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Genetic population structure of the convict surgeonfish *Acanthurus triostegus*: a phylogeographic reassessment across its range.

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This study investigates the genetic population structure and connectivity of *Acanthurus triostegus* in five Indo-Pacific biogeographic regions (western and eastern Indian Ocean, western, central and eastern Pacific Ocean), using a mitochondrial DNA marker spanning the ATPase8 and ATPase6 gene regions. In order to assess the phylogeography and genetic population structure of *A. triostegus* across its range, 35 individuals were sampled from five localities in the western Indian Ocean and complemented with 227 sequences from two previous studies. Results from the overall analysis of molecular variance (AMOVA) without *a priori* grouping showed evidence of significant differentiation in the Indo-Pacific, with 25 (8.3 %) out of 300 pairwise Φ_{ST} comparisons being significant. However, the hierarchical AMOVA grouping of Indian and Pacific Ocean populations failed to support the vicariance hypothesis, showing a lack of a genetic break between the two ocean basins. Instead, the correlation between pairwise Φ_{ST} values and geographic distance showed that dispersal of *A. triostegus* in the Indo-Pacific Ocean follows an isolation-by-distance model. Three haplogroups could be deduced from the haplotype network and phylogenetic tree, with haplogroup 1 and 2 dominating the Indian and the Pacific Ocean, respectively, while haplogroup 3 exclusively occurring in the Hawaiian Archipelago of the central Pacific Ocean.

KEYWORDS

Genetic diversity, Indo-Pacific barrier Kenya, Madagascar, mtDNA, Tanzania.

1 | INTRODUCTION

The Indo-Pacific barrier (IPB) hinders the movement of tropical marine organisms between the Indian and the Pacific Ocean. Its exact location in the Indo-Australian Archipelago (IAA) is still being debated, but it is widely recognized that the efficacy of this barrier increased during the Pleistocene sea-level low stands (Gaither *et al*., 2010). During the Pleistocene glacial cycles (*c.* 2.6 million to 11 700 years ago), sea level repeatedly dropped as much as120 m below present, exposing the shallow Sunda and Sahul shelves. At the same time, the Torres Strait between New Guinea and Australia was closed and acted as a land bridge for 90 000–100 000 years until its inundation *c.* 7000 years ago (Voris, 2000). The strong upwelling of cold water at the base of the Indonesian arc limited dispersal of tropical marine organisms through the few open narrow channels in the eastern Indonesian islands (Fleminger, 1986; Voris, 2000). This barrier divided populations that once freely exchanged migrants for tens of thousand years (Benzie, 1999). Although phylogeographic surveys across the Indo-Pacific are still at a nascent stage (Carpenter *et al*., 2011), studies on several taxa have shown a concordant genetic partition between the Indian and the Pacific Ocean. These include teleosts (McMillan & Palumbi, 1995; Planes & Fauvelot, 2002; Kochzius *et al.*, 2003; Bay *et al.*, 2004; Timm & Kochzius, 2008; Timm *et al.*, 2008; Gaither *et al.*, 2010; Mirams *et al.*, 2011), echinoderms (Benzie, 1999; Crandall *et al.*, 2008*b*; Kochzius *et al*., 2009; Otwoma & Kochzius, 2016), molluscs (Kochzius & Nuryanto, 2008; Nuryanto & Kochzius, 2009; Hui *et al*., 2016, 2017), crustacean (Lavery *et al.*, 1996) and seagrass (Hernawan *et al.*, 2017).

Although this concordant phylogeographic structure in numerous marine taxa may indicate that genetic divergence between the two ocean basins was caused by extrinsic factors such as the sea-level fluctuations during the Pleistocene (Hernawan *et al.*, 2017), a number of species lack this phylogeographic break. These include echinoderms *Eucidaris metularia* (Lessios *et al.*, 1999) and *Diadema savignyi* (Lessios *et al.*, 2001), marine gastropods *Echinolittorina reticulata* (Reid *et al.*, 2006) and *Thyca crystallina* (Kochzius *et al.*, 2009) and the teleosts *Naso vlamingii* (Valenciennes 1835) (Klanten *et al.*, 2007), *Naso brevirostris* (Cuvier 1829) and *Naso unicornis* (Forsskål 1775) (Horne *et al.*, 2008). The lack of genetic divergence in some of the species that span the Indo-Pacific has been interpreted as the loss of one of the two divergent lineages due to local extinction or selective sweeps (Grant & Bowen, 1998), or re-establishment of gene flow after the barriers were dissipated by sea-level rise (DeBoer *et al.*, 2008; Gaither *et al.*, 2011*a*; Liu *et al.*, 2012). On the other hand, it is also possible that the ranges of these species did not span the IAA during Pleistocene multiple glaciations (Crandall *et al.*, 2008*a*).

Several studies on marine shallow-water species show a higher degree of genetic differentiation among the Indian Ocean populations as compared with their counterparts in the Pacific Ocean (Williams & Benzie, 1998; Benzie, 1999; Hui *et al.*, 2016; Huyghe & Kochzius, 2017; Otwoma & Kochzius, 2016). This suggests that not only are populations from the Indian and Pacific Oceans separated, but that species in each basin exhibit different patterns of population connectivity. The higher genetic differentiation in the Indian Ocean is attributed to the fewer reefs and island archipelagos available in this basin to facilitate long-distance dispersal through the stepping-stone model (Williams & Benzie, 1998; Benzie, 1999). This is particularly true for species that disperse across the Indian Ocean while possessing a limited pelagic larval duration (PLD). Such species show limited larval exchange within the Indian Ocean (Williams & Benzie, 1998; Benzie, 1999; Hui *et al.*, 2016; Huyghe & Kochzius, 2017), possibly due to the vast distance between their suitable habitats (Spalding *et al.*, 2007). On the other hand, species with a PLD reaching 40–90 days show genetic uniformity across the Indian Ocean, suggesting that great dispersal ability may play a role in connecting eastern and western Indian Ocean population (Craig *et al.*, 2007; Horne *et al.*, 2008; Gaither *et al.*, 2010; Gaither *et al.*, 2011*b*; DiBattista *et al.*, 2016). However, the relationship between PLD and genetic population structure is not straightforward (Selkoe *et al.*, 2014), as a positive correlation between the two is reported in some studies (Gaither *et al.*, 2010; Gaither *et al.*, 2011*b*), but not in others (Barber *et al.*, 2002; Weersing & Toonen, 2009). This ambiguity suggests that larval dispersal in marine species is not only influenced by PLD but also local oceanographic current conditions (Otwoma & Kochzius, 2016; DiBattista *et al.*, 2017), larval behaviour (Fisher *et al.*, 2005) and historical processes (Otwoma & Kochzius, 2016).

The convict surgeonfish *Acanthurus triostegus* (L. 1758) is widely distributed in the lagoon and seaward reefs of the Indo-Pacific Ocean. It feeds predominantly on filamentous algae growing on coral reefs, thus helps to keep them in the coral-dominated state. Reproduction in this species occurs through large spawning aggregations that result in clouds of pelagic fertilized eggs (Hartup *et al.*, 2013). Studies on its post-recruitment stages report an average larval swimming speed of 0.56 m s^{-1}, which can be sustained for up to 194 hours (Leis & Carson-Ewart, 1997; Stobutzki & Bellwood, 1997; Fisher & Hogan, 2007). This suggests that *A. triostegus* larvae are capable of actively influencing their dispersal and settlement (Fisher *et al.*, 2005). Otherwise, its pelagic larval phase of 40 to 60 days (McCormick, 1999) would facilitate long-distance dispersal, when the mean speed of ocean currents exceeds the average swimming speed of the larvae. The great dispersal potential and wide distribution of *A. triostegus* makes it a suitable model to investigate the forces that shape the genetic structure and evolution of marine organisms in the Indo-Pacific Ocean. Previous genetic analyses of this species were based on allozymes (Planes, 1993; Planes *et al.*, 1998; Planes & Fauvelot, 2002) or mtDNA (Lessios & Robertson, 2006; Mirams *et al.*, 2011; Liggins *et al.*, 2016) and mainly focused on assessing the genetic structure of *A. triostegus* in the eastern Indian Ocean (EIO), western Pacific (WP), central Pacific (CP) and eastern Pacific (EP) (Planes, 1993; Planes *et al.*, 1998; Lessios & Robertson, 2006; Mirams *et al.*, 2011; Liggins *et al.*, 2016). Although the study by Planes & Fauvelot (2002) covers the whole Indo-Pacific Ocean, only one population was sampled from the Indian Ocean (Mozambique).

In this study, newly sampled sequences from the western Indian Ocean (WIO) were added to published sequences from two previous studies (Lessios & Robertson, 2006; Liggins *et al.*, 2016), in order to determine the genetic population structure of *A. triostegus* across its entire range. The aim was to assess the connectivity of *A. triostegus* among WIO reefs and the role contemporary or physical barriers (long-distance between suitable habitats) play in shaping its genetic structure. In addition, the influence of historical barriers on the phylogeography of *A. triostegus* across the IAA was examined. Based on the great dispersal potential of *A. triostegus* connectivity within Indian and Pacific Basins was expected. However, the dispersal ability could have played a negligible role in connecting the Indian and Pacific *A. triostegus* populations during the Pleistocene sea-level low stands. Therefore, intraspecific divergence between the two ocean basins was anticipated.

2 | MATERIALS AND METHODS

2.1 | Sampling and DNA extraction

Adult *A. triostegus* were caught between June and December 2015 by local fishermen using spear gun, gill net, basket trap and beach seine from 5 localities in the WIO region [Figure 1(b) and Table 1]. Fin clips were cut from each individual and stored in 96% ethanol prior to DNA extraction. The genomic DNA was extracted by the standard salting precipitation method (Sunnucks & Hales, 1996).

2.2 | Amplification and sequencing

A fragment of 842 bp of the ATPase8 and ATPase6 gene regions was amplified through PCR using the primers described by Lessios & Robertson (2006): ATP8.2 (5′ AAAGCRTYRGCCTTTTAAGC 3′) and CO3.2 (5′ GTTAGTGGTCAKGGGCTTGGRTC 3′). All PCRs were conducted in a total volume of 25µl that included 2.5µl buffer C (Roboklon; www.roboklon.de), 1µl deoxynucleotide triphosphate (dNTP) (10 mM), 1µl $MgCl_2$ (25 mM), 0.5µl bovine serum albumin (BSA; 10mg ml^{-1}), 0.5µl of each primer (10 µM), 0.125µl Taq DNA polymerase (5U $µl^{-1}$) and 1 µl of DNA template (100–300 ng). The temperature profile consisted of 94° C for 5 min, 39 cycles of 94° C for 30 s, 54° C for 40 s, 72° C for 1 min and a final extension at 72° C for 5 min, as described by Lessios & Robertson (2006). Purification of the PCR products was done using the ExoSAP clean-up kit (ThermoFisher scientific; www.thermofisher.com) following the manufacturer's protocol. Sequencing was done using a DyeDeoxy terminator (Applied Biosystems; www.appliedbiosystems.com) and an automatic sequencer (ABI PRISM 310 and 3100, Applied Biosystems). These 35 sequences from five WIO localities were combined with 227 sequences (GenBank accession numbers: KJ779682.1–

KJ779871.1 and DQ111127.1–DQ111163.1) from two previous studies (Lessios & Robertson, 2006; Liggins *et al.*, 2016) (Table 1).

2.3 | Data analysis

2.3.1 | Genetic diversity

Sequences were edited, trimmed and aligned using Muscle (Edgar, 2004) as implemented in Geneious 8.1.6 (Kearse *et al.*, 2012). To ensure that only functional mtDNA sequences were used, all sequences were translated into amino acids in Squint Alignment Editor 1.0.2 (Goode & Rodrigo, 2007). Thereafter, haplotypes were identified using the online web services of FaBox 1.41 (Villesen, 2007). The haplotype (h) and nucleotide (π) diversity were calculated in Arlequin 3.5 (Excoffier & Lischer, 2010).

2.3.2 | Phylogenetic analysis

The phylogenetic inference was based on *A. triostegus* haplotypes, with sequences from the three sister species *Acanthurus lineatus* (L. 1758) (EU273284.2), *Acanthurus nigricans* (L. 1758) (DQ111100 and DQ111099) and *Ctenochaetus striatus* (Quoy & Gaimard 1825) (KU244260) being used as outgroups. *Ctenochaetus striatus* was used to root the tree. The Akaike and all other criteria implemented in jModelTest 2.1.10 (Posada, 2008) suggested the Hasegawa–Kishino–Yano (HKY)+I+G as the best-fit model of evolution for the ATPase sequences. Bayesian phylogenetic analyses were conducted using MrBayes 3.2.6 x64 (Huelsenbeck &

Ronquist, 2001). Priors were set according to the HKY model with a γ-distribution and allowing for invariable sites (lset nst = 2 rates = invgamma). Two times four Markov chains run in parallel, three heated and one cold, using a random starting tree. All eight chains were run simultaneously for 10 million generations, with trees being sampled every 1000 generations for a total of 80 002 trees. The first 25 % of the trees were discarded as burn-in after confirming convergence of likelihood values of each chain using the commands sump and sumt. The majority-rule consensus tree containing the posterior probabilities of the phylogeny was determined from 60 002 trees. A spreadsheet program (Microsoft Excel 2010; www.microsoft.com) was used to generate pie charts of the contribution of the different biogeographical regions for identified haplogroups [Figure 1(g)]. A minimum spanning network was created using the software PopART 1.7 (Bandelt *et al.*, 1999) with default settings [Figure 1(h)].

2.3.3 | Genetic population structure

The level of genetic differentiation among and between sampling locations was estimated by analysis of molecular variance (AMOVA), hierarchical AMOVA and pairwise Φ_{ST} values in Arlequin, with a significance level of 0.05 and 10 000 permutations. Sequences sampled in different geographical locations were hierarchically grouped in the AMOVA, according to specific biogegraphic hypotheses. The division between the Indian and the Pacific Oceans was tested by contrasting Indian (all sample sites west of Torres Strait; 10° S; 142° E) and Pacific Ocean populations (all sample sites east of the Torres Strait). Division within each Indo-Pacific Basin was tested by comparing WIO and EIO populations in the Indian Ocean and WP, CP and EP in the Pacific Ocean. Linear correlation between pairwise Φ_{ST} values and geographic distances was tested with the software package car (Fox & Weisberg, 2011) in R 3.2.2 (www.r-project.org), with the shortest marine distance between sampling locations measured to the nearest 5 km in Google Earth (www.earth.google.com). A multidimensional scaling (MDS) plot was drawn in XLstat 7.5.2 (www.xlstat-pro.software.informer.com) to visualise the genetic differences between Indo-Pacific sample sites.

3 | RESULTS

3.1 | Genetic diversity

In total, 262 individuals were used in the analyses, including 35 new sequences from the WIO region (GenBank accession numbers: MF139577-MF139611). The sequence alignment was trimmed to 796 bp, yielding 89 unique haplotypes, 91 substitutions and 88 polymorphic sites. On the one hand, haplotype diversity was mostly ≥ 0.7 at all the sample sites, with the exception of one sample site in the EP (Revillagigedos Islands; 19^{o} N; 112^{o} W). The nucleotide diversity values, on the other hand, ranged from 0 to 0.009 within sample sites. In particular, the EP region had lower nucleotide diversity values than the WIO region; while the CP and WP were characterised by nucleotide diversity values ≥ 0.002 (Table 1).

3.2 | Genetic population structure

AMOVA and pairwise Φ_{ST} values were non-significant among the WIO sample sites (Φ_{ST} = 0.024, P > 0.05; Table 2), supporting the hypothesis of genetic homogeneity. The genetic similarity between the WIO sample sites is also shown in the MDS plot, with all the five sample sites clustering together (Figure 2). In contrast, strong genetic differentiation was displayed when all sample sites from the Indian Ocean were considered (KU, MO, DS, MT, AN, AR, NI and ET, $\Phi_{ST} = 0.124$, $P < 0.05$; Table 3). Further analysis in the hierarchical AMOVA indicated genetic differentiation between the WIO and EIO populations ($\Phi_{CT} = 0.152$, $P < 0.05$) (Table 3).

Across the Pacific Ocean, AMOVA revealed $\Phi_{ST} = 0.55$ ($P < 0.05$), with 55 % of variation being among populations and 45 % within populations. However, the hierarchical analysis involving the three biogeographical regions of the Pacific Ocean, *i.e* WP, CP and EP did not reject the hypothesis of genetic homogeneity across the Pacific ($\Phi_{CT} = –0.00738$, $P > 0.05$; Table 3). In particular, the central Pacific showed genetic similarity to both the WP and EP (EP–CP $\Phi_{CT} = 0.03$, $P > 0.05$, WP–CP $\Phi_{CT} = –0.04961$, $P > 0.05$). However, the exclusion of the CP populations from the hierarchical grouping displayed a pronounced genetic structure (WP–EP $\Phi_{CT} = 0.23$, $P < 0.05$; Table 3).

On the scale of the entire Indo-Pacific Basin, the overall AMOVA without *a priori* grouping showed evidence of significant differentiation ($\Phi_{ST} = 0.53$, $P < 0.05$). The pairwise Φst estimates revealed 25 (8.3%) significant pairwise comparisons after sequential Bonferroni correction, with differences being mostly represented by Hawaii and Johnston Island (16^{o} 43′ 45″ N; 169^{o} 32′ 00″ W) (Table 2). Nevertheless, the hierarchical grouping of Indian (all samples west of the Torres Strait) and Pacific (all samples east of the Torres Strait) populations failed to support the vicariance hypothesis, showing a lack of genetic differentiation between the two ocean basins ($\Phi_{CT} = –0.02$, $P > 0.05$) (Table 3). However, the correlation between pairwise Φ_{ST} values and geographic distance was significant ($r^2 = 0.19$, $P < 0.05$; Figure 3), indicating that dispersal of *A. triostegus* in the Indo-Pacific Basin follows an isolation-by-distance model. The isolation-by-distance was also supported by the MDS plot, which showed samples sites from respective biogeographic regions clustering together (Figure 2).

In total, three haplogroups can be deduced from the majority consensus tree of the Bayesian analysis [split frequencies in the sampled trees mean S.D. = 0.007339; Figure 1(g)]. Haplogroup 1 (posterior probability = 0.98) and 3 (posterior probability = 0.99) are well supported, while haplogroup 2 appears like a conglomeration of haplotypes branching off haplogroup 1. With the exception of haplogroup 3, which is restricted to Hawaii and Johnston Island, the other two haplogroups are not arranged according to geographical locations. Haplogroup 1 has several shared haplotypes among the five biogeographical regions, with the most extreme sharing being between Panama (EP) and Kiunga, Papua New Guinea (WIO) [Figure 1(g) and Figure 1 (h)]. While haplogroup 2 is also shared between the two ocean basins, its frequency is higher in WIO sample sites [Figure 1(b),(g)]. The haplotype network is characterized by a star-like structure, with dominant haplotypes connected to several singletons [Figure 1(h)].

4 | DISCUSSION

4.1 | Genetic population structure

4.1.1 | WIO and Indian Ocean connectivity

The AMOVA analysis reveals genetic connectivity (Φ_{ST} = 0.024, P > 0.05) across three WIO ecoregions: North Monsoon Current Coast (represented by Kiunga), East African Coral Coast (represented by Mombasa, Dar es Salaam and Mtwara) and western and northern Madagascar (represented by Anakao) (Spalding *et al.*, 2007). Gene flow among the *A. triostegus* WIO population is likely to be mediated by its pelagic larval phase and prevailing ocean currents in the WIO (Supporting Information Figure S1). Although the larvae of *A. triostegus* can swim at an average speed of 0.56 m s^{-1} (Leis & Carson-Ewart, 1997; Stobutzki & Bellwood, 1997), this is considerably less than the mean speed of the East African Coast Current (1 m s^{-1}) and Mozambique channel eddies (> 0.5 m s^{-1}) (Swallow *et al*., 1991; Lumpkin & Johnson, 2013). The interaction of *A. triostegus* larvae with the strong WIO currents can limit their ability to influence dispersal and settlement (self-recruitment), favouring long-distance dispersal. However, it is unlikely that dispersal in *A. triostegus* is entirely a function of ocean currents (passive), as a large number of larvae would be lost through this mechanism, thinning out its population over ecological time scales (Cowen *et al*., 2000). It ispossible, therefore, that this species employ both active (short) and passive (long) dispersal mechanisms. Active dispersal between coral-reef habitats in the WIO might be mediated primarily by the late stages of *A. triostegus* larvae (Leis & Carson-Ewart, 1997; Stobutzki & Bellwood, 1997), which can sustain their swimming ability for up to 194 hours, covering a distance of 60 nautical miles in a single bout (Stobutzki & Bellwood, 1997). Overall, the results of genetic homogeneity in *A. triostegus* are consistent with the findings of biophysical modeling of connectivity, which indicates that population connectivity in the WIO increases with increase in dispersal ability (Crochelet *et al*., 2016; Mayorga-Adame *et al*., 2017). Genetic homogeneity in the WIO has also been observed in other reef fish such as *Lutjanus kasmira* (Forsskål 1775) (Muths *et al*., 2012), *Scarus ghobban* Forsskål 1775 (Visram *et al*., 2010), *Amphiprion akallopisos* Bleeker 1853 (Huyghe & Kochzius, 2017), *Dascyllus trimaculatus* (Rüppell 1829) (O'Donnell *et al*., 2017) and *Acanthurus* *leucosternon* Bennet 1833 (Otwoma *et al*., 2018). Nevertheless, the lack of structure found for *A. triostegus* in the WIO have to be interpreted with caution as the number of individuals analysed for this region is low.

The overall AMOVA involving all Indian Ocean sample sites show a strong genetic differentiation (Φ_{ST} = 0.124, P < 0.05), rejecting the hypothesis of genetic homogeneity within the Indian Ocean. Further analysis in the hierarchical AMOVA suggests a differentiation between EIO and WIO *A. triostegus* populations (Φ_{CT} = 0.152, P < 0.05). This genetic differentiation between EIO and WIO has previously been shown in species with PLDs not longer than 22 days such as the echinoderms *Linckia laevigat*a (22 days; Williams & Benzie, 1998; Otwoma & Kochzius, 2016) and *Acanthaster planci* (14-21 days; Benzie, 1999; Vogler *et al.*, 2012), giant clam *Tridacna* spp. (9–12 days; Hui *et al.*, 2016), *A. akallopisos* (7–22 days; Huyghe & Kochzius, 2017) and prawn *Penaeus monodon* (*c.* 14 days; Duda Jr & Palumbi, 1999; Benzie *et al.*, 2002). However, species with PLDs reaching up to 40 to 90 days display genetic homogeneity across the Indian Ocean. These include *Myripristis berndti* Jordan & Evermann 1903 (55 days; Craig *et al.*, 2007), *Naso* spp. Lacépède 1801 (60–90 days; Horne *et al.*, 2008), *Acanthurus leucosternon* (*c.* 55 days; DiBattista *et al.*, 2016), *Coris cuvieri* (Bennett 1831) (53 days; Ahti *et al.*, 2016) and *Lutjanus kasmira* (20–44 days; Gaither *et al.*, 2010). The findings of this study present the first report of an EIO–WIO differentiation in a species with great dispersal potential (*A. triostegus*; PLD 44–60 days), which is inconsistent with previous studies (Craig *et al*., 2007; Horne *et al*., 2008; Gaither *et al*., 2010; Ahti *et al*., 2016; DiBattista *et al*., 2016). This discordance of genetic patterns in different species spanning the Indian Ocean underpins the suggestion that marine species respond uniquely to the dynamic marine environment (Crandall *et al.*, 2008*a*). Besides, marine barriers solely based on distance (*e.g* the barrier between WIO and

EIO) are semipermeable in nature and may allow sporadic dispersal across them when conditions are favourable (DiBattista *et al*., 2012), leading to discordant population structures even in species possessing similar life-history characteristics (Lessios & Robertson, 2006; DiBattista *et al*., 2012). This also indicates that PLD alone cannot adequately predict the genetic population structure of marine populations.

4.1.2 | Indo-Pacific

Despite the addition of sequences from two peripheral biogeographic regions (WIO and EP) to the Liggins *et al*. (2016) dataset (a largely EIO, WP and CP dataset), the results of this study do not support the vicariance hypothesis (Φ_{CT} –0.02, $P > 0.05$). This genetic pattern largely matches the findings of an earlier study on *A. triostegus* using cytochrome oxidase I (COI) as a marker (Mirams *et al.*, 2011). The general concordance between ATPase (present study) and COI (Mirams *et al*., 2011) in inferences of the phylogeographic pattern is due to the same mode of inheritance, as both markers are found on the mitochondrial locus. In contrast, a allozyme study on *A. triostegus* across the Indo-Pacific Basin shows a significant genetic differentiation between the Indian and Pacific Ocean populations (Planes & Fauvelot, 2002). Similar discordances between mtDNA and allozymes have been shown in other marine organisms (Elliot, 1996; Williams *et al*., 2002), with allozymes displaying a higher level of genetic differentiation than mtDNA. A possible explanation for this difference is that allozymes (nuclear) take a longer time to reach equilibrium between genetic drift and migration than mtDNA (Williams *et al*., 2002; Larmuseau *et al*., 2010); consequently, they are more reflective of the effect of past historical barriers to dispersal than present-day gene flow. Overall, this finding adds to the growing number of studies that report a lack of genetic divergence at the Indo-Pacific Barrier (IPB) in other shallow-water marine taxa (Lessios *et al.*, 1999; Lessios *et al.*, 2001; Reid *et al.*, 2006; Klanten *et al.*, 2007; Horne *et al.*, 2008; Kochzius *et al.*, 2009; Gaither *et al.*, 2010; Gaither *et al.*, 2011*b*) and is in contrast to the effect of lowered sea level during Pleistocene glacial cycles. Sea level repeatedly dropped as much as 120 m below present levels, limiting genetic exchange between the Indian and Pacific Ocean populations of various taxa (reviewed extensively by Carpenter *et al*., 2011). The absence of a genetic break in *A. triostegus* is not a confirmation that the Pleistocene sea-level low stands had no effect on this species, but most likely an indication of the quick re-establishment of substantial gene flow between the Indian and Pacific Ocean populations of *A. triostegus* since the last isolation by sea-level low stands (Horne *et al.*, 2008). This hypothesis is supported by *A. triostegus* great dispersal potential and generalist nature. Unlike other habitat-specific species, *A. triostegus* can occur in highly unstable environments such as tide pools and bays that could have enabled it to quickly colonize the new habitats along the IPB during sea-level transgression (Mirams *et al.*, 2011).

A lack of a genetic break between the Indian and the Pacific Ocean is also corroborated by the geographical distribution of haplogroups in the Indo-Pacific. On the one hand, haplogroup 1 is found at all samples sites albeit at a lower frequency in the WIO. On the other hand, haplogroup 2 dominates in the WIO but is found at a lower frequency in the EIO, WP and CP and is absent in EP. Haplogroup 3 is the most divergent group and occurs exclusively in Hawaii and Johnston Island (Figure 1). These two sample sites are the documented range for the subspecies *Acanthurus triostegus sandvicensis* in which Streets (1877) noted the differences in the fin ray number and colouration pattern of *A. triostegus* from Hawaii and Johnston Island, without intergradations to *A. triostegus* from other sites (Schulz & Woods, 1948). This observation led Streets (1877) to suggest a separate species *Acanthurus sandvicensis*. However, this was disputed by Randall (1956), who attributes the differentiation to differences in water temperature and geographical isolation of Hawaii and Johnston Island and suggests the rank of a subspecies (*Acanthurus triostegus sandvicensis*). Both Lessios & Roberts (2006) and Liggins *et al*. (2016) report a genetic divergence between *Acanthurus triostegus sandvicensis* and the remaining CP, WP and EP populations (*Acanthurus triostegus triostegus*). The evolution of this subspecies in Hawaii and Johnston Island is consistent with recent evidence, indicating that peripheral habitats such as Hawaii and Johnston Island are not just evolutionary graveyards, but also produce and export new species to central biodiversity hotspots areas (Fitzpatrick *et al*., 2011; Eble *et al*., 2011; Bowen *et al*., 2013). The wide distribution of dominant haplotypes in the Indo-Pacific Basin indicates genetic exchange at small and large scale (Figures 1 and 4). This suggests that the genetic population structure of *A. triostegus* can be explained by a metapopulation migrant-pool model, where each population has an equal chance of providing colonizers. Such a dispersal mechanism could have enabled frequent larval exchange between the Indian and Pacific Ocean populations, gradually eroding the genetic break between these two basins (Horne, 2014). The great dispersal ability and cosmopolitan nature of *A. triostegus* support this view (Stobutzki & Bellwood, 1997; McCormick, 1999; Leis & Carson-Ewart, 1997; Fisher & Hogan, 2007).

Although the hierarchical AMOVA does not support the existence of a genetic break in the Indo-Pacific, the overall AMOVA without *a priori* grouping display a strong genetic differentiation in the Indo-Pacific (Φ_{ST} = 0.53, P < 0.05). This can be attributed to a dispersal model that follows isolation-by-distance in *A. triostegus* (r^2 = 0.19, P < 0.05), which has also been demonstrated in previous allozymes study (Planes & Fauvelot, 2002). The finding of isolation-by-distance is not surprising given the sample sites of this study spread across a geographic distance of more than 28 000 km that is characterised by discontinuous reef habitats. Notably, pairwise comparisons with Hawaii and Johnston Islands populations exhibit higher Φ_{ST} values even at a relatively short distance (Figure 3 and Table 2), possibly due to self-recruitment presumed to occur at these sites (Wren *et al.*, 2016). The spatial arrangement of samples sites in the MDS plot correspond to the genetic similarity of sample sites, providing further evidence of isolation-by-distance (Figure 2).

4.2 | Genetic diversity

The genetic diversity estimates revealed mostly high haplotype and low nucleotide diversity values, a pattern common to other marine fishes. High haplotype diversity in this species could be a result of mixing between the Indian and Pacific Ocean populations, which is made possible by the great dispersal ability of *A. triostegus*. These molecular diversity indices and star-shaped network signal a population expansion after a period of small effective population size, which is consistent with the effect of Pleistocene multiple glaciations (Grant & Bowen, 1998).

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SUPPORTING INFORMATION

Supporting information can be found in the online version of this paper.

FIGURE S1 Map of Indo-Pacific showing principal ocean currents (→). EAC, East Australian Current; EACC, East African Coast Current; ITF, Indonesian Throughflow; JC, Java Current; LC, Leeuwin Current; MC, Mozambique Current; MCE, Mozambique Channel Eddies; NECC, North Equatorial Counter Current; NEMC, Northeast Madagascar Current; NGCU, New Guinea Under Current;SC, Somali current; SECC, South Equatorial Counter Current.

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FIGURE 1 Map of (a) Indo-Pacific Basin, (b) western Indian Ocean (WIO), (c) eastern Indian Ocean (EIO), (d) western Pacific Ocean (WP), (e) central Pacific Ocean (CP) and (f) eastern Pacific Ocean (EP). The Pleistocene sea level low stands *c.* 120 m below present mean sea level are indicated (■) (Voris, 2000). (g) Majority rule consensus tree from the Bayesian phylogenetic analysis using the HKY+I+G model showing the three defined haplogroups. Posterior probabilities above 0.9 are shown at the respective nodes. (h) Minimum spanning network based on ATPase sequences. The size of haplotypes (●,●,●)is proportional to their absolute frequency; ▬, single mutational steps; O, missing intermediate haplotypes. Pie charts on the map [Figure 1(a)] illustrate the proportion of each haplogroup at different sampling sites, while the large pie charts on the Bayesian phylogenetic tree [Figure 1(g)] depicts the contribution of each biogeographic region to the defined haplogroups. (See Table I for biogeographical region and sample site abbreviations.)

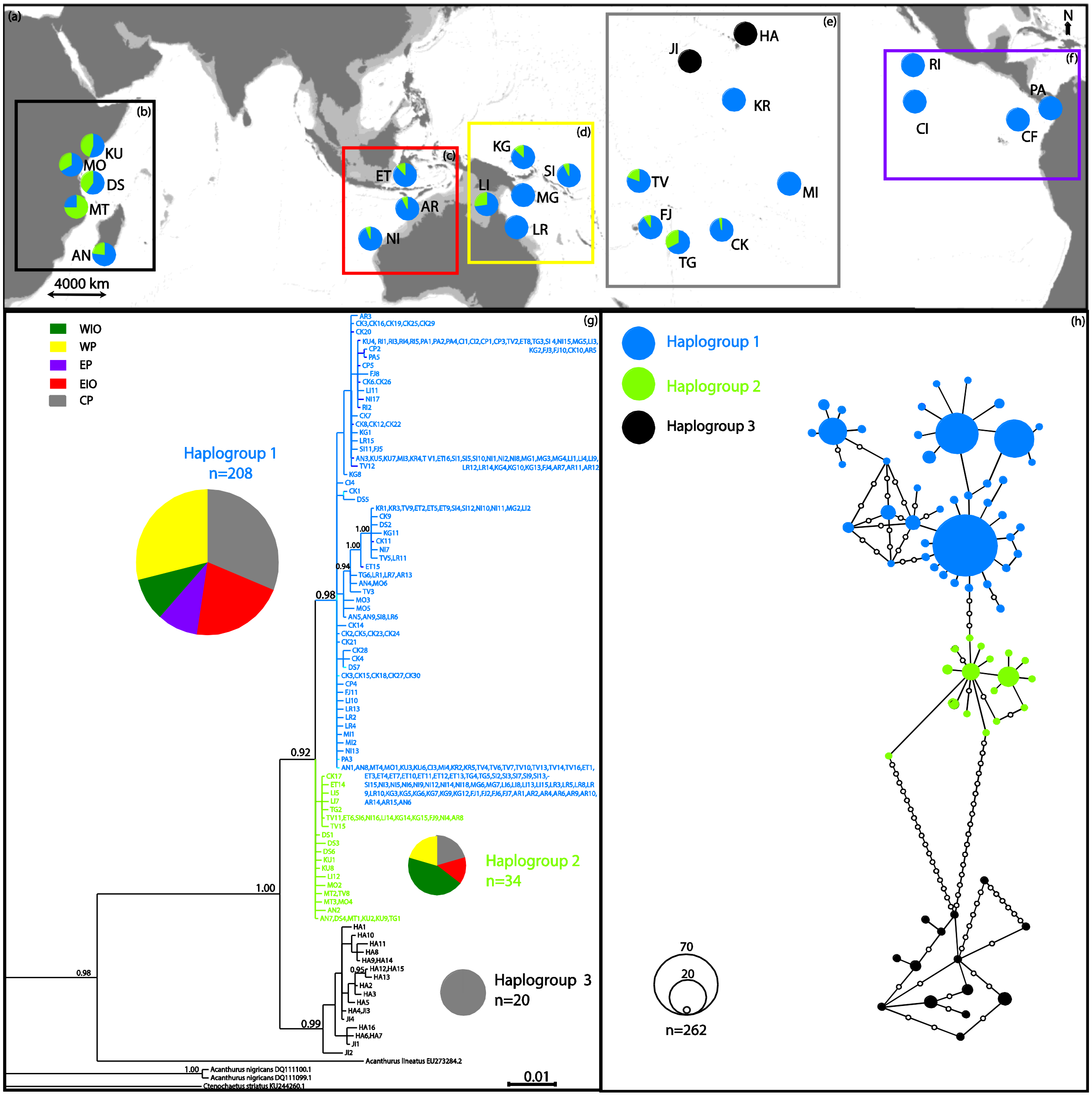


FIGURE 2 A multidimensional scale (MDS) plot for pairwise Φ_{ST} estimates among 25 populations of *Acanthurus triostegus*. Groups: I (Hawaii and Johnston Island), II (western Indian Ocean), III (central and western Pacific Ocean), and IV (eastern Pacific Ocean) (see Table I for biogeographical region and sample site abbreviations)

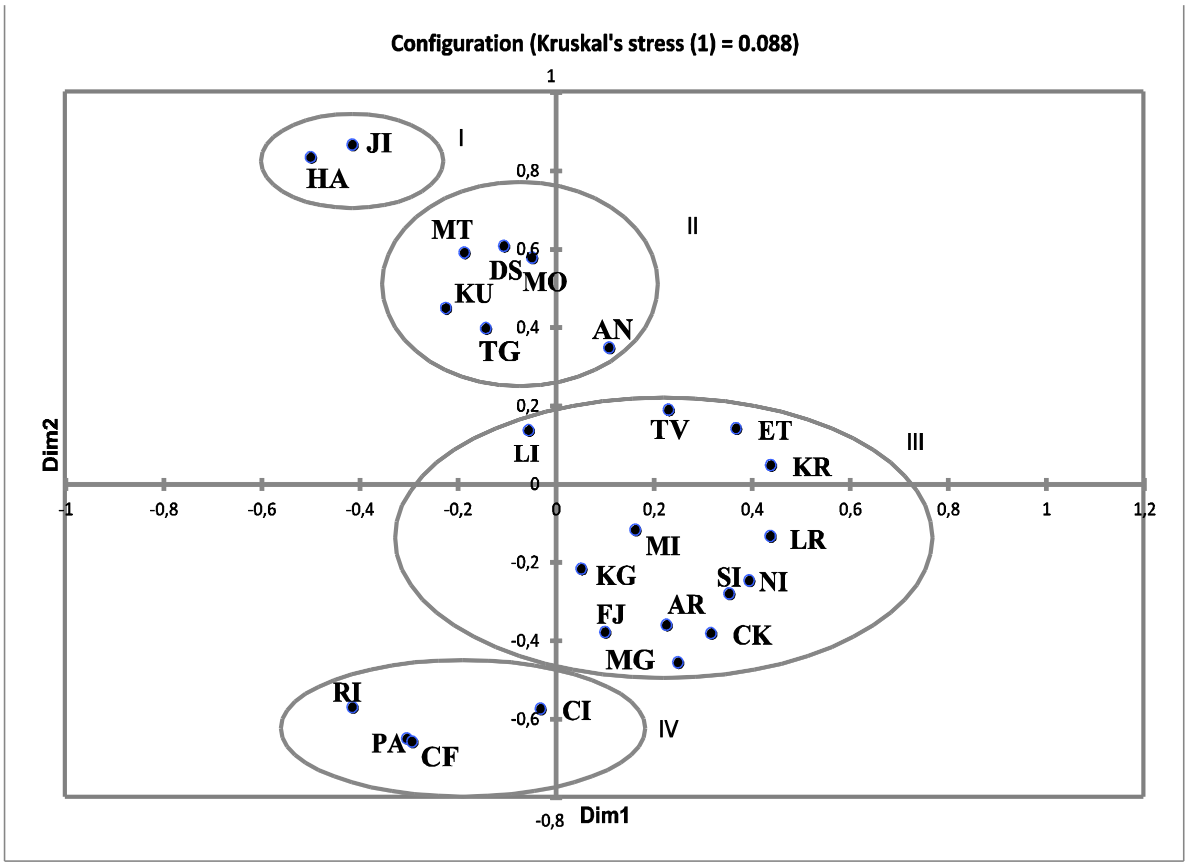
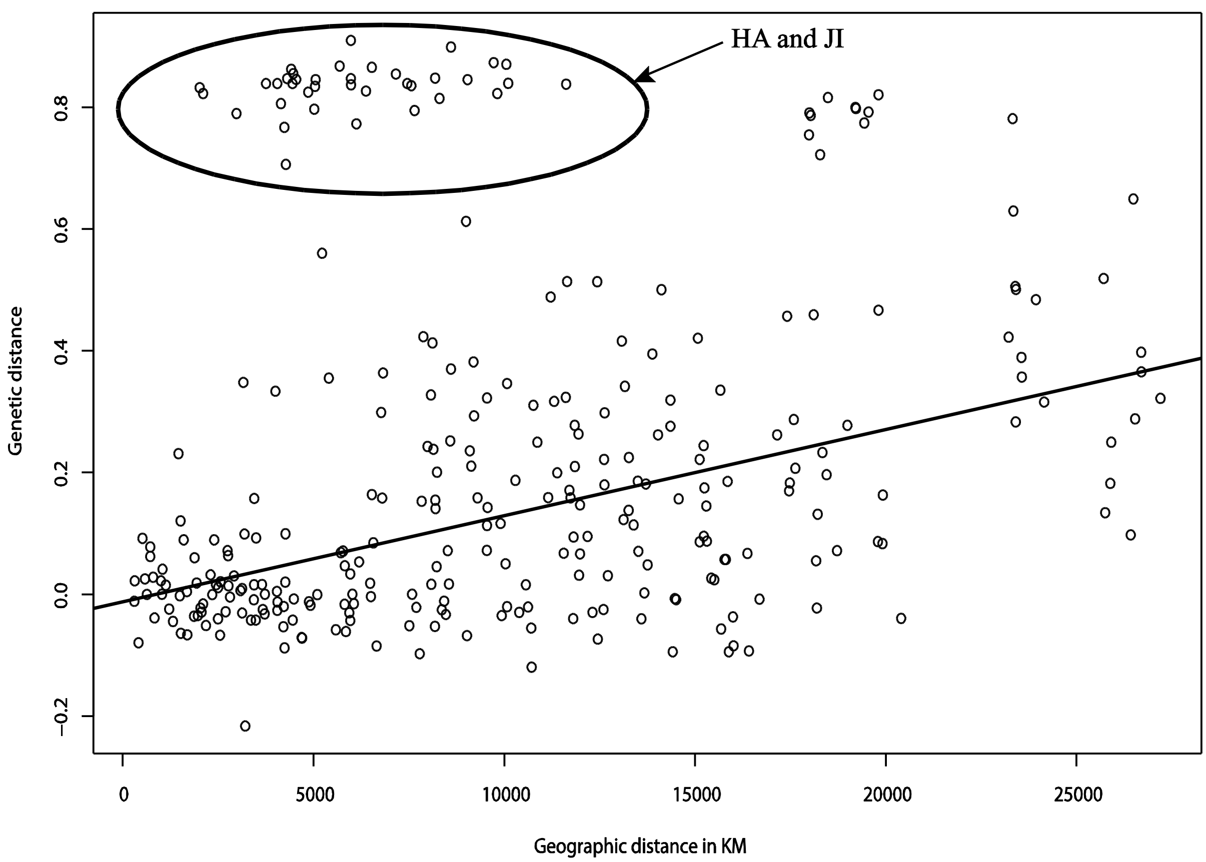

Configuration (Kruskal's stress (1) = 0.088)
Dim1
Dim2
I
II
III
IV
JI
HA
MT
DS
MO
KU
TG
AN
TV
ET
KR
LI
MI
LR
KG
SI
NI
FJ
AR
CK
MG
RI
CI
PA
CF
1
0,8
0,6
0,4
0,2
0
-0,2
-0,4
-0,6
-0,8
-1
-0,8
-0,6
-0,4
-0,2
0
0,2
0,4
0,6
0,8
1
1,2

FIGURE 3 A scatter plot of the correlation between the geographic distance (km) and pairwise Φ_{ST} estimates for the 25 sampling locations in the Indo-Pacific Basin (r^2 = 0.19, P < 0.05). HA, Hawaii; JI, Johnston Island.

Typesetter

1 X-axis: replace in KM with (km).



SUPPORTING INFORMATION

FIGURE S1. Map of Indo-Pacific showing principal ocean currents (→). EAC, East Australian Current; EACC, East African Coast Current; ITF, Indonesian Throughflow; JC, Java Current; LC, Leeuwin Current; MC, Mozambique Current; MCE, Mozambique Channel Eddies; NECC, North Equatorial Counter Current; NEMC, Northeast Madagascar Current; NGCU, New Guinea Under Current;SC, Somali current; SECC, South Equatorial Counter Current.

TABLE 1 Summary of genetic diversity indices for the georeferenced sequence samples of *Acanthurus triostegus*

Sample site	**Biogeographical region**	**Sample code**	***n***	***N*hP**	***h***	***π***	**Source of sequences**
Dar Es Salaam, Tanzania	WIO	DS	7	7	1	0.009	Present study
Kiunga, Kenya	WIO	KU	9	6	0.92	0.006	Present study
Mombasa, Kenya	WIO	MO	6	6	1	0.008	Present study
Mtwara, Tanzania	WIO	MT	4	4	1	0.005	Present study
Anakao, Madagascar	WIO	AN	9	6	0.89	0.005	Present study
Ashmore Reef, Indian Ocean	EIO	AR	15	6	0.71	0.002	Liggins *et al*., 2016
East Timor, Indonesia	EIO	ET	16	7	0.74	0.006	Liggins *et al*., 2016
Ningaloo, Australia	EIO	NI	18	9	0.84	0.005	Liggins *et al*., 2016
Kavieng, Papua New Guinea	WP	KG	15	7	0.82	0.005	Liggins *et al*., 2016
Lihou Reefs, Australia	WP	LR	15	9	0.89	0.004	Liggins *et al*., 2016
Lizard Islands, Australia	WP	LI	15	10	0.91	0.007	Liggins *et al*., 2016
Motupore Island, Papua New Guinea	WP	MG	7	4	0.81	0.004	Liggins *et al*., 2016
Solomon Islands	WP	SI	15	7	0.82	0.005	Liggins *et al*., 2016
Cook Island	CP	CK	30	16	0.93	0.005	Liggins *et al*., 2016

Hawaii, USA	CP	HA	16	13	0.98	0.006	Liggins *et al*., 2016; Lessios & Robertson, 2006
Fiji	CP	FJ	11	7	0.87	0.004	Liggins *et al*., 2016
Johnston Island, USA	CP	JI	4	4	1	0.006	Lessios & Robertson, 2006
Kiritimati, Kiribati	CP	KR	5	3	0.8	0.006	Lessios & Robertson, 2006
Marquesas Islands, France	CP	MI	4	4	1	0.002	Lessios *et al*., 2006
Tonga	CP	TG	6	5	0.93	0.007	Liggins *et al*., 2016
Tuvalu	CP	TV	16	10	0.83	0.007	Liggins *et al*., 2016
Clipperton Island, France	EP	CF	5	4	0.9	0.003	Lessios & Robertson, 2006
Cocos Island, Costa Rica	EP	CI	4	3	0.83	0.003	Lessios & Robertson, 2006
Panama	EP	PA	5	3	0.7	0.002	Lessios & Robertson, 2006
Revillagigedos Islands, Mexico	EP	RI	5	2	0.4	0	Lessios & Robertson, 2006

n , Number of sequences; *N*hP, number of haplotypes; *h*, haplotype diversity; *π*, nucleotide diversity. WIO, Western Indian Ocean; EIO, eastern Indian Ocean; WP, western Pacific Ocean; CP, central Pacific Ocean; EP, Eastern Pacific Ocean.

TABLE 2 Pairwise Φ_{ST} values of georeferenced sequence samples of *Acanthurus triostegus* in the Indo-Pacific Basin (see Table I for biogeographical region and sample site abbreviations)

Region (R)		**CP**	**CP**	**CP**	**CP**	**CP**	**CP**	**CP**	**CP**	**WP**	**WP**	**WP**	**WP**	**WP**	**EP**	**EP**	**EP**	**EP**	**EIO**	**EIO**	**EIO**	**WIO**	**WIO**	**WIO**	**WIO**
Site (S)		**HA**	**MI**	**KR**	**TV**	**TG**	**JI**	**CK**	**FJ**	**KG**	**LR**	**LI**	**MG**	**SI**	**CF**	**PA**	**CI**	**RI**	**NI**	**AR**	**ET**	**DS**	**KU**	**MO**	**MT**
R	S																								
CP	HA	0.00																							
CP	MI	0.84*	0.00																						
CP	KR	0.83*	0.09	0.00																					
CP	TV	0.81*	-0.07	0.00	0.00																				
CP	TG	0.80*	-0.03	0.10	-0.07	0.00																			
CP	JI	0.12	0.86	0.82	0.79	0.77	0.00																		
CP	CK	0.85*	-0.07	0.02	0.01	0.09	0.85	0.00																	
CP	FJ	0.83*	-0.07	0.16	0.02	0.03	0.84	0.00	0.00																
WP	KG	0.83*	-0.10	0.07	-0.03	-0.02	0.82	-0.02	-0.04	0.00															

WP	LR	0.85*	-0.05	0.03	0.01	0.09	0.87*	0.00	0.06	0.02	0.00										
WP	LI	0.79*	-0.05	0.08	-0.03	-0.09	0.77*	0.05	-0.01	-0.03	0.08	0.00									
WP	MG	0.84*	-0.03	0.02	0.02	0.10	0.85	-0.06	-0.04	-0.04	0.02	0.03	0.00								
WP	SI	0.84*	-0.08	-0.01	-0.03	0.03	0.84	-0.04	-0.02	-0.04	-0.02	0.00	-0.06	0.00							
EP	CF	0.85*	0.33	0.35	0.20	0.24	0.87	0.16	0.07	0.16	0.32	0.15	0.09	0.19	0.00						
EP	PA	0.85*	0.36	0.37	0.20	0.25	0.87	0.16	0.07	0.16	0.32	0.14	0.10	0.19	-0.22	0.00					
EP	CI	0.84*	0.00	0.15	0.02	0.05	0.85	-0.03	-0.12	-0.04	0.07	-0.01	-0.09	-0.03	-0.04	-0.04	0.00				
EP	RI	0.86*	0.71	0.56	0.33	0.41	0.91	0.30	0.25	0.31	0.49	0.26	0.32	0.35	0.00	0.00	0.35	0.00			
EIO	NI	0.84*	-0.07	-0.02	-0.02	0.05	0.84	-0.04	0.00	-0.03	-0.02	0.02	-0.05	-0.06	0.19	0.18	-0.02	0.34	0.00		
EIO	AR	0.87*	-0.06	0.21	0.05	0.16	0.90	-0.01	-0.02	-0.01	0.02	0.07	-0.03	-0.01	0.28	0.28	-0.01	0.50	0.00	0.00	
EIO	ET	0.82*	-0.03	-0.07	-0.04	0.00	0.81	0.02	0.07	0.00	0.01	0.02	0.03	-0.02	0.26	0.26	0.07	0.39	-0.02	0.09	0.00

WIO	DS	0.77*	0.16	0.20	0.09	-0.04	0.72	0.29	0.24	0.18	0.30	0.07	0.28	0.22	0.39	0.40	0.25	0.51	0.24	0.38*	0.14	0.00			
WIO	KU	0.80*	0.09	0.23	0.03	-0.09	0.79	0.17	0.09	0.05	0.22	-0.04	0.17	0.12	0.28	0.29	0.13	0.42	0.14	0.24	0.11	0.00	0.00		
WIO	MO	0.79*	0.08	0.13	0.02	-0.08	0.75	0.21	0.17	0.11	0.18	0.03	0.21	0.14	0.36	0.37	0.18	0.50	0.15	0.29	0.07	-0.01	0.02	0.00	
WIO	MT	0.80	0.47	0.46	0.22	0.06	0.79	0.46	0.42	0.34	0.51	0.16	0.51	0.42	0.63	0.65	0.52	0.78	0.42	0.61	0.32	-0.08	0.04	0.06	0.00
WIO	AN	0.82*	-0.04	0.07	-0.06	-0.09	0.82	0.05	0.06	-0.01	0.03	-0.03	0.10	0.00	0.32	0.32	0.10	0.48	0.02	0.12	-0.02	0.06	0.01	-0.05	0.23

. *P < 0.01 (after Bonferroni correction).

TABLE 3 Hierarchical analysis (AMOVA) based on nucleotide diversity of *Acanthurus triostegus* with alternative grouping of samples sites in the Indo-Pacific Basin (see Table I for biogeographical region and sample site abbreviations)

Grouping	***Φ* Statistics**	***P***
Indian Ocean		
WIO (DS,KU,MO,MT,AN)	Φ_{ST} = 0.024	> 0.05
Indian Ocean (DS,KU,MO,MT,AN,AR,ET,NI)	Φ_{ST} = 0.124	< 0.05
WIO (DS,KU,MO,MT,AN) EIO (AR,ET,NI)	Φ_{CT} = 0.152	< 0.05
Pacific Ocean		
(KG,LR,LI,MG,SI,CK,HA,FJ,JI,KR,MI,TG,TV,CF,CI,PA,RI)	Φ_{ST} = 0.55	< 0.05
WP (KG,LR,LI,MG,SI) CP (CK,HA,FJ,JI,KR,MI,TG,TV) EP (CF,CI,PA,RI)	Φ_{CT} = -0.00738	> 0.05
WP (KG,LR,LI,MG,SI) CP (CK,HA,FJ,JI,KR,MI,TG,TV)	Φ_{CT} = -0.04961	> 0.05
CP (CK,HA,FJ,JI,KR,MI,TG,TV) EP (CF,CI,PA,RI)	Φ_{CT} = 0.03	> 0.05
WP (KG,LR,LI,MG,SI) EP (CF,CI,PA,RI)	Φ_{CT} = 0.23	< 0.05
Indo-Pacific		
Indian (DS,KU,MO,MT,AN,AR,ET,NI) Pacific (KG,LR,LI,MG,SI,CK,HA,FJ,JI,KR,MI,TG,TV,CF,CI,PA,RI)	Φ_{CT} = -0.02	> 0.05
(DS,KU,MO,MT,AN,AR,ET,NI,KG,LR,LI,MG,SI,CK,HA,FJ,JI,KR,MI,TG,TV,CF,CI,PA,RI)	Φ_{ST} = 0.53	< 0.05