Predicting range-shift success potential for tropical marine fishes using external morphology

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Abstract

With global change accelerating the rate of species' range-shifts, predicting which are most likely to establish viable populations in their new habitats is key to understanding how biological systems will respond. Annually, in Australia, tropical fish larvae from the Great Barrier Reef (GBR) are transported south via the East Australian Current (EAC), settling into temperate coastal habitats for the summer period, before experiencing near-100% mortality in winter. However within 10 years, predicted winter ocean temperatures for the southeast coast of Australia will remain high enough for more of these so-called “tropical vagrants” to survive over winter. We utilised a method of morphological niche analysis, previously shown to be an effective predictor of invasion success by fishes, to project which vagrants have the greatest likelihood of undergoing successful range shifts under these new climatic conditions. We find that species from the family of butterflyfishes (Chaetodontidae), and the moorish idol, *Zanclus cornutus*, are most likely to be able to exploit new niches within the ecosystem once physiological barriers to overwintering by tropical vagrant species are removed. Overall, the position of vagrants within the morphospace was strongly skewed, suggesting that impending competitive pressures may impact disproportionately on particular parts of the native community.

Keywords: biological invasion, climate change, coral reef fishes, morphological niche, tropicalisation

1. Introduction

Human-induced warming of the planet is driving shifts in the distributional ranges of many terrestrial [1] and marine [2] organisms. Predicting which species are most likely to be successful in establishing reproducing populations within their new habitat range is a critical step in forecasting the potential changes in biodiversity and ecosystem functioning that will occur as a result of continued global warming [3-5].

In the marine environment, poleward shifts in the distribution of tropical species are already resulting in the “tropicalization” of temperate marine habitats [6].

The southeast coast of Australia lies at a known ocean warming hotspot [7-8] and is therefore likely to be particularly susceptible to the process of tropicalization. Every year tropical fish larvae are expatriated south from the GBR via the EAC, where they arrive and settle in recruitment pulses from Jan-May [9]. Currently, juvenile mortality reaches ~100% by July (Austral winter), driven by thermally induced reductions in physiological capacity. However, sea surface temperatures in this region are expected to rise by as much as 3°C by 2100, and coupled with the southward movement of the EAC [10], more of these tropical species are predicted to soon be capable overwintering at temperate latitudes. The winter ocean temperatures forecast to occur in the Sydney region by 2020-30 [8] will be above the 17°C threshold currently estimated to be the constraint on physiological survival of tropical vagrant species [11], meaning that establishment of populations of tropical reef fishes in the waters off Sydney and the southeast coast of Australia will be possible within the next 15 years. Predicting which of these vagrant species are most likely to establish breeding populations, and therefore compete with native species for food and habitat resources, is a critical issue for those concerned with managing these ecosystems into the future.

Many individual species-level traits have been proposed as predictors of geographic range shift potential, (e.g. high propagule production, generalist diet). However the predictive power of the trait-based approach across multiple ecosystems and regions has been shown to be mixed, with some traits being identified as being important in certain contexts but not in others [reviewed in 12]. Recently, Azzurro *et al.* [13] demonstrated that external morphology alone can be an accurate predictor of a species' ability to successfully colonise a novel habitat. By using morphology as a proxy for a species' ecological niche, the method maps the existing resident community in terms of its morphological niche space and examines the position of potential invading species within this morphospace. Based on present-day abundances of species that have previously invaded the Mediterranean Sea via the Suez Canal, they showed that species which established successful populations were those that either lay outside, or at the margins of, the resident morphospace. Those that were morphologically similar to residents were unlikely to establish, presumably because the ecological niche was already filled [14-15]. Here we use this method to examine the position of seasonally-invading tropical reef fish from the GBR within the morphospace of a native fish community of the southeast coast of Australia and to predict which vagrant species might be most likely to establish residency and shift their range as the physiological barriers to survival recede under global warming.

2. Material and methods

The morphological space of the native shoreline fish community of New South Wales (NSW), Australia was defined based on the species assemblage of a representative protected marine habitat (Cabbage Tree Bay, NSW, https://ctbar.wordpress.com/). A database of 110 species of bony fishes was compiled (electronic supplementary material, table S1) and an image of each species (left hand side of adult individual) was sourced from online resources. Species' morphology was then characterised using 27 anatomical landmarks with ecological significance [following 13,16,17], (electronic supplementary material, table S1). Landmarking of images was done using tpsDig v1.40 [18], and scaled via a generalised least squares procedure (generalised Procrustes) to eliminate the effect of isometric body-size variation. Relative warp analysis (tpsRelw v1.60) [19] was then used to obtain coordinates (relative warp scores) for each species within the reduced shape space [20]. The first two warps accounted for 47% of the observed morphological variation within the community and factor scores from these two warps were used to plot the position of individual species and define a morphospace of the native fish community in 2-dimensions. The convex hull of the native community (the smallest set of points enclosing all 110 species, see [21]) was then calculated using Qhull [22] and the resulting convex hull broken down into a series of Voronoi polygons to provide an estimate of the ecological space around each species [23]. For species at the periphery, Voronoi polygons are unbounded and use of the convex hull as a boundary therefore results in an underestimation of the area surrounding peripheral and hull points.

The analyses were repeated for a fish community containing the 110 native species plus the 11 tropical vagrant species most commonly observed as juveniles in the Sydney region over at least two consecutive summers in the last 15 y [24], (electronic supplementary information table S1). Relative warp analysis yielded the coordinates of the vagrant species within the 2-dimensional community morphospace, with Voronoi polygons giving conservative estimates of the amount of morphological space occupied by the vagrant species in relation to their “closest” native neighbours (polygons do not allow for overlapping niches). Based on the position of the tropical species within the convex hull of the resident community (table 1), their distance from neighbouring species, and Voronoi polygon area, the potential to establish successful populations in the future was classified (table 2). Since the receiving community could be precisely defined, and was based on a single specific habitat type, the position of vagrant species was considered in relation to the whole native fish community, rather than just in relation to pre-assigned guild members (see approach in Azzurrro et al. 2014). This meant that consideration of vagrants’ potential to establish a niche was not *a priori* constrained alongside species with an assumed similar functional role. Calculations of convex hulls, Voronoi polygons and nearest-neighbour Euclidean distances were carried out in MATLAB version 9.0.0.

3. Results and Discussion

Based on morphometric analysis, the species of tropical reef fishes with the greatest probability of exploiting an available niche within the existing resident assemblage are the butterflyfishes *Chaetodon auriga*, *C. flavirostris* and *C. vagabundus* and the zanclid *Zanclus cornutus* (figure 1, table 2). The damselfishes *Abudefduf bengalensis*, *A. sexfacsiatus,* and *A. vaigiensis* are predicted to have medium probability of establishing within the resident community, based on morphology and available niche space (figure 1, table 2). Overall, the morphological position of vagrant species were strongly skewed to the upper and lower left-hand corners of the convex hull.

Azzuro *et al.* [13] also found that species belonging to the family Chaetodontidae had a high invasion probability in the Mediterranean, but argued that habitat constraints (obligate association with coral of the species concerned) not accounted for in the methodology meant that they would remain rare. The butterflyfishes identified by our study as having strong range-shift potential actually show versatility in their habitat associations, even within reef environments. *C. auriga*, for example, can be observed in mangroves or rubble habitats, suggesting that they may be able to exploit the rocky shoreline habitats of southeast Australia, as predicted here. Additionally, they are not obligate coral feeders, exhibiting a more generalist diet including algae and invertebrates. The potential impact of climate change on the Australian temperate fish community could therefore be to expand niche opportunities for algal crevice feeders (*Z. cornutus*), algal and invertebrate feeders (*Chaetodon* spp.).

The most abundant tropical vagrant species currently found as juveniles along the NSW coast is the damselfish *A. vaigiensis*. In our analysis this species is predicted to have a moderate likelihood of establishing abundant populations within the resident community, being located within, but in close proximity to, the boundary of the convex hull of the resident assemblage. Its position lies in close proximity to the resident species *Microcanthus strigatus* and its addition to the assemblage divides the niche space of *M. strigatus* into a smaller polygon, suggesting potential competition. Juvenile *A. vaigiensis* are commonly observed in close proximity to *M. strigatus*, using similar habitat following the summer recruitment event (Smith pers. obs.) suggesting strong overlap in ecological niche and highlighting the predictive power of the morphological approach used here. Furthermore, the fact that the position of tropical vagrant species considered in the current study is strongly skewed to the upper and lower left-hand corners of the convex hull suggests that, in ecological terms, the impending escalation in competition for niche space may impact disproportionately on particular parts of the native community.

Geometric morphometrics, while a useful predictive tool, is based on the assumption that competitive interactions between residents and invaders are driving the likelihood of population establishment success. For our study system, the model assumes that all commonly observed tropical fish that can be transported to Sydney via the EAC have the potential to interact with temperate species and have equal opportunity to use resources. The model then assesses this probability relative to competitive exclusion due to morphological differences. It does not take into account environmental drivers of range-shift success. Model predictions are also critically related to the morphologies used to construct the morphospace. As Azzurro *et al.* [13] point out, morphological peculiarities not captured by the analysis can prove to be critical ecological novelties. For example the lionfish (*Pterois* spp.), predicted only to have a moderate chance of invasion success within the defined morphospace [13], has unfortunately become a highly successful invader in the Western Atlantic [25] and Mediterranean [26].

The value of the geometric morphometric approach, however, lies in the ability to generate hypotheses of range-expansion potential, which can be tested once ocean temperatures reach over-wintering levels on a consistent basis. The growth of citizen science projects such as the Range Extension Database and Mapping Project (Redmap, http://www.redmap.org.au) and ongoing data collection by Reef Life Survey (http://reeflifesurvey.com/) will be an avenue to ground-truthing the predictions made here. For the temperate marine ecosystems of Australia’s southeast coast, Redmap’s database of year-on-year numbers of adult-sized tropical vagrant fishes will provide a means by which the predictions made by the current study can be tested, once over-wintering by all vagrant species becomes a physiological reality.

Ethics: No ethics approvals were required for this study.

Data accessibility: Data deposited in Dryad: http//dx.doi.org/10.5061/dryad.q0g60

Author contributions: SS, RF, JD, DB designed the study. SS, MH and RF collected data and performed the analyses, SS, RF, JD and DB interpreted the data. All authors contributed to drafting of the manuscript, and subsequent edits made in response to reviewer comments. All authors approved the final version for publication and agree to be held accountable for the content therein.

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Table caption

Table 1: Conditions of invader position within resident morphospace corresponding to probability of invasion success.

Table 2: Predicted likelihood of range expansion by tropical vagrant fish species into temperate marine communities of the southeast coast of Australia, based on morphology alone.

Figure Legend

Figure 1: (a) Morphological position of species within the overall convex hull of a representative present-day assemblage of bony fishes from the southeast coast of Australia. Each dot represents a single species and outlines represent Voronoi polygons defining ecological niche space surrounding each species. (b) Convex hull of the present-day resident assemblage (dashed line) overlaid with assemblage including seasonally-invading tropical vagrant fish species (solid line). Numbers inside Voronoi polygons refer to species listing in table 2.