Linking the bottom to the top in aquatic ecosystems: mechanisms and stressors of benthic-pelagic coupling

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Abstract

Linkages between benthic and pelagic habitats occur in both freshwater and marine systems across multiple spatial and temporal scales, and are influenced by a number of chemical, biological, and physical forces. We identified three major mechanisms of benthic-pelagic coupling: (1) organism movement, (2) trophic interactions, and (3) biogeochemical cycling. We also explore the implications of several stressors, including invasive species and climate change that will inevitably impact the linkages between benthic and pelagic habitats. We identify critical research gaps that need to be addressed to quantify the habitat coupling of these ecosystems. We advocate for more collaboration among scientists with expertise in benthic and pelagic habitats in both freshwater and marine ecosystems to fully understand the cycles, interactions, processes, and functions of benthic-pelagic coupling in ecosystems. Finally, we suggest targeted research needs for better capturing of cross-ecosystem linkages in aquatic ecology.

Section 1. Introduction

Processes that connect benthic and pelagic habitats influence the ecology of both, particularly in ecosystems with large areas of benthic habitat relative to water volume (Vadeboncoeur et al. 2002). For example, in freshwater lakes, benthic primary production can account for up to 98% of

total primary production (Vadeboncoeur et al. 2003) and in temperate estuarine systems, benthic microalgae + cyanobacteria primary production can account for up to 50% of whole estuarine primary production (reviewed in Underwood and Kromkamp 1999). Benthic secondary production in some lakes can also contribute to upper trophic levels equally or in excess of that from pelagic production (Vander Zanden and Vadeboncoeur 2002). Less is known about the contribution of benthic communities to production in deeper marine environments. Estimates from photic zone depths suggest that benthic community net production can occur in > 33% of the global shelf area (Gattuso et al. 2006). Given that the seabed covers about 75% of the Earth's surface and can provide a vital habitat for benthic processes, it is likely that we are underestimating the ecological role of benthic habitats in the carbon and nutrient budgets of estuarine and oceanic ecosystems (Raffaelli et al. 2003). Benthic aquatic environments are also becoming well recognized as important storage banks for propagules and diapausing eggs of many water column planktonic species (Lampert 1995; Boero et al. 1996; Marcus

and Boero 1998). Moreover, treating benthic and pelagic habitats as discrete entities in ecosystems with a high benthic to pelagic habitat ratio could generate an unrealistic view of food webs. This point is illustrated by the importance of both pelagic and benthic energy pathways in food webs in small lakes (Vadeboncoeur et al. 2002), intertidal ecosystems (Riera et al. 2002), and coastal regions (Pasquaud et al. 2010; Vinagre et al. 2012).

Despite the importance of benthic habitats for overall ecosystem functioning, however, benthic-pelagic coupling (hereafter referred to as 'BPC') processes are not well understood, primarily because fewer studies have been conducted in benthic habitats versus pelagic habitats in aquatic ecosystems as a whole (Schindler and Scheuerell 2002; Vadeboncoeur et al. 2002). Early studies on BPC mainly focused on the impacts of sinking pelagic primary production to the benthic habitat (Hargrave 1973; Suess 1980; Smetacek 1985; Graf 1992). We discuss additional BPC mechanisms that are essential to the ecological understanding of the structure and function of aquatic ecosystems (Schindler and Scheuerell 2002; Chatterjee et al. 2013). There are varying definitions in the literature of what constitutes 'benthic-pelagic coupling' and the term tends to be loosely defined as any process that may influence both benthic and pelagic habitats in aquatic systems. This term has also been referred to as *bentho-pelago*, *bentho-pelagic*, *pelagic-benthic*, *benthic-pelagic relationships*, and *habitat couplings* (Schindler and Scheuerell 2002; Chatterjee et al. 2013). Here, we define BPC as benthic-pelagic coupling in aquatic ecosystems involves mechanisms of organism movement, trophic interactions, or biogeochemical cycling that connect the bottom substrate and the water column and is ultimately influenced by physical forces of depth, light, temperature, and mixing and occurs across multiple spatial and temporal scales.

We use this definition to help aquatic ecological researchers better understand the mechanisms of BPC, the physical aspects that regulate them, and their anthropogenic stressors.

In this article, we first discuss the physical controls of BPC and suggest three essential mechanisms of BPC that exist along the salinity gradient from freshwater to marine ecosystems. We also discuss how humans physically alter the two habitats. At the end of the article, we review the most significant anthropogenic stressors that likely affect these BPC mechanisms and predict potential ecological responses to these stressors. We conclude by identifying BPC research gaps and by suggesting targeted future research that will improve our understanding of BPC in diverse systems.

Section 2. Physical aspects to benthic-pelagic coupling

Benthic-pelagic coupling mechanisms are controlled by physical factors that regulate exchange across many spatial and temporal scales. Stratification frequently regulates the degree of connectivity between benthic and pelagic habitats.

Stratification is caused by processes and substances that differentially alter the density of water column layers. For example, solar radiation causes surface layers to warm more than deeper layers, inducing thermal stratification in many aquatic ecosystems. Differences in salinity between water parcels can also result stratification, with less-dense freshwater overtop of more-dense seawater.

The depth of an aquatic ecosystem is a key regulator of BPC because it determines the proximity and degree of interactions between the two environments (Schindler and Scheuerell 2002) (Fig. 1). However, even shallow ecosystems can have limited benthic-pelagic interactions, as thermal stratification can limit the exchange of water between layers in the water column. For example, many shallow dystrophic bogs are strongly thermally stratified (Read and Rose 2013), which can inhibit the flux of materials through the water column. On the other hand, BPC mechanisms can occur at large spatial scales that include the great distance between the deep ocean basins and the upper oceanic layers. The cycling of oceanic deep water as part of the 'Great Ocean Conveyor' belt is one such example (Broecker 1991).

Downward irradiance couples and regulates the ecological processes in pelagic and benthic aquatic environments (Flöder et al. 2006). Optical properties of the water column control the attenuation and spectral composition of solar radiation reaching the bottom, and thus regulate benthic primary production, oxygen dynamics, and exposure and refuges of organisms to damaging ultraviolet radiation (Gattuso et al. 2006; Yamaguchi et al. 2007; Karlsson et al. 2009; Rose et al. 2009).

Temperature and salinity gradients in the water column determine if (and how strongly) aquatic ecosystems become stratified. Thermal and density stratification regulate the exchange of dissolved and particulate substances between the pelagic and benthic environments (Imberger and Patterson 1990). Physical mixing in lake, coastal, and marine ecosystems can exhibit high temporal variability and may break down the stratification, thereby impacting the movement and distribution of substances and organisms between the pelagic and benthic habitats (Incze et al. 1995; Hamilton and Mitchell 2013). The timing of processes or the water residence time controls the amount of carbon fluxing to the bottom, when microphytobenthos are food sources for zooplankton, and when benthic suspension feeding can significantly reduce the phytoplankton standing stock (Cloern 1996; Perissinotto et al. 2003; Raffaelli et al. 2003). BPC mechanisms in aquatic ecosystems depend on the integration of these physical forces across diel and seasonal time scales (Schindler and Scheuerell 2002).

Section 3. Mechanisms of benthic-pelagic coupling

We identified three major mechanisms that drive BPC: organism movement, trophic interactions, and biogeochemical cycling (Fig. 1).
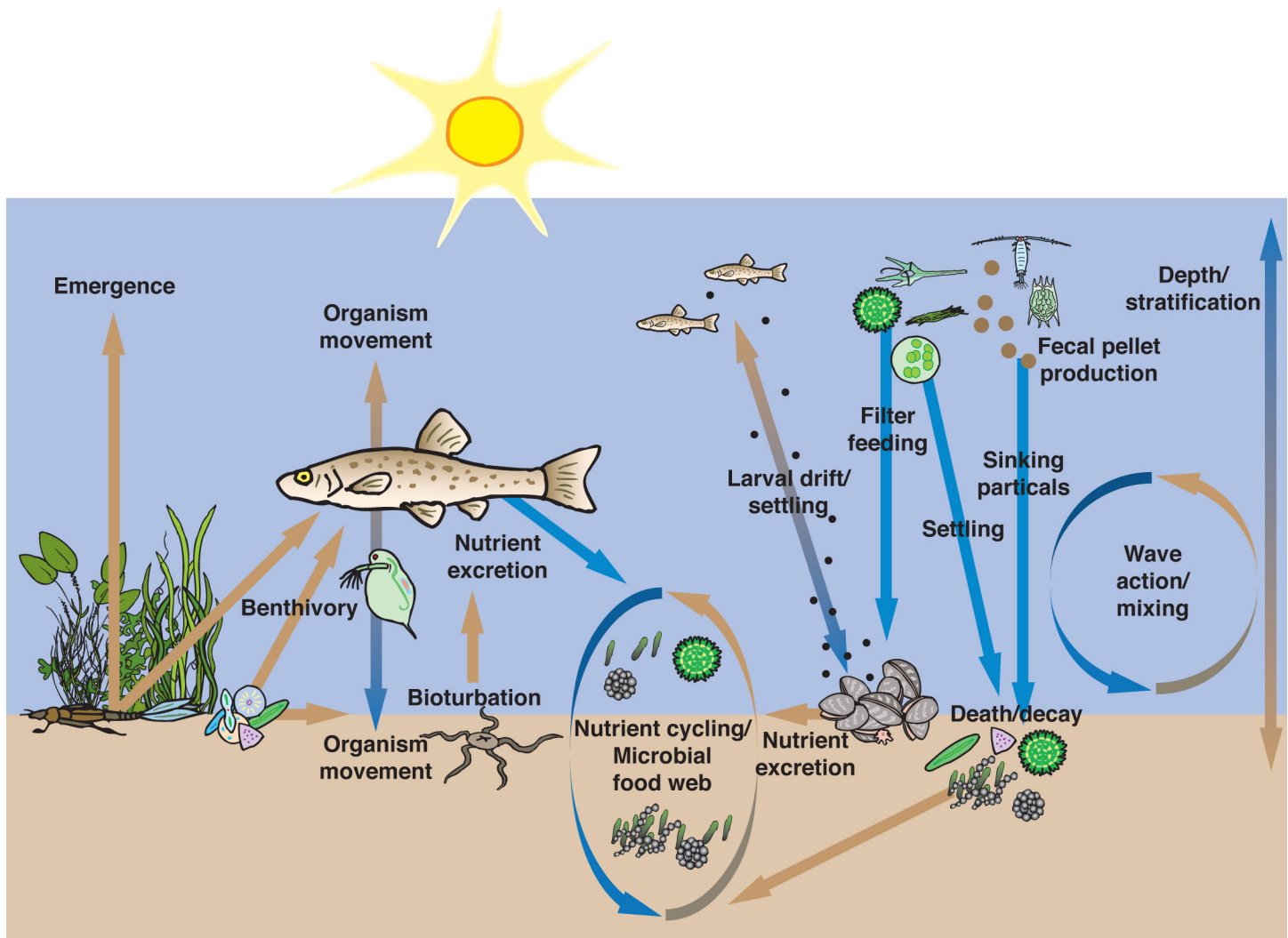
Fig. 1. Examples of processes involved with BPC mechanisms of organism movement, trophic interactions, and biogeochemical cycles in aquatic ecosystems. Blue arrows indicate pelagic-dominated processes, and brown arrows indicate benthic dominated processes.

Organism movement

Diel migrations

Benthic and pelagic habitats are connected through the movement of organisms via diel migrations (Fig. 1). Daily movements of fish and zooplankton can move substantial loads of nutrients between the benthic and pelagic zone in both freshwater and marine ecosystems (Polis et al. 1997).

The diel vertical migration (DVM) of zooplankton may be the largest daily movement of biomass on the planet (Hays 2003) (Fig. 1). Typical DVM behavior is characterized by a downward migration by day and an upward migration at night. Many different zooplankton taxa exhibit DVM behavior, in freshwater, coastal, and oceanic ecosystems and in response to a number of factors (Fiksen and Giske 1995; De Robertis et al. 2000; Williamson et al. 2011; Rose et al. 2012). Among these, predator avoidance (McLaren 1963; Zaret and

Suffern 1976), food availability (Bollens et al. 1994), and changes in the light environment (spectra, polarization pattern, absolute intensity, and rate of change in intensity) are thought to primarily drive DVM (Forward 1988; Williamson et al. 2011). For example, freshwater *Daphnia* can respond to both ultraviolet radiation and fish (Rose et al. 2012), whereas some marine copepods respond primarily to the presence of zooplanktivorous fishes (Bollens et al. 1992).

These migrations have important implications for the transport of mass and energy through the water column. DVM represents an active, rapid, and frequently occurring linkage between the benthic habitat and the upper water column. Zooplankton vertically transport items such as organic carbon, nutrients, parasites, and food resources throughout the water column (Williamson et al. 1996; Steinberg et al. 2000; Heuch et al. 2013). For example, zooplankton actively transport an average of 13% of inorganic and organic nitrogen flux

between water column layers in the Sargasso Sea (Steinberg et al. 2002). DVM organisms also couple benthic and pelagic habitats indirectly through their production of marine snow (e.g., fecal pellets) which can support microbial production at depth (Steinberg et al. 2000). In marine ecosystems, the production of particulate and dissolved organic carbon contributes to what is known as the 'biological carbon pump' (see De La Rocha and Passow 2007 for overview). These DVM examples illustrate the importance of organism movement to the ecology of benthic and pelagic habitats in both freshwater and marine ecosystems.

Life cycles

Benthic-pelagic coupling involves the movement of organisms that inhabit the benthic habitat for one part of their life cycle and the pelagic zone for another, or vice versa (Marcus and Boero 1998) (Fig. 1). Most marine benthic macrofauna have pelagic larval stages that may last from hours to months (Eckman 1996; Marcus and Boero 1998). This larval stage is critical for dispersal and has implications for inter-habitat energy transfer since pelagic larvae are prey for pelagic predators and derive nutrients from the pelagic habitat before settling to the benthic habitat.

In aquatic ecosystems, organisms connect the benthic and pelagic zones through movement driven by ontogenetic/life history stages and feeding patterns (*see also* "Trophic interactions"). Many freshwater and marine benthic macroinvertebrates spend the majority of their life in the benthic habitat, but swim up through the pelagic zone to the surface during emergence events (Corbet 1964). Pelagic fish and jellyfish prey heavily on these invertebrates during emergence, providing an influx of energy to the pelagic area from the benthic zone (*see also* "Trophic interactions," Vander Zanden and Vadeboncoeur 2002; Pitt et al. 2008). Lake fishes experience ontogenetic shifts in behavior and feeding patterns between the pelagic and benthic zones. For example, juvenile bluegill (*Lepomis macrochirus*) feed on benthic macroinvertebrates until they reach a critical size threshold and feed primarily on zooplankton thereafter (Mittelbach 1981; Werner and Hall 1988).

Many planktonic taxa in freshwater and marine systems have a benthic stage as part of their life cycle (i.e., meroplankton) and thus provide a pathway connecting the top of the water column to the bottom (Fig. 1). A number of phytoplankton taxa will produce dormant cells (thick-walled akinetes, vegetative cells, or spores) that sink to the sediments. These cells play a critical role in the long-term maintenance of populations as an evolutionary response to decreasing temperature, light, oxygen, nutrients, or a combination of these cues (Fryxell 1983; Adams and Duggan 1999; Kaplan-Levy et al. 2010). Some cells can remain viable in the sediment for potentially > 100 years (Livingstone and Jaworski 1980; Wood et al. 2009). Using different mechanisms to re-enter the water column (e.g., gas vesicles, entrainment, turbulence)

these dormant cells then form an important inoculum for water column populations (Hansson 1996; Lewis et al. 1999). Benthic recruitment from dormant stages may contribute > 50% of the surface population of some cyanobacterial species during periods of peak recruitment (Trimbee and Harris 1984; Barbiero and Welch 1992; Carey et al. 2008). Benthic resting stages have also been found in zooplankton (rotifers, tintinnids, cnidarians, cladocerans, and copepods) of fresh and marine ecosystems (Marcus and Boero 1998). Multiple scyphomedusae (Cnidaria) have a life history in which pelagic planulae settle on the bottom and become benthic polyps that then produce ephyra, the juvenile, pelagic stage of a jellyfish (Arai 1996). Other meroplanktonic taxa (e.g., crabs, bivalves, and gastropods) exhibit ontogenetic shifts in the opposite direction where pelagic larval stages recruit to the benthic habitat to mature into adult. Scyphozoan jellyfish polyps (called scyphophistma) can produce podocysts, small aggregations of epidermal cells and amoebocytes surrounded by a chitinous cuticle, that can remain viable for at least 2 years (Arai 1996). Consequently, because many organisms spend different stages of their life cycle in different habitats, the full life cycle must be taken into account when examining pelagic or benthic food webs.

Organisms who occupy both benthic and pelagic habitats as part of their life history serve as an important BPC for two reasons. First, recruitment to one habitat from the other is a primary factor maintaining adult populations, and in turn, community structure. Second, immigrating organisms also serve as inputs of allochthonous biomass and production essential for ecological interactions such as predation, competition, and parasitism. Collectively, these outcomes are essential to habitat productivity and overall ecosystem function

Trophic interactions

Even though the mechanics of food webs are similar across ecosystems, organism interactions differ based on the species involved and the spatial and temporal complexity of their habitat. Thus, we explore trophic interactions in lakes, estuaries, and marine environments separately.

Lakes

Benthic and pelagic food webs are tightly coupled at many trophic levels in lakes. At the base of the benthic food web, macrophytes and other aquatic plants are known to release part of their organic carbon as dissolved organic carbon (DOC) that can be subsequently consumed by pelagic bacteria (Findlay et al. 1986) and zooplankton (Speas and Duffy 1998). In shallow lakes, macrophytes and associated periphyton can be an important food source for pelagic bacteria and zooplankton, providing up to half of their carbon consumption (de Kluijver et al. 2015).

Many fish species traditionally associated with open waters are also feeding heavily in benthic areas (*see* "Organism movement: Life stages and cycles"; also Vander Zanden and

Vadeboncoeur 2002; Solomon et al. 2011; Vander Zanden et al. 2011). Benthic organisms constitute a substantial proportion of the diet of most fishes (Solomon et al. 2011), often with at least 50% of fish diets originating from the benthic habitat (Vander Zanden and Vadeboncoeur 2002, Henry and Bremigan unpubl. data). Zooplankton can also rely heavily on benthic food sources, such as bacteria (Rautio and Vincent 2006) and organic carbon produced by benthic algae during winter (Karlsson and Säwström 2009). These benthic food sources may be especially important to zooplankton in shallow lakes (Rautio and Vincent 2006; Cazzanelli et al. 2012).

Benthic predators can also feed heavily on pelagic prey. Zooplankton migrating to benthic areas to find refuge from pelagic visual predators, especially in shallow lakes, provide an important prey item for benthic consumers occupying nearshore areas (Van de Meutter et al. 2005). Odonates, a group of damselflies and dragonflies including several benthic predators, can feed heavily on *Daphnia*, even when *Daphnia* have the benefit of refuges in macrophytes (Burks et al. 2002). Zooplankton adapted to avoiding pelagic predators exhibit weaker avoidance behavior in the presence of littoral or benthic predators (Van de Meutter et al. 2004). Detritivores also link benthic and pelagic zones by inhabiting benthic areas but deriving energy from sinking pelagic detritus (*see also* "Biogeochemical cycling: Animal nutrient excretion and egestion.") These detritivores are then consumed by either benthic or pelagic predators, providing further evidence that benthic and pelagic zones are tightly linked via lake trophic interactions.

Estuaries

Estuarine trophic interactions can be influenced by their organic matter sources. Pelagic and benthic consumers tend to use the organic matter that is produced in the region of the estuary they reside (Deegan and Garritt 1997). For example, the upper estuarine sources of organic matter include a pelagic source of oligohaline phytoplankton and a benthic source of fresh marsh organic matter (Deegan and Garritt 1997). In lower estuaries, pelagic resources include marine phytoplankton, and benthic resources include benthic microalgae and salt marsh vegetation (Deegan and Garritt 1997). Benthic infauna from salt marshes in the Plum Island Estuary (Massachusetts, USA) relied on both phytoplankton and benthic algae, and less than *Spartina* spp. detritus, even when the infauna were found in the saltmarsh understory (Galvan et al. 2008). The pelagic rhizostome jellyfish *Catostylus mosaicus* derived 79% to 100% of their carbon from emergent demersal zooplankton in a coastal lagoon (Pitt et al. 2008). Crabs also consume both benthic and pelagic energy sources. Signa et al. (2008) found the swimming crab *Polybius henslowii* fed on a variety of pelagic and benthic prey. Vinagre et al. (2012) noted the hermit crab *Pargurus* sp. relied primarily on pelagic carbon in the Targus estuary (Bay of Biscay). The diets of European sea bass (*Dicentrarchus labrax* and *D. punctatus*), a sciaenid,

Argyrosomus regius, and the European eel (*Anguilla anguilla*), in the Gironde estuary were also a mixture of supra, epibenthic, and pelagic prey (Pasquaud et al. 2010). Benthic suspension feeders such as bivalves can exert considerable grazing pressure on phytoplankton and microzooplankton. For example, hard clams (*Mercenaria mercenaria*) and ribbed mussels (*Geukensia demissa*) cleared enough phytoplankton, ciliates, and copepod eggs to be considered an important regulatory factor on their biomass (Lonsdale et al. 2009). Bivalve grazing, in turn, can support the growth of seagrasses by improving water clarity (Wall et al. 2008). Thus, benthic and pelagic fauna can act as habitat couplers by consuming resources originating from either the water column or the sediment.

Marine systems

Marine ecosystems exhibit several examples of trophic interactions linking benthic and pelagic habitats. For example, on rocky intertidal shores, the effects of nearshore oceanographic currents on phytoplankton and sea star propagules influence the benthic community structure of mussels and predation pressure by sea stars (Menge et al. 1997, 2003). Bottom-dwelling medusa of the upside-down jellyfish (*Cassoiopea* sp.) release organic matter that is quickly taken up by the pelagic microbes and zooplankton (Niggl et al. 2010). Demersal fishes on the Bay of Biscay continental shelf are a key link to the benthic and pelagic food chains by consuming benthic epifauna and by being a prey source for pelagic top-predators (Lassalle et al. 2011). Turner (2001) reviewed food web characteristics on continental shelves and found that the percentage of pelagic primary production that enters into the pelagic food webs is linearly and positively dependent on the percentage pelagic primary production delivered to the benthic habitat. Or, in other words, the percentage of carbon flowing to the benthic habitat was in direct proportion to pelagic grazing pressure (i.e., zooplankton fecal pellets) contributing to vertical carbon flux.

In the deep sea, plankton settling from the upper water column provides an essential source of carbon to the benthic food web (Hargrave 1973; Suess 1980; Smetacek 1985). Stable isotopes provided evidence of continental shelf fish coupling benthic and pelagic production pathways (Woodland and Secor 2013) and also indicated that anthropogenic sewage pumped into the pelagic habitat from New York/New Jersey municipal barges enters the benthic food web through consumption by deep-sea urchins and cucumbers (Dover et al. 1992). In northern Baffin Bay, Arctic Circle, the benthic amphipod *Themisto libellula* was a significant source of energy and carbon to pelagic marine mammals and epi-pelagic seabirds (Hobson et al. 2002). These examples from freshwater and marine ecosystems illustrate that predator-prey interactions involving pelagic and benthic taxa inherently couples the two habitats by directly facilitating trophic energy transfer between them.

Biogeochemical cycling

Biogeochemical cycles incorporate both the pelagic and benthic habitats and thus integrate processes and interactions in both environments. Here, we focus on how microbial processes, cycling of nitrogen (N), phosphorus (P), carbon (C), and oxygen (O_2), animal nutrient excretion, organism decomposition, and bioturbation link benthic and pelagic habitats.

Nitrogen, phosphorus, and carbon cycling

There is strong cycling of nutrients and dependency between pelagic and benthic environments (Fig. 1). The benthic biogeochemical processes are essentially driven by pelagic processes, fuelled by the deposition of pelagic material (e.g., organic matter, calcium carbonate). In response, sediments transform the deposited material (such as through degradation and dissolution) back into nutrients available for uptake in the water column.

The nitrogen (N) cycle starts with the transformation of inorganic nitrogen, ammonium (NH_4^+), and nitrate (NO_3^-), into organic nitrogen during primary production by benthic and pelagic primary producers. Some specified pelagic algae (nitrogen fixers) can also fix nitrogen gas (N_2). Part of the organic nitrogen will be mineralized in the pelagic zone to NH_4^+ and another part will sink to the benthos, where it can be buried or remineralized. Mineralization takes place under oxic conditions, which is usually in the top few centimeters of the sediment. The released NH_4^+ can be transformed to NO_3^- by nitrifying bacteria if oxygen is present. Hence, sediments are usually sinks for organic nitrogen and sources for inorganic nitrogen to the water column. In anoxic parts of the sediments, a substantial part of NH_4^+ and NO_3^- is lost as N_2 via two microbial anaerobic processes: denitrification and anaerobic ammonium oxidation (anammox). Denitrification transforms NO_3^- into N_2 and anammox converts NO_2^- and NH_4^+ into N_2. Both processes have shown to be important in marine sediments, and together, they are responsible for the majority of global N loss from marine systems (Arrigo 2005; Thamdrup and Dalsgaard 2002).

Similar to N, phosphorus (P) is transformed into organic P during primary production and is remineralized in the sediment and water column. As organic P sinks to sediments, there is a cycling of inorganic P and phosphate (PO_4^{3-}) between the pelagic and benthic zones. Phosphate adsorbs to sediment particles and settling sediment particles create a large reservoir of PO_4^{3-} in the sediments. The adsorption and desorption of P is an equilibrium reaction and sensitive to pH and low oxygen. Under depleted oxygen concentrations and alterations to the redox potential, PO_4^{3-} releases from sediments and can increase and influence the overlying water chemistry in pelagic areas (Conley et al. 2002). Often the mechanisms are more complex (Hupfer and Lewandowski 2008), and an overview of uptake and release mechanisms of sedimentary P is given by Søndergaard et al. (2003).

Of particular interest is that several cyanobacterial taxa may be able to transport a substantial amount of P absorbed on the sediments into the water column during recruitment. For example, the cyanobacterium *Gloeotrichia echinulata* absorbs luxury phosphate from the sediment pore water that is transported to the water's surface during a bloom event (Whitton et al. 1991; Istvánovics et al. 1993; Pettersson et al. 1993). Consequently, recruitment of *G. echinulata* into the water column has contributed up to ~ 66% of the total yearly internal P load in two eutrophic lakes: Green Lake, Washington, USA (Barbiero and Welch 1992) and Lake Erken, Sweden (Istvánovics et al. 1993). Several other cyanobacterial taxa have also been implicated in translocating P from the sediments to the water column (e.g., Barbiero and Kann 1994; Jacobsen 1994; Istvánovics et al. 2002, Carey et al. 2014).

Carbon (C) is cycled via biological processes through primary production, respiration, and mineralization of organic matter while chemical processes take place via precipitation and dissolution of calcium carbonate in both pelagic and benthic environments. Ocean sediments represent an important reservoir for calcium carbonate. There is a strong gradient of carbon from the surface ocean toward the ocean's interior, driven by physical and biological processes, such that about two thirds of the surface-to-deep carbon gradient is caused by the biological pump (Volk and Hoffert 1985). The biological pump is the sinking of organic matter out of the euphotic zone into the deep, where it can be remineralized or buried. The vertical flux of biogenic carbon depends on rates of primary production, community respiration, and export (Rivkin and Legendre 2001). Integrated over the global oceans, export is about ~ 15% of primary production (Laws et al. 2000). The other pumps are the hard-tissue pump, which is the sinking of calcium carbonate produced by calcifying organisms and the physical temperature pump, driven by water temperature. Due to the efficient pumps, ocean sediments are long-term sinks of pelagic carbon and provide an essential role in BPC.

Oxygen cycling

The dissolved oxygen (DO) concentration of the water column is influenced by atmospheric exchange, gross primary production, and ecosystem respiration (Odum 1956; Solomon et al. 2011). When the water column is stable, DO concentrations usually vary within the water column (Staehr et al. 2010). In stratified marine and freshwater systems, oxygen in the upper water column can be an important source of oxygen to the bottom water during mixing or turn-over events (Robertson and Imberger 1994). The DO concentration of the lower water column is partially a function of the physical structure of the ecosystem. In ecosystems where sufficient light penetrates below the surface mixed layer, gross primary production can exceed respiration and result in a well oxygenated deep water layer if organic matter loads and carbon concentrations are low (Staehr et al. 2012). Lakes with a pronounced deep chlorophyll maxima exhibit a peak in DO below the surface mixed layer (Sadro et al. 2011; Staehr et al. 2012).

At the sediment-water interface, macrophytes, macroalgae, and microphytobenthos dominate benthic primary production (Cahoon 1999; Karlsson et al. 2009). These sources of oxygen allow aerobic organisms to move freely between the two habitats (Fig. 1). In ecosystems where sufficient light for primary production does not penetrate through the entire water column, respiration can exceed primary production at deeper depths with low-light conditions and result in a hypoxic or anoxic bottom-water. These oxygen dynamics, in turn, influence sediment nutrient cycling because sediments act as a nutrient source or sink depending on the redox state. Hypoxic or anoxic conditions also affect the density and diversity of organisms, with only certain taxa able to withstand low oxygen environments. Thus, the concentration of DO can help regulate how organisms and nutrients move between the benthic and pelagic environments.

Animal nutrient excretion and egestion

Nutrient excretion and egestion can link benthic and pelagic habitats via nutrient recycling or nutrient translocation (Fig. 1, *see also* "Trophic interactions: lakes.") Benthic zebra mussels (*Dreissena polymorpha*) in freshwater systems feed on pelagic phytoplankton and then excrete dissolved nutrients (P and N) back into the pelagic water column, which can then be used by phytoplankton (Arnott and Vanni 1996). Nutrient translocation moves nutrients across physical boundaries, and these nutrients are often conceptually classified as "new" nutrients stimulating new primary production (Caraco et al. 1992; Vanni 2002). Many organisms, including some benthic feeding invertebrates and fish, are considered nutrient translocators by consuming food (nutrients) trapped in the sediments and excreting these nutrients into the pelagic water column. For example, in U.S. reservoirs, gizzard shad cross-system nutrient cycling can be quantitatively important (Gido 2002) by supporting up to 39% of phytoplankton primary production through their nutrient excretion (Vanni et al. 2006). Planktivorous fish can indirectly enhance macrophyte primary productivity in estuaries through excretion of nitrogen and phosphorus in littoral areas (Pinnegar et al. 2007). Finally, marine mammals that feed at depth and defecate feces into surface waters can support new primary production (i.e., production which would not have occurred otherwise). Lavery et al. (2010) found sperm whales in the Southern Ocean defecating iron-rich feces into the pelagic habitat stimulated new primary production which was ultimately exported to the benthic zone.

Decomposition of organisms

Decomposing organisms can serve as another linkage between benthic and pelagic areas when dead pelagic organisms sink to the bottom (Fig. 1). Fully decomposing carcasses of zooplanktivorous fish can act as a source of nutrients for benthic production in shallow lakes (Vanni et al. 2013). BPC via this mechanism of nutrient cycling is likely less important

in deeper lakes because carcasses will generally decompose in profundal areas (Vanni et al. 2013). In marine ecosystems, epipelagic animal falls, such as jellyfish during bloom die offs, can transport large quantities of carbon to the bottom (Lebrato and Jones 2009). Aggregates of decaying phytoplankton also settle onto the sediment surface and supply nutrients and carbon for benthic bacteria (Brunberg 1995). In marine systems, whale carcasses can represent a significant source of organic matter to benthic areas where bacteria, macroinvertebrates, and fish congregate to feed (Smith and Baco 2003).

Bioturbation

Sediment-dwelling organisms can also be involved in BPC and biogeochemical cycling (Fig. 1). In both marine and freshwater systems, bioturbation links the benthic to the pelagic by the physical mechanism of suspending sediment that influences phytoplankton and zooplankton recruitment (Marcus and Schmidt-Gengenbach 1986; Stahl-Delbanco and Hansson 2002; Gyllstrom et al. 2008). Bioturbation stimulates mineralization of organic matter and the release of nutrients (Hansen et al. 1998; Lohrer et al. 2004; D'Andrea and DeWitt 2009), thereby affecting the growth of phytoplankton in the pelagic zone (Welsh 2003). Thus, sediment bioturbation plays an important role in biogeochemical cycling and plankton recruitment in freshwater and marine ecosystems.

Section 4: Human alterations to the benthic and pelagic environments

Any human activity that alters the physical habitats can have major ecological effects on BPC mechanisms. Such alterations include hardening of shorelines and coastal areas, extraction of natural resources (i.e., sand) and associated construction, removal of benthic habitat, and increased water withdrawal (Fig. 2).

Shoreline hardening is the placement of structures (e.g., concrete, riprap rock) along the shoreline to stabilize and prevent erosion (Fig. 2). Such shoreline hardening in lakes has increased the strength of mixing and wave action (Strayer and Findlay 2010), which can result in the uprooting of macrophytes (Jennings et al. 2003) and changes to nearshore sediments (Brauns et al. 2007). These human alterations to nearshore habitat can also alter the diversity of benthic macroinvertebrate (Brauns et al. 2011) and fish (Jennings et al. 1999) communities. Shoreline alterations, and associated effects, may result in fewer or less diverse benthic prey sources and, as a result, the loss of predators congregating in the feeding areas. In summary, shoreline hardening has the potential to affect aspects of each BPC mechanism (Fig. 1).

The development of shorelines has also resulted in the loss of physical habitat, particularly coarse woody habitat (CWH), also known as coarse woody debris (CWD) or fallen dead trees in lakes (Fig. 2). As CWH is an important refuge for prey fish, piscivores can decimate prey fish populations to the point that predators switch to a more terrestrial-based diet (Sass et al.
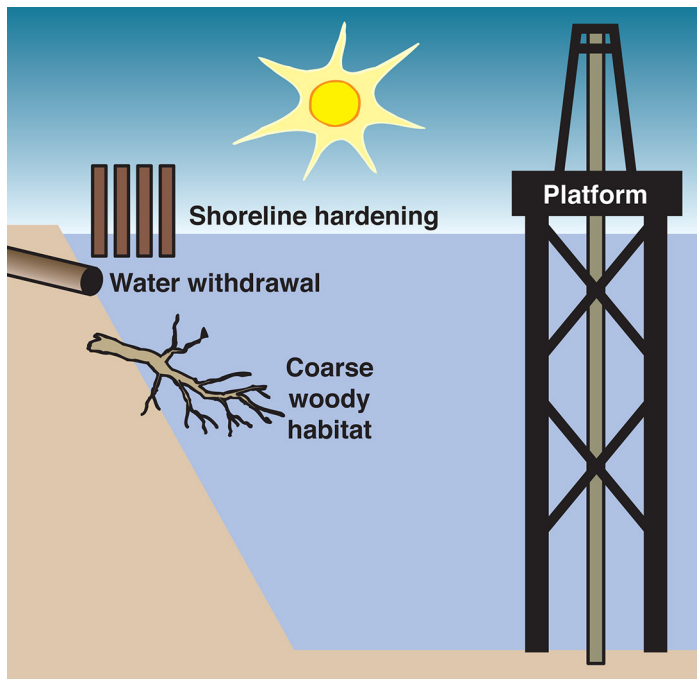
Fig. 2. Human alterations to the benthic and pelagic habitats that influence the physical constraints of the BPC mechanisms.

2006), altering the BPC mechanism of trophic interactions.

Besides removing materials, humans have introduced man-made structures that provide habitat for benthic organisms. For example, platforms associated with oil extraction and wind turbines (Fig. 2) in marine environments can provide new habitat to epibenthic prey (e.g., crabs, amphipods) and to their mobile demersal megafauna (e.g., crabs and lobsters) (Daigle et al. 2013; Krone et al. 2013). A variety of human structures (e.g., docks, aquaculture rafts, oil and gas platforms) are believed to serve as substrate for marine organisms such as jellyfish polyps. The proliferation of structures along coastlines is thought to contribute to the larger or more frequent appearance of blooms in coastal waters (Duarte et al. 2012). These benthic organisms are highly reliant on pelagic food sources (phytoplankton and zooplankton) (Arai 1996; Daigle et al. 2013), and thus provide a BPC mechanism of trophic interactions. Similarly, riprap rock seawalls used to stabilize lake shorelines can also provide habitat for benthic prey, such as macroinvertebrates (Schmude et al. 1998; Brauns et al. 2007) that are consumed by both benthic and pelagic fish species.

With a growing human population, there are a number of other demands on aquatic systems that can affect BPC mechanisms. For instance, the increased water withdrawals from freshwater systems (Fig. 2) for drinking water, industry, and agriculture (Cott et al. 2008; Morris et al. 2008), in addition to lower lake levels resulting from climate change (Angel and Kunkel 2010), will negatively influence the volume and levels

of water in lakes and reservoirs and likely affect the physical aspect of depth that regulates many BPC mechanisms (Fig. 1).

Section 5: Stressors to benthic-pelagic coupling mechanisms

Marine and freshwater ecosystems are subjected to a variety of anthropogenic stressors that ultimately impact the BPC mechanisms (Lake et al. 2000; Vadeboncoeur et al. 2002). Below we review six major stressors that impact BPC (Table 1). Interactions among these stressors, such as between eutrophication and climate change, are also likely to occur and influence the mechanisms involved in BPC. Other stressors, such as the role of ultraviolet radiation are not discussed, but may also have important global implications for the state of aquatic ecosystems (Williamson and Rose 2009; Llabrés et al. 2013).

Nutrients and eutrophication

The enrichment of nutrients, such as nitrogen and phosphorus, and the ecological response via eutrophication in aquatic ecosystems has profound impacts on the BPC mechanisms of organism movement, trophic interactions, and biogeochemical cycles (Table 1).

Impacts to organism movement

In both fresh and marine ecosystems, the increase of toxins in the sediments from decomposing toxic phytoplankton that are often associated with eutrophication, may inhibit invertebrate grazers that feed among benthic substrate (Hallegraeff 1993; Heisler et al. 2008; Trainer et al. 2012) and their movement within the benthic habitat and to the water column. The combination of decreasing light levels and lower oxygen concentrations that result from nutrient enrichment may inhibit recruitment of phytoplankton and zooplankton from resting states in the sediments (*see* "Life cycles") to the water column as part of their life cycle (McQuoid et al. 2002; Kaplan-Levy et al. 2010).

Impacts on trophic interactions

Overall, eutrophication results in an increase in phytoplankton biomass and blooms, altered phytoplankton community structure, and a decrease in benthic primary production. As a result, whole-lake production can, under some circumstances, decrease at higher P levels (Vadeboncoeur et al. 2003). Eutrophication can cause a transition in shallow lakes from macrophyte to phytoplankton-dominated alternate stable states (Scheffer et al. 1993). In the phytoplankton dominated state, low light prevents macrophytes from growing and resuspension of unprotected sediments by fish and storms further decrease water transparency. Sediment nutrient release via resuspension also promote pelagic primary production. With fewer macrophytes, zooplankton do not have a refuge and become more susceptible to grazing by planktivorous fish. If the euphotic zone reaches the bottom, nutrients can

Table 1. Examples of how stressors impact the benthic-pelagic coupling mechanisms in freshwater and marine ecosystems. BP = benthic production; PP = pelagic production; OM = organic matter.

Stressors	Benthic-pelagic coupling mechanisms		
	Organism movement	Trophic interactions	Biogeochemical cycles
Nutrients and eutrophication	Increased sinking of phytoplankton (1)	Shift BP to PP. Increased food for zoobenthic organisms. Decreased pelagic trophic efficiency (2).	Increased flow of pelagic OM to sediments, transfer of N and P between sediments and water by cyanobacteria (3)
Hypoxia and anoxia	Nekton move horizontally or vertically away (4)	Decrease sessile benthic organisms for demersal predators (5)	Release of NH_4 and P from sediments (6)
Invasive Spp.	Increased bioturbation (7) Increase or decrease in abundance of organisms with high movement rates	Increased/Increase of benthic primary production (8) Increased/ Increase of pelagic primary production via trophic cascades (9)	Transfer nutrients from pelagic to benthic zones (10) Increased nutrient release from sediments via bioturbation (11) Decrease oxygen availability via shading (12)
Overfishing	Alter abundance (13) or behavior (14) of migratory organisms	Removal of top predators (15)	Removal of filter-feeding organisms (16)
Climate change	Expatriation of taxa (17). Distributional shifts (18)	Phenological shifts (19). Trophic match/mis-match (20)	Decrease vertical flux of carbon (21)
Ocean acidification	Hypothetical: reduced movement between life stages (22)	Potential increase in benthic and pelagic production. Reduced calcification (23)	Increased export OM and decreased export $CaCO_3$ alteration of nutrient uptake and release sediments (24)

1 = Heip et al. (1995), 2 = Turner (2001); Chandra et al. (2005), Vadeboncoeur et al. (2003), 3 = Heip et al. (1995); Carey et al. (2008), 4 = Craig and Crowder (2005); Kimmel et al. (2009), 5 = Pihl (1994); Powers et al. (2005), 6 = Middelburg and Levin (2009), 7 = Weber and Brown (2009), 8 = Inderjit et al. (2006), 9 = Roohi et al. (2008), 10 = Higgins and Vander Zanden (2010), 11 = Matsuzaki et al. (2007), 12 = Kasulo (2000), 13 = Worm et al. (2009), 14 = Madin et al. (2010), 15 = Estes and Duggins (1995), 16 = Rotschild et al. (1994), 17 = Doney et al. (2012), 18 = Grebemeir et al. (2010), 19 = Kirby et al. (2007), 20 = Edwards and Richardson (2004), 21 = Fulweiler and Nixon (2009), 22 = Kroeker et al. (2010), 23 = Fabry et al. (2008); Andersson et al. (2011); Riebesell and Tortell (2011), 24 = Riebesell et al. (2007); Widdicombe and Needham (2007).

stimulate growth of benthic primary producers and cause a shift in community structure. Nuisance macroalgae species tend to benefit from eutrophication and replace macrophytes, seagrasses, corals, and red/green algae (Valiela et al. 1997). Increased N loads to estuarine and marine systems can also induce a shift in the composition and habitat of primary producers, and therefore, impact the food webs (Valiela et al. 1992; McClelland and Valiela 1998).

Harmful algal blooms (HABs) and cyanobacterial blooms are predicted to increase as a result of eutrophication and climate change (Paerl and Huisman 2008; Brookes and Carey 2011). When the phytoplankton community shifts from edible to non-edible phytoplankton (De Bernardi and Giussani 1990), such as cyanobacteria, the sedimentation of (dead) phytoplankton cells increase, thus increasing pelagic food availability for benthic consumers. Chandra et al. (2005) found a shift from 27% to 62% carbon contribution of pelagic sources to zoobenthic organisms after decades of eutrophication in Lake Tahoe. A tight coupling between land-derived nitrogen and estuarine benthic prey and predators was also shown with stable isotopes by Martinetto et al. (2006). Increases in inedible phytoplankton biomass as a result of eutrophication may weaken trophic linkages and the transfer of nutrients and carbon to higher trophic levels. Higher nutrient loading may also shift carbon flow within and through the 'microbial loop' (Turner 2001).

The effect on zoobenthic organisms from nutrient enrichment and eutrophication depends on the amount and quality of the sinking organic matter. For example, high quality organic matter is consumed by suspension feeders, while more refractory organic matter (from seagrass and macrophytes) is a food source for deposit feeders. With increasing organic matter input to the sediment, the abundance of zoobenthic organisms will peak and then decline, but biodiversity continually decreases (Pearson and Rosenberg 1978; Heip 1995). When organic matter input is high, bacterial remineralization and respiration will consume oxygen and become greater than oxygen production, thus stimulating hypoxic/anoxic conditions, and leading to the decline of benthic fauna.

Impacts to biogeochemical cycles

In general, the biogeochemical coupling between benthic and pelagic habitats seems to be significantly altered with eutrophication. After phytoplankton bloom events, a net transport downwards of nutrients and organic matter will occur from the pelagic zone to the benthic zone as phytoplankton sediment out of the water column and decompose. Because eutrophication will favor cyanobacterial dominance in both marine and freshwater systems (Paerl and Huisman 2008), and many cyanobacteria transfer sequestered P and fixed N from the sediments to the water column (Barbiero and Welch 1992; Istvánovics et al. 1993, 2002; Carey et al. 2008),

it is possible that cyanobacteria will create a positive feedback in which they increase epilimnetic nutrient concentrations during bloom events and potentially accelerate or intensify eutrophication (Carey et al. 2008; Carey and Rengefors 2010).

Increased benthic production can largely uncouple biogeochemical cycling between the sediments and the water column (Valiela et al. 1997). Macrophytes (growing in benthic zones) can reduce internal P loading in lakes by preventing sediment resuspension (Horppila and Nurminen 2003; Søndergaard et al. 2003), through the uptake of P from the sediment (Horppila and Nurminen 2003), and by oxidizing the sediment-water interface, further encouraging the binding of P to Fe (Carpenter et al. 1983; Søndergaard et al. 2003; Boros et al. 2011). In the heavily eutrophicated Skive Fjord (Denmark), especially severe cases of oxygen depletion take place in years with mass occurrence of jellyfish because the jellyfish eliminate the grazing impact of zooplankton on the blooming algae. The algae settle to the bottom where they are subsequently decomposed, leading to more severe oxygen depletion and filter-feeding mussel death. This further escalates the issue and impacts the ecosystem services the mussels provide (Møller and Riisgård 2007).

Hypoxia and anoxia

Bottom-water hypoxia (≤ 2.0 mg O_2 L^{-1}) or the lack of oxygen (anoxia) impacts the BPC of aquatic ecosystems (Diaz and Rosenberg 2008; Zhang et al. 2010) by directly affecting the behavior and survivability of pelagic and benthic organisms and their movement between the habitats (life stages or life cycles; diel migrations; resting stages). This subsequently interferes with their interactions in the local food webs. Hypoxia thresholds vary greatly across benthic organisms. Whereas 2.0 mg O_2 L^{-1} is frequently used as a hypoxia threshold, this concentration is below an empirical sublethal or lethal limit for about 50% of species, implying that the extent of hypoxia may be greatly underestimated (Vaquer-Sunyer and Duarte 2008). Low-oxygen concentrations in the bottom water and sediment surface alter the biogeochemical cycles dependent on the redox state and concentrations of solutes in the pelagic and benthic habitats.

Impacts to organism movement

Many pelagic and benthic nekton detect low oxygen conditions and move horizontally or vertically away, thus forcing them into new habitat and predator-prey interactions (Craig and Crowder 2005; Craig et al. 2005; Switzer et al. 2009). Mesozooplankton also avoid the deeper hypoxic bottom waters (Kimmel et al. 2009). The meroplankton of the common polychaete, *Paraprionospio pinnata* delayed settlement in the northern Gulf of Mexico and remained in the water column until higher oxygen concentrations (>2.0 mg O_2 L^{-1}) returned (Powers et al. 2001), thus influencing the dynamics of the water column by remaining there longer and affecting the sediment community composition by delaying their arrival. When benthic organisms are stressed under low oxygen conditions, they tend to reduce their efforts of bio-irrigation and bioturbation, which has profound impacts to the biogeochemical cycles (Middelburg and Levin 2009) such as decreasing the exchange of nutrients and oxygen between the sediment and overlying water (Aller 2001).

Impacts to trophic interactions

Bottom-water hypoxia in marine coastal waters significantly decreases the abundance, diversity, and biomass of sessile benthic infauna such as barnacles, polychaetes, and molluscs (Diaz and Rosenberg 1995; Rabalais et al. 2001; Baustian and Rabalais 2009; Seitz et al. 2009), which can impact demersal predators by decreasing and changing the composition of their available prey (Pihl 1994; Powers et al. 2005; Baustian et al. 2009). However, some demersal predators, such as spot (*Leiostomus xanthurus*) and cownose rays (*Rhinoptera bonasus*) in marine systems and mudminnows (*Umbra limi*) in lakes, may take advantage of the stressed benthic fauna and dive into hypoxic bottom water to forage (Pihl et al. 1992; Rahel and Nutzman 1994; Craig et al. 2010). In Lake Erie, hypoxic bottom water forced yellow perch to increase their amount and proportion of zooplankton (pelagic prey source) from their typical benthic prey sources of macroinvertebrates (Roberts et al. 2009), thus illustrating that hypoxia can decouple the trophic interactions between benthic prey and pelagic predators. Hypoxia can also affect the structure of coastal marine food webs by excluding some taxa and favoring those relatively more tolerant of low oxygenated waters such as jellyfish (Graham et al. 2001; Purcell et al. 2007). Low oxygenated waters may indirectly enhance consumption of hypoxia-stressed zooplankton and fish early life stages by reducing their ability to escape predation.

Impacts to biogeochemical cycles

Hypoxia and anoxia alter the oxidative states and biogeochemical processes that link the benthic and pelagic environments. During anoxia, nitrification rates decline with the consequence that denitrification rates decrease (Middelburg and Levin 2009). This loss of denitrification implies a higher recycling efficiency of nitrogen at the ecosystem level and can promote the eutrophication potential (Soetaert and Middelburg 2009). Hypoxia also results in release of manganese, iron, and elements such as phosphorus that are intimately linked to metal oxides. In the Baltic Sea, annual changes in dissolved inorganic phosphate water pools have been positively correlated with deep-water oxygen concentrations (Conley et al. 2002). Enhanced recycling of ammonium and phosphate under hypoxic bottom waters may lead to secondary eutrophication phenomena (Cloern 2001; Kemp et al. 2005; Middelburg and Levin 2009). Anoxia is often coupled to increased CO_2 release and therefore exacerbates ocean acidification at the seafloor (Cai et al. 2011).

Invasive species

Invasive species pose a major threat to both freshwater and marine ecosystems (Dudgeon et al. 2006; Molnar et al. 2008). The mechanisms by which invasive species impact BPC are species-specific; some invaders may influence all three mechanisms, whereas others may impact only one (Table 1). The direction of their effects on BPC mechanisms is also species-specific; some invasions result in greater integration of benthic and pelagic energy pathways, whereas others reduce connections. The following section illustrates the range of impacts of invasive species on BPC, but is not an exhaustive review.

Impacts to organism movement

Invasive species that exhibit any of the behavioral or life history traits listed in the "Organism Movement" section (above) that can link benthic and pelagic energy pathways have the potential to influence BPC. For example, common carp (*Cyprinus carpio*) are a widely introduced freshwater species that reduce the contribution of the benthic production to overall ecosystem productivity via their activity of bioturbation. Carp disturb benthic sediments and uproot macrophytes through their foraging behavior, reducing light penetration and suppressing macrophyte growth (e.g., Weber and Brown 2009). In combination, the foraging behaviors of carp decouple benthic processes from pelagic and shift systems from macrophyte- to phytoplankton-dominated states (Scheffer et al. 1993).

Impacts to trophic interactions

A number of invasive species alter food webs. Perhaps the best freshwater example of an invasive species altering BPC via effects on trophic interactions is the zebra mussel. These bivalves are native to the Ponto-Caspian region but have invaded inland lakes and streams throughout Europe and North America (Hebert et al. 1989; Karatayev et al. 1997). Zebra mussels are filter-feeders capable of removing high volumes of phytoplankton from the water column. In doing so, they can cause "benthification" of invaded systems (e.g., Mills et al. 2003; Higgins and Vander Zanden 2010); that is, a drastic reduction in pelagic production and increase in benthic production. Although zebra mussel larvae (known as veligers) are pelagic, consume pelagic phytoplankton, and serve as a diet item for pelagic fishes (Molloy et al. 1997), the transfer of energy and nutrients from the pelagic to the benthic zones caused by the filter feeding rates of adult mussels far outweighs the impact of larval veligers moving from the benthic to the pelagic environment (MacIsaac et al. 1992). In marine systems, invasive oysters (Family Ostreidae) can cause benthification via similar mechanisms (e.g., Ruesink et al. 2005; Sousa et al. 2009).

In some cases, invasive species can truncate food webs and decouple energy pathways. For example, the invasive marine benthic macroalga *Caulerpa taxifolia* can cover large portions of benthic substrates in coastal zones at extremely high biomass, outcompeting native taxa such as seagrass (Bax et al. 2003; Inderjit et al. 2006). Although *Caulerpa* increases benthic primary production, benthic secondary production is reduced due to declines in many benthic invertebrates and fishes that cannot effectively consume the invasive algae (e.g., Boudouresque et al. 1995). Conversely, invasive predators can increase pelagic primary production via classic predator-driven trophic cascades (cf. Carpenter et al. 1985). For example, in European marine systems, predation by the invasive comb jelly *Mnemiopsis leidyi* (Phylum Ctenophora) on crustacean zooplankton decreased zooplankton grazing pressure on phytoplankton, leading to increased pelagic production and reducing light to the benthic habitat (Roohi et al. 2008). However, these increases in primary production do not correspond with increased secondary production of consumers, because invasive comb jellies are associated with the collapse of pelagic fishes (Shiganova et al. 2004).

Impacts to biogeochemical cycling

Invasive species can impact biogeochemical cycles in addition to altering trophic interactions and/or organism movement. For example, through their foraging behaviors, common carp release nutrients from sediments, increasing nutrients available for phytoplankton growth (Matsuzaki et al. 2007). Conversely, zebra mussels concentrate nutrients from the pelagic habitat to the benthic habitat through excretion of pseudo-feces (Higgins and Vander Zanden 2010). Invasive floating aquatic plants such as water hyacinth (*Eichhornia spp.*) alter oxygen cycling by shading out other forms of primary production, leading to increased decomposition of phytoplankton and increase in the frequency and severity of anoxic conditions (Kasulo 2000).

Overfishing

Similar to invasive species, the mechanism by which overfishing influences BPC is specific to the species being fished and the method of fishing. We highlight here some of the best known examples of ways in which overfishing can affect benthic and pelagic energy pathways, but this is not intended to be an exhaustive list.

Impacts to organism movement

Fishing can alter the abundance (e.g., Anderson et al. 2008; Worm et al. 2009) and the behavior (e.g., Uusi-Heikkilä et al. 2008; Madin et al. 2010) of target organisms and their prey, both of which can alter the magnitude of energy transfer between the benthic and pelagic zones due to changes in organism movement.

Impacts to trophic interactions

Fishing directly influences the BPC by altering trophic interactions (Table 1). In many cases, fishing targets predators and their removal can lead to trophic cascades. For example,

historical overharvest of sea otters reduced their predation pressure on urchin populations, leading to reductions in benthic primary production via urchin destruction of kelp forests (Estes and Duggins 1995). Similarly, overharvest of sharks has led to increased ray populations, which have devastated benthic mollusc populations along U.S. East Coast (Myers et al. 2007). Although the effects of overfishing in fresh waters are not well understood (Allan et al. 2005), fishing of inland waters can certainly influence pelagic primary productivity and thus BPC mechanisms of trophic interactions and biogeochemical cycles (e.g., Carpenter and Kitchell 1996).

Impacts to biogeochemical cycling

Overfishing can alter biogeochemical cycling through effects on target organisms and indirect effects on habitat. For example, overfishing played a role in the massive decline of American oysters in the Chesapeake Bay, leading to subsequent decreases in benthic production and increase in eutrophication as the filtering capacity of phytoplankton by the oyster stock declined (Rotschild et al. 1994). Fishing methods such as bottom trawling can alter benthic habitat and production (Jennings et al. 2001). Bottom trawling impacts the BPC mechanism of biogeochemical cycles via altering the benthic carbon, nitrogen and oxygen fluxes, and the mechanism of organism movement by eliminating the bioturbators (Duplisea et al. 2001; Lohrer et al. 2004).

Climate change

Few studies have reported impacts of climate change to the BPC in aquatic ecosystems (Edwards and Richardson 2004; Fulweiler and Nixon 2009; Nixon et al. 2009) and far more research has focused on pelagic systems (Grall and Chauvaud 2002). Here, we describe how changes (i.e., temperature, precipitation, and wind speed) in climate both directly and indirectly affect physical characteristics and mechanisms of BPC.

Climate changes can directly impact the physical characteristics of aquatic ecosystems that regulate benthic-pelagic interactions, such as light attenuation and wind speed, and in many aquatic ecosystems, they may already be changing. For example, a warmer climate may increase water-column stratification and extend the duration of ice-free periods (Magnuson 2000; Jankowski et al. 2006). Widely observed changes in dissolved organic carbon, resulting from changes in temperature, precipitation, soil moisture, and solar radiation (reviewed in Jennings et al. 2010), may be altering water-column transparency, which has indirect implications for benthic-pelagic interactions (Rose et al. 2009).

Greater variability in precipitation could also lead to flooding and drought conditions. With flooding or sea-level rise, BPC may increase over short timescales as increased precipitation inundates and produces new benthic areas (Ackleson 2003). However, flooding or sea-level rise could also limit BPC because it may increase the depth or distance between the pelagic and benthic habitats. Drought will likely reduce these

habitats and decrease the depth of the water column, but it could increase the benthic-pelagic interactions per unit of volume. Therefore, we still have much to learn about how water levels will influence the coupling between benthic and pelagic habitats (Miranda et al. 2001). Not only does climate change impact these physical characteristics of aquatic ecosystems, it also affects the three key BPC mechanisms.

Impacts to organism movement

Reduced sea ice as a result of increased water temperatures in polar ecosystems provide the most stark examples of how climate change is affecting organism movement as a BPC mechanism. In the northern Bering Sea ecosystem, where the majority of ice-edge primary production is consumed by benthic organisms (due to limited zooplankton grazing in early spring), reduction in sea ice has caused a shift from an ice-dominated system favoring benthic communities to an open-water system favoring pelagic species (Grebmeier et al. 2006; for review see Doney et al. 2012). The distribution of pelagic and demersal fishes has expanded poleward (Grebmeier et al. 2006; Grebmeier et al. 2010). Declines in benthic prey due to a reduction in phytoplankton carbon supply from surface waters has caused apex predators dependent on benthic prey, such as gray whales, to shift their foraging ranges northward (Moore et al. 2013). Years with reduced sea ice in the Chukcki Sea caused Pacific walrus (*Odobenus rosmarus*) to arrive earlier and stay longer and highly concentrate foraging efforts in nearshore areas rather than offshore waters (Jay et al. 2012).

Impacts to trophic interactions

Climate changes will impact trophic interactions in many ways and cross trophic levels, from phytoplankton to fish (Kirby et al. 2007). Changes in stratification, concurrent with changes in temperature and wind speeds, will alter phytoplankton community structure, as nutrient-limited taxa will likely be negatively affected by the increased stratification. Climate determines the latitudinal distribution of marine eukaryotic phytoplankton taxa by regulating wind-driven turbulent mixing, which in turn, regulates nutrient fluxes that determine distributions of optimal cell sizes and species abundance (Falkowski and Oliver 2007). In response to rising temperatures, smaller phytoplankton species are expected to increasingly dominate (Moran et al. 2010). For example, in warm, oligotrophic waters, picophytoplankton are expected to become much more important contributors to total biomass and production (Agawin et al. 2000).

Rising temperatures will likely also shift the timing of phytoplankton blooms and the recruitment time of consumers. The level of responses to temperature will differ throughout the benthic and pelagic communities and the seasonal cycle, leading to a mismatch between trophic levels and functional groups (Edwards and Richardson 2004). For example, Winder and Schindler (2004) showed that increasingly warmer springs

disrupted phytoplankton-zooplankton trophic interactions due to different sensitivities to warmer water temperature. Climate changes can also directly impact the BPC of food webs by altering the growth and survival of organisms (or life-stages within an organism's life cycle) in either benthic or pelagic habitats. For example, Kirby et al. (2007) showed that benthic echinoderm larvae thrived as a result of warmer conditions and affected both the quantity and quality of phytoplankton food resources.

Impacts to biogeochemical cycling

Changes in temperature might have direct effects on metabolism of organisms and timing of biological events. Given that respiration has higher activation energy than primary production (Yvon-Durocher et al. 2012; Vaquer-Sunyer and Duarte 2013), climate change is also expected to affect the metabolic balance of aquatic ecosystems, and warmer climates may shift more systems to net heterotrophy. These results, coupled with greater duration of stratification and lower transparency, may increase eutrophication and hypoxia in both freshwater and marine ecosystems. Additionally, warming is expected to shift the partitioning of organic carbon between the particulate and dissolved phase toward an enhanced accumulation of dissolved organic carbon (Zhang et al. 2010). Observed widespread increases in dissolved organic carbon of lakes may be reducing transparency, thereby reducing benthic production and benthic-pelagic exchange of energy and mass (Monteith et al. 2007; Read and Rose 2013). This shift may cause a decrease in the vertical flux of particulate organic matter to the benthic habitat and a decrease in remineralization depth (from Riebesell et al. 2009). Warmer winters and increased cloudiness in the last 100 years of Narragansett Bay has been shown to change the timing of phytoplankton blooms and decrease their biomass during blooms. Thus, decreased carbon loading to the benthic habitat has decreased sediment oxygen consumption and nutrient fluxes (Fulweiler and Nixon 2009; Nixon et al. 2009). As temperature increases, the microbial biomass and activity become more important in the water column and because they have lower sinking rates than phytoplankton, they will negatively influence the benthic productivity (Wiklund et al. 2009).

Ocean acidification

Rising atmospheric CO_2 is causing changes in seawater chemistry including decreasing pH (hence acidification), increasing CO_2 (carbonation) and dissolution of calcium carbonate. Changes in seawater chemistry might have a range of biological effects, some related to direct impacts of pH changes on physiological processes of organisms. Other direct effects could be on carbon-related processes, such as calcification or photosynthesis. An indirect effect might be a pH induced change of substrate availability, due to kinetic effects on nutrient and metals speciation. A recent meta-analysis shows that ocean acidification leads to decreased survival, calcification,

growth, development, and abundance in a broad range of marine organisms (Kroeker et al. 2013). Indirect effects are also very important. For example, species interactions, nutritional status, source population, and water temperature affect taxa-specific responses (Kroeker et al. 2013). Despite these effects, there is also reason to believe that marine biota may be more resistant to ocean acidification than many early studies have predicted because active biological processes and small-scale temporal and spatial pH variability may protect marine biota in situ (Hendriks et al. 2010).

Impacts to organism movement

Very little is known about potential impacts of ocean acidification on organism movement. Based on general knowledge and few studies, the expected effect is likely a decrease organism movement. Early-life history stages of some invertebrates might be more sensitive to CO_2 than juveniles or adults (Kroeker et al. 2010). Early settlement mortality in bivalves was found to be affected by a reduction in the aragonite saturation state at the sediment surface (Green et al. 2009). However, greater sensitivity of early life history stages is not universal across taxa (Kroeker et al. 2013).

Impact on trophic interactions

Most CO_2 perturbation studies focused on single species or small communities, so food web predictions are mostly based on hypotheses. However, evidence suggests that interactions are an important regulator of individual species responses (Kroeker et al. 2013). Ocean acidification might change phytoplankton production and composition. Experiments with single plankton species indicate that some species benefit from ocean acidification because of increased CO_2 availability, while others are harmed, i.e., by reduced calcification (see review by Riebesell and Tortell 2011). Benthic primary producers might respond differently and could benefit from increased CO_2. Seagrasses, which appear to be limited by CO_2 availability, respond positively to increased CO_2 (reviewed in Andersson et al. 2011). These changes in autotrophic community composition might affect consumers, but these effects are not well studied. de Kluijver et al. (2013) found slightly lower grazing by zooplankton at higher CO_2 in mesocosm experiments. Grazers were found to mediate both ocean acidification and climate change effects on seagrasses (Alsterberg et al. 2013).

Noncalcifying organisms are likely favored over calcifying ones; for example, negative effects of ocean acidification are found on calcifying organisms—both in pelagic and benthic environments—such as coral, molluscs, pteropods, calcifying algae (Kroeker et al. 2010). Lowering of the calcium carbonate saturation state hampers calcification, and dissolution of existing calcium carbonate structures can occur when systems become undersaturated; the latter are conditions expected for future deep and/or polar regions (reviewed in Fabry et al. 2008). In systems with natural CO_2 gradients, such as around volcanic vents, typical tidal communities with calcareous

organisms shifted to communities with higher seagrass production and less calcareous organisms (Hall-Spencer et al. 2008). How shifting carbonate chemistry affect trophic interactions in BPC remains a critical knowledge gap.

Impacts on biogeochemical cycling

A reduction in seawater pH can directly affect biochemical processes and was found to increase the nitrate uptake and ammonium release in sediments and to decrease nitrite release and phosphate uptake (Widdicombe and Needham 2007). An increase in CO_2 availability can increase the biological consumption of carbon relative to N and P (Riebesell et al. 2007), with an increased export potential depending on the state of the food web (Thingstad et al. 2008). Consequently, ocean acidification or ocean carbonation might stimulate the biological pump and the flux of organic carbon to the seafloor. Indeed, a small increase in the sinking of fresh material with increasing CO_2 was observed by de Kluijver et al. (2013). In a modeling study, the export of material with high carbon content could potentially increase bottom-water hypoxia (Oschlies et al. 2008). However, ocean acidification causes dissolution of $CaCO_3$ in the water (and sediment), so the strength of the carbonate pump could also be reduced (Riebesell et al. 2009).

Section 6: Conclusions

By reviewing and synthesizing the available literature, we found that the BPC processes can be classified into three main mechanisms: organism movement, trophic interactions, and biogeochemical cycling. Interactions with physical forcing, such as light levels, thermal stratification, and mixing regime, are essential for controlling how the benthic and pelagic habitats interact across various spatial and temporal scales.

Although studies focused on benthic-pelagic connections have increased over the last several decades, some topics remain largely unexplored. The linkages between pelagic and benthic habitats in food webs tend to be better studied in freshwater lakes than marine systems, whereas the role of benthic microalgae in food webs, such as diatoms, tends to be better researched in marine coastal systems (Vadeboncoeur pers. comm.). Whereas there have been a number of studies on impacts of stressors such as climate change and ocean acidification on benthic or pelagic environments, very little research has been conducted on how the coupling will be affected. For example, climate change in freshwater and marine ecosystems will cause fluctuations in water level, likely triggering large effects on BPC mechanisms of organism movement, trophic interactions, and biogeochemical cycles. It is also unknown how the interactive effects of multiple stressors will impact BPC mechanisms, but given that multiple stressors frequently affect organisms and biogeochemical cycles, it is likely that BPC will also be affected in multi-stressor scenarios.

Proper quantification and development of novel tools are needed to refine methodology in researching the BPC mechanisms (Raffaelli et al. 2003). For example, quantification of BPC strength and duration needs further research. Integration of BPC mechanisms in aquatic ecological research is important during both hypothesis development and project planning (Boero et al. 1996; Raffaelli et al. 2003). To address these research gaps and needs, we advocate for more collaboration among benthic and pelagic habitat specialists and fresh and marine ecologists because it can greatly improve holistic approaches in aquatic ecosystem ecology (Peterson et al. 2000; Raffaelli et al. 2003).

References

Ackleson, S. G. 2003. Light in shallow waters: A brief research review. Limnol. Oceanogr. 48:323-328 [doi:10.4319/lo.2003.48.1_part_2.0323].

Adams, D. G., and P. S. Duggan. 1999. Tansley review no. 107. Heterocyst and akinete differentiation in cyanobacteria. New Phytol. 144:3-33 [doi:10.1046/j.1469-8137.1999.00505.x].

Agawin, N. S. R., C. M. Duarte, and S. Agustí. 2000. Nutrient and temperature control of the contribution of picoplankton to phytoplankton biomass and production. Limnol. Oceanogr. 45:591–600 [doi:10.4319/lo.2000.45.3.0591].

Allan, J. D., R. Abell, Z. E. B. Hogan, C. Revenga, B. W. Taylor, R. L. Welcomme, and K. Winemiller. 2005. Overfishing of inland waters. BioScience 55:1041-1051 [doi:10.1641/0006-3568(2005)055[1041:OOIW]2.0.CO;2].

Aller, R. C. 2001. Transport and reactions in the bioirrigated zone, p. 269-301. *In* B. P. Boudreau and B. B. Jørgensen [eds.], The benthic boundary layer: transport processes and biogeochemistry. Oxford Univ. Press.

Alsterberg, C., J. S. Eklöf, L. Gamfeldt, J. N. Havenhand, and K. Sundbäck. 2013. Consumers mediate the effects of experimental ocean acidification and warming on primary producers. PNAS 110:8603-8608 [doi:10.1073/pnas.1303797110].

Anderson, C. N. K., and others. 2008. Why fishing magnifies fluctuations in fish abundance. Nature 452:835-839 [doi:10.1038/nature06851].

Andersson, A. J., F. T. Mackenzie, and J.-P. Gattuso. 2011. Effects of ocean acidification on benthic processes, organisms, and ecosystems, p. 122-153. *In* J. P. Gattuso and L. Hansson [eds.], Ocean acidification. Oxford Univ. Press.

Angel, J. R., and K. E. Kunkel. 2010. The response of Great Lakes water levels to future climate scenarios with an emphasis on Lake Michigan-Huron. J. Gt. Lakes Res. 36, Supplement 2:51-58 [doi:10.1016/j.jglr.2009.09.006].

Arai, M. N. 1996. A functional biology of Scyphozoa. Chapman and Hall [doi:10.1007/978-94-009-1497-1].

Arnott, D. L., and M. J. Vanni. 1996. Nitrogen and phosphorus recycling by the zebra mussel (*Dreissena polymorpha*) in the western basin of Lake Erie. Can. J. Fish. Aquat. Sci. 53:646-659 [doi:10.1139/cjfas-53-3-646].

Arrigo, K. R. 2005. Marine microorganisms and global nutrient cycles. Nature. 437:349-355 [doi:10.1038/nature04159].

Barbiero, R. P., and E. B. Welch. 1992. Contribution of benthic blue-green algal recruitment to lake populations and phosphorus translocation. Freshw. Biol. 27:249-260 [doi:10.1111/j.1365-2427.1992.tb00537.x].

———, and J. Kann. 1994. The importance of benthic recruitment to the population development of Aphanizomenon flos-aquae and internal loading in a shallow lake. J. Plankton Res. 16:1581-1588 [doi:10.1093/plankt/16.11.1581].

Baustian, M. M., J. K. Craig, and N. N. Rabalais. 2009. Effects of summer 2003 hypoxia on macrobenthos and Atlantic croaker foraging selectivity in the northern Gulf of Mexico. J. Exp. Mar. Biol. Ecol. 381:S31-S37 [doi:10.1016/j.jembe.2009.07.007].

———, and N. N. Rabalais. 2009. Seasonal composition of benthic macroinfauna exposed to hypoxia in the northern Gulf of Mexico. Estuaries and Coasts 32:975-983 [doi:10.1007/s12237-009-9187-3].

Bax, N., A. Williamson, M. Aguero, E. Gonzalez, and W. Geeves. 2003. Marine invasive alien species: a threat to global biodiversity. Mar. Policy 27:313-323 [doi:10.1016/S0308-597X(03)00041-1].

Boero, F., G. Belmonte, G. Fanelli, S. Piraino, and F. Rubino. 1996. The continuity of living matter and the discontinuities of its constituents: do plankton and benthos really exist? Trends Ecol. Evol. 11:177-180 [doi:10.1016/0169-5347(96)20007-2].

Bollens, S. M., B. W. Frost, D. S. Thoreson, and S. J. Watts. 1992. Diel vertical migration in zooplankton: field evidence in support of the predator avoidance hypothesis. Hydrobiologia 234:33-39 [doi:10.1007/BF00010777].

———, B. W. Frost, and J. R. Cordell. 1994. Chemical, mechanical and visual cues in the vertical migration behavior of the marine planktonic copepod *Acartia hudsonica*. J. Plankton Res. 16:555-564 [doi:10.1093/plankt/16.5.555].

Boros, G., M. Søndergaard, P. Takács, Á. Vári, and I. Tátrai. 2011. Influence of submerged macrophytes, temperature, and nutrient loading on the development of redox potential around the sediment–water interface in lakes. Hydrobiologia 665:117-127 [doi:10.1007/s10750-011-0609-4].

Boudouresque, C. F., A. Meinesz, M. A. Ribera, and E. Ballesteros. 1995. Spread of the green alga *Caulerpa taxifolia* (Caulerpales, Chlorophyta) in the Mediterranean: possible consequences of a major ecological event. Scientia Marina 59:21-29.

Brauns, M., X.-F. Garcia, N. Walz, and M. T. Pusch. 2007. Effects of human shoreline development on littoral macroinvertebrates in lowland lakes. J. Appl. Ecol. 44:1138-1144 [doi:10.1111/j.1365-2664.2007.01376.x].

———, B. Gücker, C. Wagner, X.-F. Garcia, N. Walz, and M. T. Pusch. 2011. Human lakeshore development alters the structure and trophic basis of littoral food webs. J. Appl. Ecol. 48:916-925 [doi:10.1111/j.1365-2664.2011.02007.x].

Broecker, W. C. 1991. The great ocean conveyor. Oceanography 4:79-89 [doi:10.5670/oceanog.1991.07].

Brookes, J. D., and C. C. Carey. 2011. Resilience to blooms. Science 334:46-47 [doi:10.1126/science.1207349].

Brunberg, A. -K. 1995. Microbial activity and phosphorus dynamics in eutrophic lake sediments enriched with Microcystis colonies. Freshw. Biol. 33:541-555 [doi:10.1111/j.1365-2427.1995.tb00412.x].

Burks, R. L., D. M. Lodge, E. Jeppesen, and T. L. Lauridsen. 2002. Diel horizontal migration of zooplankton: costs and benefits of inhabiting the littoral. Freshw. Biol. 47:343-365 [doi:10.1046/j.1365-2427.2002.00824.x].

Cai, W. J., X. Hu, W. J. Huang, M. C. Murrell, J. C. Lehrter, S. E. Lohrenz, and G. C. Gong. 2011. Acidification of subsurface coastal waters enhanced by eutrophication. Nat. Geosci. 4:766-770 [doi:10.1038/ngeo1297].

Cahoon, L. B. 1999. The role of benthic microalgae in neritic ecosystems. Oceanogr. Mar. Biol. Ann. Rev 37:47-86.

Caraco, N. F., J. J. Cole, and G. E. Likens. 1992. New and recycled primary production in an oligotrophic lake: Insights for summer phosphorus dynamics. Limnol. Oceanogr. 37:590-602 [doi:10.4319/lo.1992.37.3.0590].

Carey, C. C., K. C. Weathers, and K. L. Cottingham. 2008. *Gloeotrichia echinulata* blooms in an oligotrophic lake: helpful insights from eutrophic lakes. J. Plankton Res. 30:893-904 [doi:10.1093/plankt/fbn055].

———, and K. Rengefors. 2010. The cyanobacterium *Gloeotrichia echinulata* stimulates the growth of other phytoplankton. J. Plankton Res. 32:1349-1354 [doi:10.1093/plankt/fbq046].

———,———, H. A. Ewing, M. L. Greer, and K. L. Cottingham. 2014. Spatial and temporal variability in recruitment of the cyanobacterium *Gloeotrichia echinulata* in an oligotrophic lake. Freshw. Sci. 33:577-592 [doi:10.1086/675734].

Carpenter, S. R., J. J. Elser, and K. M. Olson. 1983. Effects of roots of *Myriophyllum verticillatum* L. on sediment redox conditions. Aquatic Bot. 17:243-249 [doi:10.1016/0304-3770(83)90060-8].

———, J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience 35:634-639 [doi:10.2307/1309989].

———, and J. F. Kitchell. 1996. The trophic cascade in lakes. Cambridge Univ. Press.

Cazzanelli, M., L. Forsström, M. Rautio, A. Michelsen, and K. S. Christoffersen. 2012. Benthic resources are the key to *Daphnia middendorffiana* survival in a high arctic pond. Freshw. Biol. 57:541-551 [doi:10.1111/j.1365-2427.2011.02722.x].

Chandra, S., M. J. V. Zanden, A. C. Heyvaert, B. C. Richards, B. C. Allen, and C. R. Goldman. 2005. The effects of cultural eutrophication on the coupling between pelagic primary producers and benthic consumers. Limnol. Oceanogr. 50:1368-1376 [doi:10.4319/lo.2005.50.5.1368].

Chatterjee, A., and others. 2013. Comparative dynamics of pelagic and benthic micro-algae in a coastal ecosystem. Est. Coast. Shelf Sci. 133:67-77 [doi:10.1016/j.ecss.2013.08.015].

Cloern, J. E. 1996. Phytoplankton bloom dynamics in coastal

ecosystems: A review with some general lessons from sustained investigation of San Francisco Bay, California. Proc. R. Soc. B. 34:127-168 [doi:10.1029/96RG00986].

———. 2001. Our evolving conceptual model of the coastal eutrophication problem. Mar. Ecol. Prog. Ser. 210:223-253 [doi:10.3354/meps210223].

Corbet, P. S. 1964. Temporal patterns of emergence in aquatic insects. Can. Entomol. 96:264-279 [doi:10.4039/Ent96264-1].

Conley, D. J., C. Humborg, L. Rahm, O. P. Savchuk, and F.Wulff. 2002. Hypoxia in the Baltic Sea and basin-scale changes in phosphorus biogeochemistry. Environ. Sci. Technol. 36:5315-5320 [doi:10.1021/es025763w].

Cott, P. A., P. K. Sibley, W. M. Somers, M. R. Lilly, and A. M. Gordon. 2008. A review of water level fluctuations on aquatic biota with an emphasis on fishes in ice-covered lakes. J. Am. Water Res. Assoc. 44:343-359 [doi:10.1111/j.1752-1688.2007.00166.x].

Craig, J. K., and L. B. Crowder. 2005. Hypoxia-induced habitat shifts and energetic consequences in Atlantic croaker and brown shrimp on the Gulf of Mexico shelf. Mar. Ecol. Prog. Ser. 294:79-94 [doi:10.3354/meps294079].

———, L. B. Crowder, and T. A. Henwood. 2005. Spatial distribution of brown shrimp (*Farfantepenaeus aztecus*) on the northwestern Gulf of Mexico shelf: effects of abundance and hypoxia. Can. J. Fish. Aquat. Sci. 62:1295-1308 [doi:10.1139/f05-036].

———, P. C. Gillikin, M. A. Magelnicki, and L. N. May. 2010. Habitat use of cownose rays (*Rhinoptera bonasus*) in a highly productive, hypoxic continental shelf ecosystem. Fish. Ocean. 19:301-317 [doi:10.1111/j.1365-2419.2010.00545.x].

D'andrea, A. F., and T. H. Dewitt. 2009. Geochemical ecosystem engineering by the mud shrimp *Upogebia pugettensis* (Crustacea: Thalassinidae) in Yaquina Bay, Oregon: Density-dependent effects on organic matter remineralization and nutrient cycling. Limnol. Oceanogr. 54:1911-1932 [doi:10.4319/lo.2009.54.6.1911].

Daigle, S. T., J. W. Fleeger, J. H. Cowan, and P.-Y. Pascal. 2013. What is the relative importance of phytoplankton and attached macroalgae and epiphytes to food webs on offshore oil platforms? Mar. Coast. Fish. 5:53-64 [doi:10.1080/19425120.2013.774301].

De Bernardi, R. D., and G. Giussani. 1990. Are blue-green algae a suitable food for zooplankton? An overview, p. 29-41. *In* R. D. Gulati, E. H. R. R. Lammens, M. L. Meyer, and E. van Donk [eds.], Biomanipulation tool for water management. Springer [doi:10.1007/BF02530326].

De La Rocha, C. L., and U. Passow. 2007. Factors influencing the sinking of POC and the efficiency of the biological carbon pump. Deep Sea Research Part II: Topical Studies in Oceanography, 54(5–7):639–658 [doi:10.1016/j.dsr2.2007.01.004].

de Kluijver, A., K. Soetaert, J. Czerny, K. G. Schulz, T. Boxhammer, U. Riebesell, and J. J. Middelburg. 2013. A

^{13}C labelling study on carbon fluxes in Arctic plankton communities under elevated CO_2 levels. Biogeosciences 10:1425-1440 [doi:10.5194/bg-10-1425-2013].

———, J. Ning, Z. Liu, E. Jeppesen, R.D. Gulati, J.J. Middelburg. 2015. Macrophytes and periphyton carbon subsidies to bacterioplankton and zooplankton in a shallow eutrophic lake in tropical China. Limnology and oceanography 00:1-20. [doi:10.1002/lno.10040].

De Robertis, A., J. S. Jaffe, and M. D. Ohman. 2000. Size-dependent visual predation risk and the timing of vertical migration in zooplankton. Limnol. Oceanogr. 45:1838-1844 [doi:10.4319/lo.2000.45.8.1838].

Deegan, L. A., and R. H. Garritt. 1997. Evidence for spatial variability in estuarine food webs. Mar. Ecol. Prog. Ser. 147:31-47 [doi:10.3354/meps147031].

Diaz, R. J., and R. Rosenberg. 1995. Marine benthic hypoxia: A review of its ecological effects and the behavioural responses of benthic macrofauna. Oceanogr. Mar. Biol. 33:245-303.

———, and ———. 2008. Spreading dead zones and consequences for marine ecosystems. Science 321:926-929 [doi:10.1126/science.1156401].

Doney, S. C., and others. 2012. Climate change impacts on marine ecosystems. Ann. Rev. Mar. Sci. 4:11-37 [doi:10.1146/annurev-marine-041911-111611].

Dover, C. L. V., J. F. Grassle, B. Fry, R. H. Garritt, and V. R. Starczak. 1992. Stable isotope evidence for entry of sewage-derived organic material into a deep-sea food web. Nature 360:153-156 [doi:10.1038/360153a0].

Duarte, C. M., and others. 2012. Is global ocean sprawl a cause of jellyfish blooms? Front. Ecol. Environ. 11:91-97 [doi:10.1890/110246].

Dudgeon, D., and others. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biol. Rev. 81:163-182 [doi:10.1017/S1464793105006950].

Duplisea, D. E., S. Jennings, S. J. Malcolm, R. Parker, and D. B. Sivyer. 2001. Modelling potential impacts of bottom trawl fisheries on soft sediment biogeochemistry in the North Sea. Geochem. Trans. 2:112-117 [doi:10.1186/1467-4866-2-112].

Eckman, J. E. 1996. Closing the larval loop: linking larval ecology to the population dynamics of marine benthic invertebrates. J. Exp. Mar. Biol. Ecol. 200:207-237 [doi:10.1016/S0022-0981(96)02644-5].

Edwards, M., and A. J. Richardson. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430:881-884 [doi:10.1038/nature02808].

Estes, J. A., and D. O. Duggins. 1995. Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. Ecol. Monogr. 65:75-100 [doi:10.2307/2937159].

Fabry, V. J., B. A. Seibel, R. A. Feely, and J. C. Orr. 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. ICES J. Mar. Sci. 65:414-432 [doi:10.1093/icesjms/fsn048].

Falkowski, P. G., and M. J. Oliver. 2007. Mix and match: how climate selects phytoplankton. Nat. Rev. Microbiol. 5:813-819 [doi:10.1038/nrmicro1751].

Fiksen, Ø., and J. Giske. 1995. Vertical distribution and population dynamics of copepods by dynamic optimization. ICES J. Mar. Sci. 52:483-503 [doi:10.1016/1054-3139(95)80062-X].

Findlay, S., L. Carlough, M. T. Crocker, H. K. Gill, J. L. Meyer, and P. J. Smith. 1986. Bacterial growth on macrophyte leachate and fate of bacterial production. Limnol. Oceanogr. 31:1335-1341 [doi:10.4319/lo.1986.31.6.1335].

Flöder, S., A. Combüchen, A. Pasternak, and H. Hillebrand. 2006. Competition between pelagic and benthic microalgae for phosphorus and light. Aquat. Sci. 68:425-433 [doi:10.1007/s00027-006-0824-7].

Forward Jr, R. B. 1988. Diel vertical migration: zooplankton photobiology and behaviour. Oceanogr. Mar. Biol. Ann. Rev 26:361-393.

Fryxell, G. A. 1983. Survival strategies of the algae. Cambridge Univ. Press.

Fulweiler, R. W., and S. W. Nixon. 2009. Responses of benthic–pelagic coupling to climate change in a temperate estuary. Hydrobiologia 629:147-156 [doi:10.1007/978-90-481-3385-7_13].

Galvan, K., J. W. Fleeger, and B. Fry. 2008. Stable isotope addition reveals dietary importance of phytoplankton and microphytobenthos to saltmarsh infauna. Mar. Ecol. Prog. Ser. 359:37-49 [doi:10.3354/meps07321].

Gattuso, J. P., B. Gentili, C. M. Duarte, J. A. Kleypas, J. J. Middelburg, and D. Antoine. 2006. Light availability in the coastal ocean: impact on the distribution of benthic photosynthetic organisms and their contribution to primary production. Biogeosciences 3:489-513 [doi:10.5194/bg-3-489-2006].

Gido, K. B. 2002. Interspecific comparisons and the potential importance of nutrient excretion by benthic fishes in a large reservoir. Trans. Am. Fish. Soc. 131:260-270 [doi:10.1577/1548-8659(2002)131<0260:ICATPI>2.0.CO;2].

Graf, G. 1992. Benthic-pelagic coupling: a benthic view. Oceanogr. Mar. Biol. Ann. Rev 30:149-190.

Graham, W. M., F. Pages, and W. M. Hamner. 2001. A physical context for gelatinous zooplankton aggregations: a review. Hydrobiologia 451:199-212 [doi:10.1023/A:1011876004427].

Grall, J., and L. Chauvaud. 2002. Marine eutrophication and benthos: the need for new approaches and concepts. Global Change Biol. 8:813-830 [doi:10.1046/j.1365-2486.2002.00519.x].

Grebmeier, J. M., and others. 2006. A major ecosystem shift in the northern Bering Sea. Science 311:1461-1464 [doi:10.1126/science.1121365].

———, S. E. Moore, J. E. Overland, K. E. Frey, and R. Gradinger. 2010. Biological response to recent Pacific Arctic sea ice retreats. EOS 91:161-162 [doi:10.1029/2010EO180001].

Green, M. A., G. G. Waldbusser, S. L. Reilly, and K. Emerson. 2009. Death by dissolution: sediment saturation state as a mortality factor for juvenile bivalves. Limnol. Oceanogr. 54:1037-1047 [doi:10.4319/lo.2009.54.4.1037].

Gyllstrom, M., T. Lakowitz, C. Bronmark, and L.-A. Hansson. 2008. Bioturbation as driver of zooplankton recruitment, biodiversity and community composition in aquatic ecosystems. Ecosystems 11:1120-1132 [doi:10.1007/s10021-008-9183-7].

Hall-Spencer, J. M., and others. 2008. Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. Nature 454:96-99 [doi:10.1038/nature07051].

Hallegraeff, G. M. 1993. A review of harmful algal blooms and their apparent global increase. Phycologia 32:79-99 [doi:10.2216/i0031-8884-32-2-79.1].

Hamilton, D. P., and S. F. Mitchell. 2013. An empirical model for sediment resuspension in shallow lakes. Hydrobiologia 317:209-220 [doi:10.1007/BF00036471].

Hansen, K., S. Mouridsen, and E. Kristensen. 1998. The impact of *Chironomus plumosus* larvae on organic matter decay and nutrient (N,P) exchange in a shallow eutrophic lake sediment following a phytoplankton sedimentation. Hydrobiologia 364:65-74 [doi:10.1023/A:1003155723143].

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 [doi:10.4319/lo.1996.41.6.1312].

Hargrave, B. T. 1973. Coupling carbon flow through some pelagic and benthic communities. J. Fish. Res. Board Can. 30:1317-1326 [doi:10.1139/f73-212].

Hays, G. C. 2003. A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations, p. 163-170. *In* Migrations and dispersal of marine organisms. Springer [doi:10.1007/978-94-017-2276-6_18].

Hebert, P. D. N., B. W. Muncaster, and G. L. Mackie. 1989. Ecological and genetic studies on *Dreissena polymorpha* (Pallas): a new mollusc in the Great Lakes. Can. J. Fish. and Aquat. Sci. 46:1587-1591 [doi:10.1139/f89-202].

Heip, C. 1995. Eutrophication and zoobenthos dynamics. Ophelia 41:113-136 [doi:10.1080/00785236.1995.10422040].

Heip, C. H. R., N. K. Goosen, P. M. J. Herman, J. Kromkamp, J. J. Middelburg, and K. Soetaert. 1995. Production and consumption of biological particles in temperate tidal estuaries. Oceanogr. Mar. Biol. Ann. Rev 33:1-149.

Heisler, J., and others. 2008. Eutrophication and harmful algal blooms: A scientific consensus. Harm. Algae 8:3-13 [doi:10.1016/j.hal.2008.08.006].

Hendriks, I. E., C. M. Duarte, and M. A. Alvarez. 2010. Vulnerability of marine biodiversity to ocean acidification: a meta-analysis. Estuar. Coast. Shelf Sci. 86:157-164 [doi:10.1016/j.ecss.2009.11.022].

Heuch, P. A., A. Parsons, and K. Boxaspen. 2013. Diel vertical migration: A possible host-finding mechanism in salmon

louse (*Lepeophtheirus salmonis*) copepodids? Can. J. Fish. Aquat. Sci. 52:681-689 [doi:10.1139/f95-069].

Higgins, S. N., and M. J. Vander Zanden. 2010. What a difference a species makes: a meta-analysis of dreissenid mussel impacts on freshwater ecosystems. Ecol. Monogr. 80:179-196 [doi:10.1890/09-1249.1].

Hobson, K. A., A. Fisk, N. Karnovsky, M. Holst, J.-M. Gagnon, and M. Fortier. 2002. A stable isotope (δ13C, δ15N) model for the North Water food web: implications for evaluating trophodynamics and the flow of energy and contaminants. Deep Sea Res. II 49:5131-5150 [doi:10.1016/S0967-0645(02)00182-0].

Horppila, J., and L. Nurminen. 2003. Effects of submerged macrophytes on sediment resuspension and internal phosphorus loading in Lake Hiidenvesi (southern Finland). Water Res. 37:4468-4474 [doi:10.1016/S0043-1354(03)00405-6].

Hupfer, M., and J. Lewandowski. 2008. Oxygen controls the phosphorus release from lake sediments–a long-lasting paradigm in limnology. Int. Rev. Hydrobiol. 93:415-432 [doi:10.1002/iroh.200711054].

Imberger, J., and J. C. Patterson. 1990. Physical limnology, p. 303-380. *In* J. W. Hutchinson and T. Y. Wu [eds.], Advances in applied mechanics. Academic Press.

Incze, L. S., P. Aas, and T. Ainaire. 1995. Turbulence-modified profiles of feeding conditions for larval cod (*Gadus morhua*) on Georges Bank during spring. CM-International Council for the Exploration of the Sea.

Inderjit, D. C., M. Ranelletti, and S. Kaushik. 2006. Invasive marine algae: An ecological perspective. Bot. Rev. 72:153-178 [doi:10.1663/0006-8101(2006)72[153:IMAAEP]2.0.CO;2].

Istvánovics, V., K. Pettersson, M. A. Rodrigo, D. Pierson, J. Padisak, and W. Colom. 1993. *Gloeotrichia echinulata*, a colonial cyanobacterium with a unique phosphorus uptake and life strategy. J. Plankton Res. 15:531-552 [doi:10.1093/plankt/15.5.531].

———, L. Somlyódy, and A. Clement. 2002. Cyanobacteria-mediated internal eutrophication in shallow Lake Balaton after load reduction. Water Res. 36:3314-3322 [doi:10.1016/S0043-1354(02)00036-2].

Jacobsen, B. A. 1994. Bloom formation of *Gloeotrichia echinulata* and *Aphanizomenon flos-aquae* in a shallow, eutrophic, Danish lake. Hydrobiologia 289:193-197 [doi:10.1007/BF00007420].

Jankowski, T., D. M. Livingstone, H. Bührer, R. Forster, and P. Niederhauser. 2006. Consequences of the 2003 European heat wave for lake temperature profiles, thermal stability, and hypolimnetic oxygen depletion: Implications for a warmer world. Limnol. Oceanogr. 51:815-819 [doi:10.4319/lo.2006.51.2.0815].

Jay, C. V., A. S. Fischbach, and A. A. Kochnev. 2012. Walrus areas of use in the Chukchi Sea during sparse sea ice cover. Mar. Ecol. Prog. Ser. 468:1-13 [doi:10.3354/meps10057].

Jennings, E., and others. 2010. Impacts of climate on the flux of dissolved organic carbon from catchments, p. 199-220. *In* G. George [ed.], The impact of climate change on European lakes. Springer Netherlands [doi:10.1007/978-90-481-2945-4_12].

Jennings, M. J., M. A. Bozek, G. R. Hatzenbeler, E. E. Emmons, and M. D. Staggs. 1999. Cumulative effects of incremental shoreline habitat modification on fish assemblages in north temperate lakes. N. Am. J. Fish. Manage. 19:18-27 [doi:10.1577/1548-8675(1999)019<0018:CEOISH>2.0.CO;2].

———, E. E. Emmons, G. R. Hatzenbeler, C. Edwards, and M. A. Bozek. 2003. Is littoral habitat affected by residential development and land use in watersheds of wisconsin lakes? Lake Reserv. Manage. 19:272-279 [doi:10.1080/07438140309354092].

Jennings, S., T. A. Dinmore, D. E. Duplisea, K. J. Warr, and J. E. Lancaster. 2001. Trawling disturbance can modify benthic production processes. J. Anim. Ecol. 70:459-475 [doi:10.1046/j.1365-2656.2001.00504.x].

Kaplan-Levy, R. N., O. Hadas, M. L. Summers, J. Rucker, and A. Sukenik. 2010. Akinetes: dormant cells of cyanobacteria. *In* E. Lubzens, J. Cerda, and M. S. Clark [eds.], Dormancy and resistance in harsh environments. Topics in Current Genetics [doi:10.1007/978-3-642-12422-8_2].

Karatayev, A., L. Burklakova, and D. Padilla. 1997. The effects of *Dreissena polymorpha* (Pallas) invasion on aquatic communities in eastern Europe. J. Shellfish Res. 16:187-203.

Karlsson, J., and C. Säwström. 2009. Benthic algae support zooplankton growth during winter in a clear-water lake. Oikos 118:539-544 [doi:10.1111/j.1600-0706.2008.17239.x].

———, P. Byström, J. Ask, P. Ask, L. Persson, and M. Jansson. 2009. Light limitation of nutrient-poor lake ecosystems. Nature 460:506-509 [doi:10.1038/nature08179].

Kasulo, V. 2000. The impact of invasive species in African lakes, p. 183-207. *In* C. Perrings, M. Williamson, and S. Dalmazzone [eds.], The economics of biological invasions. Edward Elgar Publishing.

Kemp, W. M., and others. 2005. Eutrophication of Chesapeake Bay: historical trends and ecological interactions. Mar. Ecol. Prog. Ser. 303:1-29 [doi:10.3354/meps303001].

Kimmel, D. G., W. C. Boicourt, J. J. Pierson, M. R. Roman, and X. Zhang. 2009. A comparison of the mesozooplankton response to hypoxia in Chesapeake Bay and the northern Gulf of Mexico using the biomass size spectrum. J. Exp. Mar. Biol. Ecol. 381:S65-S73 [doi:10.1016/j.jembe.2009.07.012].

Kirby, R. R., G. Beaugrand, J. A. Lindley, A. J. Richardson, M. Edwards, and P. C. Reid. 2007. Climate effects and benthic-pelagic coupling in the North Sea. Mar. Ecol. Prog. Ser. 330:31-38 [doi:10.3354/meps330031].

Kroeker, K. J., R. L. Kordas, R. N. Crim, and G. G. Singh. 2010. Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. Ecol. Lett. 13:1419-1434 [doi:10.1111/j.1461-0248.2010.01518.x].

———, and others. 2013. Impacts of ocean acidification on marine organisms: quantifying sensitivities and

interaction with warming. Glob. Change Biol. 19:1884-1896 [doi:10.1111/gcb.12179].

Krone, R., L. Gutow, T. Brey, J. Dannheim, and A. Schröder. 2013. Mobile demersal megafauna at artificial structures in the German Bight—Likely effects of offshore wind farm development. Est. Coast. Shelf Sci. 125:1-9 [doi:10.1016/j.ecss.2013.03.012].

Lake, P. S., and others. 2000. Global change and the biodiversity of freshwater ecosystems: impacts on linkages between above-sediment and sediment biota. BioScience 50:1099-1107 [doi:10.1641/0006-3568(2000)050[1099:GCATBO]2.0.CO;2].

Lampert, W. 1995. Egg bank investment. Nature 377:479-479 [doi:10.1038/377479a0].

Lassalle, G., and others. 2011. Lower trophic levels and detrital biomass control the Bay of Biscay continental shelf food web: Implications for ecosystem management. Progr. Oceanogr. 91:561-575 [doi:10.1016/j.pocean.2011.09.002].

Lavery, T. J., and others. 2010. Iron defecation by sperm whales stimulates carbon export in the Southern Ocean. Proc. R. Soc. B 277:3527-3531 [doi:10.1098/rspb.2010.0863].

Laws, E. A., P. G. Falkowski, W. O. Smith, H. Ducklow, and J. J. Mccarthy. 2000. Temperature effects on export production in the open ocean. Glob. Biogeochem. Cycle 14:1231-1246 [doi:10.1029/1999GB001229].

Lebrato, M., and D. O. B. Jones. 2009. Mass deposition event of *Pyrosoma atlanticum* carcasses off Ivory Coast (West Africa). Limnol. Oceanogr. 54:1197-1209 [doi:10.4319/lo.2009.54.4.1197].

Lewis, J., A. S. D. Harris, K. J. Jones, and R. L. Edmonds. 1999. Long-term survival of marine planktonic diatoms and dinoflagellates in stored sediment samples. J. Plankton Res. 21:343-354 [doi:10.1093/plankt/21.2.343].

Livingstone, D., and G. H. M. Jaworski. 1980. The viability of akinetes of blue-green algae recovered from the sediments of Rostherne Mere. Br. Phycol. J. 15:357-364 [doi:10.1080/00071618000650361].

Llabrés, M., S. Agustí, M. Fernández, A. Canepa, F. Maurin, F. Vidal, and C. M. Duarte. 2013. Impact of elevated UVB radiation on marine biota: a meta-analysis. Global Ecol. Biogeogr. 22:131-144 [doi:10.1111/j.1466-8238.2012.00784.x].

Lohrer, A. M., S. F. Thrush, and M. M. Gibbs. 2004. Bioturbators enhance ecosystem function through complex biogeochemical interactions. Nature 431:1092-1095 [doi:10.1038/nature03042].

Lonsdale, D. J., and others. 2009. Influence of suspension-feeding bivalves on the pelagic food webs of shallow, coastal embayments. Aquat. Biol. 6:263-279 [doi:10.3354/ab00130].

MacIsaac, H. J., G. Sprules, O. E. Johannson, and J. H. Leach. 1992. Filtering impacts of larval and sessile zebra mussels (*Dreissena polymorpha*) in western Lake Erie. Oecologia 92:30-39 [doi:10.1007/BF00317259].

Madin, E. M. P., S. D. Gaines, and R. R. Warner. 2010.

Field evidence for pervasive indirect effects of fishing on prey foraging behavior. Ecology 91:3563-3571 [doi:10.1890/09-2174.1].

Magnuson, J. J. 2000. Historical trends in lake and river ice cover in the northern hemisphere. Science 289:1743-1746 [doi:10.1126/science.289.5485.1743].

Marcus, N., and J. Schmidt-Gengenbach. 1986. Recruitment of individuals into the plankton—the importance of bioturbation. Limnol. Oceanogr. 31:206-210 [doi:10.4319/lo.1986.31.1.0206].

Marcus, N. H., and F. Boero. 1998. Minireview: the importance of benthic-pelagic coupling and the forgotten role of life cycles in coastal aquatic systems. Limnol. Oceanogr. 43:763-768 [doi:10.4319/lo.1998.43.5.0763].

Martinetto, P., M. Teichberg, and I. Valiela. 2006. Coupling of estuarine benthic and pelagic food webs to land-derived nitrogen sources in Waquoit Bay, Massachusetts, USA. Mar. Ecol. Prog. Ser. 307:37-48 [doi:10.3354/meps307037].

Matsuzaki, S.-I. S., N. Usio, N. Takamura, and I. Washitani. 2007. Effects of common carp on nutrient dynamics and littoral community composition: roles of excretion and bioturbation. Fund. Appl. Limnol. 168:27-38 [doi:10.1127/1863-9135/2007/0168-0027].

McClelland, J. W., and I. Valiela. 1998. Changes in food web structure under the influence of increased anthropogenic nitrogen inputs to estuaries. Mar. Ecol. Prog. Ser. 168:259-271 [doi:10.3354/meps168259].

McLaren, I. A. 1963. Effects of temperature on growth of zooplankton, and the adaptive value of vertical migration. J. Fish. Board Canada 20:685-727 [doi:10.1139/f63-046].

McQuoid, M., A. Godhe, and K. Nordberg. 2002. Viability of phytoplankton resting stages in the sediments of a coastal Swedish fjord. Eur. J. Phycol. 37:191-201 [doi:10.1017/S0967026202003670].

Menge, B. A., B. A. Daley, P. A. Wheeler, E. Dahlhoff, E. Sanford, and P. T. Strub. 1997. Benthic-pelagic links and rocky intertidal communities: Bottom-up effects on top-down control? Proc. Nat. Acad. Sci. 94:14530-14535 [doi:10.1073/pnas.94.26.14530].

———, and others. 2003. Coastal oceanography sets the pace of rocky intertidal community dynamics. Proc. Nat. Acad. Sci. 100:12229-12234 [doi:10.1073/pnas.1534875100].

Middelburg, J. J., and L. A. Levin. 2009. Coastal hypoxia and sediment biogeochemistry. Biogeosciences 6:3655-3706 [doi:10.5194/bgd-6-3655-2009].

Mills, E. L., and others. 2003. Lake Ontario: food web dynamics in a changing ecosystem (1970-2000). Can. J. Fish. Aquat. Sci. 60:471-490 [doi:10.1139/f03-033].

Miranda, L. E., J. A. Hargreaves, and S. W. Raborn. 2001. Predicting and managing risk of unsuitable dissolved oxygen in a eutrophic lake. Hydrobiologia 457:177-185 [doi:10.1023/A:1012283603339].

Mittelbach, G. G. 1981. Patterns of invertebrate size and abundance in aquatic habitats. Can. J. Fish. Aquat. Sci.

38:896-904 [doi:10.1139/f81-121].

Møller, L. F., and H. U. Riisgård. 2007. Impact of jellyfish and mussels on algal blooms caused by seasonal oxygen depletion and nutrient release from the sediment in a Danish fjord. J. Exp. Mar. Biol. Ecol. 351:92-105 [doi:10.1016/j.jembe.2007.06.026].

Molloy, D. P., A. Y. Karatayev, L. E. Burlakova, D. P. Kurandina, and F. Laruelle. 1997. Natural enemies of zebra mussels: Predators, parasites, and ecological competitors. Rev. Fish. Sci. 5:27-97 [doi:10.1080/10641269709388593].

Molnar, J. L., R. L. Gamboa, C. Revenga, and M. D. Spalding. 2008. Assessing the global threat of invasive species to marine biodiversity. Front. Ecol. Environ. 6:485-492 [doi:10.1890/070064].

Monteith, D. T., and others. 2007. Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. Nature 450:537-540 [doi:10.1038/nature06316].

Moore, S. E., J. M. Grebmeier, and J. R. Davies. 2013. Gray whale distribution relative to forage habitat in the northern Bering Sea: current conditions and retrospective summary. Can. J. Zool. 81:734-742 [doi:10.1139/z03-043].

Moran, X. A. G., A. Lopez-Urrutia, A. Calvo-Diaz, and W. K. W. Li. 2010. Increasing importance of small phytoplankton in a warmer ocean. Glob. Change Biol. 16:1137-1144 [doi:10.1111/j.1365-2486.2009.01960.x].

Morris, T. J., S. P. Mohapatra, and A. Mitchell. 2008. Conflicts, costs and environmental degradation—impacts of antiquated ground water allocation policies in the Great Lakes Basin. Water Policy 10:459-479 [doi:10.2166/wp.2008.059].

Myers, R. A., J. K. Baum, T. D. Shepherd, S. P. Powers, and C. H. Peterson. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. Science 315:1846-1850 [doi:10.1126/science.1138657].

Niggl, W., M. S. Naumann, U. Struck, R. Manasrah, and C. Wild. 2010. Organic matter release by the benthic upside-down jellyfish *Cassiopea* sp. fuels pelagic food webs in coral reefs. J. Exp. Mar. Biol. Ecol. 384:99-106 [doi:10.1016/j.jembe.2010.01.011].

Nixon, S. W., R. W. Fulweiler, B. A. Buckley, S. L. Granger, B. L. Nowicki, and K. M. Henry. 2009. The impact of changing climate on phenology, productivity, and benthic–pelagic coupling in Narragansett Bay. Est. Coast. Shelf Sci. 82:1-18 [doi:10.1016/j.ecss.2008.12.016].

Odum, H. T. 1956. Primary production in flowing waters. Limnol. Oceanogr. 1:102-117 [doi:10.4319/lo.1956.1.2.0102].

Oschlies, A., K. G. Schulz, U. Riebesell, and A. Schmittner. 2008. Simulated 21st century's increase in oceanic suboxia by CO_2-enhanced biotic carbon export. Global Biogeochemical Cycles 22 [doi:10.1029/2007GB003147].

Paerl, H. W., and J. Huisman. 2008. Blooms like it hot. Science 320:57-58 [doi:10.1126/science.1155398].

Pasquaud, S., M. Pillet, V. David, B. Sautour, and P. Elie. 2010. Determination of fish trophic levels in an estuarine system. Est. Coast. Shelf Sci. 86:237-246 [doi:10.1016/j.ecss.2009.11.019].

Pearson, T. H., and R. Rosenberg. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr. Mar. Biol. Ann. Rev 16:229-311.

Perissinotto, R., C. Nozais, I. Kibirige, and A. Anandraj. 2003. Planktonic food webs and benthic-pelagic coupling in three South African temporarily-open estuaries. Acta Oecologica 24(1):S307-S316 [doi:10.1016/S1146-609X(03)00028-6].

Peterson, C. H., and others. 2000. Synthesis of linkages between benthic and fish communities as a key to protecting essential fish habitat. Bull. Mar. Science 66:759-774.

Pettersson, K., E. Herlitz, and V. Istvánovics. 1993. The role of *Gloeotrichia echinulata* in the transfer of phosphorus from sediments to water in Lake Erken. Hydrobiologia 253:123-129 [doi:10.1007/BF00050732].

Pihl, L. 1994. Changes in the diet of demersal fish due to eutrophication-induced hypoxia in the Kattegat, Sweden. Can. J. Fish. Aquat. Sci. 51:321-336 [doi:10.1139/f94-033].

———, S. P. Baden, R. J. Diaz, and L. C. Schaffner. 1992. Hypoxia-induced structural changes in the diet of bottom-feeding fish and Crustacea. Mar. Biol. 112:349-361 [doi:10.1007/BF00356279].

Pinnegar, J. K., N. V. C. Polunin, J. J. Videler, and J. J. De Wijes. 2007. Daily carbon, nitrogen and phosphorus budgets for the Mediterranean planktivorous damselfish *Chromis chromis*. J. Exp. Mar. Biol. Ecol. 352:378-391 [doi:10.1016/j.jembe.2007.08.016].

Pitt, K. A., A.-L. Clement, R. M. Connolly, and D. Thibault-Botha. 2008. Predation by jellyfish on large and emergent zooplankton: implications for benthic–pelagic coupling. Est. Coast. Shelf Sci. 76:827-833 [doi:10.1016/j.ecss.2007.08.011].

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Ann. Rev. Ecol. Syst. 28:289-316 [doi:10.1146/annurev.ecolsys.28.1.289].

Powers, S. P., D. E. Harper, and N. N. Rabalais. 2001. Effect of hypoxia/anoxia on the supply and settlement of benthic invertebrate larvae, p. 185-210. *In* N. N. Rabalais and R. E. Turner [eds.], Coastal and estuarine studies. American Geophysical Union.

———, C. H. Peterson, R. R. Christian, E. Sullivan, M. J. Powers, M. J. Bishop, and C. P. Buzzelli. 2005. Effects of eutrophication on bottom habitat and prey resources of demersal fishes. Mar. Ecol. Prog. Ser. 302:233-243 [doi:10.3354/meps302233].

Purcell, J. E., S.-I. Uye, and W.-T. Lo. 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. Mar. Ecol. Prog. Ser. 350:153 [doi:10.3354/meps07093].

Rabalais, N. N., L. E. Smith, D. E. Harper, and D. Justic. 2001. Effects of seasonal hypoxia on continental shelf benthos, p.

211-240. *In* N. N. Rabalais and R. E. Turner [eds.], Coastal and estuarine studies. American Geophysical Union.

Raffaelli, D., and others. 2003. The ups and downs of benthic ecology: considerations of scale, heterogeneity and surveillance for benthic–pelagic coupling. J. Exp. Mar. Biol. Ecol. 285-286:191-203 [doi:10.1016/S0022-0981(02)00527-0].

Rahel, F. J., and J. W. Nutzman. 1994. Foraging in a lethal environment: fish predation in hypoxic waters of a stratified lake. Ecology 75:1246-1253 [doi:10.2307/1937450].

Rautio, M., and W. F. Vincent. 2006. Benthic and pelagic food resources for zooplankton in shallow high-latitude lakes and ponds. Freshw. Biol. 51:1038-1052 [doi:10.1111/j.1365-2427.2006.01550.x].

Read, J. S., and K. C. Rose. 2013. Physical responses of small temperate lakes to variation in dissolved organic carbon concentrations. Limnol. Oceanogr. 58:921-931.

Riebesell, U., and others. 2007. Enhanced biological carbon consumption in a high CO_2 ocean. Nature 450:545-548 [doi:10.1038/nature06267].

———, A. Körtzinger, and A. Oschlies. 2009. Sensitivities of marine carbon fluxes to ocean change. Proc. Nat. Acad. Sci. 106:20602-20609 [doi:10.1073/pnas.0813291106].

———, and P. D. Tortell. 2011. Effects of ocean acidification on pelagic organisms and ecosystems, p. 99-121. *In* J. Gattuso and L. Hanson [eds.], Ocean acidification. Oxford Univ. Press.

Riera, P., L. J. Stal, and J. Nieuwenhuize. 2002. $\delta^{13}C$ versus $\delta^{15}N$ of co-occurring molluscs within a community dominated by *Crassostrea gigas* and *Crepidula fornicata* (Oosterschelde, The Netherlands). Mar. Ecol. Prog. Ser. 240:291-295 [doi:10.3354/meps240291].

Rivkin, R. B., and L. Legendre. 2001. Biogenic carbon cycling in the upper ocean: Effects of microbial respiration. Science 291:2398-2400 [doi:10.1126/science.291.5512.2398].

Roberts, J. J., T. O. Höök, S. A. Ludsin, S. A. Pothoven, H. A. Vanderploeg, and S. B. Brandt. 2009. Effects of hypolimnetic hypoxia on foraging and distributions of Lake Erie yellow perch. J. Exp. Mar. Biol. Ecol. 381:S132-S142 [doi:10.1016/j.jembe.2009.07.017].

Robertson, D. M., and J. Imberger. 1994. Lake number, a quantitative indicator of mixing used to estimate changes in dissolved oxygen. Int. Rev. Hydrobiol. Hydrograph. 79:159-176 [doi:10.1002/iroh.19940790202].

Roohi, A., Z. Yasin, A. E. Kideys, A. T. S. Hwai, A. G. Khanari, and E. Eker-Develi. 2008. Impact of a new invasive ctenophore (*Mnemiopsis leidyi*) on the zooplankton community of the Southern Caspian sea. Mar. Ecol. 29:421-434 [doi:10.1111/j.1439-0485.2008.00254.x].

Rose, K. C., C. E. Williamson, S. G. Schladow, M. Winder, and J. T. Oris. 2009. Patterns of spatial and temporal variability of UV transparency in Lake Tahoe, California-Nevada. J. Geohys. Res. B 114 [doi:10.1029/2008JG000816].

———, and others. 2012. The role of ultraviolet radiation and fish in regulating the vertical distribution of Daphnia. Limnol. Oceanogr. 57:1867-1876 [doi:10.4319/lo.2012.57.6.1867].

Rotschild, B., J. Ault, P. Goulletquer, and M. Heral. 1994. Decline of the Chesapeake Bay oyster population: a century of habitat destruction and overfishing. Mar. Ecol. Prog. Ser. 111:29-39 [doi:10.3354/meps111029].

Ruesink, J. L., H. S. Lenihan, A. C. Trimble, K. W. Heiman, F. Micheli, J. E. Byers, and M. C. Kay. 2005. Introduction of non-native oysters: ecosystem effects and restoration implications. Ann. Rev. Ecol. Evol. Syst. 36:643-689 [doi:10.1146/annurev.ecolsys.36.102003.152638].

Sadro, S., J. M. Melack, and S. Macintyre. 2011. Depth-integrated estimates of ecosystem metabolism in a high-elevation lake (Emerald Lake, Sierra Nevada, California). Limnol. Oceanogr. 56:1764-1780 [doi:10.4319/lo.2011.56.5.1764].

Sass, G. G., J. F. Kitchell, S. R. Carpenter, T. R. Hrabik, A. E. Marburg, and M. G. Turner. 2006. Fish community and food web responses to a whole-lake removal of coarse woody habitat. Fisheries 31:321-330 [doi:10.1577/1548-8446(2006)31[321:FCAFWR]2.0.CO;2].

Scheffer, M., S. H. Hosper, M. L. Meijer, B. Moss, and E. Jeppesen. 1993. Alternative equilibria in shallow lakes. Trends Ecol. Evol. 8:275-279 [doi:10.1016/0169-5347(93)90254-M].

Schindler, D. E., and M. D. Scheuerell. 2002. Habitat coupling in lake ecosystems. Oikos 98:177-189 [doi:10.1034/j.1600-0706.2002.980201.x].

Schmude, K. L., M. J. Jennings, K. J. Otis, and R. R. Piette. 1998. Effects of habitat complexity on macroinvertebrate colonization of artificial substrates in north temperate lakes. J. N. Am. Benthol. Soc. 17 [doi:10.2307/1468052].

Seitz, R. D., D. M. Dauer, R. J. Llansó, and W. C. Long. 2009. Broad-scale effects of hypoxia on benthic community structure in Chesapeake Bay, USA. J. Exp. Mar. Biol. Ecol. 381:S4-S12 [doi:10.1016/j.jembe.2009.07.004].

Shiganova, T. A., H. J. Dumont, A. F. Sokolsky, A. M. Kamakin, D. Tinenkova, and E. K. Kurasheva. 2004. Population dynamics of *Mnemiopsis leidyi* in the Caspian Sea, and effects on the Caspian ecosystem, p. 71-111. *In* H. J. Dumont, T. A. Shiganova, and U. Niermann [eds.], Aquatic invasions in the Black, Caspian, and Mediterranean Seas. Springer Netherlands [doi:10.1007/1-4020-2152-6_3].

Signa, G., J. E. Cartes, M. Solé, A. Serrano, and F. Sánchez. 2008. Trophic ecology of the swimming crab Polybius henslowii Leach, 1820 in Galician and Cantabrian Seas: Influences of natural variability and the Prestige oil spill. Cont. Shelf Res. 28:2659-2667 [doi:10.1016/j.csr.2008.08.008].

Smetacek, V. S. 1985. Role of sinking in diatom life-history cycles: ecological, evolutionary and geological significance. Mar. Biol. 84:239-251 [doi:10.1007/BF00392493].

Smith, C. R., and A. R. Baco. 2003. Ecology of whale falls at the deep-sea floor. Oceanogr. Mar. Biol. 41:311-354.

Soetaert, K., and J. J. Middelburg. 2009. Modeling eutrophication and oligotrophication of shallow-water marine systems: the importance of sediments under stratified

and well-mixed conditions. Hydrobiologia 629:239-254 [doi:10.1007/978-90-481-3385-7_20].

Solomon, C. T., and others. 2011. Terrestrial, benthic, and pelagic resource use in lakes: results from a three-isotope Bayesian mixing model. Ecology 92:1115-1125 [doi:10.1890/10-1185.1].

Søndergaard, M., J. P. Jensen, and E. Jeppesen. 2003. Role of sediment and internal loading of phosphorus in shallow lakes. Hydrobiologia 506-509:135-145 [doi:10.1023/B:HYDR.0000008611.12704.dd].

Sousa, R., J. Gutiérrez, and D. Aldridge. 2009. Non-indigenous invasive bivalves as ecosystem engineers. Biol. Invas. 11:2367-2385 [doi:10.1007/s10530-009-9422-7].

Speas, D. W., and W. G. Duffy. 1998. Uptake of Dissolved Organic Carbon (DOC) by *Daphnia pulex*. J. Freshw. Ecol. 13:457-463 [doi:10.1080/02705060.1998.9663642].

Staehr, P. A., and others. 2010. Lake metabolism and the diel oxygen technique: State of the science. Limnol. Oceanogr. Methods 8:628-644 [doi:10.4319/lom.2010.8.0628].

———, L. Baastrup-Spohr, K. Sand-Jensen, and C. Stedmon. 2012. Lake metabolism scales with lake morphometry and catchment conditions. Aquat. Sci. 74:155-169 [doi:10.1007/s00027-011-0207-6].

Stahl-Delbanco, A., and L. A. Hansson. 2002. Effects of bioturbation on recruitment of algal cells from the "seed bank" of lake sediments. Limnol. Oceanogr. 47:1836-1843 [doi:10.4319/lo.2002.47.6.1836].

Steinberg, D. K., C. A. Carlson, N. R. Bates, S. A. Goldthwait, L. P. Madin, and A. F. Michaels. 2000. Zooplankton vertical migration and the active transport of dissolved organic and inorganic carbon in the Sargasso Sea. Deep Sea Res. I 47:137-158 [doi:10.1016/S0967-0637(99)00052-7].

———, S. A. Goldthwait, and D. A. Hansel. 2002. Zooplankton vertical migration and the active transport of dissolved organic and inorganic nitrogen in the Sargasso Sea. Deep-Sea Res. 49:1445-1461 [doi:10.1016/S0967-0637(02)00037-7].

Strayer, D. L., and S. E. G. Findlay. 2010. Ecology of freshwater shore zones. Aquat. Sci. 72:127-163 [doi:10.1007/s00027-010-0128-9].

Suess, E. 1980. Particulate organic carbon flux in the oceans—surface productivity and oxygen utilization. Nature 288:260-263 [doi:10.1038/288260a0].

Switzer, T. S., E. J. Chesney, and D. M. Baltz. 2009. Habitat selection by flatfishes in the northern Gulf of Mexico: Implications for susceptibility to hypoxia. J. Exp. Mar. Biol. Ecol. 381:S51-S64 [doi:10.1016/j.jembe.2009.07.011].

Thingstad, T. F., and others. 2008. Counterintuitive carbon-to-nutrient coupling in an Arctic pelagic ecosystem. Nature 455:387-390 [doi:10.1038/nature07235].

Thamdrup, B., and Dalsgaard, T. 2002. Production of N_2 through anaerobic ammonium oxidation coupled to nitrate reduction in marine sediments. Appl. Environ. Microb. 68:1312-1318 [doi:10.1128/AEM.68.3.1312-1318.2002].

Trainer, V. L., S. S. Bates, N. Lundholm, A. E. Thessen, W. P. Cochlan, N. G. Adams, and C. G. Trick. 2012. Pseudo-nitzschia physiological ecology, phylogeny, toxicity, monitoring and impacts on ecosystem health. Harm. Algae 14:271-300 [doi:10.1016/j.hal.2011.10.025].

Trimbee, A. M., and G. P. Harris. 1984. Phytoplankton population-dynamics of a small reservoir—use of sedimentation traps to quantify the loss of diatoms and recruitment of summer bloom-forming blue-green-algae. J. Plankton Res. 6:897-918 [doi:10.1093/plankt/6.5.897].

Turner, R. E. 2001. Some effects of eutrophication on pelagic and demersal marine food webs, p. 371-398. *In* N. N. Rabalais and R. E. Turner [eds.], Coastal and estuarine studies. American Geophysical Union.

Underwood, G. J. C., and J. Kromkamp. 1999. Primary production by phytoplankton and microphytobenthos in estuaries, p. 93-153. *In* D. B. Nedwell and D. G. Raffaelli [eds.], Advances in ecological research. Academic Press [doi:10.1016/S0065-2504(08)60192-0].

Uusi-Heikkilä, S., C. Wolter, T. Klefoth, and R. Arlinghaus. 2008. A behavioral perspective on fishing-induced evolution. Trends Ecol. Evol. 23:419-421 [doi:10.1016/j.tree.2008.04.006].

Vadeboncoeur, Y., M. J. Vander Zanden, and D. M. Lodge. 2002. Putting the lake back together: reintegrating benthic pathways into lake food web models. BioScience 52:44-54 [doi:10.1641/0006-3568(2002)052[0044:PTLBTR]2.0.CO;2].

———, E. Jeppesen, M. J. V. Zanden, H.-H. Schierup, K. Christoffersen, and D. M. Lodge. 2003. From Greenland to Green Lakes: cultural eutrophication and the loss of benthic pathways in lakes. Limnol. Oceanogr. 48:1408-1418 [doi:10.4319/lo.2003.48.4.1408].

Valiela, I., and others. 1992. Couplings of watersheds and coastal waters: Sources and consequences of nutrient enrichment in Waquoit Bay, Massachusetts. Estuaries 15:443-457 [doi:10.2307/1352389].

———, J. McClelland, J. Hauxwell, P. J. Behr, D. Hersh, and K. Foreman. 1997. Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. Limnol. Oceanogr. 42:1105-1118 [doi:10.4319/lo.1997.42.5_part_2.1105].

Van De Meutter, F., R. Stoks, and L. De Meester. 2004. Behavioral linkage of pelagic prey and littoral predators: microhabitat selection by Daphnia induced by damselfly larvae. Oikos 107:265-272 [doi:10.1111/j.0030-1299.2004.13221.x].

———, ———, and ———. 2005. Spatial avoidance of littoral and pelagic invertebrate predators by Daphnia. Oecologia 142:489-499 [doi:10.1007/s00442-004-1738-5].

Vander Zanden, M. J., and Y. Vadeboncoeur. 2002. Fishes as integrators of benthic and pelagic food webs in lakes. Ecology 83:2152-2161 [doi:10.1890/0012-9658(2002)083[2152:FAIOBA]2.0.CO;2].

———, ———, and S. Chandra. 2011. Fish reliance on littoral–benthic resources and the distribution of primary production in lakes. Ecosystems 14:894-903 [doi:10.1007/

s10021-011-9454-6].

Vanni, M. J. 2002. Nutrient cycling by animals in freshwater ecosystems. Ann. Rev. Ecol. Syst. 33:341-370 [doi:10.1146/annurev.ecolsys.33.010802.150519].

———, and others. 2006. Nutrient cycling by fish supports relatively more primary production as lake productivity increases. Ecology 87:1696-1709.

———, G. Boros, and P. B. Mcintyre. 2013. When are fish sources versus sinks of nutrients in lake ecosystems? Ecology 94:2195-2206 [doi:10.1890/12-1559.1].

Vaquer-Sunyer, R., and C. M. Duarte. 2008. Thresholds of hypoxia for marine biodiversity. Proc. Nat. Acad. Sci. U.S.A. 105:15452-15457 [doi:10.1073/pnas.0803833105].

———, and ———. 2013. Experimental evaluation of the response of coastal Mediterranean planktonic and benthic metabolism to warming. Estuar. Coasts 36:697-707 [doi:10.1007/s12237-013-9595-2].

Vinagre, C., C. Máguas, H. N. Cabral, and M. J. Costa. 2012. Food web structure of the coastal area adjacent to the Tagus estuary revealed by stable isotope analysis. J. Sea Res. 67:21-26 [doi:10.1016/j.seares.2011.09.003].

Volk, T., and M. I. Hoffert. 1985. Ocean carbon pumps: Analysis of relative strengths and efficiencies in ocean-driven atmospheric CO_2 changes, p. 99-110. *In* E. Sundquist and W. Broecker [eds.], The carbon cycle and atmospheric CO_2: Natural variations archean to present. American Geophysical Union.

Wall, C. C., B. J. Peterson, and C. J. Gobler. 2008. Facilitation of seagrass *Zostera marina* productivity by suspension-feeding bivalves. Mar. Ecol. Prog. Ser. 357:165-174 [doi:10.3354/meps07289].

Weber, M. J., and M. L. Brown. 2009. Effects of common carp on aquatic ecosystems 80 Years after "Carp as a Dominant": Ecological insights for fisheries management. Rev. Fish. Sci. 17:524-537 [doi:10.1080/10641260903189243].

Welsh, D. T. 2003. It's a dirty job but someone has to do it: The role of marine benthic macrofauna in organic matter turnover and nutrient recycling to the water column. Chem. Ecol. 19:321-342 [doi:10.1080/0275754031000155474].

Werner, E. E., and D. J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. Ecology 69(5):1352-1366 [doi:10.2307/1941633].

Whitton, B. A., S. L. J. Grainger, G. R. W. Hawley, and J. W. Simon. 1991. Cell-bound and extracellular phosphatase-activities of cyanobacterial isolates. Microb. Ecol. 21:85-98 [doi:10.1007/BF02539146].

Widdicombe, S., and H. R. Needham. 2007. Impact of CO_2-induced seawater acidification on the burrowing activity of *Nereis virens* and sediment nutrient flux. Mar. Ecol. Prog. Ser. 341 [doi:10.3354/meps341111].

Wiklund, A. K. E., K. Dahlgren, B. Sundelin, and A. Andersson. 2009. Effects of warming and shifts of pelagic food web structure on benthic productivity in a coastal marine system. Mar Ecol Prog Ser 396:13-25 [doi:10.3354/meps08290].

Williamson, C. E., R. W. Sanders, R. E. Moeller, and P. L. Stutzman. 1996. Utilization of subsurface food resources for zooplankton reproduction: Implications for diel vertical migration theory. Limnol. Oceanogr. 41:224-233 [doi:10.4319/lo.1996.41.2.0224].

———, and K. C. Rose. 2009. Ultraviolet insights: Attempting to resolve enigmatic patterns in pelagic freshwaters—the historical context and a view to the future. Int. Rev. Hydrobiol. 94:129-142 [doi:10.1002/iroh.200811099].

———, J. M. Fischer, S. M. Bollens, E. P. Overholt, and J. K. Breckenridge. 2011. Toward a more comprehensive theory of zooplankton diel vertical migration: Integrating ultraviolet radiation and water transparency into the biotic paradigm. Limnol. Oceanogr. 56:1603-1623 [doi:10.4319/lo.2011.56.5.1603].

Winder, M., and D. E. Schindler. 2004. Climate change uncouples trophic interactions in an aquatic ecosystem. Ecology 85:2100-2106 [doi:10.1890/04-0151].

Wood, S. A., K. Jentzsch, A. Rueckert, D. P. Hamilton, and S. C. Cary. 2009. Hindcasting cyanobacterial communities in Lake Okaro with germination experiments and genetic analyses. FEMS Microbiol. Ecol. 67:252-260 [doi:10.1111/j.1574-6941.2008.00630.x].

Woodland, R. J., and D. H. Secor. 2013. Benthic-pelagic coupling in a temperate inner continental shelf fish assemblage. Limnol. Oceanogr. 58:966-976 [doi:10.4319/lo.2013.58.3.0966].

Worm, B., and others. 2009. Rebuilding global fisheries. Science 325:578-585 [doi:10.1126/science.1173146].

Yamaguchi, H., S. Montani, H. Tsutsumi, K.-I. Hamada, N. Ueda, and K. Tada. 2007. Dynamics of microphytobenthic biomass in a coastal area of western Seto Inland Sea, Japan. Est. Coast. Shelf Sci. 75:423-432 [doi:10.1016/j.ecss.2007.05.025].

Yvon-Durocher, G., and others. 2012. Reconciling the temperature dependence of respiration across timescales and ecosystem types. Nature 487:472-476 [doi:10.1038/nature11205].

Zaret, T. M., and J. S. Suffern. 1976. Vertical migration in zooplankton as a predator avoidance mechanism. Limnol. Oceanogr 21:804-813 [doi:10.4319/lo.1976.21.6.0804].

Zhang, J., and others. 2010. Natural and human-induced hypoxia and consequences for coastal areas: synthesis and future development. Biogeosciences 7:1443-1467 [doi:10.5194/bg-7-1443-2010].