

# Increasing ocean temperatures allow tropical fishes to survive overwinter in temperate waters

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## Abstract

The southeast coast of Australia is a global hotspot for increasing ocean temperatures due to climate change. The temperate incursion of the East Australian Current (EAC) is increasing, affording increased connectivity with the Great Barrier Reef. The survival of tropically sourced juveniles over the winter is a significant stumbling block to poleward range shifts of marine organisms in this region. Here we examine the dependence of overwintering on winter severity and prewinter recruitment for eight species of juvenile coral reef fishes which are carried into temperate SE Australia (30–37°S) by the EAC during the austral summer. The probability of persistence was most strongly influenced by average winter temperature and there was no effect of recruitment strength. Long-term (138 years) data indicate that winter water temperatures throughout this region are increasing at a rate above the global average and predictions indicate a further warming of  $>2^{\circ}\text{C}$  by the end of the century. Rising ocean temperatures are resulting in a higher frequency of winter temperatures above survival thresholds. Current warming trajectories predict 100% of winters will be survivable by at least five of the study species as far south as Sydney (34°S) by 2080. The implications for range expansions of these and other species of coral reef fish are discussed.

*Keywords:* butterflyfish, coral reef fish, damselfish, ocean warming, overwinter survival, range expansion, SE Australia, tropical expatriates

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## Introduction

The geographic range of a species is determined by complex interactions among ecological factors within evolutionary processes (Holt, 2003). For a species to expand its present range, the new area must meet a minimum set of biophysical requirements. It must contain adequate habitat and food to support survival of all life stages and reproduction of adults. The environment must also fall within the present range of tolerance of all factors affecting the physiology of the organism (Angilletta *et al.*, 2002) such as temperature, moisture, oxygen, nutrients and in the cases of photosynthesizing organisms, sunlight. Lastly the species must be capable

of surviving within the biological community (predators and competitors) of the new environment (Preston *et al.*, 2008). Where these basic criteria are met, range expansions are theoretically possible.

While range shifts can occur even without strong directional environmental change (Holt, 2003), there is evidence that recent global climate change is responsible for shifts of a large variety of taxa in terrestrial and marine systems (Parmesan & Yohe, 2003; Parmesan, 2006). Many observed range shifts are due to the movement of juveniles or adults both on land and in the sea (Attrill & Power, 2002; Crozier, 2004; Perry *et al.*, 2005; Agatsuma & Hoshikawa, 2007), however, marine organisms also have the potential for especially rapid and dramatic range shifts due to their highly mobile larval phase. Survival of larvae which settle (transition from pelagic to benthic environment) in novel habitat has been associated with range shifts for sea urchins on the northwest coast of Japan (Agatsuma & Hoshikawa, 2007) and sea anemones on the west coast of the United States (Sagarin *et al.*, 1999).

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There is strong potential for the pelagic larval phase to drive range expansions of marine organisms wherever major ocean currents facilitate long-distance dispersal. Previous work along the SE coast of Australia has demonstrated the important role of the East Australian Current (EAC), a western boundary current, in driving larval settlement pulses of many species of tropical coral reef fish each summer (Booth *et al.*, 2007). The presence and at least short-term (one season) persistence of these species at these sites which are well outside of their range indicates that the biophysical environment is suitable for at least the juvenile stages. However, the failure of these species to consistently survive their first winter after settlement indicates that, as has been demonstrated for other species of fish (Ludsin & DeVries, 1997; Hurst & Conover, 2001; Pratt & Fox, 2002), winter is a key bottleneck for survival and population establishment of these fishes.

Here we present the results of a 6-year study of the overwinter survival of several commonly summer-occurring tropical coral reef fish species along the SE coast of Australia at six locations, from the Solitary Islands (30°S) to Merimbula (37°S) including Lord Howe Island (Fig. 1). We examine the roles of the number of newly arrived juveniles before winter (hereafter referred to as 'prewinter' juveniles) as well as several measures of winter severity based on water temperature in determining the number of fish present after the winter (hereafter referred to as 'winter survivors'). We then evaluate the potential for range shifts of these species as well as their rate in light of ocean temperature increase at different latitudes using a long-term (138 years) sea surface temperature (SST) data set.

## Materials and methods

### *Estimating fish abundance*

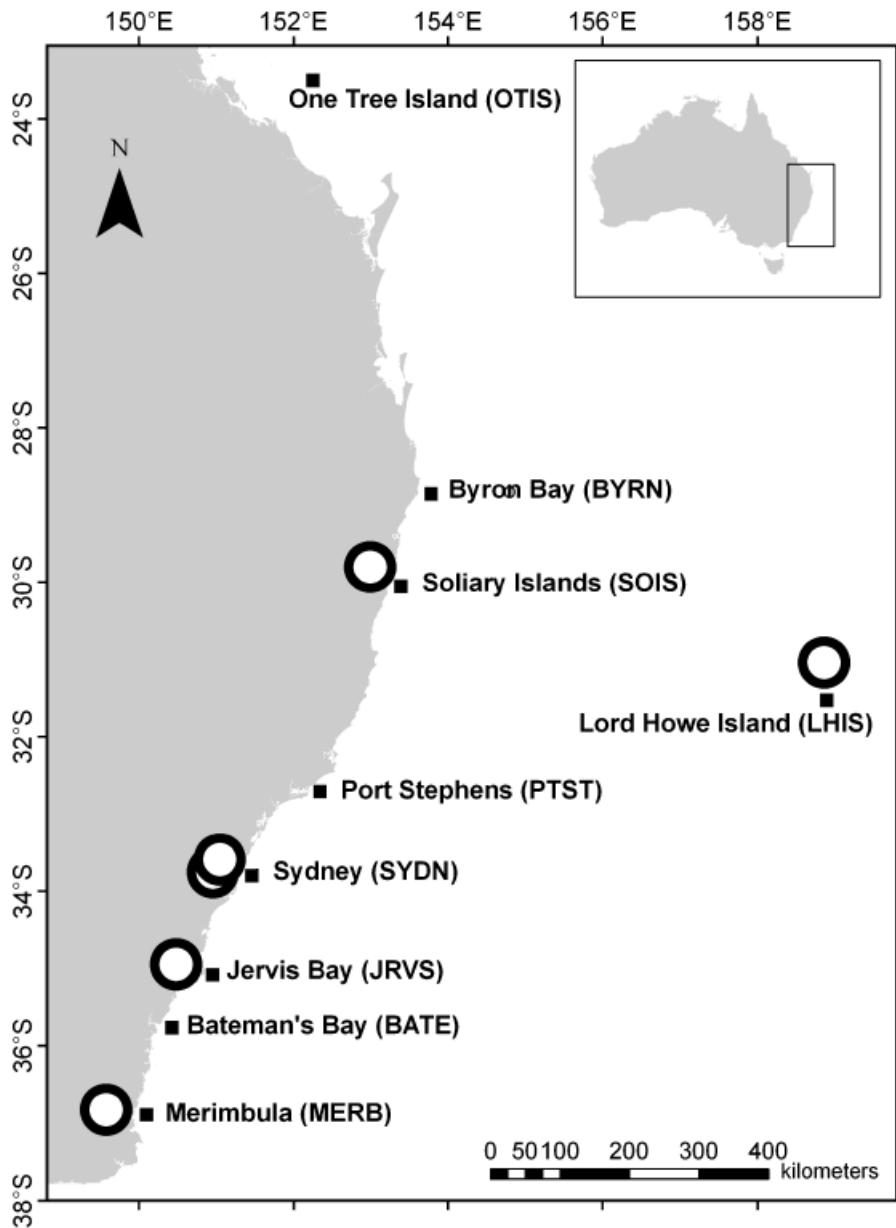
Abundance estimates were derived from data series collected by the authors (Lord Howe Island, Sydney, Jervis Bay and Merimbula) and others (Solitary Islands, data courtesy of H. Malcolm) as part of ongoing underwater visual censuses for tropical fish at each of the locations. These locations were areas in which tropical fish were known to recruit each summer based upon previous studies (Booth *et al.*, 2007). During these surveys a single individual on snorkel or SCUBA (depending on the site) methodically swam a predefined area using either transect tape or local landmarks (above and below water) for reference and counted tropical fish species categorizing them as either juveniles or as adults based upon size. In all cases censuses were conducted on fixed areas which did not change in location or extent from one survey to the next. The total

area surveyed for these censuses ranged from 150 to 1600 m<sup>2</sup> depending upon the location. Surveyed habitat was shallow (<9 m) nearshore (or near-island for the Solitary Islands and Lord Howe Island) coastal rocky reef (as described in Booth *et al.*, 2007). At Long Reef, Shelly Beach and Merimbula, surveys were conducted weekly between December and June from 2003 to 2008. At the other locations surveys were conducted annually, typically in March or April, from 2002 to 2007 for the Solitary Islands, from 2002 to 2006 for Lord Howe Island and from 2002 to 2005 for Jervis Bay. Where multiple sites were surveyed at one location, values were averaged. This was done for the Solitary Islands (14 sites), Lord Howe Island (eight sites), Shelly Beach (two sites) and Jervis Bay (two sites).

Using these abundance data we identified species for which juveniles were present in at least half of the locations and which occurred in significant numbers (>20 individuals per census on average) at those locations. This was done to ensure adequate sample sizes for analyses of trends across years and locations. For each of these species at each location at which juveniles occurred we estimated (1) the number of prewinter juveniles and (2) the number of overwinter survivors. Overwinter survivors were easily identifiable (categorized as adults) as they were much larger than the juveniles, which were at most 5–6 months old by the onset of winter. Note that exceptionally warm winters never occurred back to back in our data set and thus given the typically small number of adults occurring in a census it was possible to assure that adults had only survived one winter (i.e. had settled last season) based the absence of any adults previous to the winter in question. For locations with weekly surveys, the number of overwinter survivors and the number of juveniles present before winter was taken as the average number from the first four and last four surveys of the recruitment season (December–June), respectively.

### *On-site temperature logger data*

Daily average water temperatures for each survey site were obtained using data loggers (Stowaway Tidbit; –5 to 37 °C, ±0.2 °C; Onset (R), Pocasset, MA, USA) maintained in fixed locations adjacent to fish habitat at each location (2–9 m deep depending on location). In two locations, Jervis Bay and Lord Howe Island, logger data series were shorter than the survey period. In order to establish time series for these locations which spanned the time series of survey data we evaluated the relationship between the logger data which was available for these sites (2 years at both sites) and SST data obtained from the Pathfinder AVHRR satellite (details discussed below). There was a very strong



**Fig. 1** Map of study area. Sea surface temperature data for all locations listed were obtained from both data series as explained in 'Materials and methods'. Visual census surveys for tropical fish were conducted at locations marked by the hollow circles (note two locations in Sydney, Shelly Beach and Long Reef).

correlation between logger and SST data from which seasonality had been removed (Jervis Bay:  $R^2 = 0.80$ ,  $P < 0.001$ ; Lord Howe Island:  $R^2 = 0.90$ ,  $P < 0.001$ ) with the offshore SST data being consistently warmer than that recorded inshore by the logger. Therefore the Pathfinder data were used for each of these locations in the analyses after being adjusted by the average difference to the logger (differences were 0.14 and 1.6 °C for Lord Howe Island and Jervis Bay, respectively). The larger difference at Jervis Bay is the result of the logger (and fish habitat) being located inside the Bay

as compared with Lord Howe Island where the logger and the habitat were exposed to much more mixing due to the oceanic nature of this area.

#### *Threshold temperature analysis*

The type and quality of habitat is very likely to influence observed levels of abundance of the various species at each site. While we attempted to account for this by surveying similar habitat types, the exact area surveyed at each site was slightly different. There

may also be nuances of larval supply that lead to different levels of possible recruitment at each location and also among years, habitat issues aside. Thus in order to make abundance comparisons across sites and years, abundance data for each species were normalized by the maximum seasonal abundance observed at each location over the course of the study. We then used general linear models (GLM) to examine the effect of prewinter abundance, location, species and each of five measures of winter severity on the abundance of winter survivors. Separate models were run for each of the measures of winter severity, (1) the coldest week of the year, and four metrics based upon the temperature during the period July–August, (2) average, (3) standard deviation, (4) minimum and (5) maximum. Individual analyses were run because many of the variables describing winter severity were highly correlated. We arcsine square root transformed both the index of winter survivors and that of prewinter juvenile abundances to meet the assumptions of homogeneity of variance for the GLM.

As indicated in the results, average winter temperature had the most strongly significant effect of all the severity metrics in the GLM; however, there was a significant location  $\times$  species interaction ( $F_{11,87} = 2.8$ ,  $P = 0.004$ ). Therefore relationships between winter survivors and average winter temperature were explored further for individual species using a nonlinear sigmoidal model. The model had two parameters;  $x_0$  (the inflection point), and  $dx$  (the slope) and had its minimum and maximum fixed at 0 and 1, respectively (in accordance with the abundance indices). Because temperature is inherently confounded with location, we included a dummy variable in the model fit to test for an effect of location:

$$\text{Survivors} = 1 - \frac{1}{1 + e^{\frac{\text{Temp} - (x_0 + \beta_1 \times \text{Location})}{dx}}}$$

where survivors is the number of fish present after winter; *Temp* the average winter temperature (July–August); *Location* the code for each location;  $x_0$  the point of inflection for sigmoidal curve;  $dx$  the slope of sigmoidal curve at the point of inflection;  $\beta_1$  the coefficient for the *Location* dummy variable.

The model was fit with a least squares loss function in STATISTICA (version 7.1, Statsoft Inc., Tulsa, OK, USA) and where the coefficient on the *Location* parameter ( $\beta_1$ ) did not differ significantly from zero, the model was fit for all locations combined. Where it was significant, the model was fit to data for each location individually.

#### Long-term SST analysis

SST data were obtained for nine locations (Fig. 1) from two sources: NOAA Pathfinder and Met Office Hadley

Centre's HadISST1 data set (Rayner *et al.*, 2003). NOAA Pathfinder data were Level 3 mapped, 4 km, 7-day resolution, 1985–present, value used was the average of a  $4 \times 4$  cell grid located 10 km offshore (Fig. 1) of each location. A point 10 km offshore was selected to avoid poor-quality data which can occur at the extent of the remotely sensed data due to land effects. The Met Office Hadley Centre's SST data set was HadISST1,  $1^\circ$ , monthly resolution, 1870–present, value used was for nearest  $1^\circ$  cell to each location which did not overlap land.

The higher spatial resolution Pathfinder data were used to visualize concordance in coastal patterns of warming (relative to our sampling locations) over the period of the data set and to identify the relatively warm winters (taken as the average temperature from July to August) experienced in recent years. As indicated above, it was also used to generate complete time series of temperature data for Lord Howe Island and Jervis Bay. We used the HadISST1 data set to examine the long-term trends in coastal warming at all our sample locations. We extracted the average winter temperature (July–August) at all locations (Fig. 1) and calculated the location-specific temperature changes (in  $^\circ\text{C}$ ) based on the comparison of the average of the last 10 years of data with that of the first 10 years. We then calculated the frequency of winters warmer than a threshold value at each location over the course of the entire data set. This threshold temperature value was based on the average value observed from the significant sigmoidal model fits for all the mainland species but was corrected to account for the fact that the offshore water temperatures from the HadISST1 data set are, on average,  $1.5^\circ\text{C}$  warmer than those measured with the loggers at the study sites due both to the influence of the EAC as well as the very large offshore area represented by the one HadISST1 data point (approximately  $150 \text{ km}^2$ ). The frequency of winters that were warmer than this threshold value was calculated using a running 25-year window centered around the target year. We estimated the time at which the frequency of warm winters would equal 100% in Sydney using a linear fit to the Sydney frequency data beginning in 1985 (when the frequency became  $>0$ ). Given climate predictions for SE Australia (Poloczanska *et al.*, 2007) and the current accelerating nature of the frequency curve for Sydney, this is a conservative approach.

#### Results

Eight species of tropical coral reef fish were observed to commonly ( $> 20 \text{ fish location}^{-1} \text{ season}^{-1}$ ) settle in at least half of the locations (Fig. 1) during the study period. Six of these species were damselfishes (family Pomacentridae) – *Abudefduf bengalensis*, *Abudefduf vaiigiensis*,

**Table 1** Summary of general linear model (GLM) analysis results explaining spatial and temporal patterns of reef fish overwintering as a function of winter severity, prewinter abundance, location, and species

Winter variable	Effects of variables						
	Focal variable			Other variable's <i>P</i> -values			
	MS	<i>F</i> <sub>1,87</sub>	<i>P</i>	Juveniles previous winter	Location	Species	Site × species
Coldest week	0.1	0.5	0.468	0.686	0.032	0.248	0.029
Average temperature	3.6	33.7	<0.000	0.423	0.445	0.247	0.003
SD temperature	0.0	0.2	0.627	0.677	0.030	0.248	0.030
Minimum temperature	3.6	34.0	<0.000	0.670	0.671	0.249	0.003
Maximum temperature	2.9	25.6	<0.000	0.428	0.329	0.247	0.006

Each row gives the results of one of the five GLMs, each using a different measure of winter severity (as indicated in column one). The mean squared error (MS) and resulting *F* and *P*-values are given for each of the primary winter severity variables. Also given are the *P*-values of each of the other variables in each of the respective models. The degrees of freedom (numerator, denominator) for each of the other variables in each model were juveniles (1, 87), site (5, 87), species (7, 87), site × species (11, 87).

*Abudefduf sexfasciatus*, *Abudefduf whitleyi*, *Pomacentrus coelestis* and *Stegastes gascoyni* – and two were butterflyfishes (family Chaetodontidae) – *Chaetodon auriga* and *Chaetodon flavirostris*. All of these species occur on the southern Great Barrier Reef and are generally found in rocky/rubble habitat among and peripheral to coral reefs (Randall *et al.*, 1997). With exception of *S. gascoyni* all the pomacentrids are planktivorous and generally occur in groups of 5–25 individuals. *S. gascoyni* are omnivorous and typically found alone defending a territory (Randall *et al.*, 1997). The two chaetodontids are facultative corallivores which inhabit rubble and rocky structures and feed on a variety of benthic invertebrates with coral being only a minor component of their diet (Cole *et al.*, 2008). In total these species accounted for >97% of the total abundance of all tropical fish species at all locations. Some overwintering occurred at all locations except the most southern one in Merimbula (37°S) and for all species except *A. sexfasciatus*. One or more of the other five species of damselfish were observed to overwinter at all other locations while the two butterflyfishes were observed to overwinter only at Lord Howe Island.

Of the five winter severity metrics used in the GLMs, only average, minimum and maximum winter temperatures were significant (Table 1). The number of juveniles present before the winter was not a significant factor in any of the models but there were significant site × species interactions in all of them. As indicated in the methods section, because of the site × species interaction, we used nonlinear sigmoidal models for each of the species separately to more fully explore the relationships between winter survivors and winter severity. The significance of average, minimum and maximum winter temperature in the GLMs was not surprising given

that these variables are highly correlated. For this reason and because it showed the strongest effect based on comparison of mean squared errors (Table 1), we used the average winter temperature in the sigmoidal model fits. Model fits were significant for all species except *A. sexfasciatus* (Table 2, Fig. 2d). There was no effect of location for any of the *Abudefduf* or *Chaetodon* species, and threshold temperature values ( $x_0$  parameter, point of inflection) were about 17 and 19.5 °C for the two groups, respectively (Table 2). Model fits were different by location for *P. coelestis* and *S. gascoyni*. There was no significant fit to the *P. coelestis* data from the Solitary Islands (Fig. 2g, crosses, Table 2) and both these species had a higher threshold temperature at Lord Howe Island (~19.5 °C) than at the mainland location where they occurred (~17 °C).

The nearshore temperature profiles from the Pathfinder SST data set indicated that two of the warmest winters in this series (since 1985) were in 2001 and 2006, and that this signal is strongly evident at the more southern locations: Merimbula (37°S) to the Solitary Islands (30°S), only weakly so at Byron Bay (29°S) and absent at One Tree Island (23°S) on the southern end of the Great Barrier Reef (Fig. 3a). There is little concordance with this latitudinal trend for Lord Howe Island, which is consistent with the fact that the EAC separates from the coast near the Solitary Islands before heading into the Tasman Sea toward Lord Howe Island (Ridgway & Dunn, 2003).

The HadISST1 data set indicates significant global warming of about 0.5 °C between 1870 and 2000 (Rayner *et al.*, 2003) and a winter (July–August) warming trend of between 0.7 and 1.5 °C for the locations explored in this study (Fig. 3b) confirming previous observations that this area is a hotspot for increasing ocean temperatures

**Table 2** Summary of nonlinear, sigmoidal, model fits of overwinter survival for each species on average winter temperature and location

Species	Location effect		Best fit model statistics							
			Location	N	P ( $\chi^2$ )	$r^2$	$x_0$		dx	
							Estimate	P	Estimate	P
<i>A. bengalensis</i>	0.992	ns	10	0.806	0.93	16.5	<0.001	0.190	0.023	
<i>A. vaigiensis</i>	0.989	ns	10	0.699	0.97	17.1	<0.001	0.170	0.005	
<i>A. whitleyi</i>	0.995	ns	5	0.958	0.99	17.5	<0.001	0.207	0.074	
<i>A. sexfasciatus</i>	Fit not possible (all response values = 0)									
<i>C. auriga</i>	0.377	ns	24	0.929	0.64	19.6	<0.001	0.574	0.005	
<i>C. flavirostris</i>	0.584	ns	24	0.854	0.53	19.9	<0.001	0.557	0.015	
<i>P. coelestis</i>	0.017	Jervis Bay	4	0.761	0.97	16.7	<0.001	0.398	0.082	
		Lord Howe Island	5	0.540	0.96	19.4	<0.001	0.308	0.019	
		Solitary Islands	6	0.041	0.12	Nonsignificant fit				
<i>S. gascoyni</i>	< 0.001	Long Reef	5	0.767	0.97	17.1	<0.001	0.277	0.158	
		Shelly Beach	5	0.884	0.22	17.3	<0.001	0.815	0.551	
		Lord Howe Island	5	0.373	0.96	19.9	<0.001	0.035	0.983	

ns, location parameter was nonsignificant, model fit to data from all locations combine.

Statistics are given for fits to data from all locations combined where the coefficient for the location variable was nonsignificant ( $P > 0.05$ , 'Location effect  $P$ -value') and for individual locations where it was. The sample size ( $N$ ), quality of fit (probability of two-tailed  $\chi^2$ ) and variance explained ( $r^2$ ) of each model is given along with the estimate and  $P$ -value for the inflection ( $x_0$ ) and slope (dx) parameters of the sigmoid equation.

(Smith, 2000; Poloczanska *et al.*, 2007). Average increases at our study locations were (in °C): One Tree Island +0.75, Byron Bay +0.98, Solitary Islands +1.02, Lord Howe Island +0.66, Port Stephens +1.07, Sydney +1.22, Jervis Bay +1.32, Batemans Bay +1.50 and Merimbula +1.48. The general cooling observed until the mid-1920s means these changes would be an additional 0.5–1.0° greater over the last 90 years.

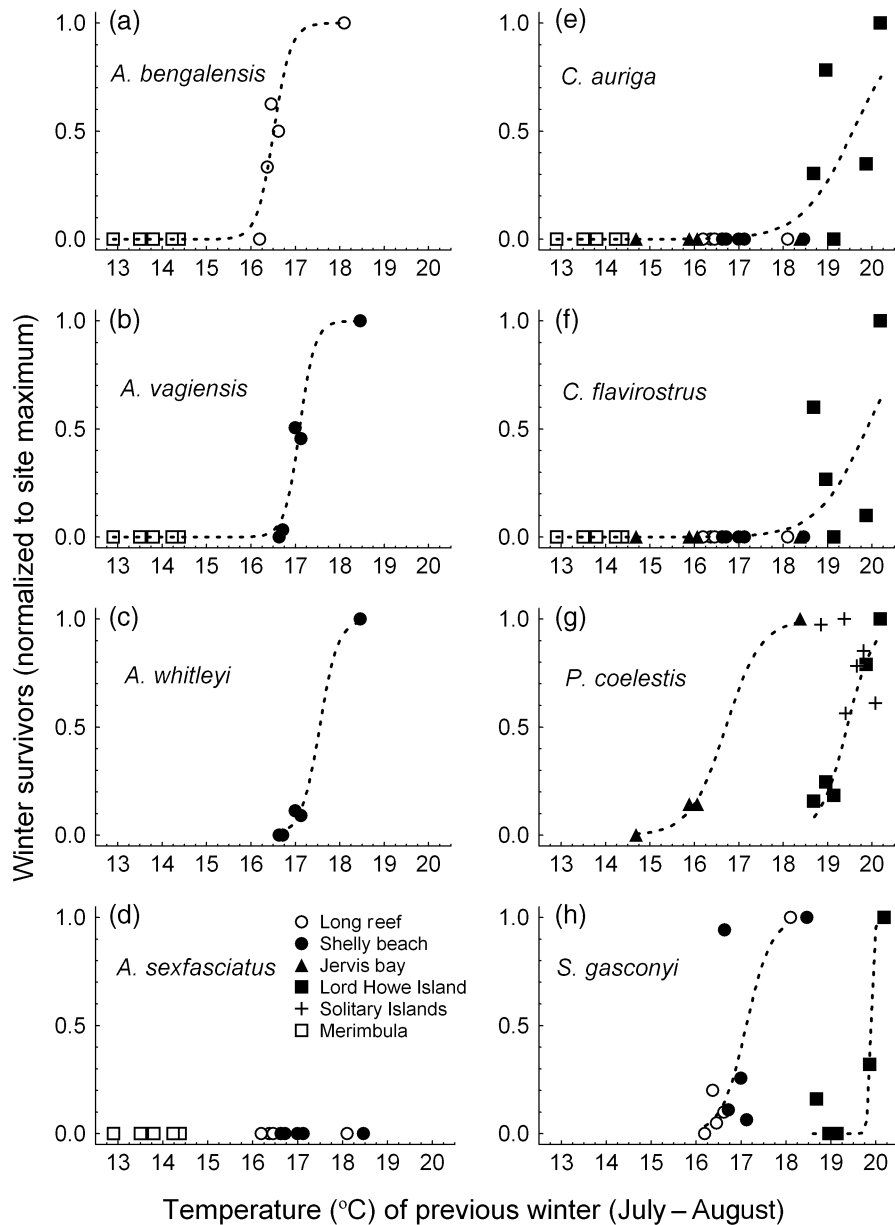
As the average water temperature increased over the last 90 years, the type of winter which a tropical fish can survive became increasingly more common (Fig. 3c). The average threshold overwintering temperature for all species in this study on mainland Australia was about 17°C and at northerly locations like One Tree Island, Byron Bay and the Solitary Islands, winters have always been warmer than this value. Indeed, year-round populations are present from the Solitary Island northwards, and this temperature seems to be necessary for strong overwinter survival. On the contrary, in Merimbula (37°S), where no overwinter survival was observed, and also Batemans Bay to the north, temperatures have never exceeded this minimum. However, in the mid-temperate locations such as Port Stephens, Sydney and Jervis Bay, the frequency of warm winters has steadily increased since the mid-1980s. This warming has already resulted in an increased incidence of overwinter survival during warm years. However, the establishment of persistent populations has so far been

hindered by ensuing cold winters. If the present ocean warming trend continues at the same rate (as predicted, Lough, 2008), then minimum threshold winter temperatures would be reached every winter in Sydney by about 2080 (linear fit to Sydney data in Fig. 3c;  $n = 23$ ,  $r^2 = 0.92$ ,  $P < 0.001$ ; increase in frequency of warm winter is 0.9% yr<sup>-1</sup>).

## Discussion

Based on these results we conclude that, (a) the ability of four common species of tropical damselfishes to overwinter at temperate latitudes increases with average winter temperatures and seems to do so substantially between 16.5 and 17.5°C, (b) this does not seem to be the case for one species, *A. sexfasciatus* which was never observed to overwinter at our study locations, (c) that the two butterflyfish species observed require temperatures warmer than 19°C to successfully overwinter and (d) that present warming trends will steadily increase the frequency of survivable winters, thus opening the door for potential range expansions of these species provided the biophysical requirements of the adult stage are also met (especially for reproduction).

The lack of a temperature effect on overwintering for *P. coelestis* at the northern-most location, Solitary Islands, is not surprising given that average winter temperatures at this latitude (30°S, Fig. 3a) are always

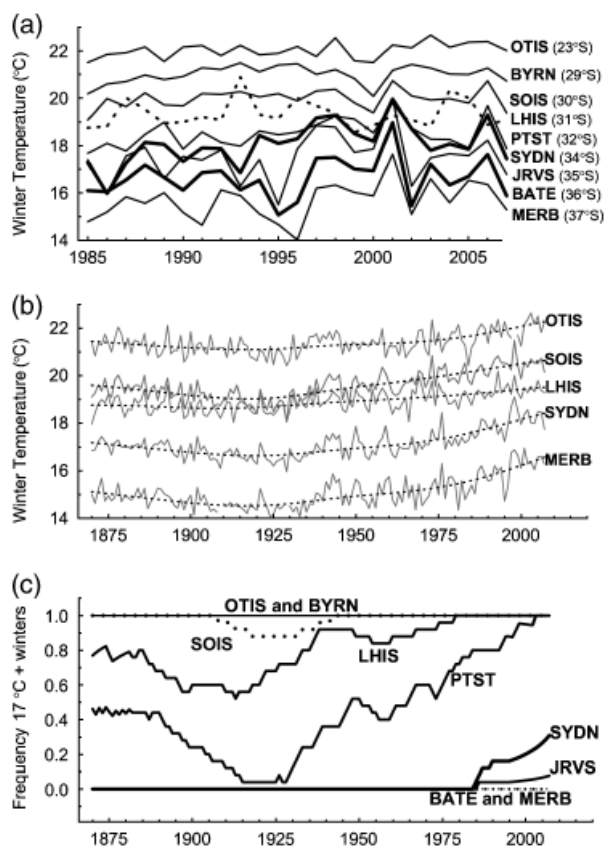


**Fig. 2** Summary of relationship between the number of winter survivors of each species (a-h, one species per panel) at each location (normalized to the maximum number observed at that location) and the average winter temperature at that location. Species are as listed for each plot and points are coded by location as given in (d). Dashed curves are best fit from significant ( $P < 0.05$ ) sigmoidal model fits as described in the text.

greater than threshold temperatures for overwinter survival and year-round breeding populations are known to exist there (W. Figueira, personal observation). The lack of a fit for *S. gascoyni* at Shelly Beach in Sydney was due to survival being unusually high, not only over the warm winter of 2006 (18.5 °C) but also over the relatively cold winter of 2007 (16.6 °C). Given that starvation endurance is positively size dependent (Biro *et al.*, 2004), this pattern may indicate that bottleneck overwinter temperatures are for only the first year

after establishment. Thus for some species, even one very warm year followed by even a mildly cold one will be enough to allow survival over multiple years.

The higher threshold temperature for *P. coelestis* and *S. gascoyni* at Lord Howe Island (where the average winter temperature never fell  $< 18.5$  °C) suggests these fish may be adapted to warmer waters. While the mainland populations are very likely sourced from common upstream locations (Booth *et al.*, 2007), local recruitment (return and settlement of larvae to



**Fig. 3** Winter temperature summaries for locations along the east coast of Australia based upon (a) the Pathfinder sea surface temperature (SST) data set and (b) the HadISST1 data set (dashed line distance weighted average, not all locations shown for clarity). (c) Frequency of winters with an average temperature  $> 17^{\circ}\text{C}$  for each of the locations based upon the HadISST1 data set. Location abbreviations are as follows OTIS, One Tree Island; BYRN, Byron Bay; SOIS, Solitary Islands; LHIS, Lord Howe Island; PTST, Port Stephens; SYDN, Sydney; JRVS, Jervis Bay; BATE, Batemans Bay; MERB, Merimbula.

their natal habitat) does occur to Lord Howe Island, both for endemic and nonendemic fishes (Patterson & Swearer, 2007).

Larval supply is certainly an important factor for fish population dynamics (Doherty & Fowler, 1994) (though to a lesser extent where populations are not recruitment limited, Caselle, 1999; Hixon & Jones, 2005) and certainly a key factor for driving range shifts of marine organisms (Dunstan & Bax, 2007). However, in this study there was no indication that variations in the supply of settlers to locations, as measured by the prewinter abundance of juveniles, affected the number ultimately surviving the winter. Previous work however has generally concerned established populations, well within their range where the physiological constraints imposed by reduced winter temperatures appear to be not as important as

they are for the expatriate populations of tropical fish studied here.

Temperature is but one aspect of the biophysical environmental which must match the requirements of a species for a range shift to occur. For all organisms, and coral reef fish are no exceptions, habitat quality (food and refuge availability, competitor and predator density) strongly affects factors such as the abundance, size structure and species composition (e.g. Connell & Jones, 1991; Hixon & Beets, 1993; Friedlander & Parrish, 1998), survival (e.g. Hixon & Beets, 1993; Nemeth, 1998; Figueira *et al.*, 2008), and even growth and fecundity (e.g. Jones, 1986; Schultz & Warner, 1991; Figueira *et al.*, 2008). In combination, these factors thus affect not only the presence/absence of species but also the nature of postsettlement dynamics (Eklund, 1997). It is important to note, however, that in novel thermal environments, interaction between an individual and its environment will be modified by temperature due to its metabolic and physiological effects (Angilletta *et al.*, 2002). Reduced temperatures will result in lower growth (Angilletta *et al.*, 2002) and can cause reduced escape ability of prey (e.g. Batty & Blaxter, 1992; Lyon *et al.*, 2008) both of which will lead to increased mortality. These ecological interactions help to explain the difference between the overwinter survival threshold temperatures observed in this field study ( $\sim 17^{\circ}\text{C}$ ) and the critical thermal minimum (limits of physiological survival) of between  $12.2$  and  $15.9^{\circ}\text{C}$  which have been established for similar coral reef fish species (Eme & Bennett, 2008; Figueira *et al.*, in press).

In the case of the juvenile tropical reef fish observed in this study, it would seem that the minimum biophysical environmental requirements have been met as evident by their presence at the study locations. Ontogenetic changes in these biophysical environmental factors can of course alter the predictions regarding the success or failure of range shifts in response to climate change (Snover, 2008). Thus for any range shift to occur for the species discussed in this study, the biophysical environment would have to be appropriate for the adult stages as well. In fact for all of the species described, juvenile and adult habitat and food requirements do not differ substantially. Adults of all species continue to occupy rocky reef habitats though the movement range for the *Abudefduf* damselfishes and *P. coelestis* as well as both of the butterflyfishes does expand slightly (author's personal observation). Also, mortality is generally reduced in adult stages of reef fish relative to juveniles (Jones, 1991) and adults are more thermally robust (Hurst, 2007).

Two remaining questions pertaining to the potential for range expansion of the species in this study are those which concern the ecological interactions of



adults and their reproductive potential. While ecological interactions are certainly minimal at present due to the rarity of adults at most southern locations, observation of the adult populations of *A. vaigiensis* and *P. coelestis* which do occur in the Solitary Islands would indicate they do have the ability to integrate into the community of predators and competitors which occur in these rocky nearshore habitats. As for breeding potential, there is evidence that reproductive capacity is more sensitive to temperature than survival (Mora & Ospina, 2002). In addition, several of these socially breeding species may require minimum densities for successful reproduction (Tyler, 1995). However, breeding does occur for two damselfishes *A. vaigiensis* and *P. coelestis* in the Solitary Islands where average winter temperatures were typically about 18 °C. Therefore if threshold temperatures for reproduction are greater than those observed for survival, it would seem to be only a difference of 0.5° or so, at least for *A. vaigiensis* and *P. coelestis*.

This study highlights a consistent relationship for at least seven coral reef fish species between winter temperatures and overwinter survival at temperate latitudes and identifies ecologically relevant threshold temperatures of between 17 and 19 °C depending on the species and location. SST is predicted to rise between 1 and 3 °C by 2100 on the Great Barrier Reef, with increases likely to be even greater to the south and during the winter (Poloczanska *et al.*, 2007; Ridgway, 2007; Lough, 2008). With the frequency of warm winters increasing, the possibility grows for southward populations of these species to become established year-round. For this to occur, conservatively 100% of winters would need to be above this threshold (assuming adult overwinter survival threshold temperatures are the same as juveniles). Under present ocean-warming predictions, year-round persistence would be possible for the species in this study as far south as Sydney (34°S) by about 2080. While there are not enough data from this study to assess adult overwinter survival thresholds, because of storage effects (Warner & Chesson, 1985), if adult thresholds are slightly lower than those for juveniles (Hurst, 2007), then not every winter would need to be over this threshold and year-round persistence may well occur before the predicted date.

The evidence described above would suggest that reproduction would be possible at or perhaps slightly above the indicated threshold temperatures for at least some of the species described in this study. As a consequence, the range of reproductively active populations would substantially increase. A range shift of this magnitude (about 175 km decade<sup>-1</sup>) would be among the most rapid of those observed to date (Parmesan & Yohe, 2003) and is driven by the long-distance connectivity afforded to these populations by the EAC. Of

course climate change is likely to affect not just coastal temperatures but will also change patterns of connectivity through a variety of mechanisms (Munday *et al.*, in press). Increasing temperatures will enhance larval growth, thus reducing larval durations (O'Connor *et al.*, 2007; Munday *et al.*, 2008) but are also likely to alter ocean currents in a manner that may enhance or retard dispersal depending on location (Munday *et al.*, 2008). Thus while the exact nature of connectivity changes are hard to predict, the EAC will remain a dominant feature of the system (Cai *et al.*, 2005) and the tropical-temperate connectivity observed in this study will remain in some form. Given adequate larval supply and the apparent availability of suitable food and habitat, overwinter survival will remain as a primary bottleneck to any range shift for the tropical coral reef fish species described in this study.

The observations of this study would suggest that in regions with long-distance connectivity afforded by dominant boundary currents, climate-induced range shifts have the capacity to be rapid and dramatic. The range of taxa for which shifts can occur will depend strongly upon their biophysical environmental requirements, especially for food, habitat and reproduction. Thus while such shifts would not be expected for specialists such as obligate corallivorous coral reef fish, for the types of habitat and dietary generalists (especially planktivores) identified in this study, range expansions are a very real possibility. Further study would be required to determine what effects such range expansions may have on local community structure and diversity. Where impacts are likely to be large, elucidating their causes, consequences and dynamic nature will be key to understanding and managing coastal ecosystems under climate change.

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