





'Stick with your own kind, or hang with the locals?' Implications of shoaling strategy for tropical reef fish on a range-expansion frontline

Shannen M. Smith¹  | Rebecca J. Fox^{1,2}  | David J. Booth¹  | Jennifer
M. Donelson^{1,3} 

¹School of Life Sciences, University of Technology Sydney, Ultimo, NSW, Australia

²Division of Ecology and Evolution, Research School of Biology, Australian National University, Canberra, ACT, Australia

³ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Qld, Australia

Correspondence

Shannen M. Smith, School of Life Sciences, University of Technology Sydney, Ultimo, NSW, Australia.
Email: shannen.m.smith@outlook.com

Present address

Shannen M. Smith, Centre for Marine Bio-Innovation, Evolution and Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW, Australia.

Funding information

UTS School of Life Sciences; Ian Potter Foundation Science; UTS Chancellor's Postdoctoral Research Fellowships

Abstract

Range shifts of tropical marine species to temperate latitudes are predicted to increase as a consequence of climate change. To date, the research focus on climate-mediated range shifts has been predominately dealt with the physiological capacity of tropical species to cope with the thermal challenges imposed by temperate latitudes. Behavioural traits of individuals in the novel temperate environment have not previously been investigated, however, they are also likely to play a key role in determining the establishment success of individual species at the range-expansion forefront. The aim of this study was to investigate the effect of shoaling strategy on the performance of juvenile tropical reef fishes that recruit annually to temperate waters off the south east coast of Australia. Specifically, we compared body-size distributions and the seasonal decline in abundance through time of juvenile tropical fishes that shoaled with native temperate species ('mixed' shoals) to those that shoaled only with conspecifics (as would be the case in their tropical range). We found that shoaling with temperate native species benefitted juvenile tropical reef fishes, with individuals in 'mixed' shoals attaining larger body-sizes over the season than those in 'tropical-only' shoals. This benefit in terms of population body-size distributions was accompanied by greater social cohesion of 'mixed' shoals across the season. Our results highlight the impact that sociality and behavioural plasticity are likely to play in determining the impact on native fish communities of climate-induced range expansion of coral reef fishes.

KEYWORDS

behaviour, biological invasion, competition, coral reef fish, range-shift, social system, vagrant fish

1 | INTRODUCTION

Biological community structure is being rapidly altered on a global scale by the impacts of climate change. Increasing global temperatures have caused both terrestrial and marine organisms to undergo latitudinal and altitudinal range expansion (e.g. Baird, Sommer, & Madin, 2012; Hickling, Roy, Hill, & Thomas, 2005; Last et al., 2011;

Pitt, Poloczanska, & Hobday, 2010; Wernberg et al., 2011; Yamano, Sugihara, & Nomura, 2011), with existing communities and 'invading' organisms being forced to interact as they compete for available resources (Zeidberg & Robinson, 2007). The consequences of these climate-induced biological invasions have already been documented in a number of ecosystems where the arrival of novel species into new locations has resulted in complete phase shifts and changes in

ecosystem functionality (e.g. Johnson et al., 2011; Ling, 2008; Saintilan, Wilson, Rogers, Rajkaran, & Krauss, 2014; Vergés et al., 2014), particularly in marine ecosystems (Poloczanska et al., 2013; Sorte, Williams, & Carlton, 2010). Predicting the extent and pace of climate-induced range-shifts of species is necessary to understand the potential changes in ecosystem functioning that could result from these biological invasions. This now represents a significant challenge for ecologists within the anthropocene. Successfully predicting species' range-shift patterns relies not only on an understanding of how adaptation to abiotic environmental variables might affect the successful establishment of a species beyond its existing range, but also how behaviour, and the potential for plasticity of expression of behavioural traits, might interact with the new environment (Holway & Suarez, 1999; Melles, Fortin, Lindsay, & Badzinski, 2011; Wong & Candolin, 2015).

For 'invading' species, successful range expansion requires the establishment of a sustainable population despite initial low densities. Evidence suggests that population density can limit range-shift success for individuals arriving at a new location (Johnson, Liebold, Tobin, & Bjørnstad, 2006; Keitt, Lewis, & Holt, 2001; Lewis & Kareiva, 1993). This can be in part due to 'Allee effects' (Allee, 1931, 1938), and thus overcoming Allee effects following expansion to a new location can be critical to biological invasion success. One behavioural strategy that can enhance survival is engagement in group living. Although the benefits gained through social grouping vary depending on the size of groups and familiarity of individuals within it (Krause & Ruxton, 2002), it is generally accepted that individuals living in groups can benefit from reduced stress (Hennessy, Kaiser, & Sachser, 2009), improved threat detection (Ward, Herbert-Read, Sumpter, & Krause, 2011), reduced individual risk (predator 'dilution', Foster & Treherne, 1981), improved acquisition of information (Brown & Laland, 2003) and reduced physiological cost of movement (Marras et al., 2015), albeit at the cost of increased competition for space and food (Krause & Ruxton, 2002). Most organisms are observed to form conspecific groups, with many showing a further preference for grouping with related individuals, for example such as in fish (Frommen & Bakker, 2004; Thünken, Hesse, Bakker, & Baldauf, 2016; Ward & Hart, 2003) and domesticated animals (Bøe & Færevik, 2003). This preference for similarity is believed to reduce the 'oddity effect' and minimize the risk that an individual will stand out and increase their risk of predation (Landeau & Terborgh, 1986; Theodorakis, 1989). In some cases, however, usually when resource niche overlap is minimal, heterospecific groups are observed, for example in fishes (Overholtzer & Motta, 2000; Sweatman, 1983), birds (Fitzgibbon, 1990) and marsupials (Coulson, 1999).

For species experiencing climate-induced range shifts, where environmental novelty imposes a further challenge in terms of population establishment, forming heterospecific groups with native species may provide benefits in terms of (1) increasing densities when conspecifics are scarce, allowing 'invaders' to experience the benefits of group living listed above; and (2) providing social learning cues that offset the gaps in 'invaders' knowledge associated

with being in a novel environment with novel predators and resources. Of course, any such benefits have to be weighed against the potentially greater costs of being in competition with group members who are in their native environment and are therefore likely to have home advantage (e.g. Olden, Larson, & Mims, 2009). Whether the benefits outweigh the costs will determine whether conspecific grouping represents an adaptive behavioural strategy for range-shifting species. Should you stick with your own kind, or should you hang with the locals?

In this study, we examined the effect of shoaling strategy on the population dynamics of juvenile tropical reef fishes that are transported annually by the East Australian Current (EAC) from the Great Barrier Reef to temperate waters off the south east (SE) coast of Australia (Booth, Figueira, Gregson, Brown, & Beretta, 2007; Feary et al., 2014; Figueira & Booth, 2010). This annual 'invasion' is just one of several expatriations of tropical fishes to temperate waters that occur worldwide (Japan: Yamano et al., 2011; Nakamura, Feary, Kanda, & Yamaoka, 2013; Western Australia: Hutchins & Pearce, 1994 and North America: Eme & Bennett, 2008). In recent years, SE Australia has seen an increase both in the numbers of 'invaders' and in their survival through the temperate winter season and into the next summer season (termed overwintering) (Booth et al., 2007), due to both the strengthening of the EAC (Ridgeway, 2007) and faster-than-average warming of ocean waters at this global hot-spot (Hobday & Pecl, 2014). The climate-mediated poleward range-shift of coral reef fishes is therefore fast becoming a reality (Hobbs, 2010; Lough, 2008; Munday, Jones, Pratchett, & Williams, 2008; Vergés et al., 2014, 2016). To date, however, research has been concentrated on monitoring of tropical species' arrivals and laboratory testing of the physiological capacity of particular species to cope with the thermal fluctuations associated with temperate latitudes (Figueira, Biro, Booth, & Valenzuela, 2009; Figueira & Booth, 2010). There have been very few previous field-based investigations of the behavioural strategies of these so-called tropical 'vagrants' in their novel environment (however see Beck, Feary, Fowler, Madin, & Booth, 2016; Beck, Feary, Nakamura, & Booth, 2016).

One species of tropical fish larvae that is regularly transported to temperate waters off the SE Australian coast is the Indo-Pacific sergeant damselfish, *Abudefduf vaigiensis* (*Pomacentridae*). Juveniles of this species start to appear in coastal rocky reef habitats around Sydney in January of each year (Austral summer). These juveniles are observed to form shoals, in some cases comprised only of conspecifics (hereafter referred to as 'tropical' shoals), but in other cases *A. vaigiensis* juveniles join heterospecific shoals with morphologically similar temperate native species such as the Australian Mado, *Atypichthys strigatus* (*Kyphosidae*), and, less commonly, the Eastern hulafish, *Trachinops taeniatus* (*Plesiopidae*) (hereafter referred to as 'mixed' shoals). Both types of shoals can be observed within meters of each other in the same stretch of habitat and dynamics of the shoals change through the season as new recruits enter and older juveniles grow. The aim of this study was to determine whether juvenile *A. vaigiensis* derive any benefits from shoaling with native species, either in larger shoals with resident temperate species, (in terms of avoiding low-

population density costs) or though behavioural benefits from shoaling with knowledgeable residents (e.g. knowledge of predators). Specifically, we documented the composition and behavioural attributes of tropical and mixed shoals containing juvenile *A. vaigiensis* over a 20 week period as water temperatures fell towards their winter minimum, and compared the effect of behavioural shoaling strategy on the underlying demographic dynamics (changes in distribution of body-sizes and abundance of shoal members through time) of *A. vaigiensis* recruiting to temperate shorelines.

2 | MATERIALS AND METHODS

2.1 | Study species and location

The planktivorous damselfish, *A. vaigiensis*, is one of the most abundant of the species of juvenile tropical reef fishes observed at temperate latitudes over the summer months (Booth et al., 2007). In its native environment the species is site-attached (Allen, Steene, Humann, & DeLoach, 2003) and reaches up to 20 cm in length as an adult (Kuitert, 1993). The temperate native species *A. strigatus* and *T. taeniatus* are both very common along the SE Australian coastline growing up to 25 cm and 10 cm, respectively, as adults (Kuitert, 1993). *T. taeniatus* is planktivorous, but is less commonly observed forming shoals with tropical vagrant *Abudefduf* species compared to the omnivorous *A. strigatus*, potentially due to the greater visual likeness between *A. vaigiensis* and *A. strigatus* (Figure S4 provides a visual comparison of the three species).

Shoaling behaviour of juvenile *A. vaigiensis* was observed through time at locations within Little Manly (33°48'27"S, 151°17'13"E), and Cabbage Tree Bay (33°48'01"S, 151°17'51"E), which are representative of the shallow coastal marine habitats into which seasonally invading juvenile tropical reef fish settle each year and into which there has been consistent tropical recruitment since 1935 (Feary et al., 2014). The topographic structure and benthic community composition of the census locations consists of large exposed rock and areas with high macroalgal cover as well as rocky substrate covered in low-lying turfing algae. Mean daily water temperature was similar across survey locations until May (end of the Austral autumn) when the temperature at Little Manly declined at a faster rate and remained on average $1.0 \pm 0.04^\circ\text{C}$ lower throughout winter than Cabbage Tree Bay. Minimum winter temperatures for the two sites of 15.3°C and 16.2°C , respectively, occurred in July (Figure 1).

2.2 | Quantifying shoal characteristics

The characteristics of 'tropical' and 'mixed' shoals were quantified by a single observer on snorkel (the same observer collected all data; sites <3 m depth). A 'mixed' shoal was defined as a group of at least five fishes comprising both the focal tropical species *A. vaigiensis* and temperate species *A. strigatus* (or *T. taeniatus*), while a 'tropical' shoal was defined as more than five individuals belonging to the *Abudefduf* genus (NB very few *Abudefduf* spp. individuals not of the study species (i.e. *A. bengalensis*, *A. sexfasciatus*, *A. whitleyi* (*Pomacentridae*))

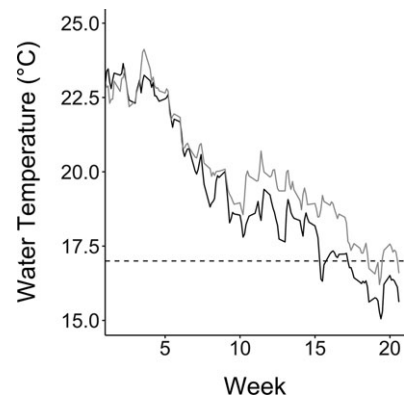


FIGURE 1 Profile of water temperatures recorded every 30 mins at Little Manly (black line) and Cabbage Tree Bay (grey line) over the 20-week study period (Mar–Jul 2015). Temperature was recorded using HOBO TidbiT v2 Data Loggers (64K Temp-alarm data logger; temperature logged every 30 mins) positioned at a depth of 2–3 m. The dotted line at 17°C represents the current threshold estimate for juvenile tropical species' survival (Figueira & Booth, 2010)

were observed and those that were did not persist past week 12 of the study). Starting in March 2015, shoals containing *A. vaigiensis* individuals within a fixed stretch of coastline (~115 m at Little Manly and ~180 m at Cabbage Tree Bay) were censused weekly for a period of 20 weeks (final observations carried out in July 2015) and always between the hours of 08:00–14:00. Upon arrival at a shoal, the observer recorded (1) total abundance of individuals within the shoal, (2) number of *A. vaigiensis* in the shoal and (3) body size (total length in mm) of each individual within the shoal (to nearest 5 mm size class). Reliability of observer size estimates were tested in a separate exercise conducted at a third site where fish body sizes were estimated and then compared to actual, measured sizes (Figure S1; Pearson's correlation coefficient $r = .967$, $p = .014$).

2.3 | Quantifying *A. vaigiensis* behaviour and shoal cohesion

Following on from the documentation of shoal characteristics (during which time the fishes had acclimatized to the presence of the snorkeler), a 10 min period of behavioural observations was conducted. At 1 min intervals within this period, the observer selected an *A. vaigiensis* individual within the shoal at random, recording its position in the water column in terms of distance from nearest point of shelter (defined as nearest obscuring structure representing a refuge from predators, following Beck, Feary, Fowler, et al., 2016; Beck, Feary, Nakamura, et al., 2016). At the end of the 10 min period, the total area over which the shoal had been observed swimming was mapped, using a system of landmarking (following Madin, Gaines, & Warner, 2010). For each shoal at least five landmark points were marked and the distance between points measured at the end of the observations period so as to avoid influencing behaviour of the shoal. If an individual left the shoal (i.e. swam outside the visual range of the observer and the focal shoal) and returned (i.e. an excursion), this was included in the

home range measurement, however, if an individual did not return, this was not included as part of the census (i.e. transience was ignored).

To investigate the effect of shoal type on overall shoal cohesion, we first calculated a home range (HR) area of each shoal on each census date, based on the measurements taken in the field (using minimum convex polygons). The social cohesion of the shoal was calculated as $\frac{\log(\text{home range})}{\text{total abundance}}$, where higher values are indicative of lower social cohesion within the group.

2.4 | Statistical analyses

The influence of shoal type (tropical or mixed) on the underlying demographic dynamics of *A. vaigiensis* populations was examined by comparing the change in body size distributions through time of *A. vaigiensis* individuals. Body size distributions were utilized due to their established link to population trends in ecology (Condit, Sukumar, Hubbell, & Foster, 1998; White, Ernest, Kerkhoff, & Enquist, 2007), providing a way to compare the fundamental demographic processes occurring at the shoal scale over the season and hence the relative likelihoods of persistence of particular populations of tropical invaders. Four time-points within the study period (weeks 1, 6, 11 and 16) were selected to represent the initial, middle and final phases of the tropical vagrant season, corresponding to observed step-changes in water temperature recorded at the study sites (see Figure 1). For each of the two shoal types in turn, observed *A. vaigiensis* were grouped into 10 mm size classes, the number of individuals within each size class summed across all shoals and these totals converted to a proportion of the overall number of *A. vaigiensis* observed in that shoal type. Potential differences in the resulting distributions of body sizes between shoal types at each time period were tested for using a two-sample Kolmogorov–Smirnov test in *SPSS* Statistics 23.

The influence of shoal type on the behaviour (boldness, HR and social cohesion of individuals within a particular shoal) and abundance of *A. vaigiensis* through time was investigated using a series of linear regression models, all with Gaussian error structure. Specifically, we ran a series of linear models to test how shoal type affected the behaviours of *A. vaigiensis* individuals, with proximity to shelter (as a measure of relative boldness), shoal cohesion and log HR as our response variables, with shoal type and time (week of survey) as fixed factors and individual shoals as replicates. We also tested for the effect of shoal type on total abundance of individuals in a shoal (i.e. Allee effects) and the number of *A. vaigiensis* censused per shoal (proxy for survival) with shoal type and time (week of survey) again as fixed factors. Linear models were run using R package “base” (R Core Team, 2012).

3 | RESULTS

3.1 | Effect of shoaling strategy on *A. vaigiensis* population dynamics

At the commencement of the study (week 1) there was a significant difference in the distribution of body sizes of *A. vaigiensis* censused between ‘tropical’ and ‘mixed’ shoals, with ‘tropical’ shoals having

higher proportions of the larger recruits (Figure 2a; $D_{53,68} = 0.273$, $p = .014$). Over the next 2 months, this gap was closed, with no significant differences in the distribution of body sizes of *A. vaigiensis* between ‘mixed’ and ‘tropical’ shoals observed in week 6 (Figure 2b; Kolmogorov–Smirnov two-sample test, $D_{75,109} = 0.169$, $p = .140$), or week 11 (Figure 2c; Kolmogorov–Smirnov two-sample test, $D_{25,37} = 0.096$, $p = .998$). Finally, by week 16 of the study, a significant difference was again evident in the distribution of body-sizes of *A. vaigiensis* within ‘mixed’ and ‘tropical’ shoals, but this time with ‘mixed’ shoals containing higher proportions of larger-sized individuals (Figure 2d; Kolmogorov–Smirnov two-sample test, $D_{50,28} = 0.491$, $p = .0002$).

Up to 63 individuals were observed in a shoal throughout the observation period. The total number of individuals within both shoal types reduced over time as water temperature declined towards winter minima ($F_{3,102} = 6.009$, $p < .001$, adjusted $R^2 = .13$), with the total number of individuals in the shoal on average decreasing by 1.3 individuals per week (Figure 3a; week: $t = -2.122$, $p = .036$). There was no significant difference in the number of individuals in the two shoal types (shoal type: $t = -1.313$, $p = .19$) or between the two shoal types in the rate of this decline (week*shoal type: $t = 1.017$, $p = .31$). These patterns were similar when considering only the number of tropical individuals within both shoal types (Figure 3b; $F_{3,103} = 6.728$, $p < .001$, adjusted $R^2 = .14$; week: $t = -2.260$, $p = .026$). The number of tropical individuals in a shoal

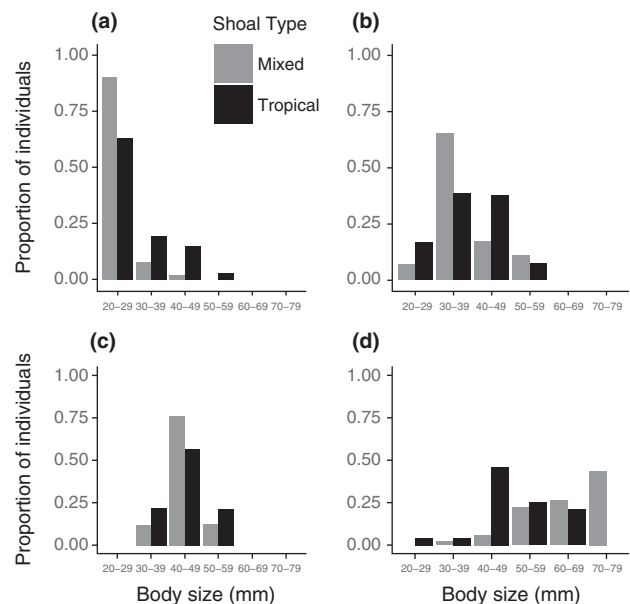


FIGURE 2 Body size (TL in mm) frequency distributions of *Abudefduf vaigiensis* individuals observed within ‘tropical’ and ‘mixed’ shoals at (a) week 1, (b) week 6, (c) week 11, and (d) week 16. Selected time-points correspond to the step-changes in water-temperature recorded at the study sites, with week 16 being the final week at which temperatures at both sites were above the current estimate of critical thermal minimum for tropical vagrant species. Frequency distributions display the proportion of *A. vaigiensis* individuals in size classes within each shoal type

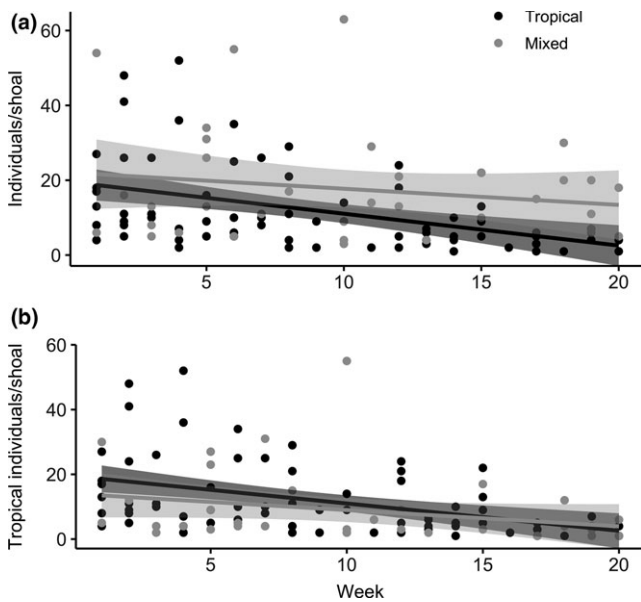


FIGURE 3 Observed abundance through time of (a) total number of individuals and (b) number of *Abudedefduf vaigiensis* per shoal for 'tropical' (solid trendline) and 'mixed' shoals (dashed trendline)

was similar regardless of mixed vs. tropical shoal type (shoal type: $t = -1.313$, $p = .19$) or the rate of decline in abundance of *A. vaigiensis* between the two shoal types (week*shoal type: $t = 0.946$, $p = .346$).

3.2 | Effect of shoaling strategy on *A. vaigiensis* behaviour

The distance from the nearest shelter of *A. vaigiensis*, did not show a significant decline (Figure 4a; $F_{3,101} = 5.916$, $p < .001$, adjusted $R^2 = .12$; week: $t = -1.861$, $p = .07$), however visually, both shoals did tend to remain closer to available shelter towards the end of the season (Figure 4a). There was no significant effect of either shoal type on distance from shelter ($t = -1.128$, $p = .26$) or the pattern of distance from shelter through time (week*shoal type: $t = 0.604$, $p = .55$).

The social cohesion of 'mixed' and 'tropical' shoals were observed to be similar at the start of the study (Figure 4b; $F_{3,100} = 9.333$, $p < .001$, adjusted $R^2 = .20$), but diverged significantly through the season depending on shoal type (week*shoal type: $t = -2.793$, $p = .006$). While 'mixed' shoals maintained a similar cohesion level throughout the season, 'tropical' shoals became less cohesive as time progressed (higher values of the response variable on the y-axis are indicative of lower social cohesion) (Figure 4b). This difference in shoal cohesion was due to changes in both log HR (Figure S2) and total abundance (Figure 1) in combination, since neither one was significant on its own (see total abundance above; log HR: $F_{3,102} = 4.024$, $p = .009$, adjusted $R^2 = .09$; week: $t = -1.152$, $p = .25$; shoal type: $t = 0.285$, $p = .78$; week*shoal type: $t = -0.24$, $p = .81$). Specifically 'tropical' shoals had a tendency to maintain the same home range area through time despite declining numbers of

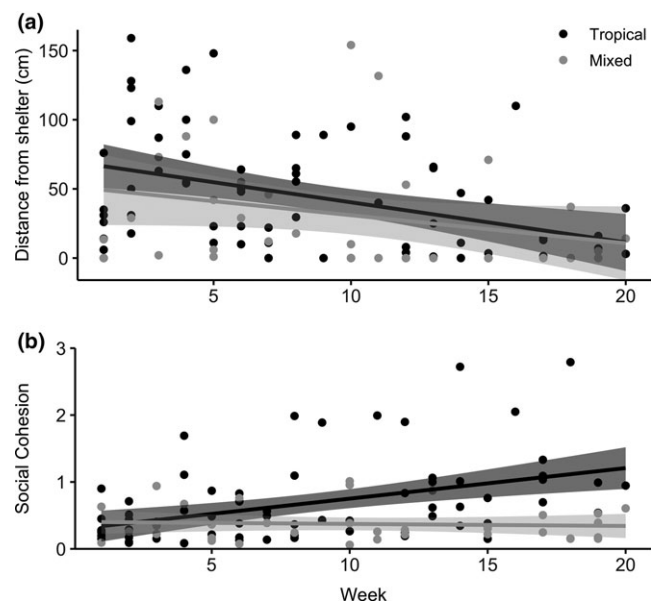


FIGURE 4 Change in behaviour of *Abudedefduf vaigiensis* in 'tropical' (solid line) and 'mixed' (dashed line) shoals over the 20 week study period, in terms of (a) average distance from shelter of *A. vaigiensis* individuals within the two types of shoals and (b) social cohesion exhibited by the two types of shoals

shoal members while 'mixed' shoals exhibited a decrease in home range area as the season progressed as well as a higher total abundance towards the end of the season.

All shoals were observed using a large proportion of the water column over the study period, with the mean height of the shoal above the substratum ranging from 9 – 240 cm (Figure S3). Obviously the upper bound of this range was governed by tidal state, but the spread of measures obtained over the course of study was similar for both shoal types. Measures of distance from the substratum were therefore poorly described by the model including shoal type and week of the season ($F_{3,95} = 0.240$, $p = .864$, adjusted $R^2 = -.02$). There was no effect of shoal type ($t = 0.154$, $p = .788$) on distance of shoal above the substratum and no change in the position of shoals above the substratum was observed across the season (week: $t = 0.217$, $p = .83$).

4 | DISCUSSION

The distributions of shifting marine species in the future will depend not only on predicted changes in sea surface temperatures, but also on the outcome of behavioural interactions between resident and invading species. Here, we show that the behavioural shoaling strategy adopted by seasonally invading *A. vaigiensis* can impact on underlying population dynamics, with *A. vaigiensis* in mixed shoals displaying larger body sizes by the end of the recruitment season than individuals that shoaled with only tropical conspecifics. This is likely to be an important benefit for invading tropical fishes, as increased body size is typically positively associated with fitness

benefits, including survival probability (McCormick & Hoey, 2004), fecundity (Cole & Sadovy, 1995; Persson, Byström, Wahlström, Andersson, & Hjelm, 1999) and reproductive success (Kuwamura, Karino, & Nakashima, 2000): the so-called “bigger is better” pattern (Kingsolver & Huey, 2008). We suggest that the mechanism behind this enhanced body size effect is not driven by population Allee effects as hypothesized, since we found no evidence that group size was driving observed benefits to tropical species in mixed shoals. Rather it appears to occur through a social learning effect, with *A. vaigiensis* in mixed shoals expressing greater social cohesion with shoal mates. The benefits of mixed shoaling did not translate into greater overall levels of survival in the current study, but this is likely due to the fact that water temperatures eventually fell below the critical minimum thermal limit for *A. vaigiensis* (~17°C; Figueira & Booth, 2010).

It is already well-known that behavioural traits and patterns can contribute to the success of biological invasions (Holway & Suarez, 1999) and that successful range expansion is linked to the adaptive behaviour of individuals on the invasion front-line (Alford, Brown, Schwarzkopf, Phillips, & Shine, 2009; Llewelyn, Phillips, Alford, Schwarzkopf, & Shine, 2009; Phillips, Brown, Travis, & Shine, 2008). Although there has been considerable research previously on the question of why it might be adaptive for individuals to join groups of a particular composition, no previous study has examined the shoaling behaviour of seasonally invading tropical reef fishes and the fitness implications of this behavioural trait in the context of range-expansion population dynamics on the invasion front-line. The results of our study suggest that the behavioural strategy of ‘hanging with the locals’ may be an adaptive one for tropical marine fishes expanding their range into temperate habitats. The consequences of this preference could be surprising, given the potential ‘oddy effect’ costs of being in a heterospecific group in terms of greater vulnerability to predation. However, our findings are in agreement with previous studies showing that invasive species can derive benefits from joining heterospecific groupings with native locals and can succeed in “overriding the oddity effect” (sensu Mathis & Chivers, 2003). For example, invasive guppies (*Poecilia reticulata*) in Mexico derive benefits in foraging efficiency (Camacho-Cervantes, Garcia, Ojanguren, & Magurran, 2014) and boldness (Camacho-Cervantes, Ojanguren, & Magurran, 2015) by joining heterospecific shoals with native topminnows. The apparent absence of an ‘oddy effect’ in the present study could be due to the critical driver of shoaling benefit being similarity in body size of individuals, rather than absolute species identity (Rodgers, Ward, Askwith, & Morrell, 2011). In fact, the juvenile mado, that *A. vaigiensis* commonly shoaled with, were always within 2 cm size of the tropical vagrants, in addition to possessing similar morphological body shape (Smith, Fox, Donelson, Head, & Booth, 2016) and colour patterns (one with horizontal black stripes, the other with vertical black stripes, Figure S4).

The mechanism that we propose as being responsible for the observed differences in *A. vaigiensis* population dynamics (body size) between the two shoal types is behavioural interactions. A difference in social cohesion was observed between the two shoal

types as the season progressed, with tropical shoals becoming less cohesive through time and mixed shoals maintaining cohesion. Rather than contracting their overall home range size as group numbers fell over the season, individuals within ‘tropical’ shoals continued to defend the same total area of territory even though individuals were being lost from the shoal, thereby increasing metabolic cost of individual territory defence (see Bilhete & Grant, 2016). This reduction in cohesion, and consequent increase in distance between individuals, would make individuals within tropical shoals at greater risk of predation, with predators more easily able to distinguish individuals within the group (dilution of predator confusion effect Krakauer, 1995). It is likely that other social benefits not measured in the present study were also obtained by *A. vaigiensis* when shoaling with local resident species such as social learning of predators. For example, it is known that tropical damselfish can gain survival benefits from social learning (Manassa & McCormick, 2013) and learn from heterospecifics (Manassa, McCormick, & Chivers, 2013), however, requires further research in this novel temperate setting.

Our results suggest that benefits of shoaling with the natives cannot simply be attributed to a method of overcoming the Allee effect. We found no evidence that mixed shoals were significantly larger than tropical ones, with both shoal types attaining similar sizes (recorded maximum of 63 and 52 individuals respectively). It may be that in this case where group sizes are all too small to experience positive density effects, that they simply did not manifest over the time frame of our study in this early life stage or were made redundant by the cost/benefit relationships caused by grouping in a novel context (Hoare, Couzin, Godin, & Krause, 2004; Killen, Marras, Nadler, & Domenici, 2017). We expect, however, that Allee effects could be influential as winter water temperatures in the SE Australian region begin to warm above the critical thermal minimum for tropical species. This is a study area that warrants further investigation.

It might be expected that the difference in body size observed between fish in both shoal types could be attributed simply to resource availability differing between them. While it was not possible in the context of the current study to determine the relative foraging efficiency of individuals, for planktivorous species, position in the water column is known to influence feeding efficiency (Goldstein, D’Alessandro, & Sponaugle, 2017) and shoal dynamics (Gregson & Booth, 2005). However, there was no observable distinction in vertical space usage (depth) for the two shoal types, and they maintained similar home ranges on average, so likely access to resources (such as food and/or shelter) would have been similar. Furthermore, while the distribution of body sizes at the beginning of the season will reflect recruitment pulses in 2 months prior to surveys commencing, the process of recruitment typically slows by May (i.e. week 9 of our study) (Booth et al., 2007). After that time, the population dynamics of both shoal types are expected to be more affected by local processes such as individual growth and predation (Hoey & McCormick, 2004; Holmes & McCormick, 2010; Mitchell, McCormick, Ferrari, & Chivers, 2011), thus we expect differences in

body-size distributions observed towards the end of the study period to have been driven by factors affecting population dynamic processes. This could, however, include behavioural complexity not directly tested for in this study that includes 'large' tropical individuals choosing to join mixed species shoals later in the season. This does require further investigation, however, is unlikely driving overall body size differences, since shoals becoming more abundant at the expense of another was not observed.

It is interesting to note that our results suggest shoaling with resident species is unlikely to be innately preferred by these juvenile tropical vagrant fishes. During the first part of the recruitment season (weeks 1–8), we observed greater numbers of *A. vaigiensis* in 'tropical' than in 'mixed' shoals, perhaps reflecting the natural preference that individuals have to group with conspecifics (Buston, Fauvelot, Wong, & Planess, 2009; Magurran, Seghers, Shaw, & Carvalho, 1994) or may be a combined result of conspecific recognition and habitat selection of tropical larvae in temperate reefs (Beck, Feary, Nakamura, et al., 2016). Recording recruitment patterns of *A. vaigiensis* at the commencement of the season at a finer (i.e. daily) temporal scale would enable observations of interactions occurring at the time of shoal selection, such as priority effects (Geange, Poulos, Stier, & McCormicj, 2017). We suggest that future research should be directed towards this area, including exploring the mechanisms for which temperate shoal mates are also chosen. Intraspecific competition may become more important at later life stages, as ecological function changes ontogenetically and the distinction between shoaling with *A. strigatus* or *T. taeniatus*, for example becomes more important considering one is of competing trophic guild (*T. taeniatus*) and the other is not (*A. strigatus*). Furthermore, although these fish have not been recorded reproducing at this latitude to date, predicted ocean temperature during winter at this location will soon be above critical thermal minima, meaning that understanding the reproductive advantages to mixed shoal choice and shoal selection of second generation tropical fish larvae would allow for more accurate predictions of the likely future interactions between tropical 'invaders' and the temperate ecosystem.

Presently, thermal physiology (i.e. the ability to survive winter water temperatures) remains the ultimate constraint on survival of these seasonally invading species and, by extension, the range-shift potential of tropical marine fishes along the SE coast of Australia. However, projected increases in ocean temperatures at this location will see winter sea surface temperatures remain above the 17°C survival threshold estimated for tropical marine fishes in the near future. Consequently, the behavioural strategies employed by tropical 'invaders' will become increasingly relevant as factors determining the relative range-shift success potential of individual species, and in predicting the likely ecological impacts on native fish communities along this SE coast of Australia. As winter season die-off is reduced and social groups retain density further into the season, benefits associated with social living such as reductions in stress response associated with reduced condition (Hansen, Schaerf, & Ward, 2015) or lower metabolic costs of (Nadler, Killen, McClure, Munday, & McCormick, 2016) may have an even greater impact on survival and

persistence. This study provides an insight into the potential impacts that behaviour could have on the population dynamics of these 'invaders' on the front line of a range expansion that is likely to have significant consequences for native fish communities in shallow temperate marine habitats.

ACKNOWLEDGEMENTS

We thank G. Polewski and S. Philp for assistance in the field, W. Figueira for water temperature data and reviewers at the Australian Coral Reef Society Student Writing Retreat for helpful comments on an earlier draft of the manuscript. This study was funded by UTS School of Life Sciences (research award to S.M.S) and the Ian Potter Foundation Science Grant (J.M.D). J.M.D. and R.J.F. were supported by UTS Chancellor's Postdoctoral Research Fellowships. This research was carried out under Ethics Permit UTS ACEC 2013-552 and Fisheries Permit F94/696.

ORCID

Shannen M. Smith  <http://orcid.org/0000-0003-1583-2785>

Rebecca J. Fox  <http://orcid.org/0000-0003-3442-4189>

David J. Booth  <http://orcid.org/0000-0002-8256-1412>

Jennifer M. Donelson  <http://orcid.org/0000-0002-0039-5300>

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Smith SM, Fox RJ, Booth DJ, Donelson JM. 'Stick with your own kind, or hang with the locals?' Implications of shoaling strategy for tropical reef fish on a range-expansion frontline. *Glob Change Biol*. 2018;24:1663–1672. <https://doi.org/10.1111/gcb.14016>