

# Marine Science Review – 194

## Miscellaneous publications



### In this review:

- A. Recent articles – no abstract available
- B. Recent articles with abstracts

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## A. Recent articles – no abstract available

Kolber, Z.S. **Getting a better picture of the ocean's nitrogen budget.** *Science* 312(5779): 1479-1480, 2006.

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## B. Recent articles with abstracts

Jordan, F., Liu, W.C., and Davis, A.J. **Topological keystone species: measures of positional importance in food webs.** *Oikos* 112(3): 535-546, 2006.

**Notes:** The local extinction or large fluctuation in abundance of a species may seriously affect other species in the community. The effects spread through the community by direct and indirect interactions. The network perspective on ecology can help map the pathways of these effects, for food webs, the pathways of indirect trophic interactions. Indirect interactions typically decay in intensity as they spread. Therefore, there is a conceptual maximum range in topological space beyond which interactions have no effects, even though all species remain connected. Neither the local characteristics of species, nor the global characteristics of entire webs, suitably quantify this range. We therefore apply intermediate scale indices that reflect the limitations imposed by effect damping in networks. We present a complex analysis of the topological positional importance of species in the Chesapeake Bay web. This web is a carbon-flow network that represents trophic interactions. We present several different indices reflecting different properties and discuss which questions the different indices best answer. We look for the best indices for identifying the key players in ecosystem functioning. Our study contributes to the quantification of relative species importance and provides an exact and a priori determination of a class of candidate keystone species that can inform applied and conservation ecology as well as theoretical concerns.

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Pakchung, A.A.H., Simpson, P.J.L., and Codd, R. **Life on earth. Extremophiles continue to move the goal posts.** *Environmental Chemistry* 3(2): 77-93, 2006.

**Notes:** The discovery of an abundance of microorganisms that flourish in a diverse range of environments, from the frigid waters of the Antarctic, to the superheated waters of the hydrothermal vents, at the bottom of 11-km deep ocean trenches and in salt-saturated lakes, has fuelled research aimed to understand the novel survival strategies evolved by these extreme-loving (extremophilic) organisms. Adaptations of biomolecules (proteins, nucleic acids, membranes and small molecules) evolved by extremophiles are wide ranging. Compared with a protein from a 'regular' organism, the extremophilic analogue might feature changes to the relative frequencies of amino acid residues that modulate the properties (e.g. conformational flexibility and stability) of the protein under conditions of the specific environmental challenge. The integrity of RNA and DNA from extremophiles may be maintained by subtle structural changes to RNA nucleobases and, in the case of (hyper)thermophiles, the expression of the enzyme reverse gyrase, which catalyses positive DNA supercoiling. The expression of small molecular weight heat-shock or related caretaker proteins also features as a common adaptive strategy for maintaining cell viability at environmental extremes. Membrane architecture in extremophiles can be modulated by the environmental temperature, with additional thermal stability in membranes from some hyperthermophiles conferred by novel (cyclised) lipid chains. In addition,

a selection of osmolytes and small molecules are biosynthesised or sequestered by extremophilic organisms that have adapted to conditions of high salt and/or micronutrient deprivation.

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Pedrós-Alió, C. **Marine microbial diversity: can it be determined?** *Trends in Microbiology* 14(6): 257-263, 2006.

**Notes:** Estimates of the order of magnitude for the total number of microbial species on Earth range from  $10^5$  to  $10^9$ . Despite global dispersal of microorganisms, this number is probably rather large. The total biodiversity of an ecosystem is composed of two elements: first, a set of abundant taxa that carry out most ecosystem functions, grow actively and suffer intense losses through predation and viral lysis. These taxa are retrievable with molecular techniques but are difficult to grow in culture. Second, there is a seed bank of many rare taxa that are not growing or grow extremely slowly, do not experience viral lysis and predation is reduced. Such taxa are seldom retrieved by molecular techniques but many can be grown in culture, which explains the dictum 'everything is everywhere'.

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Foissner, W. **Biogeography and dispersal of micro-organisms: A review emphasizing protists.** *Acta Protozoologica* 45(2): 111-136, 2006.

**Notes:** This review summarizes data on the biogeography and dispersal of bacteria, microfungi and selected protists, such as dinoflagellates, chrysophytes, testate amoebae, and ciliates. Furthermore, it introduces the restricted distribution and dispersal of mosses, ferns and macrofungi as arguments into the discussion on the postulated cosmopolitanism and ubiquity of protists. Estimation of diversity and distribution of micro-organisms is greatly disturbed by undersampling, the scarcity of taxonomists, and the frequency of misidentifications. Thus, probably more than 50% of the actual diversity has not yet been described in many protist groups. Notwithstanding, it has been shown that a restricted geographic distribution of micro-organisms occurs in limnetic, marine, terrestrial, and fossil ecosystems. Similar as in cryptogams and macrofungi, about 30% of the extant suprageneric taxa, described and undescribed, might be morphological and/or genetic and/or molecular endemics. At the present state of knowledge, micro-organism endemism can be proved/disproved mainly by flagship species, excluding sites (e.g., university ponds) prone to be contaminated by invaders. In future, genetic and molecular data will be increasingly helpful. The wide distribution of many micro-organisms has been attributed to their small size and their astronomical numbers. However, this interpretation is flawed by data from macrofungi, mosses and ferns, many of which occupy distinct areas, in spite of their minute and abundant means of dispersal (spores). Thus, I suggest historic events (split of Pangaea etc.), limited cyst viability and, especially, time as major factors for dispersal and provinciality of micro-organisms. Furthermore, the true number of species and their distribution can hardly be estimated by theories and statistics but require reliable investigations on the number of morphospecies in representative ecosystems. Generally, the doubts on Beijerinck's famous metaphor "in micro-organisms everything is everywhere" can be focussed on a simple question: If the world is teeming with cosmopolitan unicells, where is everybody?

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Zhang, Y. and Kling, G.W. **Dynamics of lake eruptions and possible ocean eruptions.** *Annual Review of Earth and Planetary Sciences* 34: 293-324, 2006.

**Notes:** Dissolved gas in liquid is able to power violent eruptions. Two kinds of such gas-driven eruptions are known in nature: explosive volcanic eruptions driven by dissolved H<sub>2</sub>O in magma at high temperatures and lake eruptions driven by dissolved CO<sub>2</sub> in water at low temperatures. There are two known occurrences of lake eruptions, one in 1984 (Lake Monoun) and one in 1986 (Lake Nyos), both in Cameroon, Africa. The erupted CO<sub>2</sub> gas asphyxiated ~1700 people in the Lake Nyos eruption and 37 people at Lake Monoun. Here we review experimental simulations of CO<sub>2</sub>-driven water eruptions and dynamic models of such eruptions, and a bubble plume theory is applied to the dynamics of lake eruptions. Field evidence, experimental results, and theoretical models show that lake eruptions can be violent, and theoretical calculations are consistent with the high exit velocities and eruption columns inferred from observations. Furthermore, the dynamics of lake degassing experiments are consistent with theoretical models. Other kinds of gas-driven eruptions are possible and may have occurred in nature in the past. A concentrated and large release of methane gas or hydrate from marine sediment may result in an ocean eruption. Furthermore, injection of liquid CO<sub>2</sub> into oceans might also lead to ocean eruptions if care is not taken. The various kinetic and dynamic processes involved are examined and quantified.

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Lafferty, K.D., Dobson, A.P., and Kuris, A.M. **Parasites dominate food web links.** *Proceedings of the National Academy of Sciences [USA]* 103(30): 11211-11216, 2006.

**Notes:** Parasitism is the most common animal lifestyle, yet food webs rarely include parasites. The few earlier studies have indicated that including parasites leads to obvious increases in species richness, number of links, and food chain length. A less obvious result was that adding parasites slightly reduced connectance, a key metric considered to affect food web stability. However, reported reductions in connectance after the addition of parasites resulted from an inappropriate calculation. Two alternative corrective approaches applied to four published studies yield an opposite result: parasites increase connectance, sometimes dramatically. In addition, we find that parasites can greatly affect other food web statistics, such as nestedness (asymmetry of interactions), chain length, and linkage density. Furthermore, whereas most food webs find that top trophic levels are least vulnerable to natural enemies, the inclusion of parasites revealed that mid-trophic levels, not low trophic levels, suffered the highest vulnerability to natural enemies. These results show that food webs are very incomplete without parasites. Most notably, recognition of parasite links may have important consequences for ecosystem stability because they can increase connectance and nestedness.

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Boogert, N.J., Paterson, D.M., and Laland, K.N. **The implications of niche construction and ecosystem engineering for conservation biology.** *BioScience* 56(7): 570-578, 2006.

**Notes:** Although strategies to conserve biodiversity (e.g., the establishment of reserves and the management of flagship, umbrella, indicator, and keystone species) are valuable, they entail practical and conceptual difficulties. A focus on niche construction and ecosystem engineering, however, could provide new insights and methods for conservation biology. Many organisms modulate the availability of resources to other species by causing state changes in biotic or abiotic materials (ecosystem engineering), in the process frequently changing the selection to which the ecosystem engineers and other organisms are exposed (niche construction). We describe growing evidence that organisms have significant nontrophic impacts on ecosystem structure, function, and biodiversity, and outline established means of identifying key species involved in niche construction. On the basis of this engineering perspective, we propose a number of measures that could be employed to enhance conservation efforts.

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Worden, A.Z. **Picoeukaryote diversity in coastal waters of the Pacific Ocean.** *Aquatic Microbial Ecology* 43(2): 165-175, 2006.

**Notes:** The extraordinary molecular phylogenetic diversity of picoeukaryotes and their contributions to marine processes have been highlighted recently. Herein, picoeukaryotic diversity in the coastal Pacific Ocean is characterized for the first time. Close to full length small subunit ribosomal RNA (ssu rRNA) gene amplicons were cloned and sequenced from size fractionated samples (< 2 µm) taken between September 2000 and October 2001. Sequences belonging to the order Mamiellales were abundant, with *Micromonas pusilla*-like sequences in all 5 libraries (4 operational taxonomic units, OTUs, at ≥ 99% sequence similarity), *Ostreococcus* in 4 (1 OTU) and *Bathycoccus* in 2 (1 OTU). Phylogenetic reconstruction showed distinct *Micromonas* clades at this site (although not for other Mamiellales), supporting the idea that the designation *M. pusilla* harbors cryptic species. In combination with picophytoplankton dynamics previously reported for the same period, the data indicates that picoplanktonic primary production at this site is likely to be dominated by prasinophytes. Furthermore, a *Micromonas*-clade with no cultured representatives was identified bearing highest identity to Sargasso Sea shotgun clone sequences. Comparison of the Pacific sequences with the shotgun clones showed *Ostreococcus* and *Micromonas* at 1 Sargasso site with elevated chlorophyll (chl) levels, but not at other Sargasso sites. Other Pacific clones were primarily Novel Alveolate Group II, which were highly diverse based on OTU analyses. Novel Alveolate Group 1, Ciliophora, Cercozoa-like and stramenopile sequences were also retrieved. Although picoeukaryotic diversity has been characterized in only 1 other Pacific Ocean sample (equatorial Pacific), most stramenopile and alveolate sequences corresponded to previously identified phylogenetic clades from studies conducted in other oceans and for which no cultured representatives exist.

Massana, R., Terrado, R., Forn, I., Lovejoy, C., and Pedros-Alio, C. **Distribution and abundance of uncultured heterotrophic flagellates in the world oceans.** *Environmental Microbiology* 8(9): 1515-1522, 2006.

**Notes:** Heterotrophic flagellates play fundamental roles in marine ecosystems as picoplankton grazers. This recognized importance contrasts with our ignorance of the taxonomic composition of this functional group, which remains mostly unidentified by microscopical and culturing approaches. Recent molecular marine surveys based on 18S rDNA genes have retrieved many sequences unrelated to cultured organisms and marine stramenopiles were among the first reported uncultured eukaryotes. However, little is known about the organisms corresponding to these sequences. Here we determine the abundance of several marine stramenopile lineages in surface marine waters using molecular probes and fluorescent in situ hybridization. We show that these protists are free-living bacterivorous heterotrophic flagellates. They were widely distributed, occurring in the five world oceans, and accounted for a significant fraction (up to 35%) of heterotrophic flagellates in diverse geographic regions. A single group, MAST-4, represented 9% of cells within this functional assemblage, with the intriguing exception of polar waters where it was absent. MAST-4 cells likely contribute substantially to picoplankton grazing and nutrient re-mineralization in vast areas of the oceans and represent a key eukaryotic group in marine food webs.

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Hudson, P.J., Dobson, A.P., and Lafferty, K.D. **Is a healthy ecosystem one that is rich in parasites?** *Trends in Ecology and Evolution* 21(7): 381-385, 2006.

**Notes:** Historically, the role of parasites in ecosystem functioning has been considered trivial because a cursory examination reveals that their relative biomass is low compared with that of other trophic groups. However there is increasing evidence that parasite-mediated effects could be significant: they shape host population dynamics, alter interspecific competition, influence energy flow and appear to be important drivers of biodiversity. Indeed they influence a range of ecosystem functions and have a major effect on the structure of some food webs. Here, we consider the bottom-up and top-down processes of how parasitism influences ecosystem functioning and show that there is evidence that parasites are important for biodiversity and production; thus, we consider a healthy system to be one that is rich in parasite species.

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Acevedo-Whitehouse, K., Spraker, T.R., Lyons, E., Melin, S.R., Gulland, F., Delong, R.L., and Amos, W. **Contrasting effects of heterozygosity on survival and hookworm resistance in California sea lion pups.** *Molecular Ecology* 15(7): 1973-1982, 2006.

**Notes:** Low genetic heterozygosity is associated with loss of fitness in many natural populations. However, it remains unclear whether the mechanism is related to general (i.e. inbreeding) or local effects, in particular from a subset of loci lying close to genes under balancing selection. Here we analyse involving heterozygosity-fitness correlations on neonatal survival of California sea lions and on susceptibility to hookworm (*Uncinaria* spp.) infection, the single most important cause of pup mortality. We show that regardless of differences in hookworm burden, homozygosity is a key predictor of hookworm-related lesions, with no single locus contributing disproportionately. Conversely, the subsequent occurrence of anaemia due to blood loss in infected pups is overwhelmingly associated with homozygosity at one particular locus, all other loci showing no pattern. Our results suggest contrasting genetic mechanisms underlying two pathologies related to the same pathogen. First, relatively inbred pups are less able to expel hookworms and prevent their attachment to the intestinal mucosa, possibly due to a weakened immune response. In contrast, infected pups that are homozygous for a gene near to microsatellite Hg4.2 are strongly predisposed to anaemia. As yet, this gene is unknown, but could plausibly be involved in the blood-coagulation cascade. Taken together, these results suggest that pathogenic burden alone may not be the main factor regulating pathogen-related mortality in natural populations. Our study could have important implications for the conservation of small, isolated or threatened populations, particularly when they are at a risk of facing pathogenic challenges.

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Wagner-Döbler, I. and Bieb, H. **Environmental biology of the marine *Roseobacter* lineage.** *Annual Review of Microbiology* 60: 255-280, 2006.

**Notes:** The *Roseobacter* lineage is a phylogenetically coherent, physiologically heterogeneous group of  $\alpha$ -Proteobacteria comprising up to 25% of marine microbial communities, especially in coastal and polar oceans, and it is the only lineage in which cultivated bacteria are closely related to environmental clones. Currently 41 subclusters are described, covering all major

marine ecological niches (seawater, algal blooms, microbial mats, sediments, sea ice, marine invertebrates). Members of the *Roseobacter* lineage play an important role for the global carbon and sulfur cycle and the climate, since they have the trait of aerobic anoxygenic photosynthesis, oxidize the greenhouse gas carbon monoxide, and produce the climate-relevant gas dimethylsulfide through the degradation of algal osmolytes. Production of bioactive metabolites and quorum-sensing-regulated control of gene expression mediate their success in complex communities. Studies of representative isolates in culture, whole-genome sequencing, e.g., of *Silicibacter pomeroyi*, and the analysis of marine metagenome libraries have started to reveal the environmental biology of this important marine group.

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Bartsch, I. **Halacaroida (Acari): a guide to marine genera.** *Organisms Diversity and Evolution* 6(2): U159-U365, 2006.

**Notes:** Halacarid mites (Halacaroida: Halacaridae) are meiobenthic organisms. The majority of species and genera are marine, only few are restricted to freshwater. Halacarid mites are present from the tidal area to the deep sea. It is the only mite family completely adapted to permanent life in the sea. The first record was published more than 200 years ago. At present, 51 marine and brackish water genera of halacarid mites are known, including more than 1000 species. The genera are Acanthohalacarus, Acanthopapirus, Acarocheilopodia, Acaromantis, Acarothrix, Actacarus, Agaue, Agauides, Agauopsis, Anomalohalacarus, Arenihalacarus, Arhodoeporus, Atelopsalis, Australacarus, Bathytialacarus, Bradyagaue, Camactognathus, Caspihalacarus, Coloboceras, Colobocerasides, Copidognathides, Copidognathus, Corallihalacarus, Enterohalacarus, Halacarus, Halacarellus, Halacaroides, Halacaropsis, Halixodes, Isobactrus, Lohmannella, Metarhombognathus, Mictognathus, Parhafixodes, Pelacarus, Peregrinecarus, Phacacarus, Rhombognathides, Rhombognathus, Scaptognathides, Scaptognathus, Simognathus, Spongihalacarus, Thalassarachria, Thalassophthirus, Tropihalacarus, Werthella, Wedheloidea, Winlundia, and Xenohalacarus. The guide, which includes marine and brackish water genera, starts with an introduction to methods of collection, extraction and examination of halacarid mites, an outline of the external morphology and life history, and an overview of the commonly used terminology. Both a dichotomous key and tabular keys to the genera are presented. The keys have been prepared on the basis of adults. In general, in adults and nymphs the outline of idiosoma, gnathosoma and legs is similar, whereas the outline of plates, the sculpturing and number of setae on idiosoma and legs differ. In the tabular keys idiosoma, gnathosoma, palps, legs, tarsi and shape of claws are treated separately. The major part of the guide deals with descriptions of the 51 genera. Each genus is diagnosed and illustrated, namely a dorsal and ventral aspect of the idiosoma, the gnathosoma, leg I and tarsi I, II and IV. The diagnoses mention both, characters expected to be relevant in a phylogenetic sense and those thought to be mainly correlated with environment and mode of life. Rare character variants are included in the diagnoses; more variants are expected to be found in the future. In addition to the diagnoses, short notes are given on biology and geographical distribution, on similar-looking genera, and distinguishing characters. At the end of the presentation of a genus, relevant and most recent descriptive or phylogenetic references are listed.

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Head, I.M., Jones, D.M., and Röling, W.F.M. **Marine microorganisms make a meal of oil.** *Nature Reviews Microbiology* 4(3): 173-182, 2006.

**Notes:** Hundreds of millions of litres of petroleum enter the environment from both natural and anthropogenic sources every year. The input from natural marine oil seeps alone would be enough to cover all of the world's oceans in a layer of oil 20 molecules thick. That the globe is not swamped with oil is testament to the efficiency and versatility of the networks of microorganisms that degrade hydrocarbons, some of which have recently begun to reveal the secrets of when and how they exploit hydrocarbons as a source of carbon and energy.

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Ward, A.C. and Bora, N. **Diversity and biogeography of marine actinobacteria.** *Current Opinion in Microbiology* 9(3): 279-286, 2006.

**Notes:** The actinomycetes, although not all the Actinobacteria, are easy to isolate from the marine environment. However, their ecological role in the marine ecosystem is largely neglected and various assumptions meant there was little incentive to isolate strains for search and discovery of new drugs. However, the marine environment has become a prime resource in search and discovery for novel natural products and biological diversity, and marine actinomycetes turn out to be important contributors. Similarly, striking advances have been made in marine microbial ecology using molecular techniques and metagenomics, and actinobacteria emerge as an often significant, sometimes even dominant, environmental clade. Both

approaches - cultivation methods and molecular techniques - are leading to new insights into marine actinobacterial biodiversity and biogeography. Very different views of actinobacterial diversity emerge from these, however, and the true extent and biogeography of this are still not clear. These are important for developing natural product search and discovery strategies, and biogeography is a hot topic for microbial ecologists.

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Jax, K. **Ecological units: Definitions and application.** *Quarterly Review of Biology* 81(3): 237-258, 2006.

**Notes:** Concepts of ecological units, such as population, community, and ecosystem, are at the basis of ecological theory and research and have increasingly, become the focus of conservation strategies. Concepts of these units still suffer from inconsistencies and confusions over terminology. The different concepts are treated here together as a common "conceptual cluster" with similar ecological functions (roles) and similar problems in their definition and use. An analysis of the multitude of existing terms and concepts that have been developed for these units reveals that they differ with respect to at least four basic criteria: (i) the questions as to whether they are defined statistically or via a network of interactions; (ii) if their boundaries are drawn by topographical or process-related criteria; (iii) how high the required internal relationships are; and (iv) if they are perceived as "real" entities or abstractions by an observer. The various definitions cannot be easily sorted into just a few types, but they can be characterized by several independent criteria. I argue that serious problems arise if the different possibilities of defining ecological units are not recognized and if the concepts are perceived as self evident. The different concepts of ecological units should be defined and used in a philosophically informed manner: I propose a dual approach to the use of ecological units. Generic meanings of the main concepts (especially population, community, and ecosystem) should be retained only as heuristically useful perspectives, while specific and "operational" definitions of the concepts as units should be developed, depending on specific purposes of their use. Some thoughts on the basic requirements for such definitions and the domains of their uses are briefly explained

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Frederiksen, M., Edwards, M., Richardson, A.J., Halliday, N.C., and Wanless, S. **From plankton to top predators: bottom-up control of a marine food web across four trophic levels.** *Journal of Animal Ecology* 75(6): 1259-1268, 2006.

**Notes:** 1. Abundant mid-trophic pelagic fish often play a central role in marine ecosystems, both as links between zooplankton and top predators and as important fishery targets. In the North Sea, the lesser sandeel occupies this position, being the main prey of many bird, mammal and fish predators and the target of a major industrial fishery. However, since 2003, sandeel landings have decreased by > 50%, and many sandeel-dependent seabirds experienced breeding failures in 2004. 2. Despite the major economic implications, current understanding of the regulation of key constituents of this ecosystem is poor. Sandeel abundance may be regulated 'bottom-up' by food abundance, often thought to be under climatic control, or 'top-down' by natural or fishery predation. We tested predictions from these two hypotheses by combining unique long-term data sets (1973-2003) on seabird breeding productivity from the Isle of May, SE Scotland, and plankton and fish larvae from the Continuous Plankton Recorder survey. We also tested whether seabird breeding productivity was more tightly linked to sandeel biomass or quality (size) of individual fish. 3. The biomass of larval sandeels increased two- to threefold over the study period and was positively associated with proxies of the abundance of their plankton prey. Breeding productivity of four seabirds bringing multiple prey items to their offspring was positively related to sandeel larval biomass with a 1-year lag, indicating dependence on 1-year-old fish, but in one species bringing individual fish it was strongly associated with the size of adult sandeels. 4. These links are consistent with bottom-up ecosystem regulation and, with evidence from previous studies, indicate how climate-driven changes in plankton communities can affect top predators and potentially human fisheries through the dynamics of key mid-trophic fish. However, the failing recruitment to adult sandeel stocks and the exceptionally low seabird breeding productivity in 2004 were not associated with low sandeel larval biomass in 2003, so other mechanisms (e.g. predation, lack of suitable food after metamorphosis) must have been important in this case. Understanding ecosystem regulation is extremely important for predicting the fate of keystone species, such as sandeels, and their predators.

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Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C., Halpern, B.S., Jackson, J.B.C., Lotze, H.K., Micheli, F., Palumbi, S.R., Sala, E., Selkoe, K.A., Stachowicz, J.J., and Watson, R. **Impacts of biodiversity loss on ocean ecosystem services.** *Science* 314(5800): 787-790, 2006.

**Notes:** Human-dominated marine ecosystems are experiencing accelerating loss of populations and species, with largely unknown consequences. We analyzed local experiments, long-term regional time series, and global fisheries data to test how biodiversity loss affects marine ecosystem services across temporal and spatial scales. Overall, rates of resource collapse increased and recovery potential, stability, and water quality decreased exponentially with declining diversity. Restoration of biodiversity, in contrast, increased productivity fourfold and decreased variability by 21%, on average. We conclude that marine biodiversity loss is increasingly impairing the ocean's capacity to provide food, maintain water quality, and recover from perturbations. Yet available data suggest that at this point, these trends are still reversible.

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Thrush, S.F., Hewitt, J.E., Gibbs, M., Lundquist, C., and Norkko, A. **Functional role of large organisms in intertidal communities: Community effects and ecosystem function.** *Ecosystems* 9(6): 1029-1040, 2006.

**Notes:** In marine soft sediments, large organisms are potentially important players in the nonlinear interactions that occur among animals, their food, and their chemical environment, all of which influence the contribution of benthos to ecosystem function. We investigated the consequences of removing large individuals of two functionally contrasting benthic communities on nutrient regeneration, microphyte standing stock, and macrobenthic community composition. The experiment was conducted at two adjacent sites that were physically similar but biologically different, one dominated by large deposit feeders and the other by large suspension feeders. Chemical fluxes were measured in experimental plots, and sediments were sampled to assess changes in macrofauna, sediment grain size, organic content, and microphyte standing stock. Our results demonstrate that the removal of large suspension feeders or deposit feeders influenced the flux of nitrogen and oxygen, surficial sediment characteristics, and community composition. In the deposit-feeder community, interactions between nutrient regeneration and grazing highlight important feedbacks between large macrofauna and biogeochemical processes and production by microphytes, indicating that the loss of large infauna driven by increased rates of anthropogenic disturbance may lead to functional extinction and cause shifts in community structure and ecosystem performance.

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Carpenter, S.R. and Brock, W.A. **Rising variance: a leading indicator of ecological transition.** *Ecology Letters* 9(3): 308-315, 2006.

**Notes:** Regime shifts are substantial, long-lasting reorganizations of complex systems, such as ecosystems. Large ecosystem changes such as eutrophication, shifts among vegetation types, degradation of coral reefs and regional climate change often come as surprises because we lack leading indicators for regime shifts. Increases in variability of ecosystems have been suggested to foreshadow ecological regime shifts. However, it may be difficult to discern variability due to impending regime shift from that of exogenous drivers that affect the ecosystem. We addressed this problem using a model of lake eutrophication. Lakes are subject to fluctuations in recycling associated with regime shifts, as well as fluctuating nutrient inputs. Despite the complications of noisy inputs, increasing variability of lake-water phosphorus was discernible prior to the shift to eutrophic conditions. Simulations show that rising standard deviation (SD) could signal impending shifts about a decade in advance. The rising SD was detected by studying variability around predictions of a simple time-series model, and did not depend on detailed knowledge of the actual ecosystem dynamics.

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Trussell, G.C., Ewanchuk, P.J., and Matassa, C.M. **Habitat effects on the relative importance of trait- and density-mediated indirect interactions.** *Ecology Letters* 9(11): 1245-1252, 2006.

**Notes:** Classical views of trophic cascades emphasize the primacy of consumptive predator effects on prey populations to the transmission of indirect effects [density-mediated indirect interactions (DMII)]. However, trophic cascades can also emerge without changes in the density of interacting species because of non-consumptive predator effects on prey traits such as foraging behaviour [trait-mediated indirect interactions (TMII)]. Although ecologists appreciate this point, measurements of the relative importance of each indirect predator effect are rare. Experiments with a three-level, rocky shore food chain containing an invasive predatory crab (*Carcinus maenas*), an intermediate consumer (the snail, *Nucella lapillus*) and a basal resource (the barnacle, *Semibalanus balanoides*) revealed that the strength of TMII is comparable with, or exceeds, that of DMII. Moreover, the sign and strength of each indirect predator effect depends on whether it is measured in risky or refuge habitats. Because habitat shifts are often responsible for the emergence of TMII, attention to the sign and strength of these

interactions in both habitats will improve our understanding of the link between individual behaviour and community dynamics.

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Seehausen, O. **Losing biodiversity by reverse speciation.** *Current Biology* 16(9): R334-R337, 2006.

**Notes:** A large fraction of the world's species diversity is of recent evolutionary origin, and has evolved as a by-product of divergent adaptation in heterogeneous environments. Recent research provides a dire warning that homogenizing environments may cause the rapid loss of such species through a reversal of the speciation process.

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Hay, S. **Gelatinous bells may ring change in marine ecosystems.** *Current Biology* 16(17): R679-R682, 2006.

**Notes:** Gelatinous plankton are critical components of marine ecosystems. Recent studies are providing evidence of increased population outbursts of such species. Jellyfish seem to respond when an ecosystem is over-fished, and their ecology is under-researched.

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Byers, J.E. and Pringle, J.M. **Going against the flow: retention, range limits and invasions in advective environments.** *Marine Ecology Progress Series* 313: 27-41, 2006.

**Notes:** Increasing globalization has spread invasive marine organisms, but it is not well understood why some species invade more readily than others. It is also poorly understood how species' range limits are set generally, let alone how anthropogenic climate change may disrupt existing species boundaries. We find a quantitative relationship that determines if a coastal species with a benthic adult stage and planktonic larvae can be retained within its range and invade in the direction opposite that of the mean current experienced by the larvae (i.e. upstream). The derivation of the retention criterion extends prior riparian results to the coastal ocean by formulating the criterion as a function of observable oceanic parameters, focusing on species with obligate benthic adults and planktonic larvae, and quantifying the effects of iteroparity and longevity. By placing the solutions in a coastal context, the retention criterion isolates the role of 3 interacting factors that counteract downstream drift and set or advance the upstream edge of an oceanic species' distribution. First, spawning over several seasons or years enhances retention by increasing the variation in the currents encountered by the larvae. Second, for a given population growth rate, species with a shorter pelagic period are better retained and more able to spread upstream. And third, prodigious larval production improves retention. Long distance downstream dispersal may thus be a byproduct of the many propagules often necessary to ensure local recruitment and persistence of a population in an advective environment.

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Harley, C.D.G. **Effects of physical ecosystem engineering and herbivory on intertidal community structure.** *Marine Ecology Progress Series* 317: 29-39, 2006.

**Notes:** Physical ecosystem engineers play dominant roles in a wide variety of communities. While many of the direct, positive effects of ecosystem engineers are readily apparent, the roles of engineers are often mediated by indirect interactions stemming from the facilitation of one or a few key species. Although direct and indirect effects are both critical drivers of community dynamics, they are rarely considered together with regards to ecosystem engineering. In the present study barnacle and herbivorous gastropod densities are experimentally manipulated to investigate the direct positive effects of habitat provision by barnacles as well as indirect effects mediated by molluscan grazers. Molluscan grazers (*Littorina* spp.) and herbivorous arthropods were positively influenced by the presence of barnacles. Arthropod abundance and species richness were lower when *Littorina* spp. were present. This pattern was not influenced by barnacle cover, suggesting that competition among herbivore functional groups was strong but independent of biogenic habitat complexity. In addition, *Littorina* spp. had strong negative effects on the filamentous alga *Urospora penicilliformis*, but this effect was only seen in the absence of barnacles. Finally, *Littorina* spp. reduced the recruitment of the principal habitat-forming barnacle *Balanus glandula*, suggesting that *Littorina* spp. may mediate a negative feedback loop in *B. glandula* population dynamics. Given the ubiquity of ecosystem engineers, similar combinations of direct and indirect influences may have far-reaching consequences for community dynamics and species richness in a wide range of systems.

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Paulay, G. and Meyer, C. **Dispersal and divergence across the greatest ocean region: Do larvae matter?** *Integrative and Comparative Biology* 46(3): 269-281, 2006.

**Notes:** For marine, benthic animals, duration of planktonic larval stages is expected to correlate with dispersal ability, and thus species ranges, at least where planktonic dispersal is necessary to reach habitats. Yet past analyses of larval duration and species ranges across the insular Pacific show at most a weak correlation. So, do larvae matter in determining species ranges in such an island setting? We analyze an extensive dataset on cowries and find, again, that estimated larval duration does not correlate with species ranges. Several factors can obscure a real correlation, however, including estimation error, intraspecific variation, other factors affecting dispersal, poor taxonomy, and remote endemics. We show that taking these into consideration greatly improves correlation. Further evidence for the importance of larval duration comes from diversity and speciation patterns. Diversity of poor dispersers drops more rapidly eastward across the Pacific and leads to taxonomic differences in community composition across the basin. Geographic scale of differentiation is strongly influenced by larval duration and leads to the most rapid diversification at intermediate dispersal capacities. A major lesson from the phylogenetically corrected cowrie dataset is that without accurate and appropriate taxonomy, clear and important distributional and diversity patterns can become obscured. Inappropriate taxonomic scale can also obscure macroecological patterns: cowrie tribes/subfamilies show substantial variation in the steepness of their diversity cline across the Pacific and in their proportional local abundance, showing the importance of ecological traits in controlling distributions. In contrast such variation was not evident in a study focused at the family level in corals and fishes.

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Levin, L.A. **Recent progress in understanding larval dispersal: new directions and digressions.** *Integrative and Comparative Biology* 46(3): 282-297, 2006.

**Notes:** Larvae have been difficult to study because their small size limits our ability to understand their behavior and the conditions they experience. Questions about larval transport focus largely on (a) where they go [dispersal] and (b) where they come from [connectivity]. Mechanisms of transport have been intensively studied in recent decades. As our ability to identify larval sources develops, the consequences of connectivity are garnering more consideration. Attention to transport and connectivity issues has increased dramatically in the past decade, fueled by changing motivations that now include management of fisheries resources, understanding of the spread of invasive species, conservation through the design of marine reserves, and prediction of climate-change effects. Current progress involves both technological advances and the integration of disciplines and approaches. This review focuses on insights gained from physical modeling, chemical tracking, and genetic approaches. I consider how new findings are motivating paradigm shifts concerning (1) life-history consequences; (2) the openness of marine populations, self-recruitment, and population connectivity; (3) the role of behavior; and (4) the significance of variability in space and time. A challenge for the future will be to integrate methods that address dispersal on short (intragenerational) timescales such as elemental fingerprinting and numerical simulations with those that reflect longer timescales such as gene flow estimates and demographic modeling. Recognition and treatment of the continuum between ecological and evolutionary timescales will be necessary to advance the mechanistic understanding of larval and population dynamics.

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Dornelas, M., Connolly, S.R., and Hughes, T.P. **Coral reef diversity refutes the neutral theory of biodiversity.** *Nature* 440(7080): 80-82, 2006.

**Notes:** The global decline of coral reefs highlights the need to understand the mechanisms that regulate community structure and sustain biodiversity in these systems. The neutral theory, which assumes that individuals are demographically identical regardless of species, seeks to explain ubiquitous features of community structure and biodiversity patterns. Here we present a test of neutral-theory predictions with the use of an extensive species-level data set of Indo-Pacific coral communities. We show that coral assemblages differ markedly from neutral-model predictions for patterns of community similarity and the relative abundance of species. Within local communities, neutral models do not fit relative abundance distributions as well as the classical log-normal distribution. Relative abundances of species across local communities also differ markedly from neutral-theory predictions: coral communities exhibit community similarity values that are far more variable, and lower on average, than the neutral theory can produce. Empirical community similarities deviate from the neutral model in a direction

opposite to that predicted in previous critiques of the neutral theory. Instead, our results support spatio-temporal environmental stochasticity as a major driver of diversity patterns on coral reefs.

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France, K.E. and Duffy, J.E. **Diversity and dispersal interactively affect predictability of ecosystem function.** *Nature* 441(7097): 1139-1143, 2006.

**Notes:** Theory and small-scale experiments predict that biodiversity losses can decrease the magnitude and stability of ecosystem services such as production and nutrient cycling. Most of this research, however, has been isolated from the immigration and emigration (dispersal) processes that create and maintain diversity in nature. As common anthropogenic drivers of biodiversity change - such as habitat fragmentation, species introductions and climate change - are mediated by these understudied processes, it is unclear how environmental degradation will affect ecosystem services. Here we tested the interactive effects of mobile grazer diversity and dispersal on the magnitude and stability of ecosystem properties in experimental seagrass communities that were either isolated or connected by dispersal corridors. We show that, contrary to theoretical predictions, increasing the number of mobile grazer species in these metacommunities increased the spatial and temporal variability of primary and secondary production. Moreover, allowing grazers to move among and select patches reduced diversity effects on production. Finally, effects of diversity on stability differed qualitatively between patch and metacommunity scales. Our results indicate that declining biodiversity and habitat fragmentation synergistically influence the predictability of ecosystem functioning.

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Montoya, J.M., Pimm, S.L., and Sole, R.V. **Ecological networks and their fragility.** *Nature* 442(7100): 259-264, 2006.

**Notes:** Darwin used the metaphor of a 'tangled bank' to describe the complex interactions between species. Those interactions are varied: they can be antagonistic ones involving predation, herbivory and parasitism, or mutualistic ones, such as those involving the pollination of flowers by insects. Moreover, the metaphor hints that the interactions may be complex to the point of being impossible to understand. All interactions can be visualized as ecological networks, in which species are linked together, either directly or indirectly through intermediate species. Ecological networks, although complex, have well defined patterns that both illuminate the ecological mechanisms underlying them and promise a better understanding of the relationship between complexity and ecological stability.

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Cardinale, B.J., Srivastava, D.S., Duffy, J.E., Wright, J.P., Downing, A.L., Sankaran, M., and Jouseau, C. **Effects of biodiversity on the functioning of trophic groups and ecosystems.** *Nature* 443(7114): 989-992, 2006.

**Notes:** Over the past decade, accelerating rates of species extinction have prompted an increasing number of studies to reduce species diversity experimentally and examine how this alters the efficiency by which communities capture resources and convert those into biomass. So far, the generality of patterns and processes observed in individual studies have been the subjects of considerable debate. Here we present a formal meta-analysis of studies that have experimentally manipulated species diversity to examine how it affects the functioning of numerous trophic groups in multiple types of ecosystem. We show that the average effect of decreasing species richness is to decrease the abundance or biomass of the focal trophic group, leading to less complete depletion of resources used by that group. At the same time, analyses reveal that the standing stock of, and resource depletion by, the most species-rich polyculture tends to be no different from that of the single most productive species used in an experiment. Of the known mechanisms that might explain these trends, results are most consistent with what is called the 'sampling effect', which occurs when diverse communities are more likely to contain and become dominated by the most productive species. Whether this mechanism is widespread in natural communities is currently controversial. Patterns we report are remarkably consistent for four different trophic groups (producers, herbivores, detritivores and predators) and two major ecosystem types (aquatic and terrestrial). Collectively, our analyses suggest that the average species loss does indeed affect the functioning of a wide variety of organisms and ecosystems, but the magnitude of these effects is ultimately determined by the identity of species that are going extinct.

Grenyer, R., Orme, C.D.L., Jackson, S.F., Thomas, G.H., Davies, R.G., Davies, T.J., Jones, K.E., Olson, V.A., Ridgely, R.S., Rasmussen, P.C., Ding, T.S., Bennett, P.M., Blackburn, T.M., Gaston, K.J., Gittleman, J.L., and Owens, I.P.F. **Global distribution and conservation of rare and threatened vertebrates.** *Nature* 444(7115): 93-96, 2006.

**Notes:** Global conservation strategies commonly assume that different taxonomic groups show congruent geographical patterns of diversity, and that the distribution of extinction-prone species in one group can therefore act as a surrogate for vulnerable species in other groups when conservation decisions are being made. The validity of these assumptions remains unclear, however, because previous tests have been limited in both geographical and taxonomic extent. Here we use a database on the global distribution of 19,349 living bird, mammal and amphibian species to show that, although the distribution of overall species richness is very similar among these groups, congruence in the distribution of rare and threatened species is markedly lower. Congruence is especially low among the very rarest species. Cross-taxon congruence is also highly scale dependent, being particularly low at the finer spatial resolutions relevant to real protected areas. 'Hotspots' of rarity and threat are therefore largely non-overlapping across groups, as are areas chosen to maximize species complementarity. Overall, our results indicate that 'silver-bullet' conservation strategies alone will not deliver efficient conservation solutions. Instead, priority areas for biodiversity conservation must be based on high-resolution data from multiple taxa.

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