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REVIEW

Advancing bioenergetics-based modeling to improve climate change projections of marine ecosystems

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ABSTRACT: Climate change has rapidly altered marine ecosystems and is expected to continue to push systems and species beyond historical baselines into novel conditions. Projecting responses of organisms and populations to these novel environmental conditions often requires extrapolations beyond observed conditions, challenging the predictive limits of statistical modeling capabilities. Bioenergetics modeling provides the mechanistic basis for projecting climate change effects on marine living resources in novel conditions, has a long history of development, and has been applied widely to fish and other taxa. We provide our perspective on 4 opportunities that will advance the ability of bioenergetics-based models to depict changes in the productivity and distribution of fishes and other marine organisms, leading to more robust projections of climate impacts. These are (1) improved depiction of bioenergetics processes to derive realistic individual-level response(s) to complex changes in environmental conditions, (2) innovations in scaling individual-level bioenergetics to project responses at the population and food web levels, (3) more realistic coupling between spatial dynamics and bioenergetics to better represent the local- to regional-scale differences in the effects of climate change on the spatial distributions of organisms, and (4) innovations in model validation to ensure that the next generation of bioenergetics-based models can be used with known and sufficient confidence. Our focus on specific opportunities will enable critical advancements in bioenergetics modeling and position the modeling community to make more accurate and robust projections of the effects of climate change on individuals, populations, food webs, and ecosystems.

KEY WORDS: Bioenergetics · Modeling · Climate change · Fish · Projections · Challenges · Agent-based

1. INTRODUCTION

Global climate change is perturbing marine ecosystems through unprecedented rates of warming, intensification of marine heatwaves, changes to ocean chemistry, and altering the timing, availability, and quality of prey resources (Gattuso et al. 2015, IPCC 2021, 2022). Understanding the cumulative impact of these changes at the scales of marine organisms, populations, communities, and coupled socio-ecological systems remains an important goal for science and management (Charles 2012, Doney et al. 2012, Hollowed et al. 2013, 2020, Poloczanska et al. 2016, Barange et al. 2018, Karp et al. 2019). Interactions

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among multiple abiotic and biotic factors, with either reinforcing (i.e. synergistic) or counteracting (i.e. antagonistic) effects, can lead to non-linear and non-intuitive ecological responses (Pörtner et al. 2014, Côté et al. 2016, Hewitt et al. 2016, Glibert et al. 2022, IPCC 2022). Projecting marine ecosystem dynamics remains challenging (Planque 2016, Baag & Mandal 2022), and we contend that projections of marine (and freshwater) species abundances and distributions generated by models that explicitly depict the impacts of climate change drivers on biological processes and trophic interactions are warranted to advance our understanding of future shifts (Hollowed et al. 2009, Mouquet et al. 2015). The challenge is ensuring that the models generate projections under unprecedented and novel environmental regimes that are sufficiently accurate and precise.

A variety of different modeling approaches are now being used (e.g. Plagányi et al. 2011, 2014, Lotze et al. 2019) to project species responses to climate change. A common approach is species distribution modeling (and related habitat suitability and bioclimate envelope modeling), which relates a species' abundance (or presence–absence) to the local observed or modeled environmental conditions (e.g. Fernandes et al. 2013, Jones & Cheung 2015, Morley et al. 2018, Melo-Merino et al. 2020). While habitat-based approaches such as species distribution models provide useful first-order predictors of habitat suitability for a species in a future climate, they often do not consider the growth, mortality, reproduction, and movement or migration processes underlying population dynamics (Planque 2016, Peck et al. 2018). Rather, such habitat-based modeling approaches use purely statistical relationships between historically observed species presence or abundance and environmental variables, representing a theory that is assumed rather than tested (Bar-Yam 2016) to make projections of population-level impacts on habitat. Increasingly, the models being used to project climate impacts on marine species and ecosystems, including species distribution models, attempt to resolve at least some of the ecological mechanisms known to be influenced by climate change by integrating abiotic and biotic factors into the models (Kearney & Porter 2009, Fernandes et al. 2013, Gamliel et al. 2020).

Projected environmental conditions under climate change often fall outside the historical range of observations (Williams & Jackson 2007, Kwiatkowski et al. 2020). Predictions of how such non-analog (i.e. unprecedented environmental and ecological) conditions will affect individuals necessitate more mechanistic approaches than habitat-based and other methods grounded in historical conditions (Jørgensen et al. 2012, Russell et al. 2012, Urban et al. 2016, Johnston et al. 2019, Dahlke et al. 2020, Little et al. 2020). Statistical models often perform well with historical data but are sensitive to misspecification when used to extrapolate outside the range of observed data. Bioenergetics modeling provides a more mechanistic framework based on first principles for making climate change projections because it is based on the physiological and behavioral responses of an individual to its environment in response to ecological interactions (Baltar et al. 2019, Lefevre et al. 2021, Kroeker & Sanford 2022).

In this paper, we provide our perspective on opportunities that would advance the ability of bioenergetics-based models to support robust projections of climate impacts on organisms, populations, and food webs. Future directions for modeling bioenergetics of fish have been periodically reviewed (e.g. Brandt & Hartman 1993, Hartman & Kitchell 2008) but there have been important advances in data collection and developments in numerical modeling since then, and climate change presents new challenges.

In this forward-looking review, we identify 4 categories of opportunities (Table 1) for advancing the field of bioenergetics modeling to understand marine organismal- to system-level responses to climate change: (1) improved depiction of bioenergetics processes to derive realistic individual-level response(s) to complex changes in environmental variability; (2) innovations in scaling organismal-level bioenergetics to improve the skill in projecting responses at the population and food web levels; (3) more realistic coupling between spatial dynamics (movement) and bioenergetics to better represent the local- to regional-scale differences in the effects of climate change on the spatial distributions of organisms; and (4) new ideas about model validation to ensure that the next generation of bioenergetics-based models can be used with known and sufficient confidence. As with all ecological modeling, the complexity and detail in a model depend on the questions being asked (Collie et al. 2016, Planque et al. 2022). Our suggestions for advancing bioenergetics modeling to project the responses of marine organisms to climate change are an inclusive list from which only a few may apply to a specific situation.

2. CONTEMPORARY BIOENERGETICS MODELING

Although there are many versions of bioenergetics models, all relate to the basic, balanced energy budget of an individual (Fig. 1):

Table 1. The specific approaches discussed in the paper for advancing bioenergetics modeling, listed according to their general opportunity category and the issue they address

General opportunity	Issues	Specific approaches (discussed within the text)			
		1	2	3	4
Individual responses to a changing environment	Formulation of temperature effects	Revisit common formulations and use of thermal windows	Subprocess effects combine to an overall effect	Mean and other aspects of temperature (e.g. variance, extremes) as drivers	Inter-individual variability
	Temperature and tolerance	Derivation of thermal thresholds indicative of tolerance	Incorporation of abiotic factors into ecological performance versus aerobic scope		
	Multiple stressors	Bioenergetics formulations capable of novel temperatures and various combinations of multiple stressors	Role of field and lab data		
	Intrinsic and extrinsic factors affecting tolerance	Influence of life stage, exposure, body size, and environmental conditions on thermal tolerance	Local adaptation and acclimation	Phenotypic plasticity	
Innovations in scaling from individuals to populations and food webs	Population dynamics models	Interactions among individuals affected by bioenergetics and that affect bioenergetics (e.g. disease, foraging, predator avoidance, schooling)			
	Multi-generational	Density dependence	Inheritable traits that determine phenotypic plasticity		
	Multi-species interactions (food webs)	Climate change indirectly affecting populations through its effects on other species in the food web	Number of parameters with multiple species		
Combining movement ecology and bioenergetics	Two-way coupling	Decisions of movement behavior can be determined by bioenergetics considerations; realized movement trajectories influence bioenergetics			
Assessing realism via model validation	Validation with new data streams	Incorporation of fine-scale data and new types of data on the health and behavior of individuals related to energetics			
	Revisiting validation strategies	New strategies to ensure validation shows quality of model predictions with new formulations under climate change			
	Uncertainty and model complexity	Assessment of new formulations to show their added value to model performance and to confirm the added complexity is needed			

$$E_C = (E_{som} + E_{gon}) + (E_S + E_{SDA} + E_A) + E_E + E_F \quad (1)$$

where the rate of energy (E, J ind.$^{-1}$ time^{-1}) gained by food consumption E_C equals the sum of the growth of

somatic tissue E_{som} and/or gonadal tissue E_{gon}, metabolism terms E_S, E_{SDA}, E_A and losses due to excretion (E_E) of nitrogenous wastes and egestion (E_F); total aerobic metabolism includes the costs of standard
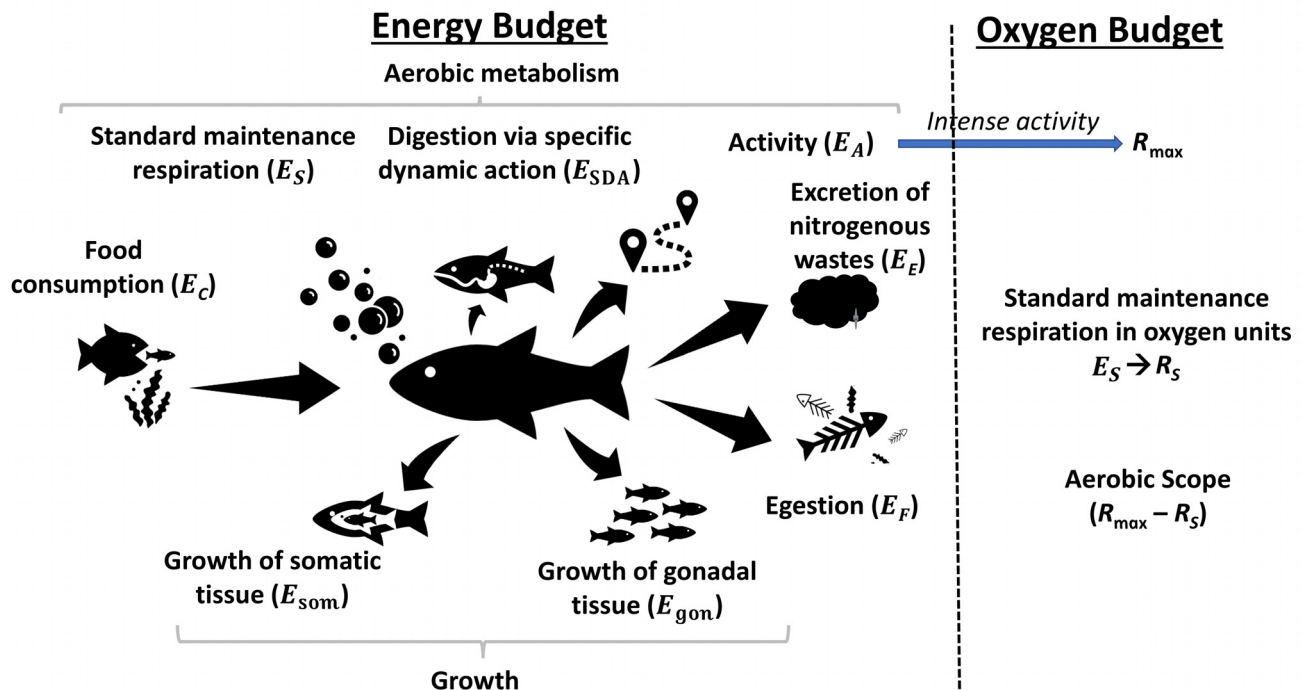
Fig. 1. Basic energy budget of an individual fish, showing the major subprocesses that comprise any bioenergetics model. Also shown are the components of the oxygen budget related to the energy budget terms that determine aerobic scope

(maintenance) respiration (E_S), digestion via specific dynamic action (E_{SDA}), and activity (E_A). E_A includes different levels of activity, from longer-term 'routine' swimming to shorter-term intense physical activity, which often is considered 'maximum aerobic metabolism' and denoted E_{max}. Note that E_S and E_{max} are also often expressed in units of mg (or ml) of O_2 per mass of the individual per unit time (R_S and R_{max}) and used as part of the oxygen budget of an individual (Holt & Jørgensen 2015) and to derive aerobic scope (Clark et al. 2013).

All of the rate processes in Eq. (1) are influenced by various intrinsic and extrinsic factors that integrate into a measure of ecological performance (Fig. 2). A wide range of metrics have been proposed as ecological performance indicators (Rezende & Bozinovic 2019, Desforges et al. 2023), including behavior, swimming speed, metabolism, fecundity, and growth; our focus is on growth and reproduction and their role in bioenergetics. To date, bioenergetics models have mostly focused on the intrinsic factors of developmental stage and body mass and the extrinsic factors of temperature and food availability. Once derived (often from laboratory experiments), these relationships are used to estimate the growth, food consumption, and/or reproduction responses of individuals and can estimate the physiological (fundamental niche; as opposed to observed or realized niche) tol-

erable thermal window of individuals characterized by empirical estimates of the preferred and critical minima and maxima temperatures (T_{pref}, CT_{min}, and CT_{max}, respectively).

Three commonly used bioenergetics models for aquatic organisms are the Wisconsin energy budget (WEB) model, which has been extensively used for fish (Kitchell et al. 1977, Hanson et al. 1997, Deslauriers et al. 2017), the dynamic energy budget (DEB) model, which has been used for a wide diversity of organisms (van der Meer 2006, Kooijman 2009, Nisbet et al. 2010, 2012, Kooijman 2020), and the physiological energy budget model (Sibly et al. 2013, Boyd et al. 2020). All 3 approaches capture the physiological processes represented in Eq. (1) (e.g. consumption, growth, metabolism, and egestion), with parameters that depend on life stage or age and are able to simulate daily to seasonal growth physiology (e.g. losses, gains) of individuals (Brownscombe et al. 2022). We focus on bioenergetics used in agent-based (also known as individual-based) modeling in this review because of their accelerating use (An et al. 2021) and because they simulate processes at the individual level (Martin et al. 2012, DeAngelis & Diaz 2019, Railsback & Grimm 2019). While the details depend on the model approach and the specific formulations used within the model, the issues and opportunities dis-
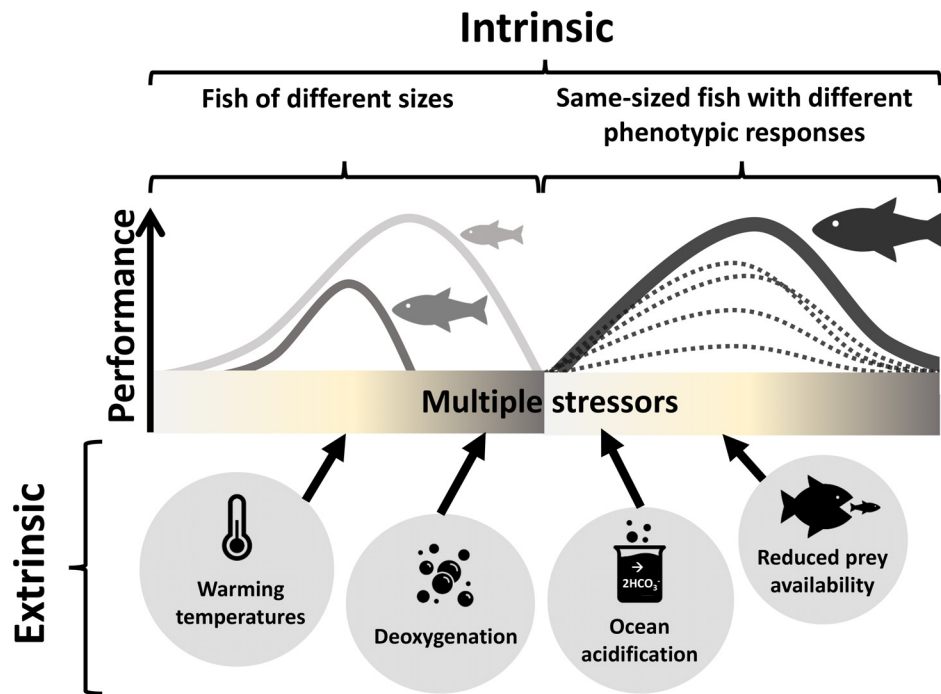
Fig. 2. Some of the major intrinsic and extrinsic factors that affect the physiological and ecological performance of individual fish. The extrinsic factors are shown as stressors expected from climate change. The left example shows possible body size effects on the response to the multiple stressors and the right example depicts how phenotypic variation could influence responses. The focus to date in bioenergetics models includes the intrinsic factor of size and the extrinsic factors of temperature and food

cussed below apply across many types of models besides agent-based (e.g. age-structured) that incorporate bioenergetics formulations (Fig. 3).

3. OPPORTUNITY 1: INDIVIDUAL RESPONSES TO A CHANGING ENVIRONMENT

Physical and biogeochemical models for depicting climate-driven changes in environmental features that are often used to force higher trophic level models continue to increase in skill and spatial resolution (Bonan & Doney 2018, Swearer et al. 2019, Hewitt et al. 2020, Hood et al. 2021, Justic et al. 2022). This increased temporal and spatial accuracy and resolution of temperature, as well as other abiotic variables, provides an opportunity to better formulate how these variables impact the bioenergetics processes of individuals. We expand below on 4 pressing issues with using bioenergetics models for predicting how individuals will respond to climate change: (1) formulation of temperature effects; (2) temperature as a foundation of environmental tolerance; (3) multiple stressors and their interaction with temperature; and (4) intrinsic and extrinsic factors impacting environmental tolerance.

3.1. Formulation of temperature effects

The effect of temperature is often explicitly included in the multiple sub-processes (e.g. consumption, respiration; see Eq. 1) of bioenergetics models. When combined, these can lead to complicated responses in terms of organism growth in response to projected warming, particularly concerning energy utilization and allocation of energy between growth and reproduction.

Common formulations for temperature effects on physiological processes are the Q_{10} coefficient and the Arrhenius relationship (Brown et al. 2004, Clarke 2017). Both Q_{10} and Arrhenius represent the effect as a non-linear monotonic increase in bioenergetics rates (e.g. consumption, metabolism) with increasing temperature. Some have argued that complex physiological changes with temperature interact with ecological constraints to produce outcomes that are unlikely to be predicted from the Arrhenius equation or metabolic theory alone (Rall et al. 2012, Dell et al. 2014, Neubauer & Andersen 2019). An example of an ecological constraint is the foraging parameters (e.g. attack rates) inherent in a species that determine the functional response and therefore its consumption (Rall et al. 2012). To address some of the limitations of
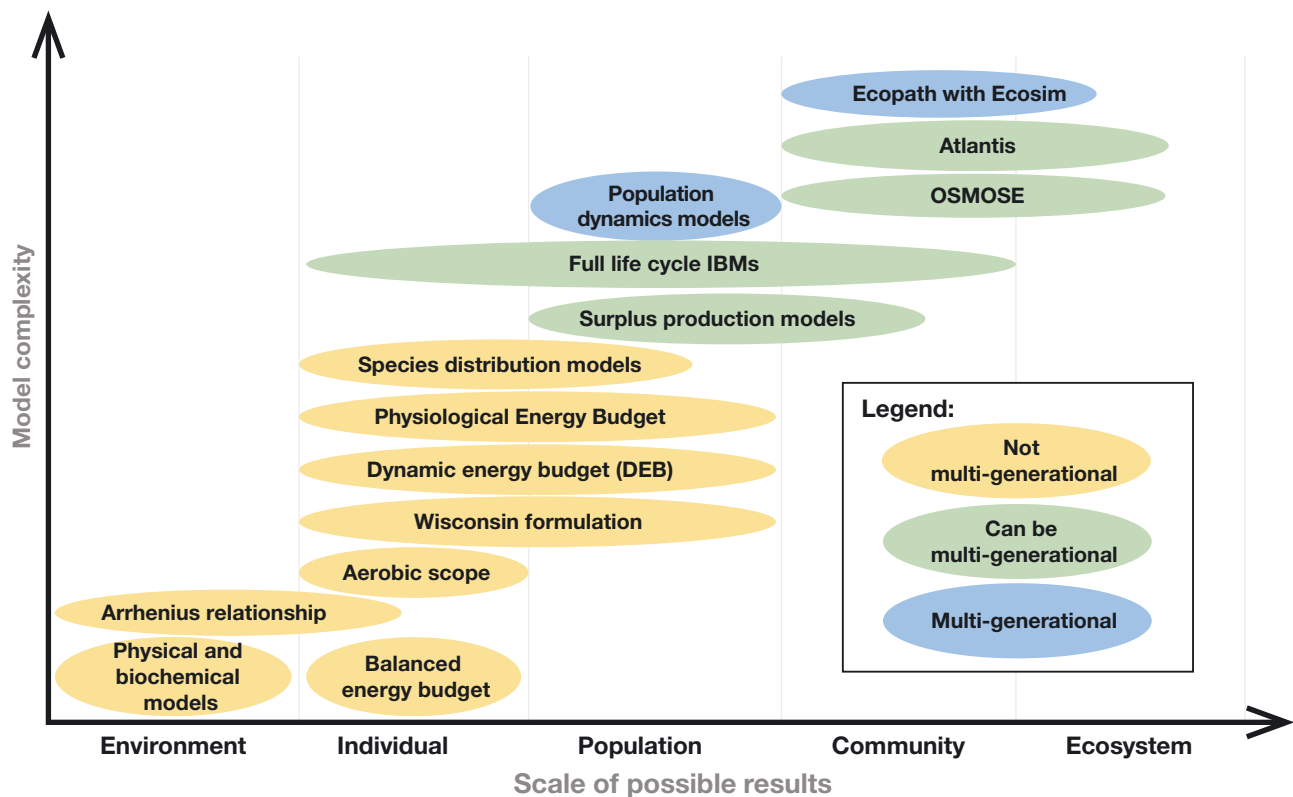
Fig. 3. Complexity of commonly used modeling approaches that incorporate bioenergetics-related formulations versus the level of biological organization of their predictions (environment to ecosystem). The color shows the degree to which multi-generational aspects are typically (or can be) included

the Arrhenius formulation, laboratory experiments have been used to increase its realism by specifying limits directly on growth in models (e.g. Akimova et al. 2016) or specifying limits to feeding that determine growth such as the maximum consumption rate (e.g. Peck & Daewel 2007, Mesa et al. 2013).

Many biological processes in organisms, particularly those related to growth and/or performance, are better described by a thermal window or optimum curve (Brown et al. 2004, Clarke 2017). DeLong et al. (2017) proposed a formulation based on enzyme-pool kinetics that generates dome-shaped relationships, and both the WEB (Deslauriers et al. 2017) and DEB (www.bio.vu.nl/thb/deb/, www.debtox.info/debkiss_appl.html) have libraries of formulations including various dome-shaped functions for temperature effects on maximum rates of consumption. A wide variety of shapes of the temperature response function(s) has been proposed (Padfield et al. 2021), and the selected formulation should be carefully corroborated with observations at high temperatures, as both gradual warming and extreme marine heat waves will push organisms into a region of the relationship likely not often tested under present-day conditions.

For all formulations, assessing the effects of warming on individual-level bioenergetics necessitates considering 3 critical issues. First, temperature has different, non-linear effects on each of the sub-processes of bioenergetics (Eq. 1). Thus, the shape of the temperature effect on consumption differs from that for metabolism. This is especially important for warming, which can have accelerating or even opposite effects (below or above the peak) depending on the sub-process. How these non-linear effects of warming on the bioenergetics sub-processes then combine to generate the resultant growth and reproduction responses should be carefully evaluated and verified.

The second consideration relates to what aspects of warming are important in determining bioenergetics responses. Bioenergetics models to date have largely focused on predicting the responses to changes in the mean temperature and other averaged environmental conditions that are experienced at each time step. Daily thermal fluctuations, more than mean daily temperature, are thought to contribute to salmonid growth and survival (Boughton et al. 2007, Wehrly et al. 2007, Geist et al. 2010, Holsman & Danner 2016). Also, responses often depend on not just the tempera-

ture experienced in the present but also the lagged effect of the advective (environmental) history that determines the exposure of an individual (Holsman & Danner 2016). Lagrangian approaches that follow the trajectories of individuals are increasingly being used to study the behavior, energetics, and exposure of individuals moving within complex environmental fields (Joo et al. 2022). Expanding and refining bioenergetics models to depict the effect of variability and past exposure to temperature will become important as climate change affects not only the averages but also the variability and the extremes of temperature (IPCC 2021).

The third issue is the long-standing approach of ignoring inter-individual variability in the simulation of bioenergetics responses. Physiological variability among individuals is not well understood (see Tyler & Bolduc 2008) and, despite bioenergetics models being based on individuals, most bioenergetics-based approaches assume that temperature changes will impact all individuals within a stage or size grouping in the same way (Peck et al. 2018). This representation of the response of the average individual can distort the population responses to climate change by missing individual adaptation due to, for example, phenotypic variation or adaptation scope at the extremes of the distribution of responses such as growth rate (Fig. 2).

3.2. Temperature as the foundation of environmental tolerance

Formulating the subprocesses of the bioenergetics model to ensure realistic responses of growth and respiration to warming is important for determining whether critical temperature thresholds will be exceeded. Aerobic scope is a measure of the amount of oxygen available above maintenance costs (i.e. Scope $= R_{max} - R_S$) to support feeding, growth, and other processes and has been offered as a general framework for defining thermal habitats suitable for (and tolerated by) organisms such as fishes (Deutsch et al. 2015). With warming, R_S is typically assumed to increase exponentially or with a peak, and R_{max} (e.g. during strenuous exercise) will likely change in a different, non-linear fashion that can reduce aerobic scope. Although the relationship between performance and aerobic scope versus temperature is species-specific (e.g. Jutfelt et al. 2018), the result is often a right-shifted, dome-shaped curve (Kroeker & Sanford 2022). This curve can be related to measures of thermal performance made using standard protocols applied at the organismal level (i.e. CT_{min}, T_{pref}, and

CT_{max}; Moyano et al. 2017, Volkoff & Rønnestad 2020). This window of positive aerobic scope is sensitive to the components of bioenergetics and how they combine into growth or other measures of ecological performance. Also relevant to climate change is how bioenergetics can be extended to multiple dimensions by including other abiotic factors and stressors, such as dissolved oxygen, pH, and salinity, that either increase or decrease R_S or R_{max} (Pörtner & Peck 2010, Deutsch et al. 2015, Kroeker & Sanford 2022).

Performance curves, thermal windows, and preferred and critical temperatures have been widely applied to model the temperature tolerance of larval (Moyano et al. 2017, Quinn 2017), juvenile, and adult fish (Pörtner & Peck 2010, McBryan et al. 2013, Vinagre et al. 2015, Ern et al. 2016). Many of these were estimated and derived from the sub-processes represented in the energy-based and oxygen-based bioenergetics modeling. The species- and life-stage-specific relationship between the aerobic scope of individuals and temperature has been used in models projecting changes in the distribution and productivity of specific populations (e.g. Cucco et al. 2012, Holt & Jørgensen 2014) or across many populations (Cheung et al. 2009). Physiologists have taken note of the broad-scale global modeling and have suggested improvements based on more recent bioenergetics measurements (Lefevre et al. 2017, 2021, Alfonso et al. 2021) such as the capacity of fish species to maintain large aerobic scopes (with a high metabolic rate) at warm temperatures across a range in body sizes (Lefevre et al. 2017). Aerobic scope can help define the thermal window of many aquatic poikilothermic organisms (those that cannot regulate body temperature) (Peck et al. 2018, Teal et al. 2018), and their performance and tolerance can be used to compare responses to anticipated temperatures under a future climate (Neuheimer et al. 2011, Pörtner 2021).

There is considerable debate about the physiological mechanisms that create an optimum temperature and that set limits to growth and performance of fish at colder and warmer temperatures. The gill-oxygen limitation theory (GOLT) can be derived from the von Bertalanffy growth function and has been used to describe various growth traits of fish based on oxygen demand and oxygen supply to fish tissues via gill surface area (Pauly 2021). The oxygen and capacity-limited thermal tolerance (OCLTT) theory provides a framework for explaining critical thermal limits based on reductions in aerobic scope (Pörtner 2010). Finally, the maintain aerobic scope and regulate oxygen supply (MASROS) framework suggests that the growth trajectories of fish have been evolutionarily

adapted to avoid oxygen limitation at warm temperatures (Lefevre et al. 2021). One implication of these alternatives relevant to global climate change is whether aerobic scope starts to decrease slowly or sharply after temperatures exceed optimal temperatures. If measurements of aerobic scope are available for the same species across large ranges in body sizes and temperatures, then the oxygen-based metabolism relationships can be formulated and the empirical information used to evaluate these alternative views of how oxygen poses limits to thermal performance curves. In cases when the available data are insufficient to distinguish among the frameworks, models will need to state assumptions on the physiological mechanism limiting the growth or performance of target species at warm and cold temperatures. Thermal thresholds and preferences will play a major role in assessing climate change effects, and the bioenergetics and metabolic rates must therefore be carefully tested for use under anticipated future conditions.

3.3. Multiple stressors and their interaction with temperature

Climate change is amplifying the multi-stressor exposure by requiring models to account for simultaneous and asynchronous events of not only warming but also ocean acidification, deoxygenation, sea level rise, habitat fragmentation, and other stressors (Sampaio & Rosa 2020, Glibert et al. 2022). The multi-stressor effects on the sub-processes represented in bioenergetics and on the resultant projection of growth can be additive, synergistic, or antagonistic (Côté et al. 2016). We suggest that a critical exploration of multi-stressor effects in bioenergetics models is overdue, especially considering the widespread use of thermal thresholds, their incorporation into population and food web models, and the recent critiques of their formulations (Jutfelt et al. 2018, Audzijonyte et al. 2019b).

Some progress has been made in expanding bioenergetics modeling beyond temperature to account for additional environmental factors. For example, DEB model parameter sets have been created based on the effects of multiple drivers (e.g. temperature, pollutants, feeding level) on freshwater invertebrates (Goussen et al. 2020), sublethal effects of stressors (Watson et al. 2020), hypoxia effects (Thomas et al. 2019), and migration costs from river blockages and reduced ocean food (Chaparro-Pedraza & de Roos 2021). Jørgensen et al. (2012) documented how aero-

bic scope could be used with bioenergetics models to examine the impacts of interacting factors (e.g. hypoxia, ocean acidification, heatwaves, cold snaps) on the fitness and performance of fish. Holt & Jørgensen (2014, 2015) used maximization of expected lifetime reproductive success with a bioenergetics model to find the optimal foraging behavior and energy allocation between growth and reproduction. They demonstrated that estimated optimal temperatures for growth and fitness in Atlantic cod *Gadus morhua* were lower than when only aerobic scope was considered; optimal behavior needed to further fulfill the requirements of foraging, avoiding predation, and reproduction. Neubauer & Andersen (2019) used behavioral optimization (by adjusting activity to maximize fitness) with an ecophysiological model to separately simulate the response of individuals to temperature and oxygen limits, indicating that various performance measures (e.g. growth, efficiency) depended on species traits, ontogenetic stage, and stressors.

The critical and most-pressing limitation to progress in treating multiple stressors is the availability and practicality of obtaining empirical information. There are few laboratory experiments specifically designed to measure organismal-level performance across the species' thermal window while also evaluating intraspecific variability in performance under interacting factors such as low pH, reduced dissolved oxygen, and salinity (Catalán et al. 2019, Cominassi et al. 2020). The number of studies examining the synergistic impacts of ocean acidification and warming (e.g. Walther et al. 2009, Di Santo 2015, Gobler et al. 2018) and dissolved oxygen and temperature (e.g. He et al. 2015, Tremblay & Abele 2016, Li et al. 2019b) is increasing. Many of these studies focus on integrative measures of performance (e.g. growth), and further resolving responses into the sub-processes of bioenergetics will enable robust formulations. Studies are also continuing to add realism into experimental design, such as *in situ* light levels and food, and more complex representations of short-term diel and seasonal changes in stressors (e.g. Wehrly et al. 2007, Geist et al. 2010, Miller et al. 2016, Lifavi et al. 2017) as well as combinations of different stressors (e.g. Reum et al. 2014, Lifavi et al. 2017, Baumann 2019). Multiple responses and realistic designs will yield valuable ecophysiological data for formulating how simultaneous variation in environmental stressors in nature can affect the sub-processes of bioenergetics (Holsman & Danner 2016, Catalán et al. 2019). For example, diel variability in pH in combination with temperature impacts marine shellfish differently compared to mean conditions (Gazeau et al. 2013). Additionally,

studies should focus on assessing the responses to highly dynamic conditions found in shallow waters of estuarine and coastal habitats relative to different magnitudes, durations, frequencies, variance, and predictability of conditions (Baumann et al. 2015, Bednaršek et al. 2022a).

Field studies from across the environmental gradients and natural analogs can additionally complement and expand our understanding obtained from multi-stressor laboratory experiments. While establishing cause-and-effect relationships from field studies is very challenging (Eberhardt & Thomas 1991) due to multicollinearity, they are valuable for documenting realistic (i.e. *in situ*) exposures for use in modeling and laboratory experiments and for defining realistic bounds on organismal responses. Examples include comparisons across fish populations experiencing different combinations of stressors within European river systems (Schinegger et al. 2016) and changes in macrozoobenthic assemblages along gradients in temperature, dissolved oxygen, and pH (pCO$_2$) at continental margins (Sperling et al. 2016). Natural *in situ* gradients offer an opportunity to study biological responses *in situ*, but it is essential to develop and apply as many different biomarkers (i.e. genetics, cellular, sub-cellular) that would allow for stress detection in the field. Spatially extensive marine heat waves or El Niño events can be used as analogs for future thermal conditions that are expected to occur more frequently in the near future (Hobday et al. 2016, Oliver et al. 2018). When marine heat waves or other extremes overlap with covarying *in situ* drivers (e.g. low pH), the combination can provide unique multifaceted settings that include interactive effects on organisms (Bednaršek et al. 2018), often driving rapid population-level responses (e.g. Bednaršek et al. 2022b).

Representing the many possibilities needed to estimate robust relationships with multifactor experiments might always have limitations due to collinearity, preventing determination of how specific stressors affect bioenergetics. This means that a strategic approach is needed that cleverly combines or synthesizes across temporal and spatial scales to advance beyond the bounds of collinearity limitations. Ultimately, field-based empirical responses (e.g. an individual's biomarkers of performance) should be combined with experimentally driven mechanistic laboratory responses and bioenergetics-based modeling to maximize our understanding of intra- and interspecific ecophysiological responses to the changes in the mean, variance, and extreme values of multiple factors (Glibert et al. 2022).

3.4. Intrinsic and extrinsic factors impacting environmental tolerance

Evidence from laboratory and field studies suggests that thermal windows are not merely species-specific but can also shift with life stage (Dahlke et al. 2020), duration of exposure, body size, food availability, and other environmental conditions (Peck et al. 2012). For example, field and laboratory evidence for European sprat *Sprattus sprattus* in the Baltic Sea suggest different optimal and tolerable temperatures for embryos, young larvae, young-of-year juveniles, and adults that pose constraints on life history scheduling (Peck et al. 2012). Decreases in tolerable and optimal temperatures with increasing fish size in laboratory and field studies are also well-documented (Paul et al. 1988, Farley et al. 2016, Hurst et al. 2018), and specific life stages of fish and invertebrates may have narrower ranges in tolerable temperatures than other stages (Rijnsdorp et al. 2009, Dahlke et al. 2020).

While these intrinsic and extrinsic factors are an important aspect of developing bioenergetics-based models, a larger challenge is incorporating the intrinsic factors of acclimation and adaptation to local and regional conditions (Munch & Conover 2002, Somero 2010). Adaptation and acclimation are critical because they are key to generating accurate growth and reproduction responses to climate change and are especially limited by empirical information and being poorly represented in models (Stitt et al. 2014, Neubauer & Andersen 2019). Acclimation involves individual phenotypic plasticity that can help an individual maintain fitness under novel conditions, whereas adaptation involves selection for genetic variation that results in a shift in the average phenotype of a population towards a peak in fitness (Munday 2014). Within adaptation, 2 possibilities are distinguished: (1) local adaptation, whereby fixed genetic differences between populations can account for variation in traits, such as heat tolerance, that can result in the movement of individuals from locally adapted populations into surrounding areas, and (2) adaptation arising from genetic polymorphism that leads to individuals within the local population having different phenotypes with different environmental tolerances (Somero 2010).

How acclimation and adaptation would modulate responses to changes in temperature, along with the interactive stressors, is typically not represented in current bioenergetics modeling frameworks. There are a few examples that use simple representations (Huse & Ellingsen 2008, Fulton & Gorton 2014) and the exploration of more detailed approaches within

the context of evolutionary dynamics is underway (e.g. predation and fishing; Forestier et al. 2020).

Bioenergetics models have great potential to explain regional variation in traits by disentangling adaptation and plasticity effects. Models allow multiple drivers to be tested and can also be used to simulate virtual transplant experiments. For example, by forcing a European anchovy *Engraulis encrasicolus* bioenergetics model with regional food and temperature across European waters, Huret et al. (2019) explained part of the variability in size-at-age observed in field data, with the remaining unexplained part being attributed to genetic adaptation. Similarly, an energy allocation model fitted to size-at-age data for 8 populations of common sole *Solea solea* across a broad range of latitudes quantified the variation in some physiological processes and explained differential growth and reproductive traits among distinct populations (Mollet et al. 2013).

Using a combination of laboratory experiments and bioenergetics modeling provides the best opportunity to quantify and separate the contributions of adaptation versus plasticity (Merilä & Hendry 2014, Donelson et al. 2018). Increasing the knowledge base of within-species variation in thermal tolerance is critical. The effect of acclimation and adaptation has only been explored under realistic conditions in a few laboratory experiments (Anttila et al. 2014, Huey & Buckley 2022). Generally, counter-gradient variation is observed in individual growth in the field as a result of the genetic adaptation counteracting the effect of decreasing temperature or the shortened length of the growing season (Conover et al. 2009). In combination with temperature, recent bioenergetics studies highlight the importance of prey quality (Huret et al. 2019) as well as daylight hours and prey size (Ljungström et al. 2024) to explain the tendency of small pelagic fish to be larger with increasing latitude. Most studies analyzing this pattern either use populations from different latitudes in common garden experiments or field transplants in reciprocal environments (e.g. Munch & Conover 2002). However, many fish species are unsuitable for selection experiments due to their complex reproduction and long generation times. Recently, the adaptive potential of unsuitable species for selection experiments has been determined by incorporating tolerance to past environments and evaluating individual performance rather than averaged performance (Paula et al. 2019). Ultimately, bioenergetics models could allow the study and understanding of the selection processes that lead to regional phenotypic and genetic differences to advance our capability to make robust projections of individual-level responses to future climate-driven changes.

4. OPPORTUNITY 2: INNOVATIONS IN SCALING FROM INDIVIDUALS TO POPULATIONS

Understanding climate change impacts on marine ecosystems requires translating effects on individual organisms to responses at the population, community, and food web levels (Fig. 4). Multiple demographic characteristics of populations are integrated outcomes of bioenergetics tradeoffs at the individual level. Bioenergetics represents the feeding, growth, and reproduction of an individual, which are all potentially influenced by movement and mortality risk. Scaling from the bioenergetics of a single individual to many individuals uses individual-level outcomes of bioenergetics (e.g. size) that influence population-level processes (Persson et al. 2014). The advantages and challenges of representing the bioenergetics of an individual described above continue to apply here, with the addition of new opportunities as part of the 'scaling-up' process when used in population and food web models. We categorize opportunities for advancing bioenergetics for scaling up into 3 interdependent issues: (1) embedding bioenergetics into population dynamics models; (2) multi-generational considerations; and (3) multi-species interactions in food webs. For discussion purposes, we distinguish between population and food-web level models that predict responses for single years (e.g. present-day versus 2100 conditions), using either user-specific reproduction or recruitment inputs to start each year (e.g. Hollowed et al. 2009, Xu et al. 2015, Koenigstein et al. 2016, Adamack et al. 2017), and the models that generate multi-generational predictions with the survivors of each year producing the young in the model for the next year (e.g. Aarflot et al. 2022).

4.1. Embedding bioenergetics in population dynamics models

With multiple individuals, individual differences in bioenergetics can also influence interactions among these individuals that, in turn, can affect bioenergetics. When accumulated at the population level, the growth and reproduction rates of the individuals (i.e. bioenergetics) affect the biomass and reproductive output of the population. Activity, movement, foraging behavior, predator avoidance, and exposure to environmental conditions experienced by an indi-
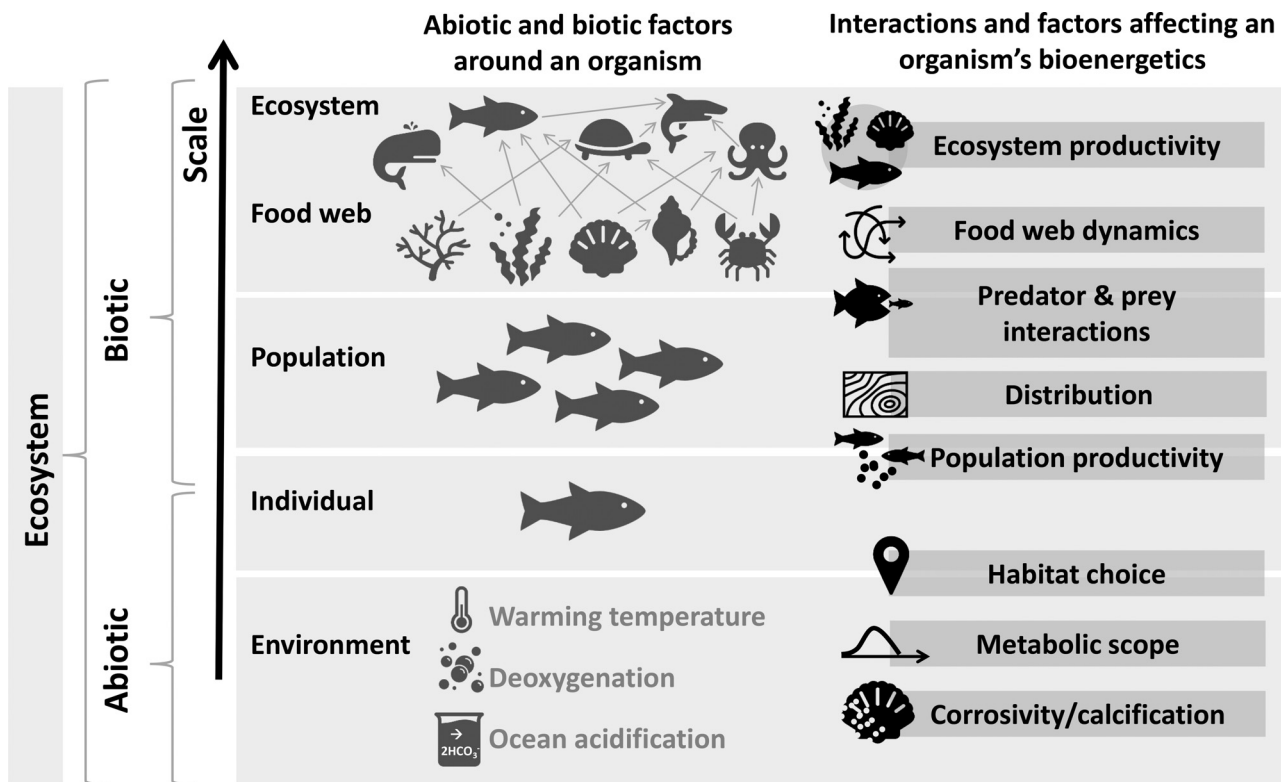
Fig. 4. Progression from individuals to ecosystems (left column) and examples of typical processes and response variables at each level (right column) that require both robust climate projections and models that incorporate representation of bioenergetics

vidual can all be affected by the presence of interactions with other individuals. Some examples include mortality from disease that depends on the presence of other individuals (transmission) and also the bioenergetic condition of the individual (Chapman et al. 2021), density-dependent growth and mortality due to crowding (Rose et al. 2001), and mating success in some crustacean species that is size-based (Jinbo et al. 2017, Sørdalen et al. 2018). A challenge in scaling up from individuals to the population involves adequately considering how inter-individual variation and interactions among individuals can affect bioenergetics. While the list of possibilities is long, likely only a few apply in any specific situation.

Full life-cycle agent-based models emulate how bioenergetics at the individual level can be scaled up to population dynamics by embedding bioenergetics and by being forced by physical—biogeochemical models. These have been developed and corroborated with extensive observations made on various components of individuals (e.g. growth, feeding, reproduction, movement) and lower trophic level prey field characteristics (Kishi et al. 2011, Hjøllo et al. 2012, Utne et al. 2012, Aarflot et al. 2022). These models have the capacity to investigate detailed individual-

and population-level mechanistic processes leading to variability in the abundance and productivity of populations and can receive global climate model outputs as inputs (e.g. Bueno-Pardo et al. 2020). However, the representation of inter-individual effects outside of experiences and size, age, and stage (e.g. genetic; Chambers 1993) is currently limited and simplified (Semeniuk et al. 2011) but provides a good starting point to further delve into how to represent bioenergetics with interacting individuals, especially under possible future climate conditions.

4.2. Multi-generational considerations

Multi-generational simulations are fundamental to assessing the long-term dynamics of populations and food webs. Multi-generational simulations differ from a sequence of 1 yr simulations in that in multi-generation simulations, the reproductive output in one year becomes the young for the next year. One year simulations have the advantage of focusing on specific life stages (e.g. egg to recruitment) without requiring the representation of the rest of the life cycle, which adds further uncertainties. For some questions or some life

histories that use many distinct habitats, predicting larval or recruitment dynamics (e.g. Daewel et al. 2008, Xu et al. 2015) or predicting adult dynamics given an assumed level of recruitment (e.g. Adamack et al. 2017) is well-suited for comparing future conditions to present-day conditions. However, the inherent limitation with 1 yr simulations is that there is no carry-over; each year restarts from the specified initial conditions. Many species of interest are long-lived (multiple years) and have complex life cycles with life stages that use different habitats (Pihl et al. 2002, Whitfield 2020). Long-term dynamics that result from multi-generational simulations allow the full manifestation of the response to climate change at the biological levels relevant to management (e.g. equilibrium endpoints) and the generation of cumulative responses to specific temporal patterns of environmental conditions (sequence of year-types) and management actions. While we have advanced in the bookkeeping aspects of biomass and even agent-based food web models that run in a multi-generation mode (Rose et al. 2015, Aarflot et al. 2022), there remain unresolved opportunities for representing density dependence and linking phenotypic variation to parents.

Compensatory density dependence at the single-species level is a negative feedback on population dynamics and operates as increasing abundance or density reduces growth, survival, or reproduction, and/or also affects movement (Rose et al. 2001). Depensatory density dependence is a positive feedback and destabilizes populations when they are at low abundance levels (Liermann & Hilborn 2001). Mortality and reproduction affect population abundance, while growth affects size, which influences mortality and reproduction. Movement can also affect growth, mortality, and reproductive success by determining the habitats used by individuals.

Representing density dependence involves specifying compensatory and depensatory processes (e.g. growth, mortality, reproduction) that can occur in multiple life stages (Brooks & Powers 2007, Lorenzen 2008, Grossman & Simon 2020). For example, young-of-year sprat can be much more abundant than older age classes, and these younger fish can have a competitive advantage for limited prey resources due to their increased weight-specific foraging and metabolic rates compared to larger conspecifics, thereby potentially exerting density-dependent control (via depletion of prey resources) on spawning stock biomass (Peck et al. 2012). In general, bioenergetics formulations that directly determine growth, reproduction, predation risk, and often movement behavior must have the capability to play their critical role in

generating density-dependent feedback in multiple life stages.

A wide range of traits related to bioenergetics are potentially subject to the genetic makeup and experiences of the parents and, in some situations, should be accommodated in the next generation's bioenergetics. Munday (2014) documented transgenerational plasticity whereby the experiences of parents shape the reaction norm of their offspring. The number of studies reporting how the environment experienced by parents affects the physiological tolerance and bioenergetics of offspring via transgenerational plasticity is growing (Donelson et al. 2012, Salinas & Munch 2012, Bell & Hellmann 2019, Harmon & Pfennig 2021). In one example, Miller et al. (2012) demonstrated that transgenerational acclimation could help to overcome behavioral impairment (poor escape responses) observed in juvenile anemone fish *Amphiprion melanopus* exposed to high CO_2. For practical reasons, there are limitations to laboratory exploration of transgenerational phenomena (Donelson et al. 2018). Most of the studies revealing this type of transgenerational acclimation on the performance (and bioenergetics) of offspring have been performed on relatively small-bodied, short-lived organisms under simplified environmental conditions. A recent study used long-term (multi-generational) temperature and pH exposure experiments on the relatively long-lived European sea bass *Dicentrarchus labrax* (Howald et al. 2022). Inter-generational temperature effects are better documented (e.g. Burt et al. 2011) but most studies have examined only eggs or embryos.

Although such plasticity and genetic effects have the potential to attenuate the impacts of changes in the environment over the long term, the inheritability and transferability from parent to offspring of traits, leading to phenotypic variation (plasticity and genetic effects) in responses at the individual level, is rarely incorporated into multi-generational bioenergetics-based models (e.g. Holt & Jørgensen 2014, Huse et al. 2018, Aarflot et al. 2022). As the evidence base grows, multi-generational models need to be ready to incorporate variation, as it may be key to revealing the adaptive capacity of populations to changes in abiotic factors (e.g. temperature, pH, oxygen) and biotic factors (e.g. prey detection) and therefore to adequately project ecological responses to climate change. Alternatively, exploring the implications of different levels of plasticity allows for targeted research to determine if those dynamics are observed in nature. This is similar to how advances have been made in extending our understanding of the effects of fishing by beginning to incorporate

multi-generational impacts of commercial fishing gear and fisheries-induced evolution, including reductions in size-at-maturity and increased growth rate (e.g. Kuparinen & Hutchings 2012, Marty et al. 2015), into models of fished stocks and communities. Thus, regularly combining diverse approaches that examine the multi-generational impacts of both fishing and climate on individuals would represent a step-change in our ability to use models to disentangle the multiple drivers of climate change in marine populations.

4.3. Multi-species interactions in food webs

Predicting the responses of populations to climate change often involves incorporating how other populations (e.g. predators and prey) will respond to climate change and to the response of the population of focus (Pörtner & Peck 2010). This, then, can render the simplifications (e.g. constant predation mortality rate) inherent in a purely population approach questionable. In a simple example, Akimova et al. (2016) used an individual-based model (IBM) of larval and juvenile cod encountering predator fields constructed from survey data in the North Sea and concluded that while warming led to faster growth of cod, it also led to higher rates of mortality since predator appetites (gut evacuation rates) increased faster with temperature than cod growth rates.

Inter-specific interactions that determine bioenergetics will be affected by climate change due to individuals showing different species-specific physiological, behavioral, and kinematic responses to temperature (warming), ocean acidification, and increasing hypoxia. These interactions underlie predator–prey interactions and competition that, in turn, influence the consumption and metabolism terms in bioenergetics. While the idea of altered competition is considered conceptually (Baag & Mandal 2022), the evidence for competition from empirical studies remains elusive due to general issues with quantifying competition (Wootton & Emmerson 2005).

In contrast to competition, there is extensive information from experimental approaches on how climate change would affect encounters (attacks) by the predator and escape by the prey (Nagelkerken & Munday 2016, Allan et al. 2017, Draper & Weissburg 2019). Dell et al. (2014) provided a general 2-species population modeling framework for consumer–resource species interactions that focused on how asymmetries in thermal sensitivities and the relative body velocities of consumer and resource (catego-

rized as grazer, sit-and-wait, or active-capture predation) greatly affected the equilibrium biomasses of the predator and prey populations. Domenici et al. (2019) used empirical evidence with coral reef fish and a generalized conceptual model and concluded that there will be an overall increase in predator–prey interactions under warming due to more attacks and reduced escape capabilities. When the multiple stressors of climate change are combined with the many detailed steps and events of predator–prey interactions, there emerges a long list of possible ways climate change can differentially affect the species involved, which translates into altered bioenergetics of the focal species and its prey and predators. The implication is that all of these effects (mechanisms of predator–prey interactions, competition) are mediated through and affect bioenergetics and can lead not only to altered growth and population dynamics of the focal species but also to restructuring of communities and the energetics of food webs (Tunney et al. 2014, Nagelkerken & Munday 2016).

Climate change will also differentially affect the spatial distributions and phenology of species that then affect bioenergetics and can also translate into population- and higher-level responses. Durant et al. (2007) examined the timing of predators and their prey on seasonal time scales and adapted the classic match–mismatch hypothesis to show how components of the food chain will shift their phenology at different rates and how this becomes a driver of increasing asynchrony. This will have concomitant effects on consumption, bioenergetics, growth of predators, and mortality of prey.

Climate change affecting the distribution and connectivity of habitats will also affect predator–prey interactions and competition. Selden et al. (2018) used habitat modeling of long-term monitoring data for the Northeast US shelf to show how the historical overlap of key fish predators with their prey species will be differentially affected by climate change. For example, Atlantic cod *Gadus morhua* would show decreased overlap relative to historical conditions, while spiny dogfish *Squalus acanthias* would show increased overlap. In terms of potential competition, Milazzo et al. (2013) assessed the interactions between 2 sympatric fish species: the cool-water species *Coris julis* and the warm-water species *Thalassoma pavo*. These wrasses are widespread and co-occur in Mediterranean nearshore waters. They used correlative and experimental approaches and showed that warmer temperatures and high relative dominance of the warm-water species (3× higher) acted synergistically and caused the cool-water species to relocate to

less preferred habitat (apparently to reduce competition) and to alter its behavioral activity, which would affect its foraging and metabolism.

When interspecific interactions need to be explicitly accounted for, model developers typically either expand the formulations of processes in the bioenergetics model of the focal species to account for other species or move to a food web approach that explicitly simulates multiple interacting species. Agent-based models have progressed to representing multiple (2–10) species as individuals, with object-oriented simulator of marine ecosystems (OSMOSE) following schools as individual units in a full food web with up to dozens of species and functional groups (Moullec et al. 2019, 2023, Morell et al. 2023).

More commonly, Eulerian approaches, such as Ecopath with Ecosim (EwE), are used for simulating the many species in complex food webs (Colléter et al. 2015, Stock et al. 2023). Eulerian approaches simulate the rates of change of biomass or abundances as a single state variable for the total population or for state variables corresponding to the population divided into subclasses such as age, stage, or size (Carlotti & Poggiale 2010, Galic et al. 2010). Atlantis, another ecosystem modeling approach, takes an intermediate approach, representing the responses of an average individual (or a small number of morphs) and scaling to the entire population from that basis (Audzijonyte et al. 2019a, Hansen et al. 2019). Mizer, a size and trait-based approach to food-web modeling, takes a somewhat similar approach (Scott et al. 2014).

Regardless of the exact form of the representations, the shift to many species requires simplification of the representation of the population dynamics of each species (e.g. Thompson et al. 2012, Collie et al. 2016). However, making sure the simplification still accurately predicts responses is an increasing concern, as there is increasing focus on food web dynamics under climate change and the importance of representing both species- and community-scale processes. For example, many food-web modeling analyses have shown the potential importance of predation and inter-specific competition on responses to climate change (e.g. Busch et al. 2013, Bossier et al. 2020, Chagaris et al. 2020).

Opportunities for scaling bioenergetics from the organism level to the population level were discussed above and they continue to apply here. In addition, scaling to multiple interacting populations raises several new pressing challenges. First, a practical issue with scaling from organismal-level bioenergetics to the food web is simply the substantial increase in the number of parameters needed to represent each additional species. Food web models require the repre-

sentation of multiple (sometimes many) species and must realistically represent how each of these species will respond to climate change. Because physiological processes and predator–prey interactions scale strongly with individual body size, size-based models have been promoted as an information-efficient tool to scale-up individual-level energetics to the community and ecosystem level (Blanchard et al. 2017, Andersen 2019). Second, many of the processes assumed to be fixed or static in a population modeling analysis (e.g. natural mortality rate, diets) must now be formulated to deal with how other species (e.g. prey, predators) dynamically determine these rates and are themselves affected by climate change. Negative feedback on populations can arise from interspecific interactions, such as community-level competition for food and predators shifting their pressure to species when those species are abundant (Dingsør et al. 2007, De Santis et al. 2021). Robust representation of bioenergetics is needed so that all of the represented populations can adequately respond to the direct effects of climate change as well as to the indirect effects that arise from interacting with other populations.

5. OPPORTUNITY 3: TWO-WAY COUPLING OF MOVEMENT AND BIOENERGETICS

Rapid and large-scale redistribution of species in response to climate-driven change in marine environments is increasingly being reported (Pecl et al. 2017, Li et al. 2019a, Stevenson & Lauth 2019, Pinsky et al. 2020). Observed spatial distributions are the result of geographic differences in population productivity, as well as direct movement either through passive transport, behaviorally driven movement of individuals, or both. The distributions of early life stages for many species (e.g. pelagic larvae) are determined by physical transport, and additionally impacted by vertical migration and navigational behaviors (Staaterman & Paris 2014, Cresci et al. 2021). Older life stages, such as juvenile and adult fish, move based on behavioral responses to cues. Many species exhibit complex life cycles, whereby each life stage may use unique habitat (e.g. offshore feeding areas separated from spawning areas separated from shallow coastal nursery areas), resulting in a complex mix of impacts of climate change over the life cycle (Petitgas et al. 2013).

Most movement algorithms used to date in population and food web models are rigid and use limited cues that are predicated on spatial patterns observed under current conditions (Huse et al. 2004, Lehodey et al. 2008, Utne et al. 2012, Rose et al. 2015). The use

of forced movement cues creates challenges for how to couple movement and bioenergetics because behaviorally mediated or physiologically based responses are not employed and the previous *in situ* spatial patterns that were used to create movement rules may be maladaptive in a future climate.

A key aspect of simulating realistic movement under changing climate conditions is that the representation of movement is behaviorally adaptive (Beever et al. 2017, Railsback & Harvey 2020). This is conceptualized and implemented in models by using bioenergetics to provide ecological valuation and tradeoffs for different movement decisions (DeAngelis & Diaz 2019, Malishev & Kramer-Schadt 2021). Bioenergetics is the calculator that combines factors and stressors into the integrated currency of growth and reproduction so that options can be compared in a formal or informal optimization evaluation of movement options (e.g. fish move towards high-growth areas). Thus, bioenergetics must include factors typically included as cues (e.g. temperature), likely at unprecedented levels, as well as new factors and stressors (e.g. low dissolved oxygen, different food types) that gain importance under climate change. Once the movement decisions are made, bioenergetics must also be capable of then using the experienced values of factors and stressors to simulate the growth and reproduction of the individual so its state can be updated.

Physiological and ecological benefits of movement to organisms can be relatively short-term, such as when organisms move to avoid unfavorable temperatures (Kotwicki et al. 2005, Dulvy et al. 2008, Nye et al. 2011) and stressful pH (Bednaršek & Ohman 2015), or to search for more productive feeding grounds to optimize their energy intake (Trenkel et al. 2014, Aoki et al. 2017). In contrast, long-distance migrations between foraging and reproductive areas (i.e. connectivity) can be energetically costly, with the net benefit or cost to offspring survival and fitness not becoming apparent for months or years (Corkeron & Connor 1999). There may be a trade-off between energy reserves, fecundity, and migration distances, such that the largest individuals migrate the farthest in order to reach the most distant but most favorable reproductive areas (Slotte & Fiksen 2000). Understanding how climate change will impact these costs and benefits of short-term and migratory movements at the individual level requires consideration and modeling of bioenergetics over a range of time lags and multiple life stages (e.g. juvenile growth affecting later migration and reproduction).

Movements and migrations can be initiated by a wide variety of cues, including local *in situ* environmental conditions (e.g. temperature, photoperiod), developmental state, accumulation of sufficient energy reserves, genetically determined internal cues, and social learning (Bauer et al. 2011, Winkler et al. 2014, Cooke et al. 2022). Whereas movements are primarily driven by animals following real-time changes in suitable thermal or foraging habitats as cues (Nøttestad et al. 1999, Bauer et al. 2011), energy costs and benefits are more easily represented using bioenergetics models. This type of adaptive behavior may also confer better resilience to long-term shifts in environmental gradients due to climate change. Alternatively, migrations may be genetically hardwired to follow evolutionarily favorable routes, with higher bioenergetics costs and reduced adaptive capacity, and thus higher vulnerability to climate change. This strategy may involve a period of energy gain, in which an animal builds up body stores before migrating, and then a period of energy loss, during which the accumulated condition is expended during migration and reproduction (van Ginneken et al. 2005, Wallace et al. 2006, Golet et al. 2007). As a result, environmentally determined bioenergetic costs and benefits for long-distance migrators are less impactful in near real-time but are important over the reproductive cycle, presenting a challenge for effective bioenergetics modeling that attempts to account for the costs and benefits of movement.

While agent-based models are computationally expensive for simulations of large spatial domains or multiple trophic levels, they have the advantage of being better able to simulate the complex movement patterns of higher trophic level animals for *in silico* experiments (Rose et al. 2010). In addition, the bioenergetics history of each individual or group can be retained, allowing the calculation of growth, condition, maturity, and energy reserves through time. Mechanisms of movement of marine species are still unclear, but it is possible to couple and dynamically link bioenergetics with marine species movement models. Some considerations include defining cues for movement and migration decisions, understanding the pathways in which a species responds to climate change, as well as ensuring that the resulting behavior can be linked to the organism's bioenergetics regarding distance traveled, swimming speed, environmental conditions experienced, and energy consumption. Examples that illustrate the 2-way coupling of bioenergetics and movement with IBMs (albeit very simplified) include the simulation of the feeding migration of Japanese sardine *Sardinops melanostictus* (Okunishi et al. 2009, 2012) and the examination of the role of zooplankton and tempera-

ture in the spawning migration of European anchovy in the Bay of Biscay (Politikos et al. 2015).

6. OPPORTUNITY 4: ASSESSING THE REALISM OF MODEL PREDICTIONS

A major challenge with the use of all ecological models, especially to inform management, has been the effective assessment of model skill through model validation and sensitivity analyses (Rykiel 1996, Eker et al. 2018, An et al. 2021). Validation often involves a comparison of model output to empirical data to determine model skill and confidence with respect to model projections (Bennett et al. 2013, Augusiak et al. 2014). However, not just numerical models but also observations are imperfect and, thus, agreement of model−data comparisons informs us about agreement between 2 models; the resemblance of these models to reality requires further evaluation (Lynch et al. 2009). Therefore, when comparing field and model estimates, variance and uncertainty need to be assessed for both observation data and predicted model data (Skogen et al. 2021). On the other hand, as models are built from published information, they also represent a framework for knowledge validation (Aarflot et al. 2022), where a misfit model with observations also can be regarded as a test of possible inconsistencies between independent studies and observational data sets.

Multiple impacts of climate change pose further challenges to model validation because of the importance of disentangling direct drivers (e.g. abiotic environmental factors such as temperature) and indirect drivers (e.g. predator abundance) of organismal performance under novel conditions. When models are linked or coupled to hydrodynamics and biogeochemical (water quality) models, a critical aspect of all validation exercises is the evaluation of hydrodynamics and biogeochemistry, especially for how its predictions are being used in the biological component. The hydrodynamics and biogeochemical predictions used as forcing often play a major role in determining the performance of coupled physical−biological models (Skogen & Moll 2005, Friedrichs et al. 2006).

Troost et al. (2023) recently proposed a general set of protocols for performing and reporting validation of agent-based models. A key aspect of validation is comparing model predictions to independent field-based survey data sets not used for model development or calibration (Schmolke et al. 2010). The data for validation (as well as calibration) include values of state variables (e.g. biomass), process rates (e.g. pri-

mary production, growth via weight-at-age data of fish), spatial distributions, and emergent system-level properties (e.g. food web structure, shape of the spawner−recruit relationship). While sufficient data for validation is always challenging for models of lower trophic levels, rigorous validation is especially challenging for models that include upper trophic levels, as most of the data are from annual or seasonal-scale surveys that use sampling locations designed to derive broad indices of abundance. Many highly resolved, upper trophic level models employ 'pattern matching' (Grimm et al. 2005), which can be a semi-quantitative technique and often uses all available data, reducing opportunities for independent validation (Fulton et al. 2011, Peck et al. 2018).

We discuss 3 issues as part of assessing the realism of model predictions. These are (1) validation of bioenergetics-based models with new data streams, (2) revisiting the traditional strategy for model validation, and (3) uncertainty and model complexity. The first 2 directly relate to model validation, while the third focuses on model structure and quantifying uncertainty; all of which enable assessment of model realism.

6.1. Validation of bioenergetics-based models with new data streams

Measurement capabilities related to bioenergetics are rapidly expanding (Cooke et al. 2016) and these offer an opportunity for collaborative efforts to ensure the data can be also leveraged for the calibration, and especially validation, of the next generation of bioenergetics models. These emerging data technologies include molecular approaches (e.g. metabarcoding, metatranscriptomics, ultra-performance liquid chromatography) applied to various types of samples (e.g. eDNA, gut contents, lipids), remote sensing, optical and acoustic sampling, biosensors, bio-logging and autonomous underwater vehicles (Danovaro et al. 2016, Moustahfid et a. 2020). Accelerometers on archival tags can provide estimates of energy dissipation from swimming and can detect specific behaviors such as feeding (e.g. Whitlock et al. 2015, Horie et al. 2017). The temporal and spatial scales of results from these different data sources vary and they include qualitative, presence−absence, and quantitative information. Furthermore, many remain limited by cost and therefore generate information that is representative of limited conditions observed during measurements, and thus difficult to extrapolate, and highly uncertain due to small sample size. How the availability of subsets of these data for a specific application can

be combined into a model validation that enables statements about overall model confidence is challenging.

Furthermore, growth is a primary predictor of bioenergetics, and growth histories for model evaluation can be reconstructed from otolith daily microstructure analysis. When used in conjunction with bioenergetics and movement modeling, otolith analysis can reconstruct the food and temperature history of individuals (e.g. Pecquerie et al. 2012) and movement patterns (e.g. Ito et al. 2018, Higuchi et al. 2019). Chung et al. (2019a,b) determined that the carbon isotope ratio precipitated in otolith daily rings has the potential to provide metabolic rate information for teleost fishes, and stable nitrogen isotope ratio of phenylalanine in vertebral centra of teleost may be able to provide organism diet information (Matsubayashi et al. 2017). Direct and rapid measurement of fat content or energy density represents a proxy to capture the variability in the condition of organisms that represent an integrative measure of growth (Peig & Green 2010, Clancey & Byers 2014) and is directly comparable to predictions from the DEB model (Gatti et al. 2017). Even when these new technologies do not monitor the focal organisms of interest, they can provide an empirical foundation for processes (e.g. transport, generation of prey fields) important for bioenergetics modeling.

6.2. Revisiting the traditional strategy for model validation

We suggest developing new validation strategies for bioenergetics-based models that incorporate the traditional survey data on monthly to annual scales with the finer-scale measurements (e.g. tracks of individuals) emerging from new monitoring and telemetry technologies (e.g. Chimienti et al. 2020). A key to advancing bioenergetics models will be how well the sampling and analysis of the observations can be used to inform the mechanistic representations, and ultimately the validation of the assumptions and performance, of the bioenergetics modeling. Monitoring is typically motivated and designed for purposes other than informing bioenergetics modeling, and effective use will require collaborative efforts of field scientists and modelers in the planning of monitoring programs. Often, with some moderate modifications or additions, monitoring can fulfill its needed objectives and also simultaneously provide valuable data to the modeling.

We illustrate this idea of creative validation strategies by describing a 'divide and conquer strategy'

and the idea of using comparisons tailored to climate change questions. The 'divide and conquer' idea uses designed simulation experiments that evaluate the performance of individual modules and then perform additional simulation experiments that allow assessment of the behavior of the fully coupled system (Lorscheid & Meyer 2016). Rose et al. (2013a,b) used a simple version of this approach and calibrated an agent-based population model of delta smelt *Hypomesus transpacificus* to available data. Separate simulation experiments were used to calibrate the growth (and diets) of an individual over its lifetime under averaged food and then daily movement in response to fixed salinity fields to confirm movement behavior, and then the calibrated modules were used together under artificially increasing spawning to determine density-dependent mortality that resulted in a realistic spawner—recruit relationship. The full model was then run for a 21 yr historical period and compared to long-term monitoring data. Following the lead of Chimienti et al. (2020), one can envision how reconstructed growth histories from otolith data, telemetry information, and condition (fat content) could be added to these simulation experiments.

Part of a new validation strategy can also make use of observed extreme conditions (Tommasi et al. 2017, Becker et al. 2018, Harris et al. 2018). Rather than the traditional mindset of focusing on the model skill for long-term average conditions or how the model fits many of the years of the observations, the historical data can be partitioned to allow testing for extreme conditions that may push model evaluation closer to the anticipated novel conditions expected under climate change. For example, exceptionally warm years can be simulated in sequence, or years with extended heatwaves (Smith et al. 2023) can provide data for model testing of possible responses to warming. Perhaps this can be combined with the approach proposed by Dietze et al. (2018), who discussed how validation using more readily available short-term predictions can be used to provide additional credibility to longer-term forecasts.

6.3. Uncertainty and model complexity

Computing power and efficient Monte Carlo methods are enabling formal uncertainty analyses of increasingly complex models (Pianosi et al. 2016); quantifying uncertainty in model predictions greatly helps the interpretation. Using different carbon emission scenarios with an ensemble of projections from different physical climate models (Hermann et al.

2019, Hollowed et al. 2020) can also enable bounding of the bioenergetics-based model projections (Holsman et al. 2020). Ensemble modeling and comparing the outputs of multiple models is another approach for assessing the trade-offs of more detailed representations (Gårdmark et al. 2013, Spence et al. 2018). The FISH-MIP project provides a template for using multiple ecosystem models to predict responses to climate change (Tittensor et al. 2021).

Finally, many of the ideas presented in this paper involve adding complexity to existing bioenergetics models or developing relatively complex new models. While only a few issues apply to any specific situation, this raises the long-standing and well-reviewed question of what the most parsimonious approach is (i.e. optimal level of complexity) for ecological models (Fulton et al. 2003, Plagányi et al. 2011, Collie et al. 2016). As part of a new strategy for model validation, a procedure to formally assess new model formulations for their added value is needed. This can involve better documentation of model development and validation performance (e.g. Grimm et al. 2014, Planque et al. 2022) and analytical methods. For example, Getz et al. (2018) proposed that coarse graining, commonly used in chemistry and biophysics, could be useful for simplifying ecological models to determine simplified formulations that capture the benefits of added process detail and complexity without actually needing to represent all of the details. In addition, increasing model complexity and diversity elevates the importance of conducting open science. Where communities of practice collaborate to move projects forward by sharing data, code, and model validation practices, more rapid progress can be made (Wolkovich et al. 2012, Hampton et al. 2015, Lowndes et al. 2017).

7. APPLICABILITY TO EULERIAN MODELS

The opportunities we described above using agent-based modeling as the context also apply to Eulerian models that include biomass, structured (e.g. age, stage, size), and trait-based approaches (Nisbet et al. 2000, Koenigstein et al. 2016, Blanchard et al. 2017, Smallegange et al. 2017). As one adds species — from population to multiple species to food web to end-to-end models — the representation tends to move from agent-based to Eulerian in order to accommodate simulating many species. Commonly used Eulerian or hybrid (some representation of individual-level dynamics) food web models are EwE and Atlantis; many of these models include a bioenergetics formulation im-plemented for classes of individuals (e.g. ages, average individual). Our ability to configure and validate models with many species (i.e. community, food web) using agent-based approaches is progressing, but spatially explicit, agent-based, full food web models remain a challenge (Fulton et al. 2011, Grimm et al. 2017); Eulerian approaches will play a critical role in assessing responses to climate change at the food web and ecosystem levels (Heymans et al. 2020).

While there are differences in the details and solutions, Eulerian-oriented models are challenged with the same conceptual opportunities that were described above using agent-based models. For example, introducing movement into spatially explicit bioenergetics models of individuals (Lagrangian) is conceptually straightforward: imposing movement algorithms (e.g. swim speed, direction) on each individual. Algorithms can use environmental gradients, recent history of exposure, or nearby individuals as cues (Watkins & Rose 2013, Calovi et al. 2014).

With climate change, Eulerian approaches also must address the challenges of simulating movement and migration in novel environmental conditions and consider acclimation, adaptation, 2-way linking of movement with bioenergetics, and adaptive behavior. However, Eulerian approaches generally treat movement as flows or fluxes of organisms among spatial cells (e.g. advection—diffusion—reaction equations) with stronger behavioral movements towards suitable habitats (e.g. Dueri et al. 2014). The representation of these fluxes is often simple and mostly habitat-based (Lehodey et al. 2008, Walters et al. 2010, Audzijonyte et al. 2019a, Coll et al. 2020), and retaining information on conditions experienced by individuals and representing adaptive behavior is difficult. Encouragingly, Scutt Phillips et al. (2018) demonstrated that Eulerian and agent-based models can generate similar patterns of migration of skipjack tuna *Katsuwonus pelamis*.

Similarly to movement, the opportunities related to representing temperature effects, multiple stressors, and validation also apply to the Eulerian approaches. Advances in modeling that allow for hybrid models that seamlessly shift from Eulerian to Lagrangian (and, more recently, purely statistical and artificial-intelligence-based) as needed at specific times during a single simulation mean that the behavior dynamics and information content of an agent-based approach can be married with the computational savings of Eulerian representations (Gray & Wotherspoon 2012, 2015). This may also prove a fruitful way forward for gaining the power of bioenergetics representations and coupling without relying on increasing computing power alone to make it feasible.

Advancing bioenergetics and addressing these opportunities in Eulerian models is possible. Like agent-based models, Eulerian models will continue to evolve (Coll et al. 2020, Perryman et al. 2021, Stock et al. 2023), and the opportunities presented here offer specific areas to ready the models for assessing living resource responses to climate change. Further incorporation of bioenergetics into these Eulerian models, along with consideration of the opportunities described above, would enable a more realistic and robust simulation of responses of populations, and especially communities and food webs, to new climate-driven conditions.

8. CONCLUDING REMARKS

There are many challenges in the field of bioenergetics, and we consider the ideas outlined here as opportunities because, with focused efforts, significant advances in our understanding of climate change impacts on marine ecology can be achieved. These opportunities will move the relatively established field of bioenergetics into a modern era of advanced experimentation and monitoring and assessment of climate change responses. The advent of new technologies such as tagging, autonomous underwater vehicles and gliders, and molecular and biochemical biomarkers and techniques provide new and invaluable covariant data streams and contextualize organism behavior *in situ*. There have been many recent advancements in modeling and the computational capacity and efficiency of computers that make it possible (if needed) to add complexity to models.

We described 4 categories of opportunities to advance bioenergetics modeling. A refined quantitative understanding of temperature effects, alone and in combination with other stressors, on physiological processes (Opportunity 1) will elucidate many ecological processes and provide robust projections of species distributions, population abundances, and productivity in response to climate change. In addition, focused efforts are needed to develop a mechanistic understanding of how multiple stressors combine to affect physiological to population- and ecosystem-level processes. Scaling from the individual- to population- and ecosystem-level processes (Opportunity 2) has always been a grand challenge in marine ecology, but advances in population and ecosystem modeling and more computing power now make this challenge achievable. Local adaptations, plasticity, and acclimation are also important areas of continued research under multiple stressors. Ad-

vances in tagging, particle tracking modeling, and an exponential increase in monitoring of the oceans have opened a tremendous opportunity to combine the well-established principles of bioenergetics with environmental conditions and movement ecology (Opportunity 3) at a much higher spatial and temporal resolution than was possible even a decade ago. Finally, model validation (Opportunity 4) remains a challenge to fields beyond bioenergetics, but new innovative data and data analysis techniques and greater reliance on scenario-testing and model comparison in addition to the goodness of fit tests will increase our confidence in bioenergetics-based models and associated projections.

The time is ripe for a renewed focus on bioenergetics modeling as we face global climate change. The opportunities are many and important. We presented specific opportunities that offer critical advancement of bioenergetics modeling and its use in projecting the effects of climate change on individuals to ecosystems. Addressing the subset of these opportunities appropriate for a given situation as part of the development, formulation, and testing of bioenergetics models, used alone or with population and food web modeling, will increase confidence in predictions and provide robust science-based advice for climate adaptation and mitigation. Progress is only possible with a coordinated effort that combines field data collection, laboratory experiments, and modeling innovations and testing. The data aspects are progressing rapidly and now the modeling needs to be updated and, if necessary, expanded to ensure maximum use of the data to inform the next generation of bioenergetics models.

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