The vulnerability of ecosystem trophic dynamics to anthropogenically induced environmental change: A comparative approach

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Abstract

We employed a comparative approach to review the vulnerability of the trophic interactions within aquatic systems to global threats associated with anthropogenic activities. The goal of this chapter was to identify and characterize mechanisms by which human-mediated environmental threats may modulate trophic dynamics across aquatic ecosystems. Trophic dynamics include some of the most obvious and pervasive factors influencing ecosystems and were used as a metric because of their importance and commonality across all aquatic environments. Our use of trophic dynamics proved to be insightful, illustrating that the flow of energy through aquatic food webs will be (or already has been) altered by invasive species, land use change, nutrient loading, exposure to ultraviolet radiation, overharvesting, acidification, and increasing global temperatures. The response of trophic dynamics to these threats was often similar across oceans, estuaries, lakes, and rivers. This similarity proved to be interesting given the differences in both the level of concern expressed by scientists and the predicted variability in environment-specific responses. As the trophic interactions of an ecosystem are at the root of its function and structure, examining trophic dynamics could be an informative method for evaluating the response of aquatic environments to global threats. If future analyses validate the use of trophic dynamics as a metric, it is our hope that trophic dynamics can be used by scientists and politicians to mitigate the effects of human actions.

Introduction

Humans are altering the Earth in several ways, and the effects of our actions are imprinted on many of the planet's ecosystems. Unfortunately, aquatic ecosystems are no exception, as they are experiencing extreme threats associated with climate change and other anthropogenic influences, including increasing surface temperature and ocean acidification and eutrophication. Generating a comprehensive picture of the effects of these changes on aquatic environments has been difficult. One reason for this difficulty is that aquatic scientists tend to specialize in working within a particular habitat, and communication between these different groups of scientists has been limited. Further complicating the generation of a global picture is the fact that specific human-mediated threats are predicted to affect the different aquatic habitats to varying degrees (Keister et al. 2010, this volume). For example, eutrophication will continue to be an issue for lakes and coastal environments but may have less impact on open ocean

environments, which are beyond the direct influence of nutrient-rich terrestrial runoff. However, all aquatic ecosystems are connected and as such are susceptible to these global threats. Investigating the commonalities that do exist may be useful in shedding new light on the effects of human activities across ecosystems, and making progress toward mediating them.

We will examine the commonality of trophic dynamics to illustrate the similarities and differences in how anthropogenic threats impact aquatic ecosystems. Trophic dynamics (also called trophodynamics) is the study of how energy flows through an ecosystem. It includes some of the most obvious (e.g., predator-prey relationships) and pervasive factors influencing ecosystem structure and function. Because of the commonality and importance of trophic dynamics across aquatic environments, using trophic dynamics as a proxy for ecosystem vulnerability is particularly useful, because it encompasses both the direct and indirect ecosystem responses to anthropogenic threats.

The goal of this chapter is to identify and characterize mechanisms by which human-mediated environmental threats may modulate trophic dynamics across aquatic ecosystems. Unfortunately there are many examples of global threats to aquatic ecosystems. In this chapter we highlight just a few that fall within our areas of expertise and were identified by our Eco-DAS colleagues as imminent and particularly worrisome (see the chapter by Keister et al. 2010, this volume). These threats include invasive species, land use changes, global temperature alterations, nutrient loading, ultraviolet (UV) radiation, overfishing, and acidification. Each global threat is discussed below in the context of how it affects trophic dynamics in different ecosystems. This comparative approach examines the vulnerability of trophic interactions to anthropogenically induced global changes. Ultimately, we aim to synthesize results, highlight areas of special concern that deserve future attention, and determine if we can use this approach to develop effective mitigation strategies against future changes.

Temperature

The effects of temperature change on ecosystems can be substantial because major metabolic (organism) and ecological (ecosystem) functions are temperature dependent. The temperatures of aquatic systems are increasing for various reasons, yet the predominant cause is increasing atmospheric carbon dioxide (CO_2) levels due to anthropogenic activities. Regardless of the mechanism behind the change, a few of the potential outcomes of temperature changes are discussed as they affect trophic dynamics.

Ecosystems rely on organisms interacting to create ecosystem structure and to provide system functionality. In general, overlapping species ranges provide opportunity for trophic interaction. According to the Match-Mismatch hypothesis (Cushing 1990), any decoupling between organisms that require interaction with each other may limit or eliminate the

functional response between the two. A change in temperature of only a few tenths of a degree can drastically expand or contract species' localized and geographic home ranges (Gilman et al. 2006; Wethey and Woodin 2008) or phenology (Edwards and Richardson 2004), thereby eliminating or creating trophic interactions. Furthermore, warming may also reduce suitable habitat by increasing or altering stratification (e.g., open ocean, lakes, and shallow coastal embayments).

Not only can temperature change be thought of as a threat to aquatic ecosystems through its impact on the distribution of organisms, but it may modulate the response of organisms to other threats. For example, temperature is known to increase estuarine invertebrate toxicity to metals (Mclusky et al. 1986) and reduce photoenzymatic repair of UV damage (Connelly et al. 2009), as well as cause and expedite hypoxic and anoxic situations in shallow and poorly mixed aquatic systems (Justic et al. 2005). Because organisms have differential responses to oxygen stress and toxicity, it is highly likely that community structure will change in response to the modified environment. In this way, temperature can help shape the trophic landscape by eliminating and replacing species from a food web, possibly removing critical linkages between trophic levels or minimizing the functional output of a keystone species.

Temperature has been shown to strongly influence metabolism of aquatic organisms. In general, increases in temperature should increase oxygen consumption rates. The standard metric for this effect is the Q10, defined as the factor by which a physiological rate changes with a 10°C increase in temperature. Q10 values from 2 to 3 indicate thermal effects on biochemical reactions, and Q10 values approximating 1 suggest relative temperature insensitivity. For most invertebrates, Q10 = 2.5 (Arai 1997). Marshalonis and Pinckney (2007) estimated Q10 values around 4.7 for multiple hydromedusae species from a relatively pristine tidal creek estuary. These data suggest the metabolic rates for hydromedusae populations are extremely sensitive to temperature; increases in predation rates relative to prey growth could cause shifts in community composition and food web structure or "balance." Interestingly, temperature impacts were strong for both summer and winter communities, suggesting that the species in these communities are well adapted to the temperature range they frequently encounter. Seasonal abundances of species in this study corroborate this hypothesis (Springer-Hester 1976), implying that temperature changes can differentially modulate trophic interactions (e.g., increased predation by gelatinous zooplankton) because of species-specific metabolic shifts.

Other organisms also respond metabolically to temperature regime shifts. Temperature has been demonstrated as the main factor governing growth rate in marine copepods (Huntley and Lopez 1992). Furthermore, Brander (1997) showed cod stocks to be causally linked to mean temperature off the coast of West Greenland; an increase of 1.0 to 1.5°C caused a twofold increase in the weight of four-year-old cod. Such

warming events might provide equally drastic and devastating results to species that prefer colder waters (North Atlantic salmon; Todd et al. 2008) or have a narrower thermal tolerance (Purcell 2005). Saiz et al. (1997) found that egg production of the copepod *Acartia grani* increased three- to fourfold between temperatures of 13 to 23°C. Thus, rising temperatures may lead to overall increases in ecosystem productivity. Such changes may be wanted (increased fisheries landings) or unwanted (eutrophication and accumulation of nuisance biomass such as red tides or jellyfish blooms).

Oceans and estuaries—Can rising temperatures cause noticeable effects in trophic dynamics via ecosystem structure (e.g., species diversity as well as magnitude and distribution of populations) and function (e.g., productivity, nutrient recycling, and predation)? One model population that may provide insight is the group collectively known as gelatinous zooplankton, consisting mostly of cnidarians and ctenophores. Regime shifts in the temperature of the North Sea have modified the structure of planktonic cnidarians (Attrill and Edwards 2008). Purcell et al. (2007) provide an excellent global review of instances where gelatinous zooplankton populations are increasing in response to warming aquatic environments, presumably because of changes to the frequency, duration, and timing of reproductive cycles (Purcell 2005). Known for their capability to reproduce rapidly, coupled with their extremely high prey-consumption rates, gelatinous zooplankton may shunt energy and nutrients away from fish and other commercially important species in marine environments (Gordina et al. 2005; Purcell et al. 2001).

Predation, an important mechanism by which aquatic food webs are constructed, is also modulated by temperature. For example, ingestion rates for hydromedusae have been shown to significantly increase in response to higher temperatures (Marshalonis and Pinckney 2008). These results, coupled with seasonal hydromedusae-abundance data, indicate that summer populations of hydromedusae graze more heavily on prey than winter populations, while also assimilating more carbon into their tissue. Thus, increased temperatures magnify trophic linkages between gelatinous animals and their prey.

Modeling efforts by Marshalonis et al. (unpubl. data) examined whether hydromedusae can alter phytoplankton community composition through grazing on smaller zooplankton. Results show shifts in algal community composition from smaller nanophytoplankton to larger microphytoplankton and reduced mesozooplankton biomass when hydromedusae grazing rates were greater than 0.095 d^{-1}. Rates below this threshold yielded communities dominated by nanophytoplankton and mesozooplankton. Based on these results, the authors suggest that natural communities of gelatinous predators seasonally regulate plankton communities through top-down control due to differences in species-specific grazing rates and seasonal abundances. Temperature regime shifts that extend the duration of optimal conditions for select predators, like hydromedusae, or enlarge the spatial extent of species

with higher ingestion rates would result in changes in community structure and function similar to those seen in this theoretical exercise.

Effects of increased predation within a food web may include modification of trophic structure, shifts in algal community composition, and decline in ecosystem stability. In situ trophic manipulation experiments in a microbial-dominated estuarine system by Marshalonis et al. (unpubl. data) show indirect top-down control on phytoplankton by hydromedusae to be negligible compared to grazing by nano- and micrograzers. In most estuaries, interactions between top level and subordinate predators are complex and dictate the effectiveness of top-down control in creating significant changes down the food web. Nonlinear trophic interactions are complicated by compensatory predation and algal growth, which may be strongly influenced by temperature. Thus the complexity of such systems may provide protection from ecosystem functional imbalance through redundancy.

Open ocean trophic dynamics are also not immune to temperature regime shifts. The El Niño and North Atlantic Oscillation phenomena are excellent examples of ocean trophic structure shifting to a markedly different state as a result of climate variability. Although these shifts are transient, expected global temperature increases lead us to question whether such changes to ecosystems in the future may be more persistent.

Freshwater lakes—Temperature effects have been shown to alter a wide variety of aquatic ecosystems in addition to estuarine environments. Thackeray et al. (2008) showed that changes in the composition of lake phytoplankton communities and shifts in phenology to earlier times of the year occur in response to climatic change due to species-specific responses to driving mechanisms. Shifts from cold stenothermal fishes to fishes with greater thermal tolerances have been observed in springs and groundwaters as a result of warming temperatures (Buisson et al. 2008; Tixier et al. 2009). Additionally, home ranges for diadromous fishes of Europe, North Africa, and the Middle East have shrunk in size and migrated poleward (Lassalle and Rochard 2009). McCullough et al. (2009) provide an excellent review of the well-studied effects of temperature on freshwater fishes.

Temperature effects on aquatic community structure are evident in European boreal springs, where there has been a loss of benthic macroinvertebrate diversity and a replacement of less thermally tolerant species with those more thermally tolerant (Ilmonen et al. 2009). Increased stream temperatures can cause species-specific freshwater mussel community shifts in various ecosystem services, including increased biodeposition, increased NH_3 excretion, and increased nitrogen:phosphorous excretion rates (Spooner and Vaughn 2008).

The trophic dynamics in freshwater lakes also have been altered through increasing temperatures. Lake eutrophication has led to increased cladoceran reproduction and growth (Visconti et al. 2008). Increases in zooplankton population abundances and concurrent shifts in zooplankton

community composition and increases in body size in Canadian lakes have been attributed to temperature increases (Rusak et al. 2008).

Trophic dynamics, a complex blend of biologically mediated reactions that dictate energy and material flow within ecosystems, is strongly influenced by temperature. The relative temperature dependence for each trophic linkage, and in turn the relative "sensitivity" of trophic structure to each linkage, dictates how the overall ecosystem will react to changes in temperature. In light of the current concern over widespread global temperature regime shifts, it is imperative that research focus on how aquatic trophic structure and function will change.

Land use change

Land use or land cover change is generally defined as the anthropogenic altering or modification of terrestrial systems to suit different human needs. For example, throughout human history, forested areas have been converted to cropland to increase food production for a growing human population. Almost all of the world's land has been influenced by anthropogenic changes (Richards 1990). This alteration of the land can result in changes to the hydrology, biogeochemistry, and biodiversity of the area undergoing modification. The land cover of a watershed can greatly affect water quality (Hunsaker et al. 1992). Because aquatic ecosystems are inherently connected to their watersheds, changing watershed landscapes can have pronounced effects on aquatic ecosystems. Of particular concern is the conversion of any natural land, especially wetlands, and the conversion of agricultural land to suburban or urban land.

On a historical scale, global land use change has resulted in an increase in the development of natural land to agriculture and residential areas. As populations continue to grow, the loss of natural land to agriculture and then from agricultural to residential use continues to add stress to aquatic ecosystems. In the US, the demand to convert agricultural land is ever increasing. From 1997 to 2007, 32.5 million acres of farmland were taken out of agricultural production (US Department of Agriculture [USDA]). From 1987 to 2002, farmland acreage increased in value from a national average of $599 per acre to $1,210 per acre (in 1987 adjusted dollars; USDA) due to an increased demand for land resources. At the peak of residential construction in January 2006, privately owned housing starts were as high as 2,276,000, a 55% increase from January 1996 (US Census Bureau 2006). This increased demand and cost for land has resulted in the conversion of agricultural land to urban and suburban land use. This conversion, especially of row-crop farmland, results in added stress to aquatic ecosystems.

While land use change can result in anthropogenic succession and the fragmenting of ecosystems, the conversion of agriculture and wetlands to urban and suburban land uses can increase water runoff velocity and volume (Hollis 1975;

Franklin 1992; Arnold and Gibbons 1996; McCarthy and Johnson 2009), affect nutrient and sediment quality, transport, and delivery (Omernik 1976; Karr and Schlosser 1978; Peterjohn and Correll 1984), and introduce pollutants (Sprague and Nowell 2008) to receiving aquatic environments. These hydrologic alterations caused by land use change can then negatively affect aquatic ecosystems. In fact, the US Environmental Protection Agency (US EPA) has listed agricultural practices, hydrological modifications, and urban run-off/storm sewers as major causes of impairment to aquatic ecosystems.

In particular, changes in hydrology can greatly affect phytoplankton productivity. The accumulation of algal biomass is dependent on a net balance of several gain processes (i.e., phytoplankton production and advective inputs) and loss processes (i.e., advective output or hydraulic flushing, respiration, grazing, sinking, and other sources of mortality) (Jassby and Goldman 1974; Crumpton and Wetzel 1982). Hydrological modifications alter growth conditions and loss rates and as a result disrupt the natural flow of nutrients and energy from the lowest trophic level.

For aquatic systems whose watersheds have recently undergone land use changes, their natural disturbance regimes can be greatly affected, resulting in seasonality that was once stable or predictable becoming increasingly punctuated by greater and more frequent deliveries of sediments, nutrients, and water. The most immediate changes to ecosystem trophic levels would occur in primary productivity. In aquatic ecosystems where water delivery causes increases in hydraulic flushing, increased advective flow can influence species composition and population dynamics. Zohary et al. (1996) and Hambright and Zohary (2000) showed that Hartbeesport Dam reservoirs (South Africa), which underwent events of hydraulic flushing, had reduced summertime dominance of *Microcysits aeruginosa* and increased diversity. However, the greatest effect of disturbance may not be in changes to the chemical and nutrient environment alone, but to the combined effect of a change in limiting resources (nutrients and light) and the physical loss of phytoplankton from hydraulic flushing and mixing into the tropholytic zone. For instance, mixing of algae into deeper, darker water can cause losses of algal biomass but can also spur growth when nutrient-rich deep water is mixed to the surface; inflow can increase flushing losses of algae but also deliver new sources of nutrients to spur further growth. Grover and Chrzanowski (2004) suggest that the cumulative effect of coupling limnological disturbances to resource availability leads to large, shared influences on phytoplankton diversity. These studies show that disturbances such as those caused by changes in watershed hydrology can limit lake productivity and result in changes to species diversity, thus, affecting the flow of nutrients and energy from lower trophic levels.

Freshwater lakes—The effects of hydrological changes on primary productivity are clearly evident in freshwater lakes

and reservoirs. In freshwater lakes and reservoirs, changes in phytoplankton population dynamics can affect zooplankton populations. The relationship between phytoplankton diversity and zooplankton populations has been well documented (e.g., Burns 1968; Gliwicz 1977; Haney and Trout 1985) with many studies showing that zooplankton choose between edible, poorly edible, and inedible phytoplankton species (e.g., DeMott 1986; DeMott 1990; Lampert 1987; Gliwicz and Lampert 1990). As phytoplankton population dynamics are altered, zooplankton populations and higher trophic levels will also be affected. A recent study by Dickman et al. (2008) showed that food-chain efficiency in a three-level experimental system was highest when phytoplankton communities consisted of high-quality food such as Cryptomonads, other small flagellates, and diatoms. In contrast, phytoplankton populations comprised mostly of cyanobacteria (poor food quality) resulted in lower energy-transfer efficiency. Dickman et al. (2008) concluded that understanding how environmental perturbations affect light and nutrient supply are important in understanding fishery yields and other ecosystem services constrained by food-chain efficiency. Because primary productivity is light and nutrient dependent, hydrological alterations of watersheds will likely affect trophic dynamics and overall ecosystem function by modulating phytoplankton community structure.

Coastal ocean—In coastal ecosystems, the effect of bottom-up controls on trophic dynamics is well documented, especially in coral reef systems. In coral reef systems where watershed land use has resulted in an influx of terrigenous nutrients and sediments into receiving waters, entire reef ecosystems have declined (e.g., Rogers 1990; McLaughlin et al. 2003; Pelley 2004; Fabricius 2005). The effects of terrigenous nutrients and sediments can have a cascading effect on higher trophic levels, the reduction in light for photosynthesis, and the smothering of reef organisms, and can lead to an overall collapse of the reef framework (Rogers 1990). The phenomenon of land use and land use change in the watersheds feeding the Great Barrier Reef (Australia) show that nutrient loads are disproportionately related to agriculture and the percentage of residential areas without sewers, and modeled fluxes of nutrients are as high as six times those of predeveloped conditions (Hunter and Walton 2008). This increase in suspended sediments and nutrients to the Great Barrier Reef changes primary productivity and can affect higher trophic levels. For example, along water quality gradients from watersheds of differing degrees of agricultural land use, Fabricius et al. (2005) showed that macroalgae increased and octocoral and hard coral abundance decreased with increasing nutrients.

Open ocean—Effects on trophic interactions caused by land use change and its subsequent alterations in the quality and delivery of water to receiving aquatic ecosystems is likely not confined to near-shore environments. These effects can be seen in coastal oceans and even the pelagic open ocean as runoff and terrigenous nutrients and sediments are transported with currents. For example, in coastal waters of the east North Pacific (from the coast of California to Alaska), bottom-up controls of phytoplankton are the highest predictor of variability in fish yields: 87% of long-term fish yields can be explained by annual chlorophyll *a* concentrations (Ware and Thomson 2005). As land use continues to change in major watersheds that feed the world's oceans, effects on coastal ocean productivity and trophic interactions in near-shore environments could then affect the productivity and health of interconnected ecosystems.

While we hypothesize that the effects of land use change would be most pronounced in aquatic ecosystems closely linked to specific watersheds that are undergoing land use change (such as lakes, reservoirs, coastal systems, and estuaries), the interconnectedness of aquatic ecosystems suggests that effects on trophic structure may be present across all major aquatic ecosystems. As climate change is predicted to affect rainfall intensity and distribution (Bates et al. 2008), the coupled effects of land use change and altered precipitation patterns could further stress aquatic ecosystems and ultimately change ecosystem function. These changes in ecosystem function can be defined, observed, and measured by understanding trophic interactions. As demonstrated above, understanding how a threat (here land use change) can affect primary productivity and, thus, higher trophic levels, can provide insight to the viability and health of our aquatic ecosystems.

Nutrient loading

Nutrients exert a bottom-up control on the biomass of primary producers in all ecosystems. As the base of most food webs, primary producers use energy from the sun to convert inorganic nutrients into organic nutrients, which are incorporated into higher trophic levels through consumption. As such, nutrients are key components of trophic dynamics.

In aquatic ecosystems, the nutrients phosphorous, nitrogen, iron, and copper are of particular interest. These nutrients are critical components of DNA, RNA, ATP, amino acids, proteins, and enzymes (Frausto da Silva and Williams 1991; Sterner and Elser 2002). Furthermore, phosphorous, nitrogen, iron, and copper limit phytoplankton growth because they are among the nutrients in the shortest supply (Schindler 1977; Martin and Fitzwater 1988; Vitousek and Howarth 1991). Nutrients enter lakes, rivers and oceans from both internal and external sources. Internal sources include upwelling, sediments, and microbial-mediated cycling through the particulate and dissolved organic matter pools (Wetzel 2001). Aeolian inputs are an external source of nutrients, as are components of the hydrological cycle, including precipitation, runoff, and groundwater (Wetzel 2001). The quantity of nutrients entering an aquatic system over a given period is called nutrient loading.

Nutrient loading is seen as an imminent threat to aquatic ecosystems (Millennium Ecosystem Assessment [MEA] 2005;

Parry et al. 2007; Keister et al. 2010, this volume). In general, nutrient loading is considered a threat because there have been drastic and rapid increases in the quantity of nutrients entering our waters due to anthropogenic activities such as agriculture, urban development and even climate change (MEA 2005; Parry et al. 2007). For example, agricultural activities have caused a 5- to 17-fold increase in the flux of nitrogen entering rivers and coastal oceans (Howarth 2008); unfortunately this is not an isolated incident and many more examples exist.

In this section, the effects of nutrient loading on the trophic dynamics of different aquatic ecosystems are discussed in order to synthesize the nature of this threat across environments. This approach is necessary to create a comprehensive picture that can be used for future mitigation, the necessity of which is obvious given that current climate change simulations predict severe alterations to the Earth's hydrology cycle (MEA 2005; Parry et al. 2007).

Freshwater lakes and coastal oceans—Human-mediated activities have significantly altered the rate and concentration of nutrients entering aquatic environments. As precipitation runs off of farms, lawns, and other anthropogenically impacted lands, concentrations of nitrogen and phosphorous within the water increase substantially prior to reaching nearby aquatic ecosystems (Smith 2003; Howarth 2008; Smith and Schindler 2009). This increase is largely due to our excessive use of fertilizers (MEA 2005; Howarth 2008). Elevated nutrient loading rates can cause a system to become eutrophic, negatively impacting the trophic dynamics of streams, rivers, lakes, and estuaries.

Excessive nutrients cause a shift in the composition of the phytoplankton community, often to organisms that are inedible or toxic. In lakes, filamentous and toxic cyanobacteria bloom outcompete other phytoplankton (Schindler 1977; Smith 2003) and bloom because they are not consumed by zooplankton or ciliates (Laws 2008). Cyanobacteria blooms also occur in coastal oceanic water (Smith 2003; Smith 2006), with similar effects. However, alternations to phytoplankton communities are not restricted to cyanobacteria, as eukaryotic phytoplankton can also bloom with high nutrient loading rates. In the early 1990s, North Carolina's estuarine and coastal phytoplankton communities were substantially altered by high nitrogen loading rates that were associated with breached sewage ponds of hog farms. A dinoflagellate (*Pfiesteria piscicida*) that produces a neurotoxin then bloomed (Burkholder et al. 1992). As a result, a large fish kill occurred, which added to the near complete disruption of the trophic interactions in these waters. In general, the increase in primary producer biomass caused by excessive nutrient loading does not translate into increased consumer biomass; as a result, the trophic structure and stability of the system are negatively affected.

Under the conditions described above with high phytoplankton abundance and low grazing rates, senescence and

viral infections are the major agents of phytoplankton mortality. As cells senesce, they are decomposed by bacteria (Chen and Wangersky 1996). Bacterial respiration rates increase with increasing numbers of senescing cells. Under certain conditions, high rates of bacterial decomposition can quickly deplete dissolved oxygen (DO) concentrations (Dodds 2006). Zooplankton, fish and benthic invertebrates suffocate and die in low-oxygen bottom waters (Diaz and Rosenberg 2008). The huge (20,000 km²; Dodds 2006) Gulf of Mexico dead zone associated with the agricultural runoff entering the Gulf is an infamous example of these low DO zones (Diaz and Rosenberg 2008). Unfortunately, the number of these dead zones have been doubling every decade since the 1960s, to >400 of these low oxygen incidents from <10 in the 1910s (Diaz and Rosenberg 2008). In this case, nutrient loading affects trophic dynamics indirectly through the death of several taxa of consumers at various trophic levels.

Viral infections can be the other major agent of phytoplankton mortality in some eutrophic systems. Viral-mediated cell lysis of phytoplankton (both eukaryotic and prokaryotic) cycles nutrients into the dissolved organic matter pool (Wilhelm and Suttle 1999). This pool is bioavailable to bacteria (Thingstad et al. 1993; Suttle 2007). The net result is that viruses divert energy from phytoplankton to heterotrophic bacteria before entering the grazer food web via consumption of the bacteria by ciliates (rotifers) and zooplankton (Suttle 2007). It could be argued that this additional step (through the microbial community) decreases trophic efficiency. Regardless of the specific details, it is clear that eutrophication shifts trophic interactions from consumers to decomposers by fuelling the microbial loop.

Although nutrient loading may increase primary producer biomass in lakes, estuaries, rivers and coastal oceans, trophic dynamics may be negatively affected because of shifts in phytoplankton community composition, consumer death, and even increased microbial interactions. The concern about the threat of nutrients loading seems justified.

Open ocean—Open oceanic waters are located far from major land sources. As a result, there is little direct evidence regarding the effects of nutrient loading on the trophic dynamics and interactions in the open ocean. However, as the nutrient concentrations of coastal waters continue to increase (MEA 2005), advection of these waters may eventually contribute to a measurable increase in the nutrient concentrations of the open oceans. Ultimately, an increase in nutrients could stimulate a slight increase in primary producer biomass and, thereby, potentially affect trophic interactions. If this process occurs at all, it would be slow due to the enormous volume of the world's oceans.

Unlike phytoplankton in coastal oceans, phytoplankton growth in the open ocean is often limited by micronutrients such as iron and copper (Martin and Fitzwater 1988). This limitation is due to the extreme distance these waters lie from iron- and copper-rich terrestrial crusts (Loktka 1925). Due to

climatic conditions and prevailing winds, dust from the deserts of Africa provide regions of the open oceans with iron and copper (Jickells et al. 2005). Current climate change models predict that tropical and subtropical climates will become drier (MEA 2005). If the frequency and intensity of drought conditions in Africa increases, oceanic dust inputs may also increase (Jickells et al. 2005). An increase in the introduction of iron- and copper-rich dust will stimulate phytoplankton growth in these waters. This response in not unprecedented; similar changes in ocean productivity occurred on glacial and interglacial time scales as climatic conditions changed (Jickells et al. 2005). Needless to say, any increase in phytoplankton biomass will affect trophic interactions.

Human-mediated activities are increasing nutrient-loading rates. Aquatic ecosystems located inland or near land will experience increased primary production, which may have a negative effect on trophic structure and stability. The effect of increased nutrient loading on trophic dynamics is so similar across lakes, estuaries, and coastal ocean ecosystems that we chose to group these ecosystems together in this section. This pattern clearly demonstrates the utility of trophic dynamics as a metric to compare threats across ecosystems. However, it remains to be seen how (and if) trophic dynamics in the open ocean will be affected by nutrient loading.

Overharvesting

Among the most evident impacts occurring across all aquatic ecosystems are those resulting from humankind's growing appetite. Overharvesting of aquatic species (often termed overfishing, regardless of species) can have far-reaching consequences, not only for the population or species directly harvested but for other components of the ecosystem as well. This connectedness is due to trophic interactions within the ecosystem, and the disruption of these interactions can have cascading effects to food web components that are not harvested. The potential for such trophic disruptions and trophic cascades (referring to effects translated through at least three trophic levels) are at the heart of this review. Any altering of energy pathways in an ecosystem, whether by overharvesting or any other threats, can manifest itself in the entire ecosystem. Overharvesting within aquatic ecosystems is one of the clearest mechanisms by which trophic disruptions occur, and it is increasingly apparent that all of the major types of aquatic ecosystems are at risk.

Freshwater lakes—Although the occurrence and effects of overharvesting in marine waters have been well-documented (e.g., Pauly et al. 1998; Myers and Worm 2003), much less attention has been paid to overharvesting in freshwater habitats or the resulting ecosystem effects (Allan et al. 2005). This is despite the fact that inland waters of the developing countries in Asia and Africa are experiencing substantial and dangerous levels of commercial and artisanal harvesting, while other areas of the world have declining rates of commercial removal but an increase in recreational fishing (Allan et al. 2005).

As is often the case in marine waters, the large, long-lived and, as a result, most vulnerable fishes of freshwater ecosystems are the most frequently and heavily impacted components of inland aquatic food webs. Often these species are the top predators of their system, playing a crucial top-down role in regulating the abundance and stability of lower trophic levels (Halpern et al. 2005). Alternatively, these large organisms are herbivores, yet due to their size still serve as important grazers in the community. Many such examples occur in the Mekong River Basin and other productive and highly diverse freshwater systems near lower latitudes and within developing countries (Allan et al. 2005).

Because many fishes exhibit diadromy, or the movement between fresh and marine waters, at some point in their life history, our divisions by ecosystem type are less appropriate for some taxa. However, such migratory species are some of the most heavily exploited, and just as exploitation can occur over the range of ecosystems these species occupy, so can the cascading effects of their exploitation. One of the most notable examples involves the overharvesting of salmon. After several years of development in the open ocean, salmon return to natal rivers and tributaries to spawn and die. These generally oligotrophic freshwater ecosystems are dependent on the nutrients provided by the carcasses of dead, post-spawn salmon. The reduction of this input, often due to fishing, has been shown to affect primary productivity, macroinvertebrate abundances, the growth and survival of the recently spawned juvenile salmon and other fishes, the survival of terrestrial animals (especially bears), and even tree growth rates (Cederholm et al. 1999). Additionally, salmon have been shown to exert top-down control of zooplankton in the open ocean, in turn influencing the abundances of phytoplankton (Shiomoto et al. 1997). Although cascading effects can be difficult to document, it seems plausible that the documented intense harvesting of other key diadromous fishes such as sturgeons, striped bass, shads, smelts, and freshwater eels is affecting the trophic interactions of their ecosystems.

Due to the high vulnerability of freshwater ecosystems to other anthropogenic influences (e.g., damming, land use change, and nutrient input), it may be difficult for many scenarios of trophic disruptions to solely implicate overharvesting; however, the many observed direct effects of overharvesting indicate that removal of aquatic organisms by humans is a significant threat, adding to the general degradation of freshwater ecosystems.

Coastal waters—Estuarine and other near-coastal aquatic ecosystems are generally very productive, resulting in high abundances and fast growth rates of organisms that have, in turn, become important resources for humans. Anthropogenic effects on coastal waters and their ecosystems are numerous and largely well documented (Pinnegar et al. 2000; Jackson 2001; Jackson et al. 2001). As such, we provide only a brief review of the effects that the overharvesting of coastal organisms has been shown to have on the trophic structure within these ecosystems.

Within estuaries, there are several important commercial fisheries for species of shrimp, clams, oysters, and finfish that depend on healthy habitats such as seagrass beds and mangrove forests. Estuarine seagrass habitats, which are thriving ecosystems that provide an important refuge for the larval and juvenile stages of many species, depend on the grazing of large aquatic organisms to maintain their important ecological functions. Green turtles, manatees and dugongs, all substantial grazers of seagrasses, are thought to have played a vital role in minimizing the buildup of detritus and in maintaining blade lengths that reduce self shading and infection (Jackson 2001). However, due to extremely high levels of harvesting of these organisms by humans, population sizes of green turtles, manatees, and dugongs are so low that their former role is left unfilled and, consequently, seagrass die offs are a common occurrence in lower latitudes.

One of the clearest trophic cascades in coastal waters has occurred on coral reefs, and it has enormous implications for the survival and functioning of these entire ecosystems. The corals themselves provide the structure and habitat for coral reef ecosystems, but their growth is very slow and competition with macroalgae for space and light is fierce. Historically and evolutionarily, herbivorous fishes and invertebrates, such as sea urchins, graze the macroalgae, keeping algal levels low so that corals are not overgrown and killed. Unfortunately, the harvesting of fishes on coral reefs (which are easily seen and occupy a habitat easily found) has drastically thrown off this evolved balance (Jackson 2001; Pandolfi et al. 2005). Large grazing fishes have been overfished on many reefs for decades, but until the 1980s in the Caribbean, grazing by *Diadema* sea urchins appeared to increase and compensate for the losses. A disease struck the large populations of *Diadema* and the resulting die off released the grazing pressure on macroalgae, which then rapidly grew and killed much of the coral, causing a decline of up to 100% of the coral cover in many areas (Hughes 1994; Jackson et al. 2001).

While coral reef ecosystems are often discrete locations and generally occupy small areas, the benthos of the entire continental shelves is extensive. However, nearshore shelf ecosystems are also highly exploited, often with fishing gear that not only indiscriminately removes the inhabiting organisms, but also destroys the substrata on which the ecosystem is built (e.g., Watling and Norse 1998). Although data are somewhat limited in demersal soft-bottom habitats, a common trophic disruption seen in some areas is the removal of fish leading to an abundance of cephalopods (Pinnegar et al. 2000). Much more is known about kelp forest systems where trophic cascades are frequent. Kelp forests that were extensive in the Northwest Atlantic were habitat to large populations of cod and other large fishes, but intense fishing that began in the 1920s removed most of the large fishes. This removal allowed sea urchin populations to boom and resulted in the near complete removal of the kelp forests due to their grazing (Jackson 2001). Kelp forests in the Northeast Pacific have experienced

similarly destructive cascades due to the removal of sheepshead and otters, which were the predators of sea urchins in those ecosystems (Estes and Palmisano 1974). In Alaska, killer whales have contributed through a recent switch to consuming sea otters, which has further released the predation pressure on sea urchins in these waters (Estes et al. 1998). The likely reason for the killer whale diet switch is the declines in sea lion and seal populations that appear to be due to the overfishing of *their* predominant prey.

Open ocean—Evidence for overharvesting effects on the trophic structure in the open ocean is very limited. Although it is possible that the well-documented collapse of many populations of fishes and mammals is not having broader effects on their ecosystems, it seems more likely that the observation of such effects, and the collection of necessary data, has just been more difficult in the open ocean. In one analysis of worldwide declines in populations of large, predatory fishes, there were several indications that compensation for the removal of one species occurred with an increase in the population size of another species (Myers and Worm 2003), likely through the trophic-related mechanism of predation release and reduced competition. As mentioned above, another example of an open ocean trophic cascade partly due to overharvesting is the salmon-zooplankton-phytoplankton food chain of the North Pacific, where top-down influences can occur.

Over the vast Scotian Shelf, there is evidence for a trophic cascade extending from the benthos to the pelagic waters overhead. Frank et al. (2005) showed that the overharvesting of large predators had cascading effects through the entire community and involved four trophic levels plus nutrients. The large predators (mainly cod) were removed from the ecosystem due to overharvesting, and, correspondingly, the abundance of small pelagic fishes and macroinvertebrates increased, large herbivorous zooplankton decreased, phytoplankton increased, and nitrate decreased.

Also shown to be related to overharvesting, there has been an increase in the abundance of jellyfish in certain locations worldwide, with the suggestion that drastic regime shifts are also occurring (Richardson et al. 2009). In these ecosystems, the small pelagic fishes that once competed with jellies for zooplankton prey, or would exert predation pressure on the jellies themselves, are removed from the food web by fishing. With a surplus of food and little top-down control, the jelly populations are free to explode, which often results in complete transformations of the entire ecosystem (Bakun and Weeks 2004; Lynam et al. 2006).

Clearly, overharvesting in all aquatic ecosystems, even of individual species, can have effects that spread throughout the food web. These effects are in addition to the more obvious implications of collapsed fisheries, reduced food supplies for developing countries, and the aesthetic loss of diversity and charismatic species. Despite the awareness of our actions, progress toward changing them has been slow. We hope that

continued research and increased public awareness can increase the pace of this change.

UV radiation

UV light, a component of sunlight, is electromagnetic radiation that has a wavelength shorter than light in the visible spectrum, and excessive or prolonged exposure can be detrimental. UV can directly destroy DNA by causing nucleotides to fuse, creating basepair dimers (Giese et al. 1957). These dimers deform the phosphate backbone of the nucleotides, which inhibits the ability of DNA polymerase to transcribe the strand (Giese et al. 1957). As a result, UV exposure can cause DNA mutation and, ultimately, cell death (MacFadyen et al. 2004). Fundamentally, the effect UV has on ecosystems depends on the degree of exposure, which varies with both natural and anthropogenic processes.

In aquatic environments, the degree and intensity of UV exposure is determined by both the amount of incoming radiation and the depth to which it penetrates. The ozone layer acts as a UV filter, decreasing the amount of radiation that reaches the surface of the Earth. However, chemicals (like chlorofluorocarbons) have drastically thinned stratospheric ozone concentrations, creating the much publicized ozone "holes" over the North and South poles (Solomon 2004). As a result, the amount of UV radiation reaching the biosphere has increased (Parry et al. 2007). Since the Montreal protocol, which banned the release of chlorofluorocarbons and other ozone-harming chemicals, stratospheric ozone concentrations have started to increase (McKenzie et al. 2007). However, this recovery may be fleeting, because the ozone layer may continue to shrink because of increasing concentrations of anthropogenic carbon dioxide in the atmosphere (Austin et al. 1992).

The concentration of atmospheric ozone is a global phenomenon affecting all aquatic systems. A large part of the variability in UV exposure (at least at similar latitudes) is attributed to differences in UV penetration depths. This section will focus on this component of UV exposure, since it is the one that varies among aquatic ecosystems (Morris et al. 1995; Wetzel 2001; Hader et al. 2007). UV attenuation is a function of angle of incidence and the absorption of UV radiation by particles in the water. The concentration of these biological and/or chemical particles is influenced by anthropogenic processes, such as runoff, eutrophication, and sedimentation (Hader et al. 2007). Because these processes vary across ecosystems, the resulting differences in UV exposure could affect trophic dynamics. Two aquatic ecosystems (lakes and open oceans) are discussed below to examine the effects UV radiation has on trophic dynamics across different ecosystems.

Open ocean—In general, small organisms (like phytoplankton) could be vulnerable to UV radiation if they lack the ability to vertically migrate below UV-penetration depths. Open ocean planktonic organisms are susceptible to UV radiation because these waters are ultra-oligotrophic, containing few biological or chemical particles that can absorb incoming UV radiation (Tedetti and Semper 2006). As a result, UV penetration depths are maximized. All organisms within these depths are exposed to potentially detrimental doses of UV radiation. For example, phytoplankton growth and primary production is inhibited by UV, likely due to damaged DNA, the inhibition of photosystem II, and/or inhibition of the production of RUBISCO (ribulose-1,5-bisphosphate carboxylase oxygenase) (Hernando et al. 2006; Hader et al. 2007). In addition, UV radiation affects the composition of phytoplankton communities. Phytoplankton species that can produce sunscreen pigments (e.g., scytonemin) dominate communities in open oceanic water because these pigments allow them to tolerate prolonged exposure to UV radiation (Hernando et al. 2006; Hader et al. 2007). Despite this mechanism to dampen the effect of UV radiation, overall phytoplankton production is low because making sunscreen pigments is energetically costly (Garcia-Pichel 1994; Wetzel 2001). Depressed primary production rates affect higher trophic levels, decreasing the amount of energy moving through open ocean food webs.

Visual predators, such as zooplankton and fish larvae, are also susceptible to UV radiation (Hader et al. 2007) because they hunt within the photic zone. However, zooplankton can vertically migrate below UV penetration depths and, therefore, limit their exposure. In addition, many zooplankton accumulate sunscreen pigments within their tissues, which offer further protection (Hader et al. 2007). Zooplankton with these pigments walk a fine line between the benefits of UV protection and loss of the invisibility that shields them from predators. Finally, viruses are a major source of mortality in aquatic environments (Suttle 2007). Bacteria, cyanobacteria, and eukaryotic phytoplankton are particularly susceptible to viral infections (Wommack and Colwell 2000; Brussaard 2004; Weinbauer 2004). Most infections lead to cell lysis, which shuffles nutrients away form the grazer food chain into the microbial loop via the viral shunt (Thingstad et al. 1993; Wilhelm and Suttle 1999). However, UV radiation is the primary mechanism by which aquatic viruses are destroyed (Suttle and Chen 1992). Because viruses have few mechanisms for photorepair, UV exposure may keep viral-mediated mortality to a minimum. Any increase in UV radiation affects the transfer of energy to higher trophic levels by depressing the number of viral infections and, therefore, viral-mediated mortality. However, the relationship between viruses and UV radiation is not simple. Evidence suggests that not only do some viruses have the ability to quickly recover from UV exposure, but others can also increase the UV resistance of their host cells (Wilhelm et al. 1998; Jacquet and Bratbak 2003). Clearly further research is necessary to elucidate how UV radiation and viruses interact. This research is ecologically and evolutionarily interesting because viruses are significant components of the global gene pool (Breitbart et al. 2004; Angly et al. 2006; Suttle 2007).

Freshwater lakes—As in the open ocean, in freshwater lakes prolonged exposure to UV negatively affects viruses, phytoplankton, and zooplankton (Williamson et al. 1994; Wetzel 2001; Maranger et al. 2002; Hader et al. 2007). However, unlike the open ocean, most lakes (and coastal oceans) are heavily influenced by terrestrial inputs. Large complex organic carbon compounds (called humics) enter the ecosystems via rivers, estuaries, and runoff, and become dissolved organic carbon (DOC). DOC compounds significantly decrease UV penetration depths because they readily absorb incoming UV radiation (Brinkmann et al. 2003; Leavitt et al. 2003; Hader et al. 2007). Waters that have low DOC concentrations do not receive the same protection from UV radiation (Morris et al. 1995). These ecosystems, including high alpine lakes and other lakes surrounded by low DOC soils, experience UV effects on trophic dynamics similar to those described for the open ocean. However, DOC-rich waters have high phytoplankton biomass because the phytoplankton communities experience less of the detrimental effects of UV radiation (Hader et al. 2007). Additionally, protection provided by DOC decreases the need to produce energetically costly internal sunscreen pigments (Wetzel 2001). The associated reallocation of energy stimulates growth and can cause shifts in the composition of both the phytoplankton and zooplankton communities.

However, DOC and UV may interact by an entirely different mechanism that may actually stimulate trophic dynamics in high-DOC waters. Surface DOC is degraded by UV, which breaks down large complex DOC compounds into small labile compounds (Brinkmann et al. 2003) that are readily used by bacteria (Klug 2005). These labile compounds can stimulate the bacterial community (De Lange et al. 2003), resulting in increased bacterial biomass. This stimulation may be a mechanism by which UV positively affects trophic dynamics in lakes and coastal oceans, or at least is required to maintain the evolved balance in these systems.

UV exposure in aquatic systems is affected by the amount of radiation reaching the surface and the depth to which the radiation penetrates. The small organisms unable to vertically migrate are at the greatest risk for UV-induced DNA damage. In open oceans, UV exposure decreases trophic interactions by inhibiting phytoplankton growth and primary production. On the other hand, in lakes (and coastal oceans) terrestrial DOC inputs act as external sunscreen pigments and protects plankton from UV. Additionally, UV radiation may enhance microbial biomass through photodegradation of DOC compounds. Current climate-change models predict alternations in both stratospheric ozone concentrations and attenuation depths (Austin et al. 1992; MEA 2005; Parry et al. 2007). It remains to be seen how any alteration in UV radiation will further affect trophic dynamics; it appears, however, that the effect of UV exposure on trophic dynamics varies across ecosystems. This difference may have interesting ecological implications, and further research is warranted.

Invasive Species

Biological invasions are of widespread concern in aquatic ecosystems. The term "invasive species" is applied to the subset of introduced species that are likely to cause ecological or economic harm. Invaders can alter ecosystem structure and function (Ruiz et al. 1997) by changing habitat structure, species composition, and species interactions, all of which can lead to cascading trophic effects (Wallentinus and Nyberg 2007) and changes in patterns of energy flow (MacIsaac 1996) and nutrient cycling (Conroy et al. 2005).

Introductions of invasive species result from multiple anthropogenic vectors and vary by aquatic ecosystem. In marine/open ocean ecosystems, commercial shipping, aquaculture, fisheries activities, drilling, canals, aquarium industries, recreational boating, and floating debris are all sources of introductions (Bax et al. 2003; Molnar et al. 2008). Estuarine introductions most likely result from the shipping, boating, aquaculture, aquarium trade, and live seafood and bait industries (Williams and Grosholz 2008). In freshwater ecosystems such as the Great Lakes, ballast water exchange from the shipping industry and unintentional release are cited as the two most likely vectors (Munawar et al. 2005).

Aquatic ecosystems have been plagued by species invasions of various plants, algae, diseases, invertebrates, and fishes. More than 400 nonindigenous species have been identified in the US along the Pacific, Atlantic, and Gulf coasts (Ruiz et al. 1997). An additional 388 nonindigenous species have been reported in the Chesapeake Bay (Maryland and Virginia), Coos Bay (Oregon) and San Francisco Bay estuaries (Ruiz et al. 1997). In the Great Lakes, Munawar et al. (2005) detailed 170 invasive species. The number of invasions are expected to only increase with increased shipping and transportation (Molnar et al. 2008) and human-induced global change (Dukes and Mooney 1999; Occhipinti-Ambrogi 2007).

Aquatic invasive species can have a wide variety of ecological impacts. Individual invaders may have differing effects in different habitats and ecosystems, but when categorized into functional groups such as clonal/weedy, filter feeders, predators, and ecosystem engineers (Williams and Grosholz 2008), these aquatic invasive functional groups appear to have similar impacts on a wide variety of aquatic ecosystems. Certain algal and plant species (e.g., a tropical green alga strain, *Caulerpa taxifolia*, in the Mediterranean Ocean, and Eurasian Watermilfoil, *Myriophyllum spicatum*, in US freshwaters) are clonal, weedy species that overgrow and outcompete native fauna and can alter species diversity and primary production. Filter feeders (e.g., Asian clam, *Corbula amurensis*, in the San Francisco Bay Estuary, and zebra mussels, *Dreissena polymorpha,* in US freshwaters) have a top-down influence on aquatic ecosystems by reducing phytoplankton, which then cascades back up, altering zooplankton biomass and potentially affecting fishes. Predator species (e.g., green crab, *Carcinus maenas*, along the US West Coast, and Nile perch, *Lates niloticus*, in

Lake Victoria, Uganda) have top-down effects on lower trophic levels, causing dramatic decreases in species diversity and negative effects on commercial fisheries. Last, ecosystem engineers (e.g., smooth cord grass, *Spartina alterniflora*, along the US West Coast, Pacific oyster, *Crassostrea gigas*, along the US coastline, and the common reed, *Phragmites australis*, in wetlands and riparian areas) convert mudflats and shorelines or create reefs, effectively outcompeting native flora and fauna by altering the habitat architecture. Below we discuss two specific examples of invasive species and their effects on ecosystem structure and trophic dynamics: the zebra mussel in freshwaters of the US and the comb jelly in the Black Sea.

Freshwater lakes—Zebra mussels are one example of an invasive species that has had a wide range of impacts on the trophic dynamics of freshwater ecosystems. First detected in Lake St. Clair, Michigan, USA, in 1988 (Herbert et al. 1989), zebra mussels quickly established populations in all five of the Great Lakes and several major river systems (e.g., Hudson, Mississippi, and Ohio Rivers) (Ludyanskiy et al. 1993), and soon began to invade smaller inland lakes (Kraft and Johnson 2000). Economic losses in the Great Lakes basin due to damage and control costs are estimated to be US $500 million per year (Pimentel 2005).

Zebra mussels are efficient filter feeders that consume large quantities of algae and small zooplankton. Phytoplankton biomass usually declines following zebra mussel invasion, and water clarity increases (Nicholls and Hopkins 1993; Caraco et al. 1997; Idrisi et al. 2001). At the same time, zebra mussels can promote blooms of the toxic colonial cyanobacterium *Microcystis aeruginosa* in lakes with low-to-moderate nutrient levels (Vanderploeg et al. 2001; Raikow et al. 2004; Sarnelle et al. 2005; Knoll et al. 2008).

Due to their efficient filtering and production of feces and pseudofeces, zebra mussels can divert energy from pelagic to benthic communities (MacIsaac 1996) by enhancing nutrient fluxes to the benthos (Conroy et al. 2005) and increasing benthic algal abundance and primary productivity (Fahnenstiel et al. 1995; Lowe and Pillsbury 1995) in shallow environments. Additionally, the increased habitat heterogeneity created by their colony formation coupled with the production of nutrient-rich feces and pseudofeces results in increased biomass of benthic macroinvertebrates (Stewart and Haynes 1994; Ricciardi et al. 1997; Thayer et al. 1997; Stewart et al. 1998a, 1998b).

Zooplankton dynamics can be affected both directly and indirectly by zebra mussels. Microzooplankton are directly consumed by zebra mussels, resulting in decreased biomass of this trophic level (Pace et al. 1998). Most macrozooplankton are too large to be consumed by zebra mussels (MacIsaac et al. 1991; MacIsaac et al. 1995), but zebra mussels indirectly affect their abundance (Bridgeman et al. 1995; Thorp and Casper 2003) and fecundity (Horgan and Mills 1999) by reducing food availability. Eventually, decreased macrozooplankton abundance affects species in higher trophic levels in the food web, including fish (Rutherford et al. 1999).

Studies of the effects of zebra mussels on fish growth in lakes and rivers are few and contradictory. Fish growth in the presence of zebra mussels decreased, increased, or remained the same for species in different life stages and ecosystems (Graham et al. 1999; Mercer et al. 1999; Trometer and Busch 1999; Mayer et al. 2000; Pothoven et al. 2001; Strayer et al. 2004). This variation most likely results from many indirect pathways through which fish can be affected by zebra mussels (Strayer et al. 2004).

Zebra mussels have fundamentally transformed freshwater food webs and the biogeochemistry of lakes and rivers since their invasion in the US (Strayer 2009). The biomass of lower trophic levels (algae, microzooplankton) has suffered greatly due to predation, yet others (macroinvertebrates) have benefited due to increased nutrient availability and habitat complexity. The impacts of zebra mussels on higher trophic levels (macrozooplankton, fish) are less well understood, and may be influenced by many indirect pathways. Although the zebra mussel invasion has been well studied for the last 20 years, we still have much to learn about the ecological and economic impacts of zebra mussels, especially on higher trophic levels (Strayer 2009).

Oceans and estuaries—The comb jelly, *Mnemiopsis leidyi*, has had a dramatic impact on the trophic dynamics of marine systems. It is native to estuaries along the western Atlantic coast from the northern US to the Valdés peninsula in Argentina. Likely introduced from ballast water exchange in the Black Sea in 1982, the comb jelly has since spread through eastern, central, and northern European waters (Bilio and Niermann 2004; Hansson 2006; Kube et al. 2007). The comb jelly is carnivorous and feeds on crustacean zooplankton, other comb jellies, fish eggs, and larval fish (Purcell et al. 2001). In 1989, comb jelly densities reached 300 individuals m^{-3} in the Black Sea (Vinogradov et al. 1989). That same year, zooplankton biomass decreased dramatically, zooplankton species composition changed, and the commercially important anchovy (*Engraulis encrasicholus*) fishery crashed (Kideys 1994; Vinogradov et al. 1995; Shiganova 1998). The crash of the fishery most likely resulted from multiple factors, including comb jelly predation on early life stages of anchovies, resource competition, and overfishing (Bilio and Niermann 2004). The anchovy fishery in the Black Sea has since rebounded after the 1997 invasion of a predator of the comb jelly (*Beroe ovata* or *Beroe cucumis*), which is also native to the northwestern Atlantic (Kideys 2002). It is still unknown how the comb jelly will affect newly invaded regions, such as the Baltic Sea (Hansson 2006; Kube et al. 2007). However, it is clear that the comb jelly has the potential to greatly alter the biomass and species composition of zooplankton and fishes in marine systems, resulting in trophic cascades and major changes to food web dynamics.

The introduction of invasive species alters the trophic dynamics of aquatic ecosystems. Once established, invaders prey on native species or outcompete with them for resources, altering biomass, species composition, and species interac-

tions, and ultimately ecosystem structure and function. Species invasions continue to occur despite efforts by the scientific community to educate the public and politicians about their devastating effects. Until we can curtail invasions, aquatic ecosystems will remain at risk.

Acidification

The acidification of aquatic ecosystems is now a threat across all types of environments, from fresh waters to the open ocean. However, the mechanisms by which acidification is occurring in these ecosystems are distinctly different, as are the threats to the ecosystems and their resident organisms. As such, examining the effects of acidification across ecosystems is somewhat inappropriate. However, ocean acidification is becoming one of the clearest future threats to marine ecosystems worldwide, with potentially major implications, and to ignore its potential impact on the trophic structure in marine waters would be a mistake.

Ocean acidification is caused by the increase in atmospheric CO_2 resulting from the burning of fossil fuels. By contrast, in fresh waters the major cause of acidification is acid rain (or other precipitation). Acid rain is caused by nitrogen and sulfur oxides in fossil-fuel emissions that acidify the precipitation, which in turn directly acidifies waters or interacts with regional- and ecosystem-specific factors such as water and soil chemistry to ultimately acidify the waters. In freshwater lakes, rivers, and streams, acidification is not a new threat (Likens and Bormann 1974); however, substantial and successful measures have reduced the culprit chemicals in emissions such that acid rain is much less of a concern today than it was in the past. Despite the reduced occurrence of harmful acid rain, ecosystems that have been affected in the past often exhibit lengthy and incomplete recoveries (Keller et al. 1999). Because the effects of acid rain include the reduction in the survival and reproduction of certain species, and even their complete elimination, there are many cases of disruptions to the trophic structure of freshwaters (Schindler 1988). The mechanism by which higher acidity affects the organisms is usually through disruption to acid-base and water-salt balances or toxic aluminum levels that originate from the acid-induced release of aluminum by soils. Physiological effects on organisms are not surprising considering the pH of acidified freshwaters can approach 5.0.

In stark contrast to freshwaters, oceanic waters have a high buffering capacity and a resulting stable pH of about 8.1 (in fresh waters, pH levels can occur well below and above the more common range of 6 to 8). Although disruptions to acid-base regulation of marine organisms may be a substantial effect of acidification (Fabry et al. 2008), much more concern is given to the potential effects of acidification on calcifying organisms. These include corals, but also important planktonic species of pteropods, coccolithophores, and foraminifera, in addition to many benthic invertebrates (mollusks and echinoderms) and other organisms (fish, squid, zoo-

plankton) that form nonskeletal calcium carbonate structures for balance and hearing (Fabry et al. 2008).

As aqueous CO_2 increases following the increase in atmospheric CO_2 concentrations, the availability of CO_3^{2-} used for calcium carbonate secretion is reduced. A reduced availability of CO_3^{2-} will lower the saturation state of calcium carbonate, yielding slower rates of accretion or the complete inability for calcification. If waters become undersaturated with respect to the specific forms of calcium carbonate (the form aragonite would be first affected), dissolution of existing calcium carbonate structures could occur.

The well-studied chemical processes involved with ocean acidification and the resulting potential effects on certain organisms (e.g., Orr et al. 2005; Kleypas et al. 2006; Fabry et al. 2008) are beyond the scope of our synthesis. However, the general implications that ocean acidification may have for altering marine food webs are worthy of discussion. Such alterations are inherently speculative because the direct effects on vulnerable species have yet to occur, and how these changes may indirectly affect trophic interactions in their ecosystems is even more speculative. There are some clear likely effects if ocean acidification plays out as predicted. Among the most vulnerable taxa are the pteropods of higher latitudes, especially those in the Southern Ocean. These waters are predicted to be undersaturated with respect to aragonite, and these pteropods, due to their high abundance in a low-diversity system, are extremely important components of planktonic food webs in these waters (Orr et al. 2005).

Another main area of concern involves reef-building corals and their ability to grow at rates fast enough for coral reef ecosystems to continue to exist and function (Kleypas et al. 2006). Clearly, any major disruption to corals' ability to grow could eliminate coral reef ecosystems altogether, with major implications for food web structure in and near these systems. A decrease in growth rate or disease resistance, or disruptions to the delicate symbiotic relationship with zooxanthellae, could reduce the ability for corals to outcompete macroalgae, leading to the increased prevalence of regime shifts on coral reefs noted previously in the overharvesting section. Adding to the threat is evidence that acidification can exert physiological stress on the symbiosis of zooxanthellae with corals and crustose coralline algae, completely separate from its effects on the calcification process (Anthony et al. 2008).

A major focus of future marine research will undoubtedly be related to the far-reaching effects of ocean acidification. Although we are only in the beginning stages of discovering and predicting the effects of ocean acidification, it is obvious that the trophic structure within marine ecosystems is largely at the heart of why this is one of greatest threats to the world's oceans.

Summary

Although the public, policy, and scientific communities still debate the specific mechanisms and consequences of cli-

mate and other anthropogenic environmental changes, the fact that our actions are threatening aquatic ecosystems is undeniable. The purpose of this chapter was to examine the potential and currently observed effects of several topical ecosystem threats to aquatic environments. We employed a comparative approach to review the vulnerability of aquatic systems to global threats associated with anthropogenic activities. Our use of trophic dynamics as a common, albeit qualitative, metric proved to be insightful, illustrating that the flow of energy through aquatic food webs will be (or already has been) altered by the introduction of invasive species, land use change, and increasing global temperatures, nutrient loading, exposure to UV radiation, overharvesting, and acidification.

The response of trophic dynamics to anthropogenic influence was often similar across oceans, estuaries, lakes, and rivers. This similarity was somewhat surprising given the differences in both the level of concern expressed by scientists and the predicted variability in environmental-specific responses. Some of the responses were so similar that the different environments could be combined in our analysis. For example, all environments were lumped together in the discussion of the effects of acidification on trophic dynamics. Because the trophic interactions of an ecosystem are at the root of its function and structure, this suggests that examining trophic dynamics can be an excellent method for evaluating the response of aquatic environments to anthropogenic changes. However, threats need to be evaluated on an individual basis, and further research is necessary to determine the frequency of observed responses to global threats.

It should be noted that we considered the effect of each threat on trophic dynamics independently, yet a synergistic analysis would be necessary to truly evaluate the utility of trophic dynamics. For example, Kirby and Beaugrand (2009) have suggested that trophic dynamics in the North Sea can be influenced by both increasing sea surface temperature and overfishing. This type of multifaceted approach was beyond the scope of this chapter but we believe it is the next logical step. Finally, there are other environmental threats that were not addressed in this chapter, including sedimentation, pollution, and sea level rise.

Ultimately, our goal was to assess global threats using a common metric. If future analyses validate the use of trophic dynamics as this metric, it is our hope that it can be used by scientists and politicians to mitigate the effects of human actions. We believe (and hope) that a global perspective is a necessary step in developing effective mitigation strategies against future changes.

Glossary

Artisanal harvesting. Small-scale, locally-based harvesting that utilizes traditional techniques.
Dead zones. Low-oxygen (< 2 mL L^{-1}) areas of the Earth's oceans.
Eutrophication. An increase in the concentration of chemical nutrients (nitrogen and/or phosphorous) in an aquatic ecosystem.

Food chain efficiency. The proportion of energy fixed by primary producers transferred to the top trophic level
Invasive species. Species that have been introduced outside their native range through human activity.
Land use change (or land cover change). The anthropogenic altering or modification of terrestrial systems to suit different human needs.
Nutrient loading. The quantity of nutrients entering an aquatic system over a given period.
Ocean acidification. The term used to describe the decreasing pH of the Earth's oceans.
Overharvesting (also called overfishing). The harvesting of species at levels beyond what is sustainable.
Q10. The factor by which a physiological rate changes with a 10°C increase in temperature.
Senescencing. Biological aging, including programmed cell death (PCD).
Trophic dynamics. The flow of nutrients and energy within an ecosystem, predominantly through food webs.
Trophodynamics. See trophic dynamics.
Ultraviolet (UV) radiation. Electromagnetic radiation that has a wavelength shorter than light in the visible spectrum.

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