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Research Paper

Unravelling the effects of gene flow and selection in highly connected populations of the silver-lip pearl oyster (*Pinctada maxima*)

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ABSTRACT

Many marine organisms often display weak levels of population genetic structuring as a result of both environmental characteristics (*e.g.*, ocean currents) and life history traits (*e.g.*, widely dispersed planktonic larval stages) maintaining high levels of gene flow. This can lead to the assumption that these organisms can be managed as a single stock based on high levels of population connectivity. However, this neglects to account for other micro-evolutionary forces such as selection, which also shape these populations. This study utilizes 1130 genome-wide SNP loci to unravel the effects of gene flow and selection shaping three highly connected populations of the silver-lip pearl oyster (*Pinctada maxima*) in the ecologically and economically important Indo-Pacific region (Aru, Bali, and West Papua). Twenty-two loci under directional selection were identified amongst the populations, providing further supporting evidence of strong local adaptation (*i.e.*, G × E effects) among populations in this region. Global F_{st} values for directional outliers (0.348) were up to eight times greater than for neutral markers (0.043). Pairwise F_{st} comparisons between Aru and Bali revealed the largest directional differences (0.488), while Bali and West Papua had the least (0.062). Unrooted neighbour-joining (NJ) distance trees and genetic diversity indices of directional outliers revealed that individuals from Bali and West Papua had reduced allelic variation ($MAF_{avg} = 0.144$, $H_o = 0.238$ and $MAF_{avg} = 0.232$, $H_o = 0.369$, respectively) compared to Aru ($MAF_{avg} = 0.292$, $H_o = 0.412$). This indicates that directional selection is most likely acting upon genetic variation within the Bali and West Papua populations. NJ distance trees, discriminant analysis of principal components, and F_{st} analyses of directional outliers revealed two divergent groups ("Bali/West Papua"; "Aru") that had previously gone unrecognized. This study not only illustrates that relatively strong local adaptive forces are occurring despite high gene flow, but identifies the populations that are most likely experiencing selection. Additionally, this study highlights the need to understand all micro-evolutionary forces acting on populations when resolving stock structure.

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1. Introduction

Identifying discrete management units (MUs) or stocks in marine ecosystems is sometimes more difficult than in terrestrial systems due to high levels of connectivity generated by ocean currents and life history traits (Gray, 2000; Kool et al., 2011). This high degree of connectivity can lead to the general assumption of population panmixia, or where all individuals are potential mates due to limited physical and ecological boundaries (Kritzer and Sale, 2004), that can be managed as a single meta-population (Kritzer and Sale, 2010). High connectivity is thought to negate selective pressures and reduce local adaptation through large amounts of gene flow (Lenormand, 2002). However, the effects of heterogeneous environments (*i.e.* marine systems) influencing selective pressures and local adaptation must also be considered. Recent genetic studies have shown that animal geographic proximity and dispersal patterns may be insufficient to accurately determine overall patterns of population genetic variation for many marine taxa (Toonen et al., 2011). One of the major shortcomings of these factors is that they neglect to account for local adaptation, or when genotype by environment (G × E) interactions result in populations displaying traits which are advantageous to their local environments (Nielsen et al., 2009).

Local adaptation can occur within populations that are highly connected if the effects of directional selection are stronger than the homogenizing effects of gene flow (Limborg et al., 2012). Under this model, genetic differentiation amongst populations is primarily due to selection acting upon specific genes within a population, and consequently those loci physically linked to them in strong linkage disequilibrium (*i.e.* hitchhiker effect; Smith and Haigh, 1974; Barton, 2000). In recent years, the identification of population genetic divergence has become easier to detect on a finer-scale due to advancements in the field of population genomics through improved accuracy, speed, and the reduced cost of genome-wide single nucleotide polymorphism (SNP) genotyping (Helyar et al., 2011).

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Traditional genetic analyses mostly rely on neutral loci (*i.e.* those alleles which do not have an established advantageous nor disadvantageous effect on a species' fitness; Hedrick, 2001), while genomic analyses are typically also able to identify outlier loci (*i.e.* those loci which are influenced by selective processes and can affect the fitness of an organism; Butlin, 2010). Characterisation of outlier loci is becoming an important tool towards fully understanding all the micro-evolutionary forces that are at play within a population (Pujolar et al., 2014; Funk et al., 2012). Traditional genetic markers (*e.g.* allozymes, microsatellite loci, amplified fragment length polymorphisms, and mitochondrial DNA) are restricted by technological limitations which can only process a limited number of markers (Zarraonaindia et al., 2012). In contrast, genome-wide SNP genotyping uses information from thousands to millions of loci, thereby increasing its analytical power (Luikart et al., 2003; Frazer et al., 2007; Stranger et al., 2007). These SNP markers cover a larger portion of the genome and allow for the detection of fine-scale gene flow and selection signatures (Stapley et al., 2010). This enhancement in genetic resolution improves our understanding of population structure, and can ultimately be used to create better defined MUs and subsequently, more effective and tailored management regimes for marine species (Waples et al., 2008; Funk et al., 2012).

Improving marine management practices is particularly important in biodiversity "hotspots", those areas with exceptionally high concentrations of species richness (Myers et al., 2000; Allen, 2008; Renema et al., 2008). These "hotspots" provide a number of ecosystem services and functions, which are important for both marine life and human food security (Moberg and Folke, 1999). In order to preserve and maintain these ecosystem services and functions, it is essential that the biodiversity in these "hotspots" be conserved, as it plays a key role in both preserving and regulating ecosystem processes (Mace et al., 2012). Therefore, it is important that we understand population dynamics in these areas in order to improve upon current management regimes.

In particular, the Indo-Pacific region is one such "hotspot" and incorporates a geographic region known as the "Coral Triangle", a well-recognized global centre of marine biodiversity (Allen, 2008; Veron et al., 2009). One common, and commercially valuable organism found in this area is the silver-lip pearl oyster, *Pinctada maxima* (Shirai, 1994; Lind et al., 2007). This organism produces the Indo-Pacific's economically important and lucrative "white" South Sea pearls (Taylor and Strack, 2008). Sessile during its adult stage, *P. maxima is* a broadcast spawner that relies upon its extended planktonic larval stage (17–24 days) and oceanic currents to disperse throughout the Indo-Pacific (Rose and Baker, 1994). It is in this stage that populations are subjected to new immigrants and additions to the population (Treml et al., 2008; Selkoe and Toonen, 2011). However, the planktonic larvae are highly vulnerable to environmental conditions, leading to differential survival among different families (Lind et al., 2010). The potential for high gene flow observed in *P. maxima* and many other marine taxa, has resulted in much debate concerning the proper management and definition of marine MUs, or stocks, for these wild organisms (Gosling, 2015). Some require only genetic distinctiveness among populations, while others consider more biological differences amongst the organisms. However, the ability to fully resolve both is becoming necessary for stocks to be clearly discriminated. Currently, a stock for marine taxa with a sessile adult stage can be as large as an entire geographic region where gene flow is possible during planktonic juvenile stages to as small as a single settlement (*e.g.* bivalve bed; Waldman, 2005; Gosling, 2015). Understanding and incorporating knowledge of both gene flow and functional evolutionary change (i.e. local adaptation) of these and all marine taxa is vital for improving management regimes and efforts to enhance stock performance (Waples et al., 2008).

A study by Lind et al. (2007) using six polymorphic microsatellite genetic markers revealed very weak genetic structuring amongst individuals from Aru, Bali, and West Papua within the Coral Triangle region (average $F_{st} = 0.0036$), whereby all sampled individuals could be considered part of a single homogeneous population. However, for the silver-lip pearl oyster, genetic differentiation among populations may not be limited by the effects of gene flow alone. A recent G × E study by Kvingedal et al. (2010) observed variations in *P. maxima* grow-out potential (*i.e.* variations in growth rate) when families originating from the three aforementioned Indonesian regions were translocated from their native environments to new locales in Bali and Lombok. The authors detected significant G × E effects among these populations, with individuals from both Bali and West Papua growing significantly larger than those from Aru in both grow-out locations, indicating that local adaption may be at play. Other marine species such as, Atlantic cod (*Gadus morhua*; Nielsen et al., 2009) and Atlantic herring (*Clupea harengus*; Limborg et al., 2012), have demonstrated that local selection pressures can in fact negate the effects of high levels of gene flow and cause selection to occur at a limited number of loci, while all other loci in the organism's genome remain unaffected by selective forces. This selection can in turn lead to a reduction in offspring fitness through outbreeding of genetically mismatched individuals, *i.e.* individuals adapted to different local environments or conditions (Gharrett et al., 1999; Edmands and Timmerman, 2003; Edmands, 2007). Consequently, to fully understand how different micro-evolutionary forces are shaping *P. maxima* populations in this region, it is essential to perform robust population genomic analysis. This genomic information will not only assist in defining relevant commercial *P. maxima* stock MUs, but it will also serve as a model for other sessile, broadcast spawning marine invertebrates.

This study aims to unravel the effects of gene flow and selection currently shaping silver-lip pearl oyster (*P. maxima*) populations in the Indo-Pacific region. Genome-wide SNP loci were used to examine population diversity statistics and population differentiation at both neutral and outlier loci in order to understand the micro-evolutionary forces acting on these populations, their interactions, and the implications for management of *P. maxima* and similar marine taxa.

2. Methods

2.1. Data collection and SNP validation

In order to quantify the effects of gene flow and local adaption as previously demonstrated in *P. maxima* populations in the Indo-Pacific (Lind et al., 2007; Kvingedal et al., 2010), a total of 85 adult silver-lip pearl oysters from the same families as those individuals in the three previously evaluated wild populations in the Indo-pacific region were obtained: Aru (27 specimens; 6.43′S, 134.63′E); Bali (33 specimens; 8.32′S, 114.92′E); and West Papua (25 specimens; 1.13′N, 130.54′E; Fig. 1). High-quality genomic DNA was extracted from all individuals using a revised CTAB protocol, DNA samples were genotyped as per manufacturer's instructions using the Illumina 3K iSelect custom arrays at PathWest Medical Laboratories, Perth, Western Australia (Steemers and Gunderson, 2007), and genotypes were calculated using GenomeStudio V2011.1 by Illumina Inc. as detailed by Jones et al. (2013a). Additionally, genetic linkage maps were constructed as described by Jones et al. (2013b). In brief, SNPs were only utilised for this study if they amplified successfully, each locus had a call rate (*i.e.* the proportion of genotypes with non-missing data; Anderson et al., 2010) of >90%, returned distinct and unduplicated genotype calling clusters, globally conformed to Mendelian expectations, and were polymorphic across all three populations (Jones et al., 2013a). Additionally, only those SNPs with a minor allele frequency (MAF) >0.02 across populations and which conformed to Hardy–Weinberg Equilibrium (HWE) in at least one population were included. This stringent filtering process was to ensure that any identified outlier loci were a result of selective forces on populations and not genotyping or genomic artefacts. In total, 1130 SNPs met these criteria and were included in all subsequent analysis.

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