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Bivalve Impacts in Freshwater and Marine Ecosystems

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Abstract

Bivalve molluscs are abundant in marine and freshwater ecosystems and perform important ecological functions. Bivalves have epifaunal or infaunal lifestyles but are largely filter feeders that couple the water column and benthos. Bivalve ecology is a large field of study, but few comparisons among aquatic ecosystems or lifestyles have been conducted. Bivalves impact nutrient cycling, create and modify habitat, and affect food webs directly (i.e., prey) and indirectly (i.e., movement of nutrients and energy). Materials accumulated in soft tissue and shells are used as environmental monitors. Freshwater mussel and oyster aggregations in rivers and estuaries are hot spots for biodiversity and biogeochemical transformations. Historically, human use includes food, tools, currency, and ornamentation. Bivalves provide direct benefits to modern cultures as food, building materials, and jewelry and provide indirect benefits by stabilizing shorelines and mitigating nutrient pollution. Research on bivalve-mediated ecological processes is diverse, and future synthesis will require collaboration across conventional disciplinary boundaries.

INTRODUCTION

Biodeposits: feces and pseudofeces; pseudofeces are filtered particles that are rejected before ingestion, usually in a mucilaginous matrix

Bivalves (class Bivalvia) are marine and freshwater molluscs with two hinged shells (e.g., mussels, clams, oysters, and scallops) that show a diverse array of life history characteristics and perform important ecological functions (Dame 2012, Gosling 2003, Strayer 2008, Vaughn 2018). Bivalves have both epifaunal and infaunal lifestyles. Infaunal bivalves bury themselves in the benthic substrate, whereas epifaunal bivalves use byssal threads or adhesive to attach themselves to hard surfaces or one another. Bivalves are largely filter feeders, although some species, especially infaunal organisms, feed on detritus (i.e., deposit or pedal feeding). Most taxa are largely sedentary as adults, with movement documented for foraging, reproduction, and predator escape. Juvenile stages are more likely to show mobility that is critical for dispersal. Finally, bivalve assemblages can occur in high densities with ecological impacts at large spatial scales. For example, epifaunal bivalves such as estuarine oysters (e.g., eastern oyster, *Crassostrea virginica*) and freshwater dreissenid mussels (e.g., zebra and quagga mussels, *Dreissena polymorpha* and *Dreissena bugensis*, respectively) form dense assemblages of individuals in reefs attached to hard surfaces, including spent shells of previous generations. The three-dimensional structure of reefs and the activity of dense populations have major implications for associated organisms and ecosystem energetics (Dame 2012, Karatayev et al. 2002). In freshwaters, infaunal mussels of the order Unionoida also form dense assemblages, often consisting of many different species, which are critical to secondary production and element cycling in freshwater ecosystems (Strayer 2008).

Research on bivalve-mediated ecosystem processes spans freshwater and marine ecosystems and covers a wide diversity of taxa, and a synthesis of studies that bridge conventional boundaries in ecological disciplines has been lacking. Here, we summarize impacts of bivalves in freshwater and marine environments and consider similarities of species with epifaunal and infaunal lifestyles. We review major categories of bivalve impacts separately and present two in-depth case studies, the importance of freshwater mussel beds in rivers and of oyster reefs in estuaries. Finally, we discuss ecosystem services to past and present human societies provided by bivalves and end with a summary of research opportunities.

BIOFILTRATION

Physiology

Bivalves couple benthic and pelagic systems by filtering particles and by excreting and depositing nutrients. Detailed reviews of bivalve feeding are available (Cranford et al. 2011, Evan Ward & Shumway 2004). Understanding bivalve feeding physiology is a prerequisite to quantifying their ecosystem impacts. Bivalves feed on suspended particles (i.e., filtration), sediment (i.e., pedal or deposit feeding), or a mixture. Intake occurs via an aperture, siphon, or proboscides, then cilia and mucus move particles toward the labial palps and stomach (Evan Ward & Shumway 2004). Bivalves show changes in filtration rate, preferential filtration, and pre-ingestion sorting based on factors such as particle size, shape, surface chemistry, and filtrate composition, although these sensory processes are not entirely understood. Rejected particles encapsulated in mucus are expelled as pseudofeces before ingestion. Post-ingestion sorting also occurs. Less nutritious items are moved to the intestine for rapid egestion as feces, and higher quality material goes to the diverticula for complete digestion (Evan Ward & Shumway 2004). Collectively, feces and pseudofeces repackage nutrients and are termed biodeposits. Thus, although bivalves are largely stationary, their selective filtration, ingestion, and digestion choices are analogous to foraging by mobile animals, with important ecological consequences (Dame 2012).

Foraging

A vast literature shows that rates of clearance, rejection, ingestion, assimilation, and egestion vary widely, according to extrinsic factors (e.g., temperature, filtrate composition) and intrinsic factors (e.g., body size, growth stage) and the methodology used to measure feeding dynamics. For example, zebra mussels (*D. polymorpha*) can selectively reject the toxic cyanobacterium *Microcystis aeruginosa* in pseudofeces, which can exacerbate algal blooms (Vanderploeg et al. 2013). With increasing silt concentrations, the hard clam *Mercenaria mercenaria* can reduce gill pumping rate. In contrast, the common cockle *Cerastoderma edule* can respond to higher silt concentrations by maintaining the same clearance rates but producing more pseudofeces (Grizzle et al. 2001). Overall, feeding by bivalves is not a binary condition (i.e., feeding or not feeding) but varies continuously in intensity and selectivity with a variety of environmental and internal factors, which affect individuals, populations, and ecosystems.

Clearance

Clearance rates (L g^{-1} h^{-1}) and filtering rates (mg g^{-1} h^{-1}) are commonly scaled by individual dry mass to describe filtration capacity, which is then compared with water residence time and human-mediated water filtration rates. Wide variation in clearance rates according to species, methods, and calculation are a constant feature of the data sets, and direct measurements are urged (Riisgård 2001). A meta-analysis of clearance rates reported central tendencies of 2.3–4.2, 3.6–7.9, 1.1–4.8, and 2.8–6.0 L g^{-1} h^{-1} for marine mussels, scallops, cockles, and oysters, respectively (Cranford et al. 2011). Zebra mussels in the Laurentian Great Lakes showed clearance rates of 0.5–22.6 L g^{-1} h^{-1} (Johengen et al. 2014), and two unionoid species showed rates of 1.8–3.7 L g^{-1} h^{-1} in an urban river (Hoellein et al. 2017). Clearance rates are scaled from individuals to populations to quantify ecosystem effects. Zu Ermgassen et al. (2013) estimated the capacity of historical and modern oyster populations to filter water volume relative to residence time in US estuaries. Vaughn (2010) found that unionoid mussels in an Oklahoma River filtered water 10 times as it flowed over beds during low flow, and Newton et al. (2011) estimated that unionoid filtration rates in the upper Mississippi River can exceed rates of treated wastewater discharge. Bivalve aggregations with these clearance rates can filter most of the overlying water column. For example, oysters and mussels in the relatively small Marennes-Oléron Bay, France, can filter all the water in the bay within 2.7 days, whereas it is estimated that depleted oyster populations need 3.5 years to turn over all of the water in the much larger Delaware Bay, United States (Dame 2012).

Bioremediation

There is a growing interest in using large aggregations of bivalves as biofilters for chemicals, metals, and pathogens. Bivalves tolerate and accumulate contaminants and, because they are sessile and widely distributed, can be used in programs for monitoring (see the section titled Bivalves as Sentinels of Environmental Change) (O'Connor 2002) and removal of contaminants (i.e., bioextraction) (Gifford et al. 2007). Animals are cultured and removed to harvest contaminants, similar to the process of nutrient removal via shellfish harvest (see the section titled Nutrient Cycling and Storage). Asian clams (*Corbicula fluminea*) accumulated metals in water from acid mine drainage effluent (Rosa et al. 2014). Yesso scallop (*Patinopecten yessoensis*) is a major aquaculture product in northern Japan that bioaccumulates cadmium in the hepatopancreas, which is removed during meat processing. The hepatopancreas is hazardous waste, but new methods can remove the accumulated cadmium for reuse in manufacturing and recycle the processed tissue as fertilizer (Gifford et al. 2007). Harvest of bioaccumulated contaminants in bivalves is one component in the toolbox of ecosystem managers for sustainable water remediation and merits further study.

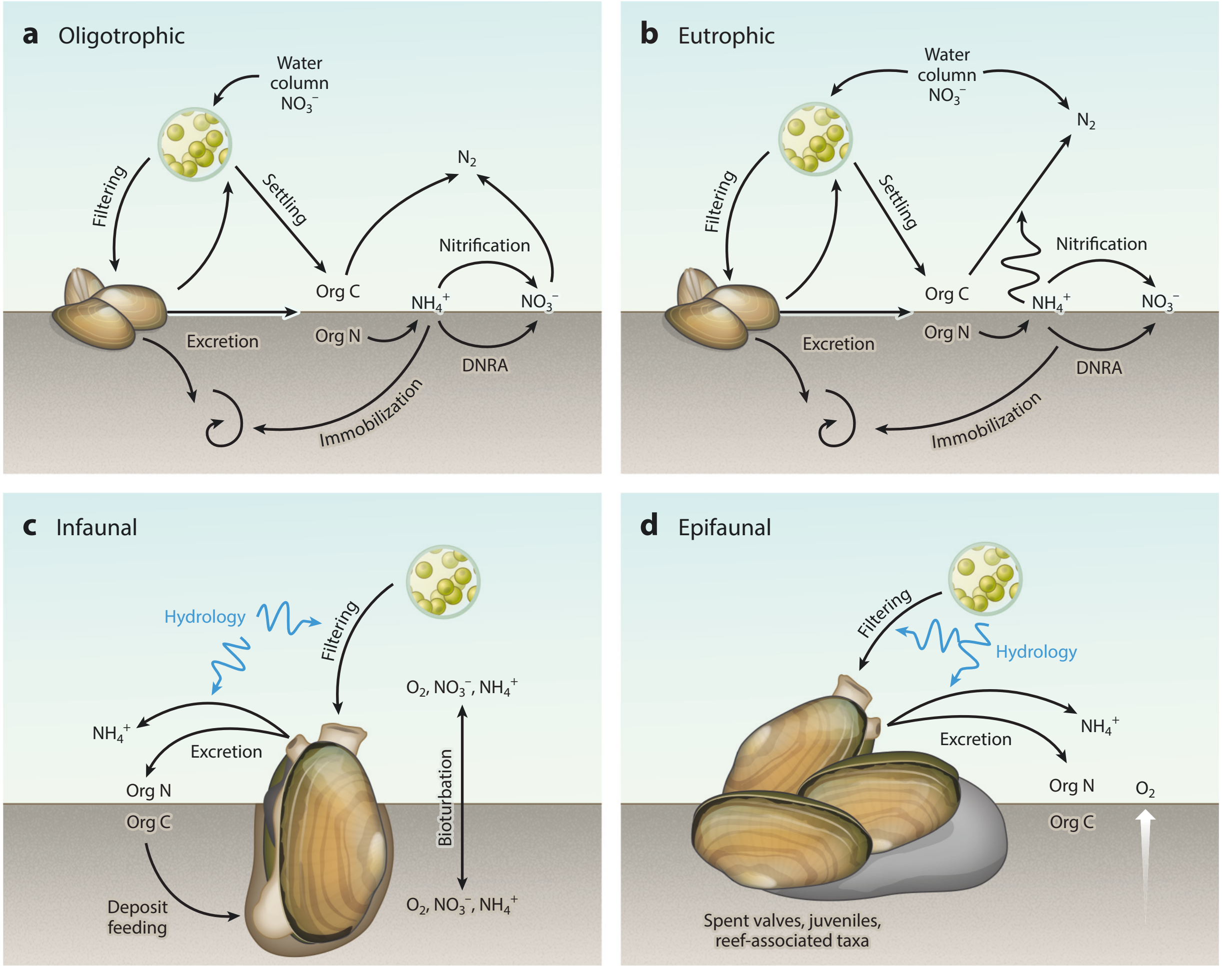


Figure 1

Biogeochemical transformations associated with bivalves, with examples regarding nitrogen (N) cycling for oysters reefs under (*a*) oligotrophic conditions and (*b*) eutrophic conditions and for (*c*) infaunal and (*d*) epifaunal bivalves. Fluxes include filtration, settling, excretion, immobilization, mineralization, ammonium (NH_4^+) efflux, nitrification, denitrification, dissimilatory nitrate (NO_3^-) reduction to ammonium (DNRA), hydrology, bioturbation, deposit feeding, and sediment oxygen (O_2) concentrations. Panels *a* and *b* adapted from Hoellein & Zarnoch (2014).

NUTRIENT CYCLING AND STORAGE

Bivalves are critical for nutrient translocation, storage, and transformation (**Figure 1**). Bivalves' role in nutrient cycling has been reviewed for unionoids (Strayer 2014), zebra mussels (Strayer et al. 1999), marine bivalves (Newell 2004), and aquacultured bivalves (Gallardi 2014). The roles of bivalves in nutrient cycling are driven by many factors such as lifestyle (i.e., infaunal and epifaunal), habitat (e.g., river, intertidal zone), eutrophication, and hydrodynamics.

Translocation

Suspension feeding (i.e., biofiltration of the water column) and deposit feeding (i.e., sediment consumption) move nutrients from pelagic and benthic zones, respectively, into bivalves, where elements are assimilated or egested (**Figure 1**). Taxa with especially dense colonies such as invasive and aquacultured species offer insight into bivalves' influence on nutrient dynamics at large scales. In the Laurentian Great Lakes, dreissenid mussels in shallow coastal waters and littoral habitats filter nutrients from terrestrial input and the water column at high rates. Mussels' egesta and corpses enrich the littoral benthic zone, a phenomenon termed the nearshore shunt (Hecky et al. 2004). Labile carbon in the biodeposits of Pacific oysters (*Magallana gigas*, previously *Crassostrea gigas*), invasive to Ireland, increased flux of carbon dioxide, methane, and ammonium from mud flats and native mussel beds (Green et al. 2013). In rope or raft-based aquaculture of epifaunal bivalves, biodeposits can shift nutrients from surface water to the benthos, sustaining sediment anoxia and ammonium efflux (Newell 2004).

Infaunal bivalves conduct both suspension and deposit feeding and live at or beneath the sediment water interface (SWI). Their role in translocation of nutrients via feeding varies by ingestion mode and is strongly driven by hydrodynamics (**Figure 1**). For example, nitrogen (N) from the unionoid *Lampsilis siliquoidea* supplied 74% of N demand in a N-limited stream (Atkinson et al. 2014c). A similar effect was shown in a N-limited estuary, where hard clam feeding reduced light and N limitation of adjacent eelgrass (*Zostera marina*) (Carroll et al. 2008).

Sediment water interface (SWI): the boundary between the water column and the benthic surface

Bioturbation: the disturbance of sediment particles by benthic organisms

Biofilm: a mixture of bacteria, archaea, fungi, and algae in a mucilaginous matrix, which colonizes all submerged surfaces in aquatic habitats

Storage in Soft Tissue and Shells

Storage of elements in bivalves' soft tissues and shells affects their role in nutrient stoichiometry and sequestration. The nutrient content of tissues and shells varies by site, season, growth stage, and reproductive status (Dame 2012, Strayer 2014). The stoichiometry of nutrients in bivalve tissues and biodeposits enables inferences on their role in nutrient dynamics. For example, in North America, the invasive Asian clam *C. fluminea* had higher C:N (carbon:nitrogen) ratios in tissue relative to a native unionoid mussel (*Elliptio crassidens*) and more N in biodeposits. Combined with a short life span, *C. fluminea* stored less N and increased N bioavailability relative to the unionoid (Atkinson et al. 2010). Similarly, zebra mussels can enhance phosphorus (P) limitation of surrounding waters via retention of P in soft tissues relative to N (Naddafi et al. 2008). Finally, die-offs and reproduction events can represent significant pulsed release of stored nutrients (Novais et al. 2015, Strayer 2014).

Shells are long-term sinks of nutrients from aquatic environments when buried or harvested. For example, eastern oyster (*C. virginica*) shell content (by dry weight) is 12.2–12.3% C, 0.2–0.3% N, 0.04–0.1% P (Higgins et al. 2011, Newell et al. 2005). Shell content for two unionoid species (*Lasmigona complanata*, *Pyganodon grandis*) averaged 14.6% C, 1.1% N, and 0.004% P (Hoellein et al. 2017). Scaling nutrient content from individuals to populations allows estimate of nutrient removal or sequestration via shell harvest or burial, respectively. Shells can persist for long time periods. Powell et al. (2011) measured shell degradation over 13 years for 4 bivalve species including ocean quahog (*Arctica islandica*), blue mussel (*Mytilus edulis*), tiger lucine (*Codakia orbicularis*), and bay scallop (*Argopecten irradians*), with high variation among species and important implications for carbonate cycling and fossil formation. Atkinson et al. (2018) estimated that decay rates for shells of two abundant unionoid species (*Actinonaias ligamentina*, *Amblema plicata*) in Oklahoma rivers were ~31.6 years at the SWI.

Biogeochemical Transformations

Bivalves affect biogeochemical transformations in sediment via alterations to redox conditions from biodeposits, bioturbation (for infaunal taxa), and activity of gut and shell biofilms (Heisterkamp et al. 2013, Newell 2004, Welsh 2003). Redox profiles that vary with sediment depth couple complementary microbial metabolism pathways, driven by contrasting abundance of oxygen and

NITRIFICATION–DENITRIFICATION

Nitrification is the oxidation of ammonium to nitrate. Denitrification is the reduction of nitrate to dinitrogen gas. In marine ecosystems where nitrate is low, nitrification provides nitrate for denitrifiers—thus, the term coupled nitrification–denitrification. Nitrification requires oxygen, whereas denitrification requires anoxia. Coupled nitrification–denitrification requires adjacent anoxic–oxic microsites at the sediment water interface.

labile C (Herbert 1999). Bivalves can enhance sediment oxygen demand via biodeposit accumulation (Kellogg et al. 2014) and supply via bioturbation (**Figure 1**). With aerobic conditions at the SWI, bivalve wastes facilitate coupled redox reactions such as nitrification–denitrification (see the sidebar titled Nitrification–Denitrification). However, anaerobic conditions at the SWI sustained by organic matter enrichment inhibit nitrification and support efflux of reduced compounds and phosphate (Hoellein & Zarnoch 2014). In highly reduced sediments, accumulation of hydrogen sulfide and ammonium can be toxic (Newell 2004, Strayer 2008). Sediment redox gradients are interrupted via bioturbation of infaunal bivalves, which introduce oxygen and oxidized elements into reduced sediment layers (Welsh 2003). Finally, bivalves' gut and shell biofilms, or microbiome, conduct biogeochemical transformations. Reduced conditions in gut tissue support microbial production of gases such as nitrous oxide and methane (Heisterkamp et al. 2013). Biofilms on shells contribute to production, respiration, and nutrient dynamics, especially in dense colonies where egesta and dissolved wastes support metabolism on live and spent shells (Welsh et al. 2015).

BIVALVES AS HABITAT AND HABITAT MODIFIERS

Bivalves create and modify habitat for other organisms across wide spatial and temporal scales: Individual bivalves host microbes and protists; some have parasitic larval stages; their shell surfaces are colonized by biofilms, algae, and invertebrates; and shell accumulations can affect secondary production. Collectively, bivalve aggregations can affect neighboring habitats via their influence on hydrodynamics, light penetration/availability, and C and nutrient fluxes.

Microscopic Organisms: Internal and External Bivalve Associations

Bivalves provide habitat for symbionts found inside body cavities or tissues. Chemoautotrophic symbionts are bacteria found within bivalve tissues of species in extreme habitats, including hydrothermal vents and anaerobic, sulfide-rich environments (Dame 2012). For example, gills of the deep sea hydrothermal vent mussel (*Bathymodiolus thermophilus*) are colonized by microbial symbionts that oxidize reduced sulfur and fix C (Dame 2012). Photoautotrophic symbionts (zooxanthellae) are intercellular symbiotic dinoflagellate algae that reside in the mantle tissue of giant clams (*Tridacna gigas*) and some small Indo-West Pacific clams in the family Trapeziidae (Vermeij 2013). These clams are found near coral reefs where plankton can be limiting to growth (Dame 2012); the zooxanthellae provide photosynthates that supplement that clam's diet, while the clam provides habitat for the algae (a state known as photosymbiosis). Recently, cockles (*Clinocardium nuttallii*) in the Pacific Northwest were found to harbor green algae, but whether this relationship is symbiotic remains unknown (Vermeij 2013). We know of no studies examining symbionts within freshwater bivalves, and this area warrants exploration.

Photosymbiosis: microbial symbionts conduct photosynthesis and share fixed carbon with the host, which provides nutrition and protection to symbionts

Across taxa, changes to microbial communities in bivalves' gut and hemolymph have been examined in response to physical stress and disease (Gómez-Chiarri et al. 2015). For example, Sydney rock oysters (*Saccostrea glomerata*) infected with the protozoan QX disease (*Marteilia sydneyi*) showed reduced diversity of gut bacteria, and Pacific oysters (*M. gigas*) dying of a bacterial infection (*Vibrio* sp.) showed reduced diversity of hemolymph bacteria. Application of new molecular tools will illustrate the genotypic and epigenetic foundations of resistance to common diseases in aquaculture bivalves, including the protozoan infections caused by *Perkinsus marinus* (i.e., perkinsosis or dermo infections in oysters) and *Bonamia ostreae* (i.e., bonamiosis in oysters) and infections by herpes virus and *Vibrio* sp. bacteria (Gómez-Chiarri et al. 2015).

Microbial biofilms are found on all submerged surfaces in aquatic habitats (Battin et al. 2016), including shells and bivalve-associated sediments, and host a diverse array of metabolic pathways and elemental transformations. Shell biofilms on epifaunal and infaunal bivalves contribute to ecosystem scale C and N transformations, supplemented by nutrients from bivalve egesta (Kellogg et al. 2013, Turek & Hoellein 2015). For example, denitrification recorded in chambers with only Manila clams (*Ruditapes philippinarum*) was approximately 70% of denitrification when clams and sediment were combined (Welsh et al. 2015). Algae growing on unionoid mussel shells in streams are more N enriched than adjacent rocks or empty shells, creating spatial hot spots of food quality or quantity for higher trophic levels (Spooner et al. 2013). Finally, biodeposition, soluble wastes, and bioturbation from bivalves can affect microbial biofilm community composition in sediments. Invasion by Pacific oysters (*M. gigas*) at high density increased the diversity of genes from ammonia-oxidizing bacteria (*amoA*) in sediment without a change in overall structure of the bacterial assemblage (i.e., the 16S ribosomal RNA gene; Green et al. 2013). In eutrophic waters of New York City, eastern oysters (*C. virginica*) did not affect abundance of genes for denitrification (*nirS*, *nirK*) or dissimilatory reduction of nitrate to ammonium (*nrfA*) in sediment bacteria (Lindemann et al. 2016). Recent advancements in tools for high-throughput sequencing of functional genes from biofilm constituents, as well as other "-omics" (i.e., metagenomics, proteomics, metabolomics), are poised to greatly inform the relationship between microbial communities and bivalve-mediated ecosystem processes (Gómez-Chiarri et al. 2015).

Shell Aggregations

Shell aggregations represent unique habitats for a diversity of organisms across marine, lake, and river habitats (reviewed by Gutierrez et al. 2003). Shells generate three-dimensional complexity and environmental heterogeneity, persist in the environment, and provide a stable surface for attachment in habitats otherwise dominated by soft sediments or with space limitations (Gutierrez et al. 2003).

Bivalves were the first known reef builders. Epifaunal rudist clams formed reefs in shallow, equatorial marine environments in the late Jurassic to late Cretaceous periods that were likely as important to ancient ecosystems as coral reefs are to present-day ecosystems. Like corals, the calcium carbonate provided by rudist shells formed a stable framework that other organisms colonized and lived around (Johnson 2002). Also, similar to corals, rudists were purportedly photosymbionts, which would have aided their growth and expansion (Vermeij 2013). Rudists went extinct during the Cretaceous–Tertiary mass extinction.

Shell accumulations provide interstitial spaces that offer unique habitats of low water speed and trapped particles. Spent shells (empty bivalve shells) and shell bottom or shell hash (i.e., fragments) are terms for shell-based habitat. Experimental additions of shell hash to denuded sediments enhanced species richness in a shallow marine environment (Thrush et al. 2013). For epifaunal organisms such as oysters, attachment of juveniles to spent shells sustains reef growth, and lack of shell material for attachment can limit population growth and restoration (Grabowski et al. 2012). Experiments manipulating live and spent shell of blue mussels (*M. edulis*), zebra mussels

(*D. polymorpha*), and various unionoid mussels have found increased abundance and biomass of associated organisms with live animals relative to shells alone, attributed to bivalve biodeposition and excretion (Norling & Kautsky 2007, Spooner & Vaughn 2006, Stewart et al. 1998). Shells that fell to the sea floor from aquaculture of the New Zealand green-lipped mussel (*Perna canaliculus*) increased abundance of sea stars, attracted by presence of live mussels, mussel biodeposits, or the presence of other sea stars (i.e., reproduction) (Inglis & Gust 2003). Finally, deployments of native and invasive bivalve shells shifted macroinvertebrate functional feeding groups from collector–gatherers to shredders and predators in the Danube River, attributed to the presence of hard shell surface, which was otherwise uncommon in the benthic zone and provided refuge from predators (Bódis et al. 2014).

Connections to Other Habitats

Bivalve aggregations can modify the physical stability and prevailing environmental conditions in adjacent habitats. Oyster reefs can stabilize shorelines by buffering waves, thereby reducing salt marsh erosion (La Peyre et al. 2015). The rapid rate of reef growth relative to global sea level rise suggests reefs might be more resilient than engineered structures for long-term shoreline stabilization (Grabowski et al. 2012). Shellfish middens from indigenous Native American cultures in British Columbia support modern cedar trees (*Thuja plicata*) with greater calcium and height than trees in non-midden habitats (Trant et al. 2016). Ribbed mussels (*Geukensia demissa*) develop mutualisms with salt marsh plants (*Spartina alterniflora*) that enhance recovery of marshes following droughts (Angelini et al. 2016). Invasive dreissenid mussels have a host of effects on lake habitats, including increased water clarity, which then changes littoral habitats by increasing benthic algae (reviewed by Karatayev et al. 2002).

BIVALVES' ROLES IN FOOD WEBS

Bivalves play important roles in food webs: directly as prey to other organisms and by grazing on seston, and indirectly through the bottom-up provisioning of nutrients and energy (Dame 2012, Vaughn et al. 2008).

Bivalves as Prey

Bivalves are important prey items for a wide diversity of organisms. Pelagic marine larvae are often prey of ctenophores and jellyfish and can also be filtered by adult bivalves (Dame 2012). Shells are a major obstacle to predation on adult bivalves, and Dame (2012) summarized techniques for penetration by predators that include chipping, wedging, crushing, and boring. In marine systems, predators on adult bivalves include invertebrates, fish, birds, and mammals. Major invertebrate predators in marine ecosystems are snails and sea stars. For example, the Atlantic (*Urosalpinx cinerea*) and Japanese (*Ocenebra inornata*) oyster drills are common oyster predators and pests for aquaculture (Naylor et al. 2001). Fish predators can feed on adult bivalves by using pharyngeal teeth to crush shells or by opportunistic attacks on exposed siphons of infaunal bivalves (Dame 2012). Shorebirds in the genus *Haematopus* (oystercatchers) are important predators of mussels and oysters, as their bills are adapted for prying open bivalve shells (Waser et al. 2016).

Freshwater bivalves are preyed on by a variety of terrestrial and aquatic organisms, from flatworms to insect larvae to turtles. Diving ducks eat fingernail clams (Sphaeriidae) and zebra mussels (Strayer 2008). The most conspicuous predator on adult unionoids are muskrats (*Ondatra zibethicus*). Muskrats create middens from mussel shells, show strong size and species selectivity, and can significantly affect unionoid abundance and size structure (Haag 2012). Other important predators on freshwater bivalves include a variety of fish, turtles, and terrestrial predators such as raccoons, otters, skunks, and crows. Freshwater drum are specialized molluscivores that prey heavily on mussels but also serve as a host to unionoid larva (see the section titled The Unusual Life History of Unionoid Mussels). Thin-shelled unionoid species suffer proportionately higher predation, yet predation on all adults is relatively low. Predation on juvenile mussels, by organisms such as flatworms, insect larvae, and crayfish, is likely an important source of mortality but is understudied (Haag 2012, Strayer 2008).

Stimulation of Primary and Secondary Production

As described above (see the section titled Biofiltration), bivalves are dominant filter feeders on phytoplankton and other suspended particles. In eutrophic and turbid systems, this filtration can increase water clarity and light penetration. As filtering bivalves deplete stocks of phytoplankton from the pelagic food web, nutrients from their biodeposits and excretion provide a nutrient pulse to the benthic food web. Increased light and nutrient cycling can increase benthic and littoral primary production, which can move up the food web (Castorani et al. 2015). Marine mussels, clams, freshwater mussels, and invasive bivalves (see the following section) stimulate macrophyte growth, which increases secondary production (Murphy et al. 2016, Peterson & Heck 2001). Bivalves can also stimulate production in adjacent habitats. For example, Allen et al. (2012) found that mussels increased the abundance of benthic insects, whose winged adults transport nutrients to riparian areas and increase the abundance of predatory spiders that feed on this emergence. Finally, when bivalves die, their decomposing tissue can provide a resource pulse to both aquatic and adjacent terrestrial ecosystems (Novais et al. 2015, Sousa et al. 2012).

Invasive Species

Food web effects of bivalves are often magnified when they invade new ecosystems because invasive species can achieve very high abundance. For example, introduced Pacific oysters in northwestern Europe have altered the size structure of phytoplankton populations (Troost 2010). Filtration by invasive golden mussels (*Limnoperna fortunei*) in South America has decreased phytoplankton, enhanced light penetration, and stimulated periphyton and macrophytes (Boltovskoy & Correa 2015). Invasions have been a major driving force for research on bivalve physiology and ecology, as they can cause major ecological and economic impacts, especially in locations where aquatic ecosystem health is tightly coupled with commerce such as shipping and fisheries.

The invasion of the San Francisco Estuary by the overbite clam (*Potamocorbula amurensis*) is partially linked to the decline of the endemic, endangered delta smelt (*Hypomesus transpacificus*) (Crauder et al. 2016). Smelt feed on zooplankton in the estuary, whereas the clams filter feed on both phytoplankton and microzooplankton (Greene et al. 2011, Kimmerer & Thompson 2014). Phytoplankton abundance in the estuary declined sharply immediately after the invasion of the clams in 1986 and remains low. Zooplankton abundance has also decreased, through direct predation by clams and indirectly through food limitation from reduced phytoplankton abundance. Thus, smelt populations are now very food limited (Crauder et al. 2016).

In a now-classic example, the invasion of zebra (*D. polymorpha*) and quagga (*D. bugensis*) mussels in rivers and lakes of North America beginning in the late 1980s profoundly altered food webs by changing the dominant energy pathway from pelagic food webs dominated by phytoplankton and zooplankton to benthic food webs dominated by macrophytes and benthic invertebrates (Higgins & Vander Zanden 2010, Strayer et al. 1999). Systems invaded by zebra mussels showed large reductions in phytoplankton (reduced by 35–78%) and zooplankton (reduced by 40–77%) biomass and increases in benthic algal and macrophyte biomass (increased by 170–180%), sediment-associated bacteria (increased by ~2,000%), and non-dreissenid zoobenthic biomass (increased by 160–210%). In some cases, these changes propagated across trophic levels, affecting top predators. For example, in Lake Huron the zebra mussel invasion led to decreases in planktivorous fish and their predators, collapsing a multimillion-dollar fishery (Higgins & Vander Zanden 2010).

Invasive freshwater bivalves also can form novel trophic links or can disrupt, alter, or reduce the number of existing trophic links. For example, zebra mussels are now important in the diet of blue crabs (*Callinectes sapidus*) in the Hudson River, and in South America introduced Asian clams (*C. fluminea*) and golden mussels (*L. fortunei*) subsidize secondary consumers as an intermediate link in the food chain (Jackson et al. 2017).

BIVALVES AS SENTINELS OF ENVIRONMENTAL CHANGE

Bivalves can reveal past environmental conditions and be used to monitor future environmental change. As sessile or sedentary filter or deposit feeders, they are in constant physical and metabolic contact with water. Bioaccumulation of materials in soft tissue integrates accrual over days to months, whereas shells indicate environmental conditions over the annual growing season.

Shells

Shell growth and geochemistry record past environmental conditions over large spatial and temporal scales. Like tree rings, annual shell growth leaves bands of aragonite deposition, which reflect the temperature, hydrology, food availability, and other conditions from that season or year (Fritts et al. 2017). For example, variations in the annual shell growth of freshwater mussels from Swedish rivers were used to reconstruct past air temperatures back to 1777, with more than 50% of the variability in annual shell growth explained by temperature (Schone et al. 2004).

Shell geochemistry can also reveal past climatic and other chemical and physical conditions. Isotopic signatures of ^{18}O and ^{13}C in freshwater mussels have been used to study climatic conditions as far back as the Miocene (Blazejowski et al. 2013), and oxygen isotopes of both fossil and modern clams from the northwestern Atlantic Ocean were used to examine sea water temperature change in the eleventh, fourteenth, and nineteenth centuries relative to global climate patterns (Wanamaker et al. 2011). Metal concentrations among shell growth layers can show past exposure to metals and rare earth elements (Merschel & Bau 2015).

Soft Tissue

Bivalves can rapidly bioaccumulate nutrients, metals, and emerging stressors such as pharmaceuticals, engineered nanomaterials, and microplastic from ambient water into their soft tissues, and these tissues are often easy to nonlethally sample. In addition, because bivalves are long-lived, they can be repeatedly sampled over time. Thus, bivalves are model sentinel organisms for monitoring pollution (Zuykov et al. 2013), particularly in coastal areas where they constitute valuable commercial resources in aquaculture (Suarez-Ulloa et al. 2015). For example, N isotope signatures in unionoid mussel tissue reflect local agricultural land use (Atkinson et al. 2014a). The marine mussel *Mytilus* sp. concentrates engineered nanomaterials in its digestive gland and is being increasingly used to monitor this pollutant (Rocha et al. 2015). Bivalves are particularly useful for monitoring heavy metals because they are constantly exposed and can accumulate metals without suffering mortality (Boening 1999). As such, bivalves, particularly blue mussels and eastern oysters (Boening 1999), have long been used as metal biomonitors in the marine environment, and interest in their use in freshwater systems is emerging (Johns 2011). Finally, recent work indicates that bivalves may be good biomonitors for ecological impacts of microplastics (Rochman et al. 2017).

Ecotoxicology

Toxic effects of many materials are first apparent at the cellular and/or subcellular level and as such serve as an early warning sign of environmental problems. Although bivalves have long been used in ecotoxicology (Zuykov et al. 2013), an exciting, emerging area is the use of physiological and molecular biomarkers to assess stress or immune responses in bivalves (Fritts et al. 2015). Bivalve hemolymph and/or tissue can be easily extracted in a nonlethal manner and biomarkers monitored over time to assess changes in stressor levels. The range of biomarkers being used or investigated includes gene damage and expression, heat shock proteins, antioxidant enzymes, and stress hormones (Fernandez-Tajes et al. 2010, Fritts et al. 2015).

FRESHWATER MUSSEL BEDS AS CENTERS OF BIOLOGICAL ACTIVITY IN RIVERS

Freshwater mussels in the order Unionoida are long-lived (∼10 to >100 years), sedentary, infaunal, suspension-feeding bivalves. In many lakes and rivers, mussels spend their adult life in dense (up to 100 individuals/m^2), multispecies aggregations termed mussel beds. Mussel beds are hot spots of biological activity, providing biogenic habitat and modifying sediment, filtering the water, and storing and recycling nutrients (Atkinson & Vaughn 2015, Vaughn 2010). Historically, many eastern North American rivers contained immense mussel beds that could stretch for many miles (Haag 2012). In the present day, mussel beds are usually separated by long stream reaches with few or no mussels (Atkinson & Vaughn 2015). Mussel beds are believed to be patchily distributed in rivers because they are constrained to stable sediments with low shear stresses and because mussels recover very slowly from disturbance (Haag 2012).

Mussel Beds as Biogeochemical Hot Spots

Recent work shows that dense mussel aggregations can act as nutrient transformation hot spots in rivers, supporting the rest of the food web and altering nutrient cycling. As mussels feed, they remove living (phytoplankton and bacterioplankton) and detrital organic matter from the water column, metabolize the labile fractions, excrete dissolved nutrients back to the water, and deposit organic nutrients to the sediment as feces and pseudofeces (**Figures 1** and **2**).

In green or photosynthesis-based food webs, nutrient excretion by mussels enhances benthic primary production and influences algal species composition (Atkinson et al. 2013, Spooner & Vaughn 2006). This enhanced primary production supports higher in-stream secondary production of aquatic insects and other primary consumers (Howard & Cuffey 2006, Spooner et al. 2012). Organic energy and nutrients stored in consumers can subsequently be exported to the terrestrial environment, for example, by emerging aquatic insects (Allen et al. 2012, Vaughn 2010) (**Figure 2**). Atkinson et al. (2014c) demonstrated that this food web enhancement is due to mussel-derived nutrients. They performed a field experiment using ^{15}N to track the movement of mussel-derived N from mussel excreta throughout the food web in a stream reach. Mussel-derived N was found in most food web compartments including benthic algae, benthic macroinvertebrates, and macrophytes.

The role of mussels in brown or detritus-based food webs has received considerably less attention. Mussels in green and brown food webs may play similar roles in inorganic nutrient provision, influences on production in microorganisms (algae versus bacteria), and invertebrate secondary production (herbivores versus detritivores or bacterivores). A key difference is that, in brown food webs, mussels supply both inorganic and organic nutrients and energy (feces and pseudofeces) to invertebrates and fish detritivores. For example, Pacific lamprey (*Entosphenus tridentatus*) grow

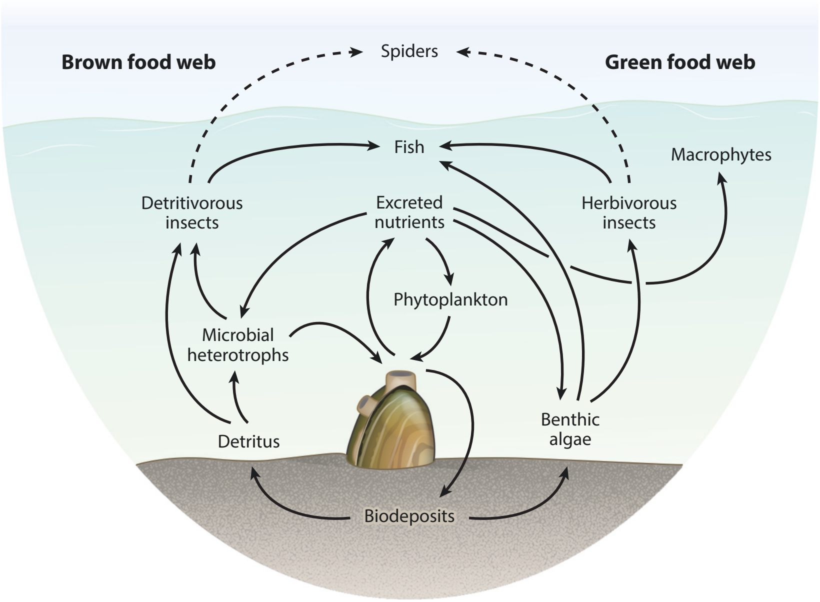


Figure 2

Pools (*terms*) and fluxes (*arrows*) associated with freshwater mussels in riverine food webs. Mussels feed on suspended seston and excrete and biodeposit nutrients that stimulate both autotrophic and heterotrophic production. This results in increased secondary production of herbivorous and detritivorous insects, which supports in-stream fish production and riparian predators.

faster in the presence of mussels, likely because they are feeding on resuspended biodeposits (Limm & Power 2011). Biodeposit particulates also may leach dissolved organic nutrients and C (van Broekhoven et al. 2015), which can be used by heterotrophic microbes (Grenz et al. 1990). Heterotrophic microbes can subsequently be consumed by grazers or detritivores (**Figure 2**). Mussels' roles in transforming and repackaging organic resources through digestive processes and the fate of these repackaged resources in brown food webs are largely unknown and merit exploration.

Nutrients retained, translocated, and transformed by mussels can alleviate nutrient limitation, decrease nutrient loss downstream, change stoichiometric nutrient ratios, and meet a significant proportion of local nutrient demand (Atkinson et al. 2013, 2018; Hoellein et al. 2017). In the stream reach modeled by Atkinson et al. (2014c) above, mussel excretion accounted for 40% of all N, with mussels supplying up to 19% of the N in specific food web compartments.

Context Dependence of Mussel Effects

Mussel effects on nutrient dynamics are context dependent and vary with environmental conditions in ways that depend on overall mussel abundance and mussel species traits. Water volume and discharge in comparison with mussel biomass influence the amount of material that mussels can filter and their role in nutrient dynamics (Strayer et al. 1999, Vaughn 2010). For example, in the Kiamichi River, a 5th-order river in the South Central United States, mussels can process the entire volume of overlying water during summer flow periods but process only a small percentage of the water when discharge is higher during spring and winter (Vaughn 2010). Mussel excretion exceeds background ambient nutrient concentration only during low flow periods (Atkinson & Vaughn 2015). Mussel effects on nutrient dynamics are spatially and temporally heterogeneous because of the patchy distribution of mussel beds, variation in mussel abundance within beds, and seasonal hydrology. Atkinson & Vaughn (2015) mapped mussel biogeochemical hot spots in the Kiamichi River. Although mussel beds make up only 1.45% of the area of the river, they play a significant role in nutrient recycling and storage. However, nutrient recycling and storage rates varied two orders of magnitude among beds, depending on mussel abundance. Mussel excretion has strong effects in nutrient-limited systems (Atkinson et al. 2013) but weak effects where nutrients are not limiting. For example, Spooner et al. (2013) examined how mussel-derived nutrients affected algae and macroinvertebrates across 14 streams in Canada that varied in nutrient loads. In more pristine areas, mussels had strong effects (i.e., increasing algal and macroinvertebrate biodiversity), which were diminished or lost in high-nutrient streams. Finally, mussel species have different physiological traits that influence their filtration and excretion rates; thus, the interaction of temperature regime with species composition can have a large influence on nutrient recycling (Spooner & Vaughn 2008).

Phoretic: a type of interspecies interaction (either mutualist or commensalism) in which one partner is physically moved by the other partner

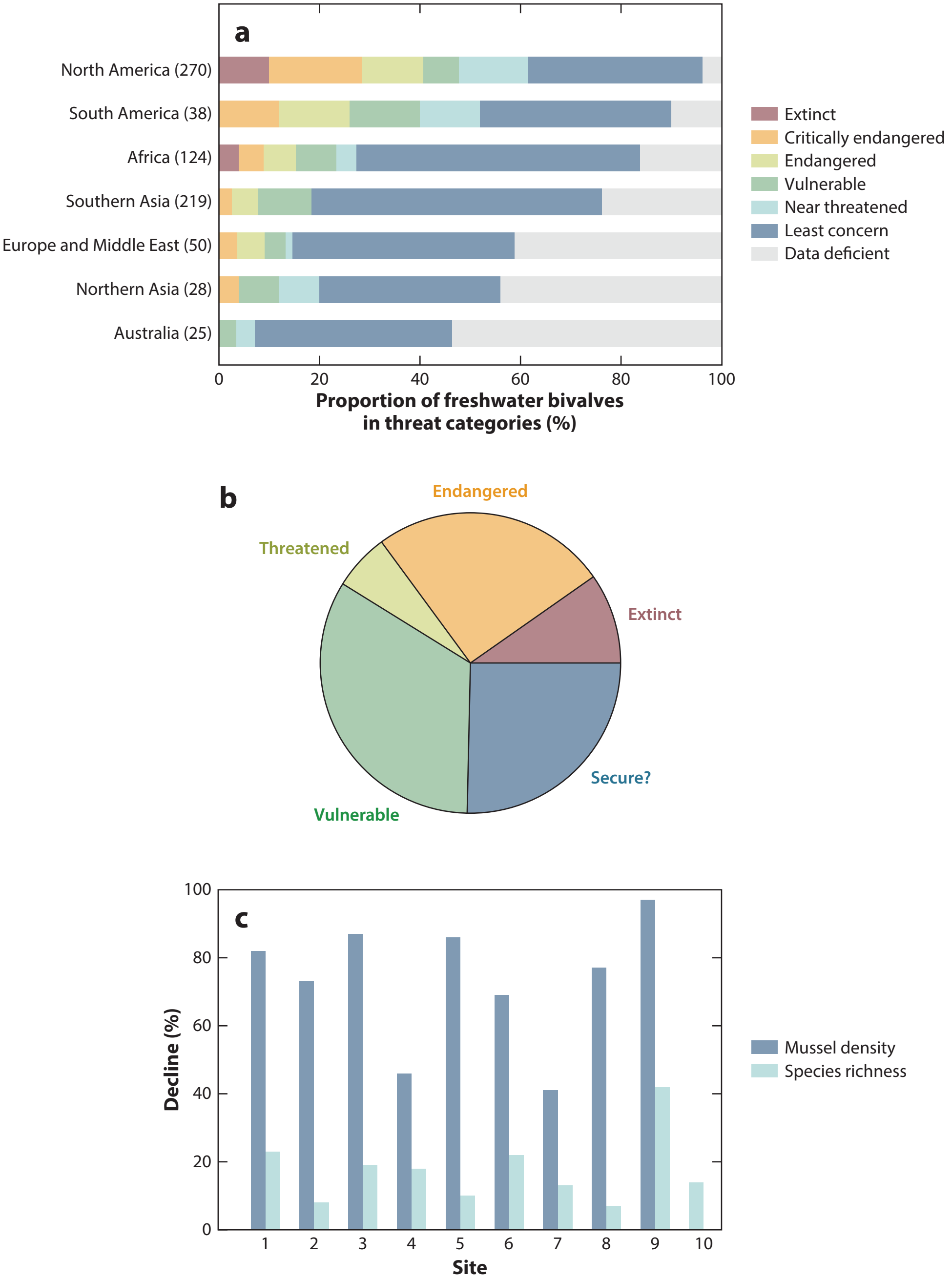
The Unusual Life History of Unionoid Mussels

A unique characteristic of unionoid freshwater mussels is their obligate, ectoparasitic larval stage (glochidia) on the gills or fins of freshwater fish. Adult mussels are sedentary, and the glochidial stage allows mussels to be dispersed to new habitats within rivers and lakes. The glochidial stage is primarily phoretic, usually does not harm the host, and can last from a few weeks to a year (Barnhart et al. 2008). Mussel species vary widely in the type and number of fish host used, the mechanism used to attract and infect the fish, and the timing of glochidial release and development (Barnhart et al. 2008). Glochidia are brooded in the mussel gills, and mussels have evolved a plethora of strategies for attracting and infecting fish hosts. Glochidia can be broadcast in the water much like many marine bivalve larvae. Some species produce aggregates of larvae (conglutinates) that physically resemble fish prey such as insect larvae. Other species form mantle lures that surround the gills and when moving in the water resemble small fish. In the case of conglutinates and mantle lures, a predatory fish bites down and the glochidia are released and become entrapped on the fish gills (Barnhart et al. 2008).

Variation in host use and host abundance has consequences for mussel dispersal and population dynamics, and the absence of mussels in an area can be due to dispersal limitation rather than unsuitable environmental conditions (Schwalb et al. 2015, Vaughn 2012, Vaughn & Taylor 2000). Plasticity in host dispersal can lead to landscape-level population persistence. For example, in Japan, the mussel *Margaritifera laevis* infects a salmonid host, *Oncorhynchus masou masou*. In response to glochidial infection, large fish increase their dispersal distances, avoiding further infection and ensuring that glochidia arrive at new patches, while small fish stay close to home and suffer decreased growth (Terui et al. 2017). Although we have learned much about mussel host requirements in the past 20 years, much more research in needed on mussel–host ecology and how it may be impacted by global change. For example, mussels and fish can respond very differently to changes in discharge and temperature, which could affect coextirpation patterns (Modesto et al. 2018, Spooner et al. 2011).

Global Declines in Mussel Populations

Fresh waters are experiencing biodiversity declines that are far greater than most terrestrial or marine systems, primarily because fresh waters are hot spots for human activities that have led to widespread habitat degradation, pollution, flow regulation, water extraction, overexploitation, and introductions of alien species (Strayer & Dudgeon 2010). Freshwater bivalves have been particularly impacted by human activities, primarily from riverine habitat loss and fragmentation and changes in water quality, and consequently have one of the highest extinction and imperilment rates of any group of organisms (Haag & Williams 2014) (**Figure 3*a***). However, considerable differences can be found in data quality and quantity among regions, and some regions with high freshwater bivalve diversity are very underexplored, particularly large areas of Asia (Lopes-Lima



(Caption appears on following page)

Figure 3 (*Figure appears on preceding page*)

(*a*) Proportion of freshwater bivalves in different threat categories globally according to the International Union for Conservation of Nature. Data downloaded and compiled by Traci Popejoy from **http://www.iucnredlist.org/** on March 5, 2018. Geographic regions are according to Abell et al. (2008). Numbers in parentheses are the number of mussel species in that region. (*b*) Proportion of freshwater mussel species in the United States that are extinct, federally listed as endangered or imperiled, considered vulnerable according to the Nature Conservancy (G1-G3 species not federally listed), or may be secure. Data from the U.S. Fish and Wildlife Service (**https://www.fws.gov/endangered/species/us-species.html**) and NatureServe (**http://www.natureserve.org/conservation-tools/data-maps-tools/natureserve-explorer**), obtained on March 5, 2018. (*c*) Declines in freshwater mussel density and species richness between 1990–1992 and 2003–2005 across 10 monitoring sites in the Kiamichi River, Oklahoma, United States. Panel *c* adapted from Galbraith et al. (2010).

et al. 2017) (**Figure 3*a***), although these regions are also the focus of increasing efforts (Zieritz et al. 2018).

With approximately 300 species, North America is the center of diversity for freshwater mussels. Many North American populations have been intensively studied, starting with mussel stock surveys for the nineteenth-century button industry (see the section titled Use of Bivalves by Humans: Past and Present), and species extinctions and population declines are well documented. In the past 100 years, 30 species have gone extinct, 95 species have been listed as federally endangered or threatened under the U.S. Endangered Species Act, and a large proportion of the remaining species are considered vulnerable (Haag & Williams 2014) (**Figure 3*b***). North American mussel populations have experienced two extinction waves: one between the 1920s and 1980s due to habitat destruction primarily from impoundments; and a second, enigmatic wave from the 1970s onward that has impacted populations even in seemingly pristine habitats. This second wave of extinction is ongoing, its causes are largely unknown, and it is an active area of research (Haag & Williams 2014). As a result of the combination of systematic habitat destruction and enigmatic declines, many mussel species now exist as only one or two small isolated populations, many of which are small and nonviable (Haag & Williams 2014). Projections of contemporary extinction rates forecast continued extinctions of as much as 50% of the remaining North American freshwater mussel species in the twenty-first century (Ricciardi & Rasmussen 1999).

In addition to the loss of species, declines in freshwater mussel populations impact their important functions in streams. The Kiamichi River, described above, is a good case study of this. In this river, a combination of drought and water management has led to more than 60% declines in mussel abundance and species richness over the past 25 years (**Figure 3*c***) (Galbraith et al. 2010, Vaughn et al. 2015). Vaughn et al. (2015) estimated that these declines have diminished mussel biofiltration, N and P recycling, and N, P, and C storage, in some cases by more than 50%. In a related study of drought effects in three small rivers, mussel declines and changes in species composition decreased availability of N and reduced P storage, potentially altering system nutrient availability (Atkinson et al. 2014b).

IMPACTS OF OYSTER REEFS IN ESTUARIES

Oyster reefs are colonies (family Ostreidae) where juveniles attach to hard surfaces and serve as epifaunal ecosystem engineers (see the sidebar titled Ecosystem Engineers) in shallow marine environments worldwide. Oyster activity and reef complexity, like freshwater mussels, affect filtration, habitat, food webs, nutrient dynamics, hydrodynamics, and harvest in coastal oceans. Although oyster reefs have declined globally, research on the ecosystem roles of oysters has grown due to interest in using aquaculture and restoration to recover ecosystem services (Beck et al. 2011, Coen

ECOSYSTEM ENGINEERS

Organisms that create, modify, or maintain habitat can be considered ecosystem engineers. Ecosystem engineers can control the availability of resources to other species by causing physicals state changes in biotic or abiotic materials. Common examples of ecosystem engineers include trees and earthworms.

et al. 2007). We use the well-studied eastern oyster (*C. virginica*) as a case study of oysters' role in ecosystem processes and services.

Oyster Reef Growth and Conservation Status

Reef building is a key component to *C. virginica*'s epifaunal life history and ecosystem effects and is sustained via larval recruitment. Adults spawn once per year, triggered by temperature cues. The larvae (i.e., veligers) are distributed by currents and settle in a crawling form (i.e., pediveligers) to the substrate, where they search for hard substrate on which they cement themselves and metamorphose into juveniles (Kennedy 1996). Thus, oyster reef growth is sensitive to anthropogenic changes in estuaries, which affect any of the stages of reproduction and recruitment. For example, dispersal and attachment are affected by alterations to water currents, reduction in availability of benthic substrate, and loss to overharvest of existing reefs. In addition, although *C. virginica* has evolved to withstand wide variability in temperature and salinity typical of estuarine habitats, anthropogenic changes to temperature and salinity regimes can have significant impacts on reproduction and larval recruitment (Shumway 1996).

The size and condition of oyster reefs have declined approximately 85% relative to historical conditions at a global scale, and restoration of historical populations is a focus of recent research (Beck et al. 2011, Zu Ermgassen et al. 2013). Common stressors to oyster reefs include overharvest of wild oyster fisheries and anthropogenic development in coastal ecosystems including dredging, anoxia, sediment, disease, and invasive species (Beck et al. 2011). The Hudson River Estuary is an example of extreme anthropogenic influence, as the historically abundant oyster reefs are now considered functionally extinct (Franz 1982, NOAA 2007). Ongoing improvements in water quality suggest oyster survivorship is now possible in New York City waterways (Hoellein & Zarnoch 2014, Levinton et al. 2011), and significant investments in restoration and research are underway (Handel et al. 2016). We further examine use of *C. virginica* reef restoration as a case study for bivalve-mediated ecosystem services in the section below titled Use of Bivalves by Humans: Past and Present.

Oyster Reefs as Biogeochemical Hot Spots: Context Dependence

C. virginica reefs are hot spots for biodiversity and biogeochemical transformations (Grabowski & Peterson 2007). Major ecosystem transformations of energy and elements include their capacity for filtration and biodeposition (i.e., benthic–pelagic coupling); three-dimensional reef structure, which provides habitat and affects hydrodynamics; and widespread use in aquaculture. Considerable research has been conducted to document the environmental factors that drive oysters' role in estuarine ecosystems (Dame 2012, Kellogg et al. 2014).

Oyster-enhanced water clarity via assimilation and transformation of nutrients is a focus of their role as a hot spot for biogeochemistry, but rates vary widely according to environmental conditions. Oyster filtration removes nutrients from seawater via harvest (i.e., removal of soft tissues and shells); burial of biodeposits, soft tissues, and shells; and production of C and N gases from microbial conversion of elements in biodeposits (DePiper et al. 2017). For example, Higgins et al. (2011) estimated that harvest of aquaculture oyster soft tissue and shell removes more N from seawater than other best management practices (e.g., cover crops) in the Chesapeake Bay when considered by area (132 kg TN/ha/year). In urban or polluted environments where harvest of oyster tissues and shells is restricted, nutrient removal by oysters is limited to burial and denitrification, which can also be significant. Cerco (2015) concluded that 28% of biodeposit N from oysters is buried or denitrified. Oyster filtration has the capacity to increase the growth of submerged aquatic vegetation (SAV), which supports nutrient removal in adjacent habitats such as seagrass and salt marshes. These vegetated habitats in turn serve as hot spots of ecological activity, by providing critical habitat variability, coastline protection, and nutrient sinks in the shallow marine environment (Grabowski et al. 2012, Zarnoch et al. 2017).

Submerged aquatic vegetation (SAV): aquatic plants that grow on the benthic surface but do not emerge above the water

The influence of oyster reefs on ecosystem processes varies by context, with factors such as density, seasonality, and hydrodynamics as overarching drivers (Green et al. 2013, Smyth et al. 2015). Reefs with dense populations have greater abundance of living and spent shells, clearance rates, habitat heterogeneity, and secondary production (Peterson et al. 2003, Zu Ermgassen et al. 2013). In very dense assemblages, however, biodeposits may generate anoxia at the SWI, stimulating efflux of reduced compounds and P. Where nitrification serves as the dominant source of nitrate for denitrification, anoxic sediments can inhibit nitrification and thereby reduce nutrient sequestration and denitrification (Higgins et al. 2013, Newell et al. 2005, Smyth et al. 2015). Seasonality drives oyster filtration, growth, and food availability. Growth rates of *C. virginica* peak in the middle of its range (i.e., Chesapeake Bay) and decline to the north and south (Dame 2012). Higher clearance under optimum conditions can increase biodeposition and N loss via denitrification (Hoellein et al. 2015, Humphries et al. 2016). However, filtering by oysters can change phytoplankton communities, reduce food availability, and alter benthic–pelagic coupling (Prins et al. 1997). Hydrodynamics affect oysters' ecosystem role via changes to particle distribution and settling, juvenile recruitment, and erosion (La Peyre et al. 2015, Lenihan 1999). In addition, water currents and tides can advect oyster biodeposits and oyster-derived nutrients to adjacent habitats (e.g., seagrass beds) (Barbier et al. 2011, La Peyre et al. 2015).

Eutrophication is a major driver of oyster filtration rates and plays a role in ecosystem biogeochemistry and reef growth (Hoellein & Zarnoch 2014, Newell et al. 2005). With high turbidity, oyster biofiltration may not affect water clarity, and individuals may suffer energetic losses from high rates of pseudofeces production (i.e., increased inability to separate high-quality food particles from nonnutritious particles in turbid waters) (Cranford et al. 2011). Additionally, shading reduces SAV. Sedimentation damages oyster reefs and reduces recruitment (Rothschild et al. 1994). Anoxia in eutrophic sediments enhances nutrient efflux and inhibits nitrification (Newell et al. 2005). In anoxic conditions, nutrients in biodeposits may be recycled (i.e., mineralized) at a greater rate than can be assimilated by SAV or denitrified (Hoellein & Zarnoch 2014). Low dissolved oxygen and changes to freshwater runoff impact survivorship and disease (Levinton et al. 2011). In Chesapeake Bay, historical losses of oyster reefs from overfishing and disease may have exacerbated phytoplankton blooms due to loss of filter feeders (Kemp et al. 2005). Finally, eutrophication often occurs with industrial and wastewater pollution, which restricts oyster harvest and consumption (Sebastiano et al. 2015).

USE OF BIVALVES BY HUMANS: PAST AND PRESENT

Historical Use

Demand for products from bivalve shells and soft tissue has driven the historical relationship between human cultures and bivalve communities in marine and freshwater environments. Bivalve shells preserve well in middens, which serve as long-term archives of their historical uses. Bivalves were an important protein source for early humans, particularly in coastal communities (Erlandson 1988, Rick et al. 2016). Shells are found in middens as far back as 110,000 years ago (Langejans et al. 2012), and Aristotle described bivalves common in the diet of ancient Greeks (Voultsiadou et al. 2010). Freshwater mussels, oysters, and clams were harvested seasonally by early Native Americans in the southeastern United States (Claassen 1986, Rick et al. 2016).

Early humans used bivalve shells as cooking pots and utensils and as blades and scrapers for cutting and skinning animal hides (Douka & Spinapolice 2012, Joordens et al. 2015). In addition, bivalve shells were one of the earliest forms of currency. Clams were used as currency by early Native Americans, and spiny oysters and Panamanian pearly oysters were traded in South America. Finally, humans have long been inspired by the symmetry and beauty of bivalve shells, and they have been used to make jewelry for thousands of years, particularly mother of pearl from oysters and freshwater unionoid mussels. Mayans carved bivalves into the walls of their public buildings, scallop shells were used as emblems in the Catholic Church, and early settlers in the southeastern United States decorated graves with freshwater mussel shells (Haag 2012).

Unionoid mussels have been harvested for natural pearls, to manufacture buttons, and to serve as nuclei for cultured pearls grown in marine oysters. North American pearl harvests began in the 1850s and subsided in the early 1900s due to overharvesting and competition from the button industry, with more than 50,000 tons of mussels harvested at the industry's peak in 1912. Beginning in the 1890s, freshwater shells from North American rivers were used to produce buttons. At this industry's peak in 1916, more than 5.75 billion buttons, valued at $230 million in today's dollars, were produced (Haag 2012). In the early 1900s, the Japanese began producing cultured pearls by planting a bead made from a thick-shelled North American mussel in the marine pearl oyster (*Pinctada*). This practice led to a resurgence of shell harvesting in North America, peaking in 1993 when 6,262 tons of shell were harvested. Commercial shell harvest in the United States declined rapidly after the 1980s, when the cultured pearl industry began using shell from China in combination with the development of nuclei-free culture techniques (Haag 2012).

Current Use

Collectively, the benefits that humans derive from healthy ecosystems are considered ecosystem services (see the Millennium Ecosystem Assessment, **https://www.millenniumassessment.org**). Present-day human cultures derive benefits from bivalves via direct and indirect use. Direct benefits include food production and commercial products such as road building material, concrete production, fertilizer, and cultured pearls. Indirect benefits of healthy bivalve communities include shoreline stabilization and nutrient mitigation.

Fishing and aquacultural production of bivalves is a billion-dollar global industry. Although estuarine bivalves make up the vast majority of bivalves consumed by humans, freshwater mussels and clams (*Corbicula* sp.) are an important food resource in southeast Asia (Zieritz et al. 2018). Global harvest (capture fisheries and aquaculture) of marine bivalves in 2015 was more than 16 million metric tons and divided among oysters (24%), mussels (18%), scallops (25%), and clams (33%) (FAO 2017). Estuaries around the world are in a state of decline following decades or more of overfishing, pollution, and climate change (Rick et al. 2016), and commercial bivalve capture has decreased. However, aquaculture production of bivalves has increased and made up 89% of the total bivalve harvest in 2015 (FAO 2017). Future bivalve aquaculture is threatened by ocean acidification from climate change, which affects carbonate mineral saturation and thus impacts shell formation. This stress will be greatest in low-latitude regions where warmer waters co-occur with the highest rates of human population growth. Some of the countries most dependent on seafood for dietary protein include developing island nations with few agricultural alternatives (Cooley et al. 2009). Revenue declines, job losses, and indirect economic costs may occur if climate change, pollution, and ocean acidification damage marine habitats, alter marine resource availability, and disrupt other bivalve-mediated ecosystem services (Cooley et al. 2009).

Oysters are often considered a prime example of ecosystem services provided by animals because their activities result in multiple benefits for humans: They filter coastal waters and recycle nutrients (described above), stabilize shorelines, and provide habitat for other organisms. We use their shells for multiple purposes, and in the end, we eat them (Grabowski et al. 2012, Humphries & La Peyre 2015). Finally, the cultural value of oysters has more recently been incorporated into the framework of ecosystem services. For example, oyster festivals occur around the globe and are important to local economies and cultural identity. Students in New York City were engaged in a program with environmentally focused community service activities including participation in neighborhood gardening, river clean ups, and oyster restoration. Students showed significantly increased ecological place meaning, or overall perceptions about nature and its importance in their community, which is linked to place-specific, pro-environmental behaviors as adults (Kudryavtsev et al. 2012).

CONCLUSIONS

The field of research on bivalve-mediated ecological processes is vast. Assembling the analytical framework to compare measurements of ecosystem function among species that vary by lifestyle, habitat, and human use is a considerable challenge. Synthesis of data requires expertise in a wide variety of disciplines including physiology, population and community ecology, biogeochemistry, landscape ecology, ecosystem management, and social science. Thus, research advancements will require greater collaboration among scientists of all types (Satz et al. 2013).

For example, both oysters and unionoids are subjects for restoration (Beck et al. 2011, FMCS 2016), yet few cross-disciplinary analyses have been conducted between freshwater and marine researchers. In addition, our assessments of ecosystem services provided by bivalves suggest that input from social scientists and economists is needed to translate ecological data for diverse audiences in research, management, and education. Although many aspects of bivalve impacts remain underexplored, the synthesis of information collected in this review led us to generate conclusions for future research. The areas listed below are topics we suggest merit particular attention in cross-disciplinary research in bivalve ecology.

FUTURE ISSUES

1. Further examination of the use of existing and restored bivalve populations as biofilters for the removal of chemicals, metals, and pathogens from the environment is needed.
2. Future research should quantify the role that bivalve individuals and assemblages play in biogeochemical transformations, particularly nitrification–denitrification, and how this may vary with background environmental conditions, bivalve population densities, and community composition.
3. Measurements should be taken of all aspects of bivalve microbiomes and associated processes, including those involved with mutualisms, parasites, nutrient transformations, and pathogen virulence.

4. The potential relationships between freshwater bivalves and endosymbiotic microorganisms should be explored.
5. Complete comparative research should be performed on how food webs change when bivalves invade new areas, particularly how this may lead to novel trophic links within aquatic ecosystems, among different aquatic habitats, and across aquatic–terrestrial connections.
6. Physiological and molecular biomarkers should be examined to assess stress or immune responses in bivalves and how these responses influence their role in ecosystem biogeochemistry.
7. The influence of global climate change on bivalve-associated organisms, including symbiosis and parasites in marine bivalves and mussel–host ecology in freshwater unionids, should be explored.
8. Researchers should standardize and assign value to ecosystem services (i.e., currency or other culturally important priorities) via direct and indirect market values for diverse bivalve taxa, not only those with a high profile in fisheries and restoration.

DISCLOSURE STATEMENT

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