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Synergistic effects of climate-related variables suggest future physiological impairment in a top oceanic predator

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By the end of this century, anthropogenic carbon dioxide (CO₂) emissions are expected to decrease the surface ocean pH by as much as 0.3 unit. At the same time, the ocean is expected to warm with an associated expansion of the oxygen minimum layer (OML). This effect is exacerbated by high temperature. Reduced aerobic and locomotory scope in warm, high-CO₂ surface waters will presumably impair predator–prey interactions with cascading consequences for growth, reproduction, and survival. Moreover, as the OML shoals, squids will have to retreat to these shallower, less hospitable, waters at night to feed and repay any oxygen debt that accumulates during their diel vertical migration into the OML. Thus, we demonstrate that, in the absence of adaptation or horizontal migration, the synergism between ocean acidification, global warming, and expanding hypoxia will compress the habitable depth range of the species. These interactions may ultimately define the long-term fate of this commercially and ecologically important predator.

Author contributions: R.R. and B.A.S. designed research; R.R. performed research; and R.R. and B.A.S. analyzed data and wrote the paper.

Supporting Information: SI Table S1

This article contains supporting information online at www.pnas.org/cgi/content/full/0806886105/DCSupplemental.

The synergistic effects of elevated CO₂, hypoxia and temperature, are, to date, completely unexplored.

The jumbo squid, Dosidicus gigas, is a large pelagic top predator endemic to the Eastern Tropical Pacific (ETP), where temperature and oxygen are already near the upper and lower extremes, respectively, found in the oceans and where climate changes are expected to be pronounced (2). D. gigas reaches >2 m in total length and 50 kg in mass. Over the last few years, it has greatly extended its tropical/subtropical range as far north as Canada and Alaska, where it is now exerting a significant top–down control on commercial fish stocks (18). Like other ommastrephid squids, D. gigas displays a high oxygen demand that reflects high activity levels dictated by the pelagic environment and low efficiency of jet propulsion relative to other forms of locomotion (19). The metabolic capacity of these muscular squids is surprising considering the limitations of their respiratory systems. Their blood has low oxygen-carrying capacity, relative to similarly active fishes, because of viscosity-related constraints associated with an extracellular respiratory protein. In fact, they use all of the oxygen carried in the blood on each cycle through the body, even at rest, leaving no venous oxygen reserve. Furthermore, blood–oxygen binding in most active squids is highly pH sensitive (supporting information (SI) Table S1), a property that facilitates oxygen release to demanding tissues, but presumably interferes with oxygen extraction from hypoxic or CO₂-rich seawater. Consequently, these organisms are thought to live chronically “on the edge of oxygen limitation” (20) and are not well poised to adapt to future environmental changes that influence oxygen supply and demand. Jumbo squids are thus expected to be particularly vulnerable to ocean acidification, global warming, and hypoxia. Surprisingly, D. gigas undergoes diel vertical migrations into zones of pronounced hypoxia at mesopelagic depths (21), known as oxygen minimum layers (OML).

To evaluate the effects of rapidly changing environmental parameters on the metabolic physiology of D. gigas, we exposed the jumbo squids to short-term (<24 h) elevations in CO₂ equivalent to pessimistic predictions for the year 2100 (0.1% CO₂, ~1000 ppm; ΔpH = 0.3), while varying temperature and oxygen levels to match the conditions currently found at their night and daytime distributions (20°-25°C, 21% O₂ and 10°C, 1% O₂, respectively).

Author contributions: R.R. and B.A.S. designed research; R.R. performed research; and R.R. and B.A.S. analyzed data and wrote the paper.

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Literature (Fig. 2) indicates predators of equivalent size, including sharks and tunas of mass-specific metabolism are higher than those of top vertebrates among the highest in the oceans (Fig. 2). The squid’s lowest rates of standard metabolic rate. Thus, IMR is, we believe, a reasonable approximation of a standard metabolic rate (RMR) (see Materials and Methods for details). The percentages chosen to designate AMR and IMR are based on levels that approximated continuous activity and apparent inactivity (modest ventilatory movements only) in the video observations. Thus, IMR is, we believe, a reasonable approximation of a standard metabolic rate.

Fig. 1. Rhythmic sinusoidal oscillations of oxygen consumption in Dosidicus gigas. (A) An 8.03-g squid at 25°C. (B) A 21.93-g squid at 20°C. (C) A 2.23-g squid at 10°C. Rates are expressed as differences between the oxygen levels (μmol liter⁻¹) recorded at the entrance and the exit of the chamber and oscillations reflect periodic activity peaks as indicated by recorded rates of mantle muscle contraction. Some specimens were exposed to two cycles of CO₂ treatment (e.g., in C) to exclude the possibility that the observed trends in oxygen consumption were not driven by decreasing stress or food deprivation after placement in the chamber.

Results and Discussion

All animals displayed a distinct periodicity of oxygen consumption rates (Fig. 1). Video analysis confirmed that the cycles, referred to here as “active cycles,” correlated with activity levels as indicated by rates of mantle contraction for jet propulsion. The occurrence of such activity peaks enabled us to quantify what we define as the maximal (MaxMR), active (AMR), routine (RMR), and inactive metabolic rates (IMR) and the mean number of active cycles per hour. These designations are based on the highest recorded rate (MRM), the average of rates expressed during peaks in the active cycles that were 20% higher (AMR) and 15% lower (IMR) than the average for the entire run (RMR) (see Materials and Methods for details). The percentages chosen to designate AMR and IMR are based on levels that approximated continuous activity and apparent inactivity (modest ventilatory movements only) in the video observations. Thus, IMR is, we believe, a reasonable approximation of a standard metabolic rate.

The jumbo squids displayed oxygen consumption rates that are among the highest in the oceans (Fig. 2). The squid’s lowest rates of mass-specific metabolism are higher than those of top vertebrate predators of equivalent size, including sharks and tunas (Fig. 2B). However, under hypoxic conditions (Fig. 3B), IMR decreased by ~80% from an average of 7.0 (control) to 1.4 μmol O₂ g⁻¹ h⁻¹ (Fig. 3A). A concomitant enhancement of glycolysis, as indicated by an accumulation of octopine (Fig. S1), compensates for only a small fraction (<10%) of the energy deficit that resulted from the decline of aerobic ATP synthesis. In the absence of reduced oxygen demand, we calculate that the rate of ventilation that would be required to meet oxygen demand, assuming complete extraction of oxygen from the respiratory stream, increases dramatically with depth (Fig. 3C). Because ventilation and locomotion are tied via contraction of the large muscular mantle (23), ventilation is a very costly part of the energy budget in squids. Excess ventilation during hypoxic exposure would drive oxygen demand up in a positive feedback loop that would presumably prohibit the maintenance of routine aerobic metabolic rates in the oxygen minimum layer. Thus, whereas the OML restricts the depth distribution of competing vertebrate predators to the upper surface layers because of their more limited hypoxia tolerance (ref. 24, Fig. 3B), D. gigas circumvents similar restrictions via metabolic suppression and spends the daytime in deep, cold, and oxygen-depleted waters (Fig. 3).

The profound hypoxia-induced metabolic suppression (Figs. 2A and 3A) extends the squid’s survival time in the OML, by conserving the finite stores of fermentable substrate, minimizing cytotoxicity and limiting the oxygen debt that must be repaid upon return to oxygen-replete surface waters. Oxygen debt typically includes the costs of replenishing substrate stores and removing toxic end products of anaerobic metabolism. Payment of such debts entails a substantial increase in oxygen consumption (25). Although the oxygen debt incurred by D. gigas is minimized by the substantial suppression of ATP-consuming
activities, it is probably not negligible and will add to the already high metabolic costs associated with warm surface temperatures.

Under the elevated CO2 conditions predicted for the end of this century, the squid’s oxygen demand was significantly reduced (Figs. 1 and 4, and Fig. S2). At 25°C, MaxMR decreased, on average, from 70 to 48 \( \mu \text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1} \) (\( P < 0.05 \); Fig. 4A), which represented a reduction of 31% (Fig. 4B). Similar CO2-induced decreases in MaxMR were attained at 10° and 20°C (\( P < 0.05 \); Fig. 4A and B). Significant reductions were also observed for all of the other measured rates and temperatures, with the*

Fig. 4. Effect of hypercapnia in the metabolic physiology of jumbo squid, Dosidicus gigas. (A) Mean oxygen consumption rates (± SE; \( \mu \text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1} \)) under control (black symbols) and hypercapnic treatments at inactive (IMR), routine (RMR), active (AMR), and maximum (MRM) levels (green, orange, red, and blue symbols, respectively). Oxygen consumption rates under control conditions are plotted against themselves and against rates of those same individuals under elevated (0.1%) CO2. Open diamonds, 10°C; solid circles, 20°C; solid triangles, 25°C (plots with individual runs are available in supporting online material). (B) Oxygen consumption rates and activity levels (number of active cycles per hour) under high CO2 expressed as a percentage of the control values at the three different temperatures. *, significant differences (paired t test, \( P < 0.05 \)); ×, nonsignificant differences (paired t test, \( P > 0.05 \)).
exceptions of RMR and IMR at 10°C (crosses in Fig. 4). The number of activity cycles per hour was also significantly reduced between 55 and 84% (P < 0.05; Fig. 4B).

Although the OML environment is characterized by both hypoxia and high CO2 levels (28), our results indicate that the effect of oxygen availability on the squid’s metabolic rate overwhelms the more subtle CO2 effect while at its cold, hypoxic daytime habitat depth. Low pH and high CO2 are common triggers of metabolic depression (27), but they do not cause a substantial metabolic depression in D. gigas while in the OML (Fig. 4B). However, at warmer temperatures, carbon dioxide becomes an important influence on D. gigas’ metabolic rate.

The effect of temperature on aerobic metabolism, expressed as a temperature coefficient (Q10), changed dramatically across the temperature range studied (Fig. 2A). Coefficients of Q10 = 2 and 7 were measured for IMR between 10°–20°C and 20°–25°C, respectively. While the former is within the normal range of metabolism in most ectotherms (28), the latter is outside this range and is not optimal for these highly aerobic animals. Field data with satellite-linked pop-up archival transmitting tags in the Sea of Cortez support this contention. Gilly and collaborators (21) reported that mitochondrial O2 consumption in squid ‘metabolic rate.

Note that pelagic predators such as D. gigas rarely stop swimming in nature and that we did not quantify locomotion continuously for any experiment in its entirety. Thus, while our inactive metabolic rates do not necessarily meet the criteria set for ‘standard’ metabolic rates in mammalian and other model organisms, we feel that they are a reasonable approximation of a standard metabolic rate.

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