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# Merging trait-based ecology and regime shift theory to anticipate community responses to warming

Running title: Merging trait and regime shift theories

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**Abstract:** Anthropogenic warming is altering species abundance, distribution, physiology, and more. How changes observed at the species level alter emergent community properties is an active and urgent area of research. Trait-based ecology and regime shift theory provide complementary ways to understand climate change impacts on communities, but these two bodies of work are only rarely integrated. Lack of integration handicaps our ability to understand community responses to warming, at a time when such understanding is critical. Therefore, we advocate for merging trait-based ecology with regime shift theory. We propose a general set of principles to guide this merger and apply these principles to research on marine communities in the rapidly warming North Atlantic. In our example, combining trait distribution and regime shift analyses at the community level yields greater insight than either alone. Looking forward, we identify a clear need for expanding quantitative approaches to collecting and merging trait-based and resilience metrics in order to advance our understanding of climate-driven community change.

**Keywords:** trait-based; regime shift; community; ecology; warming; climate; marine; North Atlantic

# Introduction

A large and growing body of research abounds with examples of anthropogenic warming-driven changes in species abundance, physiology, demography, phenology, and distribution (Poloczanska et al., 2013; Pecl et al., 2017). Warming impacts are particularly pronounced in the ocean, where species- and community-level changes outpace the global average (Blowes et al., 2019; Pinsky et al., 2019; Lenoir et al., 2020). Although most observed range shifts align with the direction of recent temperature changes (Nye et al., 2009; Pinsky et al., 2013; Poloczanska et al., 2013; Poloczanska et al., 2016; Pinsky et al., 2020), not all species are shifting at the same rates, and some are even showing so-called 'wrong-way migrations' (Pinsky et al., 2013; Fuchs et al., 2020; Thorne & Nye, 2021). Lack of synchronicity across interacting species yields new community composition and altered community dynamics (Johnson et al., 2011; Bartley et al., 2019; Pinsky et al., 2020).

Given this set of complex and concurrent changes, we need to rely on ecological theory to understand how warming has and will alter communities – tracking and predicting changes species-by-species is something of a Sisyphean quest. But, our theories are too often being developed in isolation, failing to take advantage of insights gained from alternate viewpoints. For a full picture of community responses to warming, we must pay attention to opportunities to <u>combine</u> bodies of theoretical work – especially where the strengths of one can complement the weaknesses of another. Here, we propose an analytical framework which merges two theories: (1) trait-based community ecology and (2) regime shift theory.

Trait-based ecology yields insights into community function, as well as functional responses to environmental change, that are obscured by more traditional taxonomic approaches. Rather than focusing on species, trait-based theory centers on characteristics measurable at the level of an individual organism, reflecting both genotype and phenotype. Traits of interest are often morphological (e.g., body size), behavioral (e.g., feeding strategy), physiological (e.g., thermal tolerance; Burrows et al., 2019) or life historical (e.g., income vs. capital breeding; Stearns, 1992). Traits can be classified as response or effect, depending on whether they respond to environmental factors or drive ecosystem processes (Lavorel & Garnier, 2002; Suding et al., 2008). A trait-based approach to community ecology has emerged in recent decades, largely based on observed correlations between environmental conditions and trait expression (Violle et al., 2014; Kiørboe et al., 2018). To date, most trait-based research has been descriptive; using traits to forecast future communities remains a largely aspirational goal (Green et al., 2022). Indeed, trait-based studies have grown exponentially in the last decade, in part because of their predictive potential (Sunday et al., 2015; Green et al., 2022; Palacio et al., 2022).

Progress in trait-based theory has allowed ecologists to move beyond taxonomic descriptions of communities. It has provided a means to describe the functional roles of species within an ecosystem, the correlations and trade-offs between various traits, and the evolution of community function through time (Tilman et al., 1997; Solan et al., 2004; Westoby & Wright, 2006; Allgeier et al., 2016; Dehling & Stouffer, 2018; Ward et al., 2019; Gibbs et al., 2020; Schleuning et al., 2023; Wootton et al., 2023). However, a major weakness of most trait-based analyses is that they focus on properties of a system, rather than the processes and trajectories of change. In practice, the fact that communities are governed by feedbacks, non-linearities, historical influences, and tipping points (Holling, 1973; Levin, 1999; Scheffer et al., 2001; Folke et al., 2004; Côtè & Darling, 2010; Schleuning et al., 2023) is ignored – implying smooth rather than bumpy responses to environmental change.

Regime shift theory can account for such bumps. Complex systems, including ecological communities, can abruptly shift between dramatically different stable states. For decades, ecologists have described these alternative stable states and their separation as ‘basins of attraction’. In this analogy, ecological resilience is related to the depth and width of the basin: it takes more forcing (i.e. stronger perturbation) to move a system out of a larger basin (Levin, 1999; Carpenter et al., 2001; Scheffer et al., 2001; Folke et al., 2004; Arani et al., 2021). Importantly, different forcing is often required to move the system in one direction (say, from state A to state B) than to make the reverse switch (B to A). The lack of symmetry and dependence on historical state – collectively, the temporal bumpiness – is referred to as hysteresis (Scheffer et al., 2001). A regime shift between two stable states occurs once the system passes a so-called critical transition point (Scheffer et al., 2009).

Regime shift theory has been supported by observations in ecosystems ranging from coral reefs to woodlands, lakes to deserts (Scheffer et al., 2001; Folke et al., 2004), and research looking across these diverse examples has yielded a quantitative understanding of regime shifts. Often, critical transitions are preceded by early warning signals, such as an increase in autocorrelation and variance within the system, which can serve as an early warning signals (Kubo, 1966; Scheffer et al., 2009; Dakos et al., 2012; Kéfi et al., 2014), changes in skewness and spatial patterns (Guttal & Jayaprakash, 2008; Kéfi et al., 2014), or composite signals merging multiple metrics (Drake & Griffen, 2010). Although early warning signals are most commonly calculated using abundance time series, recent studies have shown that including body size information can increase the strength and accuracy of regime shift prediction (Clements & Ozgul, 2016; Clements et al., 2017; Clements et al., 2019; Su et al., 2021). Additional work has pointed to 'exit time' – the expected lifespan of a system within a certain state – as a novel and generalizable metric of ecological resilience (Arani et al., 2021), useful for understanding the likelihood of a regime shift in response to a given set of perturbations.

Thus, in contrast with traditional trait-based approaches, regime shift theory describes and can be used to predict the dynamics of ecological change in response to stress. However, regime shift theory also falls short in isolation: it is typically applied to systems defined taxonomically rather than functionally – even when traits such as size are incorporated into early warning signal calculations (e.g., Clements & Ozgul, 2016; Clements et al., 2017; Clements et al., 2019). Given that functional traits determine ecosystem services like harvestable biomass (Brandl et al., 2022), trait-based classifications could enhance the utility of regime shift theory.

However, regime shift and trait-based community ecology theories are rarely applied in combination – limiting the descriptive and predictive power of each. Therefore, we advocate for an integrated approach that combines trait-based ecology with regime shift theory: the study of functional regime shifts. This approach will help both describe and predict community level responses to climate change. To be clear: our focus is not how community traits can be used to predict resilience or regime shifts (a unidirectional framing which can be insightful – see, for example, Su et al. (2019) and Cheng et al. (2023)), but rather how studies of trait ecology and critical transition dynamics can inform one another. We are not the first to imagine combining these two theories, but empirical work at their nexus is nascent and limited (e.g., Ma et al., 2021; Su et al., 2021; Tsimara et al., 2021). We promote an empirical approach focused on quantifying the distributions of specific traits at a community level. Further, we argue for applying quantitative measures of resilience and regime shift – such as exit time and temporal autocorrelation – to a community defined by its trait distribution. By articulating how to quantitatively fuse two bodies of literature, we aim to urge and inspire more research in this direction.

## A principled approach to merging trait-based ecology with regime shift theory

Our approach merges trait-based ecology with regime shift theory by examining biological communities according to five principles, illustrated in Figure 1:

1. Individuals express traits;
2. Trait expression responds to environmental change;
3. Trait distributions effectively describe communities;
4. Environmental conditions constrain community trait distributions;
5. Resilience dynamics influence how community traits change in response to new conditions.

Below, we will first describe each principle in the abstract, and then walk through examples from research on fish and plankton communities in the rapidly warming North Atlantic. Finally, we will discuss how this approach can be applied in other ecosystems.

## Principles

### *1: Individuals express traits*

Trait expression depends on both genotype and phenotype and fluctuates across an individual's lifetime, in response to both internal and external forcing. At any given moment, an individual's traits affect its ability to feed, grow, reproduce, and survive – collectively, they determine its fitness (Litchman et al., 2013). By definition, traits are measured at the level of the individual; with enough measurements, we can estimate population- or species-level parameters, such as maximum length or average brood size (Violle et al., 2007).

Indeed, when trait parameters are ascribed to populations or species, patterns tend to emerge. In part, this is because individual-level traits can alter population fitness: for example, individual mobility constrains the dispersal potential of a population (Tzanatos et al., 2020). Within-community analyses often find that traits are correlated or clustered, suggesting functional groupings (Benedetti et al., 2016; Tzanatos et al., 2020). Comparisons across communities reveal correlations between habitat types and trait complexes (Brind'Amour et al., 2011; Henseler et al., 2019) as well as variation along latitudinal gradients (e.g., Roman et al., 2002). These insights help develop predictions of how trait expression will respond to continued climate change.

### *2. Trait expression responds to environmental change*

Changing environmental conditions, such as rising temperatures, leads to observable changes in trait expression at the individual level, with ramifications for populations and species. In general, warming raises the metabolic demands and decreases the size of ectotherms (Atkinson, 1994; Daufresne et al., 2009; Sheridan & Bickford, 2011; Horne et al., 2015). Phenology is often controlled, at least in part, by temperature, and warming-driven changes in life histories have been widely observed (Bunker & Hirst, 2004; Pankhurst & Munday, 2011; Asch, 2015). Some environmental stressors disproportionately affect individuals with certain traits, such as the strong negative impact of ocean acidification on shell-forming organisms (Kroeker et al., 2010, Kroeker et al., 2011). Trait expression changes at the individual level in turn influence fitness and function of populations (Violle et al., 2007; Villéger et al., 2017; Tzanatos et al., 2020).

However, populations do not respond to environmental conditions in a vacuum. Altered metabolism, size, phenology, and demographics of one population impacts not only its fitness but also its interactions with other populations and thus their fitness (Hillerislambers et al., 2013; Pinsky et al., 2020). For example, phenology changes can yield timing mismatches between predators and prey (Edwards & Richardson, 2004; Staudinger et al., 2019). Ocean acidification disrupts pre-existing food webs by impacting organisms differentially (Olsen et al., 2016; Vizzini et al., 2017). Range shifts are one of the hallmarks of global change (Poloczanska et al., 2013); not all species are shifting at the same rates (Sunday et al., 2015; Thorne & Nye, 2021), yielding novel spatial overlaps and ecological interactions. Thus, the fitness of a given population under new environmental conditions is a complex result of individuals' traits, the within-population variability in trait expression, and how fit the new traits are within an altered community. The multifaceted and interdependent nature of population-level response to environmental change can make prediction difficult; often, it is useful to zoom further out and describe traits at the community level – this approach captures interspecific interactions without explicitly describing them (Visser et al., 2020).

### *3: Trait distributions can effectively describe communities*

At the community level, we can quantify trait distributions such as the size spectrum, number of generalists vs. specialists, or proportion of the individuals that are residents vs. migrators (Visser et al., 2020). In this context, numerical, rather than categorical, traits and trade-offs are especially useful. For example, size is frequently referred to as a 'master trait' (Miller et al., 1988; Brown et al., 2004; Barton et al., 2013; Andersen et al., 2016), and various size metrics can be (relatively) easily measured. At the community level, we can calculate a size spectrum: how abundance changes within a community as we move from small to large individuals. The rate at which abundance declines with size (spectrum slope) describes the efficiency of energy transfer between individuals within a community, without regard to species identity or to the details of interspecies interactions (Sheldon et al., 1972; Brown et al., 2004; Andersen & Beyer, 2006; Sprules & Barth, 2016). An observed steepening of the slope indicates a shift towards smaller organisms and/or a decline in abundance among larger individuals. Metabolic and ecological theory underpin the norms and constraints of the size spectrum slope, which has been observed to express consistent trends tied to the environmental conditions and to be sensitive to disturbance (Marquet et al., 2005; Blanchard et al., 2017). Similarly, the distribution of metabolics can quantitatively illuminate community structure and function (Brandl et al., 2022), though empirical measurements are far more limited. Development of these and other macroecological approaches to describe trait distributions of communities is needed for trait-based theory to become more useful in predictive contexts (Green et al., 2022).

### *4: Environmental conditions constrain community trait distributions*

Co-occurrence of certain environmental conditions with observed trait distributions imply that the former constrains the latter. For example, warmer waters are correlated with steeper size spectrum slopes as well as with species with opportunistic life histories (Yvon-Durocher et al., 2011; Beukhof et al., 2019; Visser et al., 2020). As illustrated in Figure 1, changes in environmental conditions support different trait distributions at both the species and community levels. If individuals within a species can only express traits that are inconsistent with those supported by warmer conditions, then it will have low fitness and the species will be highly vulnerable. However, individuals of a new species may be able to express traits which confer high fitness, allowing it to establish a novel population. Further understanding these relationships promises to aid in both description and prediction of community responses to climate change (Burrows et al. 2019, Green et al., 2022).

### *5: Resilience dynamics influence how community traits change in response to new conditions*

Given that environmental conditions constrain community trait distributions, it follows that changing environmental conditions will alter these distributions. Additionally, observed correlations between traits imply that we should expect warming to indirectly influence trait distributions without known links to temperature. However, the responses are neither immediate nor linear – instead, we must anticipate abrupt and perhaps irreversible regime shifts. For example, although we can describe a general relationship between size spectrum and temperature, we do not expect a size spectrum shift to be precisely contemporaneous nor perfectly correlated with warming, as myriad other factors relate to size (Marquet et al., 2005). Even under gradual warming, we expect community trait responses to be bumpy, rather than smooth. They will likely be characterized by hysteresis. A community's response will be largely governed by its resilience: by definition, a more resilient system will stay more constant than a less resilient one – even under the same set of environmental perturbations.

This begs the question: how do we know how resilient a system is in its current state? Some elements of resilience are conferred by trait distributions themselves. In freshwater systems, for example, macrophyte community traits such as phosphorus regulation, morphological complexity, and morphological plasticity are linked with high resilience (Su et al., 2019; Cheng et al., 2023). More broadly, we expect functional diversity conferred by the trait and trade-off distributions to increase resilience. Food webs with high omnivory and weak interactions tend to have higher resilience (Fagan, 1997; McCann, 2000). Though these broad insights are helpful, a finer-grained understanding of a specific system's resilience must be determined empirically: through measuring a system over time, and tracking its response to various levels of disturbance (Arani et al., 2021). Currently, most empirical studies on community-level disturbance response describe communities taxonomically, rather than in terms of their traits. More work is urgently needed to track and analyze the dynamics of trait distribution responses, facilitating a more holistic understanding of warming impacts on communities.

## Application to North Atlantic Zooplankton and Fish Communities

Below we take a place-based (i.e. Eulerian) approach and apply these five principles to understand warming impacts on zooplankton and fish communities in the North Atlantic. In many parts of the North Atlantic, sea surface temperature has been rapidly rising for decades, and the Northwest Atlantic has experienced extended marine heatwaves in 2012 and in many subsequent years. In some cases, heatwave conditions have spanned nearly an entire year (Mills et al., 2013; Pershing et al., 2015). Given the transition into a persistently warmer state and the high sensitivity of ectothermic zooplankton and fish to warming (Sunday et al., 2015; Pinsky et al., 2019), the North Atlantic is a fitting context from which to derive an understanding of how rising temperature alters communities – lessons which can be applied elsewhere.

As in many similarly well-monitored and studied marine ecosystems, zooplankton and fish data are collected using gear that target specifically sized individuals. In the examples discussed below, zooplankton data are derived from bimonthly 333µ mesh net sampling (Ejsymont & Sherman, 2010; Perretti et al., 2017), while fish abundance and distribution are obtained from fisheries-independent bottom trawl surveys (Nye et al. 2009; Henderson et al., 2017). As a result, the delineation of community is based on co-occurrence as well as on size. Trait-based analyses to date have also centered on size. Marine systems serve as a prime example of how to use size in a quantitative trait-based approach as marine food webs are strongly size-structured, and this trait has been studied extensively in the ocean (Sheldon et al., 1972; Litchman et al., 2013; Andersen et al., 2016). With these broad data and analytical tools, we can apply the steps above to the zooplankton and fish communities before and during recent warm decades.

Following Principles 1 and 2, we observe certain traits expressed by individuals prior to contemporary warming, as well as changes in trait expression in recent years. Historically and especially during cold regimes, the copepod *Calanus finmarchicus* dominated North Atlantic zooplankton communities, with typifying traits of individuals including large size, high lipid storage, and dormancy (Reid et al., 2003; Pershing et al., 2021). Within fish communities, Atlantic cod (*Gadus morhua*) were highly successful prior to warming (Rosenberg et al. 2005). Cod are relatively long-lived, slow-growing large top predators. In the contemporary time period, cod are much smaller and exert less trophic control in the system (Shackell et al., 2009; Pershing et al., 2015; Han et al., 2021), and there has been a switch from large copepods like *Calanus finmarchicus* to smaller zooplankton individuals

(Pershing et al., 2005; Mountain & Kane, 2010; Greene et al., 2013; Perretti et al., 2017; Meyer-Gutbrod et al., 2021).

Principles 3 and 4 invite us to describe community trait distributions and how these distributions relate to environmental conditions. Applying principle 3, we calculated size spectra of fish communities in four ecoregions of the Northwest Atlantic, using data from the Northwest Fisheries Science Center. Looking at the 1970-2000 period, prior to contemporary warming, we found the northernmost region (Gulf of Maine) had the shallowest size spectrum slope, and that slopes steepened with decreasing latitude – evidence that the distribution of size with the fish community follows the constraints of temperature (Table 1). For zooplankton, previous work has grouped copepods into general large and small size categories and used their relationship to describe the community (Link et al., 2006; Perretti et al., 2017). Prior to 2000, the estimated large:small copepod biomass ratio in the Gulf of Maine was more than twice that of its southern neighbors (Link et al., 2006), aligning with global observations that copepod community size metrics increase with latitude (Brandão et al., 2021; Ratnarajah et al., 2023).

As waters warm and heatwaves become more frequent, changes to community traits are both predicted and observed. Broadly, we expect a trait distribution within an ecosystem to become more analogous to that previously ascribed to its poleward neighbor, as has been shown empirically for fish and macroinvertebrate communities in the North Atlantic (Lucey & Nye, 2010; McLean et al., 2019). One simple prediction is that the Northwest Atlantic's recent warming should result in smaller body size within the fish community, and this indeed has been observed (Shackell et al., 2009; Friedland et al., 2023). Similarly, we would expect the zooplankton community to become smaller – more dominated by small zooplankton – like its southern counterparts. This too is observed as warming accelerated in recent years (Perretti et al., 2017; Figure 2).

Importantly, these trait changes emerge from *both* direct physiological effects of temperature and more indirect consequences of changing species interactions. In the fish community, for example, Friedland et al. (2023) ascribe decreased size to the greater taxonomic diversity, and thereby increased interspecific competition, in the warming Northwest Atlantic. Likewise, climate-induced size reductions among western Scotian Shelf fish has been linked to a trophic cascade, altering both the size and feeding traits of zooplankton (Shackell et al., 2009).

Principle 5 reminds us that trait changes are often neither instantaneous nor linear – that we should expect lags as well as abrupt shifts in ecological systems, depending on their resilience. Changes in plant (Bertrand et al., 2011; Alexander et al., 2018) and animal (Menéndez et al., 2006; Devictor et al., 2016) communities more often than not lag warming trends. In the North Atlantic, the community temperature index – an index of the temperature affinity of the community – has lagged increases in bottom temperature (Flanagan et al., 2018). Longer summers induced poleward shifts and biomass changes only when lags of 2-3 years were considered (Henderson et al., 2017). When looking taxonomically at the fish communities, we find that the 2012 heatwave did *not* meaningfully impact community composition, even on a 5 year lag (Fenwick et al., in review). This is evidence of resilience within the community. In our fish size spectrum analyses, we observe the persistence of a steeper slope (~ -0.95) in the Gulf of Maine during the recent period of elevated temperatures, similar to results shown in Friedland et al. (2023). For copepods in the Gulf of Maine, size metrics are not well correlated with temperature; rather, two regime shifts between a large- and a small-copepod dominated regime have been identified since 1980 (Perretti et al., 2017; Figure 2).

Critically, our understanding of warming impacts on the Gulf of Maine fish and zooplankton communities is richest when we apply *both* regime shift theory and a trait-based approach to the data. If we use regime shift theory without a trait-based lens, we miss the functional shift to smaller fish size that began around the year 2000 (Friedland et al., 2023). If we incorporate trait-based theory on its own, it is difficult to understand why the size spectrum does not continue to change as the system warms – an observation easily explained by hysteresis. Further time series analysis will determine whether the size spectrum shift was preceded by an increase in autocorrelation and/or variance, which, had it been detected, might have served as an early warning signal. Looking forward, monitoring such signals in the trait-based features of the community, such as the size spectrum, can alert us to potential impending functional regime shifts.

These examples are meant to be illustrative; they are by no means exhaustive or complete. More work is needed to develop a full trait-based description of zooplankton and fish communities at multiple scales, and to analyze resilience dynamics of these functional communities. Additionally, in the discussion above we have ignored social-ecological connections and the important role of fishing in this region. Tsimara et al. (2021) provide a useful example of how commercial fisheries can be considered its own system, with identifiable traits and resilience dynamics – adding this component would no doubt enhance our understanding. Our example analyses also ignore food web traits, and how these influence resilience, which we are working to understand using trophic models. Our aim here is to advocate for and catalyze future work at the intersection of trait-based and regime shift theories.

## Concluding remarks

What is needed to apply the combination of trait-based and regime shift approaches more widely? First, we recommend researchers take a Eulerian view. Such a view can integrate community dynamics and related time lags, and is also able to inform place-based management. Once a region of interest is demarcated, the next step is to define the most salient environmental conditions – past, present, and future. Above, we have focused on temperature, which is not necessarily the most important factor in all systems, and on size, which is by no means the only quantifiable trait.

In order for this approach to succeed, we must measure traits and trade-offs in observational studies and estimate community trait properties. Trait databases have been proliferating and sometimes diverging (eg., Frimpong & Angermeier, 2009; Madin et al., 2016; Brun et al., 2017); rather than develop new databases, often the greater need is data alignment. The literature of trait-based work on plants provides a good model for such cohesion (Green et al., 2022). Another challenge is that many traits are categorical, rather than ordinal or numeric – and the distributions associated with categorical traits have few parameters of interest. So, we argue that future work should focus on quantifying numeric traits including size and metabolism (Brandl et al., 2022). Further, we encourage trait-based approaches that are independent of species identities in order to facilitate describing the distribution of traits of the community as a whole. Traits can vary within species in ways that are likely important to ecosystem properties, including its resilience. Such quantitative approaches will allow us to move beyond description and towards prediction.

Third, when developing and testing hypotheses about future community traits, we need to recognize that functional communities are resilient. We cannot expect responses to environmental change to be smooth – but by applying a regime shift lens to time series of trait-based data, we can start to observe and heed early warning signs of functional regime shifts. Only then can we hope to maintain critical ecosystem services in the face of persistent climate change.

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**Data availability** – All data used in this opinion piece are publicly available at https://www.fisheries.noaa.gov/inport/item/22560 and https://www.ncei.noaa.gov/access/metadata/landing-page/bin/iso?id=gov.noaa.nodc:0187513

# Tables & Figures

*Table 1.* Abundance size spectrum slopes of fish communities in four adjacent regions of the Northwest Atlantic, in the period prior to contemporary warming (1970-2000). Spectra are calculated based on biomass and abundance data from the Northeast Fisheries Science Center's annual bottom trawl surveys. Note that the slope is steeper (more negative) in lower latitude regions. SD = standard deviation.

| **Region (high to low latitude)** | **Slope mean (SD) 1970-2000** |
|---|---:|
| Gulf of Maine | -0.895 (0.063) |
| Georges Bank | -0.926 (0.064) |
| Southern New England | -1.030 (0.046) |
| Mid-Atlantic Bight | -1.070 (0.050) |

*Figure 1*. Conceptual figure of the 5 principles for merging trait-based ecology and regime shift theory, and how the principles relate to one another. Here, size is an example trait, the community size spectrum slope is a trait distribution parameter, and temperature is a changing environmental variable (see text for further discussion). Principle 1 describes individuals in terms of traits (here, by measuring size); Principle 3 applies that lens to the community. Principles 2 and 4 state that both individual and community traits respond to environmental change - we expect smaller sizes-at age and a steeper size spectrum slope under warming. Principle 5 describes the dynamics of a communities shift between a shallower and a steeper size spectrum, with 4 possible pathways: 1) linear response (gray solid); 2) non-linear response (base case; black dashed); 3) non-linear response of a more resilient system (green dashed); 4) non-linear response of a less resilient system (purple dashed). Note that the environment (here, temperature) is constraining though not determining the size spectrum values in both cold and warm conditions.

*Figure 2*. The annual copepod size index (small copepod abundance anomaly minus the large copepod anomaly) in the Gulf of Maine, based on long-term, bimonthly plankton sampling conducted by the Northeast Fisheries Science Center (after Perretti et al., 2017). Vertical lines indicate different size structure regimes.

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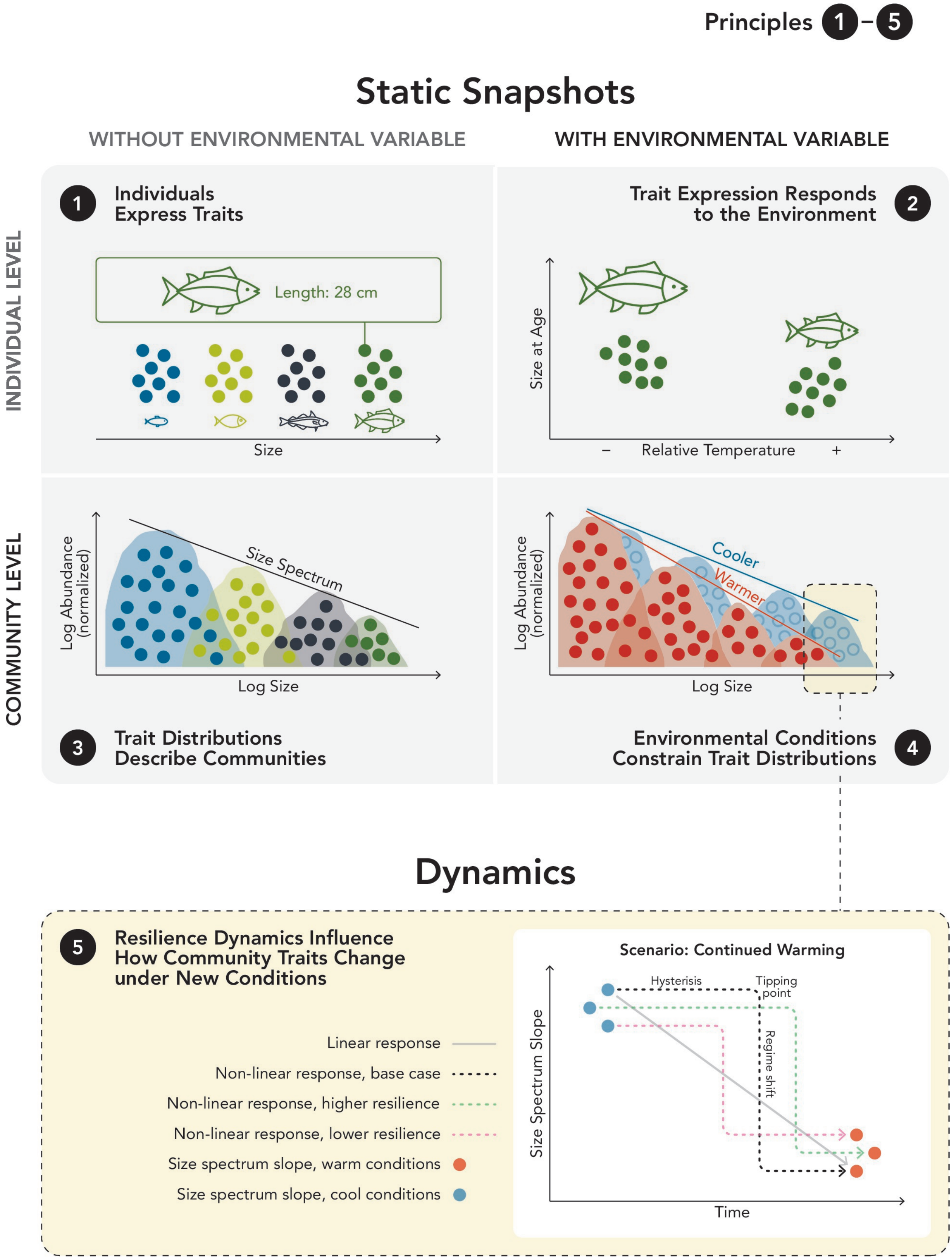

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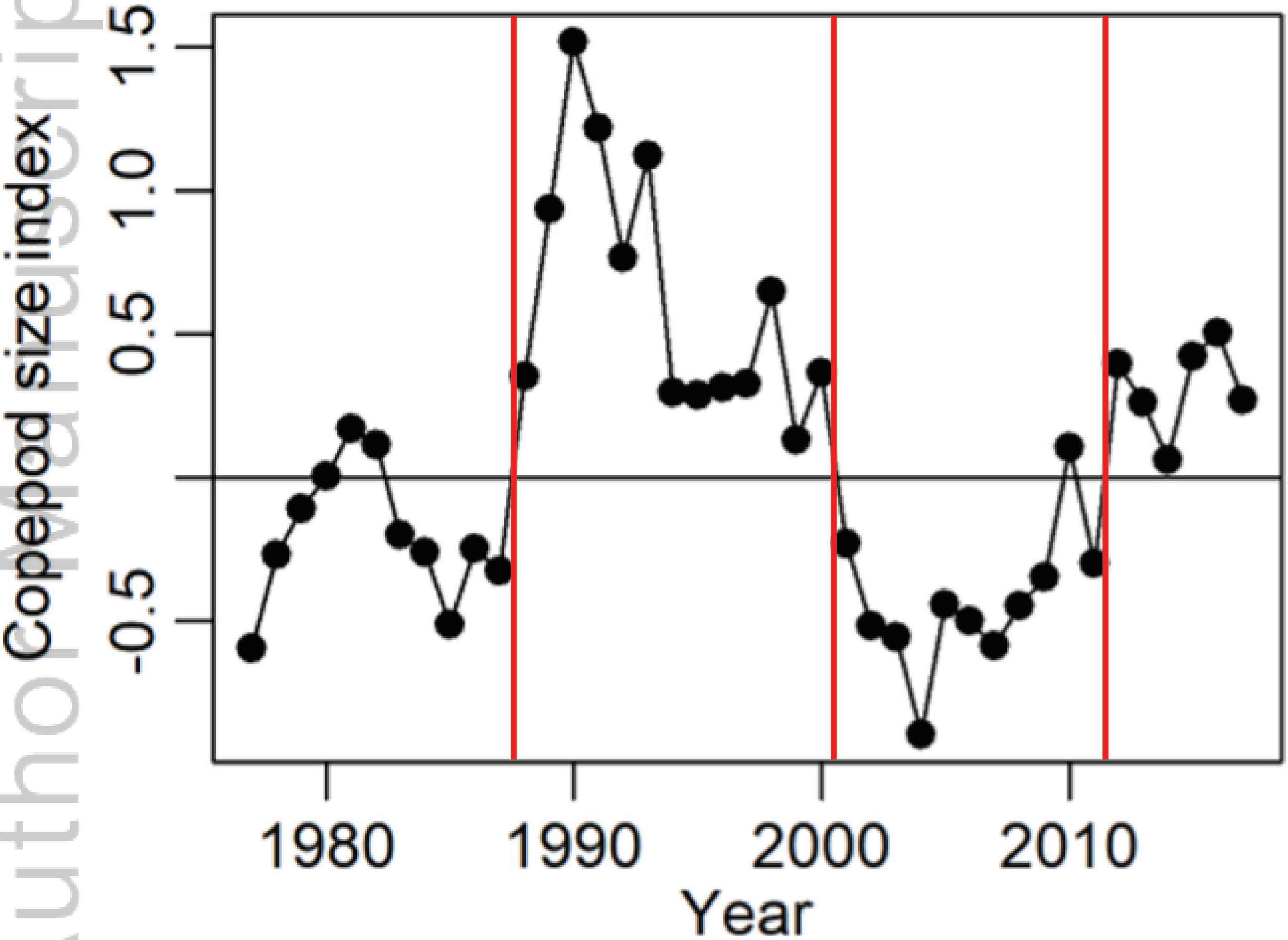

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