A

ADAPTIVE GOVERNANCE

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Definition

Adaptive governance integrates scientific and other types of knowledge into policies to advance the common interest in particular contexts through open decision-making structures. It is considered as an alternative to and a reaction to the predominant approach to natural resource management in the twentieth century, often referred to as "scientific management." Scientific management emphasized the isolation of a single best practice through rational consideration of the problem and technical expertise, often times developed and implemented by few persons or entities, in a centralized power context (Brunner and Steelman, 2005).

Adaptive governance is best understood as a pattern of practices that emphasizes the adaptation of policy decisions to a diversity of those people who are affected by the decision(s) in question. Any policy must be flexible enough to react to ongoing experiences occurring on the ground. So that managers have the ability to react to unexpected outcomes, enacted policies should be modest and incremental, rather than broad, sweeping, long lasting, and rigid. Authorities and participants must also plan for and budget for monitoring and evaluation of decisions so that policies can be terminated, modified, or nurtured, as the case may be.

Adaptive governance sees the role of science as important and critical but not sufficient in and of itself. Important policy decisions inherently involve values, not just rational consideration of information; no problem is seen as "technical" only. Therefore, adaptive governance depends on and makes use of bottom-up endeavors such as community-based initiatives so that disparate values are brought into the open and considered as part of any policy decision. Moreover, adaptive governance proceeds with the assumption that decision power is fragmented, not centralized.

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ADAPTIVE MANAGEMENT

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Synonyms

Adaptive resource management

M.J. Kennish (ed.), *Encyclopedia of Estuaries*, DOI 10.1007/978-94-017-8801-4,

Definition

Adaptive management is a decision-making process centered upon learning from the outcomes of management actions. Information from monitoring and research is systematically incorporated into future decisions to improve the effectiveness of management.

Description

Adaptive management (AM) is recommended when resource management decisions must be made despite significant uncertainty. AM programs collect information about a system while implementing management actions and apply that information to reduce uncertainty and improve future decisions. AM frameworks typically include monitoring, research, and conceptual and numerical modeling to collect and organize knowledge about a system and incorporate it into future decisions (Williams et al., 2009).

Structured decision making is recommended for the development and ongoing operation of AM programs. Structured decision making is a process in which problems, objectives, management alternatives, and key uncertainties are systematically identified (Gregory et al., 2012). The process includes projecting the consequences of alternative actions into the future to determine the range of likely outcomes and trade-offs while identifying acceptable levels of risk. As resource management has political, social, and economic considerations, formal engagement with stakeholders in the structured decision making process and the development and implementation of an AM program increases the chances that the program will succeed.

AM approaches can be categorized as active or passive. Practitioners of active approaches seek to optimize learning through management experiments, assigning higher value to management actions that will provide the most useful information. Passive approaches use information gained through monitoring of actions and outcomes; however, they generally do not choose actions based on their potential for increasing knowledge. While passive approaches gather information more slowly, they may be beneficial in cases where experimentation is impractical or impossible. Both approaches follow a cyclical pattern of action and assessment. Such a cycle might consist of (1) a planning phase to develop conceptual models, objectives, and management alternatives; (2) a design phase to choose and develop specific actions; (3) an action implementation and monitoring phase; (4) an assessment phase, in which new information is combined with existing information to evaluate the outcomes of actions relative to the objectives; and (5) an adjustment phase to make changes to actions as necessary to improve outcomes. Assessment and adjustment may apply to the current action, returning the cycle to the design phase. Less frequently, managers may use the assessment and adjustment phases to evaluate the AM program itself and revisit the planning phase.

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Cross-references

Adaptive Governance

AEROBIC ENVIRONMENTS

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Synonyms

Aerial environment

Definition

An aerobic environment is one characterized by the presence of free oxygen (O_2), in contrast to an anaerobic environment which is one devoid of free oxygen (WKU, 2013). Aerobic organisms grow or metabolize only in the presence of molecular oxygen (Mekone and Kandel, 1986; Talaro and Talaro, 1993), such as in the upper few centimeters of estuarine bottom sediments where concentrations of free oxygen are significant and chemically oxidizing processes prevail (EPA, 1990). In this environment, aerobic bacteria readily decompose organic matter, breaking down the organic molecules to simple inorganic constituents (Talaro and Talaro, 1993). These organisms require oxygen as their terminal electron acceptor. Anaerobes (anaerobic bacteria), however, grow or metabolize only in the absence of molecular oxygen, such as in the deeper sediment layers of estuarine and marine environments (EPA, 1990).

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Cross-references

Anaerobic Environments

AGE

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Definition

Age. The time elapsed since a water parcel or constituent particle entered a defined water body (Bolin and Rodhe, 1973; Zimmerman, 1976; Takeoka, 1984).

Essential concepts, applications, and methods of estimation

"Age" is a hydrodynamic transport time scale commonly used to characterize the time elapsed between release of a substance (e.g., a pollutant) into a water body and its arrival at a location of concern (Shen and Haas, 2004). Parcels and particles may be released from origin *regions* as well as from point sources; therefore, in addition to the definition provided above, age has also been defined as the time elapsed since a parcel or particle left the region in which its age is prescribed to be zero (Delhez et al., 1999; Deleersnijder et al., 2001). As the time taken by a parcel since entering a water body to reach location **x**, age is commonly considered the complement to "residence time," if residence time is defined as the time taken by a water parcel originating at **x** to leave the water body; the sum of the two time scales is called "transit time" (Takeoka, 1984; Sheldon and Alber, 2002).

Age is unique to each water parcel, spatially heterogeneous within a water body (Monsen et al., 2002; Banas et al., 2007), dependent on source location (Zimmerman, 1976; de Brye et al., 2012), and time dependent (Delhez et al., 1999). Moreover, given that diffusive processes can cause exchange of particles between fluid parcels as they travel through a water body, a parcel is likely to contain particles of different ages (Deleersnijder et al., 2001). Also important are the facts that (1) water is a mixture of different constituents including pure water, salts, dissolved chemicals, biological and mineral particulates, and chemicals sorbed to particles and (2) age of each constituent varies in space and time (Delhez et al., 1999; Delhez and Wolk, 2013). These different constituents are subject to their own unique production and destruction processes, further altering distributions of particle histories – and therefore ages – within a given water parcel (Deleersnijder et al., 2001).

Age is one of several diagnostic transport time scales that can be estimated to distill the details of estuarine hydrodynamic circulation and exchange and to aid in the understanding of linked physical, biological, and chemical processes (e.g., Banas et al., 2007; Lucas et al., 2009; Delhez and Wolk, 2013). This time scale can be used, for example, to backcast release times for substances detected in particular locations (Delhez and Deleersnijder, 2002), assess locations and times of increased estuary vulnerability to river-derived nutrient inputs (Shen and Haas, 2004), understand spatial variations in larval settlement (Banas and Hickey, 2005), and interpret complex hydrodynamic circulation patterns (Deleersnijder et al., 2001; Andutta et al., 2013). Age of water parcels originating at the water surface ("ventilation age," DeVries and Primeau, 2010) is also commonly used to provide insight into ventilation rates in ocean basins (Haine and Hall, 2002; Mouchet and Deleersnijder, 2008).

In estuaries, variability in age may be influenced by freshwater discharge (de Brye et al., 2012), gravitational circulation and stratification (Shen and Haas, 2004), wind (Andutta et al., 2013), bathymetry (Shen and Haas, 2004), tides (Banas and Hickey, 2005), and bottom friction (Andutta et al., 2013). Age is commonly computed with numerical models, using both traditional Lagrangian-based particle tracking techniques (e.g., Andutta et al., 2013) and Eulerian approaches (e.g., Delhez et al., 1999; de Brye et al., 2012). Models representing a broad range of complexity have been used to assess age, including box (Zimmerman, 1976), one-dimensional (Mouchet and Deleersnijder, 2008; Delhez and Wolk, 2013), two-dimensional (Monsen et al., 2002), and three-dimensional (Shen and Haas, 2004) models. Age may also be assessed in the field using substances such as passive dyes (Kratzer and Biagtan, 1997) and radioactive tracers (Delhez et al., 2003; de Vries and Primeau, 2010; Xu et al., 2013).

Summary

Age is a hydrodynamic transport time scale used to convey the time elapsed since a water parcel or particle was introduced to a defined water body. This time scale may be estimated using field or computational techniques to gain insight into the transport and dynamics of substances such as pollutants that are released into surface waters. Age is also used as an interpretive tool for better understanding complex hydrodynamic flows.

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Cross-references

Residence Time
Timescale

AIRBORNE LASER TERRAIN MAPPING (ALTM)

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Synonyms

Airborne laser scanning; Airborne laser swath mapping; Airborne light detection and ranging; Laser altimetry; Laser radar

Definition

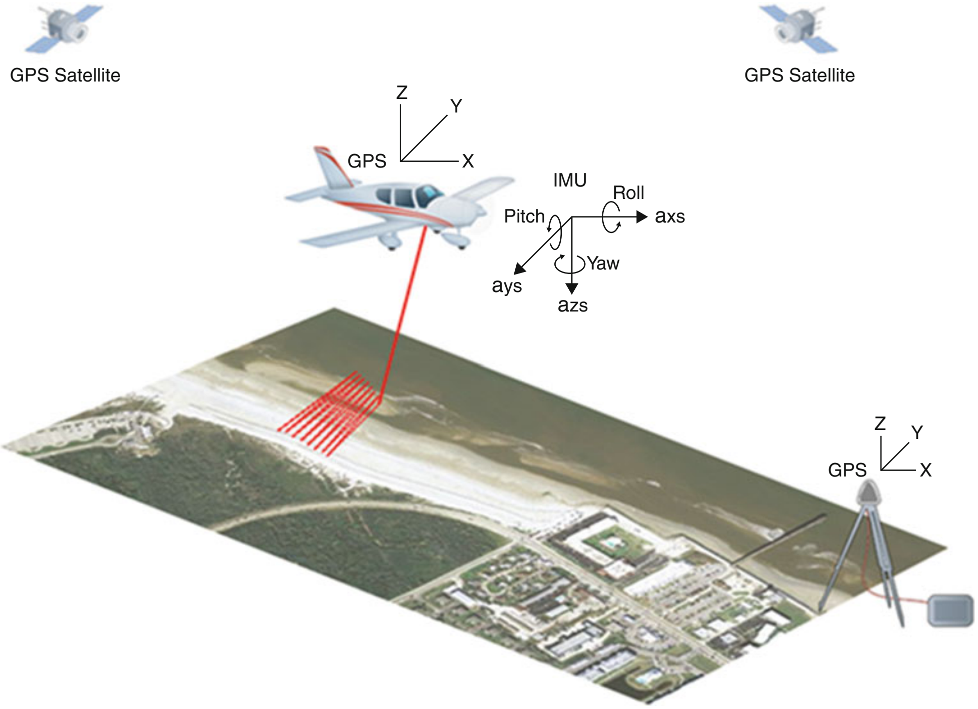
Airborne laser terrain mapping (ALTM) is an active remote sensing technology that employs light detection and ranging (see Light Detection and Ranging (LIDAR)) to measure topography at high spatial resolution over large areas. ALTM pulses a laser to measure the range between an airborne platform and the Earth's surface at many thousands of times per second. Using a rotating mirror or other scanning mechanism inside the laser transmitter, the laser pulses can be made to sweep through an angle, tracing out a line or other patterns on the reflecting surface. With the scan line oriented perpendicular to the direction of flight, it produces a sawtooth pattern of ranges within a strip centered directly along the flight path (Figure 1). An integrated global positioning system (GPS) and inertial navigation unit are used to accurately determine the aircraft position and attitude as each laser pulse leaves the aircraft. This information is then combined with the scan angle and range for each pulse to derive the georeferenced location of the sample points on the reflecting surface (Baltsavias, 1999; Wehr and Lohr, 1999). The result is a densely sampled three-dimensional (3D) point cloud of *x,y,z* values representing the ground and land cover. In addition to spatial information, ALTM systems typically provide a relative measure of the reflection intensity for each surface point based on the return pulse amplitude.

History

ALTM is commonly referred to as airborne lidar mapping. The first airborne lidar systems were developed in the late 1960s as a way to measure height profiles of ice packs and underwater surfaces (bathymetry) where traditional sonar techniques failed due to shallow water depths. The development of profiling bathymetric lidar systems continued through the 1970s. The first system to incorporate a scanning mechanism was the NASA Airborne Oceanographic Lidar (AOL) that became operational in 1977 (Fernandez-Diaz et al., 2013). Terrestrial experiments were conducted starting in 1980 to evaluate the capability of the AOL system to derive topographic maps in areas not suited for photogrammetric methods, such as forested regions. Early results encouraged researchers to develop lidar systems with specific design characteristics targeted for terrestrial applications. However, it was not until the mid-1990s that commercially manufactured units became fully operational (Shan and Toth, 2009). Starting in the 1990s, rapid advancements in enabling technologies such as GPS, IMUs, solid-state lasers, photodetectors, and optical scanners paved the way for the modern-day ALTM system.

System components

ALTM systems consist of three main components. First, the laser ranging unit consists of the laser transmitter, scanner (e.g., oscillating mirror), and a receiver to record the reflected energy. Second, the position and orientation



Airborne Laser Terrain Mapping (ALTM), Figure 1 Example of airborne laser terrain mapping (ALTM) using an oscillating mirror to scan the surface. The GPS on the ground is used to differentially correct the airplane GPS measurements.

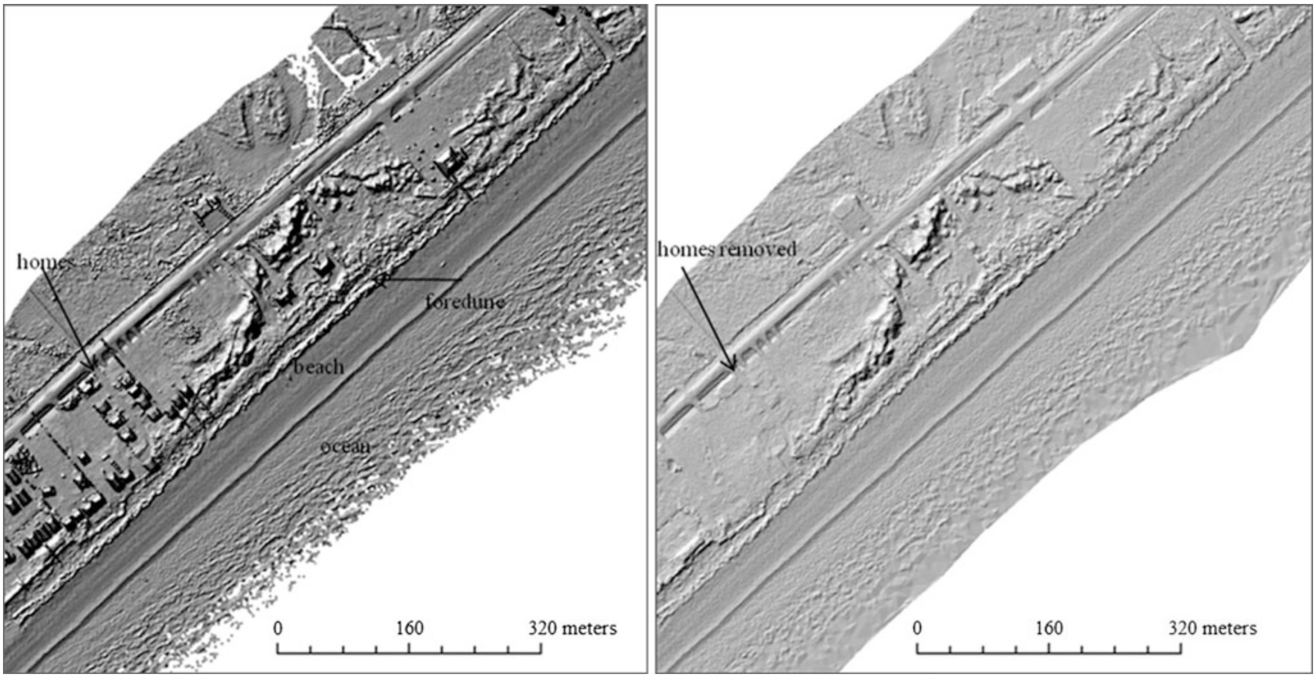
system (POS) consists of a GPS to acquire aircraft positional information and an inertial measurement unit (IMU) to record aircraft orientation (roll, pitch, and yaw). Third, the control and data acquisition unit consists of the onboard hardware and software used to operate the system and record the collected data (Shan and Toth, 2009).

System types

ALTM systems are broadly classified into two groups, those targeted at mapping topography and those targeted at mapping bathymetry. Topographic systems generally operate in the near-infrared wavelengths (e.g., 1,064 nm) of the electromagnetic spectrum that allow for easier compliance with eye safety regulations and where vegetation and other components of the land surface can be highly reflective (Fernandez-Diaz et al., 2013). Bathymetric lidar systems operate in the blue-green range of the electromagnetic spectrum (e.g., 532 nm) to achieve water penetration. However, it should be noted that there are both single- and dual-frequency ALTM systems. For example, some bathymetric systems employ an infrared laser to better detect the water surface and a blue-green laser to map submerged features.

ALTM systems can be further classified into discrete-return and full-waveform systems. Discrete-return ALTM systems typically record multiple returns per an emitted pulse, including a first and last return. Take, for example, a discrete-return system mapping over a forest that can record up to two returns per an emitted pulse. The emitted laser pulse can first interact with the forest canopy resulting in some of the pulse energy being backscattered to the sensor resulting in a measurable return (first return). The remaining pulse energy can subsequently propagate to the land surface below the canopy resulting in a second measurable return (last return). Modern discrete-return systems can record up to four or more returns per an emitted pulse. In contrast, currently available full-waveform systems digitize the entire backscattered laser pulse at very high sampling rates (e.g., 1 GHz). The advantage of this technique is that it provides a much more detailed and complete record of each received signal as it interacts with the landscape. However, this information comes at the expense of increased data storage and increased post-processing requirements. Therefore, full-waveform digitization is not advantageous for all applications, such as those concerned only with mapping the ground surface (Pack et al., 2012).

ALTM systems are generally referred to as small-footprint lidar systems. Small-footprint ALTM systems generate a laser pulse with a smaller beam divergence to reduce the spreading of the pulse as it propagates from the sensor to the surface below. This results in a smaller-diameter laser footprint on the reflective surface, thereby enabling higher-density spatial sampling. The actual diameter of the laser footprint on the surface will be



Airborne Laser Terrain Mapping (ALTM), Figure 2 (*Left*) Shaded-relief image of an ALTM-derived 1-m resolution digital elevation model (DEM) of a section of beach along the Texas coast. (*Right*) Objects, such as homes and vegetation, can be removed through a process called filtering to generate a bare-earth DEM.

a function of the aircraft flying height and the beam divergence. Small-footprint ALTM systems can enable topographic mapping with average spatial resolutions greater than 1 point per meter squared and achievable positional accuracies in the range of 15–30 cm horizontal (x, y) and 5–10 cm vertical (z) (Slatton et al ., 2007).

Data applications

ALTM surveys generate irregularly spaced *x,y,z* point cloud data representing the ground and land cover. The desired end product for many scientific and engineering applications is to derive a bare-earth digital elevation model (DEM) from the data. For multiple return ALTM systems, typically only the last return points are utilized because they have a higher probability of reflecting from the true ground surface. Prior to DEM generation, the point data typically undergo a process called filtering to try and remove non-ground points due to such things as buildings, vegetation, and other occluding objects (Slatton et al., 2007). Many different filtering algorithms have been proposed for ALTM data (e.g., Sithole and Vosselman, 2004). Once the ground points are obtained through filtering, an interpolation method is applied to generate a regularly spaced grid of bare-earth elevations (Figure 2). The achievable spatial resolution of the resultant bare-earth DEMs will depend on the ALTM sampling density and properties of the land cover, but achievable resolutions exceed 1 m. In addition to bare-earth DEMs, the first return points are often used to generate digital surface models (DSMs) of the land cover elevation, such as forest canopy or buildings in urban areas. Furthermore, the ALTM intensity values for each point can be used to derive information about the relative surface reflectance and applied to segment objects captured in the point cloud data.

Summary

ALTM is a well-established mapping solution for large-scale acquisition of topographic elevation data at high spatial resolution. Data derived from such systems have enabled the development of digital elevation models at unprecedented spatial detail. This capability has revolutionized the scientific community's ability to measure land surface dynamics. ALTM system development continues to evolve at a rapid pace including new lidar modalities, such as flash lidar (Pack et al., 2012). This progression in technology will lead to new mapping capabilities and applications.

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Cross-references

Light Detection and Ranging (LIDAR)

ALGAL BLOOMS

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Synonyms

Harmful algal blooms; Nuisance algal blooms; Phytoplankton blooms; Red tides; Spring blooms

Definition

Algal blooms refer to the increase in biomass of algae due to increased growth or due to physical aggregation, leading to an above-normal accumulation and generally adverse ecosystem effects.

Introduction

Algae are a normal part of the aquatic ecosystem; they form the base of the aquatic food web. Of this large and diverse group of organisms, most are microscopic in size, but some are macroscopic. The microscopic algae are most often single cells, but some can form chains or colonies. Most microalgae live in the water column, while others live in or near to the sediment or attached to surfaces for some or all of their life cycle. Macroalgae can be multicellular and complex, the largest of which are the seaweeds.

Algal blooms are an important and natural component of the production of all aquatic systems, but especially those of temperate, subpolar, and coastal waters. Spring blooms are triggered by seasonal warming, increased light availability, water column stratification, and increased nutrient availability from riverine runoff or other sources. These blooms are important for energy and material transport through the food web, and they also play an important role in the vertical flux of material out of the surface waters. These blooms are distinguished from those that are deemed "harmful." Algae form harmful algal blooms, or HABs, when either they accumulate in massive amounts that alone cause harm to the ecosystem or the composition of the algal community shifts to species that make compounds (including toxins) that disrupt the normal food web or to species that can harm human consumers (Glibert and Pitcher, 2001). HABs are a broad and pervasive problem, affecting estuaries, coasts, and freshwaters throughout the world, with effects on ecosystems and human health, and on economies, when these events occur. This entry focuses on those algal blooms that are HABs. After an introduction to types of HABs and their effects, an emphasis is placed on the ecology and dynamics of the planktonic HABs, their global expansion, and approaches to their prediction and control.

Types of HABs (representative species groups and their effects)

Terminology

The term HAB is an operational one, not a technical one due the diversity of HAB types and effects. Due to the complexity of toxic or ecosystem effects, with the exception of a few species, there are no formal definitions of the concentrations of cells that determine a "bloom." Many HAB events were formerly referred to as "red tides" because of their pigmentation, but this terminology has been supplanted because not all HABs are red; some may be green, yellow, or brown depending on their specific pigmentation.

While colors are used less frequently to distinguish different types of HABs, toxic properties are gaining favor as a way of distinguishing different types of HABs. By definition, all HABs cause harm, either to ecological, economic, or human health. *Toxic* HABs are those that involve toxins or harmful metabolites, such as toxins linked to wildlife death or human seafood poisonings, as described in more detail below. Of the tens of thousands of algal species, only a few percent have been documented to be toxic, although new toxins are being identified regularly (Landsberg, 2002). Some algal toxins are extremely potent, and thus toxic HABs can occur at cell densities that would not normally be taken to be in "bloom" proportion; they can, for example, sometimes cause poisonings at concentrations as low as a few hundred cells per liter.

Nuisance algal blooms, or NABs, do not produce toxins (or such toxins have not yet been identified), but are able to cause harm through the development of high biomass, leading to foams or scums, the depletion of oxygen as blooms decay, or the destruction of habitat for fish or shellfish such as by shading of submersed vegetation. Another distinction that some investigators have found useful is the group of HAB species that are not necessarily toxic but do cause disruption to the grazer community and thus to trophic transfer and the food web in general. Such blooms have been coined *ecosystem disruptive algal blooms*, EDABs (Sunda et al., 2006).

Adding to the confusing terminology associated with HABs, some HABs are technically not "algae" at all, but rather small animal-like microbes that obtain their nutrition by grazing on other small algae or bacteria; they either do not photosynthesize at all or only do so in conjunction with grazing. These complex and diverse nutritional strategies are described in more detail below. Other "HABs" are more bacteria-like. These are the cyanobacteria (*CyanoHABs*), some of which have the ability to "fix" nitrogen from the atmosphere as their nitrogen source. All of these complexities underscore that the term "HAB" is simply an operational term, recognizing the group of species (not all of which are strictly algae) that can cause harm – to health, to the environment, or to the economy.

Common species groups and harmful properties

Of the thousands of species of marine phytoplankton from hundreds of genera, only a few can be highlighted here. Diatoms are the most common organisms associated with "spring blooms." Diatoms are capable of rapid growth rates. They have a silicate shell and thus have a unique requirement for this element among the algae. Most diatoms are not harmful, but large spring blooms are associated with hypoxia or "dead zones" when the biomass sinks to deeper waters where it decomposes in oxygen-consuming processes. The annual development of summer hypoxia in Chesapeake Bay, for example, is due to these large spring bloom events (Kemp et al., 2005).

Diatoms may also be toxic, as is the case of *Pseudo-nitzschia* spp. that produce *domoic acid* that is responsible for the human illness called *amnesic shellfish poisoning* (Trainer et al., 2012). Exposure to this HAB group is now being linked to seizure and memory loss in laboratory animals and to premature births and strandings in animals such as sea lions (Johnson et al., 2010; Bargu et al., 2012).

Dinoflagellates are among the more common toxic HABs as well as NABs. Dinoflagellates all possess two dissimilar flagella; they often display complex life cycles and typically have much slower growth rates than diatoms. Many produce toxins that can kill fish directly or that intoxicate seafood with toxins that can be passed onto human consumers. One toxic dinoflagellate that causes significant human health effects is *Karenia brevis*, which produces large blooms along the coast of the Gulf of Mexico. This species produces a neurotoxin, brevetoxin, that is responsible for the human illness called *neurotoxic shellfish poisoning* (Backer and McGillicuddy, 2006). Several dinoflagellate species, including *Alexandrium* spp. and *Pyrodinium bahamense* (var. *compressum*), produce saxitoxin, responsible for *Paralytic Shellfish Poisoning* (PSP) (Backer and McGillicuddy, 2006). PSP has been particularly problematic in Southeast Asia, where many human fatalities have been reported over the past several decades (Azanza and Taylor, 2001). Another example of a toxigenic dinoflagellate is *Karlodinium veneficum*. This species has been implicated in fish-kill events in the Chesapeake Bay area (Adolf et al., 2008) as well as in coastal waters of Southwest Africa, Europe, United States, Western Australia, and other temperate coastal environments.

Many HAB dinoflagellates develop large-scale blooms but do not produce toxins that have significant human effects. *Prorocentrum minimum* is one such globally distributed species. This species can produce high biomass blooms that affect the food web by altering ingestion rates and/or growth rates of consumers especially at the larval stages (Heil et al., 2005; Glibert et al., 2008). Benthic species of this genus are known toxin producers, however (Glibert et al., 2012).

Another significant group of HABs is the prymnesiophytes. Many, if not most, *Prymnesium* species are toxic to gill-breathing organisms and thus are responsible for many fish kills around the world, especially in eutrophic waters. For example, *Chrysochromulina polylepis* has been the cause of fish kills along the Norwegian coast, and *Prymnesium parvum* (Carter) is responsible for reoccurring fish kills in coastal and inland waters worldwide (reviewed by Edvardsen and Paasche, 1998; Edvardsen and Imai, 2006; Roelke et al., 2007). Along the North Sea coast, blooms of *Phaeocystis* spp. are common. Because they are mucilage rich, water can turn viscous, and beaches can be drenched in foam from decaying blooms (Lancelot, 1995).

The raphidophytes are yet another common HAB group distributed worldwide. These organisms have often caused large-scale fish mortalities, both in aquaculture settings and in natural environments. Among the more common HAB raphidophytes are *Heterosigma akashiwo* and *Chattonella* spp. The fish-killing properties of these species are due to their production of neurotoxins or to their production of reactive oxygen or other hemolytic agents (Edvardsen and Imai, 2006).

The CyanoHABs are increasingly an important nuisance and toxic HAB group affecting both freshwaters and estuarine and coastal systems worldwide. The most common toxins associated with this group of HABs are hepatotoxins, such as microcystin, nodularin, and cylindrospermopsin, but some species may also produce neurotoxins, such as anatoxin and saxitoxin (O'Neil et al., 2012). The world's largest estuary, the Baltic Sea, is now annually affected by massive CyanoHAB blooms, including species such as *Nodularia*, *Anabaena*, and *Aphanizomenon*. One of the most common HAB types in freshwater as well as in upper estuaries and one exemplifying the effect of both direct and indirect contact is *Microcystis* spp. Exposure to water with this HAB or its toxin can cause skin irritation or respiratory irritation, but prolonged, repeated, or intensive exposure to the HAB toxin has been associated with tumor promotion, especially liver cancer (Backer and McGillicuddy, 2006). As this toxin and other related toxins can affect the nervous system, there has been a suggestion that some neurological diseases such as Parkinson's disease or dementia may also be related to some of the toxic and bioreactive compounds originating from this HAB group (Ibelings and Chorus, 2007). Among the CyanoHAB group are also some species that attach to seagrass, corals, or sediment, such as *Lyngbya* which is also capable of producing a wide array of toxic or potentially toxic compounds, including Lyngbyatoxin and saxitoxin.

Although this entry is focused on planktonic HABs, for the sake of completeness, it is important to mention macroalgal HABs. Macroalgae also dominate the flora of many shallow estuaries, lagoons, and upper embayments, coral reefs, and rocky intertidal/subtidal habitats especially in polluted environments. A well-documented example of such a bloom occurred in 2008, when the macroalgal species *Enteromorpha prolifera* (also called *Ulva prolifera* or sea lettuce) occurred at the venue of the Olympic Games sailing competition, almost blanketing the water with filamentous scum (Hu et al., 2010). Blooms of this magnitude in this region had not previously been observed but have since reoccurred on a near annual basis associated with expanding aquaculture industries and eutrophication. It has been estimated that the cost associated with the management of the *E. prolifera* event in 2008 was greater than $100 million.

Ecology and dynamics of HABs

For decades, HABs have been studied in all areas of the globe, but there is still much that is not well understood regarding the underlying processes behind the development or outbreak of species or species groups. In the simplest terms, the success of HABs lies at the intersection of their physiological adaptations of the HABs, the environmental conditions, interaction with co-occurring organisms, and physical dynamics of the water body.

Physiological adaptations

In order to grow and make new biomass, algae need to have the necessary materials and energy to make new biomass. The classic paradigm of algal blooms is that of microscopic "plants" or primary producers, dependent on light and the uptake of dissolved nutrients. However, as noted above, many HABs (the diatoms being the primary exception) may both engage in photosynthesis but may also graze on particles, including bacteria, cyanobacteria, other algae, or even bits of fish tissue. This complex nutrition or *mixotrophy* (the mix of different modes of nutrition) imparts advantages to organisms under conditions of low light (when photosynthesis would be reduced), under low nutrients (when inorganic nutrient uptake may be limited), or under conditions of imbalanced nutrient supply. Some species only use mixotrophy as a supplement, while others rely exclusively or nearly so on mixotrophic nutrition (Burkholder et al., 2008). Some of these "algae" in fact do not make their own chlorophyll at all, but rather borrow their chloroplasts from the food they eat, a process termed *kleptochloroplasty*. Most all the major groups of eukaryotic phytoplankton, including most HABs, engage in mixotrophy to some extent (Flynn et al., 2013). Importantly, when an organism undertakes primary production (photosynthesis) and grazing, the two processes provide "more than the sum of the parts" in terms of benefits to the organisms (Mitra and Flynn, 2010), and thus these modes of nutrition have important consequences for understanding HAB success and in modeling the flow of energy and materials in microbial food webs (Flynn et al., 2013).

In addition to the complex nutrition of mixotrophy, the development of specific algal species may be a function of availability of specific nutrient forms. Using sources of nutrients not available to competitors may impart an advantage for certain species or species groups (Glibert and Burkholder, 2011). Many HABs have the ability to utilize organic forms of nitrogen and phosphorus, but mechanisms may vary. Some species have species enzymes for transport or metabolism of certain forms of organic nitrogen or phosphorus, while other species have the capability for the breakdown of organic compounds at the cell surface (Glibert and Legrand, 2006). Yet other species appear to be stimulated when complex organic molecules are provided in conjunction with inorganic nutrients. For example, in mesocosm experiments, Granéli et al. (1985) showed that dinoflagellate populations, including *Prorocentrum minimum*, were stimulated by inorganic nitrogen only when added in combination with humic acids.

Furthermore, the mechanisms for nutrient acquisition and the extent of dependence by a HAB on mixotrophy or on specific dissolved nutrient forms depend not only on the species, but also prevailing environmental factors such as temperature or light (Glibert and Burkholder, 2006). Thus, a given suite of nutrients may have different impacts in different sites and at different times. Smayda (2002) has suggested that different HAB dinoflagellates can be classified into a matrix, based on preferences organized by a nearshore/offshore gradient in decreasing nutrients, reduced mixing, and increasing light. In this matrix, estuarine species are defined as the dinoflagellates that are better adapted to low-light high-nutrient waters, but oceanic species are better adapted to high-light low-nutrient waters.

Many algae, including HABs, also have complex life cycles and behaviors that have important implications for their occurrence, distribution, and dynamics. Among life cycle stages for some algae are benthic cysts or other resting stages that give cells capability to withstand hostile or unfavorable environmental conditions. The metabolic switch from resting stages to motile stages often occurs for a population at or around the same time, allowing actively dividing cells to initiate a bloom. These cysts or spores provide a recurrent seed source or inoculum for planktonic populations, and this characteristic may be a critical factor in determining not only the geographic distribution of species but also their eventual abundance.

Some species form colonial stages during parts of their life cycle that have implications for grazers or may deter or protect species from viral or bacterial infection (Lancelot et al., 2002). Many HAB species are motile, and under certain environmental conditions, their swimming behavior or buoyancy may result in the formation of high-density patches (e.g., Franks, 1992; Kamykowski et al., 1998). Some cyanobacterial species are able to regulate their vertical positioning by synthesis and collapse of gas vesicles. Vertical movement by cells in a stratified environment may help to maximize encounter frequencies for sexual reproduction, minimize grazing losses, and allow cells to obtain nutrients at depth and light at the surface. All of these behaviors have important implications for species and bloom success and serve to underscore the deep complexity of the biology of these seemingly "simple" organisms.

Trophic interactions

The proliferation of HABs reflects the metabolism and specific growth of the "algal" cells, but also the dynamics of the species that are co-occurring with the HAB. It has long been argued that production of allelopathic exudates allows some harmful species to outcompete co-occurring phytoplankton (e.g., Granéli and Johansson, 2003). The ability of a HAB species to build their population under specific conditions is therefore related to the availability of sufficient nutrients to sustain it and to reduction in mortality rates. The response of zooplankton and other grazers to toxic algae is often species specific in terms of behavioral responses and toxin susceptibility. Many HAB species produce more toxins under stress, thereby allowing them to avoid predation and competition by killing their predators and the competing algal species (Granéli and Johansson, 2003). Fish and zooplankton avoid dense concentrations of certain HAB species, and some toxic species are rejected by predators or grazers. Grazing control of HABs can also depend on the population density of the harmful algae, as demonstrated for the brown tides in Narragansett Bay, USA, where suppression of grazing occurs above a threshold concentration (Tracey, 1988). A threshold effect may also occur if the daily production of new harmful cells becomes large enough to saturate the ingestion response of the grazers and the ability of grazers to increase their populations. In that case, population growth can accelerate dramatically (Donaghay, 1988).

Bacteria play an important role in controlling many HABs and regulating their impacts, including their toxicity. Bacteria may also interact with HABs in a positive manner by stimulating their growth. CyanoHABs, in particular, establish mutually beneficial consortia of microorganisms (Paerl and Millie, 1996). A different type of bacterial interaction with HAB species was described by Bates et al. (1995) who showed that the toxicity of the diatom *Pseudo-nitzschia* was dramatically enhanced by the presence of bacteria in laboratory cultures. Likewise, viruses are also now known to have significant impacts on the dynamics of marine communities, and some have been found to infect algae and have been implicated in the demise of red or brown tide blooms (Fuhrman and Suttle, 1993). The extent to which any of the above interactions occur in natural waters and affect HAB dynamics is not well known and represents an important line of inquiry.

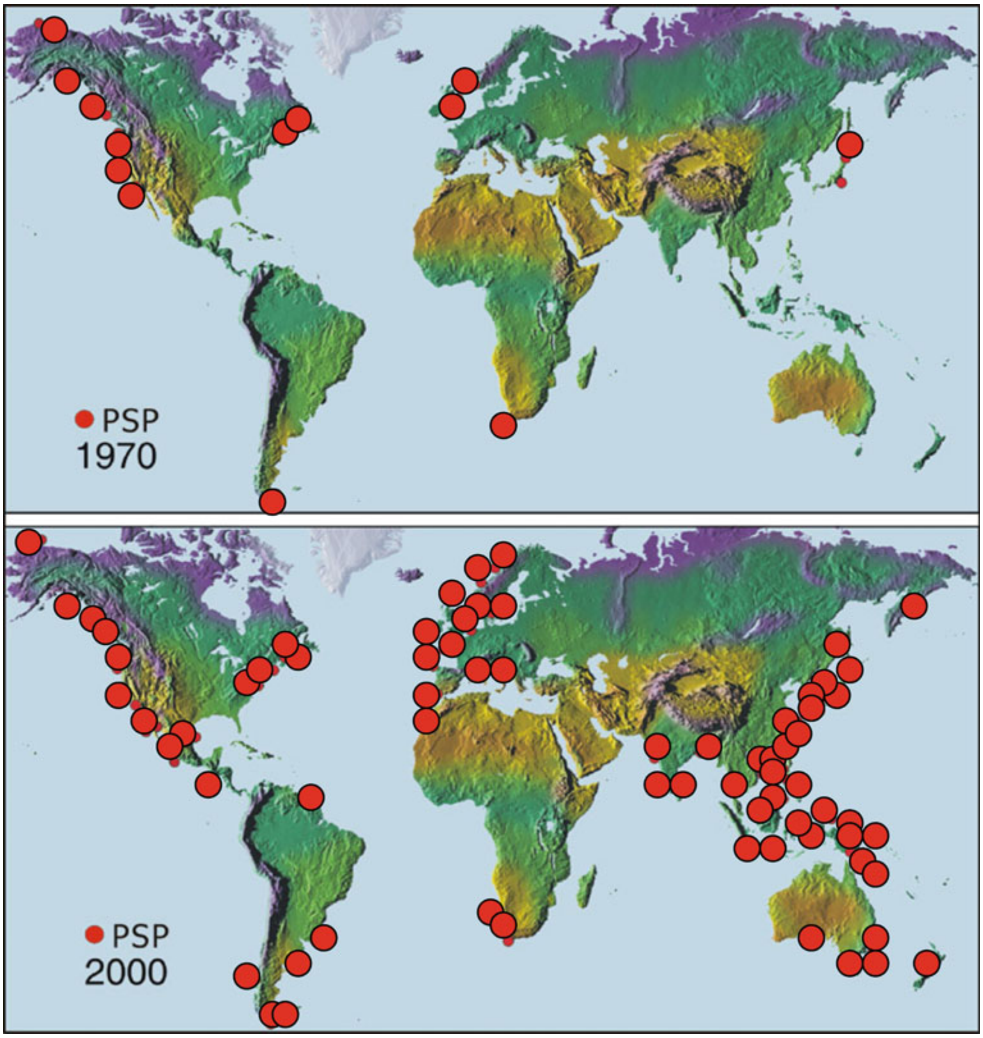
Physical dynamics

The physical environment is also intrinsically intertwined with the biology and ecology of algae. Many large-scale features have direct relevance to HABs or their likelihood for formation, including such features as tidal fronts, coastal jets, and upwelling. Some HABs tend to aggregate subsurface in thin layers. For example, in the Baltic Sea, the heterotrophic dinoflagellate *Dinophysis* may only be found in a 1–2 m layer, but at a depth of 20–25 m (Gisselson et al., 2002). As another example, it has been found off the coast of France that some subsurface layers are comprised of up to 100 % dinoflagellates, most of which are harmful and all of which are mixotrophic, a so-called magic carpet of toxic HABs (Gentien et al., 2008 and references therein). Stratification and mixing have pronounced effects on the distribution and success of HABs. Turbulence, also, has significant consequences for the growth and decline of HABs through its influence on the transport of nutrients, the mixing of phytoplankton through gradients of light, and even through direct impairment of growth. Many questions remain about the specific adaptations of cells to these local environments and the interplay between physics and biology in maintaining these microstructures.

Global expansion of algal blooms, HABs, and their effects

Both toxic and nuisance HABs are increasing throughout much of the world. For example, global occurrences of PSP increased dramatically over the three-decade period from 1970–2000 (Figure 1, Glibert et al., 2005a). Dead zones, another effect of high biomass algal blooms, are also increasing worldwide. The number of dead zones from excessive algal production has doubled each decade since the 1960s. Some systems have shown a progression from episodic to seasonal hypoxia and then, with increased nutrient enrichment, to more and more sustained hypoxia. Dead zones are now found in waters across the globe (Diaz and Rosenberg, 2008).

Although some of the factors contributing to the global expansion are natural, such as biological species dispersal, many others are considered to be a result of human activities, among which nutrient pollution is the most important. The exploitation of natural fish stocks has also, in some cases, led to a decrease in the control of HAB species by removal of the primary grazers through trophic cascade effects. Global climate change may also be important in the increase in HABs.



Algal Blooms, Figure 1 The global expansion of paralytic shellfish poisoning (PSP), one of the many harmful syndromes caused by harmful algal blooms (Figure reproduced from Glibert et al. (2005a) with permission of the Oceanography Society).

Links to eutrophication and altered nutrient stoichiometry

Overenrichment of coastal waters by nutrients is considered a major pollution problem worldwide (Howarth, 2008) and one of the most important factors contributing to global HAB increases (Anderson et al., 2002; Glibert et al., 2005b; Glibert and Burkholder, 2006; Heisler et al., 2008). Nutrient pollution is on the rise because of dramatic increases in human populations in many regions and concomitant increasing demands for energy, increases in nitrogen (N) and phosphorus (P) fertilizer use for agriculture, changes in diet that are leading to more meat production and animal waste, and expanding aquaculture industries (e.g., Howarth, 2008; Glibert et al., 2010; Bouwman et al., 2011; Bouwman et al., 2013). These industries have altered ecosystems through input of feed and feces, only a small percentage of which is incorporated in food biomass.

Increases in total nutrient load can support higher HAB biomass, and alterations in nutrient form can lead to a nutrient regime favoring HAB growth relative to other algal species. At the simplest level, harmful phytoplankton may increase in abundance due to nutrient enrichment, but remain in the same relative fraction of the total phytoplankton biomass. Even though non-HAB species are stimulated proportionately, a modest increase in the abundance of a HAB species can promote noticeable differences in the ecosystem because of its harmful or toxic effects. More frequently, a species or group of species dominates in response to nutrient enrichment or a change in the ratios of nutrient enrichment (Anderson et al., 2002).

The number of examples of algal blooms linked to eutrophication globally is long, and only a few are highlighted here. A species now well documented to be associated with nutrient enrichment is the dinoflagellate *Prorocentrum minimum*. Globally, it is found in regions of the world where the coasts are receiving elevated nutrients from anthropogenic sources (Glibert et al., 2008). In the Chesapeake Bay, blooms of this species now appear to be 10- to 100-fold higher in maximum density than blooms recorded a few decades ago, and these increases track the nutrient load to the bay over the past several decades (Heil et al., 2005). In Puget Sound, Washington, a striking correlation has been found between the growth in documented cases of PSP over four decades and the growth in human population, based on US census statistics, strongly indicative of nutrient loading and eutrophication as the causative agent of change (Trainer et al., 2003). Based on analyses of frustules preserved in cores, blooms of the diatom *Pseudo-nitzschia* spp. in the Gulf of Mexico were also rare prior to the 1950s, but have increased significantly in abundance and frequency since then as nutrient loads from the Mississippi River have risen (Parsons et al., 2002). The Baltic Sea, the Aegean Sea, the Northern Adriatic, and the Black Seas have all experienced increases in HABs coincident with increases in nutrient loading (Granéli et al., 1999; Heil et al., 2005). In Northern European waters, blooms of the mucus-forming HAB species *Phaeocystis globosa* have been shown to be directly related to the excess nitrate content of riverine and coastal waters, that is, the nitrate remaining after other species of algae deplete silicate (Lancelot, 1995). One region where expansion of eutrophication-related HABs has been particularly pronounced has been along the Asian coast, where blooms have expanded in recent years in areal extent (from square kilometers to tens of square kilometers), in duration (days to months), in species, and in harmful impacts (Furuya et al., 2010). These increases all parallel the increase in the use of anthropogenic fertilizers and the accelerated development of China.

On shorter time scales, there are also examples of HABs responding rapidly to injections of nutrients from pulsed events. Beman et al. (2005) reported, during a 5-year study, a strong positive relationship between nitrogen-rich agricultural runoff to the Gulf of California and the development, within days, of extensive phytoplankton blooms. Similarly, *Pseudo-nitzschia pseudodelicatissima* was found a week after elevated ammonium levels were reported in these waters (Trainer et al., 2007), and in Chesapeake Bay, blooms of *Prorocentrum minimum* have been found to follow within days of elevated levels of urea following agricultural applications (Glibert et al., 2001).

Another important consideration in nutrient effects is the relatively recent phenomenon of changing stoichiometry of nutrient supplies. In many parts of the developed world, phosphorus reductions have been undertaken as a means to reduce or control algal blooms (e.g., in sewage effluents and laundry detergents), whereas nitrogen loads often are allowed to remain elevated. Thus, not only have many systems undergone eutrophication, but many are showing signs of reversal due to this single nutrient reduction. The consequence is that many receiving waters are now not only enriched with nutrients, but these nutrients are in proportions that differ from those of decades past – and also diverge considerably from those that have long been associated with phytoplankton growth (Glibert and Burkholder, 2011). Many types of harmful algae appear to be able to thrive when nutrient loads are not in classically defined ideal proportions. Not only are many HABs able to access nutrients not available to competitors through mixotrophy, some species increase toxin production when growing in a state of nutrient imbalance. As examples, toxin production by the flagellates *Prymnesium parvum* and *Chrysochromulina polylepis* increases under both P and N stress, relative to toxin production in more nutrient-balanced growth conditions (Granéli and Flynn, 2006). As another example, in the dinoflagellate *Alexandrium tamarense*, the production of saxitoxin has been shown to increase by three to fourfold under phosphorus deficiency (Granéli and Flynn, 2006).

Adding to the complexity of nutrient effects, in some cases anthropogenic nutrients may not directly stimulate HABs, but may become linked to their growth and abundance following biogeochemical processing or following the stimulation of other components of the food web on which they may depend, or anthropogenic nutrients may be displaced in time and space leading to blooms that are displaced from their nutrient sources. It has recently been found, for example, that *Noctiluca*, the species responsible for classic "red" water, may well be a coastal or offshore manifestation of eutrophication, a mixotroph responding to successional planktonic changes in nutrient availability (Harrison et al., 2011). Relatedly, regulation of single nutrients (e.g., controlling phosphorus without controlling nitrogen) may lead to a situation where an estuary or inshore coastal environment is effectively phosphorus limited and blooms are controlled, but the nitrogen is displaced downstream where it eventually may help to support offshore blooms. Such effects have been documented for the Neuse River Estuary, the mid-region of the Chesapeake Bay, and the southern Baltic Sea region; all of these regions have experienced either episodic or sustained reductions in inshore blooms, but parallel increases in offshore blooms (Glibert et al., 2011 and references therein).

Links to climate

Climate ultimately controls the fundamental parameters regulating algal growth, including water temperature, nutrients, and light, and thus can be expected to result in changes in the species composition, trophic structure, and function of marine ecosystems. Examples can be found through the US and European coasts, where correlations between shifts in HAB species and the timing of their outbreaks and increases in mean water temperature have been documented. In addition, changing greenhouse gases, pH, as well as temperature are related to changes in stratification, vertical exchange, upwelling, precipitation, and related trends, all of which can also influence the habitat for particular HABs (Moore et al., 2008). Moreover, some HABs, especially CyanoHABs, such as *Microcystis* spp., may become more toxic under higher temperatures (Davis et al., 2009).

Climate change may influence HAB expansion, and therefore, the frequency of some blooms may reflect the major changes in ecosystem structure that occur in response to interannual oscillations, such as those related to the El Niño Southern Oscillation (ENSO), or longer term cycles, such as North Atlantic Oscillation (NAO) and the Pacific Decadal Oscillation (PDO). In the northern Iberian Peninsula, for example, the abundance of the harmful dinoflagellate *Gymnodinium catenatum* was high during the mid-1980s when there was a transition from downwelling-favorable conditions to upwelling-favorable conditions following a shift in the NAO index (Alvarez-Salgado et al., 2003). In California, there is circumstantial evidence that a massive domoic acid event in Monterey Bay in 1998 was triggered by post-El Niño runoff (Scholin et al., 2000).

Estuaries: notable examples of sustained HABs in retentive habitats

Estuaries throughout much of the world are sites of frequent HABs (of all forms, including toxic, nuisance, and ecosystem disruptive). Estuaries – whether they be classic river-dominated systems, fjords, coastal embayments, or rias – have many unique features that may be promotive of HABs. Many estuaries are experiencing increasing nutrient loading from pressures of increasing population and housing developments, intensive agriculture in the watershed, and increased aquaculture production. Estuaries may receive considerable riverine input or may be highly retentive with minimal freshwater input or oceanic exchange. The comparatively shallow nature of estuaries (compared to open coasts and offshore regions) means that benthic processes as well as water column processes may be important in providing nutrients for bloom development or maintenance. As a generality, in estuaries and enclosed coastal embayments, exogenous nutrients are often necessary for high biomass blooms to be initiated, but due to long-term buildup of nutrients in estuaries, leading to large sediment reserves of nutrients, recycling and regeneration may sustain blooms at higher densities and for longer periods of time than in years past. Reinforcing feedbacks in estuaries can lead to an acceleration and/or maintenance of eutrophic conditions. For example, increased algal productivity may lead to depressed water column oxygen which, in turn, may result in increased recycling of nitrogen and phosphorus by changes in redox potential, or pH (Kemp et al., 2005; Glibert et al., 2011; Gao et al., 2012). These fluxes will then positively reinforce an ecosystems degradation trajectory and may contribute to blooms being sustained for long periods of time.

One such example is the bloom of *Aureoumbra lagunensis* evident in Laguna Madre, Texas, that lasted for approximately 8 years in the 1990s. Intense rains after years of drought led to a sequence of blooms, and benthic regeneration led to sustained suitable ecosystem conditions (e.g., Buskey et al., 2001). Similarly, a bloom of *Synechococcus* was observed in eastern Florida Bay that followed an injection of phosphorus from two apparent sources: high freshwater discharge from Hurricanes Katrina, Rita, and Wilma that impacted south Florida in 2005 and a very high organic loading from a unique situation of road construction that required mulching of significant amounts of mangroves (Madden, 2010). Consequently, chlorophyll concentrations rose and were sustained at levels roughly eightfold higher than pre-bloom levels for up to 18 months, while such an increase in phosphorus concentration was only observed during the initiation stages of the bloom and then declined.

Detection, prediction, mitigation, and control

Rapid advances are being made in the ability to detect HABs and, in some cases, predict their occurrence and potentially reduce their impacts. Rapid detection capabilities have evolved from classic microscopic methods to detection involving specific molecules and genomes. For example, numerous methods have been developed targeting antibodies against cell surface antigens that are specific for a specific HAB or HAB group that can be detected with a fluorescent signal (reviewed by Sellner et al., 2003). Additionally, molecular probes have been developed for many species, targeting the ribosomal RNA genes and/or their transcriptional products. Many taxon-species probes have been developed.

New methods have been advanced for detection of toxins as well, and some are field based. Additionally, much progress has been advanced in the use of remote sensing capabilities, both remote imagery as well as moored packages and arrays that can detect and provide real-time information on species as well as associated chemistry and physical parameters. Such packages include both moored arrays and remotely operated vehicles that can survey areas more efficiently than was possible from classic shipboard approaches (Sellner et al., 2003). A suite of over 50 such probes in the State of Maryland is allowing managers and the public alike to monitor trends in Chesapeake Bay and rapidly respond when conditions warrant (www.eyesonthebay.net). In situ nutrient sensors are also advancing, with capability developing for some organic forms of nutrients as well as inorganic forms, so that relationships between pulses in nutrient delivery and alterations in salinity due to rainfall, for example, are now possible to establish (Glibert et al., 2005b; Glibert et al., 2008).

Models and forecasting of blooms are advancing very rapidly. There are two general types of HAB models that are useful for management applications. The first is the development of models that predict "general likelihood of occurrence" of HAB species, whereas the second is the development of models that include "explicit" predictions of HAB occurrence in time or space. The former is useful for management in application of long-term actions to reduce the likelihood of future occurrences, i.e., prevention. The latter requires more refinement to understand the physics, biology, and chemistry of the environment, but it can be of more value at the local community level. Coupling the knowledge of the biology of the organisms of interest with robust circulation models of the area of interest has allowed real-time forecasts to be possible. An excellent example of this developing skill is the model that has been developed for *Karenia brevis* blooms off the coast of Florida. This model uses satellite imagery together with a regional circulation model, predicted wind fields, and several biological parameters to forecast where blooms may be found in a several-day period. Operational forecasts are now provided to the public for Florida and several other regions of the United States where similar capabilities are advancing (http://tidesandcurrents.noaa.gov/hab/).

Understanding and predicting algal blooms is important, but the ultimate goal is reducing their occurrence or their impacts once they do occur. The most effective strategy for reducing their likelihood is nutrient reduction. The best cited example illustrating the effectiveness of nutrient reduction is from the Seto Inland Sea in Japan. Between 1965 and 1976, the number of "red tide" outbreaks (high biomass blooms) increased sevenfold, in parallel with the increase in industrial production, but in 1973, Japanese authorities instituted the Seto Inland Sea Law to reduce loadings to half of the 1974 levels over a 3-year period. The number of red tides began to decrease in 1977, eventually falling to less than 30 % of the peak frequency, which had been in excess of 300 blooms per year (reviewed by Imai et al., 2006).

Bloom control strategies may also take the form of mechanical control, the use of filters or booms to remove or exclude cells from certain areas and use of chemical compounds to kill or inhibit bloom cells, or biological control, the use of organisms or pathogens that can lyse, kill, or remove the HABs. Some efforts are finding success with the use of clays that flocculate and remove the HAB cells from the area. Use of clays is well advanced in Korean waters where clay application is used to protect fish cages when HABs develop (Kim, 2006). Overall, however, all of these control measures may have uncertain or unknown environmental impacts, and all such approaches are in early stages of research and development.

Summary and conclusions

In sum, while some algal blooms, such as spring blooms, are natural characteristics of many temperate and coastal waters, and critically important for food webs of marine and freshwater ecosystems, HABs are, in large part, a consequence of anthropogenic activities. HABs are increasing in frequency, magnitude, and ecological and economic effects throughout the world. Understanding of toxins, human health impacts, and the socioeconomic consequences of these blooms – to fisheries and economies – is emerging, but many questions remain unanswered, particularly as new toxins are discovered or characterized. One of the most significant factors contributing to their expansion – particularly in estuaries – is increased nutrient loading from sewage effluent, agriculture, animal operations, and aquaculture. What is clear is that the historic view of phytoplankton responses to eutrophication – increased nutrients promotes increased chlorophyll and high biomass blooms, leading to oxygen deduction and losses in habitat (e.g., Cloern, 2001) – is too simplistic for understanding how HABs respond to the major changes in nutrient loads, forms, and stoichiometry that many systems are now sustaining. Nutrient form and proportion matter and many HABs have physiological mechanisms that enable them to thrive in these environments that are being dramatically altered by human influence. Furthermore, the interplay of biology and physics is only understood at a limited scale, with much to be learned about local scales, microstructures, as well as mesoscale features. Climate changes are adding additional factors that may enhance the likelihood for blooms, and the complexity of ecosystem changes with climate changes means that much is yet to be learned about the direct and indirect effects of climate on HABs. New technologies are advancing toward improved monitoring and prediction, but many such technologies are sophisticated and expensive. Although considerable advances have been made in understanding the biology of HABs, and their interactions with other members of the community at all levels of the food web, there is still much to be learned about how and why specific species respond to specific conditions.

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Cross-references

Ecological Stoichiometry
Eutrophication

ALKALINITY

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Definition

Alkalinity is the name given to the quantitative capacity of water to neutralize an acid to the equivalence point of carbonate or bicarbonate (Water Quality Association, 2000). The total alkalinity of sea water was defined by Dickson (1981) as "... the number of moles of hydrogen ion equivalent to the excess of proton acceptors (bases formed from weak acids with a dissociation constant $K \leq 10^{-4.5}$ at 25 °C and zero ionic strength) over proton donors (acids with $K > 10^{-4.5}$) in 1 kg of sample." For the compounds found in water, the total alkalinity (A_T) is expressed as:

$$\begin{aligned} A_T = {} & [HCO_3^{-}] + 2\left[CO_3^{-2}\right] + \left[B(OH)_4^{-}\right] + [OH^{-}] \\ & + \left[HPO_4^{-2}\right] + 2\left[PO_4^{-3}\right] + [H_3SiO_4^{-}] + [NH_3] \\ & + [HS^{-}] - [H^{+}]_F - [HSO_4^{-}] - [HF] - [H_3PO_4] \end{aligned}$$

where $[H^+]_F$ is the free concentration of the hydrogen ion (Dickson, 2010).

In natural waters, carbonate alkalinity, $A_C = [HCO_3^{-}] + 2[CO_3^{-2}]$, tends to comprise most of the A_T due to the common occurrence and dissolution of carbonate rocks and presence of carbon dioxide in the atmosphere. Other common natural components of A_T are borate, hydroxide, phosphate, silicate, nitrate, ammonia, sulfide, and the conjugate bases of some organic acids. In anoxic conditions the relative role of sulfide, ammonia, and phosphate components of A_T increases (Volkov et al., 1998). In coastal regions, especially estuaries, dissolved organic matter can significantly contribute to A_T (Kim and Lee, 2009).

Alkalinity can be measured by titrating a sample with a strong acid until all the buffering capacity of the aforementioned ions above the pH of bicarbonate or carbonate is consumed (i.e., total titratable alkalinity). This point is functionally set to pH 4.5. At this point, all the bases of interest have been protonated to the zero level species; hence, they no longer cause alkalinity.

An addition (or removal) of CO_2 to a solution does not change the alkalinity. Addition of CO_2 to a solution in contact with a solid can affect the alkalinity, especially for carbonate minerals in contact with groundwater or seawater. The dissolution (or precipitation) of carbonate rock has a strong influence on alkalinity. In open ocean waters, alkalinity can be connected with salinity and temperature with a functional dependence (Lee et al., 2006). Rivers can act as either a source or a sink of alkalinity.

The actual units for the alkalinity titration are moles or equivalents per volume ($mol\ L^{-1}$ or $Eq\ L^{-1}$). They can be converted to $mol\ kg^{-1}$ or, in terms of calcium carbonate, to $mg\ CaCO_3\ L^{-1}$.

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Cross-references

pH
Water Quality

AMPHIPODS

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Synonyms

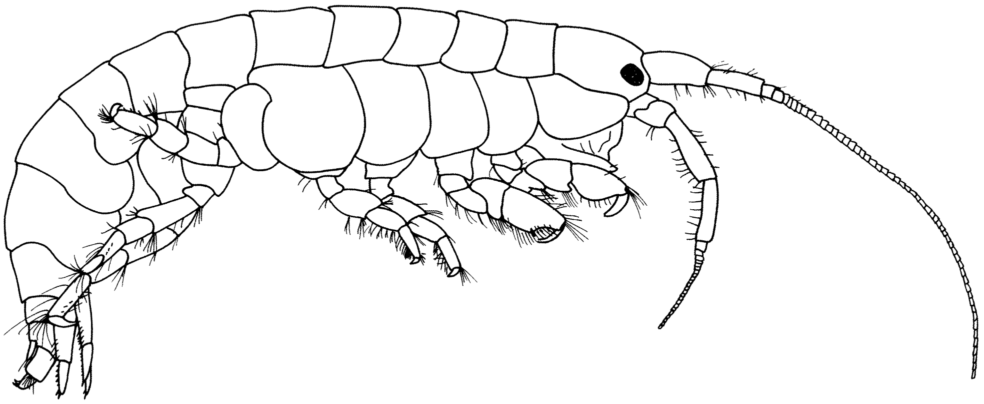
Beach fleas; Beach hoppers; Sand fleas; Sand hoppers; Side swimmers; Scuds; Skeleton shrimps

Definition

Amphipods are crustaceans from the order Amphipoda (Arthropoda, Crustacea, Malacostraca, Peracarida).

Amphipods are a diverse group of small crustaceans that are important members of most aquatic communities. They are mostly small (less than 2 cm) and laterally flattened with no carapace, a thoracic region with seven pairs of pereopods (walking legs) and an abdominal region bearing three pairs of pleopods and three pairs of uropods (Figure 1). The sexes are separate and frequently dimorphic, with males having an enlarged gnathopod involved in mate guarding. Following mating, their eggs are brooded within a marsupium and develop directly after hatching.

Amphipods are highly abundant in most estuarine sediments (up to 100,000 individuals per square meter),



Amphipods, Figure 1 Grazing amphipods from the family Ampithoidae are abundant in estuarine seagrass beds.

occurring as members of the epibenthic community or as burrowing infauna. They are one of the most conspicuous members of the invertebrate fauna inhabiting sandy or muddy beaches where they burrow into sediments or are closely associated with seagrass and algal wrack. Amphipods are abundant as fouling organisms on hard substrates and often numerically dominate the epifauna of seagrasses and macroalgae. Many species are also commensal with benthic invertebrates including sponges, ascidians, and bryozoans. Relatively few species are exclusively planktonic. While they have no larval stage that disperses in the water column, benthic amphipods are often highly mobile and colonize new habitats quickly.

Amphipods display a great diversity of feeding strategies. They include detritivores, suspension feeders, scavengers, predators, herbivores, and parasites (rarely). Those that process sediments play an important role as bioturbators in estuaries, altering the physical and chemical conditions, and thus nutrient fluxes, of the sediments. Grazing amphipods in vegetated habitats can alter the composition of primary producers and play an important role in limiting the abundance of epiphytes that can negatively affect seagrass health. Amphipods frequently comprise a large component of the diets of predatory fish and birds and thus play an important role in the transfer of energy from primary producers to higher trophic levels.

Due to their short generation times, direct development, ease of culture, and intimate associations with sediments, amphipods are routinely used in ecotoxicology as test organisms for evaluating sediment and water quality and as biomonitors for environmental contamination.

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ANADROMOUS

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Definition

Organisms such as fishes which hatch in fresh water and migrate to higher salinities such as the sea to mature and then migrate back into fresh water to spawn.

Background

Originating in the nineteenth-century Russian literature and refined from the original term ("contranatant"; Meek, 1916; Subnikov, 1976) by Meyers (1949), anadromous is one of the three types of migration between the sea and fresh water (McDowall, 1987). The directed movement by anadromous fish between these markedly different habitats is specifically associated with reproductive phases of their life cycle. Of the approximately 20,000 species of fish around the world (Cohen, 1970), McDowall estimated that 54 % are anadromous. They are most common in northern subpolar and cooler temperate waters.

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ANAEROBIC ENVIRONMENTS

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Synonyms

Non-aerial environment

Definition

An anaerobic environment is characterized by the absence of free oxygen but may contain atomic oxygen bound in compounds such as nitrate (NO_3), nitrite (NO_2), and sulfites (SO_3), in contrast to an aerobic environment where free oxygen is available (WKU, 2013).

Description

Some organisms are successfully adapted to anaerobic environments (EPA, 2012). These organisms do not use O_2 as their electron acceptors. There are a number of substances that they will use as a substitute for O_2, including (among others) nitrate (NO_3), ferric iron (Fe_3^+), manganese (Mn_2^+), sulfate (SO_4^{2-}), and carbon dioxide (CO_2) (Scharf, 2000). Bacteria use sulfate as an acceptor for electrons in place of oxygen under anaerobic conditions. As the reduced organic tissue is oxidized to CO_2, the sulfate is reduced to sulfide (Nietch, 2000).

In bottom waters of stratified estuaries, oxygen consumed primarily by bacteria will exceed oxygen input via atmospheric and photosynthetic reoxygenation. While the anoxia/hypoxia that develops will eliminate almost all estuarine and marine organisms, a large number of bacteria and protists can still remain active in these areas by changing their metabolism to anaerobic respiration (Dang et al., 2008). If oxygen becomes so low that the system becomes anoxic, which occurs frequently in shallow turbid estuaries in the summer time, anaerobic mechanisms for decomposition become important. Carbon turnover occurs continuously in subtidal and intertidal sediments where oxygen is depleted just a few millimeters below the sediment surface. Much of the organic matter undergoes decomposition in an estuarine anaerobic environment via sulfate reduction (Nietch, 2000). Preservation of skeletal remains in these environments appears to be correlated with the abundance of dissolved organic matter rather than with high sedimentation rates (Simon et al., 1994).

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Cross-references

Anaerobic Environments
Anoxia, Hypoxia, and Dead Zones

ANOXIA, HYPOXIA, AND DEAD ZONES

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Synonyms

Anoxic; Anoxic basins; Euxina; Hypoxic, Low dissolved oxygen; Oxygen minimum layer; Oxygen minimum zone

Definition

Anoxia is a condition of no, or at times very little, dissolved oxygen in marine or freshwater systems, which has drastic consequences to normal ecosystem functioning including biogeochemical cycling.

Hypoxia is a condition of low dissolved oxygen concentrations in marine or freshwater systems, which has adverse consequences to normal ecosystem functioning including biogeochemical cycling that range from mild to severe disruption.

Dead zone is an area of hypoxia or anoxia that is related to anthropogenic activity.

Introduction

Oxygen is necessary to sustain the life of fishes and virtually all higher invertebrates. When the supply of oxygen is cut off from bottom waters, usually from temperature and/or salinity stratification of the water column that separates surface and bottom layers, or consumption of oxygen through respiration exceeds resupply, oxygen concentrations can decline below levels that will sustain animal life. This condition of low oxygen is known as hypoxia. Water devoid of oxygen is referred to as anoxic. Ecologists have borrowed the term hypoxia from the medical community, but the meaning and processes for the environment are the same. The medical condition is a deficiency in the amount of oxygen reaching tissues. Similarly, a water body can be deprived of adequate oxygen for proper ecosystem functioning.

Hypoxic areas are sometimes referred to as dead zones. A term first applied to the northern Gulf of Mexico hypoxic area, which is related to excess agricultural and municipal nutrients discharged from the Mississippi and Atchafalaya Rivers (Rabalais et al., 2002, Rabalais et al., 2010), and refers to the fact that fish and shrimp avoid and migrate out of hypoxic areas. When fishermen trawl in these zones, little to nothing is caught. The term dead zone is best applied to coastal waters affected by anthropogenic activities where oxygen depletion occurs in otherwise normoxic (well oxygenated) waters and not to naturally occurring oceanic oxygen minimum zones.

The migration of mobile fishes and invertebrates can be obvious, and mortality of smaller sessile invertebrates can be overlooked, but in the absence of larger fauna, smaller species (e.g., foraminiferans and nematodes) and microbes persist and thrive, such that hypoxic areas are not truly dead or devoid of life. In addition, the fully oxygenated upper water column continues to support diverse communities, including productive fisheries. Globally, there are four basic types of low-oxygen marine environments:

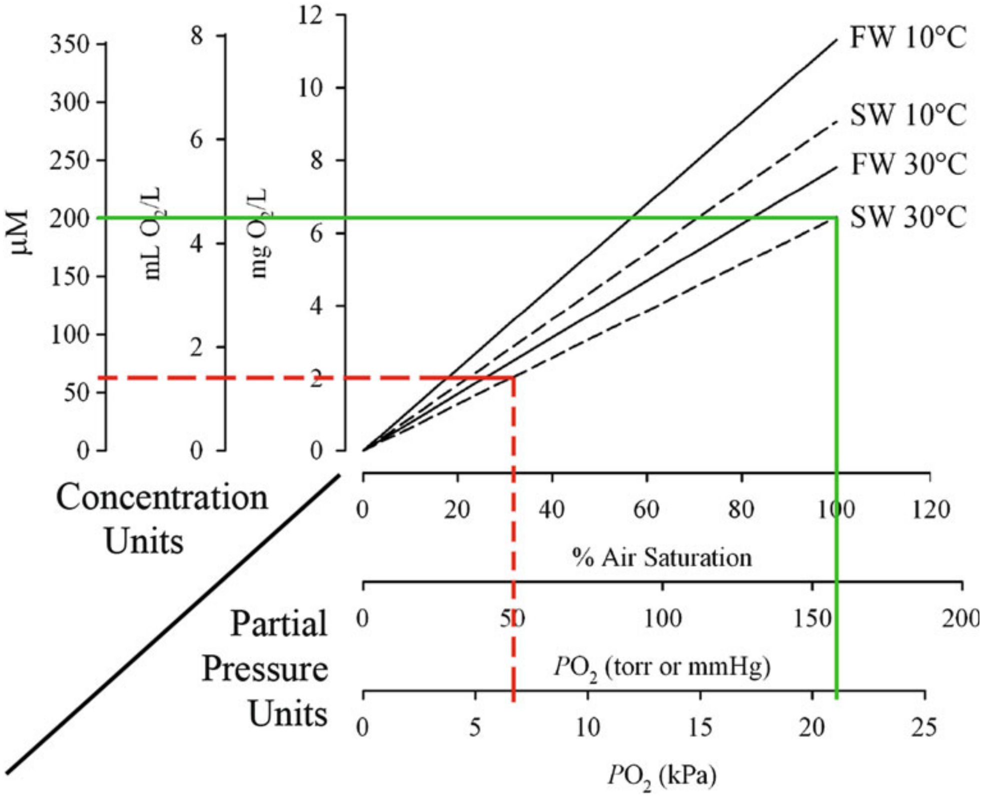
- Naturally occurring oceanic oxygen minimum zones
- Naturally occurring coastal upwellings
- Naturally occurring anoxic deep basins
- Anthropogenic-related coastal, estuarine, and brackish water hypoxia

Dead zones are just one of many consequences of anthropogenic activities (MA, 2005). Human population is expanding exponentially, recently passing six billion, and will likely exceed 8-10 billion by the year 2050. This expansion has lead to an exponential modification of landscapes at the expense of ecosystem function and services including pervasive effects from fuelling coastal primary production with excess nutrients, the primary factor leading to formation of hypoxia, to fishing down the food web (Vitousek et al., 1997; Jackson et al., 2001; Foley et al., 2005; Lotze et al., 2006). Long-term records of nutrient discharges provide compelling evidence of a rapid increase in the fertility of many temperate coastal ecosystems starting about 50 years ago (Galloway et al., 2004; Galloway et al., 2013). On a global basis, by 2050, coastal marine systems are expected to experience, from today's levels, a 2.4-fold increase in nitrogen and 2.7-fold increase in phosphorus loading from this population expansion (Tilman et al., 2001), with serious consequences to ecosystem structure and function. The question asked by Foley et al. (2005) is as follows: are land-based activities degrading the global environment in ways that undermine ecosystem services, which in turn undermine human welfare? When it comes to dissolved oxygen and the development of dead zones, the answer is yes.

Dissolved oxygen concentrations

While many authors and water quality regulations focus on concentrations of oxygen below 2–3 mg O_2/L (see Figure 1 for conversions to other units) as a threshold value for hypoxia in marine and brackish water environments, such arbitrary limits may be unsuitable when examining potential impacts of hypoxia on any one given species (Vaquer-Sonyer and Duarte, 2008). Hypoxia becomes detrimental when behavioral and physiological responses result in altered behavior or negative impacts, such as reduced growth, loss of reproductive capacity, mortality, reduced biodiversity, loss of secondary production, and stressed fisheries. For example, Atlantic cod (*Gadus morhua*) growth in St. Laurence is reduced below about 7 mg O_2/L or 70 % air saturation (Chabot and Dutil, 1999). Shrimp and fish avoid dissolved oxygen below 2 mg O_2/L (approximately 30 % air saturation) in the northern Gulf of Mexico hypoxic zone, while sharks and rays emigrate from the area at oxygen concentrations below 3 mg O_2/L (Rabalais et al., 2001).

Because of the low solubility of oxygen in water, small changes in the absolute amount of oxygen dissolved in water lead to large differences in percent air saturation. For freshwater at 20 °C, 9.1 mg of oxygen (O_2) will dissolve in a liter of water, so a 1 mg O_2/l drop is about an 11 % decline in saturation. In addition, oxygen solubility is strongly dependent on temperature and the amount of salt dissolved in the water. Saturation declines about 1 mg O_2/L from 20 to 26 °C and about 2 mg O_2/L from freshwater to seawater at similar temperatures (Benson and Krausse, 1984). Therefore, depending on temperature and salinity, water contains 20–40 times less oxygen by volume and diffuses about 10,000 times more slowly through water than air (Graham, 1990). Thus, what appear to be small changes in oxygen can have major consequences to animals living in an oxygen-limited milieu (Rabalais and Gilbert, 2009). Physiologically, higher temperatures also increase metabolic requirements for oxygen



Anoxia, Hypoxia, And Dead Zones, Figure 1 Nomogram for dissolved oxygen in freshwater (*FW*) and seawater (*SW*) at 10 °C and 30 °C (Modified from Diaz and Breitburg, 2009). Concentration units are on y-axis, and partial pressure units are on x-axis. *Red dotted line* is 2 mg O_2/L and *green solid line* is 100 % solubility of oxygen in seawater at 30 °C.

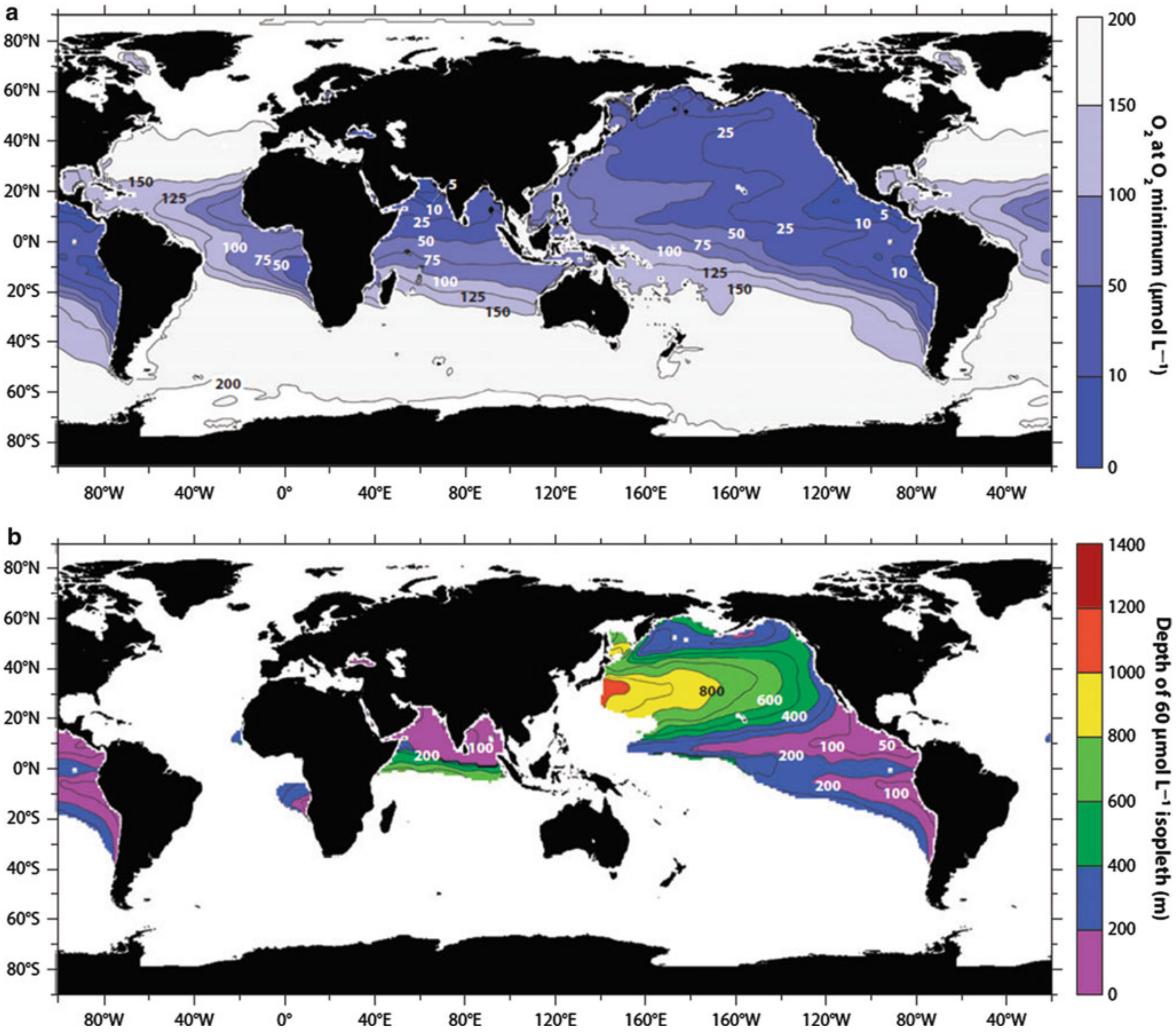
and increase rates of microbial respirations and, therefore, oxygen consumption. For salmonid fishes, oxygen can become limiting at relatively high values, and even air saturation can be limiting at higher temperatures (Fry, 1971). Concentrations of dissolved oxygen below 2-3 mg O_2/L are a general threshold value for hypoxia for marine and estuarine organisms and 5-6 mg O_2/L in freshwater. However, species and life stages differ greatly in their basic oxygen requirements and tolerances (Vaquer-Sonyer and Duarte, 2008).

Naturally low dissolved oxygen environments

By any definition, oceanic oxygen minimum zones (OMZs) are the largest low dissolved oxygen areas on earth and cover about 30 million square kilometers of open ocean (Figure 2), much of which is not near the continents (Paulmier and Ruiz-Pino, 2009). Globally, where OMZs contact the bottom, about 1,148,000 km^2 of continental margin seafloor is estimated to have bottom water oxygen concentrations <0.7 mg O_2/L (Helly and Levin, 2004). The principal factors that lead to the formation of OMZs are high surface productivity, old water mass age, and limited circulation. In addition, upwelling associated with continental margins leads to higher productivity and greater oxygen demand and also contributes to a thicker OMZ and lower oxygen concentrations (Helly and Levin, 2004).

Upwelling areas can also develop extensive hypoxia as deepwater nutrients are added to surface waters increasing production that eventually sinks and decomposes. Hypoxia associated with upwelling is not as long-lived and stable as that associated with OMZs but can periodically reoccur. The best known upwelling is along the coast of Peru and Chile associated with El Niño. Hypoxia associated with this type of coastal upwelling is not as long-lived and stable as that associated with OMZs. Upwelling can interact strongly with low-oxygen water masses to produce intense shelf hypoxia; this is observed off of Oregon, USA (Grantham et al., 2004), and Chile (Fuenzalida et al., 2009), Africa (Monteiro et al., 2008), and India (Naqvi et al., 2000).

Upwelling associated with both the Humboldt (Escribano et al., 2004) and Benguela Current systems (Chapman and Shannon, 1985; Monteiro et al., 2008) develops extensive severe hypoxia and anoxia that adversely affect pelagic and benthic species (Arntz et al., 2006). For example, in 1994, persistent and pronounced hypoxic conditions developed off the coast of central and northern Namibia over much of the continental shelf. These conditions displaced



Anoxia, Hypoxia, And Dead Zones, Figure 2 General global distribution of oxygen minimum zones (60 µmol/L). (**a**) *Colors* indicate oxygen concentrations at the depth of minimum oxygen. (**b**) Depth of the 60 µmol/L isoline in meters (From Keeling et al., 2010).

juvenile Cape hake (*Merluccius capensis*) offshore from their typical inshore habitat, subjecting them to heavy mortalities from predation by larger hake and from commercial trawling (Hamukuaya et al., 1998). Lobsters (*Jasus lalandii*) were trapped by low-oxygen waters advecting onshore that caused a "walkout" and mass mortality (Cockroft, 2001).

Today, there are a number of isolated ocean basins that are hypoxic/anoxic due to restricted water circulation combined with high primary production in surface waters. Among them are the permanently anoxic Black Sea and Cariaco Basin and several smaller basins along the California, USA, coast (Santa Monica, Santa Barbara, San Pedro, San Nicolas basins) that are reoxygenated periodically (Berelson, 1991). Some deep fjords that are permanently anoxic, such as the Framvaren, Norway, have a similar biogeochemistry to oceanic anoxic basins (Skei, 1983). But, most fjords have some seasonal deepwater renewal, which keeps them from being anoxic all year.

In the case of the Black Sea, anoxic conditions occur beneath 100–200 m of oxygenated surface waters in the open sea area. The restricted connection with the Mediterranean Sea, strong stratification, and geomorphology make the Black Sea a sink for nutrients and other materials (Richards, 1965; McQuatters-Gollop et al., 2008). The persistent anoxic basin in the open Black Sea is the largest naturally occurring anoxic area on earth. It covers about 75 % of the basin's area and is distinct from and not related to the eutrophication-related seasonal hypoxia that has occurred on the shallow northwestern continental shelf (Tolmazin, 1985; Zaitsev, 1992; Mee, 2001, 2006). The Cariaco Basin also supports a large persistent anoxic area below 250 m. Restricted circulation and high primary production within the basin support this anoxia (Müller-Karger et al., 2001; Müller-Karger et al., 2004). This naturally occurring anoxic basin allows for sediments to be deposited without bioturbation, forming varves of alternating light and dark color, which correspond to the dry or rainy season (Haug et al., 2001). Because of water column anoxia, anoxic basins have a unique biogeochemistry that resembles that of anaerobic sediments (Madrid et al., 2001; Stoeck et al., 2003). Bacteria inhabit both the oxic and anoxic portions of the water column, with a maximum in the suboxic interface (Taylor et al., 2001). The suboxic layer oscillates between 200 and 300 m in the Cariaco Basin and 150 and 200 m in the Black Sea (Oguz, 2005).

Recently, a troubling decline in the oxygen content in the open ocean is becoming apparent. Much of the decline is related to global climate change but declining trends near the coastline may be stronger and related to human activities (Stramma et al., 2008; Stramma et al., 2012; Gilbert et al., 2009; Keeling et al., 2010). The upper depth limit of OMZs has major implications for fisheries. Expansion of OMZs toward the surface in the eastern tropical Pacific has limited the depth distribution of tropical pelagic marlins, sailfish, and tunas into a narrower surface layer of oxic water about 50-100 m thick (Prince and Goodyear, 2006). The high-performance physiology of these fishes leads to a relatively high hypoxic threshold (Brill, 1996), making any reduction in oxygen problematic. Declining oxygen and expansion of the OMZ in the tropical northeast Atlantic Ocean toward the surface are also restricting usable habitat of billfishes and tunas. From 1960 to 2010, Stramma et al. (2012) found hypoxia-based habitat compression to decreasing their suitable habitat by 15 %. The combination of shallowing of OMZs encroaching onto outer continental shelves and increased coastal eutrophication-induced hypoxia will eventually reduce suitable habitat space for both pelagic and demersal fishes.

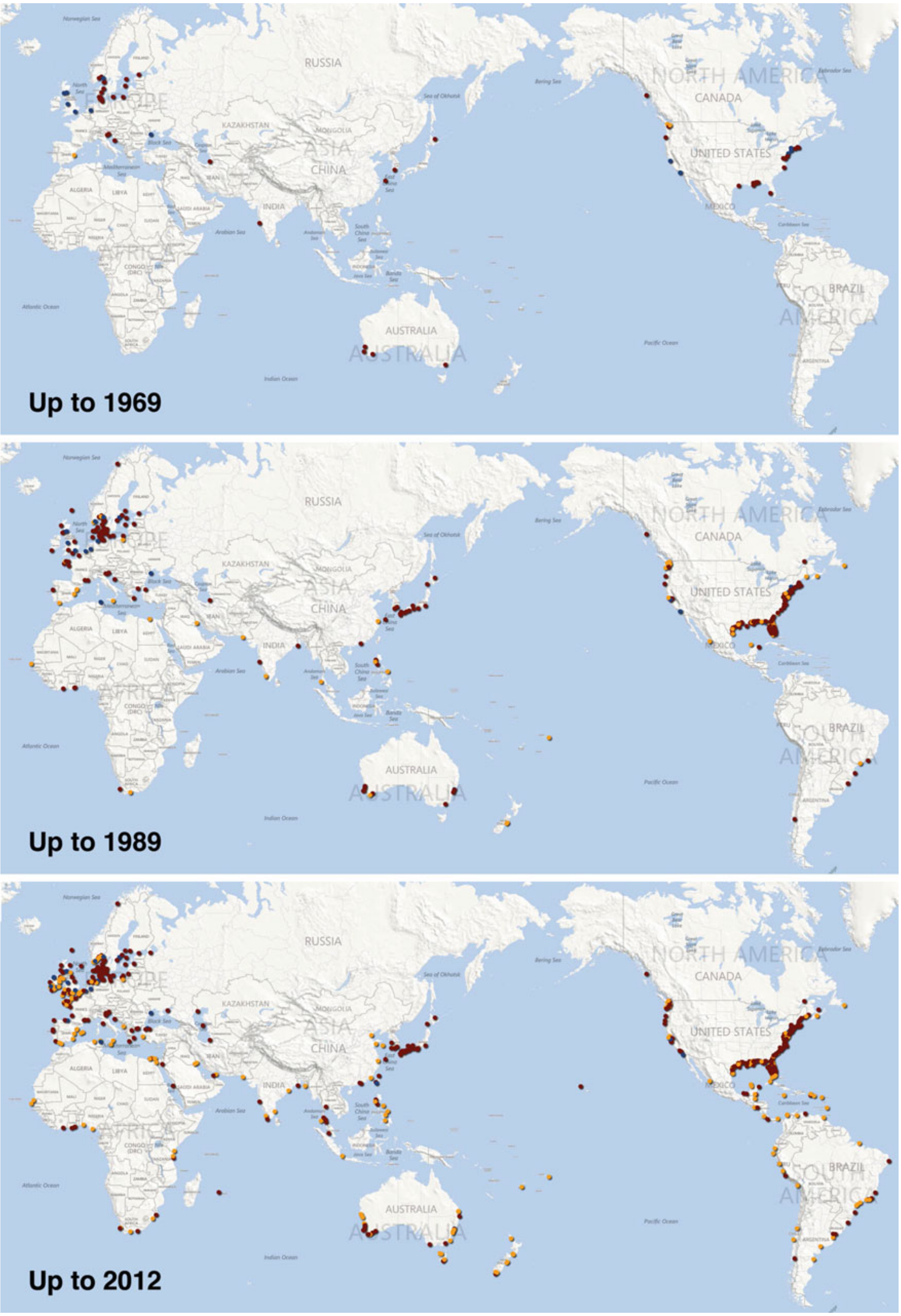
Anthropogenic influence on dissolved oxygen

In contrast to OMZs, upwelling zones, and deep basins, much of the hypoxia and anoxia in shallow coastal marine areas have developed within the last 50 years and are closely associated with anthropogenic activities. Diaz and Rosenberg (1995) noted that no other environmental variable of such ecological importance to estuarine and coastal marine ecosystems has changed so drastically in such a short period of time. Through time, there have been consistent trends of increasing severity in duration, intensity, or extent of hypoxia in areas with long-term data, for example, the northern Adriatic Sea (Justić et al., 1987). Once a system develops hypoxia, it can quickly become an annual event and a prominent feature affecting energy flow (Elmgren, 1989; Baird et al., 2004). Currently, there are over 600 hypoxia areas associated with anthropogenic activities in the world's coastal areas covering more than 245,000 km^2 of sea bottom (Diaz and Rosenberg, 2008; Diaz et al., 2010; Conley et al., 2011; Figure 3).

The worldwide distribution of coastal hypoxia is related to major population centers or is closely associated with developed watersheds that export large quantities of nutrients, specifically nitrogen and phosphorus. Up to 1970, there were scattered reports of hypoxia in North America and northern Europe. By the 1990s, coastal hypoxia was prevalent in North America, northern Europe, and Japan. By the 2000s, there were increased reports of hypoxia in South America, southern Europe, and Australia (Figure 3). Considering the close association of human population and hypoxia, it is likely that Asia and the Indo-Pacific have many unreported hypoxic areas.

Eutrophication can be defined as the increase in the rate of production of organic matter and accumulation of that organic carbon within an ecosystem (Nixon, 1995; Rabalais, 2004). This is typically in excess of what an ecosystem is normally adapted to processing and is only part of a complex web of stressors that interact to shape and direct ecosystem level responses to stressors (Cloern, 2001). The primary driver of eutrophication in both freshwater and marine systems is excess nutrient enrichment, but physical conditions that limit reaeration of bottom water are also necessary for the development of hypoxia. Phosphorus is generally the limiting nutrient in freshwater (Schindler, 1977), and increases in anthropogenic phosphorus have caused increased algal production and eutrophication in freshwater ecosystems worldwide (Carpenter et al., 1999; Smith et al., 2006). For marine systems the limiting nutrient tends to be nitrogen (Howarth and Marino, 2006). This basic difference is related to the physical properties of phosphorus and nitrogen compounds and their biogeochemical cycling through the freshwater and marine environments. Basically, phosphorus tends to be more limiting in fresher, brackish waters and river plumes, and nitrogen is more likely to be limiting in the marine end member of an estuary or a freshwater-dominated coastal system.

Eutrophication and associated hypoxia in freshwater systems became widespread in the twentieth century, but effective nutrient management has reversed this trend where it has been rigorously implemented (Jeppesen et al., 2005). In tidal portions of rivers and other water bodies near dense population centers, severe hypoxia and anoxia have been caused by discharge of raw sewage, which is high in both nutrients and organic matter. Areas devoid of fishes were reported as early as the late 1800s, for example, the Mersey Estuary, UK, and persisted until improvements in sewage treatment were implemented (Jones, 2006). Much of the hypoxia and anoxia in shallow coastal marine and estuarine areas are recent in origin and related to a combination of nitrogen and phosphorus from agriculture and human waste and atmospheric deposition of nitrogen.



Anoxia, Hypoxia, And Dead Zones, Figure 3 (Continued)

Annual hypoxia does not appear to be a natural condition for marine waters except for those systems previously described. Even in Chesapeake Bay, which had hypoxia when oxygen measurements were first made in the 1910s in the Potomac River (Sale and Skinner, 1917) and 1930s in the main stem channel (Officer et al., 1984), the geological record suggests that low oxygen was not an annual, seasonally persistent feature of the system prior to European colonization (Cooper and Brush, 1991; Zimmerman and Canuel, 2000). Geochronologies from the hypoxic area on the continental shelf of the northern Gulf of Mexico also indicate that the current seasonal hypoxia, which can cover over 20,000 km^2, did not form annually prior to the 1950s (Sen Gupta et al., 1996), and models indicate not earlier than the 1970s (Justić et al., 2001, Scavia et al., 2003; Turner et al., 2006). Hypoxia was recorded with the first oxygen measurement made in the area in the summer of 1973 on the central Louisiana continental shelf (Rabalais et al., 2002) and remains an annual event.

Many systems that are currently hypoxic were not so when first studied. For systems with historical data from the first half of the twentieth century, declines in oxygen concentrations started in the 1950s and 1960s for the northern Adriatic Sea (Justić et al., 1987), between the 1940s and 1960s for the northwest continental shelf of the Black Sea, and in the 1970s for the Kattegat (Baden et al., 1990). Declining dissolved oxygen levels were noted in the Baltic Sea as early as the 1930s (Fonselius, 1969), but it was in the 1950s that hypoxia became widespread (Karlson et al., 2002). Other systems had hypoxia since the beginning of oxygen measurements, for example, in the 1900s for Kamak Bay, Korea (Lim et al., 2006); 1910s for Oslofjord, Norway (Mirza and Gray, 1981); 1920s for Thames Estuary, England (Andrews and Rickard, 1980); 1930s for Chesapeake Bay (Newcombe and Horne, 1938); and 1970s for the northern Gulf of Mexico (Turner et al., 2008).

The negative effects of hypoxia include loss of suitable and required habitat for many bottom-dwelling fishes and benthic fauna, habitat compression for pelagic fishes, direct mortality, increased predation, decreased food resources, altered trophic energy transfer, altered bioenergetics (physiological, development, growth, and reproductive abnormalities), and altered migration. These result in stressed fisheries species (Jørgensen, 1980; Caddy, 1993; Rabalais and Turner, 2001; Cheng et al., 2002; Kodama et al., 2002; Breitburg et al., 2009). Increasing nutrient loads that also change the nutrient ratios can affect the composition of the phytoplankton community and can shift trophic interactions (Turner et al., 1998). Hypoxia also alters or interrupts ecosystem functions and services such as nutrient cycling and bioturbation (Gutiérrez et al., 2000; Rabalais, 2004; Nizzoli et al., 2007; Middelburg and Levin, 2009; Weissberger et al., 2009; Sturdivant et al., 2012). Much of the alteration in functions from hypoxia can be observed in time-lapse videos captured with Wormcam by Sturdivant et al. (2012).

The frequency and duration of hypoxic events vary among systems, over time, and with varying nutrient loads or organic accumulation. Hypoxia ranges from aperiodic events with years to decades between reoccurrences to a persistent year-round feature that can last for years or centuries at a time. Dominant faunal responses differ by type of hypoxia (Figure 4). Aperiodic hypoxia, resulting from unusual or uncommon climate conditions, elicits the most dramatic response of mass mortality in sessile and, at times, mobile species. For benthic invertebrates, this dramatic response is due to the large numbers of sensitive species usually present prior to the hypoxic event. For example, the onetime hypoxic event in the New York Bight in 1976 that covered about 1,000 km^2 caused mass mortality of many commercial and noncommercial species (Boesch and Rabalais, 1991).

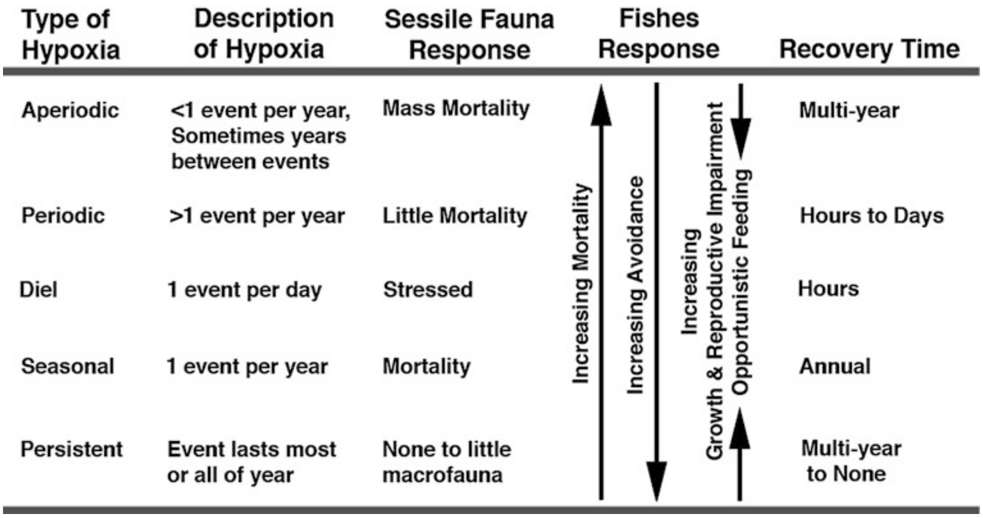
Summary

Hypoxia occurs in a wide range of systems and varies in temporal frequency, seasonality, and persistence. In temperate latitudes, bottom waters can remain hypoxic or anoxic for hours to months during summer and autumn.

There is no doubt that the increase in the areas within coastal and open oceans with hypoxia is real. Coastal water quality with regard to oxygen is currently on the decline, and the future, based on the continued increase in the global occurrence of hypoxia and current and projected increased loads of nutrients, is trending to more hypoxia. The formation of hypoxic areas has been exacerbated by any combination of interactions that increase primary production and accumulation of organic carbon leading to increased respiratory demand for oxygen below a seasonal or permanent pycnocline.

The overall forecast is for hypoxia to worsen, with increased occurrence, frequency, intensity, and duration. The consequences of global warming and climate change are effectively uncontrollable at least in the near term. On the other hand, the consequences of eutrophication-induced hypoxia can be reversed if long-term, broad-scale, and persistent efforts to reduce substantial nutrient loads are developed and implemented. The need for water and resource managers to reduce nutrient loads even if at a minimum, to maintain the current status, is critical in view of globally expanding hypoxia.

Anoxia, Hypoxia, And Dead Zones, Figure 3 Global distribution of documented cases of hypoxia related to human activities, *red dots*. Systems that have recovered from hypoxia through management of nutrient and organic loadings are *blue dots*. Systems that are eutrophic and in danger of becoming hypoxic are *yellow dots*. The number of hypoxic areas is cumulative for the successive time periods (From Diaz et al., 2010).



Type of Hypoxia	Description of Hypoxia	Sessile Fauna Response	Fishes Response	Recovery Time
Aperiodic	<1 event per year, Sometimes years between events	Mass Mortality		Multi-year
Periodic	>1 event per year	Little Mortality		Hours to Days
Diel	1 event per day	Stressed		Hours
Seasonal	1 event per year	Mortality		Annual
Persistent	Event lasts most or all of year	None to little macrofauna		Multi-year to None

Anoxia, Hypoxia, And Dead Zones, Figure 4 Types of hypoxia and generalized faunal response. Sessile fauna are primarily macrobenthos. *Arrows* indicate direction of increased impact on fishes. Mortality in fishes is more likely from aperiodic hypoxia, with complete avoidance of persistent hypoxia. Physiological impairment and opportunistic feeding are greatest for periodic and diel hypoxia (Modified from Diaz and Breitburg, 2009).

The future pervasiveness of hypoxia in all ecosystems will depend upon a combination of climate change and land management. Climate change will affect water column stratification, organic matter production, nutrient discharges, and rates of oxygen consumption. Land management will also affect the concentrations of nutrients through agriculture.

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Cross-references

Climate Change
Dissolved Oxygen
Eutrophication
Nitrogen
Nutrient Dynamics
Nutrients
Oxygen Depletion
Phosphorus

ANTHROPOGENIC IMPACTS

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Definition

Anthropogenic impacts in this volume refer to the adverse effects of human activities on estuarine environments.

Introduction

Estuaries rank among the most heavily impacted aquatic ecosystems on earth, being affected by a wide array of anthropogenic activities both in adjoining coastal watersheds and in the water bodies themselves (Kennish, 2002). Most of these activities can be linked to ongoing rapid human population growth and development of the coastal zone. For example, about four billion people live within 60 km of the world's coastlines (Kennish, 2002; Kennish et al., 2008). In the USA, more than 125 million people now reside in coastal counties nationwide. People inhabiting low-lying coastal areas are more vulnerable to sea-level rise, coastal storms and storm surges, inundation and flooding, and other coastal hazards.

While many people simply prefer to live near the ocean, others inhabit the coastal zone for economic opportunity involving tourism, recreational and commercial fisheries, mariculture, transportation and shipping, domestic and industrial construction, electric power generation, oil and gas recovery, and other human activities. Escalating human settlement has altered land use/land cover in coastal watersheds, creating impervious surfaces that facilitate nonpoint-source pollution input to estuaries. Much of this is coupled to developing infrastructure such as construction of roadways and bridges, electric utilities, as well as water, sewer, and gas lines. Other major pollutant delivery systems are point-source inputs. Some human activities have physically altered estuarine shorelines and habitats, impacting biotic communities. Included here are the construction of bayshore housing, lagoons, bulkheads and other shore protection features, harbor and marina development, dredging and dredged material disposal, wetland reclamation, and channel and inlet stabilization. Upland modifications (e.g., dams and reservoirs, deforestation and habitat fragmentation, and channelization) can significantly exacerbate other anthropogenic stresses leading to greater pressures in estuarine systems. Increasing freshwater diversions for agriculture and other human needs, such as in California (USA), can significantly alter salinity, circulation, and biotic communities in estuaries.

Estuarine impacts

Kennish et al. (2014a) identified 12 major anthropogenic stressors on estuarine ecosystems. These include (1) eutrophication; (2) sewage and organic wastes; (3) habitat loss and alteration, shoreline hardening, and erosion; (4) chemical contaminants; (5) human-induced sediment/particulate inputs; (6) overfishing; (7) intensive aquaculture; (8) introduced/invasive species; (9) human-altered hydrological regimes; (10) climate change; (11) coastal subsidence; and (12) floatables/debris. An additional stressor of importance is a group of pathogens that can impact human use of estuaries. According to Kennish and Paerl (2010), anthropogenic stressors can be categorized into those that degrade water quality and are primarily chemical and biological in nature (e.g., nutrient enrichment, chemical contaminants, and pathogens), impact habitat and are mainly physical factors (e.g., shoreline hardening, lagoon construction, dredging and dredged-material disposal), and alter biotic communities and are effectively driven by multiple stressors (e.g., overfishing, introduced/invasive species, human-altered hydrological regimes, and climate change).

Eutrophication

Nutrient enrichment, notably nitrogen and phosphorus, has led the eutrophication of many estuaries, particularly shallow systems with long water residence times (Kennish and de Jonge, 2011). Reactive nitrogen inputs to estuaries have been increasing through time, resulting in escalating eutrophication of estuarine water bodies (Howarth et al., 2002a; Rabalais, 2002; Bricker et al., 2007; Burkholder et al., 2007; Howarth, 2008; Anderson et al., 2010). Of the 138 estuaries in the USA examined by Bricker et al. (2007), 84 were determined to be highly eutrophic. Greater nitrogen and phosphorus loads to estuaries and coastal marine waters are attributed to accelerating coastal development and intensification of agriculture (Howarth et al., 2002b; Galloway et al., 2008; Howarth, 2008; Anderson et al., 2010). Aside from agriculture sources, these nutrients derive from lawn fertilization, stormwater runoff, municipal and industrial wastewaters, malfunctioning septic systems, groundwater seepage, and atmospheric deposition. The eutrophication of estuaries is manifested by an array of damaging cascading changes in ecosystem structure and function such as decreased dissolved oxygen levels, increased microalgal and macroalgal abundance, occurrence of harmful algal blooms (HABs), loss of seagrass habitat, reduced-biodiversity, declining fisheries, imbalanced food webs, altered biogeochemical cycling, and diminished ecosystem services (Kennish and de Jonge, 2011).

Sewage and organic wastes

Sewage and organic wastes also increase nutrient and organic carbon loading that can exacerbate estuarine eutrophic conditions (Kennish, 2001a). Organic carbon enrichment is coupled to elevated biochemical oxygen demand and depleted dissolved oxygen levels in some water bodies. These wastes derive from domestic and industrial sources, livestock and fish processing facilities, wildlife inputs, aquaculture operations, and other sources. Hypoxia of estuarine and coastal marine environments has increased worldwide over the past several decades due to eutrophication driven by nutrient enrichment and organic carbon loading (Diaz and Rosenberg, 1995, 2008).

The calefaction of estuarine waters by the release of heated effluent from electric generating stations and other industrial facilities can also deplete dissolved oxygen levels. Thermal discharges from electric generating stations have commonly increased mortality of susceptible estuarine organisms in near-field regions of outfall sites. Aside from increased mortality due to reduced dissolved oxygen, heat-shock and cold-shock mortality at electric generating stations has occasionally caused mass mortality of finfish populations which cannot adapt to the rapid changes in water temperature associated with abrupt changes in station operation (Kennish, 1992).

Habitat loss and alteration

Coastal population growth and development have led to substantial estuarine habitat loss and alteration, impacting biotic communities. Physical alteration is associated with the dredging of channels and other subtidal areas, the construction of hardened shorelines, and the removal of vegetation and soils during construction of buildings, roadways, and other infrastructure elements in watersheds that convert natural habitats to impervious cover and increase erosion, runoff, and nonpoint pollution to estuarine water bodies. Water quality is often degraded as a result. Other adverse effects include habitat fragmentation, ecosystem isolation, and functional degradation of upland and wetland complexes (Kennish, 2001a). Some of these changes can be intractable.

Historically, salt marshes and other wetland habitat bordering estuarine basins have been altered extensively by grid ditching, marsh diking, draining and filling (for agriculture), impoundments for wildlife, and reclamation for domestic and industrial development. The hydrology of wetland systems has been invariably changed by construction of impoundment dikes, water-control embankments, levees, dams for flood control, as well as canals and spoil banks. Tidal flooding, water flow, and drainage are often modified, reducing sediment loading to the marsh surface and even arresting vertical accretion and hastening marsh submergence (Kennish, 2001b). Concomitantly, the loss of marsh in many regions is accelerating due to climate change-driven sea-level rise. Human activities have eliminated more than 50 % of the original tidal marsh habitat in the USA and more than 70 % of the mangroves fringing the coast of Puerto Rico (Kennish, 1997; Alongi, 1998). The destruction of wetland habitat decreased substantially in the USA after enactment of the 1972 Clean Water Act.

Localized areas along estuarine shorelines have been affected by construction and use of docks, piers, boat ramps, and marinas. Other shorelines have been modified by marine engineering structures such as bulkheads and revetments for bank stabilization, jetties at inlets, stormwalls, and other protective features. Constructing physically static structures in dynamic estuarine environments has impacted the function of sensitive habitats often diminishing their ecological value.

Chemical contaminants

Many estuaries receive a wide range of chemical contaminants because they are located in close proximity to heavily populated metropolitan centers and other developed coastal areas. Urbanized estuaries are often the most heavily impacted. Major sources and delivery systems include agricultural and urban runoff, municipal and industrial discharges, groundwater inputs, riverine inflow, and atmospheric deposition. Chemical contaminants entering estuaries may concentrate in the water column, accumulate in bottom sediments and organisms, or exit to coastal waters. Bottom sediments of estuaries are typically repositories of chemical contaminants because many of these substances are particle reactive, sorbing to grain surfaces, and ultimately settling to the estuarine floor.

Among the most important groups of chemical contaminants found in estuarine environments are halogenated hydrocarbons, polycyclic aromatic hydrocarbons (PAHs), and metals. These contaminants are potentially damaging to estuarine habitats and hazardous to estuarine and marine organisms. Substances such as aromatic and aliphatic hydrocarbons derived from oil spills and seepages, as well as volatile organic compounds, can be acutely toxic to biotic communities (Kennish, 1997).

The halogenated hydrocarbons are a ubiquitous group of environmental contaminants consisting of low- to high-molecular-weight compounds. Examples are organochlorine biocides (insecticides, herbicides, and fungicides), low-molecular-weight compounds (chlorofluorocarbons), and high-molecular-weight chemicals (chlorinated aromatics and chlorinated paraffins). PCBs and DDT are two of the most notable halogenated hydrocarbons that have historically impacted estuarine environments (Kennish, 2001a).

PAHs consist of a group of chemical carcinogens, mutagens, and teratogens that originate from both natural (e.g., volcanic activity and oil seeps) and anthropogenic sources, although the inputs from anthropogenic sources (e.g., fossil fuel combustion, waste incineration, municipal and industrial wastewaters, and land runoff) typically predominate in estuaries (Kennish, 1992). The low-molecular-weight PAHs are more toxic than the high-molecular-weight forms. Hepatic neoplasia and other diseases in aquatic organisms have been attributed to PAH exposure (Kennish, 1997). A range of biochemical, physiological, behavioral, and other sublethal responses has also been documented in estuarine organisms that can adversely affect biotic community structure.

Oil spills and leakages from marine vessels and fixed installations, as well as from nonpoint-source inputs from coastal watersheds, are hazardous to estuarine organisms and habitats. The lethal and sublethal effects of polluting oil on estuarine and marine organisms are well established (Kennish, 1992, 1997, 2001a). Both aromatic and aliphatic components are problematic as noted above. Benthic organisms are particularly susceptible to oil accumulation, and contaminated habitats such as salt marsh systems can be adversely impacted by the oil for decades due to oil-contaminated sediments which are hazardous to settlement and recruitment of the organisms.

Metals

The literature is replete with pathological responses of estuarine and marine organisms to toxic levels of metals, including neurological, digestive, reproductive, and respiratory disorders, tissue inflammation and degeneration, and developmental abnormalities. Feeding behavior and growth inhibition are commonly observed. Transition metals (e.g., copper, cobalt, iron, and manganese), metalloids (e.g., arsenic, cadmium, lead, mercury, selenium, and tin), and organometals (e.g., methylmercury, tributyltin, and alkylated lead) can be toxic, particularly the organometals (Kennish, 1997; Kennish, 1998; Kennish et al., 2008). Metals are persistent in estuarine environments. They tend to bioaccumulate in organisms, and some metals such as methylmercury undergo biomagnification, with highest levels found in upper-trophic-level organisms that often serve as a food source for humans. Hence, the health of humans consuming metal-contaminated seafood can be impaired. There are many potential sources of metals in estuaries, including industrial activity (e.g., mining, smelting, refining, and electroplating operations), fossil fuel combustion, landfill leachates, shipping, marinas, and ash disposal. Delivery pathways are river discharges, groundwater inputs, and atmospheric deposition.

Human-induced sediment/particulate inputs

Human activities in coastal watersheds have facilitated inputs of sediments and other particulates to estuaries. The removal of natural vegetation and increase in impervious cover with watershed development hasten the delivery of sediments to estuarine basins. Silviculture operations, particularly in developing countries, have dramatically increased sediment loads to coastal areas (Kennish et al., 2008). One of the adverse effects is altered water and sediment quality. An increase in water column turbidity leads to the attenuation of light and shading of the estuarine floor that can reduce primary production and cause a decline of seagrasses and other essential benthic habitat. For example, Moore et al. (2012, 2014) correlated dieback of seagrasses in the Chesapeake Bay system in part to elevated turbidity levels.

Overfishing

Overfishing or overharvesting of finfish and shellfish populations not only results in depleted stocks but also the alteration of the food web structure of estuaries. While estuaries historically have had exceptional recreational and commercial fisheries, overexploitation of the biotic resources has been a concern through time. In mid-Atlantic coastal bays, overharvesting of shellfish, together with disease and predation, has been implicated in the dramatic decline of oyster and hard clam populations. Overfishing may have played an important role in the decline of Chinook salmon (*Oncorhynchus tshawytscha*), delta smelt (*Hypomesus transpacificus*), and striped bass (*Morone saxatilis*) fisheries in San Francisco Bay (USA) after the 1970s. Similarly, overfishing may have been a factor in the reduction of commercial finfisheries in Albemarle-Pamlico Sounds, North Carolina, and Sarasota Bay, Florida (Kennish, 2000).

Intensive aquaculture

A significant amount of the seafood consumed by humans (>25 %) now derives from aquaculture, which may partially compensate for overfishing (Engelman et al., 2008). Shellfish aquaculture predominates in countries of the Far East (e.g., China, Vietnam, and the Philippines). Much finfish aquaculture also occurs in countries of the Far East, but in many other countries as well. Intensive aquaculture has caused considerable coastal pollution, water and sediment quality degradation, and diseases resulting from the feces and uneaten food of the feedlot operations (New, 2002).

Aside from degraded water and sediment quality, aquaculture operations also cause habitat conversion and changes in hydrological regimes.

Introduced/invasive species

Organisms that are not endemic to an estuary, but are introduced or invade the water body, can have significant ecological impacts. Many species are introduced for commercial or recreational interests, an example being the introduction of the striped bass (*Morone saxatilis*) to San Francisco Bay (USA). In fact, the dominant species of organisms in San Francisco Bay are mainly introduced forms, with more than 200 nonindigenous species now inhabiting bay waters and wetland habitat (Kennish, 2000). Some exotic species inhabiting estuaries have been accidentally introduced via ballast water or some other means. Nearly all estuaries are affected by introduced or invasive species (Carlton and Geller, 1993; Kennish, 2002; Kennish et al., 2008)

Introduced and invasive species can be a danger to the stability and biodiversity of an estuarine ecosystem. In those cases where native controls are lacking, these species can have a significant competitive advantage, often rapidly dominating plant or animal communities. The food web structure is commonly disrupted, and native species may be displaced or greatly reduced in abundance. Changes in species composition and distribution commonly occur (Cohen and Carlton, 1998). Species diversity in these systems may drastically decline as well via intense competition and predation. For instance, the Asian clam (*Potamocorbula amurensis*), introduced into Suisun Bay (USA), has decimated the phytoplankton community and outcompeted the native shellfish species (*Macoma balthica* and *Mya arenaria*).

The introduction or invasion of exotic species is expected to increase in the future due to an expanding world population, the effects of climate change, and greater shipping and other human activities at sea and in estuaries. These changes will likely promote additional ecological disruption. More mariculture ventures, particularly in developing countries, will also add to these effects (Kennish, 2002).

Human-altered hydrological regimes

As population growth increases in coastal regions, so does the demand for freshwater to meet domestic, industrial, and agricultural needs. The urbanization of coastal watersheds also results in greater impervious land cover leading to accelerated freshwater runoff and higher river discharges. The increase in freshwater flow decreases the water residence time in estuaries, while increasing their capacity to dilute, transform, or flush contaminants (Kennish, 2000). In contrast, dams and reservoirs constructed upland reduce downstream freshwater flow. Other changes that can significantly alter water-flow regimes along coasts include channelization, marsh impoundment, and wetland habitat destruction which affect natural water storage capacity (Kennish et al., 2008). Shifts in water quality and quantity are important drivers of change in the abundance, distribution, reproductive success, and productivity of estuarine organisms (Kennish, 2000). Estuarine circulation can also significantly change. The impact of freshwater diversions is perhaps best exemplified by San Francisco Bay (USA), where 50 % of the freshwater flow has been diverted for human use, resulting in a modified salinity regime as well as altered biotic communities in the bay.

Freshwater diversions are used for ecological applications as well, such as coastal wetland restoration. Teal et al. (2012), for example, discuss diversions of river water into coastal wetlands as part of plans to mollify the areal loss of coastal wetlands in Louisiana by reversing or slowing the rates of degradation. However, freshwater diversions such as those noted by Teal et al. (2012) can cause major changes in estuarine water quality, notably large reductions in salinity and increased nutrient availability that affect plant communities, herbivory, and overall marsh stability.

The use of flood control structures has been shown to completely modify some estuarine ecosystems. For example, acute changes in water inflow to the Haringvliet, Grevelingenmeer, and Oosterschelde estuaries in southwest Netherlands occurred subsequent to the construction of dikes to avert flooding problems, such as those incurred in 1953, resulting in major changes in the physical-chemical conditions and biotic communities of the water bodies. While the Oosterschelde remained a productive estuary after these structural changes, the Haringvliet basin was altered to a highly polluted freshwater body, and the Grevelingenmeer became a saltwater system. Tidal marshes and tidal flat habitats also changed considerably (Kennish et al., 2008). Changes such as those observed in the Haringvliet, Grevelingenmeer, and Oosterschelde estuaries demonstrate the magnitude of human influence on coastal environments, particularly in regard to human-altered hydrologic regimes.

Climate change

An accumulating database indicates that human factors are important drivers of change of world climate (Skinner, 2012). Increasing global temperatures, ascribed in large part to carbon dioxide emissions, have been linked to greater frequency and severity of damaging storms, coastal flooding, droughts and fires, and other hazards projected by climate forecasting models for the twenty-first century (IPCC, 2007). Extreme climate events and ongoing sea-level rise will be hazardous to coastal communities worldwide.

During the twentieth century, global sea-level rise amounted to 0.5–30 cm, being largely attributed to the increase in global surface temperatures (mean = +0.6 ± 0.2 °C), melting of glaciers and ice sheets, and thermal expansion of the oceans (IPCC, 2007). Global sea-level rise during the twenty-first century is projected to increase by 52–98 cm (IPCC, 2013). Relative sea-level rise will be even greater in some regions due to coastal subsidence, as in the case of New Jersey and other mid-Atlantic states in the USA.

Rising sea level and coastal inundation will lead to significant loss of some coastal wetlands, eliminating buffer and rendering coastal communities more vulnerable to extreme events. Human-induced climate change will also alter temperature and salinity regimes and the structure and function of biotic communities in estuaries (Kennish, 2002). Configurations of estuarine basins will be modified as they widen and deepen. Shifts will occur in nutrient and sediment supply as well as freshwater inputs. Tidal prisms and tidal ranges will change in many systems. More frequent flooding and inundation of bayshore areas will pose hazards to vulnerable coastal communities worldwide (Kennish et al., 2008).

Coastal subsidence

Subsiding coasts result in similar impacts as rising sea level on estuarine and wetland systems. For example, as coastal subsidence increases, estuarine shoreline retreats and land submergence accelerates causing the loss of fringing wetland habitat. The wet surface area of the estuary expands, together with the basin volume, thereby altering the system bathymetry and configuration. The salinity regime, circulation, and other physical-chemical characteristics of the estuary can change considerably as well, which will also affect biotic communities.

The effects of coastal subsidence are becoming more evident around the world with accelerating population growth and development in coastal watersheds. Human activities have contributed greatly to the subsidence problems in some areas via excessive groundwater withdrawal for domestic and agricultural use and oil and gas extraction. Natural factors, such as subsurface sediment compaction, crustal (tectonic) movements, and sinkhole formation by karst processes, are more significant in some regions. In the USA, subsidence has been well chronicled at Galveston Bay, Texas, due to oil and gas extraction (Shipley and Kiesling, 1994), along the Louisiana coast due to sediment compaction (DeLaune and Pezeshki, 1994), and at Chesapeake Bay due to groundwater withdrawal and other factors (Boon et al., 2010).

Significant coastal subsidence has also been documented in other countries (e.g., Po Delta, Italy, and Tokyo, Japan) (Kennish et al., 2008). Coastal subsidence problems will take on added significance during the twenty-first century, exacerbating those due to eustatic sea-level rise (Kennish, 2002). Subsidence rates, such as those noted by Boon et al. (2010) at Chesapeake Bay (−1.3 to −4.0 mm year), will likely continue unabated into the future. It will be necessary for coastal decision makers to carefully consider the management options necessary to reduce their impacts.

Floatables/debris

Marine debris, notably plastics, has become an international problem in estuarine and marine environments. The use of plastic products has reached an all-time high in many developed countries; plastic debris has been an ongoing problem in coastal waters of the USA (Ribic, 1998; Kennish, 2001a). Plastics are particularly damaging to aquatic environments because they essentially do not degrade, thereby polluting habitats for many years. They pose a threat to many organisms, particularly fish, turtles, birds, and mammals that ingest some of the materials or become entangled in fishing line, nets, and packing bands. Some organisms mistake floatables for prey (Shaw and Day, 1994). The ingestion of plastics and other marine debris can suffocate the animals or obstruct their digestive systems, causing death.

Pathogens

Estuaries worldwide are susceptible to the entry of pathogenic microorganisms (i.e., bacteria and viruses) from land runoff and sewage wastes that pose a risk to human health. Fecal pollution (i.e., fecal coliform bacteria, enterococci, and coliphage) and human enteric pathogens and enteroviruses can greatly impair human use of impacted estuarine and coastal marine waters (Lipp et al., 2001). Faulty septic systems, sewage treatment plant effluent, and wildlife wastes often degrade estuarine water quality, which must be continually monitored. Treated municipal wastewater and urban stormwater runoff may contain more than 100 enteric pathogens (National Research Council, 1993). These organisms, which are widely distributed by coastal storms (Fries et al., 2007), pose a hazard to humans who swim in contaminated estuarine waters or consume contaminated seafood products.

Parasites, notably helminths and protozoa, are commonly associated with waterborne diseases as well. Helminths linked to untreated sewage in estuarine and other aquatic systems include hookworms, roundworms, tapeworms, and whipworms. Pathogenic enteric protozoa derived from sewage contamination can be equally devastating to human health.

Summary

A wide array of anthropogenic factors contributes to estuarine degradation. Chief among these are (1) nutrient loading and eutrophication; (2) sewage and organic wastes; (3) habitat loss and alteration, shoreline hardening, and erosion; (4) chemical contaminants; (5) human-induced sediment/particulate inputs; (6) overfishing; (7) intensive aquaculture; (8) introduced/invasive species; (9) human-altered hydrological regimes; (10) climate change; (11) coastal subsidence; and (12) floatables/debris. Pathogens coupled to human waste discharges and wildlife are also significant since they adversely affect water quality. Anthropogenic stressors can be categorized into those that degrade water quality and are primarily chemical and biological in nature (e.g., nutrient enrichment, chemical contaminants, and pathogens), impact habitat and are mainly physical factors (e.g., shoreline hardening, lagoon construction, dredging and dredged-material disposal), and alter biotic communities and are effectively driven by multiple stressors (e.g., overfishing, introduced/invasive species, human-altered hydrological regimes, and climate change). Human activities can significantly impact the structure, function, and ecological health of estuaries.

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Cross-references

Anoxia, Hypoxia, and Dead Zones
Biochemical Oxygen Demand
Bulkheads
Clean Water Act
Climate Change
Dredging
Eutrophication
Extreme Events (Hurricanes)
Invasive Species
Marsh Sediment Toxicity
Nonpoint Source Pollution
Oil Pollution
Pathogens
Polycyclic Aromatic Hydrocarbons
Revetments
Storm Surges
Toxic Blooms
Trace Metals in Estuaries
Water Quality
Wetlands Reclamation

ARCHAEA

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Synonym

Archaebacteria

Definition

Archaea constitute one of the three domains of life, as phylogenetically distinct from the domains Bacteria and Eukarya (Woese and Fox, 1977; Woese et al., 1990).

Etymology

Archaea (singular: archaeon) are derived from Greek ἀρχαῖος – ancient, primitive.

The term was coined to reflect the apparent antiquity of traits in archaeal species and their aptness to inhabit environments like those presumed for early Earth.

Phylogeny

On the phylogenetic tree of organisms, Archaea form one of the three fundamental branches called domains (Woese et al., 1990). Further branching within the archaeal domain is largely based on ribosomal RNA sequences, but also relies on evidence from comparative analysis of protein sequences. Typical markers in archaeal phylogeny are ribosomal proteins, histones, and components of the transcription system and the cell division apparatus (Brochier-Armanet et al., 2011). In addition to the initially recognized phyla Crenarchaeota and Euryarchaeota (Woese et al., 1990), four candidate phyla have been proposed: Kor-, Nano-, Thaum-, and Aigarchaeota (Brochier-Armanet et al., 2011). Given the small number of 187 sequenced archaeal genomes (Genomes OnLine Database; May 2013), archaeal phylogeny continues to be uncertain.

Physiology and metabolism

Archaea are single-celled organisms showing prokaryotic structure, but differ from bacterial cells by the absence of peptidoglycan from their cell wall and by the presence of histones associated with their DNA. In contrast to the phospholipid bilayer confining bacterial and eukaryotic cells, archaeal cell membranes consist of a single layer of isoprenoid diethers and tetraethers. Most archaeal genomes contain clustered, regularly interspaced palindromic repeats (CRISPR) that confer adaptive immunity against virus infections (Sorek et al., 2008; Marraffini and Sontheimer, 2010).

No chlorophyll-like pigments or photosynthetic electron transport chains are known in Archaea. However, some archaea possess bacteriorhodopsin, which functions as light-driven proton pump across the cell membrane. The reflux of protons can be exploited for ATP synthesis, completing the conversion of light energy into chemical energy for cellular metabolism.

Archaea show diverse forms of chemotrophic metabolism, including both the formation and the anaerobic oxidation of methane, both oxidation and reduction of CO, the aerobic oxidation of H_2 (knallgas reaction), most of the oxidative and reductive processes in the N and S cycle, and redox reactions of various metals and metalloids (Amend and Shock, 2001; Stolz et al., 2006; Oelgeschläger and Rother, 2008; Conrad, 2009; Knittel and Boetius, 2009; Bini, 2010).

In sulfur-based energy metabolism, oxidized and intermediate S compounds (sulfate, sulfite, thiosulfate, and elemental sulfur) are reduced by H_2 or organic compounds, while reduced and intermediate S compounds (sulfide, elemental sulfur, and thiosulfate) can be oxidized by O_2, nitrate, or ferric iron (Amend and Shock, 2001). Oxidation and reduction of S compounds are widely used energy sources for archaea in hydrothermal and marine ecosystems.

Several processes of nitrogen-based energy metabolism are known in archaea inhabiting extreme and moderate environments, including aerobic ammonia oxidation, dissimilatory reduction of nitrate to nitrite and of nitrite to ammonium, and all steps of denitrification. Archaea may also use nitrate assimilation or N_2 fixation to meet their cellular N demand (Zumft, 1997; Amend and Shock, 2001; Philippot, 2002; Cabello et al., 2004; Francis et al., 2005). One handful of cultured and numerous uncultured members of Thaumarchaeota share the metabolic capacity of aerobic ammonia oxidation. Given their ubiquity and abundance in diverse habitats, archaeal ammonia oxidizers may play a major role in the global N cycle (Francis et al., 2005; Prosser and Nicol, 2008; Stahl and de la Torre, 2012).

Methanogenesis is catalyzed exclusively by Archaea and may proceed via three different pathways: reduction of CO or CO_2, reduction of methyl groups in small organic compounds, or cleavage of acetate. The strictly anaerobic methanogenic archaea occur abundantly in natural and agricultural wetlands, hydrothermal environments, and the digestive tracts of ruminants and termites (Liu and Whitman, 2008; Conrad, 2009). The oxidation of methane with O_2 is known only in Bacteria, whereas its anaerobic oxidation with sulfate, iron, or manganese is catalyzed by diverse and mostly uncultured Archaea, with or without the help of bacterial symbionts (Beal et al., 2009; Knittel and Boetius, 2009; Milucka et al., 2012).

Ecology

Archaea occur in virtually any habitat that supports life. They are adapted to salt concentrations of up to 5.2 M, to temperatures above 120 °C, and to life in permafrost environments. Archaeal species inhabit mine drainage of pH <0 and soda lakes of pH >11 and thrive at hydrostatic pressures of up to 120 MPa in the deep sea and below the sea floor (Valentine, 2007; Lipp et al., 2008; Bowers and Wiegel, 2011; Takai and Nakamura, 2011). Although best known for their endurance of one or more extreme conditions, Archaea are also ubiquitous and vital parts of communities in moderate environments. Their metabolic activities contribute to the major element (C, N, S, Fe) cycles on local to global scales.

Representatives of Cren-, Eury-, Nano-, and Thaumarchaeota engage in mutualistic and parasitic symbioses with ruminants, insects, corals, sponges, molluscs, ciliates, sulfate-reducing and sulfide-oxidizing bacteria, and among archaea (Moissl-Eichinger and Huber, 2011; Wrede et al., 2012). Archaea are also hosts of diverse viruses (Pina et al., 2011) and subject to predation by zooplankton and zoobenthos. To date, neither predatory nor pathogenic Archaea are known.

Current knowledge on Archaea in moderate marine, estuarine, and freshwater environments is largely confined to methanogenic Euryarchaeota and ammonia-oxidizing Thaumarchaeota. Methanogens grow in the strict absence of O_2 and rely on H_2 or acetate produced by fermenting organisms. Their effective competition for these substrates decreases with increasing availability of electron acceptors other than CO_2. Between the three metabolic types of methanogenic archaea, relative abundance and activity appear to depend on redox potential, pH, temperature, salinity, and the concentrations of phosphate, sulfate, and organic C compounds (Liu and Whitman, 2008; Torres-Alvarado et al., 2013).

The ubiquity, abundance, and diversity of ammonia-oxidizing archaea in aquatic environments have largely been inferred from abundance and diversity of archaeal *amoA*, a gene encoding the key enzyme of aerobic ammonia oxidation. Although the postulated activity was confirmed in all four cultured species, the biochemistry of this enzyme allows for the turnover of several other substrates, including methane. The archaeal enzyme shows much higher substrate affinity than its bacterial counterpart, making archaea strong competitors at low concentrations of ammonium or O_2. Distribution patterns of archaeal and bacterial *amoA* suggest greater tolerance to sulfide, acidity, and high temperatures in archaeal compared to bacterial ammonia oxidizers (Francis et al., 2005; Erguder et al., 2009; Martens-Habbena et al., 2009; Pester et al., 2011; Hatzenpichler, 2012; Stahl and de la Torre, 2012). In estuaries, steep gradients of multiple environmental factors coincide to confound evidence for possible effects of salt or sulfide (Bernhard and Bollmann, 2010).

Summary

Archaea constitute one of the three domains of life, as distinct from the domains Bacteria and Eukarya both phylogenetically and by cell structure. Still limited sequence information suggests six phyla within the archaeal domain.

Archaea show diverse forms of chemotrophic metabolism, including both the formation and the anaerobic oxidation of methane, oxidation and reduction of CO, aerobic oxidation of H_2, many oxidative and reductive processes in the N and S cycle, and redox reactions of various metals and metalloids. Bacteriorhodopsin facilitates a simple mechanism of phototrophic energy conversion without assimilation of CO_2.

While Archaea are most famous for enduring extreme temperature, salinity, pH, or pressure, they are also widespread in a broad range of moderate habitats. Their metabolism makes a relevant contribution to global biogeochemical cycles. Archaea interact with members of all domains in mutualistic or parasitic symbioses, host viruses, and fall prey to bacterivores, but are not known in the roles of predator or pathogen.

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Cross-references

Nitrate Reduction
Nitrification
Symbiosis

ARTIFICIAL REEF

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Synonyms

Artificial habitats; Artificial reef structures; Man-made habitats; Man-made reefs

Definition

"An artificial reef is one or more objects of natural or human origin deployed purposefully on the seafloor to influence physical, biological, or socioeconomic processes related to living marine resources" (Seaman and Jensen, 2000, 5). While this definition is directed toward the marine environment, a few modifications to include "estuarine and freshwater" resources make it applicable to the estuarine environment as well. Also, it should be noted that artificial reefs are not always "deployed purposefully" as "accidental" deployments of ships or other objects sunk by storms, acts of war, or other episodic events can also create submerged structure that function under the banner of artificial reefs. Additionally, a broader appreciation of the utility of artificial reefs would certainly make them useful to disciplines which are not mutually exclusive. Thus, artificial reefs can simultaneously influence physical, biological, *and/or* socioeconomic processes.

Introduction

Artificial reefs have likely been deployed for the purposes of enhancing fishing for millennia. Most probably, fish associated with naturally occurring debris in rivers and lakes were recognized early in human history as functioning as preferred structure for some fish species. It would have been intuitive to help Mother Nature along by deploying similar-looking, natural structures in aquatic habitats to further enhance fishing. The modern impetus for artificial reef seems to have come from the congregations of reef fishes observed around sunken ships and downed warplanes resulting from sea battles during the World War II in the Pacific Ocean. For example, Chuuk (Truk) Lagoon in Micronesia, where 32 merchant ships and 249 aircraft were sunk, has become a diver's "paradise" since the early 1970s (Trumbull, 1972). The advent and popular use of scuba by the general populace since the late 1950s helped the general recognition that artificial reefs were a "good thing" when it came to fisheries, but there were few data and studies directed toward truly establishing the verifiable reasons for their deployment. Of late, artificial reefs have garnered attention by natural resource managers, aquatic scientists, and the fishing public to improve fishing and fisheries around the world. The popular mantra is that "more reefs will mean more fish" without regard for the effects of these structures on other natural processes. Lastly, the "proof" of artificial reefs as an effective management tool is wanting, largely owing to the lack of scientifically valid opportunities to test various hypotheses.

Kinds of artificial reefs

Artificial reefs are generally of two basic types: benthic (i.e., located on the majority of mid-water/surface Fig. 1). The majority of mid-water and surface reefs serves as fish-aggregating device (FADs) and is directed primarily at the pelagic and epipelagic game fishes in coastal areas. Benthic reefs have been the subject of much effort in design and planning. A broad variety of structure have been used in artificial reefs, but generally they can be considered as either structure of opportunity (i.e., made of refuse materials) or designed and engineered specifically to serve as artificial reefs. Structure of opportunity include (but are not limited to) ships, automobiles, and other vehicles (e.g., railroad cars and airplanes), derelict oil and gas platforms, bridge rubble, remnant construction materials (e.g., broken sewer pipe), scrap metal of various composition and gauges, white goods (refuse household appliances such as washing machines, stoves, and refrigerators), vehicle tires, fiberglass materials, porcelain, and any materials considered dense enough to sink and withstand some degree of wave action or current surge.

Engineered structures can run the gamut of all of the above but are generally composed of structures thought to have a longer life span (durability) and greater stability (density) than reefs composed of structures of opportunity. Engineered structures are most often composed of concrete, concrete and rock aggregate, and heavy gauge steel.

Generally, artificial reefs are deployed as modules or units of a size and shape readily transportable and deployable. These modules are then organized into sets of two or more modules, and the sets are often organized into groups. Lastly, the groups of sets and modules comprise the entire reef complex that may be of considerable extent, covering several kilometers (Grove et al., 1991).

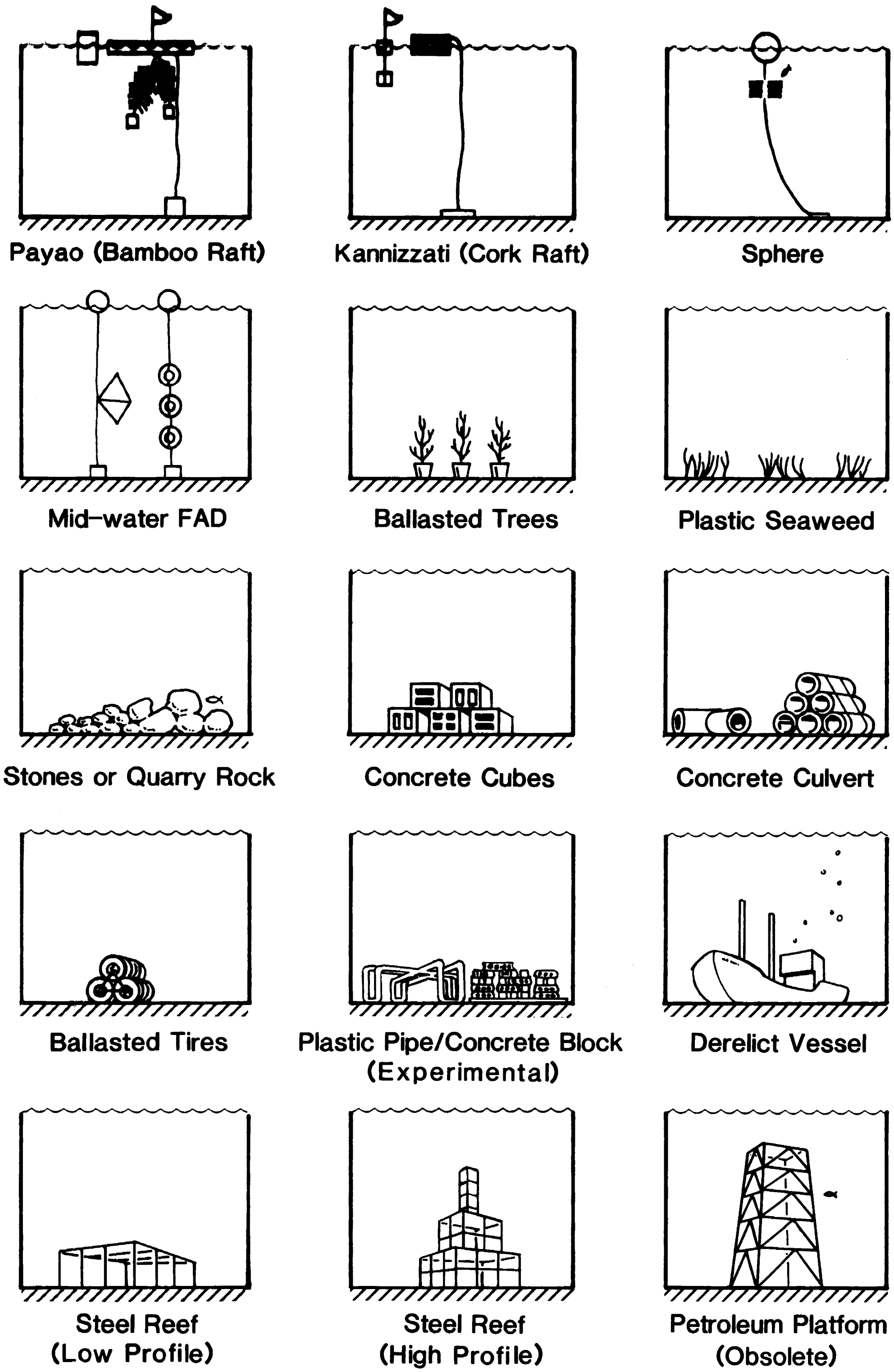
Locations of artificial reefs

Artificial reefs have been deployed in virtually every aquatic ecosystem from freshwater streams, rivers, ponds, and lakes to estuaries, fjords, bays, and the open ocean (both near coastal and far offshore). The substrate type upon which the reefs are deployed is an important consideration, as some substrates are easily eroded or scoured, and the reef can become quickly covered so as to become nonfunctional as an artificial reef.

Position of the reef in proximity to other biota is often a deployment consideration to facilitate colonization by juveniles, adults, or prey items. Depending on the intended function of the reef, positioning the reef to facilitate (or prohibit) access by users is often a consideration as well.

Functions of artificial reefs

Artificial reefs can have many functions via the ecosystem services they provide. Often a chief function is to enhance fisheries for fishing opportunities for both the commercial and recreational fishing public. Environmentally, artificial reefs can serve to mitigate damage to natural areas, serve to enhance biotic community diversity, or fulfill other goals of resource managers. Artificial reefs have been used as objects to deter various fishing activities such as the protection of seagrass beds from trawling (Fabi and Spagnolo, 2011). Recreationally, artificial reefs can serve as scuba and snorkeling sites, especially to enhance areas void of "interesting substrate" or as alternative dive sites to protect natural areas from potential damage by divers. Artificial reefs can provide a substrate to allow settling



Payao (Bamboo Raft)

Kannizzati (Cork Raft)

Sphere

Mid-water FAD

Ballasted Trees

Plastic Seaweed

Stones or Quarry Rock

Concrete Cubes

Concrete Culvert

Ballasted Tires

Plastic Pipe/Concrete Block (Experimental)

Derelict Vessel

Steel Reef (Low Profile)

Steel Reef (High Profile)

Petroleum Platform (Obsolete)

Artificial Reef, Figure 1 Examples of various artificial reefs, including FADs or fish-aggregating device deployed chiefly to attract pelagic or epipelagic fish (From Seaman and Sprague, 1991).

of sessile (attached) organisms such as bivalve mollusks (Relini et al., 1994). Japanese researchers have investigated the deployment of artificial reefs as structures to help divert ocean currents to facilitate upwelling that brings nutrients nearer to the surface to enhance phytoplankton productivity and, in turn, increase coastal fish abundance and growth (Okano et al., 2011).

The complete use of artificial reefs has yet to be fully explored. Interestingly, at least one company (www.eternalreefs.com) makes use of artificial reefs as human burial sites.

Concepts

The general idea behind deploying artificial reefs to enhance fisheries is related to either one or both of the two assumptions long argued by fisheries scientists. These assumptions are that artificial reefs attract fishery resources to a site, or they increase the productivity of fisheries resources. Clearly both concepts are viable and each can have utility in fisheries management. To date, however, both these assumptions are recognized, but little scientific testing has been done to allow proper rejection of either hypothesis in the attraction versus production debate (Bortone, 2006; Bortone, 2011).

Bohnsack (1989) diagrammatically summarized the general perspective of the attraction and production perspectives based on observations and published research. His perspective was that attraction and production were either ends of a continuum with regard to several attributes. In summary, artificial reefs that functioned more for production than attraction had low reef availability and low fishing intensity. They were inhabited by species that were habitat limited (as opposed to recruitment limited), more reef dependent, and, behaviorally, more territorial, demersal, and with high site affinity (philopatry). Polovina (1991) further clarified the attraction/production argument relative to fisheries. He indicated that if artificial reefs merely served to concentrate fish in an area, then the same biomass could be caught with less effort. If the artificial reef attracted fish from other areas, then fishing yield could increase as long as fishing effort increased. Lastly, if artificial reefs increased the carrying capacity of an area, then both total biomass and exploitable biomass should occur.

The presumption by both Bohnsack (1989) and Polovina (1991) is that attraction is the opposite of production. Bortone (2008) proposed that attraction and production were both at play in the response species made to the presence of artificial reef structure. He reasoned that some species could be both attracted to structure and that, for some species, the carry capacity of an area could also allow an increase in biomass as well (e.g., octopus and spiny lobster). Oppositely, some species are neither attracted nor do their populations increase because of the presence of artificial reefs (e.g., species that show no affinity for reefs). Most certainly, a variety of species show varying degrees of attraction to artificial reefs with varying degrees of biomass facilitation because of the reef's presence.

The conundrum might be resolved if resource managers could determine the features of target species that are enhanced by deploying artificial reefs. This means that some species and their associated fisheries may, indeed, benefit from the deployment of an artificial reef, in terms of both attraction and production, while others may not. This implies that, at least if fisheries enhancement is the goal of an artificial reef deployment, each reef should have an objective directed toward a particular species and its life history feature that can be enhanced because of the reef.

Special features of estuarine artificial reefs

While there has been some attention given to the deployment of artificial reefs in estuaries (e.g., Bortone et al., 1994; Chapman and Clynick, 2006), they have received only passing attention to date, although artificial reefs have been used as mitigation in estuaries (Foster et al., 1994). It should be noted that the principles applied to artificial reefs in other aquatic systems are probably no different when applied to estuaries. Generally, diversity issues are less important in estuaries, and changes in salinity, tidal flow, and turbidity add extra dimensions when considering the results of artificial reef deployments. Their more recent usage in estuaries has been via the deployment of oyster reefs (Coen and Luckenbach, 2000). This is a popular estuarine enhancement activity conducted by many resource managers. The extrapolation of deploying oyster reefs as consideration of an estuarine artificial reef should not be overlooked by artificial reef researchers.

Current investigations

Research on artificial reefs continues, but, as Bortone (2011) warned, unless clear objectives are included in these investigative efforts, the resolution of the attraction versus production argument will remain elusive. Particularly disconcerting is the feature that current research results are unable to answer many of the questions resource managers face. While artificial reefs have long been touted as offering a solution to many fisheries management issues, their lack of specific prescription in management will continue to exclude artificial reefs from the proverbial "managers toolbox" until these and many other issues associated with artificial reefs are programmatically resolved.

Gaps in current knowledge

Bohnsack and Sutherland (1985) and Bortone (2006, 2001) presented arguments for new directions in artificial reef research. Each of these reviews indicated the overriding gap in artificial reef research is the lack of application of artificial reefs as a reliable and predictable option for natural resource managers. Resolution of the attraction/production hypotheses plays a prominent role in resolving this issue. More importantly, however, is the need to determine the life history "bottlenecks" that are likely to be relieved by the deployment of a reef. One example of how the future might look with regard to artificial reefs in fisheries can be seen in the example off South Korea (Kim et al., 2011). In this study, artificial reefs were deployed to enhance spawning success in a bottom-dwelling fish species. The reef deployment, coupled with fishing restrictions, is part of a long-term plan to increase a depleted fish stock. Similar investigations may give purposeful direction to future artificial reef designs and deployments.

Summary

Objects of various materials, shapes, and dimensions have been deployed in nearly every aquatic environment in all parts of the world to serve as artificial reefs. Few artificial reefs have been deployed in estuaries. Nevertheless, oyster shell material, deployed to improve oyster settlement can be considered an artificial reef or at least an artificial substrate that behaves similar to other objects deployed as artificial reefs. Artificial reefs have received considerable attention among aquatic scientists and natural resource managers to facilitate fisheries. However, there remain several issues relative to the attraction versus production nature of artificial reefs that need to be resolved before they become part of a regularly prescribed option for estuarine resource management.

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Cross-references

Fringing Reef
Oyster Reef

AUTOTROPHIC

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Definition

Autotrophic organisms use an inorganic carbon compound for their sole carbon source (Okafar, 2011). The corresponding pathways of carbon metabolism are also referred to as autotrophic.

Etymology: from Greek αυτός, self, and Greek τροφή, nourishment.

The carbon sources of autotrophic metabolism comprise carbon dioxide (CO_2), carbon monoxide (CO), and carbon disulfide (CS_2). A majority of autotrophic organisms rely on CO_2 to cover their demand of cellular carbon. Examples include plants, algae, and photosynthetic bacteria, as well as a broad variety of chemotrophic microorganisms. CO-dependent autotrophs are metabolically, ecologically, and phylogenetically diverse (King and Weber, 2007). They convert CO to CO_2 and sometimes methane (CH_4) or acetate (Sokolova et al., 2009; Techtmann et al., 2009). Comparatively few bacteria are known to use CS_2 in their autotrophic metabolism (Cox et al., 2013).

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Cross-references

Heterotrophic
Macroalgae
Microphytobenthos
Phytoplankton