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Spatiotemporal patterns of abundance and ecological requirements of a labrid's juveniles reveal conditions for establishment success and range shift capacity



Katherine Cure^{a,b,*}, Jean-Paul A. Hobbs^c, Tim J. Langlois^a, David V. Fairclough^{c,d}, Emma C. Thillainath^a, Euan S. Harvey^c

- a UWA Oceans Institute & School of Biological Sciences, The University of Western Australia, 35 Stirling Highway, Crawley, 6009, WA, Australia
- b Australian Institute of Marine Science, Indian Ocean Marine Research Facility, The University of Western Australia, 35 Stirling Highway, Crawley, 6009, WA, Australia
- ^c Department of Environment & Agriculture, Curtin University, Kent Street, Bentley, 6102, WA, Australia
- d Science and Resource Assessment, Department of Primary Industries and Regional Development, 39 Northside Drive, Hillarys, 6025, WA, Australia

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ABSTRACT

Distribution shifts of demersal fishes are important adaptive responses to warming oceans for species' persistence. Shifts are facilitated by factors such as adult movement and dispersal of pelagic larvae to normally cooler regions, where increasing ocean temperatures are now enhancing larval and juvenile survival. However, successful recruitment (i.e. larval settlement) at these new regions can be constrained by resource availability, specialisation (food, habitat) and ecological interactions (competition, predation). Evaluating the capacity or likelihood of a species to successfully shift or expand its range, provides information relevant to biodiversity conservation and fisheries management, and is particularly important for species with restricted ranges. Choerodon rubescens (Günther, 1862) is an exploited labrid endemic to ~1400 km of the west Australian coastline, encompassing 13° of latitude and a 6°C temperature gradient. This region recently experienced a rapid warming event of ~3°C, which lasted 3 months and mirrored ocean temperatures expected in the next 50 years. Following this event, high levels of recruitment of C. rubescens occurred towards its southern, cooler distribution limit. Juvenile abundances were surveyed in this study to evaluate: (1) the effect of elevated temperatures on recruitment success across shallow water habitats spanning the species' distribution, (2) temporal variation in recruitment success in the typically cooler, southern part of its range and (3) ecological characteristics important to recruit survival, including habitat preferences, diet and behaviour. Juvenile C. rubescens were significantly more abundant at the margin between reef and sand and towards the cooler southern range end. Reef margin habitat provides access to shelter from predators within the reef and to sand-associated invertebrate prey in adjacent soft sediments, where most feeding activity occurred. Juveniles were abundant (0.3 to 4 fish/40 m²) in reef margin habitats of the southern cooler region for three consecutive years, with individuals represented by multiple cohorts, indicating suitable environmental conditions for ongoing recruitment and survival. Juveniles at this habitat were able to compete effectively with other co-occurring labrids for invertebrate prey. As oceans warm, the number of recruits arriving and surviving beyond the existing cooler range limit will be dependent on factors such as successful spawning, larval delivery and survival, and availability of reef margin habitat with associated prey; these factors will determine the successful range shift or expansion of C. rubescens. We present an example of how range-wide spatiotemporal ecological studies of juvenile fish can identify range shift capacity and inform management adaptive to climate change.

1. Introduction

Climate induced changes in ocean conditions are causing shifts, particularly poleward, in the distribution and abundance of many marine fishes and fishery resources (Last et al., 2011; Perry et al., 2005; Poloczanska et al., 2013). Two main mechanisms facilitate these shifts: poleward-flowing currents disperse eggs and larvae into normally cool waters (Johnson et al., 2011; Ling et al., 2009) and warming oceans

E-mail address: k.cure@aims.gov.au (K. Cure).

^{*} Corresponding author at: Australian Institute of Marine Science, Indian Ocean Marine Research Facility, The University of Western Australia, 35 Stirling Highway, Crawley, 6009, WA, Australia.

enable survival of newly settled recruits in these previously unsuitable environments (Booth et al., 2007; Figueira and Booth, 2010). Distributional shifts are an important "response" to localised warming, particularly for endemic species (Graham et al., 2011; Munday et al., 2008; Thomas et al., 2004). However, successful shifts may not be possible for many fish species because their survival is dependent on specific resources (e.g. food, habitat) which may not be available at locations beyond their current range (Feary et al., 2014).

Demersal fish species typically have little migration capacity as adults, with small home ranges and local-scale association with resources such as food and habitat (Bryars et al., 2012; Meyer and Holland, 2005). For these species, successful poleward shifts in their distributions require sustained larval recruitment to habitats in normally cooler environments and their establishment of populations via subsequent growth, maturation and reproduction (Crooks and Rilov, 2009). However, larval recruitment strength is highly variable in space and time, particularly in long-lived demersal species (Doherty, 1991; Jones, 1984; Russell et al., 1977; Trip et al., 2014; Williams and Sale, 1981), and these variations have subsequent effects on population size (Attrill and Power, 2002; Figueira et al., 2009; Hixon et al., 2012). Furthermore, despite warmer waters bringing larvae to novel areas, many recruits fail to survive because of the unsuitability of a range of ecological factors, including winter water temperatures, resource availability (food and habitat) and ecological interactions (competition and predation) (Caselle and Warner, 1996; Figueira et al., 2009; Hixon et al., 2012; Jones, 1984; Ross, 1986; Wilson et al., 2010).

Recruitment success (i.e. larval settlement) is typically highly variable across the geographic range of fishes, particularly for species distributed along a latitudinal gradient (Compton et al., 2007), because of the metabolic effects of a gradient in water temperatures on fish growth and survival (Lek et al., 2012; Phillips et al., 2014; Pörtner and Knust, 2007; Wakefield et al., 2017). For this reason, species tend to have thermal restrictions on their distribution, with recruitment being generally low and sporadic towards both low and high temperature extremes of their distribution (Shepherd and Brook, 2007; Zacherl et al., 2003; but see Sagarin and Gaines, 2002; Sagarin et al., 2006), where local environmental conditions are often not optimal for recruit survival (Figueira and Booth, 2010; Jones, 1984; Nantel and Gagnon, 1999).

The demersal baldchin groper Choerodon rubescens (Labridae) is endemic to ~1400 km of the west Australian coastline (WA) spanning a tropical to subtropical latitudinal gradient (18-24°C), where it is an important fisheries target (Fig. 1, Allen and Swainston, 1988; Edgar, 2000; Fairclough et al., 2014). It is most abundant towards the centre of its range at \sim 28°S and rare at both range edges (i.e. at 21 and 34°S) (Cure et al., 2018). While it undergoes pelagic dispersal during its egg and larval stages, juvenile and adults are considered to have restricted home ranges (Fairclough et al., 2011; Gardner et al., 2015; Hutchins, 2001). As with several other fish species along this coast, the distribution centroid of C. rubescens is predicted to shift poleward in response to gradual increases in water temperature (Cheung et al., 2012). Such future warming scenarios were recently simulated by the 2011 marine heat wave (2011 Mhw), a rapid warming event in the eastern Indian Ocean. During this event the poleward flowing Leeuwin Current (LC), which is the dominant ocean current off WA, strengthened resulting in summer water temperature anomalies of up to 3°C warmer (Feng et al., 2013; Zinke et al., 2014).

During the heatwave, fish, invertebrate and coral mortalities occurred at central latitudes along this coastline (\sim 28°S, Abdo et al., 2012; Pearce et al., 2011). Further south along the coast, high abundances of recruits of a range of tropical and subtropical demersal species, including *C. rubescens*, were observed during the years following the 2011 Mhw in areas where they were previously in low abundance or not recorded (e.g. *Chaetodon assarius* at \sim 30°S, Wernberg et al., 2013, and *C. rubescens* at \sim 32°S, Cure et al., 2018, 2015). Although water temperatures have returned to their normal range since the 2011 Mhw, these rapid increases in recruit abundance suggest that such

species are capable of undergoing poleward distribution shifts in response to warming temperatures if recruitment at southern locations is sustained by ongoing influx of recruits and/or self-recruitment. However, in order to determine range shift capacity, comparative information on recruitment patterns of such species throughout their distribution is needed, together with an assessment of the ecological requirements of newly settled recruits, to assess whether recruitment to and beyond the current cooler (southern) ends of their distribution could be sustained. Such information is crucial for developing species conservation initiatives and adapting management strategies to take into account distribution and range size changes in response to rapidly warming oceans (Poloczanska et al., 2016).

To evaluate the potential for a future range shift in *C. rubescens*, the density of juveniles and their habitat associations in shallow water lagoons where juveniles are most likely to settle (Cure et al., 2015), were first investigated across the full distribution of the species during elevated water temperatures subsequent to the 2011 Mhw. Secondly, interannual recruitment variability was examined at the cooler (southern) range end (at ~32°S) in consecutive years of elevated temperatures (2013-2015), as a proxy for the scenario of future increased water temperature conditions that may influence recruitment patterns of this species. Thirdly, to identify other specific ecological requirements of juveniles, the diet and behaviour of recruits in southern waters were determined. Data were then used to test the following hypotheses: (1) that following the 2011 Mhw, juvenile C. rubescens across all habitats sampled would show the previously identified pattern of higher abundance in the cooler (southern) part of the species' range rather than any other area along their distribution (Cure et al., 2018, 2015), (2) that habitats occupied by juveniles in lagoonal areas would be consistent across the species range, and (3) that as water temperatures remained higher than average, annual recruitment to the cooler (southern) end would be sustained after the high recruitment event following the 2011 Mhw (Cure et al., 2018, 2015). The detailed ecological information presented in this study will be valuable for evaluating range shift predictions and the ecological changes that may occur at receiving locations. It further highlights the need for detailed ecological data of species undergoing range shifts globally, particularly those that are exploited or occupy small ranges, such as endemics (Bates et al., 2014; Poloczanska et al., 2016).

2. Materials and methods

2.1. Study species

The baldchin groper Choerodon rubescens is a large subtropical protogynous wrasse (Labridae) endemic to the west coast of Australia and one of the most important recreational and commercial fisheries targets in the region (Fairclough et al., 2014). Its distribution spans a latitudinal temperature and habitat gradient from tropical coral reefs at ~21°S to temperate rocky reefs at ~34°S (Fig. 1; Allen and Swainston, 1988; Edgar, 2000; Hutchins, 2001), with abundance being highest towards the range centre and low at both range edges (Cure et al., 2018). Juveniles are common in shallow (< 3 m) protected habitats, such as lagoons (Cure et al., 2015; Fairclough, 2005; Hutchins and Swainston, 2008), and adults typically inhabit deeper and more exposed reefs up to 100 m depth (Fairclough et al., 2008). Maximum total length (L_T) and age is about 700 mm (Hutchins and Swainston, 2008) and 25 years, respectively (Fairclough et al., 2014). Juveniles attain sexual maturity as females at a minimum size of $\sim 229 \text{ mm L}_T$ (Fairclough, 2005). Reproduction at the centre of C. rubescens range occurs mostly during the austral spring to mid-summer (October to January) and juveniles settle onto the reef in summer and early autumn, i.e. December to April (Cure et al., 2015; Fairclough, 2005).

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