Biological traits of marine benthic invertebrates in Northwest Europe

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Biological traits analysis (BTA) provides insight into causes and consequences of biodiversity change that cannot be achieved using traditional taxonomic approaches. However, acquiring information on biological traits (i.e., the behavioural, morphological, and reproductive characteristics of taxa) can be extremely time-consuming, especially for large community datasets, thus hindering the successful application of BTA. Here, we present information on ten key biological traits for over a thousand marine benthic invertebrate taxa surveyed in Northwest Europe (mainly the UK shelf). Scores of 0 to 3 are provided to indicate our confidence that taxa exhibit each possible mode of trait expression. The information was acquired over a decade through an extensive appraisal of relevant sources, including peer-reviewed papers, books, online material and, where necessary, professional judgement. These data may be inspected, used, and augmented by fellow researchers, thus assisting in the wider application of BTA in marine benthic ecology.

Background & Summary

Biological traits (i.e., morphological, behavioural, and life-history characteristics) determine how species respond to environmental variation and how they influence ecosystem functioning. The study of biological traits can therefore be used to elucidate causes and consequences of biodiversity change that would go undetected using traditional analyses of community composition. Biological traits analysis (BTA) originated in freshwater and terrestrial systems but is now frequently applied to marine systems, particularly the marine benthos. Its application has advanced our understanding of human impacts on marine biodiversity and ecosystem functioning. With the seafloor globally subjected to increasing anthropogenic pressures and ecosystem functioning becoming ingrained within contemporary policy drivers for marine conservation (e.g., ecosystem-based fisheries management, the EU Marine Strategy Framework Directive), the number of benthic ecological studies applying BTA is likely to continue to rise.

A pre-requisite to BTA is acquiring the necessary biological trait information. Compiling information from primary sources (i.e., reports on laboratory or field observations) is time-consuming and often prohibitive given the large numbers of invertebrate taxa that typically comprise benthic assemblages. Secondary sources, such as online databases (e.g., BIOTIC http://www.marlin.ac.uk/biotic), provide repositories where compiled trait information can be readily accessed. However, extensive gaps have been highlighted in such databases regarding the basic biology of well-studied taxa, with up to 20% of demersal species surveyed in British marine waters completely lacking information for eight fundamental traits. When information cannot be obtained from primary or secondary sources, trait expression can be inferred from the traits of closely related taxa. However, such inferences require knowledge on the biology of taxonomic groups and must be applied with caution when there is variation in trait expression across species from the same group.

This paper aims to assist researchers in sourcing biological trait information for large numbers of marine benthic invertebrate taxa. A freely accessible data matrix is provided, describing trait expression by 1,025 taxa that typically comprise benthic assemblages. Secondary sources, such as online databases (e.g., BIOTIC), provide repositories where compiled trait information can be readily accessed. However, extensive gaps have been highlighted in such databases regarding the basic biology of well-studied taxa, with up to 20% of demersal species surveyed in British marine waters completely lacking information for eight fundamental traits. When information cannot be obtained from primary or secondary sources, trait expression can be inferred from the traits of closely related taxa. However, such inferences require knowledge on the biology of taxonomic groups and must be applied with caution when there is variation in trait expression across species from the same group.

This paper aims to assist researchers in sourcing biological trait information for large numbers of marine benthic invertebrate taxa. A freely accessible data matrix is provided, describing trait expression by 1,025 taxa (recorded at the genus level and above) for each of ten biological traits (Supplementary Table 1). This information has been acquired over a ten-year period, largely by benthic ecologists working at Cefas on projects with aims ranging from assessing the impacts of bottom trawling and aggregate dredging to mapping the functional characteristics of the benthos across broad-scale management boundaries. The provision of the resulting database augments other comparable initiatives (e.g., the Polytraits database) and is intended to provide a reliable source of trait information to facilitate future application of BTA in marine benthic ecology.

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Methods

Biological traits information was obtained for the 1,025 taxa studied within projects undertaken by the authors of this paper. These projects focused on the ecology of sedimentary habitats in Northwest Europe, primarily UK shelf seas. Ten biological traits (maximum body size, morphology, longevity, egg development location, larval development location, living habit, sediment position, feeding mode, mobility, and bioturbation mode) were selected to address the ecological questions raised by the aims of these projects. Consequently, the ten traits cover a range of widely studied biological characteristics that determine how species respond to environmental variation and/or influence ecosystem functioning. Each trait was divided into between 3 and 6 categories, each representing a possible mode of trait expression or, for quantitative traits, a range of trait values (Supplementary Table 1).

Trait information was obtained using primary literature (i.e., papers and theses reporting on in situ observations and laboratory experiments\textsuperscript{21–30}), secondary literature (i.e., textbooks and online databases\textsuperscript{302–344}) and professional judgement (i.e., traits inferred from the traits of closely related taxa). Primary literature was given precedence over secondary literature when compiling trait information, and professional judgement was used only when information could not be obtained from the other two sources. Trait information was compiled at the genus level and above, accounting for the range of trait expression at lower taxonomic levels. For example, entries at the genus level captured any species-level variation in trait expression, while entries at the family level captured any variation in trait expression at the genus and species levels. Trait information was not compiled at the species level because members of the same genus tend to have consistent trait expression for the categorical traits used, and any apparent interspecific differences may equally be explained by all members of a genus having context-specific trait expression (discussed in the Usage Notes). As traits were assigned to taxa surveyed in Northwest Europe, trait information from sources pertaining to this region was prioritised.

To describe trait expression, taxa were given a numerical score for each category of all ten biological traits. The score ranged from 0 to 3, depending on the strength of the evidence that the taxon exhibits a trait category (0 = no evidence, 3 = strong evidence). For example, a taxon established as having planktotrophic larvae in the primary literature would be scored ‘3’ for ‘planktotrophic’, whereas a taxon for which there were unsubstantiated accounts of planktotrophic larval development in the secondary literature would be given a score of ‘2’. Scores of ‘1’ were given when professional judgement was required or when the literature suggests that trait expression by a taxon may vary across its constituent species. However, in cases where trait expression is identical among studied members of a taxonomic group (e.g., brooding of eggs by Amphipoda), members of the same taxonomic group for which direct evidence is lacking were assumed with confidence to also express the trait in the same way.

Data Records

A matrix of biological traits information for 1,025 marine benthic invertebrate taxa, resulting from Methods described above, can be accessed online via the Cefas Data Portal at https://data.cefas.co.uk/view/21362. Taxonomic nomenclature in this dataset was obtained from the World Register of Marine Species (WoRMS; http://www.marinespecies.org) on the 21\textsuperscript{st} of January 2022.

Technical Validation

Trait information was compiled using the most reliable information available at the time of sourcing. A full list of sources used to compile trait information is provided in the References\textsuperscript{21–344}. Outputs of analyses that used earlier versions of the accompanying trait matrix have been widely peer-reviewed and have improved our understanding of how benthic assemblages respond to anthropogenic pressures and influence ecosystem functioning\textsuperscript{14–17,246–354}. The trait matrix has been augmented and refined over time as the list of taxa has expanded and new trait information has become available, culminating in a final review by authors in October 2021 to ensure that entries were consistent with our knowledge of the biology of the taxa. The identification of any entries as potentially erroneous was followed by a reinspection of the literature to resolve the uncertainty.

Due to the evolving nature of the trait matrix over the past decade and its various contributors, a limitation of the dataset is that a detailed account of the sources(s) of each entry (i.e., expression of an individual trait by an individual taxon) is not available. However, if users flag potentially erroneous entries with the corresponding author, then the literature will be reinspected, entries will be amended (if appropriate), and more detailed information on the sources of disputed entries will accompany future versions of the matrix. Moreover, it should be noted that despite primary and secondary sources being widely reviewed throughout the process of compiling trait information, many trait entries in the final matrix result from professional judgement. Such entries will also be amended in future iterations of the matrix if they are superseded by new information made available in the primary or secondary literature. Therefore, while the current matrix is intended to provide a useful and up-to-date resource for the scientific community, the process of refining this resource is ongoing.

Usage Notes

The accompanying matrix does not cover an exhaustive list of ecologically important traits, but rather a subset of traits that are relevant to the ecological questions addressed by the authors of this paper under the auspices of several projects. We advocate that the choice of traits is carefully tailored to each application. Not all the ten traits will be appropriate for use in every study, while traits not included in the matrix may require consideration if they are relevant to the questions being addressed. Users should therefore draw on the information provided here only if it helps to achieve the specific aims of their research.

In compiling biological trait information, priority was given to trait expression by species in Northwest Europe, which is the region where the associated projects were conducted. Therefore, the information presented for a taxon in the accompanying matrix primarily reflects trait expression by species within this region. Species
that occur only outside the region may express traits differently to congeners that occur only within the region, while populations of the same species located outside the region may also express traits differently. These possibilities should be considered if the information presented here is used to assign biological traits to taxa found outside of Northwest Europe.

Users of the accompanying matrix should consider the possible implications of taxa having multiple modes of expression (categories) for a single trait. This does not necessarily mean that each mode is equally likely in all environments, as trait expression may depend on abiotic or biotic context. For example, a species may alter its feeding mode in response to anthropogenic disturbance, hydrodynamic conditions, water temperature and chemistry, or interspecific interactions. Reliable information on the conditions in which taxa express traits in specific ways is rarely available and was therefore not incorporated into the accompanying trait matrix. This may affect the reliability of BTA outputs, depending on the ecological questions addressed.

Finally, we reiterate that the associated trait matrix reflects the best information available to the authors at the time this paper was submitted. The matrix will continue to be augmented and refined over time as the taxon list grows and new information about trait expression becomes available. It is our intention to make updated versions accessible through the Cefas Data Portal (https://data.cefas.co.uk) and for these future versions to be ‘signedposted’ on the page where the current matrix can be accessed (https://data.cefas.co.uk/view/21362). We therefore encourage users to check, verify, and, if necessary, amend the trait information provided here prior to use. Other researchers working independently of the authors of this paper have compiled and published trait information for marine benthic invertebrates, focussing on specific taxonomic groups or traits that influence specific ecological processes. We advise that users crosscheck between sources and review the primary literature to attempt to resolve any areas of disagreement. We also advise that users are particularly cautious when using information from the accompanying matrix that has a low score of ‘1’. This low score should be taken as a prompt to review the literature for information that may have been made available since the publication of this paper and may be used to direct future empirical research on the traits of marine benthic invertebrates. Any evidence that corroborates or contradicts information in the trait matrix provided here, particularly that which is derived from empirical research, is welcomed via email to the corresponding author. This evidence will be incorporated into future versions of the trait matrix.

Code availability
No custom code was used to generate or process the data described in the manuscript.

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References
1. Violle, C. et al. Let the concept of trait be functional! Oikos 116, 882–892 (2007).
2. Diaz, S. et al. Functional traits, the phylodynamics of function, and ecosystem service vulnerability. Ecol. Evol. 3, 2958–2975 (2013).
3. Mouillot, D., Villéger, S., Scherer-Lorenzen, M. & Mason, N. W. H. Functional structure of biological communities predicts ecosystem multifunctionality. PLoS One 6, e17476 (2011).
4. Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H. & Bellwood, D. R. A functional approach reveals community responses to disturbances. Trends Ecol. Evol. 28, 167–177 (2013).
5. Statzner, B., Resh, V. H. & Roux, A. L. The synthesis of long-term ecological research in the context of concurrently developed ecological theory: design of a research strategy for the Upper Rhone River and its floodplain. Freshw. Biol. 31, 253–263 (1994).
6. Townsend, C. R. & Hildrew, A. G. Species traits in relation to a habitat template for river systems. Freshw. Biol. 31, 265–275 (1994).
7. McIntyre, S., Lavoie, S. & Tremont, R. M. Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. J. Ecol. 83, 31–44 (1995).
8. Bremner, J., Rogers, S. I. & Frid, C. J. Assessing functional diversity in marine benthic ecosystems: a comparison of approaches. Mar. Ecol. Prog. Ser. 254, 11–25 (2003).
9. Bremner, J., Rogers, S. I. & Frid, C. J. Assessing functional diversity of marine benthic invertebrates. Cefas Data Portal.
10. Frid, C. J. et al. Incorporating ecological functioning into the designation and management of marine protected areas. Biodivers. Data J. 2, e1024 (2014).
11. Marchini, A., Munari, C. & Mistri, M. Functions and ecological status of eight Italian lagoons examined using biological traits analysis (BTA). Ecol. Indic. 6, 609–622 (2006).
12. van der Linden, P. et al. A biological trait approach to assess the functional composition of subtidal benthic communities in an estuarine ecosystem. Ecol. Indic. 20, 121–133 (2012).
13. Paganelli, D., Marchini, A. & Occhibinti-ambrogi, A. Functional structure of marine benthic assemblages using Biological Traits Analysis (BTA): A study along the Emilia-Romagna coastline (Italy, North-West Adriatic Sea). Estuar. Coast. Shelf Sci. 96, 245–256 (2012).
14. Bolam, S. G. & Eggleton, J. D. Macrofaunal production and biological traits: spatial relationships along the UK continental shelf. J. Sea Res. 88, 47–58 (2014).
15. Bolam, S. G., McIlwaine, P. S. O. & Garcia, C. Application of biological traits to further our understanding of the impacts of dredged material disposal on benthic assemblages. Mar. Pollut. Bull. 105, 180–192 (2016).
16. Bolam, S. G. et al. Differences in biological traits composition of benthic assemblages between unimpacted habitats. Mar. Environ. Res. 136, 1–13 (2017).
17. Kenny, A. J. et al. Assessing cumulative human activities, pressures, and impacts on North Sea benthic habitats using a biological traits approach. ICES J. Mar. Sci. 75, 1080–1092 (2018).
18. Halpern, B. S. et al. Recent pace of change in human impact on the world's oceans. Sci. Rep. 9, 11609 (2019).
19. Tyler, E. H. M. et al. Extensive gaps and biases in our knowledge of a well-known fauna: implications for integrating biological traits into macroecology. Glob. Ecol. Biogeogr. 21, 922–934 (2012).
20. Faulwetter, S., Markantonatou, V., Pavlouli, C. & Papageorgiou, N. Polytraits: a database on biological traits of marine polychaetes. Biodivers. Data J. 2, e1024 (2014).
21. Aberson, M. J. R., Bolam, S. G. & Hughes, R. G. The dispersal and colonisation behaviour of the marine polychaete Nereis diversicolor (O. F. Müller) in south-east England. Hydrobiologia 672, 3–14 (2011).
66. Chesman, B. S. & Langston, W. J. Intersex in the clam Scrobicularia plana: a sign of endocrine disruption in estuaries? Biol. Lett. 2, 420–422 (2006).
67. Christie, G. A comparative study of the reproductive cycles of three Northumberland populations of Chaceotzone setosa (Polychaeta: Cirratulidae). J. Mar. Biol. Assoc. UK 65, 239–254 (1985).
68. Christie, G. The reproductive biology of a Northumberland population of Sphaeroderma gracilis (Rathke, 1843) (Polychaeta: Sphaerodidae). Sarsia 69, 117–121 (1984).
69. Clark, R. B. Observations on the food of Nephtys. Limnol. Oceanogr. 7, 380–385 (1962).
70. Coelho, J. P., Rosa, M., Pereira, E., Duarte, A. & Pardal, M. A. Pattern and annual rates of Scrobicularia plana mercury bioaccumulation in a human induced mercury gradient (Ria de Aveiro, Portugal). Estuar. Coast. ShelfSci. 69, 629–635 (2006).
71. Corey, S. The comparative life histories of three Cumacea (Crustacea): Cumaspis goodsi (Van Beneden), Pseudocuma tripinosa (Goodis), and Pseudocuma longicornis (Bate). Can. J. Zool. 47, 695–704 (1969).
72. Crawford, G. I. The fauna of certain estuaries in West England and South Wales, with special reference to the Tanaidae, Isopoda and Amphipoda. J. Mar. Biol. Assoc. UK 21, 647–662 (1937).
73. Culliney, J. L. Comparative larval development of the shipworms Bankia gouldi and Teredo navalis. Mar. Biol. 29, 245–251 (1975).
74. Dales, R. P. The reproduction and larval development of Nereis diversicolor O. F. Müller. J. Mar. Biol. Assoc. UK 29, 321–360 (1950).
75. Dashtgard, S. E., Ginsgar, M. K. & Pemberton, S. G. Grain-size controls on the occurrence of bioturbation. Palaeogeogr. Palaeoclimatol. Palaeoecol. 257, 224–233 (2008).
76. Dauvins, D. M. Biological criteria, environmental health and estuarine macrobenthic community structure. Mar. Pollut. Bull. 26, 249–257 (1993).
77. Dauvins, D. M. Functional morphology and feeding behavior of Scolelepis squamata (Polychaeta: Sionidae). Mar. Biol. 77, 279–285 (1983).
78. Dauvins, D. M., Mahon, H. K. & Sarda, R. Functional morphology and feeding behavior of Streblotopus bidenticulatus and St. subulosis (Polychaeta: Sionidae). Hydrobiologia 496, 207–213 (2003).
79. Daunin, J. C. Impact of Amoco Cadiz oil spill on the muddy fine sand Abra alba - Melinna palmata community from the Bay of Morlaix. Estuar. Coast. Shelf Sci. 14 (2018).
80. Daunin, J.-C. & Gentil, F. Long-term changes in populations of subtidal bivalves (Abra alba and A. prismatica) from the Bay of Morlaix (Western English Channel). Mar. Biol. 103, 63–73 (1989).
81. Daunin, J.-C. Biological, dynamique et production d'une population d'Abra alba (Wood) (mollusque-bivalve) de la baie de Morlaix (Manche occidentale). J. Exp. Mar. Biol. Ecol. 97, 151–155 (1986).
82. Daunin, J.-C. & Gentil, F. Long-term changes in populations of subtidal bivalves (Abra alba and A. prismatica) from the Bay of Morlaix (Western English Channel). Mar. Biol. 103, 63–73 (1989).
83. Davis, R. W. The role of bioturbation in sediment resuspension and its interaction with physical shearing. J. Exp. Mar. Biol. Ecol. 171, 187–200 (1993).
84. Dean, D. Migration of the sandworm Nereis virens during winter nights. Mar. Biol. 45, 165–173 (1978).
85. Dekker, R. & Beukema, J. Relations of summer and winter temperatures with dynamics and growth of two bivalves, Tellina tenuis and Abra tenuis, on the northern edge of their intertidal distribution. J. Sea Res. 42, 207–220 (1999).
86. Delgado, L., Guerra, G. & Ribera, C. The Gammaridea (Amphipoda) fauna in a Mediterranean coastal lagoon: considerations on population structure and reproductive biology. Crustacea 82, 191–218 (2009).
87. Dewarumez, J.-M. Etude biologique d’Abra alba (Wood) Mollusque lamellibranché du littoral français de la mer du Nord. Université des Sciences et Techniques de Lille, Doctoral Thesis, 139pp (1979).
88. Dinneen, P. Peresialla clymeodes Harmelin, 1968: A capitellid polychaete new to Ireland and Great Britain. Irish Nat. J. 20, 471–475 (2019).
89. Dobbs, F. C. & Scholly, T. A. Sediment processing and selective feeding by Pectinaria koreni (Polychaeta: Pectinariidae). Mar. Ecol. Prog. Ser. 29, 165–176 (1986).
90. Domingues, P. M., Turk, P. E., Andrade, J. P. & Lee, P. G. Culture of the mysid, Mysidopsis almyra (Wood) (mollusque-bivalve) de la baie de Morlaix (Manche occidentale). J. Exp. Mar. Biol. Ecol. 336, 33–41 (2006).
91. Eckert, G. L. Effects of the planktonic period on marine population fluctuations. Ecology 84, 372–383 (2003).
92. Esselink, P. & Zwartz, L. Seasonal trend in burrow depth and tidal variation in feeding activity of Nereis diversicolor. Mar. Ecol. Prog. Ser. 56, 243–254 (1989).
93. Farke, H. & Berghuis, E. M. Spawning, larval development and migration behaviour of Arenicola marina in the laboratory. Netherlands J. Sea Res. 13, 512–528 (1979).
94. Fauchald, K. & Jumars, P. A. The diet of worms: A study of polychaete feeding guilds. Oceanogr. Mar. Biol. an Annu. Rev. 17, 193–284 (1979).
95. Fauchald, K. Life diagram patterns in benthic polychaetes. Proc. Biol. Soc. Washington. 96, 160–177 (1983).
96. Fetzer, I. & Arntz, W. Reproductive patterns of benthic invertebrates in the Kara Sea (Russian Arctic): adaptation of reproduction modes to cold water. Mar. Ecol. Prog. Ser. 356, 189–202 (2008).
97. Fish, J. D. & Mills, A. The Reproductive Biology of Corophium Volutator and C. Arenarum (Crustacea: Amphipoda). J. Mar. Biol. Assoc. UK 59, 355–368 (1979).
98. Fish, S. The biology of Eurylische Pulcher [Crustacea: Isopoda]. J. Mar. Biol. Assoc. UK 50, 753–768 (1970).
99. Franceschi, O. & Lopez-Jamar, E. Dynamics, growth and production of Abra alba and Abra nitida from La Coruna, NW of Spain. Biol. del Inst. Exp. Oceanogr. 7, 101–113 (1991).
100. François, F., Gerino, M., Stora, G., Durbec, J. P. & Poggiale, J. C. Functional approach to sediment reworking by gallery-forming macrobenthic organisms: Modeling and application with the polychaete Nereis diversicolor. Mar. Ecol. Prog. Ser. 229, 127–136 (2002).
101. Frid, C. J. Foraging behaviour of the spiny starfish Marthasterias glacialis in Lough Ine, Co. Cork, Mar. Behav. Physiol. 19, 227–239 (1992).
102. Funder, S., Demidov, I. & Yelovicheva, Y. Hydrography and mollusc faunas of the Baltic and the White Sea–North Sea seaway in the Eernian. Palaeogeogr. Palaeoclimatol. Palaeoecol. 184, 275–304 (2002).
103. Gemmill, J. F. I. The development of the starfish Solaster endeca Forbes, Trans. Zool. Soc. London 20, 1–29 (1912).
104. Gendron, L. Determination of the size at sexual maturity of the waved whelk Buccinum undatum Linnaeus, 1758, in the Gulf of St. Lawrence, as a basis for the establishment of a minimum catchable size. J. Shellfish Res. 11, 1–7 (1992).
285. Wanamaker, A. D. et al. Very long-lived mollusks confirm 17th century AD thera-based radiocarbon reservoir ages for north Iceland shelf waters. Radiocarbon 50, 399–412 (2008).

286. Warren, L. M., Hutchings, P. A. & Doyle, S. A revision of the genus Mediomastus Hartman, 1944 (Polychaeta: Capitellidae). Rec. Aust. Museum 46, 227–256 (1994).

287. Warwick, R. M. The partitioning of secondary production among species in benthic communities. Netherlands J. Sea Res. 16, 1–17 (1982).

288. Warwick, R. M. & George, C. L. Annual macro-fauna production in an Abra community. In Industrialised embayments and their environmental problems: a case study of Swansea Bay (eds. Collins, M. B., Banner, F. T., Tyler, P. A. & James, A. E.) 517–538 (Pergamon Press, 1980).

289. Weinberg, S. & Weinberg, F. The life cycle of a Gorgonian: Eunicella Singularis (Esper, 1794). Bild. tot Dierkd. 48, 127–137 (1979).

290. Wernberg, S. A., Janssen, R. & Budd, G. E. Hatching and earliest larval stages of the priapulid worm Priapulus caudatus. Invertebr. Biol. 128, 157–171 (2009).

291. Whithatch, R. B. Food-Retrieval partitioning in the deposit feeding polychaete Pectinaria gouldii. Biol. Bull. 147, 223–235 (1974).

292. Widicome, S. et al. Importance of bioturbators for biodiversity maintenance: Indirect effects of fishing disturbance. Mar. Ecol. Prog. Ser. 275, 1–10 (2004).

293. Williams, G. On the occurrence of Scopelocheirus hopei and Cirvola borea in living Acanthias vulgaris (spiny dogfish). Irish Nat. J. 7, 89–91 (1938).

294. Wilson, D. P. The larval development of three species of Magelona (Polychaeta) from localities near Plymouth. J. Mar. Biol. Assoc. UK 62, 385–401 (1982).

295. Wilson, W. H. Sexual reproductive modes in polychaetes: classification and diversity. Bull. Mar. Sci. 48, 500–516 (1991).

296. Yonge, C. M. Observations on Sphyria binghamii Turton. J. Mar. Biol. Assoc. UK 30, 387–392 (1951).

297. Yonge, C. M. On the Habits and Adaptations of Aliudia (Corbula) gibba. J. Mar. Biol. Assoc. UK 26, 358–376 (1946).

298. Yonge, C. M. On the structure and adaptations of the Tellinacea, deposit-feeding Eulamellibranchia. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 234, 29–76 (1949).

299. Yonge, C. M. On the structure, biology and systematic position of Pharus legumen (L.). J. Mar. Biol. Assoc. UK 38, 277–290 (1959).

300. Zenetos, A. The American piddock Petricola pholidiformis Lamark, 1818 spreading in the Mediterranean Sea. Aquat. Invasions 4, 385–387 (2009).

301. Zwarts, L. Burying depth of the benthic bivalve Scrobicularia plana (da Costa) in relation to siphon-cropping. J. Exp. Mar. Bio. Ecol. 101, 25–39 (1986).

302. Ansell, A. D., Gibson, R. N. & Barnes, M. Oceanography and Marine Biology: An Annual Review volume 35 (UCL Press, 1997).

303. Beesley, P. L., Ross, G. J. B. & Glasby, C. J. Echinoderms Through Time (CRC Press, 2019).

304. Budd, G. C. In Polychaetes & Allies: The Southern Synthesis (eds. Y oung, C. M.) Ch. 2 (Academic Press, 2002).

305.Carrier, T. J., Reitzel, A. M. & Heyland, A. Evolutionary Ecology of Marine Invertebrate Larvae (Oxford University Press, 2008).

306. David, B., Guille, A., Féral, J.-P. & Roux, M. The Biology of Mollusca: Caudofoveata, Solenogastres, Polyplacophora and Scaphopoda: keys and notes for the identification of species (Linnean Society of London and the Estuarine and Brackish-Water Sciences Association, 1987).

307. Dame, R. F. D. Ecology of Marine Bivalves: an Ecosystem Approach (CRC Press, 1996).

308. Dave, B., Guille, A., Féraul, J.-P. & Roux, M. Echinoderm Nutrition (Springer Science & Business Media, 2003).

309. David, B., Guille, A., Féral, J.-P. & Roux, M. Echinoderms Through Time (Balkema, 1994).

310. Dorestejezn, A. W. C. & Westeinde, W. Reproductive Strategies and Developmental Patterns in Annelids (Springer Netherlands, 1999).

311. Fauchald, K. The polychaete worms. Definitions and keys to the orders, families and genera Science Series 28 (Natural History Museum of Los Angeles, 1977).

312. Fauchald, K. The polychaete worms. Definitions and keys to the orders, families and genera Science Series 28 (Natural History Museum of Los Angeles, 1977).

313. Food and Agriculture Organization of the United Nations. FAO fisheries synopsis (Food and Agriculture Organization of the United Nations, 1984).

314. Giese, A. C. & Pearse, J. S. Reproduction of Marine Invertebrates. Volume 5. Molluscs: Pelecypods and Lesser Clades (Academic Press, 1979).

315. Gordon, J. Handbook of the marine fauna of north-west Europe (Oxford University Press, 1995).

316. Holtmann, S. et al. Atlas of the zoobenthos of the Dutch continental shelf (Ministry of Transport, Public works and Water management, 1996).

317. Jangoux, M. & Sirey, J. M. Echinoderm Nutrition (Balkema, 1982).

318. Jones, A. M. & Baxter, J. M. Molluscs: Caudofoveata, Solenogastres, Polyplacophora and Scaphopoda: keys and notes for the identification of species (Linnean Society of London and the Estuarine and Brackish-Water Sciences Association, 1987).

319. Little, C. The Biology of Soft Shores and Estuaries (Oxford University Press, 2000).

320. Maldonado, M. & Bergquist, P. R. In Atlas of Marine Invertebrate Larvae (ed. Young, C. M.) Ch. 2 (Academic Press, 2002).

321. MarLIN. BIOTIC - Biological Traits Information Catalogue. Marine Life Information Network. Plymouth: Marine Biological Association of the United Kingdom. http://www.marlin.ac.uk/biotic (2006).

322. MBA (Marine Biological Association). Plymouth Marine Fauna. (Marine Biological Association of the United Kingdom, 1957).

323. MollassucBase eds. MollassucBase: Abra tenuis (Montagu, 1803). https://www.molluscabase.org/aphia.php?p=taxdetails&uid=114139 (2019).

324. Morton, B. The Bivalvia: Proceedings of a memorial symposium in honour of Sir Charles Maurice Yonge (Hong Kong University Press, 1990).

325. Müller, H.-G. World Catalogue and Bibliography of the Recent Pycnogonida (Wissenschaftlicher Verlag, 1993).

326. Oliver, P. G., Holmes, A. M., Killeen, I. J. & Turner, J. A. Marine Bivalve Shells of the British Isles. Ameg Magicia - National Museums Wales http://naturalhistory.museumwales.ac.uk/britishbivalves (2016).

327. Pandian, T. J. Reproduction and Development in Annelida (CRC Press, 2019).

328. Poore, G. C. B., Ah Yong, S. T. & Taylor, J. The Biology of Squat Lobsters (CSIRO Publishing; Melbourne and CRC Press, 2011).

329. Purcell, S., Samyn, Y. & Conand, C. Commercially important sea cucumbers of the world. FAO Species Catalogue for Fishery Purposes No. 6 (Food and Agriculture Organization of the United Nations, 2012).

330. Puchon, R. The Biology of Mollosus (Pergamon, 1977).

331. Richards, S. in Marine Life Information Network: Biology and Sensitivity Key Information Reviews (eds. Tyler-Walters, H. & Hiscock, K.) https://www.marlin.ac.uk/species/detail/32 (2007).

332. Rouse, G. & Pleijel, F Reproductive Biology and Phylogeny of Annelida (Science Publishers, 2006).

333. Rouse, G. & Pleijel, F Polychaetes (Oxford University Press, 2001).

334. Ruppert, E. E., Fox, R. S. & Barnes, R. D. Invertebrate Zoology: A functional evolutionary approach 7th Ed (Thomson Learning, 2004).

335. Ryland, J. S. & Tyler, P. A. Recruitment in Abra tenuis (Montagu) (Bivalvia, Semelidae), a species with distinct development and a protruded meiobenthic phase. Proceedings of the 23rd European Marine Biology Symposium (Olsen and Olsen, 1989).

336. Shalla, C. Cumacea. Identification guide to British cumaceans (Dove Marine Laboratory, 2011).

337. Sigvaldáddottir, E. & et al. Advances in Polychaete Research (Springer Science & Business Media, 2003).

338. Smith, J. D. & Sumner-Rooney, J. H. In Structure and Evolution of Invertebrate Nervous Systems (eds. Schmidt-Rhaesa, A., Harzsch, S. & Purschke, G.) Ch. 18 (Oxford University Press, 2016).

339. Simpson, A. Reproduction in Octocorals (Subclass Octocorallia): A Review of Published Literature. Deep-Sea Corals Portal http://www.uclouisiana.edu/~scf4101/Bambooweb/ (2009).
337. Tebble, N., British Bivalve Seashells: A Handbook for Identification 2nd ed (1976).
338. Thiel, M. & Watling, L. Lifestyles and Feeding Biology: The Natural History of the Crustacea volume 2 (Oxford University Press, 2015).
339. Thorson, G. & Jørgensen, C. B. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the Sound (Oresund) (C. A. Reitzel, 1946).
340. Wigham, G. D. & Graham, A. Synopsis of the British Fauna Volume 60, Marine Gastropods 1: Patellogastropoda and Vetigastropoda. (Field Studies Council, 2017).
341. Wigham, G. D. & Graham, A. Synopsis of the British Fauna Volume 61, Marine Gastropods 2: Littorinimorpha and Other, Unassigned, Caenogastropoda. (Field Studies Council, 2017).
342. Wigham, G. D. & Graham. A Synopsis of the British Fauna Volume 62, Marine Gastropods 3: Neogastropoda. (Field Studies Council, 2018).
343. Yonge, C. M. & Thompson, T. E. Living Marine Molluscs (Collins, 1976).
344. Young, C. M. & Eckelbarger, K. J. Reproduction, larval biology, and recruitment of the deep-sea benthos (Columbia University Press, 1994).
345. Clare, D. S. et al. Ten key biological traits of marine benthic invertebrates surveyed in Northwest Europe. V2. Cefas Data Hub https://doi.org/10.14466/Cefas.dataHub.123 (2022).
346. Rijnsdorp, A. D. et al. Estimating sensitivity of seabed habitats to disturbance by bottom trawling based on the longevity of benthic fauna. Ecol. Appl. 28, 1302–1312 (2018).
347. Hiddink, J. G. et al. Assessing bottom trawling impacts based on the longevity of benthic invertebrates. J. Appl. Ecol. 56, 1075–1084 (2019).
348. van Denderen, P. D. et al. Evaluating impacts of bottom trawling and hypoxia on benthic communities at the local, habitat, and regional scale using a modelling approach. ICES J. Mar. Sci. 77, 278–289 (2020).
349. Bolam, S. G. Macrofaunal recovery following the intertidal recharge of dredged material: A comparison of structural and functional approaches. Mar. Environ. Res. 97, 15–29 (2014).
350. van Denderen, P. D. et al. Similar effects of bottom trawling and natural disturbance on composition and function of benthic communities across habitats. Mar. Ecol. Prog. Ser. 541, 31–43 (2015).
351. Rijnsdorp, A. D. et al. Towards a framework for the quantitative assessment of trawling impact on the seabed and benthic ecosystem. ICES J. Mar. Sci. 73, 1172–1138 (2016).
352. Sciberras, M. et al. Impacts of bottom fishing on the sediment infaunal community and biogeochemistry of cohesive and non-cohesive sediments. Limnol. Oceanogr. 61, 2076–2089 (2016).
353. Eggleton, J. D., Depestele, J., Kenny, A. J., Bolam, S. G. & Garcia, C. How benthic habitats and bottom trawling affect trait composition in the diet of seven demersal and benthivorous fish species in the North Sea. J. Sea Res. 142, 132–146 (2018).
354. Howarth, L. M. et al. Effects of bottom trawling and primary production on the composition of biological traits in benthic assemblages. Mar. Ecol. Prog. Ser. 402, 31–48 (2018).
355. Wohlgemuth, D., Solan, M. & Godbold, J. A. Species contributions to ecosystem process and function can be population dependent and modified by biotic and abiotic setting. Proc. R. Soc. B Biol. Sci. 284, 20162805 (2017).
356. Cassidy, C., Grange, L. J., Garcia, C., Bolam, S. G. & Godbold, J. A. Species interactions and environmental context affect intraspecific behavioural trait variation and ecosystem function. Proc. R. Soc. B Biol. Sci. 287, 20192143 (2020).
357. Cesar, C. P. & Frid, C. L. J. Benthic disturbance affects intertidal food web dynamics: implications for investigations of ecosystem functioning. Mar. Ecol. Prog. Ser. 466, 35–41 (2012).
358. Tornroos, A., Nordström, M. C., Aarnio, K. & Bonsdorff, E. Environmental context and trophic trait plasticity in a key species, the tellinid clam Macoma balthica L. J. Exp. Mar. Bio. Ecol. 472, 32–40 (2015).
359. Clare, D. S., Spencer, M., Robinson, L. A. & Frid, C. L. J. Species-specific effects on ecosystem functioning can be altered by interspecific interactions. PLoS One 11, e0165739 (2016).
360. Queirós, A. M. et al. A bioturbation classification of European marine infaunal invertebrates. Ecol. Evol. 3, 3958–3985 (2013).

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Author contributions

David S. Clare – compilation of data, validation of data, writing the manuscript. Stefan G. Bolam – compilation of data, validation of data, writing the manuscript. Paul S.O. McIlwaine – validation of data, revision of the manuscript. Clement Garcia – validation of data, revision of the manuscript. Joanna Murray – validation of data, revision of the manuscript. Jacqueline D. Eggleton – compilation of data, validation of data, revision of the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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