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REVIEWS

Effects of climate change on four New England groundfish species

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Abstract Multiple groundfish stocks in New England remain depleted despite management measures that have been effective elsewhere. A growing body of research suggests that environmental change driven by increasing concentrations of carbon dioxide in the atmosphere and ocean is unfolding more rapidly in New England than elsewhere, and is an important factor in the failure of these stocks to respond to management. We reviewed research on effects of changes in temperature, salinity, dissolved oxygen, pH, and ocean currents on pelagic life stages, post-settlement life stages, and reproduction of four species in the New England groundfish fishery: Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), winter flounder (*Pseudopleuronectes americanus*), and yellowtail flounder (*Limanda ferruginea*). The volume of research on cod was nearly equal to that on the other three species combined. Similarly, many more studies examined effects of temperature than other factors. The majority of studies suggest adverse outcomes, with less evidence for mixed or positive effects. However, for all of the factors other than temperature, there are more knowledge gaps than known effects. Importantly, most work to date examines impacts in isolation, but effects might combine in nonlinear ways and cause stronger reductions in stock productivity than expected. Management strategies will need to account for known effects, nonlinear interactions, and uncertainties if fisheries in New England are to adapt to environmental change.

Keywords Climate change · Groundfish · New England · Temperature · Productivity · Fisheries management

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Introduction

Fisheries management in the United States has evolved in important ways over the past few decades. Rebuilding plans for overfished species managed at the federal level have been required since statutory revisions to the Magnuson Stevens Act in 1996, a strategy aimed at deterring management inaction and accelerating recovery (Safina et al. 2005). The effectiveness of rebuilding plans initially proved disappointing because fishing mortality could not be kept to

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sufficiently low levels in practice (Rosenberg et al. 2006). However, further revisions to federal law in 2007 required that risk-averse buffers be included within catch limits, a strategy that can account for the often considerable scientific uncertainties underlying management (Restrepo and Powers 1999). The 2007 revisions also required that management plans include accountability measures for quota overages. This has motivated increased use of both output controls and incentive-based allocation systems, also known as ‘catch shares’, across US fisheries, approaches that are more effective at meeting fishing mortality targets (Worm et al. 2009; Melnychuk et al. 2012), reducing risk of collapse (Costello et al. 2008), dampening inter-annual variability (Essington 2010; Essington et al. 2012), and improving socio-economic outcomes (Gutierrez et al. 2011; Grimm et al. 2012). As a result of these accumulated changes, the economic and biological performance of fisheries in the United States has continually improved over the past decade (NOAA 2015).

A notable exception to the generally positive trends in US fisheries is the New England groundfish fishery (NOAA 2015), the oldest commercial fishery in the nation. Management of the groundfish fishery includes all of the elements outlined above that have contributed to success in many other US fisheries: rebuilding plans, risk-averse buffers in catch limits, output controls, and catch shares. Yet, many stocks not only remain severely depleted but are also trending downward (NEFSC 2015). Stocks at very low levels of biomass can be the least responsive to management measures and are most vulnerable to environmental variability (Vert-pre et al. 2013), which might explain the disappointing outcomes. Furthermore, environmental changes linked to rising concentrations of CO_2 in the atmosphere and ocean are especially pronounced in the waters off New England (see “Ecosystem context” below). The magnitude of these changes recently motivated a comprehensive assessment of the vulnerability of 82 species in the waters off New England to the effects of climate change (Hare et al. 2016).

Climate change can affect stock productivity, potential yield and management targets (Pörtner and Peck 2010; Sumaila et al. 2011; Doney et al. 2012; Pinsky and Mantua 2014). Fogarty et al. (2008) re-estimated biological reference points for Atlantic cod (*Gadus morhua*) accounting for predicted effects of increased temperature on growth and recruitment. Their results suggest that maximum sustainability yield (MSY) and the fishing mortality rate that will produce MSY (F_{MSY}) will be lower with a 2 °C increase relative to baseline conditions. Pershing et al. (2015) corroborated these results and illustrated that management strategies that have not accounted for these changes are partly to blame for the continued decline of the Gulf of Maine cod stock. In contrast, the vulnerability assessment by Hare et al. (2016) suggests that groundfish species might be affected less than other functional groups, notably benthic invertebrates and diadromous species. However, the authors also noted that more detailed empirical and process-oriented studies focused on individual species might yield different outcomes. Such studies are especially needed for groundfish in light of their poor status and high economic, cultural, and ecological importance.

To help guide future research and management strategies for New England groundfish that account for ongoing environmental change, we conducted a structured literature review of evidence for the effects of climactic and oceanographic factors on four of the most economically important species in the New England groundfish complex. We considered two gadoids, Atlantic cod and haddock (*Melanogrammus aeglefinus*), and two pleuronectoids, winter flounder (*Pseudopleuronectes americanus*) and yellowtail flounder (*Limanda ferruginea*). Our objectives were to identify and synthesize what is known about the positive and negative effects of climactic and oceanographic changes on each species, trends that are consistent across species or unique to each, and knowledge gaps that require future research.

Ecosystem context

The marine waters off New England are defined by two prominent geographic features: the Gulf of Maine and Georges Bank (Fig. 1). The Gulf of Maine is bound by the coastlines of the U.S. states of Massachusetts, New Hampshire and Maine to the west and north, the Scotian Peninsula and Scotian Shelf in Canada to the north and east, and Georges Bank to the south. Canada’s Bay of Fundy opens into the Gulf of Maine, which itself extends into the wider Atlantic Ocean by the Northeast Channel. The Gulf is strongly influenced by freshwater input from more than a dozen

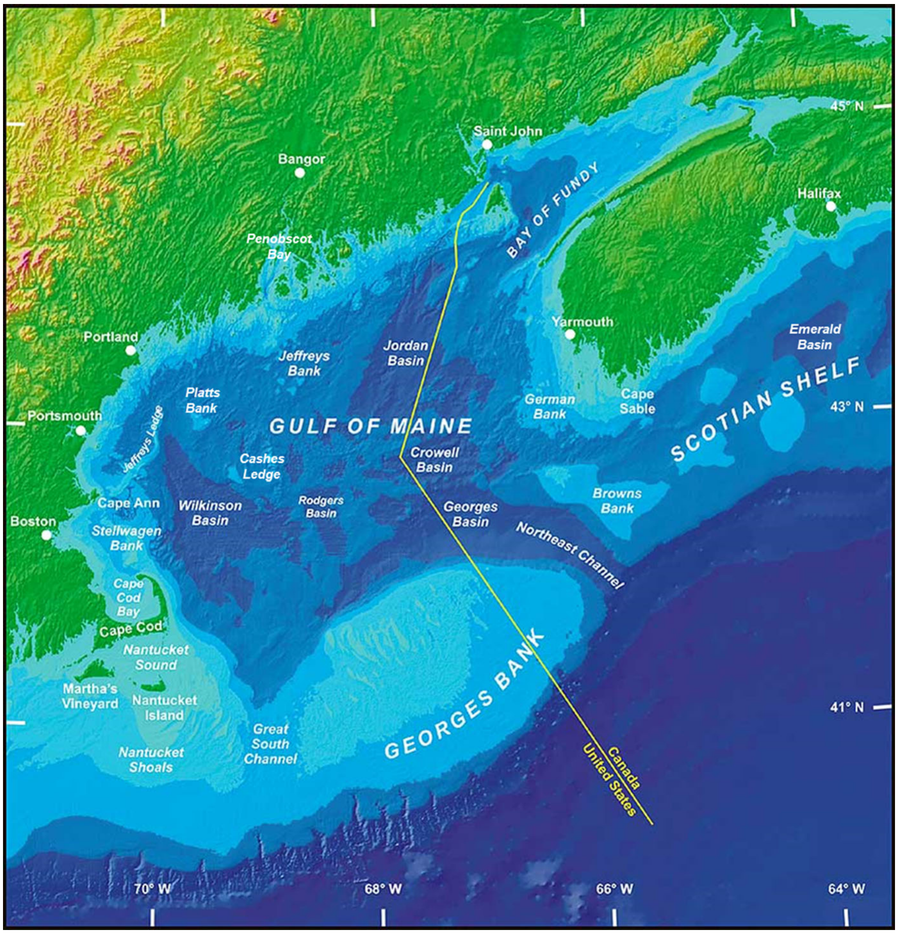

Fig. 1 Geography and topography of the coastal and marine waters off New England, USA

large rivers and many smaller tributaries. Its seafloor includes underwater banks, ledges, shoals, basins and other features, providing considerable topographic complexity. In contrast, Georges Bank is a considerably more uniform sandy underwater plateau, albeit with important variation in substrate composition and diversity.

As the North Atlantic as a whole is a comparatively young marine system, the region exhibits relatively low marine biodiversity (Witman et al. 2004). However, the historical fisheries productivity of the region was remarkably high (e.g., Rosenberg et al. 2005), bolstered by the strong linkages with freshwater ecosystems (Hall et al. 2012; Ames and Lichter 2013). Multiple anthropogenic stressors have altered ecosystem structure and function in the centuries since European colonization of the region, including overfishing, coastal development, pollution, and other watershed manipulations. For example, kelp forests in the Gulf of Maine that were once dominated by large predatory fish have become increasingly dominated by lower trophic level crustaceans (Steneck et al. 2004).

More recently, climactic and oceanographic effects of rising concentrations of greenhouse gases are increasingly altering the marine ecosystems off New England. In the Gulf of Maine, sea surface temperatures have increased at a rate of 0.026 °C year^{-1} over the last 30 years, accelerating to 0.26 °C year^{-1} between 2004 and 2012 (Mills et al. 2013), a rate faster than almost anywhere else on the globe. Average annual precipitation has increased about 5 % in the Northeast since 1991 (Walsh et al. 2014), and is expected to increase by 5–10 % by 2050 according to IPCC forecast models (Fernandez et al. 2015). Precipitation is also becoming more variable, resulting in more flood and drought years (Balch et al. 2012). Stronger precipitation events have already caused ocean freshening (Balch et al. 2012), and continued decreases in salinity are expected due to melting of the Arctic ice cap and freshening of the Labrador Current (Nummelin et al. 2016). Oceans have become about 0.1 pH units more acidic worldwide and continued increases in CO_2 concentration and decreases in salinity are expected to cause a further reduction of 0.2–0.3 pH units (Feeley et al. 2009; also see Caldeira and Wickett 2003, 2005).

Climate change can also result in lower levels of dissolved oxygen due to the reduced solubility of warmer waters. Increased nutrient runoff from increased precipitation can exacerbate hypoxic conditions in coastal waters, while alterations to water column stratification resulting from temperature and salinity changes can expand deeper hypoxic zones into shallower depths (Rabalais et al. 2010; Doney et al. 2012). Increased prevalence of hypoxia in coastal or offshore waters has not been widely reported for the New England region, but those changes might unfold as other climatic and oceanographic changes progress. Likewise, increased warming of the upper water column combined with changes in wind stress and salinity has the potential to one day alter the velocity and direction of ocean currents (Hoegh-Guldberg and Bruno 2010).

These changes in the physical environment have already resulted in measurable ecological alterations, such as decline in abundance of zooplankton species that are important prey for larval fish (Friedland et al. 2013). Many fish species are also exhibiting substantial shifts in their distribution (Nye et al. 2009; Kleisner et al. 2016), and these shifts are happening faster in the waters off New England than anywhere else in the United States (Pinsky et al. 2013). These changes are altering species composition and trophic guild structure (Garrison and Link 2000; Kleisner et al. 2016), and likely altering the system state to one dominated by lower trophic level pelagic species over higher trophic level demersal groundfish (Choi et al. 2004).

Literature review

We searched Web of Science using combinations of the scientific and common names of our four focal species with a geographic constraint (Gulf of Maine, Georges Bank, New England), and specific (temperature, temp*, salinity, ocean acidification, hypoxia, dissolv* oxygen) and general (environment* effects, environ*, climate change) topical search terms. Using references lists from the resulting literature base, we identified additional sources for topics with few studies in the initial search, allowing a wider geographic range across the North Atlantic. The waters off New England are toward the southern extent of the range of all four species we considered, especially Atlantic cod. However, cold water delivered south toward New England by the Labrador Current, combined with warm water moved away from the region by the Gulf Stream and North Atlantic Drift, mean that the New England region has historically maintained temperature profiles similar to many locales at higher latitudes across the North Atlantic. Therefore, studies from those locales can likely provide useful insights. Finally, in addition to published papers, we also reviewed relevant grey literature, such as Essential Fish Habitat source documents and stock assessment reports.

The search resulted in 136 core references, the topics of which are summarized in Table 1. The majority of these focused on Atlantic cod, with winter flounder a distant second. Many were empirical studies addressing effects of environmental attributes more generally, rather than the outcomes of climate change or other directional environmental change specifically, but we utilized these empirical findings to evaluate the likely effects of ongoing and forthcoming environmental change. Fewer studies used projections or otherwise worked within the context of climate change explicitly. Effects of temperature received the most research attention, with a dearth of literature addressing effects of hypoxia and especially ocean acidification. Additional research on the effects of these factors exists for other components of the ecosystem (species, habitats, processes) that can affect our species of interest, but we concentrated on studies that addressed the focal species directly.

Temporal trends in the studies we considered (Fig. 2) show that the considerable attention given to temperature effects over others has generally been maintained through time. However, the volume of studies increased dramatically from the 1980s to the 1990s. More importantly, the number of studies examining interacting effects of different environmental factors also increased substantially more recently. This is a promising trend in light of the multiple changes unfolding in the ecosystem.

Table 1 Number of studies addressing effects of changing environmental conditions on four species of New England groundfish

Species	Environmental factors								
	Temperature	Salinity	Acidification	Hypoxia	Currents	Multiple or interacting effects	Climate change projections	Other effects	Total
Atlantic cod	22 (15)	13 (4)	1	2 (2)	2	13 (7)	3	2	65
Haddock	10 (4)	3	1	1	6	7 (1)	0	0	24
Winter flounder	11 (9)	4	0	3 (3)	1	10 (1)	0	0 (2)	30
Yellowtail flounder	11	2 (1)	0	1	0	7 (3)	0	2 (1)	17
Total	74	25	2	11	9	41	3	7	

Numbers in parentheses are studies focused on areas other than the North American continental shelf. Some references provided information on more than one effect or species, and therefore the total number of references per species or factor is not a direct sum of the cells in a row or column in all cases

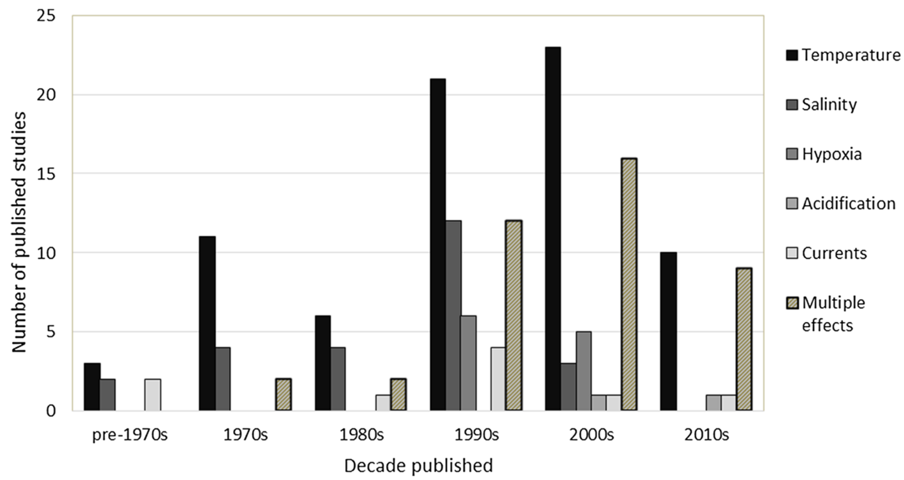

Fig. 2 Temporal trends in the number of studies considered in the literature review of effects of environmental change on four species of New England groundfish, summed across the four species. “Multiple effects” include those references addressing more than one environmental factor, and these references are reflected in the totals for each of those factors as well

Patterns in the literature

We summarize the empirical findings reported in the literature in three broad categories: Pelagic life stages (i.e., growth, development, condition, survival, and behavior of eggs and larvae), post-settlement life stages (growth, development, condition, survival, and behavior of juveniles and adults), and reproduction (maturation, fecundity, spawning and recruitment; the linkage between pelagic and post-settlement life stages). These categories are not distinct, of course. For example, growth and survival during pelagic life stages impacts recruitment, and post-settlement growth is a key determinant of fecundity. Within each of these categories, we consider temperature separately from the other environmental factors as it was focus for the majority of studies considered.

Results of the literature review are summarized in Table 2. There is considerable complexity inherent in the environmental-biological interactions we are examining. In some instances, the effects of directional change in a given environmental attribute depend upon the magnitude of the changes relative to a species’ tolerances, the rate of change, the location in question along various gradients (especially latitudinal, inshore-offshore, and depth) that determine localized adaptations, and interactions among these factors. This complexity is difficult to summarize, and the content in Table 2 is therefore generalized to a degree by necessity, although some mixed effects are

Table 2 Summary of impacts on four species of New England groundfish due to expected changes in environmental conditions based on literature review

Species	Environmental change	Pelagic stages (eggs & larvae)			Post-settlement (juveniles & adults)			Reproduction			
		Growth & development	Survival	Dispersal & settlement	Growth & condition	Survival	Behavior	Maturation	Fecundity	Spawning	Recruitment
Atlantic cod	↑ Temperature										
	↓ Salinity										
	↓ pH										
	↓ DO										
	Δ Currents										
Haddock	↑ Temperature										
	↓ Salinity										
	↓ pH										
	↓ DO										
	Δ Currents										
Yellowtail flounder	↑ Temperature										
	↓ Salinity										
	↓ pH										
	↓ DO										
	Δ Currents										
Winter flounder	↑ Temperature										
	↓ Salinity										
	↓ pH										
	↓ DO										
	Δ Currents										

Mixed effects are conveyed in some instances, but a number of factors can result in very different and even opposing outcomes (e.g., rate and magnitude of change; latitude). Therefore, these results are generalized to a degree by necessity. Green = positive effects, red = negative effects, light green or light red = indirect positive or negative effect (e.g., due to a change in another life history trait), multiple colors = evidence for different types of effects, DO = dissolved oxygen

captured. The following text attempts to delineate different outcomes expected due to the nature of environmental change and the position along environmental gradients in more detail.

Pelagic life stages

Temperature effects

Elevated ocean temperatures can increase early growth and development rates of cod (Laurence 1978; Brander 1995; Kristiansen et al. 2011), haddock (Laurence 1978; Cargnelli et al. 1999), yellowtail flounder (Colton 1959; Laurence and Howell 1981), and winter flounder (Laurence 1975; Williams 1975; Rogers 1976; Buckley et al. 1990), suggesting potential benefits of climate change. Reduced incubation and faster development reduces time in life stages when mortality and predation rates are highest, and hastens the transition to larger, free-swimming juveniles that are better at foraging and predator avoidance. Length of incubation time can be especially crucial for species such as winter flounder that are dependent on nearshore and estuarine areas where they are more susceptible to other anthropogenic impacts, such as pollution, during critical developmental periods (Pereira et al. 1999).

If warmer waters do increase growth rates, larvae will still need enough appropriately sized prey to meet size-specific metabolic needs (O'Connor et al. 2007; Kristiansen et al. 2014). In early life, failure to find food is one of the most important causes of mortality in fish larvae (Blaxter 1986). The availability of appropriately sized forage is crucial for larval feeding and growth, and therefore recruitment and year class strength, of cod (Buckley et al. 2010) and winter flounder (Laurence 1977; Stoner et al. 2001). Prey mismatches, due to temperature impacts on prey themselves, earlier spawning or rapid larval growth, can lead to larval starvation. In the North Sea, there is evidence that warming waters have caused shifts in plankton communities and in turn reduced survival of larval cod (Beaugrand et al. 2003), and may be a major driver in recent recruitment failure of cod (Nicolas et al. 2014). Similarly, changes in environmental conditions may be causing biogeographical and potentially regime shifts in copepod communities in the North Atlantic (Beaugrand et al. 2002; Beaugrand 2004) and limiting the overall production of planktonic prey (Boyce et al. 2010), with potential impacts on cod recruitment (Beaugrand et al. 2003). Kristiansen et al. (2011) determined warm years can increase prey availability and overlap with larval cod, but Friedland et al. (2013) found a recent reduction in the distribution and abundance of certain plankton in the waters off New England, resulting in localized feeding mismatches for larval cod. Changing conditions may also be limiting food availability for larval flatfish, especially in southern areas (Gibson 2013). In addition, as planktonic prey vary in caloric content, increasing temperature may also impact early life stages via the quality of prey (Nicolas et al. 2014). Furthermore, warmer temperatures may limit primary productivity (Steinacher et al. 2010; Capotondi et al. 2012), also reducing prey availability (Kristiansen et al. 2014). These impacts may vary by location and may be stronger in southern waters where temperate groundfish species are already at the limit of their environmental tolerances.

The potential benefits of warmer waters on early growth and development may be limited for other reasons as well. First, more rapid incubation, hatching and growth might occur only within a certain range of temperature increase, beyond which adverse effects unfold, as is evident for haddock (Laurence and Rogers 1976; Laurence 1978). Second, the rate at which waters warm may also be critical. For example, sudden and drastic increases in temperature can increase mortality in yellowtail flounder larvae (Colton 1959). Third, warmer waters may have other, deleterious effects. For cod, high temperatures can adversely affect fertilization, egg development (Nicolas et al. 2014), and egg size (Miller et al. 1995). Increased temperature can reduce the growth and survival of haddock (Peck et al. 2003; Eriksen et al. 2012), and hatching success (Williams 1975; Rogers 1976; Keller and Klein-MacPhee 2000), initial larval size (Buckley et al. 1990; Keller and Klein-MacPhee 2000), and larval survival (Rogers 1976; Taylor and Danila 2005; Manderson 2008) in winter founder. Fourth, changing temperature may have indirect effects. Projected rates of warming may cause earlier water column stratification in summer, potentially reducing settlement rates and increasing mortality in juvenile yellowtail flounder (Sullivan et al. 2005). Again, these possible consequences of warming waters will likely vary by location, given spatial comparisons of temperature effects on the early life history of cod (Planque and Fredou 1999; Pörtner et al. 2001, 2008) and yellowtail flounder (Steves et al. 2000).

Finally, temperature increases may alter predation rates on larvae, which has important effects on survival of larval winter flounder (Dickie and McCracken 1955). The spawning cycle of winter flounder is timed to align with favorable environmental conditions and reduced predation (Jeffries and Johnson 1974; Jeffries et al. 1989; Collette and Klein-MacPhee 2002; Taylor and Danila 2005), which can be disrupted by changes in temperature regimes and predator dynamics. With warmer winters and earlier springs, predators move into critical estuarine nursery grounds earlier and are more active (Taylor and Danila 2005; Bell et al. 2014), resulting in lower survival and abundance of eggs and larvae (Taylor and Collie 2003; Taylor and Danila 2005). Population modeling suggests that the increased predator abundance can result in consumption of up to 50 % of flounder spawn in a single season (Taylor and Danila 2005). These effects might offset advantages of increased temperature (Rajasilta et al. 1993; Taylor and Danila 2005; Keller and Klein-MacPhee 2000).

Other environmental effects

In addition to temperature, changes in salinity may also impact the early life stages of groundfish. For cod, low salinity results in a decline in fertilization and normal development (Davenport et al. 1981; Westin and Nissling 1991), delayed hatching and increased egg mortality (Laurence and Rogers 1976; Koester et al. 2001), and caused eggs to sink more readily (Lough 2004). Winter flounder appear relatively tolerant to changes in salinity, likely due to their reliance on inshore and estuarine waters, but extreme salinities were found to cause abnormal development (Rogers 1976) and lower egg and larval survival and hatching success (Buckley 1989). Salinity and temperature may also interact to affect early life history stages. Laurence and Howell (1981) found that survival of yellowtail flounder eggs is greatly reduced in low salinities at both low and high temperatures, and Rogers (1976) discovered salinity had a stronger effect on hatching success and larval survival in winter flounder under higher temperatures.

Ocean acidification has the potential to influence calcification, acid-based regulation, blood circulation, respiration, and the nervous system in marine organisms (Frommel et al. 2012). Fish are particularly vulnerable to these impacts in early life when they lack the ability to regulate internal pH levels (Sayer et al. 1993). Frommel et al. (2012) found severe to lethal tissue damage for many internal organs in cod raised under three CO_2 levels projected for future scenarios, although adverse effects were remedied once the physiological ability to regulate pH developed within a larva. Cod in this study were from lower-latitude stocks in the northeast Atlantic, and the authors note impacts may be greater in northern populations, as rates of ocean acidification are projected to be higher there (Steinacher et al. 2009).

Finally, changes in the processes that retain larvae on or transport larvae to critical nursery grounds, such as the speed or direction of ocean currents, can also influence larval survival and ultimately recruitment success. Hjort (1914) identified transport and retention of larval fish on nursery areas as critical for recruitment, a conclusion backed by patterns of recruitment in cod (Churchill et al. 2011), haddock (Boucher et al. 2013), and winter flounder (Pearcy 1962; Crawford and Carey 1985). Adaptive responses to patterns in ocean currents allow young cod to settle in particular areas at the correct time to both avoid predators and gain access to abundant food (Lough et al. 1989), and spawning by winter flounder may be timed to utilize the hydrodynamics of small narrow estuaries to maximize egg and larval retention (Pearcy 1962; Pereira et al. 1999). Therefore, changes in currents and circulation as well as conditions in river and estuarine systems may have significant impacts on larval survival and settlement.

Post-settlement life stages

Temperature

Research assessing the impact of climate change on marine fishes often focuses on distributional shifts and behavioral responses to changing conditions (e,g, Murawski 1993; Perry et al. 2005; Harley et al. 2006; Dulvy et al. 2008; Nye et al. 2009; Harley 2011; Simpson et al. 2011; Pinsky and Mantua 2014; Kleisner et al. 2016). Groundfish often move away from even slight temperature changes in the water column, as observed for cod (Rose et al. 1994; Herbert and Steffensen 2005) and haddock (Eriksen et al. 2012). High temperatures can also alter adult winter flounder migration and distribution (McCracken 1963), and the movement of yellowtail flounder (Walsh and Morgan 2004). Additionally, winter flounder juveniles and adults respond to extreme cold or heat by moving or burying themselves (Topp 1968; Olla et al. 1969; Pereira et al. 1999).

Northward movement to avoid warming waters may come with unexpected consequences, as temperature increases will not impact all populations equally. Populations can exhibit different temperature preferences, as seen in yellowtail flounder (Johnson et al. 1999; Collette and Klein-MacPhee 2002; Simpson and Walsh 2004; Sullivan et al. 2005), and may have adapted differently to local thermal regimes, as observed for cod (Dutil and Brander 2003; Mieszkowska et al. 2009). Purchase and Brown (2000) found that, if southern cod stocks move into higher latitudes, they may be less productive and less able to cope with cold periods and thermal anomalies than stocks adapted to those areas. Temperature-driven impacts might also be exacerbated by fishing pressure (Jeffries and Terceiro 1985; Collie et al. 2008) and increased predation (Bell et al. 2014), interactions that can vary with location. Outcomes may not always be detrimental, however. Simpson and Walsh (2004) determined warming waters might have helped some northern stocks of yellowtail flounder rebound from heavy fishing pressure.

Increasing temperatures will impact more than distribution and behavior (Harley et al. 2006). Warmer waters may initially result in increased growth rates, but this may only be to a threshold temperature, after which body size declines (Huey and Berrigan 2001; Baudron et al. 2011; Eriksen et al. 2012). Consequently, adults may ultimately be smaller and less productive in warmer waters. Furthermore, as temperatures increase, other metabolic and physiological rates increase as well (Fonds et al. 1992; MacIsaac et al. 1997), and rising temperatures can therefore affect the fitness and physiology of adult cod (Sartoris et al. 2003), haddock (Baudron et al. 2011), and yellowtail flounder (MacIsaac et al. 1997), and may increase adult mortality in yellowtail flounder (Sullivan et al. 2005) and winter flounder (Nichols 1918; McCracken 1963). Jeffries and Johnson (1974) found that increased mortality of adult winter flounder with rising temperature in the mid-1960s and early 1970s explained depressed catch rates at that time, a result confirmed more recently by Bell et al. (2014).

Other environmental effects

In addition to temperature, salinity can affect juvenile and adult groundfish. Although generally tolerant to a range of salinities, very low salinity can increase adult mortality in winter flounder (McCracken 1963). Cod can endure low salinity waters (Odense et al. 1966; Dutil et al. 1992; Provencher et al. 1993), but may require sufficient acclimation time, as sudden decreases in salinity can increase mortality (Provencher et al. 1993). Even seemingly tolerable salinities can still have physiological effects, such as altering ionic and osmotic regulation in adult cod (Fletcher 1978a, b), which in turn influences the energy available for growth (Lambert et al. 1994).

Changing oxygen levels may also have consequences for groundfish. Claireaux and Dutil (1992) found nonlinear and detrimental responses in cod from the Gulf of St. Lawrence and Newfoundland waters with increasing hypoxia, including hyperventilation and metabolic acidosis. They determined that effects would be further exacerbated with the greater oxygen requirements needed for digestion, pursuit of prey, or escape from predators. In Long Island Sound, winter flounder exhibited decreased abundance and mean length during low oxygen events, as larger fish may have moved to more oxygen-rich areas (Howell and Simpson 1994). Depressed oxygen can also reduce growth rates (Bejda et al. 1992; Howell and Simpson 1994) and juvenile production (Meng et al. 2001; Stierhoff et al. 2006) in winter flounder. These problems might be exacerbated with rising temperatures if species seek out cooler and deeper waters that are more likely to be hypoxic (Claireaux and Dutil 1992).

Effects of different stressors can interact in complex and deleterious ways. For example, Deutsch et al. (2015) found the combined impact of increased temperatures and decreased dissolved oxygen levels will reduce metabolic indices in the ocean, especially in higher latitudes. Hypoxia might interact with changes in salinity and temperature to influence physiology, and the combination of conditions can exacerbate effects that would otherwise be modest in isolation. Low oxygen conditions in conjunction with unfavorable changes in salinity place added stress on important physiological processes in cod, including respiration and metabolism (Claireaux and Dutil 1992). The connection between limited oxygen and temperature also influences aerobic capacity and therefore energy budgets (Pörtner et al. 1998), which in turn affect growth, fecundity, and recruitment (Pörtner et al. 2001). Collectively, this research indicates that interactions among environmental stressors can have sub-lethal impacts that manifest as depressed stock productivity rather than direct mortality.

Finally, changes in ocean currents can also affect juvenile groundfish. Lough et al. (1989) argued that young cod and haddock expend more energy swimming in strong currents to stay over preferred bottom. This expenditure could become increasingly significant with escalating stress due to higher temperatures or lack of prey, with consequences for development, growth, condition, and survival.

Reproduction

Temperature effects

Environmental change also affects maturation, fecundity, spawning, and ultimately recruitment. Temperature is inversely correlated with age and length at maturity for cod stocks across the Atlantic (e.g. Jorgensen 1990; O'Brien 1999). When cod mature earlier, the resulting spawning stock is on average younger, smaller, less fecund, and spawns for a shorter period of time (Kjesbu et al. 1996). Similarly, in North Sea haddock, warmer waters resulted in earlier maturation and larger young haddock, but they reached a smaller maximum size overall, resulting in lower spawning stock biomass and yield (Baudron et al. 2011). Deleterious impacts of temperature on adult groundfish may also have indirect effects on reproduction and recruitment via adult condition, especially for females, as maternal contributions can drive recruitment (Brodziak and O'Brien 2005). For cod, condition of females prior to the spawning season directly impacts fecundity (Kjesbu et al. 1991), energy use during spawning (Lambert and Dutil 2000; Ratz and Lloret 2003), and post-spawning health and mortality (Krivobok and Tokareva 1972). In haddock, female fecundity is dependent upon individual body mass (Palmer and Clark 1979; Smith and Morse 1985;

Page and Frank 1989), and in yellowtail flounder there is a non-linear relationship between size and maternal contribution (egg size and yolk quantity), which can be altered by rising temperatures (Benoit and Pepin 1999).

After maturation, changing temperatures can alter the timing of spawning for cod (Hutchings and Myers 1994; Fahay et al. 1999) and haddock (Page and Frank 1989; Cargnelli et al. 1999), which can create mismatches with optimal conditions for larval dispersal, feeding, survival and growth (Rijnsdorp et al. 2009). The timing of haddock spawning is affected by the duration of fall and winter in the previous year (Smith et al. 1981). For winter flounder, abundance is negatively correlated with warmer winter temperatures during spawning (Jeffries and Johnson 1974; Keller and Klein-MacPhee 2000), and winter flounder spawning is also timed to take advantage of both cold winters and spring warming to maximize initial larval size and early growth rates (Buckley et al. 1990; Wilber et al. 2013), which would be disrupted by warmer winters and earlier springs.

Temperature effects will vary by location. Brodziak and O'Brien (2005) found the relative importance of temperature, among other environmental variables, differed across stocks for several groundfish species in the Northwest Atlantic. Warmer temperatures result in earlier recruitment of cod, especially for northern stocks in colder waters (Brander 1994; Drinkwater 2002), and this earlier recruitment may result in smaller, less fecund adults (Kjesbu et al. 1996). However, in southern waters, temperature is negatively correlated with cod recruitment (Ottersen et al. 1994; Planque and Fredou 1999; Ottersen et al. 2006). Differences in temperature effects among populations have also been found in yellowtail flounder (Sissenwine 1974; Sutcliffe et al. 1977). In southern New England winter flounder, Manderson (2008) found warmer spring temperatures correlated with increased synchrony among age-0 fish, and that such synchrony can destabilize regional age-class structure and population dynamics.

Other environmental effects

Reproductive success is affected by environmental factors other than temperature. Sutcliffe et al. (1983) and Myers et al. (1993) found cod recruitment to be positively correlated with salinity, whereas Walsh et al. (2004) found a negative correlation between salinity and yellowtail flounder recruitment. Larger scale and interacting conditions are also likely critical, as is evident for yellowtail flounder. In the Mid-Atlantic Bight, smoothed recruitment of yellowtail flounder was highly correlated with the North Atlantic Oscillation (NAO) and air temperature (Sullivan et al. 2005). Prior to the collapse of the Grand Bank yellowtail flounder stock, the NAO was strongly positive, resulting in colder air and water, extensive ice cover, and low surface salinity, impacts that were likely exacerbated by fishing pressure (Brodie et al. 2010). Collectively, this suggests the potential importance of salinity and NAO, as well as the potential for differential impacts across space. Finally, changes in currents and circulation may alter the transport to and retention of larvae on critical nursery grounds, which will ultimately impact recruitment success and stock structure of cod and haddock, which have already been altered by human impacts (Ames 1997).

Discussion

Patterns across species

Our review revealed both important insights and gaps in knowledge of the potential response of cod, haddock, winter flounder, and yellowtail flounder to ongoing climactic and oceanographic change. Temperature is one of the most important and widely studied environmental parameters influencing the biology and ecology of marine fish, affecting their physiology (e.g., Fry 1971), migration (e.g., Hoar 1953), and distribution (e.g., Nye et al. 2009). Our review suggests that rising temperatures may have some positive effects on all of the species considered by causing faster growth at multiple life stages, which can move fish through smaller and more vulnerable size classes more quickly, and achieve earlier maturation. Such outcomes can accelerate recovery from depletion through enhanced population growth. However, increased growth also entails metabolic costs, and might come at the expense of future growth, fecundity and egg quality. More importantly, research also highlights many adverse effects of warmer waters that would offset these benefits, especially as temperatures become too high and approach species' upper thermal tolerances. Other impacts driven by temperature increases might further undermine advantages, such as higher predation on larval winter flounder.

The outcomes of other climactic and oceanographic changes are less well studied than temperature, and our review found virtually no positive effects of expected decreases in pH, salinity, and dissolved oxygen, or potential changes in ocean currents. Alteration of these other environmental parameters appears to be especially important for pelagic life stages of our focal species. This is perhaps not surprising given that eggs and larvae lack well developed physiological regulation mechanisms and the ability to seek out favorable environmental conditions. Also, pelagic life stages are highly responsive to changes in the planktonic community that is similarly affected by these factors.

Collectively, our review did not reveal fundamentally different responses among the focal species to the environmental changes considered. This may be expected, as all of these species co-occur and have co-evolved within the ecosystem. Consideration of species historically rare on Georges Bank and in the Gulf of Maine but expected to become more abundant (e.g., Atlantic croaker; Hare et al. 2010) might reveal very different responses.

That is not to say that certain environmental changes will not affect some species more than others. Cod and haddock in particular exhibit narrower thermal tolerance than the flatfishes (Cargnelli et al. 1999; Fahay et al. 1999; Johnson et al. 1999; Pereira et al. 1999), and might be more vulnerable to adverse effects of warming waters. However, the flatfishes show behaviors and habitat use patterns that might increase their vulnerability to certain changes, such as spawning site fidelity and dependence on localized spawning, nursery, and feeding grounds, demonstrated by winter flounder (McCracken 1963; Howell et al. 1999; Fairchild et al. 2013), or the strong habitat-dependence (e.g. Gibson and Robb 1992; Gibson 1994), limited movements (Morgan and Walsh 1996), and concentration on preferred habitats with abundance declines (Brodie et al. 1998; Simpson and Walsh 2004; Pereira et al. 2012) of yellowtail flounder. These characteristics suggests both flounders may have limited ability to shift as conditions change, and may experience greater stress if there are mismatches between preferred thermal and physical habitat. Furthermore, yellowtail flounder show density-dependent effects on demographic traits (Myers and Cadigan 1993; Beverton 1995), which will exacerbate environmental stresses. However, other aspects of the biology and ecology of the species here might confer resilience (see “Mechanisms for adaptation” below).

Our results generally align with the conclusions of Fogarty et al. (2008), Pershing et al. (2015), and Hare et al. (2016). The latter concluded winter flounder is the most vulnerable among the four species we considered, followed by cod, with haddock and yellowtail flounder being the least vulnerable. This conclusion is not necessarily evident in the overall summary of our review (Table 2). However, winter flounder and to a lesser extent cod will be affected by changes in a greater diversity of aquatic habitats, in particular shallower nearshore areas that are being more profoundly affected by climate change and other anthropogenic impacts. Our review corroborates some of the more detailed components of the assessment by Hare et al. (2016). For example, they conclude that winter flounder will be more susceptible to changes in oceans currents than the other three species. Our review agrees with this conclusion, although the literature suggests that Hare et al. may be underestimating the effect given the more precise and limited settlement habitats used by winter flounder, and the greater influence of changes in freshwater flow on dispersal and retention.

Interactions among effects

Another critical finding of our review is the importance of understanding how changes in various environmental effects will interact. Studies examining such interactions and their collective consequences for biological attributes of our species of interest are rare. Those that do reveal nonlinear outcomes, and the number of impacts we identify suggests potential for significant cumulative effects. Understanding these combined impacts is critical, as they can result in cohort- and population-level effects that compromise resilience, ecosystem function, and economic value (e.g., Harley et al. 2006; Friedland et al. 2013; Kristiansen et al. 2014).

Figure 3 illustrates how interactions among and accumulated effects of many of the individual outcomes summarized in Table 2 might unfold to shape a population of cod. Increasing temperatures can have both positive and negative effects on the growth of

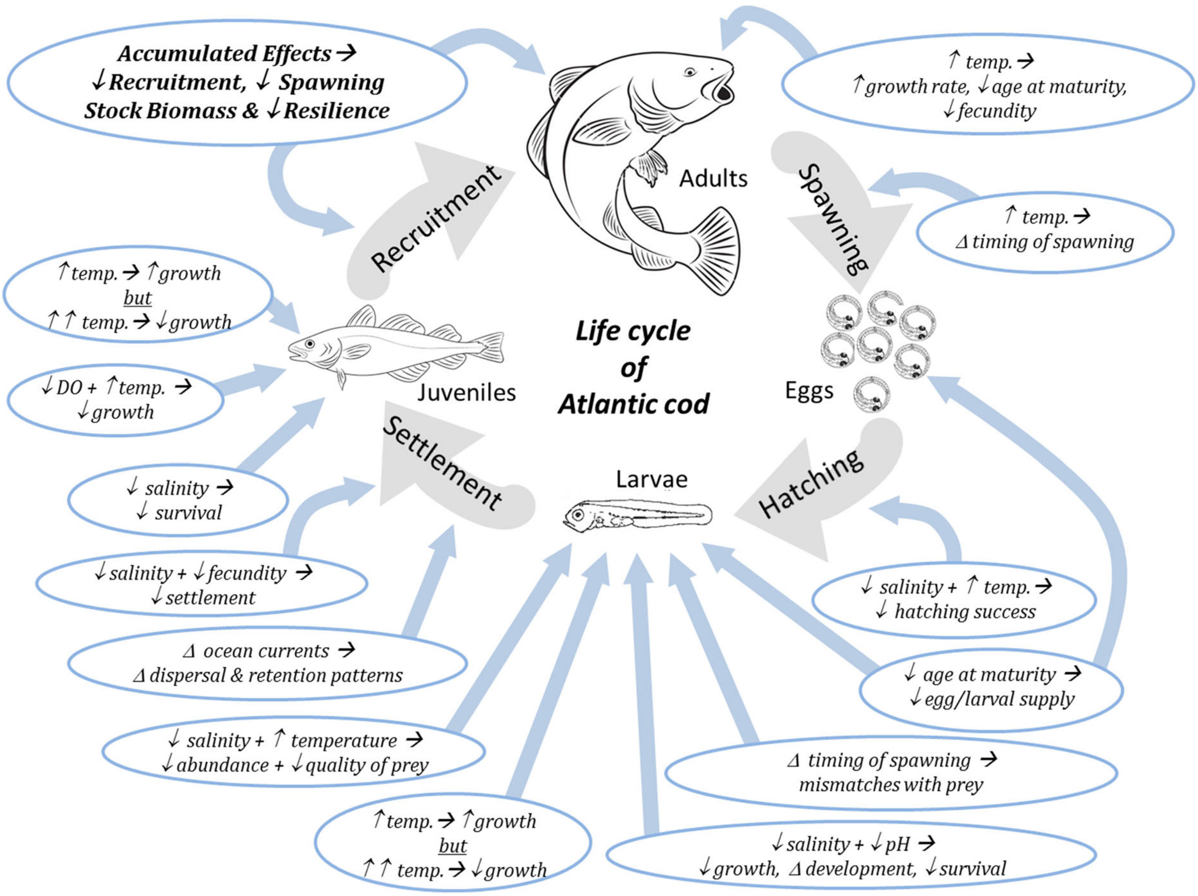

Fig. 3 Schematic diagram of many of the ways that environmental change can have positive and negative impacts over the life cycle of Atlantic cod (*Gadus morhua*), illustrating the cumulative outcomes and potentially nonlinear interactions among individual effects

larval cod, depending upon the magnitude of the increase, while acidification and especially decreasing salinity are expected to have largely negative effects. The combination of these effects is likely to be greater than that estimated for any in isolation. Higher temperatures and lower salinities are also expected to have adverse effects on survival of eggs and larvae, effects that again might be greater in combination than estimated when considering only one type of environmental change. There are also indirect consequences of interacting environmental stressors both pre- and post-settlement. For the former, the importance of body size for survivorship means that the combined growth effects are likely to reduce survivorship further than that expected due to the direct lethal effects of environmental change. Collectively, this means fewer and smaller fish available to make the pelagic-benthic transition at the end of the larval stage. The resulting reduced larval pool might further exhibit lower settlement rates due to changes in both ocean currents and water column stratification, as well as fewer or lower quality prey.

After settlement, growth rates and body size are likely to be lower if the incoming cohort of settling larvae is comprised of smaller fish. Increased temperature might offset or exacerbate this effect, again depending upon the magnitude of the increase and other external effects, such as the abundance and quality of prey. Hypoxia can further compromise growth, which can in turn compromise survivorship given size-dependence. Survivorship can also be affected directly by other changes, especially sudden decreases in salinity. On the other hand, higher temperatures can hasten maturation, minimizing the number of fish that do not reach spawning age due to lower survivorship and increasing near-term productivity. This might have short-term benefits, but at a longer term cost due to the consequences of earlier maturation for future growth, survivorship, fecundity and egg quality. In other words, an apparently counterbalancing environmental effect might mean a fundamental shift in the structure and reproductive success of the spawning population, with implications for the ability of the population to grow and withstand periods of recruitment failure over time. Also, depressed adult fitness may mean lower quality eggs and larvae over time, placing those individuals at a disadvantage from the outset as they confront future environmental stressors.

Mechanisms for adaptation

Although we identify generally adverse effects of environmental change, which may be even greater in combination, our focal species all have attributes that may help them adapt. Metapopulation structure can provide inherent resilience for a species because not all environmental changes will be experienced homogenously across a species' range (Planque et al. 2010). Subpopulations that are affected less can buffer against depletion or even localized extinction elsewhere (Kritzer and Sale 2004), although spatial population structure will not be advantageous in the face of adverse environmental changes that are experienced at the stock or metapopulation scale (Koenig 2002). Further, serial depletion of subpopulations can erode the potential for bet-hedging and recolonization benefits. Among our focal species, the spatial structure of cod populations has been especially well documented (Ames 2004; Lage et al. 2004; Wirgin et al. 2007; Kovach et al. 2010; Runge et al. 2010), which has illuminated the costs of serial depletion at the metapopulation scale (Smedbol and Wroblewski 2002; Steneck and Wilson 2010).

Spatial structure also creates the potential for behavioral and life history traits that are tailored to different conditions through localized adaptation and based upon genetic diversity (Sale et al. 2006). Localized adaptation can be a disadvantage at the individual or population scale if new conditions deviate too much from those that shaped the adaptation. However, at a larger scale across a metapopulation, a higher degree of genetic diversity increases the ability to adapt to new conditions. Spatial patterns in genetic diversity have been described for both cod (Hauser and Carvalho 2008; Kovach et al. 2010) and winter flounder (Howell et al. 1992). These differences are maintained in cod by spawning patterns (Kovach et al. 2010) and larval retention strategies (Mieszkowska et al. 2009; Runge et al. 2010), and in winter flounder by a high degree of site fidelity (Howe and Coates 1975;Phelan 1992; Gibson 2013). Unfortunately, our review suggests that both of these strategies might be compromised by changing conditions.

Although spatial structure and genetic, behavioral, and life history diversity can confer resilience and allow for adaptation at the metapopulation scale, certain behavioral and life history attributes can also contribute to resilience and adaptation at smaller scales. Winter flounder are generally viewed as an inshore spawning species, but exhibit a greater degree of spawning in deeper offshore waters than is generally appreciated (DeCelles and Cadrin 2010). This plasticity over relatively small scales might allow for localized adaptation in the future. Mobility can allow fish to seek out a better location if local conditions become unfavorable, provided of course that suitable habitat in new locations has not been unduly affected by climate change or other impacts (Kritzer et al. 2016). Cod generally exhibit the longest range movements among our focal species, especially in the Northwest Atlantic (Robichaud and Rose 2004), which should allow stronger positive responses to environmental change.

One potential downside of greater mobility is that fewer benefits of marine protected areas (MPAs) will be realized (Sherwood and Grabowski 2010). MPAs can also allow recovery of complete age and size structure (Berkeley et al. 2004), and this demographic diversity can contribute to resilience given the robustness and high reproductive value of older and larger fish (Planque et al. 2010). Fortunately, the behavioral diversity exhibited by cod has allowed some fish to benefit from spatial management in New England, resulting in more complete age and size structure within MPAs (Sherwood and Grabowski 2015). Haddock, winter flounder and yellowtail flounder all exhibit larger body size in MPAs as well (Link et al. 2005). Because impacts of environmental changes should be experienced across MPA boundaries, these outcomes underscore the continued importance of fishing pressure as a demographic driver. A recent analysis of long-term trends in cod populations across the North Atlantic reveals that effects of fishing mortality are comparable to environmental effects (Frank et al. 2016). Therefore, the observed differences in population structure across MPA boundaries suggest that spatial protection could become especially important in buffering the effects of fishing pressure in the face of rising and compounding effects of environmental change.

Implications for research and management

Our review revealed that cod is the most widely studied among the species we considered, and that effects of temperature are the most widely studied among the environmental factors. This suggests that more research on the other species and environmental factors is needed. However, the disparity in research between cod and the other species is less than that between temperature and the other factors (Tables 1, 2). Therefore, future research should focus on acidification, salinity, hypoxia, ocean currents, and their interactions. The vulnerability assessment by Hare et al. (2016) supports prioritization of research on ocean acidification in particular, given that its magnitude is expected to increase substantially in the coming decades. Furthermore, Hare et al. conclude that the exposure of all fours species to acidification will be very high, but their sensitivity will be relatively low. These divergent outcomes raise important questions about whether the effects will be significant or not, and our review reveals that the existing literature offers little direct insight (Tables 1, 2).

Future studies should examine as broad a taxonomic spectrum as possible. We considered four of the 15 groundfish species managed in New England, and among many more managed and unmanaged species in the region. We found generally consistent trends in the effects examined, at least in terms of directionality if not magnitude, but within a single functional group (c.f., Hare et al. 2016; Kleisner et al. 2016). Given the high dimensionality of a complete research matrix for the region (i.e., [environmental factors $\times$ species $\times$ life stages $\times$ life history traits], or an expanded version of Table 2), the most efficient and effective strategy will aim to extract as many general trends as possible. This would allow robust assumptions to be made where knowledge gaps inevitably remain. Furthermore, considerably more work is needed on the interactions among effects, including accumulated and synergistic impacts within and across life stages. In fact, this should arguably be the highest priority for future research, given that predictions for individual effects alone will likely underestimate aggregate outcomes (Fig. 3).

Building new science that increases understanding of the effects of climactic and oceanographic changes will take time, but management strategies will need to adapt in the near-term both to what we know and to the many uncertainties. Fishing will remain a dominant driver of groundfish population dynamics, and will interact with climate change (Harley et al. 2006; Araujo and Bundy 2012; Bundy et al. 2012) and increase the sensitivity of fish stocks to climate perturbations (Anderson et al. 2008; Hsieh et al. 2008; Pinsky and Mantua 2014). Therefore, harvest rates will need to be adjusted to contemporary productivity resulting from environmental change (Brander 2010; Planque et al. 2010; Nye et al. 2013). Fogarty et al. (2008) and Pershing et al. (2015) have re-estimated key biological parameters and reference points for cod in light of the potential impacts of climate change, illustrating the lower biomass and fishing mortality targets to which we should be managing.

In addition, the diversity of physical, chemical and biological changes unfolding in the environment means that new analytical tools will be needed to account for the impact of changes and their interactions in determining management targets. This may mean greater use of multispecies production models (e.g., Fogarty et al. 2012), especially in the face of changing species composition within management areas, supplemented by models of intermediate complexity for ecosystem assessment (MICE) to inform those models on environmental effects (Collie et al. 2014; Plaganyi et al. 2014). However, catch limits derived from either single- or multi-species models alone are unlikely to account for the full suite of changes, complexities, and uncertainties we face. Therefore, spatial management measures that protect ecosystem attributes such as habitat, biodiversity, and trophic structure (McCleod et al. 2009), and rebuild spatial structure, age structure and size structure (Kritzer and Sale 2004; Planque et al. 2010) will also be critical.

Better integration among fisheries management entities spanning municipal, state and national boundaries is already needed in light of the fact that many species do not respect these boundaries over the course of their life history (Kritzer and Liu 2013). Beyond governance of fisheries, more integrated management of different human uses that contribute to climate change and other environmental stressors will be necessary to minimize impacts on and maximize the value derived from a variety of ecosystem services (Crowder et al. 2006). In general, managers, fishermen and scientists will need to be more responsive, adaptive and risk-averse in light of ongoing environmental change and the uncertainties inherent in how it will impact groundfish and other species.

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