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Seasonally acclimated metabolic Q_{10} of the California horn shark, *Heterodontus francisci*

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ABSTRACT

Dynamic environmental thermal conditions are known to affect physiological processes in ectothermic organisms that may influence movement, distribution and energetic costs. A better understanding of their metabolic Q_{10}, temperature sensitivity, is needed in order to make realistic predictions about how some nearshore populations may respond to changing oceanographic conditions. Oxygen consumption was used as a proxy to measure acclimated standard metabolic rates (SMR) of the California horn shark (*Heterodontus francisci*) at four temperatures (14°, 16°, 20° and 22 °C) typically experienced throughout an annual cycle. Sharks were acclimated in a large holding tank at each of the desired temperatures for at least two weeks prior to the trial. All individuals tested were juveniles, ranging in size from 37 to 48 cm TL and weights of 0.41–0.94 kg. Respirometry trials ranged in length from 6 to 14 h. The estimated (± SE) resting $\dot{M}O_2$ (mg O_2 kg^{-1} h^{-1}) of the CA horn shark at each temperature treatment was 30.6 ± 3.4 (14°, n = 4), 33.9 ± 2.3 (16°, n = 10), 44.9 ± 2.4 (20°; n = 9) and 57.9 ± 2.7 (22 °C; n = 3). The metabolic Q_{10} of the CA horn shark from 14° to 22 °C is 2.01, providing a metric to generate predictive models to estimate minimum metabolic costs associated with changing thermal regimes and global sea temperature rise. Predictions from our model indicate during years 2012 to 2016, rising sea surface temperature associated with a strong El Niño Southern Oscillation (ENSO) event resulted in a 23% increase in minimum metabolic costs for the CA horn shark. The results from our model suggest the CA horn shark may need to adapt compensatory behaviors (e.g., behavioral thermoregulation) to cope with ENSO events and climate change.

1. Introduction

Temperature is a key ecological abiotic factor known to directly affect the rates of physiological processes of marine ectotherms (Brett, 1971; Di Santo, 2016; Di Santo and Bennett, 2011; Fry and Hart, 1948; Hight and Lowe, 2007; Johansen and Jones, 2011; Magnuson et al., 1979; Sibly et al., 2012; Sinclair et al., 2016). While global sea temperature is naturally dynamic, fluctuating between seasons, there is a current, consistent trend of overall increasing global ocean temperature (Boyd and Doney, 2002; Sibly et al., 2012). Because ectotherms are dependent on ambient temperatures and temperature directly affects metabolic rate, a better understanding of their metabolic temperature sensitivity (Q_{10}) is needed to make realistic predictions as to how changing thermal conditions will influence movements, distribution patterns, feeding and growth rates, and reproduction over time (Barnett et al., 2016; Parsons and Carlson, 1998; Sinclair et al., 2016). Temperature sensitivity in metabolism is quantified by calculating an organism's Q_{10}, the degree to which metabolism changes over a 10 °C change in temperature (Gillooly et al., 2001; Schmidt-Nielsen, 1997). Because there are additional costs associated with physiological temperature acclimation (Angilletta, 2009), to acquire an accurate measure of acclimated metabolic Q_{10} requires animals to be slowly acclimated to treatment temperature prior to measurement. Non-acclimated measurements of temperature sensitivity have been shown to potentially overestimate metabolic Q_{10} (Bernal and Lowe, 2015; Carlson and Parsons, 1999). Most respirometry studies previously conducted on elasmobranchs have been on non-acclimated animals (e.g., experiencing fluctuations in temperature throughout respirometry trials) (Di Santo and Bennett, 2011; Hopkins and Cech, 1994; Miklos et al., 2003; Neer et al., 2006).

Oxygen consumption rates of ectothermic elasmobranchs have been used as a proxy for metabolic rates, and thus the current physiological state of the organism (Hopkins and Cech, 1994; Lowe, 2001; Miklos et al., 2003). Coastal elasmobranch species, most of which are ectothermic, are important top and meso-level predators in marine ecosystems. For example, Cortés (1999) estimated that out of 149 coastal

Abbreviations: SMR, standard metabolic rate; ENSO, El Niño Southern Oscillation; $\dot{M}O_2$, mass specific oxygen consumption rate (mg O_2 kg^{-1} h^{-1})

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and pelagic shark species, trophic levels ranged from secondary to tertiary consumers (Trophic Level 3.1–4.7), subsequently impacting lower trophic levels through top-down processes. Therefore, determining the degree of temperature sensitivity in these species is important to be able to forecast how changing ocean temperatures may affect their behavior, and could thus have potential cascading trophic effects on these thermally dynamic ecosystems (Cortés, 1999; Ferretti et al., 2010).

This study used the California horn shark (CA horn shark; *Heterodontus francisci*) as a model species due to their importance as a meso-predator (trophic level = 3.2; Cortés, 1999) in the kelp forest ecosystem (Strong, 1990). In addition, they have a comparatively small size range (maximum TL ≤ 122 cm) and their non-obligate ram ventilation ability allows for them to exhibit long periods of inactivity making it relatively easy to quantify their minimum energetic costs (Compagno, 2001). The CA horn shark is an ectothermic, demersal, reef-associated shark that commonly uses shallow habitats (2–11 m), but may venture into deeper habitat for short periods of time (Compagno, 2001). They are found from central California to the Gulf of California (Compagno, 2001; Love, 1991), and are an important food fish in Mexican elasmobranch fisheries (Ramirez-Amaro et al., 2013). This species is currently listed as data deficient on the IUCN Red List (Carlisle, 2015), and because they are a known sea urchin predator, similar to the California sheephead (*Semicossyphus pulcher*), they may also serve as an important keystone predator in the kelp forest ecosystem as sea urchins can over graze a kelp forest if densities become too high (Compagno, 2001; Cowen, 1983; Strong, 1990; Tegner and Levin, 1983).

It is important to understand how physiologically-sensitive the CA horn shark is to temperature change in order to make realistic predictions as to how increasing ocean temperatures as well as major oceanographic events (e.g., El Niño Southern Oscillation) may affect the daily behavior (e.g., resting, foraging, mating and distribution) of these sharks. Temperate regions such as the northeast Pacific are subject to El Niño Southern Oscillation (ENSO) events, which cause a reduction in upwelling and a concurrent increase in sea surface temperatures (SST) (Tegner and Dayton, 1987). Commonly residing in shallow demersal habitats most affected by ENSO events, it is important to understand how these thermally dynamic events may alter the metabolic rates and thus the behavioral ecology of the CA horn shark. Because CA horn sharks are thought to be annual residents to southern California reefs, and are exposed to a large annual temperature range, it is hypothesized that this species should exhibit a low temperature sensitivity (≤ 2) (Strong, 1990). The goal of this study was to measure the acclimated metabolic Q_{10} of the CA horn shark across a range of seasonal water temperatures, and to model the effects of multiple ENSO events and increasing ocean temperatures on their minimum energetic costs.

2. Methods

2.1. Capture and maintenance

Sharks were collected by hand via scuba along the coast of southern California and Santa Catalina Island and were transported back to the laboratory in large aerated coolers with frequent water changes. All sharks were maintained in a 2070 L holding tank at the California State University Long Beach (CSULB) Shark Lab and were fed a diet of shrimp and squid three times a week until satiation. Water temperature of the holding tank was controlled using a Cyclone coiled chiller or a Finnex titanium heater at ± 0.5 °C of the desired temperature.

2.2. Acclimation

Sharks in this study were acclimated to each treatment temperature (14° (n = 4), 16° (n = 10), 20° (n = 9) and 22 °C (n = 3)) for at least two weeks prior to each trial (Table 1) (Rummer et al., 2014; Whitney et al., 2016). This was done to reduce the additional costs associated with physiological acclimation (Angilletta, 2009). While it was previously thought longer acclimation periods lead to lower (and less accurate) measurements of metabolic sensitivity (Burggren and Roberts, 1991; Carlson and Parsons, 1999; Neer et al., 2006; Schmidt-Nielsen, 1997), it has since been shown that adequate acclimation is necessary to not overestimate the metabolic rate, especially when working at water temperatures close to seasonal extremes (Bernal and Lowe, 2015; Chabot et al., 2016; Clarke and Fraser, 2004; Rummer et al., 2014). Temperature of the holding tank was adjusted in increments of 1 °C per day until the desired temperature was reached. Not all sharks were tested in the same order, or acclimated for the same duration of time (Table 1). The addition of two extra treatment temperatures (14° and 22 °C) were added towards the end of the study, which resulted in lower sample sizes at those temperatures.

2.3. Respirometry

To measure oxygen consumption rates of the sharks, a 90 L Loligo Brett-style swim tunnel respirometer housed at the CSULB Shark Lab was used to conduct closed respirometry (Steffensen, 1989; Svendsen et al., 2016). Individual sharks were fasted for 48 h prior to trial to eliminate any costs associated with specific dynamic action (SDA) (Chabot et al., 2016; Dowd et al., 2006; Du Preez et al., 1988). Sharks were placed in the respirometer at least 12 h prior to the start of the trial to allow for acclimation to the working chamber and an opaque sheet was placed over the chamber to reduce disturbance during the trial (Chabot et al., 2016; Du Preez et al., 1988; Neer et al., 2006; Whitney et al., 2016). Because this study aimed to determine standard (resting) metabolic rate (SMR) of the CA horn shark, water velocity inside the working chamber was kept at 0.13 m/s only to maintain a directed flow of water over the shark, preventing stratification (Steffensen, 1989), but not strong enough to induce swimming. All sharks remained resting on the bottom of the respirometer for the duration of the trial. All trials were conducted during daylight hours when these sharks are normally resting, and visual observations of the shark throughout the duration of the trial indicated movement < 5% of the time; therefore, we are confident that oxygen consumption measures are representative of true SMR (Chabot et al., 2016). A PSt3 fiber optic oxygen sensor (± 0.05 mg/L) and PT 1000 temperature sensor (± 0.5 °C) were used to measure and record dissolved oxygen (DO_2) and water temperature in the working chamber using Oxyview Precision Sensing software. Because there was a relatively high ratio of respirometer to shark volume (95–220:1), trials were run until DO_2 reached 80% saturation (Steffensen, 1989; Svendsen et al., 2016; Whitney et al., 2016). Each trial consisted of at least two oxygen consumption-resaturation events with a 15 min flush occurring after each segment to bring DO_2 levels back to ~100% saturation. Trials ranged from 6 h at 22 °C to 14 h at 14 °C, and only the second segment from each trial were used for analysis. At the end of each trial, the shark was removed from the respirometer and a one-hour blank measurement was recorded to obtain background respiration (Graham et al., 1990; Lowe, 2001). Upon removal from the respirometer sharks were weighed to the nearest kilogram and their volume was measured to the nearest 1 mL.

2.4. Data analysis

Linear regression was used to determine the rate of oxygen consumed during the second measurement of each trial, $r^2 > 0.99$ for all trials (n = 26). We then calculated the adjusted oxygen consumption rate (R = mg O_2 L^{-1} s^{-1}) of each shark using the eq. R = T-B (Graham et al., 1990). Where T (mg O_2 L^{-1} s^{-1}) represents the rate of oxygen consumed during a segment and B (mg O_2 L^{-1} s^{-1}) represents the rate of oxygen consumed during the blank. Using this adjusted oxygen consumption rate (R) we calculated the mass specific oxygen consumption rate by each shark (Steffensen, 1989):