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The North Atlantic Ecosystem, from Plankton to Whales

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Abstract

Compared with terrestrial ecosystems, marine ecosystems have a higher proportion of heterotrophic biomass. Building from this observation, we define the North Atlantic biome as the region where the large, lipid-rich copepod *Calanus finmarchicus* is the dominant mesozooplankton species. This species is superbly adapted to take advantage of the intense pulse of productivity associated with the North Atlantic spring bloom. Most of the characteristic North Atlantic species, including cod, herring, and right whales, rely on *C. finmarchicus* either directly or indirectly. The notion of a biome rests inherently on an assumption of stability, yet conditions in the North Atlantic are anything but stable. Humans have reduced the abundance of many fish and whales (though some recovery is underway). Humans are also introducing physical and chemical trends associated with global climate change. Thus, the future of the North Atlantic depends on the biome's newest species, *Homo sapiens*.

INTRODUCTION

When we were asked to write a review on the North Atlantic ecosystem, we thought, "Really, another paper on the North Atlantic?" After all, the North Atlantic is ringed by prestigious marine research institutions that pioneered the scientific study of the ocean. Major concepts like Sverdrup's critical depth theory (Sverdrup 1953), Riley's early ecosystem models (Riley 1946), and Cushing's match–mismatch hypothesis to explain variability in fish recruitment (Cushing 1990) were all developed with the North Atlantic in mind. Thus, our primary challenge is how to provide a novel perspective on an ecosystem that has been studied for so long.

Rather than trying to be encyclopedic, we decided to provide our perspective on the North Atlantic ecosystem. This perspective is informed (some might say biased) by our work on the Gulf of Maine, and we draw heavily on examples from this ecosystem. We both share an affinity for copepods and right whales, and these animals are featured prominently at the expense of many worthwhile creatures (see the sidebar titled Hey, Where'd My Favorite Species Go?).

In this review, we first explain the concept of a biome and then describe the general features of the well-defined North Atlantic biome. We then consider how these features change in the important shelf regions around the North Atlantic. Finally, we consider how human exploitation and climate change have and will alter the biome. Our aim with this ecosystem-focused overview of the region is to tie together the most prominent physical, chemical, and biological aspects of the system and highlight the impacts of natural variability, direct human activity (i.e., fishing), and indirect human influence (i.e., global warming).

THE BIOME CONCEPT

To begin, we need to define what we mean by the North Atlantic. For this article, we are specifically describing the region of the Atlantic north of the Gulf Stream/North Atlantic Current and south of the polar front (**Figure 1**). This region includes shelf regions such as the Gulf of Maine and Newfoundland shelf in the west and the North Sea and Norwegian shelf in the east. It also includes substantial open-ocean areas. While physical features like fronts and currents are a natural way of

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HEY, WHERE'D MY FAVORITE SPECIES GO?

There are many important and interesting groups of organisms that are not directly included in our review of the North Atlantic biome. Each could make for a central story line, comparable to how we have built our discussion around *Calanus* and right whales. Here are a few we considered:

- *Meganyctiphanes norvegica*, an omnivorous euphausiid species with a preference for other zooplankton, is the dominant euphausiid in the North Atlantic biome (Cabrol et al. 2019) and an important prey for fish, whales, and birds.
- Myctophid fishes are ubiquitous in the world's oceans and serve as an energetic link between zooplankton and upper trophic levels (Catul et al. 2011, Hudson et al. 2014).
- Seabirds, such as puffins, terns, and petrels (e.g., Montevecchi et al. 1992, Ronconi et al. 2010), are highly visible members of the North Atlantic shelf biome.
- Atlantic salmon (*Salmo salar*) would be a compelling alternative to right whales as a flagship species. They spawn on both sides of the Atlantic and migrate into the Labrador and Greenland Seas to feed on capelin. As with right whales, humans have depleted their populations, and they are now being disrupted by climate change (Mills et al. 2013b, Parrish et al. 1998).
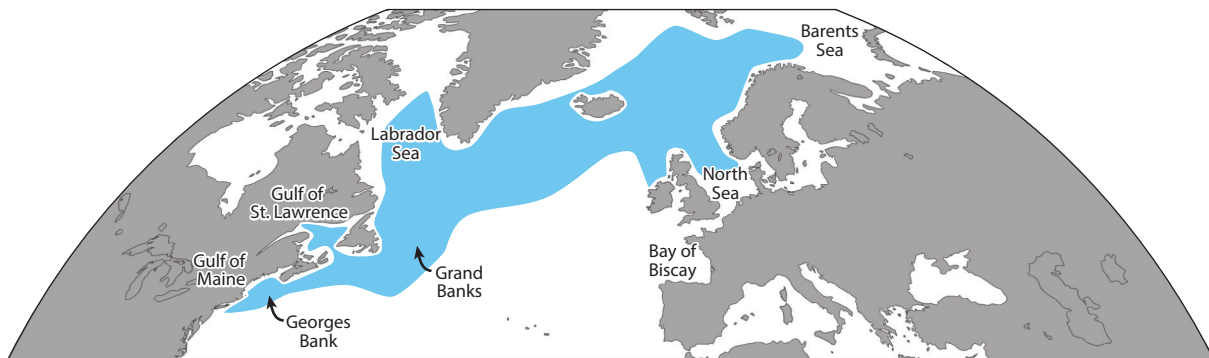
Figure 1

The geography of the North Atlantic. The blue region is the approximate location of the North Atlantic biome, defined using the distribution of *Calanus finmarchicus* (as in Record et al. 2018). Geographic regions mentioned in the text are labeled.

defining ocean regions, especially in an era with easily accessible sea surface temperature data, it is not the only way. Longhurst (1998) divided this region into five biogeochemical provinces based on annual chlorophyll cycles, all of which feature an intense spring phytoplankton bloom.

Longhurst's logic aligns with the biome concept. Terrestrial ecologists developed this concept to define distinct ecological communities resulting from succession and climate factors (Carpenter 1939, Clements 1916). The idea is that you should be able to teleport an ecologist to any part of the globe, and they should be able to look at the perennial plants around them and infer properties of the ecosystem. For example, if our teleporting ecologist sees a forest of coniferous trees, they know they are in an environment that has high precipitation and strong seasonality (e.g., Prentice et al. 1992). They can also infer properties of the animals (e.g., Fierer et al. 2009) and even the biogeochemical cycles (e.g., Luyssaert et al. 2007). The foundational vegetation of a terrestrial ecosystem serves as an energy bank that stores and shuttles carbon from one growing season to the next. Defining marine biomes based on primary producers is less clear cut. Phytoplankton communities undergo annual succession, and their total biomass varies by several orders of magnitude throughout the year. Unlike in terrestrial systems, phytoplankton stocks do not accumulate carbon on annual scales. Instead, they serve as a conduit, transferring carbon to higher trophic levels or out of the mixed layer when they sink.

As Margalef (1978) noted, one of the differences between the land and the ocean is that ocean ecosystems have more biomass stored in heterotrophs. We propose that these higher trophic levels, specifically the Metazoa, provide a more parsimonious definition of the North Atlantic biome. Specifically, we define the North Atlantic biome as the region where *Calanus finmarchicus* is the dominant mesozooplankton species (blue area in **Figure 1**). This gets closer to the terrestrial-based definition of the biome in that it is based on members of the community that are present throughout the year and that carry energy from one seasonal cycle to the next.

The biome concept envisions an ecosystem with properties that are stable when integrated over several years. Because real ecosystems vary from year to year and populations are subject to disturbance, the ecosystem we describe here is an elusive ideal. Perhaps more importantly, given the long history of industrialized fishing and other human impacts in the North Atlantic, the current ecosystem may differ in significant ways from the idealized state. We begin the review by thinking of the ecosystem without large impacts from humans but then take a broader view that includes people.

THE NORTH ATLANTIC REFERENCE BIOME

Imagine a patch of open ocean in the North Atlantic, off of the continental shelf. This patch of ocean will be subject to a repeating annual cycle of heating and cooling and wind-driven mixing (Lindemann & St. John 2014). We will assume lateral fluxes that balance the heat and nutrient budgets. This view of the ocean is similar to that represented in Evans & Parslow's (1985) idealized model of phytoplankton dynamics.

It is conventional to begin discussions of the North Atlantic ecosystem by considering winter conditions and then the physical processes that produce the spring bloom through nitrate-fueled new productivity (e.g., Sverdrup 1953, Taylor et al. 1993). Here, however, we begin our discussion in the summer because the physical, biogeochemical, and plankton community conditions are close to steady state (Evans & Parslow 1985). In this idealized steady state, the water column is strongly thermally stratified. Nitrate concentrations in the surface layer are negligible, phytoplankton abundance is very low, and primary productivity is fueled by recycled ammonia and kept in check by microzooplankton grazing (Banse 1992) and viral infection (Suttle 2005). An essential aspect of the equilibrium community is that species that become abundant create a feeding opportunity for a larger predator. We thus expect the size spectrum to be smooth, as any bumps would represent a niche that would presumably be filled if given enough time. This smooth size spectrum is an indicator of high diversity that characterizes the phytoplankton and mesozooplankton communities during this period (Beaugrand et al. 2001, Record et al. 2010). During the summer equilibrium period, there is efficient partitioning of energy, and, as is typical of systems characterized by recycled production, carbon quickly moves up the food chain (**Figure 2**) or is respired after conversion to an organic form. The stable water column also allows for vertical zonation, and this zonation is one of the reasons Hutchinson (1961) cited to explain the high diversity in phytoplankton in the apparently homogeneous ocean, i.e., the "paradox of the plankton."

In the North Atlantic, there is a second near-equilibrium community that occurs during the dark, cold winter. Phytoplankton concentrations are low during this period (**Figure 2**). The classic explanation is that phytoplankton are mixed below the critical depth, leading to light limitation (Sverdrup 1953). While this may be true on average, productivity can still occur if conditions allow phytoplankton to remain near the surface. During quiescent periods, phytoplankton growth can outpace sinking, leading to a bloom (Townsend et al. 1992). The larger volume of water in the mixed layer also lowers encounter rates between microzooplankton predators and their phytoplankton prey (Behrenfeld & Boss 2014, Lindemann & St. John 2014). Phytoplankton and mesozooplankton diversity at this time is relatively low (Beaugrand et al. 2001, Record et al. 2010).

The summer and winter equilibria exist because physical conditions, especially temperature and mixed-layer depths, are relatively constant, allowing loss terms (grazing, respiration, and cell sinking) to keep pace with primary productivity. This means that the rapid changes in the physical environment that occur in the autumn and spring disrupt the equilibria (Behrenfeld et al. 2013, Evans & Parslow 1985). Cooling and wind-driven mixing during the autumn begin the process of breaking down water column stratification, bringing nitrate into the euphotic zone and decoupling primary producers from the grazer community, which breaks the oligotrophic summer equilibrium. In most regions, phytoplankton growth is able to outpace grazing, which can lead to a phytoplankton bloom (Behrenfeld & Boss 2014, Lindemann & St. John 2014). Secondary productivity also increases, and many of the species from the high-diversity summer period proliferate during the autumn (Pershing et al. 2005).

In the spring, shoaling of the pycnocline along with increasing light levels allows phytoplankton abundance to increase rapidly. This is the famed North Atlantic spring bloom, which is fueled by nitrate brought into the euphotic zone by mixing during the winter (McGillicuddy et al. 1995)
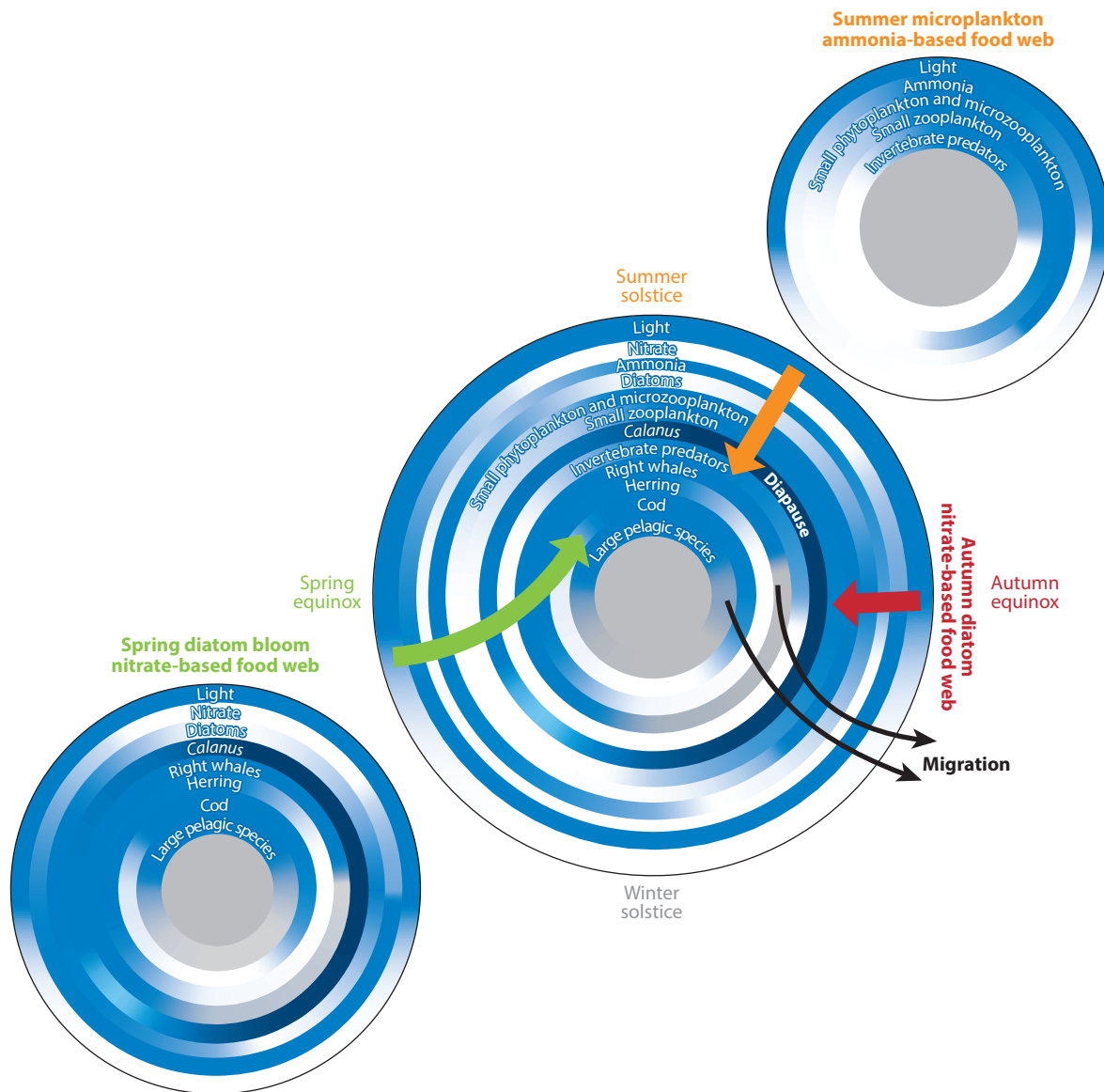
Figure 2

The seasonal flow of carbon through the North Atlantic biome. The central circle represents the food web during an average year, progressing through the seasons in a clockwise direction. Each ring indicates one ecosystem parameter (light and nutrients) or taxonomic group. The darker the color is, the more light, nutrients, or carbon is in that group at that time of year. The relative amounts are denoted by the colors, from white to blue. Navy blue highlights the high levels of carbon stored at depth in diapausing *Calanus finmarchicus* (denoted here as *Calanus*). Gray indicates the removal of carbon from the system by migratory species. Note that *Calanus* is the only group that maintains large amounts of carbon throughout the seasons, transferring fixed carbon from one year to the next and defining the North Atlantic biome. The large arrows in the central circle indicate the flow of carbon originating with new production, from the spring diatom bloom during disequilibrium (*green arrow*), recycled production produced during the summer equilibrium period of stratification (*orange arrow*), autumn new production that results from disruption of the summer equilibrium (*red arrow*), and migration (*black arrows*). The smaller circles decompose the biome into a spring nitrate-based food web (*bottom left*) and a summer ammonia-based food web (*upper right*).

(**Figure 2**). Unlike in the autumn, diversity during the spring bloom is very low. The bloom is typically dominated by a small number of large diatom species (Daniels et al. 2015, Margalef 1978). The large size and the fact that phytoplankton growth outpaces zooplankton grazing means that a significant fraction of the phytoplankton production sinks out of the mixed layer, leading to carbon export (Alkire et al. 2014, Ducklow et al. 2001).

The mesozooplankton diversity in the spring is also very low and is dominated by *Calanus finmarchicus* (hereafter generally referred to simply as *Calanus*). This species is superbly adapted to the intense seasonal cycle in the North Atlantic. A cornerstone of its ability to thrive in the North Atlantic and to take advantage of the explosive productivity of the spring bloom is its capacity for seasonal dormancy, known as diapause (reviewed in Johnson et al. 2007). During the autumn and winter period, most *Calanus* biomass is in a single life stage—the fifth copepodid stage (C5), which occurs right before maturation into an adult. In the open ocean, diapausing *Calanus* is found at great depths—from approximately 600 m down to 1,400–1,800 m (Gislason 2018, Heath et al. 2000b). *Calanus* begins to emerge from diapause prior to the spring bloom. The newly minted adults are able to quickly channel the productivity from the spring bloom into large numbers of eggs. Production rates of 45 *Calanus* eggs per individual per day have been observed in the field (Ohman & Runge 1994), and rates of 73 eggs per individual per day have been measured in the laboratory (Campbell et al. 2001). A newborn *Calanus* reaches maturity in 20–60 days, depending on temperature (Campbell et al. 2001). The generation born from these eggs produced in spring is typically the peak *Calanus* abundance during the year (Heath et al. 2000a, Pershing et al. 2005). Because temperature is increasing during the spring, stage durations decrease, allowing individuals spawned late in the bloom to catch up to those born earlier in the bloom, accentuating the peak in abundance (Pershing et al. 2009). A portion of this generation completes the maturation process, producing a second generation. However, many will pause development and enter diapause (Ji 2011).

During diapause, *Calanus*'s metabolic rate is suppressed (Jónasdóttir 1999) and then further reduced by the cold temperatures at depth (Saumweber & Durbin 2006). However, even with these reduced rates, *Calanus* must accumulate a substantial energy reserve in order to survive for several months without feeding. This species stores energy in the form of lipids, specifically wax esters, in an oil sac in its prosome (Miller et al. 2000).

The diapausing strategy requires specific oceanographic conditions. It is easy to see why a high abundance of diatoms or other phytoplankton is a prerequisite, allowing *Calanus* to accumulate lipids. But large body size is a more subtle and dynamic part of the diapause story. Copepod body size is controlled by two factors: the accumulation of biomass through feeding and the rate at which an individual transitions between developmental stages (Maps et al. 2012). Both growth and development depend on food quantity and temperature, but growth is more sensitive to food, and development is more sensitive to temperature (Campbell et al. 2001). This means that the same species of copepod grown in warm water will mature more quickly but at a smaller terminal body size. Thus, cold water is just as much of a requirement for diapause as food availability. In fact, a simple model using temperature and chlorophyll is able to reproduce the map of where the lipid-diapause strategy occurs (Ji 2011, Record et al. 2018).

The high productivity and cool temperatures in the spring in the North Atlantic allow *Calanus* to employ diapause, but this does not explain why it uses this strategy. After all, while in diapause, *Calanus* is not reproducing, so this strategy must increase fitness in other ways. It is tempting to think of diapause as an adaptation that simply allows *Calanus* to avoid the summer oligotrophic period, but its importance is twofold. Increases in copepod predators such as euphausiids, chaetognaths, ctenophores, and fish during the late spring and summer create a dangerous environment for copepods (Ji 2011, Kaartvedt 2000). The development of this predator community is part of

the progress toward the summer equilibrium. Life-history theory suggests that, to be successful in a high-mortality environment, a species should mature at a younger age (Kiørboe & Sabatini 1995). In order to be large, *Calanus* must develop slowly (Maps et al. 2014), which means that it must have a longer generation time than smaller copepods. Thus, the fitness of a *Calanus*-sized copepod decreases rapidly as predator abundance increases. Altogether, these factors create a positive evolutionary feedback. In order to employ diapause, *Calanus* must be large, but in order to be large, *Calanus* must undergo diapause. This means that there are two viable copepod strategies for the North Atlantic: be large and employ diapause or be small and stay active.

The biomass of diapausing *Calanus* is one of the main ways that carbon from the spring bloom is stored and transferred from one year to the next (**Figure 2**). Because of its large size, *Calanus* produces large fecal pellets that sink relatively rapidly, especially when ballasted by diatom frustules (Bienfang 1980, Komar et al. 1981), which contribute to the export of carbon from the mixed layer (Brun et al. 2019, Stamieszkin et al. 2015). Diel vertical migration by *Calanus* and other large mesozooplankton and micronekton further contributes to export of carbon (through respiration and defecation at depth) and nitrogen (through excretion) (Steinberg et al. 2000).

The presence of large, oily copepods is a good sign that you are in a subpolar biome, just as oak and maple trees tell you that you are in a temperate forest. In the North Pacific, *Neocalanus cristatus*, *Neocalanus plumchrus*, and *Neocalanus flemingeri* fill this role, while it is filled in South Atlantic African upwelling regions by *Calanoides carinatus* (Auel et al. 2005, Verheye et al. 1991). If the large diapausing copepod happens to be *Calanus finmarchicus*, then you are in the North Atlantic biome.

THE NORTH ATLANTIC SHELF REFERENCE BIOME

While oceanographers might think of *Calanus finmarchicus* as the species that defines the North Atlantic biome, if you were to ask people living around its perimeter, they would probably name one of the iconic fish species, like Atlantic herring (*Clupea harengus*) or Atlantic cod (*Gadus morhua*). The presence of these species, as well as seasonal predators like right whales (*Eubalaena glacialis*), humpback whales (*Megaptera novaeangliae*), and bluefin tuna (*Thunnus thynnus*), is one main difference between the biome on the continental shelves and the open ocean.

Physical processes like fronts, internal waves, and tidal mixing on the continental shelf bring nutrients into the euphotic zone, leading to enhanced primary production in the shelf biome (Franks & Chen 2001, Longhurst 1998). While the enhanced production is necessary, it is not sufficient on its own to allow for the survival of large fish and whales. Rather, the physics directly contributes to the success of large predators in the shelf biome.

To see the role that physics plays in the shelf biome, let us consider the world from the point of view of the northern right whale (*Eubalaena glacialis*) (see the sidebar titled North Atlantic Right Whales as a Flagship Species of the North Atlantic Biome). These whales, which can weigh more than 30 tons, feed almost exclusively on lipid-rich C5 and adult *Calanus*. Prior to the start of commercial whaling, they were found on both sides of the Atlantic (Hacquebord 1999), but now they are found only in the west. In the Gulf of Maine, the primary feeding ground for the remnant population, the average concentration of C5 *Calanus* during the early summer is 25 individuals per cubic meter (Pershing et al. 2005)—higher than the average concentration for the North Atlantic (Helaouet & Beaugrand 2007) but not enough for a right whale. Right whales require an estimated 1.28×10^8 *Calanus* per day, which they acquire primarily from April to October (Kenney et al. 1986). Assuming a mouth gape of 1 m^2, a right whale must cover 5,225 km each day to meet its nutritional goals, which would require swimming at a sustained speed of 218 km per hour.

NORTH ATLANTIC RIGHT WHALES AS A FLAGSHIP SPECIES OF THE NORTH ATLANTIC BIOME

We propose the North Atlantic right whale as a flagship species for the North Atlantic biome. While the conservation utility of flagship species is debatable (Andelman & Fagan 2000, Caro & O'Doherty 1999), the right whale captures many of the defining characteristics of the North Atlantic ecosystem, including a reliance on *Calanus*, a long history of human impacts, and the emerging challenges of climate change. It is easy to dismiss right whales as esoteric animals, but this view is a symptom of shifting-baseline syndrome (Pauly 1995). Like descriptions of massive schools of old cod from 400 years ago or the high catch rates of giant pelagic fish in 1950s (Fagan 2008, Myers & Worm 2003), the notion of abundant right whales on both sides of the Atlantic is hard to fathom. Yet these amazingly efficient hunters of *Calanus* were once an important component of the North Atlantic shelf biome and likely had a significant influence on upper-ocean biogeochemistry (Pershing et al. 2010, Roman et al. 2016). This functionality is now effectively gone. The trajectory of the right whale population thus reflects the interplay among human activity, climate change, and the biota of the North Atlantic biome.

Rather than swimming at race-car-like speeds, right whales swim at whale-like speeds while searching for superdense concentrations of *Calanus*. Concentrations of up to 32,000 individuals per cubic meter have been measured in the path of a feeding right whale (Mayo & Marx 1990). Tidal mixing fronts, thermal fronts, freshwater plumes, and internal waves all have the potential to concentrate plankton by several orders of magnitude (Stevick et al. 2008, Wishner et al. 1995). These features are essential for transferring the carbon in *Calanus* and other zooplankton to fish and whales.

As interesting as right whales are, they are not the most important vertebrate predator of *Calanus* in the North Atlantic shelf biome. That honor is shared by three small pelagic fish: Atlantic herring (*Clupea harengus*), sand lance (*Ammodytes* spp.), and capelin (*Mallotus villosus*) (Pedersen & Fossheim 2008). These species vary in their habitat preferences, but all three have a high lipid content that comes directly from *Calanus* (Dalpadado et al. 2000, Danielsen et al. 2016, O'Driscoll et al. 2001). They are in turn prey for larger fish, including mackerel, cod, and tuna as well as many species of seabird and whale (Link 2002, Wassmann et al. 2006). The food webs in these ecosystems have a characteristic wasp-waist structure, with reduced diversity at middle trophic levels and higher diversity at upper trophic levels (Bakun 2006) (**Figure 3**).

Atlantic cod (*Gadus morhua*) is the most iconic North Atlantic fish species. Its distribution maps almost perfectly onto that of *Calanus* (Beaugrand & Kirby 2010, Record et al. 2018). Depending on the location, cod spawn in the winter or spring, which allows their planktonic larvae to feed on the early life stages of *Calanus* produced during the spring bloom. A sustained period of elevated *Calanus* abundance from the mid-1960s through the mid-1980s led to an increase in cod in the North Sea (Beaugrand et al. 2003). Adult cod also depend on lipid-rich forage fish to support reproduction, adding an indirect dependence on *Calanus* (Sherwood et al. 2007).

All of the vertebrates in the North Atlantic must grapple with the fact that food resources are strongly seasonal. Like *Calanus*, most have evolved some ability to store energy reserves to help them through the low-productivity period. Herring and capelin have very high lipid concentrations in their tissues. Whales have thick layers of blubber. Cod and the other gadoid fish have large, oily livers. As with *Calanus*, body size plays an important role in these overwintering strategies. Larger species largely avoid the cold period altogether by migrating to temperate or subtropical regions. Avoiding the cold period is especially important for their offspring, whose high surface-area-to-volume ratio makes them more sensitive to the cold (Clapham 2001), although keeping
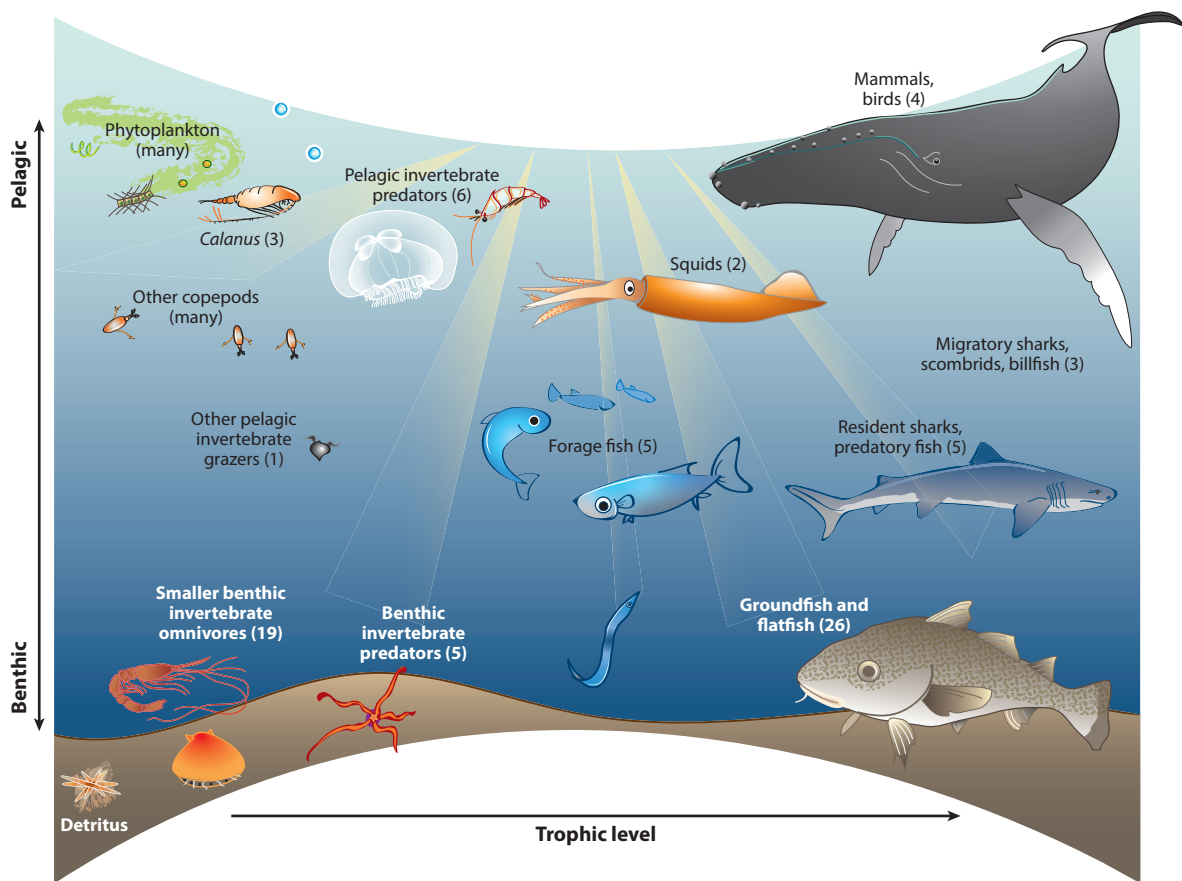
Figure 3

The characteristic food web of the North Atlantic shelf biome. The horizontal axis represents trophic level, increasing from left to right, and the vertical axis represents benthic (*bottom*) to pelagic (*top*) communities. The numbers in parentheses represent the number of taxa or species, also grouped by approximate trophic level and vertical habitat (modified from Link 2002). In this figure, *Calanus* is primarily *C. finmarchicus* but also includes *C. hyperboreus* and *C. glacialis*. Note the higher total number of species at the lower (*left*) and upper (*right*) ends of the food web, with relatively few species in the middle—a classic wasp-waist system. Original artwork by K. Stamieszkin.

vulnerable offspring away from high-latitude predators may also be a factor (Corkeron & Connor 1999). Thus, all of these migratory species spawn during the winter in warmer southern waters, temporarily removing their biomass from the North Atlantic biome (**Figure 2**).

Fish, whales, and other nonmicroscopic fauna also participate in the cycling of carbon and nutrients in the North Atlantic. They accumulate carbon and nitrogen through feeding and channel these elements to growth and reproduction. Because of their large size and daily and seasonal movements, they can transfer material through space and time. For example, Roman & McCarthy (2010) described a whale pump in which humpback whales feeding on herring and sand lance release nitrogen into the euphotic zone through their feces. The whale pump transfers nitrogen that has accumulated in the tissues of their prey into a dissolved form that is available to phytoplankton. This process becomes especially interesting when the whales feed on aggregations of spawning fish. In this case, the whales may be fertilizing the plankton community that the larval fish will use as their food. Along the Norwegian coast, spawning herring release eggs containing

considerable quantities of nitrogen into the environment, nitrogen that was acquired by feeding offshore (Varpe & Fiksen 2010). As the eggs are consumed or decomposed, a portion of the nitrogen will become available to phytoplankton. Long-distance seasonal migrations also transfer nitrogen from the North Atlantic shelf biome to tropical or subtropical regions (Roman et al. 2014). Finally, natural mortality among the vertebrates may contribute to carbon export. We calculated that preindustrial populations of sei, fin, blue, humpback, minke, and right whales in the North Atlantic (330,000 individuals) would have stored 75,000 tons of carbon in their tissues and exported 13,000 tons per year through sinking carcasses (data in Pershing et al. 2010).

The other important vertebrate in the North Atlantic biome is *Homo sapiens*, a large primate that uses sophisticated technology to transit and interact with the ecosystems in the North Atlantic, especially in the North Atlantic shelf biome (A.J. Pershing & K. Stamieszkin, personal observation). For most of the last 12,000 years, human influence was confined to a tiny band surrounding the North Atlantic basin. As we show in the next section, as human populations expanded and technology advanced, the influence of this species as both a predator and agent of disturbance expanded rapidly.

TRENDS IN THE NORTH ATLANTIC

The discussion above envisioned ecosystems with species that have adapted to stationary conditions (stable mean and variance over many generations) and have had enough time for population dynamics to adjust to these conditions. But conditions in the North Atlantic are no longer stationary—there are now strong trends in both ecological and physical conditions, all of which can be linked to the influence of humans.

Trends in Fishing and Whaling

After the retreat of the glaciers, humans established settlements along the North Atlantic coasts of North America and Europe. Many of these settlements relied on the productivity of the North Atlantic for food (Jackson et al. 2001). Communities in both Europe and North America ventured out in small boats to catch cod and other fish using hooks and lines. Limited numbers of humans and limited technology kept the impact of humans confined to the nearshore region; archaeological data show that there were no major trends in the coastal marine food web connected to overharvesting in the western part of the North Atlantic biome during this period (Lotze & Milewski 2004).

Human abundance and technological capacity then increased rapidly in Europe, putting expanding pressure on the North Atlantic ecosystem (Fagan 2008). While technology, including larger ships, was an important factor, the expansion of trade routes was the main reason impacts accelerated. By 1100, cod from Norway's Lofoten Islands were being exported via Bergen to markets across Europe (Fagan 2008). The expansion of commerce connected larger numbers of people to the coastal ecosystem. Rather than a few Norwegians catching cod for their own tables, people living next to abundant cod or herring resources were the conduit by which the entire European population was connected to the sea (Fagan 2008). The expansion of commercial fishing and whaling has been the most significant impact on the North Atlantic biome (especially the shelf biome) since the retreat of the glaciers.

Herring and cod have historically been the most important commercial species. These species could be caught in vast quantities and preserved by pickling or drying for transport to faraway markets, satisfying increasing demand for fish by devout Catholics (who were prohibited from eating other meat on Fridays and during other religious holidays) and inexpensive protein for Europe's growing militaries (Fagan 2008). Initially, these species were caught from small boats ranging

from shore using hooks and lines or small nets. Fishing technology advanced with other industrial developments. Motorized boats towing large trawl nets replaced wooden boats and handlines (Thurstan et al. 2010), which greatly increased the ability of humans to harvest fish and expanded fishing away from the coast. By 1980, herring were nearly extirpated on Georges Bank (Melvin & Stephenson 2007). In 1990, the northern cod stock off of Newfoundland collapsed due to both climate variability (cooling) and overfishing (Rose et al. 2000).

During the latter half of the twentieth century, the nations around the North Atlantic began deliberate efforts to reduce overfishing, though they have met with varying degrees of success (Dell'Apa et al. 2012, Salomon et al. 2014). Herring stocks were rebuilt on Georges Bank (Melvin & Stephenson 2007) and off Norway (Skagseth et al. 2015). Cod stocks in the North Sea have begun to recover (Brander 2018). In theory, modern fishery management based on scientific stock assessments and strict (and strictly enforced) catch limits should be able to bring fishing into balance with stock productivity. However, this theory assumes a stationary or slowly varying environment, an assumption that is no longer valid in the North Atlantic (Pershing et al. 2015).

The development of whaling paralleled the development of commercial fishing. During the Middle Ages, Basques developed commercial whaling, and *Eubalaena glacialis* became the right whale to hunt because of its coastal habitat preferences and the fact that it floats when killed. Commercial whaling expanded across the North Atlantic and eventually around the globe. By the early 1800s, right whales were already severely depleted in the North Atlantic. American whalers caught only 180 right whales in the North Atlantic during the entire nineteenth century; by contrast, they harvested 19,000 Pacific right whales (*Eubalaena japonica*) during the same period (Best 1987). Norwegians introduced the exploding harpoon in the 1870s, which, when coupled with fast ships, enabled whalers to hunt the faster and less buoyant rorqual whales, like blue whales (*Balaenoptera musculus*) and fin whales (*Balaenoptera physalus*) (Reeves & Smith 2006). By the mid-twentieth century, the population of large whales in the North Atlantic was reduced by an estimated 66–90%, with biomass reduced by 85% (Christensen 2006, Roman et al. 2014).

The decline of whale populations did not go unnoticed. Harvesting of right whales was banned in 1935, the United States ended its commercial whaling with the passage of the Marine Mammal Protection Act in 1972, and the International Whaling Commission banned commercial whaling in 1982. Though Iceland and Norway still have commercial hunts, populations of many species have been recovering. Humpback whales have done particularly well under these protections (Stevick et al. 2003). The main exception is the right whale. Its coastal distribution and feeding behavior expose this species to human-caused mortality from ship strikes and entanglement in the ropes used by lobster and crab fisheries (Knowlton et al. 2012, Parks et al. 2011).

Understanding the impact of commercial harvesting of fish and whales on the North Atlantic is surprisingly challenging. First, it is hard to quantify exactly how abundant these species were in the past. Historical records of harvests are incomplete, but they clearly show a dramatic decline in abundance. In the Gulf of Maine, annual harvests of cod from wooden ships exceeded 60,000 tons in the late 1800s (Alexander et al. 2009). By contrast, the spawning stock biomass of Gulf of Maine cod is now estimated to be less than 4,000 tons (NEFSC 2017). Jennings & Blanchard (2004) used metabolic theory to argue that North Sea fish biomass is less than 10% of what the ecosystem could theoretically produce. Reconstructions of whale populations based on reported catches estimate that the preindustrial population of humpback whales numbered around 16,000 individuals (Christensen 2006), but genetic estimates suggest the abundance could have been an order of magnitude higher (Ruegg et al. 2013). In the early 1980s there were only 7,000 humpbacks, but the current population likely exceeds 13,000 (Bettridge et al. 2015, Stevick et al. 2003). The right whale population in the western Atlantic may have numbered as many as

10,000 (Reeves et al. 2007), compared with the current abundance of 411 individuals (Pettis et al. 2018). In addition to smaller populations, we are also dealing with populations that are made up of smaller individuals, especially among commercial fish (Jackson et al. 2001, Jennings & Blanchard 2004). Added mortality from fishing reduces the abundance of older fish, an effect that is amplified by a bias toward catching larger individuals (Pauly et al. 1998). Finally, fishing creates selective pressure, and there is evidence that some fish species now mature earlier and have a smaller maximum body size because of that pressure (Heino et al. 2015).

While we might not know exactly how many whales or cod there were in the past, we do know that we are studying an ocean with far fewer of these animals. The most obvious consequence is that the populations are less resilient to both fishing and climate change (Le Bris et al. 2015) and are now more sensitive to interannual variability (Ottersen et al. 2006). Harvesting also reduced the impact of vertebrate populations on carbon and nutrient cycling (Pershing et al. 2010, Roman et al. 2014). In the North Atlantic, the capacity for lateral and vertical nutrient transfer by marine mammals has decreased by 86% and 72%, respectively (Doughty et al. 2016), and Varpe et al. (2005) hypothesized that the low abundance of Norwegian herring in the 1960s reduced the transfer of nutrients into coastal waters, leading to lower lobster abundance.

Climate Trends

In addition to the human-induced trend toward fewer large fish and whales, the North Atlantic is experiencing trends in temperature, water chemistry, and circulation associated with anthropogenic climate change. While warming, acidification, and deoxygenation are occurring globally, these factors are playing out in a distinctive way in the North Atlantic, owing to the region's unique role in the global climate system.

During winter, cold, dry continental air masses pass over the North Atlantic, leading to intense fluxes of heat out of the ocean. In the Labrador and Greenland Seas, the cooling can create very dense water that travels south in the deep ocean circulation (Schulze et al. 2016). This water is the descending limb of the Atlantic meridional overturning circulation (AMOC), a key feature of the global climate system (Rahmstorf et al. 2015). The strength of the AMOC depends on the interplay among surface cooling, the transport of high-salinity water from the south, and the supply of fresh water from Greenland and the Arctic. Sediment cores indicate that the AMOC has been getting steadily weaker since the early 1900s and is well below levels that have existed since the last ice age (Thibodeau et al. 2018). Most climate models project continued weakening of the AMOC, and the weakening is especially pronounced in a recent high-resolution projection (Saba et al. 2016).

Weakening of the AMOC leads to a distinct pattern of sea surface temperatures that is visible both in climate projections (Saba et al. 2016) and, perhaps more disturbingly, in recent observations (Caesar et al. 2018, Pershing et al. 2018). In the last 20 years, the periphery of the North Atlantic biome, notably the northwest Atlantic shelf and Barents Sea, has warmed at several times the global rate, while the center of the ecosystem has cooled (Caesar et al. 2018, Pershing et al. 2015) (**Figure 4a**). The cold-center/warm-edge pattern leads to distinct and contrasting trajectories for the ecosystems. As an indicator of the North Atlantic biome, we followed Record et al. (2018) and computed the probability of *Calanus finmarchicus* undergoing diapause under recent (2012–2016) temperature conditions using the Ji (2011) model. We contrasted the recent probabilities with those from 1998–2002. These calculations suggest that the North Atlantic biome has expanded northward in both the Labrador and Barents Seas (**Figure 4b**).

As indicated in **Figure 4**, the Barents Sea is now firmly part of the North Atlantic biome. Warm Atlantic water now penetrates farther into the Arctic (Årthun et al. 2018), and ecosystem
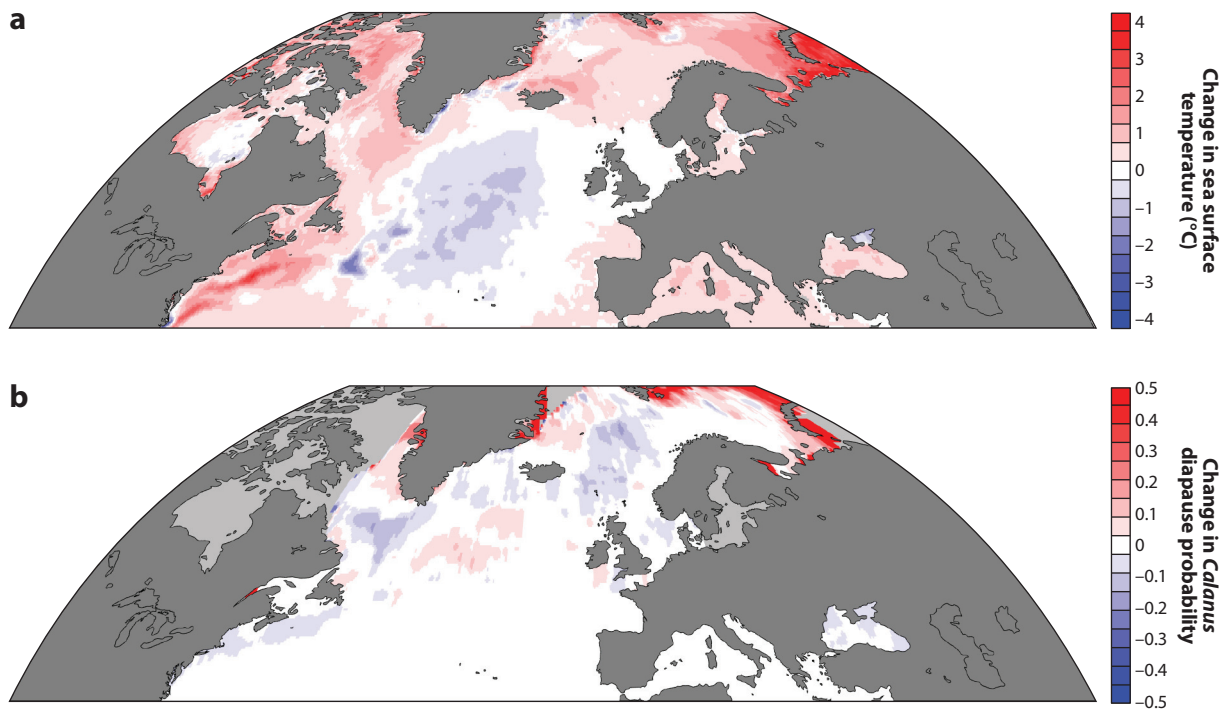
Figure 4

Recent changes in the North Atlantic. (*a*) Mean difference in monthly sea surface temperatures between 1998–2002 and 2012–2016. Red indicates where recent conditions are warmer. (*b*) Change in *Calanus finmarchicus* (denoted here as *Calanus*) diapause probability between the two periods using the Ji (2011) model (as in Record et al. 2018). Red indicates a higher fitness for the diapausing trait in the recent period and therefore higher potential fitness for *Calanus*. The code and data for this figure are available at **https://github.com/gulfofmaine/2019-Ann-Rev-North-Atlantic-Ecosystem**.

properties also reflect this change. *Calanus*, capelin, and cod have all expanded northward into the Barents Sea, while polar species like polar cod (*Boreogadus saida*) and Greenland halibut (*Reinhardtius hippoglossoides*) have retreated farther north (Eriksen et al. 2017, Fossheim et al. 2015, Hop & Gjøsæter 2013). During the 2012 North Atlantic heat wave (Mills et al. 2013a), bluefin tuna followed the warmer temperatures and their prey into waters off eastern Greenland (MacKenzie et al. 2017), further pointing to a northerly shift in the North Atlantic biome. While thermal conditions in the Arctic may now be within the tolerances of many North Atlantic species, it remains to be seen how the biome will function in the high Arctic's distinct annual light cycle (Sundby et al. 2016).

By contrast, the northwest Atlantic is at the warm edge of the biome. Temperatures in this region have warmed at nearly four times the global average rate since 1980, with much of the warming occurring in the last 15 years (Pershing et al. 2015, 2018). The region also experienced notable marine heat waves in 2012 (Mills et al. 2013a), 2016 (Pershing et al. 2018), and again in 2018 (A.J. Pershing, personal observation). In the Gulf of Maine, warming has been linked to a decline in the summer and fall abundance of *Calanus*, especially after 2010 (Record et al. 2019). Somewhat surprisingly, the abundance of *Calanus* in the winter has increased during this period, especially along the coast (Record et al. 2019, Runge et al. 2015). After a decade of strong calf production, right whale reproduction has plummeted—no calves were born during the

2017–2018 season, and the whales have largely abandoned the traditional late-summer feeding ground and are spending more time in the Gulf of St. Lawrence (Davies & Brillant 2019, Record et al. 2019). Because right whales were historically rare in the Gulf of St. Lawrence, the lobster and crab fisheries were not using whale-safe practices, leading to several fatal entanglements, though the Canadian fishery responded swiftly (Davies & Brillant 2019). The increase in mortality is threatening the viability of the species (Meyer-Gutbrod & Greene 2018). The warming has also contributed to the record low abundance of cod in the Gulf of Maine (Pershing et al. 2015), and herring recruitment has similarly declined since 2012 (NEFSC 2018). While additional attribution work is needed, when viewed in aggregate, the declines in *Calanus*, right whales, cod, and herring look very much like an ecosystem losing its North Atlantic character. This assertion is supported by the increased prominence of temperate species, including black sea bass (*Centropristis striata*), silver hake (*Merluccius bilinearis*), and longfin squid (*Doryteuthis pealeii*) (Mills et al. 2013a, Nye et al. 2011, Pinsky et al. 2013).

At one level, the loss of North Atlantic characteristics as the ecosystem warms is not surprising, but is it just a simple response of warming, such as species tracking their preferred temperatures? We hypothesize that indirect effects of warming—specifically, enhanced stratification—are likely the main driver of ecosystem changes. Our hypothesis is supported by a similar ecosystem transition that occurred in the Gulf of Maine in the 1990s. During the 1990s, the transport of relatively fresh water equatorward along the Canadian shelf increased (Greene & Pershing 2007, MERCINA Work. Group 2012), leading to enhanced vertical stratification, especially in the fall and winter. The increased stratification supported elevated phytoplankton abundance during the fall and winter but less intense spring blooms (Greene & Pershing 2007, Ji et al. 2007). *Calanus* abundance was average to above average during the fall and winter, while abundance in the summer and fall decreased (Pershing et al. 2005). The result was a more diverse zooplankton community (Record et al. 2010) with reduced potential to export carbon (Stamieszkin et al. 2015). The 1990s shift in *Calanus* phenology is nearly identical to the recent observations of Runge et al. (2015). During the 1990s, right whale calf production (Meyer-Gutbrod et al. 2015) and cod recruitment (Mountain & Kane 2010) declined as well.

FUTURE DIRECTIONS FOR THE NORTH ATLANTIC AND NORTH ATLANTIC SCIENTISTS

The rapid pace of change in the North Atlantic means that this ecosystem will experience changes before many other regions. Thus, the North Atlantic provides a laboratory to understand the processes that structure marine ecosystems and how ecosystems respond to changes in these processes.

Our review has emphasized the impact of temperature and warming on the ecosystem. The limited studies of ocean acidification on the major North Atlantic species suggest that temperatures are likely to become limiting before pH does and that interactions between these environmental variables have more impact than each alone. For example, simulated acidification did not affect adult *Calanus finmarchicus* but did affect the hatching success of its eggs, especially when temperatures were high (Preziosi et al. 2017). Direct impacts of acidification on cod vary depending on how drastic the drop in pH is, the life stage considered, and the subpopulation studied (Frommel et al. 2012, 2013), and detrimental interactions of pH and temperature together have been seen in embryonic cod (Dahlke et al. 2017). A meta-analysis of acidification studies showed that calcifying organisms are more affected than noncalcifiers and that negative responses to pH are exacerbated by elevated temperature (Kroeker et al. 2013).

Oxygen is another confounding factor tied to temperature; warmer water holds less oxygen, so it is possible that many of the reported temperature impacts are in fact due to declining

dissolved oxygen. Deutsch et al. (2015) suggested that oxygen limitation may explain the southern biogeographic limit of North Atlantic species, including cod. Studies exploring the complex effects of changing temperature, oxygen, and pH in many combinations will be essential to understanding the state of the North Atlantic biome in the future.

Ecosystem studies that incorporate multiple methods—experiments, observational data sets, and modeling—are imperative to capturing the extent of change in the North Atlantic. Experiments are suited to disentangling compounding effects of environmental parameters on biota, as described in the paragraph above. Observational data sets, particularly long-term studies, are essential to documenting change. Management relies on understanding the influences of ecosystems on endangered species and fish stocks. If it were not for zooplankton and environmental monitoring programs in both the United States and Canada, we would still be guessing why the North Atlantic right whale drastically altered its seasonal migration. Knowing now that they are tracking *Calanus* (Record et al. 2019) could enable preemptive management to prevent any further upticks in human-caused mortality. Finally, modeling can tie experiments together with large-scale ecosystem observations. For example, theoretical models of *Calanus* diapause (Ji 2011, Record et al. 2018) (e.g., **Figure 4b**) and empirical models of *Calanus* habitat (Helaouet & Beaugrand 2007, Reygondeau & Beaugrand 2011) can be used to track the movement of the North Atlantic biome.

We would be remiss if we failed to note the interaction between the direct impacts of humans on fish and whale populations and the indirect impacts through the warming trend. Our analysis of the decline of Gulf of Maine cod in response to recent warming (Pershing et al. 2015) was not, as some have asserted (e.g., Brander 2018), just about warming. Warming led to a decline in the productivity of the stock (reduced recruitment and increased mortality), an association that was detected several years before (Fogarty et al. 2008). The decline in productivity meant that the stock could sustain lower levels of fishing. While the management system did adjust fishing mortality downward, the point of our analysis was that these adjustments were not able to keep pace with the rapid decline in productivity. In a similar way, it took several right whale deaths to prompt actions to reduce entanglement as the whales shifted their distributions in response to rising temperatures (Davies & Brillant 2019, Record et al. 2019). While there are strong fishery management and conservation policies in the North Atlantic, these policies and the technical practices that support them (such as stock assessments) are based on historical conditions. The trajectory of the North Atlantic ecosystem now depends on our ability to predict future conditions and react appropriately in how we manage both marine resources and carbon emissions.

DISCLOSURE STATEMENT

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during the development of the greatest proposal never funded. Much like the North Atlantic food web, *Calanus finmarchicus* is the lipid-rich center of this paper. The notion that it is the most interesting animal on the planet reflects our apprenticeship under Jeffrey Runge, the Zen master of the lipidscape. We humbly dedicate this article to him.

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