

Contents lists available at ScienceDirect

# Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv



# Eat more, often: The capacity of piscivores to meet increased energy demands in warming oceans

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## HIGHLIGHTS

# G R A P H I C A L A B S T R A C T

- Physiological limits posited to underlie global 'shrinking of fishes' as oceans warm
- Projected physiological limits for piscivore foraging examined during thermal stress
- Whole-animal energy demand and acquisition rates evaluated during marine heatwaves
- Contrary to theory, physiological flexibility lets piscivores eat more as oceans warm
- Species ecology, not physiology, may dictate global body-size declines of piscivores

# ARTICLE INFO

Editor: Julian Blasco

Keywords: Global change-induced extreme events Coral reefs Piscivory Physiology Ecology Aerobic capacity Digestive limitations



# ABSTRACT

Marine heatwaves (MHWs) profoundly disturb tropical coral reefs, imperilling species fitness and survival. Ectothermic piscivorous reef fishes are particularly vulnerable to MHWs since all aspects of their survival are dictated by ambient temperature. Severe +4 °C MHWs are projected to escalate daily energy demands by  $\sim$ 32–55 %, compelling piscivores to pursue larger or more frequent prey to survive. However, the feasibility of these responses have been questioned, as evolved predation and digestive strategies are constrained to specific prey types and sizes to safeguard residual aerobic scope (AS) during digestion for other vital processes. Instead, prevailing theory proposes appetite reductions at temperatures above optimal, preserving AS at the expense of growth and/or fitness. We investigated this dichotomy in the thermal foraging responses of Arc-eye hawkfish (*Paracirrhites arcatus*) and blacktail snapper (*Lutjanus fulvus*), evaluating energetic demand (standard metabolic rate, SMR), AS, appetite (meal mass intake), and capacity for digestion (specific dynamic action, SDA). Spanning a thermal gradient encompassing present-day winter (24.0 ± 0.1 °C), summer (27.5 ± 0.1 °C), and MHW (31.0 ± 0.1 °C), we show that SMR increased by ~65 % from winter to MHW for both species, while AS increased by ~31–67 %. Contrary to predictions of reduced appetite, both species consumed ~106 % larger meals, yielding a ~ 35–105 % greater SDA magnitude. Surprisingly, increased appetite did not encroach on residual AS as both

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https://doi.org/10.1016/j.scitotenv.2025.179105

Received 7 June 2024; Received in revised form 9 January 2025; Accepted 9 March 2025 Available online 18 March 2025

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species maintained the physiological flexibility to process larger meals while retaining ~45–60 % of AS at the post-prandial peak. Although larger meals take longer to digest, both species exhibited faster digestion with rising temperatures resulting in a maintained or shortened SDA duration during MHWs, simultaneously enabling increased feeding rates while preserving aerobic reserves to support heightened predation. Our findings underscore the physiological feasibility of increasing appetite for some piscivores, while highlighting the ecological challenge of increasing prey numbers and sizes amid declining prey densities and prey size-reductions caused by ocean warming.

# 1. Introduction

Piscivorous coral reef fishes serve as a vital source of sustenance and livelihood for millions of people residing in coastal communities worldwide, while also playing a pivotal role in shaping the trophic dynamics of coral reef ecosystems (Hixon, 2015; Hoegh-Guldberg et al., 2017). However, these ectothermic organisms and the services they provide face a significant threat from prolonged discrete anomalously warm water events better known as marine heatwaves (MHWs; Hobday et al., 2016; Smale et al., 2019). Predicted to escalate in frequency, intensity, extent, and duration due to ongoing anthropogenic climate change (Frölicher and Laufkötter, 2018; Laufkötter et al., 2020; Oliver et al., 2018), these extreme thermal events have been documented to instigate drastic declines in both the abundance and diversity of coral reef fishes globally (Feary et al., 2014; Genin et al., 2020; Graham et al., 2015; Habary et al., 2017; Magel et al., 2020; Pearce and Feng, 2013; Pratchett et al., 2011; Robinson et al., 2019).

Across evolutionary timescales, the majority of tropical reef ecosystems have experienced <4 °C seasonal changes in water temperatures (Donner, 2011; Lough, 2012). As a result, most piscivorous coral reef fishes are expected to be limited in their physiological and ecological capacity to deal with thermal changes beyond the conditions for which they are evolved (Pörtner and Peck, 2010; Tewksbury et al., 2008). For instance, as water temperatures rise, the metabolic demands associated with maintaining homeostasis (i.e., standard metabolic rate, SMR) typically increases exponentially in ectotherms (i.e.,  $Q_{10}$  of ~2-3; Seebacher et al., 2015). As a result, a typical MHW with a mean peak temperature anomaly of 4 °C will, if not lethal (Genin et al., 2020; Pearce and Feng, 2013), increase SMR of coral reef fishes by  $\sim$ 32 to 55 % (Pratchett et al., 2015; Seebacher et al., 2015). These increased metabolic demands must be met with appropriate increases in energy acquisition (e.g., via increases in meal size and/or feeding frequency), reductions in energy expenditure (e.g., by reducing activity), or through the catabolism of energy reserves to allow survival through the long durations (weeks to months) of typical MHWs (Frölicher and Laufkötter, 2018; Johansen et al., 2015; Laufkötter et al., 2020; Oliver et al., 2018; Pörtner and Peck, 2010).

While rising temperatures increase energetic demand, these conditions are simultaneously hypothesized to cause reductions in their scope for aerobic performance (i.e., aerobic scope, AS; Pörtner and Farrell, 2008; Pörtner and Peck, 2010; Pratchett et al., 2015). AS represents the surplus energy available for critical tasks beyond that required for maintaining homeostasis, and thus reductions in AS directly limits their capacity for swimming, foraging and digestion (Clark et al., 2013; Johansen and Jones, 2011; Jutfelt et al., 2021). Indeed, thermallyinduced reductions in AS of  $\sim$ 24 to 65 % have been shown to align with concurrent declines in maximum swimming speed across a wide range of damselfishes (Johansen and Jones, 2011), while large piscivorous coral reef fishes are known to become lethargic and reduce foraging activity at elevated temperatures (e.g., common coral trout, Plectropomus leopardus; Johansen et al., 2014; Scott et al., 2019). Such impairments of piscivorous fishes that hunt mobile prey are expected to decrease prey encounters and capture rates, particularly if the prey species exhibit a higher thermal tolerance, leading to diminished energy available for maintenance, growth, and reproduction (Johansen et al., 2014, 2015; Pörtner and Peck, 2010).

Piscivorous fishes often exhibit a 'feast and famine' foraging strategy (Armstrong and Schindler, 2011), necessitating sufficient AS to accommodate the substantial metabolic demands associated with consuming prey (McCue, 2006; Secor, 2009). Following prey capture, metabolism rapidly increases and remains elevated for an extended period of time, before eventually returning to pre-feeding levels. This increase in postprandial metabolism is termed 'specific dynamic action' (SDA) and encompasses the energetic expenditure of all activities related to the ingestion, digestion, absorption, and assimilation of a meal (McCue, 2006; Secor, 2009). Previous studies have demonstrated that the magnitude of the SDA response in fishes increases with meal size (Fu et al., 2005; Norin and Clark, 2017) and that the post-prandial peak oxygen demand for a given meal size rises with temperature (Pang et al., 2010, 2011). This presents an added dilemma for piscivorous fishes during thermal stress, as they must augment feeding to satisfy heightened energy demands, yet the digestion of larger meals may be impeded by rising digestive costs concurrent with thermally-induced decreases in AS. Indeed, the SDA response has been shown to occupy 100 % of AS during acute temperature elevations in shorthorn sculpin (Myoxocephalus scorpius) leaving the species unable to conduct any other critical activities (e.g., foraging, predatory avoidance and inter-/intraspecific competition; Sandblom et al., 2014). To protect residual AS for other essential aerobic processes, it has been proposed that the appetite of piscivorous fishes may be reduced at temperatures above optimal (i.e., 'Aerobic Scope Protection' hypothesis; Jutfelt et al., 2021) leading to growth impairments that may, at least in part, underlie the 'shrinking of fishes' phenomenon wherein elevated temperatures cause a decline in the maximum size of individuals (Cheung et al., 2013). Alternatively, fishes may adapt by opting for smaller, more frequent meals to sustain continuous, low-level SDA that retains sufficient post-prandial residual AS while maximizing nutrient intake (Norin and Clark, 2017). Given the impacts of either strategy on trophic structuring, functioning and fisheries productivity (Cheung et al., 2013; Pörtner and Peck, 2010; Verberk et al., 2021), there is an urgent need to evaluate the post-prandial metabolic responses of piscivorous fishes to ocean warming (Jutfelt et al 2021)

Here we evaluate the resilience of representative piscivorous coral reef fishes to MHWs by elucidating changes in the energetic demand, physiological scope for aerobic performance, food intake and metabolic costs of digestion within and beyond their current thermal window (*i.e.*, seasonal temperature changes *vs.* MHW, respectively). We hypothesize that while rising temperatures will increase the energetic demands for survival in piscivorous coral reef fishes, their physiological scope for aerobic performance will decline when exposed to water temperatures beyond current thermal conditions, ultimately resulting in a reduction in appetite to protect residual AS during the ingestion, digestion, absorption, and assimilation of prey.

# 2. Materials and methods

### 2.1. Study species, collection and holding conditions

Arc-eye hawkfish (*Paracirrhites arcatus*) and blacktail snapper (*Lutjanus fulvus*) were selected for this study. Both species adopt a 'feast and famine' approach to foraging (*i.e.*, intermittently consume single large meals consisting of fish, crustaceans or other invertebrates), are from

distinct evolutionary lineages (Cirrhitidae and Lutjanidae, respectively), and are found in high abundance on shallow water reefs throughout the equatorial Pacific (Armstrong and Schindler, 2011; Randall, 1998; Sheppard et al., 2017). Fish were collected with hand nets and barrier nets by scuba divers during the winter (January–March) and summer (July–September) of 2021 and 2022 from reefs around Kāne 'ohe Bay on the eastern coast of O'ahu, Hawai'i (main collection site for *L. fulvus*: 21.414234, -157.784047 and *P. arcatus*: 21.477181, -157.791538).

Following collection, fish were transported to the Johansen Fish Resilience Laboratory at Moku o Lo'e in Kane'ohe Bay, and housed in groups of four individuals in large conical holding tanks (height: 86.0 cm; diameter: 82.5 cm; volume: 260 L) containing sections of PVC pipe for shelter. Tanks were supplied with flow-through, filtered, aerated and UV-sterilized seawater and subjected to a 12 h:12 h light:dark photoperiod. Water within the holding tanks were maintained at 24.0  $\pm$  0.1  $^\circ\text{C}$ and 27.5  $\pm$  0.1 °C during the winter and summer, respectively, reflecting mean seasonal sea surface temperatures (SST) of Kane'ohe Bay (data retrieved online from tidesandcurrents.noaa.gov; Moku o Lo'e weather station; ID: 1612480; depth = 1 m; 21.433° N, 157.786° W). Water temperature within each tank was regulated using temperature control relays (WH1436, Willhi, China) that activated to either heat or cool the tank when water temperatures were not within the desired range. Heating within each tank was achieved with an 800 W aquarium heater (TH-08005, Finnex Inc., USA), whereas cooling was achieved with a submersible pump (D08V045CD, Kedsum, China) that circulated water from within the tank through a stainless-steel coil that was submerged in a 95 L external reservoir held at 5 °C by a water chiller (ECO-1 1/2HP, Ecoplus, USA).

Fish were allowed two weeks to acclimate to laboratory conditions during which they were fed to satiation on a daily basis with  $\sim$ 0.2–1.0 g pieces of Pacific squid (*Loligo opalescens*). Animal care and all of the experimental procedures described below and in Supp. Info. 1 complied with the ethical standards of the Institutional Animal Care and Use Committee at the University of Hawai'i at Mānoa, approved under the permit number 3200.

# 2.2. Treatment groups

Following acclimation to laboratory conditions, fish were individually assigned to large conical treatment tanks that were identical to the aforementioned holding tanks and conditions. Fish collected in winter were assigned to the 'winter' treatment (i.e.,  $24.0 \pm 0.1$  °C for 7 days), whereas fish collected in summer were randomly assigned to either the 'summer' (i.e., 27.5  $\pm$  0.1 °C for 7 days) or 'MHW' treatment (i.e., a simulated MHW for 7 days). A simulated MHW in this study was defined as a discrete, prolonged warm water anomaly above the climatological mean with a minimum duration of five days (following Hobday et al., 2016). Based on the characterization of MHWs in Kane ohe Bay between 1994 and 2020 (Tran and Johansen, 2023), MHWs were simulated by increasing water temperature  $\sim 0.9$  °C per day from mean summer SST to the peak of the MHW (31.0  $\pm$  0.1 °C), whereafter water temperatures were maintained at the peak of the MHW for at least three more days. These conditions closely matched the mean duration (days), maximum heating rate (°C day<sup>-1</sup>), and maximum intensity (°C) for MHWs detected on the reefs within Kane'ohe Bay, ensuring that MHW simulations followed real-world conditions (Tran and Johansen, 2023).

The treatment groups described above were selected to reflect ecologically relevant field conditions for both species, capturing the stable thermal environments typically encountered during winter and summer, as well as the extreme thermal events that are increasingly prevalent in their natural habitats. Mean seasonal SSTs were chosen for the winter and summer treatments because fish are capable of avoiding unfavourable daily temperature fluctuations through behavioural thermoregulation (*e.g.*, by moving to deeper and more thermally stable waters; (Haesemeyer, 2020). This mobility minimizes the ecological relevance of daily temperature variability for these treatments. Conversely, the MHW treatment was included to simulate an unavoidable thermal stress scenario, as these extreme thermal events are known to penetrate the entire water column at reefs within Kāne'ohe Bay (Bahr et al., 2015), leaving fish with no thermal refuge. By including both stable seasonal SSTs and an MHW scenario, the study design ensures ecological relevance and captures the range of thermal conditions these species are likely to encounter in their natural habitats.

# 2.3. Intermittent-flow respirometry

Oxygen uptake rates ( $\dot{M}_{O2}$ ) of *P. arcatus* and L. *fulvus* were measured using best practices for intermittent-flow respirometry (Clark et al., 2013; Roche et al., 2013; Svendsen et al., 2016). Specifically, respirometry trials were conducted in a temperature-controlled room containing two experimental tanks (length: 97 cm, width: 53 cm, height: 37 cm) supplied with flow-through, filtered, aerated and UV-sterilized seawater under a 12 h:12 h light:dark photoperiod. Water temperature within the experimental tanks were maintained within 0.1 °C of winter, summer, and peak MHW treatment temperatures. Each experimental tank contained either two large cylindrical acrylic respirometers for L. fulvus (length: 22.0 cm, diameter: 10.0 cm, volume: 1.600 L) or four smaller respirometers for *P. arcatus* (length: 10.6 or 14.6 cm, diameter: 3.8 or 3.8 cm, volume: 0.166 or 0.214 L for small and large individuals, respectively). To feed fish within the respirometer, a 1 cm hole was drilled into the top of the anterior end of the respirometer, which was sealed with an oxygen impermeable rubber stopper when obtaining  $\dot{M}_{02}$ measurements. Water was continuously circulated through each respirometer using an in-line submersible pump (AD20P-1230E, DollaTek, USA) within a recirculation loop to ensure a homogenous concentration of oxygen throughout the respirometer. Automated flush pumps intermittently refreshed the water within each respirometer according to specific flush cycles (see 2.4. Experimental protocol) set in the AquaResp software (v3.04, https://github.com/bigb8/AquaResp). This ensured that oxygen levels in the respirometers always remained above 80 % air saturation. The partial pressure of oxygen in the water within each respirometer was measured continuously at 1 Hz using a fiber optic oxygen sensor mounted in the recirculation loop where the flow is sufficient to ensure a rapid response time of the sensor. The optode was connected to a 4-channel Firesting Optical Oxygen Meters (Pyro Science, Germany), which in turn were connected to a PC that logged the data. Oxygen measurements were automatically compensated for temperature (via a Pt100 temperature probe connected to the temperature port of the oxygen meter) and salinity (via manual input of water salinity into the Firesting logger software). Mass-specific  $\dot{M}_{02}$  were then automatically calculated by the AquaResp software from the linear decline in the partial pressure of oxygen during the measurement period when the flush pumps were off. Only  $\dot{M}_{02}$  calculations with an R<sup>2</sup> of >0.95 were kept for further analysis.

# 2.4. Experimental protocol

Based on pilot trials, all fish were fasted during the final three days of the treatment period to avoid the confounding effects of specific dynamic action on pre-prandial whole-animal aerobic metabolic rates (Secor, 2009). Following the treatment period, the experimental protocol consisted of initially determining pre-prandial whole-animal aerobic metabolic rates such as maximum metabolic rate (MMR, day 1) and SMR (days 2–3), and then subsequently determining post-prandial whole-animal aerobic metabolic rates to evaluate SDA (days 4–6) for each fish.

To determine MMR, fish were individually transferred from their treatment tank to an identical tank with a reduced water level ( $\sim$ 15 cm) and subjected to a 'chase protocol' (Clark et al., 2013; Norin and Clark, 2016; Roche et al., 2013). This protocol consisted of chasing the fish by hand for three minutes followed by a period of air exposure for one minute during which they were weighed and measured. Fish were then

placed into respirometers and  $\dot{M}_{O2}$  were obtained overnight with the AquaResp software set to 'MMR mode' (*i.e.*, 'Wait' = 0.5 min, 'Measure' = 1 min, and 'Flush' = 2.5 min). Then to determine SMR,  $\dot{M}_{O2}$  measurements were obtained for 48 h starting the following day at 07:00 HST with the AquaResp software set to 'SMR mode' (*i.e.*, 'Flush' = 5 min, 'Wait' = 1 min, and 'Measure' = 1 min).

Following the evaluation of pre-prandial whole-animal aerobic metabolic rates, fish were fed inside the respirometers by gently removing the rubber stopper from the hole in the respirometer and inserting ~0.2–1.0 g pieces of Pacific squid until the individual was satiated. Fish were deemed to be satiated when a piece of squid within the respirometer was not consumed within 15 min, whereafter unconsumed pieces of squid were gently removed and the respirometer was resealed with the rubber stopper. The feeding process typically took ~30 min. To determine SDA, post-prandial  $\dot{M}_{O2}$  measurements were then obtained for another 72 h with the AquaResp software set to 'SMR' mode. At the end of the experiment, fish were removed from the respirometers for subsequent release back into the wild at the approximate location of capture.

To account for background respiration, linear regression over time using measures of bacterial  $\dot{M}_{O2}$  obtained from empty respirometers before and after each respirometry trial were subtracted from all  $\dot{M}_{O2}$  measurements. To limit background respiration rates, all equipment was disinfected with a 1 % bleach solution, thoroughly rinsed with freshwater, and allowed to dry before commencing further trials.

# 2.5. Determining pre-prandial responses

A total of 44 individual *P. arcatus* (n: winter = 14, summer = 17, MHW = 19) and 35 *L. fulvus* (n: winter = 11, summer = 12, MHW = 12) were used to determine pre-prandial metabolic rates. MMR was defined as the highest pre-prandial  $\dot{M}_{O2}$  measurement (Norin and Clark, 2016, 2017), while the 20 % quantile method on  $\dot{M}_{O2}$  measurements obtained during the 48 h pre-prandial period yielded the most consistent SMR estimates based on visual inspection of  $\dot{M}_{O2}$  and the cumulative variance of the mean lowest normal distribution (Chabot et al., 2016). In addition,  $Q_{10}$  was calculated (*i.e.*,  $Q_{10} = (R_2/R_1)^{\text{II}0/(\text{T})}$  using mean SMR values for each species between winter and summer (*i.e.*,  $R_1$ : SMR<sub>winter</sub>;  $R_2$ : SMR<sub>summer</sub>; T<sub>1</sub>: 24.0 °C; T<sub>2</sub>: 27.5 °C), as well as between summer and at the peak of a simulated MHW (*i.e.*,  $R_1$ : SMR<sub>summer</sub>; R2: SMR<sub>peak of MHW</sub>; T<sub>1</sub>: 27.5 °C; T<sub>2</sub>: 31.0 °C). AS was calculated as MMR minus SMR (Clark et al., 2013).

In order to accurately quantify SDA (see 2.6. Determining postprandial responses below), it is recommended to account for the 'metabolic circadian rhythm' of the study organism to account for brief periods of spontaneous activity (Roe et al., 2004). This was achieved for each individual by calculating an hourly moving median of the  $\dot{M}_{O2}$ measurements obtained during the 48 h pre-prandial period. From the smoothed data, parameters of the 'metabolic circadian rhythm' such as the mesor (*i.e.*, mean of the circadian rhythm) and amplitude (*i.e.*, difference between the mesor and peak of the 'metabolic circadian rhythm') were calculated for each individual. Likewise, routine metabolic rate (RMR) was calculated for each individual by subtracting SMR from the mesor of the 'metabolic circadian rhythm' to evaluate rates of surplus energy expenditure (*i.e.*, energetic expenditure in excess of that required for maintaining homeostasis).

### 2.6. Determining post-prandial responses

Following exclusion of individuals due to high background respiration (*i.e.*, background respiration >10 % of SMR, likely due to the presence of faeces within some respirometers), noisy  $\dot{M}_{O2}$  measurements (*i.e.*,  $R^2 < 0.95$ ), or lack of feeding, a total of 36 individual *P. arcatus* (n: winter = 12, summer = 14, MHW = 10) and 32 *L. fulvus* (n: winter = 10, summer = 11, MHW = 11) were used to determine post-prandial metabolic rates.

To account for brief periods of spontaneous activity during the SDA period, an hourly moving median was applied to post-prandial  $\dot{M}_{02}$ measurements. The post-prandial response of an individual was then defined as the period of elevated  $\dot{M}_{02}$  occurring directly after feeding until post-prandial values had returned to pre-prandial levels - defined as >8 consecutive smoothed post-prandial  $\dot{M}_{02}$  values (>1 h of measurements) that were  $\leq$  'metabolic circadian rhythm' of that individual (*i.e.*, median + median deviation of pre-prandial  $\dot{M}_{O2}$  expected for that time of day). The accumulated energy expended from the ingestion, digestion, absorption and assimilation of a meal (SDA<sub>absolute</sub>) was calculated from the amount of oxygen consumed above the 'metabolic circadian rhythm' during the entire post-prandial response, and converted to units of energy with a conversion factor of 20.083 kJ L  $O_2^{-1}$ (Schmidt-Nielsen, 1997). The proportion of AS that was occupied by the SDA response (SDA<sub>relative</sub>) was calculated by dividing the total amount of oxygen consumed above SMR by AS during the entire post-prandial response. The absolute peak of the post-prandial response (SDAabsolute <sub>peak</sub>) was defined as the highest smoothed value of  $\dot{M}_{O2}$  during the postprandial response, and was also calculated as a percentage of AS (SDA<sub>relative peak</sub>). The duration of the post-prandial response (SDA<sub>dura-</sub> tion) was calculated as the period of time between feeding and the completion of the post-prandial response. The efficiency of the SDA response (SDA<sub>coefficient</sub>) was calculated by dividing SDA<sub>absolute</sub> by the amount of digestible meal energy (e.g., kJ SDA<sub>absolute</sub>/kJ Pacific squid), which was 2.510 kJ g<sup>-1</sup> based on the nutritional information provided on the packaging (Emerald Calamari, Del Mar Seafoods, Inc., Watsonville, CA, USA) and assuming a conversion factor of 4.184 kJ kcal<sup>-1</sup> (Schmidt-Nielsen, 1997).

# 2.7. Statistical analyses

All statistical analyses were performed using R. Detailed descriptions of the statistical analyses used for pre-prandial (*i.e.*, SMR, MMR, AS, RMR, as well as the mesor and amplitude of 'metabolic circadian rhythm'), prandial (*i.e.*, meal size), and post-prandial data (*i.e.*, SDA<sub>ab-solute</sub>, SDA<sub>relative</sub>, SDA<sub>coefficient</sub>, SDA<sub>absolute</sub> peak, SDA<sub>relative</sub> peak, and SDA<sub>duration</sub>) are provided in the supplementary information (*e.g.*, R packages used, data exploration, model fitting, model selection, model checking, model inference and model predictions; see Supp. Info. 2–3).

Briefly, pre-prandial and prandial linear regression models were fit using various combinations of body mass, treatment temperature, and species, as well as the interactions between them (Supp. Info. 4). Postprandial linear regression models were fit using various combinations of body mass, meal size, treatment temperature, and species, as well as the interactions between them (Supp. Info. 4). The best-fitting models were selected based on Akaike's Information Criterion (AIC) and model assumptions were checked (Anderson and Burnham, 2002). All variables with the exception of treatment temperature, species and SDA duration were log transformed to meet model assumptions.

The main inferences from the most parsimonious models are reported throughout the text, while back-transformed model predictions are displayed in the figures. For detailed model summary outputs and extensive model inferences refer to Supp. Info. 2–4, respectively. Planned contrasts were conducted to investigate treatment temperature differences for an average sized individual (*i.e.*, mean body masses of 9 or 45 g for *P. arcatus* or L. *fulvus*, respectively) and/or meal size (*i.e.*, mean meal sizes of 0.53 or 3.63 g for *P. arcatus* or *L. fulvus*, respectively) for each species. The *p*-values resulting from the planned contrasts were subjected to False Discovery Rate (FDR) adjustment using the Benjamini-Hochberg procedure to account for multiple testing (Benjamini & Hochberg, 1995).

# 3. Results

# 3.1. Pre-prandial responses

# 3.1.1. Energy demand

SMR of both species increased by ~28 % from winter to summer, and by ~29 % from summer to peak of MHW (Treatment temperature:  $F_{2,79}$  = 119.239, p < 0.001, Supp. Info. 4), equating to an increase of ~65 % from winter to the peak of a MHW and a  $Q_{10}$  of 2.0 for both species (Fig. 1A).

# 3.1.2. Aerobic capacity

MMR and AS of both species increased across temperatures, although the magnitude of the responses differed between species (Interaction<sub>species x temperature</sub> for MMR:  $F_{2,78} = 7.276$ , p = 0.001 and AS:  $F_{2,78} = 6.045$ , p = 0.004, Supp. Info. 4). Specifically, from winter to the peak of a MHW, *P. arcatus* exhibited increases of ~36 % in MMR and ~ 31 % in AS, whereas these parameters increased in L. *fulvus* by ~70 % and 67 %, respectively (Fig. 1A).

# 3.1.3. 'Metabolic circadian rhythm'

The mesor of the 'metabolic circadian rhythm' increased from winter to the peak of a MHW in *P. arcatus* and L. *fulvus* by  $\sim$ 52 and 90 %, respectively (Interaction<sub>species x</sub> temperature: F<sub>2,77</sub> = 3.451, *p* = 0.037,

Supp. Info. 4, Fig. 1B). The amplitude of the 'metabolic circadian rhythm' did not differ across temperatures for *P. arcatus*, while it increased from winter to summer for L. *fulvus*, after which it plateaued with a further rise in temperature from summer to peak MHW (Interaction<sub>species x temperature</sub>:  $F_{2,78} = 11.225$ , p < 0.001, Supp. Info. 4, Fig. 1B).

# 3.1.4. Surplus energy expenditure

RMR of *P. arcatus* did not significantly differ across temperatures (Planned contrasts:  $p_{24.0^{\circ}C}$  vs  $_{27.5^{\circ}C} = 0.331$ ,  $p_{27.5^{\circ}C}$  vs  $_{31.0^{\circ}C} = 0.635$ ,  $p_{24.0^{\circ}C}$  vs  $_{31.0^{\circ}C} = 0.163$ ), whereas it increased by ~85 % from winter to summer for *L. fulvus*, but then plateaued with a further rise in temperature from summer to peak MHW ( $p_{24.0^{\circ}C}$  vs  $_{27.5^{\circ}C} = 0.003$ ,  $p_{27.5^{\circ}C}$  vs  $_{31.0^{\circ}C} = 0.069$ ,  $p_{24.0^{\circ}C}$  vs  $_{31.0^{\circ}C} < 0.001$ , Supp. Info. 4).

# 3.2. Prandial responses

# 3.2.1. Energy intake

Average meal size increased by ~106 % from winter to the peak of a MHW for both species (Treatment temperature:  $F_{2,63} = 85.523$ , p < 0.001, Supp. Info. 4, Fig. 2A-D). In addition, meal size substantially increased with body mass in both species (Body mass:  $F_{1,63} = 1936.012$ , p < 0.0001, Supp. Info. 4). The allometric scaling relationship between meal size and body mass was consistent across species and treatments (*i. e.*, slope = 1.037, denoting a 1 % increase in body mass corresponds to a



**Fig. 1.** Pre-prandial metabolic rates of *P. arcatus* and L. *fulvus*. (A) Standard metabolic rate (SMR, circles), maximum metabolic rate (MMR, squares), aerobic scope (AS, text) and (B) 'metabolic circadian rhythms' (solid line = smoothed rhythm, dashed line = mean of rhythm, arrows = amplitude of rhythm) of an average sized *P. arcatus* (left panel, 9 g individual) and *L. fulvus* (right panel, 45 g individual) during winter ( $24.0 \pm 0.1 \degree$ C, blue symbols and lines), summer ( $27.5 \pm 0.1 \degree$ C, orange symbols and lines), and at the peak of a MHW ( $31.0 \pm 0.1 \degree$ C, red symbols and lines). Data points for SMR, MMR and AS represent the estimated marginal means $\pm 95$  % C.I., while statistical differences between treatments for each species (p < 0.05, based on models 1–5 in Supp. Info. 4) are represented by different lower-case letters (SMR, mean of 'metabolic circadian rhythm'), upper-case letters (MMR, amplitude of 'metabolic circadian rhythm') or number of asterisks (AS). Sample size (n) of each treatment for (A-B) are displayed at the top of the figure for each species.



**Fig. 2.** Meal size and associated post-prandial responses of *P. arcatus* and *L. fulvus*. (A) The relationship between meal size and body mass, as well as (B—D) preprandial 'metabolic circadian rhythms' (solid black lines), post-prandial metabolic rates (solid coloured lines and shading, mean  $\pm$  95 % C.I.), SMR (grey dashed lines) and MMR (grey solid lines) of *P. arcatus* (left column) and *L. fulvus* (right column) during winter (24.0  $\pm$  0.1 °C, blue lines), summer (27.5  $\pm$  0.1 °C, orange lines), and at the peak of a MHW (31.0  $\pm$  0.1 °C, red lines). Solid coloured lines and shading in (A) represent the back-transformed mean  $\pm$  95 % C.I., respectively, predicted by linear regression model 7 in Supp. Info. 4, while statistical differences between treatments for each species when controlling for body mass are represented by different lower-case letters (p < 0.05). Solid and dashed lines in (B—D) represent the mean responses of an average sized individual for each species (9 and 45 g for *P. arcatus* and *L. fulvus*, respectively). Note that in (B—D) the time of day at 0 h is 07:00 HST, average feeding time was ~9:30 HST, and fish were fed *ad libitum* with mean meal sizes displayed as a proportion of body mass  $\pm$  95 % C.I. within each plot. Sample size (n) of each treatment for (A-D) are displayed at the top of the figure for each species.



**Fig. 3.** Accumulated energy expended during the post-prandial response and the efficiency of digestion in *P. arcatus* and *L. fulvus*. (A) Absolute and relative SDA (black and grey lines, respectively), as well as (B) SDA coefficient (black lines) of *P. arcatus* (left column) and *L. fulvus* (right column) across their respective meal size ranges. Lines and shading represent the back-transformed mean  $\pm$  95 % C.I., respectively, predicted by linear regression models 8 (SDA<sub>absolute</sub>), 9 (SDA<sub>relative</sub>) and 10 (SDA<sub>coefficient</sub>) in Supp. Info. 4. The transparent rectangles illustrate the 95 % C.I. for meal sizes of an average sized individual for each species (9 and 45 g for *P. arcatus* and *L. fulvus*, respectively) during winter (24.0  $\pm$  0.1 °C, blue rectangles), summer (27.5  $\pm$  0.1 °C, orange rectangles), and at the peak of a MHW (31.0  $\pm$  0.1 °C, red rectangles). Sample size (n) of each treatment for (A-B) are displayed at the top of the figure for each species.

1.037 % increase in meal size), with the differences in intercepts reflecting baseline variations in meal size across species and treatments. Consequently, the largest individuals of *P. arcatus* and L. *fulvus* ingested meals that were  $\sim$  321 and 376 % larger than those consumed by their smallest conspecifics, respectively (Fig. 2A).

# 3.3. Post-prandial responses

# 3.3.1. Metabolic costs of the post-prandial response

Thermally induced increases in meal size caused a significant rise in SDA<sub>absolute</sub> of *P. arcatus* and *L. fulvus*, although the magnitude of the response differed between species (*i.e.*, slopes of 1.034 and 0.413, respectively; Interaction<sub>species x meal size for SDA<sub>absolute</sub>:  $F_{1,62} = 10.333$ , p = 0.002, Supp. Info. 4). As temperatures rose from winter to the peak of a MHW, so too did the average meal size, resulting in SDA<sub>absolute</sub> increases from ~0.19 to 0.39 kJ for *P. arcatus* and ~ 1.69 to 2.28 kJ for L. *fulvus* (Fig. 3A). The thermally induced increases in meal size also led to a larger proportion of AS being occupied by the post-prandial response in both species (Meal size:  $F_{1,63} = 20.616$ , p < 0.001, Supp. Info. 4). Specifically, the proportion of AS that was occupied by the SDA incurred from an average sized meal during winter increased from ~17 and 29 % to ~24 and 35 % at the peak of a MHW for *P. arcatus* and *L. fulvus*, respectively (Fig. 3A).</sub>

# 3.3.2. Metabolic efficiency of the post-prandial response

SDA<sub>coefficient</sub> of *P. arcatus* remained at ~18 % irrespective of thermally induced increases in meal size, whereas for L. *fulvus* it decreased from ~25 % to 17 % following the consumption of an average sized meal in winter compared to at the peak of a MHW, respectively (Interaction<sub>species x meal size</sub>: F<sub>1,62</sub> = 10.333, *p* = 0.002, Supp. Info. 4, Fig. 3B). Neither body mass nor the interaction between body mass and species significantly contributed to the variation in SDA<sub>coefficient</sub> (Body mass:  $F_{1,62} = 0.926$ , p = 0.340; Interaction<sub>body mass x species</sub>:  $F_{1,62} = 0.587$ , p = 0.446).

#### 3.3.3. Peak of post-prandial response

SDA<sub>absolute peak</sub> of both species increased by ~27 % from winter to summer, and by ~26 % from summer to peak of MHW (Treatment temperature:  $F_{2,63} = 56.456$ , p < 0.001, Supp. Info. 4), equating to an increase of ~60 % from winter to the peak of a MHW (Fig. 4A). Despite these substantial absolute differences in SDA<sub>absolute peak</sub>, the proportion of AS occupied during the peak post-prandial response did not differ across temperatures as it remained at  $40 \pm 3$  % for *P. arcatus* and  $55 \pm 4$ % for *L. fulvus* from winter to the peak of a MHW (Supp. Info. 4).

# 3.3.4. Duration of post-prandial response

SDA<sub>duration</sub> was impacted by the counteracting effects of treatment temperature and meal size (Fig. 4B). When controlling for meal size, SDA<sub>duration</sub> decreased from winter to the peak of a MHW by 42 and 35 % in *P. arcatus* and *L. fulvus*, respectively (Treatment temperature:  $F_{2,60} =$ 4.785, p = 0.012, Supp. Info. 4, Fig. 4A). In contrast, SDA<sub>duration</sub> increased with meal size in both species, albeit this response was more pronounced in *P. arcatus* (Interaction<sub>species x meal size;  $F_{1,60} = 11.861$ , p =0.001, Supp. Info. 4, Fig. 4A). Consequently, when incorporating both the direct (*i.e.*, thermal temporal compression of post-prandial response) and indirect effects of treatment temperature (*i.e.*, prolonged postprandial response due to thermally induced increases in meal size), SDA<sub>duration</sub> ranged between ~28–33 h for *P. arcatus* while it decreased from ~43 h in winter to 30 h at the peak of a MHW for L. *fulvus* (see coloured dashed lines in Fig. 4B).</sub>



**Fig. 4.** Magnitude and duration of the post-prandial response in *P. arcatus* and *L. fulvus*. (A) The relationship between SDA<sub>absolute peak</sub> and body mass, as well as (B) the relationship between SDA<sub>duration</sub> and meal size of *P. arcatus* (left column) and *L. fulvus* (right column) during winter  $(24.0 \pm 0.1 \,^{\circ}\text{C})$ , blue lines), summer  $(27.5 \pm 0.1 \,^{\circ}\text{C})$ , orange lines), and at the peak of a MHW ( $31.0 \pm 0.1 \,^{\circ}\text{C}$ , red lines). Solid coloured lines and shading in (A-B) represent the back-transformed mean  $\pm 95 \,^{\circ}\text{W}$  C. I., respectively, predicted by linear regression model 11 (SDA<sub>absolute peak</sub>) and 13 (SDA<sub>duration</sub>) in Supp. Info. 4, while statistical differences between treatments for each species when controlling for either body mass (SDA<sub>absolute peak</sub>) or meal size (SDA<sub>duration</sub>) are represented by different lower case letters (p < 0.05). Dashed coloured lines in (B) illustrate the SDA<sub>duration</sub> following the consumption of an average sized meal at each specific treatment temperature. Sample size (n) of each treatment for (A-B) are displayed at the top of the figure for each species.

# 4. Discussion

Understanding the impact of ocean warming on the fitness and productivity of piscivorous coral reef fishes is crucial for ecosystem health and global fisheries. These species are expected to have limited to no metabolic capacity for increasing prey consumption to meet elevated energetic demands as oceans warm, with consequential theoretical predictions of reduced appetite at temperatures beyond evolved conditions. Yet, contrary to theoretical predictions, we found increasing appetite and no constraints to oxygen supply prior to, or during, the ingestion, digestion, absorption, and assimilation of increasingly large meals as temperatures increased within and beyond their evolved thermal window. Instead, both species were physiologically capable of ingesting both larger and more frequent meals regardless of temperature rises. If broadly applicable across species, these findings suggest physiological limitations may not be the primary driver of declining fitness of large bodied individuals in warming oceans, instead pointing to alternate factors including species ecology.

As water temperatures rise, coral reef fishes experience heightened energetic demands for survival, but face strong challenges to meet these demands (Pörtner and Peck, 2010; Pratchett et al., 2015; Rummer et al., 2014). Indeed, basal energetic demands of both species increased by ~28 % from winter to summer (*i.e.*,  $Q_{10}$  of ~2.0) and by an additional ~29 % during the MHW (*i.e.*,  $Q_{10}$  of ~2.0), aligning with previously documented thermally-induced physiological rate elevations in fish (Seebacher et al., 2015). Such rising demands, requires an ability to capture and digest more prey, both of which are fuelled by surplus AS. However, AS is also projected to decline at temperatures above evolved thermal windows, rendering species less able to function and perform activities (e.g., swimming) to capture more prey (Johansen et al., 2014; Johansen and Jones, 2011; Scott et al., 2019). Yet, contrary to our own hypothesis and prior findings in other coral reef fishes (Gardiner et al., 2010; Habary et al., 2017; Johansen and Jones, 2011; Nilsson et al., 2009; Rummer et al., 2014), both species of piscivores examined here were able to expand their AS both within and beyond their current thermal window (*i.e.*, from winter to summer to the peak of a MHW). As a result, these species appear unconstrained by oxygen supply during MHWs and, hence, more physiologically resilient to ocean warming than many other coral reef fishes (Pörtner and Peck, 2010).

As energetic demands increase, so too does the need to feed. However, oxygen limitations imposed by the metabolic costs associated with the ingestion, digestion, absorption and assimilation of a meal has also been implicated in loss of residual AS needed for critical physiological and ecological processes. For instance, the 'Aerobic Scope Protection' hypothesis (Jutfelt et al., 2021) suggests that observed growth reductions of water-breathing ectotherms at warmer-than-optimal temperatures (Audzijonyte et al., 2019; Baudron et al., 2014; Cheung et al., 2013; van Rijn et al., 2017) may be due to a reduced appetite in order to conserve post-prandial residual AS for other essential aerobic processes (e.g., foraging, predatory avoidance and inter-/intra-specific competition). Accordingly, we hypothesized that while rising temperatures would increase the energetic demands for survival in piscivorous coral reef fishes, their physiological scope for aerobic performance would also decline when exposed to water temperatures beyond current thermal conditions, ultimately resulting in a reduction in appetite to protect residual AS during the ingestion, digestion, absorption, and assimilation of prey. However, no such reductions in appetite were observed in the present study, as both species substantially increased energy intake across the examined temperature range (*i.e.*, meal size increased by  $\sim 106$  % from winter to the peak of a MHW in summer). These thermally-induced increases in food intake are also similar to those previously reported for another piscivorous coral reef species allowed to voluntarily feed to satiation (*i.e.*, leopard coral grouper, *Plectropomus leopardus*; Johansen et al., 2015).

Processing larger meals as temperatures rise is expected to result in post-prandial responses that are of greater magnitude and more temporally compressed, inevitably resulting in higher peak postprandial oxygen uptake rates and corresponding reductions in postprandial residual AS (Jutfelt et al., 2021; McCue, 2006; Sandblom et al., 2014; Secor, 2009). Indeed, as meal size and temperature increased, both species displayed post-prandial responses of greater magnitude (i.e., SDAabsolute increased from winter to the peak of a MHW by ~105 % for P. arcatus and ~ 35 % for L. fulvus) and higher postprandial peak oxygen uptake rates (i.e., SDAabsolute peak was ~60 % higher at the peak of a MHW during summer when compared to winter). However, contrary to expectations, both species of piscivores were still able to retain a substantial surplus of residual AS at the peak of the postprandial response (i.e., P. arcatus and L. fulvus retained ~60 and 45 % of their AS, respectively, regardless of treatment temperature), which indicates that the metabolic costs associated with processing larger meals does not impose an oxygen supply limitation for these species during a MHW. This unexpected retention of residual AS suggests that these species may possess physiological mechanisms that enable them to effectively regulate oxygen delivery and metabolic demands during digestion. An intriguing direction for future research would be to investigate these mechanisms further, which may involve factors such as the controlled release of digesta by the pyloric caeca to modulate metabolic costs (Buddington and Diamond, 1986) or the possibility of gastrointestinal perfusion limitations (Brijs et al., 2018), whereby the capacity to deliver additional oxygen to the gastrointestinal system may

become constrained during the peak of the post-prandial response. These mechanisms may, at least in part, play a crucial role in enabling piscivores to protect their residual AS during digestion, even under heightened thermal stress.

Interestingly, the piscivorous coral reef fishes examined here exhibited excess digestive capacity across the temperature range studied, meaning that energy derived from a single meal substantially exceeded metabolic demands. This was especially pronounced in larger individuals, as they gained an estimated  $\sim$ 59–72 % surplus energy from each meal, allowing them to energetically sustain themselves for  $\sim$ 12–45 h after the complete digestion of each meal before new prey is required (see Fig. 5A). This excess digestive capacity likely reflects an evolutionary adaptation of piscivorous fishes to a cyclical pattern of prey abundance and scarcity, enabling them to thrive in an environment characterized by intermittent episodes of meal satiation and deprivation (i.e., a 'feast and famine' foraging strategy; Armstrong and Schindler, 2011). This adaptation to survive periods of fasting may also provide an unexpected advantage in the face of ocean warming, provided that adequate prev can be captured. While not directly assessed in the present study, this excess digestive capacity may, at least in part, result from the ability of the gastrointestinal system to dynamically adjust its structure and/or capacity in anticipation of seasonal increases in resource availability and energy demands (Armstrong and Bond, 2013; Caceres et al., 1994; Furey et al., 2016; Olsson et al., 2007; Zaldúa and Naya, 2014). Indeed, the seasonal phenotypic flexibility of the gastrointestinal system has been suggested to facilitate rapid and efficient adaptive responses to environmental change (Fernandes et al., 2024), highlighting a promising avenue for future research into the physiological mechanisms underpinning resilience to global warming.

While our study reveals the physiological capacity of both species of piscivores to process larger-than-necessary meals in response to rising temperatures, a critical question persists regarding their ability to



**Fig. 5.** Excess metabolic capacity and compressed digestive patterns allows piscivores to satisfy thermally-induced elevations in metabolic demands. (A) The proportion of meal energy required for satisfying basal energetic demands (solid coloured lines, calculated across body masses by dividing SMR with meal energy and adjusting for the costs of digestion and an energy absorption coefficient of 0.86, see (Knight et al., 2021), the buffer time between the completion of the post-prandial response and the next feeding bout (dashed coloured lines, calculated across body masses by determining the time taken to utilise all of the energy from a meal minus the duration of the respective post-prandial response), and (B) absolute daily resource demands required from the environment for *P. arcatus* (left column) and *L. fulvus* (right column) during winter ( $24.0 \pm 0.1 \degree$ C, blue lines), summer ( $27.5 \pm 0.1 \degree$ C, orange lines), and at the peak of a MHW ( $31.0 \pm 0.1 \degree$ C, red lines). Lines in (A) and (B) were calculated using the linear regression equations for SMR (model 1), absolute meal size (model 7), SDA coefficient (model 10) and SDA duration (model 13) across the range of body masses examined in this study for each species.

acquire sufficient energy from the environment during periods of thermal stress. Here, we estimate that on a daily basis, P. arcatus and L. fulvus need to acquire  $\sim$ 29 and 23 % more energy from the environment, respectively, during a MHW with a peak temperature anomaly of 3.5 °C above summer SST (Fig. 5B). These absolute resource demands may be exacerbated in larger individuals, with energy requirements estimated to rise by  $\sim$ 13 and 4 % per gram of body mass increase in *P. arcatus* and L. fulvus, respectively. Consequently, the largest individuals of each species in this study may respectively require up to  $\sim \! 154$  and 296 % more energy on a daily basis compared to smaller conspecifics (Fig. 5B). In light of projections indicating reduced productivity of coral reefs in response to ocean warming (Lo-Yat et al., 2011; Mellin et al., 2022; Millington et al., 2022), coupled with the documented declines in the abundance and biomass of coral reef fishes during MHWs (Genin et al., 2020; Magel et al., 2020; Pearce and Feng, 2013), it is plausible that prey availability for piscivorous fishes will become increasingly restricted in the future (Johansen et al., 2015). Furthermore, as temperatures rise, piscivorous fishes may display increased lethargy and reduced foraging activity (Johansen et al., 2014; Scott et al., 2019). Indeed, this trend appeared reflected in our study as rates of surplus energy expenditure (RMR) plateaued with increasing temperatures, indicative of diminished activity. As such, irrespective of the unexpected capacity to survive on larger, but infrequent meals, the reality of dwindling prey density, and reduced prey capture ability, compounded by a higher per capita resource demand, may disproportionately impact the ability of larger individuals to meet their energetic demands compared to their smaller conspecifics which rely on smaller and relatively more abundant prey.

Interestingly, the causative factors driving growth reductions of water-breathing ectotherms and ecosystem wide shifts to smaller maximum sized adults at warmer-than-optimal temperatures (i.e., the temperature-size-rule; Atkinson, 1994; Watt et al., 2010) is a topic of vigorous discussion among scientists (Berrigan and Charnov, 1994; Jutfelt et al., 2021; Lefevre et al., 2017; Pauly, 2021; Scheuffele et al., 2021; Verberk et al., 2021; Wootton et al., 2022). In accordance with our findings here, recent data have suggested that this global 'shrinking of fishes' phenomenon may be driven more by ecological factors than by physiological limitations. For instance, Johansen et al. (2024), suggested that once physiological limitations for residual AS are overcome (as also demonstrated by piscivores in this study), then resource acquisition and limitation becomes the primary driver for body-size reductions at elevated temperature, highlighting the need for a combined eco-physiological approach to elucidate ocean-warming consequences for species fitness and ecosystem productivity.

While the consequences of ocean warming and extreme thermal events remain uncertain for many species, this study provides a critical foundation for advancing our understanding of species-specific responses. However, significant gaps remain in our ability to predict the impacts of future thermal stressors on coral reef ecosystems with precision. For example, in the species investigated here, a deeper understanding is needed of the physiological mechanisms that enable P. arcatus and L. fulvus to substantially increase meal size while safeguarding residual AS. Do these mechanisms persist across more vulnerable seasonal life stages or ontogenetic phases (Dinh et al., 2023; Tran and Johansen, 2023), where physiological capacities may be constrained? Additionally, how might these responses shift when compounded by multiple stressors, such as habitat degradation and prey scarcity? Expanding beyond the species investigated, intriguing questions arise regarding how the capacity for flexible physiological responses to warming varies across trophic levels. For example, might species with more stable resource availability, such as herbivores, exhibit fundamentally different physiological trade-offs or limitations compared to piscivores, whose adaptations hinge on fluctuating prey abundance in accordance with a feast-and-famine life history?

## 5. Conclusions

Our study systematically investigated changes in energetic demand, aerobic performance, appetite, and metabolic costs of digestion for piscivorous fishes within and beyond their current thermal window to elucidate theoretical physiological limitations in energy availability for growth and fitness enhancing processes. In contrast to the anticipated physiological constraints and heightened energetic demands imposed by elevated temperatures, both species demonstrated increased appetite and excess digestive capacity, likely an artefact of their evolutionary adaptation to thrive in fluctuating prey availability scenarios. Nevertheless, challenges lie ahead for piscivorous fishes, particularly larger individuals, in securing ample energy from the environment as temperatures continue to rise. These challenges will be exacerbated by the projected escalation in the frequency, intensity, extensiveness, and duration of MHWs towards the end of the century, compounded by dwindling numbers of prey species (Genin et al., 2020; Magel et al., 2020; Pearce and Feng, 2013).

To comprehensively grasp species- and size-specific responses to prolonged ocean warming and extreme thermal events, our study underscores the necessity for a theoretical framework that integrates aspects of both oxygen limitation theory (emphasizing the importance of adequate aerobic surplus for sustaining critical ecological activities) and ecological resource limitation theory (highlighting the critical balance between energetic demand and acquisition for ensuring optimal growth, development, and survival) (*e.g.*, see Protect Aerobic Scope and Limit Energy Demand [PASLED] theory by Johansen et al., 2024).

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2025.179105.

# CRediT authorship contribution statement

Jeroen Brijs: Writing - review & editing, Writing - original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. Chloe Moore: Writing - review & editing, Writing - original draft, Visualization, Validation, Investigation. Mathias Schakmann: Writing - review & editing, Writing - original draft, Visualization, Validation, Investigation. Taylor Souza: Writing - review & editing, Writing - original draft, Visualization, Validation, Investigation. Katherine Grellman: Writing - review & editing, Writing - original draft, Visualization, Validation, Investigation. Leon L. Tran: Writing - review & editing, Writing - original draft, Visualization, Validation, Investigation. Philip T. Patton: Writing - review & editing, Writing - original draft, Visualization, Validation, Methodology, Formal analysis, Data curation. Jacob L. Johansen: Writing - review & editing, Writing - original draft, Visualization, Validation, Supervision, Resources, Project administration. Methodology, Funding acquisition, Formal analysis, Conceptualization.

# Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work Jeroen Brijs used ChatGPT 3.5 by openai.com in order to improve the grammar and readability of sections within the introduction and discussion of this manuscript. After using this tool/service, the author reviewed and edited the content as needed and takes full responsibility for the content of the publication.

# Funding

This work was funded by a University of Hawai'i at Mānoa startup grant awarded to Jacob L. Johansen [#009454] and a U.S. National Science Foundation grant to Jacob L. Johansen (#2210070).

# Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

# Acknowledgements

The authors acknowledge this research was done in the ahupua'a of He'eia in Ka-waha-o-ka-manō (known today as Kāne'ohe Bay), and would also like to thank the staff at the Hawai'i Institute of Marine Biology on Moku o Lo'e for logistical assistance.

# Data availability

The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.j3tx95xp8

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J. Brijs et al.

 
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