FRONTIERS OF BIOGEOGRAPHY
The scientific journal of
The International Biogeography Society

Frontiers of Biogeography 19, 2026,
e174247 | DOI 10.21425/fob.19.174247

RESEARCH ARTICLE

Global biogeography of zoantharians indicates a weak genetic differentiation between the Atlantic and Indo-Pacific oceans, and distinct communities in tropical and temperate provinces

Maria E. A. Santos[1,2], Hiroki Kise[2], Chloé Julie Loïs Fourreau[2], Bogdan Kiriukhin[3], Marcelo Visentini Kitahara[4], David Michael Baker[5], Robert J. Toonen[1], Pi Jen Liu[6], Arthur Chang[6], Ting-Hsuan Tu[6], Widiastuti[7], Kadek Miko Purnama Agustini[7], Brian W. Bowen[1], James D. Reimer[2,8]

1 *ToBo Lab, Hawai'i Institute of Marine Biology, University of Hawai'i at Mānoa, Hawai'i, USA*
2 *Molecular Ecology and Invertebrate Systematics Laboratory, University of the Ryukyus, Okinawa, Japan*
3 *AquaBioSafe Laboratory, University of Tyumen, Tyumen, Russia*
4 *Center for Marine Biology, University of São Paulo, São Paulo, Brazil*
5 *The Swire Institute of Marine Science, University of Hong Kong, Hong Kong, Hong Kong*
6 *Graduate Institute of Marine Biology, National Dong Hwa University, Checheng, Taiwan*
7 *Graduate School of Marine Science, Universitas Udayana, Bali, Indonesia*
8 *Tropical Biosphere Research Center, University of the Ryukyus, Okinawa, Japan*

Corresponding author: Maria E. A. Santos (santos.mariaea@gmail.com)

Editor Mark John Costello
Received 8 October 2025 ♦ **Accepted** 7 December 2025 ♦ **Published** 30 January 2026

Abstract

Biogeographic patterns for marine fishes and scleractinian stony corals are well-established, but it is still unclear whether these patterns apply to the understudied marine invertebrates. Here we investigate the distribution of zoantharians (=zoanthids), an order of cnidarians that are distributed globally from tropical coral reefs to deep temperate oceans. We examined the available literature, along with new records and morphological and DNA sequence data, to establish their first global biogeographical assessment. Two striking results emerged that contrast with previously known marine biogeographical patterns. The first was that several zoantharian genera are cosmopolitan, inhabiting most biogeographic provinces within and between ocean basins. Although the highest diversity was observed in the Indo-Pacific Ocean (IPO), concordant with biogeographic assays of reef fishes and stony corals, the distribution of genera was not significantly different between the Atlantic (ATO) and the IPO. Secondly, there were multiple sibling species complexes between the ATO and the IPO. At species and population scales, a long pelagic larval duration, asexual reproduction modes, and rafting abilities, may at least partly explain the low levels of genetic differences between ocean basins. As some zoantharian species can play a significant role in phase shifts, filling knowledge gaps on species distributions is essential to support monitoring of reef ecosystems.

Highlights

- Our study revealed that several Zoantharia genera, and most families, are globally distributed.
- This is highly distinct from the pattern previously observed for common reef animals, such as stony corals and fishes, where the Indo-Pacific Ocean has several times the number of familes/genera compared to the Atlantic Ocean.
- Some zoantharian species, especially in the genera *Palythoa* and *Zoanthus*, have dispersal strategies that allow for broad distributions within ocean basins, while the vicariant events of the rise of the Isthmus of Panama and the appearance of the Benguela upwelling likely prompted the speciation of sibling lineages between the oceans.

Keywords

Biogeographical Barriers, Marine Provinces, Niche, Sibling Species, Vicariance, Zoanthids

Introduction

Understanding the processes that produce and maintain biodiversity is one of the main goals of evolutionary biologists. Parapatry has been suggested as one of the key speciation mechanisms in the marine realm, occurring when divergence in alternate habitats can continue in the face of ongoing gene flow (Gavrilets et al. 2000). Most biogeographic barriers in the marine realm are soft and species with extensive larval dispersal abilities may readily traverse such barriers (Rocha and Bowen 2008). For instance, widespread marine species usually have larvae that are transported by sea currents across great ocean distances, with some dispersing for more than 5000 km from the central to eastern Pacific during El Niño episodes (Lessios and Robertson 2006). However, physical barriers cannot be crossed by marine taxa and may lead to allopatric speciation via vicariant isolation (Coyne and Orr 2004).

One relatively recent vicariant isolation event was the rise of the Isthmus of the Panama, which removed the tropical connection between the Atlantic and Pacific basins (~3.5 mya; O'Dea et al. 2016). This event led to the evolution of sibling species pairs in several marine groups, including fishes and sea urchins (Jordan 1908; Bernardi et al. 2008; Lessios 2008). However, no such clear pattern has been observed for benthic cnidarians such as scleractinian stony corals (Fukami et al. 2004) or *Millepora* fire corals (Arrigoni et al. 2018). Some stony coral genera have a high genetic divergence between ocean basins among genera/families. However, zoantharians (= zoanthids; Cnidaria; Anthozoa; Zoantharia), hexacorals related to stony corals, are an exception to this pattern as several sibling species (or species complexes) inhabit distinct ocean basins yet share highly similar DNA sequences (Reimer et al. 2010; Reimer et al. 2012a; Santos et al. 2016; Dudoit et al. 2022). To date, no detailed investigations of these zoantharian sibling species across the order have been performed, and their diversity and overall distributions remain uncertain. Zoantharians are among the most abundant non-calcifying hexacorals in shallow-water ecosystems, with colonies of some species able to cover dozens of square meters in tropical and temperate regions (Burnett et al. 1997; Oigman-Pszczol et al. 2004), and there is also high diversity known from deep to abyssal waters (Carlgren 1901; Reimer et al. 2007a).

Although biogeographical patterns of many shallow-water reef groups such as fishes and stony corals are relatively well-known (Randall 1998; Briggs and Bowen 2012; Veron et al. 2015; Cowman et al. 2017), zoantharians and many other marine invertebrates are understudied in most regions (Knowlton 2001), and this extends especially into deeper waters (Reimer et al. 2019). An exception to that is the zoantharian distribution across Atlantic subtropical and tropical provinces (Santos et al. 2016, 2019), which have some biogeographic partitions similar to reef fishes (Floeter et al. 2008), stony corals (Veron et al. 2015), and fire corals (De Souza et al. 2017). Examples of this concordance among organismal groups include both range limits and biodiversity patterns: 1) Thermohaline properties of South Atlantic water masses may limit the southern distribution of tropical zoantharians in this region (Santos et al. 2016), and 2) the Caribbean province is the zoantharian biodiversity center of the Atlantic, while oceanic islands have the lowest species richness (Santos et al. 2019). In contrast to prevailing biogeographic patterns, a lower endemism rate among provinces was observed in Atlantic Zoantharia compared to other common reef groups. The most widespread species were *Palythoa caribaeorum* Duchassaing & Michelotti, 1860, *P. grandiflora* (Verrill, 1900), and *Zoanthus sociatus* (Ellis, 1768), all with amphi-Atlantic distributions (Santos et al. 2019). Despite these basin-wide efforts, no study has connected the biogeographic patterns of zoantharians on a global scale.

Due to their wide distribution, zoantharians provide opportunities to examine evolution at large geographical scales (Swain 2010; Santos et al. 2019, 2024). The order has nine families and is subdivided into the suborders Brachycnemina and Macrocnemina (Fig. 1). Most species of Brachycnemina are associated with the Symbiodiniaceae microalgae (Muscatine and Hand 1958; LaJeunesse et al. 2018), also known as zooxanthellae, and are restricted to shallow waters. On the other hand, macrocneminans have a broader distribution into the deep sea and polar regions, and are mostly azooxanthellate (Swain 2010). Additionally, several Macrocnemina genera, and one Brachycnemina genus (*Acrozoanthus*), display epizoic symbioses, in which the polyps attach to other benthic invertebrates, including crabs, hydroids, octocorals, sponges, or tubes of polychaete worms (West 1979; Sinniger et al. 2010; Swain 2010; Kise et al. 2023). These associations are often obligatory, and the zoantharian species is only found associated with a specific genus or family of invertebrate hosts. For example, *Umimayanthus chanpuru* Montenegro, Sinniger & Reimer, 2015 is always associated with sponges, while *Epizoanthus illoricatus* Tischbierek, 1930 is only found growing on eunicid worm tubes.

Herein, we used morphological and molecular data combined with a comprehensive literature review to investigate the global biogeography of Zoantharia. We also aimed to indicate which are the zoantharian sibling species complex between the Atlantic (ATO) and the Indo-Pacific (IPO) ocean basins. We then discussed hypotheses of how ecological traits influence dispersal and evolution of zoantharians in (primarily) shallow and (where possible) deep waters, illuminating the processes that led to these biogeographical patterns.

Methods

Shallow water and deep-sea surveys

Surveys were conducted using snorkeling or SCUBA diving at depths of 0 to 40 m in five regions: Yucatan, Mexico (2013), Hong Kong, Hong Kong SAR (2015 and 2024), Cebu, Philippines (2017), South Africa (2019), Bali, Indonesia (2019 and 2024) and Kenting, Taiwan (2024). Whenever possible,

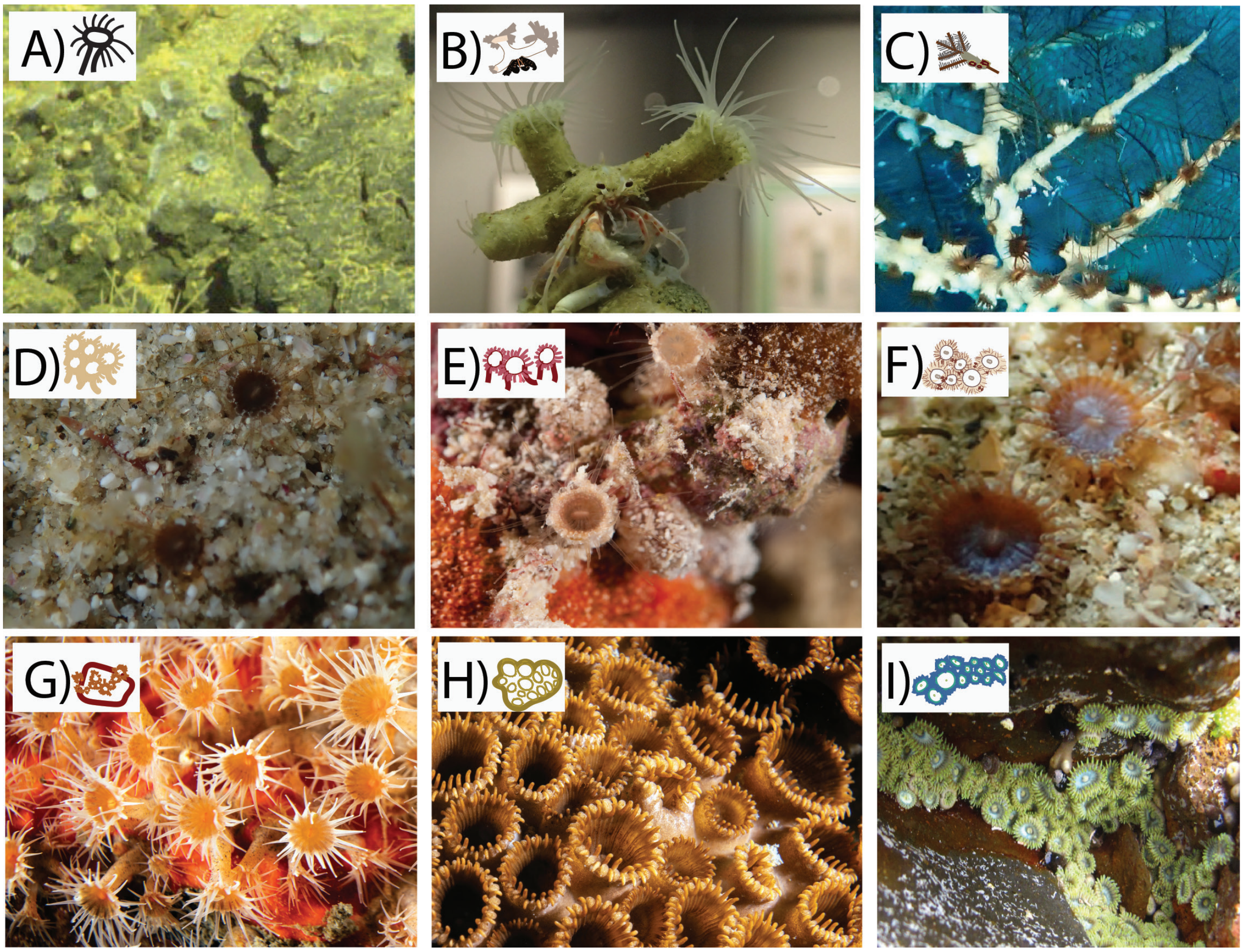

Figure 1. Representatives of the nine zoantharian families. Abyssoanthidae (**A.** *Abyssoanthus convallis* Reimer & Sinniger, 2010); Epizoanthidae (**B.** *Epizoanthus paguricola* Roule, 1900 associated with a hermit crab), Hydrozoanthidae (**C.** *Hydrozoanthus gracilis* (Lwowsky, 1913) with hydrozoan), Microzoanthidae (**D.** *Microzoanthus* sp.), Nanozoanthidae (**E.** *Nanozoanthus*), Neozoanthidae (**F.** *Neozoanthus uchina* Reimer, Irei &. Fujii, 2012), Parazoanthidae (**G.** *Parazoanthus swiftii* (Duchassaing de Fonbressin & Michelotti, 1860) symbiotic with sponges), Sphenopidae (**H.** *Palythoa tuberculosa* (Esper, 1805)), and Zoanthidae (**I.** *Zoanthus sociatus* (Ellis, 1768)). Image credits: JD Reimer (**A** and **E**), T Moritaki (**B**), MEA Santos (**C**, **F**, and **I**), T Fujii (**D**), and MV Kitahara (**G** and **H**).

we followed the roving observer technique to observe as many species as possible (Schmitt et al. 2002). Additionally, *in situ* high-resolution images were taken, and a small fragment of the colony was collected (non-lethal sampling) and preserved in 90–99% ethanol for further analyses (Suppl. material 1). We also examined zoantharian specimens deposited at the Bernice Pauahi Bishop Museum (BPBM) in O'ahu, Hawai'i. To improve the understanding of deep-sea (>200 m) zoantharians, we investigated specimens deposited at the Smithsonian National Museum of Natural History (SNMNH) collected by the Okeanos 2016 expedition in the Pacific Ocean, and at the National Museum of Rio de Janeiro (MNRJ) collected in Brazilian waters (Suppl. material 1).

Literature review and biogeographical analyses

We compiled records of Zoantharia for global marine biogeographical provinces (Suppl. material 2). We followed the provinces as described in Briggs and Bowen (2012) because this work has a special focus on reef ecosystems, and the provinces defined by >10% endemism align well with phylogeographic breaks recovered in fishes and crustaceans (Bowen et al. 2016; Iacchei et al. 2016). Due to the high number of inadvertent Zoantharia species redescriptions combined with a lack of surveys focusing on this group (Burnett et al. 1997; Hibino et al. 2013a, b; Santos et al. 2019), data were analyzed at the taxonomic level of families and genera, and not to species level. We then summarized the relationship among global biogeographical provinces based on the number of shared zoantharian taxa common to the pair of areas using Jaccard dissimilarity index (Jaccard 1908) and Unweighted Pair Group Method with Arithmetic Mean (Sneath and Sokal 1973). We also applied a non-metric multidimensional scaling analysis (nMDS) of the dissimilarity distances to plot similarities in zoantharian composition by ocean basin (ATO or IPO) and seawater temperature (tropical or temperate). Statistical differences were tested with pairwise Adonis

(Martinez Arbizu 2020) with the package vegan 2.6-10 (Oksanen et al. 2025). Due to the patchiness of deep-sea data (Reimer and Sinniger 2010; Carreiro-Silva et al. 2017; Reimer et al. 2019b), we focused analyses of the biogeography and sibling species complexes only in the shallow-water data.

Morphology, phylogenetic analyses, and sibling species complexes

Morphology was used to identify zoantharian specimens to the lowest taxonomic level possible using the following characters: number of tentacles, size range of oral disk, oral disk color, and form of the polyp as 'liberae', 'intermediae', or 'immersae' (Pax 1910; West 1979; Burnett et al. 1997; Reimer 2010; Reimer et al. 2013). Additionally, we retrieved molecular sequences from NCBI for the most common markers for Zoantharia: mitochondrial cytochrome oxidase subunit I (COI) and 16S ribosomal DNA (16S rDNA), and the nuclear ribosomal internal transcribed spacer (ITS rDNA). The sequences and species are listed in Suppl. material 3. We selected mainly sequences from previous authors' publications, and for which we were confident in species identifications (e.g. had voucher specimens). Sequences were aligned using Geneious v8.1 (Kearse et al. 2012), using the global alignment tool with free-end gaps and default settings. A concatenated alignment was generated and missing data was replaced with "N" (excluding gaps). All output alignments were visually inspected and manually curated, totaling 120 sequences and 3,219 sites. Phylogenetic reconstructions were performed using this concatenated alignment for maximum-likelihood (ML; 1000 bootstrap replicates) in Geneious v8.1, with the GTR model of nucleotide substitution as selected using TOPALi v2.5 (Milne et al. 2009). The newick dataset is available at the Figshare repository (https://doi.org/10.6084/m9.figshare.30811127). We defined a sibling species complex in the phylogeny as sister clades composed of at least one ATO and one IPO species (or species' group) that had a similar overall morphology (partial or total overlap of at least three out of the four following traits: number of tentacles, size range of oral disk, oral disk color, and form of the polyp). Morphological characters for described species and distribution data were compiled from the literature and newly collected specimens (Suppl. material 4).

Results

Biogeography of zoantharians

Our results revealed that 6 out of the 8 Zoantharia families reported in shallow-waters were cosmopolitan (Figs 2, 3; Suppl. material 2), with the exception of Nanozoanthidae and Neozoanthidae, which, so far, only have been reported in the IPO (but see Discussion; they are most likely also distributed in the ATO). The diversity center for Zoantharia in shallow waters was the INP province in the Central IPO (Fig. 2A, B). Within the ATO, CAR was the province with the highest diversity. However, a different pattern is observed for deep waters (Fig. 2C, D) where the most diverse provinces were SNJ (7 genera), LUS (6), and HAW (5).

With the exception of the families Abyssoanthidae, Epizoanthidae, and Parazoanthidae, zoantharians were restricted to shallow waters (Fig. 3). Parazoanthidae was the most diverse family (16 genera) and the most widely distributed, with reports across 19 provinces (Figs 3, 4). Of the 31 Zoantharia genera, 14 were found only in shallow waters, 11 only in deep waters, and 6 across both depth zones (Suppl. material 2). Among the 20 genera observed in shallow waters, 6 were so far only reported to the IPO and one to the ATO.

The clustering of shallow biogeographical provinces retrieved two main groups; one with all warm global provinces, in addition to the temperate provinces AGU, COR, and LUS, and the other with the remaining temperate/polar provinces (Fig. 4). Adonis analyses showed no significant differences in the composition of genera and families between the ATO and IPO, yet tropical and temperate provinces had significant differences (Suppl. material 5).

Phylogeny and sibling species complexes

The phylogenetic reconstruction confirmed that the suborder Brachynemina is monophyletic (families Neozoanthidae, Sphenopidae, and Zoanthidae), while the suborder Macrocnemina (families Epizoanthidae, Hydrozoanthidae, Microzoanthidae, Nanozoanthidae, and Parazoanthidae) is paraphyletic with the family Hydrozoanthidae residing within brachycnemic zoantharians (Fig. 5). Although the family Abyssoanthidae is not assigned to any suborder, species were phylogenetically within Macrocnemina. At least four shallow-water families had sibling species complexes (Suppl. material 4).

In the suborder Brachycnemina, three genera from two families had species reported in ATO and IPO. These three genera had sibling species groups: *Palythoa* from the family Sphenopidae, and *Zoanthus* and most likely *Isaurus* (discussed below) from Zoanthidae (Fig. 6; Suppl. material 4). The suborder Macrocnemina had at least two sibling species groups, one from the family Hydrozoanthidae and another from Parazoanthidae. With the exception of *Hydrozoanthus antumbrosus* (Swain 2009), which has so far only been reported in the CAR, zoantharian sibling species had extensive distributions including at least two biogeographic provinces. The sibling pair *P. caribaeorum* (ATO) and *P. tuberculosa* (Esper, 1805) (IPO) had the most extensive distribution among zoantharians analyzed herein, with reports across all tropical and subtropical provinces (Fig. 6, Suppl. material 4).

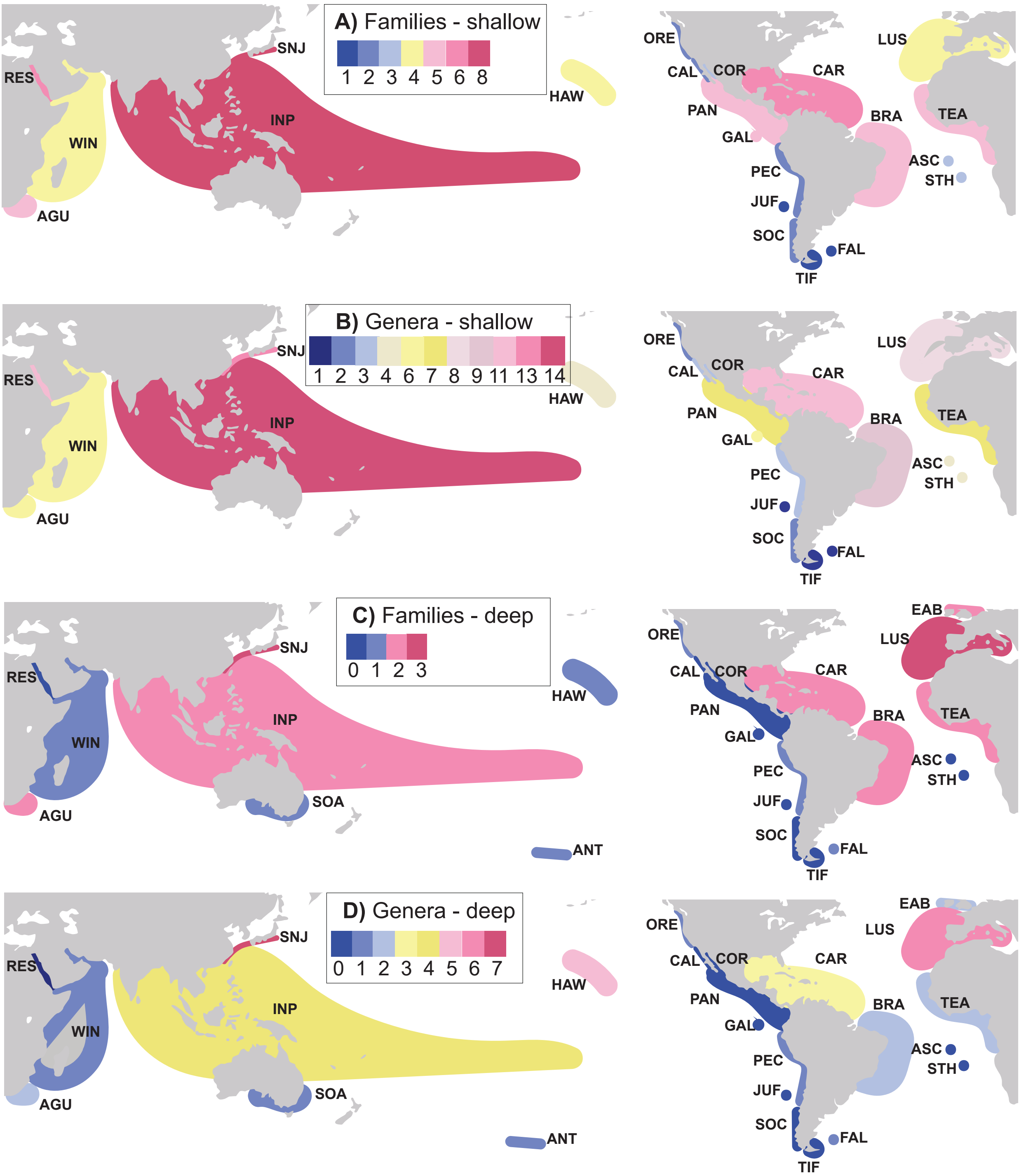

Figure 2. Global distribution of zoantharians. Total number of families and genera in shallow (**A** and **B**) and deep waters (**C** and **D**). Colors represent the number of families/genera reported for each province. Subtropical and tropical provinces were Ascension (ASC), Brazilian (BRA), Caribbean (CAR), Lusitania (LUS), Saint Helena (STH), Tropical Eastern Atlantic (TEA), Galapagos (GAL), Hawaiian (HAW), Indo-Polynesian (INP), Red Sea (RES), Sino-Japanese (SNJ) and Western Indian Ocean (WIN), while in temperate/polar waters were Agulhas Province (AGU), Antarctic Province (ANT), California (CAL), Cortez (COR), Easter Atlantic Boreal (EAB), Falkland Islands (FAL), Juan Fernandez (JUF), Oregon (ORE), Panamanian (PAN), Peru-Chilean (PEC), Southeastern Australian (SOA), Southern Chile (SOC), and Tierra del Fuego (TIF).

Discussion

Global marine biogeography

We observed a higher diversity of Zoantharia in shallow waters in the IPO compared to the ATO, with the global hotspot in the INP province (Fig. 2A, B), similarly to global patterns observed for marine fishes, corals, and macroinvertebrates (Roberts et al. 2002; Bowen et al. 2013; Briggs and Bowen 2013; Veron et al. 2015). Nevertheless, the composition of genera and families between the IPO and ATO was not significantly different (Fig. 4 and Suppl.

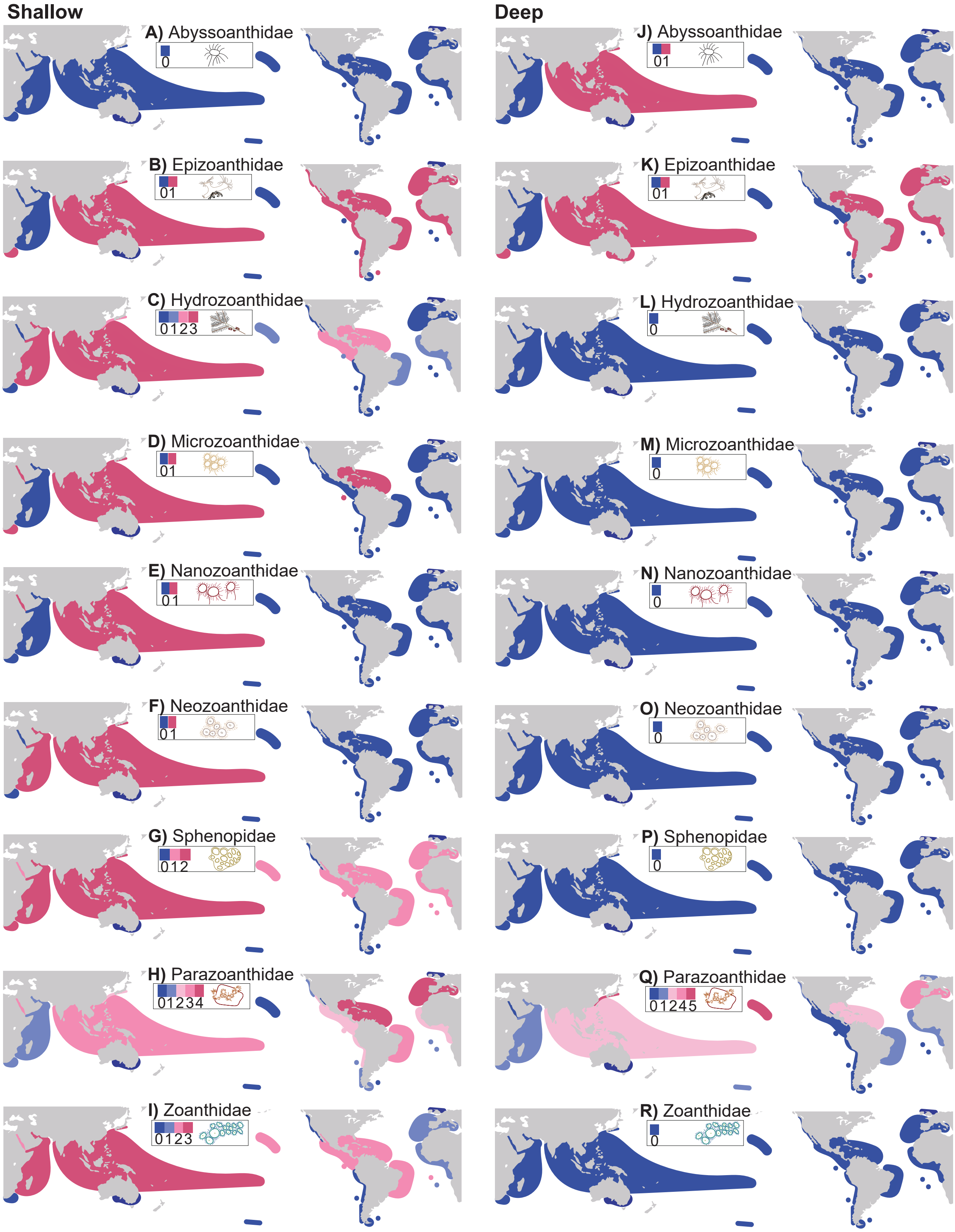

Figure 3. Global distribution of zoantharians for each family in shallow (**A–I**) and deep (**J–R**) waters. Colors represent the number of families/genera reported for each province. Subtropical and tropical provinces were Ascension (ASC), Brazilian (BRA), Caribbean (CAR), Lusitania (LUS), Saint Helena (STH), Tropical Eastern Atlantic (TEA), Galapagos (GAL), Hawaiian (HAW), Indo-Polynesian (INP), Red Sea (RES), Sino-Japanese (SNJ) and Western Indian Ocean (WIN), while in temperate/polar waters were Agulhas Province (AGU), Antarctic Province (ANT), California (CAL), Cortez (COR), Easter Atlantic Boreal (EAB), Falkland Islands (FAL), Juan Fernandez (JUF), Oregon (ORE), Panamanian (PAN), Peru-Chilean (PEC), Southeastern Australian (SOA), Southern Chile (SOC), and Tierra del Fuego (TIF).

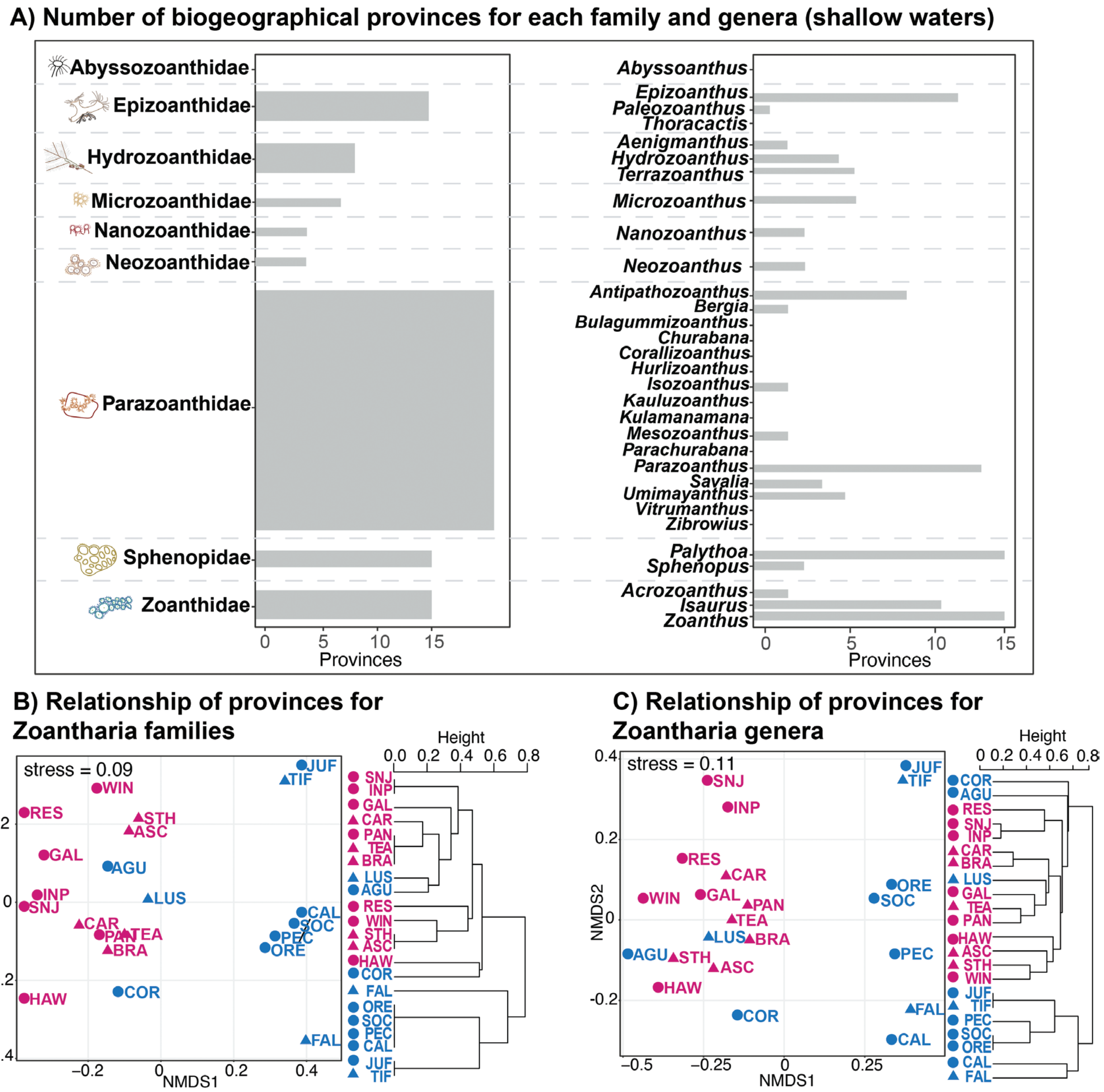

Figure 4. Relationship of the global biogeographic provinces based on Zoantharia distribution in shallow waters. Total number of provinces records for (**A**) each family (left) and genera (right). The thickness of the barplot for each family is proportional to its number of genera. Taxa with no records in shallow waters were reported only in the deep sea. The relationship among biogeographical provinces was summarized for families (**B**) and genera (**C**), based on a non-metric multidimensional scaling analysis (left) and Jaccard dissimilarity index and Unweighted Pair Group Method with Arithmetic Mean (right). Tropical/subtropical provinces are shown in pink, and temperate/polar provinces in blue. Provinces from the Atlantic Ocean are indicated by a triangle, and from the Indo-Pacific by a circle. Subtropical and tropical provinces were Ascension (ASC), Brazilian (BRA), Caribbean (CAR), Lusitania (LUS), Saint Helena (STH), Tropical Eastern Atlantic (TEA), Galapagos (GAL), Hawaiian (HAW), Indo-Polynesian (INP), Red Sea (RES), Sino-Japanese (SNJ) and Western Indian Ocean (WIN), while in temperate/polar waters they they were Agulhas Province (AGU), Antarctic Province (ANT), California (CAL), Cortez (COR), Easter Atlantic Boreal (EAB), Falkland Islands (FAL), Juan Fernandez (JUF), Oregon (ORE), Panamanian (PAN), Peru-Chilean (PEC), Southeastern Australian (SOA), Southern Chile (SOC), and Tierra del Fuego (TIF).

material 5), contrasting with prevailing biogeographical patterns that indicate strong vicariance between these ocean basins (Cowman and Bellwood 2013; Costello et al. 2017). Most, if not all, zoantharian families had a global distribution in shallow waters, which is remarkable and distinct from most other common marine animals.

We hypothesize that low or moderate genetic diversity may partially explain this pattern of low divergence between ocean basins. Anomalously low mutation rates have been observed in a diversity of taxa including plants (Wolf et al. 1987; Xu et al. 2019), cnidarians (Tseng et al. 2005) and vertebrates (Avise et al. 1992; Feng et al. 2017). A low mtDNA mutation rate may prevail in most anthozoan orders, including stony corals and zoantharians (Shearer et al. 2002; Huang et al. 2008). Likewise, hybridization and incomplete lineage sorting may obscure

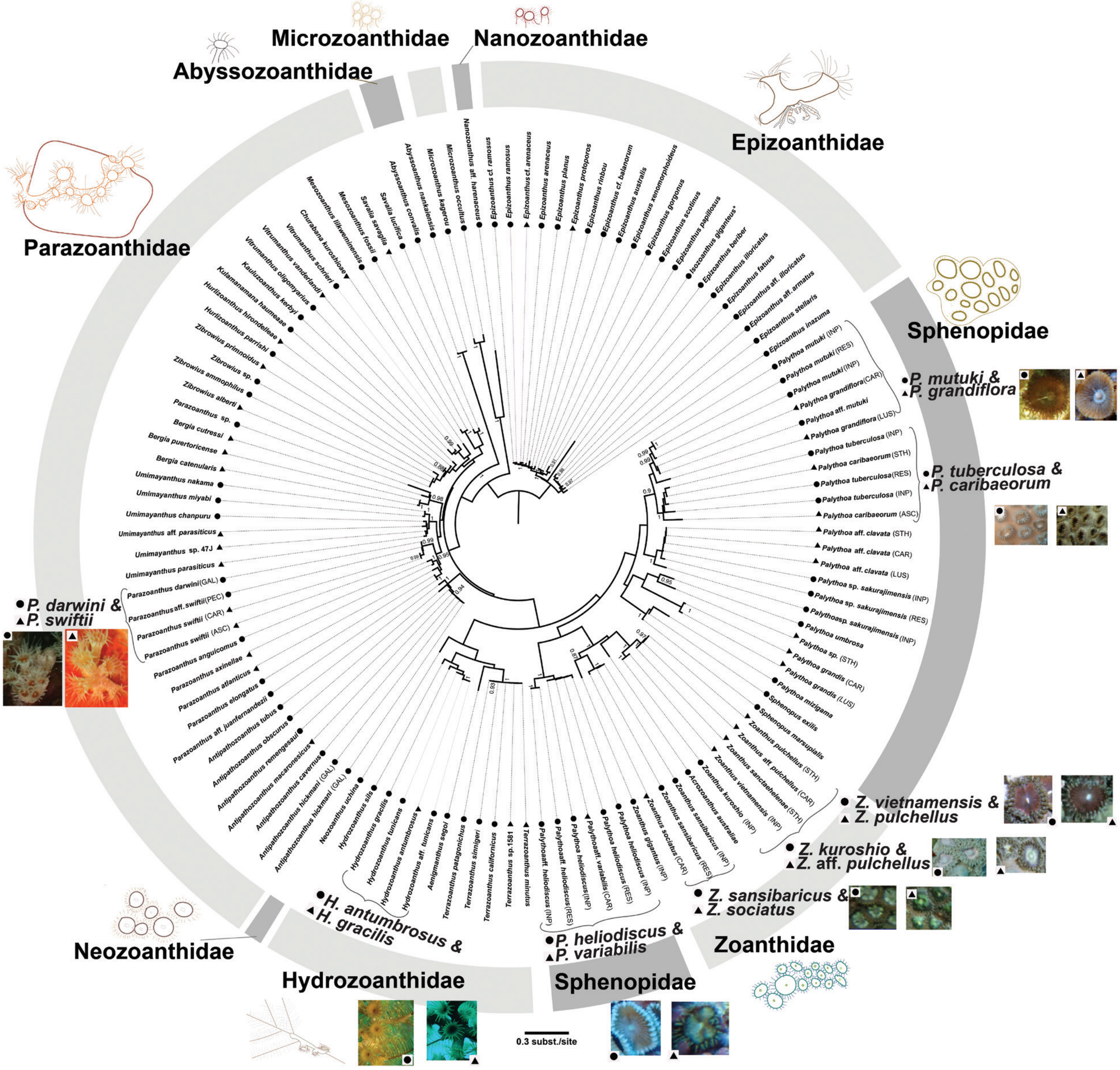

Figure 5. Phylogeny of the order Zoantharia. Phylogenetic tree obtained from a concatenated alignment of the mitochondrial markers of COI, 16S-rDNA, and the nuclear ITS-rDNA. Values at nodes represent ML bootstrap values >75%, respectively. Species distributed in the Atlantic Ocean are indicated by a triangle, and in the Indo-Pacific Ocean by a circle. Sibling species complexes are indicated with curly brackets. *Family Parazoanthidae.

evolutionary relationships for many *Palythoa* and *Zoanthus* lineages (Reimer et al. 2007b; Shiroma and Reimer 2010; Mizuyama et al. 2018), as well as for some stony coral species (Vollmer and Palumbi 2002; Johnston et al. 2017; Terraneo et al. 2025). Additionally, many Zoantharia lineages have evolved high ecological plasticity, adapting to distinct habitats/environment settings. For instance, endosymbiosis with Symbiodiniaceae and epizoism have been gained and lost multiple times in several distinct genera/families (Swain 2010; Kise et al. 2023). However, genomic studies of zoantharians are still scarce (Fourreau et al. 2023; Yoshioka et al. 2024), hampering our ability to compare their gene repertoire with other groups such as stony corals. For example, the evolutionary mechanisms that promote a lower mutation rate in zoantharian lineages, and/or facilitate generalist ecological strategies. Therefore, further research on this topic is needed to shed light on the puzzling evolution of Zoantharia and the apparent unusual low levels of DNA evolutionary rates between the IPO and ATO.

Which processes might have driven the sibling species pattern?

There was a striking pattern in zoantharians having sibling evolutionary lineages between ocean basins (Figs 5, 6), which is far different from that observed in stony corals and fire corals (Fukami et al. 2004; Arrigoni et al. 2018). In a genetic survey of 35 marine vertebrates and invertebrates,

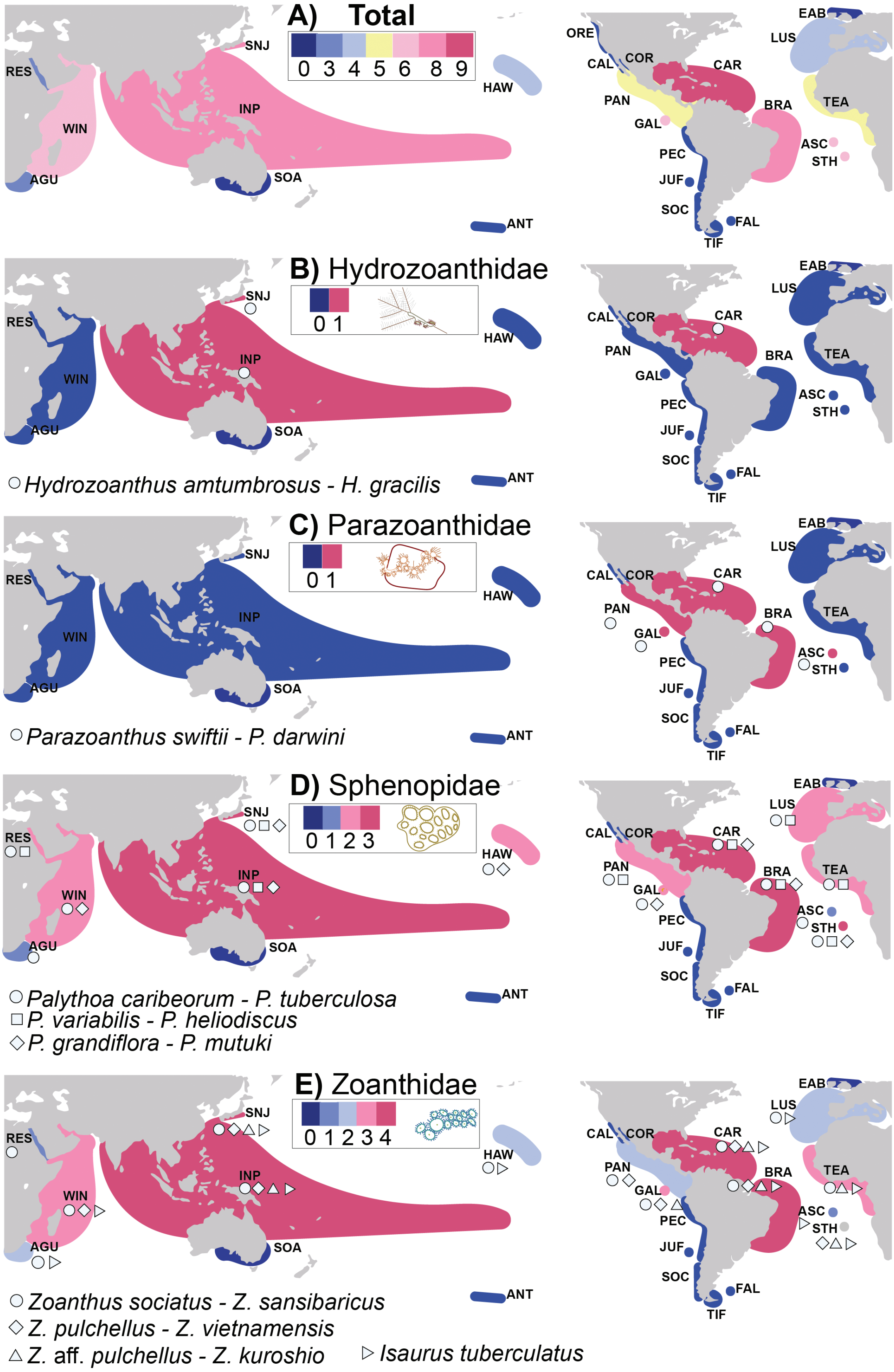

Figure 6. Global distribution of zoantharian sibling species complexes (**A**) and for each family (**B–E**). Colors represent the number of species reported for each province. Subtropical and tropical provinces were Ascension (ASC), Brazilian (BRA), Caribbean (CAR), Lusitania (LUS), Saint Helena (STH), Tropical Eastern Atlantic (TEA), Galapagos (GAL), Hawaiian (HAW), Indo-Polynesian (INP), Red Sea (RES), Sino-Japanese (SNJ) and Western Indian Ocean (WIN), while in temperate/polar waters were Agulhas Province (AGU), Antarctic Province (ANT), California (CAL), Cortez (COR), Easter Atlantic Boreal (EAB), Falkland Islands (FAL), Juan Fernandez (JUF), Oregon (ORE), Panamanian (PAN), Peru-Chilean (PEC), Southeastern Australian (SOA), Southern Chile (SOC), and Tierra del Fuego (TIF).

Selkoe et al. (2014) reported that at most 50% of population dispersal could be attributed to pelagic larval duration (PLD). Research on zoantharian PLDs is limited, but an extended planktonic larval phase of more than 100 days is known for *P. tuberculosa* (Polak et al. 2011). Plankton tows also indicate long PLDs for the families Sphenopidae and Zoanthidae (Ryland et al. 2000). Asexual reproduction may promote local dispersal and increase substrate occupancy (Ryland 1997), and this trait has been described for genera such as *Palythoa*, *Parazoanthus*, and *Zoanthus* (Garrabou 1999; Acosta et al. 2005a; Acosta and González 2007). Additionally, some zoantharians have a high rafting potential (Santos and Reimer 2018). Many coastal organisms, including stony corals and reef fishes, are able to disperse for hundreds to thousands of kilometers attached to drift material such as volcanic pumice, seaweed, logs, or man-made objects (Jokiel 1990; Hoeksema et al. 2012). Combined, a long PLD, asexual reproduction modes, and rafting, at least partly explain the apparent low levels of genetic differentiation between ocean basins and the widespread distribution of several species (Fig. 6).

The low molecular and morphological divergence observed between zoantharian sibling species may also reflect a similar use of resources (e.g., related niches). For example, *P. tuberculosa* is often the most abundant zoantharian in shallow waters of the IPO, including Okinawa (Irei et al. 2011; Yang et al. 2013), Taiwan (Reimer et al. 2011a; Reimer et al. 2017a), Malaysia (Wee et al. 2017), and Red Sea (Reimer et al. 2017b). A similar trend was observed in the ATO sibling *P. caribaeorum*, which is widespread along the Brazilian and Caribbean coasts (Suchanek and Green 1981; Acosta et al. 2005b; Santos et al. 2016; Reimer et al. 2018), the Mid-Atlantic ridge (Reimer et al. 2014; Santos et al. 2019), and the East Atlantic (Reimer et al. 2010). Both species have been reported as generalists found in diverse environments from the backreef moat to the outer reef, and from the intertidal zone to more than 20 m deep (Sebens 1982; Yang et al. 2013; Santos et al. 2016, 2019, 2021; Reimer et al. 2017b). In contrast, the siblings *P. mutuki* (Haddon & Shackleton, 1891) and *P. grandiflora* are relatively less abundant than *P. tuberculosa* and *P. caribaeorum*, respectively, and occur most commonly on intertidal reef crests or exposed habitats in both ocean basins (Oigman-Pszczol et al. 2004; Shiroma and Reimer 2010; Irei et al. 2011; Santos et al. 2016). Additional ecological studies will help to understand if sibling zoantharians share other traits, such as reproduction cycles, trophic ecology, and interaction with symbiotic partners (Santos et al. 2021).

Speciation driven by ecological differentiation is documented in marine habitats (Rocha et al. 2005; Bowen et al. 2013). However, considering that most zoantharians are widely distributed across regions, and might share similar traits, it is unlikely that these sibling species result from ecological differences between the ATO and IPO. On the other hand, processes on a geological time scale are important in allopatric evolution. Due to the high molecular and morphological similarities between the zoantharian sibling species, and the widespread species distribution within each ocean basin, their ancestors may have had a cosmopolitan distribution before the comparatively recent separation of the tropical ocean basins, prompting the allopatric processes generating this sibling species pattern.

The vicariant rise of the Panama Isthmus, along with the cold Benguela Current in southern Africa, are the most likely barriers that lead to the sibling zoantharian pairs and/or groups. The Isthmus of Panama connects the North and South American landmasses and its rise closed the tropical exchange between the ATO and IPO via the Central American Sea approximately 3.5 mya (Keigwin 1978; O'Dea et al. 2016). The Benguela upwelling zone started approximately 2 mya and encompass the South Atlantic coast of Angola, Namibia, and South Africa (Etourneau et al. 2009; Hutchings et al. 2009), and its cold water is an environmental barrier to many tropical marine species (Floeter et al. 2008). Nevertheless, water exchange from the Indian Ocean to the South ATO still occurs due to rings and filaments of the warm Agulhas Current that occasionally intrude into the Atlantic (Lutjeharms 1996), possibly connecting reef fish populations (Cord et al. 2025). Another vicariant event that could have influenced the sibling zoantharians' speciation process was the closure of the Tethys Sea. However, this is a much older event (20 to 12 mya; Dercourt et al. 1986; Cowman and Bellwood 2013b), which would have likely resulted in higher genetic differentiation than has been observed from zoantharian siblings.

Main gaps on biogeography of zoantharians

There is no information on the connectivity of zoantharian populations at large scales. Studies describing high-quality whole genomes of Zoantharia species will further support phylogenomic trees and population genomic analysis. Such work is crucial to clarify how biogeographical barriers affect the gene flow and evolution of species and populations. Although our study is a first attempt to characterize the morphological similarities of sibling zoantharians, we highlight that additional work on the taxonomy and ecology of these species is much needed.

Zoantharians are often overlooked in ecological surveys, and their distributions as reported here are still underestimated. In particular, there is a paucity of research in the African coasts (Southeastern Atlantic and Western Indian), and Polynesian archipelagos. There is also great potential for discovering additional zoantharian species within cryptic habitats, such as caves (Kise et al. 2017), rubble zones (Fujii and Reimer 2013), and turf (Vaga et al. 2021). Although deep-sea research in HAW (Sinniger et al. 2013) and LUS (Carreiro-Silva et al. 2017) provinces have reported and described several species, the high diversity at these locations could be biased due to a paucity of zoantharian research in the mesophotic and deep-sea zones across most other provinces (Reimer et al. 2019).

It is most likely that the two current IPO-endemic families, Nanozoanthidae and Neozoanthidae, are cosmopolitan. Combined with the lack of focused surveys on

Zoantharia, species of the family Nanozoanthidae are difficult to spot due to a pale/translucid color and a small polyp size (<1 mm; Fujii and Reimer 2013). Molecular data have also pointed that the species *Isozoanthus sulcatus* found off the coast of western Europe likely belongs to Nanozoanthidae (Fujii and Reimer 2013). Likewise, phylogenetic analyses indicated that the family Neozoanthidae should be reassigned to the cosmopolitan family Zoanthidae (Reimer et al. 2011b, 2012b).

At the suborder level, Brachycnemina was recovered as a monophyletic group but several phylogenetic studies have shown that Macrocnemina is a polyphyletic clade (Sinniger et al. 2005; Swain 2010; Fourreau et al. 2023). Our results also retrieved Macrocnemina as a polyphyletic group (Fig. 5). Although our tree showed Parazoanthidae and Sphenopidae (genera *Palythoa*) as non-molophyletic clades, these nodes had poor support, while previous studies have endorsed the monophyly of these families (Sinniger et al. 2005; Poliseno et al. 2019; Forreau et al. 2023). Previous studies have also called for research to determine whether: (1) the monospecific genus *Acrozoanthus* is actually within *Zoanthus* (family Zoanthidae; Reimer et al. 2011c); (2) the monospecific genus *Sphenopus* is actually within *Palythoa* (family Sphenopidae; Reimer et al. 2012c; Fujii and Reimer 2016; Poliseno et al. 2019); (3) the monospecific genus *Paleozoanthus* is actually within *Terrazoanthus* (families Epizoanthidae and Hydrozoanthidae, respectively; Low et al. 2016; Fourreau et al. 2023); (4) the monospecific genus *Thoracactis* of the family Epizoanthidae is actually within Parazoanthidae (Kise et al. 2024); (5) *Isaurus tuberculatus* Gray, 1828, originally described from the ATO and later reported across the IPO, is likely a sibling species group (yet only mitochondrial sequences had been published; Reimer et al. 2008); (6) putative *P.* sp. 'sakurajimensis' (IPO) and *P.* aff. *clavata* (ATO) while not formally described, are part of a sibling species clade (Fig. 5); and (7) there are additional shallow-water zoantharian species with records from both oceans (e.g., *Epizoanthus paguricola* Roule, 1900 has been recorded from ATO and New Zealand, but no molecular data are available for these specimens). Lastly, species of *Palythoa* and *Zoanthus* play a significant ecological role in phase shifts from coral to zoantharian-dominated reefs (Cruz et al. 2016; Oliveira et al. 2022). With ongoing environmental changes, such phase-shifts may become more common in coral reefs worldwide (Reimer et al. 2021). Filling knowledge gaps on the distributions and biology of zoantharians will be essential to support monitoring and management of marine ecosystems.

Conclusions

We reported unusual low DNA divergence for zoantharian lineages between the ATO and the IPO. Additional research is needed to reveal the processes behind this pattern, such as investigating whole-genomes of representatives of Zoantharia families, which could reveal low rates of molecular evolution. At the species level, we hypothesize that some zoantharians have evolved generalist niches to survive in distinct biogeographical provinces across a wide range of environmental conditions, such as nutritional interactions with symbionts (Santos et al. 2021). Some species, particularly in *Palythoa* and *Zoanthus*, have dispersal strategies that allow for broad distributions within ocean basins, while the vicariant events of the rise of the Isthmus of Panama and the appearance of the Benguela Current upwelling likely prompted the speciation of sibling lineages between the ATO and the IPO.

Acknowledgements

We are thankful for support from Florence Evacitas (University of the Philippines Cebu, Philippines); Debora Pires (National Museum of Rio de Janeiro, Brazil); Allen Collins, Annie Evankow, Rebecca Bernardos (Smithsonian National Museum of Natural History, U.S.A); and Jan Vicente and Holly Bolick (Bernice Pauahi Bishop Museum, Hawai'i, U.S.A). This work was supported in part by a grant from the Japan Society for the Promotion of Science (23H03821) to JDR. MVK also thanks the support of the São Paulo Research Foundation (FAPESP, Process #2021/06866-6), and the National Council for Scientific and Technological Development (CNPq #303461/2025-0). Comments from the editor and two reviewers improved an earlier version of this manuscript.

Author contributions

All authors have contributed equally.

Data accessibility statement

All of the data that support the findings of this study are available in the main text or Supplementary Information.

References

Acosta A, Sammarco PW, Duarte LF (2005a) New fission processes in the zoanthid *Palythoa caribaeorum*: description and quantitative aspects. Bulletin of Marine Science 76(1): 1–26.

Acosta A, Casas M, Vargas CA, Camacho JE (2005b) Lista de Zoantharia (Cnidaria: Anthozoa) del Caribe y de Colombia. Biota Colombiana 6(2): 147–161.

Acosta A, González AM (2007) Fission in the Zoantharia *Palythoa caribaeorum* (Duchassaing and Michelotii, 1860) populations: a latitudinal comparison. Bulletin of Marine and Coastal Research 36: 151–166. https://doi.org/10.25268/bimc.invemar.2007.36.0.204

Arrigoni R, Maggioni D, Montano S, Hoeksema BW, Seveso D, Shlesinger T, Terraneo TI, Arrigoni R (2018) An integrated morpho-molecular approach to delineate species boundaries of *Millepora* from the Red Sea. Coral Reefs 37(4): 967–984. https://doi.org/10.1007/s00338-018-01739-8

Avise JC, Bowen BW, Lamb T, Meylan AB, Bermingham E (1992) Mitochondrial DNA evolution at a turtle's pace: evidence for low genetic variability and reduced microevolutionary rate in the Testudines. Molecular Biology and Evolution 9: 457–473.

Bernardi G, Alva-Campbell YR, Gasparini JL, Floeter SR (2008) Molecular ecology, speciation, and evolution of the reef fish genus *Anisotremus*. Molecular Phylogenetics and Evolution 48(3): 929–935. https://doi.org/10.1016/j.ympev.2008.05.011

Bowen BW, Rocha LA, Toonen RJ, Karl SA (2013) The origins of tropical marine biodiversity. Trends in Ecology and Evolution 28(6): 359–366. https://doi.org/10.1016/j.tree.2013.01.018

Bowen BW, Gaither MR, DiBattista JD, Iacchei M, Andrews KR, Grant WS, Toonen RJ, Briggs JC (2016) Comparative phylogeography of the ocean planet. Proceedings of the National Academy of Sciences 113(29): 7962–7969. https://doi.org/10.1073/pnas.1602404113

Briggs JC, Bowen BW (2012) A realignment of marine biogeographic provinces with particular reference to fish distributions. Journal of Biogeography 39(1): 12–30. https://doi.org/10.1111/j.1365-2699.2011.02613.x

Burnett WJ, Benzie JAH, Beardmore JA, Ryland JS (1997) Zoanthids (Anthozoa, Hexacorallia) from the Great Barrier Reef and Torres Strait, Australia: systematics, evolution and a key to species. Coral Reefs 16: 55–68. https://doi.org/10.1007/s003380050060

Cord I, Araujo GS, Silva FC, Kurtz YR, Rocha CR, Pinheiro HT, Rocha LA, Floeter SR (2025) Biogeography and evolution of reef fishes on tropical Mid-Atlantic Ridge islands. Proceedings of the Royal Society B: Biological Sciences 292(2051): 20250756. https://doi.org/10.1098/rspb.2025.0756

Costello MJ, Tsai P, Wong PS, Cheung AKL, Basher Z, Chaudhary C (2017) Marine biogeographic realms and species endemicity. Nature Communications 8(1): 1–9. https://doi.org/10.1038/s41467-017-01121-2

Cowman PF, Bellwood DR (2013) Vicariance across major marine biogeographic barriers: temporal concordance and the relative intensity of hard versus soft barriers. Proceedings Biological Sciences of The Royal Society 280: 20131541. https://doi.org/10.1098/rspb.2013.1541

Cowman PF, Parravicini V, Kulbicki M, Floeter SR (2017) The biogeography of tropical reef fishes: Endemism and provinciality through time. Biological Reviews 92(4): 2112–2130. https://doi.org/10.1111/brv.12323

Coyne J, Orr H (2004) Speciation (Sinauer (ed.)). [ISBN 0-87893-091-4]

Cruz ICS, Meira VH, de Kikuchi RKP, Creed JC (2016) The role of competition in the phase shift to dominance of the zoanthid *Palythoa* cf. *variabilis* on coral reefs. Marine Environmental Research 115: 28–35. https://doi.org/10.1016/j.marenvres.2016.01.008

De Souza JN, Nunes FLD, Zilberberg C, Sanchez JA, Migotto AE, Hoeksema BW, Serrano XM, Baker AC, Lindner A (2017) Contrasting patterns of connectivity among endemic and widespread fire coral species (*Millepora* spp.) in the tropical Southwestern Atlantic. Coral Reefs 36(3): 701–716. https://doi.org/10.1007/s00338-017-1562-0

Dercourt J, Zonenshain L, Riocu L, Kazmin V, Le Pichon X, Knipper A, Grandjacquet C, Sbortshikov I, Geyssant J, Lepvrier C, Pechersky D, Boulin J, Sibuet J, Savostin L, Sorokhtin O, Westphal M, Bazhenov M, Lauer J, Biju-Duval B (1986) Geological evolution of the Tethys Belt from the Atlantic to the Pamirs since the LIAS. Tectonophysics 123: 241–315. https://doi.org/10.1016/0040-1951(86)90199-X

Dudoit A, Santos MEA, Reimer JD, Toonen RJ (2022) Phylogenomics of *Palythoa* (Hexacorallia: Zoantharia): probing species boundaries in a globally distributed genus. Coral Reefs 41(3): 655–672. https://doi.org/10.1007/s00338-021-02128-4

Etourneau J, Martinez P, Blanz T, Schneider R (2009) Pliocene-Pleistocene variability of upwelling activity, productivity, and nutrient cycling in the Benguela region. Geology 37(10): 871–874. https://doi.org/10.1130/G25733A.1

Feng C, Pettersson M, Lamichhaney S, Rubin CJ, Rafati N, Casini M, Folkvord A, Andersson L (2017) Moderate nucleotide diversity in the Atlantic herring is associated with a low mutation rate. ELife 6: 1–14. https://doi.org/10.7554/eLife.23907

Floeter SR, Rocha LA, Robertson DR, Joyeux JC, Smith-Vaniz WF, Wirtz P, Edwards AJ, Barreiros JP, Ferreira CEL, Gasparini JL, Brito A, Falcón JM, Bowen BW, Bernardi G (2008) Atlantic reef fish biogeography and evolution. Journal of Biogeography 35: 22–47. https://doi.org/10.1111/j.1365-2699.2007.01790.x

Fourreau CJL, Kise H, Santander MD, Pirro S, Maronna MM, Poliseno A, Santos MEA, Reimer JD (2023) Genome sizes and repeatome evolution in zoantharians (Cnidaria: Hexacorallia: Zoantharia). PeerJ 11. https://doi.org/10.7717/peerj.16188

Fujii T, Reimer JD (2013) A new family of diminutive zooxanthellate zoanthids (Hexacorallia: Zoantharia). Zoological Journal of the Linnean Society: 509–522. https://doi.org/10.1111/zoj.12075

Fujii T, Reimer JD (2016) A new solitary free-living species of the genus *Sphenopus* (Cnidaria, Anthozoa, Zoantharia, Sphenopidae) from Okinawa-jima Island, Japan. ZooKeys 4: 11–24. https://doi.org/10.3897/zookeys.606.9310

Fukami H, Budd AF, Paulay G, Sole A, Chen CA, Iwao K, Knowlton N (2004) Conventional taxonomy obscures deep divergence between Pacific and Atlantic corals. Nature 427: 832–835. https://doi.org/10.1038/nature02339

Garrabou J (1999) Life-history traits of *Alcyonium acaule* and *Parazoanthus axinellae* (Cnidaria, Anthozoa), with emphasis on growth. Marine Ecology Progress Series 178: 193–204. https://doi.org/10.3354/meps178193

Gavrilets S, Li H, Vose M (2000) Patterns of parapatric speciation. Evolution 54: 1126–1134. https://doi.org/10.1111/j.0014-3820.2000.tb00548.x

Hibino Y, Todd PA, Yang S, Benayahu Y, Reimer JD (2013a) Molecular and morphological evidence for conspecificity of two common Indo-Pacific species of *Palythoa* (Cnidaria: Anthozoa). Hydrobiologia 733(1): 31–43. https://doi.org/10.1007/s10750-013-1587-5

Hibino Y, Todd P, Ashworth CD, Obuchi M, Davis J (2013b) Monitoring colony colour and zooxanthellae (*Symbiodinium* spp.) condition in the reef zoanthid *Palythoa tuberculosa* in Okinawa, Japan. Marine Biology Research 9(8): 794–801. https://doi.org/10.1080/17451000.2013.766344

Hoeksema BW, Roos PJ, Cadee GC (2012) Trans-Atlantic rafting by the brooding reef coral *Favia fragum* on man-made flotsam. Marine Ecology Progress Series 445: 209–218. https://doi.org/10.3354/meps09460

Hutchings L, van der Lingen CD, Shannon LJ, Crawford RJM, Verheye HMS, Bartholomae CH, van der Plas AK, Louw D, Kreiner A, Ostrowski M, Fidel Q, Barlow RG, Lamont T, Coetzee J, Shillington F, Veitch J, Currie JC, Monteiro PMS (2009) The Benguela Current: An ecosystem of four components. Progress in Oceanography 83(1–4): 15–32. https://doi.org/10.1016/j.pocean.2009.07.046

Iacchei M, Gaither MR, Bowen BW, Toonen RJ (2016) Testing dispersal limits in the sea: Range-wide phylogeography of the pronghorn spiny lobster *Panulirus penicillatus*. Journal of Biogeography 43(5): 1032–1044. https://doi.org/10.1111/jbi.12689

Irei Y, Nozawa Y, Reimer JD (2011) Distribution patterns of five zoanthid species at Okinawa Island, Japan. Zoological Studies 50(4): 426–433.

Jaccard P (1908) Nouvelles recherches sur la distribution florale. Bulletin de la Société vaudoise des sciences naturelles 44: 223–270.

Johnston EC, Forsman ZH, Flot JF, Schmidt-Roach S, Pinzón JH, Knapp ISS, Toonen RJ (2017) A genomic glance through the fog of plasticity and diversification in *Pocillopora*. Scientific Reports 7(1): 5991. https://doi.org/10.1038/s41598-017-06085-3

Jokiel PL (1990) Long-distance dispersal by rafting: reemergence of an old hypothesis. Endeavour 14: 66–73. https://doi.org/10.1016/0160-9327(90)90074-2

Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Meintjes P, Drummond A (2012) Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28(12): 1647–1649. https://doi.org/10.1093/bioinformatics/bts199

Keigwin LD (1978) Pliocene closing of the Isthmus of Panama, based on biostratigraphic evidence from nearby Pacific Ocean and Caribbean Sea cores. Geology 6(10): 630–634. https://doi.org/10.1130/0091-7613(1978)6%3C630:PCOTIO%3E2.0.CO;2

Kise H, Fujii T, Masucci GD, Biondi P, Reimer JD (2017) Three new species and the molecular phylogeny of *Antipathozoanthus* from the Indo-Pacific Ocean. ZooKeys 725: 97–122. https://doi.org/10.3897/zookeys.725.21006

Kise H, Santos MEA, Fourreau C, Iguchi A, Goto R, Reimer JD (2023) Evolutionary patterns of host switching, lifestyle mode, and the diversification history in symbiotic zoantharians. Molecular Phylogenetics and Evolution 182: 107732. https://doi.org/10.1016/j.ympev.2023.107732

Kise H, Montenegro J, Corrêa PVF, Clemente MVC, Sumida PYG, Hoeksema BW (2024) A taxonomic revision of the sponge-associated genus *Thoracactis* Gravier, 1918 (Anthozoa: Zoantharia) based on an integrated approach. Contributions to Zoology 152(2): 1–23. https://doi.org/10.1163/18759866-bja10059

Knowlton N (2001) The future of coral reefs. Proceedings of the National Academy of Sciences of the United States of America 98(10): 5419–5425. https://doi.org/10.1073/pnas.091092998

LaJeunesse TC, Parkinson JE, Gabrielson PW, Jeong HJ, Reimer JD, Voolstra CR, Santos SR (2018) Systematic revision of Symbiodiniaceae highlights the antiquity and diversity of coral endosymbionts. Current Biology 28(16): 2570–2580.e6. https://doi.org/10.1016/j.cub.2018.07.008

Lessios HA (2008) The great American schism: Divergence of marine organisms after the rise of the Central American Isthmus. Annual Review of Ecology, Evolution, and Systematics 39(1): 63–91. https://doi.org/10.1146/annurev.ecolsys.38.091206.095815

Lessios HA, Robertson DR (2006) Crossing the impassable: Genetic connections in 20 reef fishes across the eastern Pacific barrier. Proceedings of the Royal Society B: Biological Sciences 273(1598): 2201–2208. https://doi.org/10.1098/rspb.2006.3543

Low MEY, Sinniger F, Reimer JD (2016) The order Zoantharia Rafinesque, 1815 (Cnidaria, Anthozoa: Hexacorallia): supraspecific classification and nomenclature. ZooKeys 641: 1–80. https://doi.org/10.3897/zookeys.641.10346

Lutjeharms JRE (1996) The exchange of water between the South Indian and South Atlantic oceans. In: Wefer G, Berger WH, Siedler G, Webb DJ (Eds) The South Atlantic. Springer, Berlin, Heidelberg, 125–162. https://doi.org/10.1007/978-3-642-80353-6_8

Martinez Arbizu P (2020) pairwiseAdonis: pairwise multilevel comparison using adonis. R. Package Version 0.4.

Milne I, Lindner D, Bayer M, Husmeier D, McGuire G, Marshall DF, Wright F (2009) TOPALi v2: a rich graphical interface for evolutionary analyses of multiple alignments on HPC clusters and multi-core desktops. Bioinformatics 25(1): 126–127. https://doi.org/10.1093/bioinformatics/btn575

Mizuyama M, Masucci GD, Reimer JD (2018) Speciation among sympatric lineages in the genus *Palythoa* (Cnidaria: Anthozoa: Zoantharia) revealed by morphological comparison, phylogenetic analyses and investigation of spawning period. PeerJ: 6: e5132. https://doi.org/10.7717/peerj.5132

Muscatine L, Hand C (1958) Direct evidence for the transfer of materials from symbiotic algae to the tissues of a coelenterate. Zoology 44: 1259–1263. https://doi.org/10.1073/pnas.44.12.1259

O'Dea A, Lessios HA, Coates AG, Eytan RI, Restrepo-Moreno SA, Cione AL, Collins LS, de Queiroz A, Farris DW, Norris RD, Stallard RF, Woodburne MO, Aguilera O, Aubry M-P, Berggren WA, Budd AF, Cozzuol MA, Coppard SE, Duque-Caro H, Finnegan S, Gasparini GM, Grossman EL, Johnson KG, Keigwin LD, Knowlton N, Leigh EG, Leonard-Pingel JS, Marko PB, Pyenson ND, Rachello-Dolmen PG, Soibelzon E, Soibelzon L, Todd JA, Vermeij GJ, Jackson JBC (2016) Formation of the Isthmus of Panama. Science Advances 2(8): e1600883. https://doi.org/10.1126/sciadv.1600883

Oigman-Pszczol SS, Figueiredo MADO, Creed JC (2004) Distribution of benthic communities on the tropical rocky subtidal of Armação dos Búzios, Southeastern Brazil. Marine Ecology 25(3): 173–190. https://doi.org/10.1111/j.1439-0485.2004.00018.x

Oksanen J, et al. (2025) vegan: Community Ecology Package. R package version 2.6-10.

Pax F (1910) Studien an westindischen Actinien. Zoologische Jahrbucher Supplement 11: 157–330.

Polak O, Loya Y, Brickner I (2011) The widely-distributed Indo-Pacific zoanthid *Palythoa tuberculosa*: a sexually conservative strategist. Bulletin of Marine Science 87(3): 605–621. https://doi.org/10.5343/bms.2010.1088

Poliseno A, Santos MEA, Kise H, MacDonald B, Quattrini AM, McFadden CS, Reimer JD (2020) Evolutionary implications of analyses of complete mitochondrial genomes across order Zoantharia (Cnidaria: Hexacorallia). Journal of Zoological Systematics and Evolutionary Research 58(4): 858–868. https://doi.org/10.1111/jzs.12380

Randall JE (1998) Zoogeography of shore fishes of the Indo-Pacific region. Zoological Studies 37(4): 227–268.

Reimer JD, Sinniger F, Fujiwara Y, Hirano S, Maruyama T (2007a) Morphological and molecular characterisation of *Abyssoanthus nankaiensis*, a new family, new genus and new species of deep-sea zoanthid (Anthozoa: Hexacorallia: Zoantharia) from a north-west Pacific methane cold seep. Invertebrate Systematics 21(3): 255. https://doi.org/10.1071/IS06008

Reimer JD, Takishita K, Ono S, Tsukahara J, Maruyama T (2007b) Molecular evidence suggesting interspecific hybridization in

Zoanthus spp. (Anthozoa: Hexacorallia). Zoological Society of Japan 24(4): 346–359. https://doi.org/10.2108/zsj.24.346

Reimer JD, Ono S, Tsukahara J, Iwase F (2008) Molecular characterization of the zoanthid genus *Isaurus* (Anthozoa: Hexacorallia) and associated zooxanthellae (*Symbiodinium* spp.) from Japan. Marine Biology 153: 351–363. https://doi.org/10.1007/s00227-007-0811-0

Reimer JD, Todd PA (2009) Preliminary molecular examination of zooxanthellaete zoanthids (Hexacorallia: Zoantharia) and associated zooxanthellae (*Symbiodinium* spp.) diversity in Singapore. The Raffles Bulletin of Zoology 22: 103–120.

Reimer JD (2010) Key to field identification of shallow water brachycnemic zoanthids (Order Zoantharia: Suborder Brachycnemina) present in Okinawa. Galaxea Journal of Coral Reef Studies 12(1): 23–29. https://doi.org/10.3755/galaxea.12.23

Reimer JD, Hirose M, Wirtz P (2010) Zoanthids of the Cape Verde Islands and their symbionts: previously unexamined diversity in the Northeastern Atlantic. Contributions to Zoology 79(4): 147–163. https://doi.org/10.1163/18759866-07904002

Reimer JD, Obuchi M, Irei Y, Fujii T, Nozawa Y (2011a) Shallow-water brachycnemic zoanthids (Cnidaria: Hexacorallia) from Taiwan: A Preliminary Survey 50(3): 363–371.

Reimer JD, Hirose M, Irei Y, Obuchi M, Sinniger F (2011b) The sands of time: rediscovery of the genus *Neozoanthus* (Cnidaria: Hexacorallia) and evolutionary aspects of sand incrustation in brachycnemic zoanthids. Marine Biology 158: 983–993. https://doi.org/10.1007/s00227-011-1624-8

Reimer JD, Ishikawa SA, Hirose M (2011c) New records and molecular characterization of *Acrozoanthus* (Cnidaria: Anthozoa: Hexacorallia) and its endosymbionts (*Symbiodinium* spp.) from Taiwan. Marine Biodiversity 41(2): 313–323. https://doi.org/10.1007/s12526-010-0069-5

Reimer JD, Foord C, Irei Y (2012a) Species diversity of shallow water zoanthids (Cnidaria: Anthozoa: Hexacorallia) in Florida. Journal of Marine Biology 2012: 1–14. https://doi.org/10.1155/2012/856079

Reimer JD, Irei Y, Fujii T (2012b) Two new species of *Neozoanthus* (Cnidaria, Hexacorallia, Zoantharia) from the Pacific. ZooKeys 246: 69–87. https://doi.org/10.3897/zookeys.246.3886

Reimer JD, Lin M, Fujii T, Lane DJW, Hoeksema BW (2012c) The phylogenetic position of the solitary zoanthid genus *Sphenopus* (Cnidaria: Hexacorallia). Contributions to Zoology 81(1): 43–54. https://doi.org/10.1163/18759866-08101003

Reimer JD, Sinniger F, Irei Y (2013) Preliminary list of macrocnemic zoanthids diversity (Anthozoa: Hexacorallia: Zoantharia) from Southern Shikoku, Japan. Kuroshio Biosphere 9: 1–10.

Reimer JD, Santos MEA, Kise H, Neo ML, Chen CA, Soong K (2017a) Diversity of Zoantharia (Anthozoa: Hexacorallia) at Dongsha Atoll in the South China Sea. Regional Studies in Marine Science 12: 49–57. https://doi.org/10.1016/j.rsma.2017.02.006

Reimer JD, Montenegro J, Santos MEA, Low MEY, Herrera M, Gatins R, Roberts MB, Berumen ML (2017b) Zooxanthellate zoantharians (Anthozoa: Hexacorallia: Zoantharia: Brachycnemina) in the northern Red Sea. Marine Biodiversity 47: 1079–1091. https://doi.org/10.1007/s12526-017-0706-3

Reimer JD, Wee HB, García-Hernández JE, Hoeksema BW (2018) Zoantharia (Anthozoa: Hexacorallia) abundance and associations with Porifera and Hydrozoa across a depth gradient on the west coast of Curaçao. Systematics and Biodiversity 16(8): 820–830. https://doi.org/10.1080/14772000.2018.1518936

Reimer JD, Kise H, Santos MEA, Lindsay DJ, Pyle RL, Copus JM, Bowen BW, Nonaka M, Higashiji T, Benayahu Y (2019) Exploring the biodiversity of understudied benthic taxa at mesophotic and deeper depths: Examples from the order Zoantharia (Anthozoa: Hexacorallia). Frontiers in Marine Science 6: 1–12. https://doi.org/10.3389/fmars.2019.00305

Reimer JD, Wee HB, López C, Beger M, Cruz ICS (2021) Widespread *Zoanthus* and *Palythoa* dominance, barrens, and phase shifts in shallow water subtropical and tropical marine ecosystems. In: S. J. Hawkins et al. (Eds) Oceanography and marine biology: an annual review. CRC Press, 533–557. https://doi.org/10.1201/9781003138846

Roberts CM, Mittermeier CG, Schueler FW (2002) Marine biodiversity hotspots and conservation priorities for tropical reefs. Science 295: 1280–1284. https://doi.org/10.1126/science.1067728

Rocha LA, Bowen BW (2008) Speciation in coral-reef fishes. Journal of Fish Biology 72(5): 1101–1121. https://doi.org/10.1111/j.1095-8649.2007.01770.x

Rocha LA, Robertson DR, Roman J, Bowen BW (2005) Ecological speciation in tropical reef fishes. Proceedings of the Royal Society B: Biological Sciences 272(1563): 573–579. https://doi.org/10.1098/2004.3005

Ryland JS (1997) Reproduction in Zoanthidea (Anthozoa: Hexacorallia). Invertebrate Reproduction & Development 31(1–3): 177–188. https://doi.org/10.1080/07924259.1997.9672575

Ryland JS, Putron S, Scheltema RS, Chimonides PJ, Zhadan DG (2000) Semper's (zoanthid) larvae: pelagic life, parentage and other problems. Hydrobiologia 440: 191–198. https://doi.org/10.1023/A:1004171127777

Santos MEA, Reimer JD (2018) Rafting in Zoantharia: a hitchhiker's guide to dispersal? Marine Pollution Bulletin 130: 307–310. https://doi.org/10.1016/j.marpolbul.2018.03.041

Santos MEA, Kitahara MV, Lindner A, Reimer JD (2016) Overview of the order Zoantharia (Cnidaria: Anthozoa) in Brazil. Marine Biodiversity 46(3): 547–559. https://doi.org/10.1007/s12526-015-0396-7

Santos MEA, Wirtz P, Montenegro J, Kise H, López C, Brown J, Reimer JD (2019) Diversity of Saint Helena Island and zoogeography of zoantharians in the Atlantic Ocean: Jigsaw falling into place. Systematics and Biodiversity 17(2): 165–178. https://doi.org/10.1080/14772000.2019.1572667

Santos MEA, Baker DM, Conti-Jerpe IE, Reimer JD (2021) Populations of a widespread hexacoral have trophic plasticity and flexible syntrophic interactions across the Indo-Pacific Ocean. Coral Reefs 40(2): 543–558. https://doi.org/10.1007/s00338-021-02055-4

Santos MEA, Reimer JD, Kiriukhin B, Wee HB, Mizuyama M, Kise H, Kitahara MV, Iguchi A, Dudoit A, Toonen RJ, Husnik F (2024) Coral microbiomes from the Atlantic and Indo-Pacific oceans have the same alpha diversity but different composition. BioRxiv: 1–14. https://doi.org/10.1101/2024.08.16.608269

Schmitt EF, Sluka RD, Sullivan-Sealey KM (2002) Evaluating the use of roving diver and transect surveys to assess the coral reef fish assemblage off southeastern Hispaniola. Coral Reefs 21(2): 216–223. https://doi.org/10.1007/s00338-002-0216-y

Sebens KP (1982) Intertidal distribuition of zoanthids on the Caribbean coast of Panamá: effects of predation and desiccation. Bulletin of Marine Science 32(1): 316–335.

Selkoe KA, Gaggiotti OE, Bowen BW, Toonen RJ (2014) Emergent patterns of population genetic structure for a coral reef community.

Molecular Ecology 23(12): 3064–3079. https://doi.org/10.1111/mec.12804

Shearer TL, Van Oppen MJH, Romano SL, Wörheide G (2002) Slow mitochondrial DNA sequence evolution in the Anthozoa (Cnidaria). Molecular Ecology 11(12): 2475–2487. http://www.ncbi.nlm.nih.gov/pubmed/12453233

Shiroma E, Reimer JD (2010) Investigations into the reproductive patterns, ecology, and morphology in the zoanthid genus *Palythoa* (Cnidaria: Anthozoa: Hexacorallia) in Okinawa, Japan. Zoological Studies 49(2): 182–194.

Sinniger F, Montoya-burgos JI, Chevaldonné P, Pawlowski J (2005) Phylogeny of the order Zoantharia (Anthozoa, Hexacorallia) based on the mitochondrial ribosomal genes. Marine Biology 147: 1121–1128. https://doi.org/10.1007/s00227-005-0016-3

Sinniger F, Reimer JD, Pawlowski J (2010) The Parazoanthidae (Hexacorallia: Zoantharia) DNA taxonomy: description of two new genera. Marine Biodiversity 40: 57–70. https://doi.org/10.1007/s12526-009-0034-3

Sinniger F, Ocaña OV, Baco AR (2013) Diversity of zoanthids (Anthozoa: Hexacorallia) on Hawaiian seamounts: description of the Hawaiian gold coral and additional zoanthids. PLOS ONE 8(1): e52607. https://doi.org/10.1371/journal.pone.0052607

Sneath PHA, Sokal RR (1973) Unweighted Pair Group Method with Arithmetic Mean. Numerical Taxonomy. San Francisco, CA, USA: WH Freeman and Co.

Soares MO, Kitahara MV, Santos MEA, Bejarano S, Rabelo EF, Cruz ICS (2022) The flourishing and vulnerabilities of zoantharians on Southwestern Atlantic reefs. Marine Environmental Research 173: 105535. https://doi.org/10.1016/j.marenvres.2021.105535

Suchanek TH, Green DJ (1981) Interspecific competition between *Palythoa caribaeorum* and other sessile invertebrates on St. Croix reefs, U.S. Virgin Islands. Proceedings of the 4th International Coral Reef Symposium 2: 679–684.

Swain TD (2010) Evolutionary transitions in symbioses: dramatic reductions in bathymetric and geographic ranges of Zoanthidea coincide with loss of symbioses with invertebrates. Molecular Ecology 19: 2587–2598. https://doi.org/10.1111/j.1365-294X.2010.04672.x

Terraneo TI, Benzoni F, Arrigoni R, Berumen ML, Mariappan KG, Antony CP, Harrison HB, Payri C, Huang D, Baird AH (2025) A genomic approach to *Porites* (Anthozoa: Scleractinia) megadiversity from the Indo-Pacific. Molecular Phylogenetics and Evolution 203: 108238. https://doi.org/10.1016/j.ympev.2024.108238

Tseng CC, Wallace CC, Chen CA (2005) Mitogenomic analysis of *Montipora cactus* and *Anacropora matthai* (Cnidaria; Scleractinia; Acroporidae) indicates an unequal rate of mitochondrial evolution among Acroporidae corals. Coral Reefs 24: 502–508. https://doi.org/10.1007/s00338-005-0499-x

Veron J, Stafford-Smith M, DeVantier L, Turak E (2015) Overview of distribution patterns of zooxanthellate Scleractinia. Frontiers in Marine Science 1: 1–19. https://doi.org/10.3389/fmars.2014.00081

Vollmer SV, Palumbi SR (2002) Hybridization and the evolution of reef coral diversity. Science 296(5575): 2023–2025. https://doi.org/10.1126/science.1069524

Wee HB, Reimer JD, Safuan M, Saidin J, Tan CH, Bachok Z (2017) Zoantharian abundance in coral reef benthic communities at Terengganu Islands, Malaysia. Regional Studies in Marine Science 12: 58–63. https://doi.org/10.1016/j.rsma.2017.02.005

Wolfe KH, Li W-H, Sharp PM (1987) Rates of nucleotide substitution vary greatly among plant mitochondrial, chloroplast, and nuclear DNAs. Proceedings of the National Academy of Sciences of the United States of America 84: 9054–9058. https://doi.org/10.1073/pnas.84.24.9054

West DA (1979) Symbiotic zoanthids (Anthozoa: Cnidaria) of Puerto Rico. Bulletin of Marine Science 29(2): 253–271.

Xu S, Stapley J, Gablenz S, Boyer J, Appenroth KJ, Sree KS, Gershenzon J, Widmer A, Huber M (2019) Low genetic variation is associated with low mutation rate in the giant duckweed. Nature Communications 10(1): 8–13. https://doi.org/10.1038/s41467-019-09235-5

Yang SY, Bourgeois C, Ashworth C, Reimer JD (2013) *Palythoa* zoanthid 'barrens' in Okinawa: examination of possible environmental causes. Zoological Studies 52(39): 1–12. https://doi.org/10.1186/1810-522X-52-39

Yoshioka Y, Yamashita H, Uchida T, Shinzato C, Kawamitsu M, Fourreau CJL, Castelló GM, Fiedler BK, van den Eeckhout TM, Borghi S, Reimer JD, Shoguchi E (2024) Azooxanthellate *Palythoa* (Cnidaria: Anthozoa) genomes reveal toxin-related gene clusters and loss of neuronal genes in hexacorals. Genome Biology and Evolution 16(9): 1–10. https://doi.org/10.1093/gbe/evae197

Supplementary materials

Supplementary material 1

ESM table S1: Sampling information. We conducted surveys using snorkeling and SCUBA diving at depths between 0–40 m following the roving technique to observe as many species as possible in the following locations: Yucantan, Mexico (2013 and 2017), Hong Kong, Hong Kong SAR (2015 and 2024), Cebu, Philippines (2017), Bali, Indonesia (2019) and Kenting, Taiwan (2024). Whenever possible, in situ high-resolution images were taken and samples were collected and preserved in 90–99% ethanol for further analyses. We also examined specimens from the Smithsonian National Museum of Natural History (SNMNH), Museu Nacional do Rio de Janeiro (MNRJ), Brazil, and Bernice Pauahi Bishop Museum (BPBM), Hawai'i (.xlsx)

Link: https://doi.org/10.21425/fob.19.174247.suppl1

Supplementary material 2

ESM table S2: Compiled records of Zoantharia for 25 global marine biogeographical provinces for shallow and deep waters. Subtropical and tropical provinces were Ascension (ASC), Brazilian (BRA), Caribbean (CAR), Lusitania (LUS), Saint Helena (STH), Tropical Eastern Atlantic (TEA), Galapagos (GAL), Hawaiian (HAW), Indo-Polynesian (INP), Red Sea (RES), Sino-Japanese (SJA) and Western Indian Ocean (WIN), while in temperate waters were Agulhas Province (AGU) Tierra del Fuego (TIF) and Falkland Islands (FAL), California (CAL), Cortez (COR), Juan Fernandez (JUF), Panamanian (PAN), Peru-Chilean (PEC), Southern Chile (SOC), and Southeastern Australian (SOA), and the cold temperate Antarctic (ANT), Eastern Atlantic Boreal (EAB), and Oregon (ORE) provinces (.xlsx)

Link: https://doi.org/10.21425/fob.19.174247.suppl2

Supplementary material 3

ESM table S3: GenBank accession numbers of the zoantharian sequences used in this study (.xlsx)
Link: https://doi.org/10.21425/fob.19.174247.suppl3

Supplementary material 4

ESM table S4: List of zoantharian sibling species along with their associated Symbiodiniaceae, and morphological and distribution data. Morphological data examined in this study (polyp form, oral disk color, and tentacle number) are shown in bold. Subtropical and tropical provinces were Ascension (ASC), Brazilian (BRA), Caribbean (CAR), Lusitania (LUS), Saint Helena (STH), Tropical Eastern Atlantic (TEA), Galapagos (GAL), Hawaiian (HAW), Indo-Polynesian (INP), Red Sea (RES), Sino-Japanese (SNJ) and Western Indian Ocean (WIN), while in temperater warm were Agulhas Province (AGU) Tierra del Fuego (TIF) and Falkland Islands (FAL), California (CAL), Cortez (COR), Juan Fernandez (JUF), Panamanian (PAN), Peru-Chilean (PEC), Southern Chile (SOC), and Southeastern Australian (SOA), and the cold temperate/polar provinces Antarctic (ANT) and Oregon (ORE) provinces (.docx)
Link: https://doi.org/10.21425/fob.19.174247.suppl4

Supplementary material 5

ESM table S5: Summary of the Adonis results for the distribution of zoantharians in shallow waters tested for Ocean (Atlantic or Indo-Pacific) and localities (Temp; tropical or temperate provinces). Test under reduced model with 999 permutations. Signif. codes: 0 ‘*’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1 (.xlsx)**
Link: https://doi.org/10.21425/fob.19.174247.suppl5