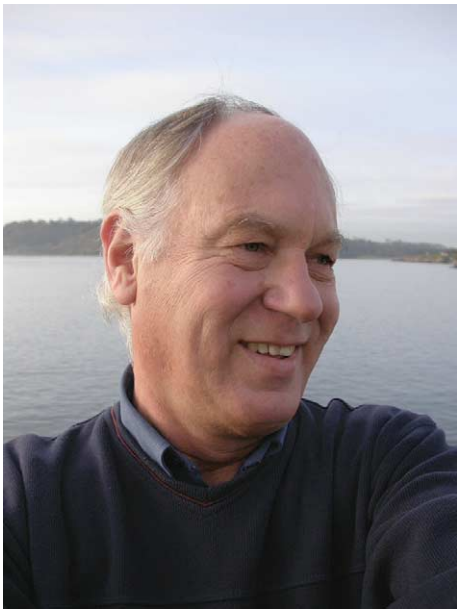
ELSEVIER

Journal of Experimental Marine Biology and Ecology 330 (2006) 3 – 11

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

www.elsevier.com/locate/jembe

Richard Martyn Warwick: A short biography



That one cannot consider the meiobenthos without encountering and appreciating the contributions of Richard Warwick speaks volumes regarding his talents as a scientist and mentor. The enthusiasm expressed by his friends and colleagues for the special symposium in his honour, and their subsequent contributions to this volume are testament to the high esteem in which he is held. A gifted writer and teacher, he has given generously of his time and expertise over several decades to further scientific knowledge, train students and inspire colleagues, collaborators and others. He also provided untold assistance to scientists worldwide during his 7-year tenure as one of the Editors-in-Chief of the *Journal of Experimental Marine Biology and Ecology*.

Richard received his B.Sc. (First Class Honours) from the University of Exeter and remained there for his doctoral studies, completing his degree in 1968. After a 4-year period in the Zoology Department at the University of Newcastle upon Tyne, he joined the Plymouth Marine Laboratory (formerly the NERC Institute for Marine Environmental Research) where he established a research program on the meiobenthos and where he and his team continue their studies. His earlier contributions to the field were recognized in 1984 with the awarding of a D.Sc. from the University of Exeter.

His research has embraced the whole size range of metazoan benthos, but his early work focussed on the ecology of the meiobenthos, particularly free-living marine nematodes. While they represent one of the most abundant and diverse group of metazoans in the sea, relatively little was known about them at the time Richard started his Ph.D. studies. This early work inevitably involved a considerable amount of alpha taxonomy of the group, since species were difficult to identify using the scattered literature sources, and many of the ones he encountered proved to be new to science. His many taxonomic publications are enhanced with beautiful (and accurate!) drawings of nematodes. His taxonomic work has culminated in recent years with the production of three volumes on free-living marine nematodes in the Linnean Society ‘Synopses of the British Fauna’ series which utilize novel pictorial keys and have made this group of animals, which has traditionally been regarded as one of the most taxonomically difficult, far more accessible to non-specialist ecologists. This work alone has furthered the discipline of meiobenthic study enormously and the keys are essential for those studying meiobenthic nematodes. Richard has continued to maintain this specialty, since nematodes have proved for various reasons to be excellent practical and theoretical models for studying general problems of community ecology and biodiversity.

Two areas of Richard's work on the functional ecology of the benthos are particularly important. First,

doi:10.1016/j.jembe.2005.12.012

the quantification of production rates in macrobenthic communities using the techniques of cohort growth analysis for all the major species in each assemblage. These still stand as the only studies of their kind, such that the production/biomass ratios derived from them are widely used for short-cut estimates of benthic production. Second, his detailed analysis of energy flow through the benthos of an estuarine mud-flat revealed, for the first time, the importance of energy flow through the smaller size component, the annual production of the meiobenthos being about twice that of the macrobenthos. This work involved laboratory experimentation on the energetics of meiobenthic organisms (using, for example, Cartesian diver respirometry and laboratory culture techniques) which were then extrapolated to standing stocks in the field, and also field manipulative experiments to investigate trophic pathways to predators such as fish and crabs.

One of his most important findings on the structural attributes of marine benthic communities was the discovery of a highly conservative bimodal pattern of species size distributions. Such conservatism can only result from the evolutionary optimization of size-related life history and feeding characteristics that are dichotomized between large and small species.

Richard has also undertaken a series of observational studies and manipulative experiments in the field and laboratory to investigate both anthropogenic and natural constraints on benthic biodiversity and community structure. Field studies include investigations of the relationship between the fractal dimensions of macroalgae and the community composition and diversity of the macrofauna and meiofauna associated with them. One important conclusion from an examination of relationships between body size, species abundance and diversity in sedimentary macrobenthic assemblages is that species richness increases linearly with body size (on log scales). This would be an inevitable consequence, in samples of fixed areal cover, of patterns of spatial dispersion scaling with organism size. Microcosm experiments have shown that community responses to disturbance are quite specific to the type of disturbance (physical disturbance, biological disturbance, organic enrichment, and chemical pollution), and differential responses have even been demonstrated for specific heavy metals. The response also depends upon the nature of the receiving assemblage and their degree of 'pre-adaptation' to particular types of environmental insult such as physical disturbance or organic enrichment events. In these studies, free-living nematodes have emerged as models, because of their amenability to community-level experiments conducted on relatively small spatial and temporal scales.

In the course of his work, Richard has supervised numerous Ph.D. students from various universities, and served as an external examiner for many doctoral dissertations. He has always excelled at promoting and leading high-quality science with his research group at the Plymouth Marine Laboratory. He has been particularly successful in bringing out the best in his colleagues, and developing important synergies within these collaborations. This has been most obvious in his more recent collaborative work with Dr K.R. Clarke, a statistician, focussing on the analysis of various structural attributes of benthic communities and, in particular, the development of protocols for detecting and monitoring the effects of natural and anthropogenic disturbance. This work has been applied to data on a variety of organism types, including reef corals, fish and macro- and meiobenthos. The range of methodologies developed has been incorporated into a software package (PRIMER) which is now routinely used worldwide in more than 60 countries for the analysis of community data, particularly in environmental impact studies. The techniques have also been used to address more fundamental problems of community ecology. For example, a measure of structural redundancy in community composition has been developed, which may be an indirect measure of the resilience or compensation potential within an assemblage. Finally, new biodiversity indices have been developed, reflecting the taxonomic relatedness of species in a community sample rather than the number of species present. Taxonomic distinctness is significantly reduced in degraded environments, and these new indices have a number of advantages over the traditionally used species richness measures. In particular, they are not at all sensitive to sample size or sampling effort, and this may be of particular significance for historic (diffusely collected) species lists from different localities or regions, which at first sight may seem unamenable to valid diversity comparison. Nematodes again proved to be valuable models for testing these ideas. Richard is currently exploring these indices as methods for rapid assessment of biodiversity using indicators such as recent and fossil death assemblages of molluscs.

Generous with his time and expertise, Richard has been a member of many scientific panels, committees and editorial boards. In 2001, he resigned as a senior research leader at Plymouth Marine Laboratory to become a research fellow. By shedding his administrative responsibilities, Richard is able to enjoy and fully

pursue the science he so relishes. We thank Richard for his intellectual and societal contributions to date and wish him continued good fortune as we look forward to his future contributions!

Publications of Richard M. Warwick

Agard, J.B.R., Gobin, J., Warwick, R.M., 1993. Analysis of marine macrobenthic community structure in relation to oil pollution, natural oil seepage and seasonal disturbance in a tropical environment (Trinidad, West Indies). Mar. Ecol., Prog. Ser. 92, 233–243.

Austen, M.C., Warwick, R.M., 1989. Comparison of univariate and multivariate aspects of estuarine meiobenthic community structure. Estuar. Coast. Shelf Sci. 29, 23–42.

Austen, M.C., Warwick, R.M., 1995. Effects of experimental manipulation of food supply on estuarine meiobenthos. Hydrobiologia 311, 175–184.

Austen, M.C., Warwick, R.M., Rosado, M.C., 1989. Meiobenthic and macrobenthic community structure along a putative pollution gradient in southern Portugal. Mar. Poll. Bull. 20, 398–405.

Austen, M.C., Warwick, R.M., Ryan, K.P., 1993. Astomonema southwardorum sp. nov., a gutless nematode dominant in a methane seep area in the North Sea. J. Mar. Biol. Assoc. U.K. 73, 627–634.

Austen, M.C., McEvoy, A.J., Warwick, R.M., 1994. The specificity of meiobenthic community responses to different pollutants: results from microcosm experiments. Mar. Poll. Bull. 28, 557–563.

Bayne, B.L., Warwick, R.M. (Eds.), 1998. Feeding and growth of bivalves: observations and modelsJ. Exp. Mar. Biol. Ecol. (Special Issue), vol. 219. 261 pp.

Bayne, B.L., Addison, R.F., Capuzzo, J.M., Clarke, K. R., Gray, J.S., Moore, M.N., Warwick, R.M., 1988. An overview of the GEEP workshop. Mar. Ecol., Prog. Ser. 46, 235–243.

Brown, B.E., Clarke, K.R., Warwick, R.M., 2002. Serial patterns of biodiversity change in corals across shallow reef flats in Ko Phuket, Thailand, due to the effects of local (sedimentation) and regional (climatic) perturbations. Mar. Biol. 141, 21–29.

Buchanan, J.B., Warwick, R.M., 1974. An estimate of benthic macrofauna production in the offshore mud of the Northumberland coast. J. Mar. Biol. Assoc. U. K. 54, 197–222.

Chia, F.S., Warwick, R.M., 1969. Assimilation of labelled glucose from seawater by marine nematodes. Nature 224, 720–721.

Clarke, K.R., Warwick, R.M., 1994. Similarity based testing for community pattern: the 2-way layout with no replication. Mar. Biol. 118, 167–176.

Clarke, K.R., Warwic, R.M., 1998a. Quantifying structural redundancy in ecological communities. Oecologia 113, 278–289.

Clarke, K.R., Warwick, R.M., 1998b. A taxonomic distinctness index and its statistical properties. J. Appl. Ecol. 35, 523–531.

Clarke, K.R., Warwick, R.M., 1999. The taxonomic distinctness measure of biodiversity: weighting of step lengths between hierarchical levels. Mar. Ecol., Prog. Ser. 184, 21–29.

Clarke, K.R., Warwick, R.M., 2001. A further biodiversity index applicable to species lists: variation in taxonomic distinctness. Mar. Ecol., Prog. Ser. 216, 265–278.

Clarke, K.R., Warwick, R.M., Brown, B.E., 1993. An index showing breakdown of seriation, related to disturbance, in a coral-reef assemblage. Mar. Ecol., Prog. Ser. 102, 153–160.

Dawson Shepherd, A.R., Warwick, R.M., Clarke, K.R., Brown, B.E., 1992. An analysis of fish community responses to coral mining in the Maldives. Environ. Biol. Fisches 33, 367–380.

Dernie, K.M., Kaiser, M.J., Richardson, E.A., Warwick, R.M., 2003a. Recovery of soft sediment communities and habitats following physical disturbance. J. Exp. Mar. Biol. Ecol. 285, 415–434.

Dernie, K.M., Kaiser, M.J., Warwick, R.M., 2003b. Recovery of benthic communities following physical disturbance. J. Anim. Ecol. 72, 1043–1056.

Faubel, A., Warwick, R.M., 2005. The marine flora and fauna of the Isles of Scilly: free-living Platyhelminthes ("Turbellaria"). J. Nat. Hist. 39, 1–45.

Feller, R.J., Warwick, R.M., 1988. Energetics. In: Higgins, R.P., Thiel, H. (Eds.), Introduction to the Study of Meiofauna. Smithsonian Institution, Washington DC, pp. 181–196.

Field, J.G., Clarke, K.R., Warwick, R.M., 1982. A practical strategy for analysing multispecies distribution patterns. Mar. Ecol., Prog. Ser. 8, 37–52.

Gee, J.M., Warwick, R.M., 1984. Preliminary observations on the metabolic and reproductive strategies of harpacticoid copepods from an intertidal sandflat. Hydrobiologia 118, 29–37.

Gee, J.M., Warwick, R.M., 1994a. Metazoan community structure in relation to the fractal dimensions of marine macroalgae. Mar. Ecol., Prog. Ser. 103, 141–150.

Gee, J.M., Warwick, R.M., 1994b. Body-size distribution in a marine metazoan community and the fractal

dimensions of macroalgae. J. Exp. Mar. Biol. Ecol. 178, 247–259.

Gee, J.M., Warwick, R.M., 1996. A study of global biodiversity patterns in the marine motile fauna of hard substrata. J. Mar. Biol. Assoc. U.K. 76, 177–184.

Gee, J.M., Warwick, R.M., Schanning, M., Berge, J.A., Ambrose Jr., W.G., 1985a. Effects of organic enrichment on meiofaunal abundance and community structure in sublittoral soft sediments. J. Exp. Mar. Biol. Ecol. 91, 247–262.

Gee, J.M., Warwick, R.M., Davey, J.T., George, C.L., 1985b. Field experiments on the role of epibenthic predators in determining prey densities of an estuarine mudflat. Estuar. Coast. Shelf Sci. 21, 429–448.

Gee, J.M., Austen, M., De Smet, G., Ferraro, T., McEvoy, A., Moore, S., Van Gausbeki, D., Vincx, M., Warwick, R.M., 1992. Soft sediment meiofauna community responses to environmental pollution gradients in the German Bight and at the site of a former Dutch oil rig. Mar. Ecol., Prog. Ser. 91, 289–302.

George, C.L., Warwick, R.M., 1985. Annual macrofauna production in a hard–bottom reef community. J. Mar. Biol. Assoc. U.K. 65, 713–735.

Goss-Custard, J.D., Warwick, R.M., Kirby, R., McGrorty, S., Clarke, R.T., Pearson, B., Rispin, W. E., Le V. Dit Durell, S.E.A., Rose, R.J., 1991. Towards predicting wading bird densities from predicted prey densities in a post-barrage Severn Estuary. J. Appl. Ecol. 28, 1004–1026.

Gourbault, N., Warwick, R.M., 1994. Is the determination of meiobenthic diversity affected by the sampling method in sandy beaches? P.S.Z.N.I. Mar. Ecol. 15, 267–279.

Gourbault, N., Warwick, R.M., Helléouet, M.-N., 1995. A survey of intertidal meiobenthos (especially Nematoda) in coral sandy beaches of Moorea (French Polynesia). Bull. Mar. Sci. 57, 476–488.

Gourbault, N., Warwick, R.M., Helléouet, M.-N., 1998. Spatial and temporal variability in the composition and structure of meiobenthic assemblages (especially nematodes) in tropical beaches (Guadeloupe, FWI). Cah. Biol. Mar. 39, 29–39.

Gray, J.S., Aschan, M., Carr, M.R., Clarke, K.R., Green, R.H., Pearson, T.H., Rosenberg, R., Warwick, R.M., 1988. Analysis of community attributes of the benthic macrofauna of Frierfjord/Langesundfjord and in a mesocosm experiment. Mar. Ecol., Prog. Ser. 46, 151–165.

Gray, J.S., Clarke, K.R., Warwick, R.M., Hobbs, G., 1990. Detection of initial effects of pollution on marine benthos: an example from the Ekofisk and Eldfisk oilfields, North Sea. Mar. Ecol., Prog. Ser. 66, 285–299.

Guo, Y.Q., Warwick, R.M., 2001. Three new species of free–living nematodes from the Bohai Sea, China. J. Nat. Hist. 35, 1575–1586.

Heip, C., Warwick, R.M., Carr, M.R., Herman, P.M.J., Huys, R., Smol, N., Van Holsbeke, K., 1988a. Analysis of community attributes of the benthic meiofauna of Frierfjord/Langesundfjord. Mar. Ecol., Prog. Ser. 46, 171–180.

Heip, C., Warwick, R.M., d'Ozouville, L., 1998b. A European science plan on marine biodiversity. EMaPS Position Paper, vol. 2. European Science Foundation. 20 pp.

Hummon, W.D., Warwick, R.M., 1990. The marine flora and fauna of the Isles of Scilly: Gastrotricha. J. Nat. Hist. 24, 519–525.

Jayasree, K., Warwick, R.M., 1977. Free-living marine nematodes of a polluted sandy beach in the Firth of Clyde, Scotland. Description of seven new species. J. Nat. Hist. 11, 289–302.

Joint, I.R., Gee, J.M., Warwick, R.M., 1982. Determination of fine-scale vertical distribution of microbes and meiofauna in an intertidal sediment. Mar. Biol. 72, 157–164.

Kramer, K.J.M., Brockmann, U.H., Warwick, R.M., 1994. Tidal Estuaries: Manual of Sampling and Analytical Procedures. A.A. Balkema, Rotterdam. 304 pp.

Kendall, M.A., Widdicombe, S., Davey, J.T., Somerfield, P.J., Austen, M.C.V., Warwick, R.M., 1996. The biogeography of islands: preliminary results from a comparative study of the Isles of Scilly and Cornwall. J. Mar. Biol. Assoc. U.K. 76, 219–222.

Kendall, M.A., Warwick, R.M., Somerfield, P.J., 1997. Species size distributions in Arctic benthic communities. Polar Biol. 17, 389–392.

Kirby, R., Henderson, P.A., Warwick, R.M., 2004. The Severn, UK: Why is the estuary different? J. Mar. Sci. Environ. C2, 3–17.

Leonard, D.R.P., Clarke, K.R., Somerfield, P., Warwick, R.M. (in press). The application of an indicator based on taxonomic distinctness for UK marine biodiversity assessments. J. Env. Manag.

McIntyre, A.D., Warwick, R.M., 1984. Meiofauna techniques, In: Holme, N.A., McIntyre, A.D. (Eds.), Methods for the Study of Marine Benthos, 2nd ed. IBP Handbook, vol. 16. Blackwell, Oxford, pp. 217–244.

Mu, F.-H., Somerfield, P.J., Warwick, R.M., Zhang, Z.-N., 2002. Large-scale spatial patterns in the community structure of benthic harpacticoid copepods in the Bohai Sea, China. Raffles Bull. Zool. 50, 17–26.

Netto, S.A., Warwick, R.M., Attrill, M.J., 1999a. Meiobenthic and macrobenthic community structure in carbonate sediments of Rocas Atoll (north-east Brazil). Estuar. Coast. Shelf Sci. 48, 39–50.

Netto, S.A., Attrill, M.J., Warwick, R.M., 1999b. Sublittoral meiofauna and macrofauna of Rocas Atoll (NE Brazil): indirect evidence of a topographically controlled front. Mar. Ecol., Prog. Ser. 179, 175–186.

Netto, S.A., Attrill, M.J., Warwick, R.M., 1999c. The effect of a natural water-movement related disturbance on the structure of meiofauna and macrofauna communities in the intertidal sand flat of Rocas Atoll (NE Brazil). J. Sea Res. 42, 291–302.

Netto, S.A., Attrill, M.J., Warwick, R.M., 2003. The relationship between benthic fauna, carbonate sediments and reef morphology in reef-flat tidal pools of Rocas Atoll (north-east Brazil). J. Mar. Biol. Assoc. U.K. 83, 425–432.

Platt, H.M., Warwick, R.M., 1980a. The significance of free-living nematodes to the littoral ecosystem. In: Price, J.H., Irvine, D.E.G., Farnham, W.F. (Eds.), The Shore Environment. Ecosystems, vol. 2. Academic Press, Cambridge, pp. 729–759.

Price, R., Warwick, R.M., 1980b. Temporal variations in annual production and biomass in estuarine populations of two polychaetes, Nephtys hombergi and Ampharete acutifrons. J. Mar. Biol. Assoc. U.K. 60, 481–487.

Platt, H.M., Warwick, R.M., 1983. Freeliving Marine Nematodes: Part 1. British Enoplids. Synopses of the British Fauna, vol. 28. Cambridge. Univ. Press. 307 pp.

Platt, H.M., Warwick, R.M., 1988. Freeliving Marine Nematodes: Part II. British Chromadorida. Synopses of the British Fauna, vol. 38. Brill. 502 pp.

Platt, H.M., Warwick, R.M., Clarke, K.R., Agard, J., Gobin, J., 1990. Benthic communities and disturbance in a subtropical marine environment. Prog. Underw. Sci. 15, 43–54.

Potter, I.C., Claridge, P.N., Warwick, R.M., 1986. Consistency of seasonal changes in an estuarine fish assemblage. Mar. Ecol., Prog. Ser. 32, 217–228.

Price, R., Warwick, R.M., 1980. The effect of temperature on the respiration rate of meiofauna. Oecologia 44, 145–148.

Rowden, A.A., Warwick, R.M., Gordon, D.P., 2004. Bryozoan biodiversity in the New Zealand region and implications for marine conservation. Biodivers. Conserv. 13, 2695–2721.

Savage, C., Field, J.G., Warwick, R.M., 2001. Comparative meta-analysis of the impact of offshore marine mining on macrobenthic communities versus organic pollution studies. Mar. Ecol., Prog. Ser. 221, 265–275.

Schratzberger, M., Warwick, R.M., 1998a. Effects of physical disturbance on meiofaunal communities in sand and mud: a microcosm experiment. Mar. Biol. 130, 643–650.

Schratzberger, M., Warwick, R.M., 1998b. Effects of the intensity and frequency of organic enrichment on two estuarine nematode assemblages. Mar. Ecol., Prog. Ser. 164, 83–94.

Schratzberger, M., Warwick, R.M., 1999a. Impact of predation and sediment disturbance by Carcinus maenas (L.) on free-living nematode community structure. J. Exp. Mar. Biol. Ecol. 235, 255–271.

Schratzberger, M., Warwick, R.M., 1999b. Differential effects of various types of disturbances on the structure of nematode assemblages: an experimental approach. Mar. Ecol., Prog. Ser. 181, 227–236.

Solan, M., Germano, J.D., Raffaelli, D.G., Warwick, R. M. (Eds.), 2003. Benthic Dynamics: In Situ Surveillance of the Sediment–Water InterfaceJ. Exp. Mar. Biol. Ecol. (Special Issue), vol. 285–286. 511 pp.

Somerfield, P.J., Gee, J.M., Warwick, R.M., 1994a. Soft sediment meiofaunal community structure in relation to a long-term heavy metal gradient in the Fal estuary system. Mar. Ecol., Prog. Ser. 105, 79–88.

Somerfield, P.J., Gee, J.M., Warwick, R.M., 1994b. Benthic community structure in relation to an instantaneous discharge of waste water from a tin mine. Mar. Poll. Bull. 28, 363–369.

Somerfield, P.J., Rees, H.L., Warwick, R.M., 1995. Interrelationships in community structure between shallow-water marine meiofauna and macrofauna in relation to dredgings disposal. Mar. Ecol., Prog. Ser. 127, 103–112.

Thrush, S.F., Warwick, R.M. (Eds.), 1997. The ecology of soft-bottom habitats: matching spatial patterns with dynamic processesJ. Exp. Mar. Biol. Ecol. (Special Issue), vol. 216. 259 pp.

Villano, N., Warwick, R.M., 1995. Meiobenthic communities associated with the seasonal cycle of growth and decay of Ulva rigida Agardh in the Palude della Rosa, Lagoon of Venice. Estuar. Coast. Shelf Sci. 41, 181–194.

Warwick, R.M., 1969a. Two new species of Pseudonchus Cobb (Nematoda, Choanolaimidae) from the British coast. Cah. Biol. Mar. 10, 375–382.

Warwick, R.M., 1969b. The marine nematode *Eurystomina terricola* (de Man, 1907) and its distribution on British shores. Hydrobiologia 34, 392–400.

Warwick, R.M., 1970a. Fourteen new species of free-living marine nematodes from the Exe estuary. Bull. Br. Mus. Nat. Hist., Zool. 19, 137–177.

Warwick, R.M., 1970b. The genus Paramesacanthion Wieser (Nematoda, Enoplidae) off the coast of Northumberland. Cah. Biol. Mar. 11, 187–194.

Warwick, R.M., 1970c. Two new species of freeliving marine nematodes from the Northumberland coast. J. Nat. Hist. 4, 593–598.

Warwick, R.M., 1971a. The Cyatholaimidae (Nematoda, Chromadoroidea) off the coast of Northumberland. Cah. Biol. Mar. 12, 95–110.

Warwick, R.M., 1971b. Nematode associations in the Exe estuary. J. Mar. Biol. Assoc. U.K. 51, 439–454.

Warwick, R.M., 1973. Freeliving marine nematodes from the Indian Ocean. Bull. Br. Mus. Nat. Hist. (Zoology) 25, 85–117.

Warwick, R.M., 1977a. Some free-living marine nematodes from the Isles of Scilly. J. Nat. Hist. 11, 381–392.

Warwick, R.M., 1977b. The structure and seasonal fluctuations of phytal marine nematode associations on the Isles of Scilly. In: Keegan, B.F., O Ceidigh, P., Boaden, P.J.S. (Eds.), Biology of Benthic Organisms. Pergamon, Oxford, pp. 577–585.

Warwick, R.M., 1978. The taxonomic requirements of ecologists. Ann. Soc. R. Zool., Belg. 108, 191.

Warwick, R.M., 1980. Population dynamics and secondary production of benthos. In: Tenore, K.R., Coull, B.C. (Eds.), Marine Benthic Dynamics. Univ. S. Carolina Press, Columbia, pp. 1–24.

Warwick, R.M., 1981a. Survival strategies of meiofauna. In: Jones, N.V., Wolff, W.J. (Eds.), Feeding and Survival Strategies of Estuarine Organisms. Plenum, New York, pp. 39–52.

Warwick, R.M., 1981b. The nematode/copepod ratio and its use in pollution ecology. Mar. Poll. Bull. 12, 329–333.

Warwick, R.M., 1981c. The influence of temperature and salinity on energy partitioning in the marine nematode Diplolaimelloides bruciei. Oecologia 51, 318–325.

Warwick, R.M., 1982. The partitioning of secondary production among species in benthic communities. Neth. J. Sea Res. 16, 1–16.

Warwick, R.M., 1983a. The implications of resource partitioning for the structure of a sand-beach meiofauna community. In: McLachlan, A., Erasmus, T. (Eds.), Sandy Beaches as Ecosystems. W. Junk, The Hague, pp. 753–754.

Warwick, R.M., 1983b. Sampling and analysis of benthic communities. Practical Procedures for Estuarine Studies. The Natural Environment Research Council, pp. 185–212.

Warwick, R.M., 1984a. Species size distributions in marine benthic communities. Oecologia 61, 32–41.

Warwick, R.M., 1984b. The benthic ecology of the Bristol Channel. Mar. Poll. Bull. 15, 70–76.

Warwick, R.M., 1986. A new method for detecting pollution effects on marine macrobenthic communities. Mar. Biol. 92, 557–562.

Warwick, R.M., 1987. Meiofauna: their role in marine detrital systems. In: Moriarty, D.J.W., Pullin, R.S.V. (Eds.), Detritus and Microbial Ecology in Aquaculture. ICLARM, Manila, pp. 282–295.

Warwick, R.M., 1988a. The structure and dynamics of marine benthic communities. Nova Thalassia 7 (Suppl. 3), 31–42 (dated 1985).

Warwick, R.M., 1988b. The level of taxonomic discrimination required to detect pollution effects on marine benthic communities. Mar. Poll. Bull. 19, 259–268.

Warwick, R.M., 1988c. Effects on community structure of a pollutant gradient – introduction. Mar. Ecol., Prog. Ser. 46, 149.

Warwick, R.M., 1988d. Analysis of community attributes of the macrobenthos of Frierfjord/Langesundfjord at taxonomic levels higher than species. Mar. Ecol., Prog. Ser. 46, 167–170.

Warwick, R.M., 1988e. Effects on community structure of a pollutant gradient – summary. Mar. Ecol., Prog. Ser. 46, 207–211.

Warwick, R.M., 1989. The role of meiofauna in the marine ecosystem: evolutionary considerations. Zool. J. Linn. Soc. 96, 229–241.

Warwick, R.M., 1993. Environmental impact studies on marine communities: pragmatical considerations. Aust. J. Ecol. 18, 63–80.

Warwick, R.M. (Ed.), 1996. Marine BiodiversityJ. Exp. Mar. Biol. Ecol. (Special Issue), vol. 202. 95 pp.

Warwick, R.M., 1996. Biodiversity and production on the sea floor. In: Hempel, G. (Ed.), The Oceans and the Poles. Gustav Fischer Verlag, Jena, pp. 217–227.

Warwick, R.M., 2000a. Using data and information for research. In: Hiscock, K. (Ed.), Using Marine Biological Information in the Electronic Age. MBA Occasional Publication, vol. 7. Marine Biological Association of the United Kingdom, Plymouth, pp. 5–6.

Warwick, R.M., 2000b. Are loriciferans paedomorphic (progenetic) priapulids? Vie et Milieu 50, 191–193.

Warwick, R.M., 2001a. Scaling of marine biodiversity. Océanis 24, 51–59.

Warwick, R.M., 2001b. Evidence for the effects of metal contamination on the intertidal macrobenthic assemblages of the Fal estuary. Mar. Poll. Bull. 42, 145–148.

Warwick, R.M., 2001c. Pollution: effects on marine communities. In: Steele, J., Thorpe, S., Turekian, K. (Eds.), Encyclopedia of Ocean Sciences. Academic Press, London, pp. 2222–2229.

Warwick, R.M., Bayne, B.L. (Eds.), 1993. Changes in Marine CommunitiesJ. Exp. Mar. Biol. Ecol. (special issue), vol. 172. 232 pp.

Warwick, R.M., Buchanan, J.B., 1970. The meiofauna off the coast of Northumberland: I. The structure of the nematode population. J. Mar. Biol. Assoc. U.K. 50, 129–146.

Warwick, R.M., Buchanan, J.B., 1971. The meiofauna off the coast of Northumberland: II. Seasonal stability of the nematode population. J. Mar. Biol. Assoc. U.K. 51, 355–362.

Warwick, R.M., Buchanan, J.B., 1973. Population stability in offshore meiobenthic nematodes. Proc. Challenger Soc. 4, 111.

Warwick, R.M., Clarke, K.R., 1991. A comparison of some methods for analysing changes in benthic community structure. J. Mar. Biol. Assoc. U.K. 71, 225–244.

Warwick, R.M., Clarke, K.R., 1993. Comparing the severity of disturbance: a meta-analysis of marine macrobenthic community data. Mar. Ecol., Prog. Ser. 92, 221–231.

Warwick, R.M., Clarke, K.R., 1993. Increased variability as a symptom of stress in marine communities. J. Exp. Mar. Biol. Ecol. 172, 215–226.

Warwick, R.M., Clarke, K.R., 1994. Relearning the ABC: taxonomic changes and abundance/biomass relationships in disturbed benthic communities. Mar. Biol. 118, 739–744.

Warwick, R.M., Clarke, K.R., 1995a. New 'biodiversity' measures reveal a decrease in taxonomic distinctness with increasing stress. Mar. Ecol., Prog. Ser. 129, 301–305.

Warwick, R.M., Clarke, K.R., 1995b. Multivariate measures of community stress and their application to marine pollution studies in the East Asian region. Phuket Mar. Biol. Cent. Res. Bull. 60, 99–113.

Warwick, R.M., Clarke, K.R., 1996. Relationships between body size, species abundance and diversity in marine benthic assemblages: facts or artifacts? J. Exp. Mar. Biol. Ecol. 202, 63–71.

Warwick, R.M., Clarke, K.R., 1998. Taxonomic distinctness and environmental assessment. J. Appl. Ecol. 35, 532–543.

Warwick, R.M., Clarke, K.R., 2001. Practical measures of marine biodiversity based on relatedness of species. Oceanogr. Mar. Biol. Ann. Rev. 39, 207–231.

Warwick, R.M., Coles, J.W., 1975. Notes on the free-living marine genus *Euchromadora* de Man, 1886 and its allies, with descriptions of two new species (Chromadoridae: Nematoda). J. Nat. Hist. 9, 403–412.

Warwick, R.M., Coles, J.W., 1977. The marine flora and fauna of the Isles of Scilly. Free-living Nematoda. J. Nat. Hist. 11, 393–407.

Warwick, R.M., Davies, J.R., 1977. The distribution of sublittoral macrofauna communities in the Bristol Channel in relation to the substrate. Estuar. Coast. Mar. Sci. 5, 267–288.

Warwick, R.M., Gage, J.D., 1975. Near–shore zonation of benthic fauna, especially Nematoda, in Loch Etive. J. Mar. Biol. Assoc. U.K. 55, 295–311.

Warwick, R.M., Gee, J.M., 1984. Community structure of estuarine meiobenthos. Mar. Ecol., Prog. Ser. 18, 97–111.

Warwick, R.M., George, C.L., 1980. Annual macrofauna production in an *Abra* community. In: Collins, M.B., et al. (Ed.), Industrial Embayments and Their Environmental Problems. A Case Study of Swansea Bay. Pergamon, Oxford, pp. 517–538.

Warwick, R.M., Joint, I.R., 1987. The size distribution of organisms in the Celtic Sea: from bacteria to Metazoa. Oecologia 73, 185–191.

Warwick, R.M., Light, J., 2002. Death assemblages of molluscs on St. Martin's Flats, Isles of Scilly: a surrogate for regional biodiversity? Biodivers. Conserv. 11, 99–112.

Warwick, R.M., Platt, H.M., 1973. New and little known marine nematodes from a Scottish sandy beach. Cah. Biol. Mar. 14, 135–158.

Warwick, R.M., Platt, H.M., 1983. Third Symposium on Aquatic Nematodes, Plymouth, 7–9 September 1981Veroff. Inst. Meeresforsch. Bremerh., 19, pp. 203–207.

Warwick, R.M., Price, R., 1975. Macrofauna production in an estuarine mud-flat. J. Mar. Biol. Assoc. U.K. 55, 1–18.

Warwick, R.M., Price, R., 1979. Ecological and metabolic studies on free-living nematodes from an estuarine mud-flat. Estuar. Coast. Mar. Sci. 9, 257–271.

Warwick, R.M., Radford, P.J., 1989. Analysis of the flow network in an estaurine benthic community. In:

Wulff, F., Field, J.G., Mann, K.H. (Eds.), Network Analysis in Marine Ecology. Springer Verlag, pp. 220–231.

Warwick, R.M., Robinson, J., 2000. Sibling species in the marine pollution indicator genus Pontonema Leidy (Nematoda: Oncholaimidae), with a description of P. mediterranea sp. nov. J. Nat. Hist. 34, 641–662.

Warwick, R.M., Ruswahyuni, 1987. Comparative study of the structure of some tropical and temperate marine soft-bottom macrobenthic communities. Mar. Biol. 95, 641–649.

Warwick, R.M., Turk, S.M., 2002. Predicting climate change effects on marine biodiversity: comparison of recent and fossil molluscan death assemblages. J. Mar. Biol. Assoc. U.K. 82, 847–850.

Warwick, R.M., Uncles, R.J., 1980. The distribution of benthic macrofauna associations in the Bristol Channel in relation to tidal stress. Mar. Ecol., Prog. Ser. 3, 97–103.

Warwick, R.M., Villano, N., 2000. The meiobenthic component of the Palude della Rosa, Lagoon of Venice. In: Lasserre, and Marzollo, A. (Eds.) The Venice Lagoon Ecosystem: Inputs and Interactions Between Land and Sea. UNESCO, Paris and Parthenon Publishing, Carnforth, UK, pp. 227–246.

Warwick, R.M., George, C.L., Davies, J.R., 1978. Annual macrofauna production in a Venus community. Estuar. Coast. Mar. Sci. 7, 215–241.

Warwick, R.M., Joint, I.R., Radford, P.J., 1979. Secondary production of the benthos in an estuarine environment. In: Jefferies, R.L., Davy, A.J. (Eds.), Ecological Processes in Coastal Environments. Blackwell, Oxford, pp. 429–450.

Warwick, R.M., Davey, J.T., Gee, J.M., George, C.L., 1982. Faunistic control of Enteromorpha blooms: a field experiment. J. Exp. Mar. Biol. Ecol. 56, 23–31.

Warwick, R.M., Gee, J.M., Berge, J.A., Ambrose Jr., W. G., 1986a. Effects of the feeding activity of the polychaete Streblosoma bairdi (Malmgren) on meiofaunal abundance and community structure. Sarsia 71, 11–16.

Warwick, R.M., Collins, N.R., Gee, J.M., George, C.L., 1986b. Species size distributions of benthic and pelagic Metazoa: evidence for interaction? Mar. Ecol. Prog. Ser. 34, 63–68.

Warwick, R.M., Pearson, T.H., Ruswahyuni, 1987. Detection of pollution effects on marine macrobenthos: further evaluation of the species abundance/biomass method. Mar. Biol. 95, 193–200.

Warwick, R.M., Carr, M.R., Clarke, K.R., Gee, J.M., Green, R.H., 1988. A mesocosm experiment on the effects of hydrocarbon and copper pollution on a sublittoral soft-sediment meiobenthic community. Mar. Ecol., Prog. Ser. 46, 181–191.

Warwick, R.M., Platt, H.M., Clarke, K.R., Agard, J., Gobin, G., 1990a. Analysis of macrobenthic and meiobenthic community structure in relation to pollution and disturbance in Hamilton Harbour, Bermuda. J. Exp. Mar. Biol. Ecol. 138, 119–142.

Warwick, R.M., Clarke, K.R., Gee, J.M., 1990b. The effect of disturbance by soldier crabs, Mictyris platycheles H. Milne Edwards, on meiobenthic community structure. J. Exp. Mar. Biol. Ecol. 135, 19–33.

Warwick, R.M., Clarke, K.R., Suharsono, 1990c. A statistical analysis of coral community responses to the El Niño events of 1982–3 in the Thousand Islands, Indonesia. Coral Reefs 8, 171–179.

Warwick, R.M., Goss–Custard, J.D., Kirby, R., George, C.L., Pope, N.D., Rowden, A.A., 1991. Static and dynamic environmental factors determining the community structure of estuarine macrobenthos in SW Britain: why is the Severn estuary different? J. Appl. Ecol. 28, 329–345.

Warwick, R.M., McEvoy, A.J., Thrush, S.F., 1997. The influence of Atrina zelandica Gray on meiobenthic nematode diversity and community structure. J. Exp. Mar. Biol. Ecol. 214, 231–247.

Warwick, R.M., Platt, H.M., Somerfield, P.J., 1998. Freeliving marine nematodes: Part III. British Monhysterida. Synopses of the British Fauna, vol. 53. Field Studies Council. 296 pp.

Warwick, R.M., Ashman, C.M., Brown, A.R., Clarke, K.R., Dowell, B., Hart, B., Lewis, R.E., Shillabeer, N., Somerfield, P.J., Tapp, J.F., 2002a. Inter-annual changes in the biodiversity and community structure of the macrobenthos in Tees Bay and the Tees estuary, UK, associated with local and regional environmental events. Mar. Ecol., Prog. Ser. 234, 1–13.

Warwick, R.M., Dexter, D.M., Kuperman, B., 2002b. Freeliving nematodes from the Salton Sea. Hydrobiologia 473, 121–128.

Widdicombe, S., Austen, M.C., Kendall, M.A., Warwick, R.M., Jones, M.B., 2001. Bioturbation as a mechanism for setting and maintaining levels of diversity in subtidal macrobenthic communities. Hydrobiologia 440, 369–377.

Warwick, R.M., Emblow, C., Féral, J.-P., Hummel, H., Van Avesaath, P., Heip, C., 2003. *European Marine Biodiversity Research Sites.* Report on Worpackage 1 of BIOMARE (Implementation and networking of large scale, long term marine biodiversity research in Europe), 121 pp.

Melanie C. Austen
Plymouth Marine Laboratory, Prospect Place,
West Hoe, Plymouth, PL1 3DH, UK
E-mail address: mcva@pml.ac.uk.
Corresponding author. Tel.: +44 1752 633100;
fax: +44 1752 633101.

Robert B. Whitlatch
Department of Marine Sciences,
1080 Shennecossett Road, University of Connecticut,
Groton, Connecticut 06340, USA

10 December 2005