SYMPOSIUM

Ecosystem Engineers in the Pelagic Realm: Alteration of Habitat by Species Ranging from Microbes to Jellyfish

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Synopsis Ecosystem engineers are species that alter the physical environment in ways that create new habitat or change the suitability of existing habitats for themselves or other organisms. In marine systems, much of the focus has been on species such as corals, oysters, and macrophytes that add physical structure to the environment, but organisms ranging from microbes to jellyfish and finfish that reside in the water column of oceans, estuaries, and coastal seas alter the chemical and physical environment both within the water column and on the benthos. By causing hypoxia, changing light regimes, and influencing physical mixing, these organisms may have as strong an effect as species that fall more clearly within the classical category of ecosystem engineer. In addition, planktonic species, such as jellyfish, may indirectly alter the physical environment through predator-mediated landscape structure. By creating spatial patterns of habitats that vary in their rates of mortality due to predation, planktonic predators may control spatial patterns and abundances of species that are the direct creators or modifiers of physical habitat.

Introduction

In a seminal paper, Jones et al. (1994) defined ecosystem engineers as ''organisms that directly or indirectly modulate the availability of resources to other species by causing physical state changes in biotic or abiotic materials. In doing so they modify, maintain and/or create habitats''. Although beavers were the first engineer identified in the original paper and continue to be cited as the archetypal example of an engineer, Jones et al. (1994) provided an extensive list of organisms ranging from micro-algae to forest trees, and the concept has been applied to a wide range of spatial and temporal scales and habitats (Wright and Jones 2006). Knowledge that organisms modify their physical environment certainly pre-dates the 1990s (Buchman et al. 2007), but formalization of the concept of ecological engineering has provided a language and theoretical construct to describe the ways that species that do not interact trophically or through direct competition for resources alter the availability and suitability of a habitat for other species.

In the marine realm, the concept of ecosystem engineering has most often been applied to species that either attach to, or directly interact with the benthos. Corals, bivalves, kelps, and sea grasses are classic examples of species that modify the physical habitat in a number of ways and create structured habitat for other species (Coen et al. 2007; Grabowski and Peterson 2007; Lambrinos 2007; Arkema et al. 2009; Koch et al. 2009). In addition, species that modify sediments have received increasing attention for their direct and indirect effects on the suitability of benthic habitat for other organisms (Levinton 1995; Woodin et al. 2010).

In contrast, the issue of ecosystem engineering in the pelagic realm has received far less attention, perhaps because the physical structure that is altered is not visually obvious. Jones et al. (1997) suggested

eight characteristics of systems that are likely to increase the importance of physical ecosystem engineering, only one of which applies to the pelagic realm, and suggested that the "pelagic zones of the waters of the earth, seem unlikely to be dominated by engineering effects". They did, however, provide examples of pelagic ecosystem engineers, including marine and freshwater phytoplankton, which affect light and heat within the water column, and marine zooplankton, whose sinking fecal pellets transport materials vertically within the water column (Jones et al. 1994).

Spatial variation in physical (including chemical and kinetic) properties creates important structure within water columns of the earth's oceans and estuaries, influences global climate and affects processes ranging from rates of encounter between predators and prey to the transport of organisms and materials. Features such as stratification, currents, and light penetration are commonly understood to affect behaviors, distributions, and the evolution of aquatic organisms. Water motion at scales ranging from micro-turbulence to global thermohaline circulation transports heat, materials, and organisms as well as water. The extent to which these sorts of features of the marine realm are "engineered" by biota, and how this alteration of the water column falls under that concept of ecosystem engineering has not been as thoroughly explored.

Our goal in this synthesis is to present examples indicating the range and importance of ecosystem engineers in the pelagic realm. To do this, we focus on three general classes of engineers and engineering comprising important and large-scale effects on marine ecosystems: creation of hypoxia and anoxia by microbes, alteration of the light and heat structure of the water column by phytoplankton, and mixing of water by mobile organisms within the water column. We also consider the importance of predator-mediated structure of the landscape—a case in which dominant consumers can indirectly control physical habitat through trophic control of ecosystem engineers. We use not only an inclusive definition of ecological engineering based on the original 1994 publication and its examples, but also include metabolic processes that dramatically alter the environment because these can be so important in aquatic environments. In considering the importance of the concept of ecosystem engineering to the pelagic realm, we also emphasize the kinds of structures, materials, and material transformations, as well as the temporal and spatial scales that affect organisms dwelling in the water column.

Hypoxia: microbes as ecological engineers

Low-dissolved oxygen concentrations are ubiquitous in coastal waters of the world's oceans and include near-shore/estuarine waters affected by anthropogenic enrichment of nutrients as well as permanently hypoxic oxygen-minimum zones in the open ocean. These regions are vast, and are estimated to cover over 1.1 million km^2 of sea floor (Helly and Levin 2004; Diaz and Rosenberg 2008). The prevalence and severity of hypoxia in near-shore and estuarine waters has increased substantially over the past 60 years with increases in use of fertilizers and in the size of human populations, with reports of hypoxia in over 400 systems (Diaz and Rosenberg 2008). Hypoxia (low-dissolved oxygen) and anoxia (the absence or near absence of dissolved oxygen) affect survival, growth, reproduction, and food–web interactions of a wide variety of organisms (Breitburg 2002; Breitburg et al. 2009; Levin et al. 2009). Besides lack of oxygen, some anoxic waters contain high levels of sulfides (H_2S) that are toxic to most macro-fauna. As a result, hypoxia and anoxia have qualitatively different effects on biota. The extent, severity, and effects of hypoxia are predicted to worsen with global warming because increased temperatures are associated with reduced solubility and rapid biological depletion of oxygen, increased requirements for oxygen by many species, increased water-column stratification, and a shallowing of oxygen-minimum zones (Helly and Levin 2004; Intergovernmental Panel on Climate Change 2007).

Microbial metabolism is responsible for the depletion of oxygen, the accumulation of toxic hydrogen sulfide, and the transformation of sulfides into harmless chemicals. In so doing, these microbes engineer environments in ways that affect their suitability for a wide range of organisms. Ecosystems that experience hypoxia and anoxia are commonly referred to as "dead zones" because they exclude fish and eliminate benthic organisms. These zones, however, are not really dead. In fact, the abundance and production of bacteria in anoxic waters is often greater than that in overlying oxic waters (Cole and Pace 1995; Taylor et al. 2001) due, in part, to reduced grazing pressure (Fig. 1). One negative impact of expanding dead zones in the coastal margin is a significant loss of habitat that reduces the production of fish and other valuable organisms, with losses estimated at over 9 million metric tons (wet weight) annually (Diaz and Rosenberg 2008). However, from the perspective of bacteria and other microbes, this could be considered a positive impact. Biomass that might
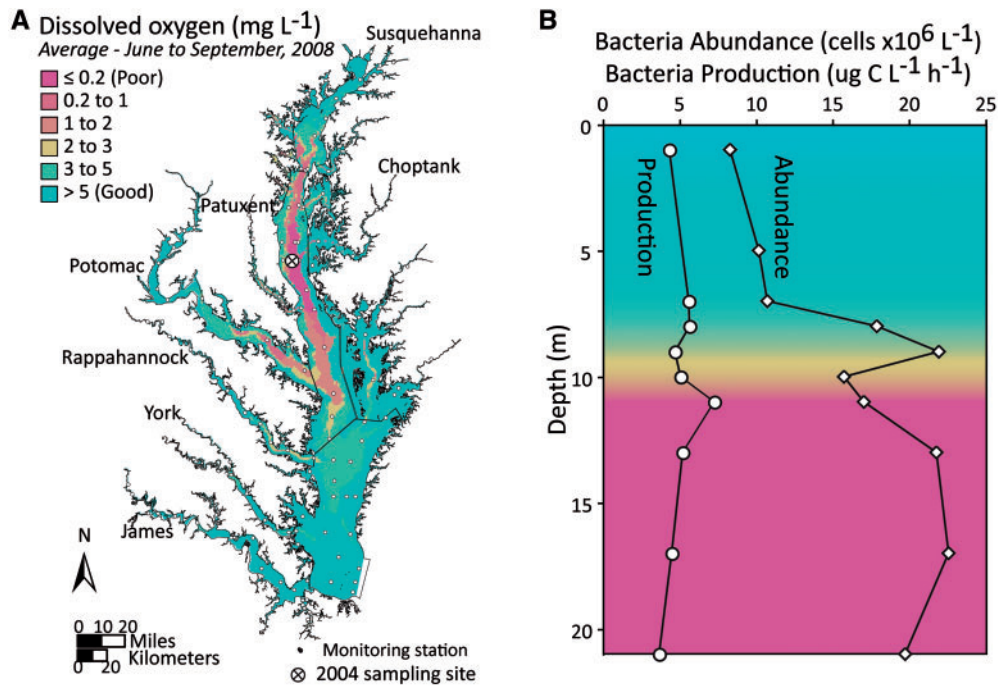
Fig. 1 During midsummer, bottom waters in Chesapeake Bay become anoxic, as shown in (**A**) for 2008 (map from Ecocheck, www .eco-check.org/reportcard/chesapeake. Data from Virginia Institute of Marine Science, http://webvims.edu/bio/sav). Samples collected in the deep central channel of the bay during July 2004 (**B**) indicated that bacterial abundance and production remained high in anoxic, sulfidic bottom waters (Figure redrawn from Crump et al. 2007).

have supported the lost secondary production instead supports microbial communities and fuels diverse microbial metabolisms that engineer the chemistry of the water column.

On the longest time scale, microbes are ultimately responsible for the oxygenated atmosphere on this planet through the evolution of oxygenic photosynthesis (Nisbet and Sleep 2001). This pool of oxygen is very large relative to global estimates of oxygen consumption by microbial respiration in aquatic systems (del Giorgio and Williams 2005). However, oxygen is not especially soluble in water, and is nearly 45 times less soluble than CO_2 at 20°C. Thus, the oxygen concentration in water is sensitive and is set by the balance between oxygen consumption by aerobic respiration and replenishment from the atmosphere and from oxygenic photosynthesis. Water becomes particularly sensitive to hypoxia and anoxia when it is sequestered from the atmosphere by stratification (see Biogenic mixing section), especially in the dark (see Modification of the light environment section). This dark, sequestered condition describes most of the volume of aquatic environments on this planet, including the bottom waters of stratified lakes and estuaries, and most of the oceans below the euphotic zone.

In many estuaries and coastal regions, stratification in summer and limited transparency of water

create hypoxia-sensitive bottom waters. Sinking algal biomass fuels aerobic respiration by heterotrophic microbes, and hypoxic/anoxic zones develop. The loss of oxygen signals a major shift in the eukaryotic biology of these ecosystems, eliminating organisms ranging from protists to fish, but it appears that for prokaryotic communities (e.g., bacteria) the change has only a limited effect.

The loss of oxygen in aquatic ecosystems does not halt respiration of organic matter because bacteria switch to alternative electron acceptors and continue to respire. A study in the Chesapeake Bay showed chemical evidence of a succession of respiratory processes that dramatically altered the chemistry of bottom waters (Crump et al. 2007). After oxygen was eliminated and the water column became sub-oxic (i.e., anoxic but with no accumulation of sulfide), microbes began using nitrate to respire organic matter, leading to the accumulation of nitrite from nitrate-based respiration, ammonia from mineralization of organic nitrogen, and N_2 from denitrification (Kana et al. 2006) and anammox (Rich et al. 2008). When nitrate was used up, microbes switched to other electron acceptors, possibly oxidized manganese and iron, resulting in the accumulation of reduced metals (Gavis and Grant 1986; Van Cappellen et al. 1998; Trouwborst et al. 2006; Crump et al. 2007). Remarkably, up to this point

in the respiratory succession, the dominant phylo-types of bacteria did not change and the community in anoxic waters remained rather similar to the community in the overlying oxic zone. This suggests that these microbes are genetically equipped to carry out several respiratory metabolisms, to remove or transform a wide range of oxidants (oxygen, nitrate, iron, manganese), and to make several major changes to the chemical conditions in the anoxic zone.

In July, however, sulfides began to accumulate in the anoxic zone and the system went through another major chemical and biological shift. Sulfides are produced by sulfate-respiring bacteria in the sediments and water column (Tuttle et al. 1987), and for much of the year they are removed from the water column through reactions with oxygen and other oxidants either chemically or by chemoautotrophic sulfur-oxidizing bacteria. Once these oxidants are used up, however, sulfides accumulate and maintain anoxic conditions by reducing all available oxygen and other oxidants (Jonas 1997). At this point, the phylogenetic composition of the microbial community changed (Crump et al. 2007). Thus, it appears that once the system becomes sulfidic, the sub-oxic microbial community can no longer thrive because of the lack of oxidants, the presence of toxic sulfides, or both. This community is replaced by a new community that can reduce sulfate and can thrive in an environment flooded with sulfides.

Changes in the chemical environment caused by heterotrophic bacteria create conditions that are unsuitable for organisms dependent on aerobic respiration but are ideal for chemoautotrophic microbes that contribute to the dramatic chemical modification of hypoxic and anoxic waters. Chemoautotrophic activity can be expected in any environment in which energetic pairs of oxidized and reduced inorganic molecules occur, and this condition is typical of hypoxic and anoxic water columns. Chemoautotrophs use the energy in these redox pairs to fix carbon in much the same way that photoautotrophs use light energy. Chemoautotrophic microbes oxidize ammonia, nitrite, sulfide, and other reduced products of respiration that use oxygen in hypoxic waters (Taylor et al. 2001; Dai et al. 2006), or nitrate and other oxidants in anoxic waters (Dalsgaard et al. 2003; Jost et al. 2010). Recent evidence suggests that, in some hypoxic and anoxic waters, chemoautotrophic production of organic matter can be high enough to fuel microbial food webs (Taylor et al. 2001; Yilmaz et al. 2006), and have major impacts on chemical conditions. In the Pearl River Estuary, for example, oxidation of ammonia and nitrite by nitrifying organisms

can be high enough to significantly reduce oxygen concentrations (Dai et al. 2006).

The Benguela system, located off the western coast of Africa, is among the most productive regions of the world's oceans (Carr 2002). Very high production of phytoplankton in that region often fuels microbial respiratory succession in sediments and bottom water. This succession can progress to a point where sulfides are highly concentrated (Bruchert et al. 2009). These events are thought to cause massive fish kills in Namibian coastal waters (Weeks et al. 2002). In fact, hypoxia and the toxic effects of this sulfide are thought responsible for low fish catch in this system relative to other eastern boundary-current regions of the world (e.g., the Humboldt current off South America) (Carr 2002). However, a recent study described "detoxifying" blooms of chemoautotrophic bacteria in anoxic waters that oxidized tremendous amounts of sulfide to form harmless sulfur and sulfate using nitrate as an oxidant (Lavik et al. 2009). It seems clear that chemical conditions in the water column, including the concentration and form of oxygen, carbon, nitrogen, sulfur, and other key elements are tightly controlled by the metabolism of heterotrophic and autotrophic microbes, and can directly impact higher trophic levels.

Modification of the light environment: phytoplankton as engineers

Phytoplankton-imposed structure on the physical environment in ways that affect the availability of resources for themselves and for other organisms, and therefore meet the formal definition of ecosystem engineers. Phytoplankton engineer the physical environment of the water column through their cellular structure and metabolic function, which may be crudely characterized as ubiquitous, pigment-bearing particles that produce organic matter and oxygen through photoautotrophy. As pigment-bearing particles residing near the surface, they affect the photic, chemical, and thermal regimes of waters in both obvious and unexpected ways.

The study of the effects of phytoplankton on the photic regime has been pursued by biological oceanographers interested in primary productivity (Ryther and Yentsch 1957) and optical oceanographers interested in developing satellite remote-sensing algorithms (Morel and Prieur 1977). All phytoplankton contain the photosynthetic pigment, chlorophyll *a*. Phytoplankton chlorophyll is one of three broad classes of materials that absorb and scatter light, the other two being colored dissolved organic matter

(CDOM) and suspended particulate matter (SPM). For the purposes of deriving remote-sensing algorithms, optical oceanographers distinguish between Case 1 waters, which are distant from terrestrial inputs of CDOM and SPM, and Case 2 waters, which are influenced by terrestrial CDOM and SPM. Case 1 waters are considered to be optically simpler, because all of the light-attenuating processes can be parameterized in terms of chlorophyll *a*.

Radiative transfer models allow us to simulate the effect of phytoplankton chlorophyll *a* on the depth of the photic zone, defined here as the depth of penetration of 1% of surface-incident photosynthetically active radiation. In Case 1 waters, the underwater light field may be simulated as a function of chlorophyll concentration alone (Fig. 2). Due to the exponential decline of light underwater and to spectral effects, a 1000-fold change in chlorophyll concentration leads to a 100-fold change in depth of the photic zone. Ecological consequences of the steepening of the light gradient by increasing concentrations of phytoplankton include a reduction in the range of depth over which primary productivity occurs. As a result, the spatial distribution of trophic interactions throughout the food web can be affected. A second direct consequence of a compressed photic zone is that the distance that vertically migrating zooplankton must swim to reach an aphotic refuge from visually orienting predatory fish is reduced (Dodson 1990), potentially opening the water column up to species having a shorter vertical range.

In coastal Case 2 waters, there are terrestrial sources of CDOM and SPM, and thus the effect of phytoplankton on the depth of the photic zone must be considered in the context of these other two
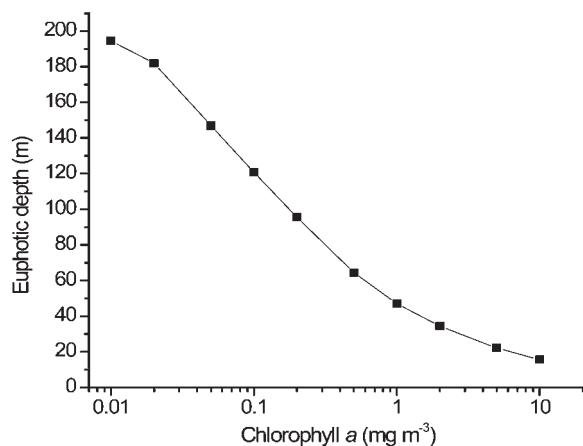
factors. Additionally, in coastal waters subject to anthropogenic nutrient loading, light attenuation caused by excessive growth of phytoplankton is viewed as detrimental to the structural complexity of the habitat afforded by submersed vascular plants (Duarte 2002). The shift from benthic to planktonic primary producers has been analyzed as examples of alternate stable states (Zaldívar et al. 2009), and of response to crossing thresholds (Kemp et al. 2004). Although clearly associated with a loss of quality of the habitat (Duarte 2002), such transitions are, nevertheless, structural modifications of the physical environment with ramifications for macroflora and macrofauna.

The light available to submersed aquatic vegetation (SAV) growing in shallow water may be modeled from a knowledge of the optical properties of the three primary attenuators of light, CDOM, chlorophyll *a*, and SPM (Fig. 3; Gallegos 1994, 2001). To do so requires some knowledge of the light requirements of the SAV at a site, variously estimated to range from 11% to 45% of average surface incident light (Duarte et al. 2007). For this example, we used 22% of surface irradiance, which is the average light requirement for SAV in mesohaline and polyhaline Chesapeake Bay (Kemp et al. 2004). Figure 3 shows
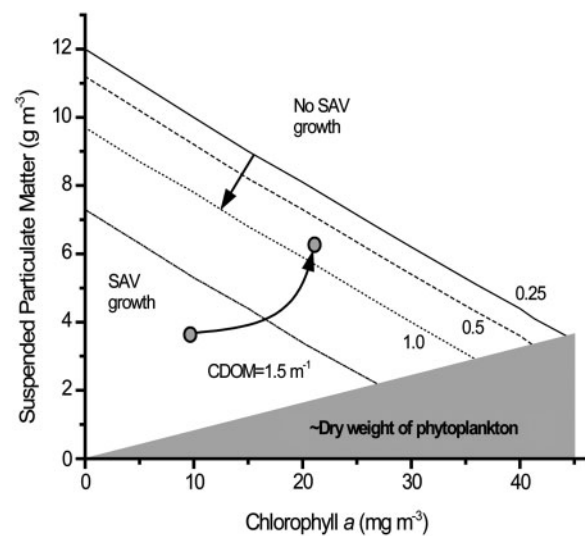

Fig. 3 Contours of concentrations of chlorophyll concentration and suspended particulate matter that allow 22% of surface incident irradiance to penetrate to a depth of 1.5 m with different concentrations of CDOM (numbers on lines). Trajectory arrows show hypothetical eutrophication in which nutrient loading results in a doubling of chlorophyll concentration; concomitant changes in SPM and CDOM may move a system from conditions that support SAV to conditions that do not (gray circles). Gray triangle represents approximate contribution of phytoplankton to SPM concentration.

Fig. 2 Depth of the euphotic zone as a function of chlorophyll concentration as simulated by the radiative transfer program Hydrolight 5.0 for Case 1 waters.

combinations of suspended solids and chlorophyll concentrations that, on average, allow enough light for SAV to grow to a depth of 1.5 m, with different line styles corresponding to a range of CDOM concentrations from 0.25 to 1.5 m^{-1} (measured as absorption at 440 nm). The complex dependence of availability of light on the concentrations of all three optical constituents in coastal and estuarine systems is readily apparent. A hypothetical trajectory is shown whereby a system initially having conditions supportive of SAV (open circle at Chl$a = 10$ mg m^{-3}, SPM $= 4$ g m^{-3}, CDOM $= 0.25$ m^{-1}) is driven by eutrophication to a state that no longer supports SAV (gray circle at Chl$a = 20$ mg m^{-3}, SPM $= 6$ mg m^{-3}, CDOM $= 1$ m^{-1}). Losses of SAV and associated changes to the physical habitat in eutrophying systems may be sudden and catastrophic (Orth and Moore 1983). Similar effects of shading due to increasing chlorophyll on microphytobenthos have been documented along a gradient of eutrophication in the Bodden (southern Baltic Sea, Germany) (Köster et al. 1997).

These examples only consider the effects of undifferentiated phytoplankton pigment on the penetration of light. At the species level, a striking example of the effects of phytoplankton on the physical environment is seen in blooms of the prymnesiophyte, *Emeliana huxleyi*. The cells of *E. huxleyi* are covered with delicately ornamented calcite plates that are highly effective at scattering light (Voss et al. 1998). During the course of a bloom, cells shed these coccoliths that may reach concentrations of 3×10^5 ml^{-1}. The intense backscattering associated with high concentrations of coccoliths turns water a milky aquamarine color that is easily recognized in satellite images, making the global distribution of *E. huxleyi* the best understood of any species of phytoplankton (Tyrrell and Taylor 1996). Blooms of *E. huxleyi* are favored under conditions of high-surface insolation (Egge and Heimdal 1994), a shallow-mixed layer (depth <20 m) and positive temperature anomalies (Raitsos et al. 2006), which are typical of northern latitude areas such as the subarctic North Atlantic and Bering Sea in summer (Tyrrell et al. 1999).

The light-scattering properties of coccoliths have a profound effect on the optical properties of the water column (Tyrrell et al. 1999). Intense scattering of light by high concentrations of coccoliths enhances scalar irradiance (i.e., light coming from all directions) near the surface (upper 5 m), and reduces irradiance at greater depths. Calculations of the effect of a bloom of *E. huxleyi* on the penetration of light showed a reduction of the euphotic depth (1% light

level) from 52 m in the absence of coccoliths to 26 m in waters containing coccoliths (100 mg m^{-3} of calcite). Enhanced scalar irradiance near the surface may increase the portion of the water column subject to photo-inhibiting light intensities from 1.2 m in the absence of coccoliths to 1.9 m with 100 mg m^{-3} CaCO$_3$-C (Tyrrell et al. 1999). Interestingly, the ability of *E. huxleyi* to form dense blooms in shallow surface layers may be due in part to their ability to photosynthesize without photoinhibition at near-surface intensities (Balch et al. 1992; Nanninga and Tyrrell 1996). In this regard, the cells may be modifying the physical environment in a way that improves their own survival relative to taxa that are sensitive to high intensities of light.

Coccolithophore blooms in the Bering Sea are thought to have affected waterfowl by changing the light field available for these visual predators. Fecundity of diving species such as the Alaskan murre was impaired due to reduced visibility underwater, while that of surface-feeding species such as kittiwakes improved, because of enhanced visual contrast that better enabled them to see their prey (http://www.noc.soton.ac.uk/soes/staff/tt/eh/press_release.html).

Biogenic mixing of the world's oceans: ecological engineering by organisms from microbes to whales

Munk (1966) is often credited with the original suggestion that aquatic animals might affect prevailing ocean currents by their swimming. Though his proposal was actually made in jest (W.H. Munk 2007, personal communication), the concept has been revived in recent years. By transporting and mixing the surrounding water as they swim, planktonic, and nektonic organisms are purported to affect the chemistry, nutrient concentrations, and turbulence of local waters. Changes in these properties potentially support a bottom-up cascade of processes leading to larger scale events as varied as eutrophication, harmful algal blooms, sequestration of carbon, and maintenance of the meridional overturning circulation of the ocean.

The feasibility of biogenic ocean mixing as a global-scale mechanism of ecosystem engineering has been supported by estimates of the total power available to marine animals to transport water while swimming and the energy generated through photosynthesis. Dewar et al. (2006) calculated net primary production from satellite measurements of phytoplankton at the ocean's surface and combined these data with theoretical models of the conversion from

chemical to mechanical energy. They concluded that nearly 1 trillion watts of power are available for biogenic mixing of the oceans globally. This input of power is comparable to the estimated global contributions from wind and tidal forcing (Munk and Wunsch 1998), suggesting that the biosphere may be an equally significant driver of oceanic currents as physical oceanographic mechanisms. J.-L. Thiffeault and S. Childress (unpublished data) estimated that if the 1 trillion watts of biomixing power is distributed throughout the top 3 km of the oceans, the effective diffusivity (i.e., mixing) is $\sim 0.2 \, \text{cm}^2 \, \text{s}^{-1}$, or five times the mixing of heat that would occur by molecular diffusion alone.

At least two distinct processes are likely to contribute to biogenic mixing of the oceans—alteration of the heat structure of the water column, and movement of water caused by swimming. In near-surface waters where photosynthesis is light-saturated, <3% of the absorbed radiant energy is typically converted to chemical energy for biosynthesis and growth. Most of the absorbed radiant energy is actually dissipated as heat, and a number of authors have considered what this might mean for the thermal regime of oceanic waters.

Among the first of these authors were Zaneveld et al. (1981) who solved the 1D heat budget for waters of various optical properties and physical boundary conditions. They concluded that a phytoplankton bloom doubling once per day could, in a matter of days, increase the heating rate of a mixed layer by $0.1°C$ per day. They speculated that in frontal zones where shallow warm and turbid layers flow over clearer and colder water masses, biological processes could affect the current dynamics via heating of the surface layer. Chang and Dickey (2004) discussed the possibility that differential heating due to light absorption by phytoplankton could enhance or erode frontal boundaries in coastal regions, depending on whether phytoplankton bloomed on the warm or on the cool side of the front. Such calculations have become quite sophisticated, incorporating dynamic feedbacks among light absorption, growth, and physical dynamics of the phytoplankton. Löptien et al. (2009) found that biologically induced differential heating generated by increased absorption of light in the upper layers of the chlorophyll-rich eastern equatorial Pacific generally improved the performance of their model of oceanic circulation with respect to temperature and circulation patterns. In particular, they found that the depth of the mixed layer is reduced by 2–18 m in the tropical Pacific in the presence of chlorophyll because of enhanced surface warming and subsurface cooling.

The physical mechanism that enables swimming animals to transport and mix the surrounding water has also come into question in recent years. It was traditionally assumed that the flapping motions of aquatic creatures' appendages created small-scale vortices that were the primary constituent of biogenic ocean turbulence. This perspective formed the basis of most theoretical and experimental studies aiming to quantify the mixing process (Huntley and Zhou 2004; Kunze et al. 2006). Visser (2007), however, identified an important shortcoming in the small-scale vortex paradigm of biogenic oceanic mixing: that water viscosity will typically suppress the motion of small-scale vortices before significant transport of fluid is achieved. Hence, it appears that the smallest—and most numerous—plankton cannot facilitate ecosystem engineering via transport of fluid.

Katija and Dabiri (2009) proposed an alternative mechanism of fluid transport that is not only unimpeded by the fluid's viscosity, it is significantly enhanced by it. The fluid mechanical principle behind their mechanism, called "induced drift," dates back to the work of Sir Charles Galton Darwin (1953) (grandson of the *Origin of Species*' author), who was a physicist interested in hydrodynamics. He showed that when a solid object moves through a fluid like water, the object tends to carry a portion of the surrounding fluid with it. The amount of fluid carried with the object relative to its size depends only on the shape of the object. Furthermore, viscosity in the fluid increases the amount of fluid transported by the solid object.

Using this mechanism as their foundation, Katija and Dabiri (2009) proposed a more direct mechanism of fluid transport by plankton and nekton: as the animals migrate, their solid bodies carry along a portion of the local fluid; hence, the local water and its contained chemicals and nutrients are also transported. This provides a potentially powerful mechanism of ecosystem engineering because it suggests that when swimming organisms transport themselves to new environments, they also take a portion of the original environment with them. Depending on the circumstances, this may either alleviate or exacerbate extreme environments, e.g., where hypoxia or eutrophication is near threshold levels. It also presents an opportunity for animals to actively support the chemical and biological processes on which they ultimately depend. For example, by transporting from deeper water the necessary nutrients to promote photosynthesis at the ocean's surface, the animals can ensure sufficient phytoplankton and the products

of photosynthesis at lower trophic levels to support their diet.

Direct evidence for the mechanism of induced drift is currently limited to the field experiments of Katija and Dabiri (2009), which studied the fluid transport achieved by jellyfish in a marine lake in Palau. By tracking dye markers delivered into the water near animals using SCUBA techniques, they observed the drifting process *in situ* (Fig. 4). Their data are consistent with the concept that animals carry the surrounding fluid with them as they migrate.

To fully appreciate the potential of marine organisms to act at engineers of their ecosystems, further research on the physics, biology, and chemistry of the mixing processes is needed. It seems likely that the diversity of animals' shapes and swimming kinematics will be reflected in varied impacts on water transport in the ocean. The sensitivity of local ecosystems to biogenic mixing will depend intimately on the population dynamics of local animals (e.g., which animals are present and to what degree), and the local water chemistry and its spatial variation. In many cases, opportunities will exist for complex feedback loops between animal populations and the surrounding milieu.

Predator-mediated landscape structure—merging food web and engineering concepts

Trophic interactions and ecosystem engineering have typically been considered distinct classes of ecological processes that alter the suitability of a habitat in quite different ways. In practice, however, the ability of consumers to affect spatial distributions of engineers, and thus the location, extent, and characteristics of the engineered landscape blur that distinction (Jones et al. 1994). Classic examples of keystone species include direct or indirect control by predators of
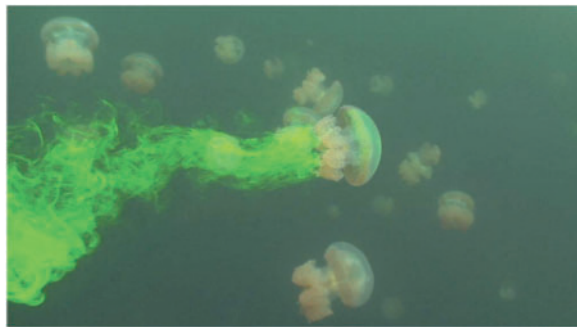
Fig. 4 Induced forward drift of dye behind a swimming *Mastigias* sp. jellyfish. Medusa bell diameter approximately 7 cm. Image adapted from Katija and Dabiri (2009).

organisms that create or modify the physical habitat in terrestrial, marine, and freshwater environments (Paine 1966; Estes and Palmisano 1974; Power et al. 1996).

A particular kind of spatially varying trophic interaction, which we call "predator-mediated landscape structure" (PMLS) may form an important link between the trophic and engineering mechanisms of ecological control. PMLS is a case in which consumers, themselves, create a landscape mosaic that varies in suitability for their prey and the species with which their prey interact. Where PMLS affects the abundance or distribution of ecosystem engineers, it can either directly or indirectly control characteristics and the landscape-level organization of the engineered environment. PMLS may be especially important in aquatic environments in which physical variation within the pelagic habitat has less effect than do trophic interactions in defining the spatial pattern of survival probabilities of species.

We provide an example of PMLS based on a study of the distribution of gelatinous zooplankton in the Patuxent River (a sub-estuary of Chesapeake Bay; Fig. 6A) and its tributaries by Breitburg et al. (2009). Two gelatinous zooplanktonic species—the scyphomedusa *Chrysaora quinquecirrha* (sea nettle) and the lobate ctenophore *Mnemiopsis leidyi* (referred to as ctenophores, below) are dominant consumers in Chesapeake Bay (Purcell and Decker 2005) that can directly and indirectly control abundances of an important ecosystem engineer, the Eastern oyster *Crassostrea virginica* (Fig. 5). Ctenophores consume oyster larvae, but sea nettles reject these prey or eject them unharmed (Purcell et al. 1991). Oysters provide a wide range of ecosystem services including creation of physical habitat and improvement of water clarity (Coen et al. 2007; Grabowski and Peterson 2007). Filtration of water by oysters also has cascading effects in an environment by affecting other ecosystem engineers such as phytoplankton and submersed macrophytes (Fig. 5).

Gelatinous zooplankton were sampled at 12 sites with a 244-μm mesh 1-m^2 Tucker trawl weekly during summer of 2004. Duplicate tows of surface and bottom layers, each lasting 90 seconds and sampling an average of 51 m^3, were taken at each site on each date. Sea nettles and ctenophores were counted in total or through sub-samples containing $\geq$200 individuals. Total volume of each species was determined, and up to 25 individuals were measured (bell diameter or length). Below, we describe the patterns found in the surface layer and near the surface in shallow waters.
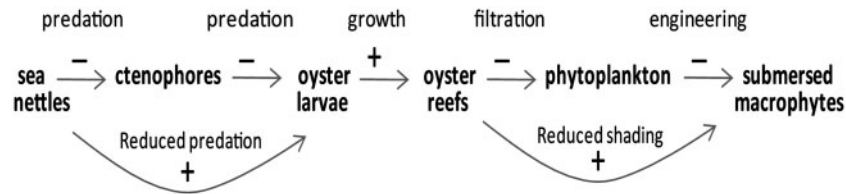
Fig. 5 Gelatinous zooplankton control of ecological engineers and the physical habitat they create or modify. Predation by sea nettles can reduce or eliminate local populations of ctenophores. Ctenophores consume oyster larvae, but sea nettles reject these prey or egest them unharmed. Sea nettles, therefore, potentially control the spatial distribution and intensity of recruitment of oysters by controlling the abundance of ctenophores. Filtration by oysters can reduce phytoplankton densities, thereby increasing water clarity and improving the light environment for SAV growth. Oysters, phytoplankton and submersed macrophytes are important ecosystem engineers in estuaries and marine systems.

The seasonal progression of abundances and spatial distributions of sea nettles and ctenophores created a temporally shifting landscape of habitat that varied in suitability for important ecological engineers, including the Eastern oyster. In mid-May, ctenophores appeared in low abundances at sampling sites in the main stem Patuxent River and one of the three sampled tributaries, but no sea-nettle medusa were collected at any site (Fig. 6B). By early June, ctenophores were abundant in surface waters at all sampling sites, including the most upstream shallow sites within each of the tributaries (Fig. 6C). Sea nettles had begun to appear in the tributaries, but were primarily small individuals averaging 2.4-cm bell diameter, and were below the 0.16 ind m^{-3} density at which they can eliminate ctenophores in the field (Breitburg and Fulford 2006). During the next few weeks, densities and sizes of sea nettles increased, especially in the tributaries so that by 11 August there was near-complete separation of the two gelatinous species with large populations of sea nettles in the tributaries and large populations of ctenophores in the main stem river (Fig. 6D).

The spatial patterning in the predation landscape created by spatial patterns of abundances and subtle differences in the diets of the two gelatinous species potentially had strong consequences for other organisms (Fig. 6E). At biovolumes found in the main stem river, ctenophores could consume the majority of oyster larvae (Breitburg and Fulford 2006), potentially reducing or eliminating local recruitment by this important ecosystem engineer. In contrast, the protective effect of sea nettles created a refuge from predation by ctenophores in tributary creeks, potentially increasing local recruitment of oysters. In the absence of filtration by oysters, a larger fraction of the phytoplankton biomass in the main stem river would likely go un-grazed, sinking into the bottom layer as cells senesce, and die, and providing substrate for microbial decomposition that consumes oxygen and leads to hypoxia or anoxia. In the presence of filtration by oysters in the tributaries, phytoplankton densities and their effect on light penetration could be reduced, thereby improving habitat suitability for submersed macrophytes.

In summary, PMLS has the potential to strongly influence the spatial pattern of ecosystem engineers and their effect in the aquatic landscape. This form of predatory control represents a potential mechanistic and conceptual bridge between trophic ecology and ecosystem engineering. The combined trophic control (by gelatinous zooplankton) and engineering (by oysters) can greatly alter the physical habitat for a wide range or organisms and have cascading effects translated through a series of engineers (oysters, phytoplankton, SAV), each affecting the other.

Conclusions

The examples we provide demonstrate the profound effects that ecosystem engineers ranging from bacteria to gelatinous zooplankton have on their environment. Ecosystem engineers in the pelagic realm and near-shore water column create physiologically meaningful oxygen structure, create and eliminate toxicity, influence water motion and circulation, and affect the penetration of light, the amount and distribution of heat, and the depth of stratification. In addition, consumers alter landscape structure through trophic control of structural ecosystem engineers. We provide the example of PMLS to highlight the importance of linkages between food web and engineering activities on aquatic landscape structure. We also intentionally include effects of microbial metabolism because they so completely transform the suitability of the water column habitat for organisms that are dependent on aerobic respiration or are susceptible to the toxic effects of sulfides. Although these microbial "engineers" are smaller, the process is fundamentally the same as described for macrophytes by Caraco et al. (2006), who suggest that the most important chemical change
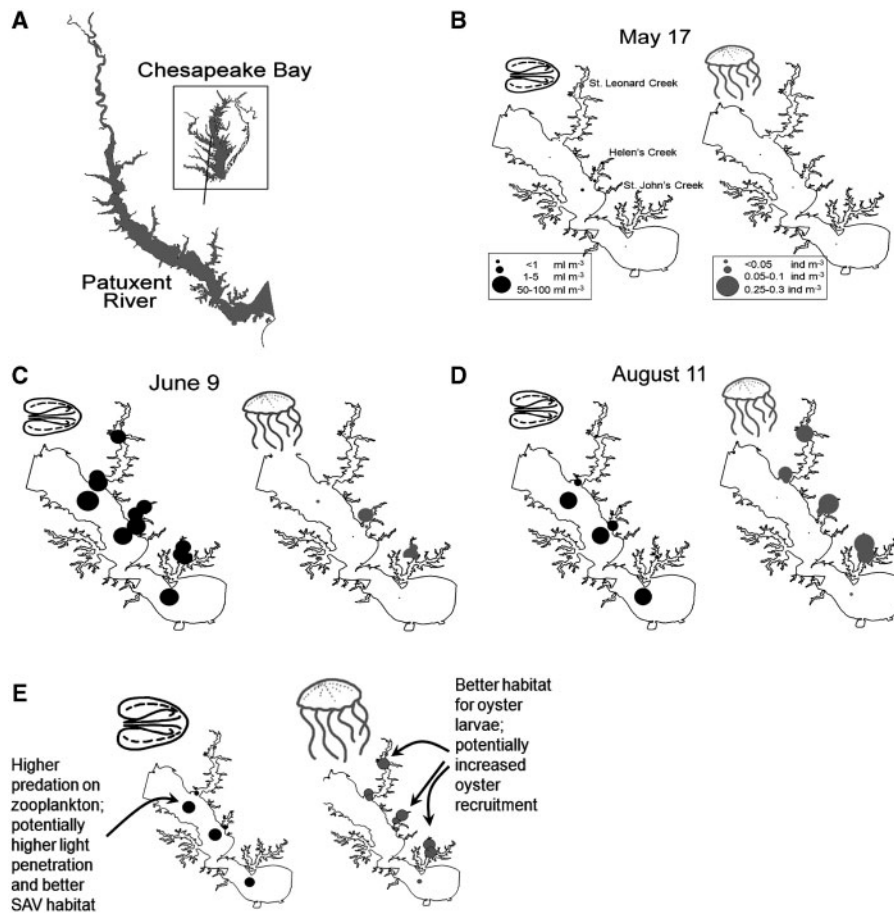
Fig. 6 The location of habitats with the highest potential for predation by gelatinous zooplankton shift over time as a result of changes in distributions and abundances. (A) Study site, (B–D) distributions and abundances of sea nettles and ctenophores on three dates during 2004, and (E) subtle differences in diet can influence spatial variation in the suitability of habitat for ecologically and economically important prey, including important ecosystem engineers that alter and create habitat.

engineered by organisms may be their effect on oxygen levels.

There are many examples of organisms that create complex 3D structure in the pelagic realm at scales ranging from millimeters to kilometers in addition to those described in detail above. For example, another way that both phytoplankton and bacteria affect the physical structure of the water column is through their role in the formation of macro-aggregates sometimes referred to as "marine snow"—an example of marine ecosystem engineering cited by Jones et al. (1997). Phytoplankton and bacteria exude certain acidic polysaccharides that, under appropriate levels of shear, form transparent exopolymer particles (Alldredge et al. 1993). Transparent exopolymer particles are very sticky and promote formation of large aggregates comprising varying proportions of phytoplankton, bacteria, detritus, and mineral particles (Wolanski 2007). The settling rate of marine snow aggregates depends on the size, dry weight, porosity, and excess density (relative to water) of the

aggregates, and is generally fast compared with that of individual phytoplankton cells (Alldredge and Gottschalk 1988). The formation of marine snow has been shown to act as a biological filter, increasing the penetration of light by clearing some fraction of the particulate matter in the water column (Ayukai and Wolanski 1997). Additionally, these large aggregates provide a rich 3D structure at the micro-scale that creates complex zones of heightened microbial activity (Davoll and Silver 1986) and grazing by zooplankton (Wolanski 2007). Modern optical and acoustical instruments have also revealed the existence of plankton in thin layers ranging from a few centimeters to <2 m in vertical thickness, extending over several kilometres in the horizontal direction and persistent for several days (McManus et al. 1996). These thin layers provide 3D physical structure and alter the optical and acoustical properties of the water column.

The ability of engineers to so completely transform pelagic habitat raises the possibility that

ecosystem engineering could be more important in the pelagic zone, away from other physical structure, than it is in terrestrial habitats, rather than less important—essentially the opposite of what was originally suggested (Jones et al. 1997). Some of the structure created by ecosystem engineers inhabiting the water column is quite transient, but the cumulative effects of many organisms and many small actions can sum up to habitat that is created or altered over large spatial and temporal scales. Using the theoretical construct of ecosystem engineering as an overarching concept that links the diverse processes by which organisms inhabiting the water column transform their environment, may provide new insight into the range of both positive and negative interactions that structure marine ecosystems.

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