Historical subtidal regime shifts echoed in adjacent intertidal community

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Data availability statement

Data and codes can be found at:

https://github.com/Julien-Beaulieu/GOM_RegimeShift_timeSeries

Conflict of interest disclosure

There are no competing interests to declare

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Abstract

Anthropogenic stressors can trigger regime shifts, causing ecosystems to reorganize into new states. Moreover, there is growing evidence of the importance of fluxes (e.g., energy, matter and nutrients) in linking adjacent systems, suggesting that regime shifts within one system may extend to neighbouring systems through cross-ecosystem interactions. However, empirical evidence supporting this hypothesis is lacking. To address this gap, we analyzed over 40 years of community data from intertidal and subtidal ecosystems at Appledore Island in the Gulf of Maine, a region that has experienced multiple subtidal regime shifts. We identified three periods of rapid change in subtidal communities that are coherent with known regime shifts in the region. In the intertidal zone, we found that 58% of island-scale directional changes in community composition exhibited offset synchrony with subtidal regime shifts, meaning they started changing during subtidal regime shifts. This pattern was also observed in key intertidal species. We suggest that these offset synchronies may be the result of cross-ecosystem linkages through trophic interactions. Our results support the notion that regime shifts can propagate across ecosystem boundaries, demonstrating the importance of considering adjacent ecosystems as drivers of changes in any ecosystem of interest, and highlighting the need to consider the indirect effects of cross-ecosystem interactions for multiple ecological phenomena.

Introduction

Regime shifts are abrupt, high amplitude shifts in the physical or ecological components of a system, which cause a transition to an alternative stable state that is difficult or virtually impossible to reverse (Beisner et al. 2003, Scheffer and Carpenter 2003, Lees et al. 2006). Regime shifts can be triggered by natural (e.g., hurricane) or anthropogenic (e.g., overharvesting) pressures (Genkai-Kato et al. 2012) and can have numerous cascading effects on biodiversity and ecosystem services. Regime shifts are difficult to reverse because they change the dominant positive feedbacks controlling the system in a way that reinforces the new state of the ecosystem even after the initial cause of the shift is removed (Scheffer and Carpenter 2003). Losses of ecosystem services caused by regime shifts can lead to substantial and persistent social and economic consequences, such as through the collapse of fisheries or resource harvesting industries (Scheffer et al. 2001, Scyphers et al. 2019, Janssen et al. 2021, Defeo et al. 2021, Kuzyk et al. 2026). However, the study of regime shifts often requires long-term datasets that are challenging to obtain, as these shifts may be difficult to distinguish from other types of changes, such as cyclic variations or reversible transitions (Biggs et al. 2009, Sundstrom et al. 2017).

Regime shifts in one ecosystem may affect adjacent ecosystems through cross-ecosystem interactions (Polis et al. 1997, Rocha et al. 2018, Rocha and Crepin 2023). Cross-ecosystem interactions occur primarily via two mechanisms: 1) transport of matter and biologically available energy or nutrients between systems; and 2) mobile animals that cross systems boundaries and have effects on nutrient cycles or community structure (Krumhansl and Scheibling 2012, Subalusky et al. 2017, Brandt et al. 2024, Cereghetti et al. 2025), often through nutrient excretion or consumption (Scherer-Lorenzen et al., 2022). These cross-ecosystem interactions can influence the dynamics and structure of an ecosystem (e.g., nutrient dynamics and food web structure) and shape their functions (e.g., pollination, Knight et al., 2005 ; metapopulation dynamics, Montagano et al., 2019; and ecosystem metabolism, Gounand et al., 2018). Despite the recognized importance of cross-ecosystem interactions in coupling the ecological dynamics of adjacent ecosystems, few studies to date have examined how temporal shifts in species composition (i.e., regime shifts) within one ecosystem may influence adjacent ecosystems through such linkages (but see Rocha et al., 2018; Rocha & Crepin, 2023). Understanding these dynamics is crucial, as cross-ecosystem interactions may initiate regime shifts in adjacent ecosystems or amplify ecological disturbances by propagating regime shifts to coupled ecosystems (Rocha et al. 2018, Rocha and Crepin 2023).

Cross-ecosystem interactions are common between intertidal and nearshore subtidal ecosystems. These adjacent ecosystems are connected by mobile predators such as fish, lobsters and crabs that regularly forage across the intertidal-subtidal boundary (Rilov and David R 2006, Rilov and Schiel 2006, Silva et al. 2008, 2010, 2014, Christie et al. 2020). Predators shape community structure in these ecosystems through top-down control (Pauly et al. 1998, Williams et al. 2004, Peller et al. 2022), and predators have previously been implicated as key players in regime shifts (Daskalov et al. 2007, Steneck et al. 2013).

At least three distinct subtidal regime shifts have been identified in the nearshore Gulf of Maine during the past fifty years (Figure 1; Dijkstra et al., 2017; Jackson et al., 2001; Pershing et al., 2015, 2016; Steneck et al., 2013). The first regime shift was driven by the overharvesting of commercial predatory fish such as Atlantic cod (*Gadus morhua*) (Jackson et al. 2001, Myers and Worm 2003). This first regime shift occurred mainly around 1975–1980, but lasted until around 1990 in the Gulf of Maine (Worm and Myers 2002). This fisheries collapse released key benthic species from predation pressure, including green sea urchins (*Strongylocentrotus droebachiensis*) (Jackson et al. 2001, Steneck et al. 2013). Abundant sea urchins defoliated kelp beds, causing shifts to urchin barrens between 1975–1990 (Steneck et al. 2013). The second regime shift occurred between 1995–2000 when urchin populations collapsed due to overharvesting, increased predation, and disease outbreaks (Scheibling and Hennigar 1997, Steneck et al. 2013). Urchin declines allowed opportunistic species and non-native macroalgae to establish on the benthos, which facilitated larger invertebrate populations through habitat provisioning (Steneck et al. 2013). The third regime shift, likely driven by ongoing rapid ocean warming (Pershing et al. 2015), occurred around 2010 as non-native filamentous red algae proliferated (Newton et al. 2013, Dijkstra et al. 2017, O'Brien et al. 2018), affecting invertebrates and, indirectly, higher trophic levels (Dijkstra et al. 2017, O'Brien et al. 2018).

While changes in the neighbouring intertidal communities have not been explicitly defined, changes in populations and community compositions occurred across the same time period. When comparing shores from the 1970s to those in 2013–2014, Sorte et al., (2017) observed a decrease in Irish moss (*Chondrus crispus*) and blue mussels (*Mytilus edulis*) and an increase in the red alga *Mastocarpus stellatus* and crustose red algae. Petraitis & Dudgeon (2020) documented warming-associated declines in the recruitment of habitat-forming filter feeders (blue mussels, *M. edulis,* and barnacles, *Semibalanus balanoides*), and ocean acidification-linked declines in the abundances of herbivorous gastropods and predatory whelks from 1996 to 2012. In addition to climate change, shifts in intertidal community composition may also be attributed to increases in harvesting, hurricane activity, and non-native species (Sorte et al. 2017).

Here, we use long-term data sets from the Gulf of Maine to examine whether shifts in intertidal communities correspond in time to documented subtidal regime shifts propagation during a 42-year monitoring program. We do so by assessing periods and rates of change in both ecosystems and how they align in time (Figure 2a). We hypothesized that subtidal regime shifts will have cascading effects on intertidal ecosystems, likely through altered trophic interactions propagating through linked food webs. We predict that if intertidal community composition is driven by cross-ecosystem interactions with subtidal communities, then changes in the intertidal community should lag behind those occurring in subtidal ecosystems in an "offset synchrony" pattern (Figure 2b). Alternatively, if intertidal community composition is largely independent of these cross-ecosystem interactions, then changes (not necessarily regime shifts) in intertidal assemblages should occur independently of subtidal transitions, if they occur at all.

Methods

Our study focuses on Appledore Island in the Gulf of Maine (42.987°N, 70.609°W), where intertidal community composition has been monitored annually along permanent vertical transects since 1980, first as part of undergraduate field courses and later as part of a regular sampling program (Shoals Marine Laboratory 2018). To identify the subtidal regime shifts over the whole study period, we used NOAA bottom-trawl survey data from transect within 100 km from Appledore Island. We then identified periods of change in mobile and sessile intertidal communities in each of the five sites distributed around the island before relating the timing of intertidal periods of changes to the subtidal regime shifts.

NOAA Bottom Trawl Communities

To identify the timing of regime shifts in subtidal and pelagic ecosystems of the Gulf of Maine, we analyzed time-series data from sampled fishes and invertebrates as part of the Seasonal Bottom Trawl Surveys conducted by the National Oceanic and Atmospheric Administration (Grosslein n.d., Johnston and Sosebee n.d., NOAA 2020). Initiated in 1963, these seasonal surveys follow a standard protocol to provide a harvesting-independent estimate of the abundances and biomasses of key fisheries species (Evans and Stauffer 2004). Each season, tows are conducted at more than 350 transects of different depths spanning the length of the northeastern US Atlantic coast from Cape Hatteras, North Carolina in the south (28.47°N) to the Canadian border in the north (44.52°N). In order to compare temporal changes in the intertidal community to those in the subtidal zone, we used only NOAA transects within 100 km of Appledore Island (42.987°N, 70.609°W) with complete survey data from 1980 onwards. With this approach, we selected six total transects: three inshore and three offshore (of a possible 56 total located within the Gulf of Maine; strata 01260, 01270, 01400, 03640, 03650, and 03660). The depth of the six transects selected were 366-549m, 549-732m, 0-27m, 110-183m, 183-366m, and 366-549m. We acknowledge that despite their proximity to Appledore Island, the communities described by the NOAA data may differ from those of the nearshore subtidal zone (e.g., more deep water species). We argue that these data are a more thorough indicator of the state of communities within the Gulf of Maine given their spatial scale and taxonomic diversity in order to characterize system-wide regime shifts (Jackson et al. 2001, Steneck et al. 2013, Pershing et al. 2015, Dijkstra et al. 2017). As a robustness check, we re-analyzed the data using only species sampled in nearshore surveys at 10m depth by the Kelp Ecosystem Ecology Network, and found the same results as analyzing the entire trawl data set with respect to timing of regime shifts (see supplementary material 3).

Data from the six NOAA transects were used to detect changes in subtidal community structure. We calculated the total number of individuals for each species captured in each transect at every sampling time. We similarly calculated the species-specific total biomass of all individuals caught in a given transect, season, and year. These values (catch and biomass) were subsequently standardized by sampling effort by dividing the value by the number of samples ("tows") taken along each transect. Finally, we averaged the standardized effort values from all strata to arrive at season-specific time series for each species included in the dataset. Because data from summer and winter surveys were sparse relative to spring and autumn (summer and winter trawls have only been conducted since 1991 and 1992, respectively), we averaged spring and autumn records for calculating annual effort-standardized catch and biomass.

Intertidal Communities

We divided Appledore Island into five regions that differ in wave exposure: Babb's Cove (BC); North-East Appledore (NE); North-West Appledore (NW); South-East Appledore (SE) and South-West Appledore (SW) (see Byrnes et al. (2024) for classification). A detailed description of the survey methods and timeline of sampling changes can be found in the open access data repository (Shoals Marine Laboratory 2018). Briefly, within each region, permanent transects were surveyed periodically from 1982–2022, for a total of 28 transects around the entire island. Within each transect, replicate 20 x 20 cm quadrats were placed every 0.3 m (1 ft) in elevation from the low to the high intertidal zone. Within quadrats, the presence and/or abundance of all observable species were documented. Mobile organisms were identified to species and counted within each quadrat. The percent cover of sessile organisms was estimated at the canopy and primary cover layers for all species with more than 3% cover. The percent cover used in this study is the sum of values for the two layers in each quadrat such that a species can have more than 100% cover. Organisms were identified to species or else the lowest possible taxonomic resolution possible (e.g., *Fucus* spp., amphipods). The number and length of transects and number of replicate quadrats within each transect surveyed varied among years. Each year, between one and 17 transects (8.3 per year on average), and between one and four replicate quadrats per tide height were sampled.

Statistical analysis

Subtidal regime shift identification

To identify the timing of subtidal regime shifts in the predator communities surrounding Appledore Island, we used ordination and multivariate generalized additive models (GAMs; Figure 2a). Fitted GAMs provided estimates of interannual community changes, and their derivatives indicated the rate and direction of those changes. Prior to analysis, we aggregated abundances to the genus level and excluded species recorded in fewer than 10 different years to reduce zero inflation (see supplementary material 1 for retained species in this analysis). Second, we performed a Principal Coordinate Analysis (PCoA) using Hellinger distance dissimilarity on the NOAA bottom trawl survey effort-corrected biomass data. The PCoA was calculated using the R package `*vegan*` (Oksanen et al. 2020). Next, we performed a time series analysis on the first two ordination axes using Bayesian multivariate Gaussian Generalised Additive Model (GAM) with the three first PCoA axes as dependent variables and year as predictor with a smoothing term. All time series models are listed in Table 1. The first three PCoA axes were used because they all explained significant variation in community composition and had eigenvalues above one. The model was fitted with the `brms` package (Bürkner 2018) in R version 4.3.3 (CoreTeam 2020).

Proper identification of regime shifts is difficult as it requires demonstrating rapid and substantial changes in the community, in addition to the establishment of an alternative stable state (Scheffer and Carpenter 2003) and often an increase in variance and autocorrelation preceding the shift (Dakos et al. 2012, Guttal et al. 2013). In this study system, drastic changes in the subtidal community have been previously defined as regime shifts (Jackson et al. 2001, Steneck et al. 2013, Pershing et al. 2015, Dijkstra et al. 2017). Consequently, we define subtidal regime shifts as the periods of time when the rate of community change is at its highest while transitioning from one extreme to another (i.e., the maximum of the first derivative of the curve) (Figure 2a). To identify the timing of the subtidal regime shifts, we calculated the derivative (i.e., rate of change) of 1000 draws of the posterior prediction of the time series for subtidal community PCoA axis one and two using forward difference. The regime shift interval was identified as the period during which 95% of the derivatives of those 1000 draws were maximal or minimal (Figure 1a).

Timing of the changes in the intertidal community

To identify periods of change in intertidal communities, we again used PCoA and GAMs to estimate the magnitude of interannual community changes. First, we made one PCoA for sessile organisms and one PCoA for mobile organisms using Hellinger dissimilarity for each quadrat. Species present in less than 2.5% of the intertidal quadrats over the entire sampling period were removed from those analyses to reduce zero-inflation. Next, we used two separate multivariate hierarchical GAMs (HGAMs) for change analysis in sessile and mobile intertidal communities on the first three axes of the PCoA. All time series models are listed in Table 1. We accounted for spatial variability in these time series—both within and among transects—by including tide height as a smoothing term and a random intercept for each transect. We used leave-one-out cross-validation (LooIC) to select between models with different structures for time effects: 1) a shared temporal trend and similar smoothness between site; 2) a shared trend and different smoothness between sites; and 3) different trends and smoothness between sites (Pedersen et al. 2019). For all of the following analyses, the model with different trends and smoothness between sites (model 3 above) was selected (Table 1).

Because some taxa were numerically dominant and/or participate in key trophic interactions linking intertidal and subtidal communities, we generated additional time series for eleven focal taxa : *Amphipoda*; *Isopoda*; *Mytilus edulis*; *Semibalanus balanoides*; *Nucella lapillus*; *Littorina spp.*; *Carcinus maenas*; *Mastocarpus stellatus*; *Fucus* spp.; *Chondrus crispus*; and *Ascophyllum nodosum.* We used the same GAM formulation to generate focal taxa time series data, accounting for spatial heterogeneity across different transects by including transect ID as a random intercept and across different intertidal heights using a smoothing term. We also allowed different trends and smoothness between sites. We modeled mobile species with count data using the zero-inflated negative binomial distribution. The exception was *Littorina* spp., for which we used a zero-inflated Poisson distribution, as these data were not overdispersed. We modelled percent cover of sessile invertebrates using the zero-inflated beta distribution, and algae were modeled with gamma hurdle distribution. All priors were non-informative and weakly regularizing (see supplementary material 7).

Comparison of Subtidal and Intertidal Periods of Change

To test whether regime shifts from the subtidal zone propagated to the intertidal zone, we identified periods of changes in subtidal and intertidal communities as changes in temporal trend direction (second derivative different from zero) of the previously described time series models. A useful framework to assess whether or not a time series influences another is Granger causality (Granger 1969). However, this approach requires high data frequency and linear causal relationships (Maziarz 2015), which are lacking here. Instead, we compared the timing of changes in temporal trends in intertidal community composition over time with the timing of subtidal community changes. We assumed that if intertidal communities are influenced by trophic interactions with subtidal predators, subtidal regime shifts will lead to corresponding intertidal shifts beginning when the rate of subtidal change is at its maximum. (Figures 2a–b). Changes in the temporal trend direction (forming an “elbow” shape) can be quantified using the second derivative, with a second derivative significantly different than zero implying a shift in trend direction. A non-zero second derivative of the intertidal community during a subtidal regime shift therefore indicates that intertidal community composition begins to change at the same time as the subtidal regime shift occurs, implying cross-ecosystem interactions. We expect that intertidal community change will not be synchronous with subtidal regime shifts, but delayed, as the intertidal community starts changing when the changes in the subtidal community are occurring most rapidly. This pattern—hereafter referred to as offset synchrony—indicates a potential propagation of the subtidal regime shift to the intertidal system and corresponds to the concept of Granger causality, wherein changes in one ecosystem precede and potentially influence another ecosystem. Offset synchrony is also coherent with our hypothesis of regime shift propagation through altered trophic interactions between the subtidal and intertidal zones, as changes in abundance due to trophic interactions inherently includes a lag in time (Wangersky 1978).

To identify shifts in trend direction, we calculated the second derivative for each intertidal time series using the central difference method across 1000 posterior predictive draws. This included site by species combinations where a significant interaction between the two factors was detected. Changes in the second derivative that were completely asynchronous with a subtidal regime shift were attributed to variables unrelated to the subtidal regime shift. Finally, as the intertidal and subtidal community compositions were quantified using Hellinger dissimilarity, the magnitude of the changes in community composition over time can therefore be compared by looking directly at the magnitude of changes over time.

Results

Subtidal regime shift identification

Subtidal community composition around Appledore Island (i.e., pelagic and benthic fishes and invertebrates from the NOAA trawl survey) was nonstationary over the 40-year period, as demonstrated by constant change on the first or the second ordination axes (Figure 3). Rates of community change were also variable through time, with the first derivative (slope) reaching a maximum around the year 2000 on the first ordination axis, and around 1990 and 2010 on the second axis (Figure 3, supplementary material 2). For the remainder of this study, we considered these periods of particularly fast changes in community composition in 1990, 2000 and 2010 as the first, second, and third subtidal regime shifts (see Supplementary Figures S1 and S4). Driven by the first regime shift (~1990), the subtidal predator community changed on the second ordination axis from an assemblage characterized by a higher abundance of large predatory and benthic invertivore fish (e.g., *Gadus morua, Pollachius virens,* and *Cyclopterus lumpus*) to one characterized by invertebrates (e.g., crabs, shrimps, squid)(Figure 3, Tables S1 and S2). This trend was reversed ~20 years later during the third regime shift (~2010), when predatory fish again became more abundant. The second regime shift (~2000) drove a change from a community characterized by a higher abundance of large vertebrate and invertebrate predators (e.g., *Lumpenus spp, Scomber scombrus, Brosme brosme, Cancer* spp. crabs and *Lithodes maja*), to a community characterized by a high abundance of invertebrates (e.g., *Bathypolypus arcticus, Maurolicus weitzmani*, *Sepiolidae*, *Lycenchelys verrilli*, *Lebbeus polaris***,** *Pontophilus norvegicus* and *Spirontocaris liljeborgii*) and barndoor skate (*Dipturus laevis*)(Figure 3 and S1).

Comparison of Intertidal and Subtidal Regime Shifts and Changes in Intertidal Communities

Mobile invertebrate intertidal community

The composition of the intertidal mobile invertebrate community changed through time across all sites (Figure 4) on the first and third ordination axis. We identified 10 changes in the second derivative of the mobile intertidal community, 4 of which displayed offset synchrony with the three subtidal regime shifts (Figure 4, Supplementary Material 6, and a table with all the second derivative values for each regime shift is available in the data repository hereafter referred to as repository table). Moreover, all six intertidal mobile invertebrate genera that we analyzed exhibited changes corresponding to offset synchrony with the subtidal regime shifts (Figure 5, Supplementary Material 6, repository table).

The offset synchrony varied across species and sites, with a tendency for the focal taxa to exhibit a more offset response at the SE Appledore site (figure 5). However, spatial variation (i.e., intertidal height and site) was the primary factor shaping the intertidal mobile organism community, which varied between higher intertidal communities characterized by a low abundance of mobile organisms and lower intertidal communities characterized by a higher abundance of *Nucella, Amphipoda* and *Littorina* on the first two ordination axis (Figure S3). However, accounting for spatial variation allowed us to isolate temporal trends (Figure 4, Supplementary Material 4).

The magnitude of island-wide shifts in species composition, measured in Hellinger distance, were less pronounced in the intertidal community than in the subtidal community over the study period. Intertidal community changes ranged between -0.1 to 0.1 on the first axis and -0.2 and 0.2 on the second axis, approximately five to ten times smaller than changes in the subtidal community (-1 to 1 on both axes) (Figures 3, 4).

Sessile intertidal community

We identified two changes in the sessile intertidal community, both along the first ordination axis (Figure 6). Island-wide shifts in the intertidal sessile community composition showed offset synchrony with subtidal regime shifts along the first ordination axis in 1990, but not in 2000 nor 2010 (Figure 6, Supplementary Material 6). No corresponding changes were detected on the second or third ordination axes. Of the five focal sessile organisms analyzed, four displayed some level of offset synchrony with subtidal regime shifts (*S. balanoides, C. crispus, M. stellatus* and *Fucus* spp.), especially for *S. balanoides* and *C. crispus* (Figure 5, Supplementary Material 6). Similar to the intertidal mobile invertebrate community, the sessile community was mainly influenced by spatial variation in intertidal height and site, and accounting for this variation allowed us to distinguish temporal trends.

Long-term community changes in the intertidal zone

Overall, 58% (7/12) of the periods of changes in both sessile and mobile whole intertidal communities (i.e., number of times the second derivative differed from zero) corresponded to offset synchrony with subtidal regime shifts (Figure 4, 6, Supplementary material 6, repository table). However, both sessile and mobile intertidal communities also tended to have changes starting around 2005 until the end of the study period that were asynchronous with the identified subtidal regime shifts (Figures 4, 6), although these changes were not significant (second derivative overlapping with zero, Figure S5). Similar patterns were observed for many focal taxa that decreased in abundance post-2005 in some sites: *C. crispus*; *M. edulis*; *N. lapillus*; and amphipods, although their abundance started decreasing at the beginning of the study (1980). At the same time, there was an increase in *Fucus sp.* presence. These changes lasted until the end of the study period, although the mobile invertebrate community began to stabilize towards 2020 (Figure 4, Supplementary material 6). There were also variable changes in abundance over time for *C. crispus, Fucus* spp. and *Littorina* spp. around 1995 that did not overlap with any subtidal regime shifts, but these changes were short-lived, and a subsequent abundance change in 2000 occurred in offset synchrony with the second subtidal regime shift (Supplementary Material 6).

Discussion

Regime shifts are often examined in isolation within individual habitats, limiting our understanding of how a shift in one habitat may influence shifts in others. In our analyses of a 42-year dataset of subtidal and intertidal ecosystems in the Gulf of Maine, we found that 58% of the changes in intertidal communities (at the island and community wide scale) were in offset synchrony with subtidal regime shifts, and thus could be due to cross-ecosystem interactions by species that move between both ecosystems. These findings reveal that there is offset synchrony in regime shifts between intertidal and subtidal communities, a pattern that was consistent across three distinct regime shifts and among key intertidal species. Regardless of mechanism, this pattern suggests that species interactions are capable of propagating change between subtidal and intertidal ecosystems. The remaining 42% of directional changes in intertidal community composition were mainly long-term (~20 years) starting around 2005 and correspond to expected consequences of climate change on intertidal communities rather than linkages to the subtidal community (Passarelli et al. 2017, Petraitis and Dudgeon 2020).

Subtidal regime shifts identification

We identified three periods of rapid change in the subtidal community composition since 1980 in the Appledore Island area. These changes correspond with previous benthic and pelagic documented regime shifts (Jackson et al. 2001, Steneck et al. 2013, Pershing et al. 2015, Dijkstra et al. 2017). The first regime shift, detected around 1990, is attributed to the collapse of larger fish due to overharvesting (Jackson et al. 2001, Myers and Worm 2003). Despite the fisheries collapse between 1970 and 1980, there was a second smaller collapse between 1980 and 1990 in the Gulf of Maine (Worm and Myers 2002). The second regime shift, detected around 2000, aligns well with the collapse of urchins and the rise of invasive macroalgae as the ecosystem reorganized (Steneck et al. 2013, Dijkstra et al. 2017). While we used trawl data to characterize regime shifts, these shifts were likely felt in multiple parts of the system, and our analysis of the subtidal community when selecting only species commonly present in the nearshore subtidal zone of AppledoreIsland shows the same result (Supplementary material 3). The third subtidal regime shift, detected around 2010, appears to coincide with the introduction and proliferation of exotic filamentous red algae (Dijkstra et al. 2017) and warming oceans (Pershing et al. 2015, Greene 2016, Bianchi et al. 2023).

By using multivariate approaches for whole-community analyses, we found that the subtidal community composition has experienced continuous change over the last 40 years. Some components of the community had periods of relative stability, but consistent structural changes over this period suggest stressors occurred at a greater frequency than the ability of the community to stabilize. The absence of a stable state points towards the need to promote ecosystem resilience in the Gulf of Maine in the face of ongoing changes in climate (Caddy and Seijo 2005). Within dynamic communities there is growing evidence of the importance of ecosystem-based- (Curtin and Prellezo 2010) and adaptive management approaches (Williams 2011) for bolstering ecosystem resilience to external perturbations (DeYoung et al. 2008, Pace et al. 2015) and prevent new regime shifts as anthropogenic stressors erode ecosystem resilience (DeYoung et al. 2008).

Regime shift propagation and changes in intertidal communities

We identified changes in the intertidal community that occurred both independently and in offset synchrony with the changes to the subtidal community, offering support for the idea of propagation of regime shifts between ecosystems. However, all three periods of change in the subtidal community were followed by changes in intertidal community composition, which were smaller in magnitude but may reflect a change in top-down trophic pressure from the subtidal to the intertidal zone. The smaller magnitude of these shifts may be attributed to stabilizing interactions, which can dampen the effects of subtidal regime shifts as they cross ecosystem boundaries (Gladstone-Gallagher et al. 2023), or higher spatial heterogeneity in the intertidal zone, which can promote stability by increasing overall richness and providing a range of refugia (Oliver et al. 2015). Whether these changes in the intertidal zone constitute regime shifts or not is beyond the scope of this study. Formal identification of regime shifts requires showing fast and major changes (as here) in addition to the reach of an alternative stable state, which is often accompanied by an increase in variance and autocorrelation before the shift, or multimodal relationships with control factors (Scheffer and Carpenter 2003). While we observed substantial shifts in intertidal community composition, the reversibility of the changes is impossible to determine with the data available, the temporal frequency of the data is too low and the sampling effort too variable to assess changes in autocorrelation and variance, and the drivers for each period of change in the intertidal zone are too uncertain to test multimodality.

Potential mechanism for regime shifts propagation from the subtidal to the intertidal zone

We identified offset synchrony between the intertidal and the subtidal communities for all three subtidal regime shifts at both the whole island and community scale, although the sites and species impacted differed. While our data does not address specific interactions that would cause the shifts *per se*, based on the natural history of the system and cross-correlations in species abundances, we hypothesize that the propagation of subtidal regime shifts to the intertidal ecosystem is through cascading consequences of changes in cross-ecosystem top-down regulation (supplementary material 8). We identified 60 subtidal consumer species present around Appledore Island that feed on taxa identified in the intertidal zone (Fig. S92). Among those 60 consumers, 39 were identified to be impacted by one or two subtidal regime shifts based on the ordinations and subtidal time series (Fig. S92). Of those 39 species' biomass, 31 were negatively cross-correlated with the abundance of some of their intertidal prey (suggesting top-down regulation) and impacted by the same regime shift at one or more sites. Yet, among those 31 species potentially linking the subtidal to the intertidal, six were detected in the nearshore subtidal zone during a visual survey between 2014 and 2018 and their predation on intertidal organisms could have cascaded through intertidal food webs and altered grazing dynamics (Lubchenco 1978, 1980, Ellis et al. 2007). Forexample, *Cancer borealis* is a known top-down regulator of intertidal communities at Appledore Island (Ellis et al. 2007), but the impact of the five other species (*Homarus americanus, Pollachius virens, Pseudopleuronectes americanus, Tautogolabrus adspersus* and *Urophycis regia*) on intertidal communities is untested, partly because intertidal surveys are being done at low tide. However, as communities from shallow subtidal and deeper subtidal zones differ, the offshore NOAA bottom trawl surveys may not capture all nearshore species that contribute to trophic linkages by foraging in the intertidal zone.

We acknowledge that cross-ecosystem linkage through trophic interactions in this article remains speculative. We also acknowledge that some intertidal community change could result from effects that are confounded with subtidal changes, qualities inherent to any time series analysis. However, our finding of offset synchrony in intertidal communities across all three subtidal regime shifts, combined with our knowledge of the ecological relationships between subtidal and intertidal species, provides compelling circumstantial evidence that subtidal regime shifts are influencing adjacent intertidal ecosystems. Our findings suggest that further investigations of the impacts of regime shifts on adjacent ecosystems, particularly the mechanisms by which those impacts propagate, are worthy of investigation.

Independent changes in the intertidal communities

Many (42%) of the changes in direction of the intertidal community composition at the island- and community-wide scales did not correspond to offset synchrony with subtidal regime shifts. These longer-term tendencies are coherent with the expected consequences of climate change, as we have seen an increase in warm-affinity species and a decrease in cold-affinity species on Appledore Island (Lawlor et al. 2026). Here, we found a general tendency for change starting around 2005 that lasted until the end of the study period in sessile and mobile communities.

These changes include a decreased abundance of many key intertidal taxa (*C. crispus*, *M. edulis*, Amphipoda, and *Nucella sp.*), all of which are likely negatively impacted by increasing temperatures, either in their adult stage (Khan et al. 2018), as planktonic larvae (Petraitis and Dudgeon 2020), or indirectly through increased susceptibility to parasites (Lavaniegos and Ohman 1998, Mouritsen et al. 2005). Other abiotic factors including acidity and salinity may contribute to declines in *Nucella* and Amphipoda (Passarelli et al. 2017, Petraitis and Dudgeon 2020). The reduction in *M. edulis* may also be attributable to the increased abundance of predatory *Cancer borealis* (Ellis et al. 2007), from 2005 to the end of the study period.

Conclusion

The propagation of regime shifts has been theorized (Rocha et al. 2018, Rocha and Crepin 2023) but empirical evidence has been lacking. Our results offer some support for cross-ecosystem interactions between subtidal and intertidal systems, wherein all major community changes in the subtidal zone were followed by corresponding changes in the intertidal zone, and abundance of subtidal consumers was negatively cross-correlated with abundance of their intertidal prey. Propagation of regime shifts from subtidal to intertidal ecosystems is plausible due to top-down control from subtidal predators feeding in the intertidal zone at high tide (Rilov and David R 2006, Rilov and Schiel 2006, Silva et al. 2008, 2010, 2014, Christie et al. 2020). Importantly, through our analyses we were able to distinguish between changes in intertidal communities that are likely attributable to subtidal regime shifts, and changes that are likely attributable to other causes, particularly climate change. This result demonstrates the broad importance of considering community regime shifts in adjacent ecosystems as putative drivers of change in any ecosystem of interest and a renewed need to consider the indirect effects of cross-ecosystem interactions for multiple ecological phenomena.

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Author contribution

All authors played a role in Conceptualization (supporting), Writing - Review & Editing (supporting). JEKB, JBB and EKB participated in Project Administration. JEKB also played a role in Formal Analysis (supporting), and Funding Acquisition. JEKB, JAD and KB had a role in Supervision. JB did conceptualization (lead), formal analysis (lead), visualization (lead), writing - original draft (lead).

Conflict of interest

The authors declare no conflict of interest.

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Tables

Table 1: Models ran and their performance. The GS model is a model with a shared trend and similar smoothness between sites, the GI model has a shared trend and different smoothness between sites, and the I model has different trends and smoothness between sites.

Variable	**Model type**	**looIC**	**Bayes R^2**
Subtidal predators community	-	30.5	0.83
Sessile community	GS	28084.9	0.55
Sessile community	**GI**	**18803.5**	**0.55**
Sessile community	I	18826.0	0.55
Mobile community	GS	19593.5	0.16
Mobile community	**GI**	**19553.8**	**0.17**
Mobile community	I	19659.9	0.16
Ascophyllum	I	12594.4	0.52
Chondrus	I	20301.6	0.50
C. maenas	I	3632.0	0.13
Fucus	I	48214.2	0.31
Littorina	I	114252.1	0.11
Mastocarpus	I	17553.3	0.36
Mytilus	I	9067.3	0.38
Nucella	I	16017.7	0.30
Semibalanus	I	8689.5	0.39
Amphipoda	I	77154.3	0.16
Isopoda	I	11816.8	0.42

Figure captions

Figure 1. Timeline of subtidal regime shifts within the Gulf of Maine since 1980 based on Dijkstra et al. (2017); Pershing et al. (2015); Petraitis & Dudgeon (2020); Steneck & Wahle (2013).

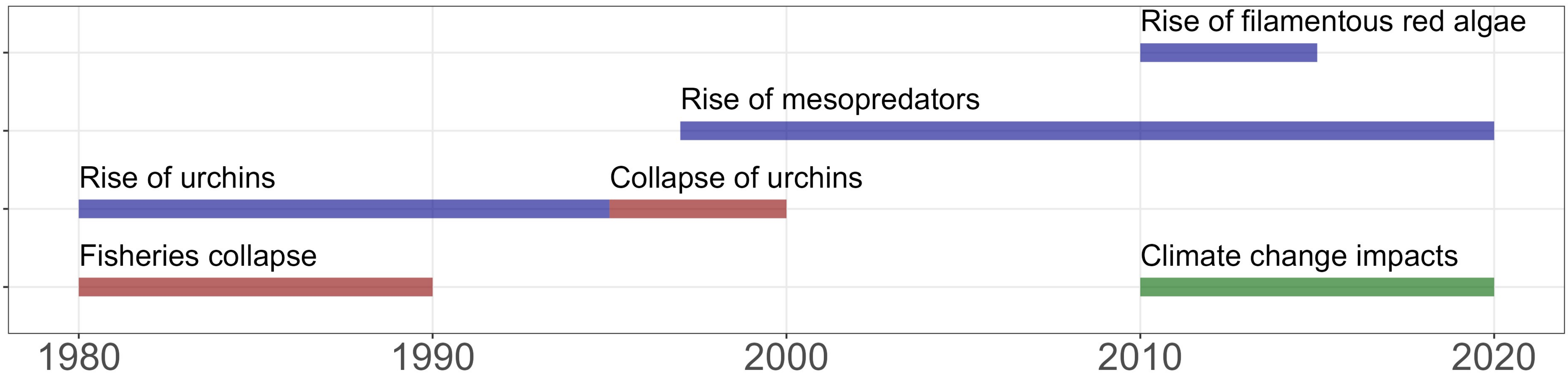
Figure 2. Illustrated hypotheses and timing of regime shifts within the Gulf of Maine. a) a hypothetical temporal trend with the corresponding first and second derivatives. b) conceptual figure of the hypothesis of where the subtidal regime shifts impact the intertidal community and the alternative hypothesis where the changes in intertidal community are the result of the direct effects of a stressor on the intertidal.

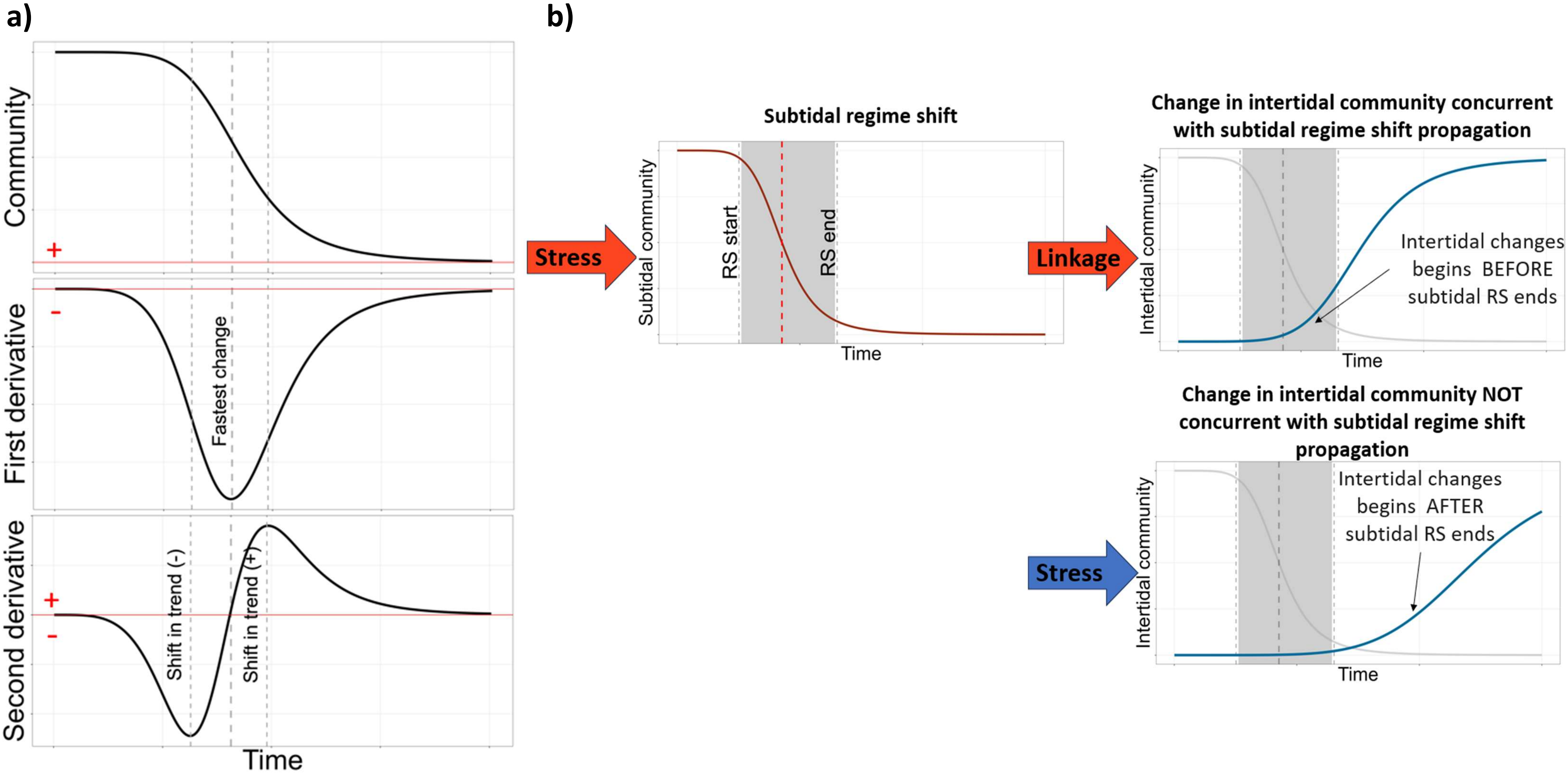
Figure 3. Changes in the subtidal predator community through time, as shown through PCoA axes. The first ordination axis is in (a), and the second ordination axis is in (b). The shaded area represents the 95% credible interval of the centered posterior predicted trends (without the intercept). The red dashed lines represent the moments when the rate of change was particularly fast (regime shifts) and the red shaded area around this line represents its 95% credible interval.

Figure 4. Island-wide changes in the intertidal mobile community through time, as shown through PCoA axes. In a) island-scale trend in PCoA axis 1, in b) island-wide trend in PCoA axis 2, and in c) island-wide trend in PCoA axis 3. The blue shaded area represents the 95% credible interval of the centered posterior predicted trends (without the intercept). The red and grey shaded areas represent the 95% CI of the subtidal regime shifts. This area is red when we detected offset synchrony and grey if we did not. The small grey lines at the bottom are times where there were significant changes in direction (second derivative different from zero). The site specific trends are in supplementary material 4.

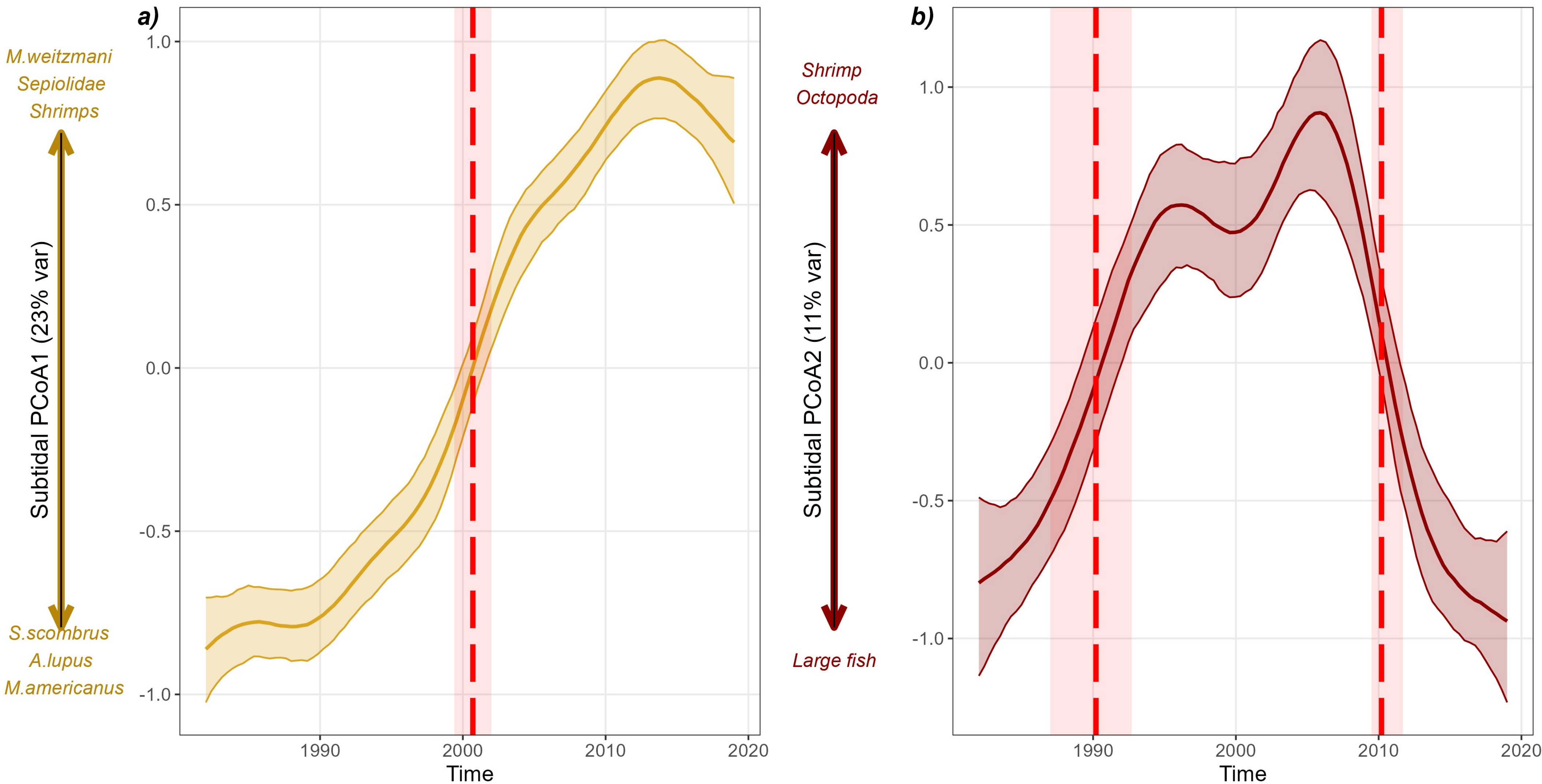
Figure 5. Heatmap of the offset synchrony of intertidal species changes in abundance for each subtidal regime shift. The sites are on the y-axis and the focal groups in the x-axis. Red represents a shift toward a higher abundance, blue represents a shift toward a lower abundance, and white represents the absence of shift. We considered a shift in direction as significant when the 95% credible interval of the second derivative differed from zero during the time period of a subtidal regime shift.

Figure 6. Island-wide changes in the intertidal sessile community through time, as shown through PCoA axes. In a) island-scale trend in PCoA axis 1, in b) island-wide trend in PCoA axis 2, and in c) island-wide trend in PCoA axis 3. The blue shaded area represents the 95% credible interval of the centered posterior predicted trends (without the intercept). The red and grey shaded areas represent the 95% CI of the subtidal regime shifts. This area is red when we detected offset synchrony and grey if we did not. The small grey lines at the bottom are times where there were significant changes in direction (second derivative different from zero). The site-specific trends are in supplementary material 4.

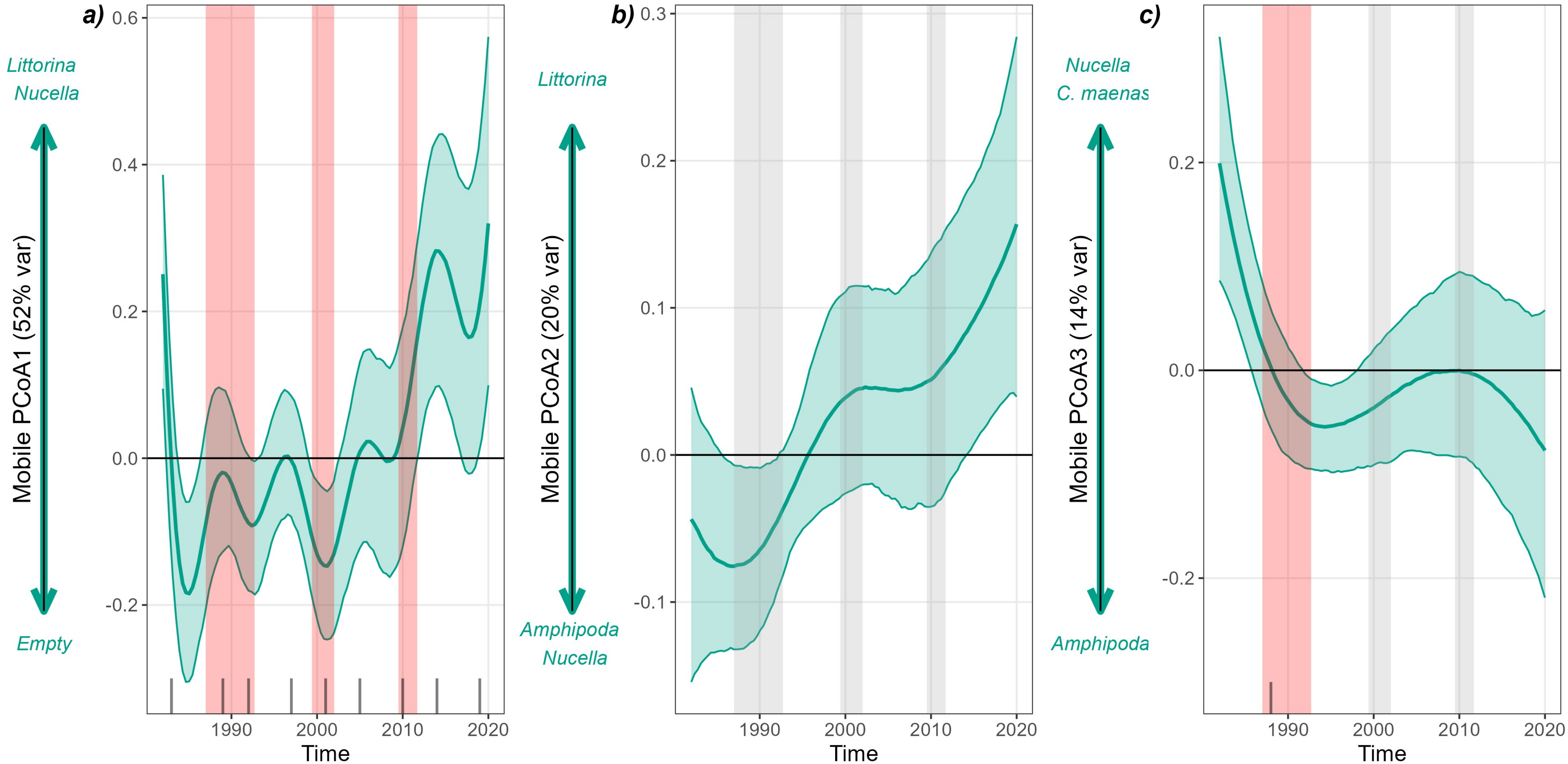

Rise of filamentous red algae
Rise of mesopredators
Rise of urchins
Collapse of urchins
Fisheries collapse
Climate change impacts
1980
1990
2000
2010
2020



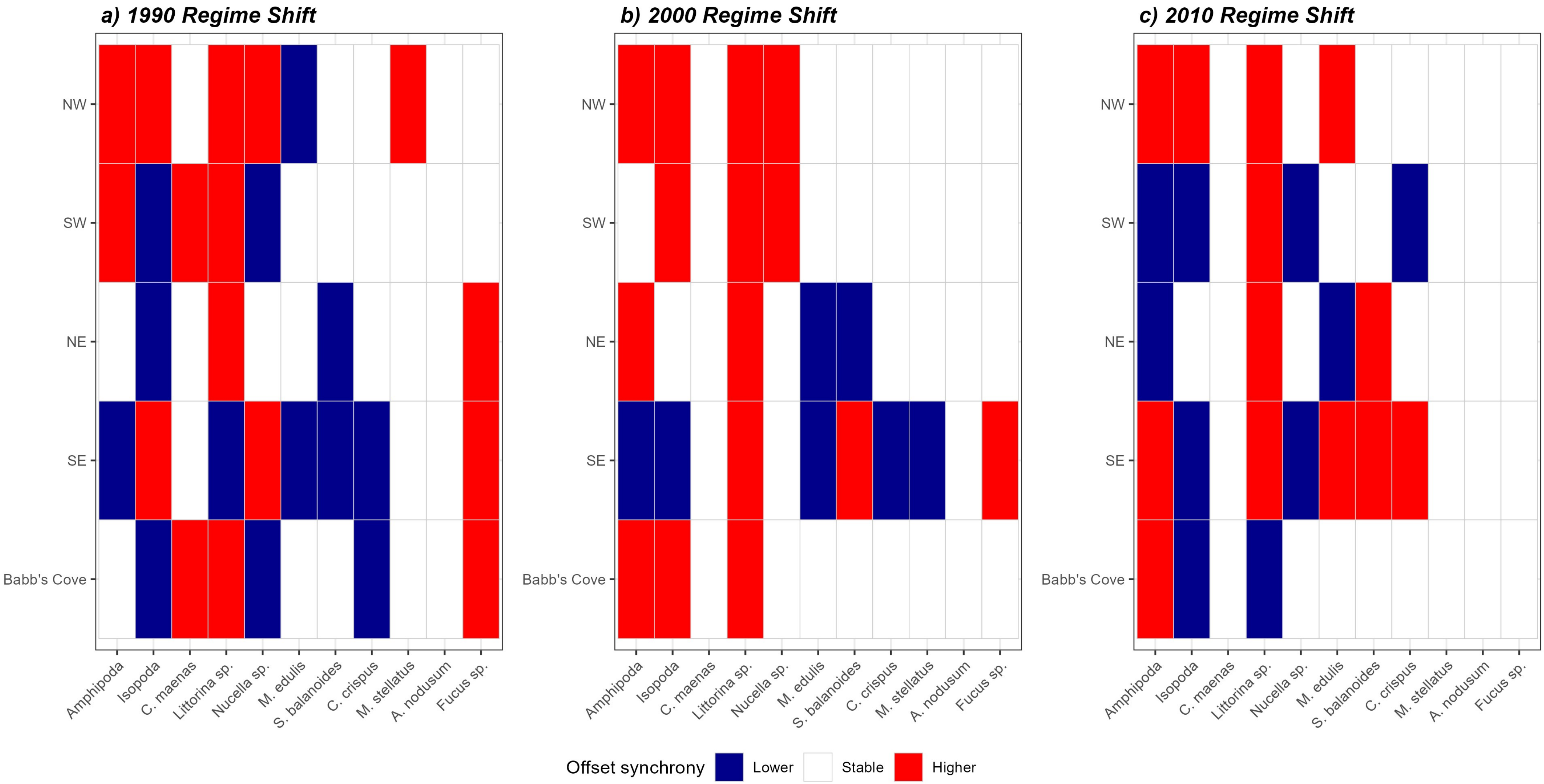
a)
b)
Community
First derivative
Second derivative
Time
+
-
Fastest change
Shift in trend (-)
Shift in trend (+)
Stress
Subtidal regime shift
Subtidal community
RS start
RS end
Time
Linkage
Change in intertidal community concurrent with subtidal regime shift propagation
Intertidal community
Intertidal changes begins BEFORE subtidal RS ends
Time
Change in intertidal community NOT concurrent with subtidal regime shift propagation
Stress
Intertidal community
Intertidal changes begins AFTER subtidal RS ends
Time



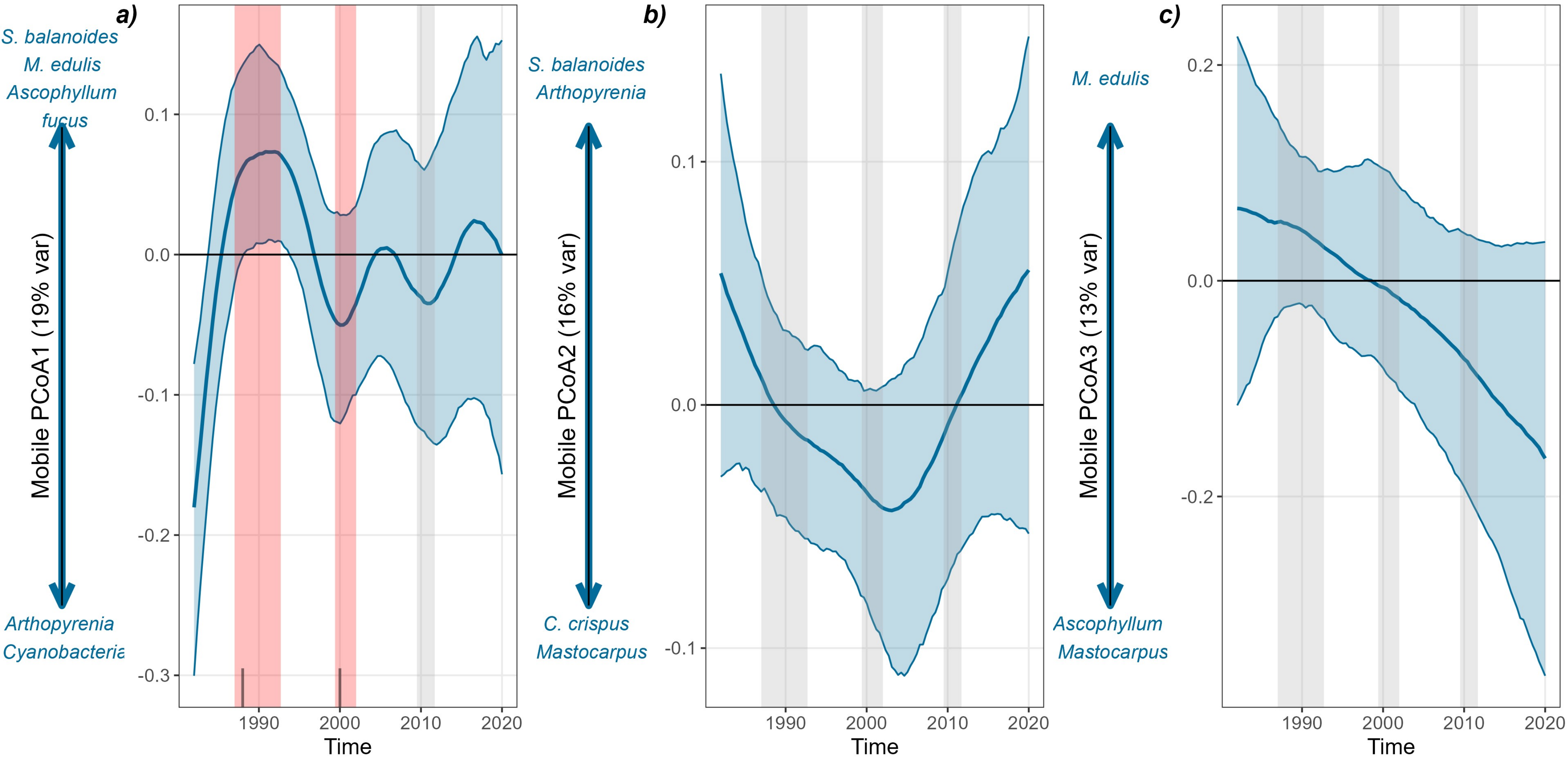
a)
M.weitzmani
Sepiolidae
Shrimps
S.scombrus
A.lupus
M.americanus
Subtidal PCoA1 (23% var)
1.0
0.5
0.0
-0.5
-1.0
1990
2000
2010
2020
Time
b)
Shrimp
Octopoda
Large fish
Subtidal PCoA2 (11% var)
1.0
0.5
0.0
-0.5
-1.0
1990
2000
2010
2020
Time



a)
Littorina
Nucella
Empty
Mobile PCoA1 (52% var)
0.6
0.4
0.2
0.0
-0.2
1990
2000
2010
2020
Time
b)
Littorina
Amphipoda
Nucella
Mobile PCoA2 (20% var)
0.3
0.2
0.1
0.0
-0.1
1990
2000
2010
2020
Time
c)
Nucella
C. maenas
Amphipoda
Mobile PCoA3 (14% var)
0.2
0.0
-0.2
1990
2000
2010
2020
Time



a) 1990 Regime Shift
b) 2000 Regime Shift
c) 2010 Regime Shift
NW
SW
NE
SE
Babb's Cove
Amphipoda
Isopoda
C. maenas
Littorina sp.
Nucella sp.
M. edulis
S. balanoides
C. crispus
M. stellatus
A. nodusum
Fucus sp.
Offset synchrony
Lower
Stable
Higher



a)
S. balanoides
M. edulis
Ascophyllum
fucus
Mobile PCoA1 (19% var)
Arthopyrenia
Cyanobacteria
0.1
0.0
-0.1
-0.2
-0.3
1990
2000
2010
2020
Time
b)
S. balanoides
Arthopyrenia
Mobile PCoA2 (16% var)
C. crispus
Mastocarpus
0.1
0.0
-0.1
1990
2000
2010
2020
Time
c)
M. edulis
Mobile PCoA3 (13% var)
Ascophyllum
Mastocarpus
0.2
0.0
-0.2
1990
2000
2010
2020
Time