Worldwide genetic differentiation in the common fouling barnacle, *Amphibalanus amphitrite*

Hsi-Nien Chen, Ling Ming Tsang, Ving Ching Chong and Benny K.K. Chan

*Institute of Ecology and Evolutionary Biology, National Taiwan University, Taipei, Taiwan, ROC; Institute of Marine Biology, National Taiwan Ocean University, Keelung, Taiwan, ROC; Institute of Ocean and Earth Sciences, University of Malaya, Kuala Lumpur, Malaysia; Biodiversity Research Center, Academia Sinica, Taipei, Taiwan, ROC

(Received 13 May 2014; accepted 15 September 2014)

*Amphibalanus amphitrite* is a common fouling barnacle distributed globally in tropical and subtropical waters. In the present study, the genetic (mitochondrial cytochrome oxidase subunit I) and morphological differentiation in *A. amphitrite* from 25 localities around the world were investigated. The results revealed three clades within *A. amphitrite* with a genetic divergence of ~ 4% among clades, whereas there were no diagnostic morphological differences among clades. Clade 1 is widely distributed in both temperate and tropical waters, whereas Clade 3 is currently restricted to the tropical region. The deep divergence among clades suggests historical isolation within *A. amphitrite*; thus, the present geographical overlaps are possibly a result of the combined effects of rising sea level and human-mediated dispersals. This study highlights the genetic differentiation that exists in a common, widely distributed fouling organism with great dispersal potential; future antifouling research should take into account the choice of lineages.

Keywords: genetic differentiation; fouling; *Amphibalanus amphitrite*; model species; biogeography

Introduction

*Amphibalanus amphitrite* (= *Balanus amphitrite*; for nomenclature see Clare & Høeg 2008; Carlton & Newman 2009) is a model barnacle species used in biofouling (eg De Gregoris et al. 2011; Dash et al. 2012; Petrone et al. 2013) and invertebrate larval biology studies (eg Chaw et al. 2011; Maruzzo et al. 2011; Chen et al. 2014). The barnacle is the laboratory test organism of choice for antifouling (AF), toxicity (Zhang et al. 2011) and larval settlement assays (Holm et al. 2000; Petrone et al. 2013) since larvae are easy to culture and the life cycle can be completed in the laboratory (Qiu & Qian 1999). *A. amphitrite* can produce numerous larvae throughout the year (Karande 1965; Rittschof et al. 1992; Qiu & Qian 1999), and settlement of the cyprids can easily be manipulated under laboratory conditions (Rittschof et al. 1992; McDonald et al. 2009; De Gregoris et al. 2011; Maruzzo et al. 2012).

*A. amphitrite* is distributed in tropical and warm temperate waters worldwide, suggesting that it is dispersed through human-mediated activities via ballast water (larvae) and attached individuals on vessels plying long distance routes. It is believed that the global trade expansion in the twentieth century had transported *A. amphitrite* from the Indo-Pacific waters to those of Europe and even to North and South America (Carlton et al. 2011). The fouling behavior of the species is hypothesized to increase gene flow among distant populations, and thus homogenizes genetic structuring.

The morphology of *A. amphitrite* has long been known to be variable, with presumptive subspecies names given to various populations by Darwin (1854) and later workers (see summary in Newman and Ross, 1976). However, extensive revisionary work based on morphological analyses by Henry & McLaughlin (1975) reduced all names, except *A. amphitrite saltonensis*, to the nominate stem species *Amphibalanus amphitrite*. They chose to retain *A. amphitrite saltonensis* on grounds of morphological differences. Later, Flowerdew (1985), Van Syoc (1992) and Raimondi (1992) demonstrated elegantly through genetic, morphological, and experimental work that *saltonensis* is not a distinct ‘subspecies’ (clade), leaving *A. amphitrite* currently perceived as a single global species.

To date, no extensive molecular study has examined the genetic differentiation in *A. amphitrite* populations worldwide (but see Flowerdew 1985). Therefore, it remains unclear whether *A. amphitrite* consists of a homogeneous meta-population across the globe or maintains some geographically restricted lineage distributions despite frequent human-mediated dispersals. It is important to understand the extent of any differentiation, as such structuring could be associated with variation in characters of interest to, for example, scientists using *A. amphitrite* as a model organism in research on biofouling control or larval biology. *A. amphitrite* exhibits significant, apparently genetic variation in characters such as larval attachment and metamorphosis (Holm et al. 2000).