



An aerobic scope-based habitat suitability index for predicting the effects of multi-dimensional climate change stressors on marine teleosts



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ABSTRACT

Climate change will expose many marine ecosystems to temperature, oxygen and CO₂ conditions that have not been experienced for millennia. Predicting the impact of these changes on marine fishes is difficult due to the complexity of these disparate stressors and the inherent non-linearity of physiological systems. Aerobic scope (the difference between maximum and minimum aerobic metabolic rates) is a coherent, unifying physiological framework that can be used to examine all of the major environmental changes expected to occur in the oceans during this century. Using this framework, we develop a physiology-based habitat suitability model to forecast the response of marine fishes to simultaneous ocean acidification, warming and deoxygenation, including interactions between all three stressors. We present an example of the model parameterized for *Thunnus albacares* (yellowfin tuna), an important fisheries species that is likely to be affected by climate change. We anticipate that if embedded into multispecies ecosystem models, our model could help to more precisely forecast climate change impacts on the distribution and abundance of other high value species. Finally, we show how our model may indicate the potential for, and limits of, adaptation to chronic stressors.

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1. Introduction

1.1. Habitat quality is central to conservation biology

Habitat alteration is the dominant driver of species extinction in our time (Homyack, 2010) and is likely to only increase in importance in the future due to the perturbations brought about by global climate change (Thomas et al., 2004; Travis, 2003). The ubiquity of habitat quality models (i.e. those that attempt to simulate species distribution based on habitat variables) across different disciplines of ecology reflects this importance. For example, one of the simplest forms of the habitat quality model is the climate envelope model (CEM), which correlates presence/absence data against the spatial distribution of environmental variables to try to define the limits of a species distribution (Thomas et al., 2004). A generalized form of the CEM is the habitat suitability model, which attempts to simulate not only the limits of

a species' distribution but also its probability of occurrence/abundance within its range (Hirzel and Le Lay, 2008).

These habitat suitability models can be incorporated into more complex models either as a single-species add on to a fisheries assessment model (Link et al., 2011) or as part of a niche model that adds bionomic factors (resource limitation or predation pressures that define a Grinnellian niche) through interactions with other species whose distribution and abundance is partially driven by habitat suitability models incorporating scenopoetic factors (e.g. temperature and oxygen limits that define an Eltonian niche) (Hutchinson, 1957). When enough niche models are aggregated to represent the full breadth of trophic levels existing in an ecosystem, these are then termed end-to-end ecosystem models (see Lehodey et al., 2008; Link et al., 2010; Maury, 2010) and may be used to perform large-scale simulations of ecosystem-responses to climatic or biogeochemical shifts (Lehodey et al., 2010).

Finally, a special application of habitat suitability models are those required fisheries biologists who need to disentangle habitat effects from stock abundance in order to constrain their estimates of optimum yield. These so-called habitat-based standardizations (Hinton and Nakano, 1996) generally take the form of correction factors to a "catchability" term that are used to ensure that the

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catch per unit effort at a given location and time is more reliably indicative of abundance (Maunder et al., 2006).

1.2. Physiology is a key constraint for climate-change studies

While all of the model types discussed above can be applied both to current and future environments, habitat suitability models that attempt to tackle the problem of climate change face fundamentally different challenges than those that are primarily concerned with current or historical environments. This is because applying habitat suitability models to a climate change future is inherently extrapolative – that is, future habitats are likely to involve either novel states (e.g. temperature or $p\text{CO}_2$ levels not previously experienced in a given region) or novel combinations of states (e.g. unusually high temperatures combined with low oxygen) for which species distribution data is not currently available (Kearney and Porter, 2009). The inherent non-linearity of physiological control mechanisms (typically involving some tolerable range of environmental stressors bounded by *pejus* limits beyond which fitness rapidly declines (Nagarajan, 2002; Pörtner, 2002)) and the fact that the regulatory machinery involved in responding to distinct stressors often overlap (leading to complex interactions when multiple environmental variables are perturbed simultaneously; see (Claireaux and Lagardère, 1999; Kato et al., 2005; Lefrançois and Claireaux, 2003; Perry and Gilmour, 1996; Roch and Maly, 1979)) make these extrapolations highly uncertain. To make matters worse, many of the environmental variables used to inform habitat suitability models (e.g. temperature, oxygen, $p\text{CO}_2$) exhibit high spatial correlation (Prince and Goodyear, 2006; Schmittner et al., 2008), compromising the ability to assign a gradient in species abundance to a specific variable. Indeed, many studies have demonstrated large variability in estimated abundance when extrapolating statistical models trained on current observations to future states (Thuiller, 2003; Thuiller, 2004; Thomas et al., 2004; Hijmans and Graham 2006).

One way to ameliorate these problems is to constrain the results of statistical habitat suitability models with information from organismal physiology (Denny and Helmuth, 2009; Hijmans and Graham, 2006). Physiological relationships provide a mechanistic (or semi-mechanistic) basis for understanding changes in abundance for which (in the absence of substantial genetic or epigenetic adaptation) we can assume stationarity into the relatively distant future (Kearney and Porter, 2009). Furthermore, because organismal physiology is principally modified by genetic or epigenetic processes, physiology-based models address a major weakness in statistical habitat suitability models by allowing us to ask questions such as (1) which physiological parameters could play a role in mitigating the changes to habitat suitability caused by climate change, and (2) is the currently observed variability in these parameters (indicative of the range of phenotypic plasticity) sufficient to adapt to future climate change even in the absence of genotypic or epigenetic modification (Kearney and Porter, 2009)?

1.3. Aerobic scope is an integrative index of abiotic habitat suitability

Implicit in the concept of linking organismal physiology to habitat suitability (and, after consideration of bionomic factors, to abundance) is the criteria that the metric of physiological state used must be linked to fitness (Homyack, 2010). The most popular methods utilize some measure of energetic state, such as the metabolic cost of key fitness-determining behaviors including digestion, hibernation, flight, and foraging; or of benchmark metabolic states such as standard (minimum) or active (maximum) metabolism (Braaten et al., 1997; Homyack, 2010; Rosenfeld et al., 2005). In this paper we utilize aerobic scope (the difference between maximal aerobic metabolism and the minimum metabolic expenditure needed for survival (Fry, 1947)) as an integrative index of habitat suitability with strong ties to

fitness. Because the machinery that underlies aerobic metabolism is conserved across metazoan taxa (Thannickal, 2009), much of the discussion below is broadly applicable.

The correspondence between aerobic scope and the other energetic indicators discussed above can be seen by partitioning an organism's energy budget into four parts: (1) the proportion of total energy required to maintain essential life processes, (2) the proportion that can be devoted to foraging and somatic growth, (3) the proportion dedicated to reproduction either in the form of gonadal growth or activities such as maintaining a territory, and (4) the energy available for storage (Homyack, 2010). In vertebrates, almost all of these energetic costs must be paid for through aerobic metabolism (Pörtner, 2010), either by directly powering these activities or via excess post-exercise oxygen consumption (EPOC: Gaesser and Brooks, 1983; Lee et al., 2003). The aerobic scope can be thought of as the total potential metabolic expenditure available for fueling portions 2–4 in excess of that required for portion 1. Reductions in aerobic scope either through an increase in minimum metabolism (a rise in portion 1) or a decrease in maximum metabolism (a decline in the total available energy output) therefore imply a reduction in the maximum rate for one of the processes (growth, reproduction, or energy storage) that drives current and future fitness. Furthermore, aerobic scope defines physical limits to long-term habitation at the critical limits (conditions under which aerobic scope is zero) beyond which maintenance of essential life processes is only possible by drawing down stored oxygen reserves or relying (temporarily) upon anaerobic capacity (Pörtner, 2010). This definition is only a slight variation on what is termed the fundamental niche: the space where, in the absence of biotic interactions, an organism can survive and reproduce (Kearney and Porter, 2009). These properties make aerobic scope a strong metric on which to base a physiological habitat-suitability model.

1.4. *Thunnus albacares* as a model organism for aerobic scope modeling

While a number of species could conceivably be used to parameterize an aerobic scope model, we chose the yellowfin tuna *Thunnus albacares* for this study due to the wealth of physiological data available on this species as well as the multiple environmental changes that are likely to befall portions of its habitat due to climate change. These include increased surface ocean temperatures, surface ocean and thermocline deoxygenation, and increased hypercapnia (high levels of $p\text{CO}_2$) both in the surface ocean and especially in the thermocline and oxygen minimum zones where high levels of dissolved carbon dioxide have already substantially depleted the buffering capacity of seawater (Brewer and Peltzer, 2009; Cai et al., 2011; Gruber, 2011). We rely on well-established physiological equations to create an aerobic scope estimator from already available laboratory data, and incorporate both the mean and variability of this data to create not just an estimate of how these complex environmental perturbations could affect habitat suitability for *T. albacares* but also some indications of the extent to which the observed variability in these parameters could compensate for future climate change.

While this paper provides one example of an aerobic-scope based habitat suitability model parameterized for a single species at a single location, we have designed this model to be applicable to a wide range of teleosts in many different marine environments with very little modification, and we hope broader aspects of the model can be useful for an even wider range of taxa.

2. Methods

We developed a three-box model of a tuna consisting of a conceptually infinite seawater reservoir, a gill reservoir, and a reservoir for the working tissues (principally the muscles). The

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