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Projected impacts of climate change on marine fish and fisheries

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This paper reviews current literature on the projected effects of climate change on marine fish and shellfish, their fisheries, and fishery-dependent communities throughout the northern hemisphere. The review addresses the following issues: (i) expected impacts on ecosystem productivity and habitat quantity and quality; (ii) impacts of changes in production and habitat on marine fish and shellfish species including effects on the community species composition, spatial distributions, interactions, and vital rates of fish and shellfish; (iii) impacts on fisheries and their associated communities; (iv) implications for food security and associated changes; and (v) uncertainty and modelling skill assessment. Climate change will impact fish and shellfish, their fisheries, and fishery-dependent communities through a complex suite of linked processes. Integrated interdisciplinary research teams are forming in many regions to project these complex responses. National and international marine research organizations serve a key role in the coordination and integration of research to accelerate the production of projections of the effects of climate change on marine ecosystems and to move towards a future where relative impacts by region could be compared on a hemispheric or global level. Eight research foci were identified that will improve the projections of climate impacts on fish, fisheries, and fishery-dependent communities.

Keywords: climate change, fish, fisheries, fisheries-dependent communities, uncertainty, vulnerability assessment.

Introduction

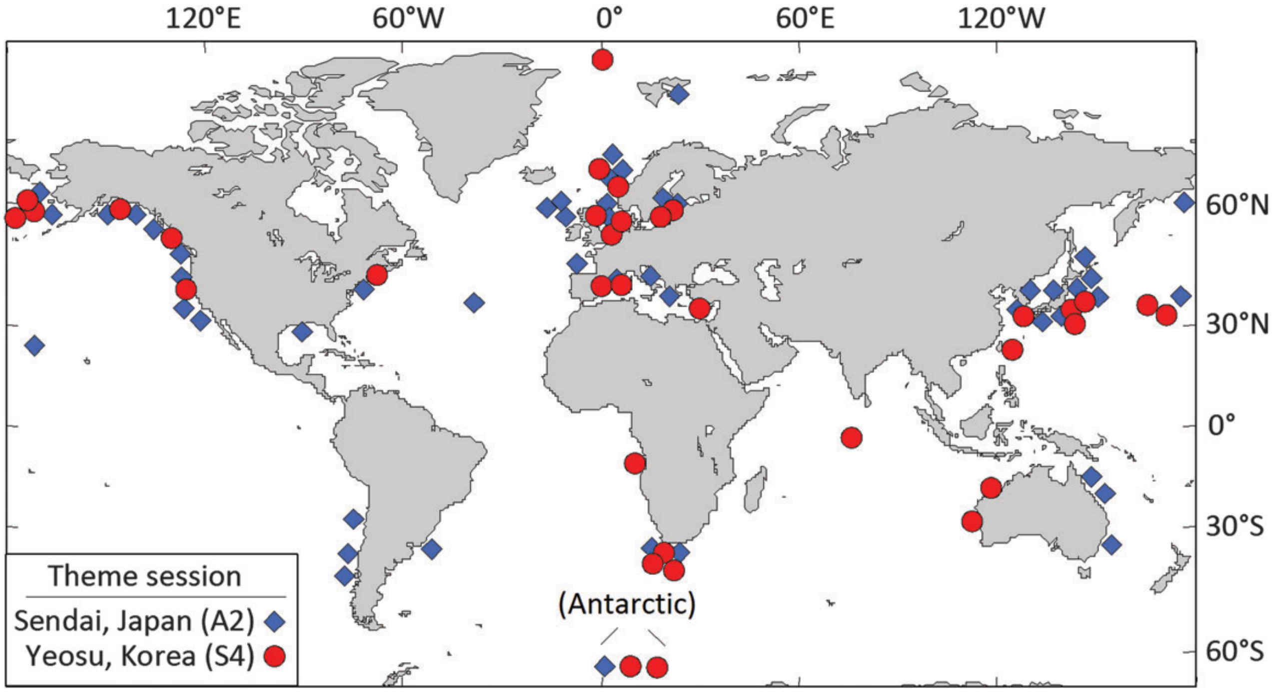
The marine science community now regularly uses climate change projections released by the Intergovernmental Panel on Climate Change (IPCC; IPCC, 2007) to make qualitative and quantitative projections of marine ecosystem responses to environmental changes associated with the accumulation of greenhouse gases in the atmosphere (e.g. climate change and ocean acidification). These projections indicate that climate change will affect fish, fisheries, and fisheries-based economies around the globe as well as broader components of marine ecosystems (ACIA, 2005; Allison *et al.*, 2009; Cochrane *et al.*, 2009; Drinkwater *et al.*, 2010; Blanchard *et al.*, 2012; Doney *et al.*, 2012; Merino *et al.*, 2012). The potential implications of climate change for marine ecosystems, and goods and services derived from marine ecosystems, have prompted the formation of integrated interdisciplinary research partnerships to quantify these impacts in many regions throughout the world (Figure 1; Barange *et al.*, 2011; Wiese *et al.*, 2012). Several international organizations [e.g. the International Council for Exploration of the Sea (ICES), the North Pacific Marine Science Organization (PICES), the Intergovernmental Oceanographic Commission (IOC), the World Meteorological Organization (WMO), and the Food and Agriculture Organization of the United Nations (FAO)] and international research programmes (e.g. Ecosystems Studies of Sub-Arctic Seas, ESSAS) have sponsored symposia focused on climate change effects on marine ecosystems to encourage international research partnerships and to widely disseminate new research findings (Valdés *et al.*, 2009; Hollowed *et al.*, 2011; Drinkwater *et al.*, 2012; Salinger *et al.*, in press).

In this paper, we synthesize existing information to elucidate the expected effects of climate change on fish and fisheries to guide future research. Other international (e.g. the IPCC) and national climate assessment teams have provided a comprehensive evaluation of climate change impacts on marine and terrestrial ecosystems on regional (e.g., Arctic Climate Impact Assessment; ACIA, 2005; Arctic Monitoring Assessment Program; AMAP, 2011; and National Climate Assessment; Howard *et al.*, 2013) and global scales (IPCC, 2007). Our synthesis focuses on the implications on a limited set of components of marine ecosystems and the goods and services they provide. We consider the following themes: (i) expected impacts on ecosystem productivity and habitat quantity and quality; (ii) impacts of changes in production and habitat on marine fish and shellfish species including effects on the community species composition, spatial distributions, interactions, and vital rates of fish and shellfish; (iii) impacts on fisheries and their associated communities; (iv) implications for food security and associated changes; and (v) uncertainty and modelling skill assessment. Using this synthesis of information, key research activities are identified that may serve to guide future investigations.

Impacts on ecosystem productivity and habitat

In a world with high atmospheric CO_2 levels, global physical models project increased sea temperatures in many regions, changes in locations and magnitudes of wind patterns and ocean currents, loss of sea ice in Polar Regions, and a rise in the sea level (IPCC, 2007). The accumulation of CO_2 in the atmosphere and associated climate changes is expected to cause ocean acidification and expansion of oligotrophic gyres (Doney *et al.*, 2012). These physical and chemical changes are expected to result in shifts in the timing, species composition, and magnitude of seasonal phytoplankton production (Figure 2; Cochrane *et al.*, 2009; Wang and Overland, 2009; Polovina *et al.*, 2011; Doney *et al.*, 2012). Changes in phytoplankton species composition may include shifts to smaller sizes that could lengthen food chains and increase assimilation losses to higher trophic levels (Morán *et al.*, 2010; Bode *et al.*, 2011).These physical, and resulting biological, changes will occur at different spatial and temporal scales throughout the world's oceans (Burrows *et al.*, 2011; Gnanadesikan *et al.*, 2011; King *et al.*, 2011). Changes in temperature, nutrient supply, mixing, light availability, pH, oxygen, and salinity are expected to affect the ecological functions and, consequently, the sustainable harvests available from the ocean's biological communities (Cochrane *et al.*, 2009; Brander, 2010; Denman *et al.*, 2011; Doney *et al.*, 2012). Exposure of marine organisms to ocean acidification and oxygen depletion will vary regionally, and other anthropogenic impacts (e. g., eutrophication) may also contribute. The vulnerability of species to these changes varies considerably (Whitney *et al.*, 2007; Feely *et al.*, 2008; Vaquer-Sunyer and Duarte, 2008; Levin *et al.*, 2009; Ries *et al.*, 2009; Rabalais *et al.*, 2010).

Regional differences in primary production are also anticipated. In mid-latitudes the mixed layer depth (MLD) is projected to shoal, which could decrease nutrient supply and ultimately primary production. For example, an intercomparison study of 11 models projected that the ocean's MLD will change (decrease or shoal) in most regions of the North Pacific during the 21st century as the result of increased stratification resulting from warming and/or freshening of the ocean surface and changes in the winds (Jang *et al.*, 2011). A study using four Earth System Models (ESMs) found a similar pattern in the North Atlantic (Steinacher *et al.*, 2010). Capotondi *et al.* (2012) also provide a global treatment of stratification changes. Primary production in mid-latitudes is expected to be reduced by this MLD shoaling through decreased nutrient supply (Hashioka and Yamanaka, 2007; Barange and Perry, 2009). However, production may increase in higher latitudes especially in seasonally ice-covered areas through increased light levels and a longer period of production and changes in the ice-edge bloom (Perrette *et al.*, 2011). Increased stratification caused by sea surface freshening and/or warming is also a main driver of ocean deoxygenation through decreased ventilation (Whitney *et al.*, 2007). Rykaczewski and Dunne (2010) hypothesized that decreased ventilation in upwelling zones may increase production due to increased residence times (the period where producers are retained in the high production zone) and nutrient remineralization; however, we note that these benefits could be offset by reduced nutrient supply. There remain important questions regarding how physical and biological processes are incorporated



Species/group	A2	S4	Species/group	A2	S4	Species/group	A2	S4
American lobster		1	European eel	1		Rabbitfish		1
Arrowtooth flounder	1	1	European hake	1		Red mullet	1	
Atlantic cod	3	2	European lobster		1	Sablefish		1
Atlantic herring	2	1	European sardine		1	Saffron cod	1	
Atlantic mackerel	1		European sprat	1		Pacific sardine	1	1
Bigeye tuna	1		Haddock		1	Seaweeds	1	
Black rockfish	1		Japanese anchovy	5		Sciaenid fishes	1	
Blue marlin	1	1	Japanese sardine	4	1	Snake pipefish	1	
Blue whiting	1		Japanese squid	2		Sockeye salmon	1	
Bluefin tuna	1		Moon jellyfish		1	Spear squid		1
Chilian hake	1		Pacific cod	2		Spiny lobster		1
Chilian sardine	1		Pacific hake	1		Striped marlin		1
Chinook salmon	1		Pacific halibut	1		Swordfish	2	
Chum salmon	1		Pacific herring	3		Skipjack tuna		1
Daubed shanny	1		Pacific oyster	1		Walleye pollock		1
Echinoderms		1	Pacific saury	1		Yellowfin tuna	2	1
Euphausids	1		Pink salmon	1		Yellowtail	2	
European anchovy		2	Plaice	1		Interspecific	14	16

Figure 1. Overview of species and geographic location of investigations presented at the 2010 ICES/PICES/FAO symposium in Sendai, Japan (session A2) and the 2012 ICES/PICES/IOC symposium in Yeosu, Korea (session S4) (also see special volume Hollowed *et al.*, 2011).

into projection models (e.g. temperature response; Taucher and Oschlies, 2011) and how these models represent coastal and shelf sea areas (e.g. Holt *et al.*, 2012).

The responses of secondary production to climate change are not clear, partially because the data available for zooplankton are more limited and the mechanisms linking secondary production to ocean conditions are complex. In the North Atlantic, the total abundance of zooplankton changed with sea surface temperature (SST) change (Richardson and Schoeman, 2004). However, this overall pattern masks important trends in the zooplankton community where the abundance of both herbivorous and carnivorous copepods increased with phytoplankton abundance but the abundance of neither group was directly correlated with SST. Several authors have recognized that the phenology of zooplankton may also be affected by a changing climate in both the Atlantic and Pacific (Chiba *et al.*, 2004; Edwards and Richardson, 2004; Mackas *et al.*, 2007). Although climate change results in an earlier onset of production cycles, the actual timing and changes in the magnitude of production

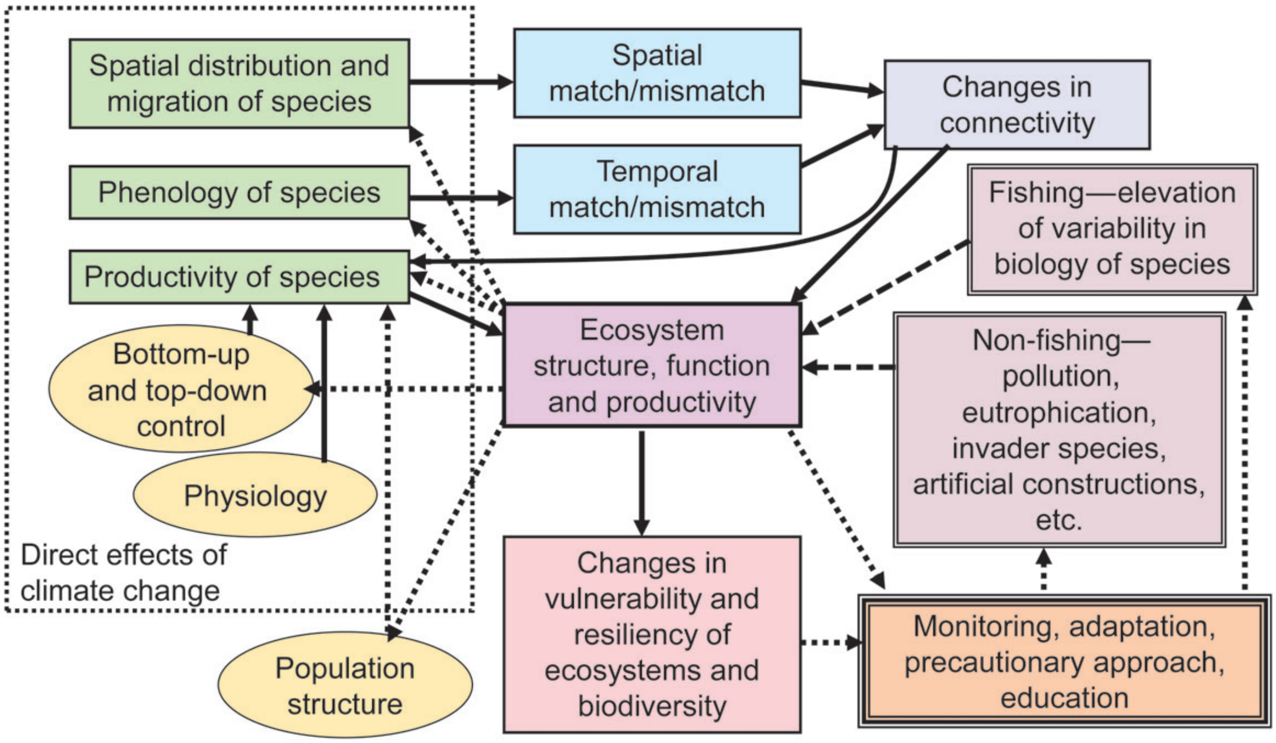


Figure 2. Conceptual pathways of direct and indirect effects of climate change and other anthropogenic factors on marine ecosystems, with their implications to adaptation and management. Solid arrows, consequences of climate change; dotted arrows, feedback routes.

varied in direction and was influenced by different mechanisms among regions (Richardson, 2008). Our limited understanding of the trophodynamic linkages between phytoplankton and zooplankton adds considerable uncertainty to projections of the responses of these groups to global change (Ito *et al.*, 2010).

Impacts on marine fish and shellfish

Climate-driven changes in the environment may affect the physiology, phenology, and behaviour of marine fish and shellfish at any life-history stage, and any of these effects may drive population-level changes in distribution and abundance (Loeng and Drinkwater, 2007; Drinkwater *et al.*, 2010; Jørgensen *et al.*, 2012). Fish and shellfish will be exposed to a complex mix of changing abiotic (e.g. temperature, salinity, MLD, oxygen, acidification) and biotic (shifting distribution, species composition, and abundance of predators and prey) conditions making it difficult to predict the responses.

Many climate-related changes have already been observed (Table 1; Perry *et al.*, 2005; Mueter and Litzow, 2008; Barange and Perry, 2009; Nye *et al.*, 2009). Kingsolver (2009) identified three types of potential responses of species to climate change: distribution changes in space and time, productivity changes, and adaptation. The extent of population-level changes may be mediated by the capacity for individual species/populations to adapt to changes in important abiotic and biotic factors through changes in the phenology of important life-history events (e.g. migration, spawning), or through changes in organismal physiology (e.g. thermal reaction norms of key traits such as growth; Pörtner, 2010) and/or through acclimation (Donelson *et al.*, 2011). Mismatches may occur when shifts in the environment lack consistent patterns or out-pace the species ability to adapt or acclimate to change (Burrows *et al.*, 2011; Duarte *et al.*, 2012).

Changes in life cycle dynamics will occur in concert with climate-induced expansion, contraction, and/or shifts in the quality and quantity of suitable habitat, and different life stages may be affected differently by changes in habitat characteristics (Petitgas *et al.*, 2013). Moreover, in some regions, changes in temperature will be accompanied by changes in other abiotic factors. For example, expected regional changes in precipitation could lead to decreases or increases in local salinities which will have major impacts on distributions and productivities of fish species in coastal and estuarine areas. Thus, perhaps future thermal conditions may be suitable for new immigrant species, but shifts in salinities could make these waters uninhabitable, illustrating the challenges of projecting future trends in species richness of fish communities.

Table 1 summarizes recent literature on observed and expected shifts in spatial distributions of marine fish and shellfish. Although there are many accounts of temperate species moving to higher latitudes, presumably in response to warming (Table 1; e.g. Beare *et al.*, 2004; Perry *et al.*, 2005), there is less evidence of contraction of ranges of boreal species (Genner *et al.*, 2004; Rijnsdorp *et al.*, 2010). The distributional changes may be the result of either active migration of living marine resources to higher latitudes or from differential productivity of local populations in lower and higher latitudes (Petitgas *et al.*, 2012), and usually the causal factors are poorly documented. The sensitivity of fish and shellfish stocks to climate change may differ depending on whether the stock is at the leading, trailing or center of the species range (Beaugrand and Kirby, 2010). In some cases, latitudinal shifts will exacerbate mismatches due to concurrent changes in the light cycle and the duration of the growing season (Kristiansen *et al.*, 2011; Shoji *et al.*, 2011).

Table 1. Recent studies of climate impacts on spatial distribution of marine fish and shellfish.

Reference	Publication year	Region	LME	Type	# Species
Cheung *et al.*	2009	Global	NA	Retrospective and Projection	
Hollowed *et al.*	In press b	Arctic/Subarctic	Barents Sea, Bering Sea, Arctic	Vulnerability	17
Huse and Ellingsen	2008	Arctic/Subarctic	Barents Sea	Retrospective and Projection	1
Ciannelli and Bailey	2005	Subarctic	E. Bering Sea	Retrospective	1
Mueter and Litzow	2008	Subarctic	E. Bering Sea	Retrospective	46
Spencer	2008	Subarctic	E. Bering Sea	Retrospective	5
Sundby and Nakken	2008	Subarctic	Norwegian Sea	Retrospective	1
Drinkwater	2005	Subarctic	North Atlantic	Projection	1
Drinkwater	2006	Subarctic	Northern North Atlantic	Retrospective	24
Dulvy *et al.*	2008	Subarctic	North Sea	Retrospective	29
Engelhard *et al.*	2011	Subarctic	North Sea	1913–2007	2
Petitgas *et al.*	2012	Subarctic	North Sea	Retrospective	1
Perry *et al.*	2005	Subarctic	North Sea	1977–2001	36
Welch *et al.*	2001	Subarctic	North Pacific Ocean	Retrospective and Projection	1
Tseng *et al.*	2011	Subarctic	Oyashio Current	Retrospective and Projection	1
Fogarty *et al.*	2008	Temperate	NE US Continental Shelf	Retrospective and Projection	1
Hare *et al.*	2012a	Temperate	NE US Continental Shelf	Projection	1
Nye *et al.*	2009	Temperate	NE US Continental Shelf	Retrospective	36
Hare *et al.*	2010	Temperate	NE US Continental Shelf	Retrospective and projection	1
Last *et al.*	2011	Temperate	Australian Shelf	Retrospective	45
Ito *et al.*	2010	Subarctic / Subtropical	Kuroshio/Oyashio current, Kuroshio Extension	Projection	1
Okunishi *et al.*	2012	Subarctic / Subtropical	Kuroshio/Oyashio current, Kuroshio Extension	Projection	1
Yatsu *et al.*	2013	Subtropical / Subtropical	Kuroshio/Oyashio current, Kuroshio Extension	Vulnerability	4
Hare *et al.*	2012b	Subtropical	SE US Continental Shelf	Projection	1
Agostini *et al.*	2008	Subtropical	California Current	Retrospective	1
King *et al.*	2011	Subtropical	California Current	Vulnerability	8
Hsieh *et al.*	2009	Subtropical	California Current	Retrospective	34
Stewart *et al.*	2012	Subtropical	California Current	Retrospective	1
Muhling *et al.*	2011	Tropical	Gulf of Mexico	Retrospective and Projection	1
Su *et al.*	2011	Tropical	Pacific Ocean	Retrospective and Projection	1
Lehodey *et al.*	2012	Tropical	Pacific Ocean	Retrospective and Projection	1

The aforementioned impact of climate change on MLD and ocean chemistry has been shown to exacerbate vertical habitat compression for some highly migratory species of billfish and tunas in the tropical Northeast Atlantic Ocean. Initial work demonstrated how the near-surface density of many high-oxygen demand species of pelagic fish was much higher in the eastern than in the western tropical Atlantic (Prince *et al.*, 2010). Eastern boundary current conditions off the west coast of Africa create an oxygen minimum zone that is much closer to the surface than in the western tropical Atlantic. The habitat compression has led to higher vulnerabilities to surface fishing gear and artificially high indications of abundance. Stramma *et al.* (2011) reported that a decrease in the upper ocean layer dissolved oxygen occurred in the tropical Northeast Atlantic. This change equated to an annual habitat loss of ~15% over the period 1960–2010. Climate change is expected to further expand the Atlantic oxygen minimum zone due to increased ocean temperatures and decreased oxygen levels, potentially threatening the sustainability of the pelagic fisheries and their associated ecosystems.

Climate change may also influence recruitment success, which will impact population productivity (e.g. Hare *et al.*, 2010; Mueter *et al.*, 2011). The resilience to shifts in production may vary by region. In many regions, fish and shellfish have evolved within systems impacted by intermittent (1–2 years) or longer term events that occur on decadal or multidecadal timescales (Baumgartner *et al.*, 1992; Hare and Mantua, 2000;

Greene and Pershing, 2007; Di Lorenzo *et al.*, 2008; Hatun *et al.*, 2009; Overland *et al.*, 2010; Alheit *et al.*, 2012). These events will probably continue to occur in the future. It is unclear whether species and communities that have experienced such variability in the past will be better adapted to future climate change. In some well-documented cases, climate variability is thought to provide opportunities for dominance switching and ecosystem reorganization (Skud, 1982; Southward *et al.*, 1988; Anderson and Piatt, 1999; Rice, 2001; Stenseth *et al.*, 2002; Chavez *et al.*, 2003). Climate change may interrupt or accelerate these cycles of dominance switching with unknown implications for both dominant and subordinate species within each phase of a cycle.

The responses of individual marine species to climate change will vary by species and region resulting in a broad spectrum of potential shifts in geographic ranges, vertical distributions, phenologies, recruitment, growth, and survival. Thus, alterations in both the structure (i.e. assembly and connectivity) and function (i.e. productivity) of biological communities are expected (Figure 2). Community responses are the most uncertain types of ecosystem responses to climate change because they involve more players (all the species in the community and the habitats that are used), their interactions, and direct as well as indirect effects of climate drivers (Stock *et al.*, 2011), as well as the spatial and temporal complexity of responses (Burrows *et al.*, 2011; Gnanadesikan *et al.*, 2011). However, there is some evidence that community assemblages tend to move in concert based on retrospective studies of species spatial patterns and species richness (Hofstede *et al.*, 2010; Lucey and Nye, 2010).

Impacts on fishers, fisheries, and fishery-dependent communities

Fisheries and fishery-dependent communities have been subjected to fluctuations in fish stocks, extreme weather events, and natural changes in climate and sea-level throughout history. Coastal livelihoods have depended on the capacity to cope with such changes through the alteration of fishing practices or switching to alternative livelihoods (Allison *et al.*, 2009; Perry *et al.*, 2011). The capacity for human communities to respond to changes in the species composition, abundance, and availability of marine resources vary regionally (Daw *et al.*, 2009). Climate change effects on fish and fisheries will occur within the context of existing and future human activities and pressures, as well as the combined effects of multiple stressors and natural agents of change acting directly and through feedback pathways (Figure 2; Ruckelshaus *et al.*, 2013). In coastal ecosystems, pollution, eutrophication, species invasions, shoreline development, and fishing generally play more important roles as drivers of change than on the high seas.

It will be difficult to tease out the additional effect of climate change from other anthropogenic activities (such as fishing; Rogers *et al.*, 2011). In some cases, where time-series are long enough or can be re-constructed, the relative importance of different forcings can be quantified (e.g. Eero *et al.*, 2011). Hare *et al.* (2010) examined the combined effects of fishing and climate in a modelling context and found that fishing likely remains the dominant pressure, especially at the historically high fishing levels. Other researchers found that it was difficult to separate the influence of anthropogenic climate change from decadal environmental variability and fishing even with a century of data (Engelhard *et al.*, 2011; Hofstede and Rijnsdorp, 2011), whereas others note that fisheries can amplify or moderate climate signals (Ottersen *et al.*, 2006). Some promising alternative approaches to address these issues include: comparative studies, experiments, and opportunistic studies of major natural or anthropogenic events (Megrey *et al.*, 2009; Murawski *et al.*, 2010). Ainsworth *et al.* (2011) used five Ecopath with Ecosim models to simulate changes in primary production, species range shifts, zooplankton community size structure in response to ocean acidification, and/or ocean deoxygenation. Fishing pressure was also included as an additional perturbation to the modelled foodweb. Their study revealed that responses to the cumulative effects of climate change and fishing may result in different patterns than would have been predicted based on individual climate effects, indicating possible interactions.

The degree to which fisheries are managed sustainably varies globally (Worm and Branch, 2012). In many regions, efforts are underway to prevent overfishing, rebuild overfished stocks, and implement an ecosystem approach to management (Murawski, 2007). In the future, the detrimental effects of climate change on fish stocks may, to some extent, be buffered in stocks that have a large and productive spawning-stock biomass, a less truncated age structure, and sustainable exploitation rates (Costello *et al.*, 2012). For example, cod have remained abundant with wide size/age structure in some areas (i.e. Øresund) where exploitation has been low, although temperatures have increased and while abundance has declined and age structure has narrowed in neighbouring areas (North Sea, Baltic Sea; Lindegren *et al.*, 2010).

Natural scientists and economists are partnering to develop the projections of how fishers may respond to changes in fish distribution and abundance (Haynie and Pfeiffer, 2012). It is unclear how complex management systems involving measures such as catch shares, bycatch limits, mixed species catch or effort limits, and spatial or temporal closures will perform as the species composition, distribution, and abundance of fish species change (Criddle, 2012). An equally challenging issue is predicting how different nations will utilize the broad range of ecosystem services that marine ecosystems provide (Halpern *et al.*, 2012). Multispecies management strategy evaluations can be used to evaluate the expected performance of management frameworks with respect to balancing these complex issues (Plagányi *et al.*, 2011). However, selecting the functional form of responses necessary to predict how fishers will respond to changes in marine resources will continue to be challenging.

The fish stocks, fisheries, and marine ecosystems that coastal communities depend on can be described as components of coupled marine social-ecological systems (Perry *et al.*, 2011). This is a particularly useful representation when considering the policy goals of preserving the health of the marine ecosystem while maintaining the supply of desirable goods and services that support human livelihoods. The representation requires specifying the scale of the system, its properties (e.g. resilience, biodiversity, productivity, social capital), how it is, or can be, governed, and what structures and information are required for such governance. Management and governance approaches may need to be adapted to the available scientific and management capacity (including financial and social resources). While strengthening capacity may put extra demands on management agencies and stakeholders, it also brings with it greater sustainable benefits through reduced uncertainty (Cochrane *et al.*, 2009, 2011). Anthropogenic climate change is an increasingly influential driver of change in such social-ecological systems, added to an already complex set of natural and anthropogenic drivers. The impacts of climate drivers are manifested on time-scales that are generally longer than most other anthropogenic drivers to which these social-ecological systems routinely respond.

There is growing recognition of the need for much stronger integration of social and ecological sciences in developing adaptation options for industries and coastal communities (Allison *et al.*, 2009; Daw *et al.*, 2009; Miller *et al.*, 2010; Gutierrez *et al.*, 2011). In this context, there may be much to learn from the dynamics of small-scale fisheries in coastal communities. Institutions such as the FAO and Worldfish are active in working on climate change adaptation in such systems. Adaptation and mitigation depend on actions and behavioural choices by the communities who are exploiting the marine resources (whether for fisheries, tourism, or other goods and services), as well as a supportive wider governance environment to address threats and constraints to adaptation and mitigation that are outside the control of local communities. Resource users and communities, within the context of an integrated ecosystem approach, must have the capacity and the will to adapt and mitigate. Viable adaptation and mitigation actions require the identification of vulnerabilities at levels from the household to macroeconomic ability to diversify livelihoods for income and the availability of environmentally sustainable livelihoods and development options. For example, "co-benefits" of both adaptation and mitigation can arise from biodiversity conservation, and protection and restoration of mangroves, and other coastal vegetation (Ruckelshaus *et al.*, 2013). Coastal resources governance can be encouraged to develop community-based disaster risk management and to integrate climate change issues into the local and national socio-economic development planning. These actions may help to prepare communities for climate change impacts on livelihoods that depend on marine resources.

Implications for future security of the food supply

The expansion of the world's human population and current levels of hunger in many parts of the world have raised concerns over the security of the food supply in the future (OECD, 2008; Godfray *et al.*, 2010, 2011). Fish currently provide essential nutrition to 4 billion people and at least 50% of the animal protein consumed by 400 million people (Laurenti, 2007; FAO, 2012), currently contributing ~17 kg of fish per capita and year. Most of the expected increase in the human population to 2050 occurs in regions where fish provide most of the non-grain dietary protein (UN-DESA, 2009; UN-WHO, 2002). The extent to which marine fisheries will be able to provide fish for the world's population in the future will depend on climate-driven changes to the productivity of the world's oceans and the performance of fisheries management systems (Bell *et al.*, 2009; Worm *et al.*, 2009; Costello *et al.*, 2012). Several scientists have used outputs from IPCC global climate models to explore quantitatively or qualitatively the potential consequences of climate change on fish and fisheries production and the implications in terms of food security targets (e.g. Merino *et al.*, 2012). These studies concluded that even with improved management, there is only a modest scope for increases in sustainable global yields for capture fisheries (Rice and Garcia, 2011; Brander, 2012). However, innovation in both large-scale and small-scale aquaculture may support a continued increase in production from marine and freshwater systems (FAO, 2008a, b; OECD, 2008; Garcia and Rosenberg, 2009; Rice and Garcia, 2011; Merino *et al.*, 2012). At present, global aquaculture production is very unevenly distributed with Asia accounting for 89% of world production (FAO, 2012). In addition, the effects of climate change on prospects for fisheries and aquaculture show strong regional differences (Merino *et al.*, 2012). Substantial political and financial investment in aquaculture will be required in suitable climatic and environmental regions if it is to provide greater contributions to food security and meet the growing demand for fish and seafood products. Growing international trade in fish products and fishing fleet capacities is accentuating regional differences in potential fish consumption (OECD-FAO, 2009; Kim, 2010). Hence, in addition to direct impacts of climate change on fish populations and communities, and thus food production, there can be indirect impacts through changes to the availability of alternative sources of protein, to the conditions suitable for intensive culture of fish and shellfish, and even to the complex interactions of climate on the global trade in food.

Uncertainty and skill assessment

Almost all attempts to forecast the impacts of climate change on fish and fisheries involve models of one form or another, and all these models will include uncertainties in both model structure and parameter values. A range of model types is used in fisheries research, from simple empirical relationships through population dynamics models to detailed system models (Hollowed *et al.*, in press a). Consideration of the diverse and complex interactions that occur between the underlying drivers of climate change and their ultimate impacts on fish and fisheries tends to require the use of relatively complex models in an effort to achieve scientific realism. However there are trade-offs since increasing model complexity to achieve greater realism can reveal additional uncertainty associated with incomplete knowledge of both the functional form and parameterization of the model (FAO, 2008a, b; FAO, 2009).

There are many such uncertainties in assessing impacts of climate change on marine ecosystems. For example, physical–biological pathways are elucidated for only a few species or functional groups. Our empirical knowledge may also not apply beyond previously observed ranges of environmental factors, or outside of historical rates and amplitudes of environmental change. Adaptation of a species to new environmental conditions is one of the most difficult issues to evaluate, especially when attempting to project connectivity among ecosystem components (Planque *et al.*, 2011). Furthermore, projecting climate change effects on fish and fisheries is challenging due to the cumulative effects of climate change, other anthropogenic activities, and feedback mechanisms (Fulton, 2011).

When physical–biological pathways are known, analysts must consider what long-range forecast and a modelling method should be used to project future states of nature. Long-term quantitative forecasts of climate change effects are generally based on outputs from one or more global circulation models (GCMs) providing boundary conditions for species or ecosystem predictive models. Inferences about biological responses to climate change based on GCM outputs commonly deal with uncertainty in the emission scenario forcing the GCMs (Hawkins and Sutton, 2009), structural uncertainty in the GCMs, internal variability, and the generally coarse resolution of the GCM, as well as uncertainty in modelling the biological responses. The relative importance of different sources of uncertainty associated with GCM predictions depend on the temporal and spatial scales of interest. Although these have not been quantified in coupled atmosphere-ocean GCMs, climate model predictions on both global and regional spatial scales have been shown to be dominated by internal variability in the climate over short time-scales (5–15 years), by model uncertainty on intermediate scales (15–40 years), and by scenario uncertainty on longer time-scales (Hawkins and Sutton, 2009). Although sensitive to emissions scenarios, there is broad agreement among climate models for some parameters such as temperature, even at short time-scales and on regional spatial scales (Deser *et al.*, 2012). Similarly, GCMs provide credible projections for regional ocean temperatures (Wang *et al.*, 2012). In contrast, derived quantities computed from the GCM output (e.g. MLD) can vary widely among models if they are based on parameters that are poorly estimated by GCMs (Jang *et al.*, 2011). Moreover, there is generally a mismatch in spatial scales between the output of the GCMs, which tend to have skill at an ocean-basin scale, and the need for resolution of finer scale ocean processes on the coastal shelves needed to project impacts on fish and fisheries (Stock *et al.*, 2011; MacKenzie *et al.*, 2012; Meier *et al.*, 2012). Although there is a clear need to capture regional-scale processes, there is no guarantee that high-resolution regional models will provide improved predictions of regional climate changes compared with GCMs (Racherla *et al.*, 2012). Therefore, it is important that scientists investigating fish responses to climate change correctly understand the robustness and uncertainty of GCM-derived variables when they use these variables to predict biological responses.

In addition to uncertainty in GCM outputs, many sources of uncertainty exist in models of biological responses (Planque *et al.*, 2011) and these should be accounted for when making projections (Hare *et al.*, 2012b). Various approaches have been used to quantify the uncertainty associated with the projections of the potential impacts of changing ocean conditions on marine fish and shellfish (e.g. Loukos *et al.*, 2003; Cheung *et al.*, 2009, 2010; Lindegren *et al.*, 2010; Fulton, 2011; Blanchard *et al.*, 2012). These include bioclimate envelope models to determine expected shifts in species distributions as a result of changes in the availability of preferred temperatures (Cheung *et al.*, 2009, 2011; Jones *et al.*, 2012), fish population models and end-to-end ecosystem models coupled to regionally downscaled climate-physical oceanographic models (e.g., MacKenzie *et al.*, 2012; Meier *et al.*, 2012). Methods used to address uncertainty include, but are not limited to, the following:

(i) Hierarchical models: these models, using a fully Bayesian or a empirical Bayes approach, provide a powerful tool for quantifying uncertainty in the estimated responses of fish populations to climate variability across multiple stocks, regions, or other "replicate" units (e.g. Mueter *et al.*, 2002; Helser *et al.*, 2012). Because of the computational demands, such models are only beginning to be applied to coupled biophysical models (e.g. Fiechter *et al.*, 2009).

(ii) Multiclimate model scenarios: the most basic approach to characterizing, if not quantifying, uncertainty about potential future responses to climate change consists of presenting results and implications from the analysis of different models and comparing and contrasting the resulting patterns across models (A'mar *et al.*, 2009; Hare *et al.*, 2010).

(iii) Ensemble modelling: this approach is commonly used to characterize uncertainty in climate projections across multiple models (Hollowed *et al.*, 2009; Wang and Overland, 2009) and has recently also been used in coupled models to examine uncertainty in both climate trajectories and in the biological responses (Ito *et al.*, 2013; Mueter *et al.*, 2011). This approach is used when analysts find that some of the different oceanographic models may perform better than others to reproduce the physical or biological oceanographic variables (e. g., temperature, plankton production) that influence the fish population dynamics (MacKenzie *et al.*, 2012). Biological models in these ensemble approaches may be driven by dynamically (e.g. Ito *et al.*, 2013) or statistically downscaled climate scenarios (Meier *et al.*, 2012; MacKenzie *et al.*, 2012). An outstanding issue in ensemble modelling is the criteria to decide which models should be included in the ensemble and/or how they should be weighted. Overland and Wang (2007) reduced a set of 22 GCMs to 10 based on how well they simulated the variability of 20th century North Pacific SSTs. Depending on which particular variables are of interest, other selection criteria could of course be devised. Additionally, good model performance evaluated based on historical or present climate does not necessarily imply certainty in predictions of future climate. However, Reichler and Kim (2008) note that the retrospective assessment of the skill of simulations relative to observations is an important way to evaluate confidence in projections.

(iv) Monte-Carlo approaches: whether or not the impacts of multiple models are investigated, a simulation (Monte Carlo) approach can generally be used to quantify uncertainty when making projections. Simulations can account for known uncertainty in future climate (random draws of climate trajectories based on different emission scenarios), in population dynamics (random draws of important population parameters from multiple univariate or, better, a single multivariate distribution), and in environment–biology relationships (random draws of parameter values for estimated or assumed functional relationships from a suitable probability distribution or from historical values; Mueter *et al.*, 2011; Planque *et al.*, 2011). A simulation approach is also utilized in the context of Management Strategy Evaluations, which allows the robustness of management strategies to be tested in the face of system uncertainty, but at the expense of considerable time and processing power (Ianelli *et al.*, 2011). The reliability of such simulations depends on specifying both the functional forms and the sampling distribution of the parameters correctly, which in some data-limited situations can be more difficult than merely estimating the central moment of the distribution correctly and using other means to incorporate uncertainties in the final result (Rochet and Rice, 2009).

(v) Parameter sensitivity: estimating the sensitivity of model outputs to changes in values of parameters is the primary means for identifying particularly influential parameters (Maunder *et al.*, 2006; Haltuch *et al.*, 2009; Peck and Hufnagl, 2012). If models are particularly sensitive to a given parameter, uncertainty about the true parameter value is an important source of overall uncertainty. Sensitivity analyses are typically used to prioritize field and laboratory studies (e.g. Peck and Hufnagl, 2012), but they can also be used to quantify uncertainty in projections by repeatedly running models across different values of the important parameters to bracket possible responses. However, this requires some knowledge of the likely distribution of parameter values and it can be challenging with complex models that have multiple, important parameters that require a large number of model runs. Gibson and Spitz (2011) and Fiechter (2012) provide examples of exploring the effects of parameter uncertainty in a nutrient–phytoplankton–zooplankton–detritus (NPZD) model on estimates of phytoplankton biomass in the eastern Bering Sea and Gulf of Alaska, respectively.

Each modelling approach has strengths and weaknesses and, as for the physical realm, multimodel projections may provide additional insights into the range of impacts to fish and fisheries that could occur under future climate change (Plagányi *et al.*, 2011; Stock *et al.*, 2011; Link *et al.*, 2012; Hollowed *et al.*, in press a). A parallel alternative is the development of models that combine principles and algorithms from several modelling frameworks, such as the inclusion of size-based ecological constraints embedded in bioclimate envelope models (Fernandes *et al.*, in press). This approach helps assess the relative strengths of each model and makes predictions more realistic and robust to assumptions.

Uncertainty in fish population simulations may be more fully characterized by using a suite of models representing different components of the climate–ocean–ecosystem complex. Compounding the uncertainty of projected fish responses is the availability of multiple representations of the fish population dynamics (e.g. single-species model, predator–prey interactions model, foodweb models, etc.) which can be coupled to the outputs from the available physical oceanographic models. Consequently, the availability of different climate-physical oceanographic and ecological models for a given system presents an opportunity to investigate a wide range of climate-oceanographic and biological model assumptions and parameterisations (e.g. via sensitivity analysis), particularly by combining the different climate-oceanographic and population models (MacKenzie *et al.*, 2012; Meier *et al.*, 2012). This approach can identify both the range and similarity of possible biological responses to different model frameworks and identify critical gaps in knowledge and new hypotheses for investigation.

Recommendations

Our synthesis elucidated several research foci that will be needed to improve the projections of climate impacts on fish and fisheries. The scale and ecological importance of climate change research for the marine community will require coordination at the local, national, and international level. In many nations, research programmes are emerging that will address the data gaps and research identified below. International marine research organizations are facilitating coordination and integration of national research at the hemispheric or global level. A key element of the success of these local, national, and international research collaborations will be the formation of interdisciplinary research teams that include earth system modellers, ecologists, fisheries scientists, and fisheries managers who will work together to develop new and improved projection capabilities for the future. We identify the following key research needs.

Increased physiological measurements

Physiological measurements of key life stages of all target marine fish species are needed. Studies should examine the effects of multiple factors on growth and bioenergetics (rates of energy losses and gains). There is an urgent need to explore interactive effects (temperature $\times$ pH $\times$ O_2) on the survival and growth performance in a variety of fish and invertebrates and to gain more data on the growth physiology of all life stages. This will not only help in the short term for linking physiological responses to statistically downscaled drivers but also in the long-term to build physiologically-based models (Pörtner and Peck, 2010; Jørgensen *et al.*, 2012) that can make use of dynamically downscaled forcing variables. Longer term experiments are also needed (Denman *et al.*, 2011) to gauge the adaptive capacity of individuals and populations and test how the sensitivity to climate-driven factors may change from one generation to the next. Operational techniques to incorporate physiology directly into stock projection type models should be explored.

Integrated ecological monitoring to identify mechanisms underlying fish and shellfish responses to environmental drivers and fishing

Systematic ocean sampling of interacting physical, chemical, and biological components must be continued to improve our understanding of the key climate-driven processes underlying observed trends. The marine environment is chronically undersampled, and we have limited historical time-series to gauge the past and recent magnitude of natural variability (abundance, distribution) of marine fish and shellfish resources relative to more recent responses to multiple, anthropogenic stressors (climate, eutrophication, pollution, etc.). Efforts to establish a global network of observations (e.g. distribution, growth) are particularly useful for tracking climate change impacts on spatial distributions and abundance. In addition, continued efforts to understand critical biomass thresholds will be needed. Knowledge of the responses of key prey fields (zooplankton and forage fish) to changes in ocean conditions will be needed to adequately project shifts in the distribution and abundance of exploited fish and shellfish stocks. Efforts to identify cost-effective ways of augmenting existing fish and shellfish surveys to collect information on these prey fields is needed to fill existing gaps in knowledge for these species (e.g. Handegard *et al.*, 2012; Ressler *et al.*, 2012). Maintenance and enhancement of fish and shellfish consumption is also needed to adequately project responses to shifting prey density and species composition. Trophodynamic monitoring (e.g. combination of stomach contents and isotope ratio) is also required to detect match–mismatch changes with climate change in future.

Short-term forecasts (1–10 years) based on observed ocean conditions

Short-term projections of biological responses using observed ocean conditions are a powerful way to assess the predictive skill of functional relationships. For physical models, these short-term projections will allow analysts to test the models ability to capture the correct physics. For harvested fish and shellfish stocks, this may be part of routine stock assessments. Over time, results from these skill assessments will provide the estimates of process error for long-term projections.

Process studies to test functional relationships

Survival and growth efficiency of early life stages of marine fish and invertebrates mostly ensures a formation of year-class productivity. Despite a century of research, many key functional relationships remain uncertain and they do not appear to be static. Studies of bioenergetic responses to climate change and their effect on larval and juvenile development (especially with respect to ocean acidification), growth and reproduction are needed. Process studies of species interactions including predator-prey responses to climate change are also needed. Studies to identify the factors influencing the distribution of juveniles would provide valuable information for modelers.

Comparative studies to test hypotheses

Continued emphasis should be placed on identifying (and/or comparing) the drivers of recruitment variability between and within species. Comparative analyses among stocks can reveal broad, climate-related patterns in productivity (e.g. Dutil and Brander, 2003; Shuntov and Temnykh, 2011) that would otherwise be elusive. Furthermore, continued process-oriented investigations are necessary to reveal how various abiotic (temperature, salinity, pH) and biotic (trophodynamic) factors interact with fishing pressure to make populations most susceptible to climate-driven changes. In terms of understanding recruitment, "non-stationarity" is an important point to consider in understanding historical and current recruitment drivers (Haltuch *et al.*, 2009). Such information should help identify how various factors contribute to changes in the productivity and distribution of marine fish observed in the last two to three decades (e.g. Rose, 2005; Rijnsdorp *et al.*, 2010) and to make more robust projections of future changes.

Improvement of ESMs and/or regional coupled biophysical models

The horizontal resolution of some GCMs is too coarse to capture shelf-region ocean processes. The spatial scales are not adequate to resolve many of the important mesoscale structures such as eddies, fronts, tides, and wind-driven upwelling that are important for biological processes. This will require downscaling from GCMs to more spatially resolved regional models. Although such regional models are being developed, it is important that there be coupling (one-way or two-way) between the regional and global models to capture the correct physics.

Coupled biophysical projection models should be extended to include the responses of fish and shellfish, fishers, and managers to climate-driven change (Stock *et al.*, 2011). New classes of models that explore the synergy between climate change effects and human activities are needed to provide meaningful and realistic projections and to allow adaptation and mitigation measures and their trade-offs, and to emerge from evolving management systems (Barange *et al.*, 2010).

Vulnerability assessments for fish, fisheries, and fishery-dependent communities

Allison *et al.* (2009) provided an important preliminary estimate of the vulnerability of countries to climate change impacts on fisheries. The authors concluded that for countries depending on fisheries but without sufficient capacity to adapt, climate-related changes in fisheries are likely to result in either greater economic hardships or to those countries missing opportunities for maintaining or improving the benefits obtained from their fisheries. Further research is required to increase the resolution of the results from the Allison *et al.* (2009) study and to explore the opportunities and constraints to adaptation in the most vulnerable countries in greater detail to allow for targeted efforts to build adaptive capacity where it is most needed and will yield the greatest benefits.

Coping strategies

As presented in this paper and in references included here, there is considerable general information available on what adaptive strategies are likely to be effective in response to climate-induced changes in fisheries and aquaculture. However, to date, there are very few examples of successful, or not so successful, implementation of adaptation strategies or plans in practice. There is an urgent need to select cases, of diverse social and ecological characteristics, where climate change is already having an impact on fisheries and aquaculture social-ecological systems and to develop, implement, and monitor adaptation plans in accordance with current best practices and understanding. This will allow the existing theories to be tested and improved where required from the lessons learned. Issues of food security and marine conservation may require new approaches to satisfy the growing demand for marine resources.

ICES–PICES strategic initiative

To coordinate and encourage research to address the some of the research needs outlined in the previous section, the governing bodies of both PICES and ICES approved the formation of the first joint ICES–PICES Strategic Initiative on Climate Change effects on Marine Ecosystems (SICCME). The key deliverables for ICES and PICES are the development of sufficient knowledge and understanding to successfully predict the future implications of climate change on marine ecosystems and the ability to use this information to develop strategies for managing living marine resources under a changing climate. The SICCME is designed to facilitate and accelerate the acquisition of new knowledge and to ensure that new knowledge is communicated and published on a schedule that would allow it to be useful to, and considered by, international scientific organizations responsible for providing advice on climate change such as the IPCC and the United Nations.

Members of the SICCME will focus their work on four critical issues:

(i) identifying techniques for predicting climate change impacts in systems impacted by decadal variability,
(ii) defining the vulnerability of commercial species to climate change and identifying which species would be most likely to experience shifts in spatial distributions,
(iii) engaging the global earth system modelling community in modelling climate change effects on marine ecosystems and identifying opportunities for collaborations, and
(iv) building response scenarios for how the human community will respond to climate changes as an extension (added dimension) of RCP scenarios described by van Vuuren *et al.* (2011).

The eight key research issues identified in this paper map into the four SICCME critical issues as follows:

(i) SICCME Critical Issue a: research recommendations 2, 3, and 5
(ii) SICCME Critical Issue b: recommendations 1, 2, 3, 4, and 7
(iii) SICCME Critical Issue c: recommendation 6
(iv) SICCME Critical Issue d: recommendations 7 and 8

This suggests that the leading marine science organizations in the northern hemisphere are well poised to facilitate advancements in our ability to understand and project the effects of climate change on marine ecosystems in the future. Their track record, to date, suggests that partnerships between science organizations will lead to more rapid global dissemination of research findings and analytical approaches through workshops, symposiums, and publications.

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