

Marine Metazoan Modern Mass Extinction: Improving Predictions by Integrating Fossil, Modern, and Physiological Data

Piero Calosi,¹ Hollie M. Putnam,² Richard J. Twitchett,³ and Fanny Vermandele¹

¹Département de Biologie, Chimie et Géographie, Université du Québec à Rimouski, Rimouski, Quebec G5L 3A1, Canada; email: piero_calosi@uqar.ca, fanny.vermandele@uqar.ca

²Department of Biological Sciences, University of Rhode Island, Kingston, Rhode Island 02881, USA; email: hputnam@uri.edu

³Department of Earth Sciences, Natural History Museum, London SW7 5BD, United Kingdom; email: r.twitchett@nhm.ac.uk

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Abstract

Evolution, extinction, and dispersion are fundamental processes affecting marine biodiversity. Until recently, studies of extant marine systems focused mainly on evolution and dispersion, with extinction receiving less attention. Past extinction events have, however, shaped the evolutionary history of marine ecosystems, with ecological and evolutionary legacies still evident in modern seas. Current anthropogenic global changes increase extinction risk and pose a significant threat to marine ecosystems, which are critical for human use and sustenance. The evaluation of these threats and the likely responses of marine ecosystems requires a better understanding of evolutionary processes that affect marine ecosystems under global change. Here, we discuss how knowledge of (a) changes in biodiversity of ancient marine ecosystems to past extinctions events, (b) the patterns of sensitivity and biodiversity loss in modern marine

taxa, and (c) the physiological mechanisms underpinning species' sensitivity to global change can be exploited and integrated to advance our critical thinking in this area.

1. INTRODUCTION

There are three fundamental processes in biogeography: evolution, extinction, and dispersal. These are the means by which biotas respond to spatial and temporal dynamics of the geographic template. Thus, all the biogeographic patterns that we study derive from the effects of these processes.

—Lomolino et al. (2010, p. 167)

This review focuses on past and present extinctions and, more specifically, on the identification of macroevolutionary patterns that characterize past extinction events as well as macro- and microevolutionary patterns that are underpinned by modern species' sensitivity to global changes. It also discusses ways of identifying the putative physiological limits that underlie current and future losses of marine biodiversity.

1.1. On the Fragility of Life on Our Planet

Over the past 500 million years, multicellular life on Earth has experienced five major mass extinction episodes, where global losses of families and genera were significantly above background levels, as well as a number of other events with above-average extinctions of marine organisms (Benton 1995, Bambach 2006, Harnik et al. 2012). After each extinction interval, life evolved to pre-extinction levels of diversity and complexity, a process that took millions of years after the most severe events (Erwin 2001). Though rare, times of rapid and intense environmental change appear to have always represented a tremendous challenge for species' survival, as well as for the persistence of biotic communities and the functioning of entire ecosystems (Blois et al. 2013). These major crises in Earth's history represent fundamental turning points for the trajectory of life on our planet, when extinction selectivity differed from background levels, and left indelible signatures on subsequent evolution (Erwin 2001, Jablonski 2001).

While relatively rare, past extinction events have shaped the evolutionary landscape on our planet (Jablonski 2001). They dictated which taxa, morphs, or phenotypes were negatively selected against and which were retained for evolutionary and ecological processes to act upon during the recolonization (sensu Hutchinson 1978). However, recolonization and diversification

rely not only on the surviving species composition but also on the functional diversity remaining after these extinctions, as this diversity can influence the numbers of new taxa and lifestyles that subsequently emerge (Foster & Twitchett 2014). Extinctions have ecological and evolutionary legacies, defining and constraining the trajectory evolution can take, by influencing how the processes of post-extinction radiation will proceed (Erwin 2001).

While multicellular life has shown the ability to persist through extreme environmental events, it has also displayed a low level of resilience—the time required for an ecosystem to return to an equilibrium or steady state following a perturbation (sensu Holling 1973). This is a direct consequence of the fact that radiation and diversification of species leading to the reoccupation of ecological niches is a slow process, with speciation taking on average 2 million years to occur (Lamichhane et al. 2017; cf. Wood & Erwin 2018).

1.2. The Anthropocene

Rapid and intense environmental change and biodiversity loss are currently being caused, for the first time in Earth's history, by a single species (humans) instead of by catastrophic extraterrestrial or terrestrial events, and thus this era has been termed the Anthropocene (Waters et al. 2016). The current rate of global-scale environmental change is among the most rapid in Earth's history (Zeebe et al. 2016), matched only by instantaneous catastrophes such as bolide impacts. It is the direct (and indirect) consequence of our species' ingenuity and activity in transforming and utilizing the environment around us, and its available resources: particularly since the discovery of fossil fuels. This includes changes to the hydrological systems of most major rivers (Habersack et al. 2014), global use of fertilizers and pesticides (Waters et al. 2016), fisheries (Payne et al. 2016), and habitat utilization and destruction (Fahrig 2017). It is undeniable that humanity dominates Earth's ecosystems, for example, through industrial, geological, agriculture, and forestry activities that are driving an increase in atmospheric carbon dioxide, fixing more nitrogen than all natural terrestrial sources combined, and utilizing half of all accessible surface fresh water (Vitousek et al. 1997). As a consequence, humanity now represents "the world's greatest evolutionary force" (Palumbi 2001).

The anthropogenic nature of current environmental change, together with its unprecedented rapidity and intensity, defines new environmental and climatic landscapes and thus a new selective horizon (see Palumbi 2001, Dam 2013, Calosi et al. 2016), with potentially significant

consequences for biodiversity (Ceballos & Ehrlich 2018). In particular, the rapidity and intensity of ongoing environmental changes represent a challenge for the persistence of populations and species that will not be able to track climate (Chen et al. 2011), due to limitations in their physical dispersal ability and/or the presence of local adaptation (Gaston et al. 2009, Dam 2013, Lardies et al. 2014, Calosi et al. 2017). On the other hand, even for the species that are able to track climate, specific habitat and niche requirements (Brown 1995, Gaston 2003, Angilletta 2009) may not be met due to habitat loss and degradation caused by human resource utilization, or simply the lack of natural habitat poleward, thus representing a major threat to their persistence. More generally, species loss, locally and globally, can occur as the consequence of both direct and indirect impacts, such as the direct negative impact of climatic changes on species' physiology, phenology, development, and fitness (e.g., Pörtner & Knust 2007, Koeller et al. 2009) and the indirect negative impacts linked to, for example, the degradation of trophic networks (Dossena et al. 2012). To date, most documented evidence has been for direct impacts (Scheffers et al. 2016), while evidence for indirect impacts of global change is more difficult to come by (Smithers & Blicharska 2016).

The current ongoing mass extinction event (sensu Barnosky et al. 2011) is an anomaly when compared with past mass and major extinction events (Dirzo et al. 2014, Ceballos et al. 2015, Ceballos & Ehrlich 2018). This may represent a major disadvantage when trying to use the understanding we have acquired from past extinction events to shed light on the possible mechanisms and trends of the ongoing biodiversity loss. This forecasting challenge will be more acute the more the selective horizon generated by human activities differs from that experienced by the Earth biotas during past extinction events, as could be the case with the selectivity of fishing activities (Payne et al. 2016). Here, we discuss the utility of the paradigm that lessons from the past represent sufficiently good tools to predict the ongoing mass extinctions in marine systems, which are particularly sensitive to human impacts (Lotze et al. 2006). We further posit that a fundamental shift in our way of thinking about extinctions is required to understand the current biodiversity crisis, and that this can be accomplished by comparing paleo patterns with modern patterns of biodiversity losses for which physiological mechanisms and limitations are known (Figure 1).

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Figure 1 Conceptualization of the objectives used to produce a working framework for the

integration of fossil ecological data, modern ecological data, and modern physiological mechanisms. This framework can be used to further our understanding of the processes and consequences of extinction under climate and global change, as well as the identification of existing and new questions and hypotheses about extinction to be tested within and across these fields. Symbols originate from the Integration and Application Network, University of Maryland Center for Environmental Science (<http://ian.umces.edu/symbols>)

1.3. The Challenge of Improving Our Ability to Predict Future Biodiversity Losses

Marine systems represent critical ecosystems for human use and sustenance (e.g., food security), as well as being key indicators of species' sensitivity to global change (e.g., coral reefs and temperature-induced mass bleaching). Certainly, some general trends of marine species' responses to global change have already started emerging and may contribute to the understanding of the ongoing sixth mass extinction. For instance, patterns such as the sensitivity of tropical and polar specialists to global warming (Cheung et al. 2012, 2013), a reduction in the breadth of the geographic range and abundance of endemic species (Parmesan 2006), and a reduction in body size due to human exploitation and global warming (Payne & Finnegan 2007, Daufresne et al. 2009, Cheung et al. 2013) have been documented. Nonetheless, in order to conserve and manage, to the best of our capacity, the extant level of taxonomic and functional biodiversity in the marine environment (Solan et al. 2004), we require a broader framework to understand the processes and implications of mass extinctions in a time of climate change with no analog. Such a framework would enable greater predictive ability to elucidate the putative sequence of species and functional group loss and extinction within marine ecosystems, as a consequence of the cumulative effect of direct and indirect impacts of ongoing global change. In order to facilitate the advancement of our critical thinking with respect to evolutionary processes in oceans in the Anthropocene, this review aims to do the following:

1. Describe the fossil record of past marine extinctions during periods of environmental change when loss in biodiversity was the greatest. More precisely, we aim to highlight what lessons can be drawn from the past and how these can be relevant for biologists looking at the species' sensitivity under global change and extinction in modern biological systems.
2. Characterize our knowledge of modern patterns of sensitivity in marine species. For instance, we describe differences in functional groups or physiotypes with respect to their sensitivity to global change, including whether they are small or large, rare or common in

their climatic and geographic distributions, and calcifiers or noncalcifiers.

3. Distinguish the putative physiological limitations underpinning species' sensitivity patterns to the global change. More specifically, we propose approaches to identify mechanisms to be investigated at the cellular to organismal levels that limit the capacity of different marine species assemblages or functional groups to resist modern global change.
4. Discuss the need to integrate across paleontological, ecological, and physiological-molecular knowledge to generate a more in-depth synthesis and greater predictive ability. More specifically, we postulate that by linking our current understanding of (a) patterns of (mass) extinction under past climate change events to (b) patterns of sensitivity of modern species to the ongoing global change and (c) the physiological-molecular mechanisms underpinning such sensitivity (**Figure 1**), we will have an enhanced predictive ability regarding the uncertain fate of biodiversity under global change, and acquire a greater capacity to generate testable hypotheses about the mechanistic underpinnings that explain the ongoing sixth mass extinction. Finally, we outline several focal questions and challenges that need to be urgently addressed in order to rapidly improve our understanding of the modern climate-change-driven marine mass extinction.

2. PAST MASS EXTINCTIONS AND EMERGING BIODIVERSITY LOSS PATTERNS

The fossil record contains a time series of natural experiments on the effects of major climate and environmental changes on life on Earth (**Jablonski 2004**). Biological and chemical proxies provide key environmental data, such as atmospheric CO₂ (e.g., **McElwain et al. 1999**) and temperature (e.g., **Joachimski et al. 2012**), that, when combined with quantitative species-abundance data from the same samples, enable the responses of marine ecosystems to be assessed (**Danise et al. 2015**) at spatial and temporal scales that are beyond those of modern experiments. Understanding the past becomes especially important as atmospheric CO₂ continues to rise beyond 400 ppm, a level last recorded more than 2 million years ago, during the Pliocene. Most of the major extinction events that affected life on Earth during the Phanerozoic (the past 540 million years) are associated with evidence of global warming (**Harnik et al. 2012**). One potential drawback of using past events as analogs of the present day, or as a means of

generating predictions of future change, is that the rates and magnitudes of change, as well as the starting conditions (e.g., initial CO₂ levels, species present, global sea level, distribution of the continents, and even the nature of the carbon cycle), all differed from those of the present. Biological limitations could be highlighted, however, through the identification of coherent trends in records of multiple past events caused by a comparable environmental change (e.g., multiple past global warming events) even though those periods differed in their baseline conditions.

The key biogeochemical parameters of rising temperature, declining oxygen concentration, changing productivity, and lower pH that are a concern for the immediate future (e.g., [IPCC 2014](#)) have been documented during these past events ([Joachimski et al. 2012](#)). In addition, elevated temperature and atmospheric CO₂ results in elevated weathering rates, which would have increased turbidity and sedimentation rates in shelf seas ([Algeo & Twitchett 2010](#)). The associated nutrient flux stimulates productivity and eutrophication, leading to local hypoxic conditions ([Algeo et al. 2011](#)). Evidence is emerging that shelf seas may also have become salinity stratified, with reduced surface salinity affecting marine plankton ([van Soelen et al. 2018](#)).

2.1. Benthic Community Dynamics During Past Events

Numerous studies have demonstrated the importance of hypoxia and anoxia in the collapse and recovery of benthic marine ecosystems during past climate-driven crises (e.g., [Twitchett et al. 2004](#), [Danise et al. 2015](#)), which strongly supports current concerns (e.g., [Diaz & Rosenberg 2008](#)). Expanding dead zones are a key feature of all past warming events, and patterns of ecological change are very similar to those of modern ecosystems, despite differences in species composition and temporal and spatial scales (e.g., [Danise et al. 2013](#)). The fossil record demonstrates that during peak global warming events, benthic marine dead-zone ecosystems comprised low-diversity, low-evenness communities of small animals ([Figure 2](#)). These zones were frequently affected by anoxic events and only colonized during intervals of sufficient oxygenation (e.g., [Danise et al. 2013](#), [Pugh et al. 2015](#)). Epifaunal, surficial, suspension-feeding bivalves were the most common shelled invertebrates, and benthic organisms appear to have occupied only a very narrow zone just above and below the sediment–water interface ([Figure 2](#)). Bioturbation was very limited in depth and extent, with the trace fossil record demonstrating that infaunal communities were typically dominated by shallow-dwelling polychaetes, with only rare

small crustaceans (Twitchett & Barras 2004), implying a significant reduction in nutrient cycling and productivity (Solan et al. 2004). Recent analysis of the Early Jurassic record suggests that coupling between benthic and pelagic ecosystems may have been weaker during peak global warming (Danise et al. 2015).

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Figure 2 Benthic biodiversity in a shallow shelf sea through the Triassic–Jurassic mass extinction event and recovery. (a) Low-diversity, low-complexity ecosystems of small benthos during peak global warming. (b) High-diversity, high-complexity ecosystems following the post-extinction recovery and a return to normal atmospheric CO₂. These reconstructions are based on quantitative species-abundance data of shelled benthos (Pugh et al. 2015) and size, depth, and diversity data of burrowing infauna (Twitchett & Barras 2004, Barras & Twitchett 2007) from the Blue Lias Formation, southwest of Lyme Regis, Dorset, United Kingdom, in the Pre-*planorbis* Zone (panel a) and *Schlotheimia angulata* Zone (panel b).

Marine ecosystem recovery has been studied in detail for most of the major warming-related events at both local and global scales (e.g., Danise et al. 2013, Foster & Twitchett 2014, Pugh et al. 2015, Dunhill et al. 2018). Even during peak warming, diverse marine ecosystems living under better-oxygenated conditions have been recorded at some sites (e.g., Twitchett et al. 2004). It has been suggested that higher-latitude, shallow marine settings within the wave base may have acted as refugia due to their persistent oxygenation, at least during the Permian–Triassic event (Beatty et al. 2008). The duration of the recovery interval is governed by the rate and magnitude of CO₂ injection to the atmosphere, which are controlled by volcanic activity; the duration it takes natural processes (i.e., the weathering of silicate rocks and burial of organic matter) to remove excess CO₂ from the atmosphere; and the severity of the extinctions and the rate of evolutionary processes. Thus, global marine ecosystem recovery generally takes a few million years (Erwin 2001) but can vary with latitude, region, and habitat, with tropical reefs typically suffering the greatest extinctions and taking the longest to recover (Foster & Twitchett 2014, Dunhill et al. 2018).

2.2. Body Size Changes and Past Global Warming

One key prediction that can be tested from the fossil record is that global warming will lead to size reduction in marine organisms (see **Figure 3**). Body size is a key trait conserved during the fossilization process, enabling size data to be directly extracted from fossil remains. Size can even be estimated from partial remains, such as teeth (e.g., Chen et al. 2013), and tracks, trails

and burrows left behind by organisms that otherwise may not be preserved (e.g., Twitchett & Barras 2004, Barras & Twitchett 2007).

<COMP: PLEASE INSERT FIGURE 3 HERE>

Figure 3 Schematic representation of processes leading to body mass reduction in aquatic species during a period of global warming. Figure adapted from Sheridan & Bickford (2011), incorporating data from Algeo et al. (2011).

Numerous studies have demonstrated that marine organisms are smaller in the immediate aftermath of past mass extinction events (e.g., Twitchett 2007). In some cases, this is due to the selective loss of larger-bodied species, such as the reduction in plankton size at the end of the Cretaceous, but temporary size reduction is also widely recorded in taxa and lineages that survived an extinction event, a phenomenon termed the Lilliput effect (Urbanek 1993, Twitchett 2007). The Lilliput effect is most pronounced during past warming events, with size minima occurring during peak warming in the immediate aftermath of the main extinction event. Examples include end-Cretaceous sharks (Belben et al. 2017); Permian–Triassic brachiopods and gastropods (Metcalf et al. 2011, He et al. 2014); conodonts (Chen et al. 2013); infaunal polychaetes and crustaceans (Twitchett 2007); and Early Jurassic cephalopods (Morten & Twitchett 2009), infaunal polychaetes, and crustaceans (Twitchett & Barras 2004, Barras & Twitchett 2007). Similar results have also been observed in mesocosm experiments (e.g., Hale et al. 2011, Christen et al. 2013) and in situ in CO₂ vents (Kroeker et al. 2011). Thus, regardless of starting conditions or the rates or magnitudes of environmental change, body size reduction in marine organisms emerges as a consistent response to past global warming, strongly supporting the prediction that it will occur with continued current warming, as already appears to be the case for some taxa (see Section 3).

2.3. Selectivity of Extinction

Past episodes of global warming did not affect all taxa equally, and marine extinctions are always selective. The two most severe such events of the past 300 million years, the Permian–Triassic and Triassic–Jurassic events (Harnik et al. 2012), were selective against epifaunal, non-motile filter feeders and tropical reef ecosystems (Foster & Twitchett 2014, Dunhill et al. 2018). During both events, the loss of functional diversity was greatest in the tropics, but diversity was maintained and even increased in the mid-latitudes during peak warming (Foster & Twitchett

2014, Dunhill et al. 2018). Even the most severe warming events of the past have not managed to cause the global loss of key functional groups, and tropical ecosystems have always recovered, albeit slowly. It has been suggested that animals with heavily calcified skeletons may be more vulnerable to warming-related extinction than lightly calcified taxa, due to the metabolic costs of maintaining their skeletons under more acidic conditions (Knoll et al. 2007) (see also Section 3.3 and 4), but this is not borne out by the latest fossil data, at least for the Triassic–Jurassic interval (Dunhill et al. 2018), perhaps because body size reduction provides a mean of mitigating the physiological demands of skeletogenesis under ocean acidification conditions (Garilli et al. 2015) and reduces metabolic costs overall (Calosi et al. 2013b). Resistance to extinction varies among different taxonomic groups, and additional traits, such as having a restricted geographic distribution, have been shown to enhance extinction risk (Harnik et al. 2012) (see also Section 3.2).

3. TRENDS OF MODERN BIODIVERSITY LOSS PATTERNS

Past extinction events that were caused by similar biogeochemical changes to those that are occurring today can help us predict the effects of current global environmental change (Blois et al. 2013). Here, we focus on three observed trends of modern biodiversity loss that exhibit parallels with past extinction events: reductions in body size, loss of rare species, and the sensitivity of marine ectotherms to ocean acidification.

3.1. Reductions in Body Size with Ongoing Global Change in the Ocean

According to the Bergmann's rule (Bergmann 1847) and the temperature–size rule (Atkinson 1994), body size and temperature are intrinsically linked (Angilletta 2009). Individuals of a given species tend to be smaller under warmer conditions (lower latitudes), which implies that body size decreases with increasing temperature (Daufresne et al. 2009). This pattern has already been documented in many marine taxa in the immediate aftermath of past extinction events characterized by warmer conditions (see Section 2.2 and the discussion on the Lilliput effect). A global reduction in species' body size is thus expected in marine ecosystems under the current ocean warming trend (van Rijn et al. 2017).

Evidence of size reduction as a consequence of increasing temperature has been reported for both marine ectotherms and endotherms (e.g., Daufresne et al. 2009, Sheridan & Bickford 2011),

regardless of their life histories or trophic levels (Baudron et al. 2014). In a short-term mesocosm study, Daufresne et al. (2009) observed a negative relationship between temperature and the length of adult copepod females (*Pseudocalanus* sp.). In addition, the analyses of long-term data sets, a reduction of biomass and body size with increasing temperature were observed in herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) from the Baltic Sea (Daufresne et al. 2009), as well as in haddock (*Melanogrammus aeglefinus*), herring (*Clupea harengus*), and plaice (*Pleuronectes platessa*) in the North Sea (Baudron et al. 2014 and references therein). Furthermore, evidence to support a relationship between increasing temperatures and reductions in body size was also provided for Mediterranean fishes (van Rijn et al. 2017), further showing that maximal sea surface temperature was the best predictor for fish size and that 1°C warming is expected to cause a 5% decrease in fish length. These results are consistent with the model outputs of Cheung et al. (2013), which predicted body size reductions of 14–24% in fish assemblages globally between 2000 and 2050. Similarly, marine invertebrates are expected to undergo body size reductions of 0.5–4% per 1°C of warming (Sheridan & Bickford 2011). This pattern is supported by a multigeneration laboratory experiment that reported a reduction in body size after five generations of exposure to warming conditions in the marine polychaete *Ophryotrocha labronica* (Gibbin et al. 2017). Finally, the geographic distributions of large species in fish communities are decreasing, while those of smaller species are expanding with ocean warming trends (Daufresne et al. 2009).

Despite the compelling evidence for a pattern of body size reduction with warming, the mechanistic explanation driving such a pattern remains unclear (e.g., Angilletta et al. 2004). According to the temperature–size rule, ectotherms usually grow to a smaller size when reared at higher temperatures (Atkinson 1994) (Figure 3); however, the ubiquitous nature of this mechanism has not yet been verified. In general, growth rates and developmental rates are not equally affected by temperature: Organisms that develop faster reach sexual maturity at a smaller size (Sheridan & Bickford 2011) While this could represent a selective advantage for some species, as early maturation can enable organisms to reproduce multiple times per season (van Rijn et al. 2017), under global change such plastic (adaptive) responses would impose a chronic shift toward smaller individuals and thus affect the structure, productivity, and function of ecosystems (Dossena et al. 2012) (Figure 3). Another hypothesis is instead that size reduction is caused by oxygen limitation: As water temperature increases, oxygen solubility in the water

decreases (Baudron et al. 2014; cf. Verberk et al. 2011), while organisms' metabolic rates and thus their oxygen demands increase (Sheridan & Bickford 2011, Baudron et al. 2014) (see Section 4). This can lead to an imbalance between oxygen demand and supply (Baudron et al. 2014, van Rijn et al. 2017), which affects the aerobic scope of marine organisms (Pörtner & Knust 2007). Consequently, this imbalance limits the size of marine organisms by fixing the threshold size for which the surface-area-to-volume ratio is not sufficient to maintain a positive balance between oxygen demand and supply (Baudron et al. 2014). Considering that oxygen availability is more limited in marine environments than in terrestrial ones, the fact that body size reduction has been, up to now, steeper in marine species than in terrestrial ones fits this hypothesis.

Other factors, such as nutrient limitation and fisheries, can act as additive or synergistic effects on size reduction in marine species (Daufresne et al. 2009, van Rijn et al. 2017). Indeed, by potentially affecting growth rate, nutrient limitation could act as an additive or synergistic factor affecting body size. However, few studies have tested the relation between food limitation and size in the wild (van Rijn et al. 2017). In addition, fisheries are known to cause a selective pressure on body size by targeting large individuals and retaining smaller ones for reproduction, thus reducing the mean body size of a population (Daufresne et al. 2009). Finally, ocean-acidification conditions (i.e., low pH and elevated $p\text{CO}_2$ of seawater) appear to cause, at least in some taxa, a considerable reduction in body size, as observed in situ at CO_2 vents in polychaetes (Calosi et al. 2013b, Lucey et al. 2015) and gastropods (Garilli et al. 2015).

The ubiquitous nature of global-change-dependent body size reduction has not yet been tested broadly. Differential reductions in body size in different species and taxonomic and functional groups is expected. While we can consider it almost a certainty that body size reductions will affect marine trophic cascades and ecosystem functions (Sheridan & Bickford 2011), the uncertainty about the intensity of temperature- and ocean-acidification-dependent body size changes across the tree of life and trophic and ecological assemblages will make it more difficult to predict ecosystem-level consequences of body size shifts generated by extinction events.

3.2. Rare Species' Sensitivity to Global Change

Rare species—here broadly defined as species that are found in a restricted geographic range—are important components of regional and global biodiversity, as well as pivotal elements

defining the structure and dynamics of communities (Gaston 2003). They also carry out important and unique ecosystem functions (Mouillot et al. 2013, Leitão et al. 2016). Thus, losses in rare species will likely greatly affect marine ecosystems.

One of the favored explanations for the great variation observed within taxa in terms of species' range sizes results from differences in the breadth of their ecological niches (Brown 1984, Lomolino et al. 2010), more specifically the breadth of their fundamental (physiological) niches (Brättstrom 1968, Calosi et al. 2008, Gaston et al. 2009). As a consequence, widespread taxa should be inherently less at risk of local and global extinction events by virtue of their great physiological abilities of tolerance and regulation (Spicer and Gaston 1999, Calosi et al. 2007, 2008; Gaston et al. 2009) and the fact that, because they are present in multiple places, they have more opportunities to survive and encounter refugia (Gaston 2003). Here, we focus on the differences in the breadth of the physiological niches of rare and common species. As relevant examples for this dichotomy are relatively limited for marine species, we take advantage of examples from different habitats.

Rare species possess lower levels of tolerance to heat and cold and lower thermal plasticity (e.g., Brättstrom 1968, Calosi et al. 2008). Rare extant species appear to be more at risk of extinction when compared with their common relatives, as they possess narrower windows of physiological tolerance that make their survival more improbable in the face of the ongoing warming and extreme climatic events (e.g., heat waves) (Oliver et al. 2018). This creates a parallel with the documented loss of rare species reported during past extinctions (see Section 2).

While the relationship between rarity and temperature is relatively well understood through several empirical tests (e.g., van Dijk et al. 1999), we know comparatively little about other changing environmental drivers: i.e., pH/pCO₂, pO₂, and salinity. Differences in the breadth of osmo-ionic regulatory ability appear to help explain differences in the distribution of marine species in coastal areas, particularly intertidal habitats, coastal lagoons, and estuaries (Kinne 1963, Newell 1979). A relevant example is provided by two phylogenetically closely-related species of talitrid amphipods, one common and one rare, where the rare species shows much more limited osmo-ionic regulatory abilities than the common species (Calosi et al. 2007). Furthermore, whether ocean acidification and ocean deoxygenation will represent a further physiological challenge for rare species when compared with their common relatives remains to be determined. This said, existing evidence confirms the importance of these emerging

environmental challenges in defining species' geographic distributions and abundance, as is the case, for example, around habitats characterized by natural CO₂ gradients, such as CO₂ vents (Kroeker et al. 2010; Calosi et al. 2013a,b; Gambi et al. 2016) and bathymetric CO₂ gradients (Maas et al. 2012, Lewis et al. 2013).

Given that rare species appear to possess narrower fundamental niches (Brättstrom 1968, Calosi et al. 2008), most narrowly distributed species are found in the tropics (Stevens 1989), and their geographic ranges are shrinking with global changes (Parmesan 2006), it is reasonable to expect a significant reduction in these taxa. This reduction has important consequences for the loss of specific and functional biodiversity levels, as occurred in the paleo past (see Section 2).

3.3. Sensitivity to Ongoing Ocean Acidification

Oceanic pH and *p*CO₂ levels have been relatively stable for the last ~800,000 years, with an average of approximately 8.2 and 250 μatm, respectively, and global ocean extremes ranging between 8.3 and 8.1 for pH and between 280 and 180 μatm for *p*CO₂ (Barker & Ridgwell 2012). This general stability has created, with important exceptions (see Hofmann et al. 2011), ocean habitats characterized by lower level of selectivity. The selectivity that will characterize future marine ecosystems (Caldeira & Wickett 2003, IPCC 2014) will largely sit outside the landscape under which extant species have evolved (Barker & Ridgwell 2012). That said, species occupying habitats characterized by more frequent and greater levels of environmental fluctuations [e.g., estuaries and intertidal and coastal habitats (Hofmann et al. 2011, Duarte et al. 2013)] display a greater ability to deal with low and/or variable seawater pH and *p*CO₂ levels (Widdicombe & Spicer 2008, Thomsen et al. 2017). However, several species may not possess the necessary machinery to deal with chronic future oceanic conditions (e.g., Widdicombe & Spicer 2008). In fact, some may have reached a sort of evolutionary ceiling beyond which they may not be able to further adapt; for example, tropical terrestrial arthropods appear to have a lower evolutionary ability to further increase their thermal tolerance compared with their temperate congeners (Kellermann et al. 2009).

Evidence for species' and populations' capacity for plastic responses (within and between generations) to ocean acidification are emerging, showing that some metazoans may be capable of positive transgenerational responses (Putnam & Gates 2015, Torda et al. 2017, Donelson et al. 2018) and even rapid adaptation (De Wit et al. 2016, Thor & Dupont 2015). These abilities do not, however, appear to be ubiquitous across taxa and functional groups, and even if present may

come at a cost (Gibbin et al. 2017). For example, changes in abundance and local extinctions along natural CO₂ gradients in shallow-water benthic coastal ecosystems are relatively well documented, with many calcifiers—which are considered among the most sensitive to ocean acidification when compared with non-calcifiers (Kroeker et al. 2010, 2013; see also Sections 2.3, 4.1, and 4.2)—showing reductions in abundance and local extinction trends (Kroeker et al. 2011, 2013; Calosi et al. 2013a; Gambi et al. 2016; cf. Calosi et al. 2013b). In general, ocean acidification may contribute to reductions in local and global abundance, suggesting that it may drive several species to extinction, again this being more relevant for calcifying species, but not exclusively.

The existence of energetically demanding physiological mechanisms—including metabolic adaptations in ectotherms (Calosi et al. 2013b, 2017, Lewis et al. 2013, Maas et al. 2012), the ability to maintain an extracellular fluid acid–base balance (Calosi et al. 2013a), cellular homeostasis (Turner et al. 2015), and mineralization (Findlay et al. 2011)—that drive species' local distributions supports the idea that differences in physiological niches will help define the distinction between sensitive and tolerant taxa (see Section 4), and ultimately define their global geographic distributions and risks of extinction.

4. PUTATIVE PHYSIOLOGICAL LIMITATIONS CONTRIBUTING TO MODERN BIODIVERSITY LOSS

Global change in the ocean includes a variety of abiotic factors that have both acute and chronic consequences for marine organisms. Major stressors include hypoxia, salinity, ocean acidification, and increasing temperature (Gruber 2011). While patterns of sensitivity to ocean stressors are emerging, the mechanisms underpinning the tolerance of a variety of taxa have been less explored (Hofmann & Todgham 2010, Somero 2012). However, relevant work reveals responses at a variety of scales, ranging from transcriptomic (Padilla-Gamiño et al. 2013) and proteomic (Timmins-Schiffman et al. 2014, Wei et al. 2015) to metabolomic (e.g., Putnam et al. 2016, Calosi et al. 2017) and organism biology (Kroeker et al. 2010, Byrne 2011). Furthermore, there is an emerging understanding of the role of epigenetics (Varriale & Bernardi 2006, Putnam et al. 2016, Eirin-Lopez and Putnam 2019) and genetics (Lohbeck et al. 2012) in the plastic and selective responses, including rapid adaptation, of marine metazoans to global change. The limited accessibility of genomic resources for most marine organisms hampers the rate of

mechanistic advancement across multiple taxa to identify conserved physiological constraints that may contribute to mass extinction outcomes for key functional groups (see Section 3).

Despite a limited mechanistic understanding across marine taxa, a picture of general physiological limitations in the ability to adapt to rapid climate change are emerging and will enhance our capacity to project future communities and identify sensitive and tolerant taxa in the Anthropocene. Given projections of rapid changes in temperature and frequent heat waves (IPCC 2014, Oliver et al. 2018), ocean acidification (IPCC 2014), increased storm frequency (Knutson et al. 2010), and increased occurrence of hypoxia (Bakun et al. 2015), the capacity for marine taxa to persist will be limited by their scope for physiological tolerance of such changes, as this defines their future physiological niches (sensu Hutchinson 1978). Here, we focus on two critical areas of physiological study that present opportunities to better understand the limitations to performance in a changing ocean. First, at the broadest level, one way to advance our understanding of critical physiological sensitivities is by quantifying energetic budgets as a function of single and multiple global stressors. Second, in a specific example of a massively energetically demanding process, there can be little argument that biomineralization is a physiological limitation in warming and acidifying seas. These ubiquitous or common processes provide instructive information with which to identify mechanistic commonalities to enhance our projections of species' survival or extinction in the Anthropocene.

4.1. Energetics

Fitness is related to both the proximate concern of energy demand for the basal maintenance of functions (homeostasis) and the more ultimate energetic demands of developmental processes or metamorphosis, growth (biomass or skeletal) of the adult form, and reproduction. The energetic needs of an organism can be quantified using a basic but comprehensive energetic budget approach, as described by the following equation: Consumption = Production + Respiration + Urine + Feces (reviewed in Sokolova et al. 2012). The use of energetic budget approaches for marine organisms has a long history and provides great utility for detecting differential susceptibility across taxa and environment, including a variety of invertebrates, such as mussels (Widdows & Bayne 1971) and corals (Edmunds & Davies 1986, 1989). This approach of tracking scope for growth and shifts in budget components can highlight specific pathways and/or genes sensitive to climate change stressors (Stumpp et al. 2011b). For instance, processes expending increased energy under climate change, such as acid–base regulation (Stumpp et al.

2011b), protein synthesis (Pan et al. 2015), osmoregulation (Calosi et al. 2007), damage repair (Wood et al. 2008), and mineralization (Findlay et al. 2011), would be detected through shifts in energetic budget components and targeted for cell-level investigation.

Beyond the critical yet painstaking and detailed measurements and calculation of energy equivalents associated with energetic budgets, modeling approaches also have the potential to indicate process or pathway sensitivity. Dynamic energy budget (DEB) modeling (Kooijman 1993, Nisbet et al. 2000) is one such quantitative way forward. DEB models utilize a series of equations to describe the flux of energy from food to organismal processes such as development, maintenance, growth, and reproduction based on first principles of energy conservation. These equations or rates are responsive to life history and biotic and abiotic factors, and as such, they provide a quantifiable model and set of testable hypotheses as a function of changing environment.

DEB models have commonly been applied in marine environments (Nisbet et al. 2004), with specific examples from taxa sensitive to ocean acidification and increasing temperatures, such as shellfish (Ren & Ross 2005, Alunno-Bruscia et al. 2011) and corals (Muller et al. 2009, Cuning et al. 2017). These models can also be applied for species comparisons, where the parameter values highlight differences in species performance given the model conditions. For instance, a comparison of different Atlantic fish species identified the thermal sensitivity of the surface-area-based assimilation rate and volume-based maintenance rate, highlighting differing energetic allocations by thermal regime (Freitas et al. 2010). Given the importance of thermal tolerance in defining body size and biodiversity levels in a warming ocean (Section 3), DEB modeling provides a promising linkage between critical drivers of selection and energetic underpinnings. Furthermore, the DEB modeling approach provides the capacity to investigate size and scaling relationships and the means to incorporate trade-offs involved with energetic allocation (Wood et al. 2008), and thus models of selection can be more fully parameterized (Nisbet et al. 2000).

While shifts in energy allocation provide one avenue of detecting shared sensitivities of taxa to global change, in practice, integrative (cross-scale) measurements are necessary to detect mechanistic changes not necessarily seen at a single scale. Organism-level consequences of environmental stress, such as mortality, developmental abnormalities, changes in growth rates or size, changes in mineralization rates and type of mineralization, and changes in metabolic rate, are often indicators of gross performance issues but do not necessarily identify causative

components or even respond in expected ways (Pan et al. 2015). Furthermore, cross-scale analyses of stress responses are less common. In an integrative study, Stumpp et al. (2011b) targeted the organism-scale responses of urchin larvae through energetic estimates of scope for growth, revealing that a substantial portion of energy for growth was redirected to other processes (e.g., maintenance) at high $p\text{CO}_2$. These findings led to a mechanistic examination of physiological sensitivity through gene expression analysis of a set of genes involved in metabolism, ion homeostasis, and calcification (Stumpp et al. 2011a), specifically identifying the downregulation of calcification-related genes and upregulation of the metabolism gene set under high $p\text{CO}_2$. An integrative approach was also used by Pan et al. (2015) in a study where, surprisingly, the exposure of larval urchins to ocean-acidification conditions resulted in no single mechanism responding at the biochemical scale, but parsing the energetic demands into those necessary for protein turnover and those necessary for ion transport accounted for the majority of the available ATP. In summary, energetics-based approaches can facilitate detailed and integrative studies to elucidate phenome–genome linkages and thus evolutionary implications.

4.2. Biomineralization

The active and biologically mediated deposition of CaCO_3 represents a growing challenge under global climate change (Doney et al. 2009). As carbonate ion availability declines and H^+ availability increases, the energetic cost of building shells, skeletons, and other calcified parts increases dramatically (Stumpp et al. 2011b). Extinctions are projected to occur for the species where larval development includes mineralization and occurs over a tightly constrained temporal window (Spalding et al. 2017). Indeed, negative synergistic impacts of ocean acidification and increased temperature on marine calcifiers are more common when calcification is ongoing at the larval stage (e.g., in oysters, mussels, and urchins) than when calcification is delayed until later stages (Byrne & Przeslawski 2013, Putnam et al. 2013). Research into the mechanistic understanding of biomineralization remains paramount. Advancements in assessing species' sensitivities are now possible through novel techniques for tracking intracellular pH dyes through live imaging (Venn et al. 2013), assessment of mineralogy using nanoscale secondary ion mass spectrometry (Brahmi et al. 2012), transcriptomics of newly calcifying life stages (Mass et al. 2016), proteomic analysis of the matrix proteins (Drake et al. 2013), and spectromicroscopy of crystals (Mass et al. 2017).

As methodologies advance and genomic resources become more readily available, it will be critical to use approaches such as DEB modeling and cross-scale integration to ascertain whether common mechanisms underlie topics such as nonlinearities in organismal sensitivities in response to global change drivers, the implications of environmental heterogeneity of local conditions interacting with global change, and biological responses in the presence of multiple stressors. Through this multipronged approach, it may be possible to elucidate critical physiological limitations to persistence under global climate change.

5. A MULTIDISCIPLINARY INTEGRATIVE APPROACH AND FOCAL QUESTIONS

Common threads emerge from past extinction events under climate change, ecological biodiversity losses observed under modern global change, and the physiological constraints of marine organisms. The utilization of these coherent patterns therefore provides an invaluable approach in facilitating the identification of likely processes of extinction in the near future (**Figure 4**). This approach should help us in reducing the uncertainties of predictions and improve our ability to identify coherent patterns of biodiversity losses that have been observed over multiple extinction events, and thus are most likely to also occur under ongoing anthropogenically driven global change. This integrative approach should also enable us to acquire a more in-depth understanding of the pathways of action of global change drivers on biotic systems (organisms to ecosystem) and thus help us predict their likely consequences for marine species persistence and ecosystem functioning. The advancement of our understanding of ecological and physiological mechanisms, processes, and consequences of the ongoing sixth mass extinction will be best driven by the formal testing of hypotheses. This extends to hypotheses that were already developed within a specific research field [e.g., the existence of selectivity against infaunal organisms—particularly the reduction in bioturbators and decreases in the depth, size, and amount of bioturbation observed in the fossil record—have been partially observed in modern mesocosm experiments (**Hale et al. 2011**) and predictive models (**Solan et al. 2004**) but need to be tested more broadly; see **Figure 4**] and to *de novo* hypotheses emerging from the integration of concepts from the research fields of paleo-ecology, modern ecology, and mechanistic physiology. This is most relevant as how discussed by Pigliucci et al. (2006) “Evidence” is not simply out

there for the taking, it becomes an object of a search in light of specific hypotheses (we would do well to remember Darwin's words in a letter to Henry Fawcett: "*How odd it is that anyone should not see that all observation must be for or against some view if it is to be of any service!*")".

<COMP: PLEASE INSERT FIGURE 4 HERE>

Figure 4 Integration of the current understanding of patterns, processes, and mechanisms linked to past and current biodiversity losses under climate and global change and identification of focal questions to determine generalities that can improve our ability to predict the consequences of the ongoing anthropogenically driven sixth mass extinction. Green check marks indicate supported patterns, the red X indicates a pattern that is not supported or not ubiquitously supported, and gray question marks indicate a lack of evidence. Asterisks indicate patterns observed in situ in CO₂ vents and/or mesocosm experiments (e.g., [Kroeker et al. 2011](#), [Hale et al. 2011](#), [Christen et al. 2013](#))

Developing specific hypotheses aimed at shedding light on the ongoing mass extinction makes the integration of multiple disciplines central to the development of an approach that can produce a useful understanding to support decision-making, which should ultimately enhance the conservation of biodiversity and the sustainable use of natural resources. This is important given that extinctions have had a disproportionate importance in shaping the evolution of life on our planet, and their influence on extant biodiversity has been prominent. We propose to include a macroevolutionary perspective within the current efforts to integrate an evolutionary perspective into the research fields of global change biology, conservation biology and assisted evolution (see [van Oppen et al. 2015](#), [Calosi et al. 2016](#), [Torda et al. 2017](#), and references within) More specifically, we suggest more closely exploring past extinction events and purposefully investigating the potential presence of parallels in modern patterns of biodiversity loss, as well as attempting to identify their potential pathways of physiological impact. This approach might help develop the innovative thinking required to tackle the current biodiversity crisis ([Barnosky et al. 2011](#)), and more accurately identify future trends in biodiversity loss and changes in ecosystem functions linked to the ongoing sixth mass extinction. We also suggest that, in order to be effective in our effort, we should pragmatically target a limited number of focal questions to rapidly advance our current understanding of the processes and consequences of the ongoing extinction (**Figure 4**).

Beyond the undeniable tremendous effort already produced by the international scientific community through the Intergovernmental Panel on Climate Change (IPCC 2014), and specifically the IPCC review by the marine scientific community (Pörtner et al. 2014), there is still space to improve our ability to project future changes in marine biodiversity trends and marine ecosystem functions under global changes via cross-disciplinary synthesis using an evolutionary lens (Calosi et al. 2016, Torda et al. 2017).

DISCLOSURE STATEMENT

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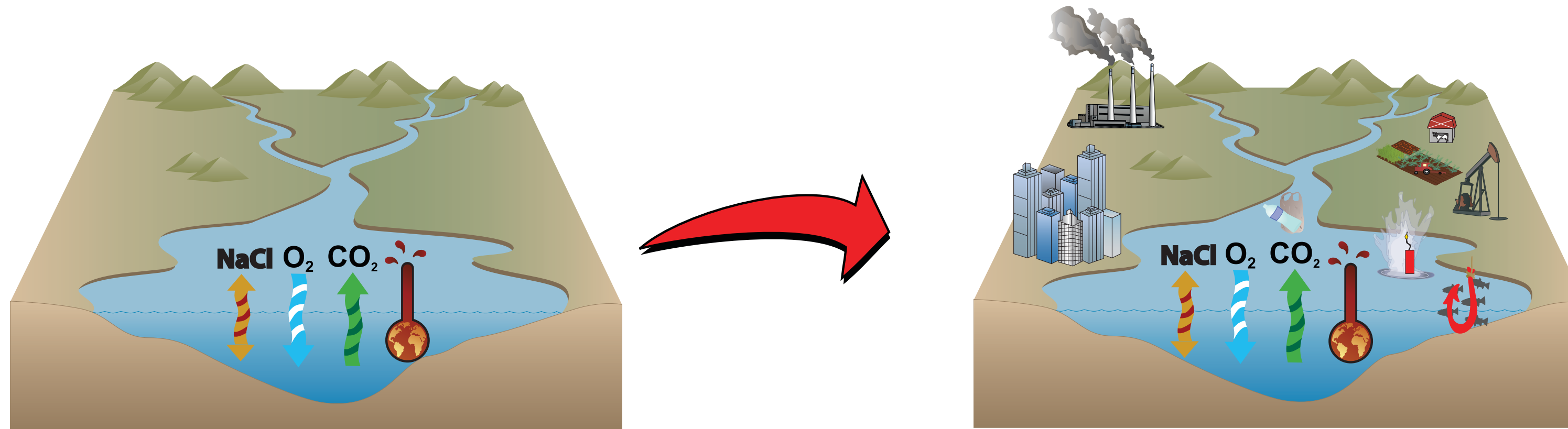
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INTENSIFYING ENVIRONMENTAL PRESSURES



Patterns of Biodiversity Loss

OBJ 1: PALEO RECORD OF CHANGES IN BIODIVERSITY

OBJ 2: MODERN RECORD OF CHANGES IN BIODIVERSITY

OBJ 3: PHYSIOLOGICAL PATHWAYS OF SENSITIVITY

Physiological Sensitivity Associated with Biodiversity Loss

Multidisciplinary Integration

OBJ 4: ENHANCED PREDICTIVE CAPACITY IN THE ANTHROPOCENE

Common Threats:

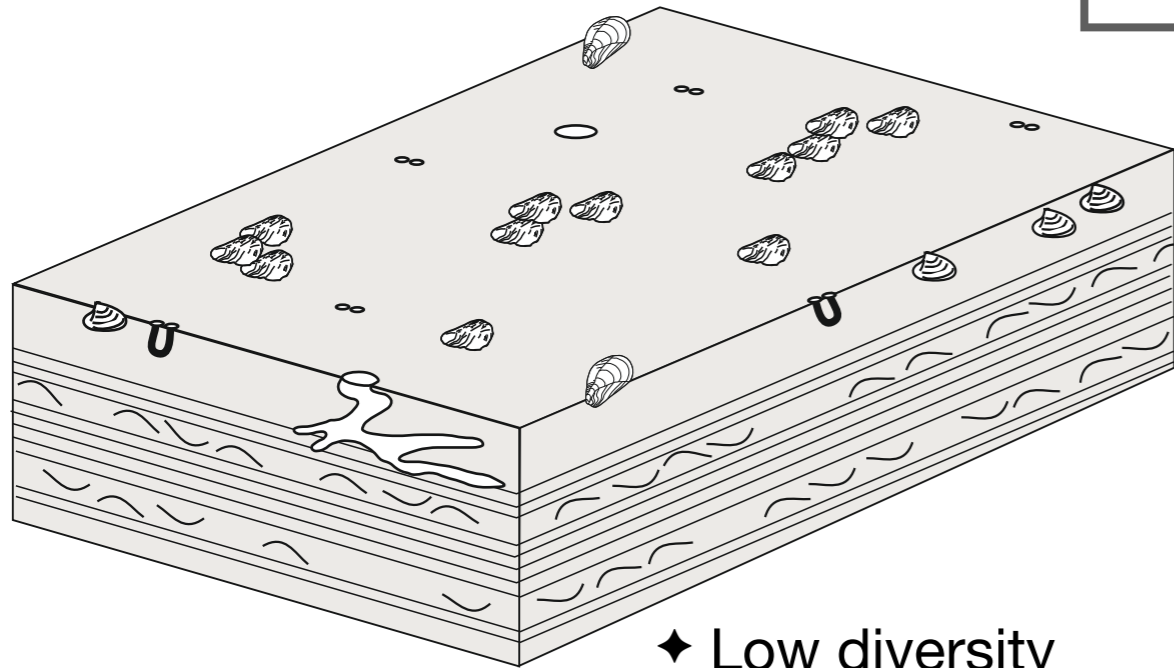
- Specific biodiversity loss
- Functional biodiversity reduction
- Rare species loss
- Body Size reduction
- Calcifiers sensitivity to ocean acidification

Early Jurassic of southwest England

a Pre-Planorbis Zone

High CO₂ (ca. 2000 ppm) & warming conditions

a

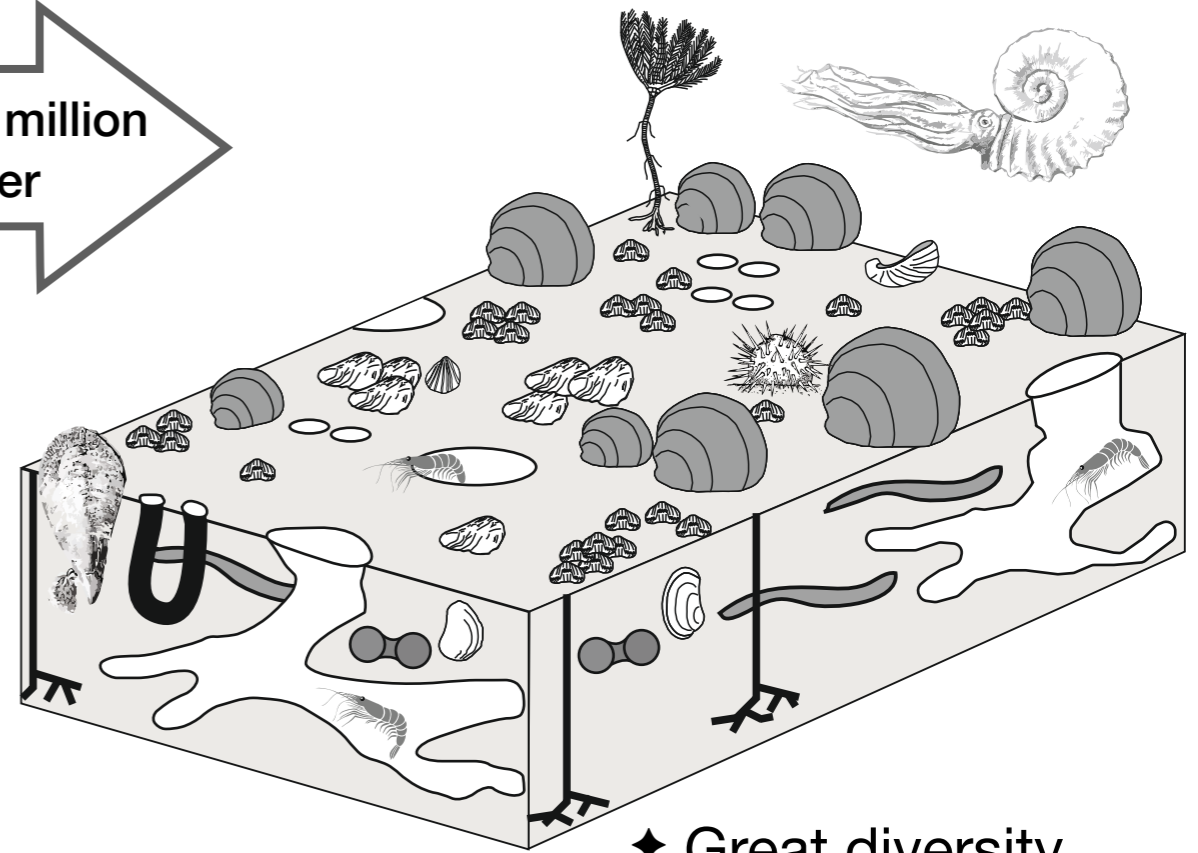


- ◆ Low diversity
- ◆ Small size of species

b Angulata Zone

“Normal” CO₂ (ca. 500 ppm) conditions

b

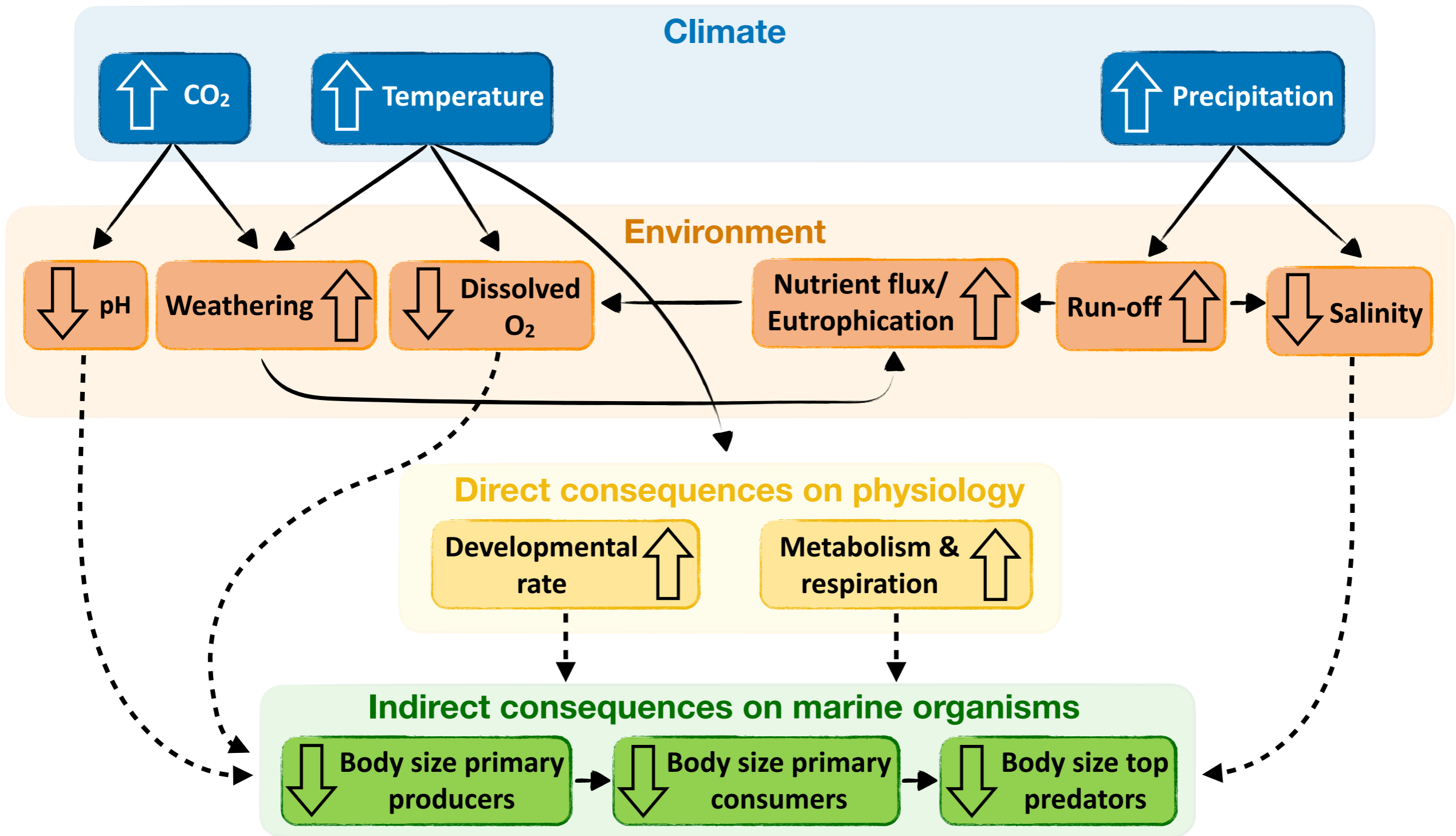


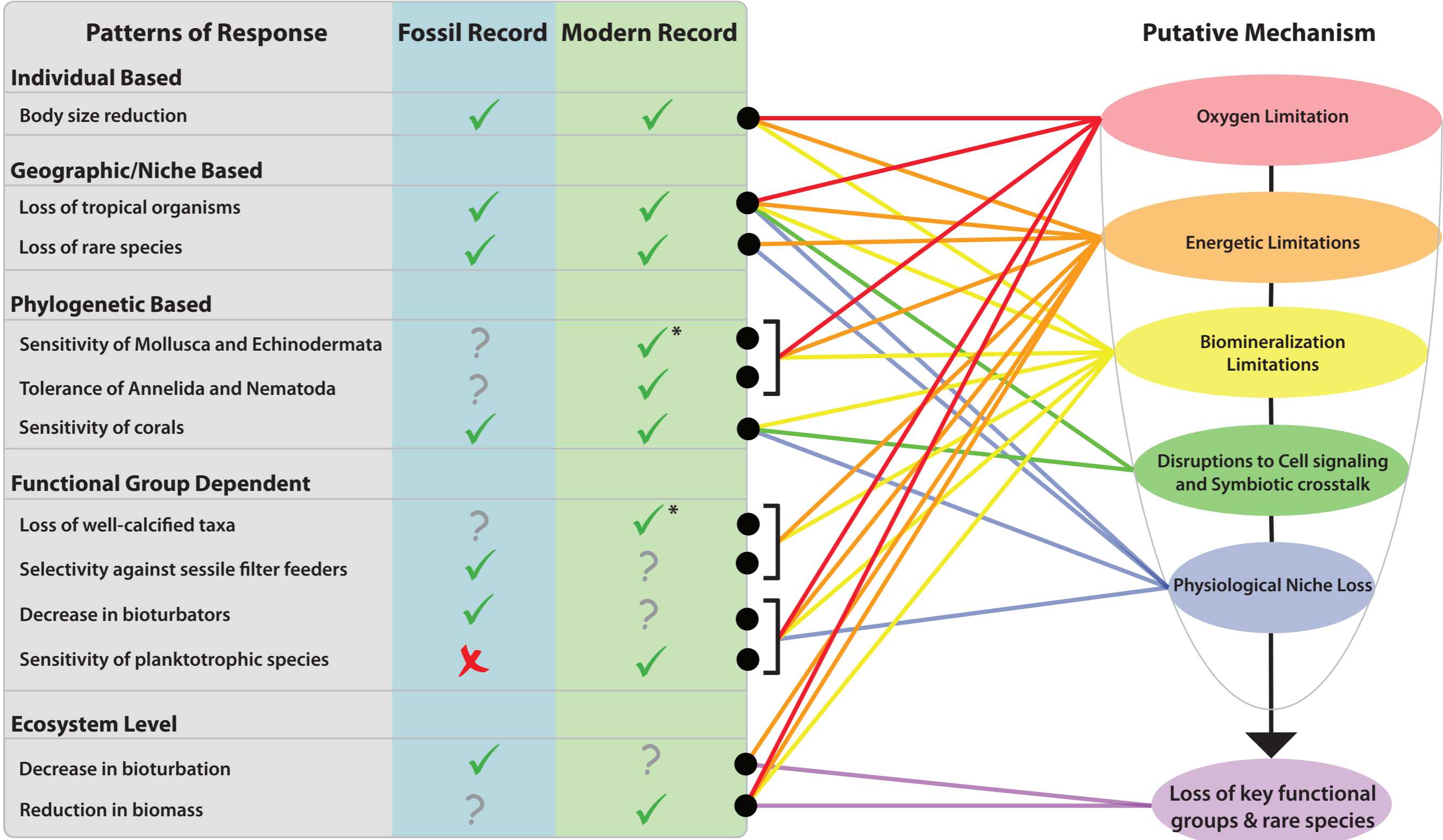
- ◆ Great diversity
- ◆ Large size of species

Recovery 1-2 million years later

Key:

- | | | | | | | | |
|--|--|--|--|--|-----------------------------|--|---------------------|
| | <i>Liostrea hisingeri</i> | | <i>Rhizocorallium</i> isp.
(burrows of crustaceans) | | <i>Plagiostoma gigantea</i> | | Echinoid |
| | <i>Modiolus minimus</i> | | <i>Palaeophycus</i> isp.
(burrows of polychaetes) | | <i>Pinna</i> sp. | | Ammonite |
| | <i>Pteromya tatei</i> | | <i>Pleuromya</i> sp. | | <i>Pholadomya</i> sp. | | Crinoid |
| | <i>Arenicolites</i> isp.
(burrows of polychaetes) | | <i>Chondrites</i> isp.
(burrows of polychaetes) | | <i>Chlamys</i> sp. | | <i>Gryphaea</i> sp. |
| | <i>Thalassinoides</i> isp.
(burrows of crustaceans) | | <i>Calcirhynchia calcaria</i> | | | | |





Emerging focal questions:

- (1) Is there evidence of selectivity against sessile filter feeders in modern time?
- (2) Are symbiotic organisms more sensitive to global change than non symbiotic ones?
- (3) Is there a decrease in bioturbators and bioturbation in modern time?
- (4) Are there ubiquitous mechanisms of cell sensitivity in rare species?