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RESEARCH ARTICLE

An appetite for invasion: digestive physiology, thermal performance and food intake in lionfish (*Pterois* spp.)

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ABSTRACT

Species invasions threaten global biodiversity, and physiological characteristics may determine their impact. Specific dynamic action (SDA; the increase in metabolic rate associated with feeding and digestion) is one such characteristic, strongly influencing an animal's energy budget and feeding ecology. We investigated the relationship between SDA, scope for activity, metabolic phenotype, temperature and feeding frequency in lionfish (*Pterois* spp.), which are invasive to western Atlantic marine ecosystems. Intermittent-flow respirometry was used to determine SDA, scope for activity and metabolic phenotype at 26°C and 32°C. Maximum metabolic rate occurred during digestion, as opposed to exhaustive exercise, as in more athletic species. SDA and its duration (SDA_{dur}) were 30% and 45% lower at 32°C than at 26°C, respectively, and lionfish ate 42% more at 32°C. Despite a 32% decline in scope for activity from 26°C to 32°C, aerobic scope may have increased by 24%, as there was a higher range between standard metabolic rate (SMR) and peak SDA (SDA_{peak}; the maximum postprandial metabolic rate). Individuals with high SMR and low scope for activity phenotypes had a less costly SDA and shorter SDA_{dur} but a higher SDA_{peak}. Feeding frequently had a lower and more consistent cost than consuming a single meal, but increased SDA_{peak}. These findings demonstrate that: (1) lionfish are robust physiological performers in terms of SDA and possibly aerobic scope at temperatures approaching their thermal maximum, (2) lionfish may consume more prey as oceans warm with climate change, and (3) metabolic phenotype and feeding frequency may be important mediators of feeding ecology in fish.

KEY WORDS: Invasive species, Metabolic phenotype, Specific dynamic action, Thermal physiology, Temperature

INTRODUCTION

Species invasions are a widely recognized and growing threat to global biodiversity (Ricciardi et al., 2017). Dozens of fish species have become invasive worldwide as the result of human activity, and many more may become invasive, with over 600 known introductions of non-native species (Gozlan, 2008). The probability of an introduced species becoming invasive depends on ecological and life history traits (e.g. niche, growth rate, reproductive capacity or tolerance to disturbance), which are underpinned by physiological characteristics (Van Kleunen et al., 2010; Kelley, 2014; Lennox et al., 2015). Characteristics of metabolic rate – the rate at which an organism expends energy, commonly measured using oxygen consumption rate ($\dot{M}_{O_2}$) – are increasingly recognized as a potential determinant of invasion success (González-Ortegón et al., 2010; Maazouzi et al., 2011; Lejeusne et al., 2014; Lagos et al., 2017). Relatively few studies have examined their relevance to invasive fish, however, which is surprising given the number and impact of invasive fish species worldwide (but see Marras et al., 2015; McCallum et al., 2017; Behrens et al., 2017; Srean et al., 2017; Nati et al., 2018; Tessier et al., 2018).

A characteristic of metabolic rate that has largely been ignored in invasive species biology is specific dynamic action (SDA): the postprandial increase in metabolic rate associated with feeding and digestion. SDA represents the total energy expenditure of numerous pre-absorptive, absorptive and post-absorptive pathways associated with feeding and digestion, and is typified by a rapid rise in metabolic rate up to a relatively short-lived peak (SDA_{peak}) followed by a longer decline (Jobling, 1981; McCue, 2006; Chabot et al., 2016) (Fig. 1). SDA is ecologically relevant because it can occupy a large proportion of a fish's energy budget in terms of its aerobic scope or scope for activity. Aerobic scope is the range between standard metabolic rate (SMR, the minimum metabolic rate required for maintenance) and maximum metabolic rate (MMR), whereas scope for activity is the range between SMR and active metabolic rate (AMR, the metabolic rate elicited from maximal exercise) (Sandblom et al., 2014; Norin and Clark, 2016). Aerobic scope and scope for activity are equivalent and interchangeable in many species (i.e. AMR=MMR); however, in some more-sedentary species, these characteristics are distinct as MMR may be achieved independently of exhaustive exercise (i.e. AMR<MMR) (Norin and Clark, 2016). As SDA increases with meal size, a trade-off occurs between feeding and maintaining a sufficient aerobic scope or scope for activity required to avoid predators, move through the environment or find the next meal (Auer et al., 2015a; Norin and Clark, 2017). This trade-off may be mediated by the environment or physiological state (Secor, 2009; Chabot et al., 2016; Metcalfe et al., 2016), but little work has investigated how this manifests in fish. The present study explores three of these factors: (1) temperature, (2) metabolic phenotype and (3) feeding frequency.

Temperature strongly influences both SDA and aerobic scope (Secor, 2009; Farrell, 2016). The effect of temperature on either aerobic scope or SDA has been described for many fish species; however, the effect of temperature on these two traits together has been described for very few (but see Pang et al., 2010, 2011; Sandblom et al., 2014), none of which have been invasive species. Changes in aerobic scope or scope for activity have major implications for fish performance and fitness (Rummer et al., 2014; Farrell, 2016; Norin and Clark, 2016). However, understanding the effect of temperature on SDA is necessary to

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List of symbols and abbreviations

ADC	apparent digestibility coefficient
AMR	active metabolic rate
M_b	body mass
MMR	maximum metabolic rate
$\dot{M}_{O_2}$	oxygen consumption rate
RMR	routine metabolic rate
SDA	specific dynamic action
SDA_{coeff}	SDA coefficient
SDA_{dur}	SDA duration
SDA_{peak}	peak SDA
SMR	standard metabolic rate

contextualize the significance of these changes in aerobic scope, as aerobic scope and SDA can vary with temperature independently and, in turn, define the roles of feeding, exercise and other energetic processes in a species' energy budget (Sandblom et al., 2014; Auer et al., 2015b; Metcalfe et al., 2016; Norin and Clark, 2017). As such, the relationship between SDA and temperature could play a significant role in the expected increase of ectothermic species invasions in aquatic ecosystems with climate change, particularly as temperature approaches species' thermal maxima, where aerobic scope or scope for activity is often reduced (Côté and Green, 2012; Marras et al., 2015).

In addition to temperature, metabolic phenotypes have been found to affect SDA in fish. Metabolic phenotypes are inherent individual variations (either genotypic or plastic) in SMR, routine metabolic rate (RMR, metabolic rate at regular activity levels), MMR, AMR and aerobic scope or scope for activity, and are important determinants of a fish species' behavior, ecology and life history (Cutts et al., 2002; Fu et al., 2008; Norin and Clark, 2016). Millidine et al. (2009) found that juvenile Atlantic salmon (*Salmo salar*) with a high SMR phenotype had an energetically costlier SDA but a shorter SDA duration (SDA_{dur}) than those with a low SMR phenotype, which in salmonids is hypothesized as a trade-off for faster growth. However, fish may express metabolic phenotypes in MMR, AMR and aerobic scope independently of their SMR phenotype (Auer et al., 2015b; Metcalfe et al., 2016), the effects of which on SDA have not been explored to date.

Along with temperature and metabolic phenotype, the effect of feeding frequency on SDA and its occupation of aerobic scope or scope for activity has been relatively understudied in fish. Most SDA studies in fish have analyzed single meals (Secor, 2009; Chabot et al., 2016), but many fish feed more frequently than the time required to fully digest a single meal, which in other ectotherms

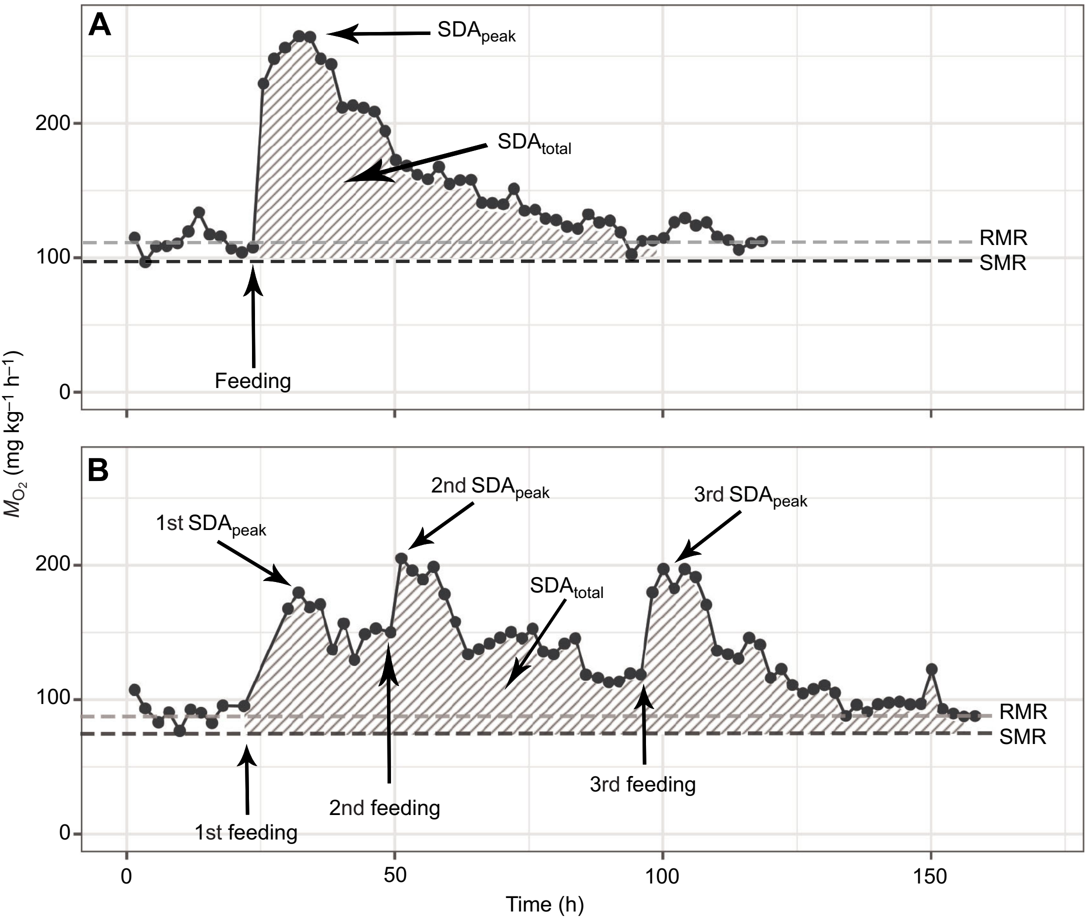

Fig. 1. Examples of specific dynamic action (SDA) curves. (A) During single feeding and (B) during repeated feeding. Metabolic rate data are oxygen consumption rate values ($\dot{M}_{O_2}$, mg kg^{-1} h^{-1}) mass-adjusted to a 140 g fish (*b*=0.835). SDA is the integral under the curve between postprandial $\dot{M}_{O_2}$ and standard metabolic rate (SMR, black line) over the duration between feeding and the third postprandial $\dot{M}_{O_2}$ value to fall below routine metabolic rate (RMR, gray line). Peak SDA (SDA_{peak}) is the highest unblocked postprandial $\dot{M}_{O_2}$ value following feeding. The single feeding curve was in response to a 7.4% body mass (M_b) meal, and the first, second and third repeated feeding curves were in response to 3.2%, 2.7% and 2.7% M_b meals, respectively.

can lower the energetic cost of upregulating gut function (Iglesias et al., 2003; Secor, 2009; Zaldúa and Naya, 2014). In turn, this may lower the cost of SDA relative to eating single, less frequent meals; however, empirical support for this in fish remains sparse. Ross et al. (1992) and Guinea and Fernandez (1997) found no difference in the cost of SDA between one meal and several smaller, more frequent meals of the same total ration in Nile tilapia (*Oreochromis iuloticus*) and gilt-headed sea bream (*Sparus aurata*), respectively; however, frequent feeding caused a higher SDA$_{peak}$ in these species, which has also been observed in frequently fed southern catfish (*Silurus meridionalis*) (Fu et al., 2005). These studies were primarily concerned with fish aquaculture, and did not consider that such increases in SDA$_{peak}$ may occupy a greater proportion of their aerobic scope or scope for activity. Such a trade-off may mediate feeding rates in species that must maintain an adequate aerobic scope or scope for activity for predator avoidance or other forms of exercise during SDA (Norin and Clark, 2017), but this has yet to be explored experimentally.

We sought to explore these paradigms in invasive lionfish (*Pterois* spp. Oken 1817). Lionfish are mid-sized demersal predators native to the Indian and Pacific Oceans that have been invasive to the western Atlantic Ocean since 2001 and the Mediterranean since 2012 (Hixon et al., 2016; Bariche et al., 2017). Their phylogeny has recently been contested (Wilcox et al., 2018), so lionfish will be referred to generically henceforth. Their invasion is driven mainly by a lack of natural predators, prey naivety, and unique hunting traits not found in native predators, which allows lionfish to spread and forage with few, if any, limits (Valdivia et al., 2014; McCormick and Allan, 2016; Green et al., 2019). Lionfish threaten western Atlantic marine ecosystems by consuming small-bodied fish and crustaceans, significantly lowering their populations and even extirpating them locally (Benkwitt, 2015; Palmer et al., 2016; Ingeman, 2016; South et al., 2017), facilitating coral-smothering algal growth by removing grazers (Kindinger and Albins, 2017), and outcompeting native mesopredators (Raymond et al., 2015; Curtis et al., 2017). Green et al. (2011) estimated that an adult lionfish could consume 8.9% of its body mass per day based on field observations in The Bahamas, which was more than twice their required daily energy intake for maintenance (i.e. SMR) as estimated by Côté and Maljković (2010). This excess energy assimilation allows lionfish to grow and reproduce much faster than native mesopredators, reaching sexual maturity in less than a year and spawning as frequently as every 4 days (Morris, 2009; Côté et al., 2013).

A broad thermal tolerance spanning almost 25°C has allowed lionfish to invade a wide latitudinal range, as well as cold mesophotic reefs as deep as 100 m (Dabruzzi et al., 2017; Tornabene and Baldwin, 2017). Barker et al. (2017) found a temperature preference of 28.7°C in invasive lionfish from Florida, similar to the 29.8°C optimum for voluntary food intake found by Cerino et al. (2013). Dabruzzi et al. (2017) found a lower temperature preference between 23°C and 24°C in Indo-Pacific lionfish; however, they found a mean critical thermal minimum (CT_{min}=12.1°C) and maximum (CT_{max}=35.3°C) similar to those of Barker et al. (2017) (CT_{min}=12.1°C and CT_{max}=36.5°C). Invasive lionfish have therefore been found to have a temperature preference and food intake optimum close to their upper thermal threshold, a typical trait in tropical fish (Norin et al., 2014; Rummer et al., 2014); however, performance-based physiological metrics such as aerobic scope or scope for activity have not been tested in lionfish across temperatures to date. Warming sea temperatures are anticipated to expand the lionfish's invasive northern and southern limits – currently set by lethally low winter temperatures – and to increase the habitability of temperature-structured ecosystems throughout their invaded range (Kimball et al., 2004; Whitfield et al., 2014; Bernal et al., 2015). Higher metabolic rates associated with increasing sea temperatures have been predicted to increase feeding rates in invasive lionfish (Côté and Green, 2012; Cerino et al., 2013); however, feeding metabolism (i.e. SDA) and its relationship to temperature have not been studied in lionfish to date.

The objective of the study was to determine the effect of temperature (26°C versus 32°C), metabolic phenotype (SMR and scope for activity) and feeding frequency (single versus repeated feeding) on SDA in invasive lionfish and whether these relationships may facilitate the invasiveness of this species as oceans warm with climate change. These temperatures were selected to represent contemporary winter and extreme summer conditions in the subtropical western Atlantic, respectively, of which the latter will become more common with climate change (Zhang et al., 2018). We hypothesized that: (1) SDA and SDA$_{dur}$ would decrease with temperature, given that lionfish optimally feed close to their upper temperature thresholds, whereas SDA$_{peak}$ would increase owing to the higher metabolic demands of increased temperature; (2) lionfish with higher SMR and larger scope for activity would have a greater SDA but shorter SDA$_{dur}$, as per the findings of Millidine et al. (2009); (3) as temperatures increase, scope for activity would decrease and, in turn, SDA would occupy a greater proportion of it; (4) the SDA of frequent feeding would be lower than that of a single feeding; (5) SDA$_{peak}$ of a repeated meal would be higher when the previous meal was larger and more recent; and (6) lionfish would eat larger repeated meals when the residual metabolic rate from the previous meal's SDA was lower and occupying less of its scope for activity, and when the previous meal was smaller and less recent.

MATERIALS AND METHODS

Animal collection and husbandry

Lionfish were collected on SCUBA with plastic hand nets from patch reefs in the Bight of Rock Sound (24°50′28N, 76°17′13W) in the winter (January–March) and summer (June–July) of 2017 and winter of 2018 (January–February) [mean=135.5±9.5 g body mass (M_b); all data are reported as means±s.e.m.; sex unidentifiable as gonadosomatic index<1% M_b in all individuals]. All collections were from less than 4 m depth to prevent barotrauma. Collected lionfish were transported to the Cape Eleuthera Institute wet laboratory and held with no more than 10 individuals per tank in outdoor circular 750 liter tanks that were aerated and continuously supplied with fresh seawater (5 l min^{-1}) at ambient temperature (see below). All lionfish were acclimated to laboratory conditions for a minimum of 5 days and held for a maximum of 22 days before metabolic rate measurements, and were fed live silversides (*Atherinomorus stipes*) to satiation (when feeding ceased after the addition of new prey) every 3 to 5 days. Live silversides were used as prey because the lionfish would not eat dead prey, a typical behavior of the species (Cerino et al., 2013; Hixon et al., 2016).

Respirometry

An eight-chambered intermittent-flow respirometry system (Loligo Systems, Viborg, Denmark) was used to measure oxygen uptake rates ($\dot{M}_{O_2}$) in individual lionfish. Chambers were custom-made from 10.15 liter polypropylene containers (Snapware, Rosemont, USA) and plumbed with vinyl tubing to 5 l min^{-1} recirculation pumps and 10 l min^{-1} flush pumps bifurcated between two chambers for an effective flush rate of 5 l min^{-1} (Eheim, Deizisau, Germany). The chamber lids had 3 cm ports sealed with rubber stoppers, through which prey fish could be fed *in situ* and with minimal disturbance during measurements. Chambers were immersed in two 570 liter raceways (300×30×60 cm) supplied with filtered and aerated seawater. Loligo mini sensor oxygen probes (Witrox, Loligo Systems) were calibrated before each measurement period to 0% and 100% air saturation using a seawater–sodium sulphite solution and air-saturated seawater, respectively. $\dot{M}_{O_2}$ was recorded in a closed loop mixed by a recirculating pump for 10 min, preceded by a 19-min flush period to restore oxygen saturation levels and a 1-min wait period. Microbial background respiration was recorded in each chamber for three measurement cycles (90 min) before and after each round of respirometry.

Experimental protocol

A single feeding experiment was conducted at 26°C (n=13) and 32°C (n=16), and a feeding frequency experiment was conducted at 26°C (n=13). The feeding frequency experiment was planned to include a 32°C treatment, but unfortunately could not be completed due to a limited timeframe. 26°C was chosen as it represents contemporary ambient winter sea temperatures in the subtropical western Atlantic. 32°C was chosen as it is representative of high summer sea temperatures both in The Bahamas and in the invasive lionfish range nearest the equator (Zhang et al., 2018), and because Cerino et al. (2013) observed a reduced prey consumption rate at 32°C. In the single feeding experiment, the 26°C treatment was performed in March and June 2017, and the 32°C treatment was performed in July 2017. The feeding frequency experiment was conducted in January and February 2018. There was no significant difference in body mass or SMR between the 26°C treatment measurement in March 2017, the 26°C treatment measurement in June 2017, and the repeated feeding treatment measured in January and February 2018 at 26°C according to Welch's *t*-tests, and there was no consistent temporal change in SMR or scope for activity between measurement rounds in any treatment, suggesting minimal possibility for an acclimation effect (Sandblom et al., 2014). All lionfish were used once.

In both experiments, lionfish were fed to satiation in their holding tanks and then fasted for 48 h prior to respirometry to ensure a post-absorptive state, which was confirmed by a plateaued $\dot{M}_{O_2}$ trace as SMR was measured (see below). Lionfish were transferred directly from their holding tank into respirometry chambers and $\dot{M}_{O_2}$ was recorded for 24 h to calculate SMR. The difference in temperature between the holding tanks and the respirometry chambers was ±2°C or less, typical of diel variation in the shallow patch reefs from which the lionfish were collected. Lionfish were then fed live silversides directly in their chambers during crepuscular hours, and $\dot{M}_{O_2}$ was immediately recorded to calculate SDA. Because lionfish would not consistently eat the meal sizes we sought to measure, we decided to feed each fish to satiation in order to capture a range of meal sizes that could be measured as a continuous variable. Meal sizes were measured by weighing individual silversides prior to putting them in the respirometry chambers. One silverside was presented to the lionfish at a time, and they were sequentially added until the lionfish ceased feeding. In the single feeding experiment, SDA was recorded over 96 h following a single feeding that occurred between 17:00 and 19:00 h. In the feeding frequency experiment, SDA was recorded for 72 h while lionfish were fed to satiation every morning between 06:00 and 08:00 h and every evening between 17:00 and 19:00 h, followed by 60 h without feeding. Rations ranged between 0.6% and 13.8% M_b (1.0–20.4 g). AMR was determined at the end of each trial by chasing each lionfish in a 150 liter tank to exhaustion, determined when their flight reflex was impaired and the caudal fin could be held and let go three times in quick succession. The lionfish were then immediately returned to their respirometry chambers and $\dot{M}_{O_2}$ was recorded.

All work was carried out under the Bahamas Department of Marine Resources permit number MAMR/FIS/17 and with approval from the Canadian Council of Animal Care and Carleton University. As they are a harmful invasive species, lionfish were euthanized after experimentation with cerebral percussion.

Prey calorimetry

The gross energy content of 10 silversides collected in winter 2017 was determined using an oxygen bomb calorimeter (Parr Instrument Co., Moline, USA). Average gross energy density was 13.79±0.87 kJ g^{-1} (wet mass), similar to the energy density of demersal western Atlantic reef fish that lionfish would prey upon (Schwartzkopf and Cowan, 2017; Welicky et al., 2018). Pettitt-Wade et al. (2011) found no difference in the energy density of small forage fish including *A. stipes* between seasons in The Bahamas, so this energy density was used for all treatments and experiments.

Data analysis

Raw $\dot{M}_{O_2}$ was corrected for microbial background respiration for each chamber in each trial. Background respiration was calculated for each chamber based on a first-order exponential trendline calculated between initial and ending average background measurements, then subtracted from the slope of each $\dot{M}_{O_2}$ measurement to calculate background-corrected $\dot{M}_{O_2}$. Per Chabot et al. (2016), the minimum r^2 to ensure linearity of the oxygen trace slope was determined for each lionfish and values below this threshold were rejected, with an absolute minimum threshold of 0.80. The average r^2 across all fish was 0.96, and the fish with the lowest average r^2 was 0.89. Background-corrected $\dot{M}_{O_2}$ was blocked by minimum values per every four measurements (2 h) to account for short bouts of activity in some fish per Eliason et al. (2007). AMR and SDA_peak were derived from unblocked $\dot{M}_{O_2}$. SMR, RMR and SDA were derived from $\dot{M}_{O_2}$ block minimums. SMR was calculated as the average of the lowest 10th percentile of $\dot{M}_{O_2}$ recorded over 24 h before feeding and following a 48 h fasting period. RMR was calculated as the average $\dot{M}_{O_2}$ of the 18 h before feeding after a 6 h recovery period following placement in the respirometer. SDA_dur was calculated as the number of hours between feeding and the third point of postprandial $\dot{M}_{O_2}$ to fall below RMR. Four lionfish in the single feeding experiment and four lionfish in the feeding frequency experiment had postprandial $\dot{M}_{O_2}$ that did not return below RMR within 96 h but were within 20% of it and trending downward, for which SDA_dur was extrapolated to the slope of the last period of declining $\dot{M}_{O_2}$ derived from a fifth-order polynomial trendline fitted to the SDA response. SDA was calculated by integrating the area under the curve of postprandial $\dot{M}_{O_2}$ over SDA_dur minus SMR (Fig. 1A). RMR was chosen as the endpoint of SDA_dur because many lionfish had postprandial $\dot{M}_{O_2}$ that did not return to SMR before the end of the experiment, but was not used as the baseline from which SDA is measured because it was consistently higher than SMR and therefore a less accurate measure of true resting metabolic rate. SDA_peak exceeded AMR in many lionfish and precluded a reliable measurement of aerobic scope, so scope for activity was used instead and calculated as the difference between AMR and SMR. The cost of SDA as a percentage of energy consumed is termed the SDA coefficient (SDA_coeff). This was calculated with the equation $\text{SDA}_\text{coeff}=(E_\text{SDA}/E_\text{meal})\times100$, where E_SDA is the energy spent on SDA assuming 1 g of O_2 is associated with the release of 13.6 kJ of energy (Cho et al., 1982), as the rate of sequential fuel use (Ferreira et al., 2019) is not known for lionfish, and E_{meal} is the energy of an ingested meal, calculated by multiplying its mass by the average gross energy density we found in our feed fish (13.79 kJ g^{-1}) and a 0.8 correction factor to account for indigestible energy (Craig et al., 1978; Jobling, 1983).

In the feeding frequency experiment, single values for SDA, meal size and $\mathrm{SDA}_{\mathrm{coeff}}$ across repeated feedings were determined by integrating all repeated meals, summing repeated meal sizes, and using these values in the equation above (Fig. 1B).

M_{b} varied 7.6-fold in the single feeding experiment (43.5–331.5 g, mean=140±11.3 g) and 3.5-fold in the feeding frequency experiment (44–155 g, mean=92.3±9.9 g). Log_{10}-transformed whole-animal SMR (mg O_2 h^{-1}) varied allometrically when regressed against $\log_{10}$-transformed M_{b} (kg) at both temperatures used in this study. $\dot{M}_{\mathrm{O_2}}$ was therefore mass-adjusted to that of a 140 g lionfish using the equation $y_{0.14\,\mathrm{kg}}=y_M\ (M\times0.14^{-1})^{(1-b)}$, where $y_{0.14\,\mathrm{kg}}$ is $\dot{M}_{\mathrm{O_2}}$ mass-adjusted to a 140 g lionfish, y_M is $\dot{M}_{\mathrm{O_2}}$ of a lionfish at mass M, and b is the allometric scaling coefficient (Rosewarne et al., 2016). The scaling coefficient was almost identical between temperatures (b=0.83 at 26°C and b=0.84 at 32°C), and so was averaged for all fish (b=0.835). Results are presented using mass-adjusted data.

Statistical analysis

Separate ANCOVA models were fit for each SDA parameter (SDA, $\mathrm{SDA}_{\mathrm{coeff}}$, $\mathrm{SDA}_{\mathrm{peak}}$ and $\mathrm{SDA}_{\mathrm{dur}}$) to test the effect of temperature, meal size, SMR and scope for activity. All but one of the parameters were normally distributed and homoscedastic, and met the assumptions of ANCOVA, with $\mathrm{SDA}_{\mathrm{coeff}}$ $\log_{10}$-transformed to meet assumptions of normality and homoscedasticity. Interactions were determined by including interaction terms between temperature and each covariate in the ANCOVA model. Relationships between the predictors were also analyzed, using Welch's t-tests or regression as appropriate. Significance was determined with P-values in all models. All statistical tests were performed in RStudio (RStudio Inc., Boston, MA, USA).

Data from the feeding frequency experiment were analyzed in three separate ways, each testing the effect of meal size, SMR and scope for activity as in the single feeding experiment. The first used multiple regression to determine whether food intake of a repeated meal was affected by residual SDA from the previous meal – measured as the percentage of scope for activity occupied by pre-feeding $\dot{M}_{\mathrm{O_2}}$ – as well as the previous meal's size, the previous meal's SDA integral and the time interval since the previous meal. The second used multiple regression to analyze the effect of the previous meal's size, the previous meal's SDA integral and the time interval since the previous meal on $\mathrm{SDA}_{\mathrm{peak}}$. Variance inflation factors were below 3. Akaike's information criterion was used to determine the optimal combination of predictors for each linear model. The third used ANCOVA models to test the effect of frequent versus single feeding on SDA and $\mathrm{SDA}_{\mathrm{coeff}}$ while controlling for meal size, SMR and scope for activity as covariates.

RESULTS

Single feeding experiment

Relationships between predictors: temperature, meal size, SMR and scope for activity

Lionfish ate significantly more (P=0.003) in the 32°C treatment than the 26°C treatment, with a 42% increase in prey consumption from 26°C (mean=4.5±0.59% M_{b}, 1.4–9.1% M_{b}) to 32°C (mean=7.8±0.81% M_{b}, 1.8–13.8% M_{b}). The lionfish expressed a range of metabolic phenotypes, with a two-fold variation in both SMR and scope for activity in either temperature treatment. Scope for activity did not significantly vary with SMR, but rather significantly increased with AMR (P<0.01). Food intake did not significantly vary with SMR or scope for activity.

SMR significantly differed between temperatures (P<0.001), with a 59% increase from the 26°C treatment (mean=69.6±4.0 mg $\mathrm{kg}^{-1}\,\mathrm{h}^{-1}$) to the 32°C treatment (mean=118.4±3.9 mg $\mathrm{kg}^{-1}\,\mathrm{h}^{-1}$), while AMR did not significantly differ between the 26°C treatment (mean=257.0±7.8 mg $\mathrm{kg}^{-1}\,\mathrm{h}^{-1}$) and the 32°C treatment (mean=245.9±7.8 mg $\mathrm{kg}^{-1}\,\mathrm{h}^{-1}$) (Fig. 2). $\mathrm{SDA}_{\mathrm{peak}}$ exceeded AMR in many lionfish and precluded a reliable measurement of true aerobic scope (MMR–SMR), so scope for activity (AMR–SMR) was used instead. Scope for activity significantly differed between temperatures (P<0.001), declining 32% from the 26°C treatment (mean=187.4±5.8 mg $\mathrm{kg}^{-1}\,\mathrm{h}^{-1}$) to the 32°C treatment (mean=127.5±6.6 mg $\mathrm{kg}^{-1}\,\mathrm{h}^{-1}$) (Fig. 2). Aerobic scope may have increased from 26°C to 32°C, however, as the range between SMR and $\mathrm{SDA}_{\mathrm{peak}}$ from the largest meals at these respective temperatures increased by 24% (26°C: $\mathrm{SDA}_{\mathrm{peak}}$=193.7 mg $\mathrm{kg}^{-1}\,\mathrm{h}^{-1}$ for a 9.1% M_{b} meal; 32°C: $\mathrm{SDA}_{\mathrm{peak}}$=262.6 mg $\mathrm{kg}^{-1}\,\mathrm{h}^{-1}$ for a 13.8% M_{b} meal).

Effects of temperature, meal size, SMR and scope for activity on SDA parameters

The effect of temperature on SDA approached significance (P=0.08). When divided by meal size to control for its positive effect (P<0.001), SDA was 29.6% lower at 32°C (mean=685.2±51.2 mg $\mathrm{kg}^{-1}\,\mathrm{h}^{-1}$ % M_{b}^{-1}) than at 26°C (mean=972.8±130.72 mg $\mathrm{kg}^{-1}\,\mathrm{h}^{-1}$ % M_{b}^{-1}) (Fig. 3A,D). $\mathrm{SDA}_{\mathrm{coeff}}$ was 15.2±1.6% and did not significantly vary with meal size (Fig. 3E). $\mathrm{SDA}_{\mathrm{coeff}}$ did not significantly differ between temperatures, but was 7% lower at 32°C (mean=15.9±2.7%) than at 26°C (mean=14.7±2.0%) (Fig. 3H).

SDA significantly varied with SMR (P=0.02) and scope for activity (P=0.01), decreasing with SMR and increasing with scope for activity when divided by meal size to control for its effect (Fig. 3B,C). Model results suggest that SDA can be up to 33% lower at the highest SMR we observed at a given temperature versus the lowest, and up to 46% lower at the lowest scope for activity versus the highest (Table S1).

$\mathrm{SDA}_{\mathrm{peak}}$ significantly differed between 26°C and 32°C (P<0.001). When divided by meal size to control for its positive effect (P<0.001), $\mathrm{SDA}_{\mathrm{peak}}$ was 30% lower at 32°C than at 26°C (Fig. 3I,L). $\mathrm{SDA}_{\mathrm{peak}}$ significantly increased with SMR (P=0.005) and increased with scope for activity, but not significantly (P=0.057) (Fig. 3J,K). $\mathrm{SDA}_{\mathrm{peak}}$ occupied the entirety of scope for activity (i.e. $\mathrm{SDA}_{\mathrm{peak}}$>AMR) in 88% of the feedings at 32°C, versus 23% at 26°C. All meal sizes created an $\mathrm{SDA}_{\mathrm{peak}}$ that occupied more than 64% of a fish's scope for activity. Model results for $\mathrm{SDA}_{\mathrm{peak}}$ suggest that meal sizes of 8.4% and 4.2% M_{b} would occupy the entirety of scope for activity at 26°C and 32°C, respectively (i.e. $\mathrm{SDA}_{\mathrm{peak}}$=AMR), for fish with average SMR and scope for activity at those respective temperatures (Fig. 2; Table S1). The average time taken to reach $\mathrm{SDA}_{\mathrm{peak}}$ after feeding was 6.6±1 h.

The effect of temperature on $\mathrm{SDA}_{\mathrm{dur}}$ approached significance (P=0.053). When divided by meal size to control for its positive effect (P=0.05), $\mathrm{SDA}_{\mathrm{dur}}$ was 45% lower at 32°C (mean=10.1±1.0 h % M_{b}^{-1}) than at 26°C (mean=18.2±2.4 h % M_{b}^{-1}) (Fig. 3M,P). $\mathrm{SDA}_{\mathrm{dur}}$ ranged from 27.9 to 109.6 h, significantly increased with scope for activity (P=0.02) and decreased with SMR, but not significantly (P=0.09) (Fig. 3N,O). For a 5% M_{b} meal, for example, our model results suggest that $\mathrm{SDA}_{\mathrm{dur}}$ would be up to 23.8 h shorter at the lowest scope for activity we observed at a given temperature versus the highest, and up to 7.7 h shorter at the highest SMR versus

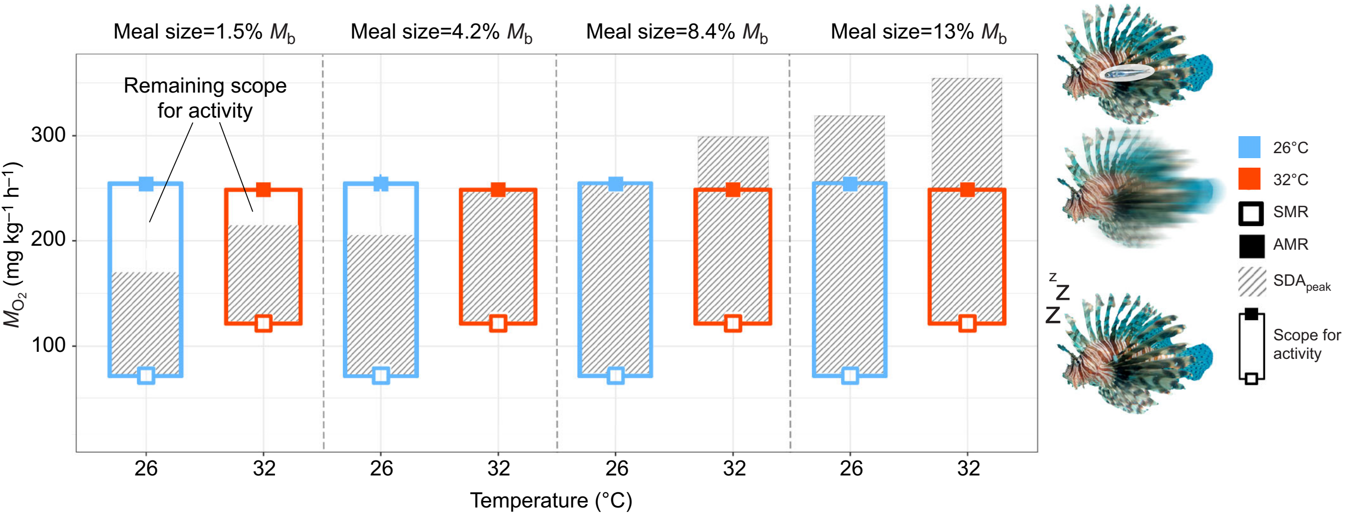

Fig. 2. Relationships between SDA$_{peak}$, scope for activity and temperature (26°C and 32°C; *n*=13 and *n*=16, respectively) as a function of meal size for single meals. Metabolic rates are illustrated for lionfish at rest (SMR, bottom), at maximal activity (AMR, middle) and at maximal digestion of a large meal (SDA$_{peak}$, top). Metabolic rate data are mass-adjusted to a 140 g fish (b=0.835). Meal size is measured as a percentage of body mass (%M_b). SMR and active metabolic rate (AMR) are $\dot{M}_{O_2}$ values (mg kg^{-1} h^{-1}). Plotted SMR and AMR values are averages from each temperature treatment. Scope for activity is the difference between AMR and SMR in an individual lionfish.

the lowest (Table S1). Although SDA$_{dur}$ for some larger meals exceeded the post-feeding 48–72 h in which SMR was measured, $\dot{M}_{O_2}$ had stabilized during this window in all lionfish and did not steadily decline as in an absorptive state, suggesting the measurement of SMR was not confounded by elevated post-feeding metabolism from the satiation feeding prior to measurement.

Feeding frequency experiment

Effects of previous meals on feed intake and SDA$_{peak}$

Twenty-seven repeated meals were recorded for 13 lionfish, which ate between two and five meals each. Nine of these were eaten within 12 h of the previous meal, eight were eaten within 24 h, and 10 were eaten within 36 to 60 h. Food intake of repeated meals ranged from 0.6% to 8.5% M_b (mean=3.7±0.3%) and varied among meals for individual lionfish. As in the single feeding experiment, individuals varied in metabolic phenotype, with a 1.5-fold variation in SMR and a two-fold variation in scope for activity. Food intake did not significantly vary with SMR or scope for activity.

Food intake had no relationship to how much of an individual's scope for activity was being occupied by residual SDA from the previous meal at the time of feeding (Fig. 4D), nor the previous meal's size, SDA integral or the interval between meals (Fig. 4A–C). SDA$_{peak}$ of repeated meals significantly increased with meal size (P<0.001), shorter intervals between meals (P=0.02) and larger scope for activity (P<0.001), and was not significantly affected by SMR, previous meal size or the SDA integral of the previous meal (Fig. 4E–G).

Frequent feeding versus single feeding

Feeding frequency significantly affected SDA (P<0.001) and was 15% lower for frequent feeding (mean=823.5±34.2 mg kg^{-1} h^{-1} % $M_b$$^{-1}$) than for one feeding (mean=972.8±130.7 mg kg^{-1} h^{-1} % $M_b$$^{-1}$) when divided by meal size to control for its positive effect (P<0.001) (Fig. 4H). There was also higher variability of SDA in the single feeding treatment (s.d.=3150 mg kg^{-1} h^{-1}) versus the repeated feeding treatment (s.d.=2641 mg kg^{-1} h^{-1}) (Fig. 4H). Consistent with the single feeding experiment, SDA significantly varied with SMR (P=0.01) and varied with scope for activity, but not significantly (P=0.06), decreasing with SMR and increasing with scope for activity when divided by meal size to control for its effect (Fig. 3A–C). SDA$_{coeff}$ across repeated meals was not significantly affected by meal size (Fig. 3E–G). Heterogeneity of variance in SDA$_{coeff}$ between single and repeated meals precluded the use of an ANCOVA model, so it was assessed qualitatively. SDA$_{coeff}$ of repeated meals (mean=10.1±0.34%) was 36% lower than that of single meals (mean=15.8±2.7%), and SDA$_{coeff}$ of single meals had much higher variability (s.d.=9.7%) than that of repeated meals (s.d.=1.1%) (Fig. 4I).

DISCUSSION

We found several lines of evidence that lionfish have physiological traits that could facilitate their invasiveness, and that they may be robust to warming temperatures from climate change owing to both their energetic and digestive physiologies. These can be broadly categorized into: (1) the relationship between SDA, energetic physiology and feeding behavior, (2) the effects of temperature, (3) the effects of metabolic phenotype and (4) the effects of feeding frequency.

SDA, energetic physiology and feeding behavior

We found that lionfish have a physiology that prioritizes feeding over movement to a greater extent than that described in most other fish species to date. MMR is attained during exhaustive exercise in most fish species and not during digestion (Norin and Clark, 2016). However, in the present study, we observed lionfish routinely attain higher metabolic rates during SDA following voluntary feeding than from exhaustive exercise, with SDA$_{peak}$ exceeding AMR by as much as 1.7 times for large meals at 32°C. Furthermore, the amount of prey a lionfish consumed was independent of how much of its scope for activity was occupied by residual postprandial metabolic rate from its previous meal, whether its scope for activity was exceeded, or how large or recent that previous meal was. In addition, the SDA we observed of even the smallest meals (<2.5% M_b) occupied at least 64% of scope for activity at 26°C and at least 80% at 32°C. Together, these findings suggest that the lionfish's

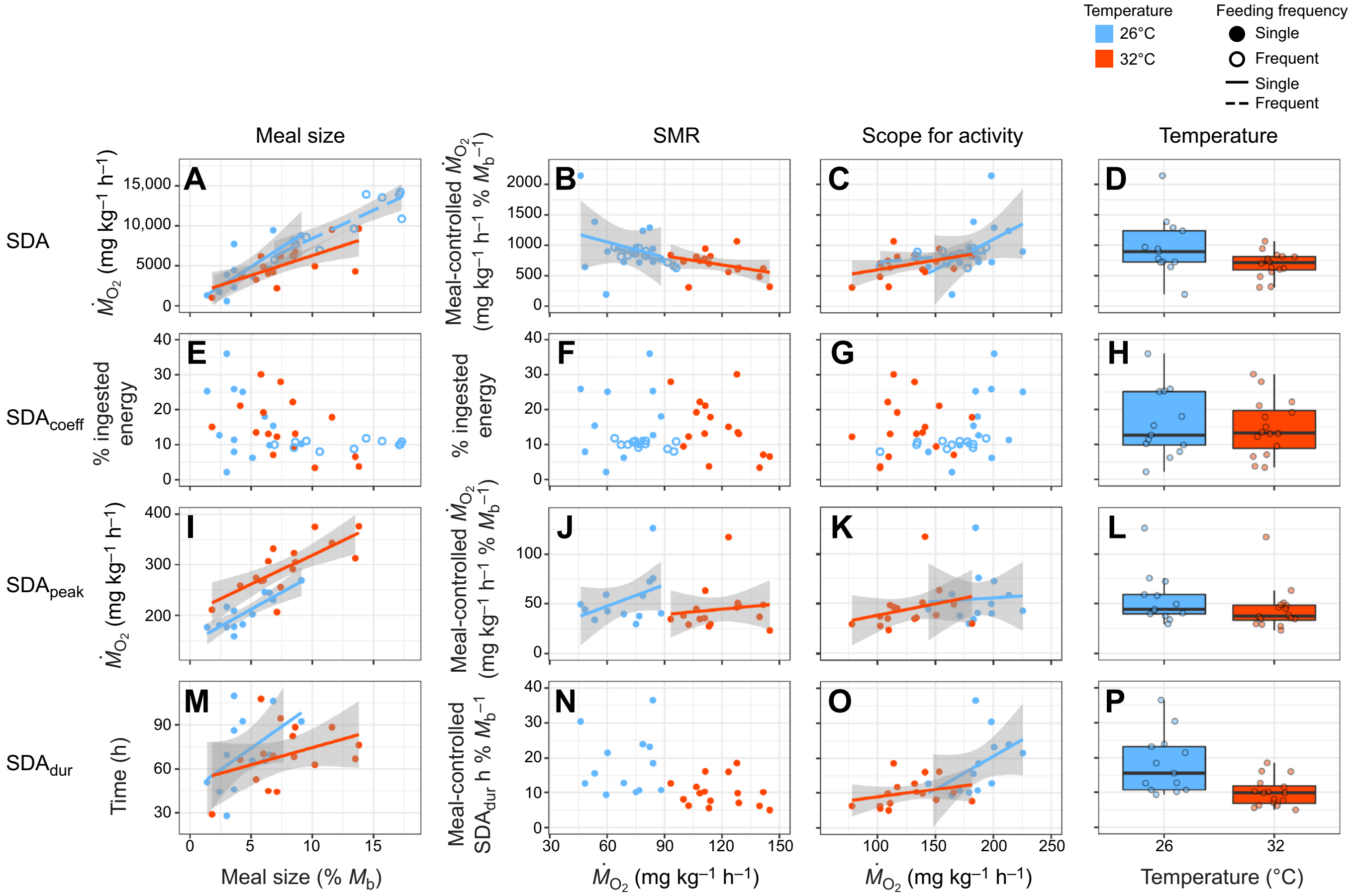

Fig. 3. Effects of temperature, meal size, SMR and scope for activity on SDA parameters. Relationships between (A–D) SDA and (A) meal size, (B) standard metabolic rate (SMR), (C) scope for activity and (D) temperature; (E–H) SDA coefficient (SDA$_{coeff}$) and (E) meal size, (F) SMR, (G) scope for activity and (H) temperature; (I–L) SDA$_{peak}$ and (I) meal size, (J) SMR, (K) scope for activity and (L) temperature; and (M–P) SDA duration (SDA$_{dur}$) and (M) meal size, (N) SMR, (O) scope for activity and (P) temperature in both single feeding (solid points and trendlines) and repeated feeding (empty points and dashed trendlines) experiments. Values derived from metabolic rate mass-adjusted to a 140 g fish (b=0.835). n=13 and n=16 for 26°C and 32°C, respectively, and n=13 for the repeated feeding treatment. Trendlines with 95% CI are included for significant relationships. Boxplots depict median (black bar), first and third quartiles (box hinges), and 1.5 interquartile range (whiskers). SDA, peak SDA (SDA$_{peak}$) and SDA$_{coeff}$ are $\dot{M}_{O_2}$ values (mg kg^{-1} h^{-1}). Data for SDA, SDA$_{peak}$ and SDA$_{dur}$ in response to SMR (B,J,N), scope for activity (C,K,O) and temperature (D,L,P) are divided by meal size to control for its effect. Meal size is measured as a percentage of body mass (%M_b). Scope for activity is the difference between active metabolic rate (AMR) and SMR in an individual lionfish.

defensive venomous spines may allow them to feed without a clear metabolic trade-off to the locomotory capacity that most other species need to preserve to avoid predators or continue moving during digestion (Millidine et al., 2009; Norin and Clark, 2017). Lionfish may retain some locomotory capacity during SDA despite exceeding the AMR we recorded, as AMR has been shown to increase in fed versus unfed fish up to 14% in European seabass (*Dicentrarchus labrax*), 23% in common carp (*Cyprinus carpio*) and 26% in southern catfish (*S. meridionalis*) (Dupont-Prinet et al., 2009; Jourdan-Pineau et al., 2009; Pang et al., 2010; Zhang et al., 2012); however, feeding has been found to have no effect on AMR in rainbow trout (*Oncorhynchus mykiss*), Chinook salmon (*Oncorhynchus tshawytscha*), goldfish (*Carassius auratus*) or qinbo (*Spinibarbus sinensis*) (Alsop and Wood, 1997; Thorarensen and Farrell, 2006; Zhang et al., 2012). As AMR was measured in fasted lionfish, we may be underestimating the meal sizes at which SDA fully occupies their scope for activity; however, their scope for activity would likely still be very small or nonexistent when digesting medium or large meals. Regardless, this lack of a clear metabolic trade-off between digestion and locomotory capacity would underpin the lionfish's high feeding rates and ability to assimilate excess energy for the rapid growth, reproduction and dispersal that fuels their invasion (Côté and Maljković, 2010; Green et al., 2011; Côté et al., 2013), and may be considered one of several traits that have made lionfish such a successful and impactful invader.

Furthermore, the readiness at which lionfish eat meals that exceed their scope for activity seems to be driven by the ability to eat exceptionally large meals, as opposed to an exceptionally low AMR or high SMR. Lionfish exhibited an SMR and AMR comparable to those of another coral reef predator at a similar temperature, leopard coral grouper (*Plectropomus leopardus*) (Messmer et al., 2017), as well as a decline in factorial aerobic scope (the proportional difference between SMR and MMR or AMR) with increasing temperature almost identical to that of another sedentary predator, shorthorn sculpin (*Myoxocephalus scorpius*) (Sandblom et al., 2014). As such, lionfish appear to readily exceed their scope for activity during SDA because they eat very large meals, suggesting this phenomenon could occur in other species with a similar scope for activity that also eat large meals. For example, Sandblom et al. (2014) found that a 5% M_b meal occupied most of the scope for activity in *M. scorpius*; however, this species has been observed to

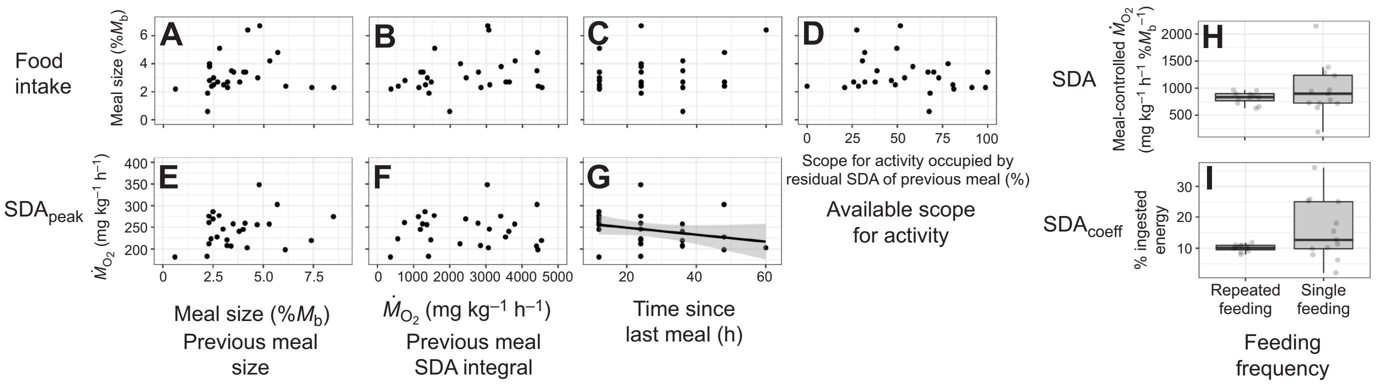

Fig. 4. Results from the repeated feeding experiment. Relationships between SDA, food intake and variables used in the repeated feeding experiment (A–D, F–H; *n*=13), as well as the relationship between SDA, SDA$_{coeff}$ and feeding frequency (E,I). *n*=13 for the repeated feeding and the single feeding treatments. Trendlines with 95% CI are included for significant relationships. Boxplots depict median (black bar), first and third quartiles (box hinges), and 1.5 interquartile range (whiskers). SDA, peak SDA (SDA$_{peak}$) and SDA$_{coeff}$ are $\dot{M}_{O_2}$ values (mg kg^{-1} h^{-1}). Data for SDA in response to temperature (E) are divided by meal size to control for its effect. Meal size is measured as a percentage of body mass (%M_b). Previous meal residual SDA is the percentage of scope for activity occupied by SDA at the time of a repeated meal.

voluntarily eat meals up to 12.7% M_b at a similar temperature (Johnston and Battram, 1993), suggesting that SDA in *M. scorpius* may exceed scope for activity to an extent similar to what we observed in lionfish.

As far as we are aware, this is the first study to experimentally test the role of the trade-off between SDA and aerobic scope or scope for activity in a fish species' feeding behavior and food intake. Contrary to what we hypothesized, lionfish did not mediate their food intake based on the occupation of SDA in their scope for activity or its exceedance of AMR. Lionfish foraging may instead be constrained by their MMR, equivalent to the SDA$_{peak}$ of the largest possible consumable meal. The largest observed meal in this study may have approached this at 13.8% M_b, which produced an SDA$_{peak}$ 1.7 times greater than that fish's scope for activity. However, observations of wild lionfish suggest that they forage below such a hypothetical limit. Green et al. (2011) observed an 8.9% M_b day^{-1} consumption rate at 26°C in wild lionfish in The Bahamas, which was spread across smaller meals during morning and evening crepuscular hours. Based on our model results, a single 8.9% M_b meal would produce an SDA$_{peak}$ only marginally above the average AMR we observed at 26°C, and far below a hypothetical MMR from maximal feeding (Fig. 2). As such, a higher foraging rate would be expected in wild lionfish, suggesting that factors other than metabolic constraints mediate their foraging. Identifying these would be necessary to fully understand how climate change and a changing ocean environment are affecting the lionfish invasion (Côté and Smith, 2018; Green et al., 2019).

Temperature

Our results showed that invasive lionfish digest meals more efficiently and rapidly at 32°C than at 26°C, suggesting that they may benefit from some ocean warming by virtue of their digestive physiology. SDA was 29.6% lower at 32°C than at 26°C when divided by meal size to correct for its effect. This decline in SDA was reflected in a 7% decrease in SDA$_{coeff}$ and a 45% decrease in SDA$_{dur}$ as well. In addition, SDA$_{coeff}$ did not differ with meal size, suggesting that the decrease in SDA, SDA$_{coeff}$ and SDA$_{dur}$ was not due to the increased food intake in the 32°C treatment. Although the underlying mechanisms of SDA are not fully understood, a majority of it has been attributed to cellular-level protein handling, which may have been more efficient at 32°C than at 26°C. A thermal optimum for protein handling has been proposed as an explanation for temperature-dependent SDA in fish, which may underpin temperature dependency in growth, aerobic scope and other physiological processes (Pannevis and Houlihan, 1992; Eliason et al., 2008; Tirsgaard et al., 2015). Lower SDA could also correspond to a lower apparent digestibility coefficient (ADC; or the percentage of prey energy assimilated versus excreted); however, ADC increases with temperature owing to enhanced enzymatic activity in the gut, suggesting that our observed decline in SDA reflects improved digestive efficiency (Hardewig and Van Dijk, 2003; Kofuji et al., 2005). Altogether, the reduced cost and duration of digestion observed in this study will likely benefit lionfish in warming ocean temperatures by allowing them to feed more frequently and allow more energy for growth, reproduction and dispersal. However, such a decrease in SDA at high temperatures may not necessarily be unique to lionfish, as research on warm-water fish species' SDA near their upper thermal limits remains sparse. Nevertheless, invasive lionfish may stand to benefit from such a decrease in SDA more than native species, given their advantages of having naïve prey, a lack of natural predators, and unique hunting traits (Côté and Smith, 2018; Green et al., 2019) and our aforementioned finding that they prioritize feeding over movement and predator avoidance to a greater extent than that described in any other species studied to date (Norin and Clark, 2016).

Relative SDA$_{peak}$ was correspondingly lower at 32°C than at 26°C (that is, SDA$_{peak}$ divided by meal size to control for its effect); however, it occupied the entirety of scope for activity in most fish at 32°C owing to a 32% decrease in scope for activity from 26°C. So although higher temperatures give lionfish lower SDA, they will simultaneously limit locomotory capacity during digestion. For example, a meal size of 4.2% M_b would fully occupy the scope for activity of an average lionfish at 32°C but leave 21% of its scope for activity free at 26°C for other energetic processes (Fig. 2), a trend similar to that observed by Sandblom et al. (2014) in shorthorn sculpin (*M. scorpius*). This trade-off is less likely to affect lionfish performance or fitness compared with other species (Norin and Clark, 2017), as we found that they feed independently of how much their scope for activity is occupied by their previous meal, as discussed above.

Although scope for activity decreased between 26°C and 32°C, we observed a higher range between SMR and SDA$_{peak}$ of the largest meal at 32°C, suggesting that aerobic scope increased from 26°C to 32°C. If so, lionfish would be robust performers in temperatures that are only a few degrees below their previously reported average thermal maximum of 35–36°C (Barker et al., 2017; Dabruzzi et al., 2017). They could hypothetically consume more prey at temperature increases projected for their invaded range in this case (Bernal et al., 2015), consistent with our observed 42% increase in average food intake from 26°C to 32°C. Cerino et al. (2013) reported the opposite in invasive lionfish, with a decrease in food intake between 29°C and 32°C; however, they used only half the sample size of our 32°C treatment and reported considerable variability in it as well. This suggests that prey consumption increases up to higher temperatures than was previously thought in lionfish, and that subsequent ecosystem models based on the food intake reported in Cerino et al. (2013) may be an underestimation of the impact invasive lionfish have at these temperatures (Bernal et al., 2015; Chagaris et al., 2017; Sancho et al., 2018). Further research is warranted to determine aerobic scope in lionfish across a broader temperature range and up to their thermal maximum to establish a thermal performance curve that would improve predictions of how their invasion will be affected by ocean warming (Jensen et al., 2017).

Metabolic phenotype

In addition to temperature, we found an effect of metabolic phenotype on SDA. Lionfish appear to face a trade-off between SMR and SDA, with higher SMR phenotypes having lower SDA with higher $\mathrm{SDA_{peak}}$ and shorter $\mathrm{SDA_{dur}}$. This is somewhat consistent with the findings of Millidine et al. (2009), where juvenile Atlantic salmon (*S. salar*) with higher SMR had higher $\mathrm{SDA_{peak}}$ and shorter $\mathrm{SDA_{dur}}$; however, they also found that higher SMR phenotypes had a costlier SDA, whereas we found the opposite. This suggests that $\mathrm{SDA_{peak}}$ and $\mathrm{SDA_{dur}}$ may vary with SMR independently of SDA, but why SMR would act on these traits differently is unclear. Individual variations in SMR may be due to individual differences in relative organ size as found by Boldsen et al. (2013) in European eel (*Anguilla anguilla*), where individuals with larger intestines and livers had higher SMR, likely due to the energetic demands of these larger organs. This may explain why lionfish with high SMR phenotypes appear to digest meals more efficiently, rapidly and with a higher $\mathrm{SDA_{peak}}$; however, such a relationship was found lacking by Norin and Malte (2011) in brown trout (*Salmo trutta*). Instead, they found that individual variation in SMR was explained by individual differences in enzyme activity in the liver, which, if consistent in gastrointestinal organs, could also explain the relationship between SMR and SDA we observed. Both processes may explain the differing effects of SMR on the cost of SDA versus its $\mathrm{SDA_{dur}}$ and $\mathrm{SDA_{peak}}$ observed between lionfish in the present study and *S. salar* in Millidine et al. (2009), and further research is warranted to explore such questions.

We also observed a relationship between scope for activity and SDA, which to our knowledge has not been assessed in fish previously. As with SMR, lionfish appear to face a trade-off between scope for activity and SDA, with lower scope for activity phenotypes having a less costly SDA, shorter $\mathrm{SDA_{dur}}$ and a smaller $\mathrm{SDA_{peak}}$. Our finding that scope for activity did not vary with SMR but significantly increased with AMR suggests that this relationship may have different mechanistic causes than that of SMR. It is possible that AMR is limited either by oxygen delivery by the cardiorespiratory system or by the maximum capacity of the mitochondrial electron transport system to utilize oxygen to produce ATP, traits that can vary among individuals (Metcalfe et al., 2016; Norin and Clark, 2016). One possibility is that inter-individual differences in relative organ sizes or enzyme activities may manifest in performance trade-offs between organ systems (Boldsen et al., 2013; Norin and Malte, 2011; Metcalfe et al., 2016), where lionfish with low scope for activity owing to limited cardiac performance invest more in gastrointestinal organ mass and performance.

Regardless of its determinants, the finding that lionfish express intraspecific variation in metabolic phenotype and that it affects SDA could have important ecological implications. Intraspecific variation in SMR is thought to give fish populations persistence under varying food availability, as lower-SMR individuals with lower energetic demands can weather periods of low food availability, while higher-SMR individuals can capitalize on periods of high food availability to grow and reproduce more quickly (Van Leeuwen et al., 2012; Metcalfe et al., 2016). Our finding that individuals with low-SMR phenotypes face up to a 33% greater energetic burden from SDA and an almost 8 h longer digestive period may counter such an effect. Less is known about the ecological implications of intraspecific variation in MMR, or in our case, AMR (Metcalfe et al., 2016). Having a two-fold phenotypic variation in scope for activity seems at odds with the sedentary nature of lionfish; however, invasive lionfish were recently discovered to engage in long, energetically demanding agonistic interactions that likely determine dominance hierarchies (Fogg and Faletti, 2018). Little is known about this behavior, but it suggests that lionfish may sometimes compete for territory and access to prey. Lionfish with a low AMR, low scope for activity and low-cost SDA would benefit from high prey densities that are typical of their invaded range and would not require them to compete interspecifically (Chappell and Smith, 2016; Hixon et al., 2016). When prey are more scarce, lionfish with a high AMR and high scope for activity may be better competitors and more able to secure access to prey that would offset their more costly SDA and longer $\mathrm{SDA_{dur}}$, which we found to be up to 46% higher and almost 24 h longer than in individuals with low scope for activity, respectively. As such, metabolic phenotypes may confer resilience to the lionfish invasion, particularly in light of past research showing they can cause local collapses in their prey populations and, therefore, variability in food availability (Green et al., 2012; Benkwitt, 2015; Ingeman, 2016; South et al., 2017).

Feeding frequency

Along with temperature and metabolic phenotype, we found an effect of feeding frequency on SDA that may manifest in ecologically relevant ways. Feeding frequently was less costly than feeding singularly, differing from the findings of Ross et al. (1992) and Guinea and Fernandez (1997) in Nile tilapia (*O. iuloticus*) and gilt-head sea bream (*S. aurata*), respectively. These studies used meal sizes of 1% M_b or less, which is below the 3.7% M_b average and 8.5% M_b maximum of this experiment, which may explain this difference. Although little work has been done on this subject in fish, gut activity has been found to affect the cost of digestion in other ectotherms such as lizards and snakes (Iglesias et al., 2003; Secor, 2009), so the difference we observed may not manifest until meal sizes larger than those in Ross et al. (1992) and Guinea and Fernandez (1997) are used. In addition, we found that the cost of frequent feeding was more consistent than that of feeding singularly, possibly because of differing downregulation of gut function during the 72 h fast before SDA was recorded. The time required to downregulate gut function varies widely among fish species, but in some such as the brown surgeonfish (*Acanthurus nigrofuscus*), gut length can decrease by as much 46.7% in as little as 60 h (Montgomery and Pollak, 1988). Given that lionfish can consume large meals and survive for at least 3 months without feeding, they may be adapted to regulate their gut rapidly and widely (Fishelson, 1997; Secor, 2001; Zaldúa and Naya, 2014; Côté and Smith, 2018). This consistency has likely selected for frequent feeding in lionfish and concords with the high foraging rates observed in their invasive population (Côté and Maljković, 2010; Green et al., 2011). Despite its lower and more consistent cost, frequent feeding posed a trade-off to maintaining a scope for activity, as $\mathrm{SDA_{peak}}$ increased with shorter intervals from the previous meal. Norin and Clark (2017) found that such a trade-off limited foraging in a way that was not optimal for energy assimilation and growth in barramundi (*Lates calcarifer*), suggesting that frequent feeding may compound such an effect. Although this is unlikely to affect lionfish because they readily exceed their scope for activity during feeding and digestion, as discussed above, it illustrates the importance of energetic physiology in mediating feeding behavior and ecology in fish (Auer et al., 2015a, 2015b; Norin and Clark, 2017).

Conclusions

In conclusion, we found physiological traits that would benefit lionfish as an invasive species and, as with past studies' findings, may partially explain how they have become successful invaders (Wilcox et al., 2018; Côté and Smith, 2018). Lionfish may be robust to and possibly benefit from some ocean warming by virtue of their digestive physiology, which concords with past physiological studies on lionfish (Cerino et al., 2013; Bernal et al., 2015; Dabruzzi et al., 2017) and other invasive species (Kelley, 2014; Marras et al., 2015). Population and ecosystem models should use physiological characteristics and their relationship to environmental variables to predict how invasive species such as lionfish impact native ecosystems; however, some assumptions in such models are based on limited knowledge of species' physiology (Lennox et al., 2015). For example, an early bioenergetic model developed for lionfish (Cerino et al., 2013) that has subsequently been incorporated into ecosystem models of its invasion (Bernal et al., 2015; Chagaris et al., 2017; Sancho et al., 2018) used an assumed $\mathrm{SDA_{coeff}}$ that was almost double what we found in lionfish that fed frequently, and reported a lower temperature-specific prey consumption rate than what we found in this study, which may have led these models to underestimate the prey consumption and ecological impact of invasive lionfish. In addition, we found that lionfish express inter-individual variability in metabolic phenotype and that this affects their SDA, which likely influences their behavior and ecology (Van Leeuwen et al., 2012; Auer et al., 2015a; Metcalfe et al., 2016) and presents another potential shortcoming of invasive lionfish ecosystem models to date. The findings of this empirical experimental study and others like it may therefore improve such models, but further research is necessary to determine whether thermal plasticity affects the magnitude of our observed temperature effect, as well as to fully develop thermal performance curves for lionfish (Sandblom et al., 2014; Auer et al., 2016; Jensen et al., 2017).

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: S.S., T.E.V., S.J.C., E.J.E.; Methodology: S.S., T.E.V., J.W.B., S.J.C., E.J.E.; Software: S.S., J.W.B.; Formal analysis: S.S., J.W.B.; Investigation: S.S.; Resources: T.E.V., S.J.C., E.J.E.; Data curation: S.S.; Writing - original draft: S.S.; Writing - review & editing: S.S., T.E.V., S.J.C., E.J.E.; Visualization: S.S.; Supervision: T.E.V., S.J.C., E.J.E.; Project administration: S.J.C., E.J.E.; Funding acquisition: S.J.C., E.J.E.

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Supplementary information

Supplementary information available online at http://jeb.biologists.org/lookup/doi/10.1242/jeb.209437.supplemental

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