Annual Review of Marine Science

Physiological Consequences of Oceanic Environmental Variation: Life from a Pelagic Organism's Perspective

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Annu. Rev. Mar. Sci. 2022. 14:4.1–4.24

The *Annual Review of Marine Science* is online at marine.annualreviews.org

https://doi.org/10.1146/annurev-marine-040221-115454

Keywords

behavior, ecological physiology, environmental gradients, performance curve, response time, variation

Abstract

To better understand life in the sea, marine scientists must first quantify how individual organisms experience their environment, and then describe how organismal performance depends on that experience. In this review, we first explore marine environmental variation from the perspective of pelagic organisms, the most abundant life forms in the ocean. Generation time, the ability to move relative to the surrounding water (even slowly), and the presence of environmental gradients at all spatial scales play dominant roles in determining the variation experienced by individuals, but this variation remains difficult to quantify. We then use this insight to critically examine current understanding of the environmental physiology of pelagic marine organisms. Physiologists have begun to grapple with the complexity presented by environmental variation, and promising frameworks exist for predicting and/or interpreting the consequences for physiological performance. However, new technology needs to be developed and much difficult empirical work remains, especially in quantifying response times to environmental variation and the interactions among multiple covarying factors. We call on the field of global-change biology to undertake these important challenges.

1. INTRODUCTION

In their quest to better understand current patterns and predict future trends for life in the sea, marine scientists must characterize a chain of effects that connects the physical environment to the performance of individuals, their ecological interactions, and the interactions among (and evolution of) populations. This is a gargantuan task. Our limited goal in this review is to analyze the first link in that chain: how the magnitude and time course of changes in environmental drivers affect the physiological performance of individual marine organisms.

We approach this task by considering two classes of fundamental questions regarding the interactions between environmental variation and physiology. The first involves accurately quantifying environmental variation from a pelagic marine organism's perspective: How much change does an individual see over the course of its lifetime? How rapidly, how frequently, and how predictably do those changes occur? In what ways do multiple factors covary? We then turn to the physiological consequences of environmental variation: How does physiological performance in a fluctuating environment differ from our predictions from static conditions? How rapidly can physiology adjust to a shifting environment? How do the effects of multiple environmental factors interact?

Answers to these questions are not easily generalized (and in some cases are altogether lacking), exposing the challenges that currently hinder attempts to understand and predict the biological consequences of environmental variation. While we do not directly address the impacts of climate change (for reviews, see Doney et al. 2012, Levin & Le Bris 2015, Boyd et al. 2016), it is clear that progress in forecasting long-term impacts of climate change on the marine ecosystem relies on a more complete, nuanced understanding of how individual organisms experience the patterns and cope with the physiological exigencies of environmental variation. In short, this exploration reveals more about what we need to know than the relatively little we currently understand.

2. PATTERNS OF ENVIRONMENTAL VARIATION IN THE SEA

Marine life is subject to the same environmental drivers as life on land, although the effects often differ greatly in magnitude. As on land, light intensity in the ocean affects visual predators' foraging ability and, by governing the rate of photosynthesis, controls the flow of energy into the food web. Much more so than air, however, seawater effectively absorbs and scatters light, so most of the ocean habitat is dark (Jerlov 1976). Unlike the terrestrial environment, where atmospheric pressure varies by at most 0.75 atm, hydrostatic pressure in the ocean increases by 1 atm with each 10 m of depth, with effects on a variety of cellular processes (Somero et al. 2017, Yancey 2020). As with other aquatic life—but in contrast to life on land—marine organisms are impacted by the concentration of dissolved materials: salts, which determine seawater's salinity (with effects on its density and organisms' osmotic balance); hydrogen ions (i.e., pH, which affects many physiological processes); oxygen (necessary for aerobic metabolism); carbon dioxide, bicarbonate, and carbonate (necessary as reactants in photosynthesis and for the production of calcareous shells and skeletons); silicate (needed for diatoms' armor); and a wide variety of mineral nutrients (e.g., nitrate and ammonium, phosphate, and iron). Interactions among these variables can be complex. For example, the concentration of nutrients can control the rate of phytoplankton's photosynthesis and growth, and thereby affect pH and the availability of O_2 and CO_2.

In addition to these factors, two properties of seawater have fundamental consequences for how organisms experience environmental variation. First, seawater's thermal conductivity is 23 times that of air (Denny 1993). As a consequence, with few exceptions (e.g., cetaceans and a few sharks and tunas), marine organisms are the same temperature as the surrounding seawater—a stark contrast to many terrestrial ectotherms, whose body temperature can be 20–40°C different from the ambient temperature (Gates 1980; Denny 1993, 2016). As a result, marine organisms' options for behavioral thermoregulation differ in scale and timing from those on land.

Second, unlike air, seawater's density is close to that of living things. Taking advantage of the resulting buoyancy, the vast majority of marine organisms (in terms of both number of individuals and taxonomic diversity) drift with the water mass in which they are embedded: a planktonic lifestyle. Small adjustments to buoyancy offer the potential for vertical migration (e.g., Villareal & Carpenter 2003, Gemmell et al. 2016), but while they move up or down, migrators still drift with any horizontal flow. As a result, many marine organisms move with the oceanic weather, reducing the variation they experience. This is a stark contrast to most terrestrial organisms, which encounter environmental variation as the weather comes to them. When addressing issues of marine environmental variability, our default should therefore be to view the world from a perspective that moves with the fluid: a Lagrangian rather than an Eulerian reference frame. As we discuss below, movement relative to the fluid (often under behavioral control) can significantly alter the variation experienced by an individual.

Lagrangian reference frame: a reference frame that moves with the fluid

Eulerian reference frame: a reference frame that is fixed in space, through which a fluid can move

The Lagrangian perspective does not apply to sessile or sedentary benthic organisms, although it does apply to their planktonic larvae. For benthic organisms living at the oceans' margins (e.g., reef-forming corals and inhabitants of intertidal rocky shores), the environment varies so drastically that its effects have garnered much attention (e.g., Helmuth 2002, Somero 2002, Lesser & Farrell 2004, Connor & Gracey 2011, Denny et al. 2011, Oliver & Palumbi 2011, Dong et al. 2017, Suggett & Smith 2020, Marshall et al. 2021). However, these hypervariable environments are not representative of the ocean as a whole, and we instead focus our attention on pelagic organisms in open-ocean habitats.

2.1. Variation from the Organism's Perspective

Although the marine environment varies through space, the gradient in a driver is seldom so steep that organisms can sense the difference from one part of their body to another. Instead, organisms experience variation through time (Dowd et al. 2015, Woods et al. 2015, Dillon et al. 2016), either as environmental drivers change at fixed points in the Lagrangian reference frame or as individuals move from one location to another within that frame. The temporal variation experienced by an organism in any environmental factor x is quantified by the total derivative, D:

$$\frac{\mathrm{D}x}{\mathrm{D}t} = \frac{\mathrm{d}x}{\mathrm{d}t} + u\frac{\mathrm{d}x}{\mathrm{d}s}. \qquad 1.$$

Here, u is speed measured along path s in the direction of travel (be it up, down, or sideways). The term $\mathrm{d}x/\mathrm{d}t$ is the rate of change of x at each point, $u(\mathrm{d}x/\mathrm{d}s)$ is the advective component of temporal variation, and the variation experienced by an individual accumulates as $\mathrm{D}x$ accrues over the individual's lifetime. Therefore, to understand the environmental variation experienced from an organism's perspective, at a minimum we need to know how fast the environment changes ($\mathrm{d}x/\mathrm{d}t$), how the environment differs from one place to the next ($\mathrm{d}x/\mathrm{d}s$), how fast the organism moves (u), and how much time the organism has to accrue experience (i.e., how long it lives).

General patterns relating body size to life span and speed allow for preliminary insights. Among marine taxa, generation time (a proxy for life span) tends to increase with body size (**Figure 1*a***). Most marine biota are small, however, and therefore have short generations. Approximately 48% of marine biomass—the bacteria, archaea, picoplankton, and ciliates that numerically dominate oceanic life—is distributed among tiny organisms (length $L < 0.1$ mm; Bar-On et al. 2018), with generation times typically less than 2.5 days. For the 75% of marine biomass comprising individuals with $L < 1$ cm—that is, for virtually all marine primary producers and herbivores and a

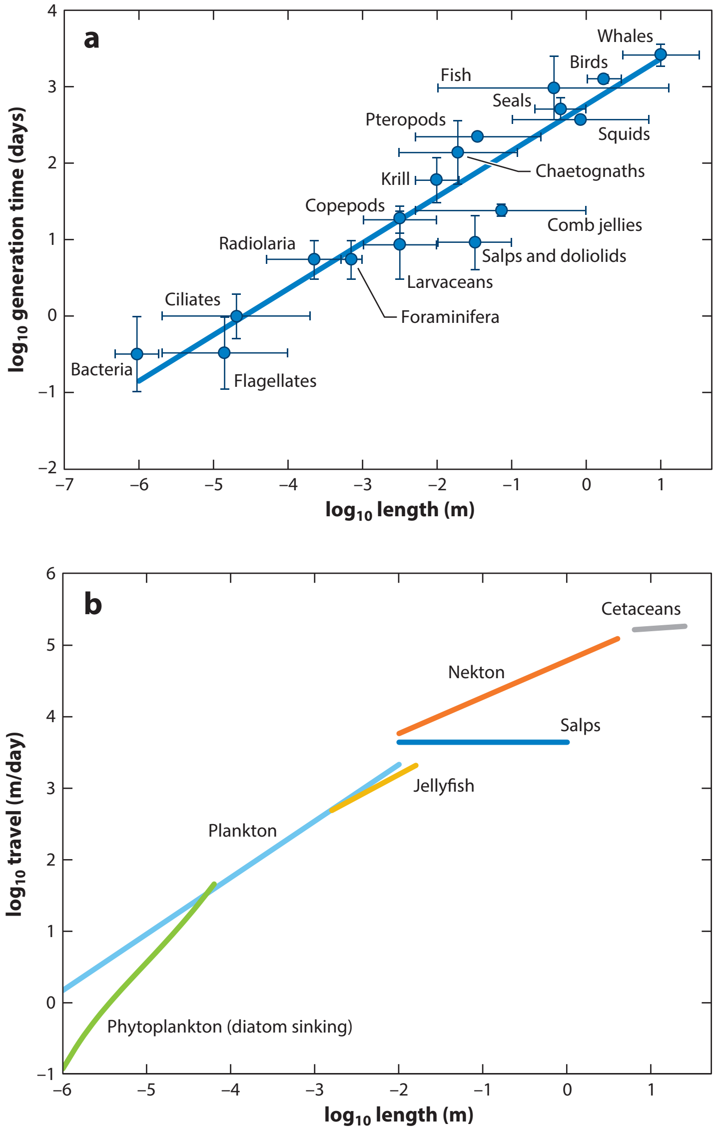

Figure 1

General trends in the generation time and speed of travel of marine organisms. (*a*) Generation time, which tends to increase with body length. To a reasonable approximation, $\log_{10} G = 0.602 \log_{10} L + 2.77$ (revised from Denny 2008), where G is generation time (in days) and L is body length (in meters). Bars denote approximate ranges in G and L. (*b*) Speed of travel. Data are from Kiørboe (2011) (plankton), Miklasz & Denny (2010) (diatom sinking), Videler (1993) and Webb (1975) (nekton), McHenry & Jed (2003) (jellyfish), Sutherland & Madin (2010) (salps), and Gough et al. (2019) (cetaceans).

substantial fraction of primary predators—the generation time is less than 40 days. Only for the rare organisms with $L > 1$ m are generation times commonly greater than a year.

The rate at which marine organisms move through the surrounding water by sinking or swimming is also positively correlated with size (**Figure 1*b***). Because most marine organisms are small, they travel slowly; the 48% of biomass with $L < 0.1$ mm typically swims or sinks less than 50 m/day, or less than 125 m in an average lifetime. This limited excursion constrains the extent of an environmental gradient they can traverse and reduces the likelihood of experiencing repeated fluctuations. Larger organisms live longer and can travel farther (e.g., ~2 km/day for $L \sim 1$ cm), potentially encountering more environmental variation overall, as well as repeated fluctuations. We note that movement relative to the fluid is often under organisms' control, so behavior can have a substantial impact on the environmental variation organisms experience.

Mixed layer: the uppermost layer of the ocean, which is subject to mixing from turbulence generated by wind and waves

With these size-dependent patterns in hand, we explore how the temporal ($\mathrm{d}x/\mathrm{d}t$) and spatial ($\mathrm{d}x/\mathrm{d}s$) gradients in marine environmental drivers affect the magnitudes and rates of variation encountered by individual organisms.

2.2. Variation Experienced by Drifting Organisms

The magnitude of temporal variation experienced by drifting organisms varies greatly depending on whether they live in the surface mixed layer (where substantial change can occur within a generation) or at greater depth (where change is often too slow to affect physiology directly).

2.2.1. Temporal variation in the mixed layer. Global average temperature in near-surface waters is increasing as the climate changes at a rate of ~0.01°C/year (Rhein et al. 2013), but in addition to that slow trend, the physical environment of the mixed layer is sufficiently dynamic that even small, short-lived planktonic organisms can experience substantial environmental variation. When the sea is calm (so that mixing is minimal), water within 1–2 m of the surface can vary by 5°C on a sunny day. Similarly, illumination in the photic zone can change substantially over the lifetime of even the shortest-lived marine organisms. Irradiance changes through the day as the sun travels across the sky (Gates 1980) and varies on a scale of minutes as clouds obscure the sun. At depths of less than ~10 m, light intensity can fluctuate multiple times per second as surface waves focus and defocus incident light, potentially amplifying intensity more than threefold (Schubert et al. 2001). As noted above, O_2 and CO_2 concentrations and pH can change through biological action, and in the surface mixed layer their rates of change, like those of illumination, can be substantial (Hofmann et al. 2011, Sutton et al. 2019).

2.2.2. Variation in the ocean interior. By contrast, for drifting organisms below the pycnocline—the rapid increase in salinity at the base of the mixed layer—most environmental drivers vary little over even the longest generation times. For instance, several physical and biological factors are leading to vertical expansion and horizontal shoaling of the oxygen minimum zone (OMZ) in mesopelagic waters (Gilly et al. 2013). But the temporal change in oxygen concentration at a given depth amounts to only 0.16–0.60% of saturation per year. The co-occurring shifts in CO_2 concentration and pH proceed at similarly sluggish rates (Doney et al. 2009). Temperature in the ocean interior is increasing due to climate change, but only slowly: 0.004°C/year in the Southern Ocean, and 0.0005°C/year as a global average (Rhein et al. 2013).

2.3. Advective Variation

If individuals are capable of moving relative to the water, the potential for encountering environmental variation increases, often drastically. The ocean contains spatial gradients in environmental drivers at scales from whole ocean basins to micrometers. When coupled with the speed at which organisms move, these gradients control the advective component of temporal variation (Equation 1). To highlight these effects, we explore five illustrative oceanic gradients.

2.3.1. Light intensity. Temporal variation in light intensity due to the sun's travel, clouds, and wave focusing is augmented by the variation encountered as phytoplankton sink or are transported vertically by internal waves and turbulence. Vertical velocities due to sinking (typically ~10^{-5} m/s) are much lower than those induced by internal waves (up to ~2 cm/s; Denman & Gargett 1983) and turbulence (up to ~3 cm/s, although typically less; D'Asaro 2001), so the latter two account for the highest rate of variation. Near the surface in clear water, a vertical velocity of 3 cm/s would cause noontime irradiance to change by 0.9 W/(m^2·s), much greater than the maximum rate of 0.07 W/(m^2·s) due to the shifting solar angle of incidence.

Thermocline: the rapid decrease in temperature with depth at the base of the mixed layer

2.3.2. The thermocline. In much of the ocean, in addition to the pycnocline and its associated vertical gradient in mineral nutrients, the thermocline provides substantial spatial variation accessible to vertically mobile animals, often as a concomitant to their diel vertical migration (DVM). Temperature differences across the thermocline vary greatly with location and season, but they can approach 20°C. The gradient in temperature is typically on the order of 0.05°C/m and can be as high as 0.5°C/m (Pickard 1964, Kennish 1989). Consider, for instance, the rate of change of temperature for copepods—the ocean's most abundant herbivores—as they swim through the thermocline during their daily vertical migration. At a garden-variety gradient of 0.05°C/m, a copepod swimming at 3 cm/s will experience a rate of change of 0.09°C/min. In a steep gradient, this could be as high as 0.9°C/min. In either case, both the magnitude and rate of change are far in excess of what it would encounter if it drifted for a day in the middle of the mixed layer (<1°C, <0.001°C/min) or moved 100 m vertically through the ocean interior (<0.1°C, <0.002°C/min). For larger organisms, faster swimming speeds translate into greater rates of encountered environmental change. For a fish or squid swimming at 1 m/s through a steep thermocline, the water temperature could change by 20°C in less than a minute—a potential thermal shock—although for large-bodied organisms (such as sharks and tunas), the corresponding rate of change of body temperature would be buffered by the animal's thermal mass (Gates 1980). Fronts—large-scale horizontal gradients often associated with mesoscale eddies and coastal currents—can be created by the convergence or divergence of water masses, providing gradients in temperature, salinity, and nutrients analogous to those of the thermocline, although these horizontal gradients are typically much less steep than those in the thermocline.

When considering temperature effects on physiology, the frequency with which the thermocline or front is crossed can be as important as the rate and magnitude of change encountered while traversing the gradient. A wide variety of organisms (everything from copepods to small fish and jumbo squid) complete one cycle of vertical migration per day (Hays 2003). Others, such as tunas and whales, may cross the thermocline tens of times per day (e.g., Howell et al. 2010, Lawson et al. 2010, Goldbogen et al. 2011).

2.3.3. Pressure. Across a variety of marine taxa, 300–800-m vertical displacements—corresponding with pressure changes of 30–80 atm—are not uncommon (e.g., Madigan et al. 2015, Maas et al. 2018, Coffey et al. 2020, Tutasi & Escribano 2020, Liszka et al. 2021). Diel movements of this amplitude occur even within the deep sea below the apparent influence of any surface-light zeitgeber (van Haren & Compton 2013, Tutasi & Escribano 2020). For these vertically migrating organisms, change in pressure often coincides with a change in temperature and/or oxygen levels (Seibel 2011).

2.3.4. The oxygen minimum zone. As dead organic matter sinks below the surface mixed layer, it is decomposed by bacteria, which consume oxygen in the process. As a result, the O_2 concentration in the water column decreases from a near-saturated value of 5–6 mg/L near the surface to a minimum near zero at a depth of 600–800 m, forming the OMZ (Gilly et al. 2013). Below that minimum, decomposition is effectively complete, so respiration is negligible, and the O_2 concentration rises with increasing depth as oxygen-rich waters of the deep ocean are encountered. Although the magnitude of change across the oxygen gradient is large—for most organisms, the difference between abundant availability and severe hypoxia—the gradient of O_2 concentration in the OMZ is shallow, typically 0.005–0.01 mg/(L·m). For a copepod migrating vertically in this gradient at 3 cm/s, the rate of change of O_2 concentration would be 0.009–0.018 mg/(L·min). As noted above, vertical migration in the OMZ and from the OMZ to the surface mixed layer (Tutasi & Escribano 2020) coincides with a considerable shift in temperature and pressure. We discuss below how this inherently multifactorial transition has potentially complex physiological ramifications.

2.3.5. Small-scale gradients. While light attenuation, the thermocline, pressure, and the OMZ have received considerable attention from oceanographers, important environmental gradients occur at the much smaller scales relevant to the numerically dominant organisms in the ocean—bacteria, archaea, phytoplankton, and protists—and these gradients have received less study. At this small scale, physiologically important solutes (e.g., oxygen, carbon dioxide, and nutrients) are transported primarily by molecular diffusion, and gradients can be extreme. For example, at night, if the ambient oxygen concentration is 6 mg/L (typical of near-surface water) and a respiring phytoplankton cell with a radius of 10 μm absorbs every oxygen molecule that arrives at its surface, the gradient 10 μm away from the cell is a whopping 3×10^5 mg/(L·m) (Kiørboe 2008). Bacteria are attracted to the carbohydrates released by phytoplankton, and in the process can traverse this gradient (Kiørboe 2008). Moving at a speed of 10 μm/s down the oxygen gradient, a bacterium would experience a rate of change of available oxygen of 4 mg/(L·s), taking less than 2 s to go from an oxygen-saturated to a nearly anoxic microenvironment. If the phytoplankter (or other organism) creating the concentration gradient sinks, the gradient is drawn out into a trail in the object's wake, but the magnitude of the gradient—and hence its effect—is similar (Kiørboe 2008). During the day, when the phytoplankter is photosynthesizing, the gradient is reversed, and the same bacterium would experience high oxygen concentrations. Thus, at this microscopic scale, organisms can experience magnitudes and rates of change far in excess of what a larger organism would experience in a vertical migration to or from the ocean's OMZ; a migrating animal would have to swim at more than 50 m/s to encounter the same rate of change. Gradients in pH, CO_2, and nutrients in the vicinity of phytoplankton (or other small organisms) can be similarly steep.

Extreme as they are, these diffusion-mediated concentration gradients become negligible at distances more than a few tens of micrometers away from the cell (or of the trail in its wake). As a result, this extraordinary spatial variability is experienced as temporal variation by only the smallest marine organisms. But, as noted above, these smallest organisms comprise approximately half of marine biomass and are a key component of marine ecosystems. Thus, diffusion-scale gradients have substantial potential to affect life in the oceans.

2.4. Describing Temporal Patterns of Variation

Although the examples explored previously describe the magnitudes of environmental change an individual organism might encounter, they amount to only snapshots of the overall time course of variation. The temporal pattern of an environmental driver can be better summarized by the factor's power spectrum. The power spectrum of a series of data (the Fourier transform of the series' autocovariance function) tells us how the series' total variance is distributed among temporal or spatial frequencies (Diggle 1990, Denny 2016). The area under the spectrum between

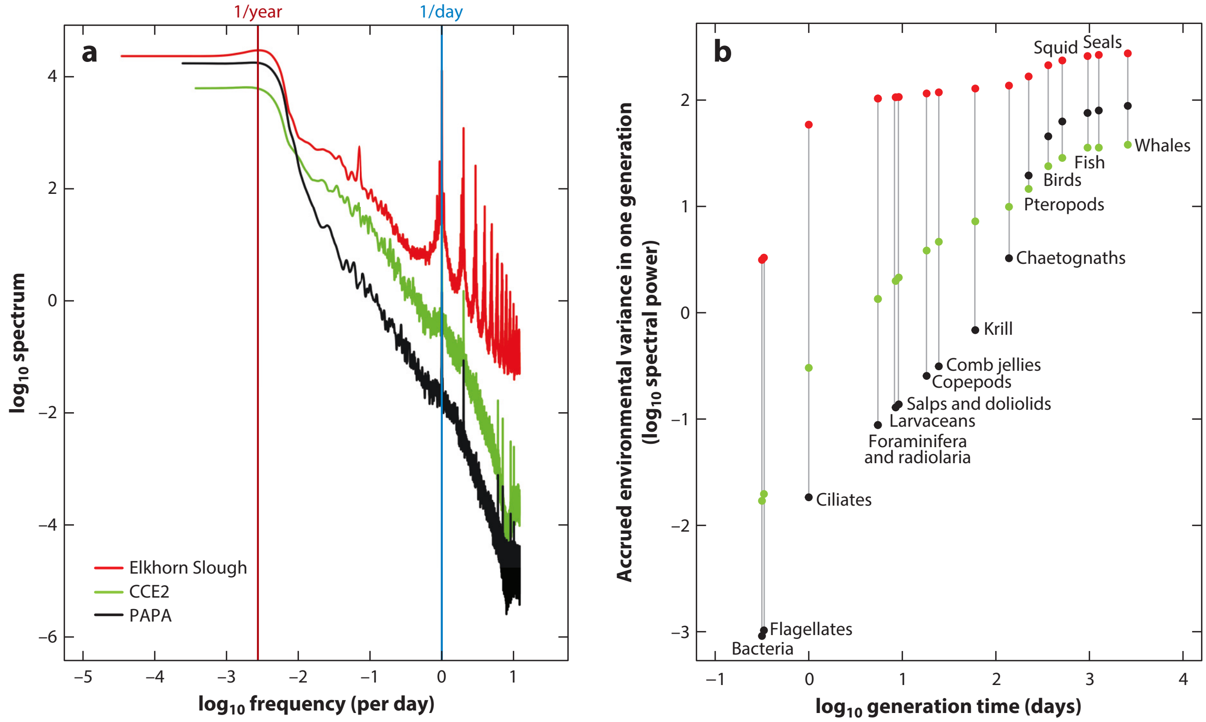

Figure 2

Frequency patterns of variation in sea-surface temperature and their relationship with generation time. (*a*) Temporal power spectra of sea-surface temperature in the North Pacific open ocean (PAPA; *black*), the California Current [California Current Ecosystem Mooring 2 (CCE2); *green*], and a California estuary (Elkhorn Slough; *red*). In all of these spectra, but especially in the estuarine spectrum, the peaks at frequencies higher than 2/day quantify fluctuations that account for the slightly non-sinusoidal pattern of the daily (1/day) and tidal (~2/day) variations, and would not themselves be noticed by organisms. For the estuary, a small peak is evident at the bimonthly spring–neap frequency of the tides. Vertical red and blue lines indicate frequencies of 1/year and 1/day, respectively. (*b*) Accrued variance in body temperature as a function of generation time for the major groups of marine organisms depicted in **Figure 1*a***. For this heuristic exercise, we unrealistically assumed that body temperature equaled sea-surface temperature. Values were generated by integrating the spectra in panel *a* between the highest frequency and the frequency (or, inversely, the period) associated with the average generation time. For example, a hypothetical copepod's physiology can adjust to changes in temperature that fluctuate once per hour, a frequency of 24/day, and the species has a generation time of 4 weeks, corresponding to a frequency of 0.036/day. Integrating the spectrum between these two frequencies quantifies the total variance in temperature relevant to this species' physiology. Oceanic data are from the NOAA Ocean Carbon Data System (Sutton et al. 2019); Elkhorn Slough data for the Azevedo Pond monitoring site are from the NOAA National Estuarine Research Reserve System (NERRS) System-Wide Monitoring Program's Centralized Data Management Office website (**http://www.nerrsdata.org**).

any two frequencies is the variance associated with that range of frequencies. Spectra for temporal variation of sea-surface temperature in the northeast Pacific Ocean provide a heuristic example (**Figure 2*a***). (These spectra represent data taken at fixed locations in the ocean; spectra from measurements taken in a Lagrangian reference frame would be preferable but are currently not available.) Several messages emerge from a comparison of spectra among these particular marine habitats. First, the overall amount of variation (the total area under the curve) differs from one location to another in this area of the ocean: little variance in open-ocean sea-surface temperature, more in a coastal current, and even more in an estuary. Second, although in each spectrum there is a peak of variation at a frequency of 1/day associated with solar heating, the bulk of variation is spread out among the lower frequencies associated with the tides and variation in atmospheric forcing (weather) and the seasons. Spectra showing this pattern of increasing variance with decreasing frequency are said to be reddened, an analogy to light spectra dominated by low-frequency (red) light. The degree of reddening is proportional to the slope of the spectrum on a log–log plot (as in **Figure 2*a***). In general, marine environmental spectra (with slopes of −0.75 to −1.5) are redder than terrestrial spectra (−0.1 to −0.75) (Steele 1985, Vasseur & Yodzis 2004).

The characteristics of marine power spectra have profound implications for the total variation experienced in an individual's lifetime. As a heuristic exercise, we used the spectra in **Figure 2*a*** to calculate the total variance in temperature an organism would encounter as a function of its lifetime. Accrued variance increases nonlinearly with increasing generation time (**Figure 2*b***), and the shape of this response differs among habitats, with total variance encountered converging only for the longest-lived organisms. Short-lived organisms might experience considerable variance associated with tidal or daily fluctuations in a coastal habitat (**Figure 2*b***), but similar organisms would experience relatively little variance in the open ocean. We look forward to similar analyses based on time series taken from the organism's perspective.

Multiple environmental factors often interact to affect physiology, but understanding the consequences of these interactions requires information about how the various factors are correlated through time. For instance, pressure, temperature, and oxygen concentration each vary with depth. As a result, during its daily vertical migrations an organism would experience cycles in these factors at the same temporal frequency (1/day). But pressure and temperature are negatively correlated—as the organism ascends, pressure decreases and temperature typically increases (i.e., their fluctuations are 180° out of phase)—and this negative correlation must be taken into account when considering the interacting physiological effects of temperature and pressure. Temperature and oxygen concentration likewise fluctuate during vertical migration, but they are typically positively correlated (in phase)—temperature and oxygen concentration both tend to increase as the animal ascends. Just as the power spectrum quantifies the characteristic frequencies at which a single environmental factor varies, the cross spectrum for two environmental factors identifies the frequencies at which the stressors are correlated, and the accompanying coherence and quadrature spectra together quantify the frequency-specific phase shifts between factors (see, e.g., Bendat & Piersol 1986).

For planktonic organisms, spectra of marine environmental drivers would ideally be calculated from time series taken in the Lagrangian reference frame relevant to the organism in question. Direct measurement of such time series is exceedingly difficult, however, resulting in the current dearth of available data on the temporal experiences of individual organisms. However, computational approaches can potentially substitute for direct measurements. For example, temporal variation in mixed-layer light intensity can be modeled from information regarding turbulence intensity and internal wave amplitude and frequency (Denman & Marra 1986), and computational methods have recently been developed for tracking surface water masses (Lagrangian coherent structures; LeHahn et al. 2018) and drifting larvae (e.g., McVeigh et. al 2017, Gary et al. 2020). Coupled with data from Argo buoys (e.g., for temperatures at depth; PacIOOS 2021), these indirect approaches have the potential to provide long-term Lagrangian time series of physiologically relevant environmental factors for planktonic organisms. For large, mobile organisms (e.g., tunas, sharks, turtles, whales, and squid), advances in technology have made it possible to attach data-logging tags that provide high-resolution time series of the factors they encounter as they sample the environment (e.g., Southwood et al. 1999, Schaefer et al. 2007, Gilly et al. 2013, Goldbogen et al. 2017). Chemical analyses of hard parts (such as otolith element or isotope ratios; Kerr et al. 2007) offer another potential avenue for describing time series of environmental experience. Developing similar approaches for the microbiota that numerically dominate in the oceans represents a significant technological challenge.

In summary, most marine organisms are small and planktonic, and the environmental variation they encounter depends in large part on how long they live. However, if an organism can move through the water, the temporal pattern of variation it experiences is often governed by its speed and the spatial gradients available to it. Lifetime, speed, and the availability of gradients are all affected by the organism's size, with both very small organisms (with the largest gradients) and very large organisms (with the greatest speeds) having perhaps the highest potential to encounter environmental variation in their lifetimes. Much work remains before marine scientists can fully translate their understanding of oceanographic patterns and processes into environmental time series for individual marine organisms.

P_{crit}: the partial pressure of oxygen below which an organism cannot sustain the normoxic rate of aerobic metabolism

3. PHYSIOLOGICAL CONSEQUENCES OF ENVIRONMENTAL VARIATION IN THE SEA

The biological consequences of the patterns of environmental variation just described remain understudied (Dowd et al. 2015, Wahl et al. 2015, Boyd et al. 2016, Morash et al. 2018). Ideally, experimental designs targeting the physiological consequences of variation should be informed by detailed knowledge of those patterns. Unfortunately, for a large fraction of marine (and other) organisms, we know too little about the rates, amplitudes, and frequencies of change encountered by individuals over a lifetime (Woods et al. 2014, Dowd et al. 2015).

Are there shortcuts to be taken from generalized oceanic patterns of variation to organismal (or ecological and evolutionary) impacts? In our opinion, no, because important biological complexities interfere at the critical step of translating environmental variation into physiological performance. First, unlike physical aspects of the environment, physiology has few general rules that can be applied across taxa. For example, it is straightforward to calculate for a given shift in temperature the resulting changes in seawater density and buoyancy (Denny 1993). But for that same temperature shift, the idiosyncrasies of physiology complicate estimation of its biological impacts. We might attempt to estimate the resulting change in metabolic rate, for instance, using the traditional Q_{10} relationship (the typical doubling-to-tripling of physiological rates for a 10°C increase in temperature) or universal allometric relationships that describe the scaling of metabolic rate as a function of body mass (Gillooly et al. 2001), but these estimates would have dubious accuracy. Q_{10} values vary among species, and within a species they may vary over ontogeny, over the range of temperatures tested (e.g., Hopkins & Cech 1994, Rosa & Seibel 2010), and between acute (e.g., during vertical migrations) and chronic (e.g., seasonal) temperature shifts (Neer et al. 2006, Costa et al. 2013). Similarly, estimates of allometric exponents range widely among species (White et al. 2019). Relationships between physiology and pH or dissolved oxygen are even less direct. For example, the critical oxygen threshold at which organisms shift from aerobic to anaerobic metabolism (P_{crit}) is species specific (Seibel 2011); the definition of hypoxia thus depends on the organism. Furthermore, unlike physical rules, physiological sensitivities to environmental shifts often have the capacity to change, either via acclimatization (or accumulated damage; Williams et al. 2016) during one individual's lifetime or via longer-term processes, including transgenerational plasticity (Salinas & Munch 2012, Ryu et al. 2018, Rivera et al. 2021) and/or evolution (Kelly et al. 2011, Schaum & Collins 2014). For example, cyclical exposure to hypoxia in qingbo fish led to a decrease in P_{crit} (Dan et al. 2014). The magnitude, rate, and persistence of these temporal adjustments also vary from one organism to the next. These physiological complexities render extrapolation directly from environmental patterns to ecological and/or evolutionary predictions challenging.

In the absence of suitable shortcuts, we advocate for a concerted empirical effort to quantify the physiological consequences of environmental variation, particularly in scenarios where organisms

Review in Advance first posted on July 27, 2021. (Changes may still occur before final publication.)

experience simultaneous fluctuations of several variables during their lifetime (Wahl et al. 2015). In the interest of space, we do not review the effects of univariate environmental shifts on specific physiological traits (Somero et al. 2017). However, several important observations emerge from this body of knowledge.

First, performance in a varying environment can differ dramatically from performance under constant conditions (e.g., Ruel & Ayres 1999, Estay et al. 2014, Vasseur et al. 2014, Dowd et al. 2015). Therefore, it is imperative that experimental designs explicitly incorporate realistic patterns of environmental variation. Unfortunately, much of our knowledge has been derived from single-step experiments in which organisms are abruptly (and unrealistically) moved from one constant environmental state to another. This approach, combined with only a few time points of analysis (as is typical), makes it impossible to discern the temporal dynamics of physiological responses in relation to natural patterns (Tanner & Dowd 2019). Other complications abound. Amplified light intensity due to focusing by surface waves can damage photosynthetic machinery and/or cause photorespiration, and the effect of light fluctuations in different frequency bandwidths is still uncertain (Walsh & Legendre 1983, Stramski et al. 1993, Graham et al. 2017). Diel vertical migrators exhibit circadian rhythms in oxygen consumption rates, even when these organisms are held in constant conditions (Maas et al. 2018).

The second observation is that few, if any, temporal environmental changes encountered by marine organisms are limited to a single variable, whereas traditional experimental designs frequently address one variable at a time. There are legitimate arguments for this reductionist experimental approach, but as we outline below, the combined effects of superimposed environmental fluctuations may not be predictable from single-variable (and single-step) experiments. In other cases, we may be neglecting altogether variables that might alter the experimental results.

3.1. Frameworks for Predicting the Physiological Effects of Environmental Variation

We discuss two promising, complementary frameworks for predicting and evaluating the effects of environmental variation on physiological performance, highlighting important underlying assumptions and limitations of each. Where possible, we offer examples of physiological insights gained from these frameworks. Ultimately, progress will most likely derive from synthetic approaches to problems of environmental variation, using these and other perspectives such as bioenergetics and dynamic energy budgets (Kooijman 2010, Nisbet et al. 2012).

3.1.1. Performance curves and scale-transition theory. Performance curves, a variant of reaction norms, quantify the effect of an environmental parameter on some metric of physiological performance. These curves have long been a standard tool in ecophysiology (Huey & Stevenson 1979), most prominently in thermal physiology (Angilletta 2009). Interest in their applicability to fluctuating environmental conditions surged following Ruel & Ayres's (1999) (re)introduction of biologists to Jensen's inequality, an inherent consequence of nonlinear averaging in which a function's value at constant average conditions does not equal the average of the function's values when conditions vary. On its own, the performance-curve framework offers one means of generating null predictions of the physiological impacts of environmental variation (Estay et al. 2014), but like all predictions, these must be evaluated against empirical data.

The first step is to measure performance (P) in a series of constant conditions to generate a performance curve. Here, we use the thermal performance curve as an example, but the approach can apply to any environmental variable. Scale-transition theory (Chesson et al. 2005) is then used to estimate performance in the presence of environmental variation (reviewed in Dowd et al. 2015).

Scale-transition theory states that, to a first approximation, average performance in a variable thermal environment, $\overline{P(T)}$, is

$$\overline{P(T)} \cong P\left(\bar{T}\right) + \frac{1}{2}P''\left(\bar{T}\right)\ \sigma_T^2. \qquad 2$$

Here, $P(\bar{T})$ is performance at the average temperature, $\bar{T}$; σ_T^2 is the variance of temperature encountered by an organism; and $P''(\bar{T})$ is the second derivative, which describes the function's curvature, evaluated at the average temperature.Several predictions have arisen from the application of Equation 2 (e.g., Ruel & Ayres 1999, Estay et al. 2014, Vasseur et al. 2014, Dowd et al. 2015). First, this framework forecasts that variation around the mean increases mean performance where the $P''(\bar{T})$ of the static performance curve is positive, and variation decreases performance where $P''(\bar{T})$ is negative. Integrative physiological traits such as growth rate—which have unimodal performance curves with a negative $P''(\bar{T})$ throughout—are substantially reduced in fishes reared in fluctuating thermal environments (Morash et al. 2018), generally supporting these predictions. Similarly, a recent thorough study of a coastal phytoplankton species showed that scale-transition theory accurately predicted decreased population growth rates in a fluctuating temperature regime (Bernhardt et al. 2018). However, there are counterexamples (Niehaus et al. 2012, Kingsolver et al. 2015, Marshall et al. 2021). Koussoroplis et al. (2017) generated a set of diagnostic tools for differentiating the underlying causes of these different outcomes. Specifically, they distinguished several categories of time-dependent effects, including reserve/inertia, stress, acclimation, and compensation. Although elegantly described, these categorizations merely facilitate post hoc analysis in the face of empirical data, rather than allowing a priori prediction of performance patterns under realistically fluctuating scenarios. A comprehensive, mechanistic explanation for why nonlinear averaging makes accurate predictions in some scenarios but not in others still eludes physiologists. To fill this gap, physiologists must account for effects of both the amplitude (i.e., whether conditions enter ranges that induce damage) and frequency (i.e., whether conditions fluctuate faster than the organism can respond) of environmental changes. Once sufficient empirical performance data are collected, it may prove possible to draw useful generalizations across organisms, environmental variables, and/or the frequencies of fluctuations; at the moment, any such generalizations would be premature.

The second prediction derived from this framework is that suboptimal is optimal—that is, organisms in fluctuating environments perform best at mean temperatures below their static optimal temperature (Martin & Huey 2008). Whether this prediction applies to marine taxa remains an open question. Bernhardt et al. (2018) found that most of the phytoplankton species in their meta-analysis were collected at locations with mean sea-surface temperatures below their static thermal optimum (4.26°C lower on average). Third, a subtle but potentially critical prediction of performance-curve approaches is that an individual's temporal variation in performance should increase as it experiences environmental fluctuations near either end of its thermal window (Dowd et al. 2015). This third prediction has received little empirical attention. In general, relatively little work has been done to evaluate the predictions of the performance-curve framework for variables other than temperature.

There are at least four important limitations to the application of performance curves and scale-transition theory. First, Equation 2 is reasonably accurate only when variation in the environment is small compared with the breadth of the performance curve. When the temporal (or spatial) series of the environmental driver is known or can be simulated, this problem can be solved by directly averaging the resulting performance values (Benedetti-Cecchi 2005). The second, and much more severe, limitation is that scale-transition theory makes the rash assumption that an organism's physiology does not adjust (or, perhaps more accurately, that it adjusts instantaneously;

Roitberg & Mangel 2016) to changes in the environment. The resulting predictions are thus purely mathematical, ignoring well-documented physiological phenomena such as acclimatization, stress hardening, and carryover effects (Schulte et al. 2011, Dowd et al. 2015, Kingsolver et al. 2015, Williams et al. 2016). Rather than approaching deviations from those predictions with skepticism, we should probably be more surprised to observe data consistent with the predictions of scale-transition theory. Important progress will be made by deducing the mechanistic causes of disparities between performance-curve-based null predictions and empirical observations (Koussoroplis et al. 2017). Third, the static performance-curve measurements are typically made in laboratory settings, which may differ in other substantive ways (e.g., food quality) from the natural environments to which we wish to extrapolate. There are no easy solutions to this limitation. Finally, scale-transition approaches on their own cannot account for the lagged physiological consequences of unusual or extreme events (Dowd et al. 2015, Kingsolver & Woods 2016).

In light of these limitations, extensions or modifications of the performance-curve framework are appealing. Roitberg & Mangel (2016) presented a model incorporating time-dependent shifts in the thermal performance curve's shape following acute heat or cold stress, but this heuristic model is not yet explicitly parameterized by empirical physiological data concerning carryover effects of thermal stress on performance metrics. When combined with measurement of physiological response times, this approach holds great promise. A second potential modification, one we have not seen implemented, would be to incorporate in the scale-transition approach only the portion of variance associated with particular frequencies. From the power spectrum of measured conditions, it would be possible to extract either the variance associated with the dominant frequencies that impact an individual in its lifetime or the fraction of total variance associated with frequencies of physiological importance. Of course, this approach would also rely on physiological data to identify those important frequencies.

3.1.2. Physiological response times. As noted above, the standard performance-curve framework fails to incorporate acclimatization and related temporal shifts in physiological state. One way to approach this shortcoming is via measurements of the characteristic physiological response time—the time required for a system to respond to change by reaching (or returning to) steady state. For example, for an organism exposed to a step increase in temperature, the consequent production of heat-shock proteins might reach 90% of its eventual maximum level within 3 h. Note that the response time of an upward change in input need not be the same as the response time to a downward change (Moyen et al. 2020a,b), and this nuance requires more thorough evaluation in physiological studies.

Knowing an organism's physiological response times allows one to appropriately assess the pattern (e.g., the spectrum; **Figure 2*a***) in which the environment varies over an organism's lifetime. The inverse of frequency (i.e., the period) indicates how much time must pass to complete one full cycle. If the period of dominant environmental fluctuations is shorter than the response time, little is gained by an organism attempting to compensate for those fluctuations (Denman & Marra 1986). By contrast, fluctuations with periods longer than the response time may be nearly perfectly compensated by physiology. Of course, this relies on the physiological response also being of sufficient magnitude to cope with the amplitude of environmental fluctuations. Other complications can intrude here. Several physiological components might respond to a shift in the environment but have different response times, making it difficult to meaningfully characterize "the" response time. Nonetheless, even approximate estimation of physiological response times can be a useful first step when exploring the interaction between environmental variation and performance.

Unfortunately, measurements of response times are rare in the literature, owing at least in part to the difficulty of repeatedly monitoring an organism's physiological status. In this respect, rapid light curves and pulse amplitude modulated (PAM) fluorescence techniques—which allow noninvasive, rapid characterization of the photosynthetic machinery's current state and its responsiveness to changing conditions—provide a distinct advantage for researchers studying response times of the ocean's primary producers (Juneau & Harrison 2005, Ralph & Gademann 2005). Using data derived from similar approaches, Denman & Marra (1986) developed a response-time model for marine phytoplankton acclimating to fluctuating light levels. The model explicitly accounted for the lagged, inhibitory effects of prior light exposure on photosynthetic capacity, and by so doing accurately predicted a reduced photosynthetic rate at midday despite high irradiance levels. Importantly, the model demonstrated that photoacclimation must occur with a response time shorter than the period of the light fluctuations if it is to rescue photosynthetic rates from the depressing effects of Jensen's inequality. In a similar example, estimates of turbulent mixing were combined with photosynthetic-rate response times to illustrate that if the physiological response is slow relative to the timescale of changes in light intensity (due to turbulence-induced depth change), cells mixed closer to the surface would be unable to capitalize on the favorable light conditions (Lewis et al. 1984). On days with less mixing, however, cells near the surface would enjoy high photosynthetic rates. Light-based techniques also benefit from a detailed mechanistic understanding of photoinhibition and other processes that govern response times (e.g., damage to the PsbA subunit of photosystem II; Key et al. 2010). Analogous, noninvasive approaches to real-time monitoring of metabolic physiology in marine animals would represent a significant leap forward. The key limitation of this response-time framework is that it demands time-consuming physiological measurements under a variety of conditions, but this should not dissuade marine scientists.

Like scale-transition theory, the response-time framework leads to predictions that can guide empirical physiological studies. First and foremost, the plasticity and flexibility of physiological performance are predicted to be a function of the dominant spectral components of experienced variation. Specifically, to have mitigating effects on average performance, the response time for physiological plasticity should be shorter than the period(s) with the highest spectral power. Environmental histories dominated by low-frequency variation—for example, a long-lived organism experiencing primarily seasonal cycles of sea-surface temperature in the open ocean (**Figure 2*a***)—would be expected to promote (or permit) slow response times. These slow responses might be overlooked by all but the longest physiological studies, perhaps being misinterpreted as a lack of physiological plasticity altogether. At the other extreme, it is unlikely that physiological plasticity would respond to fluctuations at very high frequencies; the energetic costs of constantly rewiring the biochemical infrastructure would be excessive. Instead, physiological consequences of very-high-frequency fluctuations are more likely driven by passive effects on biochemical and physiological systems (e.g., Schulte et al. 2011). In between these extremes, outcomes of fluctuating conditions likely depend on the relationship between frequency and the response times of key physiological processes (e.g., Graham et al. 2017).

Rigorous tests of these predictions again require experimental designs and timescales that match the nature of the environmental fluctuations as experienced by each type of organism. We suspect that additional physiological data from these sorts of studies will provide nuanced refinements of past observations. For example, a meta-analysis of the plasticity of thermal tolerance limits found no correlation with a rough index of seasonality (Gunderson & Stillman 2015). A more refined approach might map the kinetics of plasticity onto the dominant frequencies (and amplitudes) of variation experienced over a generation in each species' habitat. In summary, empirical physiological response times, which are relatively straightforward (albeit time-consuming) to measure, have great potential to refine our predictions of the physiological consequences of environmental variation.

3.2. Environmental Variation Is Often Inherently Multivariate

The frameworks just described are relatively well developed for single environmental factors such as temperature and light, but, as noted in Section 2.4, many environmental gradients in the sea are inherently multivariate. Covarying parameters can have complex impacts on physiological function that are difficult to predict a priori. Simultaneous or sequential shifts in multiple parameters can generate additive, antagonistic (a second factor offsets or mitigates effects of the first), or synergistic (a second factor amplifies impacts of the first) effects on physiological performance (Crain et al. 2008, Calosi et al. 2013, Todgham & Stillman 2013, Gunderson et al. 2016). For example, a prominent theory proposes that oxygen limitation should synergistically exacerbate the effects of thermal stress for aquatic organisms (Pörtner 2010). While there are data supporting this theory, there also exists a growing list of counterexamples that raise questions about the universality of this synergistic effect (Jutfelt et al. 2018 and references therein).

We explore the inherent complexity of physiological responses to multiple fluctuating parameters using two examples of broad significance to life in the oceans. The first involves phytoplankton in the ocean's surface mixed layer, where they experience vertical movements due to turbulence, internal waves, sinking, and in some cases their own behavior. These vertical movements result in roughly cyclical changes in ambient light intensity (generating fluctuations that are superimposed on the day–night cycle), nutrients (typically higher concentrations at depth), and often temperature (lower near the thermocline). For mobile dinoflagellates, vertical movements appear to balance a need for light with access to nutrients at depth (e.g., Cullen 1985, Watanabe et al. 1988), leading to an inherent temporal separation of nutrient acquisition and nutrient utilization. In the case of an experimental freshwater phytoplankton community (admittedly not marine, but one of the most comprehensive recent examples), thermal fluctuations decreased population growth rates overall, as predicted by scale-transition theory (Gerhard et al. 2019). However, the influence of temperature fluctuations interacted with N:P nutrient ratios to reshape the thermal performance function in a complex fashion. To fully capture the experience of individual phytoplankton cells in the mixed layer, physiological experiments will need to mimic fluctuations in all of these parameters simultaneously.

For the second example, we consider DVM, one of the most dramatic movements of biomass on the planet. As noted previously, this behavior is exhibited by a wide range of marine organisms, which potentially encounter daily fluctuations of several variables. Of these, the relationships between oxygen availability (less at depth, especially if DVM is of sufficient amplitude to reach the OMZ) and temperature have received the most attention (Seibel 2011). In some cases, it has been hypothesized that these factors offset one another. For example, *Calanus* copepods may benefit energetically from reduced energy expenditures during the deep, hypoxic portion of their diel cycle (∼110-m amplitude). Routine aerobic metabolic rates decreased roughly sevenfold when copepods were sequentially exposed to a 14°C decrease in temperature followed by a gradual decrease in dissolved oxygen (Svetlichny et al. 2000). Similarly, the apparent P_{crit} for Nordic krill is lower at 7°C than at 15°C due to a concomitant decrease in metabolic turnover (Strömberg & Spicer 2000), making them ostensibly more tolerant of hypoxia when in cold water. In other respects, however, physiological data suggest that animals that practice DVM might be pushing their functional limits. The amphipod *Phronima sedentaria* may tolerate elevated near-surface temperatures only for the duration of its diel residence high in the water column; longer exposures induced thermal stress (Elder & Seibel 2015). In jumbo squid, there is an 82% decline in aerobic metabolic rate under low-temperature, low-oxygen conditions typical of deep dives, with anaerobic metabolism offsetting only a small percentage (∼7%) of this metabolic depression (Rosa & Seibel 2008). The associated constraints on ATP turnover rates while at depth limit metabolic processes for much of a squid's life. Similarly, the Nordic krill mentioned above appear to approach their physiological limits for supporting metabolism via anaerobic pathways when at depth (Spicer et al. 1999). Furthermore, Spicer & Strömberg (2002) hypothesized that these krill metabolize the respiratory pigment hemocyanin when they are food limited during the deep phase of their diel cycle. This nutritional use of hemocyanin further compromises the ability to acquire oxygen to support feeding activity on the next ascent. In light of these examples, we suggest that the physiological ramifications of DVM are anything but straightforward.

Two additional points merit consideration. First, as noted above, much of what we do know about DVM physiology is derived from single-step experiments (e.g., Saborowski et al. 2000, Strömberg & Spicer 2000, Liszka et al. 2021), in which organisms are either collected at one of two depths or transferred in the laboratory between two disparate environmental conditions. The constraints of ship time and space likely play a role in these experimental-design choices, but this logistical constraint cannot be used to dismiss the need for more realistic experiments that re-create fluctuating conditions.

Second, laboratory experiments regarding the physiology of DVM have nearly always neglected to account for the effects of hydrostatic pressure changes that inherently accompany DVM. Even moderate amplitudes of migration near the surface (70–100 m; e.g., Spicer et al. 1999, Häfker et al. 2017) involve roughly order-of-magnitude changes in ambient pressure. For the wide variety of organisms that traverse even greater vertical distances each day, changes in pressure can reach nearly 100 atm. This hidden variable can impact a variety of physiological processes and structures, including enzyme substrate-binding kinetics and membrane properties (Somero 1992, Yancey 2020). For example, changes in pressure of less than 75 atm can appreciably reduce the binding affinity of metabolic enzymes for their substrates (Somero 1992). Membrane composition also shifts in a consistent manner with increasing depth of capture in fishes, implying the need for physiological compensation for pressure changes (Cossins & MacDonald 1984, Cossins & Macdonald 1986). The inner mitochondrial membrane, in particular, is packed with enzymes of the electron transport chain, and the structural flexibility of these enzymes in their lipid environment is crucial for aerobic ATP production (Somero et al. 2017). A pressure change of a few tens of atmospheres (i.e., a change in depth of a few hundred meters) can disrupt neuronal conductance and the movement of solutes across membranes of shallow-dwelling organisms (Somero 1992). Given these intricate connections, and the rapid daily pace of pressure change during DVM, it is reasonable to hypothesize that pressure effects could alter some previously documented patterns—for example, regarding combined effects of temperature and oxygen on aerobic metabolic rates. Unfortunately, the effects of pressure on the physiological function of organisms practicing DVM and other vertical movements remain almost entirely undescribed (Yancey 2020). Vertically migrating animals may modulate extrinsic factors, such as the cellular concentrations of protein-protective piezolytes [e.g., trimethylamine *N*-oxide (TMAO); Yancey et al. 2014, Yancey 2020], as they move through the water column. However, even if these mechanisms maintain roughly constant functional capacity, they may be energetically costly to adjust on a diel basis. What remains to be clarified are the effects of combined and repeated fluctuations in pressure, temperature, dissolved oxygen, and/or pH that are experienced during DVM.

Once the relevant environmental patterns are known, the greatest challenges to implementing the necessary multivariate experiments are technological. It is fairly routine to manipulate temperature, oxygen, salinity or even pH in a cyclical fashion in the laboratory. Similarly, advances in technology now allow not only for precise control of shifting irradiance levels but also for manipulation of the spectral characteristics of light reaching photosynthetic organisms. Although manipulating more than one of these factors at a time is much less common, there are recent examples of systems that enable complex experimental fluctuations (e.g., Paganini et al. 2014, Bonnefond et al. 2016, Burrell et al. 2016, Huesemann et al. 2017, Dinh et al. 2020). However, given the constraints of high-pressure chambers, combining the study of any of these parameters with fluctuations in pressure represents a much more significant hurdle. In light of the importance of the information that would result, we call on marine scientists and engineers to swiftly develop the technology necessary to include pressure in the list of covarying environmental factors that can be manipulated in physiological measurements.

Can we apply the predictive frameworks outlined above for incorporating the physiological effects of multiple covarying parameters? Fortunately, others have recently laid the foundation. For example, Koussoroplis et al. (2017) described a mathematical approach that extends scale-transition theory to include both parameter-specific and covariance effects of multiple parameters on performance. This mathematical framework allows researchers to partition the variance in performance among these contributing factors. Application of this approach to marine systems may be facilitated by the fact that many environmental drivers are strongly correlated, thereby constraining the number of possible environmental scenarios that must be evaluated.

4. CONCLUSION: RECONCILING ENVIRONMENTAL VARIATION WITH PHYSIOLOGICAL PERFORMANCE

Due to the idiosyncrasies of biological systems, there currently is no substitute for empirical physiological studies of marine organisms facing realistic patterns of environmental variation. That said, depending on the ultimate objectives, these investigations do not necessarily require a detailed, mechanistic understanding at the level of cells or molecules. Rather, in many instances it may be sufficient, at least at the outset, to treat physiological mechanisms as a black box, measuring simple, integrative, and ecologically relevant response variables such as growth rate or reproductive output. Even so, the complexity of individual environmental experiences and the nuances of multifactorial environments will demand far more complex experimental designs than are currently the norm (Dowd et al. 2015, Wahl et al. 2015, Koussoroplis et al. 2017). Once patterns are described at this integrative level, it is incumbent upon physiologists to fill in the mechanistic details that produce outputs from the black box, and specifically to better characterize response times for physiological processes such as photoacclimation, the turnover of transient carbon (Halsey & Jones 2015) in phytoplankton, membrane restructuring, and TMAO accumulation. This more detailed level of understanding may very well be needed to forecast mechanistic responses beyond the range of current conditions—for example, in the context of climatic changes that may alter the frequency, magnitude, or covariance patterns of environmental fluctuations (Wahl et al. 2015, Boyd et al. 2016).

Climate change may also increase the frequency of extreme deviations from the norm, during which environmental drivers exceed individuals' physiological tolerances (e.g., Rahmstorf & Coumou 2011). These extreme events, which we have not addressed, can have substantial consequences for population dynamics and evolution. Only recently have they become a focus for study in marine systems (e.g., Denny et al. 2009, Frölicher et al. 2018, Harris et al. 2018, Dowd & Denny 2020, Oliver et al. 2021). As with lesser variations, understanding the biological consequences of extreme events will require a mechanistic understanding of physiology.

Unfortunately, knowledge of mean patterns within a population (as discussed above) may not be sufficient to accurately predict the future. There has been relatively little consideration of regional, inter-day, and inter-individual variation in patterns of environmental variation experienced, or of variation in the physiological capabilities to cope with those environmental changes. For example, in the context of DVM, there is the possibility of partial migration within a single population (Frost 1988, Cresswell et al. 2009, Ogonowski et al. 2013). In other species, discrete life-history stages occupy different depth ranges or otherwise vary in their environmental experiences (Yancey 2020). Ultimately, marine physiologists require a better understanding of how performance varies among individuals in a population, how much of this variation among individuals is genetically (and/or epigenetically) determined, and whether the dominant axes of that inter-individual variation align with selective pressures imposed by global change.

Furthermore, our discussion has focused on patterns of variation within one individual organism's lifetime, whereas populations have the potential to respond over generations. Indeed, recent work with *Ostreococcus* demonstrated that populations adapted to fluctuating $p\mathrm{CO}_2$ levels had greater potential to respond to further shifts in $p\mathrm{CO}_2$ than populations adapted to the mean (Schaum et al. 2016). The same species exhibits greater adaptive potential in populations that have maintained higher physiological plasticity due to their exposure to environmental fluctuations (Schaum & Collins 2014). Recent work in short-lived terrestrial arthropods shows that seasonal fluctuations—which are experienced as monotonic trends by any one generation—elicit seasonally oscillating evolutionary changes in physiology (Bergland et al. 2014). More observations of these biological nuances will help to fully parameterize the potential for species to respond to global change.

To then translate species-specific patterns to larger-scale ecological forecasts, we also must better appreciate whether species within a community have similar performance responses to the same types of fluctuations and whether they experience the environmental change differently (e.g., Broitman et al. 2009, Kroeker & Sanford 2022). For example, sympatric species may differ in the typical amplitude of DVM, particularly when there is a pronounced OMZ (Tutasi & Escribano 2020).

These important long-term research goals are predicated on a more refined understanding of the patterns of present-day environmental variation in the sea—specifically, how marine organisms experience the oceanic weather (Bates et al. 2018)—and of the consequences for individuals. Barring that knowledge (and it is a high bar), our ability to predict, and thereby potentially to ameliorate, the effects of climate change will be severely constrained. We call on the field of global change biology to develop the necessary technology and undertake the difficult empirical work required to achieve these invaluable insights.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank Margaret McManus for comprehensive and constructive suggestions. M.W.D. and W.W.D. were supported by National Science Foundation grants IOS-1655529 and IOS-1655822, respectively.

LITERATURE CITED

Angilletta MJ Jr. 2009. *Thermal Adaptation: A Theoretical and Empirical Synthesis*. Oxford, UK: Oxford Univ. Press

Bar-On YM, Phillips R, Milo R. 2018. The biomass distribution on Earth. *PNAS* 115:6506–11

Bates AE, Helmuth B, Burrows MT, Duncan MI, Garrabou J, et al. 2018. Biologists ignore ocean weather at their peril. *Nature* 560:299–301

Bendat JS, Piersol AG. 1986. *Random Data: Analysis and Measurement Procedures*. New York: Wiley-Intersci.

A monumental effort to account for the distribution of biomass among all organisms on Earth.

Benedetti-Cecchi L. 2005. Unanticipated impacts of spatial variance of biodiversity on plant productivity. *Ecol. Lett.* 8:791–99

Bergland AO, Behrman EL, O'Brien KR, Schmidt PS, Petrov DA. 2014. Genomic evidence of rapid and stable adaptive oscillations over seasonal time scales in *Drosophila*. *PLOS Genet*. 10:e1004775

Bernhardt JR, Sunday JM, Thompson PL, O'Connor MI. 2018. Nonlinear averaging of thermal experience predicts population growth rates in a thermally variable environment. *Proc. R. Soc. B* 285:20181076

Bonnefond H, Moelants N, Talec A, Bernard O, Sciandra A. 2016. Concomitant effects of light and temperature diel variations on the growth rate and lipid production of *Dunaliella salina*. *Algal Res*. 14:72–78

Boyd PW, Cornwall CE, Davison A, Doney SC, Fourquez M, et al. 2016. Biological responses to environmental heterogeneity under future ocean conditions. *Glob. Change Biol.* 22:2633–50

Broitman BR, Szathmary PL, Mislan KAS, Blanchette CA, Helmuth B. 2009. Predator-prey interactions under climate change: the importance of habitat versus body temperature. *Oikos* 118:219–24

Burrell RB, Keppel AG, Clark VM, Breitburg DL. 2016. An automated monitoring and control system for flow-through co-cycling hypoxia and pH experiments. *Limnol. Oceanogr. Methods* 14:168–85

Calosi P, Turner LM, Hawkins M, Bertolini C, Nightingale G, et al. 2013. Multiple physiological responses to multiple environmental challenges: an individual approach. *Integr. Comp. Biol.* 53:660–70

Chesson P, Donahue MJ, Melobourne B, Sears AL. 2005. Scale transition theory for understanding mechanisms in metacommunities. In *Metacommunities: Spatial Dynamics and Ecological Communities*, ed. M Holyoak, MA Leibold, RD Holt, pp. 279–306. Chicago: Univ. Chicago Press

Coffey DM, Royer MA, Meyer CG, Holland KN. 2020. Diel patterns in swimming behavior of a vertically migrating deepwater shark, the bluntnose sixgill (*Hexanchus griseus*). *PLOS ONE* 15:e0228253

Connor KM, Gracey AY. 2011. Circadian cycles are the dominant transcriptional rhythm in the intertidal mussel *Mytilus californianus*. *PNAS* 108:16110–15

Cossins AR, MacDonald AG. 1984. Homeoviscous theory under pressure: II. The molecular order of membranes from deep-sea fish. *Biochim. Biophys. Acta Biomembr.* 776:144–50

Cossins AR, MacDonald AG. 1986. Homeoviscous adaptation under pressure. III. The fatty acid composition of liver mitochondrial phospholipids of deep-sea fish. *Biochim. Biophys. Acta Biomembr.* 860:325–35

Costa IASF, Driedzic WR, Gamperl AK. 2013. Metabolic and cardiac responses of cunner *Tautogolabrus adspersus* to seasonal and acute changes in temperature. *Physiol. Biochem. Zool.* 86:233–44

Crain CM, Kroeker KJ, Halpern BS. 2008. Interactive and cumulative effects of multiple human stressors in marine systems. *Ecol. Lett.* 11:1304–15

Cresswell KA, Tarling GA, Thorpe SE, Burrows MT, Wiedenmann J, Mangel M. 2009. Diel vertical migration of Antarctic krill (*Euphausia superba*) is flexible during advection across the Scotia Sea. *J. Plankton Res.* 31:1265–81

Cullen JJ. 1985. Diel vertical migration by dinoflagellates: roles of carbohydrate metabolism and behavioral flexibility. *Contrib. Mar. Sci.* 27(Suppl.):135–52

Dan X-M, Yan G-J, Zhang A-J, Cao Z-D, Fu S-J. 2014. Effects of stable and diel-cycling hypoxia on hypoxia tolerance, postprandial metabolic response, and growth performance in juvenile qingbo (*Spinibarbus sinensis*). *Aquaculture* 428–29:21–28

D'Asaro EA. 2001. Turbulent vertical kinetic energy in the ocean mixed layer. *J. Phys. Oceanogr.* 31:3530–37

Denman KL, Gargett AE. 1983. Time and space scales of vertical mixing and advection of phytoplankton in the upper ocean. *Limnol. Oceanogr.* 28:801–15

Denman KL, Marra J. 1986. Modelling the time dependent photoadaptation of phytoplankton to fluctuating light. In *Marine Interfaces Ecohydrodynamics*, ed. JCJ Nihoul, pp. 341–59. Elsevier Oceanogr. Ser. 42. Amsterdam: Elsevier

Denny MW. 1993. *Air and Water: The Physics of Life's Media*. Princeton, NJ: Princeton Univ. Press

Denny MW. 2008. *How the Ocean Works: An Introduction to Oceanography*. Princeton, NJ: Princeton Univ. Press

Denny MW. 2016. *Ecological Mechanics: Principles of Life's Physical Interaction*. Princeton, NJ: Princeton Univ. Press

Denny MW, Dowd WW, Bilir L, Mach KJ. 2011. Spreading the risk: small-scale body temperature variation among intertidal organisms and its implications for species persistence. *J. Exp. Mar. Biol. Ecol.* 400:175–90

Denny MW, Hunt LJH, Miller LP, Harley CDG. 2009. On the prediction of extreme ecological events. *Ecol. Monogr.* 79:397–421

Diggle PJ. 1990. *Time Series: A Biostatistical Introduction*. Oxford, UK: Clarendon

Dillon ME, Woods HA, Wang G, Fey SB, Vasseur DA, et al. 2016. Life in the frequency domain: the biological impacts of changes in climate variability at multiple time scales. *Integr. Comp. Biol.* 56:14–30

Dinh KV, Cuevas-Sanchez AY, Buhl KS, Moeser EA, Dowd WW. 2020. Heat tolerance and thermal preference of the copepod *Tigriopus californicus* are insensitive to ecologically relevant dissolved oxygen levels. *Sci. Rep.* 10:18885

Doney SC, Fabry VJ, Feely RA, Kleypas JA. 2009. Ocean acidification: the other CO_2 problem. *Annu. Rev. Mar. Sci.* 1:169–92

Doney SC, Ruckelshaus M, Duffy JE, Barry JP, Chan F, et al. 2012. Climate change impacts on marine ecosystems. *Annu. Rev. Mar. Sci.* 4:11–37

Dong Y, Li X, Choi FMP, Williams GA, Somero GN, Helmuth B. 2017. Untangling the roles of microclimate, behaviour and physiological polymorphism in governing vulnerability of intertidal snails to heat stress. *Proc. R. Soc. B* 284:20162367

Dowd WW, Denny MW. 2020. A series of unfortunate events: characterizing the contingent nature of physiological extremes using long-term environmental records. *Proc. R. Soc. B* 287:20192333

Dowd WW, King FA, Denny MW. 2015. Thermal variation, thermal extremes, and the physiological performance of individuals. *J. Exp. Biol.* 218:1956–67

Elder LE, Seibel BA. 2015. The thermal stress response to diel vertical migration in the hyperiid amphipod *Phronima sedentaria*. *Comp. Biochem. Physiol. A* 187:20–26

Estay SA, Lima M, Bozinovic F. 2014. The role of temperature variability on insect performance and population dynamics in a warming world. *Oikos* 123:131–40

Frölicher TL, Fischer EM, Gruber N. 2018. Marine heatwaves under global warming. *Nature* 560:360–64

Frost BW. 1988. Variability and possible adaptive significance of diel vertical migration in *Calanus pacificus*, a planktonic marine copepod. *Bull. Mar. Sci.* 43:675–94

Gary SF, Fox AD, Biastoch A, Roberts JM, Cunningham SA. 2020. Larval behaviour, dispersal and population connectivity in the deep sea. *Sci. Rep.* 10:10675

Gates DM. 1980. *Biophysical Ecology*. New York: Springer

Gemmell BJ, Oh G, Buskey EJ, Villareal TA. 2016. Dynamic sinking behavior in marine phytoplankton: rapid changes in buoyancy may aid nutrient uptake. *Proc. R. Soc. B* 283:20161126

Gerhard M, Koussoroplis AM, Hillebrand H, Striebel M. 2019. Phytoplankton community responses to temperature fluctuations under different nutrient concentrations and stoichiometry. *Ecology* 100:e02834

Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL. 2001. Effects of size and temperature on metabolic rate. *Science* 293:2248–51

Gilly WF, Beman J, Litvin SY, Robison BH. 2013. Oceanographic and biological effects of shoaling of the oxygen minimum zone. *Annu. Rev. Mar. Sci.* 5:393–420

Goldbogen JA, Cade DE, Boersma AT, Calambokidis J, Kahane-Rapport SR, et al. 2017. Using digital tags with integrated video and inertial sensors to study moving morphology and associated function in large aquatic vertebrates. *Anat. Rec.* 300:1935–41

Goldbogen JA, Calambokidis J, Oleson E, Potvin J, Pyeson ND, et al. 2011. Mechanics, hydrodynamics and energetics of blue whale lunge feeding efficiency: dependence on krill density. *J. Exp. Biol.* 214:131–46

Gough WT, Segre PS, Bierlich KC, Cade DE, Potvin J, et al. 2019. Scaling of swimming performance in baleen whales. *J. Exp. Biol.* 222:jeb204172

Graham PJ, Nguyen B, Burdyny T, Sinton D. 2017. A penalty on photosynthetic growth in fluctuating light. *Sci. Rep.* 7:12513

Gunderson AR, Armstrong EJ, Stillman JH. 2016. Multiple stressors in a changing world: the need for an improved perspective on physiological responses to the dynamic marine environment. *Annu. Rev. Mar. Sci.* 8:357–78

Gunderson AR, Stillman JH. 2015. Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming. *Proc. R. Soc. B* 282:20150401

Häfker NS, Meyer B, Last KS, Pond DW, Hüppe L, Teschke M. 2017. Circadian clock involvement in zooplankton diel vertical migration. *Curr. Biol.* 27:2194–201.e3

Halsey KH, Jones BM. 2015. Phytoplankton strategies for photosynthetic energy allocation. *Annu. Rev. Mar. Sci.* 7:265–97

Harris RMB, Beaumont LJ, Vance TR, Tozer CR, Remenyi TA, et al. 2018. Biological responses to the press and pulse of climate trends and extreme events. *Nat. Clim. Change* 8:579–87

Hays GC. 2003. A review of the adaptive significance and exosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia* 503:163–70

Helmuth B. 2002. How do we measure the environment? Linking intertidal thermal physiology and ecology through biophysics. *Integr. Comp. Biol.* 42:83745

Hofmann GE, Smith JE, Johnson KS, Send U, Levin LA, et al. 2011. High-frequency dynamics of ocean pH: a multi-ecosystem comparison. *PLOS ONE* 6:e28983

Hopkins TE, Cech JJ Jr. 1994. Effect of temperature on oxygen consumption of the bat ray, *Myliobatis californica* (Chondrichthyes, Myliobatididae). *Copeia* 1994:529–32

Howell EA, Hawn DR, Polovina JJ. 2010. Spatiotemporal variability in bigeye tuna (*Thunnus obesus*) dive behavior in the central Pacific Ocean. *Prog. Oceanogr.* 86:81–93

Huesemann M, Dale T, Chavis A, Crowe B, Twary S, et al. 2017. Simulation of outdoor pond cultures using indoor LED-lighted and temperature-controlled raceway ponds and Phenometrics photobioreactors. *Algal Res*. 21:178–90

Huey RB, Stevenson RD. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *Am. Zool.* 19:357–66

Jerlov NG. 1976. *Marine Optics*. Amsterdam: Elsevier

Juneau P, Harrison PJ. 2005. Comparison by PAM fluorometry of photosynthetic activity of nine marine phytoplankton grown under identical conditions. *Photochem. Photobiol.* 81:649–53

Jutfelt F, Norin T, Ern R, Overgaard J, Wang T, et al. 2018. Oxygen- and capacity-limited thermal tolerance: blurring ecology and physiology. *J. Exp. Biol.* 221:jeb169615

Kelly MW, Sanford E, Grosberg RK. 2011. Limited potential for adaptation to climate change in a broadly distributed marine crustacean. *Proc. R. Soc. B* 279:20110542

Kennish MJ. 1989. *Practical Handbook of Marine Science*. Boca Raton, FL: CRC

Kerr LA, Secor DH, Kraus RT. 2007. Stable isotope (δ^{13}C and δ^{18}O) and Sr/Ca composition of otoliths as proxies for environmental salinity experienced by an estuarine fish. *Mar. Ecol. Prog. Ser.* 349:245–53

Key T, McCarthy A, Campbell DA, Six C, Roy S, Finkel ZV. 2010. Cell size trade-offs govern light exploitation strategies in marine phytoplankton. *Environ. Microbiol.* 12:95–104

Kingsolver JG, Higgins JK, Augustine KE. 2015. Fluctuating temperatures and ectotherm growth: distinguishing non-linear and time-dependent effects. *J. Exp. Biol.* 218:2218–25

Kingsolver JG, Woods HA. 2016. Beyond thermal performance curves: modeling time-dependent effects of thermal stress on ectotherm growth rates. *Am. Nat.* 187:283–94

Kiørboe T. 2008. *A Mechanistic Approach to Plankton Ecology*. Princeton, NJ: Princeton Univ. Press

An innovative and thorough explanation of how mechanistic approaches can provide insight into plankton ecology.

Kiørboe T. 2011. How zooplankton feed: mechanisms, traits and trade-offs. *Biol. Rev.* 86:311–39

Kooijman SALM. 2010. *Dynamic Energy Budget Theory for Metabolic Organisation*. Cambridge, UK: Cambridge Univ. Press

Koussoroplis A-M, Pincebourde S, Wacker A. 2017. Understanding and predicting physiological performance of organisms in fluctuating and multifactorial environments. *Ecol. Monogr.* 87:178–97

An innovative extension of scale-transition theory that incorporates temporal variation among multiple environmental drivers.

Kroeker KJ, Sanford E. 2022. Ecological leverage points: species interactions amplify the physiological effects of global environmental change in the ocean. *Annu. Rev. Mar. Sci.* 14:In press

Lawson GL, Castelton MR, Block BA. 2010. Movements and diving behavior of Atlantic bluefin tuna *Thunnus thynnus* in relation to water column structure in the northwestern Atlantic. *Mar. Ecol. Prog. Ser.* 400:245–65

Lehahn Y, d'Ovidio F, Koren I. 2018. A satellite-based Lagrangian view on phytoplankton dynamics. *Annu. Rev. Mar. Sci.* 10:99–119

Lesser MP, Farrell JH. 2004. Exposure to solar radiation increases damage to both host tissues and algal symbionts of corals during thermal stress. *Coral Reefs* 23:367–77

Levin LA, Le Bris N. 2015. The deep ocean under climate change. *Science* 350:766–68

Lewis MR, Horne EPW, Cullen JJ, Oakey NS, Platt T. 1984. Turbulent motions may control phytoplankton photosynthesis in the upper ocean. *Nature* 311:49–50

Liszka CM, Robinson C, Manno C, Stowasser G, Tarling GA. 2021. Diel vertical migration of a Southern Ocean euphausiid, *Euphausia triacantha*, and its metabolic response to consequent short-term temperature changes. *Mar. Ecol. Prog. Ser.* 660:37–52

Maas AE, Blanco-Bercial L, Lo A, Tarrant AM, Timmins-Schiffman E. 2018. Variations in copepod proteome and respiration rate in association with diel vertical migration and circadian cycle. *Biol. Bull.* 235:30–42

Madigan DJ, Carlisle AB, Gardner LD, Jayasundara N, Micheli F, et al. 2015. Assessing niche width of endothermic fish from genes to ecosystem. *PNAS* 112:8350–55

Marshall KE, Anderson KM, Brown NEM, Dytnerski JK, Flynn KL, et al. 2021. Whole-organism responses to constant temperatures do not predict responses to variable temperatures in the ecosystem engineer *Mytilus trossulus*. *Proc. R. Soc. B* 288:20202968

Martin TL, Huey RB. 2008. Why "suboptimal" is optimal: Jensen's inequality and ectotherm thermal preferences. *Am. Nat.* 171:E102–18

McHenry MJ, Jed J. 2003. The ontogenetic scaling of hydrodynamics and swimming performance in jellyfish (*Aurelia aurita*). *J. Exp. Biol.* 206:4125–37

McVeigh DM, Eggleston DB, Todd AC, Young CM, He R. 2017. The influence of larval migration and dispersal depth on potential trajectories of a deep-sea bivalve. *Deep-Sea Res. I* 127:57–64

Miklasz KA, Denny MW. 2010. Diatom sinking speeds: improved predictions and insight from a modified Stokes' law. *Limnol. Oceanogr.* 55:2513–25

Morash AJ, Neufeld C, MacCormack TJ, Currie S. 2018. The importance of incorporating natural thermal variation when evaluating physiological performance in wild species. *J. Exp. Biol.* 221:jeb164673

Moyen NE, Crane RL, Somero GN, Denny MW. 2020a. A single heat-stress bout induces rapid and prolonged heat acclimation in the California mussel, *Mytilus californianus*. *Proc. R. Soc. B* 287:20202561

Moyen NE, Somero GN, Denny MW. 2020b. Mussel acclimatization to high, variable temperatures is lost slowly upon transfer to benign conditions. *J. Exp. Biol.* 223:jeb222893

Neer JA, Carlson JK, Thompson BA. 2006. Standard oxygen consumption of seasonally acclimatized cownose rays, *Rhinoptera bonasus* (Mitchill 1815), in the northern Gulf of Mexico. *Fish Physiol. Biochem.* 32:67–71

Niehaus AC, Angilletta MJ, Sears MW, Franklin CE, Wilson RS. 2012. Predicting the physiological performance of ectotherms in fluctuating thermal environments. *J. Exp. Biol.* 215:694–701

Nisbet RM, Jusup M, Klanjscek T, Pecquerie L. 2012. Integrating dynamic energy budget (DEB) theory with traditional bioenergetic models. *J. Exp. Biol.* 215:892–902

Ogonowski M, Duberg J, Hansson S, Gorokhova E. 2013. Behavioral, ecological and genetic differentiation in an open environment—a study of a mysid population in the Baltic Sea. *PLOS ONE* 8:e57210

Oliver ECJ, Benthuysen JA, Darmaraki S, Donat MG, Hobday AJ, et al. 2021. Marine heatwaves. *Annu. Rev. Mar. Sci.* 13:313–42

Oliver TA, Palumbi SR. 2011. Do fluctuating temperature environments elevate coral thermal tolerance? *Coral Reefs* 30:429–40

PacIOOS (Pac. Isl. Ocean Obs. Syst.). 2021. Water temperature forecast: western North Pacific. *PacIOOS*. **http://www.pacioos.hawaii.edu/water/model-temperature-wnpacific**

Paganini AW, Miller NA, Stillman JH. 2014. Temperature and acidification variability reduce physiological performance in the intertidal zone porcelain crab *Petrolisthes cinctipes*. *J. Exp. Biol.* 217:3974–80

Pickard GL. 1964. *Descriptive Physical Oceanography*. Oxford, UK: Pergamon

Pörtner HO. 2010. Oxygen- and capacity-limitation of thermal tolerance: a matrix for integrating climate-related stressor effects in marine ecosystems. *J. Exp. Biol.* 213:881–93

Rahmstorf S, Coumou D. 2011. Increase of extreme events in a warming world. *PNAS* 108:17905–9

Ralph PJ, Gademann R. 2005. Rapid light curves: a powerful tool to assess photosynthetic activity. *Aquat. Bot.* 82:222–37

Rhein M, Rintoul SR, Aoki S, Campos E, Chambers RA, et al. 2013. Observations: ocean. In *Climate Change 2013: The Physical Science Basis; Contribution of Working Group 1 to the Fifth Assessment of the Intergovernmental Panel on Climate Change*, ed. TF Stocker, D Qin, G-K Plattner, M Tignor, SK Allen, et al., pp. 255–315. Cambridge, UK: Cambridge Univ. Press

Rivera HE, Chen C-Y, Gibson MC, Tarrant AM. 2021. Plasticity in parental effects confers rapid larval thermal tolerance in the estuarine anemone *Nematostella vectensis*. *J. Exp. Biol.* 224:jeb236745

Roitberg BD, Mangel M. 2016. Cold snaps, heatwaves, and arthropod growth. *Ecol. Entomol.* 41:653–59

Rosa R, Seibel BA. 2008. Synergistic effects of climate-related variables suggest future physiological impairment in a top oceanic predator. *PNAS* 105:20776–80

Rosa R, Seibel BA. 2010. Metabolic physiology of the Humboldt squid, *Dosidicus gigas*: implications for vertical migration in a pronounced oxygen minimum zone. *Prog. Oceanogr.* 86:72–80

Ruel JJ, Ayres MP. 1999. Jensen's inequality predicts effects of environmental variation. *Trends Ecol. Evol.* 14:361–66

Ryu T, Veilleux HD, Donelson JM, Munday PL, Ravasi T. 2018. The epigenetic landscape of transgenerational acclimation to ocean warming. *Nat. Clim. Change* 8:504–9

Saborowski R, Salomon M, Buchholz F. 2000. The physiological response of Northern krill (*Meganyctiphanes norvegica*) to temperature gradients in the Kattegat. *Hydrobiologia* 426:157–60

Salinas S, Munch SB. 2012. Thermal legacies: transgenerational effects of temperature on growth in a vertebrate. *Ecol. Lett.* 15:159–63

Schaefer KM, Fuller DW, Block BA. 2007. Movements, behavior, and habitat utilization of yellowfin tuna (*Thunnus albacares*) in the northeastern Pacific Ocean, ascertained through archival tag data. *Mar. Biol.* 152:503–25

Schaum CE, Collins S. 2014. Plasticity predicts evolution in a marine alga. *Proc. R. Soc. B* 281:20141486

Schaum CE, Rost B, Collins S. 2016. Environmental stability affects phenotypic evolution in a globally distributed marine picoplankton. *ISME J.* 10:75–84

Schubert H, Sagert S, Forster RM. 2001. Evaluation of the different levels of variability in the underwater light field of a shallow estuary. *Helgol. Mar. Res.* 55:12–22

Schulte PM, Healy TM, Fangue NA. 2011. Thermal performance curves, phenotypic plasticity, and the time scales of temperature exposure. *Integr. Comp. Biol.* 51:691–702

Seibel BA. 2011. Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones. *J. Exp. Biol.* 214:326–36

Somero GN. 1992. Adaptations to high hydrostatic pressure. *Annu. Rev. Physiol.* 54:557–77

Somero GN. 2002. Thermal physiology and vertical zonation of intertidal animals: optima, limits, and costs of living. *Integr. Comp. Biol.* 42:780–89

Somero GN, Lockwood BL, Tomanek L. 2017. *Biochemical Adaptation: Response to Environmental Challenges from Life's Origins to the Anthropocene*. Sunderland, MA: Sinauer

Southwood AL, Andrews RD, Lutcavage ME, Paladino FV, West NH, et al. 1999. Heart rates and diving behavior of leatherback sea turtles in the eastern Pacific Ocean. *J. Exp. Biol.* 202:1115–25

Spicer JI, Strömberg J-O. 2002. Diel vertical migration and the haemocyanin of krill *Meganyctiphanes norvegica*. *Mar. Ecol. Prog. Ser.* 238:153–62

Spicer JI, Thomasson MA, Strömberg J-O. 1999. Possessing a poor anaerobic capacity does not prevent the diel vertical migration of Nordic krill *Meganyctiphanes norvegica* into hypoxic waters. *Mar. Ecol. Prog. Ser.* 185:181–87

Steele JH. 1985. A comparison of terrestrial and marine ecological systems. *Nature* 313:355–58

Stramski D, Rosenberg G, Legendre L. 1993. Photosynthetic and optical properties of the marine chlorophyte *Dunaliella tertiolecta* grown under fluctuating light caused by surface-wave focusing. *Mar. Biol.* 115:363–72

Strömberg J-O, Spicer JI. 2000. Cold comfort for krill? Respiratory consequences of diel vertical migration by *Meganyctiphanes norvegica* into deep hypoxic waters. *Ophelia* 53:213–17

Suggett DJ, Smith DJ. 2020. Coral bleaching patterns are the outcome of complex biological and environmental networking. *Glob. Change Biol.* 26:68–79

Sutherland KR, Madin LP. 2010. Comparative jet wake structure and swimming performance of salps. *J. Exp. Biol.* 213:2967–75

Sutton AJ, Feely RA, Maenner-Jones S, Musielwicz S, Osborne J, et al. 2019. Autonomous seawater $p\mathrm{CO}_2$ and pH time series from 40 surface buoys and the emergence of anthropogenic trends. *Earth Syst. Sci. Data* 11:421–39

Svetlichny LS, Hubareva ES, Erkan F, Gucu AC. 2000. Physiological and behavioral aspects of *Calanus euxinus* females (Copepoda: Calanoida) during vertical migration across temperature and oxygen gradients. *Mar. Biol.* 137:963–71

Tanner RL, Dowd WW. 2019. Inter-individual physiological variation in responses to environmental variation and environmental change: integrating across traits and time. *Comp. Biochem. Physiol. A* 238:110577

Todgham AE, Stillman JH. 2013. Physiological responses to shifts in multiple environmental stressors: relevance in a changing world. *Integr. Comp. Biol.* 53:539–44

Tutasi P, Escribano R. 2020. Zooplankton diel vertical migration and downward C flux into the oxygen minimum zone in the highly productive upwelling region off northern Chile. *Biogeosciences* 17:455–73

van Haren H, Compton TJ. 2013. Diel vertical migration in deep sea plankton is finely tuned to latitudinal and seasonal day length. *PLOS ONE* 8:e64435

Vasseur DA, DeLong JP, Gilbert B, Greig HS, Harley CDG, et al. 2014. Increased temperature variation poses a greater risk to species than climate warming. *Proc. R. Soc. B* 281:20132612

Vasseur DA, Yodzis P. 2004. The color of environmental noise. *Ecology* 85:1146–52

Videler J. 1993. *Fish Swimming*. New York: Chapman & Hall

Villareal TA, Carpenter EJ. 2003. Buoyancy regulation and the potential for vertical migration in the oceanic cyanobacterium *Trichodesmium*. *Microb. Ecol.* 45:1–10

Wahl M, Saderne V, Sawall Y. 2015. How good are we at assessing the impact of ocean acidification in coastal systems? Limitations, omissions and strengths of commonly used experimental approaches with special emphasis on the neglected role of fluctuations. *Mar. Freshw. Res.* 67:25–36

Walsh P, Legendre L. 1983. Photosynthesis of natural phytoplankton under high frequency light fluctuations simulating those induced by sea surface waves. *Limnol. Oceanogr.* 28:688–97

Watanabe M, Kohata K, Kunugi M. 1988. Phosphate accumulation and metabolism by *Heterosigma akashiwo* (Raphidophyceae) during diel vertical migration in a stratified microcosm. *J. Phycol.* 24:22–28

Webb PW. 1975. *Hydrodynamics and Energetics of Fish Propulsion*. Bull. Fish. Res. Board Can. 190. Ottawa: Fish. Res. Board Can.

White CR, Marshall DJ, Alton LA, Arnold PA, Beaman JE, et al. 2019. The origin and maintenance of metabolic allometry in animals. *Nat. Ecol. Evol.* 3:598–603

Williams CM, Buckley LB, Sheldon KS, Vickers M, Pörtner H-O, et al. 2016. Biological impacts of thermal extremes: mechanisms and costs of functional responses matter. *Integr. Comp. Biol.* 56:73–84

Woods HA, Dillon ME, Pincebourde S. 2015. The roles of microclimatic diversity and of behavior in mediating the responses of ectotherms to climate change. *J. Therm. Biol.* 54:86–97

Woods HA, Martin LB, Ghalambor CK. 2014. Conclusions: the central role of the organism in biology. In *Integrative Organismal Biology*, ed. LB Martin, CK Ghalambor, HA Woods, pp. 309–17. New York: Wiley & Sons

Yancey PH. 2020. Cellular responses in marine animals to hydrostatic pressure. *J. Exp. Zool.* 333A:398–420

Yancey PH, Gerringer ME, Drazen JC, Rowden AA, Jamieson A. 2014. Marine fish may be biochemically constrained from inhabiting the deepest ocean depths. *PNAS* 111:4461–65