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Marine hybrid hotspot at Indo-Pacific biogeographic border

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Studying hybridization is crucial to understanding speciation and almost all our knowledge comes from terrestrial and freshwater environments. Marine hybrids are considered rare, particularly on species-rich coral reefs. Here, we report a significant marine hybrid zone at Christmas and Cocos Islands (eastern Indian Ocean) with 11 hybrid coral reef fishes (across six families); the most recorded hybrids of any marine location. In most cases, at least one of the parent species is rare (less than three individuals per 3000 m²), suggesting that hybridization has occurred because individuals of the rare species have mated with another species owing to a scarcity of conspecific partners. These islands also represent a marine suture zone where many of the hybrids have arisen through interbreeding between Indian and Pacific Ocean species. For these species, it appears that past climate changes allowed species to diverge in allopatry, while recent conditions have facilitated contact and subsequent hybridization at this Indo-Pacific biogeographic border. The discovery of the Christmas–Cocos hybrid zone refutes the notion that hybridization is lacking on coral reefs and provides a natural laboratory for testing the generality of terrestrially derived hybridization theory in the marine environment.

Keywords: hybridization; Christmas Island; Cocos (Keeling) Islands; suture zone; coral reef fish; phylogeography

1. INTRODUCTION

A wide range of plants and animals hybridize, and these hybrids provide the key to understanding the barriers to gene flow and the speciation process (Arnold 1997; Seehausen 2004; Mallet 2005). Central to the study of hybridization are hybrid zones: areas where species or subspecies interbreed (Hewitt 1988; Harrison 1993). These zones often arise where there is secondary contact between allopatric species (Hewitt 1988, 2000). When

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regional biotas come into secondary contact at biogeographic borders, many species pairs may interbreed forming a cluster of hybrid zones termed a 'suture zone' (Remington 1968; Hewitt 2000).

Almost all our knowledge and theories of hybridization, hybrid zones and suture zones comes from research in the terrestrial and freshwater environments (Harrison 1993; Arnold 1997; Hewitt 2000; Seehausen 2006). Even though the marine environment covers more than 70 per cent of the planet and contains some of the world's most diverse ecosystems, hybridization has seldom been explored in the sea and this has led to the belief that marine hybridization is rare and insignificant (Arnold 1997).

Coral reef fishes comprise the most species-rich vertebrate communities on the Earth, attaining their greatest diversity in the Indonesia–Philippines region. Yet 'the seeming lack of hybridization in the swarming reef fauna of the Indo-Pacific region is amazing' (Hubbs 1955), especially given the prevalence of hybridization in freshwater fishes (Hubbs 1955; Arnold 1997; Gardner 1997; Seehausen 2006). Similarly, suture zones have not been reported in the tropical marine environment (Gardner 1997), despite obvious boundaries between major biogeographic provinces, such as the region surrounding Christmas and Cocos (Keeling) Islands in the eastern Indian Ocean, where the Indian and Pacific Ocean regional biotas abut (Marie *et al.* 2007; Rocha *et al.* 2007).

In this study, we present findings from our investigation of hybrid coral reef fishes at Christmas Island (10°30' S, 105°40' E) and the Cocos (Keeling) Islands (12°12' S, 96°54' E), which challenge the long-held belief that hybridization is rare in the marine environment. Here, we describe, to our knowledge, the first suture zone in the tropical marine environment (figure 1), determine the number of species that are hybridizing and examine the conditions that have facilitated hybridization and the formation of a suture zone.

2. MATERIAL AND METHODS

Hybrid coral reef fishes were first identified underwater based on obvious intermediate coloration, while SCUBA diving on fieldtrips to Christmas and/or Cocos Islands from 1978 to 2008. To confirm hybrid status, individuals were photographed and/or collected and compared with the published accounts, verified by expert fish taxonomists or examined genetically. Underwater observations of heterospecific groups or breeding pairs and interspecific spawnings provided additional support for hybridization. The abundance of parent species was determined through underwater surveys. For detailed methodology, see the electronic supplementary material.

3. RESULTS

Our field studies of reef fishes at Christmas and Cocos Islands identified 10 hybrids in addition to a previously reported hybrid (Yaakub *et al.* 2006). The 11 recorded hybrids belong to six reef fish families: *Acanthurus leucosternon* × *Acanthurus nigricans*, *Naso elegans* × *Naso lituratus* (Acanthuridae); *Melichthys indicus* × *Melichthys vidua* (Balistidae); *Chaetodon guttatissimus* × *Chaetodon punctatofasciatus*, *Chaetodon ornatissimus* × *Chaetodon meyeri*, *Chaetodon lunulatus* × *Chaetodon trifasciatus* (Chaetodontidae); *Thalassoma janseni* × *Thalassoma quinquevittatum* (Labridae) (Yaakub *et al.* 2006); *Centropyge flavissima* × *Centropyge eibli* (figure 2), *C. eibli* × *Centropyge vrolikii*, *C. flavissima* × *C. vrolikii*

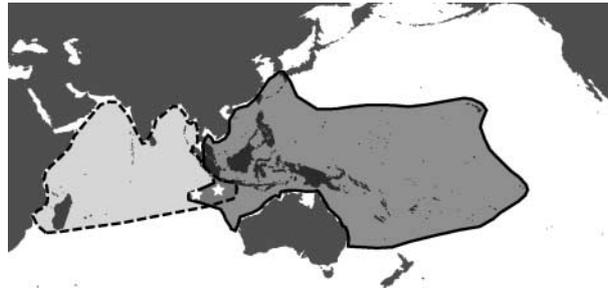


Figure 1. Christmas and Cocos Islands (represented by five-pointed stars) constitute a tropical marine suture zone located in the eastern Indian Ocean on the Indo-Pacific marine biogeographic border. At these islands, Indian (represented by lighter shaded area with dashed outline) and Pacific Ocean species (darker shaded area with solid outline) have come into contact and interbred.

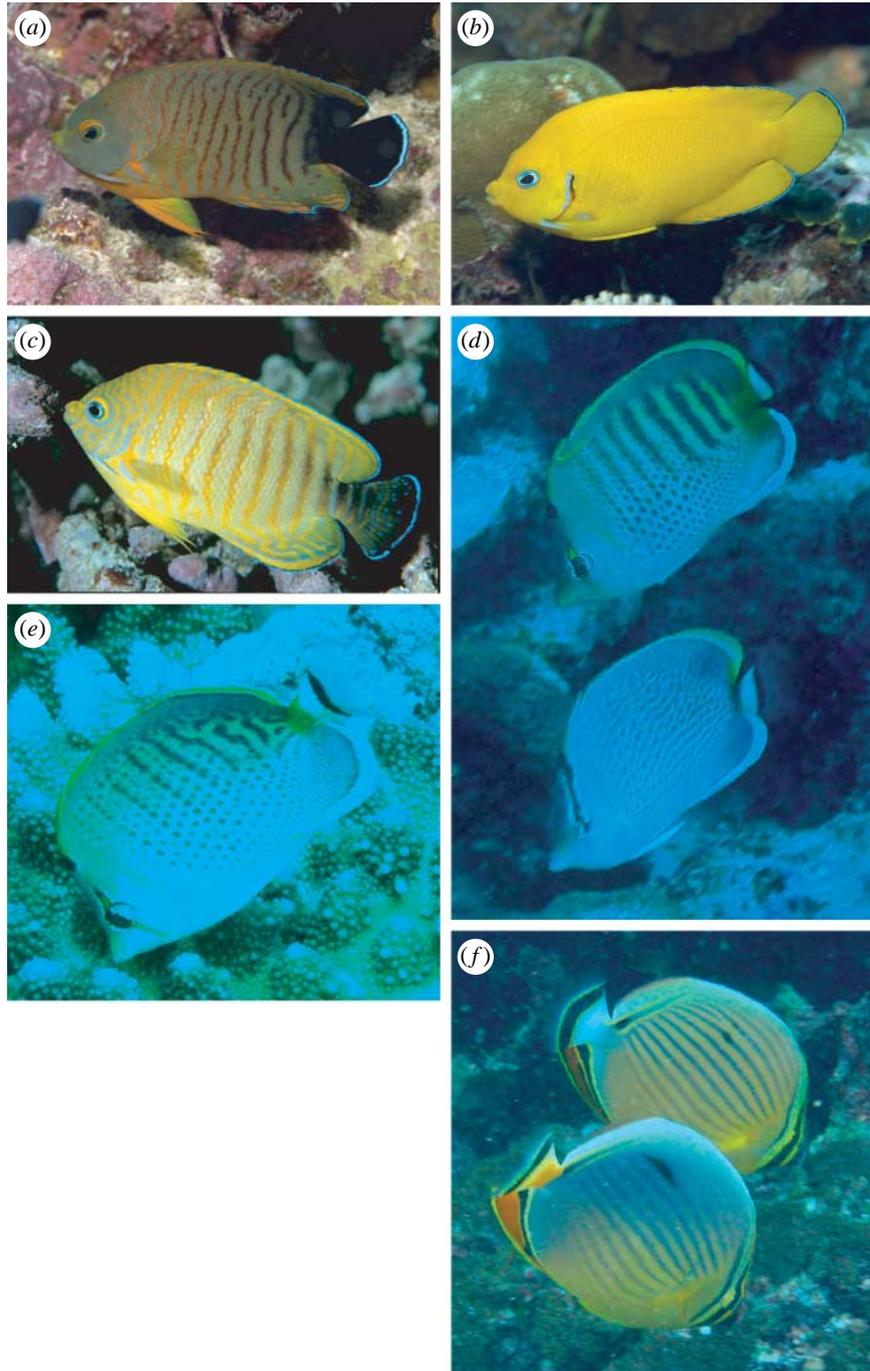


Figure 2. Christmas and Cocos Islands constitute a marine suture zone where (a) Indian Ocean (*C. eibli*) and (b) Pacific Ocean species (*C. flavissima*) come into contact and interbreed to produce (c) hybrids. (d) Heterospecific breeding pairs of *Ch. guttatissimus* (Indian Ocean: bottom) and *Ch. punctatofasciatus* (Pacific Ocean: top) produce (e) hybrids. (f) Heterospecific breeding pair of Indian (*Ch. trifasciatus*: bottom) and Pacific Ocean (*Ch. lumulatus*: top) butterflyfishes.

Table 1. The occurrence of parent species and hybrids at Christmas (CI) and Cocos Islands (CKI). (The presence of the parental species (denoted by the first letter of the species name) and hybrids (H) at each location is listed. The estimated mean densities (individuals per 3000 m²) of the parent species are presented for Christmas Island where parent species 1 is the species listed first in the hybrid column and parent species 2 is listed second. An asterisk denotes rare species whose abundance was not significantly different from zero ($t_{0.05(1),3} < 2.35$, $p > 0.05$). Geographical range of the parent species is based on the published reports (Allen *et al.* 1998; Froese & Pauly 2007). Support for each hybrid is listed as: HS, heterospecific social groups; HP, heterospecific breeding pair; IS, interspecific spawning; G, genetic confirmation; M, morphological evidence; C, intermediate coloration.)

hybrid	occurrence		mean density (per 3000 m ²)		geographical range		hybrid support
	CI	CKI	species 1	species 2	species 1	species 2	
<i>A. leucosternon</i> × <i>A. nigricans</i>	L, N, H	L, N, H	2*	23.75	Indian Ocean	Pacific Ocean	HS, G ^a , C
<i>N. elegans</i> × <i>N. lituratus</i>	E, L, H	E, L, H	2.75*	12	Indian Ocean	Pacific Ocean	HS, G ^b , C
<i>M. indicus</i> × <i>M. vidua</i>	I, V, H	I, V, H	11.5	23.25	Indian Ocean	Indo-Pacific	HS, C
<i>Ch. guttatissimus</i>	G, P, H	G, P	7.75	0.75*	Indian Ocean	Pacific Ocean	HP, C
× <i>Ch. punctatofasciatus</i>							
<i>Ch. trifasciatus</i> × <i>Ch. lumulatus</i>	T, L, H	T	0.5*	0*	Indian Ocean	Pacific Ocean	HP, C
<i>Ch. ornatissimus</i> × <i>Ch. meyeri</i>	O, M, H	O, M	11.5	14.5	Indo-Pacific	Indo-Pacific	HP, C
<i>T. janseni</i> × <i>T. quinquevittatum</i>	J, Q, H	J, Q, H	1.75*	9.5	Indo-Pacific	Indo-Pacific	HS, IS, G ^a , C
<i>C. eibli</i> × <i>C. flavissima</i>	E, F, H	E, F, H	0.5*	> 30	Indian Ocean	Pacific Ocean	HS, IS, M ^c , C
<i>C. eibli</i> × <i>C. vrolikii</i>	E, V, H	E	0.5*	0.5*	Indian Ocean	Pacific Ocean	HS, M ^c , C
<i>C. flavissima</i> × <i>C. vrolikii</i>	F, V, H	F, H	> 30	0.5*	Pacific Ocean	Pacific Ocean	HS, IS, M ^c , C
<i>Ar. nigropunctatus</i> × <i>Ar. mappae</i>	N, H	N	4*	0*	Indo-Pacific	Indo-Pacific	C

^aElectronic supplementary material.

^bS. Klanten 2008, unpublished data.

^cPyle & Randall (1994).

(Pomacanthidae); and *Arothron nigropunctatus* × *Arothron mappae* (Tetraodontidae). In six of these cases, the hybrids were formed via interbreeding between the Pacific and Indian Ocean species (table 1). The underwater surveys revealed that in nine cases, either one or both parent species were rare (abundances did not differ significantly from zero: $t_{0.05(1),3} < 2.35$, $p > 0.05$; table 1).

4. DISCUSSION

The identification of 11 hybrid fishes at Christmas and Cocos Islands represents, to our knowledge, the greatest number of hybrids reported from any marine location (Gardner 1997) and the first recorded suture zone in tropical seas. Genetic and/or morphological studies so far confirm or support the hybridization between six of these species pairs (table 1). Furthermore, genetic analyses of two hybridizing species pairs confirm that introgression has occurred (Yaakub *et al.* 2006; Marie *et al.* 2007), signifying that some hybrids are fertile and backcross with the parent species.

Contact between typically allopatric species appears to be the most plausible reason for the hybridization in 6 of the 11 cases. These hybrids generally represent interbreeding between recently diverged Pacific and Indian Ocean species (Pyle & Randall 1994; McMillan & Palumbi 1995; Klanten *et al.* 2004; Marie *et al.* 2007) and phylogenetic studies show that a concordant genetic division occurred in this region 1–3 Myr ago (McMillan & Palumbi 1995; Benzie 1999; Hewitt 2000). This timing coincides with sea-level changes that formed land bridges across the Indonesian region, thereby restricting gene flow between the Indian and Pacific

Oceans (Benzie 1999; Hewitt 2000). Christmas and Cocos Islands are apparently a tropical marine equivalent of terrestrial suture zones (Remington 1968; Hewitt 2000) where hybridization has subsequently occurred owing to recent contact between allopatric species that diverged as a result of past (probably Pleistocene) climate changes. Divergence time may have been insufficient to establish pre- or post-zygotic barriers, thus enabling hybridization following secondary contact.

In five cases, sympatric species have hybridized indicating that factors other than secondary contact are important. Hybridization can also be promoted by low abundance (Hubbs 1955; Arnold 1997; Yaakub *et al.* 2006) and our field surveys at Christmas Island revealed that either one or both the parent species were rare in 9 of the 11 cases. Consequently, individuals of the rare species may choose to mate with another closely related species owing to a scarcity of conspecific partners. However, in two cases, the parent species were abundant, occupied the same habitat, and Christmas and Cocos Islands are the only locations where hybrids of these sympatric species have been reported. It is unclear why these species are hybridizing at this location. It may represent accidental hybridization that has been suggested for other reef fish hybrids, where groups of two species have spawned in the vicinity of each other and their gametes have come into contact (Frisch & Van Herwerden 2006; Yaakub *et al.* 2007). It appears that even within the Christmas–Cocos zone, hybrids can arise owing to different reasons. Further exploration in other marine taxa and locations is required to determine what factors are most commonly responsible for hybridization in the marine environment.

The occurrence of hybridization is usually underestimated (Mallet 2005) and more cases are probably at Christmas and Cocos Islands. Hybrid individuals of many reef fishes often go undetected because they exhibit the physical appearance of one of the parent species (McMillan *et al.* 1999; Yaakub *et al.* 2006; Marie *et al.* 2007). More importantly, this study examined only reef fishes, and hybridization is probable in other marine groups. Christmas and Cocos Islands lie on the largest marine biogeographic border in the tropical Indo-Pacific (Bay *et al.* 2004; Rocha *et al.* 2007) and phylogenetic studies of a wide range of marine taxa, including invertebrates and plants, consistently report a phylogenetic break in this region (Benzie 1999; Hewitt 2000). At these islands, many tropical marine species are at the edge of their range, are low in abundance and come into contact with allopatric sister species or subspecies (Wells 1994; Hobbs & Salmond 2008); all factors that promote hybridization (Mayr 1979; Hewitt 1988; Arnold 1997).

The discovery of the Christmas–Cocos suture zone is significant because it refutes the notion that hybridization is rare in the marine environment and lacking on coral reefs (Hubbs 1955, Arnold 1997). These islands now provide a natural laboratory for testing the generality of terrestrially derived hybridization theory in the marine environment. Furthermore, these studies will provide unique insights and contribute to our understanding of evolutionary processes in the sea; such as barriers to gene flow, insular speciation processes and the formation of hybrid lineages. Finally, the location of this suture zone close to the global centre of coral reef diversity (Indonesia–Philippines) helps to explain this extraordinary diversity by identifying Pleistocene sea-level changes as a significant biodiversity contributor to this region.

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