

Hybridisation among coral reef fishes at Christmas Island and the Cocos (Keeling) Islands

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Abstract. Hybridisation is common among terrestrial and freshwater species, but is considered rare and insignificant in marine systems. Christmas and Cocos (Keeling) Islands represent a recently discovered marine suture zone that contains a high number of hybridising coral reef fishes. In this study we document a further eight species that are hybridising, bringing the total number of reported hybrid crosses to 15, involving 27 species across eight families. So far, eight of the 15 hybrid crosses have been genetically confirmed. There is a taxonomic bias to this hybridisation, with chaetodontids and acanthurids containing the greatest number of hybridising species. Hybridisation commonly involves Indian and Pacific Ocean sister species that are coming into secondary contact. In most cases, at least one parent species is rare and the lack of conspecific partners is leading to the formation of heterospecific social groups and the breakdown of assortative mating. The discovery of this hybrid hotspot provides a unique and important opportunity to examine speciation in the marine environment.

Key words. coral reef fish, hybridisation, hybrid hotspot, Indo-Pacific biogeographic border, suture zone

INTRODUCTION

Hybridisation is the interbreeding between two genetically distinct lineages or species that produces viable offspring (Arnold, 1997). Hybridisation is considered an important evolutionary process because it has the ability to both increase and decrease species diversity (Seehausen, 2004, 2006). Areas where species hybridise (hybrid zones) are considered important natural laboratories for studying speciation because they reveal the processes that are crucial to maintaining reproductive isolation (Hewitt, 1988; Arnold, 1997). Hybridisation is particularly common in regions of secondary contact (e.g., biogeographic borders) where multiple pairs of sister species interbreed (Hewitt, 2000). An area containing multiple hybrid zones is termed a ‘suture zone’ (Remington, 1968).

Hybridisation can be facilitated by a number of factors (see reviews by Arnold, 1997; Hewitt, 2000; Mallet, 2005), with secondary contact, abundance disparities and non-assortative mating among the most commonly studied. Secondary contact between sister species may lead to hybridisation because insufficient divergence during allopatry prevents the evolution of complete reproductive isolation (Hewitt, 2000). Interbreeding between species may also be triggered by low abundance because an individual of a rare species may mate

with another species due to a lack of conspecific partners (Arnold, 1997). The breakdown in reproductive isolation can also be generated by indiscriminate mate choice, which leads to non-assortative mating. Taxonomic differences in the prevalence of these factors mean that some groups are more prone to hybridise than others (Gardner, 1997; Mallet, 2005).

In the tropical marine environment, the Indo-Pacific biogeographic border represents a significant region for hybridisation (Allen et al., 2007; Hobbs et al., 2009, 2012). Located in the eastern Indian Ocean, this region (which includes Christmas and Cocos (Keeling) Islands) is a zone of secondary contact between Indian and Pacific Ocean species that have diverged in allopatry during the Plio-Pleistocene sea level changes (Hobbs & Salmond, 2008; Hobbs et al., 2009, 2010). Eleven species pairs of coral reef fishes were initially reported to hybridise at Christmas and/or Cocos (Keeling) Islands (Hobbs et al., 2009) and this high incidence of hybridisation provides the ideal opportunity to study the factors that facilitate the breakdown of reproductive isolation in the marine environment.

In this study we provide descriptions and photographs of all the reef fishes that hybridise at Christmas and Cocos (Keeling) Islands as well as their hybrids. This includes eight species not previously known to hybridise. This study provides a range of evidence supporting each case of hybridisation inferred from extensive behavioural observations and molecular studies. We also examine the role of biogeographic, ecological and behavioural factors in the promotion of hybridisation at this marine hybrid hotspot.

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MATERIAL AND METHODS

Study site and species. This study was conducted at Christmas Island (10°30'S, 105°40'E) and the Cocos (Keeling) Islands (12°12'S, 96°54'E), which are situated on the Indo-Pacific biographic border in the eastern Indian Ocean (Hobbs et al., 2012). Hybrid fishes were recorded and/or collected during underwater surveys by the authors on fieldtrips to Christmas and/or Cocos (Keeling) Islands in 1978, 1986, 1987, 1989, 2001, 2002, 2005, 2006, 2008, 2010, 2011, 2012 and 2013. Individuals suspected of being hybrids were identified by unique colouration that is intermediate of the parent species (Fig. 1.). To garner further evidence of hybridisation, in situ behavioural observations were used to determine if parent species formed heterospecific social groups, heterospecific breeding pairs, and/or spawned

interspecifically. Where available, published meristic data was obtained as evidence of intermediate phenotypes of hybrids (e.g., fin spine and ray counts; Pyle & Randall, 1994). Published and unpublished data from recent molecular studies were available for eight cases of hybridisation. These data were examined for conclusive evidence of hybridisation and genetic confirmation of the parent species.

Underwater visual surveys for hybrids and observations of heterospecific interactions focused on reef fishes inhabiting coral reefs between 0–40 m depth. A full list of reef fish species occurring at Christmas and Cocos (Keeling) Islands is provided in Hobbs et al. (2014a, 2014b, this issue). Recent taxonomic revisions mean the status of four species requires clarification. Firstly, *Chromis fieldi* has recently been described by Randall & DiBattista (2013). Previously,

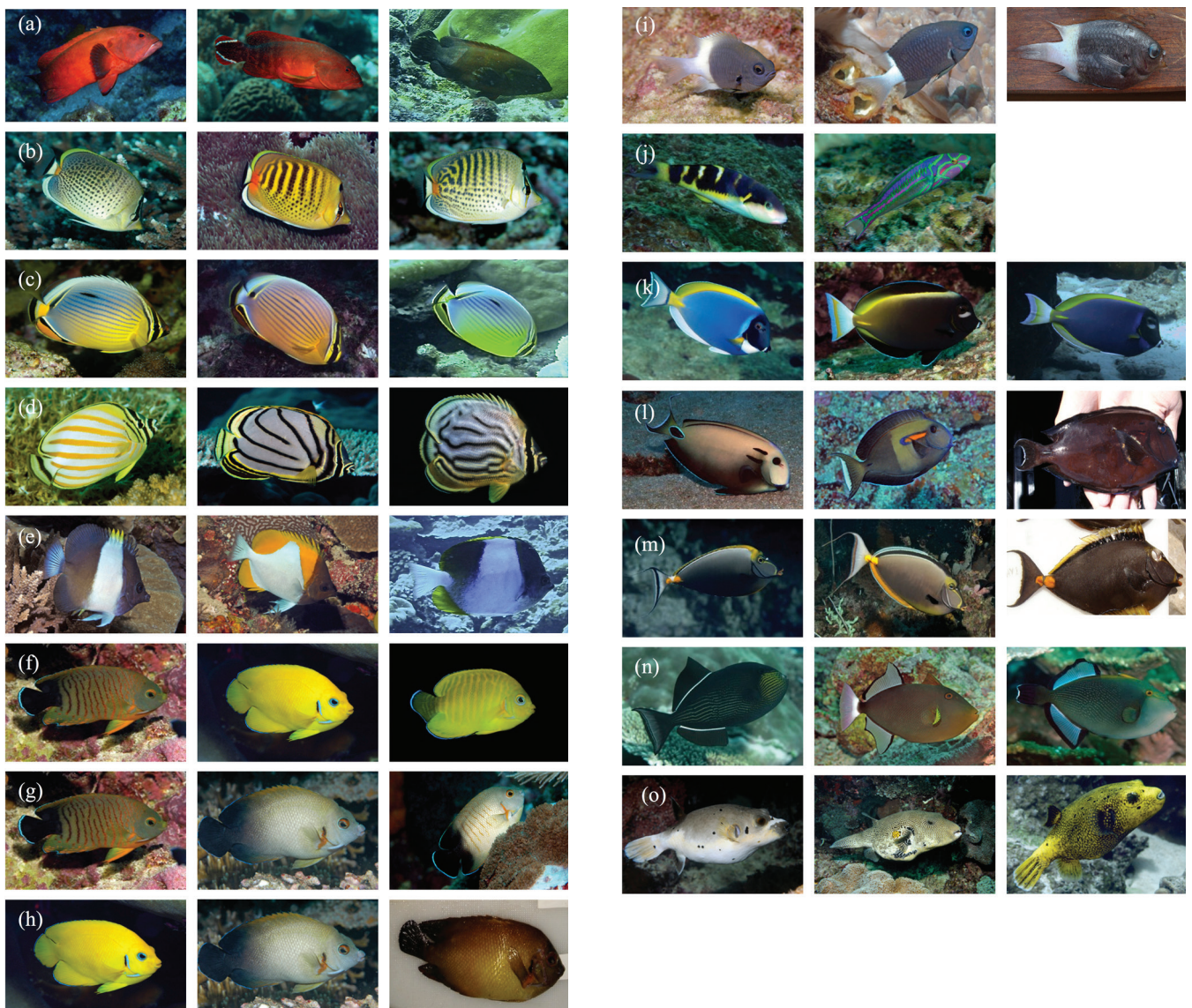


Fig 1. Hybridising coral reef fishes from Christmas and Cocos (Keeling) Islands. The first column of photographs is parent species 1 (named first), second column is parent species 2 (named second) and the third column is the hybrid. Rows are: (a) *Cephalopholis nigripinnis* × *C. urodeta*, (b) *Chaetodon guttattissimus* × *Ch. punctatofasciatus*, (c) *Ch. trifasciatus* × *Ch. lunulatus*, (d) *Ch. ornatissimus* × *Ch. meyeri* (hybrid photo: F. Walsh), (e) *Hemitaurichthys zoster* × *H. polylepis*, (f) *Centropyge eibli* × *Ce. flavissima* (hybrid photo: J. Gilligan), (g) *Centropyge eibli* × *Ce. vrolikii*, (h) *Centropyge flavissima* × *Ce. vrolikii*, (i) *Chromis fieldi* × *C. margaritifer*, (j) *Thalassoma janssenii* × *T. quinquevittatum* (no photo of hybrid), (k) *Acanthurus leucosternon* × *A. nigricans*, (l) *A. tennentii* × *A. olivaceus* (hybrid photo: M. Craig), (m) *Naso elegans* × *N. lituratus*, (n) *Melichthys indicus* × *M. vidua*, and (o) *Arothron nigropunctatus* × *A. mappa*. All photos are the authors unless stated otherwise.

this species was known as *C. dimidiata*, however molecular research has shown that the Red Sea and Indian Ocean populations are genetically distinct and warrant species level classification (Randall & DiBattista, 2013). Consequently, the Red Sea population is *C. dimidiata* and the Indian Ocean population is now *C. fieldi*. The second clarification concerns *Cephalopholis nigripinnis* and *C. urodeta*. Although these two species are sometimes considered one Indo-Pacific species (Heemstra & Randall, 1993), we prefer to consider them as separate species because they are genetically distinct (Craig & Hastings, 2007) and can be easily distinguished by their caudal fin colouration. *Centropyge flavissima* has a disjunct geographic distribution, and the Indian Ocean population, which is endemic to Christmas and Cocos (Keeling) Islands, is separated by 3000 km from the Pacific Ocean population. The Christmas-Cocos population has different colouration and is genetically distinct to the Pacific Ocean population and therefore probably represents a distinct species or sub-species (Allen et al., 1998; DiBattista et al., 2012).

Factors facilitating hybridisation. Once hybrids were identified, the roles of three factors (secondary contact, low abundance and non-assortative mating) in facilitating hybridisation were examined. Given that Christmas and Cocos (Keeling) Islands are situated on a zone of secondary contact, we used information on published geographic ranges (Froese & Pauly, 2013) to determine if hybridisation is occurring between Indian and Pacific Ocean sister species. Indian Ocean species are those that are only found in the Indian Ocean (and may also occur in the Red Sea), whereas Pacific Ocean species are those that occur in the Pacific Ocean, the waters of SE Asia and have their western range limit at Christmas or Cocos (Keeling) Islands. The geographic range of Indo-Pacific species extends from the Pacific Ocean into the Indian Ocean westward of Cocos (Keeling) Islands.

To determine if hybridisation is occurring between species with low abundance, the mean densities of the parent species were estimated from underwater surveys at Christmas Island. The mean density of each parent species was calculated based on the number of individuals encountered during a 40 min swim covering depths of 0–40 m at four sites on the north coast (Hobbs et al., 2009). This equates to an approximate survey area of 3000 m² per site. Species were considered rare if their mean density was less than three individuals per 3000 m² and if their mean abundance did not differ significantly from zero (one sample, one tailed t-test). For abundant species, counts stopped once 30 individuals were encountered at a site.

To determine if hybridisation is facilitated by a breakdown in assortative mating, underwater observations of parent species in heterospecific social groups, heterospecific breeding pairs and interspecific spawning episodes were conducted at Christmas Island in 2005, 2008, 2010, 2011, 2012 and 2013. To determine the sexual status of heterospecific breeding pairs, both partners were captured and their gonads examined. Gonads of mature females were yellow, relatively large and contained vitellogenic oocytes that were visible to naked eye, whereas mature males had relatively small

white gonads that produced milt when cut transversely and gently squeezed. If these macroscopic signs were not obvious, gonads were preserved, histologically processed and examined microscopically to determine sex and maturity (following Hobbs et al., 2004).

RESULTS

We observed four new hybrids involving eight species: *Cephalopholis nigripinnis* × *C. urodeta*, *Hemitaenichthys zoster* × *H. polylepis*, *Chromis fieldi* × *C. margaritifer*, and *A. tennentii* × *A. olivaceus*. These newly described hybrids contribute to the total of 15 hybrids observed at Christmas and/or Cocos (Keeling) Islands, involving 27 species from eight families (Fig. 1). Evidence to support the status of the hybrids has increased substantially since our initial study (Hobbs et al., 2009), and several other studies have now genetically confirmed the parent species of eight hybrid crosses (Table 1). In all cases where genetics has been used ($n = 8$), hybridisation has been confirmed.

Hybridisation was most prevalent in the chaetodontids (involving eight species) followed by acanthurids (six species) and pomacanthids (three species) (Table 1). In each of the other five families (serranids, pomacentrids, labrids, balistids and tetraodontids), hybridisation was recorded for two species. The apparent bias between locations, 14 of the 15 hybrid crosses identified at Christmas Island compared to eight observed at the Cocos (Keeling) Islands (Table 1), is probably because sampling intensity was twice as great at Christmas Island compared to the Cocos (Keeling) Islands.

Nine of the 15 cases represent hybridisation between Indian and Pacific Ocean sister species (Table 1). Two cases involve hybridisation between the endemic species *C. flavissima* and its Indian and Pacific Ocean sister species. Three cases involved hybridisation between widespread Indo-Pacific species, and the remaining case was between an Indian Ocean species and an Indo-Pacific species (Table 1).

In 12 of the 15 cases of hybridisation, either one or both of the parent species is rare at Christmas Island (mean density <3 individuals per 3000 m², Table 1). Density data is only available for hybridising angelfishes at the Cocos (Keeling) Islands and a similar result is observed: *C. flavissima* is common (mean density of >30 individuals per 3000 m²), while the species it hybridises with are rare (*C. eibli* and *C. vrolikii* mean densities of 0 individuals per 3000 m²). Although the low abundance estimate for *Hemitaenichthys polylepis* at Christmas Island is not representative of this location (this schooling species can be the most abundant butterflyfish at some sites); the species it hybridises with, *H. zoster*, is so rare that it has not yet been observed at Christmas Island, even though hybrids have. Similarly, the pufferfish *Arothron mappa* has not yet been observed at Christmas Island, but its hybrid has.

In 14 of the 15 hybrid cases, parent species were observed in heterospecific social groups indicating a breakdown in assortative mating (Table 1). This is confirmed in the harem

Table 1. Description and characteristics of hybridising reef fishes at Christmas (CI) and Cocos (Keeling) (CKI) Islands. For occurrence, the initial represents the first letter of the parent species name and "H" represents hybrid. Note the occurrence of the hybridising *Cephalopholis* and *Chromis* and their hybrids has not yet been properly investigated for CKI. For mean density, Sp. 1 is the parent species listed first in the hybrid column and Sp. 2 is listed second. An asterisk denotes rare species whose abundance was not significantly different from zero ($t_{0.05(1),3} < 2.35$, $p > 0.05$). The following abbreviations were used for geographic distributions: IO = Indian Ocean; PO = Pacific Ocean; IP = Indo-Pacific; E = endemic. Support for each hybrid is listed as: HS = heterospecific social groups; HP = heterospecific breeding pair; IS = interspecific spawning; C = intermediate colouration; M = morphological evidence (from Pyle & Randall, 1994); and G = genetic confirmation.

Family	Hybrid	Occurrence		Mean density (per 3000 m ²) at CI		Geographic range		Hybrid support
		CI	CKI	Sp. 1	Sp. 2	Sp. 1	Sp. 2	
Serranidae	<i>Cephalopholis nigripinnis</i> × <i>C. urodeta</i>	N, U, H	N	9.25	4.5	IO	PO	HS, C
Chaetodontidae	<i>Chaetodon guttatisimus</i> × <i>C. punctatofasciatus</i>	G, P, H	G, P	7.75	0.75*	IO	PO	HP, C, G – Montanari et al., 2014
	<i>C. trifasciatus</i> × <i>C. lunulatus</i>	T, L, H	T	0.5*	0*	IO	PO	HP, C, G – Montanari et al., 2012
	<i>C. ornatissimus</i> × <i>C. meyeri</i>	O, M, H	O, M	11.5	14.5	IP	IP	HP, C
	<i>Hemitaenichthys zoster</i> × <i>H. polylepis</i>	P, H	P, Z	0*	1.25*	IO	PO	HS, C
Pomacanthidae	<i>Centropyge eibli</i> × <i>C. flavissima</i>	E, F, H	E, F, H	0.5*	> 30	IO	E	HS, IS, C, M, G – DiBattista et al., 2012
	<i>Centropyge eibli</i> × <i>C. vrolikii</i>	E, V, H	E, V	0.5*	0.5*	IO	PO	HS, C, M, G – DiBattista et al., 2012
	<i>Centropyge flavissima</i> × <i>C. vrolikii</i>	F, V, H	F, V, H	> 30	0.5*	E	PO	HS, IS, M, C, G – DiBattista et al., 2012
	<i>Chromis fieldi</i> × <i>C. margaritifera</i>	F, M, H	M	2.75*	>30	IO	PO	HS, C
Labridae	<i>Thalassoma janssenii</i> × <i>T. quinquevittatum</i>	J, Q, H	J, Q, H	1.75*	9.5	IP	IP	HS, IS, C, G – Yaakub et al., 2006
Acanthuridae	<i>Acanthurus leucosternon</i> × <i>A. nigricans</i>	L, N, H	L, N, H	2*	23.75	IO	PO	HS, C, G – Marie et al., 2007
	<i>A. tennentii</i> × <i>A. olivaceus</i>	T, O, H	T, O, H	0*	16.75	IO	PO	HS, C
Balistidae	<i>Naso elegans</i> × <i>N. lituratus</i>	E, L, H	E, L, H	2.75*	12	IO	PO	HS, C, G – S. Klanten unpublished data
	<i>Melichthys indicus</i> × <i>M. vidua</i>	I, V, H	I, V, H	11.5	23.25	IO	IP	HS, C
Tetraodontidae	<i>Arothron nigropunctatus</i> × <i>A. mappa</i>	N, H	N	4*	0*	IP	IP	C

angelfishes (*Centropyge*) and pair-forming butterflyfish (*Chaetodon*) where social groups contained mature females and males of different species (Table 1). Furthermore, in the hybridising angelfishes and wrasses, deliberate spawning between the different parent species was observed in these heterospecific groups (Table 1). Hence species are choosing to partner with another species and mate with them.

DISCUSSION

Christmas and Cocos (Keeling) Islands have by far the most reported hybrid marine fishes of any location reported to date (Gardner, 1997). Hybridisation frequently occurs between Indian and Pacific Ocean sister species and in most cases, where one or both parent species is rare. The formation of heterospecific social groups and breeding pairs, combined with observations of interspecific spawning, indicates that a breakdown in assortative mating has allowed interbreeding and subsequent hybridisation.

Hybridisation is usually first detected by observing individuals with intermediate colouration but is ultimately confirmed using genetics. Genetic confirmation is particularly important for species that exhibit a range of colour variants (e.g., *Arothron nigropunctatus*; Su & Tyler, 1986) or change colour throughout their life. Genetics has confirmed hybridisation in eight of the 15 cases from Christmas and Cocos (Keeling) Islands. Most importantly, there were no cases where genetics did not confirm putative

hybrids (individuals with intermediate colouration). However, one case of hybridisation (*Thalassoma jansseni* × *T. quinquevittatum*) was “accidentally” detected during a genetic study of wrasses (Yaakub et al., 2006) before any other evidence of hybridisation was detected. This confirms previous generalisations that hybridisation frequently goes undetected and is often discovered inadvertently (Mallet, 2005). The continued discovery of hybrids at Christmas and Cocos (Keeling) Islands indicates that more cases of hybridisation are likely.

Given that hybridisation is most common among recently diverged taxa (Mallet, 2005) that come into secondary contact at biogeographic borders (Hewitt, 2000), future hybrids at Christmas and Cocos (Keeling) Islands are most likely between Indian and Pacific Ocean sister species. Likely candidates include the following fishes that have already been observed in heterospecific social groups at Christmas and Cocos (Keeling) Islands: *Acanthurus pyroferus* with *A. tristis*; *Zebrasoma desjardini* with *Z. veliferum*; *Chaetodon baronessa* with *C. triangulum*; and *C. falcula* with *C. ulietensis*. As Christmas and Cocos (Keeling) Islands represent a suture zone between Indian and Pacific marine biotas, hybridisation is also likely to be discovered in taxa other than fish (Hobbs & Salmond, 2008; Hobbs et al., 2009).

In addition to hybridisation between distinct species, hybridisation may occur between different clades and morphs that are present at Christmas and Cocos (Keeling) Islands.

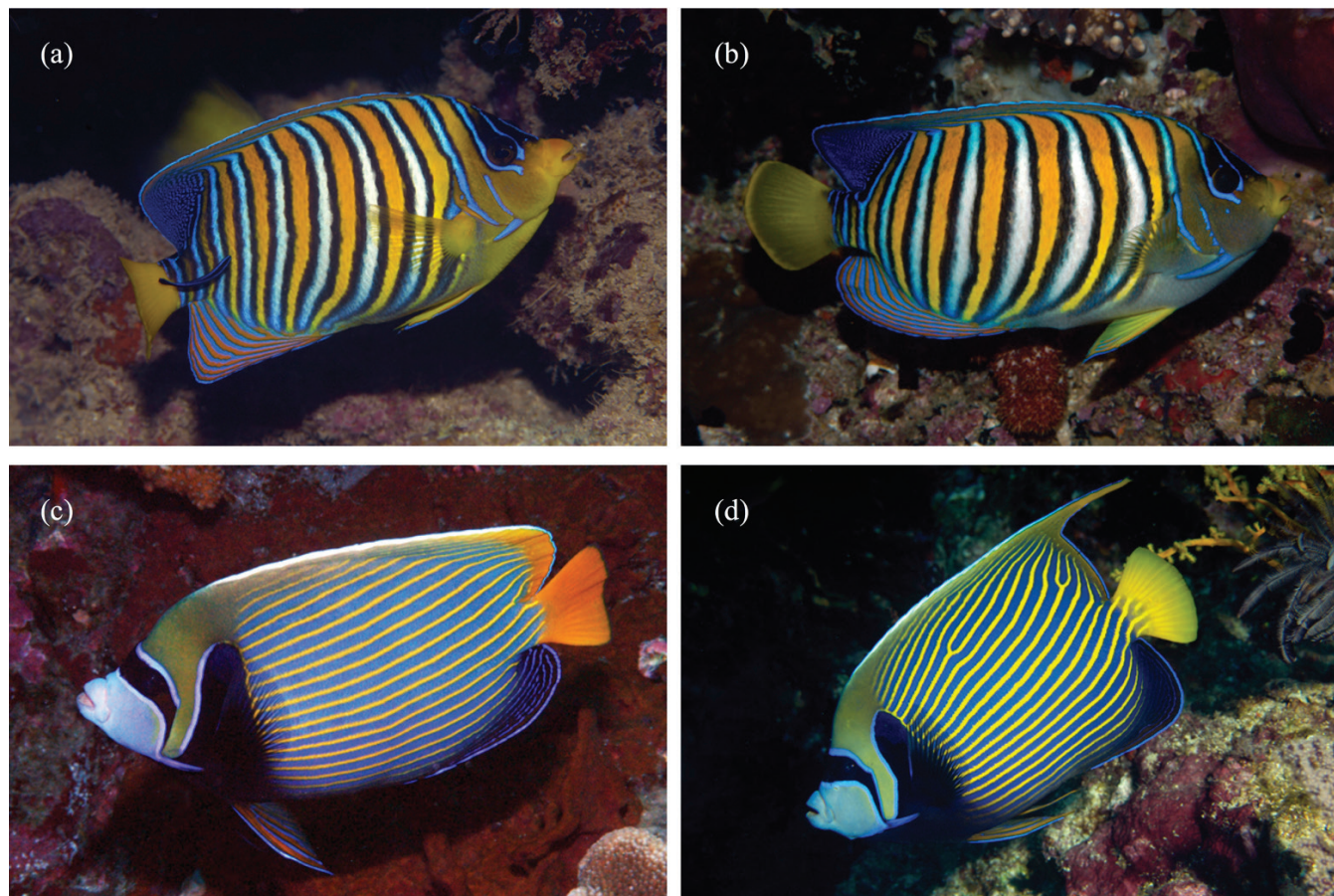


Fig 2. Examples of Indian and Pacific Ocean morphs that cohabit and potentially interbreed at Christmas Island. (a) Indian and (b) Pacific Ocean *Pygoplites diacanthus*, and (c) Indian and (d) Pacific Ocean *Pomacanthus imperator*. Photos: G. Allen.

Several widespread Indo-Pacific species that have Indian and Pacific Ocean phenotypes form heterospecific groups at Christmas and Cocos (Keeling) Islands and are likely to be interbreeding (e.g., angelfishes *Pygoplites diacanthus* and *Pomacanthus imperator*, Fig. 2). At an even finer scale, recent genetics studies have revealed that some widespread Indo-Pacific species have cryptic Indian and Pacific Ocean clades that cannot be distinguished phenotypically but co-occur at Christmas and Cocos (Keeling) Islands (e.g., Gaither et al., 2011). Hybridisation between species, colour morphs and cryptic clades represent a continuum of increasing difficulty in identification of hybrids by intermediate colouration. However, given that hybridisation is defined as the product of interbreeding between genetically distinguishable taxa (Arnold, 1997), molecular studies will be able to identify hybrid individuals where intermediate colouration is not obvious (e.g., Yaakub et al., 2006).

There is a taxonomic bias to hybridisation in the terrestrial environment (Mallet, 2005), and this also appears to be the case for reef fishes at Christmas and Cocos (Keeling) Islands. The families that have the most recorded hybridising species are not the most speciose. Chaetodontids and acanthurids have the most hybridising species (eight and six species, respectively) but at Christmas Island these are the seventh and eighth most speciose families, and at the Cocos (Keeling) Islands they are the fifth and seventh most speciose (see Hobbs et al., 2014a, 2014b, this issue). In contrast, the four most speciose families at Christmas and Cocos (Keeling) (Labridae, Gobiidae, Serranidae, Pomacentridae; Hobbs et al., 2014a, 2014b, this issue) contain a combined total of only six species known to hybridise at Christmas Island, and two hybridising species at the Cocos (Keeling) Islands. This taxonomic bias may be partly due to differences in sampling intensity and the level of cryptic behaviour or colouration. This could explain why hybrids from groups such as butterflyfish and angelfish are frequently reported (Pyle & Randall, 1994; Hobbs et al., 2013). However, this hypothesis cannot explain the scarcity of hybridising labrids and pomacentrids at Christmas and Cocos (Keeling) Islands because these speciose groups are generally well studied and not cryptic. Other factors, such as taxonomic differences in divergence rates, may also create taxonomic bias in hybridisation and require further investigation.

Rarity is commonly implicated in hybridisation because a lack of conspecific partners results in a rare species mating with another species (Arnold, 1997). For most hybridising species pairs at Christmas and Cocos (Keeling) Islands at least one of the parent species is rare. Furthermore, in all cases where at least one of the parent species is rare, we have observed them in heterospecific social groups. Thus it appears that the lack of conspecific partners is promoting the breakdown in assortative mating that leads to interbreeding. In three of the 15 cases, hybridisation is occurring between common species and it is not clear why interbreeding is occurring given the abundance of conspecific partners. Accidental hybridisation (where two species mate homospecifically in close proximity and their broadcast gametes inadvertently come into contact) may play a role.

The occurrence of so many hybrids at Christmas and Cocos (Keeling) Islands provides an ideal opportunity to investigate a number of key topics in marine speciation. Such research can provide unique insights into reproductive isolation, barriers to gene flow and the speciation process in the marine environment. Furthermore, molecular studies can determine whether hybridisation results in decreased species richness (through reverse speciation; Seehausen, 2006) or produces new lineages and species (as it has for freshwater cichlids; Seehausen, 2004). Using coral reef fishes as a model system to determine if hybridisation increases or decreases species richness in the marine environment is appropriate given that this group represents the most diverse vertebrate communities on earth.

This study concludes that Christmas and Cocos (Keeling) Islands are a hybrid hotspot for marine fishes, and the discovery of more hybrids, particularly in other taxonomic groups, is likely. The secondary contact between Indian and Pacific Ocean biotas that is occurring at the Christmas-Cocos marine suture zone, combined with the low abundance of parent species, is facilitating the formation of heterospecific groups and the breakdown in assortative mating. This hybrid hotspot provides the ideal natural laboratory for studying marine speciation because it allows comparisons between hybridising species that can overcome barriers to gene flow and non-hybridising species that can maintain reproductive isolation under the same conditions.

ACKNOWLEDGEMENTS

We are grateful to everyone who has helped us with our fieldwork at these remote islands. In particular, we thank A. Graham, G. Christie, J. Clunies-Ross, J. Gilligan, T. Hamanaka, J. Hender, E. Johari, M. Misso, R. Muller, R. Steene and A. Yon. Special thanks to Christmas Island National Park Chief Ranger M. Orchard whose encouragement, enthusiasm and knowledge has initiated and advanced marine research considerably at Christmas and Cocos (Keeling) Islands. We appreciate the logistical and financial support provided by Parks Australia and Western Australia Museum. Thanks to H. Choat and L. van Herwerden for stimulating discussions on reef fish hybridisation and M. Gaither and S. Klanten for information on unpublished molecular data. M. Craig, J. Gilligan, and F. Walsh generously provided photographs of hybrids. Thanks to T. Staeudle for assisting with manuscript preparation.

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