OCEANOGRAPHY

Climate-driven aerobic habitat loss in the California Current System

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Climate warming is expected to intensify hypoxia in the California Current System (CCS), threatening its diverse and productive marine ecosystem. We analyzed past regional variability and future changes in the Metabolic Index (Φ), a species-specific measure of the environment's capacity to meet temperature-dependent organismal oxygen demand. Across the traits of diverse animals, Φ exhibits strong seasonal to interdecadal variations throughout the CCS, implying that resident species already experience large fluctuations in available aerobic habitat. For a key CCS species, northern anchovy, the long-term biogeographic distribution and decadal fluctuations in abundance are both highly coherent with aerobic habitat volume. Ocean warming and oxygen loss by 2100 are projected to decrease Φ below critical levels in 30 to 50% of anchovies' present range, including complete loss of aerobic habitat—and thus likely extirpation—from the southern CCS. Aerobic habitat loss will vary widely across the traits of CCS taxa, disrupting ecological interactions throughout the region.

INTRODUCTION

Hypoxia in the California Current System

Climate change is warming the oceans, depleting its dissolved oxygen (O_2), lowering its pH, and altering species distributions, phenology, and interactions (*1*). Understanding how these changes affect species fitness remains a challenge for at least two fundamental reasons. First, the role of climate in shaping habitat is mediated by numerous physiological and ecological traits that are not systematically measured and are difficult to disentangle. Second, the observational records needed to detect climate-driven ecosystem changes rarely span the decadal periods of intrinsic ocean variability (*2*). Attributing past species responses to multiple climate stressors is essential to projecting future climate impacts on marine ecosystems.

The California Current System (CCS) is ideally situated to detect and attribute ecological responses to climate change. Upwelling of nutrient-rich water maintains high biological productivity and ecological diversity, but also bathes the continental shelf in waters that are naturally low in O_2 and pH, two primary stressors for many species (*3*). The CCS is also a region of strong interannual and decadal hydrographic variability driven by modes of natural climate variability spanning the Pacific Ocean (*4*). Ecological responses to this climate variability have been observed in species that form critical links in the food web (*5*–*7*). These low-frequency perturbations provide "natural experiments" that presage future climate change, and can therefore be used to calibrate thresholds for species and ecosystem responses to accelerating ocean changes.

The CCS is also uniquely suited to evaluate the role of temperature-dependent hypoxia as a driver of global marine habitat loss (*8*–*10*). Oxygen loss is projected to be especially strong in the Northeast Pacific, emerging early from the background natural variability there (*2*). Recent analyses of physiological traits of diverse marine species demonstrate a close alignment of biogeographic range boundaries with the ratios of organismal O_2 supply and demand. This suggests that species geographic ranges are commonly limited by temperature-dependent aerobic energy availability (*8*). However, this ecophysiological framework, the "Metabolic Index," has not been tested against ecological observations of species abundance changes over decadal scales. Meanwhile, O_2 fluctuations in the CCS have been statistically implicated in the historical variability of fish populations (*5*–*7*), but have yet to be linked to habitat availability based on measurable physiological traits. Here, we use the Metabolic Index to provide evidence of such a link, and present a general approach to evaluate the response of species in a region likely to undergo rapid intensification of temperature-dependent hypoxia in coming decades.

The Metabolic Index and aerobic habitat

The influences of temperature and O_2 on organism fitness are closely linked through the physiology of aerobic respiration. As temperatures rise, most species become less tolerant of low-O_2 water (*10*), because metabolic O_2 demand rises with temperature faster than organismal O_2 supply does. The temperature-dependent ratio of the potential O_2 supply to metabolic demand can be represented by the Metabolic Index [Φ; (*8*, *9*)], which must exceed a critical value (Φ_{crit}) for an environment to be ecologically habitable

$$\Phi = \frac{\text{Supply}}{\text{Demand}} = A_o \frac{pO_2}{\exp(-E_o/k_B(1/T - 1/T_{ref}))} \geq \Phi_{crit} \quad (1)$$

This index incorporates both environmental temperature (T, K) and the partial pressure of O_2 (pO_2, atm), as well as species-specific physiological traits. The coefficient A_o (atm^{-1}) is the ratio of oxygen supply to demand by an organism at a reference temperature (T_{ref}), and measures hypoxia tolerance. The change in hypoxia tolerance with temperature is described by the Arrhenius function (k_B is the Boltzmann constant), with the parameter E_o (eV) representing the temperature sensitivity of hypoxia tolerance. These two physiological parameters—hypoxia tolerance (A_o) and its temperature sensitivity (E_o)—can be calibrated using laboratory experiments, in which the

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