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High intra-ocean, but limited inter-ocean genetic connectivity in populations of the deep-water oblique-banded snapper *Pristipomoides zonatus* (Pisces: Lutjanidae)

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ABSTRACT

While many studies have investigated connectivity and subdivision in marine fish occupying tropical, shallow water reef habitats, relatively few have been conducted on commercially important deep-water species in the Indo-Pacific region. Here, we examine spatial and temporal genetic variation in the deep-water oblique-banded snapper *Pristipomoides zonatus*, collected from eight locations across the Indian and Pacific Oceans. A total of 292 individuals were screened for genetic variation at six nuclear microsatellite loci and the cytochrome c oxidase subunit 1 (COI) mitochondrial DNA (mtDNA) gene. There was evidence of low, but significant genetic differentiation between ocean basins ($F_{CT} = 0.009$) and no significant divergences between sites within oceans. The lack of population structure within ocean basins suggests *P. zonatus* has a long pelagic larval duration with high levels of connectivity between populations over large geographical distances (> 2000 km). There was no evidence of temporal variation in allele frequencies within populations. However, ephemeral genetic divergences between sites were detected, along with a significant reduction in genetic diversity at one site, suggesting there may be low effective population sizes (N_e). Our results suggest that localized declines in genetic diversity could be offset by gene flow from other locations within ocean basins, though predicting the broader impacts of localized stock depletions requires further understanding of recruitment dynamics and life history characteristics of the species.

1. Introduction

Molecular genetics has greatly increased our understanding of population structure in exploited marine taxa (Hellberg et al., 2002; Mora and Sale, 2002; Jones et al., 2009). In marine fish, the established paradigm that all populations are open and highly connected has been challenged repeatedly (Swearer et al., 2002; Hauser and Carvalho, 2008). Several shallow water species have been found to self-recruit to natal reefs and exhibit significant genetic subdivision (Johnson et al., 1994; Jones et al., 1999; Swearer et al., 1999; Palumbi and Warner, 2003; Taylor and Hellberg, 2003; Bay et al., 2004; Jones et al., 2005; Horne et al., 2011; Horne et al., 2012). However, a number of species have also been found to exhibit high population connectivity and low population subdivision (Lessios and Robertson, 2006; Craig et al., 2007; van Herwerden et al., 2009; Gaither et al., 2011b; Bentley et al., 2014).

The extent of population genetic structure in marine species can differ depending on the spatial scale examined (Bernardi et al., 2001; Johnson and Black, 2006). Population structure may be stable or temporally transient (Pujolar et al., 2006; Hedgecock and Pudovkin, 2011). Temporal variation in genetic structure has been observed in marine species over several generations to several decades (Hauser et al., 2002; Hutchinson et al., 2003; Hoarau et al., 2005; Maes et al., 2006; Christie et al., 2010). One hypothesis put forward to explain ephemeral genetic structure is the 'sweepstakes reproductive success (sweepstakes)' hypothesis (Hedgecock, 1994; Hedgecock and Pudovkin, 2011). The sweepstakes hypothesis implies that where substantial

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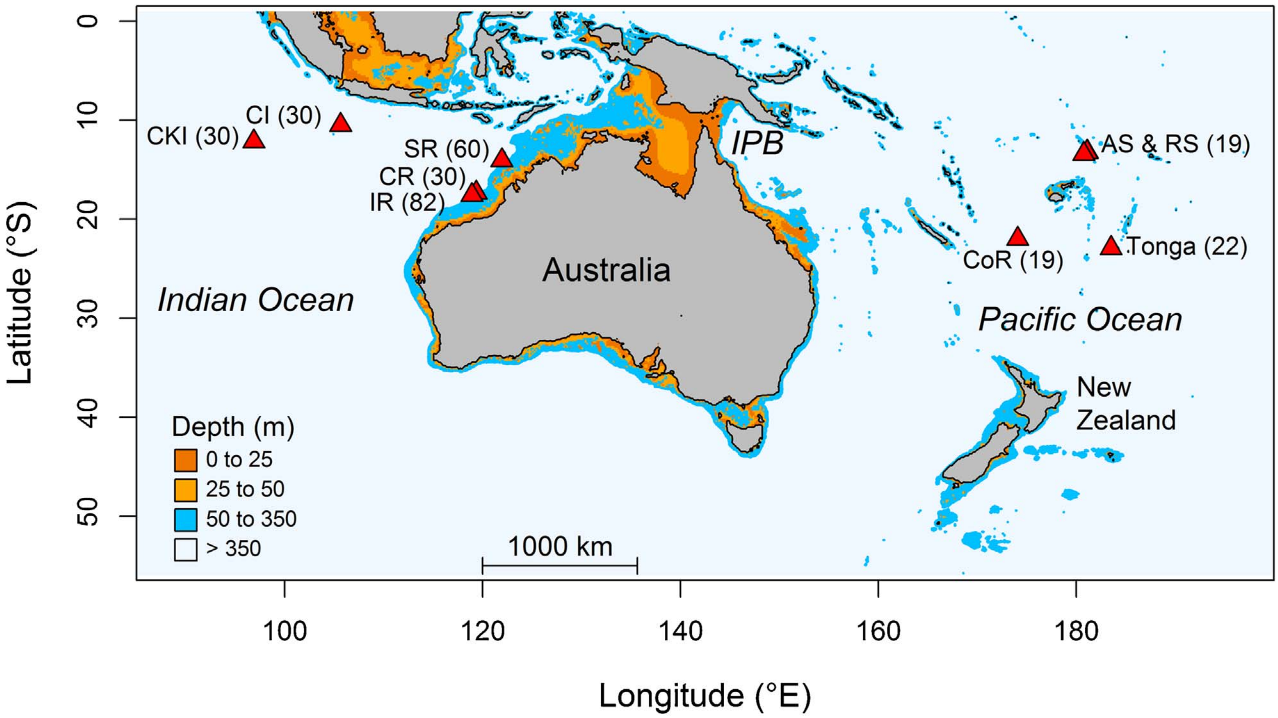

Fig. 1. Sampling locations of *P. zonatus* across the Indian and western Pacific Oceans. Sample location IDs are provided in Table 1. Numbers in parentheses are the number of individuals genotyped.

differential reproductive success occurs between reproducing individuals, this can lead to high genetic homogeneity in recruiting cohorts (Hedgecock and Pudovkin, 2011). Combined with spatially variable levels of recruitment, this leads to genetic patchiness, where genetic homogeneity exists on large spatial scales, with chaotic genetic heterogeneity over smaller spatial scales (Hedgecock and Pudovkin, 2011).

The sweepstakes hypothesis is not the only explanation for observed patterns of population structure. Life history traits (Swearer et al., 1999; Riginos and Victor, 2001; Bay et al., 2006), local oceanographic and hydrodynamic processes (Parsons, 1996; Lessios and Robertson, 2006; Gaither et al., 2010b) and historical phylogeography (Bowen et al., 2001a; Reece et al., 2010; Gaither et al., 2011a) have all been shown to affect population structure. Life history factors, such as pelagic larval duration, may provide the upper limit of potential dispersal of larvae (Magsino and Juinio-Meñez, 2008). Prevailing local oceanographic conditions (Riginos and Nachman, 2001; Thomas et al., 2015) and larval behaviour (Montgomery et al., 2001; Gerlach et al., 2007; Horne et al., 2013) may act to limit the dispersal potential.

A significant proportion of studies investigating genetic connectivity and subdivision in marine fish have focused on tropical, shallow water reef taxa (0–30 m depth). Studies that have investigated deep-water taxa (> 100 m depth) have been biased towards commercially exploited taxa of the Atlantic, such as Atlantic cod (Miller and Kapuscinski, 1997; Hutchinson et al., 2003) and plaice (Hoarau et al., 2005). In contrast, relatively few studies have investigated population subdivision of commercially important deep-water species in the Indo-Pacific region, and have shown mixed results (Newman et al., 2016). Ovenden et al. (2004) found statistically significant population structure over a relatively small geographical scale in the deep-water goldband snapper, *Pristipomoides multidens*. F_{ST} values of 0.16 and 0.17 were observed between pairs of populations separated by 191 km and 491 km respectively. Contrasting results were found by Gaither et al. (2011b) in the congenic deep-water rosy snapper, *Pristipomoides filamentosus*. In *P. filamentosus*, low, but significant population structure (F_{ST} = 0.029) was observed across 14,000 km of the Indo-Pacific. However, once the Hawaiian samples were removed from the analysis, no significant population structure was observed across the rest of the Indo-Pacific. These contrasting results are surprising given that these two species, *P. filamentosus* and *P. multidens*, have sympatric distributions and have similar estimates of pelagic larval duration, about 30–40 days (Akazaki and Iwatsuki, 1987; Leis and Lee, 1994). Differences in population structure may be tentatively attributed to behavioural differences, life-history characteristics, historical population processes or possible combinations of these factors. Different patterns of population subdivision among congeners have also been observed in shallow water taxa, despite similar life history traits such as pelagic larval duration (Muss et al., 2001; van Herwerden et al., 2006; Magsino and Juinio-Meñez, 2008).

The oblique banded snapper, *Pristipomoides zonatus*, is widely distributed throughout the subtropical and tropical waters of the Indo-Pacific region, from east Africa to the western and central Pacific (Akazaki and Iwatsuki, 1987) and inhabits rocky bottoms and steep reef slopes at depths of 70–350 m (Allen, 1985). Little is known about the life history, reproductive biology and larval ecology of *P. zonatus*. The pelagic larval duration is estimated to be similar to other *Pristipomoides* species and slightly longer than the mean larval duration of 30 days for the Lutjanidae (Martinez-Andrade, 2003). The objectives of this study were to investigate the spatial and temporal genetic variation in populations of *P. zonatus*. More specifically, we investigated the level of genetic connectivity within and between the Indian and Pacific Oceans and the temporal heterogeneity in genetic structure and genetic diversity and thus, evidence for sweepstakes reproductive success.

2. Methods

2.1. Sample collection

A total of 292 adult and sub-adult *P. zonatus* (25.4–48.4 cm fork length) were collected from eight locations within the eastern Indian Ocean and western Pacific Ocean between 1997 and 2013 (Fig. 1). Sampling locations were selected to represent a range of geographic