



Review

The ups and downs of benthic ecology: considerations of scale, heterogeneity and surveillance for benthic–pelagic coupling

Dave Raffaelli^{a,*}, Elanor Bell^b, Guntram Weithoff^b,
Asako Matsumoto^c, Juan Jose Cruz-Motta^d, Pete Kershaw^e,
Ruth Parker^e, Dave Parry^f, Malcolm Jones^f

^aEnvironment Department, University of York, Heslington, York YO10 5DD, UK

^bInstitute for Biochemistry and Biology, University of Potsdam, Maulbeerallee 2, 14469 Potsdam, Germany

^cMarine Ecosystems Research Department, Japan Marine Science and Technology Centre, 2-15 Natsushima-cho,
Yokosuka 237-0061, Japan

^dCentre for Research on Ecological Impacts of Coastal Cities, Marine Ecology Laboratories,
University of Sydney, Sydney NSW 2006, Australia

^eThe Centre for Fisheries, Environment and Aquaculture Science, Lowestoft Laboratory, Pakefield Road,
Lowestoft NR33 0HT, UK

^fPlymouth Environmental Research Centre, University of Plymouth, Drake Circus, Plymouth PL4 8AA, UK

Received 21 August 2002; received in revised form 19 October 2002; accepted 30 October 2002

1. Introduction

The seabed is the most extensive habitat on the planet. It occupies at least 75% of the Earth's surface, far more if the planar areas of the shelves and slopes are taken into account. It follows that fluxes of materials across the sediment–water interface, and the mechanisms that mediate and constrain those fluxes, are likely to have global significance. Just how important the seabed is globally has been costed for nutrient cycling, which for marine shallow water systems is >US\$ 40,000 ha⁻¹ year⁻¹, 86% of the value of this service for all terrestrial and aquatic systems (Constanza et al., 1997). To this must be added the smaller areas (<1%) occupied by the sediment–water interface of wetlands, lakes and rivers, where local fluxes can be high and their significance belies their lesser size. However, what must also be taken into account, but is often overlooked, is the contribution of living benthic particles to pelagic systems, particularly planktonic, a process which is likely to profoundly influence the dynamics

* Corresponding author. Tel.: +44-1904-434060; fax: +44-1904-432998.

E-mail address: dr3@york.ac.uk (D. Raffaelli).

of water column populations and communities (see below). Benthic organisms are often also key drivers of biogeochemical fluxes through their bioturbatory activities in sediments. An understanding of the linkages between the fluxes of inorganic materials, the fluxes of living particles and benthic patterns, and processes within the sediment will be central to a proper evaluation of the significance of the benthic environment in marine ecosystems.

These issues were the focus of a workshop held at Aberdeen 25th–29th March 2002, as part of a larger meeting *Benthic dynamics: in situ surveillance at the sediment–water interface*. The workshop specifically identified scaling, heterogeneity and the coupling of benthic and pelagic systems, focusing on the flux of living particles, as pressing research issues. In presenting the output from that workshop, we are only too aware that the area of benthic–pelagic coupling is not novel and that several excellent reviews of the topic already exist (e.g. Boero et al., 1996; Graf, 1992; Marcus and Boero, 1998). Similarly, many of the issues of scale and heterogeneity which are so pertinent to benthic ecology have been discussed at considerable length by many authors (Botsford, 2001; Chase and Leibold, 2002; Edmunds and Bruno, 1996; Ellingsen, 2001; Gaston, 2000; He and Gaston, 2000; Pascual and Levin, 1999; Pepin and Anderson, 1997; Sponseller et al., 2001; Woodward and Hildrew, 2002), and a marine benthic focus is provided in a dedicated issue of this journal (Thrush and Warwick, 1998). It is not our purpose to duplicate these fine reviews, but to highlight the ways in which the themes of heterogeneity, scale and the coupling of benthic and pelagic processes might usefully inform one another. Specifically, we provide a brief review of benthic–pelagic coupling, identify issues of patchiness and scale pertinent to our theme, discuss ways in which the integration of these areas might yield new scientific insights and reflect on the potential of surveillance methodologies in this respect.

2. Benthic–pelagic coupling

The theme of benthic–pelagic coupling acknowledges that there is a two-way exchange, or flux of matter, between the benthos and the overlying water body, which is important for both benthic and pelagic compartments. This exchange takes place across the sediment–water interface, typically viewed by macrobenthic ecologists as a planar surface. Since much of this essay focuses on the flux of living particles, especially larvae, post-larvae and sub-adults, it is this planar surface which is also the major focus, but it should be noted that the area of sediment at the seabed or lake bed in contact with the overlying water is significantly greater than that represented by the planar surface, due to the presence of burrows and the resulting active and passive bio-irrigation. Similarly, water flowing over burrow mounds and ripples can induce porewater advection, extending several centimetres deep, influencing the distribution of chemical properties (e.g. oxygen penetration) and biological phenomena (Huettel and Webster, 2001; Huettel et al., 1996; Huettel and Rusch, 2000; Rusch and Huettel, 2000; Parker et al., this volume).

Many studies have focused on the deposition of non-living organic matter to the seabed, ranging from microscopic debris through faecal pellets to very large particles,

such as whales which also create substantial habitat structure (Fujioka et al., 1993; Smith, 1992; Smith et al., 1989), the mineralisation of this organic material within the sediment and the release of nutrients back into the overlying water column, and the role of benthic invertebrates in this process. Whilst technically challenging, such investigations seem relatively tractable compared to estimates of the movement of living particles between the benthic and pelagic compartments. The flux of living organisms, both downwards and upwards is affected by a range of diel, seasonal and ontogenetic migrations which may overlap spatially to such an extent that they can be thought of as providing a ladder of migrations linking the organisms on the seafloor with those at the surface (Herring, 2002). It is only by considering this complex of fluxes that the true significance of benthic–pelagic coupling becomes apparent. Three basic categories of movement of living material between benthic and pelagic compartments can be recognised.

2.1. Active movement following a life-form shift

Ontogenetic movement from the benthic to the pelagic compartment includes hatching, excysting and larval release, as found, for example, in polyps of jellyfish (Miyake et al., in press; Dybas, 2001), and the copepods *Calanus finmarchicus* and *Neocalanus plumchirus* (Herring, 2002). Ontogenetic related movement from the pelagic to the benthic compartment includes encystment, egg and larval release across a range of taxa from protists to macrofauna, including deep-water squid, fish and shrimps. For instance, *Calanus* and *Neocalanus* live as the pre-adult stage at considerable depth, moulting to the adult form in winter and rising into the surface waters. Movement of organisms between benthic and pelagic compartments is also associated with a life-form shift in eels (Schmidt, 1922; Tsukamoto, 1992) and whales (Best et al., 1984; Rice, 1989).

2.2. Active movement without a life-form shift

Movement (active or passive) of organisms between benthic and pelagic compartments also occurs without a life-form shift, as in the regular diel vertical migrations (DVM) shown by jellyfish (Larson et al., 1992; Mackie et al., 1981; Mills and Goy, 1988; Miyake et al., 2002), the mesopelagic shrimp *Systellaspis debilis* (Foxton, 1970; Roe, 1984), whales (Rice, 1989; Roe, 1969), the copepods *Calanus pacificus* (Frost, 1988), *Eurytemora* (Vuorinen, 1987), *Euchaeta* (Bollens and Frost, 1991) and *Pseudocalanus* (Ohman, 1990) as well as in mysid and other hyperbenthic organisms (Mees and Jones, 1997). Organisms within the deep scattering layers (populations of fish, shrimp and siphonophores) can rise to the surface at dusk at rates of up to 300 m h^{-1} (Herring, 2002), whilst in the Pacific, some 43% of the individual and 47% of the biomass migrate from below 400 m by day to above this depth at night (Maynard et al., 1975). It has been estimated that there may be a vertical translocation of $25 \text{ tons km}^{-2} \text{ day}^{-1}$ from 250 m to the surface, almost $10^9 \text{ tons day}^{-1}$ over the whole world oceans (Longhurst, 1976). Animals undertaking DVM which feed at the surface (Merrett and Roe, 1974) carry the food in their guts down to depths where they void their faecal pellets, greatly increasing the export of carbon from the surface to the seafloor.

2.3. Passive processes involved in movement

Large-scale passive resuspension of individuals from the benthos to the water column can occur in extreme hydraulic events, such as storms or where tidal ranges are high (Yeo and Risk, 1979; Cacchione et al., 1987; Dobbs and Vozarik, 1983; Essink et al., 1989) and can be expected to be increased by human activities such as fishing using bottom trawls, dredging and aggregate extraction (Jennings et al., 2001a,b; Schratzberger and Warwick, 1999). Similarly, upwelling from deep-sea canyons, cold water seeps and hydrothermal vents can upwardly transport water masses and their associated organisms (Corliss et al., 1979; Fujikura et al., 1999; Paull et al., 1984; Suess et al., 1985; Tomassa et al., 2000).

Further discussion of these mechanisms can be found in Marcus and Boero (1998), Schelske et al. (1995), Hansson (1996), De Jonge and van Beusekom, (1995), Garstecki and Wickman (2001), Marcus and Schmidt-Gengenback (1986), Ogilvie and Mitchell (1998), Herring (2002) and Wainwright (1987).

This flux of living particles is likely to have consequences for the dynamics of both pelagic and benthic systems (Marcus and Boero, 1998). In addition to the trophic cross-subsidy of living material from the pelagic to the benthic and the benthic to the pelagic (Polis et al., 1997), benthic environments, in particular, serve as storage banks for propagules of water column species. Many taxa associated traditionally with an entirely water column life cycle are now known to use the benthic environment for periods of months to many years, depending on the species (Marcus, 1995; Hairston et al., 1996), as eggs, encysted individuals and pre-adults (see above). Movement of this material from the benthic storage bank to the water column could stabilise population and community dynamics in the water column and ensure long-term population persistence by repopulating areas following adverse environmental conditions in the water column. The parallels with terrestrial soil seed banks are only too obvious. As in the latter, long-term “storage” of individuals in the sediment effectively decouples the generations and Marcus and Boero (1998) explore the implications of this. Similarly, the recruitment of “non-storage” macrobenthic invertebrate larvae into the water column may stabilise models of coastal ecosystem dynamics (Warwick, 1989). Interestingly, we could find no examples of storage banks for benthic taxa in the pelagic.

The importance of living particles in the coupling of benthic and pelagic systems energised marine research programmes 20 years ago, but the theme has fallen out of fashion in recent years, rightly prompting wake-up calls from several authors (e.g. Marcus and Boero, 1998; Boero et al., 1996), and has received much less attention by freshwater ecologists (Ackerman et al., 2001; Bell and Weithoff, this volume; Finelli et al., 2002; Makino et al., 2001; Rothhaupt, 2000 and references therein; Wilhelm et al., 1999). Given developments in the field of supply-side ecology (Lewin, 1986; Roughgarden et al., 1985; Gaines and Roughgarden, 1985), the highlighting of the significance of cross-subsidies between ecosystems (Polis et al., 1997), attempts to match long-term trends in pelagic and benthic populations (e.g. Beukeema, 2002), and compelling arguments that the recruitment of benthic organisms to pelagic systems may be important for marine ecosystem dynamics (e.g. Warwick, 1989; Belmonte et al., 1995), it is surprising that benthic and pelagic ecologists have still to fully embrace the holistic approach encapsulated by benthic–pelagic coupling.

3. Methodological constraints

Perhaps one of the reasons why benthic–pelagic coupling has declined as a mainstream theme in marine ecology is that the proper quantifying of the linkages between the two compartments is not a trivial undertaking. There are many coupled links which integrate different depths within the water column and it is likely that similar coupled links occur over depth within sediments, albeit on a much smaller spatial scale. Yet the majority of the surveillance techniques and experimental methodologies available, many of which are described in detail in this volume, necessarily focus on the sediment–water interface. This is understandable given the visually disjunct nature of the sediment and water column habitat (but see also earlier comments about the pitfalls of restricting observations to planar surfaces), and the fact that surveillance techniques such as landers require a stable surface for their operation. However, by focusing on the interface itself and relying entirely on surveillance techniques, ecologists are unlikely to gain a complete appreciation of benthic–pelagic dynamics, because they only see the arrival of pelagic material to the sediment (the very endpoint of its journey) and the departure of benthic material to the water column (the starting point for this material). The processes which take place within the sediment or the water column must remain obscure. Moreover, this ‘material’ usually comprises a restricted range of organism body sizes (larvae and small adults), because of the size constraints of the recording devices of most surveillance and experimental approaches. Large particles are infrequently recorded by many devices, unless they are specifically designed to do so (e.g. [Smith, 1992](#); [Smith et al., 1989](#); [Klages et al., this volume](#); [Bailey et al., this volume](#), and references therein).

Many studies have measured the input of living material from the pelagic to the benthos using traps ([Godhe et al., 2001](#); [Hansson, 1996](#); [Norkko et al., 2001](#); [Whitlatch and Osman, 1998](#); [Whitlatch et al., this volume](#)), but there have been relatively few estimates of emergence from sediments to the pelagic compartment ([Arnott and Yan, 2002](#); [Bell and Weithoff, this volume](#); [De Stasio, 1990](#); [Duggan et al., 2002](#); [Hairston et al., 2000](#); [Head et al., 1998, 1999a,b](#)). Whilst investigations of settlement and emergence may be thought of as complementary, because they describe the movement of particles across a boundary, the two processes are quite asymmetric in the information they provide. Emergence from the benthos is measured at the sediment surface, but the settlement patterns of these individuals within the water column, perhaps many tens or hundreds of metres above, has to our knowledge not been documented at all. Similarly, the emergence or rain-out of living material from the pelagic zone, may be initiated many tens or hundreds of metres above the sediment–water interface, and the spatial patterns of this rain-out as it moves through the water column have rarely been mapped ([Hansson et al., 1994](#); [Hansson, 1996](#)). Until we can better estimate and describe the spatial structure of recruitment of benthic material to its final destination within the pelagic compartment, as well as rain-out of pelagic material to the benthos, it will be difficult to truly appreciate the dynamics of benthic–pelagic coupling. Simply knowing how much material leaves or arrives at the sediment–water interface, without following the subsequent fate of the organisms provides only a limited view of the benthic–pelagic couple.

4. Issues of patchiness and scale

One of the most important attributes of both benthic and pelagic systems is the patchiness (heterogeneity) of their biological components in space and time (e.g. Dagg, 1977; Denman, 1994; Hall et al., 1994), both vertically and horizontally. Rather than being recognised as an important feature of their systems, ecologists have long regarded patchiness as a nuisance because of the high variance it imposes on sampling programmes and because it generates autocorrelation between samples that can potentially confound any subsequent statistical analyses (Legendre, 1993). In the past, much effort has therefore been put into trying to minimise the variance between separately collected samples, for instance by increasing the number of samples, by increasing the size of the sampling unit, by simply homogenising many separately collected samples to lose the variance, or by using extremely large sampling units which integrate abundances over large areas, such as trawls. An alternative view is that between-sample variance is important information which allows a formal description of the natural heterogeneity that may hold the key to understanding the dynamics of the system under study (Legendre, 1993). We believe that this will certainly be true for the emergence and settlement processes observed at the sediment–water interface.

Benthic organisms display patchiness at a range of scales, from millimetres to kilometres and from seconds to years (Hall et al., 1994), but these are rarely explicitly acknowledged in the design and implementation of surveillance techniques including emergence and settlement traps, which often employ more pragmatic criteria (cost, weight, ease of sample processing, etc.). Whilst shallow-water ecologists at least have the potential to sample and re-sample intensively and repeatedly over a range of scales, the costs (in every sense) of sampling in deeper water makes this prohibitive, and scaling issues have usually been explored in a more constrained way by sub-sampling from larger sample units, such as a grab or a box-core, or by multi-samplers. However, the spatial separation between sub-samples (the lag) is necessarily rather small and may not describe adequately spatial patchiness at the scale appropriate for larger species or reveal the correct scale at which key ecological processes operate. Although not dealing specifically with the flux of living particles, the point is illustrated well for species that develop complex burrow systems and actively transport particulate material from the surface to depth and vice versa (e.g. *Callianassa subterranea*, *Maxmulleria lankesteri*, Atkinson and Nash, 1985; Hughes et al., 1999, 2000). Such activities bring about subtle changes in the microbiological, physical and chemical properties over very fine scales (sub-mm) across burrow walls but the phenomena occur over vertical scales of tens to hundreds of centimetres. These systems can only be observed adequately if the sampling design is appropriate, for example by using large box cores and 2–3-m-long, large-diameter gravity corers (Kershaw et al., 1983, 1984, 1999).

Given the acknowledged patchiness in the distribution of benthic organisms, it is reasonable to suppose that the spatial patterns in the departure of living particles from the sediment will be similarly heterogeneous. The extent to which this patchiness is eroded by diffusion and turbulence as the individuals leave the sediment and move up through the water column has not, to our knowledge, been documented. Likewise, the likely effects of the arrival of large patches of benthic larvae on the tropho-dynamics of their receiving pelagic system are not clear.

Relating emergence and settlement processes of macrofaunal organisms to sediment physico-chemical and microbiological features is also potentially confounded by the scale at which those features are routinely measured. For instance, oxygen electrodes record heterogeneity at the micron-scale, whilst macrofauna are often sampled with corers many centimetres in diameter. Whilst there can be no “correct” scale at which to describe ecological pattern and process (Levin, 1992), it is clear that larger-scale processes do provide the conditions in which a distributional pattern occurs, whilst the processes responsible for the pattern itself often operate at the next lowest level (O’Neill, 1989).

To explore these issues better, benthic ecologists need to adopt the landscape approaches developed by terrestrial ecologists (e.g. Forman, 1995; Pickett and Cadenasso, 1995). The framework of landscape ecology has enjoyed several decades of activity in terrestrial ecology, but only relatively recently have marine ecologists applied it to benthic systems. Over much of the seafloor, marine landscapes are typically defined by physical characteristics, rather than the biological structures (e.g. plant communities) seen in terrestrial systems (Zajac, 1999; but see also Robbins and Bell, 1994 on seagrass habitats). Several of the benthic surveillance techniques and approaches described in this volume (e.g. Cutter et al., this volume; Parry et al., this volume) offer great potential in this respect, although interpretation of the data must be made cautiously, because they tend to reflect physical rather than biological characteristics. For instance, acoustic ground discrimination systems can be used to define areas of the seabed which are acoustically different, but these boundaries between sediment classes should not be used in isolation to artificially constrain faunal assemblages. As pointed out many years ago by Gray (1974), particle size varies continuously across the seabed and co-varies with other habitat structuring factors, such as the presence of megafauna. In practice, the seabed habitat is a mosaic of different sediment grades that support different assemblages and densities of fauna that respond to spatial and temporal variation in the environment at many overlapping scales. Each scale may require different but complimentary techniques, for example RoxAnn (Greenstreet et al., 1997), QTC View (Morrison et al., 2001), side-scan sonar (Zajac et al., 2000) for broad-scale survey and video observation for intermediate scales (Parry et al., this volume).

5. Future perspectives

Given that benthic and pelagic systems are coupled, pelagic patterns and processes are also likely to affect benthic pattern and process. Hence, there is an urgent need not only to identify these patterns and processes, but also to develop protocols which link processes and patterns across different scales. If scaling rules are non-linear, then relating a pattern to a process measured at quite different scales, and extrapolating from small-scales where measurements and experiments are more tractable, to those larger scales, in which managers are interested, will involve crude approximations at best. Despite the interest in scale as an issue in benthic ecology, techniques for linking patterns and processes across even a limited range of scales (e.g. Thrush et al., 1997) still seem a long way off.

The issues of scale, heterogeneity and benthic–pelagic coupling are being increasingly considered together by managers of the marine environment. Measurements at

site-specific scales are increasingly being used to answer questions at a regional scale, because marine ecosystem managers are under pressure from directives which are increasingly concerned with human impacts. When taking measurements of these systems at the ecosystem, community and sediment–water interface scales, it is essential that these separate elements are brought together. Although landers, related surveillance techniques and the experimental methodologies currently available have the potential to facilitate measurements of benthic–pelagic coupling and heterogeneity at various temporal and spatial scales, we need to consider exactly how information recorded at these different scales can be subsequently integrated when designing programmes. This is probably best underlined by considering the impact of disturbance, which has effects over a broad range of scales. For example, large-scale trawling may impact the entire North Sea at different intensities (Jennings et al., 1999, 2000; Rijnsdorp et al., 1996), but there are potential benthic effects from the level of bacterial populations to entire benthic habitats. Trawling can also affect various aspects of benthic–pelagic coupling, such as sediment flux and biodeposition (Norkko et al., 2001), recruitment to the benthos (Marinelli and Woodin, 2002), biological structuring, production and chemical fluxes (Jennings et al., 2001a,b; Widdicombe and Austen, 2001; Duplisa et al., 2001).

As discussed above, linking across these quite different scales is likely to be problematic. Whilst approaches such as those described in Thrush et al. (1997) and new numerical tools, such as meta-analysis (Arnqvist and Wooster, 1995; Gurevitch et al., 2002), offer potential in this respect, we believe that much could also be achieved by closer collaboration between benthic and pelagic ecologists working at different scales. Our workshop included researchers working across a broad range of scales from the very precise measurement of physico-chemical processes at the millimetre scale, through mapping regions of the seabed at the landscape (kilometre scale), with every scale in between represented (see papers, this volume). Yet the opportunity for collaboration between what have become essentially sub-disciplines of benthic ecology and other disciplines is minimal, and coordinated campaigns designed to specifically address the issue of integrating information across different scales are long overdue.

Acknowledgements

This paper represents the output of a workshop in which the following also participated: Magda Bergman, Melanie Bergman, Mike Burrows, Randy Cutter, Kirsty Demie, Suzanne Eriksson, Franck Gilbert, Norma Angelia Hernandez Guevara, Michael Klages, Katja Ringdahl, Jose Alejandro Rodriguez Valencia and George Stora. We are grateful for their stimulating discussion and contribution. The manuscript was greatly improved by the comments of three anonymous reviewers. [RW]

References

- Ackerman, J.D., Loewen, M.R., Hamblin, P.F., 2001. Benthic–pelagic coupling over a zebra mussel reef in western Lake Erie. *Limnol. Oceanogr.* 46, 892–904.

- Amott, S.E., Yan, N.D., 2002. The influence of drought and re-acidification on zooplankton emergence from resting stages. *Ecol. Appl.* 12, 138–153.
- Arnqvist, G., Wooster, D., 1995. Meta-analysis—synthesizing research findings in ecology and evolution. *Trends Ecol. Evol.* 10, 236–240.
- Atkinson, R.J.A., Nash, R.D.M., 1985. Burrows and their inhabitants. *Prog. Underw. Sci.* 10, 109–115.
- Belmonte, G., Castello, P., Piccini, M.R., Quarta, S., Rubino, F., Geraci, S., Boero, F., 1995. Resting stages in marine sediments off the Italian coast. In: Ansell, A.D., Smith, C.J. (Eds.), *Biology and Ecology of Shallow Coastal Waters*. Olsen & Olsen, Denmark, pp. 53–58.
- Best, P.B., Canham, P.A.S., MacLeod, N., 1984. Patterns of reproduction in sperm whales, *Physeter macrocephalus*. *Rep. Int. Whal. Comm., Spec. Issue* (6), 51–79.
- Beukeema, J.J., Cadée, G.C., Dekker, R., 2002. Zoobenthic biomass limited by phytoplankton abundance: evidence from parallel changes in two long-term data series in the Wadden Sea. *J. Sea Res.* 48, 111–126.
- Boero, F., Belmonte, G., Fanelli, G., Piraino, S., Rubino, F., 1996. The continuity of living matter and the discontinuities of its constituents: do plankton and benthos really exist? *Trends Ecol. Evol.* 11, 177–180.
- Bollens, S.M., Frost, B.W., 1991. Oviparity, selective predation, and variable diel migration in *Euchaeta elongata* (Copepoda: Dalanoida). *Oecologia* 87, 155–161.
- Botsford, L.W., 2001. Physical influences on recruitment to California Current invertebrate populations on multiple scales. *ICES J. Mar. Sci.* 58, 1081–1091.
- Cacchione, D.A., Grant, W.D., Drake, D.E., Glen, S.M., 1987. Storm-dominated bottom boundary layer dynamics on the North Californian continental shelf: measurements and predictions. *J. Geophys. Res.* 92, 1817–1827.
- Chase, J.M., Leibold, M.A., 2002. Spatial scale dictates the productivity–biodiversity relationship. *Nature* 416, 427–430.
- Constanza, R., d’Arge, R., de Groot, R., Fraber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O’Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P., van den Belt, M., 1997. The value of the world’s ecosystem services and natural capital. *Nature* 387, 253–259.
- Corliss, J.B., Dymond, J., Gordon, L., Edmond, J.M., von Herzen, R.P., Ballard, R.D., Green, K., Bainbridge, A., Crane, K., Andel, T.H.V., 1979. Submarine thermal springs on the Galapagos Rift. *Science* 203, 1073–1083.
- Dagg, M., 1977. Some effects of patchy food environments on copepods. *Limnol. Oceanogr.* 22, 99–107.
- De Jonge, V.N., van Beusekom, J.E.E., 1995. Wind- and tide-induced resuspension of sediment and microphytobenthos from tidal flats in the Ems estuary. *Limnol. Oceanogr.* 40, 766–778.
- De Stasio Jr., B.T., 1990. The role of dormancy and emergence patterns in the dynamics of a freshwater zooplankton community. *Limnol. Oceanogr.* 35, 1079–1090.
- Denman, K.L., 1994. Scale-determining biological–physical interactions in oceanic food webs. In: Giller, P.S., Hildrew, A.G., Raffaelli, D.G. (Eds.), *Aquatic Ecology: Scale, Pattern and Process*. Blackwell Scientific Publications, Oxford, pp. 377–402.
- Dobbs, F.C., Vozarik, J.M., 1983. Immediate effects of a storm on coastal infauna. *Mar. Ecol., Prog. Ser.* 11, 273–279.
- Duggan, I.C., Green, J.D., Shiel, R.J., 2002. Rotifer resting egg densities in lakes of different trophic state, and their assessment using emergence and egg counts. *Arch. Hydrobiol.* 153, 409–420.
- Duplisea, D.E., Jennings, S., Malcolm, S.J., Parker, R., Sivyer, D.B., 2001. Modelling potential impacts of bottom trawl fisheries on soft sediment biogeochemistry in the North Sea. *Geochem. Trans.* 14, 1–6.
- Dybas, T., 2001. News from the American Society of Limnology and Oceanography. *Bioscience* 51, 313–316.
- Edmunds, P.J., Bruno, J.F., 1996. The importance of sampling scale in ecology: kilometre-wide variation in coral reef communities. *Mar. Ecol., Prog. Ser.* 143, 165–171.
- Ellingsen, K.E., 2001. Biodiversity of a continental shelf soft-sediment macrobenthos community. *Mar. Ecol., Prog. Ser.* 218, 1–15.
- Essink, K., Kleef, H.L., Visser, W., 1989. On the pelagic occurrence and dispersal of the benthic amphipod *Corophium volutator*. *J. Mar. Biol. Assoc. U.K.* 69, 11–15.
- Finelli, C.M., Hart, D.D., Merz, R.A., 2002. Stream insects as passive suspension feeders: effects of velocity and food concentration on feeding performance. *Oecologia* 131, 145–153.
- Forman, R.T.T., 1995. *Land Mosaics: The Ecology of Landscapes and Regions*. Cambridge Univ. Press, Cambridge.

- Foxton, P., 1970. The vertical distribution of pelagic decapods (Crustacea: Natantia) collected on the SoND cruise 1965: 1. The Caridea. *J. Mar. Biol. Assoc. U.K.* 50, 939–960.
- Frost, B.W., 1988. Variability and possible adaptive significance of diel vertical migration in *Calanus pacificus*, a planktonic marine copepod. *Bull. Mar. Sci.* 43, 675–694.
- Fujikura, K., Kojima, S., Tamaki, K., Maki, T., Hunt, J., Okutani, T., 1999. The deepest chemosynthesis-based community yet discovered from the hadal zone, 7326 m deep, in the Japan Trench. *Mar. Ecol., Prog. Ser.* 190, 17–26.
- Fujioka, K., Wada, H., Okano, H., 1993. Torishima whale bone deep-sea animal community assemblage—new finding by Shinkai 6500. *J. Geog.* 102, 507–517.
- Gaines, S., Roughgarden, J., 1985. Larval settlement rate: a leading determination structure in an ecological community of the marine intertidal zone. *Proc. Acad. Nat. Sci. Philadelphia* 82, 3707–3711.
- Garstecki, T., Wickham, S.A., 2001. Effects of resuspension and mixing on population dynamics and trophic interactions in a model benthic microbial food web. *Aquat. Microb. Ecol.* 25, 281–292.
- Gaston, K.J., 2000. Global patterns in biodiversity. *Nature* 405, 220–227.
- Godhe, A., Noren, F., Kuylentierna, M., Ekberg, C., Karlson, B., 2001. Relationship between planktonic dinoflagellate abundance, cysts recovered in sediment traps and environmental factors in the Gullmar Fjord, Sweden. *J. Plankton Res.* 23, 923–938.
- Graf, G., 1992. Benthic–pelagic coupling: a benthic view. *Ocean. Mar. Biol. Ann. Rev.* 30, 149–190.
- Gray, J., 1974. Animal–sediment relationships. *Oceanogr. Mar. Biol., Ann. Rev.* 12, 223–261.
- Greenstreet, S.P.R., Tuck, I.D., Grewar, G.N., Armstrong, E., Reid, D.G., Wright, P.J., 1997. An assessment of the acoustic survey technique, RoxAnn, as a means of mapping seabed habitat. *ICES J. Mar. Sci.* 54, 939–959.
- Gurevitch, J., Curtis, P.S., Jones, M.H., 2002. Meta-analysis in ecology and evolutionary biology. *Adv. Ecol. Res.* 32 (in press).
- Hall, S.J., Raffaelli, D., Thrush, S.F., 1994. Patchiness and disturbance in shallow water benthic assemblages. In: Giller, P.S., Hildrew, A.G., Raffaelli, D.G. (Eds.), *Aquatic Ecology: Scale, Pattern and Process*. Blackwell Scientific Publications, Oxford, pp. 333–375.
- Hairton, N.G., Ellner, S., Kerans, C.M., 1996. Overlapping generations: the storage effect and the maintenance of biotic diversity. In: Rhodes, O.E., Chesser, R.K., Smith, M.H. (Eds.), *Population dynamics in ecological space and time*. University of Chicago Press, Chicago, pp. 234–248.
- Hairton Jr, N.G., Hanssen, A.-M., Schaffner, W.R., 2000. The effects of diapause emergence on the seasonal dynamics of a zooplankton assemblage. *Freshw. Biol.* 45, 133–145.
- Hansson, L.-A., 1996. Algal recruitment from lake sediments in relation to grazing, sinking, and dominance patterns in the phytoplankton community. *Limnol. Oceanogr.* 41, 1312–1323.
- Hansson, L., Rudstam, G., Johnson, T.B., Soranno, P.A., Allen, Y., 1994. Patterns in algal recruitment from sediment to water in a dimictic eutrophic lake. *Can. J. Fish. Aquat. Sci.* 51, 2825–2833.
- He, F.L., Gaston, K.J., 2000. Occupancy–abundance relationships and sampling scales. *Ecography* 23, 503–511.
- Head, R.M., Jones, R.I., Bailey-Watts, A.E., 1998. The role of benthic stages in the life history of planktonic cyanobacteria. *Verh.-Int. Ver. Theor. Angew. Limnol.* 26, 1711–1715.
- Head, R.M., Jones, R.I., Bailey-Watts, A.E., 1999a. An assessment of the influence of recruitment from the sediment on the development of planktonic populations of cyanobacteria in a temperate mesotrophic lake. *Freshw. Biol.* 41, 759–769.
- Head, R.M., Jones, R.I., Bailey-Watts, A.E., 1999b. Vertical movements by planktonic cyanobacteria and the translocation of phosphorus: implications for lake restoration. *Aquat. Conserv., Mar. Freshw. Ecosyst.* 9, 111–120.
- Herring, P., 2002. *The Biology of the Deep Ocean*. Oxford Univ. Press, Oxford.
- Huettel, M., Rusch, A., 2000. Transport and degradation of phytoplankton in permeable sediment. *Limnol. Oceanogr.* 45, 534–549.
- Huettel, M., Webster, I.T., 2001. Porewater flow in permeable sediments. In: Boudreau, B.P., Jorgensen, B.B. (Eds.), *The Benthic Boundary Layer—Transport Processes and Biogeochemistry*. Oxford Univ. Press, Oxford, pp. 144–179. Chapter 7.
- Huettel, M., Zeibis, W., Forster, S., 1996. Flow induced uptake of particulate matter in permeable seabeds. *Limnol. Oceanogr.* 41, 309–322.

- Hughes, D.J., Atkinson, R.D.A., Ansell, A.D., 1999. The annual cycle of sediment turnover by the echiuran worm, *Maxmuelleria lankesteri* (Herdman) in a Scottish sea loch. J. Exp. Mar. Biol. Ecol. 238, 209–233.
- Hughes, D.J., Atkinson, R.J.A., Ansell, A.D., 2000. A field test of the effects of megafaunal burrows on benthic chamber measurements of sediment–water solute fluxes. Mar. Ecol., Prog. Ser. 195, 189–199.
- Jennings, S., Alvsvag, J., Cotter, A.J.R., Ehrlich, S., Greenstreet, S.P.R., Jarre-Teichmann, A., Mergardt, N., Rijnsdorp, A.D., Smedstad, O., 1999. Fishing effects in the northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure: III. International trawling effort in the North Sea: an analysis of spatial and temporal trends. Fish. Res. 40, 125–134.
- Jennings, S., Warr, K.J., Greenstreet, S.P.R., Cotter, A.J.R., 2000. Spatial and temporal patterns in North Sea fishing effort. In: Kaiser, M.J., De Groot, S.J. (Eds.), Effects of Fishing on Non-Target Species and Habitats: Biological Conservation and Socio-Economic Issues. Blackwell Science, Oxford.
- Jennings, S., Pinnegar, J.K., Polunin, N.V.C., Warr, K.J., 2001a. Impacts of trawling disturbance on the trophic structure of benthic invertebrate communities. Mar. Ecol., Prog. Ser. 213, 127–142.
- Jennings, S., Dinmore, T.A., Duplisea, D., Warr, K.J., Lancaster, J.E., 2001b. Trawling disturbance can modify benthic production. J. Anim. Ecol. 70, 459–475.
- Kershaw, P.J., Swift, D.J., Penreath, R.J., Lovett, M.B., 1983. Plutonium redistribution by biological activity in Irish Sea sediments. Nature 306, 774–775.
- Kershaw, P.J., Swift, D.J., Penreath, R.J., Lovett, M.B., 1984. The incorporation of plutonium, americium and curium into the Irish Sea seabed by biological activity. Sci. Total Environ. 40, 61–81.
- Kershaw, P.J., Denoon, D.C., Woodhead, D.S., 1999. Observations on the redistribution of plutonium and americium in Irish Sea sediments, 1978 to 1996: concentrations and inventories. J. Environ. Radioact. 44, 191–221.
- Larson, R.J., Matsumoto, G.I., Madin, L.P., Lewis, L.M., 1992. Deep-sea benthic and benthopelagic medusae: recent observations from submersibles and a remotely operated vehicle. Bull. Mar. Sci. 51, 277–286.
- Legendre, P., 1993. Spatial autocorrelation: trouble or new paradigm? Ecology 74, 1659–1673.
- Levin, S.A., 1992. The problem of pattern and scale in ecology. Ecology 73, 1943–1967.
- Lewin, R., 1986. Supply-side ecology. Science 234, 25–27.
- Longhurst, A.R., 1976. Vertical migration. In: Cushing, D.H., Walsh, J.J. (Eds.), The Ecology of the Sea. Blackwell Scientific Publishers, Oxford, pp. 116–137.
- Mackie, G.O., Larson, R.J., Larson, K.S., 1981. Swimming and vertical migration of *Aurelia aurita* in a deep tank. Mar. Behav. Physiol. 7, 321–329.
- Makino, W., Kato, H., Takamura, N., Mizutani, H., Katano, N., Mikami, H., 2001. Did chironomid emergence release *Daphnia* from fish predation and lead to a *Daphnia*-drive clear-water phase in Lake Towanda, Japan? Hydrobiologia 442, 309–317.
- Marcus, N.H., 1995. Seasonal study of planktonic copepods and their benthic resting stages in northern Californian coastal waters. Mar. Biol. 123, 459–465.
- Marcus, N.H., Boero, F., 1998. Minireview: the importance of benthic–pelagic coupling and the forgotten role of life cycles in coastal aquatic systems. Limnol. Oceanogr. 43, 763–768.
- Marcus, N.H., Schmidt-Gengenbach, J., 1986. Recruitment of individuals into the plankton: the importance of bioturbation. Limnol. Oceanogr. 31, 206–210.
- Marinelli, R.L., Woodin, S.A., 2002. Experimental evidence for linkages between infaunal recruitment, disturbance, and sediment surface chemistry. Limnol. Oceanogr. 47, 221–229.
- Maynard, S.D., Riggs, F.V., Walters, C.F., 1975. Mesopelagic micronekton faunal composition, standing stock, and diel vertical migration. Fish. Bull., U.S. Fish Wildl. Serv. 73, 115–126.
- Mees, J., Jones, M.B., 1997. The Hyperbenthos. Oceanogr. Mar. Biol., Ann. Rev. 35, 221–255.
- Merrett, N., Roe, T., 1974. Patterns and selectivity in the feeding of certain mesopelagic fishes. Mar. Biol. 28, 115–126.
- Mills, C.E., Goy, J., 1988. In situ observations of the behavior of mesopelagic *Solmissus narcomedusae* (Cnidaria, Hydrozoa). Bull. Mar. Sci. 43, 739–751.
- Miyake, H., Lindsay, D., Hunt, J.C., Hamatsu, T., 2002. *Scyphomedusa Aurelia limbata* (Brandt, 1838) found in deep waters off Kushiro, Hokkaido, Northern Japan. Plankton Biol. Ecol. 49, 44–46.
- Morrison, M.A., Thrush, S.F., Budd, R., 2001. Detection of acoustic class boundaries in soft sediment systems using the seafloor acoustic discrimination system QTC View. J. Sea Res. 46, 233–243.

- Norkko, A., Hewitt, J.E., Thrush, S.F., Funnell, G.A., 2001. Benthic–pelagic coupling and suspension-feeding bivalves: linking site-specific sediment flux and biodeposition to benthic community structure. *Limnol. Oceanogr.* 46, 2067–2072.
- Ogilvie, B.G., Mitchell, S.F., 1998. Does sediment resuspension have persistent effects on phytoplankton? Experimental studies in three shallow lakes. *Freshw. Biol.* 40, 51–63.
- Ohman, M.D., 1990. The demographic benefits of diel vertical migration by zooplankton. *Ecol. Monogr.* 60, 257–281.
- O'Neill, R.V., 1989. Perspectives in hierarchy and scale. In: Roughgarden, J., May, R.M., Levin, S.A. (Eds.), *Perspectives in Ecological Theory*. Princeton Univ. Press, Princeton, NJ, pp. 140–156.
- Pascual, M., Levin, S.A., 1999. From individuals to population densities: searching for the intermediate scale of nontrivial determinism. *Ecology* 80, 2225–2236.
- Paull, C.K., Hecker, B., Commeau, R., Freeman-Lynde, R.P., Neumann, C., Corso, W.P., Hoodk, J.E., Sikes, E., Curray, J., 1984. Biological communities at the Florida Escarpment resemble hydrothermal vent taxa. *Science* 226, 965–967.
- Pepin, P., Anderson, J.T., 1997. Scale-dependent variations in the precision of larval fish abundance estimates: a study of *Sebastes* sp. on Flemish Cap. *Can. J. Fish. Aquat. Sci.* 54, 1111–1120.
- Pickett, S.T.A., Cadenasso, M.L., 1995. Landscape ecology: spatial heterogeneity in ecological systems. *Science* 269, 331–341.
- Polis, G.A., Anderson, W.B., Holt, R.D., 1997. Towards an integration of landscape and food web ecology: the dynamics of spatially subsidised food webs. *Ann. Rev. Ecol. Syst.* 28, 289–316.
- Rice, D.W., 1989. Sperm whale *Physeter macrocephalus* Linnaeus, 1758. In: Ridgway, S.H., Harrison, R.J. (Eds.), *Handbook of Marine Mammals*, vol. 4. River Dolphins and the Large Toothed Whales. Academic Press, London, 430, pp. 177–233.
- Rijnsdorp, A.D., Buiji, A.M., Storbeck, F., Visser, E., 1996. Micro-scale distribution of beam-trawl effort in the southern North Sea between 1993 and 1996 in relation to the trawling frequency of the seabed and the impact on benthic organisms. *ICES 1996/mini* 11.
- Robbins, B., Bell, S., 1994. Seagrass landscapes: a terrestrial approach to the marine subtidal environment. *Trends Ecol. Evol.* 9, 301–304.
- Roe, H.S.J., 1969. The food and feeding habits of the sperm whales (*Physeter catodon* L.) taken of the west coast of Iceland. *F. Cons. Int. Explor. Met.* 33, 93–102.
- Roe, H.S.J., 1984. The diel vertical migrations and distributions within a mesopelagic community in the north east Atlantic: 2. Vertical migrations and feeding of mysids and decapod Crustacea. *Prog. Oceanogr.* 13, 269–318.
- Rothhaupt, K.O., 2000. Plankton population dynamics: food web interactions and abiotic constraints. *Freshw. Biol.* 45, 105–109.
- Roughgarden, J., Isawa, Y., Baxter, C., 1985. Demographic theory for an open marine population with space-limited recruitment. *Ecology* 66, 54–67.
- Rusch, A., Huettel, M., 2000. Advective particle transport into permeable sediments—evidence from experiments in an intertidal sandflat. *Limnol. Oceanogr.* 45, 525–533.
- Schelske, C.L., Carrick, H.J., Aldridge, F.J., 1995. Can wind-induced resuspension of meroplankton affect phytoplankton dynamics? *J. North Am. Benthol. Soc.* 14, 612–630.
- Schmidt, J., 1922. The breeding places of the eel. *Philos. Trans. R. Soc. Lond.*, B 211, 179–208.
- Schratzberger, M., Warwick, R.M., 1999. Differential effects of various types of disturbances on the structure of nematode assemblages: an experimental approach. *Mar. Ecol., Prog. Ser.* 181, 227–236.
- Smith, C.R., 1992. Whale falls—chemosynthesis on the deep seafloor. *Oceanus*, Fall 1992, 72–78.
- Smith, C.R., Kukert, H., Wheatcroft, R.A., Jumars, P.A., Deming, J.W., 1989. Vent fauna on whale remains. *Nature* 341, 27–28.
- Sponseller, R.A., Benfield, E.F., Valett, H.M., 2001. Relationships between land use, spatial scale and stream macroinvertebrate communities. *Freshw. Biol.* 46, 1409–1424.
- Suess, E., Carson, B., Ritger, S., Moore, J.C., Kulm, L.D., Cochrane, G.R., 1985. Biological communities at a vent site along the subduction zone of Oregon. *Bull. Biol. Soc. Wash.* 6, 475–484.
- Tomassa, L.D., Belmonte, G., Planques, A., Puig, P., Broero, F., 2000. Resting stages in a submarine canyon: a component of shallow–deep-sea coupling? *Hydrobiologia* 440, 249–260.

- Thrush, S.F., Warwick, R.M. (Eds.), 1998. J. Exp. Mar. Biol. Ecol., vol. 216.
- Thrush, S.F., Schneider, D.C., Legendre, P., Whitlatch, R.D., Dayton, P.K., Hewitt, J.E., Hines, A.H., Cumming, V.J., Lawrie, S.M., Grant, J., Pridmore, R.D., Turner, S.J., McArdle, B.H., 1997. Scaling-up from experiments to complex ecological systems: where to next? J. Exp. Mar. Biol. Ecol. 216, 243–254.
- Tsukamoto, K., 1992. Discovery of spawning area for the Japanese eel. Nature 356, 789–791.
- Vuorinen, I., 1987. Vertical migration of *Eurytemora* (Crustacea, Copepoda): a compromise between the risks of predation and decreased fecundity. J. Plankton Res. 9, 1037–1046.
- Wainwright, S.C., 1987. Stimulation of heterotrophic microplankton production by resuspended marine sediments. Science 238, 1710–1712.
- Warwick, R.M., 1989. The role of meiofauna in the marine ecosystem: evolutionary considerations. Zool. J. Linn. Soc. 96, 229–241.
- Whitlatch, R.B., Osman, R.W., 1998. A new device for studying benthic invertebrate recruitment. Limnol. Oceanogr. 43, 516–523.
- Widdicombe, S., Austen, M.C., 2001. The interaction between physical disturbance and organic enrichment: an important element in structuring benthic communities. Limnol. Oceanogr. 46, 1720–1733.
- Wilhelm, F.M., Hudson, J.J., Schindler, D.W., 1999. Contribution of *Gammarus lacustris* to phosphorus recycling in a fishless alpine lake. Can. J. Fish. Aquat. Sci. 56, 1679–1686.
- Woodward, G., Hildrew, A.G., 2002. Food web structure in riverine landscapes. Freshw. Biol. 47, 777–798.
- Yeo, R.K., Risk, M.J., 1979. Intertidal catastrophes: effects of storms and hurricanes on intertidal benthos of the Minas Basin, Bay of Fundy. J. Fish. Res. Board Can. 36, 667–669.
- Zajac, R.N., 1999. Understanding the sea floor landscape in relation to impact assessment and environmental management in coastal marine sediments. In: Gray, J.S. (Ed.), Biogeochemical Cycling and Sediment Ecology, vol. 59. Kluwer, Dordrecht, pp. 211–227.
- Zajac, R.N., Lewis, R.S., Poppe, L.J., Twichell, D.C., Vozarik, J., DiGiacomo-Cohen, M.L., 2000. Relationships among sea-floor structure and benthic communities in Long Island Sound at regional and benthoscape scales. J. Coast. Res. 16, 627–640.