Review

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The importance of within-system spatial variation in drivers of marine ecosystem regime shifts

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Comparative analyses of the dynamics of exploited marine ecosystems have led to differing hypotheses regarding the primary causes of observed regime shifts, while many ecosystems have apparently not undergone regime shifts. These varied responses may be partly explained by the decade-old recognition that within-system spatial heterogeneity in key climate and anthropogenic drivers may be important, as recent theoretical examinations have concluded that spatial heterogeneity in environmental characteristics may diminish the tendency for regime shifts. Here, we synthesize recent, empirical within-system spatio-temporal analyses of some temperate and subarctic large marine ecosystems in which regime shifts have (and have not) occurred. Examples from the Baltic Sea, Black Sea, Bengula Current, North Sea, Barents Sea and Eastern Scotian Shelf reveal the largely neglected importance of considering spatial variability in key biotic and abiotic influences and species movements in the context of evaluating and predicting regime shifts. We highlight both the importance of understanding the scale-dependent spatial dynamics of climate influences and key predator–prey interactions to unravel the dynamics of regime shifts, and the utility of spatial downscaling of proposed mechanisms (as evident in the North Sea and Barents Sea) as a means of evaluating hypotheses originally derived from among-system comparisons.

1. Introduction

Two of the most pressing needs in marine ecosystem research include an improved understanding of the factors that foster or thwart regime shifts (defined here as sudden changes between differing, persistent states in complex systems [1,2]) and an enhanced quantitative partitioning of the relative importance of multiple drivers of observed regime shifts. Such understanding of the how and why of regime shifts remains a precursor to reliable predictions of the differential resilience of specific ecosystems to changing ocean conditions and to exploitation [1–3], and to the development of more effective approaches to the management of large marine ecosystems and their constituent parts [4]. To date, several challenges have slowed efforts to predict and relate regime shifts in large marine ecosystems to specific drivers. Among these are limitations in the data required to detect and effectively document regime shifts [5–7], to do so in a timely manner [3,7,8], and to evaluate the relative importance of specific mechanisms underlying the changes observed [9]. One rarely addressed challenge is to account for the role of within-system spatial heterogeneity for regime shifts [1]. However, theoretical examinations suggest that such heterogeneity may thwart regime shifts if, for example, environmental characteristics vary along a smooth gradient
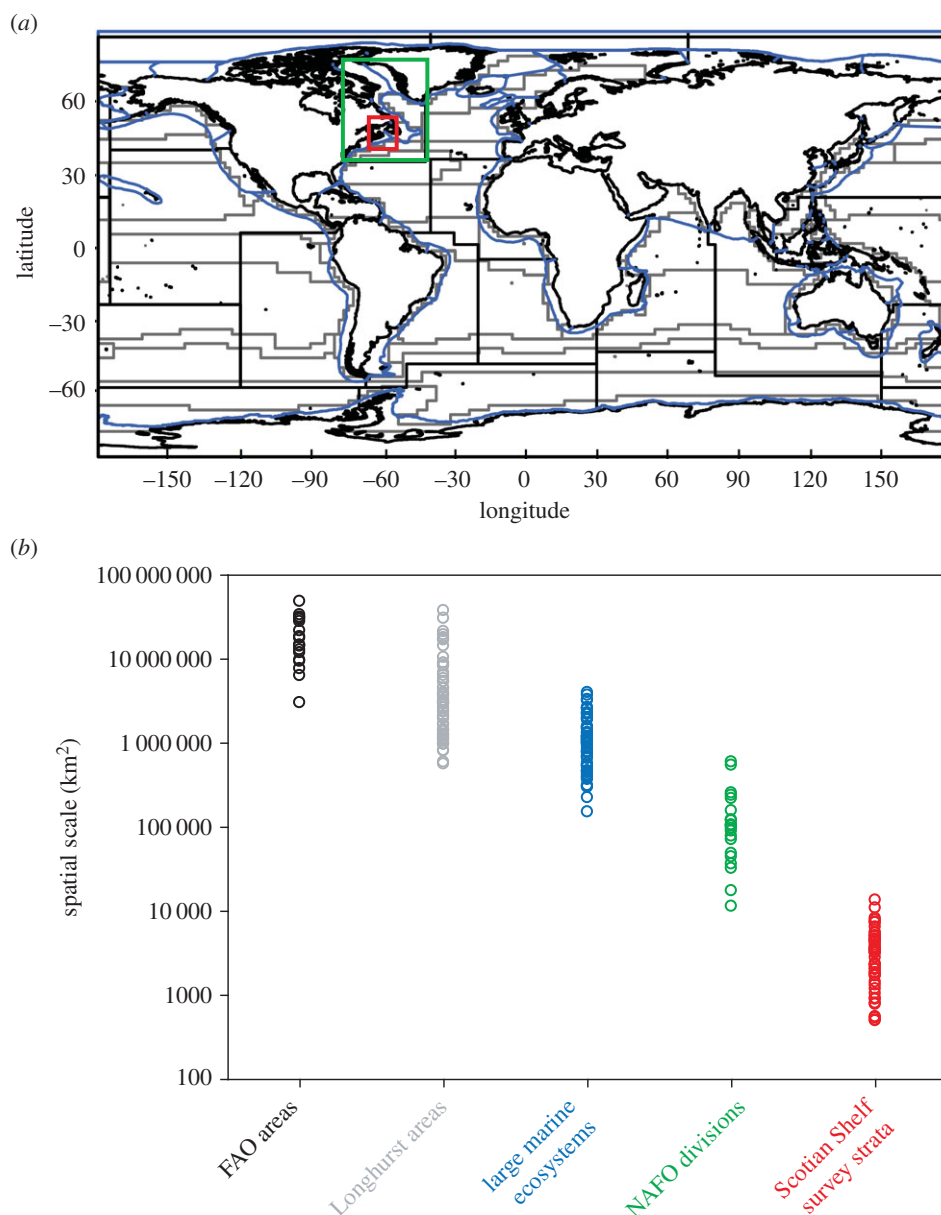
Figure 1. A subset of overlapping local to global units within which marine regime shifts and their drivers continue to be analysed. (a) Colour coding of largest areas (FAO areas: black), Longhurst areas (grey; from www.marineregions.org), large marine ecosystems (LMEs: blue), North Atlantic Fishery Organization (NAFO) areas (green box outlines area only) and Scotian Shelf survey strata (red box outlines area only). (b) Spatial scales of areas examined illustrating the extensive range of spatial scales from hundreds to tens of millions of km^2.

[10]. Also, the spatial scales at which key drivers operate are critical [11,12] as spatial averaging has a blurring effect on the evaluation of the roles of potential mechanisms [13]. Finally, both the confounding effects of events aggregated in space or time [14] and challenges associated with resolving the interacting effects of regional-to-basin-scale climate drivers on local dynamics [15–17] add to these difficulties, as large-scale regime shift drivers influence processes operating at the scale of individual organisms. Therefore, accounting for within-system spatial heterogeneity in drivers may account for some of the differential responses within and among ecosystems.

These issues associated with spatial heterogeneity and scale dependence are longstanding and ubiquitous in ecological investigations [18,19]. In the context of regime shifts, they bear on the challenges of identifying and quantifying the effects of noted large-scale drivers (e.g. climate and fishing and other types of disturbances) at relatively small spatial scales [20], within large marine ecosystems [2,9,21] (figure 1), and quantifying the factors that govern ecosystem recovery

[22,23]. Ultimately, they highlight the need for a diversity of approaches to understand and perhaps prevent undesirable regime shifts, some of which represent among the most serious of ecological surprises [3,24].

For more than a century, comparative analyses of marine ecosystem dynamics have been advocated as a vehicle for achieving an enhanced understanding of the differential dynamics of exploited large marine systems. Hjort [25], for example, provided the following as part of his motivation for serving as Director of the 1914–1915 Canadian Fisheries Expedition:

> In the course of my researches in North European waters, it has frequently occurred to me that many problems of long standing in the sphere of fishery and marine investigation might perhaps best be solved by making a comparison between the two separate areas of sea which contain the same forms of animal life, viz., the waters of northern Europe, and the range of sea from the coast of Labrador and Canada to that of Maine.   [25, p. xi]

Comparative analyses of marine system dynamics and functioning have experienced renewed emphasis in recent years

[11,26–29] and continue to provide insight into the timing [17,30] and responses of large marine ecosystems and of marine fisheries to changing ocean conditions and exploitation that together are known to contribute to regime shifts [17,30,31]. This enhanced activity is partly due to the increasing availability of time-series data for ocean climate and of survey-derived geospatial information for multiple trophic levels, and an expanding array of analytical frameworks and detection methods [2,3,7,32] that have allowed researchers to determine whether and where regime shifts have occurred. These studies have contributed materially to the understanding of the roles of multiple potential drivers of regime shifts at large spatial scales [17].

Moving beyond comparative analyses towards examinations of spatio-temporal dynamics within systems, this paper draws upon empirical examples to fulfil two aims:

(1) to briefly review novel contributions of studies conducted at scales smaller than, but complementary to, those typically employed in the rapidly evolving study of the comparative dynamics of exploited marine systems generally, and of regime shifts in particular. Focus is largely given to the North Atlantic, due in part to the relative richness of ecosystem level data and to the historic [33] and more recent accounts of regime shifts there [17], and

(2) to investigate the potential for spatial downscaling to test the generality of proposed mechanisms underlying or preventing regime shifts and possibly enhance the detection of regime shifts [1–3,6,32].

2. Spatial variation in dominant drivers

To-date, the most widely used approach to the search for potential drivers of regime shifts in large marine ecosystems has been the examination of temporal variation in climate, in species interactions and in rates of exploitation. In each of these cases, the availability of data at a sufficiently high resolution is of fundamental importance, making the maintenance and expansion of existing marine ecosystem survey series a central challenge for facilitating empirical tests of proposed mechanisms. However, recognition of spatial variation in climate influences, exploitation and species interactions is also important, because large marine ecosystems can be sufficiently climatically and biologically heterogeneous that they encompass multiple species assemblages (figure 1); such heterogeneity has been hypothesized to thwart the occurrence of regime shifts under some conditions [10]. For example, within the 1.6 million km² Barents Sea (a marine ecosystem that has not undergone a regime shift [34]) there exists up to 93% dissimilarity among six discrete fish assemblages that occupy water masses ranging in character from subarctic to temperate [35]. For this reason, analyses conducted at the spatial scale of the entire Barents Sea are unlikely to yield useful insights into the role of species variation as potential indicators of regime change. However, when this spatial heterogeneity is explored by incorporating the unique spatial detail inherent in each of the six sub-regions, the power of analyses and examinations of the utility of species variation as an indicator of the sensitivity of a particular sub-region to regime change can be effectively enhanced. This approach, when linked to effective definition of ecoregions, has now been used to set the scale for ecosystem analyses and management in other systems [36] and has recently been applied in the search for drivers of regime shifts at sub-system
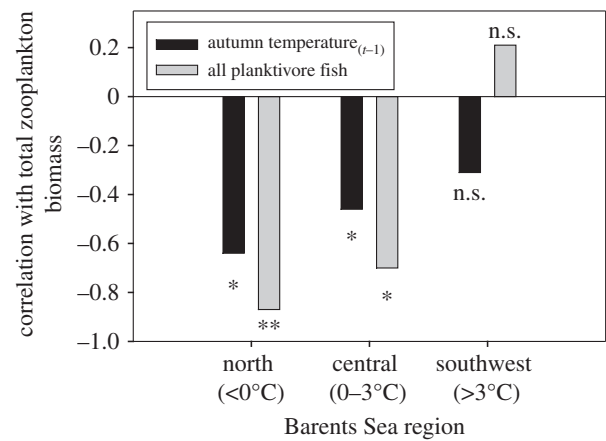

Figure 2. Spatially downscaled relationships within the Barents Sea, illustrating heterogenous temperature and predator effects on zooplankton dynamics within three areas of the Barents Sea characterized by increasing water temperature [39]. The significant negative correlations (*$p < 0.05$; **$p < 0.01$; n.s., $p > 0.05$ accounting for autocorrelation) between both planktivorous fish and water temperature occurred only in those regions characterized by relatively cold water conditions, based on model results from Stige *et al.* [39]. This finding reveals important spatial heterogeneity in zooplankton responses to changing temperatures and predators along an environmental gradient, a pattern expected to reduce the chance of a regime shift within a system [10].

spatial scales within the North Sea, the Baltic Sea and the Barents Sea [37–39].

For example, returning to the Barents Sea, Stige *et al.* [39] analysed the spatio-temporal dynamics of the several planktivorous fish complexes and their zooplankton prey within three regions (northern, central and southwest) to quantify potential within-system spatial variability in top-down control of zooplankton by fishes. Their model results indicated apparent top-down control (negative predator–prey correlations) of zooplankton by planktivorous fishes in the northern (cold water temperature) and central (intermediate water temperature) regions [35] but not in the warmer water southwestern region (positive predator–prey correlations) [39] (figure 2). Given that the characteristics of predator–prey correlations (positive versus negative) have been characterized as symptomatic of the initiation and/or maintenance of regime shifts in other ecosystems ([40–42], but see [43]), these evaluations of the predator–prey association at the scale of these ecoregions within the Barents Sea may have utility as predictors of their relative sensitivity to trophic restructuring within that system and largely confirm the findings from among-system comparisons at larger spatial scales.

The high fisheries productivity, long history of research and sensitivity to regime shifts [17,33] that characterize the North Sea has led to a major research focus on the search for, and characterization of the spatial variation in, potential drivers of regime shifts there. Fauchald [44], who studied the North Sea ecosystem as a whole, reported evidence in support of the hypothesis that the low biomass levels of North Sea cod (*Gadus morhua*) that developed in that ecosystem as a result of overfishing were being maintained by a corresponding increase in the biomass of herring (*Clupea harengus*) which, through the process of predator/prey role reversal, were acting as important predators of the early life stages of cod. Comparative analyses of the North Sea and 13 other ecosystems yielded additional support for this hypothesis, but have also revealed heterogeneity in this response among
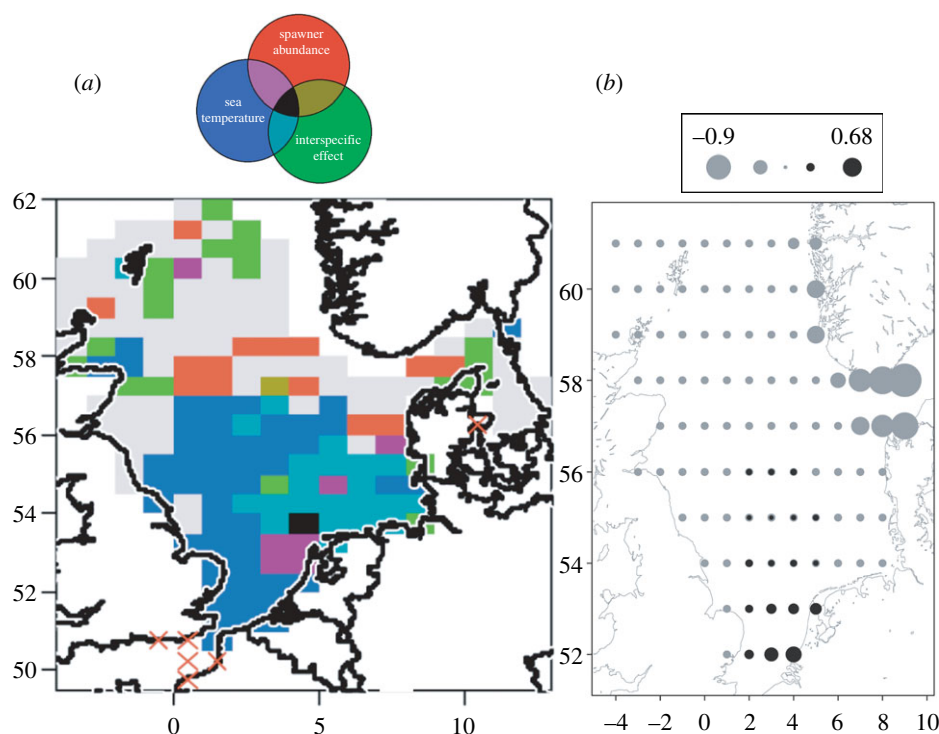
Figure 3. Spatial analyses of potential drivers of North Sea regime shifts. (a) Spatial variation in best-fit predictors of cod recruitment within North Sea grid cells averaging 3435 km^2, where colours indicate whether one or more of the three predictors was included in the model [47]. Grey cells indicate no strong relationship to any of the three predictors. (b) Spatial variation in zooplankton and phytoplankton time-series correlations from 1973 to 2004 within 95 1-degree square regions within the North Sea [38], illustrating positive correlations in the warm southern areas and negative correlations in cool northern areas, patterns that differed from the 1958–1972 period of consistent positive correlations across the North Sea.

regions and among pelagic species [45]. Recognizing the pronounced differences in the North Sea environmental conditions at multiple spatial scales and spatial autocorrelation among adjacent sites [46], Hjermann *et al.* [47] re-evaluated the generality of the herring role reversal hypothesis at smaller spatial scales and spatial variation in the relative importance of determinants of cod biomass, ranging from predominantly sea surface temperature (SST) in the southwest to combined influence of temperature and herring biomass in the east (figure 3a). Similar spatial heterogeneity in the key determinants of herring biomass was reported [47]. Taken together, these analyses illustrate the need to simultaneously evaluate the potential influences of cod parental biomass, temperature and predator biomass in a spatial context (see also [48])—factors that while acting locally may sum to determine the sensitivity of the entire ecosystem to regime shifts.

Spatial variability between sub-systems can also lead to complex mechanisms driving regime shifts based on the behavioural and productivity responses of affected populations. In the Northern Benguela, the Namibian sardine (*Sardinops sagax*) stock has fallen drastically since 1970 and never recovered to its previous size, corresponding with important ecosystem changes interpreted as a regime shift [49,50]. Correlations between sardine recruitment and environmental indices (SST, wind) have changed sign between regimes of high and low sardine abundance (from positive until the 1980s to negative in the 1990s) [49]. Sudden warming in the Gulf of Guinea has been remotely linked to environmental shifts in sardine habitat along the Namibian coast [49]. It was first hypothesized that this remote influence has led to unfavourable changes in local conditions including relaxation of upwelling and reduced productivity. However, between the two regimes, the main spawning ground of the sardine population has also

apparently moved to the north, where warmer conditions may influence it negatively, contrary to its former southern spawning location near the upwelling area [49]. This change in migratory behaviour may be a response to heavy fishing in the southern area [51] and as a result of this behavioural shift, the sardine population lost its southward-migratory tendency towards the preferred spawning ground, thereby potentially explaining the change in correlation with SST and completing a feedback loop that stabilizes the current low sardine regime.

High productivity in particular areas within a system and their exploitation by resident and migrating populations can provide key mechanisms underlying regime shifts. In the Black Sea, a pronounced regime switch from a predator-dominated to a planktivore-dominated system has been documented [52,53]. As described by Aristotle in his *Historia Animalium* [54], the main pelagic predators (bonito, bluefish and mackerel, but also bluefin tuna in the past) migrate in the spring from the southern Black Sea and Mediterranean to feed during the warm season along the most productive area of the basin—the large and shallow northwest shelf. Similar migrations are undertaken by small pelagic prey fishes, and their migrations represent the dominant driver of exploitation and export of biomass from the productive areas to subsidize less productive areas and support important fisheries. Declines in the abundances of migratory predators drove a basin-wide trophic cascade resulting in massive phytoplankton blooms in the productive northwestern Black Sea [53].

The Baltic Sea provides another important area in which to examine spatial variability, as ecosystem assessments have identified as many as 10 smaller scale regions [28]. The ecosystem structure of one of the Baltic Sea sub-basins, the Gulf of Riga, has been shown to be driven by processes occurring in one of its adjacent sub-basins, the Main Basin

[37]. The link between the two sub-basins is mediated by the main piscivore cod: when in high abundance in the Main Basin, cod increases its spatial distribution and disperses into the Gulf of Riga. Conversely, when cod abundance in the Main Basin is low, its population contracts and disappears from the Gulf of Riga. The occurrence versus absence of cod in the Gulf of Riga produces opposite chains of multi-level top-down regulations in its food web, changing its entire ecosystem structure, from planktivorous fishes down to phytoplankton [37]. This example suggests that when ecosystems are not functionally isolated, synchronous regime shifts could arise due to changes in ecological features connecting systems, as fluxes of key organisms or subsidies, and not by a common large-scale force (e.g. climate).

These examples illustrate the need to consider spatial variation in species interactions, environmental forcing and exchanges of individuals to quantify potential drivers of regime shifts and the importance of exploring within-system dynamics in large marine ecosystems in order to strengthen analyses by reducing the confounding effects of spatial averaging.

3. Spatial downscaling of proposed mechanisms

Another approach to the identification and evaluation of factors responsible for the initiation and/or maintenance of regime shifts (or lack thereof, as in the Barents Sea [34]) is that of quantifying whether mechanisms identified as being potentially important through among-system comparisons yield similar (or predicted) outcomes when assessed at the (smaller) scales at which individuals and populations interact with their local environments. This approach has been examined in theoretical approaches [10], is consistent with current approaches in analogous empirical fields linking large-scale patterns to more localized mechanisms [55] and complements analyses focused on the potential for scaling up from regional to planetary regime shifts [56]. Also of relevance is the question of whether proposed drivers produce similar outcomes at multiple spatial scales, which may not be the case if the drivers of regime shifts are species interactions [17] or show environmental heterogeneity in space [10,20]. Recent methods that seek to move beyond correlational studies to reveal causality in complex systems provide stronger tests of potential drivers of regime shifts [43,57].

In an example of the potential power of spatial downscaling to elucidate the relative strength of drivers identified in comparative studies conducted at large spatial scales, Frank et al. [40] compared and contrasted the nature of fish predator/prey in 26 data time series drawn from exploited ecosystems spanning the North Atlantic. Clear geographical variation in the strength and sign of the predator–prey correlation was evident. Strong positive correlations diagnostic of resource-controlled dynamics in exploited systems (and the expected baseline configuration in unexploited systems: see also [39]) dominated ecosystems characterized by relatively warm waters and high species richness. By contrast, strong negative correlations (diagnostic of predator-controlled top-down dynamics and prey outbreaks) dominated in relatively cold, species-poor ecosystems [40] (figure 4a). These strong among-system differences suggest a gradient in the relative resilience of these ecosystems to trophic restructuring that in some cases has been tied to regime shifts [31], with
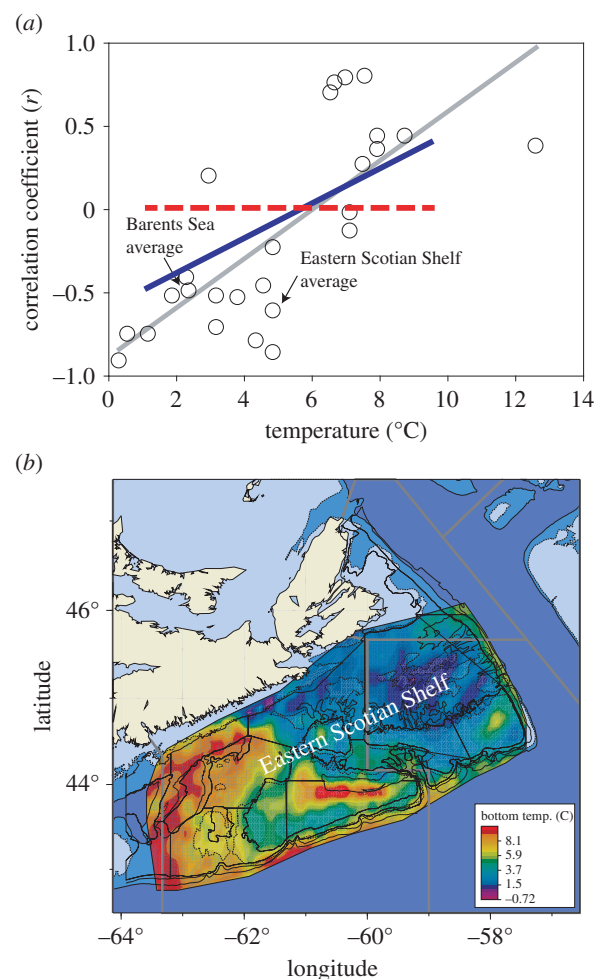

Figure 4. Illustrations of the concept of spatial downscaling to examine the roles of top-down and bottom-up drivers of potential regime shifts. (a) Positive relationship between average temperature and predator–prey time-series correlations among 26 exploited large ecosystems [40], illustrating positive correlations within systems characterized by warm water conditions and the average temperatures of the Barents Sea (range is highlighted in figure 2) and the Eastern Scotian Shelf (ESS; range highlighted by the coloured lines). (b) Spatial variability in long-term bottom water temperature among 24 ESS survey strata (outlined in black lines), showing that the within-area range of temperatures (1.4–9.2°C) among strata overlaps most of the observed range in average temperatures reported from 26 exploited large ecosystems in (a). Examinations within strata are being conducted to test whether the apparent temperature influence is maintained at smaller scales within this ecosystem. If so, it would suggest that water temperature has the same mechanistic influence at small and large spatial scales (blue line in (a)) and is therefore a general mechanism underlying spatially varying predator–prey correlations and the proposed differential resilience of ecosystems to restructuring under exploitation [40]. Alternatively, if the relationship is not maintained (red dashed line in (a)), the proposed mechanism would not be general.

northern cold water/species-poor ecosystems being more prone to such perturbations. The fact that water temperature and species richness covaried, and other interpretations are possible [43] confounds a full understanding of the primary drivers and calls for further exploration of the relative role and the generality of influence of these respective drivers at smaller spatial scales.

Similar context-dependent variations in the sign and strength of predator–prey correlations have been observed at smaller spatial scales within the North Sea. There, prior to

the 1970s, temporal correlations between phytoplankton/zooplankton abundances were consistently and strongly positive within $1° \times 1°$ boxes across the ecosystem [38]. Subsequent to 1972, however, the sign of these correlations in colder waters of the northern sectors became strongly negative, suggesting a transition from resource regulated to predator-driven control, while those in warmer waters of the southern sectors remained positive (indicative of resource-regulated (bottom-up) control [38] (figure 3b)). This within-system geographical or temperature-related pattern of spatial variation and top-down or bottom-up control of predator–prey dynamics mirrors that reported for the Barents Sea [39] (figure 2) and in among-system comparisons across the North Atlantic [40]. It is suggestive of the importance of temperature in structuring ecosystems and in their resilience to perturbation, and highlights the importance of incorporating spatial heterogeneity when seeking to identify and characterize the important regional differences in ecosystem stability and resilience in the face of perturbation. Research aimed at evaluating the generality of this temperature–diversity–resilience paradigm is now focusing on the Eastern Scotian Shelf ecosystem, across which the temperature range is similar to that observed across the entire North Atlantic [40] and which experienced a dramatic regime shift, driven largely by overfishing of groundfish during a period of cold temperatures and low productivity in the early 1990s [58]. This ecosystem is only now (more than 20 years later) exhibiting signs of a return to its former predator-dominated configuration [22]. Coordinated annual bottom trawl data based on strata ranging from hundreds to thousands of km^2 (figure 1; smallest spatial scale depicted) are available for the period 1970 to present, and make it an excellent system in which to test the generality of water temperature and/or species richness as meditators of predator/prey correlations at spatial scale orders of magnitude smaller than the original pattern among large marine ecosystems and NAFO (North Atlantic Fishery Organization) areas (figure 1). Should the relationship between water temperature and the sign and strength of predator–prey correlations prove similar at multiple smaller spatial scales (figure 4b, blue line), it would be strong evidence in support of the importance of context-dependent water temperature as a major factor structuring the resilience of marine systems to exploitation and or environmental change. Examination of such straightforward predictions at multiple spatial scales within areas having undergone regime shifts represents another method to test for the occurrence of predicted drivers [43,49,57].

4. Conclusion

The largely non-experimental nature of regime shift requires creative methods to increase understanding of mechanisms that both initiate and maintain regimes [2,4,6–11,32,43,57], as the range of spatial scales in which key regime shift drivers operate and may be detected vary by more than five orders of magnitude (figure 1), while within-system spatial heterogeneity has long been identified as a potentially important factor in analyses of regime shifts [1,10]. As the above examples have demonstrated, recent examinations of the roles of spatial heterogeneity and the movement of marine populations have implications for the initiation and detection of regime shifts, and some common features emerge. Based on spatio-temporal analyses within the Benguela, Baltic and Black Seas, seasonal and/or interannual shifts in the spatial distribution of predatory populations have contributed to initiating regime shifts and may explain shifts in associations between key population dynamics and environmental drivers [37,49,52,53]. In the North Sea [38] and Barents Sea [39], spatial downscaling of population models relating environmental and predation dynamics on key species have illustrated that relationships such as the apparent increased role of predation at lower water temperatures, first reported in among-system comparisons [40], are mirrored at smaller spatial scale orders of magnitude (figures 2 and 3). Therefore, in addition to examinations of commonalities in the timing of regime shifts [17,30], testing for important spatial variation within systems should be undertaken by downscaling potential relationships identified at larger spatial scales, as outlined using the Eastern Scotian Shelf as a future case study (figure 4). Future analyses will benefit from the application of such approaches to complement other strong tests of potential mechanisms [32,43,57] and assess their generality both among and within marine ecosystems, with the goal of anticipating future regime shifts and the factors that accentuate or thwart them.

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