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Peer reviewed|Thesis/dissertation

UNIVERSITY OF CALIFORNIA

Santa Barbara

CAUSES AND CONSEQUENCES OF SPECIES RANGE EDGE SHIFTS

IN A WARMING OCEAN

A dissertation submitted in partial satisfaction of the  
requirements for the degree Doctor of Philosophy  
in Environmental Science and Management

by

Alexa Fredston-Hermann

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March 2020

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January 2020

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I extend particular thanks to these individuals who contributed profoundly to my dissertation work. First and foremost, my “dream team” committee: Malin Pinsky, whose insightful questions helped me think more deeply and clearly about ecology; Steve Gaines, who taught me the elusive skills of ecological intuition and connecting my small projects to the big picture; and Ben Halpern, whose wisdom about ecology is matched only by his devotion to impactful and ethical science. Matt Burgess has been an invaluable mentor, sounding board, and source of encouragement. I also thank Steve Pacala for almost a decade (and counting) of steadfast guidance on ecology and changing the world.

My PhD afforded me the opportunity to cross paths with Edgar Shaghoulian, which alone would have made the experience worthwhile. Completing my dissertation from Ithaca (or Florence, or New Delhi) with Edgar was tremendous fun, thanks in large part to his extraordinary efforts to ensure I remained happy, comfortable, focused, and caffeinated.

I dedicated my undergraduate thesis to my parents eight years ago. Their unwavering, unconditional support continues to awe me. Thanks, Mom and Dad.

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Burgess, M. G., **A. Fredston-Hermann**, D. Tilman, M. Loreau, and S. D. Gaines. (2019). Broadly inflicted stressors can cause ecosystem thinning. *Theoretical Ecology* 12(2): 207-223.

Brown, C.J., S. D. Jupiter, S. Albert, K. R. N. Anthony, R. J. Hamilton, **A. Fredston-Hermann**, B. S. Halpern, H.-Y. Lin, J. Maina, S. Mangubhai, P. J. Mumby, H. P. Possingham, M. I. Saunders, V. J. D. Tulloch, A. Wenger, and C. J. Klein. (2019). A guide to modelling priorities for managing land-based impacts on coastal ecosystems. *Journal of Applied Ecology* 56: 1106-1116.

**Fredston-Hermann, A.**, S. D. Gaines, and B. S. Halpern. (2018). Biogeographic constraints to marine conservation in a changing climate. *Annals of the New York Academy of Sciences: The Year in Ecology and Conservation Biology* 1429(1): 5-17.

Burgess, M. G., **A. Fredston-Hermann**, M. Pinsky, S. D. Gaines, and D. Tilman. (2017). Reply to Le Pape et al: Management is key to preventing marine extinctions. *Proceedings of the National Academy of Sciences* 114(31): E6275-E6276.

Burgess, M. G., C. Costello, **A. Fredston-Hermann**, M. Pinsky, S. D. Gaines, D. Tilman, and S. Polasky. (2017). Range contraction enables harvesting to extinction. *Proceedings of the National Academy of Sciences* 114(15): 3945-3950.

Press coverage by *Science Daily*, *Breitbart*, *UPI*, *Futurity*, and others.

**Fredston-Hermann, A.**, C. J. Brown, S. Albert, C. Klein, S. Mangubhai, J. L. Nelson, L. Teneva, A. Wenger, S. D. Gaines, and B. S. Halpern. (2016). Where does river runoff matter for coastal marine conservation? *Frontiers in Marine Science* 3(273): 1-10.

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- 2018 Complex dynamics of the “warm” range edge in Northeast U.S. marine species under rapid climate change (poster). Gordon Research Conference on Ocean Global Change Biology in Waterville Valley, NH
- 2018 Do TURFs confer resilience to climate change? Bren PhD Student Symposium in Santa Barbara, CA (with Casey C. O’Hara)
- 2017 Marine biogeographic controls on climate-related range shifts. Ecological Society of America Meeting in Portland, OR
- 2017 How far can marine species shift their ranges in response to climate change? UCSB Grad Slam in Santa Barbara, CA
- 2017 Predicting the effects of non-climate processes on “species on the move.” Bren PhD Student Symposium in Santa Barbara, CA (Runner-Up Best Short Talk Award)
- 2016 Non-climate drivers of species distributions in the Anthropocene. Western Society of Naturalists Meeting in Monterey, CA
- 2015 A conceptual framework for understanding the relative impact of nitrogen runoff on coastal ecosystems. UCSB Grad Slam in Santa Barbara, CA (semifinalist)
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## ABSTRACT

# CAUSES AND CONSEQUENCES OF SPECIES RANGE EDGE SHIFTS IN A WARMING OCEAN

by

Alexa Fredston-Hermann

Climate change is causing species to shift their geographical distributions, with profound consequences for nature and people around the world. These climate-related species range shifts have created opportunities for some species to thrive, threatened others with extinction, and led to cascading effects through communities and ecosystems. While historical range shifts are often correlated with climate change, this relationship alone cannot always predict range shifts, forcing natural resource managers and conservation practitioners to act amidst high uncertainty about the future. I explored this uncertainty from management and ecological perspectives. First, I synthesized guidelines and evidence from global change, biogeography, and conservation planning literature to collate concrete recommendations for marine protected area design for range-shifting species. Next, I conducted some of the first analyses of species range edge dynamics over time, using long-term annual biodiversity monitoring efforts in U.S. oceans, which allowed for detection of fine-scale changes in range edge positions. I tested several biogeographical hypotheses about whether and how much cold and warm range edges will shift in response to changing temperatures. In the Northeast

U.S., I reported that cold range edges shifted further and were more closely related to temperature than warm edges. I extended this analysis to several U.S. regions with different warming histories, where I quantified edges using a spatiotemporal model and then tested for thermal niche conservatism at range edges. I found notable regional differences, but thermal niche tracking was detected even in regions that did not warm during the study period. Species varied markedly in the degree to which they tracked temperature, even among related taxa in the same region. However, thermal niche conservatism occurred more frequently at cold range edges than at warm range edges. These patterns would not have emerged from methods using fewer time points, underscoring the need to use long time-series. This work tested biogeographical theories about the fundamental drivers of range edge dynamics, identified range edges of marine species that are expected to track climate change, and provided tools for managing range-shifting species.

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# 1. Introduction

Species are on the move. Across landscapes, seascapes, and rivers, species are shifting upwards in elevation, deeper in the oceans, and generally toward the poles (Parmesan & Yohe, 2003; Scheffers et al., 2016). This global reshuffling of biodiversity is providing opportunities for some species to spread, but threatening others with extinction; upending species interactions and ecosystem functions as communities reassemble; and affecting livelihoods, culture, food provision, disease transmission, and other dimensions of human welfare and well-being (Pecl et al., 2017). Human-caused climate change is unequivocally the culprit, yet models based on climate alone cannot predict shifts in species ranges (Sofaer et al., 2018), underscoring the need to study and incorporate greater ecological complexity into forecasts (Urban et al., 2016).

In this dissertation, I conducted studies that advance both our mechanistic understanding of climate-related range shifts, and our ability to manage range shifts given uncertain predictions. To achieve the former, I focused on the dynamics of range edges, which are highly relevant to natural resource management and conservation: range edges are where the processes of extinction and colonization actually play out. Distinct and sometimes contradictory processes may limit species distributions at the cold or warm edges, and no consensus exists on which processes should be dominant at which range edges for which species (Gaston, 2009; Sexton et al., 2009). Without understanding the fundamental drivers of range edges, it is impossible to reliably predict how they will respond to future climate change. My dissertation work provided one of the first attempts to test which theories appear to best fit how range edges have actually responded to historical climate change (although see La Sorte & Jetz, 2012).

In Chapter Two, I compared temperature tracking of cold and warm range edges of marine fishes in the Northeast US using 50 years of annual survey data. I found that cold edges seem to be tracking temperature more closely than warm edges, contradicting the expectation that marine ectotherms would be equally temperature-limited at both range edges (Sunday et al., 2012). However, my approach could not differentiate between two possible explanations for poor temperature tracking at the warm edge: that edge might have been tracking temperature but with a lag due to extinction debt (Jackson & Sax, 2010), or not tracking temperature at all if the edge was historically mediated by species interactions (Louthan et al., 2015).

I tested these hypotheses more systematically in Chapter Three, using marine survey records from three US ocean regions with differing climatic histories. I estimated the “edge thermal niche” as the cold and warm extreme temperatures where each range edge was found every year. Using the degree of thermal niche conservatism over time, I then classified range edges as tracking thermal niches, tracking with a lag, or not tracking temperature. This approach detected thermal niche tracking even in regions that did not warm significantly over the study period, and could be extended to any biogeographical hypotheses that are associated with a prediction of range edge dynamics.

While this work shed light on the fundamental drivers of range edges, and the extent to which they track temperature, it will take time to be translated into improved predictions for the future. But natural resource managers and conservation practitioners need guidance now on how to respond to and plan for climate-related range shifts, which motivated Chapter One. Many conservation initiatives are spatial in nature: to protect or manage species and ecosystems, we often define them by fixed boundaries. These initiatives may be undermined

by climate change if the focal species shift out of the managed area, or new species shift in. I reviewed how biogeographical theory can inform marine spatial planning in Chapter One, and laid out a set of concrete recommendations for what areas should be protected in the future (Fredston-Hermann et al., 2018). Taken together, these three studies tested biogeographical theories of temperature tracking at range edges of marine species, and applied biogeographical insight to the design of marine protected areas for range-shifting species.

## **2. Biogeographic constraints to marine conservation in a changing climate**

### ***A. Abstract***

The siting of protected areas to achieve management and conservation objectives draws heavily on biogeographic concepts of the spatial distribution and connectivity of species. However, the marine protected area (MPA) literature rarely acknowledges how biogeographic theories underpin MPA and MPA network design. We review which theories from biogeography have been incorporated into marine spatial planning and which relevant concepts have yet to be translated to inform the next generation of design principles. This biogeographic perspective will only become more relevant as climate change amplifies these spatial and temporal dynamics, and as species begin to shift in and out of existing MPAs. The scale of climate velocities predicted for the 21<sup>st</sup> century dwarfs all but the largest MPAs currently in place, raising the possibility that in coming decades many MPAs will no longer contain the species or assemblages they were established to protect. We present a number of design elements that could improve the success of MPAs and MPA networks in light of biogeographic processes and climate change. Biogeographically informed MPA networks of the future may resemble the habitat corridors currently being considered for many terrestrial regions.

## ***B. Introduction***

Marine conservation is an inherently spatial endeavor, whether explicitly, in the case of marine spatial planning, or implicitly, by virtue of the fact that any marine policy or management plan has a spatial jurisdiction. Thus, biogeography—the study of patterns and processes in the distributions of species—should be central to conservation planning. However, biogeography has rarely been explicitly applied to marine conservation. Here, we review the challenges facing the design of marine protected areas (MPAs)—the most widely recognized form of marine spatial conservation—in the 21<sup>st</sup> century and argue that broader use of the insights from existing biogeographic principles could substantially improve the design of MPAs in the future. MPAs are geographically delineated areas that are “designated or regulated and managed to achieve specific conservation objectives” (UNEP-WCMC & IUCN, 2016), acknowledging that MPAs that prohibit fishing (i.e., marine reserves) may be more successful at achieving conservation objectives than mixed-use MPAs (Lester & Halpern, 2008).

MPA design research has primarily focused on small-scale ecological and social processes that impact the size and shape of individual MPAs or the connectivity and representation among a network of MPAs (Halpern et al., 2008). (Social and economic dimensions of MPA design, which are critical elements but fall beyond the scope of this review, have also received significant research attention (Charles & Wilson, 2009; Halpern et al., 2013; Klein et al., 2008). MPAs are typically established to achieve a set of goals related to biodiversity conservation and more recently for fisheries management (Botsford et al., 2009). Given their small-scale goals and typically small size, most single MPAs are unlikely to contribute significantly to the conservation outcomes of an entire species (Roberts et al.,



2001). Recognition of this constraint has prompted calls for larger MPAs, MPA networks, and the integration of MPAs into ecosystem-based management (Halpern et al., 2010; Halpern & Warner, 2003; Roberts et al., 2001). As MPAs are gradually applied at larger spatial scales (Wood et al., 2008) and as climate change increases the possibility of local extinction within small MPAs, understanding and predicting species range limits and future range shifts is becoming increasingly important to MPA design.

The explicit application of biogeography to marine conservation has primarily focused on defining unique assemblages of species and setting conservation targets for those assemblages. These targets are commonly embodied in the conservation planning principles of representation (which guides MPA placement to include locations with representative examples of the full suite of species) and replication (which spreads risk among multiple MPAs within a biogeographic region) (Margules & Pressey, 2000; Roberts et al., 2003). Much less directly, MPA planning also borrows principles from biogeography when accounting for and modeling larval dispersal and connectivity, but rarely in a systematic way (Gaines et al., 2010). Other active areas of research in marine biogeography, such as within-range distributions of individuals within species, are rarely acknowledged in MPA-design research despite having the possibility to profoundly influence optimization models of MPAs and MPA networks, including the differential benefits of protecting different places within a species' range (Sagarin et al., 2006; Sagarin & Gaines, 2002). In general, research on MPA design tends to incorporate more sophisticated models of physical dynamics (e.g., advection-diffusion of currents, temperature, pH) than of ecological dynamics (e.g., within-range species distributions, habitat associations, migrations and range shifts, species interactions, adult movement) (Botsford et al., 2009; Brown, Harborne, et al., 2016; Levy & Ban, 2013;

Makino et al., 2015; Mumby et al., 2011). However, ecological dynamics clearly affect the abundance and distribution of species over space and time, and thus possibly the success of MPAs in achieving diverse conservation goals. A clear example of where such dynamics are considered is with trophic cascades, where protection of top predators can have implications for the abundance and viability of prey species that may also be conservation targets (Estes et al., 2016; McDonald-Madden et al., 2016). Less dramatic but equally important predator-prey, competition, facilitation and other interactions are not typically accounted for in MPA design, yet they can profoundly affect the pace and ultimate outcome of conservation (Samhuri et al., 2017).

Biogeography will become even more important to MPA design under climate change, which is predicted to cause rapid and heterogeneous changes in species distributions, with uncertainty in these changes among climate change scenarios (García Molinos et al., 2015). Many factors will influence if or how species respond to climate change, most notably the regional intensity of climate change (Pinsky et al., 2013) but also the pressures from other human activities. Most existing studies on climate change and MPAs have suggested a focus on reducing cumulative impacts and/or building resilience within MPAs, and risk-spreading and buffering catastrophic events in MPA networks, as a way to mitigate climate impacts (Keller et al., 2009; Magris et al., 2014a; Roberts et al., 2017). Missing from this literature is consideration of how biogeographic factors may alter species responses to climate change, and thus conservation strategies. Here, we contribute a biogeographic perspective to this literature by reviewing how MPAs have adopted biogeographic principles, which principles might be useful if better incorporated, and how biogeography can inform MPA planning under climate change. To inform these recommendations, we present a simple analysis of the

spatial scale of most existing MPAs relative to species' range sizes and marine climate velocities from 1960-2009. We focus on large MPAs and MPA networks, which are relatively rare but becoming increasingly common and have outsize importance in marine conservation; there are 75 MPAs in the world that exceed 100,000 km<sup>2</sup> of protected oceans, while almost 14,000 MPAs exist under 100 km<sup>2</sup> (UNEP-WCMC & IUCN, 2016).

### ***C. How biogeography affects MPA success***

The design of MPAs and MPA networks—i.e., their size, shape, location, and spacing—ultimately rests on principles adopted from biogeography. In the theory and application of MPAs, biogeography is commonly used to subdivide oceans into areas with relatively consistent and distinct habitats, flora, and fauna. These biogeographic “regions”, “provinces”, or “zones” are often used as boundaries for defining where and how to achieve representation and replication goals (Beger et al., 2015; Fernandes et al., 2005). The most common tools used to design MPA networks—Zonation and Marxan—can be applied to achieve target levels of representation and replication, if provided with biogeographic information (i.e., the spatial extent of species and habitats) (Moilanen et al., 2009). Treating biogeographic representation and replication as a conservation target is considered the “best practice” for MPA network design and has been widely applied (Beger et al., 2015; Fernandes et al., 2005).

However, marine conservation planning has not yet applied the major caveat of using these biogeographic units: they can move on a variety of time scales (Lourie & Vincent, 2004; MacArthur, 1972). MPA planners who make decisions based on biogeographic units rarely acknowledge that the edges of species distributions, which in aggregate define

biogeographic provinces, can be quite dynamic. An MPA, or a network of MPAs, designed to represent a biogeographic province with replication might fail to do so if biotic and abiotic processes that drive range fluctuations are not considered.

Biogeography theory has also strongly influenced MPA design through aspects of the theory of island biogeography. Most notably, early MPA design models (Hastings & Botsford, 2003) made the extreme case assumption that habitats outside of MPAs had no populations, which is highly analogous to the equilibrium theory of island biogeography (MacArthur & Wilson, 1963, 1967). In that framework, populations are assumed to only persist within MPAs. Therefore, a patch model of MPAs where there is no adult survival or larval production outside of protected areas is effectively identical to a network of islands for terrestrial species.

As a discipline, biogeography has disproportionately focused on terrestrial systems, with quantitative and theory-driven marine biogeographic studies relatively rare (Pinheiro et al., 2017). More recently, marine biogeography has evolved rapidly, progressing far beyond simple models of immigration and extinction to shed light on complex dispersal processes, range dynamics, and connectivity in the sea (Cowen, Paris, & Srinivasan, 2006; Cowen & Sponaugle, 2009; Gaines, Gaylord, & Largier, 2003; Gaines et al., 2009; Kinlan, Gaines, & Lester, 2005; Siegel, Kinlan, Gaylord, & Gaines, 2003). Recent models of MPAs and MPA networks rely on metapopulation models, which in turn incorporate source-sink dynamics and persistence (Almany et al., 2009; Bode et al., 2016; Burgess et al., 2014; White et al., 2010). While the field of metapopulation dynamics is not considered a derivative of biogeography, it inevitably draws upon marine biogeographic principles regarding dispersal and connectivity when applied to spatially explicit scenarios such as MPA planning.

The treatment of dispersal in metapopulation models for MPA planning has become remarkably sophisticated (Beger et al., 2015) but has historically lacked empirical data on larval dispersal for validation (Burgess et al., 2014). Several studies have attempted to ground-truth dispersal models with real data, primarily for tropical corals and reef fish (Jones et al., 2009; Pelc et al., 2010; Sponaugle et al., 2012). These efforts to improve larval dispersal models are crucial for accurate and informed MPA planning. Unfortunately, less research exists on the spatial dynamics of adults, which can also inform metapopulation models, even for species that accomplish most of their movement as larvae. The significance of adult spatial dynamics for mobile marine species is self-evident, and has recently been incorporated into some metapopulation models (Botsford et al., 2009; Brown et al., 2016). However, within-range adult distributions of sessile species can also shed light on important dispersal processes and inform the design of MPAs.

Within-range dynamics of species, and the processes that establish range edges, have been an area of interest in biogeography for decades. In 1972, Robert MacArthur wrote that “patterns on islands, of species diversity, and of tropical communities are already clear and even moderately well understood, while patterns of single species’ ranges still seem to be catalogs of special cases” (MacArthur, 1972). MacArthur and others wrote extensively on the role of climate, habitat, and species interactions in establishing range edges, but very little was known about how individuals are arrayed within the species range. The only generalizable ecological rule on the topic is the abundant-center hypothesis, which originated in the early 20<sup>th</sup> century with the work of Grinnell and others (Grinnell, 1922) and predicts that a species’ population density is highest at the geographic center and declines toward the range edges (Guo et al., 2005; Westman, 1980). Unfortunately, the abundant-center

hypothesis is not consistently supported by data, and no universal theory has emerged to replace it (Dallas et al., 2017; Sagarin et al., 2006). In the marine environment, it is not uncommon for coastal and intertidal invertebrates to be most abundant at one range edge, possibly because their distributions are mediated by oceanographic flow regimes (Gaines et al., 2009).

Analyses of MPAs that use real data on adult and larval distributions may be able to sidestep the theoretical debate regarding the drivers of range edges and within-range abundance. However, models of MPAs and MPA networks should critically examine their biogeographic assumptions, including whether the within-range distributions (i.e., spatial population matrices) used are justified. Even the size of a species' range is rarely considered in conservation planning: a recent terrestrial study found that incorporating range size into an optimization model for conservation hotspots led to very different recommendations than using other targets such as species richness (Veach et al., 2017). The identification of marine conservation hotspots might be similarly influenced by considering range size. Embracing this and other biogeographic perspectives on marine spatial planning will almost certainly lead to management recommendations that are more realistic for the dynamic and complex oceans.

#### ***D. Biogeography and MPAs under a changing climate***

Biogeography is devoted to understanding and modeling the spatial arrangement of individuals, populations, and species. These dynamics are applicable to all MPA-design processes, but they are unequivocally crucial for anticipating the influence of climate change on MPAs. Climate change is predicted to affect species via multiple pathways at numerous

scales, including altered survivorship, growth, reproduction, spatial distributions, and species interactions (Scheffers et al., 2016). Past reviews on MPAs and climate change have made qualitative recommendations to enhance resilience via risk-spreading and MPA connectivity (Green et al., 2014; Keller et al., 2009; Magris et al., 2014b; McLeod et al., 2009). However, they have rarely addressed whether species will persist in their current distributions and abundances, or at all—a fundamental question that must be answered as a precondition to MPA planning. Predicting the future state of species and communities protected by MPAs requires modeling both their distributions and their persistence.

Persistence of populations is not widely incorporated into models of MPAs and networks, although literature on the topic is rapidly growing (Almany et al., 2009; Bode et al., 2016; Burgess et al., 2014; White et al., 2010). As described above, biogeographic theory on larval dispersal and source-sink dynamics clearly underpins this area of research on MPAs. These metapopulation models may inform the fine-scale siting of MPAs in the climate change context by predicting which habitats will be colonized by, and support persistent populations of, species that are shifting their ranges.

Modeling future species distributions has received intensive research effort in recent years, as global climate models have become widely available for use in ecology (Burrows et al., 2011; García Molinos et al., 2015). These models are becoming increasingly realistic with endeavors to incorporate species interactions, multiple climate variables, physiological responses, and other dimensions in addition to projected temperature changes (Urban et al., 2016). Although biotic processes have been a recent focus of species distribution modeling, models of physical processes associated with climate change—such as thermal exposure that might lead to coral bleaching (Magris et al., 2014b), changing patterns in oceanic currents

that could influence larval dispersal (Wilson et al., 2016), and effects of temperature on larval development times and dispersal distances (O'Connor et al., 2007)—are equally if not more sophisticated.

Indeed, distribution models using “climate velocity” (the rate and direction of thermal envelope shift predicted for a spatial cell) may have outstripped the empirical evidence for range shifts, which shows highly individualistic responses to 20<sup>th</sup> century warming, including species that do not shift their ranges at all or shift in an unexpected direction (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Lenoir & Svenning, 2015; Pinsky et al., 2013). Given the multitude of biotic and abiotic processes that influence species range edges, it is unsurprising that temperature alone does not explain all of the observed variance in Anthropocene species distributions (Urban et al., 2016). In the oceans, biogeographic processes—particularly biogeographic boundaries—may play a critical and overlooked role in mediating species’ responses to climate change. Marine biogeographic boundaries often occur at major breaks in coastal currents, which inhibit larval dispersal in one or both directions along the coastline (Gaylord & Gaines, 2000; Sorte, 2013). Due to their ability to influence dispersal, marine biogeographic boundaries may pose a particular concern for species that migrate in response to climate change. Biogeographic theory on larval dispersal can inform predictions of future species distributions and persistence, and thus improve forecasting for communities protected by MPAs.

### ***E. Recommendations for improving MPA design***

Recent efforts to evaluate the utility of MPAs in the 21<sup>st</sup> century frequently focus on building resilience and reducing cumulative impacts, which would in theory buffer the worst



effects of climate change in the oceans (Roberts et al., 2017). However, there has been relatively little analysis of the spatial scales of important processes in MPA planning, despite widespread advocacy for larger and more connected MPAs. We provide a quantitative comparison of the scale of MPAs in contrast to climate velocities and species' ranges sizes, and provide novel recommendations for MPA design given their diminutive size relative to biogeographic processes.

We examine the size distribution of existing MPAs and MPA networks relative to marine climate velocities from 1960-2009 and projected range sizes of marine species (Fig 1.1). As a simplifying first approximation, we only consider the latitudinal extent—i.e., “height”—of MPAs and species' ranges. Marine bony and cartilaginous fishes typically have very large geographic ranges, with a median range latitudinal extent of  $4384 \text{ km} \pm 2970 \text{ km}$  (standard deviation). Climate velocities from 1960-2009 exceeded 200 km/dec in some areas, although many parts of the ocean surface had minimal temperature change during this period. However, the median latitudinal extent for MPAs is just 2.7 km—several orders of magnitude smaller than many range shifts already documented in the oceans (Poloczanska et al., 2013).

With the exception of MPAs that are either very large, in networks, or in places that are not warming rapidly, this scale mismatch suggests that many MPAs are at risk of losing the species they were originally established to protect. MPAs that were created to protect geomorphological units, habitats, or assemblages (e.g., coral reefs or seamounts) are still likely to be undermined by climate-related range shifts of individual species, and the loss of the services they provision. Individual MPAs outside of networks, except in the rare cases of giant MPAs that approach the scale of a species' geographic range, appear unlikely to

provide substantial benefits to an entire species. Although individual MPAs may certainly offer local benefits to populations and ecosystem function, most do not have the spatial extent necessary to protect an entire species (except endemics with tiny ranges) from the effects of climate change.

Given this scale mismatch, we offer the following recommendations for MPA design in the Anthropocene. First, while small MPAs are unlikely to contribute materially to species-level conservation, they can nonetheless have an outsized impact if sited with consideration of climate velocity and the range size of species of interest. For example, MPAs intended to protect single species that are sited closer to the leading (often poleward) edge of the geographic range will keep that species within their boundaries far longer than MPAs sited at the trailing (often equatorward) edge (Fig. 1.2A vs. 1.2B). However, this approach is likely impractical for MPAs intended to protect diverse species assemblages, because each species has a different geographic range and range size, and tends to shift at different rates. In addition, given the scale of climate velocities (Fig. 1.1), almost no single fixed MPA can feasibly protect most marine species for decades and centuries to come.

Very large MPAs may achieve that goal, although they are exceedingly difficult to design and manage effectively (Pala, 2013; Wilhelm et al., 2014). Setting aside the complex political context of large MPAs (Leenhardt et al., 2013), our second set of recommendations address the siting and design of large MPAs should they be implemented. Many existing large MPAs are designed to be “wide” (e.g., the Mid-Atlantic Ridge North of the Azores), to cover habitats that occur at specific latitudes (e.g., reefs and seamounts), achieving replication and representation goals in the present but not necessarily protecting habitats that might be important in the future (Davies et al., 2017). To protect future populations *in places*

*where species are predicted to shift* (which may not be the case in tropical ecosystems such as coral reefs for which habitat is unavailable past certain latitudes), large MPAs should be designed as “tall” rather than “wide”. This strategy would encompass more habitat that might continue to support species of interest in the future, based on climate velocity predictions (see design of MPA “chains”, below). To cover 50% of the latitudinal extent of a median species range in our dataset, a large MPA would have to extend 4329 km in latitude, or approximately 39 degrees. For reference, the Coral Sea Commonwealth Marine Reserve—one of the world’s largest MPAs—covers 14.84 degrees of latitude. Large MPAs should also be designed to encompass features with disproportionate conservation significance (Table 1.1), discussed in more detail below. In general, we do not consider large MPAs to be the most pragmatic tools for mitigating the effects of climate change, given the extraordinary challenges in implementing and enforcing them and the massive scale of observed and predicted range shifts.

Third, MPA “chains”—networks that are at the scale of or larger than most species range sizes—along a coastline can help mitigate most of the challenges MPAs will face from shifting ranges of species. These stepping stone chains can act like terrestrial migration corridors, which have been recently proposed to protect terrestrial biota with poleward-shifting ranges (Batllori et al., 2017; Lawler et al., 2013; McGuire et al., 2016). Individual MPAs in these networks could be relatively small, as their purpose would be to serve as a stepping-stone for shifting species; and the spacing between these MPAs could be determined using biogeographically informed connectivity models (mentioned earlier) to ensure that important species can disperse between them (Andrello et al., 2017). However, the extent of such an MPA chain should encompass a substantial portion of the geographic

range of the species or assemblage of interest, in addition to a more distal area that the species or assemblage might shift into (the location and extent of which would be dictated by climate velocity projections) (Fig. 1.2C). Although an ideal scenario would involve the instantaneous creation of these MPA networks following a unified conservation plan informed by the biogeographic principles described here, we note that MPA chains that emerge from *ad hoc* or sequential planning processes are still likely to confer conservation benefits (Meir et al., 2004). However, in scenarios with high uncertainty and/or limited funding, it may be advantageous to strategically postpone conservation interventions to ensure an optimal outcome (Iacona et al., 2017).

This proposition builds upon, and far exceeds, past calls for MPA networks of up to several hundred kilometers (Halpern & Warner, 2003; McLeod et al., 2009; Shanks et al., 2003). For example, for a species whose range extends 1000 km from north to south, in a region where climate velocity has been estimated at 50 km/dec, an ideal MPA chain intended to protect the species for a century would have to extend most of the species' current range plus an additional 500 km along the path of climate velocity. Although most range-shifting marine species are moving poleward (Poloczanska et al., 2013), more refined climate velocity projections for marine assemblages are now available for the global oceans and can be used to inform the orientation of MPA chains (García Molinos et al., 2015). Climate projections have already been used to anticipate climate velocity in North American terrestrial protected areas (Batllori et al., 2017).

An MPA-chain strategy may be effective at protecting species that are shifting their ranges. However, species cannot shift their ranges indefinitely, and indeed some are tracking climate velocity slowly or not at all (Pinsky et al., 2013). Thus, our fourth recommendation is

to protect areas with high conservation value to species experiencing climate change, such as regions that harbor genetically diverse populations, or areas where species may pass through or aggregate (Table 1.1). This approach builds upon existing recommendations to protect unique biophysical features in the oceans, such as seamounts, using MPAs (Fernandes et al., 2005; Magris et al., 2014b). The broader conservation literature has also recommended the protection of populations that contribute to genetic diversity, which is generally predicted to be reduced by climate change (Arenas et al., 2012; Bellard et al., 2012), and the protection of corridors through which wildlife may migrate in response to climate change (Lawler et al., 2013; McGuire et al., 2016).

We propose additional features for protection with MPAs that, for biogeographic reasons, may aggregate individuals and species in the future and become hotspots of species richness (Table 1.1). These include biogeographic boundaries that arise from currents, particularly those that account for poleward range edges and may inhibit further range shifts (Gaylord & Gaines, 2000). Marine biogeographic boundaries are often porous and asymmetrical, so knowledge of regional dispersal dynamics and the ability of species with certain life history traits to colonize across specific boundaries will be critical (Gaines et al., 2009; Pappalardo et al., 2015; Sorte, 2013). These features are somewhat analogous to alpine regions where terrestrial species' trailing edges are shifting upslope, but their leading edges cannot extend further, leading to an overall reduction in habitat and often a concomitant population decline (Gottfried et al., 2012; Wilson et al., 2005). Similarly, because species cannot spread beyond their required habitats, the poleward edges of key marine habitats are likely to play disproportionately large conservation roles (Wernberg et al., 2011). Due to the heterogeneous nature of climate change, some parts of the ocean are predicted to warm much

faster than others, and thermal refugia—patches with climatic conditions that have not and are not predicted to change dramatically—could also accumulate species and warrant additional protection (Burrows et al., 2014), although those refugia may be rare in the oceans (Ban et al., 2016). The paths taken by species shifting in response to climate change, termed “migration corridors” in terrestrial ecology, are also likely to accumulate species in the future and contribute substantially to conservation outcomes (Lawler et al., 2013; McGuire et al., 2016). This concept is most relevant to the coastal oceans, where narrow bands of habitat (possibly along climate velocity trajectories and/or MPA chains) may serve as a conduit for many species shifting their ranges in the future.

Recognizing that most MPA planning is conducted with spatial prioritization tools that are designed for flexible applications, we stress that all of these considerations can be incorporated into Marxan, Zonation, and other software (Moilanen et al., 2009). For example, poleward range edges may be classified as distinct features with their own representation targets, and the arrangement of MPA chains may be optimized with these tools using projected future species distributions as inputs. In particular, all of the features noted in Table 1.1 can be easily classified as high-value areas for conservation with these spatial prioritization tools.

Managed relocation (also termed assisted migration or colonization) is a promising but controversial management strategy to conserve species that are declining in their historic ranges. The ecological, ethical, legal, and other challenges facing this intervention have been reviewed elsewhere (Schwartz et al., 2012). Managed relocation has typically been considered an intervention that applies to species that disperse slowly relative to climate velocity, or that have limited habitat availability, such as endemic species with small ranges

(Bellemare et al., 2017); it has been most extensively studied in the terrestrial environment, particularly for plants (Vitt et al., 2010).

From a biogeographic perspective, we note that species' ranges and dispersal patterns will influence both the need for, and the success of, managed relocation. Species with smaller geographic ranges are often more vulnerable to extinction and may need additional conservation efforts (Purvis et al., 2000). However, the success of those conservation efforts for marine species may hinge on dispersal patterns. As discussed above, biogeography can help to identify regions where marine species may get "stuck" at a dispersal barrier, providing an early flag for species that may need managed relocation. Indeed, managed relocation may be an ideal tool for helping range-shifting species to cross biogeographic boundaries. The same biogeographic principles may also be applied to identify potential habitats for relocation with suitable flow fields that favor self-recruitment.

## ***F. Conclusions***

Many present elements of MPA planning and design have been derived from biogeography, though often without recognizing that legacy. However, some concepts from biogeography have still not been incorporated into MPA models and theory, particularly regarding the spatial dynamics of marine populations. Biogeographic principles suggest concrete and novel recommendations for MPA design, including the protection of areas that are predicted to aggregate species in this century, and the establishment of massive MPA networks at scales comparable to the geographic ranges of species of interest. These recommendations build upon past calls for larger MPAs and MPA networks. Several relevant topics merit continued research efforts in order to improve MPA design, including the

within-range spatial dynamics of marine species, the role of flow fields in structuring dispersal, and the improvement of range shift predictions. By highlighting lessons learned and opportunities to apply them in the climate change context, we hope to improve the design of future MPAs.

### ***G. Tables***

Table 1.1. Unique features in the oceans that (presently or in the future) will have disproportionately high conservation value to species experiencing climate change. Most of these features are predicted to aggregate populations and thus become hotspots of species richness.



<b>Feature to Protect</b>	<b>Justification</b>	<b>Example(s)</b>	<b>References</b>
Migration corridors	Terrestrial conservation planning has combined climate velocity models with habitat and species distribution data to identify corridors through which species may shift, which should also be conservation priorities in the ocean.	The southern Appalachian Mountains, which may have served as thermal refugia in the past, are predicted to facilitate the climate-related range shift of many southeast U.S. terrestrial animals.	(Lawler et al., 2013; McGuire et al., 2016)
Biogeographic boundaries that lie in path of climate velocity	Coastal marine species that rely on larval dispersal for colonization often cannot cross major breaks in ocean currents. These species may “pile up” against a poleward biogeographic boundary if they experience mortality at the equatorward edge.	Despite experiencing substantial warming since earliest records, few intertidal species on the east coast of Australia have shifted markedly poleward. A marine biogeographic boundary in the region may be impeding larval dispersal in the direction predicted by climate velocity.	(Gaines et al., 2009; Gaylord & Gaines, 2000; Poloczanska et al., 2011; Sorte, 2013)
Poleward habitat edges	Similar to above, species may pile up at the edge of a habitat that is more climatically suitable than the rest of their historic ranges.	Australian macroalgae in the Indian and Pacific Oceans have retreated from their historic equatorward edge, but cannot colonize poleward past the edge of the continental shelf. Similarly, the ability of North Sea demersal fish to track climate velocity may be constrained by the availability (beyond their historic ranges) of suitable habitat at their preferred depths.	(Rutterford et al., 2015; Wernberg et al., 2011)
Thermal refugia / microrefugia (sites with minimal climate velocity or observed climate change) and climate sinks (sites where many climate velocity trajectories converge, representing locally “lost” climates)	Global climate models predict heterogeneous ocean warming, including thermal refugia and climate sinks that are predicted to accumulate species because they have warmed less than the surrounding environment.	Marine climate sinks may arise when equatorward coastlines block climate velocity trajectories, such as in southern France. Although many parts of the global oceans are not experiencing rapid warming, regional studies (e.g., Brazil, British Columbia) found only a tiny percentage of spatial cells studied that have not and will not experience changing climate conditions.	(Ban et al., 2016; Burrows et al., 2014; Dobrowski, 2011; Magris et al., 2015)
High genetic diversity populations	Some semi-isolated populations are genetically distinct and contribute to high beta-diversity that can increase a species’ adaptive capacity. This is sometimes true of equatorward populations of terrestrial and shallow coastal species, which may represent genetically differentiated survivors of past glacial maxima.	The southern range edge of <i>Bifurcaria bifurcata</i> , an eastern Atlantic macroalgal species, harbors most of the species’ genetic diversity; an ecological niche model for this species predicts loss of the southern population under high (but not low) emissions scenarios. Populations of <i>Macoma balthica</i> , a common intertidal bivalve in Europe, exhibit high genetic diversity at the southern range limit—where the range has also contracted due to warming.	(Arenas et al., 2012; Becquet et al., 2012; Neiva et al., 2015)

## H. Figures

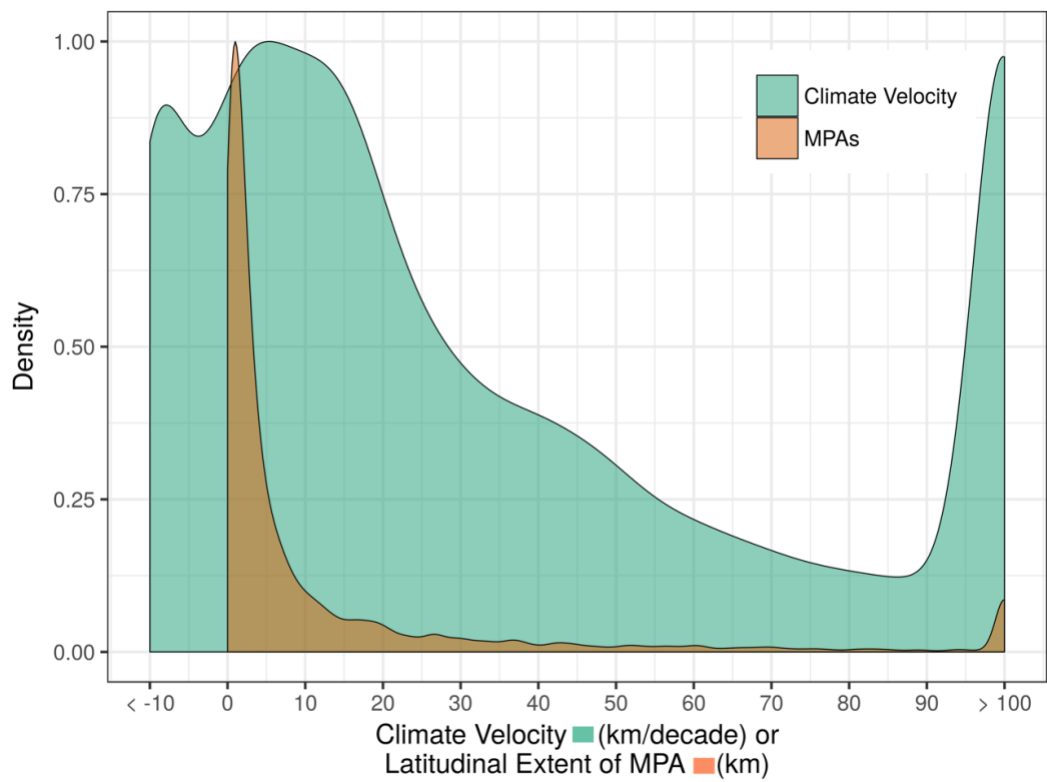
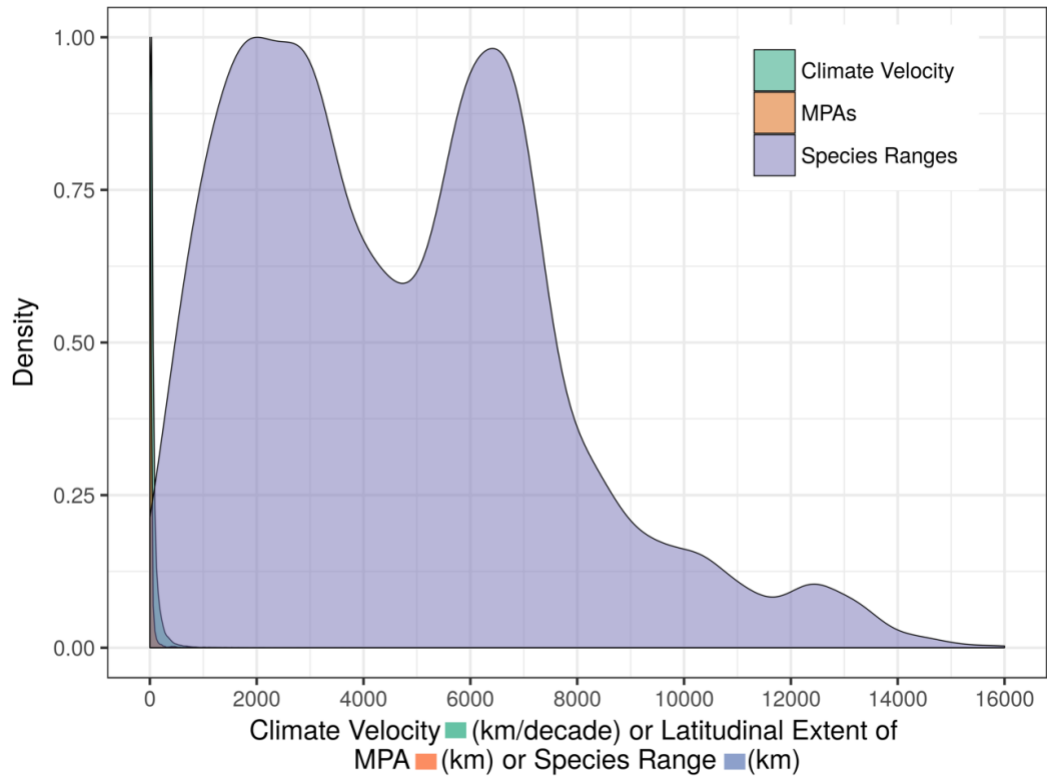


Figure 1.1. Spatial scale of MPAs (latitudinal [north-south] extent, N=5,727), marine fish species ranges (latitudinal [north-south] range extent, N=12,345), and positive (warming) climate velocities of sea surface temperature from 1960-2009 (N=43,425), displayed using a smoothed density function with the most frequent value scaled to 1 for each data series (A). Panel B shows fine-scale density distribution of MPA sizes and climate velocities, including negative (cooling) climate velocities; values greater than 100 km or km/decade and negative climate velocities (i.e., values beyond the x-axis bounds) were binned for visual purposes. Latitudinal extent of MPAs and MPA networks was extracted from the World Database of Protected Areas (UNEP-WCMC & IUCN, 2016) (WDPA) using only data on protected areas in IUCN protection classes I-IV (the stricter conservation classes that prohibit most extractive uses) (Klein et al., 2015a), and using the WDPA classification of networks (Klein et al., 2015b). MPA latitudinal extent was calculated as the difference between the maximum and minimum latitude of a bounding box drawn around each MPA in the filtered list from the WDPA; each sample in the distribution plotted here is one MPA. Range data is based on Aquamaps predicted spatial distributions for cartilaginous and bony fishes (Kaschner et al., 2016), with probabilities of occurrence below 60% excluded to be conservative. Range latitudinal extent was calculated as the difference between the maximum and minimum latitudes of spatial cells where a species' probability of occurrence was greater than or equal to 60%, measuring from the center of the half-degree square cells used in Aquamaps; each sample in the distribution plotted here is one marine bony or cartilaginous fish species' range. Climate velocity was calculated as "the ratio of the long-term temperature trend (in °C/year) to the two-dimensional spatial gradient in temperature (in °C/km, calculated over a 3°-by-3° grid), oriented along the spatial gradient" (Burrows et al., 2011) and is presented in km/dec up to 16,000 km for 1°-by-1° cells in the global oceans based on 1960-2009 data (provided by M. Burrows); each sample plotted here is the climate velocity for one marine spatial cell (Burrows et al., 2011).

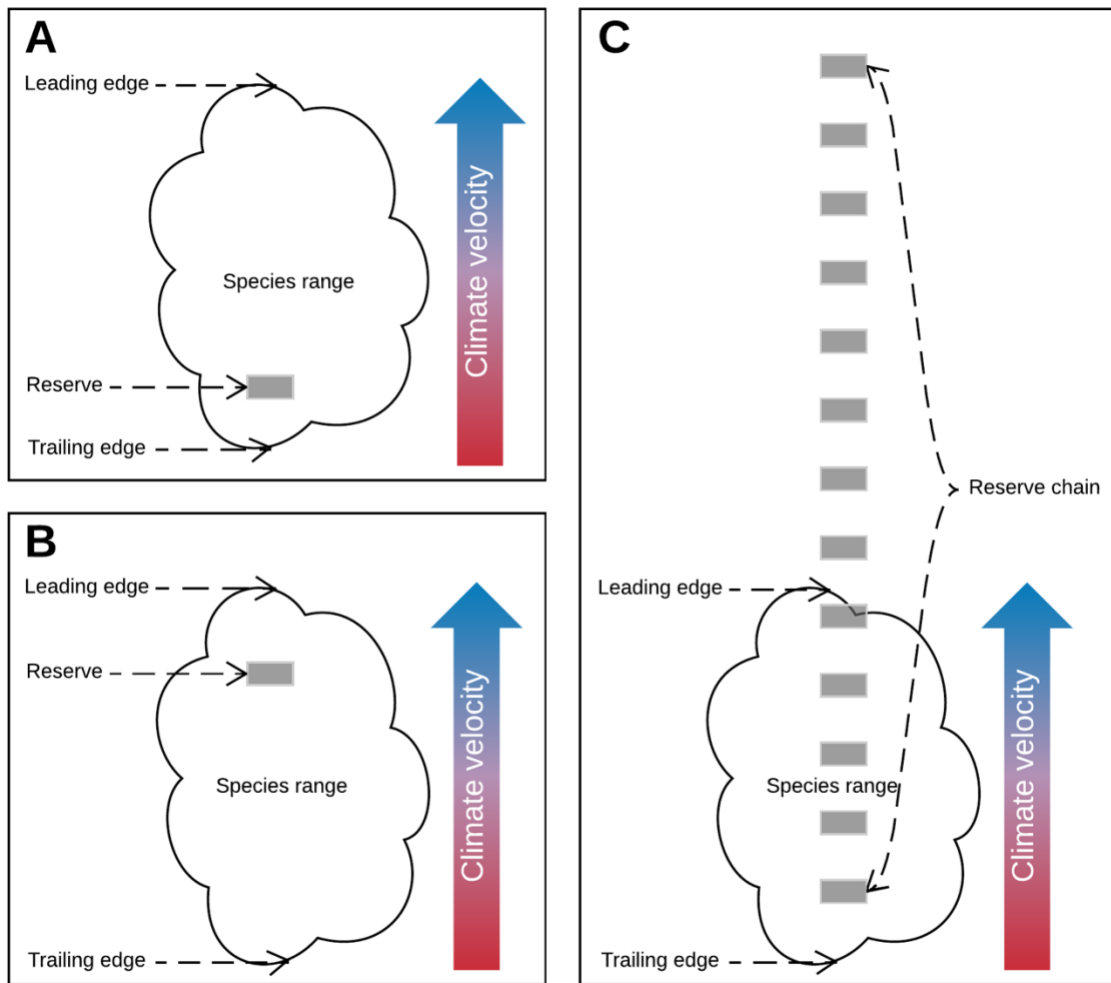


Figure 1.2. Schematic of MPA configurations in relation to the size of a species' geographic range, and the direction of climate velocity. MPAs are positioned near the trailing edge of the species range (A), the leading edge of the range (B), and in a linear chain parallel to climate velocity (C).

### **3. Cold range edges of marine fishes track climate change better than warm edges**

#### ***A. Abstract***

Species around the world are shifting their ranges in response to climate change. To make robust predictions about climate-related colonizations and extinctions, it is vital to understand the dynamics of range edges. This study is among the first to examine annual dynamics of cold and warm range edges, as most global change studies average observational data over space or over time. We analyzed annual range edge dynamics of marine fishes—both at the individual species level and pooled into cold- and warm-edge assemblages—in a multi-decade time-series of trawl surveys conducted on the Northeast U.S. Shelf during a period of rapid warming. We tested whether cold edges show stronger evidence of climate tracking than warm edges (due to non-climate processes or time lags at the warm edge; the *biogeography hypothesis* or *extinction debt hypothesis*), or whether they tracked temperature change equally (due to the influence of habitat suitability; the *ecophysiology hypothesis*). In addition to exploring correlations with regional temperature change, we calculated species- and assemblage-specific sea bottom and sea surface temperature isotherms and used them to predict range edge position. Cold edges shifted further and tracked sea surface and bottom temperature isotherms to a greater degree than warm edges. Mixed-effects models revealed that for a one-degree latitude shift in isotherm position, cold edges shifted 0.47 degrees of latitude, and warm edges shifted only 0.28 degrees. Our results suggest that cold range edges are tracking climate change better than warm range edges, invalidating the ecophysiology hypothesis. We also found that even among highly mobile marine ectotherms in a global warming hotspot, few species are fully keeping pace with climate.

## ***B. Introduction***

Species around the globe are shifting their ranges in response to warming (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Lenoir & Svenning, 2015; Parmesan & Yohe, 2003; Poloczanska et al., 2013). In the 20<sup>th</sup> century, the land and sea surfaces of our planet warmed 0.85°C on average. By 2100, the planet will almost certainly have warmed at least 2°C relative to the pre-industrial average, and could warm up to 5°C depending on the greenhouse gas emissions trajectory (Pachauri et al., 2015). Robust predictions of which species will move, where they will go, and how fast they will shift are critical for maintaining food security, controlling agricultural pests, managing disease outbreaks, preserving ecosystem function and biodiversity, and many other contributors to human well-being (Pecl et al., 2017). Because species' responses to climate change are highly individualistic and are not solely climate-mediated (Jackson et al., 2009), they can be difficult to predict.

Better predictions are likely to derive from a better understanding of the relevant processes (Urban et al., 2016) but understanding the ecological processes underlying the shifts in species distributions has been challenging in part because many studies examine shifts in the center of a species distribution (Perry et al., 2005; Pinsky et al., 2013). However, species shifts consist of colonizations at the leading edge, extirpations at the trailing edge, or both. Each of these processes is likely to be sensitive to different aspects of climate change and to differ from the processes affecting range centers (Sunday et al., 2015). If climate velocities point poleward — i.e., the region is warming and cooler climates exist toward the poles, as is the case in most parts of the world (Burrows et al., 2011) — then the leading edge is equivalent to the “cold” or “poleward” range edge, and the trailing edge to the “warm” or “equatorward” edge.

The fundamental determinants of species range edges, and their sensitivity to climate, have been active areas of ecological research for over a century (Gaston, 2009; MacArthur, 1972; Sexton et al., 2009; Wallace, 1876). Biogeographic theory developed largely in terrestrial systems suggests that cold range edges are exposed to greater abiotic stress and thus more likely to be climate-mediated than are warm range edges. By contrast, warm range edges encounter less seasonality and higher biodiversity (due to the latitudinal biodiversity gradient), so biotic interactions should have a greater influence (Cahill et al., 2014; Louthan et al., 2015); we call this the *biogeography hypothesis*. Alternatively, cold edges may respond more immediately to contemporary climate shifts while warm edges may “lag” climate because extirpation is slower than colonization (the *extinction debt hypothesis*). Climate-induced extirpation in terrestrial species can take decades to materialize for short-lived species, and more than a century for long-lived species, due to extinction debt (Fordham et al., 2016). If either of these mechanisms — the biogeography hypothesis or the extinction debt hypothesis — is operating for marine species, we would expect cold range edges to track climate better than warm range edges.

Most biogeographic research has been conducted on land, but the relative importance of climatic and biotic factors in constraining cold and warm range edges may differ systematically between terrestrial and marine ecosystems. Range edges of mobile marine ectotherms are expected to be highly correlated with climate suitability because those species experience few barriers to dispersal and tend to occupy all thermally suitable habitat (Sunday, Bates, & Dulvy, 2011, 2012). In addition, local extirpations as a result of warming were found to be twice as common in the ocean as on land (Pinsky et al., 2019), suggesting that temperature is an important driver of both extinction and colonization dynamics in

marine species. This mechanism would lead to an expectation that warm and cold range edges should track climate equally, which we term the *ecophysiology hypothesis*.

Predictions from theory are therefore equivocal about how marine species range edges are expected to change as ocean temperatures warm. One of the major challenges to testing theory about movements of range edges is the large data requirement: data are ideally collected over large spatial extents with fine-scale resolution for many species and over many years (Thomas et al., 2006). Consequently, few empirical studies have investigated the relationship between annual range edge positions and climate, and most of them focus on just one edge type (Cavanaugh et al., 2018; La Sorte & Thompson, III, 2007). One study that tested annual dynamics of cold and warm range edges for climate tracking — in tree species in the United States — found no evidence of climate-related shifts at either range edge (Zhu et al., 2012). The several empirical studies that compared both range edges using two or three time points have reported variable findings, including better climate tracking at the cold edges than the warm edges (Hickling et al., 2005; Parmesan et al., 1999); no climate tracking at either edge (Currie & Venne, 2017); and warm edge retractions without concordant cold edge extensions (Cristine & Kerr, 2015; Kerr et al., 2015). Analyzing fewer time points creates greater uncertainty about the shift of any given species and can confound stationary variability in range position with a long-term shift (Bates et al., 2015; Brown, O'Connor, et al., 2016).

We address this empirical challenge by examining whether cold and warm range edges of marine fishes have shifted predictably in response to temperature change on the Northeast US Shelf, a global warming hotspot, using annual survey data from 1968-2017. We used both sea surface and sea bottom temperatures to predict species-specific and



assemblage-wide shifts in edge position, contrasting individual responses with broader trends. On the Northeast US Shelf, severe warming since the mid-20<sup>th</sup> century has already been linked to marked shifts in distributions of marine fish, including an assemblage-wide northward shift (Bell et al., 2015; Hare et al., 2016; Lucey & Nye, 2010; Nye et al., 2009; Pinsky et al., 2013) and novel northward occurrences of many species (Mills et al., 2013). By examining trends in both cold and warm edges under climate change, we tested the ecophysiology hypothesis against the biogeography and extinction debt hypotheses. We found evidence that both cold and warm range edges of marine fishes in the Northeast US shifted north and tracked temperature in our 50-year time-series, but cold edges shifted further and exhibited a stronger relationship with temperature. This contradicts the ecophysiology hypothesis and suggests either that biotic interactions and other non-temperature-related factors are more important at the warm than at the cold range edge, or that extinction debt is causing warm range edges to lag behind temperature changes.

### ***C. Methods***

#### *Region and historical warming*

The Northeast US Shelf is a highly productive, temperate ecosystem with extensive sandy bottom that supports numerous important fisheries. It extends from Cape Hatteras to the Gulf of Maine. The region is considered a global warming hotspot, having warmed over 1°C in the 20<sup>th</sup> century (Hare et al., 2016). Some high-resolution climate models suggest that this region will continue to warm even more than previously expected (Saba et al., 2016). We used three different temperature datasets to capture three dimensions of temperature change in this region. The National Oceanographic and Atmospheric Administration (NOAA) NCEI

optimum interpolation sea surface temperature (NOAA, 2018) is available daily from 1982 onward at 0.25°x0.25° resolution; we used this to calculate temperature extremes. The Hadley Centre sea surface temperature dataset included the full length of the study period, but only monthly at 1° resolution, from which we calculated average sea surface temperatures (Rayner, 2003). We also obtained hindcast sea bottom temperature values from the Simple Ocean Data Assimilation model (version 3.4.2, available monthly from 1980 at 0.5° resolution) to test whether bottom temperature better explained the dynamics of these demersal fish species than surface temperature. Both sea surface temperature datasets were accessed using the rerddap package (Chamberlain, 2019). Bottom temperature data were provided by J. Carton (pers. comm.). Each dataset was retrieved within a bounding box of 35-45°N and 66-77°W and then cropped to exclude all points deeper than 300 m or beyond the US Exclusive Economic Zone (Bauer, 2018; Claus et al., 2019).

### *Survey data*

We used data from benthic trawl surveys conducted on the Northeast US Shelf by NOAA's Northeast Fisheries Science Center (NEFSC) from 1968-2017 (Politis et al., 2014). The NEFSC's spring survey was historically conducted at more consistent times than their fall survey, so we only used data from the spring survey (Flanagan et al., 2019). These surveys are repeated annually as random samples within pre-defined statistical regions ("strata"). There are over 100 strata across the entire Northeast US Shelf at various depths; hauls ranged from 5-542 m deep, with almost all hauls occurring between 10 and 300 m depth. The NEFSC trawl survey records observations regarding both the catch and the environment, including bottom temperature, depth, salinity, species identity, individual

length, and individual weight. Data were obtained from OceanAdapt (downloaded May 5, 2019 from <https://oceanadapt.rutgers.edu/>), a data portal to access NOAA trawl survey records.

We analyzed two distinct groups of species: those with a cold range edge in the Northeast US Shelf, and those with a warm range edge in that region. Because marine fish often have large ranges, and because we restricted our study to the Northeast US Shelf, none of the species had both a cold and a warm range edge in the study area (i.e., there is no overlap between the two groups of species studied). Most species with warm range edges in the Northeast US Shelf extend past Maine into Canadian waters (beyond the NEFSC survey area), and most species with cold range edges in this region are also found in the South Atlantic, Gulf of Mexico, or Caribbean (also beyond the NEFSC survey area). To distinguish single-species and pooled analyses, we refer to the set of species with a cold or a warm edge as a *group*, and to the set of all individuals belonging to cold- or warm-edge species pooled together (without regard to species) as an *assemblage*.

We used three approaches to check that the species to be analyzed had range edges in the study region. First, we eliminated from the warm range edge group any species recorded in the Southeast US survey (using the list of species in that region from the analogous South Atlantic bottom trawl survey conducted by the Southeast Fisheries Science Center, also obtained from OceanAdapt). To ensure that cold edge species started out well within the survey area (i.e., not already close to the edge of the US Exclusive Economic Zone), we classified species as having a cold edge in the region if they were not found above 42°N in the first year they were observed. Second, we calculated range edges from Aquamaps, a global ecological niche model of marine species ranges that projects into under-sampled

areas using environmental variables and known observations of species (Kaschner et al., 2016). Because Aquamaps range edges are imprecise, we calculated the 5<sup>th</sup> and 95<sup>th</sup> percentile of latitudes where each of these species occurs in Aquamaps with >80% probability. To eliminate species with range edges far beyond the Northeast US Shelf, we removed a warm edge species from further analysis if the Aquamaps projections placed its 5<sup>th</sup> percentile latitude below 30°N, or if Aquamaps placed a cold edge species' 95<sup>th</sup> percentile latitude above 50°N. Third, we manually compared the two lists of species to the International Union for Conservation of Nature (IUCN) and/or FishBase range maps (Froese & Pauly, 2019; IUCN, 2019). This third check primarily ruled out species with a cold edge near Nova Scotia or Newfoundland, such as Atlantic menhaden (*Brevoortia tyrannus*) and barndoor skate (*Dipturus laevis*).

We imposed a number of filters to ensure data quality and comparability among species, strata, and years. This study only used data on bony and cartilaginous fishes, which are most frequently and consistently sampled in the NEFSC survey. We excluded all observations that were missing essential data or were otherwise of poor quality [e.g., not identified to species (eliminated 28,504 records), no recorded biomass (eliminated 18,223 additional records), latitude below 36°N where survey does not regularly operate (eliminated 10,533 additional records)]. We eliminated species-year combinations where the species was observed fewer than 10 times (eliminating 4,829 additional records), because such limited observations were not sufficient to estimate the edge position. From the remaining data, we excluded species that were observed in fewer than 10 years. The final datasets used for analysis included 105,887 records of warm edge species, and 14,422 records of cold edge species. Although many species were observed in far more than 10 years, we did not impose

a stricter filter on the number of years because we wanted to include species with range edges that might have shifted into or out of the study region during the time-series.

After imposing these filters on data quality, we examined 14 cold edge species and 29 warm edge species that represented a diverse group of benthic-dwelling bony and cartilaginous fish (see Supplement). In addition to including more species, the warm edge group was better-sampled: the median number of total observations per species was 3708 (interquartile range: 964 to 5034), and over half of the species were present in all 50 years. The median number of observations of each cold edge species was 568 (interquartile range: 352 to 1324), and median years recorded per species was 27 (interquartile range: 12 to 42).

#### *Range edge position analysis*

Many methods exist to quantify the edge of a species' range, most of which are based on measuring latitudinal position (Kerr et al., 2015; Lenoir, Gégout, Pierrat, Bontemps, & Dhôte, 2009; Thomas & Lennon, 1999; Zhu et al., 2012). Because climate velocity points northeast along the shelf in this region (Burrows et al., 2011; Pinsky et al., 2013), and latitudinal response variables only capture north/south displacement, we also described range edges using distance along the coastline (Bell et al., 2015; Hare et al., 2010). For the Northeast US Shelf region, we downloaded a coarse outline of the coast using the “rnaturalearth” package in R (South, 2017) and applied a smoothing function to remove coastal features such as the Chesapeake Bay that would otherwise be counted in a measurement of coastline length. We measured the smoothed coastline using Cape Hatteras as the origin, such that a greater distance along the coastline represented a poleward shift. Each species observation was “snapped” to the smoothed coastline by minimizing the

absolute distance from the point observation (somewhere on the shelf) to the smoothed coastline. For each year, the edge position was calculated as the 95<sup>th</sup> percentile (cold edge) or 5<sup>th</sup> percentile (warm edge) of point observation distances along the smoothed coastline. We also calculated a second, independent edge metric as the 95<sup>th</sup> percentile (poleward) or 5<sup>th</sup> percentile (equatorward) of *latitudes* of observations, for use in models with isotherms, which were defined in terms of latitude.

We applied the edge calculation approach both to the observations of a single species in a year (species range edge), and to all observations of individuals belonging to species in the cold-edge or warm-edge groups in each year (assemblage range edge). For the assemblage range edges, in other words, we pooled observations across species before calculating the range edge. The assemblage range edge therefore described the range edge of an entire assemblage of species with a cold or warm range edge in this region. These assemblage edges were strongly influenced by the further poleward cold-edge species or the further equatorward warm-edge species in a given year.

We tested for edge displacement over the time-series with a linear model of edge position on year (14 linear models for the cold-edge group of species, 29 models for species in the warm-edge group, and two for the cold- and warm-edge assemblages). Our approach to estimating range edge position relied on presence and absence only. We did not use data on abundance or biomass because our focus was on range edge dynamics. The within-range distribution of abundance is poorly understood for most species (Dallas et al., 2017; Sagarin et al., 2006; Santini et al., 2019) and will not necessarily shift in concert with range edges (Simpson et al., 2011). Relative to a presence-based edge metric, an abundance-weighted edge metric (see Supplement Figures 2.1 and 2.2) would estimate less similar (i.e., further

apart) edge positions for species with the same overall geographic extent but different within-range distributions of abundance (e.g., one species concentrated toward its geographic center, one toward the edges). Our approach is also consistent with the existing literature on range edge shifts and climate change, which predominantly uses presence-based metrics (Hickling et al., 2005; Sittaro et al., 2017; Tingley & Beissinger, 2009).

### *Relationships between range edge dynamics and temperature*

We fitted a series of statistical models to examine the relationship between annual edge position and recent changes in temperature: linear models for each species-specific edge, linear mixed effects models for all species edges in the warm- or cold-edge group at once, and linear models for the edge positions of each of the two assemblages (all individuals in cold-edge or warm-edge species groups, pooled). We used two groups of predictor variables (Table 2.1): regional trends in temperature to explore the influence of temperature extremes and longer time-series, and edge-specific isotherms to test spatially explicit temperature tracking. Because the trawl survey occurs in the spring, species may be responding to conditions from the previous calendar year. To address this timing issue, all models used predictor variables calculated from the twelve-month period (March-February) before the spring survey in any given year. In other words, the edge position calculated in 1990 was compared to temperatures that occurred from March 1989 to February 1990.

Annual species- or assemblage-specific isotherms were derived from the monthly sea surface and bottom temperature datasets (Sunday et al., 2015). The isotherm analyses were repeated independently with the surface and bottom datasets, so each species and assemblage had a sea surface and a sea bottom temperature isotherm. First, using annual linear models of

sea surface or sea bottom temperature on latitude, we derived an equation that calculated the expected temperature given a latitude, or the expected latitude given a temperature. Once a range edge was described (see *Range edge position analysis*), we established a baseline temperature for that edge. For the assemblages, the baseline temperature was the sea surface or sea bottom temperature predicted by the linear model at the latitudinal position of the edge in the first year for which monthly temperature data were available. For individual species, whose edges are more variable through time, the baseline temperature was the mean of predicted temperatures calculated from the first three years when the species was observed. For species that were observed every year, the baseline reference years were 1968-1970 for sea surface temperature and 1980-1982 for sea bottom temperature. With these species- and assemblage-specific isotherms, we then calculated the latitude at which those temperatures occurred in later years, again using annual linear models of sea surface or bottom temperature on latitude. Each time-series of predicted latitudes at which a given temperature was found comprised a species- or assemblage-specific isotherm (*sensu* Sunday et al. 2015).

For the species-specific linear models, we fit linear regressions to test the correlation between each range edge position and each species' corresponding isotherm position ( $n = 14$  cold range edges and  $n = 29$  warm range edges). For each edge, we examined two models: one with the sea surface temperature isotherm as a predictor, and one with the sea bottom temperature isotherm as a predictor. In total, we fit 86 linear regressions of this type (two models by 43 individual species).

Next, we constructed linear mixed effects models across all species in a group (cold edge or warm edge) to test our hypotheses in aggregate rather than in a species-by-species manner. We used the `lmerTest` package in R, which implements linear mixed-effects models



and calculates  $p$ -values using Satterthwaite's degrees of freedom method (Kuznetsova et al., 2017). The response variable was a single-species edge position, and the explanatory variables were either sea surface or sea bottom temperature species-specific isotherm positions. Species identity was a random effect. In total, we fit four linear mixed effects models (two groups for each of two sets of predictor variables).

Finally, to explain the annual position of the assemblage edge, we compared six linear models, each run separately for the cold and warm edge assemblages. Each linear model had a different set of explanatory variables: (1) *bottom temperature only*: regional mean annual bottom temperature as the predictor variable; (2) *surface temperature only*: regional mean annual surface temperature; (3) *cold extreme*: 1<sup>st</sup> percentile regional annual surface temperature; (4) *warm extreme*: 99<sup>th</sup> percentile regional annual surface temperature; (5) *sea surface isotherms*: the assemblage edge-specific isotherm for sea surface temperature; and (6) *sea bottom isotherms*: the assemblage edge-specific isotherm for sea bottom temperature. The cold and warm extreme models tested for the influence of extreme temperatures on range edges (Pinsky et al., 2019; Sunday et al., 2019), and were based on percentiles of daily mean temperatures across the region; in other words, these predictors represented the warmest and coldest days in the Northeast US in the past year. Depending on the predictor variables in each model, response variables (edge positions) were estimated from either a percentile of distance (for regional temperatures) or of latitude (for isotherms; see *Range edge position analysis*). The assemblage models contained no species-specific information. In total, we fit 12 assemblage linear models (two species groups by six sets of explanatory variables).

### *Changes in depth and biomass*

Range shifts often coincide with shifts in the depth and abundance of populations, which can confound their interpretation (Dulvy et al., 2008; Frank et al., 2018; Ralston et al., 2017). We calculated a standardized total annual biomass for each species from the weight recorded in the survey. Each row in the raw data contained a recorded biomass in kilograms for individuals of each species in each haul. Some of these biomass values were further subdivided by sex class in the data; in these cases, we added the biomass values for each unique species and haul combination and discarded the sex class category. We then averaged those raw biomass values, producing a mean annual biomass value for each species in each stratum that included zeroes for true absences where a haul occurred but a species was not found. Up to this point, all biomass values were in units of kg/tow; to standardize by area towed, we divided the mean annual biomass value for each species in each stratum by the area of a tow (0.01 nmi<sup>2</sup>), multiplied it by the area of that stratum (available from OceanAdapt), and summed over all strata to yield a standardized estimate of each species' total annual biomass. Changes in biomass can reflect changes in abundance, changes in body size, or both (Bell et al., 2015; Shackell et al., 2010). We tested for changes in biomass over time using a linear regression of biomass on year for each species (43 species-specific linear regressions).

We then used the depth data from the NEFSC trawl surveys to calculate an annual mean depth for each species based on all its observations in that year — not just the observations at the edge (Dulvy et al., 2008). These annual depth estimates were weighted by the biomass recorded in each haul (the raw biomass values described above). For each species, we performed a linear regression of depth on year (43 species-specific linear

regressions). This analysis tested whether the biomass-weighted mean depth of each species had shifted deeper or shallower over the time-series. We compared coefficients from these linear models and those described in *Range edge position analysis* to explore whether species showed simultaneous changes in range edge position and either biomass or depth. We then calculated the Spearman rank correlation between the coefficients of biomass or depth over time and the coefficients of edge position over time from the linear models (four tests total, for biomass and depth by the two species groups).

All data analyses for this project were conducted in R version 3.6.0 (R Core Team, 2018). Code can be accessed on GitHub at: <https://github.com/afredstonhermann/neus-range-edges>.

## ***D. Results***

### *Region and historical warming*

The Northeast US Shelf region (Figure 2.1A) has a strong thermal gradient along the coast (Figure 2.1B). From 1968-2017, the annual mean of monthly sea surface temperatures on the Northeast US Shelf increased 0.030°C per year ( $\pm 0.004^\circ\text{C}$ ,  $p = 1.14 \times 10^{-8}$ , linear regression; Figure 2.1D). From 1982-2017, high (99<sup>th</sup> percentile) daily sea surface temperatures in this region warmed 0.046°C per year ( $\pm 0.01^\circ\text{C}$ ,  $p = 3.32 \times 10^{-5}$ , linear regression; Figure 2.1E). Mean annual monthly sea bottom temperatures also increased from 1980-2017, at a rate of 0.017°C per year ( $\pm 0.007^\circ\text{C}$ ,  $p = 0.024$ , linear regression). Cold extremes were less affected: the low (1<sup>st</sup> percentile) daily sea surface temperature from 1982-2017 did not significantly change ( $0.005 \pm 0.01^\circ\text{C}$ ,  $p = 0.68$ , linear regression; Figure 2.1C). These spatial and temporal changes in temperature translated into isotherms that shifted north

at least one degree of latitude during the study period (0.02-0.03 degrees latitude per year; Figure 2.1B).

### *Range edge position analysis*

Of the 14 cold edges studied, 11 (79%) shifted north during the time-series, of which 8 (57%) shifted significantly north ( $p \leq 0.05$ , linear regression) (Figure 2.2A). Only one of the three species that shifted south was statistically significant: offshore silver hake. Among the significant shifts, the estimated time trend of species edge position ranged from -7.4 km/yr to 13.1 km/yr, with standard errors ranging from  $\pm 0.6$  to  $\pm 3.5$ . In other words, over the 50-year time-series, we estimated that species' cold edges shifted up to 370 km south or 655 km north. The cold assemblage edge, calculated from species observations pooled together, moved north at  $6.7 \text{ km/year} \pm 0.8$  (standard error;  $p = 3.7 \times 10^{-11}$ , linear regression), or a total of 335 km from 1968-2017. See Supplement for all estimated range edge shifts.

In the warm edge group, 18 of 29 edges (62%) shifted north, of which 13 (45%) were statistically significant ( $p \leq 0.05$ , linear regression) (Figure 2.3A). Of the 11 warm edges that shifted south, only winter skate and barndoor skate were significant. Effect sizes of significant shifts ranged from -15.6 km/year (750 km south in total) to 11 km/year (550 km north in total), with standard errors from  $\pm 0.1$  to  $\pm 2.2$ . A linear model of the warm edge assemblage position over time revealed a non-significant relationship ( $p = 0.8$ ) with an effect size close to zero (-0.2 km/yr).

For most species in both groups, range edge position was highly dynamic over time; for many species we studied, selecting a random “old” and “new” year to compare could result in a finding of a marked northward shift, a marked southward shift, or no shift at all,

depending on the exact years chosen (Figure 2.4). All single-species time-series can be viewed in the Supplement.

### *Range edge dynamics and temperature*

Seven of the 14 cold-edge species, and 14 of the 29 warm-edge species, had a significant positive association with their sea surface temperature isotherms (Figures 2.2B and 2.3B). Fewer species in either group had a significant positive association with their sea bottom temperature isotherms (Figures 2.2C and 2.3C), although the fraction was higher in the cold edge group (5 of 14, 36%) than the warm edge group (3 of 29, 10%). In both groups, the species that did significantly track sea bottom temperature also tracked sea surface temperature and shifted significantly north. The four linear mixed-effects models across all species in a group suggested similar conclusions, with stronger relationships to surface than to bottom temperatures (Table 2.2).

In addition, the individual species models and the cross-species mixed effects models both suggested stronger temperature relationships for cold range edges than for warm range edges. The isotherm coefficients represent how far the range edge shifted in relation to a shift in the isotherm. Coefficients were larger for cold edge species in the single species models: the median edge shift for a one-degree latitude shift in isotherm position was 0.38 for sea surface temperature *versus* median estimates of only 0.14 for warm edge species (0.05 and 0.006, respectively, for sea bottom temperature). We found similar results in the mixed-effects models: coefficients for cold edge species were 0.47 and 0.13 for sea surface and sea bottom temperature isotherms, respectively, *versus* 0.28 and 0.014 for warm edge species.

However, the edges for only a small percentage of species fully kept pace with that of climate (dashed line in Figures 2.2B and 2.3B).

Sea surface temperature also emerged as a stronger predictor of the cold assemblage edge than of the warm assemblage edge (Figure 2.5, Table 2.2). The cold assemblage edge was positively and significantly associated with regional mean sea surface temperature, regional warm extreme sea surface temperature, and the sea surface temperature isotherm (Figure 2.5A, Table 2.2). It was also marginally associated with the sea bottom temperature isotherm ( $p=0.075$ , Figure 2.5A, Table 2.2). The cold assemblage edge shifted 0.6 degrees of latitude for every one-degree latitude shift in its sea surface temperature isotherm. The warm assemblage edge was only significantly associated with the sea surface temperature isotherm and the regional warm extreme sea surface temperature (Figure 2.5B, Table 2.2), and it only shifted 0.23 degrees north for every one-degree latitude shift in the sea surface temperature isotherm. Sea bottom temperature and cold extreme sea surface temperature were both poor predictors of edge position.

#### *Changes in depth and biomass*

In the cold edge group, five of 14 species had significant shifts in depth over time ( $p \leq 0.05$ , linear regressions). These shifts were all positive (i.e., deeper); one species shifted 3 m/yr deeper (dusky smooth-hound), and the other five (blueback shad, Gulf Stream flounder, summer flounder, and blackrim cusk-eel) all shifted less than 0.7 m/yr (Figure 2.6A). Six of the cold edge species showed significant changes in biomass over time ( $p \leq 0.05$ ; linear regressions); offshore silver hake and Gulf Stream flounder declined in biomass, and rosette

skate, summer flounder, chain catshark, and shortnose greeneye all increased (Figure 2.6B). See Supplement for single-species time-series of depth and abundance.

The warm edge group had stronger evidence for a depth shift, which was significant in 14 of the 29 species ( $p \leq 0.05$ ; linear regressions). Four species shifted significantly shallower (Atlantic mackerel, longhorn sculpin, haddock, and little skate), and the remaining ten shifted deeper; in either direction, significant shifts ranged from about 0.3 m/yr to 1.1 m/yr in magnitude (Figure 2.6C). This group also had stronger evidence for biomass shifts: 18 of 29 species had significant biomass changes over the time-series ( $p \leq 0.05$ ; linear regressions). Thirteen of these species declined in biomass, and only five increased (Figure 2.6D). Estimated biomass changes were also greater in magnitude than in the cold-edge group. In either group, we did not find any evidence for a relationship between the rate of edge shifts and changes in either depth or biomass over time (Spearman's rank correlation, Figure 2.6).

## ***E. Discussion***

By analyzing 50 years of range edge dynamics of marine fishes, we found that both warm and cold range edges have shifted significantly over time. However, species' cold edges shifted further north with warming, were more strongly associated with temperature, and tracked isotherms better than species' warm edges. These results suggest that cold edges are tracking ocean temperature change more readily than warm edges in the same region, lending support to either the biogeography or the extinction debt hypotheses.

Our findings of faster range edge expansions than range edge contractions are consistent with previous work demonstrating that the range sizes of North American marine fishes are expanding (Batt et al., 2017), which could be explained by cold edge shifts outpacing warm edge shifts. At the single-species level, approximately half of each group shifted north and had a significant positive association with their sea surface temperature isotherms, underscoring the highly individualistic response of fishes to the same history of warming. We also documented a number of range expansions and local extirpations in Northeast US Shelf marine fishes; some are consistent with previous literature and news reports, such as black sea bass and Atlantic cod (Bell et al., 2015; Nye et al., 2009), and others have not yet been widely highlighted, such as the warm edge retraction in Northern sand lance (a forage fish).

Cold edges of marine fishes in the Northeast US responded positively and quite consistently to historical warming in our analysis. Cold range edges predominantly shifted north, as did the cold-edge assemblage as a whole (which was unlikely to be driven by a single outlier, as several species had range edges near one another in the northern part of the study region; see Supplement). Cold edge species also tracked their sea surface and sea bottom temperature isotherms to a greater degree than warm edge species. In contrast, the warm assemblage edge was associated with sea surface temperature but not with sea bottom temperature, and northward shifts were only evident at the species-specific (not assemblage-wide) scale. The warm assemblage edge did not shift north because many of the most abundant species in the that assemblage moved north slightly or not at all or even shifted south. The assemblage edge represents the frontier of all species colonizing or becoming locally extirpated, so its position along the coastline is strongly influenced by the furthest



(i.e., most distal) species in each assemblage. Notably, although the warm assemblage edge did not significantly shift north, it showed a positive relationship with sea surface temperature, suggesting that the range edge was responding to interannual temperature variation but that longer-term changes were counterbalanced by changing species interactions or other factors that offset range contractions.

Our finding that warm edges track isotherms poorly relative to cold edges is consistent with either a localized extinction debt or with the warm edge being mediated more strongly by species interactions or other non-climate processes. The lags we find are similar to the “climatic debts” defined as the differential between regional climate velocities and realized shifts of species, an approach that also cannot distinguish between extinction debt, species interactions, and other processes (Devictor et al., 2012). Few studies have explored whether species interactions mediate range edges of demersal fishes (Louthan et al., 2015). A bioclimate envelope model applied to marine fishes predicted lesser range shifts when trophic interactions were incorporated (Fernandes et al., 2013). Evidence for delayed range contractions from localized extinction debt processes is also less clear in fishes. Many species in our dataset are relatively long-lived, but adults are also quite mobile and able to move in response to temperature change (Freitas et al., 2016). Formally testing for the presence of an extinction debt may be possible with models that include lags or life history information to explain the length of time lags (Orensanz et al., 2004). Similarly, testing for the role of antagonistic species interactions in mediating warm-edge dynamics may be possible by identifying strong interactors for each study species and then comparing the study species’ warm-edge position to the distribution of its competitor, predator, or prey (García-Valdés et al., 2015; Sanín & Anderson, 2018). While both of those lines of inquiry

are beyond the scope of this study, we can conclude that our results contradict the hypothesis that warm and cold edges of marine fishes will track climate change equally (Sunday et al., 2012).

Across a number of tests, we found that the demersal species in our analysis appeared to respond to sea surface temperature more strongly than to sea bottom temperature. We examined sea bottom temperature because the bottom trawl survey catches primarily demersal species, and yet our results suggested that sea surface temperature is a better predictor of range edge positions. Two possible explanations are that the longer time-series available for sea surface temperature aided in detecting a relationship or that the hindcast sea bottom temperatures were not be sufficiently accurate or precise for the Northeast US Shelf. However, it is also possible that a real sensitivity to sea surface temperature exists in these species, most likely in the larval phase. Temperature affects larval duration and survival (O'Connor et al., 2007), and some marine species' range edges are driven by larval distributions (Gaylord & Gaines, 2000; Hutchins, 1947; Orensanz et al., 2004; Sanford et al., 2006; Zacherl et al., 2003). While this mechanism has primarily been described in invertebrates, the distributions of fish species may also be constrained by juvenile survival (Hare et al., 2012; Wuenschel et al., 2012). Further research using improved hindcast temperature models and species with different dispersal capacities and different stage-specific thermal tolerances may shed light on this result.

Analyzing our data at the species as well as the assemblage scale, using two different metrics for edge position, and numerous temperature datasets as predictor variables allowed us to tease apart broad- and fine-scale patterns and to address common sources of error in studying range shifts (Brown, O'Connor, et al., 2016). For example, measuring edge shifts

only using latitude and not using our alongshore distance metric might have masked some range shifts that occurred in sections of the coast that slant eastward. Had we examined only northward shifts and regional warming, we might have been biased toward finding cold edge shifts, because cold edges tend to fall further north in this region which is also where the most warming has occurred. By conducting the isotherm analysis, we were able to detect that some warm edges are tracking local changes in temperature. We also tested for changes in depth, another possible response to warming. While some species — approximately one-third of each group — shifted deeper over the time-series, we did not find evidence that depth and edge shifts were correlated or that species were only shifting in one dimension or the other.

This is one of a very small number of studies to examine range edge dynamics at the annual scale (Cavanaugh et al., 2018; La Sorte & Thompson, III, 2007; Zhu et al., 2012). The vast majority of studies documenting the displacement of a cold or warm range edge in the Anthropocene use relatively few time points as a result of either binning time-series data (Alheit et al., 2012; Kerr et al., 2015) or a “resurvey” approach that revisits the site of a historic dataset and conducts a second survey for comparison (Franco et al., 2006; Freeman et al., 2018; Wernberg et al., 2011). These studies provide a valuable snapshot of change and useful baselines for historic species distributions. However, the resurvey and binning approaches mask the complexity of range edges that is only apparent in time-series analyses. In our data, using two or three time points to estimate an edge shift would have yielded results that are inconsistent with the magnitude and even the direction of change revealed by the complete time-series (Figure 2.4).

Given that our estimates of edge shifts are based on up to 50 years of data, it is surprising that we found several warm edge species that shifted south during the study period

(little skate, barndoor skate, and winter skate), or had a negative relationship with isotherm position (American plaice, tusk, alewife, and all three southward-shifting skates). Offshore hake, a cold edge species, also shifted significantly south. In other systems, shifts against the direction of climate velocity have been attributed to a positive abundance-area relationship (Blanchard et al., 2005; Thorson et al., 2016) or the species tracking a non-temperature climate factor, e.g., water availability in plants (Crimmins et al., 2011). However, the warm edge species that we studied generally decreased in biomass over the time-series or did not change (see Figure 2.6 and Supplement), which — if the changes in biomass were due to changing abundance (not body size), and if range dynamics were abundance-driven — would have led to the warm range edge contracting north, not expanding south (Ralston et al., 2017). The non-temperature climate factors most likely to influence the distributions of marine fishes include pH and dissolved oxygen; but ocean acidification in this region is primarily considered a risk to coastal marine invertebrates, not demersal fish (Hare et al., 2016). High-resolution time-series data are not readily available to test for the role of oxygen limitation (Deutsch et al., 2015).

In addition to mechanistic explanations, there may be methodological reasons why individual species do not appear to be tracking climate change. Species distributions in this region fluctuate over the year due to seasonal migrations as well as a response to seasonal stratification (Kleisner et al., 2016). The spring survey may not capture the absolute furthest position of each species' range edge. By comparing data from the same season across years, we have described the range edge position at one point in the year, but the data may miss possible climate-related spatial shifts in species distributions in other seasons. We included several predictor variables for temperature, including sea surface and bottom temperatures,

and extreme values as well as means. However, these predictors are annual summary statistics that may do a poor job of capturing the thermal conditions that are actually influencing species fitness (Helmuth et al., 2014). We avoided some of the most common sources of methodological error in detecting range shifts by using a long time-series, focusing on abundant species, and calculating edge position as a percentile rather than from the most extreme values (Bates et al., 2015; Brown et al., 2016). However, the high degree of variability that we observed in species' range edge dynamics may be as much or more due to imperfect sampling than to actual fluctuations in the species range. Range edges are difficult to quantify, and even using a 50-year survey conducted annually at a large spatial scale, our estimates are imperfect. This underscores the need to both continue these types of large-scale biodiversity surveys and intensify efforts to sample large areas at fine spatial and temporal scales. Empirical research in this field is limited by available datasets, and we strongly support the continuation of traditional biodiversity surveys such as the trawl survey we used in addition to more nontraditional programs such as citizen science efforts aimed at detecting novel colonizations (Pecl et al., 2019), recognizing, however, that efforts to document local extinctions are also needed (Thomas et al., 2006).

We found consistent evidence that cold range edges of marine fishes in the Northeast US tracked climate better than warm range edges during 50 years of historical warming. Not only do these results invalidate the ecophysiology hypothesis, they also challenge the assumption that marine fishes are shifting as fast as climate velocities: very few range edges from either group perfectly tracked an isotherm. If warm edges are lagging cold edges in marine systems as well as terrestrial systems, we may expect widespread increases in range size — at least in the short term — with cascading consequences for ecological communities

both on land and in the oceans. Our findings underscore the importance of studying non-climate processes at range edges of all taxa, including those that are often expected to keep pace with climate change.

## F. Tables

Table 2.1. Predictor variables used in the analysis. SODA: Simple Ocean Data Assimilation model 3.4.2 (Carton et al., 2018). HadISST: Hadley Centre Global Sea Ice and Sea Surface Temperature model (Rayner, 2003). OISST: NOAA NCEI optimum interpolation sea surface temperature model (NOAA, 2018).

Predictor Variable	Data Source	Years Available
Regional annual sea bottom temperature, mean	SODA	Monthly 1980-2017
Regional annual sea surface temperature, mean	HadISST	Monthly 1968-2017
Regional annual sea surface temperature, 99 <sup>th</sup> percentile (warm extreme)	OISST	Daily 1982-2017
Regional annual sea surface temperature, 1 <sup>st</sup> percentile (cold extreme)	OISST	Daily 1982-2017
Edge-specific sea surface temperature isotherms	HadISST	Monthly 1968-2017
Edge-specific sea bottom temperature isotherms	SODA	Monthly 1980-2017

Table 2.2. Results of models explaining range edge position with temperature. Model acronyms: linear model (LM), linear mixed-effects model (LMEM). Temperature acronyms: sea bottom temperature (SBT), sea surface temperature (SST). Coefficients are presented with standard errors. *p*-values below 0.05 are in bold text, and very small *p*-values are expressed in scientific notation.

Model	Response Variable	Predictor Variable(s)	Coefficient(s)	<i>p</i> -value
<i>Cold edge</i>				
LMEM	Species edges (latitude)	SST isotherm	$0.47 \pm 0.07$ °lat/°lat	<b><math>7.96 \times 10^{-10}</math></b>
LMEM	Species edges (latitude)	SBT isotherm	$0.13 \pm 0.03$ °lat/°lat	<b><math>5.51 \times 10^{-6}</math></b>
LM	Assemblage edge (distance)	Mean SST	$105.88 \pm 25.15$ km/°C	<b><math>1.11 \times 10^{-4}</math></b>
LM	Assemblage edge (distance)	Mean SBT	$37.55 \pm 38.93$ km/°C	0.34
LM	Assemblage edge (distance)	1% SST	$-12.48 \pm 34.20$ km/°C	0.72
LM	Assemblage edge (distance)	99% SST	$90.35 \pm 21.04$ km/°C	<b><math>1.45 \times 10^{-4}</math></b>
LM	Assemblage edge (latitude)	SST isotherm	$0.60 \pm 0.24$ °lat/°lat	<b>0.016</b>
LM	Assemblage edge (latitude)	SBT isotherm	$0.18 \pm 0.10$ °lat/°lat	0.075
<i>Warm edge</i>				
LMEM	Species edges (latitude)	SST isotherm	$0.28 \pm 0.04$ °lat/°lat	<b><math>4.69 \times 10^{-15}</math></b>
LMEM	Species edges (latitude)	SBT isotherm	$0.014 \pm 0.016$ °lat/°lat	0.40
LM	Assemblage edge (distance)	Mean SST	$18.65 \pm 12.05$ km/°C	0.13
LM	Assemblage edge (distance)	Mean SBT	$14.62 \pm 14.06$ km/°C	0.31
LM	Assemblage edge (distance)	1% SST	$13.54 \pm 12.37$ km/°C	0.28
LM	Assemblage edge (distance)	99% SST	$26.54 \pm 8.47$ km/°C	<b>0.0036</b>
LM	Assemblage edge (latitude)	SST isotherm	$0.23 \pm 0.10$ °lat/°lat	<b>0.027</b>
LM	Assemblage edge (latitude)	SBT isotherm	$0.02 \pm 0.05$ °lat/°lat	0.73

## G. Figures

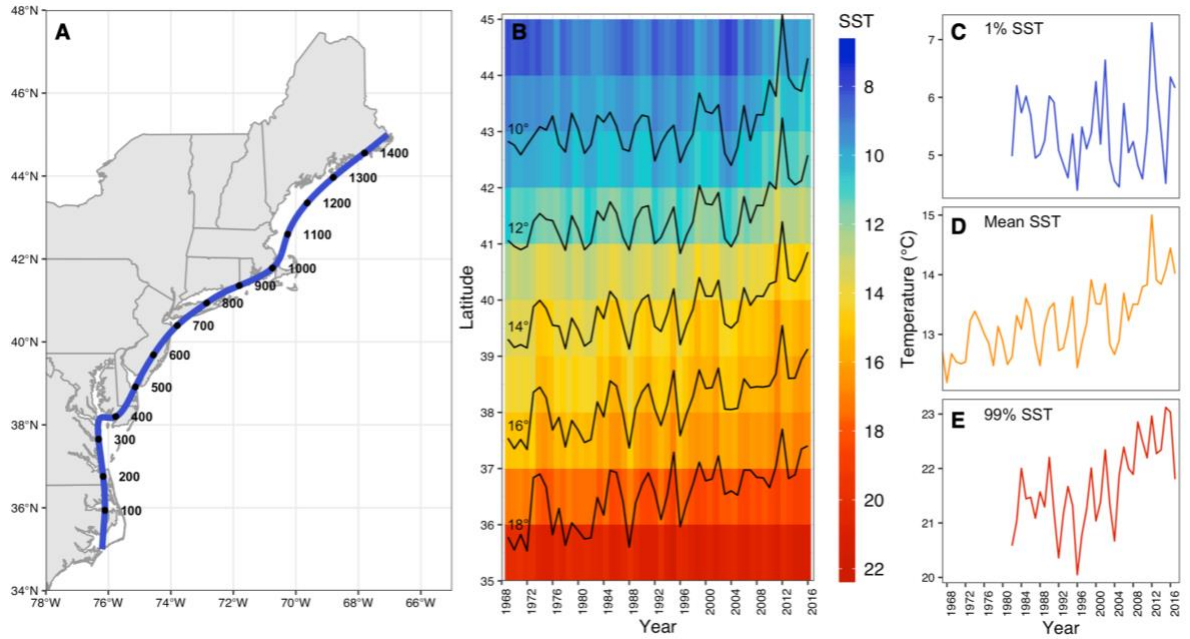


Figure 2.1. Map of study area (A), Hovmöller diagram of change in sea surface temperature during the study period (B), and time-series of 1<sup>st</sup> percentile (C), mean (D), and 99<sup>th</sup> percentile (E) sea surface temperature in the study region. The blue line on (A) shows the smoothed coastline, with dots every 100 km. Sea surface temperature data in (B) are presented as shelf-wide annual means of monthly temperatures (°C). The 10°C, 12°C, 14°C, 16°C, and 18°C isotherms plotted in black on (B) are calculated from annual linear regressions of monthly sea surface temperature on latitude.

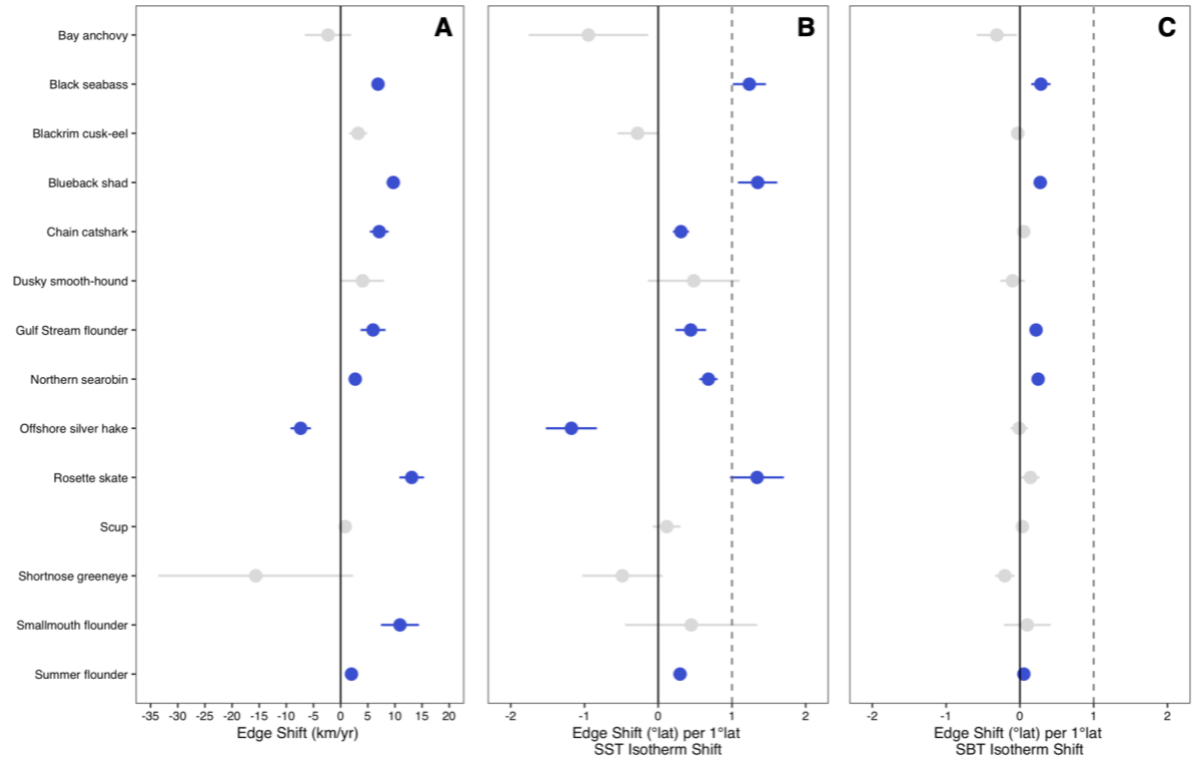


Figure 2.2. Species-specific cold edge shifts over time (A) and effect of species-specific sea surface (B) and sea bottom (C) temperature isotherms on edge position (linear models). Lines are standard errors from the model output. Blue dots represent significant results ( $p \leq 0.05$ ), and grey dots represent non-significant results ( $p > 0.05$ ). Points to the left of the vertical black line represent southward shifts (A) or negative relationships with isotherm position (B or C). In (B) and (C), a value of one (vertical grey dashed line) represents perfect climate tracking, i.e., the range edge shifted one degree in latitude for every degree that the isotherm shifted.



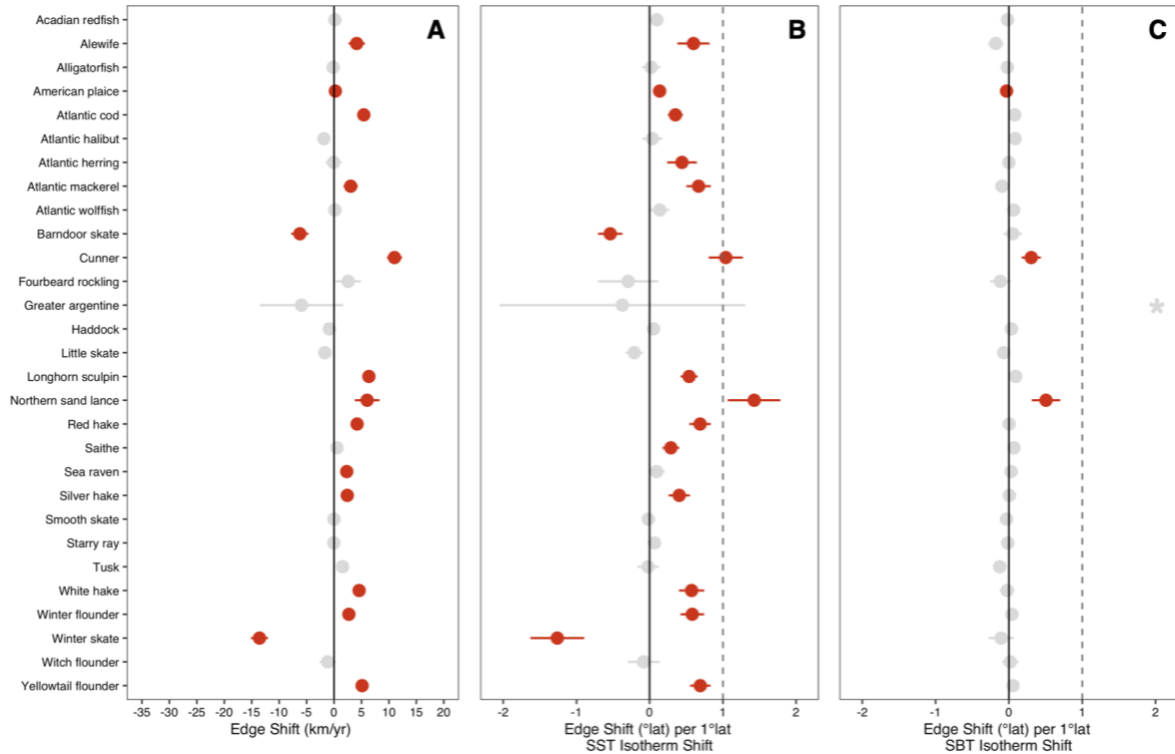


Figure 2.3. Species-specific warm edge shifts over time (A) and effect of species-specific sea surface (B) and sea bottom (C) temperature isotherms on edge position (linear models). Lines are standard errors from the model output. Red dots represent significant results ( $p \leq 0.05$ ), and grey dots represent non-significant results ( $p > 0.05$ ). Points to the left of the vertical black line represent southward shifts (A) or negative relationships with isotherm position (B or C). In (B) and (C), a value of one (vertical grey dashed line) represents perfect climate tracking, i.e., the range edge shifted one degree in latitude for every degree that the isotherm shifted. The grey asterisk for Greater argentine in (C) denotes a non-significant outlier (effect size  $4.0 \pm 2.3$ ).

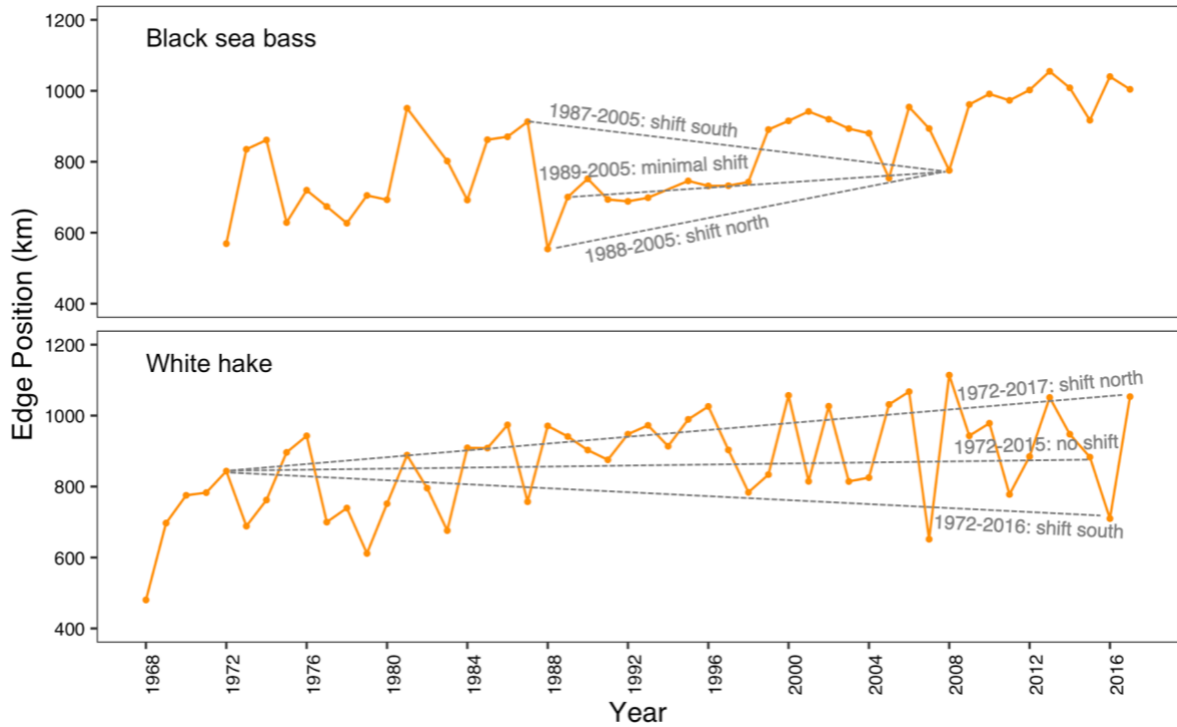


Figure 2.4. Annual cold (black sea bass) and warm (white hake) range edge position for example species chosen to represent relatively well-sampled species that show highly variable edge dynamics. Both species shifted significantly north over the time-series. Grey lines show hypothetical observed shifts in each species if only two time points had been observed: a baseline in 1987, 1988, and 1989 with a resurvey in 2005 for black sea bass, and a baseline in 1972 with a resurvey in 2015, 2016, or 2017 for white hake. See Supplement for all species' time-series.

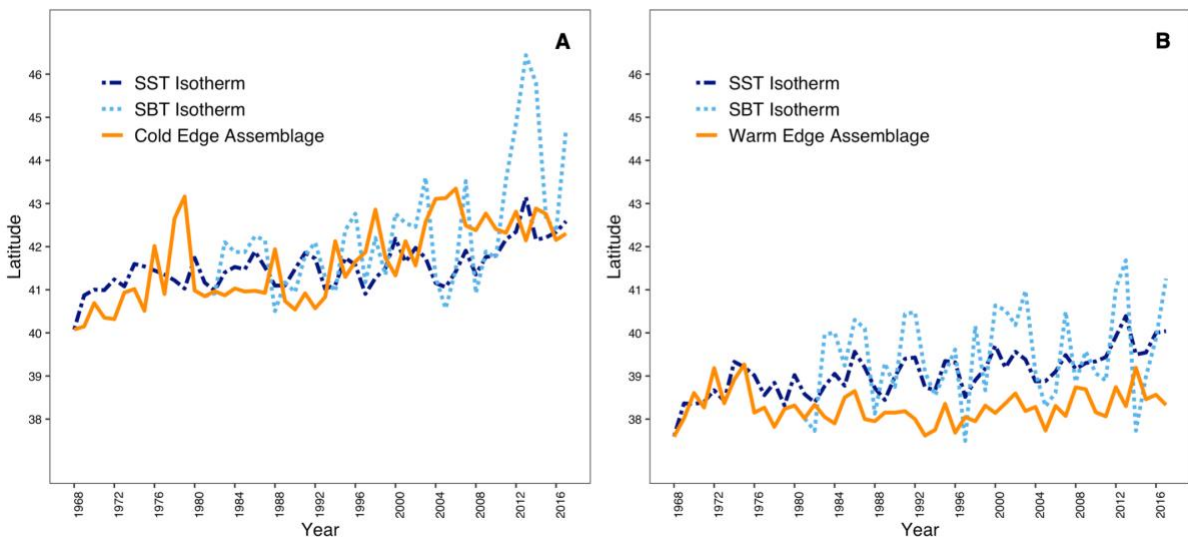


Figure 2.5. Assemblage-wide edge position (solid orange line), mean sea surface temperature isotherm position (dashed dark blue line), and mean sea bottom temperature isotherm position (dashed light blue line) for cold edge (A) and warm edge (B) species.

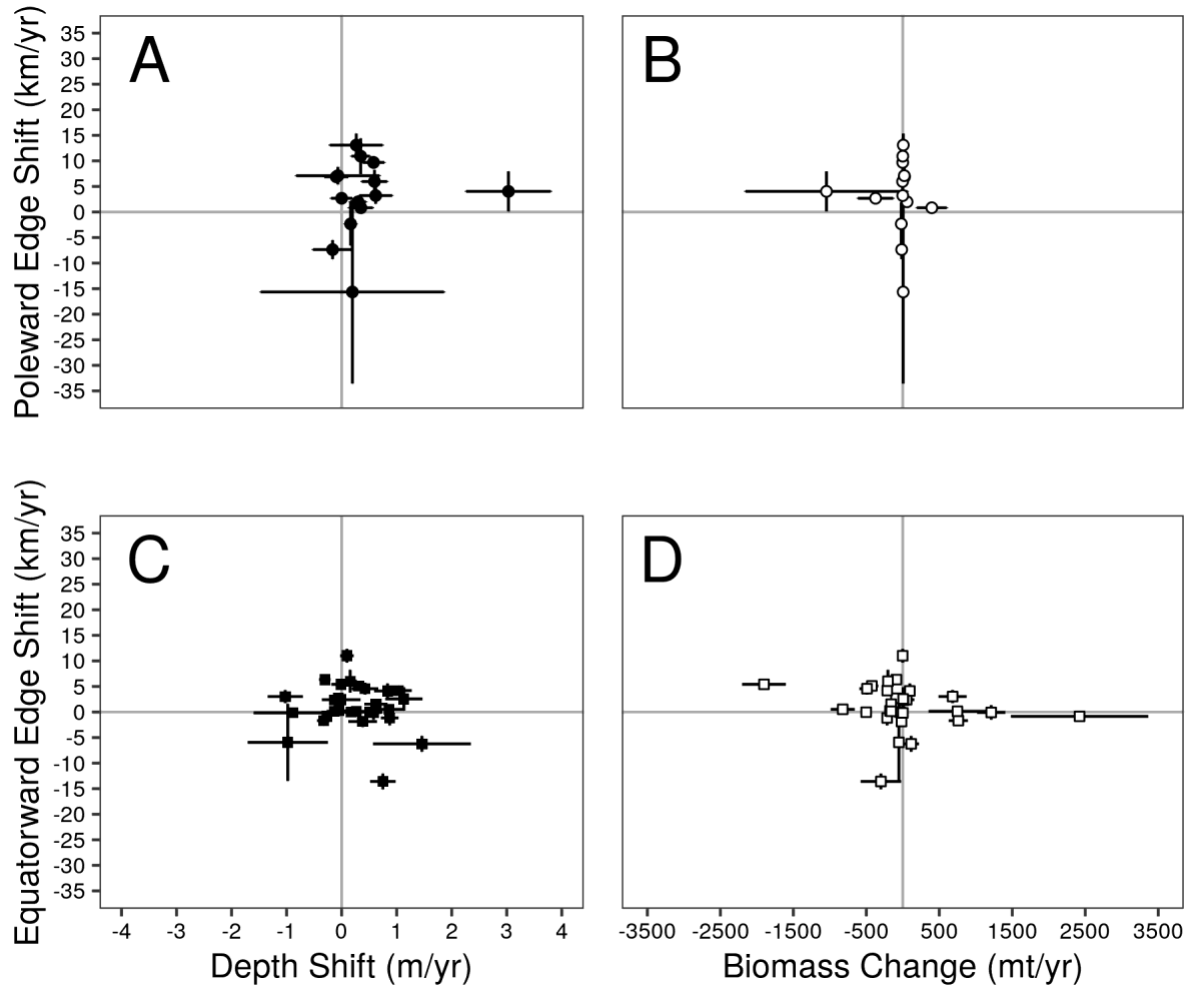


Figure 2.6. Relationships between changes in depth (meters per year; filled points) and abundance (metric tons per year; open points), and edge shifts (kilometers per year). (A) and (B) show cold edge species (circles) and (C) and (D) show warm edge species (squares). Spearman's rank correlations: (A) 0.22,  $p = 0.44$ , (B) 0.13,  $p = 0.65$ , (C) -0.06,  $p = 0.75$ , (D) -0.26,  $p = 0.18$ . Positive depth shifts are toward deeper water, and positive edge shifts are northward up the shelf. Each point is a single species, and the lines are standard errors.

## H. Supplementary Information

Latin name	Common name	Number of Observations	Number of Years
<b>Warm edge group</b>			
<i>Alosa pseudoharengus</i>	Alewife	6495	50
<i>Amblyraja radiata</i>	Starry ray	2599	50
<i>Ammodytes dubius</i>	Northern sand lance	1446	33
<i>Anarhichas lupus</i>	Atlantic wolffish	667	29
<i>Argentina silus</i>	Greater argentine	134	11
<i>Aspidophoroides monopterygius</i>	Alligatorfish	294	13
<i>Brosme brosme</i>	Cusk	656	30
<i>Clupea harengus</i>	Atlantic herring	6683	50
<i>Dipturus laevis</i>	Barndoor skate	964	21
<i>Enchelyopus cimbrius</i>	Fourbeard rockling	807	27
<i>Gadus morhua</i>	Atlantic cod	5254	50
<i>Glyptocephalus cynoglossus</i>	Witch flounder	3719	50
<i>Hemirhamphus americanus</i>	Sea raven	3913	50
<i>Hippoglossoides platessoides</i>	American plaice	4545	50
<i>Hippoglossus hippoglossus</i>	Atlantic halibut	265	19
<i>Leucoraja erinacea</i>	Little skate	8052	50
<i>Leucoraja ocellata</i>	Winter skate	4963	50
<i>Limanda ferruginea</i>	Yellowtail flounder	4681	50
<i>Malacoraja senta</i>	Smooth skate	1587	48
<i>Melanogrammus aeglefinus</i>	Haddock	3998	50
<i>Merluccius bilinearis</i>	Silver hake	10262	50
<i>Myoxocephalus octodecemspinosus</i>	Longhorn sculpin	5237	50
<i>Pollachius virens</i>	Saithe	2402	50
<i>Pseudopleuronectes americanus</i>	Winter flounder	5034	50
<i>Scomber scombrus</i>	Atlantic mackerel	3261	50
<i>Sebastes fasciatus</i>	Acadian redfish	2732	50
<i>Tautoglabrus adspersus</i>	Cunner	335	24
<i>Urophycis chuss</i>	Red hake	7281	50
<i>Urophycis tenuis</i>	White hake	3708	50
<b>Cold edge group</b>			
<i>Alosa aestivalis</i>	Blueback shad	2899	46
<i>Anchoa mitchilli</i>	Bay anchovy	154	11
<i>Centropristis striata</i>	Black seabass	1172	44
<i>Chlorophthalmus agassizi</i>	Shortnose greeneye	211	10
<i>Citharichthys arctifrons</i>	Gulf Stream flounder	1375	28
<i>Etropus microstomus</i>	Smallmouth flounder	342	12
<i>Lepophidium profundorum</i>	Blackrim cusk-eel	700	33
<i>Leucoraja garmani</i>	Rosette skate	263	11
<i>Merluccius albidus</i>	Offshore silver hake	408	25
<i>Mustelus canis</i>	Dusky smooth-hound	383	13
<i>Paralichthys dentatus</i>	Summer flounder	3227	48
<i>Prionotus carolinus</i>	Northern searobin	2051	50
<i>Scyliorhinus retifer</i>	Chain catshark	435	13
<i>Stenotomus chrysops</i>	Scup	802	37

Table 2.S1. List of species analyzed, with common and Latin names, number of years, and total number of observations. Common names were extracted from FishBase (Boettiger et al., 2012).

Common Name	Coefficient	Standard Error	Test Statistic	p-value
Bay anchovy	-2.32	4.25	-0.55	5.98E-01
Black seabass	6.88	1.09	6.28	1.55E-07
Blackrim cusk-eel	3.21	1.63	1.97	5.76E-02
Blueback shad	9.70	1.24	7.81	7.64E-10

Chain catshark	7.10	1.72	4.13	1.68E-03
Dusky smooth-hound	4.03	3.93	1.02	3.28E-01
Gulf Stream flounder	5.97	2.29	2.61	1.50E-02
Northern searobin	2.68	0.87	3.07	3.53E-03
Offshore silver hake	-7.36	1.87	-3.93	6.75E-04
Rosette skate	13.09	2.27	5.76	2.73E-04
Scup	0.83	0.96	0.86	3.95E-01
Shortnose greeneye	-15.65	17.93	-0.87	4.08E-01
Smallmouth flounder	10.92	3.50	3.12	1.08E-02
Summer flounder	1.99	0.59	3.35	1.62E-03
<i>Assemblage</i>	<i>6.69</i>	<i>0.79</i>	<i>8.52</i>	<i>3.69E-11</i>

Table 2.S2A. Estimated coefficients of cold edge species and assemblage range edges over time (linear regression). The response variable was distance along the coastline, and the units of the estimated coefficient are km/year. A negative coefficient represents a southward shift.

Common Name	Coefficient	Standard Error	Test Statistic	p-value
Acadian redfish	0.15	0.15	0.95	3.49E-01
Alewife	4.12	1.49	2.77	7.87E-03
Alligatorfish	-0.17	0.60	-0.28	7.86E-01
American plaice	0.23	0.10	2.39	2.08E-02
Atlantic cod	5.42	1.00	5.39	2.09E-06
Atlantic halibut	-1.86	1.08	-1.72	1.04E-01
Atlantic herring	-0.08	1.43	-0.05	9.57E-01
Atlantic mackerel	3.03	1.30	2.33	2.39E-02
Atlantic wolffish	0.14	0.24	0.59	5.63E-01
Barndoor skate	-6.23	1.57	-3.97	8.24E-04
Cunner	11.01	1.36	8.08	4.99E-08
Fourbeard rockling	2.56	2.30	1.11	2.76E-01
Greater argentine	-5.93	7.57	-0.78	4.53E-01
Haddock	-0.85	0.62	-1.37	1.77E-01
Little skate	-1.69	0.85	-1.97	5.43E-02
Longhorn sculpin	6.34	0.81	7.79	4.58E-10
Northern sand lance	6.03	2.24	2.69	1.14E-02
Red hake	4.20	0.95	4.43	5.42E-05
Saithe	0.53	0.27	1.93	5.94E-02
Sea raven	2.31	1.02	2.28	2.74E-02
Silver hake	2.41	1.19	2.03	4.82E-02
Smooth skate	-0.01	0.28	-0.04	9.71E-01
Starry ray	-0.04	0.22	-0.16	8.71E-01
Tusk	1.54	0.81	1.90	6.76E-02
White hake	4.57	1.16	3.93	2.74E-04
Winter flounder	2.70	0.74	3.65	6.56E-04
Winter skate	-13.58	1.55	-8.77	1.58E-11
Witch flounder	-1.15	1.48	-0.78	4.39E-01
Yellowtail flounder	5.11	0.72	7.13	4.60E-09
<i>Assemblage</i>	<i>-0.16</i>	<i>0.52</i>	<i>-0.30</i>	<i>7.64E-01</i>

Table 2.S2B. Estimated coefficients of warm edge species and assemblage range edges over time (linear regression). The response variable was distance along the coastline, and the units of the estimated coefficient are km/year. A negative coefficient represents a southward shift.

Model	Response Variable	AIC	Predictor Variable(s)	Estimate	Standard Error	Test statistic	p-value
LM	Assemblage edge (distance)	460.99	(Intercept)	838.62	310.45	2.70	1.06E-02
LM	Assemblage edge (distance)	460.99	Mean SBT	37.55	38.93	0.96	3.41E-01
LM	Assemblage edge (distance)	614.61	(Intercept)	-286.97	331.97	-0.86	3.92E-01
LM	Assemblage edge (distance)	614.61	Mean SST	105.88	25.15	4.21	1.11E-04
LM	Assemblage edge (distance)	437.13	(Intercept)	1209.23	180.18	6.71	1.21E-07
LM	Assemblage edge (distance)	437.13	1% SST	-12.48	34.20	-0.37	0.72
LM	Assemblage edge (distance)	421.73	(Intercept)	-814.67	456.36	-1.79	0.08
LM	Assemblage edge (distance)	421.73	99% SST	90.35	21.04	4.29	1.45E-04
LM	Assemblage edge (latitude)	93.74	(Intercept)	34.30	4.10	8.36	7.46E-10
LM	Assemblage edge (latitude)	93.74	SBT Isotherm	0.18	0.10	1.84	7.45E-02
LM	Assemblage edge (latitude)	133.75	(Intercept)	16.65	9.99	1.67	1.02E-01
LM	Assemblage edge (latitude)	133.75	SST Isotherm	0.60	0.24	2.50	1.58E-02
LMEM	Species edges (latitude)	665.76	(Intercept)	35.37	1.14	31.06	5.81E-95
LMEM	Species edges (latitude)	665.76	SBT Isotherm	0.13	0.03	4.63	5.51E-06
LMEM	Species edges (latitude)	665.76	(Species ID)	0.86	NA	NA	NA
LMEM	Species edges (latitude)	665.76	(Residual)	0.65	NA	NA	NA
LMEM	Species edges (latitude)	931.08	(Intercept)	21.32	3.03	7.04	1.46E-11
LMEM	Species edges (latitude)	931.08	SST Isotherm	0.47	0.07	6.36	7.96E-10
LMEM	Species edges (latitude)	931.08	(Species ID)	0.71	NA	NA	NA
LMEM	Species edges (latitude)	931.08	(Residual)	0.77	NA	NA	NA

Table 2.S3A. Full model results for cold edge group and assemblage. Horizontal lines separate different models. See main text for detailed model descriptions. Predictor variables in parentheses are other relevant terms from the model output. AIC scores are reported here but should not be compared among models with different response variables.

Model	Response Variable	AIC	Predictor Variable(s)	Estimate	Standard Error	Test statistic	p-value
LM	Assemblage edge (distance)	385.63	(Intercept)	358.59	112.12	3.20	2.93E-03
LM	Assemblage edge (distance)	385.63	Mean SBT	14.62	14.06	1.04	3.06E-01
LM	Assemblage edge (distance)	541.07	(Intercept)	238.46	159.11	1.50	1.40E-01
LM	Assemblage edge (distance)	541.07	Mean SST	18.65	12.05	1.55	1.28E-01
LM	Assemblage edge (distance)	365.93	(Intercept)	403.97	65.16	6.20	5.37E-07
LM	Assemblage edge (distance)	365.93	1% SST	13.55	12.37	1.10	0.28
LM	Assemblage edge (distance)	358.07	(Intercept)	-100.49	183.80	-0.55	0.59
LM	Assemblage edge (distance)	358.07	99% SST	26.55	8.47	3.13	0.004
LM	Assemblage edge (latitude)	28.48	(Intercept)	37.51	2.09	17.98	2.93E-19
LM	Assemblage edge (latitude)	28.48	SBT Isotherm	0.02	0.05	0.35	7.31E-01
LM	Assemblage edge (latitude)	45.56	(Intercept)	29.46	3.86	7.64	7.73E-10
LM	Assemblage edge (latitude)	45.56	SST Isotherm	0.23	0.10	2.28	2.68E-02
LMEM	Species edges (latitude)	1800.14	(Intercept)	39.39	0.72	54.88	6.13E-223
LMEM	Species edges (latitude)	1800.14	SBT Isotherm	0.01	0.02	0.86	0.39
LMEM	Species edges (latitude)	1800.14	(Species ID)	1.55	NA	NA	NA
LMEM	Species edges (latitude)	1800.14	(Residual)	0.61	NA	NA	NA
LMEM	Species edges (latitude)	2607.81	(Intercept)	28.43	1.46	19.45	1.43E-71
LMEM	Species edges (latitude)	2607.81	SST Isotherm	0.28	0.04	7.95	4.69E-15
LMEM	Species edges (latitude)	2607.81	(Species ID)	1.13	NA	NA	NA
LMEM	Species edges (latitude)	2607.81	(Residual)	0.67	NA	NA	NA

Table 2.S3B. Full model results for warm edge group and assemblage. Horizontal lines separate different models. See main text for detailed model descriptions. Predictor variables in parentheses are other relevant terms from the model output. AIC scores are reported here but should not be compared among models with different response variables.

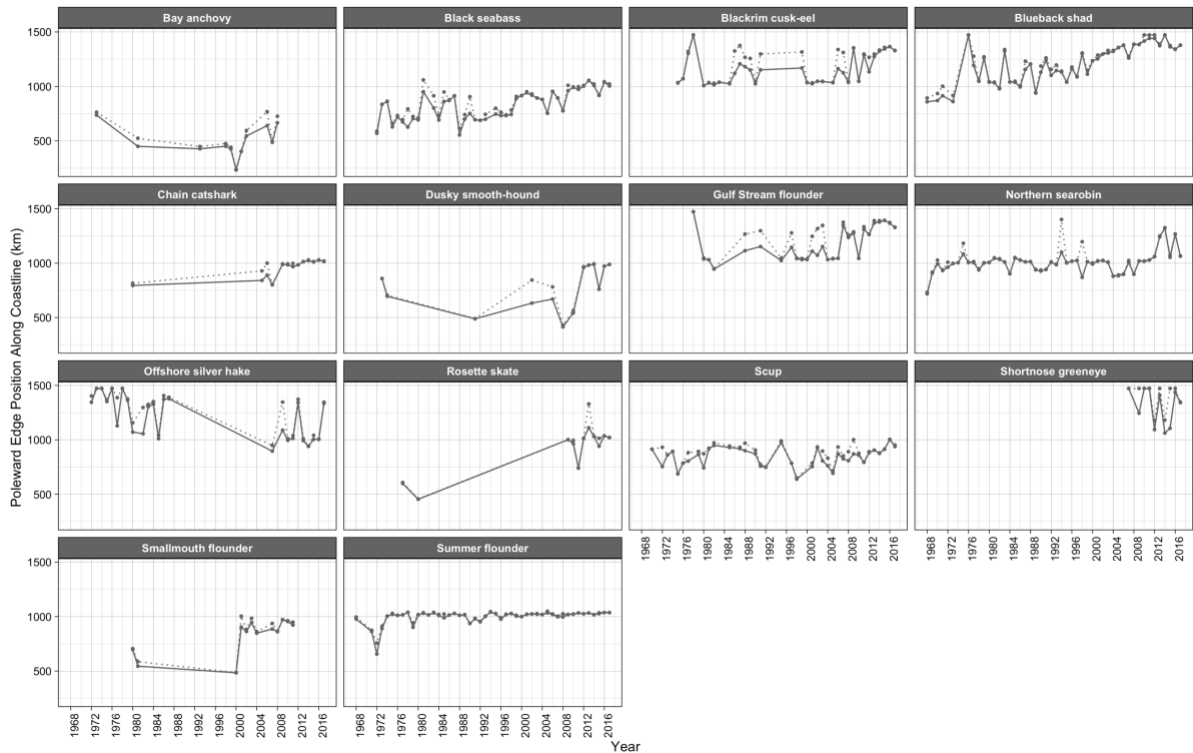




Figure 2.S1. Species' cold edge position (95<sup>th</sup> percentile of distance along coastline, calculated from all observations in a year) from 1968-2017. Solid lines denote the presence-based estimate used in the manuscript, and dotted lines denote a biomass-weighted quantile. Note that in order to be included for analysis, a species\*year combination had to have 10 or more observations, so data gaps represent years where the species was observed 0-9 times.

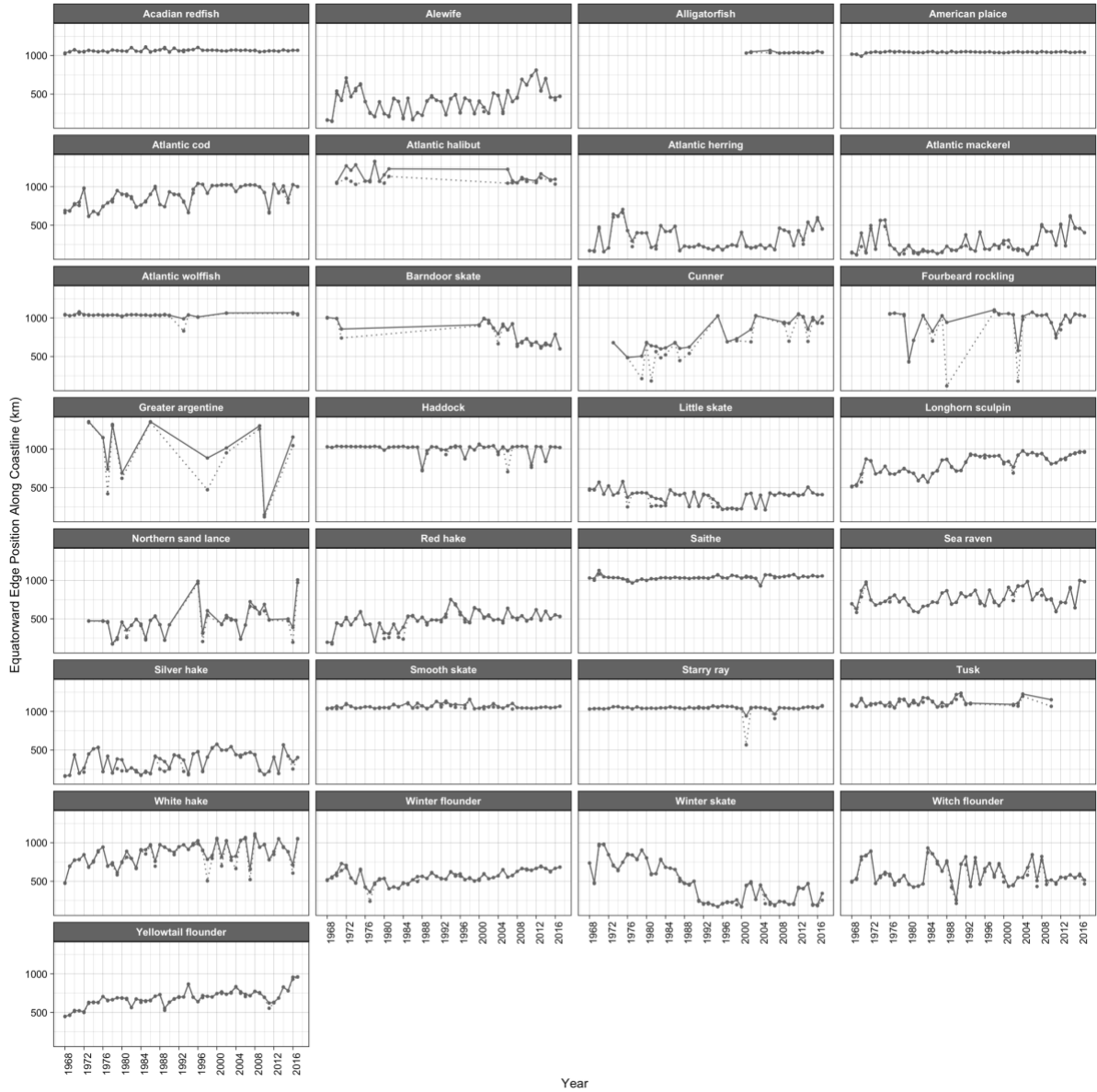


Figure 2.S2. Species' warm edge position (5<sup>th</sup> percentile of distance along coastline, calculated from all observations in a year) from 1968-2017. Solid lines denote the presence-based estimate used in the manuscript, and dotted lines denote a biomass-weighted quantile. Note that in order to be included for analysis, a species\*year combination had to have 10 or more observations, so data gaps represent years where the species was observed 0-9 times.

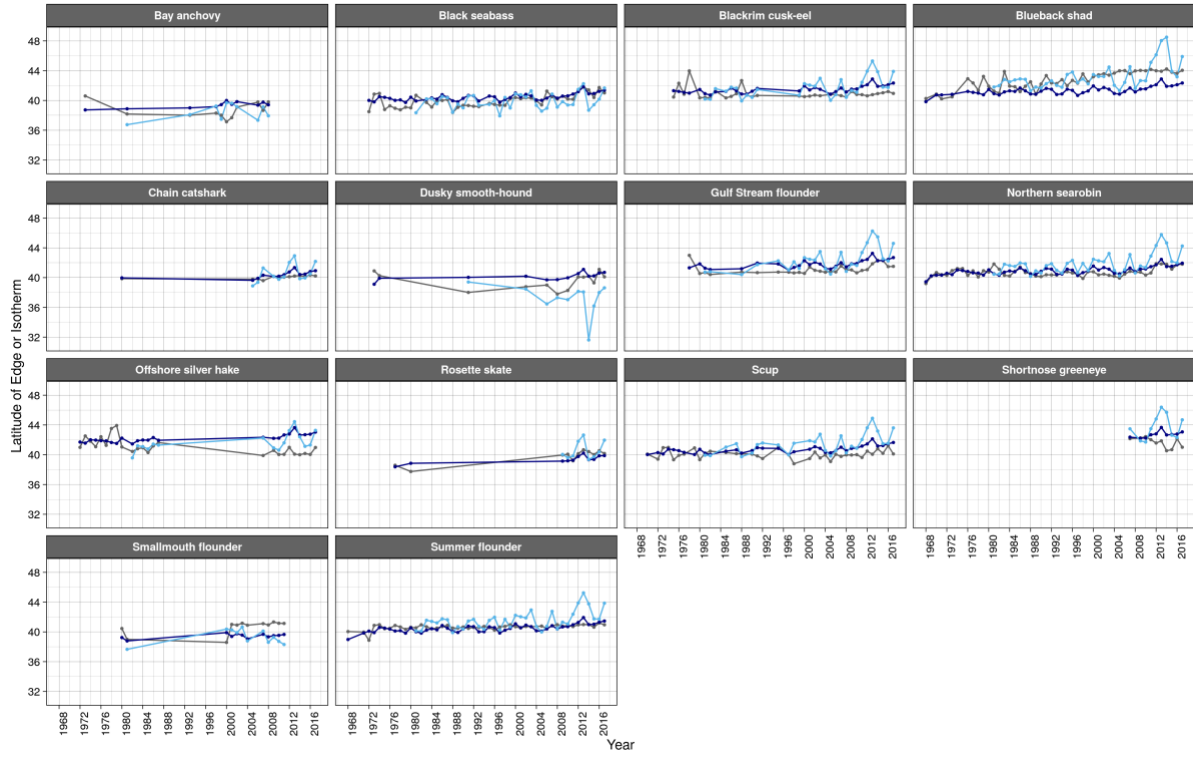


Figure 2.S3. Cold-edge species' range edges (measured as 95<sup>th</sup> percentile of latitude) and species-specific sea surface (navy) and bottom (light blue) temperature isotherms. See Methods for a description of how species-specific isotherms were calculated.

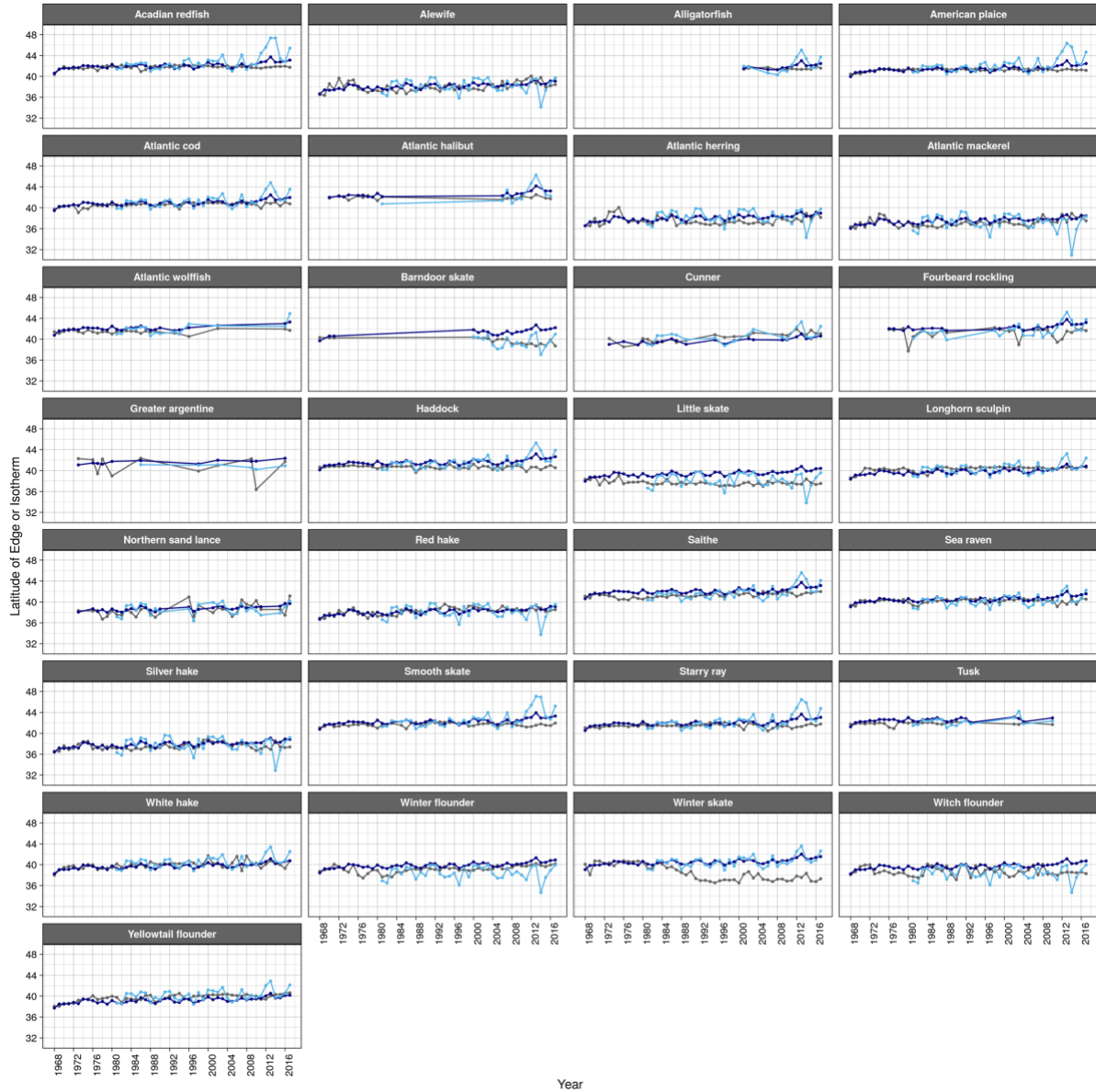


Figure 2.S4. Warm-edge species' range edges (measured as 95<sup>th</sup> percentile of latitude) and species-specific sea surface (navy) and bottom (light blue) temperature isotherms. See Methods for a description of how species-specific isotherms were calculated.

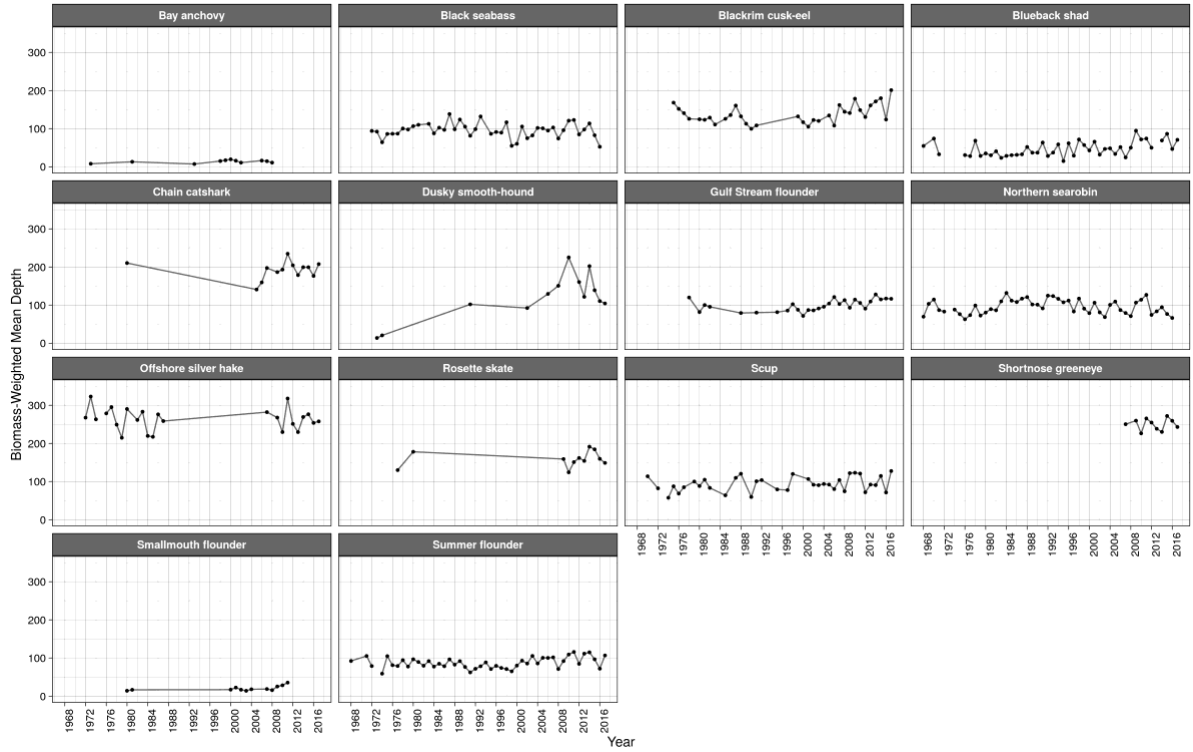


Figure 2.S5. Mean depth of cold edge species' observations each year, calculated as the mean depth of each haul where a species was found, weighted by its raw biomass in that haul.

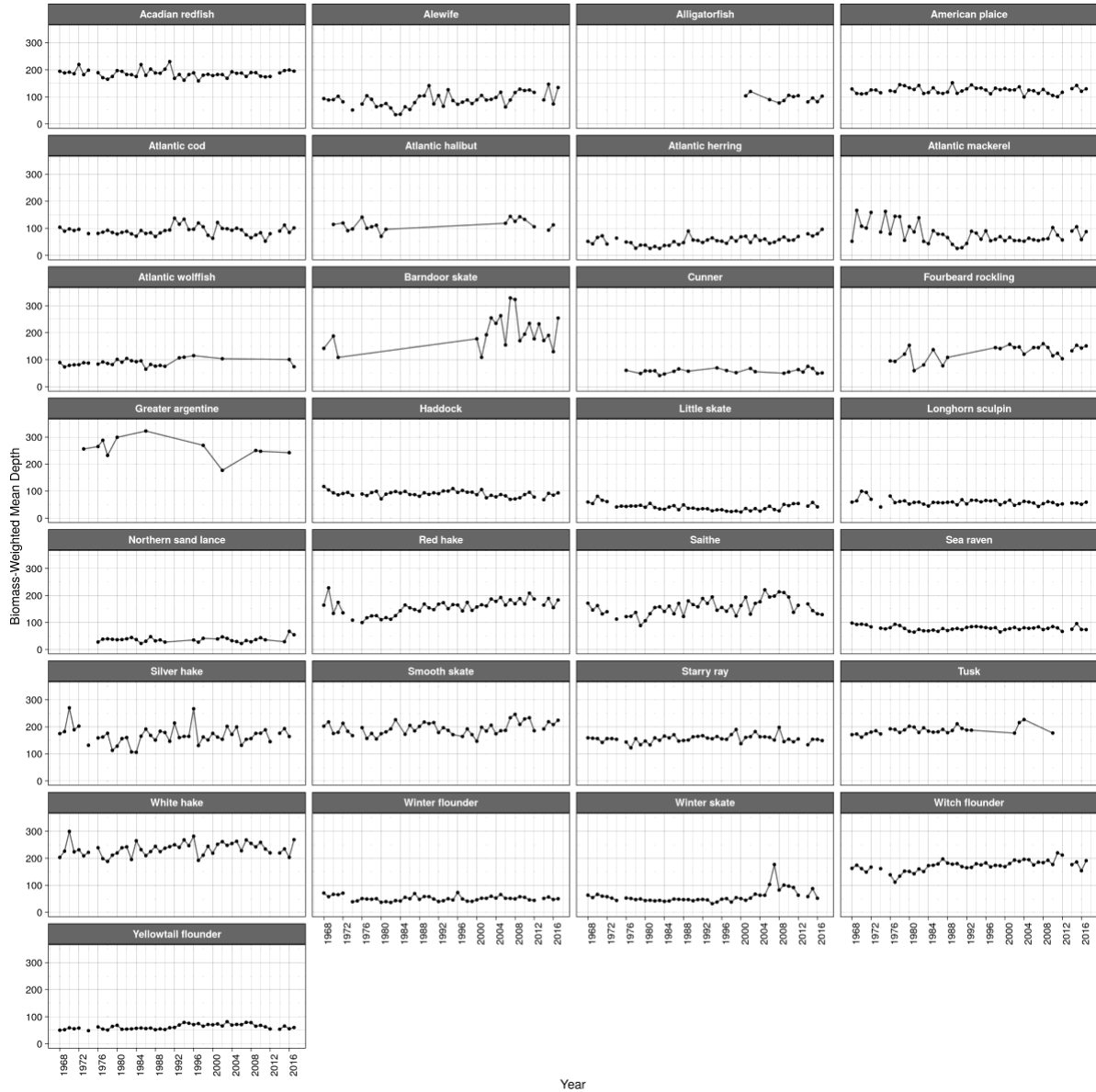


Figure 2.S6. Mean depth of warm edge species' observations each year, calculated as the mean depth of each haul where a species was found, weighted by its raw biomass in that haul.

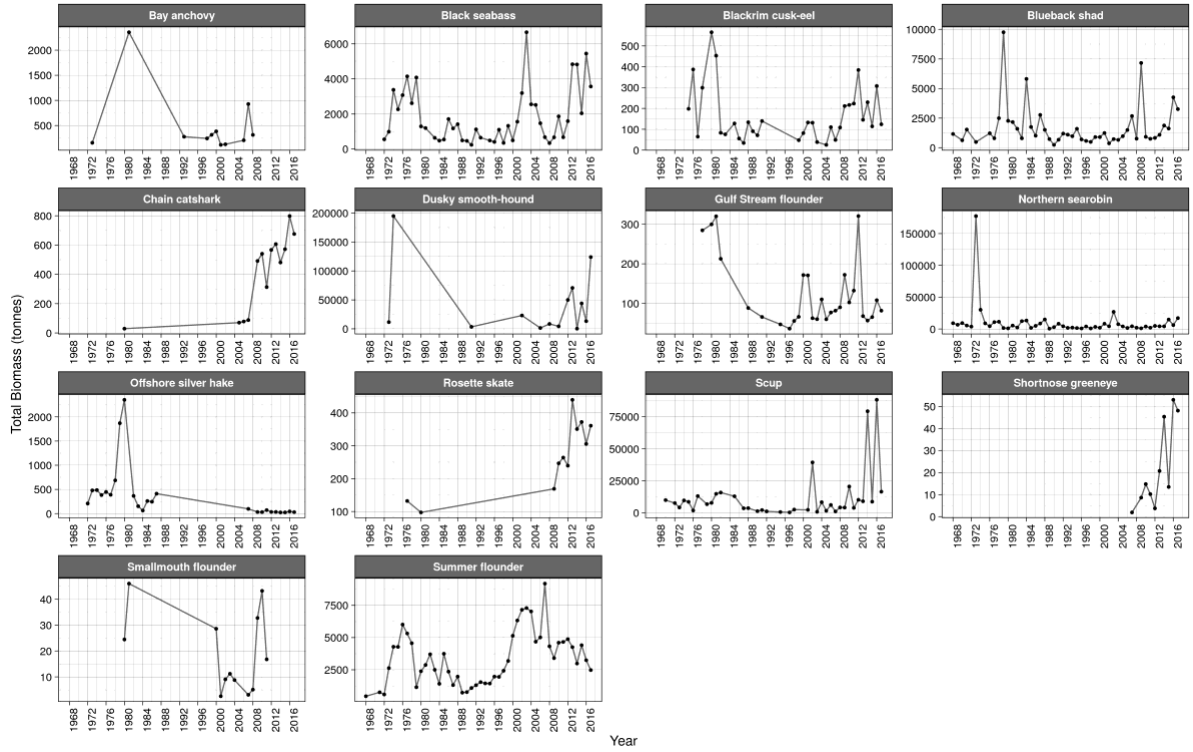


Figure 2.S7. Total biomass calculated for each cold edge species in each year (see Methods). Note that the y-axis scale varies among species.

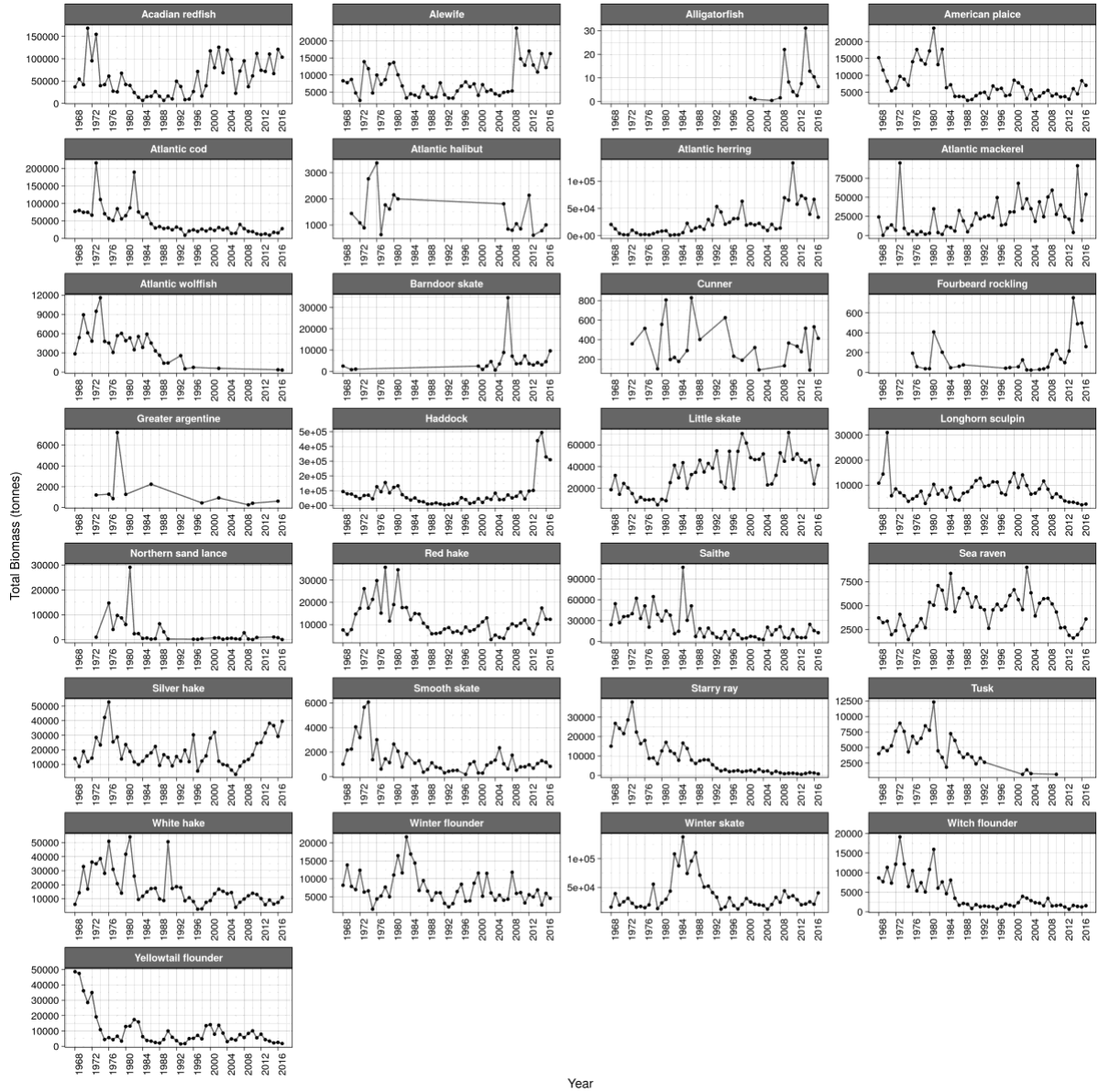


Figure 2.S8. Total biomass calculated for each warm edge species in each year (see Methods). Note that the y-axis scale varies among species.

## 4. Realized thermal niche tracking at range limits of North American marine species

### A. Abstract

Climate-related shifts in species ranges have been documented around the globe. Accurate prediction of future range shifts is important for natural resource management and conservation—and the maintenance of human welfare and well-being—in the 21<sup>st</sup> century. However, the extent to which temperature change drives range shifts remains unresolved and likely varies among systems, regions, and taxa. Temperate marine ecosystems are ideal study systems for disentangling whether range limits are temperature-mediated: many marine regions have warmed in recent decades, and marine ectotherms experience relatively few barriers to dispersal. We used three to five decades of annual survey data on 75 fish and invertebrate species from the Northeast, the West Coast, and the Eastern Bering Sea to describe range edge dynamics, quantify temperature extremes at species' range limits (representing the realized thermal niche), and test to what degree thermal niches were conserved over time. With these thermal niches of species' range limits, we investigated three hypotheses for range limit changes: the *thermal niche hypothesis* that cold and warm range limits track temperature change near-instantaneously; the *temporal lag hypothesis* that range limits track temperature change with a time lag due to extinction debt, slow dispersal or other demographic processes; and the *temperature-independent hypothesis* that range limits are mediated by non-climate processes such as biotic interactions and dispersal limitation and do not track temperature change. Almost half of all range limits were classified as temperature-independent. A higher proportion of cold range limits than warm range limits conformed to the thermal niche hypothesis. We detected thermal niche tracking



in all three regions, including the West Coast where there has been no overall warming trend. This approach classified range limits according to their degree of thermal niche conservatism and could be extended to test other hypotheses of range limits.

## ***B. Introduction***

Human-caused global climate change now affects, directly or indirectly, all biomes and levels of biological organization (Scheffers et al., 2016). One of the most profound effects has been changes in the spatial distributions of species as they follow their preferred climates up mountains, deeper in the oceans, and generally toward the poles (Parmesan & Yohe, 2003; Pecl et al., 2017). A strong correlation between regional climate change and shifting species ranges has been documented in many taxa (Chen et al., 2011; Pinsky et al., 2013). However, individualistic responses and “ecological surprises” are also common (La Sorte & Jetz, 2012; Poloczanska et al., 2011; Zhu et al., 2012), underscoring the need to consider the interplay of climatic constraints and non-climate processes in determining the limits of species ranges (Sexton et al., 2009; Urban et al., 2016).

Range limits arise where biotic or abiotic conditions prevent persistence of a species, meaning that the species has exceeded its niche. We use the definition of the fundamental niche as the range of environments in which a species could theoretically persist in the absence of biotic interactions, and the realized niche as the range of environments in which the species is actually found (Godsoe et al., 2017). Shifts in the realized thermal niche often trade off with shifts in the range: if a species is shifting its range to track temperature, it will occur at the same temperature over time, thus the realized thermal niche at will be conserved.

Conversely, if a species does not shift in concert with temperature change, the range may remain stable but the realized thermal niche will shift (La Sorte & Jetz, 2012).

Temperature extremes are more commonly theorized to be range-limiting than means (Jankowski et al., 2013; La Sorte & Jetz, 2012), but either cold or warm range limits can theoretically be limited by either cold or warm temperature extremes; e.g., a cold range limit might occur if it becomes too cold in winter for adults to survive, or if summers are not warm enough for reproduction and juvenile survival (Hutchins, 1947). We define the *edge thermal niche* as the thermal extremes found at a species' range limit.

In this study, we explore three hypotheses about how temperature mediates a species' realized niche and therefore its range limits (Table 3.1): the *thermal niche hypothesis* (TNH), which predicts that cold and warm range limits are temperature-mediated and will both track temperature change; the *temporal lag hypothesis* (TLH), which predicts that range limits will track temperature but with a lag at one or both limits; and the *temperature independent hypothesis* (TIH), which predicts that one or both range limits are set by other processes and will not shift primarily in response to temperature change. The TNH is supported by evidence that some species' range limits coincide with their physiological thermal limits (Sunday et al., 2012). The TLH may arise from several mechanisms, including a detection lag at the cold range limit (Orensanz et al., 2004) or extinction debt at the warm range limit (Jackson & Sax, 2010). The TIH implies that other processes mediate range edge dynamics, such as dispersal limitation (Poloczanska et al., 2011) or biotic interactions (Louthan et al., 2015).

Empirical studies on range limits and climate have reported results in line with each of these hypotheses. The literature includes findings that support the TNH at cold and/or

warm range limits (Atkinson et al., 2019; Cavanaugh et al., 2014; Freeman & Freeman, 2014); evidence for the TLH at both cold and warm range limits (Forero-Medina et al., 2011; Orensanz et al., 2004); better climate tracking at cold limits than at warm limits, consistent with either the TIH or the TLH (Fredston-Hermann et al., n.d.; Hickling et al., 2005); observations that species are not shifting at all in the face of pronounced warming, as predicted by the NTH (Poloczanska et al., 2011); and highly individualistic responses that did not uniformly support the TNH or any other hypothesis (Boisvert-Marsh et al., 2014; Currie & Venne, 2017; Hanberry & Hansen, 2015).

It is unlikely that any one variable will ever fully explain range limits of all species (Gaston, 2009). However, key variables may emerge as predominant in certain systems, taxa, or biogeographic scenarios. For example, marine ectotherms have latitudinal range limits that coincide well with their experimentally-derived thermal limits, but terrestrial ectotherms do not (Sunday et al., 2012). The realized thermal niche of marine fishes is correlated with their responses to recent temperature changes, also suggesting that range limits of marine species are commonly temperature-mediated (Day et al., 2018). Additionally, marine fishes have tracked historical warming (Hiddink et al., 2015; Perry et al., 2005; Pinsky et al., 2013). Motivated by this type of evidence, many models now exist that predict future ranges of marine species based on a statistical association with the temperatures and environments where those species were historically found (Cheung et al., 2009; García Molinos et al., 2015). However, responses to historical warming do vary markedly among species (Pinsky et al., 2013; Poloczanska et al., 2013), and few studies have explored which marine species might *not* be tracking temperature, or why.

To more fully test our three hypotheses, we explored variation across species and geographic regions, drawing on repeated large-scale biodiversity surveys in three North American marine regions to quantify shifts in poleward and equatorward range limits across 75 fish and invertebrate species. The three study regions have experienced divergent climatic histories that provide a natural experiment for our hypotheses: the Northeast US has warmed rapidly and almost continuously, the Eastern Bering Sea has warmed episodically, and the US West Coast has not warmed overall but periodically experiences dramatic temperature fluctuations among years. The combination of many species across three divergent climate regimes provides a rich opportunity to explore the applicability of the three range limit hypotheses. By measuring thermal extremes at range limits and testing whether they have changed over time, we quantified the degree to which edge thermal niches are conserved over time.

### ***C. Methods***

#### *Data sources*

We studied three temperate marine continental shelf regions in the US: the Northeast, the West Coast, and the Eastern Bering Sea. Each of these regions has a long-term marine survey program operated by the National Oceanic and Atmospheric Administration (NOAA). The surveys use trawl gear and a randomized stratified or fixed station sampling design in a consistent season for marine fish and invertebrates. Each of these surveys is conducted on the continental shelf targeting demersal and benthic species, up to several hundred meters deep. Northeast data (from a spring survey) were available annually from 1968-2018, Eastern Bering Sea data (from a summer survey) were available annually from 1982-2018, and West

Coast data (from a fall survey) were obtained by combining a triennial survey conducted from 1977-2004 and an annual survey available from 2003-2018. The West Coast data was trimmed to 1983 to coincide with the start of that region's temperature dataset (see below), and the Eastern Bering Sea data was trimmed to 1989 to omit years with a smaller spatial extent of sampling (Lauth & Conner, 2014). The West Coast and Eastern Bering Sea raw datasets were downloaded from FishData, and the Northeast data were downloaded from OceanAdapt (downloaded November 25, 2019 from <https://oceanadapt.rutgers.edu/>), a data portal to access NOAA trawl survey records (Keller et al., 2017; Lauth & Conner, 2014; Politis et al., 2014).

The Northeast dataset, which was pre-processed for quality control and taxonomic accuracy, contained records for 74 species. We limited our West Coast analysis to the 54 species that were recorded in both the triennial and the annual surveys. In the Eastern Bering Sea dataset, we downloaded data on the 100 most frequently observed taxa, and proceeded with analysis for the 82 taxa that were identified to species. We retrieved higher taxonomy for all 210 species from the Integrated Taxonomic Information System database, (Chamberlain & Szöcs, 2013; ITIS, 2020) revealing that study species came from ten taxonomic classes of fishes and invertebrates (see Suppl. Table 3.1).

Throughout our analysis, we compared distribution data for a given species with temperature data from the preceding twelve months. We used the 12 months preceding the earliest possible start month for each region's survey for analysis (March in the Northeast, May in the West Coast, and July in the Eastern Bering Sea). For example, range edges derived from the spring 1999 Northeast survey were compared to temperature records from March 1998 to February 1999.

To obtain environmental predictor variables, we downloaded two historical sea surface temperature (SST) datasets. The National Oceanographic and Atmospheric Administration (NOAA) NCEI optimum interpolation SST (NOAA, 2018) is available daily from 1982 onward at 0.25°x0.25° resolution; we used these data for the Eastern Bering Sea and West Coast regions. Because the Northeast survey substantially pre-dates the beginning of this high-resolution SST dataset, we used the Hadley Centre SST dataset in the Northeast. The HadISST data are available monthly at 1° resolution from 1870 to date (Rayner, 2003). To ensure comparability between the two data sources, we converted the daily SST records from the West Coast and Eastern Bering Sea regions into monthly means for each grid cell; all temperature metrics described henceforth are based on monthly mean SSTs.

Records were downloaded from NOAA (Chamberlain, 2019) within a bounding box of 34-46°N, 66-78°W for the Northeast, 30-50°N, 116-126°W for the West Coast, and 54-66°N, 154-179.5°W for the Eastern Bering Sea. Temperature records were then cropped to fall within the US Exclusive Economic Zone in water no deeper than 300 m for the Northeast and the Eastern Bering Sea. Because the West Coast shelf is so narrow that some latitudes have no grid cells with a mean depth less than 300 m, we retained temperature records for spatial cells up to 400 m depth for that region. All data processing and analyses were conducted in R version 3.6.0 (R Core Team, 2018).

Range edge dynamics were compared to warm and cold temperature extremes; these were defined as the warmest and coldest months of the 12 months preceding the survey. To generate edge-specific estimates of warm and cold extreme temperatures (see *Range edge analysis*), we constructed generalized additive models (GAMs) of maximum and minimum monthly temperatures in each year along the axis of measurement for each region (coastal

distance or northwest distance; see *Spatiotemporal reconstruction of species ranges*) using the “mgcv” package in R (Wood, 2017). Each of these GAMs predicted warm or cold temperature extremes in each year, given a position along the axis.

### *Spatiotemporal reconstruction of species ranges*

We estimated annual species ranges from the raw trawl survey data using VAST, a spatial generalized linear mixed model involving two components in a delta-model implemented in an R package (Thorson, 2019; Thorson & Barnett, 2017). This model was designed to estimate total abundance and spatial variation in density of species caught in NOAA trawl surveys. We fit VAST to data that follow either stratified-random or fixed-station designs; in both cases, VAST predicted densities over a fixed spatial domain. This analysis enabled comparison across years even when survey methodologies were revised and across regions with distinct survey protocols, and can control for differences in catchability, enabling us to combine the two historical West Coast surveys. Previous work showed that without this type of spatiotemporal model-based approach, estimating range dynamics from raw observations can yield misleading or biased results (Thorson, Pinsky, et al., 2016).

The VAST models estimated biomass density (kilograms per square-kilometer) as a two-dimensional density surface defined over the spatial domain of the survey. We used a Poisson-link delta-model that involves two log-linked linear predictors, which are then transformed to predict encounter probability and expected biomass given an encounter (Thorson, 2018). Each linear predictor involves several coefficients including: an annual intercept that follows a first-order autoregressive process (where the variance and autocorrelation are estimated), a spatial term that is constant among years (“spatial

variation”), a spatial term that varies among years (“spatio-temporal variation”), density covariates that are used to predict variation in each linear predictor, and catchability covariates that represent differences in encounter probability and/or positive catch rates but are not caused by differences in density (e.g., gear performance and deployment affecting detectability). Spatial and spatio-temporal terms are estimated as random effects, where the spatial variance and decorrelation rate are estimated. These random effects are approximated as following a Matern distribution while estimating geometric anisotropy (i.e., where decorrelation rates vary between north-south and east-west axes; Thorson et al. (2015)); to approximate this Matern distribution, we use the stochastic partial differential equation (SPDE) approach (Lindgren et al., 2011). We additionally use a predictive-process framework (Banerjee et al., 2008) where spatial variables are estimated at 100 pre-defined locations (termed “knots”) and the value of these variables at other locations is predicted using bivariate interpolation using methods from R-INLA (Lindgren, 2012). The model is implemented using R package VAST (Thorson, 2019; Thorson & Barnett, 2017), and fixed effects are estimated while integrating across random effects using the Laplace approximation as implemented using TMB (Kristensen et al., 2016). We check for evidence of non-convergence by confirming that the Hessian matrix is positive definite, and that the gradient of the marginal log-likelihood with respect to each fixed effect is low ( $<0.001$ ). Range edges are then calculated by predicting densities at every 2 km by 2 km raster cell within the spatial domain, calculating the cumulative sum of densities along a given axis, and identifying the raster cell where this cumulative sum equals a given quantile. We then calculate standard errors for these range-edge predictions by drawing 100 samples from the predictive distribution of fixed and random effects (i.e., the joint precision matrix),



recalculating the edge for each of these samples, and treating this as the predictive distribution. This study is the first to demonstrate this new feature for calculating uncertainty in range-edges using VAST, and the sample-based uncertainty generalizes previous standard-error calculations that were only feasible for differentiable transformations of model variables (Kass & Steffey, 1989). Of the 210 species across the three regions, VAST models successfully converged in all years for 170 (69 in the Northeast, 41 on the West Coast, and 60 in the Eastern Bering Sea).

### *Range edge analysis*

We quantified species range edges as the 0.05 and 0.95 quantiles of density along axes customized to each study region. Because VAST fitted each species' range edges as derived quantities in the model, the model reported an estimate and a standard error for each edge quantile (0.05 and 0.95) and each axis. For the West Coast and the Northeast, we measured range edges in distance along the coast, because parts of the coastline veer east-west. Our previous work found that distance along the coast was a better predictor of range dynamics than latitude in areas with complex coastline topographies (Fredston-Hermann et al., n.d.). For both regions, we downloaded a coarse outline of the coast using the “*naturalearth*” package in R (South, 2017) and applied a spatial kernel smoothing function from the R package “*smoothr*” (Strimas-Mackey, 2018) to remove coastal features such as the Chesapeake Bay that would be counted in a measurement of coastline length. The smoothing function used a relative scale for the degree of smoothing to be applied; we began at one and added to the degree of smoothing incrementally until all bays, estuaries, and other major coastal features were smoothed out, leading to a final smoothness value of one for the

West Coast and eight for the Northeast. We then associated points along the coastline with the northing/easting VAST grid by minimizing Euclidean distances to estimate density along the coastal distance axis. In the Eastern Bering Sea, where the shelf points almost directly northwest, we estimated density along a rotated northwest axis.

We omitted from further analysis species for which the estimated edge position was highly uncertain by comparing the standard deviation of range limits through time with the VAST-estimated standard errors around each year's estimated range limit. Species' range limits were eliminated if the mean of VAST-estimated standard errors across all years was greater than the time-series standard deviation of range limit position. This filter removed 39 Northeast species, 14 West Coast species, and five Eastern Bering Sea species.

To ensure that the species analyzed truly had at least one range edge in the study region, we also eliminated range limits with mean positions within 100 km of the edge of the study region. This removed 12 additional Northeast species, seven additional West Coast species, and 18 additional Eastern Bering Sea species. After all of these filters, we proceeded with 87 range limits—20 in the Northeast, 22 on the West Coast, and 45 in the Eastern Bering Sea—across 75 species (12 had both warm and cold range limits; See Supp. Table 3.2). For almost all species, only one range limit fell within the study region, not both (see Supp. Table 3.2). Thus, our analysis evaluates the evidence for our different hypotheses by evaluating many isolated range limits, not both range limits of a single species.

We tested whether range limit positions had significantly shifted over time with single-species Bayesian linear regressions of range limit position on time ( $n = 87$  models). Single-species models were fitted using the `rstanarm` package (Goodrich et al., 2018) with four chains, 12,000 iterations including 2,000 burn-in draws, a target average proposal

acceptance probability of 0.95, and normally distributed noninformative priors (means of 0, variance set at 10 for the intercept and 2.5 for other parameters, then scaled by the standard deviation of the response variable); all models converged (Gelman-Rubin convergence statistic below 1.1). We then pooled posterior distributions of the estimated coefficient by averaging across all single-species values at each draw position, within the three regions and each of the two types of range limits (warm or cold).

### *Edge thermal niche conservatism*

We measured the edge thermal niche—the temperature extremes found at the range limit—by predicting annual warm and cold temperature extremes from the range limit position, using region-specific GAMs (see *Data sources*). We then fitted Bayesian linear regressions to test whether either the warm or cold extreme temperature at a species' range limit had changed significantly over time ( $n = 174$ , 87 range limits by two temperature extremes). Single-species Bayesian linear regressions were fitted using the *rstanarm* package (Goodrich et al., 2018) with four chains, 40,000 iterations including 10,000 burn-in draws, a target average proposal acceptance probability of 0.99, and normally distributed noninformative priors (means of 0, variance set at 10 for the intercept and 2.5 for other parameters, then scaled by the standard deviation of the response variable); models converged for 86 of 87 range limits (Gelman-Rubin convergence statistic below 1.1). We calculated the mean and 90% Bayesian credible interval from each single-species posterior distribution of the year coefficient for either warm or cold temperature extremes. This approach identified whether either extreme of the edge thermal niche had moved into colder

or warmer waters, indicating that the range limit was shifting at a different rate than expected from temperature change.

If just one of the two temperature metrics we measured at a range limit—cold or warm extremes—was constant over time, it would imply that the range limit was tracking temperature. We differentiated among three potential patterns in edge thermal niche trends over time, which correspond to different hypotheses about what drives range limits (Figure 3.1). Our first hypothesis was that species' range limits were perfectly tracking at least one temperature extreme and thus either the warm, cold, or both temperature extremes at the range limit would not change over time (the TNH). If the estimated coefficient for either temperature extreme fell below an absolute value of 0.01 °C/year, we accepted the first hypothesis that the range limit conformed to the TNH. We chose this threshold, because it is just below rates of change in regions that did warm during the study period (see *Results*), so a finding that a species' thermal niche has shifted less than 0.01 °C/year is evidence that the range limit is shifting to stay within a constant edge thermal niche, consistent with the TNH. In other words, if the edge thermal niche was shifting more than 0.01 °C/year, the range limit might not be moving at all and the shift in edge thermal niche could simply reflect ambient changes in sea surface temperature.

The TNH was rejected if for a given range limit, neither thermal limit's coefficient of change over time had an absolute value below 0.01. In that case, we tested the second hypothesis, the TLH, predicting that species were tracking temperature with a lag. We accepted the TLH if the 90% Bayesian credible interval of the coefficient of time on either temperature extreme overlapped with zero. We note that this approach did not explicitly test for the presence of a temporal lag; rather, it reflects the finding that the edge thermal niche

was not consistent over time, but we cannot reject the possibility that the range limit is tracking temperature.

The second hypothesis was rejected if neither coefficient of the edge thermal niche had a Bayesian credible interval that overlapped with zero. In other words, there was clear evidence for a change in edge thermal niche over time: both temperature extremes showed rates of change that were far from zero and had Bayesian credible intervals that did not overlap with zero. In this case where there was no evidence of temperature tracking, we accepted the TIH.

#### ***D. Results***

From 1967 to 2018, minimum, mean, and maximum SSTs in the Northeast all increased (Figure 3.2A), translating to more than one degree Celsius of warming in each metric over the time-series (respectively,  $0.03 \pm 0.007$  °C/year,  $p = 7.43 \times 10^{-5}$ ;  $0.028 \pm 0.004$  °C/year,  $p = 2.01 \times 10^{-9}$ ;  $0.024 \pm 0.005$  °C/year,  $p = 1.65 \times 10^{-5}$ ; linear regression). On the West Coast (Figure 3.2B), no significant temperature trends occurred in any temperature metric from 1982-2018 (minimum SST  $0.005 \pm 0.01$  °C/year,  $p = 0.59$ ; mean SST  $0.003 \pm 0.009$  °C/year,  $p = 0.69$ ; maximum SST  $0.001 \pm 0.012$  °C/year,  $p = 0.91$ ; linear regression). In the Eastern Bering Sea (Figure 3.2C), warming was pronounced, particularly in warm temperature limits from 1982-2018: mean SST increased  $0.02 \pm 0.009$  °C/year ( $p = 0.029$ ), and maximum SST increased  $0.044 \pm 0.01$  °C/year ( $p = 0.0022$ ), representing over 1.5°C of warming in maximum regional temperatures in just 37 years. Minimum SST did not change significantly in the Eastern Bering Sea ( $0.002 \pm 0.008$  °C/year,  $p = 0.78$ ; all linear regressions).

### *Range edge shifts over time*

When averaged across all species in a region, range limits shifted 7.3 km/year in the Northeast (90% CI 6.8-7.8), 3.7 km/year on the West Coast (90% CI 2.0-5.4), and 0.9 km/year in the Eastern Bering Sea (90% CI 0.3-1.5; Figure 3.3A; means and credible intervals from single-species Bayesian linear regressions). Separating these posterior distributions by range limit type (cold or warm) revealed that these shifts were driven almost entirely by warm range limits; across all regions, we found no evidence of cold range limits shifting over time (Figure 3.3B). Warm range limits shifted 11.1 km/year (90% CI 10.4-11.7) in the Northeast, 5.7 km/year (90% CI 3.4-8.1) on the West Coast, and 2.3 km/year (90% CI 1.6-3.2) in the Eastern Bering Sea (Figure 3.3C; means and credible intervals from single-species Bayesian linear regressions).

### *Temperature tracking of edge thermal niche*

Of the 86 range limits included in the edge thermal niche analysis, 38 showed strong evidence of thermal niche conservatism from at least one thermal extreme over time, categorized as an estimated coefficient below an absolute value of 0.01. These edges were classified as conforming to the TNH. Another 10 did not have coefficients as low as 0.01 but had at least one thermal extreme with a Bayesian credible interval that overlapped with zero, consistent with the TLH. For the remaining 38 range limits, neither thermal extreme had a coefficient overlapping with zero (i.e., both thermal extremes changed over time), consistent with the TIH.

Range limits supported dissimilar hypotheses across the three regions (Figure 3.4). In the Northeast (Figure 3.4A), 15 of 20 range limits (75%) supported the TIH; of the remainder, one supported the TLH and four supported the TNH. The West Coast region had a more even spread (Figure 3.4B), with five range limits (23%) consistent with the TNH, eight (36%) consistent with the TLH, and nine (41%) consistent with the TIH. The Eastern Bering Sea range limits (Figure 3.4C) primarily conformed to the TNH (66%;  $n = 29$ ), with 32% conforming to the TIH ( $n = 14$ ) and just 2% to the TLH ( $n = 1$ ). The hypotheses supported by range limits were similar among taxonomic groups (39% TNH, 10% TLH, and 51% TIH for fish, and 49% TNH, 13% TLH, and 38% TIH for invertebrates). The majority of cold range limits ( $n = 40$ ) supported the TNH, while the majority of warm edges supported the TIH (60% TNH, 10% TLH, and 30% TIH for cold edges, and 30% TNH, 13% TLH, and 57% TIH for warm edges).

## ***E. Discussion***

We tested for thermal niche conservatism at range limits of a diverse group of marine fish and invertebrates across three regions, two oceans, and up to five decades of survey records. We distinguished between range limits with a high degree of thermal niche conservatism (consistent with the thermal niche hypothesis), some thermal niche conservatism (consistent with the temporal lag hypothesis), or thermal niches that shifted over time (consistent with the temperature-independent hypothesis). 48 of 86 range limits showed some degree of thermal niche conservatism, which is predicted to be widespread among marine ectotherms (Day et al., 2018; Sunday et al., 2012). Notably, the remaining 38 range limits showed no evidence of tracking temperature. We also found no evidence of

spatial shifts in cold range limits averaged across species, even while warm limits had shifted, contrary to expectations from other studies conducted with the same datasets (Batt et al., 2017; Fredston-Hermann et al., n.d.). However, cold range limits exhibited thermal niche conservatism over time much more often than warm range limits.

These results varied dramatically among regions. In the Northeast, warming has been the most consistent over time, and our previous work showed that cold range limits shifted further and tracked temperature better than warm range limits. The present results support the latter finding—that cold range limits are more likely to maintain consistent temperatures over time—but not the former. Our results on cold range limit shifts may have been affected by one species that shifted dramatically south during the time-series, *Merluccius albidus*. In addition, the spatiotemporal model estimated very large northward shifts in warm range limits in the Northeast—shifts that were so pronounced that many warm range limits in this region were classified under the TIH because they moved into much cooler waters. The Eastern Bering Sea has exhibited variable but marked warming in recent decades. Despite this variability, we found support for the TNH among most range limits in the region, suggesting that many species are keeping up with changing ocean conditions. We found fewer range limits consistent with the TNH on the West Coast, which has not warmed overall but experiences periodic warming events due to the El Niño Southern Oscillation (Hayward, 2000; Lea & Rosenblatt, 2000). We expected to find more evidence for the TNH among fishes than invertebrates, because invertebrates may have more limited dispersal (Grantham et al., 2003). However, invertebrates actually supported the TNH more frequently than fishes in our analysis. This result likely arose because most invertebrates were found in the Eastern



Bering Sea, where we also recorded the greatest degree of thermal niche conservatism at range limits overall.

Using only observational data, we could not test which mechanisms were truly driving the patterns we observed. For example, we did not characterize what caused temporal lags in the range limits attributed to the TLH, or the duration of the lag. Possible mechanisms for temporal lags include extinction debt at the warm range limit (Fordham et al., 2016) or a delay in detection (Orensanz et al., 2004). However, given that most lags between extreme temperature events and observed range shifts in marine species take less than 10 years (Day et al., 2018; Orensanz et al., 2004) and we used decades of survey data, our methods would have detected a species returning to its preferred thermal conditions at the range limit if it was indeed tracking temperature with a lag. Similarly, we did not distinguish among the myriad possible temperature-independent drivers of range edge dynamics, such as dispersal limitation (Poloczanska et al., 2011), biotic interactions (Louthan et al., 2015), and fishing (Engelhard et al., 2014).

Geographical range shifts are a common way to measure how species are responding to climate change (Lenoir & Svenning, 2015). However, species may also shift in abundance or depth to track their thermal niches, in addition to or instead of tracking temperature (Dulvy et al., 2008; Perry et al., 2005). Our previous work found that changes in abundance or depth did not frequently co-occur with range shifts, but neither did they frequently compensate for a lack of range shifts (Fredston-Hermann et al., n.d.).

While NOAA surveys are among the most extensive and long-standing biodiversity monitoring programs on Earth, they nonetheless have limitations, particularly when calculating a range limit which is inherently stochastic. The surveys are conducted in one

season, which may not capture the most distal extent of every species' range. The NOAA surveys have also changed over time in effort, survey area, and other elements of sampling design. We utilized a spatiotemporal model to address some of these sources of bias. This was a particular concern on the West Coast, where we added a catchability coefficient to the model to control for a change in survey methodology from a triennial survey (1977-2004) to an annual one with a different design (2003-2018). Because the model fit the range limit position as a derived quantity, we also estimated a standard error in range limit position, and used it to omit range limits that were too stochastic to reveal any real trends.

We systematically tested which of three biogeographical hypotheses regarding temperature tracking best explained patterns in thermal niche conservatism at range limits of marine species over time. Rather than identify a single hypothesis that is consistent among all marine species, this approach attributed individual range edges to particular hypotheses. Our results move beyond the simplistic assumption that “marine species are tracking temperature” to highlight variable—but potentially predictable—responses to temperature change. Given that marine ectotherms are often assumed to track temperature more than many taxa, our findings suggest that no taxonomic group should be expected to uniformly respond to warming; rather, we should expect individualistic responses, which may lead to divergent conservation outcomes for different species and changes in range size and community composition. Our approach could aid in managing species experiencing warming, for which different management interventions would be appropriate for species that are tracking temperature, lagging temperature, or temperature-independent. Further, our methods could be extended to any biogeographical hypothesis for which an associated range edge behavior can be described. For example, future studies with distribution data on both sides of

a biogeographic boundary could test whether range edge dynamics were consistent with a dispersal limitation hypothesis. Further work in this area will continue to reveal the biogeographic processes underlying range limits and how they respond to environmental change.

## ***F. Tables***

<b>Hypothesis</b>	<b>Description</b>	<b>Manifestation</b>	<b>References</b>
<b>Thermal niche hypothesis (TNH)</b>	The TNH assumes that a species' range limits coincide with the limits of its thermal tolerance, that range limits are primarily determined by temperature, and thus that species should closely track the thermal conditions historically present at their range limits through space.	Range limits track temperature	(Stuart-Smith et al., 2017; J. M. Sunday et al., 2012)
<b>Temporal lag hypothesis (TLH)</b>	The TLH predicts that species are tracking temperature, but with a temporal lag at one or both range edges.	Range limits track temperature, possibly lagged	(Devictor et al., 2012; Fordham et al., 2016; Jackson & Sax, 2010)
<b>Temperature-independent hypothesis (TIH)</b>	The TIH predicts that non-temperature factors mediate one or both range limits, and those range limits will not shift predictably as a result of warming.	Range limits do not track temperature	(Cahill et al., 2014; Connell, 1961; Louthan et al., 2015; MacArthur, 1972; Poloczanska et al., 2011)

Table 3.1. Summary of hypotheses investigated in the study.

## G. Figures

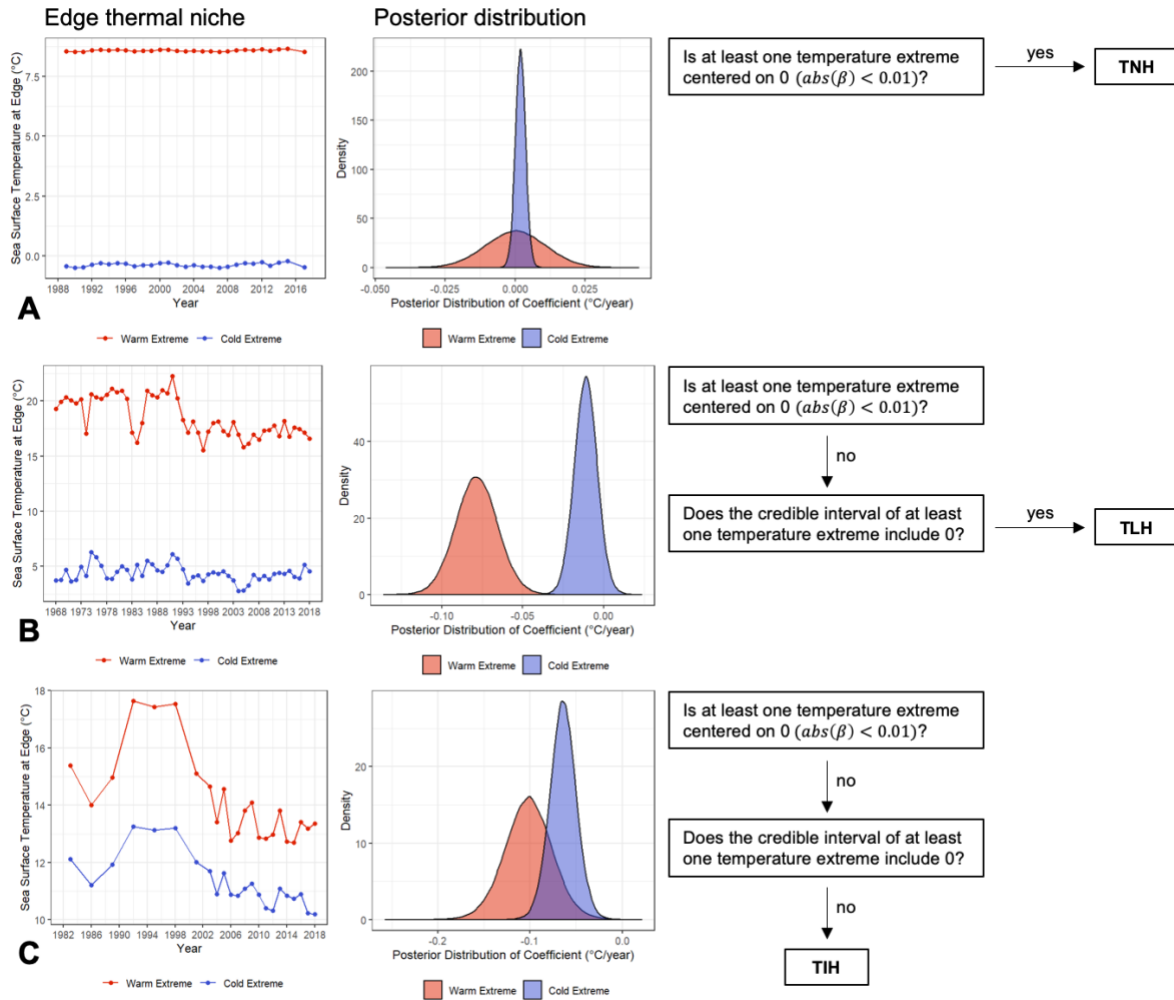


Figure 3.1. Process diagram representing how the thermal niche hypothesis (TNH), the temporal lag hypothesis (TLH), and the temperature-independent hypothesis (TIH) were tested for edge thermal niche dynamics of three example species: the cold range limit of *Gadus macrocephalus* in the Eastern Bering Sea (A), the cold range limit of *Paralichthys oblongus* in the Northeast (B), and the warm range limit of *Sebastes pinniger* in the West Coast (C). Note the different scales among plots.

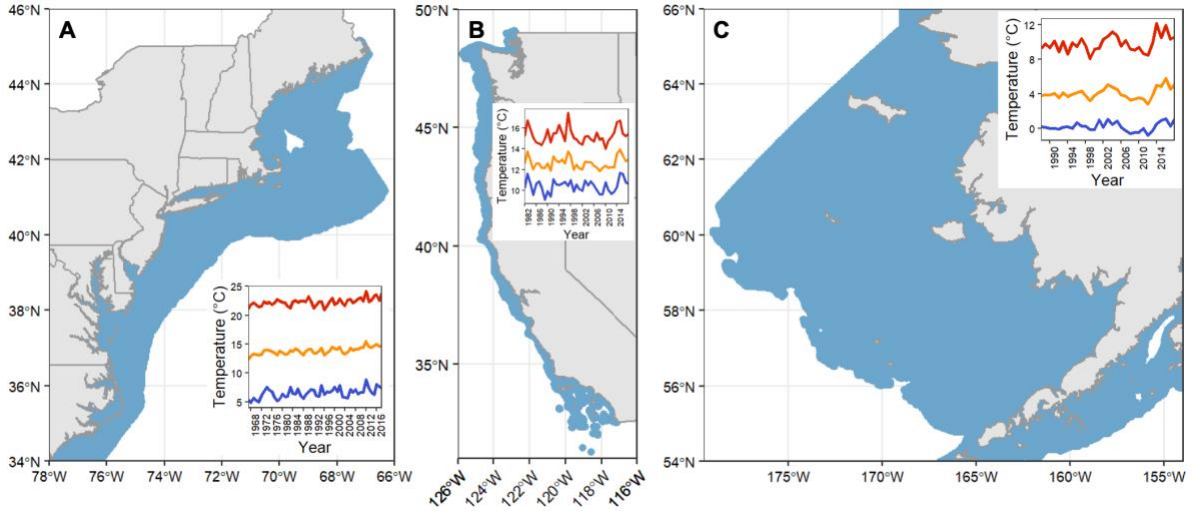


Figure 3.2. Maps of study regions—Northeast (A), West Coast (B), and Eastern Bering Sea (C)—with the continental shelf shaded in blue (300 m cutoff for Northeast and Eastern Bering Sea, 400 m for West Coast). Inset plots show regional minimum (blue), mean (orange), and maximum (red) monthly sea surface temperature (annual means). The temperature time-series begin in 1967 in the Northeast, 1982 in the West Coast, and 1989 in the Eastern Bering Sea, reflecting the data used in this analysis.

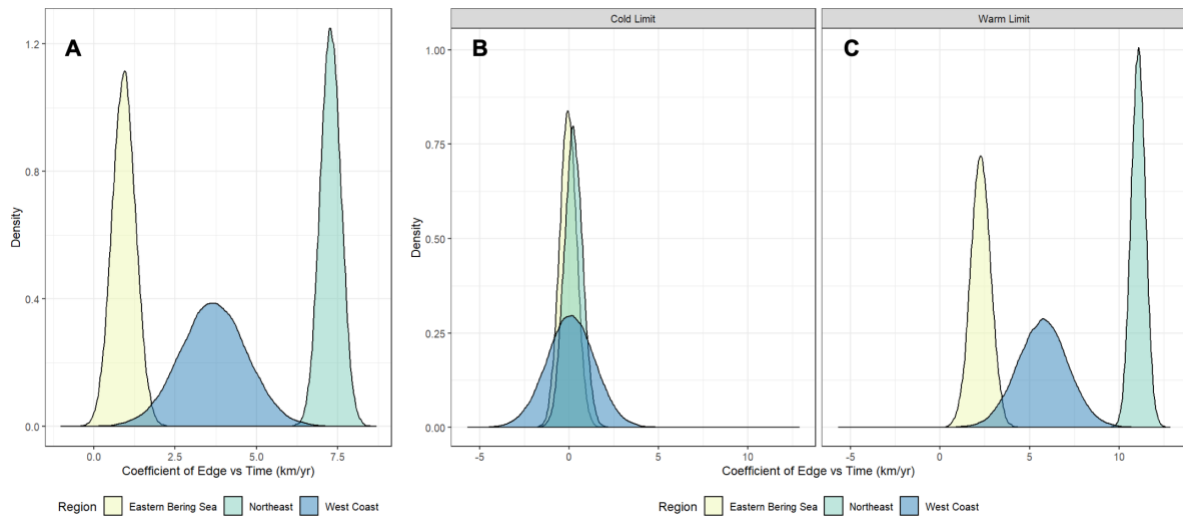


Figure 3.3. Posterior distributions of the coefficient of time on range limit position from single-species Bayesian linear regressions. Distributions are pooled among individual range limits and separated by region (A) or region and range limit type (B, C).

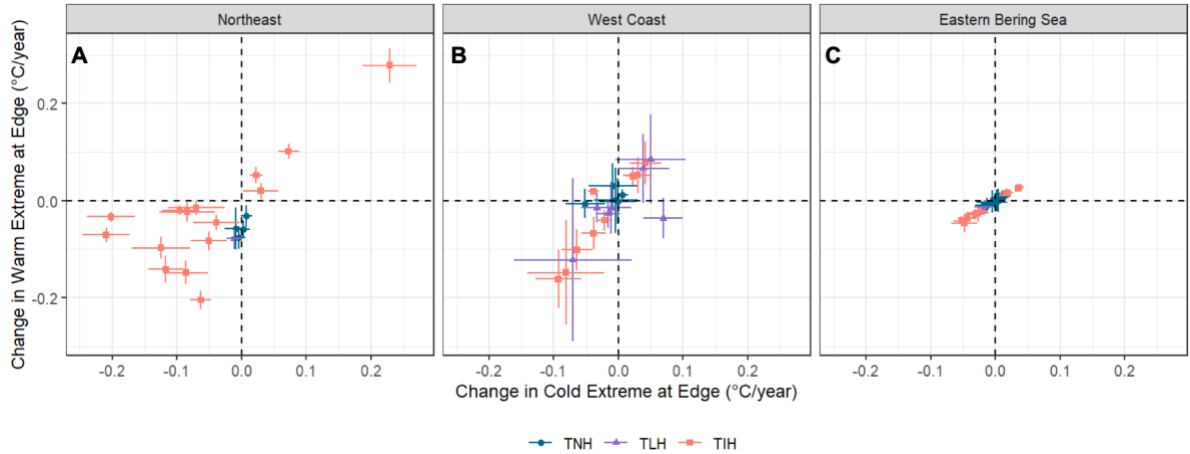


Figure 3.4. Estimated change in cold (x-axis) and warm (y-axis) extremes of edge thermal niches over time, across three regions (Bayesian linear regression coefficients; error bars are 90% Bayesian credible intervals). Patterns in extreme temperatures at species' range limits over time are classified as consistent with the TNH (at least one thermal extreme had a coefficient very near zero), the TLH (at least one thermal extreme had a credible interval overlapping zero), or the TIH (both thermal extremes changed over time; see *Methods*).

## H. Supplementary Information

Species name	Class	Region
<i>Alosa aestivialis</i>	Teleostei	Northeast
<i>Alosa pseudoharengus</i>	Teleostei	Northeast
<i>Alosa sapidissima</i>	Teleostei	Northeast
<i>Amblyraja radiata</i>	Chondrichthyes	Northeast
<i>Ammodytes dubius</i>	Teleostei	Northeast
<i>Anarhichas lupus</i>	Teleostei	Northeast
<i>Anchoa mitchilli</i>	Teleostei	Northeast
<i>Argentina silus</i>	Teleostei	Northeast
<i>Brevoortia tyrannus</i>	Teleostei	Northeast
<i>Brosme brosme</i>	Teleostei	Northeast
<i>Cancer borealis</i>	Malacostraca	Northeast
<i>Cancer irroratus</i>	Malacostraca	Northeast
<i>Centropristis striata</i>	Teleostei	Northeast
<i>Citharichthys arctifrons</i>	Teleostei	Northeast
<i>Clupea harengus</i>	Teleostei	Northeast
<i>Conger oceanicus</i>	Teleostei	Northeast
<i>Cryptacanthodes maculatus</i>	Teleostei	Northeast
<i>Cyclopterus lumpus</i>	Teleostei	Northeast
<i>Cynoscion regalis</i>	Teleostei	Northeast
<i>Dipturus laevis</i>	Chondrichthyes	Northeast
<i>Enchelyopus cimbrius</i>	Teleostei	Northeast
<i>Gadus morhua</i>	Teleostei	Northeast
<i>Geryon quinquedens</i>	Malacostraca	Northeast
<i>Glyptocephalus cynoglossus</i>	Teleostei	Northeast
<i>Helicolenus dactylopterus</i>	Teleostei	Northeast
<i>Hemirhamphus americanus</i>	Teleostei	Northeast
<i>Hippoglossoides platessoides</i>	Teleostei	Northeast
<i>Hippoglossus hippoglossus</i>	Teleostei	Northeast
<i>Homarus americanus</i>	Malacostraca	Northeast
<i>Illex illecebrosus</i>	Cephalopoda	Northeast

<i>Leiostomus xanthurus</i>	Teleostei	Northeast
<i>Lepophidium profundorum</i>	Teleostei	Northeast
<i>Leucoraja erinacea</i>	Chondrichthyes	Northeast
<i>Leucoraja garmani</i>	Chondrichthyes	Northeast
<i>Leucoraja ocellata</i>	Chondrichthyes	Northeast
<i>Limulus polyphemus</i>	Euchelicerata	Northeast
<i>Loligo pealeii</i>	Cephalopoda	Northeast
<i>Lophius americanus</i>	Teleostei	Northeast
<i>Malacoraja senta</i>	Chondrichthyes	Northeast
<i>Melanogrammus aeglefinus</i>	Teleostei	Northeast
<i>Menidia menidia</i>	Teleostei	Northeast
<i>Menticirrhus saxatilis</i>	Teleostei	Northeast
<i>Merluccius albidus</i>	Teleostei	Northeast
<i>Merluccius bilinearis</i>	Teleostei	Northeast
<i>Micropogonias undulatus</i>	Teleostei	Northeast
<i>Morone saxatilis</i>	Teleostei	Northeast
<i>Mustelus canis</i>	Chondrichthyes	Northeast
<i>Myoxocephalus octodecemspinosus</i>	Teleostei	Northeast
<i>Myxine glutinosa</i>	Myxini	Northeast
<i>Ophidion marginatum</i>	Teleostei	Northeast
<i>Paralichthys dentatus</i>	Teleostei	Northeast
<i>Paralichthys oblongus</i>	Teleostei	Northeast
<i>Peprilus triacanthus</i>	Teleostei	Northeast
<i>Peristedion miniatum</i>	Teleostei	Northeast
<i>Phycis chesteri</i>	Teleostei	Northeast
<i>Placopecten magellanicus</i>	Bivalvia	Northeast
<i>Pollachius virens</i>	Teleostei	Northeast
<i>Pomatomus saltatrix</i>	Teleostei	Northeast
<i>Prionotus carolinus</i>	Teleostei	Northeast
<i>Prionotus evolans</i>	Teleostei	Northeast
<i>Raja eglanteria</i>	Chondrichthyes	Northeast
<i>Scomber scombrus</i>	Teleostei	Northeast
<i>Scophthalmus aquosus</i>	Teleostei	Northeast
<i>Scyliorhinus retifer</i>	Chondrichthyes	Northeast
<i>Sebastes fasciatus</i>	Teleostei	Northeast
<i>Squalus acanthias</i>	Chondrichthyes	Northeast
<i>Squatina dumeril</i>	Chondrichthyes	Northeast
<i>Stenotomus chrysops</i>	Teleostei	Northeast
<i>Tautoglabrus adspersus</i>	Teleostei	Northeast
<i>Urophycis chuss</i>	Teleostei	Northeast
<i>Urophycis regia</i>	Teleostei	Northeast
<i>Urophycis tenuis</i>	Teleostei	Northeast
<i>Zenopsis conchifer</i>	Teleostei	Northeast
<i>Zoarces americanus</i>	Teleostei	Northeast
<i>Aforia circinata</i>	Gastropoda	Eastern Bering Sea
<i>Asterias amurensis</i>	Asteroidea	Eastern Bering Sea
<i>Atheresthes evermanni</i>	Teleostei	Eastern Bering Sea
<i>Atheresthes stomias</i>	Teleostei	Eastern Bering Sea
<i>Bathymaster signatus</i>	Teleostei	Eastern Bering Sea
<i>Bathyraja interrupta</i>	Chondrichthyes	Eastern Bering Sea
<i>Bathyraja parmifera</i>	Chondrichthyes	Eastern Bering Sea
<i>Boltenia ovifera</i>	Ascidacea	Eastern Bering Sea
<i>Boreogadus saida</i>	Teleostei	Eastern Bering Sea
<i>Buccinum angulosum</i>	Gastropoda	Eastern Bering Sea
<i>Buccinum polare</i>	Gastropoda	Eastern Bering Sea
<i>Buccinum scalariforme</i>	Gastropoda	Eastern Bering Sea
<i>Chionoecetes bairdi</i>	Malacostraca	Eastern Bering Sea
<i>Chionoecetes opilio</i>	Malacostraca	Eastern Bering Sea
<i>Chrysaora melanaster</i>	Scyphozoa	Eastern Bering Sea

<i>Clinopegma magnum</i>	Gastropoda	Eastern Bering Sea
<i>Clupea pallasii</i>	Teleostei	Eastern Bering Sea
<i>Ctenodiscus crispatus</i>	Asteroidea	Eastern Bering Sea
<i>Dasycottus setiger</i>	Teleostei	Eastern Bering Sea
<i>Erimacrus isenbeckii</i>	Malacostraca	Eastern Bering Sea
<i>Eunoe depressa</i>	Polychaeta	Eastern Bering Sea
<i>Eunoe nodosa</i>	Polychaeta	Eastern Bering Sea
<i>Fusitriton oregonensis</i>	Gastropoda	Eastern Bering Sea
<i>Gadus chalcogrammus</i>	Teleostei	Eastern Bering Sea
<i>Gadus macrocephalus</i>	Teleostei	Eastern Bering Sea
<i>Glyptocephalus zachirus</i>	Teleostei	Eastern Bering Sea
<i>Gorgonocephalus eucnemis</i>	Ophiuroidea	Eastern Bering Sea
<i>Gymnocanthus pistilliger</i>	Teleostei	Eastern Bering Sea
<i>Hemilepidotus jordani</i>	Teleostei	Eastern Bering Sea
<i>Hemilepidotus papilio</i>	Teleostei	Eastern Bering Sea
<i>Hemitripteris bolini</i>	Teleostei	Eastern Bering Sea
<i>Hippoglossoides elassodon</i>	Teleostei	Eastern Bering Sea
<i>Hippoglossoides robustus</i>	Teleostei	Eastern Bering Sea
<i>Hippoglossus stenolepis</i>	Teleostei	Eastern Bering Sea
<i>Hyas coarctatus</i>	Malacostraca	Eastern Bering Sea
<i>Hyas lyratus</i>	Malacostraca	Eastern Bering Sea
<i>Icelus spiniger</i>	Teleostei	Eastern Bering Sea
<i>Labidochirus splendescens</i>	Malacostraca	Eastern Bering Sea
<i>Lepidopsetta polyxystra</i>	Teleostei	Eastern Bering Sea
<i>Leptagonus frenatus</i>	Teleostei	Eastern Bering Sea
<i>Leptasterias arctica</i>	Asteroidea	Eastern Bering Sea
<i>Leptasterias polaris</i>	Asteroidea	Eastern Bering Sea
<i>Lethasterias nanimensis</i>	Asteroidea	Eastern Bering Sea
<i>Limanda aspera</i>	Teleostei	Eastern Bering Sea
<i>Limanda proboscidea</i>	Teleostei	Eastern Bering Sea
<i>Lumpenus maculatus</i>	Teleostei	Eastern Bering Sea
<i>Lycodes brevipes</i>	Teleostei	Eastern Bering Sea
<i>Lycodes palearis</i>	Teleostei	Eastern Bering Sea
<i>Lycodes ravidens</i>	Teleostei	Eastern Bering Sea
<i>Mactromeris polynyma</i>	Bivalvia	Eastern Bering Sea
<i>Mallotus villosus</i>	Teleostei	Eastern Bering Sea
<i>Myoxocephalus jaok</i>	Teleostei	Eastern Bering Sea
<i>Myoxocephalus polyacanthocephalus</i>	Teleostei	Eastern Bering Sea
<i>Myoxocephalus scorpius</i>	Teleostei	Eastern Bering Sea
<i>Neptunea borealis</i>	Gastropoda	Eastern Bering Sea
<i>Neptunea heros</i>	Gastropoda	Eastern Bering Sea
<i>Neptunea lyrata</i>	Gastropoda	Eastern Bering Sea
<i>Neptunea pribiloffensis</i>	Gastropoda	Eastern Bering Sea
<i>Neptunea ventricosa</i>	Gastropoda	Eastern Bering Sea
<i>Occella dodecaedron</i>	Teleostei	Eastern Bering Sea
<i>Ophiura sarsi</i>	Ophiuroidea	Eastern Bering Sea
<i>Oregonia gracilis</i>	Malacostraca	Eastern Bering Sea
<i>Pagurus aleuticus</i>	Malacostraca	Eastern Bering Sea
<i>Pagurus capillatus</i>	Malacostraca	Eastern Bering Sea
<i>Pagurus confragosus</i>	Malacostraca	Eastern Bering Sea
<i>Pagurus ochotensis</i>	Malacostraca	Eastern Bering Sea
<i>Pagurus rathbuni</i>	Malacostraca	Eastern Bering Sea
<i>Pagurus trigonocheirus</i>	Malacostraca	Eastern Bering Sea
<i>Pandalus eous</i>	Malacostraca	Eastern Bering Sea
<i>Pandalus goniurus</i>	Malacostraca	Eastern Bering Sea
<i>Paralithodes camtschaticus</i>	Malacostraca	Eastern Bering Sea
<i>Paralithodes platypus</i>	Malacostraca	Eastern Bering Sea
<i>Platichthys stellatus</i>	Teleostei	Eastern Bering Sea
<i>Pleuronectes quadrituberculatus</i>	Teleostei	Eastern Bering Sea



<i>Plicifusus kroyeri</i>	Gastropoda	Eastern Bering Sea
<i>Podothecus accipenserinus</i>	Teleostei	Eastern Bering Sea
<i>Pteraster obscurus</i>	Asteroidea	Eastern Bering Sea
<i>Reinhardtius hippoglossoides</i>	Teleostei	Eastern Bering Sea
<i>Strongylocentrotus droebachiensis</i>	Echinoidea	Eastern Bering Sea
<i>Styela rustica</i>	Ascidacea	Eastern Bering Sea
<i>Telmessus cheiragonus</i>	Malacostraca	Eastern Bering Sea
<i>Thaleichthys pacificus</i>	Teleostei	Eastern Bering Sea
<i>Alosa sapidissima</i>	Teleostei	West Coast
<i>Anoplopoma fimbria</i>	Teleostei	West Coast
<i>Apristurus brunneus</i>	Chondrichthyes	West Coast
<i>Atheresthes stomias</i>	Teleostei	West Coast
<i>Bathyraja interrupta</i>	Chondrichthyes	West Coast
<i>Brisaster latifrons</i>	Echinoidea	West Coast
<i>Cancer magister</i>	Malacostraca	West Coast
<i>Careproctus melanurus</i>	Teleostei	West Coast
<i>Citharichthys sordidus</i>	Teleostei	West Coast
<i>Clupea pallasii</i>	Teleostei	West Coast
<i>Eopsetta jordani</i>	Teleostei	West Coast
<i>Glyptocephalus zachirus</i>	Teleostei	West Coast
<i>Hippoglossoides elassodon</i>	Teleostei	West Coast
<i>Hippoglossus stenolepis</i>	Teleostei	West Coast
<i>Hydrolagus collii</i>	Chondrichthyes	West Coast
<i>Icelinus filamentosus</i>	Teleostei	West Coast
<i>Liponema brevicornis</i>	Anthozoa	West Coast
<i>Loligo opalescens</i>	Cephalopoda	West Coast
<i>Luidia foliolata</i>	Asteroidea	West Coast
<i>Lycodes cortezianus</i>	Teleostei	West Coast
<i>Lycodes diapterus</i>	Teleostei	West Coast
<i>Lycodes pacificus</i>	Teleostei	West Coast
<i>Lyopsetta exilis</i>	Teleostei	West Coast
<i>Merluccius productus</i>	Teleostei	West Coast
<i>Metridium farcimen</i>	Anthozoa	West Coast
<i>Microstomus pacificus</i>	Teleostei	West Coast
<i>Ophiodon elongatus</i>	Teleostei	West Coast
<i>Pandalus jordani</i>	Malacostraca	West Coast
<i>Paractinostola faeulentata</i>	Anthozoa	West Coast
<i>Parastichopus leukothele</i>	Holothuroidea	West Coast
<i>Parophrys vetulus</i>	Teleostei	West Coast
<i>Pasiphaea pacifica</i>	Malacostraca	West Coast
<i>Pleuronichthys decurrens</i>	Teleostei	West Coast
<i>Porichthys notatus</i>	Teleostei	West Coast
<i>Pycnopodia helianthoides</i>	Asteroidea	West Coast
<i>Raja binoculata</i>	Chondrichthyes	West Coast
<i>Raja rhina</i>	Chondrichthyes	West Coast
<i>Rathbunaster californicus</i>	Asteroidea	West Coast
<i>Sebastes aurora</i>	Teleostei	West Coast
<i>Sebastes babcocki</i>	Teleostei	West Coast
<i>Sebastes crameri</i>	Teleostei	West Coast
<i>Sebastes diploproa</i>	Teleostei	West Coast
<i>Sebastes elongatus</i>	Teleostei	West Coast
<i>Sebastes goodei</i>	Teleostei	West Coast
<i>Sebastes jordani</i>	Teleostei	West Coast
<i>Sebastes pinniger</i>	Teleostei	West Coast
<i>Sebastes saxicola</i>	Teleostei	West Coast
<i>Sebastes semicinctus</i>	Teleostei	West Coast
<i>Sebastolobus alascanus</i>	Teleostei	West Coast
<i>Squalus suckleyi</i>	Chondrichthyes	West Coast
<i>Strongylocentrotus fragilis</i>	Echinoidea	West Coast

<i>Stylasterias forreri</i>	Asteroidea	West Coast
<i>Zalembius rosaceus</i>	Teleostei	West Coast
<i>Zaniolepis latipinnis</i>	Teleostei	West Coast

Table 3.S1. List of species in the analysis from each region, with taxonomic class.

Species name	Range limit type	Region
<i>Alosa aestivalis</i>	Cold Limit	Northeast
<i>Alosa pseudoharengus</i>	Warm Limit	Northeast
<i>Alosa sapidissima</i>	Warm Limit	Northeast
<i>Apristurus brunneus</i>	Cold Limit	West Coast
<i>Atheresthes evermanni</i>	Warm Limit	Eastern Bering Sea
<i>Atheresthes stomias</i>	Cold Limit	Eastern Bering Sea
<i>Bathymaster signatus</i>	Cold Limit	Eastern Bering Sea
<i>Bathyraja interrupta</i>	Warm Limit	West Coast
<i>Boltenia ovifera</i>	Cold Limit	Eastern Bering Sea
<i>Brisaster latifrons</i>	Warm Limit	West Coast
<i>Brisaster latifrons</i>	Cold Limit	West Coast
<i>Buccinum polare</i>	Warm Limit	Eastern Bering Sea
<i>Buccinum polare</i>	Cold Limit	Eastern Bering Sea
<i>Buccinum scalariforme</i>	Warm Limit	Eastern Bering Sea
<i>Cancer borealis</i>	Warm Limit	Northeast
<i>Cancer irroratus</i>	Warm Limit	Northeast
<i>Cancer irroratus</i>	Cold Limit	Northeast
<i>Centropristis striata</i>	Warm Limit	Northeast
<i>Chionoecetes bairdi</i>	Cold Limit	Eastern Bering Sea
<i>Clupea harengus</i>	Warm Limit	Northeast
<i>Clupea harengus</i>	Cold Limit	Northeast
<i>Eunoe depressa</i>	Cold Limit	Eastern Bering Sea
<i>Eunoe nodosa</i>	Warm Limit	Eastern Bering Sea
<i>Eunoe nodosa</i>	Cold Limit	Eastern Bering Sea
<i>Gadus macrocephalus</i>	Cold Limit	Eastern Bering Sea
<i>Gorgonocephalus eucnemis</i>	Warm Limit	Eastern Bering Sea
<i>Gorgonocephalus eucnemis</i>	Cold Limit	Eastern Bering Sea
<i>Gymnocanthus pistilliger</i>	Cold Limit	Eastern Bering Sea
<i>Hemilepidotus jordani</i>	Warm Limit	Eastern Bering Sea
<i>Hemilepidotus jordani</i>	Cold Limit	Eastern Bering Sea
<i>Homarus americanus</i>	Warm Limit	Northeast
<i>Hyas coarctatus</i>	Warm Limit	Eastern Bering Sea
<i>Hyas coarctatus</i>	Cold Limit	Eastern Bering Sea
<i>Hyas lyratus</i>	Cold Limit	Eastern Bering Sea
<i>Icelinus filamentosus</i>	Warm Limit	West Coast
<i>Labidochirus splendescens</i>	Warm Limit	Eastern Bering Sea
<i>Labidochirus splendescens</i>	Cold Limit	Eastern Bering Sea
<i>Leptagonus frenatus</i>	Cold Limit	Eastern Bering Sea
<i>Leptasterias arctica</i>	Cold Limit	Eastern Bering Sea
<i>Leucoraja erinacea</i>	Cold Limit	Northeast
<i>Leucoraja ocellata</i>	Warm Limit	Northeast
<i>Loligo opalescens</i>	Cold Limit	West Coast
<i>Lumpenus maculatus</i>	Warm Limit	Eastern Bering Sea
<i>Lycodes brevipes</i>	Warm Limit	Eastern Bering Sea
<i>Lycodes pacificus</i>	Cold Limit	West Coast
<i>Lycodes palearis</i>	Warm Limit	Eastern Bering Sea
<i>Lyopsetta exilis</i>	Warm Limit	West Coast
<i>Mallotus villosus</i>	Warm Limit	Eastern Bering Sea
<i>Mallotus villosus</i>	Cold Limit	Eastern Bering Sea
<i>Merluccius albidus</i>	Cold Limit	Northeast

<i>Merluccius bilinearis</i>	Warm Limit	Northeast
<i>Merluccius productus</i>	Warm Limit	West Coast
<i>Metridium farcimen</i>	Warm Limit	West Coast
<i>Metridium farcimen</i>	Cold Limit	West Coast
<i>Myxine glutinosa</i>	Warm Limit	Northeast
<i>Neptunea borealis</i>	Cold Limit	Eastern Bering Sea
<i>Neptunea lyrata</i>	Cold Limit	Eastern Bering Sea
<i>Neptunea pribiloffensis</i>	Warm Limit	Eastern Bering Sea
<i>Neptunea ventricosa</i>	Warm Limit	Eastern Bering Sea
<i>Pagurus aleuticus</i>	Cold Limit	Eastern Bering Sea
<i>Pagurus capillatus</i>	Cold Limit	Eastern Bering Sea
<i>Pagurus confragosus</i>	Cold Limit	Eastern Bering Sea
<i>Pagurus rathbuni</i>	Warm Limit	Eastern Bering Sea
<i>Pagurus trigonocheirus</i>	Warm Limit	Eastern Bering Sea
<i>Pandalus eous</i>	Warm Limit	Eastern Bering Sea
<i>Pandalus goniurus</i>	Warm Limit	Eastern Bering Sea
<i>Pandalus jordani</i>	Warm Limit	West Coast
<i>Paralichthys oblongus</i>	Cold Limit	Northeast
<i>Parastichopus leukothele</i>	Warm Limit	West Coast
<i>Parophrys vetulus</i>	Warm Limit	West Coast
<i>Pasiphaea pacifica</i>	Cold Limit	West Coast
<i>Phycis chesteri</i>	Warm Limit	Northeast
<i>Pleuronectes quadrituberculatus</i>	Cold Limit	Eastern Bering Sea
<i>Podothecus accipenserinus</i>	Cold Limit	Eastern Bering Sea
<i>Prionotus carolinus</i>	Warm Limit	Northeast
<i>Raja rhina</i>	Warm Limit	West Coast
<i>Rathbunaster californicus</i>	Cold Limit	West Coast
<i>Scomber scombrus</i>	Warm Limit	Northeast
<i>Sebastes jordani</i>	Warm Limit	West Coast
<i>Sebastes pinniger</i>	Warm Limit	West Coast
<i>Squalus suckleyi</i>	Warm Limit	West Coast
<i>Strongylocentrotus droebachiensis</i>	Cold Limit	Eastern Bering Sea
<i>Strongylocentrotus fragilis</i>	Cold Limit	West Coast
<i>Styela rustica</i>	Warm Limit	Eastern Bering Sea
<i>Styela rustica</i>	Cold Limit	Eastern Bering Sea
<i>Stylasterias forreri</i>	Warm Limit	West Coast
<i>Zoarces americanus</i>	Cold Limit	Northeast

Table 3.S2. List of range limits analyzed in the study from each region.

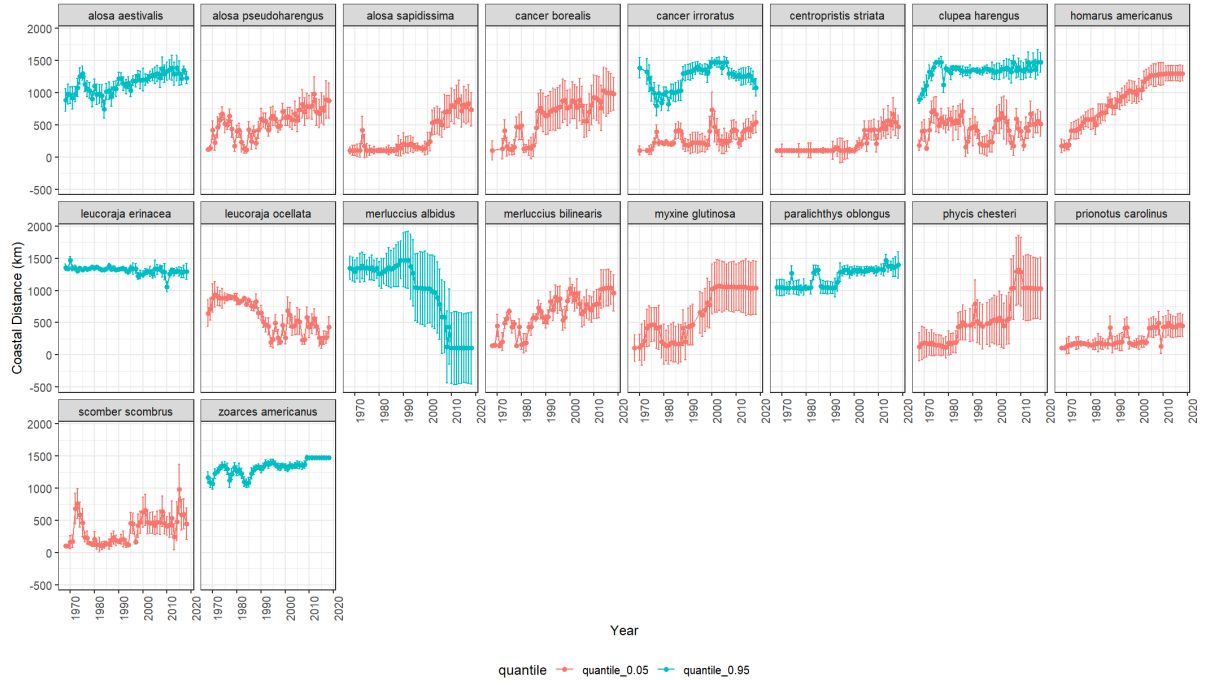


Figure 3.S1. Model-estimated range limits used in the edge thermal niche analysis in the Northeast.

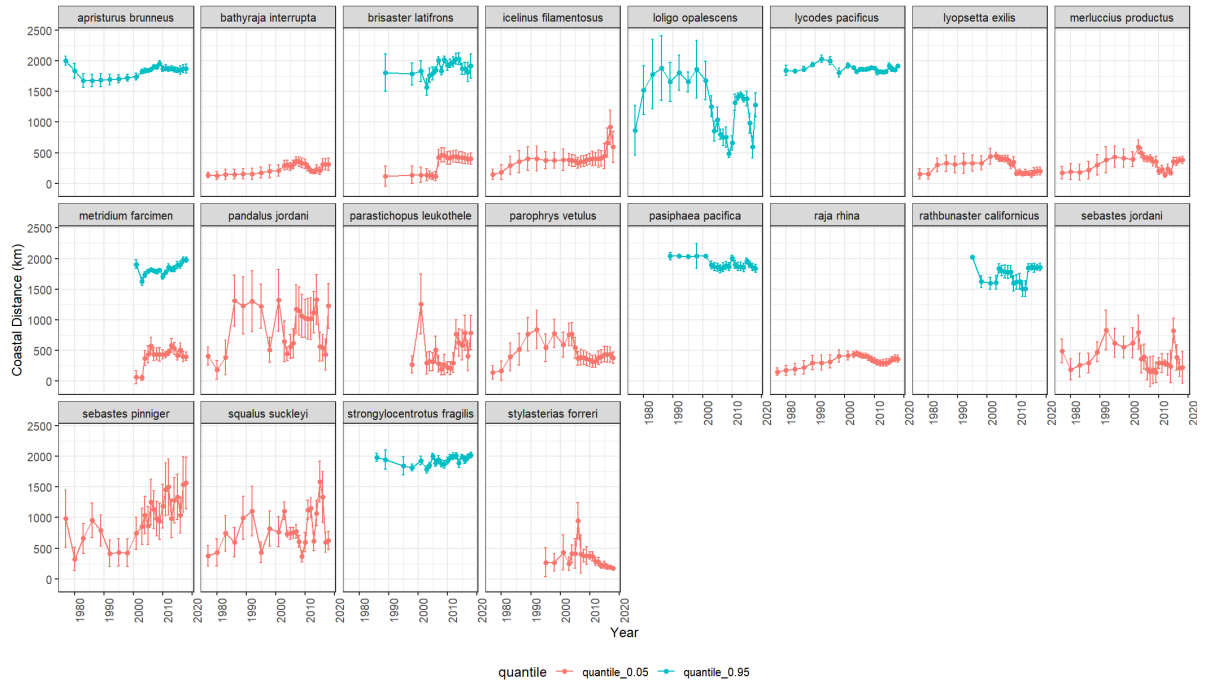


Figure 3.S2. Model-estimated range limits used in the edge thermal niche analysis in the West Coast.



Figure 3.S3. Model-estimated range limits used in the edge thermal niche analysis in the Eastern Bering Sea.

## 4. References

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