Resident lobsters dominate food competition with range-shifting lobsters in an ocean warming hotspot

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ABSTRACT: Species redistributions are one of the most prevalent changes observed in oceans worldwide due to climate change. One of the major challenges is being able to predict temperature-driven changes to species interactions and the outcome of these changes for marine communities due to the complex nature of indirect effects. In the ocean-warming hotspot of southeast Australia, the ranges of many species have shifted poleward. The range of the eastern rock lobster *Sagmariasus verreauxi* has extended into warming Tasmanian waters inhabited by the resident southern rock lobster *Jasus edwardsii*, which may lead to increased competitive interactions between the species. Using video monitoring, we investigated how the 2 species compete for food at current (18°C), future (21°C) and future heatwave (24°C) summer temperatures. Behavioural competition occurred in 80% of experiments, during which *J. edwardsii* won 84% of competitive interactions and showed more aggressive behaviour at all temperatures. This indicates that resident *J. edwardsii* is not only more dominant in direct food competition than the range-shifting *S. verreauxi* but, surprisingly, also sustains competitive dominance beyond its physiological thermal optimum under predicted future ocean warming and heatwave scenarios.

KEY WORDS: Climate change ecology · Interspecific competition · Novel species interactions · Range shifts · Spiny lobsters · Thermal performance

1. INTRODUCTION

Anthropogenic climate change alters abiotic and biotic environmental conditions at rapid rates, with far-ranging effects on marine ecosystems worldwide (Doney et al. 2012), particularly warming-driven alterations to species geographical ranges, or 'range shifts' (Parmesan & Yohe 2003, Poloczanska et al. 2013, Pecl et al. 2017, Pinsky et al. 2020). While warming can directly affect individual species performances, it may also have indirect effects through changes in species interactions (e.g. through changes in abundance; Kordas et al. 2011). Species interactions are critical to the structure and functioning of marine ecosystems; however, range shifts may alter these interactions and substantially change marine ecosystems now and in the future (Winder & Schindler 2004, Kordas et al. 2011, Milazzo et al. 2013).

Species interactions, particularly between competitors, may change with future ocean warming, either directly due to changes in individual species performance or abundance (Milazzo et al. 2013,

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Kroeker & Sanford 2022) or indirectly through the emergence of novel interactions with range-shifting species (Kordas et al. 2011, Dell et al. 2014). For example, temperate reef fish become more aggressive in the face of novel range-shifting tropical fish species (Coni et al. 2021). Predicting changes to species interactions and their potential subsequent influences on marine communities is one of the 'known unknowns' of climate change ecology (Lord et al. 2017). This is largely because the indirect effects (e.g. competitive release of species) resulting from changes to species interactions are complex, spatially variable and often difficult to predict and have hence not been as readily studied as the direct effects (e.g. physiological changes; Lord et al. 2017).

The outcomes of competitive interactions can depend on a wide range of factors, and hence many performance measures could be used to predict competitive strength or ability (Twiname et al. 2020a). Physiological parameters, such as aerobic scope, have been shown to predict competitive ability and outcomes of interspecific interactions (Kroeker & Sanford 2022), such as for Arctic sculpins (Seth et al. 2013) or tropical damselfish (Killen et al. 2014). In crustaceans, besides physiology (Seebacher & Wilson 2006), size can be a major factor in establishing interspecific competitive dominance. For instance, during competitive trials, only large American lobsters *Homarus americanus* outcompeted the invasive green crab *Carcinus maenas* for food resources, while small and medium-sized lobsters were unable to dominate and spent more time seeking shelter (Williams et al. 2009). Aggression is another factor that can influence the outcome of competitive interactions. In studies with hermit crabs or freshwater crayfish competing for food or shelter, those individuals that were more aggressive were more likely to obtain the contested resource (Usio et al. 2001, Tran et al. 2014, Greggor & Laidre 2016). Similarly, in fish, local snapper species in the Gulf of Mexico have been shown to become more aggressive in the presence of range-shifting conspecifics (Marshak & Heck 2017). The diversity of factors affecting competitive outcomes underlines the complex nature of species interactions and the difficulty in forecasting species redistributions; however, examining multiple measures will improve insight into these interactions.

In south-east Australia, the ranges of dozens of marine species have extended poleward in response to ocean warming (Pitt et al. 2010, Last et al. 2011, Robinson et al. 2015, Sunday et al. 2015, Gervais et al. 2021). One of these is the eastern rock lobster *Sagmariasus verreauxi* (Pecl et al. 2009, Robinson et

al. 2015), a species common in the waters of New South Wales, inhabiting a temperature range of approximately 14.5–21.5°C (Holthuis 1991, Reef Life Survey 2019b). This largest species of spiny lobster is currently increasing in abundance in areas historically dominated by the more commercially important southern rock lobster *Jasus edwardsii* (Robinson et al. 2015), specifically in Tasmania, where *J. edwardsii* inhabits a temperature range of approximately 9–21°C (Holthuis 1991, Reef Life Survey 2019a). How these 2 species interact currently and under future ocean warming is unknown, though it is likely that both will experience direct or indirect competition due to similar resource requirements (Booth 2006, Byrne & Andrew 2013, Jeffs et al. 2013). Competition between spiny lobsters has been observed where shelter is limited or of insufficient quality (Eggleston et al. 1990, Briones-Fourzán et al. 2007). Resource competition between spiny lobsters will be further enhanced in degraded reef habitats, such as coral reefs following bleaching (Sabino et al. 2021). Such habitat degradation is particularly problematic in Tasmanian waters, where ocean warming and the arrival of the range-extending destructive long-spined sea urchin *Centrostephanus rodgersii* has converted formerly rich underwater kelp forests to impoverished barren habitats (Johnson et al. 2005, Ling et al. 2015). This degraded habitat has already led to a decrease in spiny lobster and abalone density (Johnson et al. 2005). With novel species such as *S. verreauxi* extending into Tasmanian waters, competition for increasingly scarce resources will likely increase further. Increasing abundance of *S. verreauxi* may pose potential risks to the more valuable fishery (Plagányi et al. 2018) and ecosystem (Ling & Johnson 2012) role played by *J. edwardsii*. Thus, we need to understand present and future species interactions in order to support adaptive management of fisheries and ecosystems.

The aim of this study was to investigate competition for food between the 2 lobster species — the resident *J. edwardsii* and the range-shifting *S. verreauxi* — under current and future temperature scenarios. It was hypothesized that the individual species' competitive abilities would match the physiological thermal tolerance windows previously investigated for these species (Twiname et al. 2020b). Specifically, we expected each species to compete more successfully within a temperature range where their respective physiological performance derived from aerobic scope is highest; i.e. ~19–22°C for *J. edwardsii* and ~23–27°C for *S. verreauxi* (puerulus and juvenile aerobic scope measurements; Twiname et al. 2020b).

2. MATERIALS AND METHODS

Competitive interaction trials for food were conducted at 3 temperature treatments that encompass current summer (18°C), future summer (21°C) and future summer heatwave (24°C) ocean temperatures off eastern Tasmania (Pecl et al. 2009, Oliver et al. 2017, Oellermann et al. 2022). The trials were between 18 approximately size-matched (within 5 mm of total length) individuals of *Jasus edwardsii* and *Sagmariasus verreauxi*. Seven paired trials were run at 18°C, 6 at 21°C and 5 at 24°C. Each paired trial involved 3 repeated feeding experiments over 3 d. No lobster pairs were re-used beyond their 3 d feeding trial; i.e. pairs were not used for different temperature treatments. Different sample sizes between temperature treatments were due to the exclusion of individuals that moulted immediately before, after or during competitive trials, which critically affects their behaviour and overall performance. Competitive interactions were filmed when a food item was introduced to the tank and scored for the number of aggressive and submissive behaviours exhibited by both species, as well as the 'winner' of the interaction (individual that consumed the food).

2.1. Animal collection and holding

Adult *J. edwardsii* (n = 18; mean ± SD total length: 298.85 ± 11.95 mm) were collected in February 2017 using baited lobster pots in the Crayfish Point Scientific Reserve (42.95° S, 147.35° E), south-eastern Tasmania. Sub-adult *S. verreauxi* were purchased from commercial rock lobster fishers operating along the east coast of Tasmania from February to April 2017 (n = 18; total length: 304.17 ± 15.87 mm). All lobsters were transported live to the Institute of Marine and Antarctic Studies (IMAS) aquaculture facility and held in 5000 l coated glass fibre tanks supplied with flow-through raw seawater (salinity: 35 PSU). The 2 species were kept in separate tanks to limit any interaction prior to experimentation. Each individual was tagged ventrally behind the fifth pair of pereiopods using a unique identification number T-bar tag (to prevent the tag being shed upon moulting) as well as a larger identification number glued (Loctite 454; Henkel) onto the carapace for easy identification in the tanks and to reduce possible subsequent handling stress to the lobsters. Of the 18 individuals of each species, 10 were female and 8 were male. For *J. edwardsii*, 6 of the 10 females carried eggs. Due to biological differences between the species (*J. edwardsii*

growing to smaller overall sizes, and hence smaller sizes at maturity), no *S. verreauxi* of similar size were egg-bearing.

Before adding lobsters to the tanks, we recorded carapace length, width, total length, mass and the number of missing appendages (antennae and legs). The lobsters were fed 2–3 times wk^{-1} to excess with fresh or thawed blue mussels *Mytilus galloprovincialis* and/or thawed squid *Loligo* sp. tentacles. Prior to the competitive trials, similar-sized pairs (within 5 mm of total length) of *J. edwardsii* and *S. verreauxi* were selected. Pairs of the same sex were selected using total length and weight and were matched where possible in terms of missing appendages to eliminate any effect these losses may have had on behaviour.

2.2. Acclimation

Four matched lobster pairs were transferred into two 200 l (800 mm diameter, 400 mm deep) round acclimation tanks, species separated, until the competition trials commenced to make sure no dominance structures between paired individuals were developed before trials. The separated acclimation and competition tanks were the same size to avoid any potential behavioural changes when moving lobsters from the acclimation period to the competition phase. Tanks were supplied with flow-through filtered seawater at approximately 3 exchanges h^{-1}, an air stone and a submersible 2000 W heater (Istra Elements & Engineering) to adjust and maintain tank temperatures at the trial temperatures. Two large concrete hides with enough space for all individuals were placed on opposite sides of the tank to provide shelter. A maximum of 4 same-species individuals were acclimated at the same time in each acclimation tank and were fed with fresh or thawed blue mussels in excess every day in the afternoon. Any uneaten food was removed daily to prevent fouling of the water. Temperatures were increased by 1°C d^{-1} from ambient conditions (~11–14°C) until the trial temperature was achieved. The lobsters were left for 7 d to acclimate to this temperature. Before the start of competition trials, the lobsters were fasted for a period of 72 h (deemed a suitable time from pilot fasting trials for the lobsters to be hungry enough to approach the food source) to ensure that the lobsters would search for food during the trials. This acclimation period included a change from ambient light regimes to a 12 h light:12 h dark (red light) regime, as was implemented in the competition trials.

2.3. Competition trials

Competition trials were conducted in 20 l (800 mm diameter, 400 mm deep) tanks supplied with flow-through filtered seawater (approx. 3 exchanges h^{-1}), an air stone and 2 concrete hides placed on either side of the tank. During the experimental trials, a 12 h light:12 h dark (red light) regime was simulated, and the feeding competition trials were undertaken during the dark period. From the acclimation tanks, the size-matched pairs of *J. edwardsii* and *S. verreauxi* were introduced into 4 separate competition tanks 24 h before feeding trials began to allow them to acclimate to their new environment. No food was provided during this 24 h period. After this 24 h, one half-shell mussel was placed into the tank, at a similar distance from the 2 lobsters. The trial was then filmed for 1 h followed by removal of the mussel shell (when eaten) or the uneaten mussel. Competition feeding trials were repeated every 24 h for 72 h, resulting in 3 repeated feeding trials for each pair of lobsters. No other feeding was implemented during the trials. Competition trials were conducted in the late afternoon under red light, simulating dark conditions, as lobsters generally forage at night (Childress & Jury 2006). The air stones were removed during competition trial filming to eliminate associated water-surface disturbance, which impeded effective lobster observations. Air stones were re-introduced immediately after the trials, and the tanks received constant water flow throughout the trial to maintain oxygen levels above 90% saturation.

The trials were filmed using video cameras (GoPro Hero5) suspended directly above the tanks to view the whole tank. Video footage of the competitive interactions was viewed and different behaviours recorded, including (1) who 'won' the interaction (secured and ate the mussel), (2) how long the food item was handled (once the mussel was secured to when it was completely eaten and the empty shell discarded), (3) the number of aggressive and submissive behaviours exhibited by the pair of competitors and (4) the level of activity exhibited by both individuals (see Table 1 for descriptions). Activity level was scored from 0–4; scoring was determined by how much movement each lobster exhibited, as defined in Table 1.

2.4. Data analysis

All statistical analyses were performed in the R statistical program (R Core Team 2017). From the 18 pairs of lobsters, a total of 54 successful trials were conducted over the 3 temperature treatments. Nine trials (3 lobster pairs) were excluded due to individuals moulting immediately before, during or immediately after completion of experiments. Data was tested for normality using a Shapiro-Wilk test and, due to all data being non-parametric, generalised linear mixed models (GLMMs) were used to analyse competition outcomes using the 'lme4' package (Bates et al. 2015) and the following model description:

$$\text{Response} = \text{Species} + \text{Temperature} + \text{Damage} + (1|\text{Number}) + (1|\text{Pair}) \quad (1)$$

This model was used for different responses, where 'response' is (1) the competition outcome winner,

Table 1. Descriptions of the winner of the trials, aggressive and submissive behaviours exhibited by *Jasus edwardsii* and *Sagmariasus verreauxi* during competition trials and level of activity scoring. Descriptions of aggressive and submissive behaviours are adapted from Carter et al. (2014) and Briones-Fourzán et al. (2015)

Behaviour	Description
Winner	The lobster that secured the food first and consumed it, or the lobster that fought for the food, secured it and consumed it. This was recorded as the species that 'won', *J. edwardsii* or *S. verreauxi*, or as 'neither' if neither species secured or consumed the mussel during the 1 h trial
Aggressive behaviours	
Approach	One lobster moves towards the other
Threat	One lobster flicks antennae or lifts legs in threat display towards the other
Physical contact	One lobster physically touches with legs or antennae, grabs or attacks the other
Submissive behaviours	
Retreat	One lobster moves away from the other in response to the other approaching
Escape	One lobster utilises a tail-flick response to escape the other
Activity level scoring	
0	No movement by lobster
1	Lobster active for 1–25% of the competition period
2	Lobster active for 26–50% of the competition period
3	Lobster active for 51–75% of the competition period
4	Lobster active for 76–100% of the competition period

(2) the number of aggressive and submissive behaviours, (3) the activity level and (4) food handling time. Species, temperature and pre-trial damage are the predictor variables. The number error term indicates the day number of food competition trials (the first, second or third day) and the pair error term identifies the specific lobster identification pairs, both of which account for the repeated measures aspect of the experiments. Model covariables (total length, sex and whether the females carried eggs) were removed from the model, as none showed significance and model fits assessed by Akaike's information criteria (AIC) were not improved with their inclusion. The model for assessing the number of wins used a binomial distribution, aggressive and submissive behaviours and activity level used a Poisson distribution, and food handling time used a gamma distribution. As R^2 values are not produced using the 'lme4' package, the 'jtools' package was used to calculate R^2 values for model comparison using the 'summ' function (Long 2020). Spearman rank correlation tests were used to examine the relationship between aggressive and submissive behaviours and the number of competition wins.

3. RESULTS

Jasus edwardsii won more food competition trials than *Sagmariasus verreauxi* at all temperatures tested (36 [67%] wins for *J. edwardsii* compared to 7 [13%] for *S. verreauxi*; GLMM, species p = 0.007; Fig. 1). There was one instance where the *S. verreauxi* individual reached the food first (at 24°C) but was then attacked by the *J. edwardsii* who proceeded to secure and consume the mussel. In this case, *J. edwardsii* was considered the winner of the competitive trial. For the few *S. verreauxi* that won food competition trials, there was no effect of temperature or difference in behaviour from those that did not win. There was also no effect of the trial day number (1, 2 or 3) on which species won the trial. The effect of pre-trial appendage damage was also significant for the winner of the food competition, where *S. verreauxi* had higher numbers of damaged appendages (59% of *S. verreauxi* had limb damage compared to only 28% of *J. edwardsii*; GLMM, damage p = 0.028). Using R^2 values to calculate model variation showed that 16% of the variation was explained by the 'damage' fixed effect. The effect of appendage damage was not significant for any other model outcome and did not improve model fit via AIC and was therefore dropped for all other GLMM
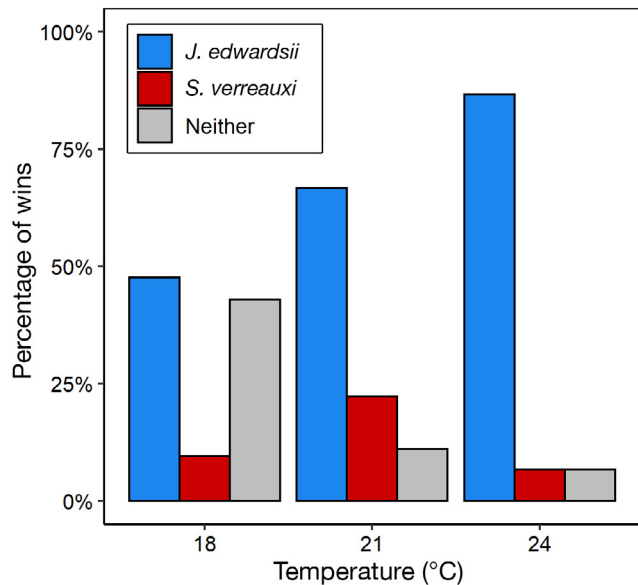

Fig. 1. Percentage of food competition wins (whereby the lobster secured and ate the mussel) by *Jasus edwardsii*, *Sagmariasus verreauxi*, or where neither lobster secured the mussel in paired competitive feed trials (at 18°C: n = 21, 7 lobster pairs; 21°C: n = 18, 6 lobster pairs; 24°C: n = 15, 5 lobster pairs) relative to temperature

analyses (aggressive and submissive behaviours, activity level or food handling time).

The species exhibited different levels of aggressive behaviours, where *J. edwardsii* exhibited more aggressive behaviours overall than *S. verreauxi* at all temperatures (*J. edwardsii*: 54 aggressive behaviours; *S. verreauxi*: 6; GLMM, species p < 0.001; Table 2, Fig. 2a). Conversely, *S. verreauxi* exhibited more submissive behaviours than *J. edwardsii* (*S. verreauxi*: 45; *J. edwardsii*: 3; GLMM, species p < 0.001; Table 2, Fig. 2b). Temperature did not significantly affect aggressive or submissive behaviour (Table 2). Results of 2 Spearman rank correlation tests showed a significant positive relationship between the number of wins and numbers of aggressive behaviours (r_S = 0.535, p = 0.001) and a significant negative relationship between the number of wins and number of submissive behaviours exhibited by individuals (r_S = −0.508, p = 0.002) for the species combined.

The relative number of different types of behaviours exhibited varied among species and temperature treatments (Table 3). There was a very high level of physical contact in the 21°C trials. This was a result of one *J. edwardsii* individual exhibiting higher levels of aggression than others (this can be seen in Fig. 2a, where there is an outlier of 11 aggressive behaviours at 21°C). This behaviour coincided with a high number of retreats by its paired *S. ver-*

Table 2. Generalized linear mixed model statistics of the effect of species (*Jasus edwardsii* and *Sagmariasus verreauxi*) and temperature on different behaviours observed during paired competitive food trials. Random effects account for the repeated measures in the trials. *p < 0.05

| Model	Random effects			Fixed effects				
	Factor	Variance	SD	Factor	Estimate	SE	t	Pr (>|z|)
Aggressive behaviours	Number	0.497	0.705	Species	−2.216	0.520	−4.262	<0.001*
	Pair	0.111	0.334	Temperature	0.153	0.093	1.642	0.101
Submissive behaviours	Number	0.000	0.000	Species	2.708	0.596	4.542	<0.001*
	Pair	0.512	0.715	Temperature	0.175	0.104	1.736	0.083
Activity level	Number	0.067	0.259	Species	−1.008	0.232	−4.343	0.001*
	Pair	0.027	0.163	Temperature	0.148	0.047	3.127	0.002*
Handling time	Number	0	0	Species	<0.001	0.015	0	1
	Pair	0.007	0.085	Temperature	0.018	0.016	1.181	0.238
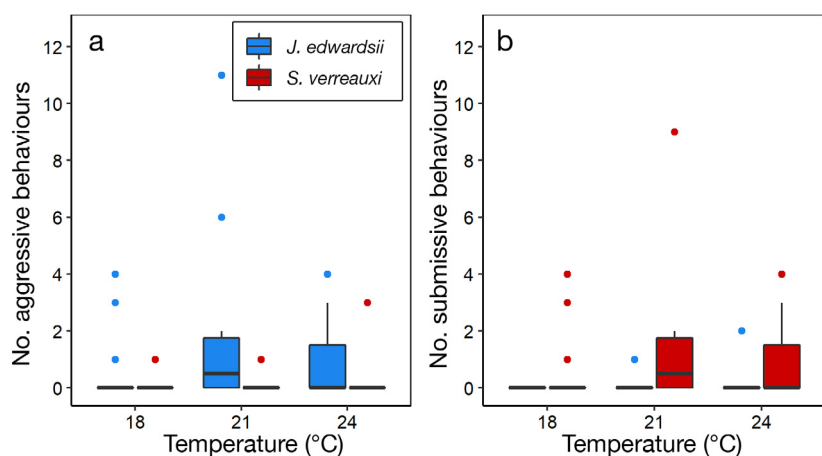
Fig. 2. Mean (±SE) number of (a) aggressive and (b) submissive behaviours (described in Table 1) exhibited by *Jasus edwardsii* and *Sagmariasus verreauxi* in competitive feeding trials at 18, 21 and 24°C (n = 21, 18 and 15, respectively). Dots indicate data outliers

Table 3. Total number of aggressive and submissive behaviours (as described in Table 1) exhibited by *Jasus edwardsii* and *Sagmariasus verreauxi* in competitive feeding trials at 18, 21 and 24°C (n = 21, 18 and 15, respectively), by behavioural type

Behaviour	J. edwardsii			S. verreauxi		
	18°C	21°C	24°C	18°C	21°C	24°C
Aggressive						
Approach	3	4	8	1	1	1
Threat	3	8	4	1	0	0
Physical contact	4	15	4	0	0	2
Total aggressive	10	27	16	2	1	3
Submissive						
Retreat	0	1	1	8	15	13
Escape	0	0	1	1	6	2
Total submissive	0	1	2	9	21	15

reauxi at 21°C, where, interestingly, that individual was more likely to just retreat rather than actively escaping using a tail-flick response (Table 2).

The level of activity exhibited was significantly affected by both species and temperature (GLMM, species p = 0.001; temperature p = 0.002; Table 2, Fig. 3a). *J. edwardsii* individuals were more active than *S. verreauxi* during all temperature trials, while *S. verreauxi* did not move for the 1 h filmed period for more than half of the trials (Fig. 3a). Activity level at 18°C was significantly less than activity level at 24°C (Tukey method, significance between 18 and 24°C, p = 0.005). Food handling time did not vary with species or temperature (GLMM, species p = 1.000, temperature p = 0.238; Fig. 3b).

4. DISCUSSION

We demonstrated that the resident lobster species *Jasus edwardsii* dominated over range-shifting *Sagmariasus verreauxi* when competing directly for food both at current summer temperatures and future warming and heatwave scenarios for south-east Australia. *J. edwardsii* was more aggressive and won more paired competitive feeding trials across the full range of tested temperatures, unlike *S. verreauxi*, which was significantly more submissive. Also, resident lobsters intensified food competition towards future and heatwave temperatures. Very few *S. verreauxi* individuals won food competitions, and these indi-
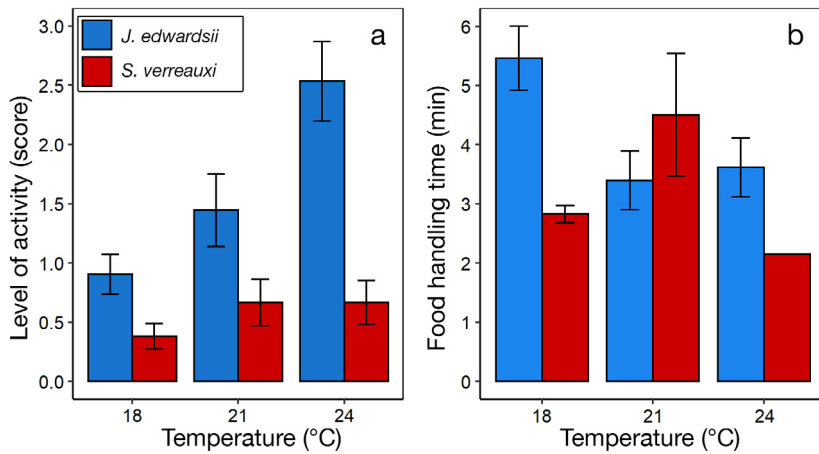
Fig. 3. Mean (±SE) (a) activity level (from 0–4 behavioural score) and (b) food handling time (both described in Table 1) exhibited by *Jasus edwardsii* and *Sagmariasus verreauxi* in competitive feeding trials at 18, 21 and 24°C (level of activity: n = 21, 18 and 15, respectively; food handling time: n = 12, 16 and 14, respectively). Note there was only one replicate, and therefore no error bar for food handling time for *S. verreauxi* at 24°C

viduals did not exhibit any behaviours that differed from those that did not win. Similarly, the effect of trial day did not affect the trial winner; e.g. even with a greater fasting duration due to lack of competitive success, behavioural dominance did not change between the lobster pair over the 3 d trial. Overall, these results indicate that resident spiny lobsters show unexpected resilience to direct food competition with range-extending species in the face of rapidly warming oceans and future heatwaves.

4.1. Competitiveness beyond physiological optima

In contrast to our original hypothesis, we found that *J. edwardsii* sustains competitive dominance beyond its optimal physiological performance. In juvenile *J. edwardsii*, aerobic scope—indicative of oxygen-dependent physiological capacity—peaks at ~20°C (Twiname et al. 2020b). Other temperature-dependent physiological performance indicators, such as growth and feed-conversion ratios, peak at 20.6 and 19.3°C, respectively in post-pueruli *J. edwardsii* (Thomas et al. 2000). Given that *J. edwardsii* continues to be the dominant competitor up to 24°C, these physiological performances do not necessarily predict competitive outcomes. However, at higher sub-optimal temperatures, metabolic energy demand and the need to feed increase disproportionally (Oellermann et al. 2020), which may explain higher aggression levels and competitive dominance, similar to cold-temperate resident

reef fish (Coni et al. 2021). Juvenile *S. verreauxi* showed parallel increases in feed consumption and metabolic rates with rising temperatures (Fitzgibbon et al. 2017, Oellermann et al. 2020). However, the poor competitiveness of *S. verreauxi* with increasing temperatures may be explained by a combination of a generally more submissive or inactive behavioural phenotype and lower metabolic demands relative to *J. edwardsii* at identical temperatures (Oellermann et al. 2020). Moreover, even though *J. edwardsii* maintained dominance, the presence of *S. verreauxi* may increase the general frequency of competitive interactions as well as activity and aggression levels of *J. edwardsii*, leading to increased long-term energetic costs and reduced energy stores (Su et al. 2020), which may hamper growth and performance (Vøllestad & Quinn 2003), particularly at physiologically sub-optimal temperatures. Thus, at longer acclimation periods exceeding 1 wk (this study), energetic deficiencies or phenotypic shifts (Oellermann et al. 2022) may alter competitive performance and outcomes.

4.2. Effect of damage on competitive outcomes

Missing appendages (legs and antennae) affected the outcome of the food competition winner in this study: 59% of *S. verreauxi* were damaged (6 individuals missing 1 appendage and 4 missing 2 appendages) while only 28% of *J. edwardsii* were damaged, all with only 1 missing appendage. The majority of these missing appendages were legs. Previous research on *J. edwardsii* behaviour found that unlike clawed lobsters that are dependent on their large foreclaws, their aggressive behaviours involved pushing and clasping their opponents (Carter et al. 2014). Additionally, in contrast to other spiny lobster species, *J. edwardsii* do not use their antennae offensively. In other crustacean species, missing appendages or limbs have been found to affect aggression, vulnerability to attack, foraging and mating (Juanes & Smith 1995 and references within, Briones-Fourzán et al. 2015). Higher levels of limb damage are likely a result of commercial fisheries handling (Juanes & Smith 1995 and references within), as *S. verreauxi* individuals were purchased from commer-

cial fishers and *J. edwardsii* were collected during routine scientific sampling. However, while the effect of damage was significant for the 'winner' of the food competition (GLMM, damage p = 0.028; 16% of model variance explained by the 'damage' term), it was not significant for any other statistical analysis (i.e. aggressive behaviours, submissive behaviours, activity level and food handling time), suggesting that limb damage was not a strong driving factor in our study.

4.3. Aggressive behaviour

Resident *J. edwardsii* dominated competition with range-shifting *S. verreauxi*, supported by its more aggressive behaviour. Aggression is considered a key factor in the successful outcomes of competitive interactions within and between species, such as hermit crabs, where aggressive individuals are more commonly the winner of a food resource (Kaiser et al. 1998, Tran et al. 2014) or resident temperate reef fish being more aggressive in face of range shifting tropical species (Coni et al. 2021). While it has been observed that food restrictions increased intraspecific dominance in *J. edwardsii* (Thomas et al. 2003), other studies have found that limited food in aquaculture situations did not affect aggressive behaviours among conspecifics (Carter et al. 2014). The lack of intraspecific aggression observed in Carter et al. (2014) combined with the high levels of aggression observed in this study indicate differences between intra- and interspecific competitive behaviours in *J. edwardsii*.

Interestingly, mature *J. edwardsii* have been shown to have higher oxygen consumption rates than *S. verreauxi* at—for *J. edwardsii*—relatively high temperatures ranging from 20–23°C (Oellermann et al. 2020). This is in line with *J. edwardsii* having higher activity and more aggressive feeding behaviour found in this study (Figs. 2 & 3), to satisfy an increased demand for food caused by raised metabolic costs at higher temperatures. Atlantic salmon apply a similar high-cost/high-return feeding strategy (Metcalfe 1986), where individuals with high standard metabolic rates were also more aggressive and competitively dominant (Cutts et al. 1998). In contrast, *S. verreauxi* juveniles with higher metabolic rates did not have a growth advantage in communal settings, suggesting that metabolic phenotype does not provide a competitive advantage (Tuzan et al. 2019). Rather, this species employs a 'compensation' strategy to minimise energetic costs and dominance and channel energetic re-

sources towards growth (Tuzan et al. 2019). In comparison, at temperatures beyond which physiological performance declines (e.g. >20°C for aerobic scope; Twiname et al. 2020b), increased activity of *J. edwardsii* may deplete energetic resources for other essential processes such as growth, reproduction or health. Therefore, despite *J. edwardsii* being competitively dominant in the short run, novel interactions with *S. verreauxi* may enhance energetically costly behaviours that may lead to long-term trade-offs at warmer temperatures. This may be compounded by the fact that at warmer temperatures *S. verreauxi* are likely to grow faster and larger than *J. edwardsii*, thus enhancing an important competitive trait that could overpower dominance by *J. edwardsii*.

4.4. Submissive behaviour

The range-shifting *S. verreauxi* was less active, more submissive and competed poorly for food with resident *J. edwardsii*. Low activity rates by *S. verreauxi* marked by stationary behaviour in or along the side of the shelters can be triggered by colder temperatures (e.g. Smith et al. 1999, Seth et al. 2013, Wang et al. 2016), as a means to conserve energy to reduce feeding needs (Sogard & Olla 1996) and exposure to predators (Lozano-Álvarez & Briones-Fourzán 2002, Briones-Fourzán et al. 2006, Briceño et al. 2018). This may be particularly relevant to leading-edge populations for *S. verreauxi* suffering from limited access to familiar prey or low levels of conspecific group protection. Also, because optimal temperatures for various traits of *S. verreauxi* were higher than for *J. edwardsii* (e.g. 24.3 vs. 19.6°C for aerobic scope; Twiname et al. 2020b), the challenge to consume sufficient food to meet increased metabolic needs may not be as critical as for *J. edwardsii*. Therefore, low activity paired with submissive behaviours may be due to a combination of conserving energy, lower metabolic demand, reduced feeding needs and predator avoidance.

4.5. Limitations and future research

Two limitations of this study will need to be addressed in future studies. First, approximately half of the *J. edwardsii* females carried eggs (6 of 10). Although there was no apparent impact in this study, egg-bearing females may behave and compete differently, requiring further study (Campbell 1990, Figler et al. 1997, Mello et al. 1999). Second, due to

different growth rates and size at maturity between *J. edwardsii* and *S. verreauxi* (Montgomery 1992, Gardner et al. 2006), matched size pairs of lobsters were of different ages and not at the same stage of sexual maturity in this study. However, since size is an important predictor of competitive dominance in crustaceans (Thomas et al. 2003), future studies will need to assess this factor by simulating natural size variations.

Further investigations may validate these laboratory results in the wild and consider other factors affecting competitive outcomes, including physiological and behavioural plasticity, mating, brooding, spawning, moulting and life stage. Also, although *J. edwardsii* dominated food competition over *S. verreauxi* up to 24°C, they do not typically range into such warm habitats, suggesting that other factors or long-term exposure limit its distribution.

4.6. Conclusions

This study found that resident spiny lobsters show unexpected resilience to direct food competition with range-extending species in the face of rapidly warming oceans and future marine heatwaves. We provided evidence that climate-driven species redistribution is not only shaped directly by the impacts of changing abiotic conditions but also indirectly by biotic barriers arising from novel species interactions.

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