

# EQUILIBRIA OR NOT? HOW WILL DEEP-SEA MINING AFFECT BENTHIC MARINE COMMUNITIES?

K. ROHDE<sup>1\*</sup>, D. VAUGHAN<sup>2,3</sup>

<sup>1</sup> Zoology, University of New England, Armidale NSW, Australia

<sup>2</sup> School of Access Education, Central Queensland University, QLD, Australia

<sup>3</sup> Coastal Marine Ecosystems Research Centre, Central Queensland University, QLD, Australia

\* Corresponding author: [krohde@une.edu.au](mailto:krohde@une.edu.au)

MEIOFAUNA  
BIODIVERSITY  
DEEP-SEA MINING  
EQUILIBRIUM VS. NONEQUILIBRIUM

**ABSTRACT.** – Attempts are underway for large-scale industrial mining for rare earth elements on the ocean floor. Using data from marine meiofauna, we examine whether communities disturbed or destroyed by localized mining will recover and re-establish the original equilibria. Studies of beach meiofauna are more detailed than comparable studies of deep-sea meiofauna, permitting the conclusion that many meiofaunal species do not produce many offspring fast nor disperse widely. Cosmopolitan species are rare. Previous studies have shown an enormous species diversity and the presence of many new taxa. Detailed surveys are necessary of more beach and deep-sea habitats including biological observations. Environmental DNA studies of deep-sea sediments are essential but cannot replace taxonomic studies using morphology and DNA analysis of species. Discovery rates of new species are not a reliable measure for completeness of estimates in largely unexplored biomes. Since we do not even know the taxonomic composition of the benthic fauna, it is impossible to determine whether habitats are in equilibrium or not. However, high endemism and limited dispersal suggest that equilibrium conditions are uncommon. Therefore, it is illusory to expect that habitats will return to an equilibrium after mining. Industrial exploitation on the ocean floor should be preceded by detailed and long-term taxonomic and biological studies.

## INTRODUCTION

Efforts are beginning to mine the deep-sea floor on a large (industrial) scale for rare earth elements, although sporadic mining for such minerals in several areas have already been done. The UN is trying (so far without success), to arrive at consensus about an international treaty regulate such efforts (<https://www.abc.net.au/news/2022-06-28/united-nations-chief-says-egoism-preventing-global-ocean-treaty/101189426>). Some small Pacific nations have strongly protested expressing fears that delicate marine ecosystems may be disturbed (<https://www.abc.net.au/news/2022-07-02/outgunned-island-states-vow-to-fight-deep-sea-mining/101203290>). They have been calmed by assuring them that the seafloor is well known, containing mainly bacteria, and that observations over extended periods have been done. However, this is demonstrably wrong, as shown in the following.

## DEFINITION OF EQUILIBRIUM

Rohde (2005) has discussed the definition of equilibrium systems given by various authors. Here we define an equilibrium system as one which returns to its original state after a disturbance. If the deep-sea ecosystem is in equilibrium, even major disturbances such as those caused by mining (dredging) will only lead to temporary

loss of diversity, because the flora and fauna will soon be replaced by individuals of the same species from adjacent undisturbed habitats. If the ecosystem is not in equilibrium, the loss is permanent, *i.e.*, the gap can only be filled in evolutionary time.

## DIVERSITY AND BIOLOGY OF MARINE MEIOFAUNA

Early estimates of marine biodiversity differ widely. Thus, Lamshead (1993) estimated that the total for macrofauna could reach 10 million species, and the total meiofauna 'an order of magnitude higher'. Briggs (1994), on the other hand, using specialist advice for the various taxa, gave estimates for the total terrestrial species fauna of 1 million, and the total marine diversity as less than 200,000. Recent reviews (Appeltans *et al.* 2012, Costello & Chaudhari 2017), again using specialists' advice but also rates of discovery, seem to have settled the question: marine biodiversity is much lower than terrestrial plus freshwater diversity.

And "...discoveries of cryptic, deep-sea, microscopic, and parasitic diversity will not alter the overall pattern of species richness", because microscopic species, and perhaps other taxa, have high local but low global species richness compared with larger taxa. Reasons given are a supposed homogeneous structure of deep-sea habitats

compared with terrestrial ones. However, some marine habitats may well look homogeneous to humans, but are in fact highly complex for small organisms living in them. For example, the interstitial micro- and meiofauna of sandy beaches face two gradients, a physical-horizontal and a chemical-vertical gradient (Fenchel *et al.* 1967, Armonies & Reise 2000) which explains the astonishing species diversity in beaches. Benthic habitats in the deep sea may differ in depth, currents, types of substrata (rocky, muddy, sandy with different grain size etc.), reflected by remarkable adaptations of meiofaunal animals (*e.g.*, Rohde *et al.* 1993).

The methods used (expert estimates, rates of discovery of new species) may lead to wrong conclusions because some large biomes have been severely underexamined and may be practically unknown. New species may be discovered at decreasing rates in relatively well-known biomes, but who discovers them in biomes which have been more or less ignored? These include coastal and deep-sea meiofauna and their parasites. Rohde (2016) pointed this out with special reference to parasites of deep-sea and coastal meiofauna. Concerning benthic communities, the deep-sea fauna of the Mediterranean has been better explored than that of most other seas, but Sevastou *et al.* (2012) concluded that the Mediterranean “deep-sea floor remains largely unexplored”, and they stress that it is a complex system with wide habitat heterogeneity. These authors compared spatial patterns of the dominant small-size components of deep-sea benthos, metazoan meiofauna and bacteria 4 km in depth at 73 stations and found high diversity. Microbial richness tends to increase with depth, and there is a gradual change of meiofauna structure towards abyssal stations (further references for studies on Mediterranean new deep-sea meiofauna in that review paper). Bianchelli *et al.* (2010) examined the metazoan meiofauna in six deep-sea canyons and five adjacent open slopes of three deep-sea regions along more than 2500 km on the Portuguese to the Catalan and South Adriatic margins, from the shelf break to about 5000 m depth. They found great differences in abundance, biomass and species diversity, determined by food sources and topographic features. However, taxa were identified only to the level of large taxa (*e.g.*, Turbellaria, Cnidaria). Nematodes and harpacticoid copepods represented up to 98% of the abundance. Curini-Galletti *et al.* (2012) examined soft-bodied meiofauna from littoral beaches and rock pools to sublittoral sediments to a depth of c.37 m along the northwestern coast of Sardinia, Mediterranean, and found that numerous species of Proseriata appear to be limited in their distribution to a small sector of the study area, suggesting a high degree of endemism. Rohde (2002) discussed earlier findings for deep-sea diversity (further references therein).

In the following, we concentrate on the intertidal micro- and meiofauna of beaches, a biome that may look barren to the human observer but in fact is a complex sys-

tem, very ancient with a long evolutionary history. Few thorough studies of these faunas have been made, but among them is one that is more thorough than that of any deep-sea habitat and can therefore serve as a model for comparable studies in the deep-sea.

By far the most thorough study of the micro- and macrofauna of a sandy beach, conducted by many research workers over many years, is that of the Island of Sylt, North Sea. In this study, 652 species were recorded from the intertidal zone of one beach, including Turbellaria (32 % of all species), Nematoda (27 %), Ciliata (11 % – however, the smallest species were not included), Copepoda (10 %), Gastrotricha (7 %) and 9 other taxa. 25 times as many meiofaunal than of macrofaunal interstitial species were recorded, among them 148 new species, and not only the taxonomy, but the biology (at least of some species) was studied. The results were published in many papers and reviewed by Armonies & Reise (2000). Very similar congeneric species may occur in the same habitat, with only minor differences in the choice of prey, which shows that only very careful taxonomic and ecological studies can reveal the true number of species. The authors estimate that 850 species compose the entire interstitial fauna at the “particularly well studied” beach at Sylt. Concerning the platyhelminths alone, Reise (1988) recorded 435 species from around the entire island (compared with 207 from the well-studied beach), which included beaches with a range of characteristics. Armonies & Reise (2000) estimate that there may be about 1600 interstitial species around the entire island. A re-examination about 15 years later of some groups revealed almost no additional species.

Of 74 species of turbellarians at the well-studied beach, 60 % reproduced only once and 15 % twice a year (Armonies & Reise 2000). These species do not have pelagic larvae. Hence, these authors conclude, absence of rapid dispersal “implies, on an evolutionary time scale, ample possibilities for founder effects and genetic drift in small populations, generating a high number of species” in an ancient habitat “which persisted essentially unchanged since the beginning of metazoan life”.

As documented in the review by Westheide (1991), although not as exhaustive as the studies at Sylt, similar studies on the Galapagos Islands, largely by some of the same group of researchers, have identified about 390 species of meiofauna, most of them new species. However, almost 95 % of the identified species are from genera already described from elsewhere. These islands are only 2-3 million years old, and at least some of the species may have evolved at the islands, although comparative studies in the eastern Pacific are inadequate and the proportion of endemic species and genera can therefore not be accurately given (Westheide 1991). For the Platyhelminthes, one of the most abundant and species-rich groups, almost all species were new including some new genera.

The land faunas of small islands are typically very species-poor, whereas the intertidal meiofauna of the Galapagos Islands is rich in species, although species numbers of Platyhelminthes at the Galapagos Islands are markedly smaller than at Sylt. Very few meiofaunal species have pelagic larvae, and since the Galapagos Islands are oceanic, the shortest distance to the American continent of 1000 km and without a known landbridge to a continent in the past, species must have arrived over the last three million years by some other means, most likely on drifting material.

Dittmann (1991) examined meiofauna of beaches in northeastern Australia, but species were not identified to the species level. Blome, Faubel & Schleier (unpubl)<sup>1</sup> examined the meiofauna of beaches along the Australian east coast, but the study was not completed because of lack of funding (Blome, Faubel & Schleier unpubl). Nematodes were the most diverse and abundant group, followed by copepods and platyhelminths. Some species descriptions of platyhelminths have been published, including that of a new and unique turbellarian (Miller & Faubel 2003). Faubel (pers comm) found 202 species between Thursday Island and Batemans Bay. None of them are known from Sylt and other European localities, although some belong to genera and families known from boreal and temperate latitudes in Europe. There appear to be latitudinal differences in species composition.

In samples of the benthos taken at 20, 50 and 100 m along thirteen positions off the South African east coast off KwaZulu Natal over several years, meiofauna were dominant, constituting at least 70 % of benthic composition (McClurg 1988). Nematodes were the most numerous, followed by annelids and arthropods. Taxa were not identified to species level.

Worldwide, a high proportion of all described species, are parasitic, which makes the parasitic way of life one of the most successful on Earth (Poulin & Morand 2004, Rohde and Vaughan, in press). There were at least 60 independent transitions from free-living to obligate parasitism (Poulin & Morand 2004). None have been described from marine meiofauna in coastal and deep-sea habitats. Perhaps meiofaunal animals are too small and their habitats too difficult to access for successful infections. Alternatively, parasitic species may be common but no systematic surveys to find them have been made. At Sylt, small ciliates were found but not described, and they are the most likely candidates among the observed species to be parasitic.

Rohde (2013) has described many examples of communities in equilibrium or in nonequilibrium. Marine meiofauna should be added as an example of communi-

ties of uncertain 'status': too little is known. And this is probable for most communities, whether on land or in the sea. Studies of environmental DNA have shown major gaps in our taxonomic knowledge of deepsea meiofauna (Sinniger *et al.* 2016), and Rohde (2010) has shown how little we know about marine parasite diversity.

## CONCLUSION

We conclude that the interstitial meiofauna of beaches and probably the ocean floor generally has very high local and probably global diversity, because many small meiofaunal animals do not disperse widely and do not produce many offspring. Rohde (2005 and further references therein) has discussed characteristics of communities that make nonequilibrium conditions more likely. Among them are a high degree of endemism and limited scope for dispersal, as likely to be found in the benthic marine meiofauna. Long evolutionary history under conditions that have not changed as drastically as those on land, on the other hand, may make the establishment of equilibria more likely. Taxonomic and biological studies are urgently required of the meiofauna of beaches and in the deep-sea. With regard to planned large-scale exploitation for rare earth elements on the ocean floor, we strongly urge that any such enterprise should be preceded by careful taxonomic and biological studies of benthic organisms. In view of our scanty knowledge, it is impossible to predict whether an oceanic benthic habitat will return to an equilibrium after mining. The role of benthic meiofauna in the oceans is practically unknown, but it is likely that benthic meiofauna is a food source for larger animals higher up in the food chain. It is possible and indeed likely that cascade effects may have significant effects on communities of such larger animals, with potentially global implications. After all, the oceans cover about two thirds (71 %) of the Earth's surface, and many countries depend on marine ecosystems for their main food source.

ACKNOWLEDGEMENTS. - We thank A Faubel, Hamburg University, for information on Australian meiofauna and permission to use that information, and W Armonies, Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, for advice on beach meiofauna. We are also grateful to S Fennessy, Oceanographic Research Institute, South African Association for Marine Biological Research, for information on South African meiofauna.

## REFERENCES

- Appeltans W, Ah Yong ST, Anderson GA, Angel MV, Artois T, Bailly N, Bamber R, Barber A, Bartsch I, Berta A, Blaazewicz-Paszkowycz M, Bock P, Boxshall G, Boyko CB, Nunes Brandão S, Bray RA, Bruce NL, Cairns SD, Chan Y-Y, Cheng L, Collins AG, Cribb T, Curini-Galletti M, Dahdouh-Guebas F, Davie PJF, Dawson MN, De Clerck O, Decock

<sup>1</sup> Blome D, Faubel A, Schleier U (unpublished). Investigations of eulittoral meiobenthos of exposed sandy beaches of eastern Australia: including catalogues of free-living marine nematode, gastrotrich, and turbellarian genera.

- W, De Grave S, de Voogd NJ, Domning DP, Emig CC, Erséus C, Eschmeyer W, Fauchald K, Fautin DG, Feist SW, Franssen CHJM, Furuya H, Garcia-Alvarez O, Gerken S, Gibson D, Gittenberger A, Gofas S, Gómez-Daglio L, Gordon DP, Guiry MD, Hernandez F, Hoeksema BW, Hopcroft RR, Juane D, Kirk P, Koedam N, Koenemann S, Kolb JB, Kristensen RM, Kroh A, Lambert G, Lazarus DB, Lemaitre R, Longshaw M, Lowry J, Macpherson E, Madin LP, Mah C, Mapstone G, McLaughlin PA, Mees J, Meland K, Messing CG, Mills CE, Molodtsova TN, Mooi R, Neuhaus B, Ng PKL, Nielsen C, Norenburg J, Opresko DM, Osawa M, Paulay G, Perrin W, Pilger JF, Poore GCB, Pugh P, Read GB, Reimer JD, Ruis M, Rocha RM, Saiz-Salinas JI, Scarabino V, Schierwater B, Schmidt-Rhaesa A, Schnabel KE, Segers H, Self-Sullivan C, Shenkar N, Siegel V, Sterrer W, Stöhr S, Swalla B, Tasker ML, Theusen EV, Timm T, Antonio Todara M, Turon X, Tyler S, Uetz P, van der Land J, Vanhoorne B, van Ofwegen L, van Soest RWM, Vanaverbeke J, Walker-Smith G, Chad Walker T, Warren A, Williams GC, Wilson SP, Costello MJ 2012. The magnitude of global marine species diversity. *Curr Biol* 22: 2189-2202. <https://doi.org/10.1016/j.cub.2012.09.036>
- Armonies W, Reise K 2000. Faunal diversity across a sandy shore. *Mar Ecol Prog Ser* 196: 49-57.
- Bianchelli S, Gambi C, Zeppilli D, Danovaro R 2010. Metazoan meiofauna in deep-sea canyons and adjacent open slopes: a large-scale comparison with focus on rare taxa. *Deep Sea Res* 1 57: 420-433. <https://doi.org/10.1016/j.dsr.2009.12.001>
- Briggs JC 1994. Species diversity: land and sea compared. *Syst Biol* 43: 130-135. <https://doi.org/10.1093/sysbio/43.1.130>
- Costello, MJ, Chaudhary C 2017. Marine biodiversity, biogeography, deep-sea gradients and conservation. *Curr Biol* 27: R511-R527. <https://doi.org/10.1016/j.cub.2017.04.060>
- Curini-Galletti M, Artois T, Delogu V, De Smet WH, Fontaneto D, Jondelius U, Leasi F, Martinez A, Meyer-Wachsmuth I, Nilsson KS, Tongiorgi K, Todara MA 2012. Patterns of diversity in soft-bodied meiofauna: Dispersal ability and body size matters. *PLOS ONE* 7: e33801. <https://doi.org/10.1371/journal.pone.0033801>
- Dittmann S 1991. Spatial and temporal patterns of platyhelminth assemblages in intertidal sediments of northeast Australia. *Hydrobiologia* 227: 369-374. <https://doi.org/10.1023/A:1003473929312>
- Fenchel TM, Jansson BO, Thun WJ 1967. Vertical and horizontal distribution of the metazoan microfauna and of some physical factors in a sandy beach in the northern part of the Öresund. *Ophelia* 4: 227-243. <https://doi.org/10.1080/00785326.1967.10409622>
- Lamshead PJD 1993. Recent developments in marine benthic biodiversity research. *Oceanis* 19: 5-24.
- McClurg TP 1988. Benthos of the Natal continental shelf. In Schumann EH Ed, Coastal Ocean Studies off Natal, South Africa. Vol 26, Springer: 280 p.
- Miller W, Faubel A 2003. Six new species of Proseriata (Platyhelminthes) from eastern Australia. *Mitt Hamb Zool Mus Inst* 100: 27-57.
- Poulin R, Morand S 2004. Parasite Diversity. Washington, Smithsonian Inst.
- Reise K 1988. Platyhelminth diversity in littoral sediments around the island of Sylt in the North Sea. *Prog Zool* 36: 469-480.
- Rohde K 2002. Ecology and biogeography of marine parasites. *Adv Mar Biol* 43: 1-86. [https://doi.org/10.1016/S0065-2881\(02\)43002-7](https://doi.org/10.1016/S0065-2881(02)43002-7)
- Rohde K 2005. Nonequilibrium Ecology. Cambridge University Press, Cambridge.
- Rohde K 2010. Marine parasite diversity and environmental gradients. In Morand S, Krasnov BR Eds, The Biogeography of Host-Parasite Interactions. Oxford University Press: 277 p.
- Rohde K 2013. The Balance of Nature and Human Impact. Cambridge University Press, Cambridge. <https://doi.org/10.1017/CBO9781139095075>
- Rohde K 2016. Ecology and biogeography, future perspectives: Example marine parasites. *Geoinform Geostat: An Overview* 4: 2. <https://doi.org/10.4172/2327-4581.1000140>
- Rohde K, Vaughan D in press. Parasitism. Encyclopedia of Biodiversity, 3<sup>rd</sup> ed. Elsevier.
- Rohde K, Watson NA, Faubel A 1993. Ultrastructure of the statocyst in an undescribed species of Luridae (Platyhelminthes: Rhabdocoela: Luridae). *Aust J Zool* 41: 215-224. <https://doi.org/10.1071/ZO9930215>
- Sevastou K, Lampadariou N, Polymenakou PN, Tselepides A 2012. Benthic communities in the deep Mediterranean Sea: exploring microbial and meiofaunal patterns in slope and basic ecosystems. *Biogeosci Discuss* 9: 17539-17581. <https://doi.org/10.5194/bg-10-4861-2013>
- Sinniger F, Pawlowski J, Harii S, Gooday AJ, Yamamoto H, Chevalloné P, Cedhagen T, Carvalho G, Creer S 2016. Worldwide analysis of sedimentary DNA reveals major gaps in taxonomic knowledge of deep-sea benthos. *Front Mar Sci* 3: e92. <https://doi.org/10.3389/fmars.2016.00092>
- Westheide W 1991. The meiofauna of the Galapagos. In James MJ Ed, Galápagos Marine Invertebrates. Taxonomy, Biogeography, and Evolution in Darwin's Islands. Plenum Press, New York: 473 p.

Received on November 28, 2022

Accepted on May 17, 2023

Associate editor: J Orignac