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Hybridization in coral reef fishes: Introgression and bi-directional gene exchange in *Thalassoma* (family Labridae)

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Abstract

Hybrids in coral reef fishes have traditionally been described based on external features using meristic characters and colouration to identify putative parental contributors. This study utilised molecular genetic techniques to verify hybrid status and identify putative parental species for five hybrid specimens (Labridae: *Thalassoma*) collected from Holmes Reef in the Coral Sea. Phylogenetic analyses support hybrid origins of the specimens. Mitochondrial COI gene, nuclear S7 (intron 1) and nuclear copy of mitochondrial (NUMT) D-loop region corroborate the identity of *T. quinquevittatum* as the maternal and *T. jansenii* as the paternal contributor. Backcrossing to parental species by hybrids and bi-directional gene exchange between the Holmes Reef populations of *T. jansenii* and *T. quinquevittatum* was detected, suggesting that hybrids are fertile and able to reproduce successfully. F_1 hybrids display a mixture of the colouration attributes of the two parental species, but subsequent backcrossed individuals were unrecognisable as hybrids and displayed colouration of either parental species. A large numerical imbalance exists between the putative parental species at Holmes Reef, with *T. quinquevittatum* outnumbering *T. jansenii* by approximately 25:1. In this case study, hybridization appears to be driven by ecological rather than evolutionary factors.

Keywords: Hybridization; Coral reef fishes; Backcrossing; Introgression; Molecular genetics; Ecology

1. Introduction

A hybrid is formed through interbreeding between individuals from two populations, or groups of populations, which are distinguishable based on one or more heritable characters (Arnold, 1997). It then follows that a hybrid zone is an area of spatial overlap of two or more populations, which cross to form viable offspring of mixed ancestry (Arnold, 1997; Harrison, 1993). Hybridization and hybrid zones are of interest to evolutionary biologists because of the opportunity to observe the interplay of selection and gene exchange and its implications for the evolutionary process (Futuyma, 1998).

While there have been several reviews and books on the topic of natural hybridization and its role in the evolutionary process (Arnold, 1997; Barton and Hewitt, 1985; Harrison, 1990, 1993; Hewitt, 1988), the focus of these studies have been on terrestrial biota. Hybridization is traditionally thought to be a rare occurrence in the marine environment (Mayr, 1999; Randall et al., 1977). A review on hybridization in the marine environment (Gardner, 1997) and several recent papers on hybridization in marine taxa (Bierne et al., 2003; Frisch and van Herwerden, in press; Nielsen et al., 2003; Planes et al., 2001; van Herwerden et al., 2002; van Herwerden and Doherty, 2005; van Oppen et al., 2000, 2001, 2002) have highlighted the potential for hybridization in marine systems. Nevertheless, it is important to make the

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distinction between the formation of natural hybrids and the formation of a hybrid zone as the latter has consequences for speciation and the evolutionary fate of the species involved. Hybrid zones indicate that beyond the initial hybridization, there is the component of gene exchange, selection and/or dispersal, with implications for the hybridizing populations as well as neighbouring populations (Arnold, 1997; Harrison, 1993).

Studies on hybridization in marine taxa often involve commercially important species such as temperate cod (*Gadus morhua*) (Nielsen et al., 2003), mussels (*Mytilus* sp.) (Bierne et al., 2003; Gilg and Hilbish, 2003) and coral trout (*Plectropomus* sp.) (Frisch and van Herwerden, in press; van Herwerden et al., 2002). In the case of coral reef taxa, extensive work has been done on scleractinian corals, where reticulate evolution has been implicated in the evolutionary histories of several extant coral genera (Medina et al., 1999; van Oppen et al., 2000, 2001, 2002; Wallace and Willis, 1994). Although well documented in certain reef fish families such as the Chaetodontidae (McMillan and Palumbi, 1995; McMillan et al., 1999) and Pomacanthidae (Pyle and Randall, 1994), evidence of hybridization in coral reef fishes is relatively scarce (Fig. 1). The Chaetodontidae and Pomacanthidae are atypical in this respect, with the high number of reported hybrids possibly due to their popularity with underwater photographers and in the aquarium trade. Most reef fishes have not been reported to hybridize frequently (Fig. 1), highlighted by the relatively low proportion of hybridizing species found in some of the more species rich families such as the Labridae, Pomacentridae, and Serranidae, and by the absence of hybrids in families such as the Apogonidae, Blennidae, and Gobiidae. Patterns of hybridization outside of the Chaetodontidae and Pomacanthidae indicate that hybridization is restricted to a few genera within each family (Frisch and van Herwerden, in press; van Herwerden and Doherty, 2005). Within the Labridae for example, most of the hybridizing species belong to the genus *Thalassoma* (Walsh and Randall, 2004).

A study on hybridization is most useful when the attributes of its model organisms are characteristic of a broader range of taxa. Wrasses (family Labridae) are a diverse group of more than 600 species in 82 genera and display a range of body shapes, sizes, colours, and habitat preferences (Parenti and Randall, 2000; Wainwright et al., 2004). They are quintessential reef fishes and make-up a considerable proportion of the typical reef fish assemblage, second only to the gobies (family Gobiidae) on the Great Barrier Reef (Bellwood and Wainwright, 2002; Randall et al., 1996). Labrids also display life history characteristics that are shared by most other coral reef fishes (Leis, 1994). Wrasses of the genus *Thalassoma* (family Labridae, subfamily Julidini) have a circumtropical distribution and are characteristic inhabitants of both coral reefs and rocky shores. All 27 species within the genus share similar morphological and meristic characters but display a wide variety of colour patterns. Species in this genus are distinguished largely based on colour patterns (Randall et al., 1996), and recent work on the molecular phylogenetic relationships between species has confirmed the validity of currently recognised species (Bernardi et al., 2004; Costagliola et al., 2004).

Both inter-specific and inter-generic hybrids have been documented in the genus *Thalassoma*. Hybrids have been documented from crosses between *T. lunare* × *T. ruppellii* in the Red Sea (Randall and Miroz, 2001), *T. hardwicke* × *T. quinquevittatum* in Micronesia (Myers, 1999), *T. duperrey* × *T. lutescens* in Hawaii (Randall, 1996), *T. duperrey* × *T.quinquevittatum* at Johnston Atoll (Lobel, 2003), and between *Gomphosus varius* × *T. lunare* in northwestern Australia (Randall and Allen, 2004). *Gomphosus* is a derived lineage within *Thalassoma*, and may be placed within the genus (Bernardi et al., 2004).

Between 2000 and 2004, five *Thalassoma* hybrid specimens were discovered on Holmes Reef, an isolated atoll in the Coral Sea. From an evolutionary standpoint, hybridization success is theoretically more likely between closely

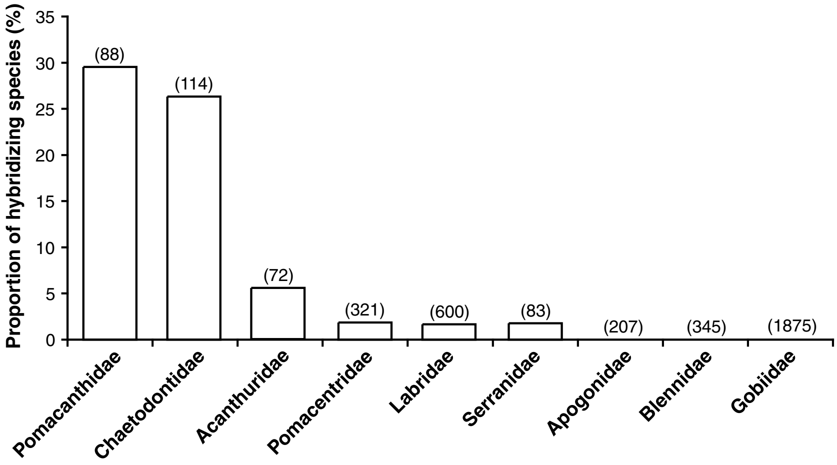

Fig. 1. Hybridization in nine coral reef fish families expressed as a percentage of the total number of species in each family reported as hybrid contributors. Numbers in parentheses are the total number of species in each family. Data combined from Pyle and Randall (1994), Gardner (1997), Allen et al. (1998), Kuiter (2002), and Fishbase (2005).