Performance of tropical fish recruiting to temperate habitats: role of ambient temperature and implications of climate change

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ABSTRACT: The warming of coastal oceans due to climate change is increasing the overwinter survival of tropical fishes transported to temperate latitudes by ocean currents. However, the processes governing early post-arrival mortality are complex and can result in minimum threshold temperatures for overwinter survival, which are greater than those predicted based upon physiological temperature tolerances alone. This 3.5 mo laboratory study monitored the early performance of a tropical damselfish *Abudefduf vaigiensis* that occurs commonly during austral summer along the SE Australian coast, under nominal summer and winter water temperatures, and compares results with a co-occurring year-round resident of the same family, *Parma microlepis*. Survivorship, feeding rate, growth and burst swimming ability (as a measure of predator escape ability) were all reduced for the tropical species at winter water temperatures compared to those in summer, whereas the temperate species experienced no mortality and only feeding rate was reduced at colder temperatures. These results suggest that observed minimum threshold survival temperatures may be greater than predicted by physiology alone, due to lowered food intake combined with increased predation risk (a longer time at vulnerable sizes and reduced escape ability). Overwinter survival is a significant hurdle in pole-ward range expansions of tropical fishes, and a better understanding of its complex processes will allow for more accurate predictions of changes in biodiversity as coastal ocean temperatures continue to increase due to climate change.

KEY WORDS: Damselfishes · *Parma microlepis* · *Abudefduf vaigiensis* · Overwinter survival · Burst swimming · Tropical vagrants · Marine fishes

INTRODUCTION

The production of pelagic larvae is a ubiquitous feature of the life history of marine fishes (Leis 1991) and one which allows for the transport and settlement (transition from pelagic to benthic existence) of benthic fish recruits (newly settled fish) to areas well outside the established breeding range of adult populations. This phenomenon has been documented in situations where tropical fishes are transported large distances by ocean currents to temperate habitats during the summer (Hutchins 1991, Hutchins & Pearce 1994, McBride 1996, McBride & Able 1998, Nakazono 2002, Booth et al. 2007).

Tropical fishes are frequently transported 100s of km south by the East Australian Current (EAC) to temperate latitudes along the SE coast of Australia where average winter temperatures of between 13 and 16°C (depending on location) typically result in nearly 100% mortality of tropical fishes, even in years with high settlement (Booth et al. 2007). However, this coastal region is a global hot-spot for increases in coastal

ocean temperatures (Lough 2007, Ridgway 2007), with 2 of the warmest winters since 1848 (~1.4°C warmer than the long-term average) having occurred in the past 6 yr, during which tropical fishes experienced high survivorship (with death in subsequent cold winters; Figueira & Booth 2009).

Eme & Bennett (2008) indicated critical thermal minima for several Indo-Pacific damselfishes of ≤15°C. Figueira & Booth (2009) analysed 6 yr of overwinter mortality data for tropical fish in temperate waters and identified minimum threshold average winter temperatures for the survival of 5 damselfish species between 17 and 17.5°C. While these 2 studies do not have any species in common, they do contain the congeneric species *Abudefduf sordidus* and *A. vaigiensis*. The critical thermal minimum value for *A. sordidus* was 13.0°C (Eme & Bennett 2008). Assuming this would be similar for *A. vaigiensis*, this represents a difference of about 3.5°C between the physiological minimum and that actually observed in the field.

The discrepancy between minimum physiological tolerance, which is ultimately determined by physiological factors (loss of osmotic balance; Hurst 2007), and field observations is likely due to biophysical interactions related to the effect of temperature on feeding, growth and swimming ability. The temperature sensitivity of metabolic rate in ectotherms means there will be a positive relationship between temperature and feeding that is required to supply metabolic demand (Angilletta et al. 2002). This can result in dramatic reductions in feeding rates as temperatures drop, even in the presence of abundant food supplies. For instance, Eme & Bennett (2008) looked at the lower thermal tolerances of 8 Indo-Pacific damselfishes and noted that, while critical thermal limits (the limits of physiological survival) were ≤15°C for all fish, fish stopped feeding at between 3 and 5°C warmer than these temperatures. Thus, starvation, due to metabolically induced reductions in feeding, is likely to be an agent of overwinter mortality in expatriated fishes.

Starvation risk is not the only potential source of mortality for warm-adapted fishes finding themselves in cool waters. The same metabolic response to reduced temperature that leads to reduced feeding also leads to reduced growth. As predation is typically size dependent in fish, reduced growth can extend periods of vulnerability to gape-limited predators (Sogard 1997). In addition, reduced temperature can also compromise the escape ability of prey from more optimally temperature-adapted predators. Several studies have demonstrated reduced kinetic activity at low temperatures, which leads to lower maximum escape or 'burst-swim' speeds and distances (e.g. Batty & Blaxter 1992, Lyon et al. 2008). Reduced temperature has also been

demonstrated to increase the sensitivity of a fish to threat stimuli, making it more likely to react, but often with greater direction error (e.g. towards the simulated predator; Preuss & Faber 2003). In aggregate, these predator-mediated effects mean that at low temperatures, fish are likely to spend more time at sizes vulnerable to predation and be less able to escape in the event of a predation attempt.

Starvation- and/or predation-mediated overwinter mortality for tropical fishes at the temperate latitudes described above could explain the loss of tropical fish recruits in temperate waters. While ever more studies have been focussed on the effects of increased water temperatures on fish growth, reproduction and survival (e.g. Nakano et al. 2004, Biro et al. 2007, Munday et al. 2008a,b) there are relatively few that have considered the lower temperature tolerances of tropical fishes or the interaction of ecology and physiology in the process of low temperature mortality. Thus, mechanisms favouring and disfavouring survival at marginal thermal habitats are poorly understood, because it is not clear what the relative impacts of starvation, acute thermal stress and reduced growth and escape ability/predation play in the overwintering mortality observed in these fishes.

In this study, we first present field data from temperate coastal waters linking temperature declines over time to the loss of the tropical species *Abudefduf vaigiensis* and contrast this pattern with a local temperate species. Next, because the processes driving the overwinter mortality of this tropical damselfish are difficult to study *in situ*, we examined, in the laboratory, the temperature sensitivity of feeding, growth and burst swimming ability of *A. vaigiensis* relative to a co-occurring temperate-adapted member of the same family, *Parma microlepis*. By comparing the temperature-specific performance responses of the 2 species, we can evaluate whether starvation (related to impaired feeding), reduced growth, reduced escape ability, or all 3 together could explain increased mortality in the field, at temperatures well above their critical thermal minima. Based on the arguments discussed previously, we expected that the tropical species, but not the temperate one, would show reduced feeding at low temperatures and would experience starvation-related mortality as a result, though this mortality would be below the 100% expected in the field, due to the absence of predation in the laboratory studies. We also predicted that lower temperatures would reduce growth and burst swimming ability in the tropical, but not in the temperate species (i.e. significant interactions between species and temperature), which would demonstrate the mechanisms by which the proposed increased predation risk at low temperatures would occur in the field.

MATERIALS AND METHODS

Study species. *Abudefduf vaigiensis* is a tropical/sub-tropical species that is broadly distributed throughout the Indo-Pacific (including the Red Sea) from Japan to Australia and has occurred in Hawaii since the early 1990s (Maruska & Peyton 2007). Along the east coast of Australia its distribution is generally believed to be restricted to the Great Barrier Reef, though reproducing adults are known to occur as far south as the Solitary Islands (W. Figueira & D. Booth pers. obs.). It is predominately planktivorous (Noda et al. 1990) and occurs annually via sporadic recruitment pulses at highly variable densities of between 1 and 50 ind. 100 m^{-2} (W. Figueira & D. Booth unpubl. data), during the summer and early winter months (December to June) at sites all along the coast of New South Wales, Australia (densities average between 0.6 and 12 ind. 100 m^{-2} at sites around Sydney; see Fig. 1a). The present study is chiefly interested in establishing the relative performance of tropical fish under 2 different temperature regimes; however, we include the temperate-adapted con-familial *Parma microlepis* in order to compare the effect of temperature between the 2 species. *P. microlepis* is a benthic feeder (Moran & Sale 1977, Buckle & Booth 2009) found year-round on rocky reef habitats from northern New South Wales to north-eastern Tasmania to a depth of at least 30 m (Kuiter 2000). It co-occurs at sites with *A. vaigiensis* at densities of about 20 ind. 100 m^{-2} (for Sydney sites; E. Buckle unpubl. data), and, given its similar size and habitat associations, it likely shares predators with *A. vaigiensis.*

Seasonal abundance. We quantified the seasonal abundance patterns of each of the study species using existing visual census data from Shelly Beach, Sydney. *Abudefduf vaigiensis* was surveyed approximately weekly during summer (December to June) and monthly during winter since 2003, within a fixed area of approximately 1700 m^2 as part of the tropical fish visual survey program described in Booth et al. (2007). *Parma microlepis* was surveyed monthly in 2002 along five 90 m × 2 m transects (E. Buckle unpubl. data). These data were used to determine the average density per census point (week or month) for each species at Shelly Beach. As both species are highly site attached (E. Buckle unpubl. data, K. Gledhill unpubl. data), mortality is unlikely to be confounded by migration.

Experimental procedures. Ten juvenile *Parma microlepis* and 20 juvenile *Abudefduf vaigiensis* were collected from Long Reef, Sydney, Australia, in late April of 2007. Only a total of 30 ind. were used due to limited laboratory space and ethical considerations of housing fish individually for 17 wk. The additional *A. vaigiensis* were used to compensate for their predicted lower survival. The lack of a strong recruitment pulse for either species immediately prior to the collection period resulted in the use of fish that had settled over the previous 4 to 6 wk (based on length; D. Booth unpubl. data), though individuals, which were recent recruits, were still growing rapidly as they were below their asymptotic size. Fish total length (TL) at the commencement of the experiment ranged from 41.3 to 60.3 mm (mean = 50.5 mm, SD = 6.95) for *P. microlepis* and from 27.0 to 68.2 mm (mean = 46.4 mm, SD = 9.42) for *A. vaigiensis.* The average wet masses ranged from 1.7 to 4.9 g (mean = 3.1 g, SD = 1.15) for *P. microlepis* and from 0.4 to 5.3 g (mean = 2.1 g, SD = 1.22) for *A. vaigiensis.* Fish were held individually in plastic, opaque-walled 14 l aquaria with low-flow filters to continuously oxygenate the water. Tanks were kept on shelving racks in a temperature-controlled laboratory at the University of Technology, Sydney, from May to August 2007 (a total of 17 wk), with lighting on a 12 h light:12 h dark cycle. Location on shelves was randomly assigned with respect to species and temperature treatments (discussed below). Each tank contained a 10 cm section of PVC tubing (6 cm diameter) for shelter, a thermometer and a 12 W aquarium heater. Fish were fed to excess with Spectrum marine fish food pellets (high-quality protein source, 1 mm diameter) 5 times d^{-1}. Uneaten food was siphoned off twice per week and three-fourth water changes were carried out weekly using water of the same temperature as that in the tank. Filters were cleaned every 2 wk, and water chemistry (pH and ammonia) was monitored weekly.

Temperature treatments were created by randomly designating half the individuals of each species to 1 of 2 treatments: 'ambient' or 'elevated'. The elevated temperature treatment was maintained at about 20°C with aquarium heaters, representing the average minimum winter water temperature experienced by tropical fish on the southern Great Barrier Reef (D. Booth's temperature logger data from One Tree Island research station, 2000 to 2007). The ambient temperature treatment mimicked water temperatures at the collection site and was achieved by gradually (approximately weekly) lowering the room air temperature such that tank water temperatures matched those observed at Long Reef, Sydney (based on average 2002 to 2007 daily water temperatures from *in situ* temperature loggers) that reached a low of about 16°C (above the critical thermal minimum for congener tropical fishes; Eme & Bennett 2008; but below threshold mortality values observed in the field; Figueira & Booth 2009). Water temperatures were recorded daily (Fig. 1b).

Fish size and mass were monitored by removing fish from tanks and measuring total length, standard length (to the nearest 0.1 mm with calipers) and wet

mass (to the nearest 0.01 g) approximately weekly. Growth was estimated over each interval as the instantaneous growth rate (G_{Inst}) based on the mass of fish at the beginning (M_1) versus the end (M_2) of the interval of length Δt (in days):

$$G_{Inst} = \frac{\ln\left(\dfrac{M_2}{M_1}\right)}{\Delta t} \qquad (1)$$

Because fish readily fed as soon as food was put into the tank, the feeding rate was assessed for individual fish by supplying food in excess and counting the number of bites (equal to the number of pellets) taken in 30 s after the addition of food. To ensure uniform responses each time, excess food was cleaned from the tank and fish were not fed for 12 h before the test. The feeding rate was estimated for all fish approximately twice per week beginning in Week 11 (a different technique was used unsuccessfully prior to this).

Burst swimming was assessed by video-recording the startle response of individual fish approximately every third week during the experiment. Fish were transferred individually to a narrow, opaque-walled glass aquarium (25 cm deep, 80 cm long, 50 cm tall) with a gridded background (for reference), and water was kept within 0.5°C of their treatment temperature. The tank was shielded from disturbances using black sheeting with a small hole cut out to allow a tripod-mounted Sony DCR-PC350E digital camera lens to protrude. After a 5 min acclimation period, fish were recorded by video for 1 min. Next, fish were startled with a small weight dropped on the side nearest the fish's current position using a remote release system and recorded for an additional minute. The video, shot at 24 frames s^{-1} (adequate to assess burst swimming in fish; Lyon et al. 2008), was analysed to determine the distance moved (and therefore velocity), each frame beginning with the dropping of the weight as a common reference point. The maximum velocity attained during the 2 s following the release of the weight (burst swimming behaviour was completed by this point) was taken as the maximum burst-swim speed for the fish on that trial. Analyses were conducted for all fish in the study at each time point.

Statistical analyses. Since the response variables of interest in the present study (feeding, growth and burst swimming) were not measured simultaneously in all cases, we identified 3 temporal periods over which we could compare fish responses for each of these variables across temperature treatments and species. The selection of these intervals was based upon the most parsimonious overlap of measured responses. The intervals used for analyses were 0 to 8 wk (Week 8), 9 to 13 wk (Week 13) and 14 to 16 wk (Week 16). The use of a repeated-measures factor (the intervals in this case)

also provides additional power to detect the effects of temperature over the duration of the experiment.

In order to test for any differential effects on mortality of temperature between the 2 species, the raw binomial mortality data were analysed using Proc Genmod (SAS Institute), and tested for the effects of temperature treatment, mass and the interaction, specifying a binomial probability distribution, Type III sums of squares to assess significance of effects and a logit link function (Allison 1995). Because there was no mortality for *Parma microlepis* (see 'Results'), there was an infinite likelihood associated with that estimate, and therefore it was not possible to include a species effect in the model. Therefore, the 95% confidence interval (CI) for the estimates for *Abudefduf vaigiensis* mortality were compared at each temperature to assess whether they differ from the zero mortality obtained for *P. microlepis*.

Any differential effect of temperature on feeding between the 2 species was assessed by calculating the feeding rate (bites 30 s^{-1}) for each time interval as the average rate for all observations conducted during the interval (which varied from 2 to 4). The feeding response was then evaluated using a general linear model (GLM), with average feeding rate as the response variable, mass (Ln transformed) as a continuous predictor variable (covariate), species and temperature treatment as fixed factors, and time (week number) as a within-subjects (repeated-measures) factor. Assumptions of homogeneity of variance were evaluated in all cases (including models below) using residual plots and Levine's test. Unless indicated, this assumption was satisfied. Note that feeding data were only available for 2 time intervals, Week 13 and Week 16. Where results indicated significant interactive effects, *a priori* contrasts were used to test for differences between temperature treatments for species in each temporal period as necessary. The GLM was run using only fish that survived for the duration of the entire experiment. To assess if the necessary exclusion of non-surviving fish from the GLM biased the results, the feeding rates of fish that did not survive the entire experiment were compared with those that did survive at each time interval prior to the last (at which time all non-surviving fish were dead, and thus no comparison was possible as there were no data on feeding for those fish from that interval). In the case of feeding, this was only possible for the Week 13 interval.

In order to test for any differential effects of temperature on growth between the 2 species, instantaneous growth data were Ln + 1 transformed (to account for the ln–ln linear relationship between growth and size in fish) and were used as the response variable in a GLM with the same structure as that described above for feeding. *A priori* contrasts and comparisons between surviving and non-surviving fish were also used as described for feeding.

Any differential effect of temperature on burst-swimming ability between species was assessed by calculating an average maximum burst-swim speed (in cm s^{-1}) for each individual from all tests performed during the interval. This average value was used as the response variable in a GLM with the same structure as that described for feeding and growth above. *A priori* contrasts and comparisons between surviving and non-surviving fish were also used as described for feeding and growth. It is not uncommon to see burst swimming speeds quantified as specific speeds, in body lengths per second. This study uses centimeters per second rather than specific speed due to its more direct relevance to escaping a predator, which is fundamentally a matter of how fast a fish can move a specific distance (away from a predator) and, as such, is independent of size.

RESULTS

Seasonal abundance

Density of the temperate damselfish *Abudefduf vaigiensis* was relatively high and declined only slightly over time from December through January (Fig. 1a). In contrast, the tropical damselfish increased in density between January and May, with episodic spikes in recruitment present though June, but declined quickly to near zero by August (Fig. 1a) as the water temperature dropped (Fig. 1b). Abundance of the tropical damselfish declined sharply as temperatures dropped below 17°C, suggesting a critical temperature affecting their survival (Fig. 1b).

Fig. 1. *Abudefduf vaigiensis*, *Parma microlepis*. (a) Average density (±SE) at Shelly Beach, Sydney (2003 to 2007 for *A. vaigiensis*, only 1 yr for *P. microlepis*). (b) Average water temperatures (±SE) at nearby Long Reef during the same period, with experimental temperatures overlaid. (c) Proportion of experimental fish surviving over time, by treatment and species (note *x*-axis zoomed relative to Panels a,b)

Mortality

In the laboratory, there was no mortality for the temperate damselfish, whereas mortality was observed for the tropical species at cool winter temperatures (Fig. 1b,c). The highest mortality occurred in the ambient temperature treatment for *Abudefduf vaigiensis* (4 out of 10 died) followed by the elevated temperature treatment (1 out of 10 died; Fig. 1c).
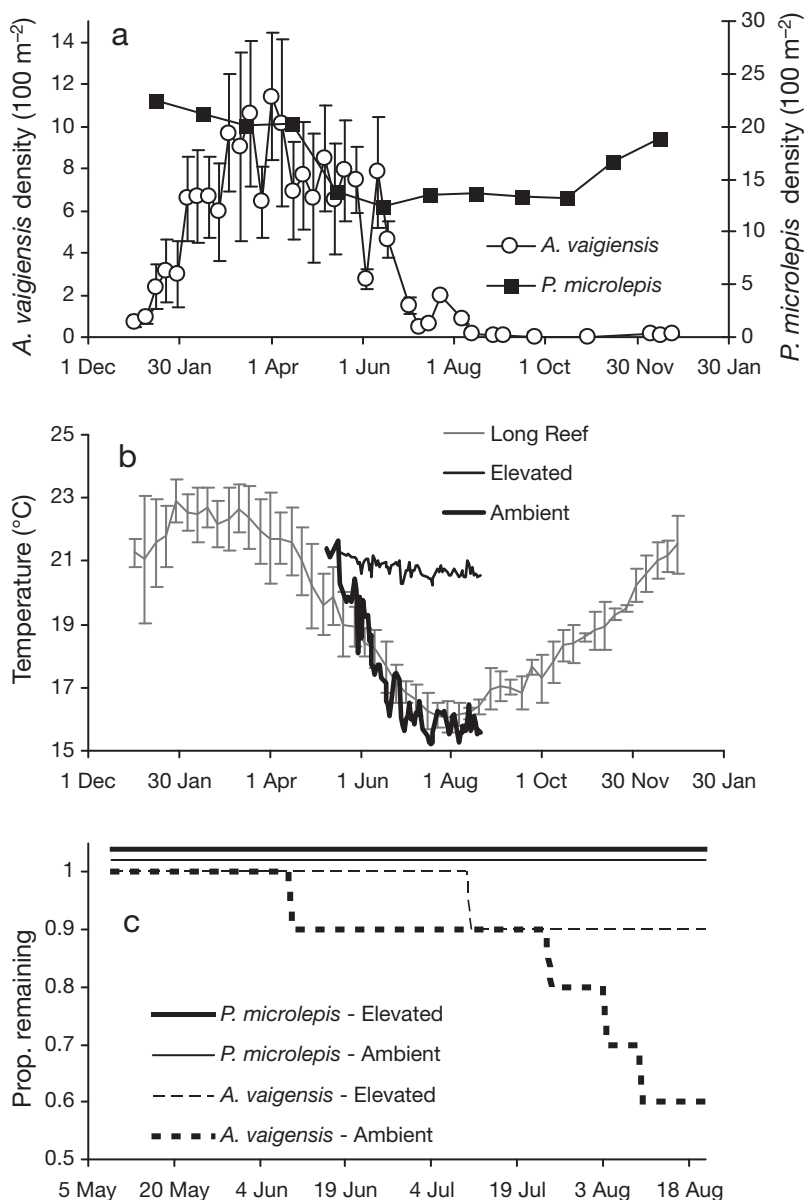
Despite this difference, mortality of *A. vaigiensis* did not differ significantly between temperature treatments, and there was no effect of individual mass or the interaction of the 2 factors (all $\chi_1^2 < 2.6$, all p > 0.1). The model with only species identity as a predictor was fit to obtain 95% CI for each; as predicted, mortality of *A. vaigiensis* was significantly greater than for *Parma microlepis*, which did not experience any mortality (p < 0.05).

Feeding

Feeding rates were greater in the elevated than in the ambient temperature treatment ($F_{1,21} = 7.19$, p = 0.014; Fig. 2, Table 1), and there was no interaction between temperature and species ($F_{1,21} = 0.98$, p = 0.335), which indicates both species showed a similar pattern. Overall, feeding rate was greater for *Parma microlepis* than for *Abudefduf vaigiensis* ($F_{1,21} = 7.00$, p = 0.015), and there was no effect of time ($F_{1,21} = 2.60$, p = 0.122; Table 1). The strong effect of temperature existed after controlling statistically for mass, which showed that larger fish consume more food than smaller fish, as expected ($F_{1,21} = 13.43$, p = 0.001). As there was no interaction and only 2 treatments per factor, no contrast tests were necessary. The comparison of surviving and non-surviving fish (to assess bias from the exclusion of non-surviving fish from analysis) indicated that there was no significant difference in feeding rates
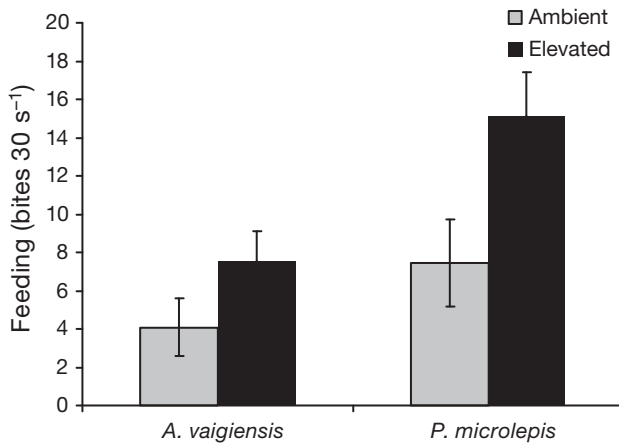
among these 2 groups at Week 13 ($t = 1.01$, df = 15, p = 0.325). Thus, there is no indication that observed feeding effects were due to the exclusion of non-surviving fish from the analysis.

Growth

After statistically controlling for the expected declines in growth rate with increasing mass ($F_{1,20} = 4.55$, p < 0.045; Table 1), a significant Species × Temperature interaction was revealed ($F_{1,20} = 30.19$, p < 0.001). There was also a significant within-subjects effect of time, with growth rates slowing at the end of the experiment ($F_{2,40} = 7.48$, p = 0.002). A priori comparisons indicated that growth of the tropical species *Abudefduf vaigiensis* was significantly less in the ambient than in the elevated treatment at all time points (Week 8: $F_{1,20} = 8.75$, p = 0.008; Week 13: $F_{1,20} = 87.07$, p < 0.001; Week 16: $F_{1,20} = 8.01$, p = 0.010), but, for the temperate species *Parma microlepis*, there were no differences at any time point (Week 8: $F_{1,20} = 0.09$, p = 0.766; Week 13: $F_{1,20} = 0.35$, p = 0.563; Week 16: $F_{1,20} = 0.03$, p = 0.870; Fig. 3).

Growth rates were compared among the surviving and non-surviving groups as described above for feeding. There were no significant differences in instantaneous growth (Ln + 1 transformed) at either the Week 8 ($t = 1.00$, df = 17, p = 0.329) or Week 13 ($t = 1.68$, df = 15, p = 0.114) time points. Thus, there is no indication that observed growth effects were due to the exclusion of non-surviving fish from the GLM analysis.

Burst swimming

There was no significant effect of either mass (Ln transformed, $F_{1,20} = 0.47$, p = 0.502; Table 1) or species ($F_{1,20} = 0.62$, p = 0.441) on maximum burst swimming ability. While there was an effect of temperature ($F_{1,20} =$

Fig. 2. *Abudefduf vaigiensis, Parma microlepis.* Average (±SE) feeding rates (least-squares means from general linear model, GLM) in each temperature treatment across both temporal periods for which feeding data were available (Weeks 13 and 16). The GLM indicated a significant (p < 0.05) effect of both temperature and species, but no interaction (see 'Results — Feeding')

Table 1. *Abudefduf vaigiensis, Parma microlepis.* General linear model results for the 3 response variables: feeding rate, instantaneous growth rate and maximum burst swimming speed. df values are given along with *F*-values and the corresponding p-value for each factor. Interactions with time and other factors have been excluded as none were significant. *Italics*: significant (p < 0.05)

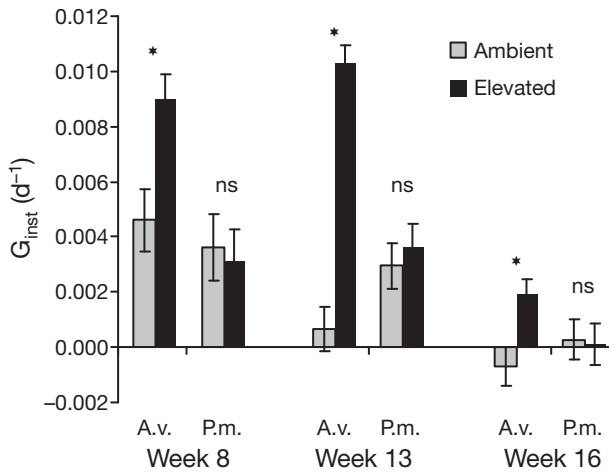| Factor	Feeding			Growth			Burst swimming		
	df	*F*	p	df	*F*	p	df	*F*	p
Temperature	*1*	*7.19*	*0.014*	*1*	*30.84*	*0.000*	*1*	*6.66*	*0.018*
Species	*1*	*7.00*	*0.015*	*1*	*16.64*	*0.001*	1	0.62	0.441
Temperature × Species	1	0.98	0.335	*1*	*30.09*	*0.000*	*1*	*4.63*	*0.044*
Mass	*1*	*13.43*	*0.001*	*1*	*4.55*	*0.045*	1	0.47	0.502
Error	21			20			20		
Time (within subjects)	1	2.60	0.122	*2*	*7.48*	*0.002*	2	0.36	0.699
Error (within subjects)	21			*40*			40		

Fig. 3. *Abudefduf vaigiensis* (A.v.), *Parma microlepis* (P.m.). Average (±SE) instantaneous growth, G_{inst} (least-square means from general linear model, see 'Results — Growth') in each temperature treatment over the 3 temporal periods (Weeks 8, 13 and 16). Results of *a priori* comparisons between temperatures for each species at each temporal period are indicated as either significant (*p < 0.05) or non-significant (ns)

6.66, p = 0.018), there was also a significant Species × Temperature interaction ($F_{1,20}$ = 4.63, p = 0.044), indicating this response was not the same for each species. There was no effect of time ($F_{2,40}$ = 0.36, p = 0.699). *A priori* contrasts indicated that *Abudefduf vaigiensis* in the ambient temperature had maximum burst-swim speeds half those in the elevated treatment ($F_{1,20}$ = 10.77, p = 0.004), whereas *Parma microlepis* swam at similar speeds at both temperatures ($F_{1,20}$ = 0.10, p = 0.750; Fig. 4). Comparisons between surviving and
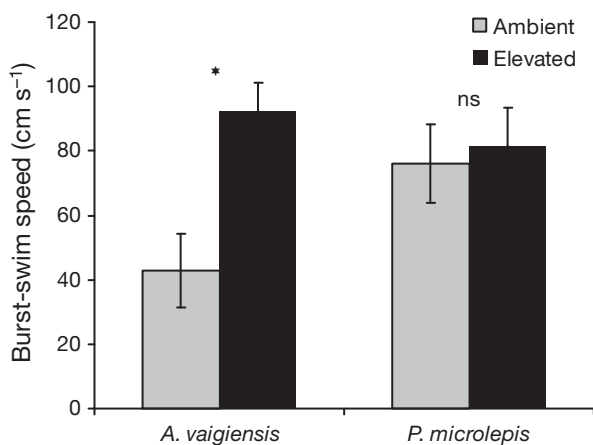

Fig. 4. *Abudefduf vaigiensis*, *Parma microlepis*. Average (±SE) maximum burst-swim speed (least-squares means from general linear model, see 'Results — Burst swimming') in each temperature treatment across all time periods (Weeks 8, 13, 16). Results of *a priori* comparisons between temperatures for each species are indicated as either significant (*p < 0.05) or non-significant (ns)

non-surviving fishes indicated no difference in burst-swim speeds at either Week 8 (t = 1.25, df = 17, p = 0.229) or Week 13 (t = 0.34, df = 15, p = 0.739). Therefore, as with growth and feeding, there was no indication that observed burst swimming effects were due to the exclusion of non-surviving fish from the GLM analysis. Analyses were also conducted on specific size (body length s⁻¹) with identical results.

DISCUSSION

We observed a precipitous decline in the abundance of the tropical vagrant fish *Abudefduf vaigiensis* when temperatures declined below 17°C during winter, leading to the complete loss of recruited cohorts (Fig. 1a,b; Figueira & Booth 2009). In contrast, the co-occurring temperate damselfish *Parma microlepis* experienced no such decline in numbers with declines in temperature. A detailed laboratory experiment that mimicked this seasonal temperature decline over 17 wk examined performance traits that might explain the differential loss of the tropical damselfish. Figueira & Booth (2009) observed nearly 100% mortality of *A. vaigiensis* at temperatures <17.5°C in the field. In the present study mortality was 40%, even at temperatures reaching 16°C. The fact that survival was greater in the laboratory than in the field indicates that thermal stress and the subsequent loss of osmotic balance are not solely to blame for overwinter mortality of these tropical fishes at temperate latitudes. Indeed, other laboratory studies have demonstrated that critical lower temperatures for other similar tropical species including the congener *A. sordidus* and 7 other confamilials were between 12.2 and 15.9°C (Eme & Bennett 2008). The discrepancy in mortality between the minimum threshold temperatures observed in laboratory and field can be accounted for by starvation mortality due to reduced feeding and increased susceptibility to predation due to slowed growth and reduced escape ability.

As predicted by metabolic theory (Angilletta et al. 2002), lower temperatures reduced the feeding rate of both species. However, it was only the tropical species that experienced any increase in mortality as a result of this reduction. While not significant, *Abudefduf vaigiensis* mortality in the ambient temperature treatment was 4 times greater than in the elevated temperature treatment (10 vs. 40%). The fact that these reductions in feeding and subsequent mortality occurred even in the face of abundant food indicates that starvation due solely to reduced intake (independent of food abundance) will be an important mortality factor for these tropical fishes.

Predation is also well known to be a powerful force structuring reef fish communities in both temperate

and tropical waters (Hixon & Jones 2005) and can be even more important for novel species such as tropical fish in temperate environments (Almany & Webster 2004). Our study highlights 2 mechanisms by which predation risk may be enhanced for tropical fishes in temperate habitats relative to co-occurring temperate fishes: increased exposure due to reduced growth and reduced escape ability.

Temperature-mediated growth is the norm for ectotherms, although the effect of a temperature change will depend strongly upon the magnitude of the new temperature relative to the performance response curve and inherent optimal temperature of the organism (Angilletta et al. 2002). In the case of the temperate damselfish, it is likely that the temperature at which growth is optimized is within the range of the test temperatures used in the present study, and thus tested temperatures are situated on either side of this optimum, thereby showing no real differences. This would make sense since these temperatures span winter and summer temperatures at the temperate field location, thus bounding those experienced by a year-round resident. The optimum temperature for the tropical species is clearly much higher than that for the temperate species and is likely much higher than the elevated temperature (20 to 21°C) used in this experiment. There are no studies describing optimal growth for *Abudefduf vaigiensis*; however, 1 study on this species in Japan demonstrated reduced growth at temperatures above about 31°C, indicating optimal growth occurs somewhere below this point (Nakano et al. 2004). Medvick (1979) indicates that the optimal temperature for growth of the congeneric species *A. abdominalis* in Hawaii is 30.1°C. Thus, while it is able to grow much faster than the temperate species when fed to satiation at the elevated temperature, its growth rate drops dramatically (from 50 to 95% depending upon the temporal period) under temperatures typical of a Sydney winter (15 to 16°C). This reduction in growth will increase the time spent at sizes vulnerable to predation, thereby increasing mortality risk (Sogard 1997).

The outcome of predator–prey interactions is mediated by many factors, but one of the most important is the prey's ability to react to an impending threat and to escape with sufficient speed (Domenici & Blake 1997). We observed a roughly 60% reduction in burst swimming speed at winter water temperatures for *Abudefduf vaigiensis*, relative to warmer temperatures. This reduction in maximum burst swimming speed, which occurred as a result of reduced temperatures, is also consistent with the metabolic theory of swimming performance and occurs due to the direct relationship between muscle contraction times, tail beat frequency and temperature (Batty & Blaxter 1992). As with growth, the species-specific responses to temperature

observed in the present study are the result of the burst swimming performance function of *Parma microlepis* likely straddling temperature treatments used in the experiment, while that for *A. vaigiensis* is likely shifted far to the right of this, with an optimum occurring at temperatures nearer to average temperatures within its adult range (26°C and above). In addition, while not quantified in our study, low temperatures not only reduce burst-swim speeds, but can also dramatically increase error in reaction direction, further reducing the capability of prey escape (Preuss & Faber 2003). In combination, these factors will lead to an increase in susceptibility to predation at cooler temperatures.

The present study illustrates the challenges confronting newly settled tropical fishes at temperate latitudes attempting to survive their first winter. By demonstrating reductions in feeding, growth and escape ability, our study helps to explain the failure of these tropical fishes to survive winters, the temperatures of which would be at the low end but still within their range of tolerance. The warming of the coastal oceans due to climate change has stimulated much scientific research into the potential direction and magnitude of range shifts in marine species (Parmesan & Yohe 2003, Perry et al. 2005, Parmesan 2006). The predicted 1 to 3°C rise in ocean temperatures over this century in tropical regions (Lough 2007) is likely to severely stress many species that may already be at or near their thermal maximum (Munday et al. 2008a). At the same time, these increases are likely to allow poleward expansion of some species (Munday et al. 2008a). The pelagic larval phase of the life history of most fishes, and indeed many marine organisms, provides them with the ability to colonize distant locations. Climate change may alter patterns of connectivity by increasing larval growth rates (O'Connor et al. 2007, Munday et al. 2008a) and altering ocean currents (Munday et al. 2008a), but a certain amount of long-distance transport will remain. Thus, for the majority of tropical species, overwinter survival will likely remain the ultimate population bottleneck, as shown for fish in temperate fresh- and saltwater habitats (Ludsin & DeVries 1997, Hurst & Conover 2001, Pratt & Fox 2002, Biro et al. 2004). It will, therefore, be increasingly important to understand the complex set of physical and biological factors, the interactions of which ultimately determine ecologically relevant temperature thresholds. Only with this understanding will we be able to accurately predict the nature of the changes in local community structure that are likely to occur due to climate change.

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