

Diversity and ecology of zoantharians in the Canary Islands, and their potential to proliferate in a climate change context

Doctoral Thesis
Cataixa López Batista

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**Universidad
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 Departamento de Biología
Animal, Edafología y Geología
Universidad de La Laguna

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La Laguna, diciembre 2019

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Los Drs. D. Alberto Brito Hernández Catedrático de Zoología y Dña. Sabrina Clemente Martín, Profesora Ayudante Doctor, ambos del Departamento de Biología Animal, Edafología y Geología, y el Dr. Mariano Hernández Ferrer, Catedrático de Genética del Departamento de Bioquímica, Microbiología, Biología Celular y Genética, todos de la Universidad de La Laguna

CERTIFICAN

Que la tesis doctoral titulada "*Diversity and ecology of zoantharians in the Canary Islands, and their potential to proliferate in a climate change context*" presentada por la Licenciada Dña. Cataixa López Batista, ha sido realizada bajo su dirección en los Departamentos de Biología Animal, Edafología y Geología, y de Bioquímica, Microbiología, Biología Celular y Genética de la Universidad de La Laguna.

Y para que conste a los efectos oportunos, firman la presente en San Cristóbal de La Laguna a, 07 de noviembre de 2019.

Fdo.

Dr. Alberto Brito Hernández
Dra. Sabrina Clemente Martín
Dr. Mariano Hernández Ferrer

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empujado para que al final esta tesis saliera adelante. Han sido, sin lugar a dudas, los mejores directores que una alumna pueda tener.

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A mi madre y mis abuelos,
que lo han hecho posible

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General Introduction

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Biogeographic patterns and advantages of isolation: the case of the Canary Islands

Marine conservation requires a thorough knowledge of species' biogeographic patterns, in order to develop suitable management strategies (Brito 2010). This involves the understanding of how species are distributed and their populations are connected within geographic regions. In a recent study by Spalding et al. (2007), a nested system was proposed to organize global marine biota based on the taxonomic configuration of species, which is influenced by their evolutionary history, patterns of dispersal and isolation. In this hierarchical system, composed by realms, provinces and ecoregions, the marine environment of the Macaronesian region has been separated in two ecoregions: (1) Azores, Madeira, Selvagens and the Canary Islands within the Lusitanian province of the Temperate Northern Atlantic realm (hereafter referred as the Macaronesia); (2) and an ecoregion within the West African Transition province of the Tropical Atlantic realm constituted only by Cape Verde Islands (Fig. 1), due to high levels of endemism and the tropical affinities of their biota. However, the two ecoregions share many geological and oceanographic characteristics such as small insular platforms with deep bottoms near to the coastline, oligotrophic waters with slight influence of the African upwelling and quite stable temperatures during the year (Brito 2010). Indeed, Cape Verde is usually included in the Macaronesia region when considering terrestrial ecosystems (Friedlander et al. 2017).

The biodiversity and communities of the Canary Islands are the most diverse within the Macaronesia ecoregion, mainly because of their subtropical latitude, the larger surface area, environmental heterogeneity and closer proximity to the African continent (MacArthur and Wilson 1967; Brito 2010). Moreover, during glacial and interglacial periods, in which colonization and extinction processes greatly contributed to the high degree of their endemism (Domingues 2007), Madeira and the western islands of the Canaries could have acted as a climate refuge, harbouring higher species diversity (Brito 2010). On the contrary, the Azores have the lowest diversity of species and communities in many taxa due to its northward geographical position and higher level of isolation (Carine and Schaefer 2009; Borges et al. 2010). The knowledge of these isolated biogeographic ecoregions and how species interconnect among them, is crucial for developing ecologically representative networks of protected areas, especially in coastal

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and neritic zones where the greatest levels of both biodiversity and human pressure are concentrated.

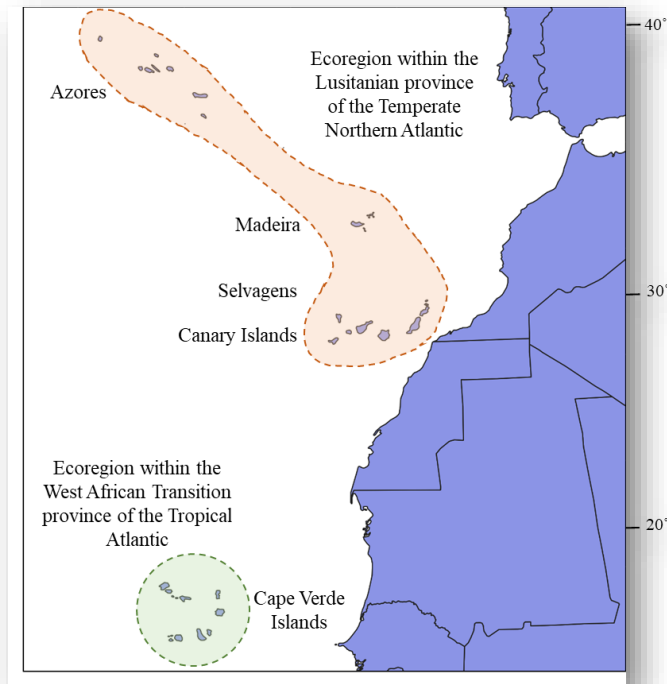


Fig. 1: Map of the archipelagos constituting each ecoregion and belonging to two different provinces within the North Atlantic Ocean (Spalding et al. 2007).

The current huge diversity of marine biota from the Canary Islands is the result of the peculiar oceanographic and climate conditions surrounding the Archipelago. The Islands are located around 28°N of latitude (Fig. 1), where the Canary Current, trade winds and the Saharian upwelling converge giving rise to a wide regional and local environmental variability (Barton et al. 1998, 2004). In this context, the eastern islands are characterized by higher nutrient concentrations and lower sea surface temperatures (SST), which can reach a difference of 2°C compared to the western islands, mainly because their proximity to the African coast and the Saharian upwelling (Braun and Molina 1984; Barton et al. 1998; Hernández-León 2007). Following this temperature

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gradient, the marine biota of Lanzarote and Fuerteventura show temperate affinities, with many species shared with the Mediterranean Sea and higher latitudes, highlighting the large biological effects of even subtle temperature differences. In this context, temperate species such as the fish *Symphodus mediterraneus* and the sea anemone *Actinia equina* are frequently found, while there are not populations of these species in the westernmost islands (Falcón 2015; Ocaña et al. 2005). On the other hand, the marine fauna and flora from El Hierro and La Palma show warmer affinities, with higher abundances of tropical species such as the Atlantic cornetfish *Aulostomus strigosus* or the seaweed *Lobophora* spp. (Sangil et al. 2011; Falcón 2015). Besides this longitudinal variability, SST in the northern coasts of the islands are slightly cooler than in the south-western sides due to the so-called “island mass effect” (Doty and Oguri 1956; Aristegui et al. 2009), except in the western coast of Lanzarote and Fuerteventura that are influenced by a local upwellings. This phenomenon is produced by the interaction among the islands with the cold Canary Current and the flow of the trade winds, especially during summer when intensity of trade winds is higher (Stramma and Siedler 1988; Aristegui et al. 1994).

Oceanic archipelagos are considered natural laboratories because their relative youth and geographical isolation lead to an overall low diversity and high endemism levels, which make ecological and evolutionary patterns easier to interpret (Losos and Ricketts 2009; Pinheiro et al. 2017). Their biota is the result of immigration, speciation and local extinction processes, being discrete units that simplify natural processes that take place in continents or the open ocean (MacArthur and Wilson 1963, 1967; Whittaker and Fernández-Palacios 2007; Whittaker et al. 2008). However, it has been suggested that islands are particularly susceptible to biological invasions. This is partially due to the smaller pool of native species, higher proportion of vacant niches typical of insular systems and the absence of specific functional groups that result in available resources and lack of natural competitors (Sax et al. 2002; Inglis et al. 2006). Such is the case of the aggressive pantropical crab *Cronius ruber* that recently arrived to the Canary Islands (González et al. 2017). Its successful colonization is probably due to its intrinsic biological characteristics (Spiridonov et al. 2014) combined with an unstructured sublittoral ecosystem (González et al. 2017). In the last decades the colonization of different organisms on islands has been accelerated by anthropogenic vectors such as shipping, oil platforms and species trade (Molnar et al. 2008; Pajuelo et al. 2016; Brito et al. 2017). In the Canaries several tropical species have been recently found related to

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marine traffic, such as the African hind *Cephalopholis taeniops* (Brito et al. 2011), the African sergeant *Abudefduf hoefleri* (Pajuelo et al. 2016) or the sun coral *Tubastraea* spp. among other stony coral species (Brito et al. 2017). Although most introductions usually fail because of the inhospitable climate in the host region, global warming is now facilitating settlement of many invasive species by means of generating the adequate environmental conditions and becoming one of the biggest threats to marine biodiversity and ecosystems' functions worldwide (Seebens et al. 2013; Thomsen et al. 2014). In this context of greater vulnerability, combined with worldwide increased anthropogenic impacts, islands biota can be currently considered under severe threat.

Human impacts and their effect on marine ecosystems

The progressive demographic development and the improvement of economic processes since the industrial revolution, have led to an unsustainable life style that is irreversibly modifying global ecosystems (Hofmann et al. 2010). Human populations have risen almost to 8 billion people during the last few decades, which implies an increase in food production, global material extractions, use of fossil fuels (Fig. 2) and the corresponding discharges of wastes and emissions (Ayres and Simonis 1994; Fischer-Kowalski and Haberl 2007; Krausmann et al. 2009). Anthropogenic greenhouse emissions are releasing high concentrations of atmospheric carbon dioxide (CO₂), methane (CH₄) and nitrous oxide (N₂O). These changes in the atmosphere chemistry lead to several direct and indirect effects in both land and oceans, causing what is called climate change. In particular, the high concentrations of atmospheric CO₂ keep part of the heat energy that would otherwise re-radiate to the atmosphere, causing a process of global warming (Fig. 3a). The increase in global temperatures of our planet is driving a significant rise in ocean levels as consequence of glaciers melt, more intense tropical storms, stratification of the water column that limit nutrient availability, among others (Behrenfeld et al. 2006) (Fig. 3b).

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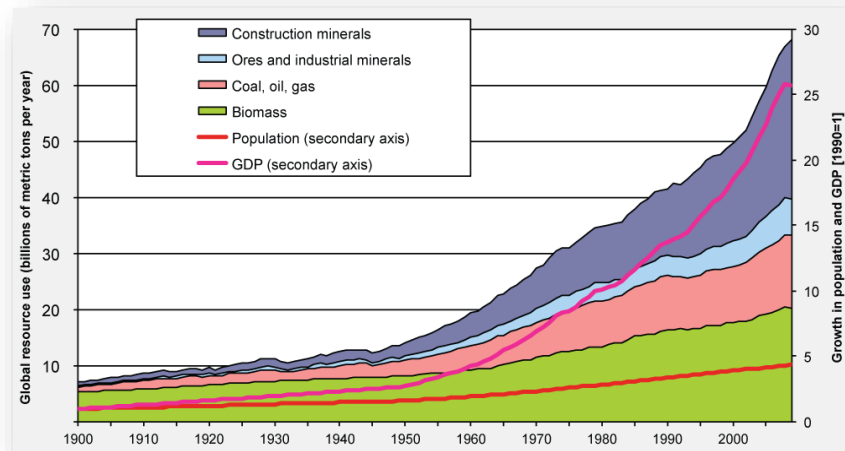


Fig. 2: Trends of global increasing resources' consumption and human population sizes. The left axis shows global resource use between 1900 and 2009 measured in billions of metric tons per year. The right axis shows the growth in population and Gross Domestic Product (GDP), as defined as a measure of the monetary value of final goods and services produced. Data source: <http://www.igbp.net/news/features/features/addictedtoresources.5.705e080613685f74edb800059.html> based on Krausmann et al. 2009 and updated using data available at <http://www.uni-klu.ac.at/socec/inhalt/3133.htm>.

Increasing ocean temperature is the most evident effect of climate change in the marine environment because it modifies species distribution, abundances and phenology according to their thermal tolerance and ability to adapt (McCarty 2001; Harley et al. 2006; Poloczanska et al. 2013). Warmer temperature regimens enable northward expansions and settlement of tropical species in new ecosystems (tropicalization process) (Walther et al. 2009; Horta and Gonçalves 2013), processes also facilitated by changes in main ocean currents (Bindoff et al. 2007). On the other hand, in subtropical and temperate regions, populations of some native species with tropical affinities have been able to proliferate within their own geographic range (meridionalization process) given the more appropriate environmental conditions. Both tropicalization and meridionalization processes can cause the displacement of native species with temperate habits (Southward et al. 1995; Hiddink and Hofstede 2008; Yapici et al. 2016), threatening their survival and persistence, especially when they already live close to their maximum limits of thermal tolerances (Hughes et al. 2003; Harley et al. 2006).

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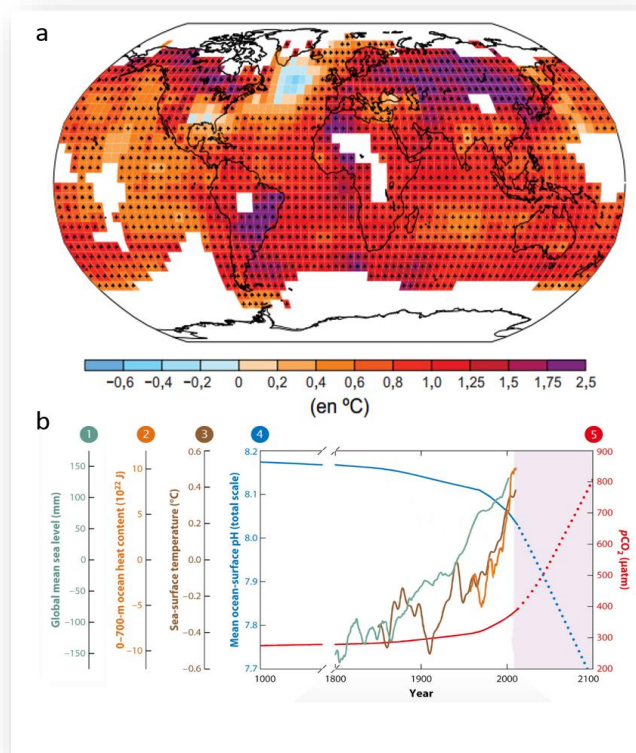


Fig. 3: a) Changes in global SST observed between years 1901-2012 (Source: <http://www.ipcc.ch/>) b) Changes in (1) global mean sea level (teal line; Jevrejeva et al. 2008), (2) ocean heat content at depths 0–700 m (orange line; Levitus et al. 2009), (3) sea-surface temperature (brown line; Rayner et al. 2006), (4) mean ocean-surface pH (blue line; Natl. Res. Council. 2010) and (5) atmospheric pCO₂ (red line; Petit et al. 1999). Light purple shaded region denotes projected changes in pH and pCO₂ consistent with the Intergovernmental Panel on Climate Change’s twenty-first-century A2 emissions scenario with rapid population growth. Source: modified from Doney et al. 2012.

Fossil fuel combustion and industrial processes are responsible of the 78% of released greenhouse emissions, currently reaching the highest concentrations recorded history (410.83 ppm) (Lüthi et al. 2008; <https://www.esrl.noaa.gov/>). These emissions have been partially mitigated by plants and soils but especially by the ocean, which has been able to absorb about 1/3 of total releases (Sabine et al. 2004; Feely et al. 2009; Hoegh-Guldberg and Bruno 2010) (Fig. 4). However, this uptake of anthropogenic CO₂

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by the ocean drives changes in sea water chemistry with important consequences to marine species and communities. CO_2 reacts with sea water causing a decrease in concentrations of carbonate ion (CO_3^{2-}), as well as an increase in dissolved inorganic carbon (DIC) and hydrogen ions (H^+) that leads to ocean acidification (Fig. 4). Global average of ocean pH has dropped approximately 0.1 units since preindustrial decades, and it is expected to further decrease 0.3 - 0.4 units depending on the climate change scenario (Caldeira and Wickett 2003; Orr et al. 2005) (Fig. 3b). Lower pH levels promote the dissolution of calcium carbonate (CaCO_3) from shells and skeletons of many marine organisms (Feely et al. 2004; Doney et al. 2012) (Fig. 4) leading them more susceptible to environmental pressures and predation (Welladsen et al. 2010). Moreover, numerous studies have revealed dramatic reductions in calcifications rates due to the lower CO_3^{2-} concentrations in several calcareous organisms, including corals, invertebrates and coralline algae (Gazeau et al. 2007; Kuffner et al. 2008). However, the effects of decreased sea water pH greatly vary among species and communities (Kayanne et al. 2005) and some taxa have even shown enhanced net calcification of their structures at high $p\text{CO}_2$ (Iglesias-Rodríguez et al. 2008; Ries et al. 2008; Wood et al. 2008).

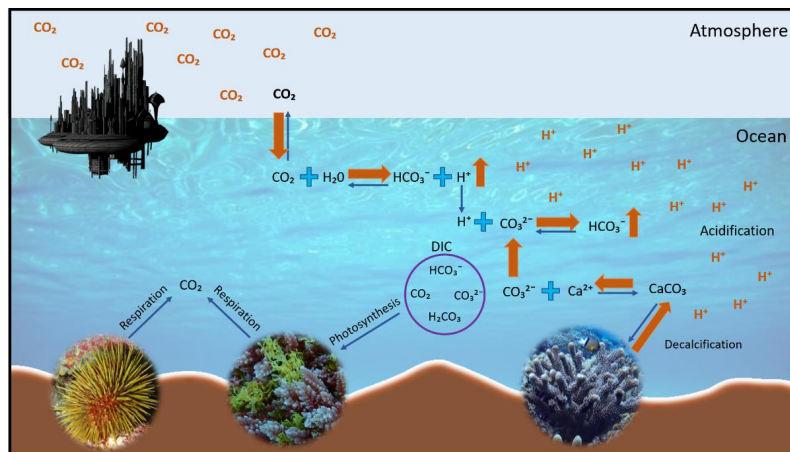


Fig. 4: Simplified diagram of the inorganic carbon cycle in marine ecosystems. Orange arrows illustrate alterations in sea water chemistry and related processes due to the increase in CO_2 derived from industrial activities. DIC: dissolved inorganic carbon.

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Not only structural modifications that threaten the persistence of complex systems such as coral reefs, but also ethological alterations are caused by ocean acidification. For example, in marine fish elevated CO₂ can cause a reduction in anti-predator behaviour, loss of learning and even altered olfactory and auditory capacities (Heuer et al. 2014; Nagelkerken and Munday 2016). In the case of photosynthetic organisms, responses to high CO₂ concentrations are even more complex and greatly depend of their ability to exploit different sources of carbon. Autotrophic organisms are able to utilize both CO₂ and additionally HCO₃⁻ by means of carbon-concentrating mechanisms (CCMs) (Fig. 4) (Leggat et al. 1999), developed as an offset against low levels of dissolved CO₂ available in sea water for photosynthesis (Badger and Price 2003; Giordano et al. 2005). These CCMs depend on the organisms involved and vary in their efficiency but, in general, low pH causes three kinds of responses: (1) high growth rates without effect in photosynthetic function, (2) increment in photosynthetic rates without increasing growth, (3) or absence of response to acidification (Brading et al. 2011; Gattuso and Hansson 2011; Kroeker et al. 2013). Because of these changes are species-specific and, taking into account that ocean acidification is no occurring in isolation to other impacts, it is expected that communities respond in different complicated ways to climate change (Ries et al. 2008; Doney et al. 2012).

Effects of climate change in the Canary Islands

Although consequences of acidification due to climate change have not been noticed yet in the marine environment of the Canary Islands, the influence of ocean warming is already patent in many ways. Sea water temperature has experienced an increase of 0.28°C per decade since 1970 (Fig. 5), being more noticeable during summer months. As a consequence, several species from tropical latitudes have been able to settle stable populations in the Archipelago, with important effects upon local ecosystems. For instance, in 2003 three colonies of the fire coral *Millepora alcicornis* were recorded for the first time in the Canary Islands (Clemente et al. 2010a). Phylogenetic analyses showed that the colonization was the result of a very recent and strong founder effect of one specimen from the Caribbean (López et al. 2015), which was able to effectively expand

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its population up to a total of 40 colonies recorded until now. *Millepora* spp. are considering reef-building corals that outcompete algae stands for space, so the expansion and spread of their populations may trigger changes in the Canarian ecosystems, potentially causing phase-shifts from algae to fire coral-dominated communities. Temperate species from oceanic islands are particularly susceptible to this kind of biota reorganization processes, due to the less favourable warming conditions, exacerbated by a greatly limited ability to displace to other regions as a consequence of a deep water barrier surrounding the islands.

Disturbed ecosystems are less resilient to any kind of impacts, especially when the organisms affected are habitat-forming species, e.g. scleractinian corals, sea grasses and mangroves (Alongi 2008; Hoegh-Guldberg and Bruno 2010; Telesca et al. 2015). In this context, some organisms have demonstrated to be more tolerant to habitat degradation, such as colonial anemones belonging to the genus *Palythoa* (Anthozoa: Zoantharia) (Sebens 1982), which are known to take advantage in areas where environmental factors make it difficult for the settlement of scleractinian corals (Cruz et al. 2015, 2016). These deviations in ecosystems' organization involve dramatic changes in marine communities, shifting to an alternative structure that usually causes loss of ecosystem functions. Ecosystems' phase-shifts from coral reefs to algae-dominated systems, or from erect algae assemblages to sea urchin barrens due to intense grazing, are widely recognized phenomena (Mumby et al. 2007; Filbee-Dexter and Scheibling 2014; Verges et al. 2014; Enochs et al. 2015) and constitute the best documented examples of ecosystems' reorganization and loss of resilience due to disturbances. The knowledge of transitions from coral reefs to zoantharian-dominated areas is scarce, despite studies recording these phase-shifts are currently increasing (Cruz et al. 2015, 2016). However, nothing is known about phase-shifts caused by zoantharian dominance in temperate or subtropical areas where macroalgae are main ecosystem engineers. The variability of oceanographic conditions surrounding the Canary Islands allows tropical, subtropical and temperate species to cohabit in a relatively small region, which combined to its geographical isolation that limit the number of factors influencing species distribution, make the Canary Islands an ideal location to study the effects of this tropicalization process.

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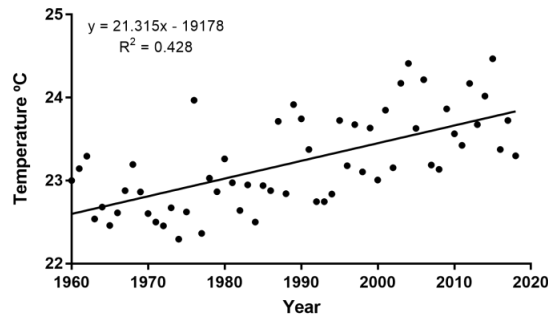


Fig. 5: Increase in ocean temperatures recorded for the summer season (mean SST from July to October) in the Canary Islands region from the year 1960 to 2019.

Characteristics of the Order Zoantharia: species in current expansion

The order Zoantharia (Cnidaria: Anthozoa) is composed by benthic cnidarians widely distributed in tropical and subtropical regions around the world, from intertidal zones to the deep sea (Ryland et al. 2000; Reimer and Sinniger 2010; Koupaei et al. 2014). It is an order of hexacorals known as colonial sea anemones due to their resemblance to actinarians (Reimer and Fujii 2017), but having two rows of tentacles around the oral disk and a single ventral siphonoglyph (Fig. 6a). Most of the species are colonial with polyps connected by a common tissue (coenenchyme) which can be: (1) well-developed with polyps ‘immersae’, (2) poorly developed and polyps ‘liberae’ or (3) polyps in an intermediate state (Pax 1910) (Fig. 6b). Based on the organisation of septa, Zoantharia are divided in two suborders, Macrocnemina and Brachycnemina (Haddon and Schackelton 1891), showing the fifth pair of septa complete and incomplete, respectively (Fig. 6). The suborder Macrocnemina is represented by several families and genera that include many epibiotic and parasite organisms, especially associated with molluscs, crustaceans, polychaetes, hydroids, sponges, black corals and octocorals (Sinniger et al. 2010; Ocaña and Brito 2018). Species belonging to this suborder are, in general, less studied due to mostly occurring in relative deep waters or cryptic environments (Reimer et al. 2017a). However, the number of studies that address Macrocnemina species is currently increasing (e.g. Montenegro et al. 2015; Kise et al. 2018; Ocaña and Brito 2018).

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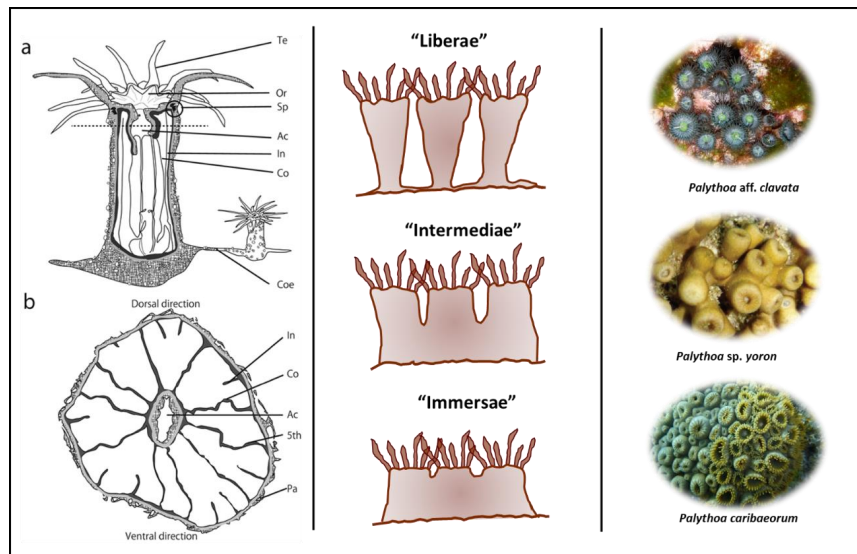


Fig. 6. Left diagrams correspond to a Zoantharia (Macrocnemina) polyp, obtained from Reimer and Fujii (2017). (a) Longitudinal and (b) cross horizontal sections of a polyp of *Microzoanthus kagerou* Fujii and Reimer (2013). The ectoderm layer is shown in mesh pattern, mesoglea in grey, and endoderm in black. The Actinopharynx (Ac), complete mesentery (Co), coenenchyme (Coe), incomplete mesentery (In), oral disc (Or), sphincter muscle (Sp), tentacle (Te), 5th dorsal mesentery (5th) are shown. Note that in Brachycnemina the fifth mesentery from the dorsal directive would be incomplete. Middle diagrams show the degree of coenenchyme development following Pax (1910) and images to the right show species as examples of each morphological type. Image of *Palythoa* sp. *yoron* taken by M. Mizuyama (Mizuyama et al. 2018).

Most common zoantharian species belong to the suborder Brachycnemina; their symbiosis with zooxanthellae limit their distribution to shallow illuminated waters facilitating their study and species identification (Reimer et al. 2006a). However, because of low levels of genetic variation for mitochondrial DNA genes in Anthozoa (Shearer et al. 2002; Neigel et al. 2007; Huang et al. 2008), often used as Barcode, and their high intraspecific plasticity that hinder species delimitation (Ryland and Lancaster 2003; Ong et al. 2013), zoantharian biodiversity is currently far from being known. For these reasons, many authors have opted for combining morphological, molecular and ecological approaches to better differentiate species (Sinniger et al. 2005; Koupaei et al. 2014; Santos et al. 2016). Currently there are recognized three Brachycnemina families: Neozoanthidae Herberts, 1972 (*Neozoanthus*); Sphenopidae Hertwig, 1882 (*Palythoa* and *Sphenopus*); and Zoanthidae Rafinesque, 1815 (*Acrozoanthus*, *Isaurus* and *Zoanthus*).

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Sphenopidae species are characterized by having sand grains, spicules and other particles in their body wall while Zoanthidae species do not have any sand incrustations (Haywick and Mueller 1997), showing the family Neozoanthidae an intermediate state with less abundant incrustations in the outer mesoglea (Herberts 1972; Reimer et al. 2011). Most of the studies about the group have been carried out in the Indo-Pacific region and the information about Brachycnemina from the Atlantic Ocean are mainly restricted to the East American coast (eg. Reimer et al. 2012a; Santos et al. 2016) and south Atlantic oceanic islands (Reimer et al. 2017a; Santos et al. 2019). Only two studies that combine phylogenetic and morphology analyses have been performed in the East North Atlantic until now, both conducted with specimens from Cape Verde Archipelago (Reimer et al. 2010; López et al. 2018).

The genera *Palythoa* and *Zoanthus* include the most studied zoantharian species since they play a relevant ecological role in many benthic ecosystems. Because of the lack of carbonate in their body walls, combining with effective asexual and sexual reproductions (Bastidas and Bones 1996; Haywick and Mueller 1997; Polak et al. 2011), populations of some species are able to rapidly increase and cover massive extensions of the substratum in short periods of time. In fact, there are specific locations where *Z. sociatus* and *Z. solanderi* cover large areas conforming extensive mats, the so-called “*Zoanthus zone*” (Karlson 1981; López et al. 2018). Regarding the genus *Palythoa*, *P. caribaeorum* from the Atlantic and its sister species from the Indo-Pacific, *P. tuberculosa*, have also been reported as mat builders covering large areas in both intertidal and subtidal zones (Sebens 1982; Acosta 2001; Irei et al. 2011). These species are important components of coral reefs systems in both the Atlantic and Indo-Pacific Oceans (Reimer et al. 2012b), but any uncontrolled increase in their population would significantly modify abundances and compositions of local communities (González-Delgado et al. 2018).

Brachycnemina species in the Canary Islands

Information about Brachycnemina species from the Canary Islands can be obtained from a total of 23 scientific documents. However, most of them are local scientific-technical reports that addressed records of colonies of the two zoantharian species catalogued as species of interest for the Canarian ecosystems, *Palythoa*

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caribaeorum and *P. canariensis* (BOE-A-2010-9772). Regarding scientific publications, a total of 12 documents provide some information about brachynectic zoantharians, but only four of them have focused in certain aspects of their ecology (González-Delgado et al. 2018) or toxicity (Villar et al. 2003; Cen-Pacheco 2014; Fraga et al. 2017).

The most extensive study about zoantharian biodiversity in the Canary Islands was carried out in 1984 by Dr. Alberto Brito, in which the author made a thorough morphological description of the species and their distributions. Although only five Brachynectina Zoantharia are currently recognized in the Archipelago: *Palythoa canariensis* Haddon & Duerden 1896, *P. caribaeorum* Duchassaing & Michelotti 1860, *P. grandis* Verrill 1900, *Isaurus tuberculatus* Gray 1828 and *Zoanthus* sp. Lamarck 1801, Brito (1984) described four new potential brachynectic species based on morphological characteristics: *P. perezdionisi*, *Z. musculosus* and an unknown *Palythoa* and *Zoanthus* species. Because the high morphological plasticity of Zoantharia species may lead to misidentification and possible synonyms, studies including phylogenetic analyses, morphological and ecological aspects are necessary to correctly identified species and their populations' status.

Aim and thesis structure

Anthropogenic impacts are causing changes in climate with profound effects in marine ecosystems, including decreases in ocean productivity, alterations in food web dynamics, homogenization of the biota and reduction in habitat-forming species. These direct and indirect effects are irreversible on ecological timescales and require immediate actions to partially mitigate the consequences, and to secure the wellness of future generations. In the current context, Zoantharia species seem to be more resistant and some species are becoming dominant in benthic tropical and subtropical ecosystems. Because of the lack of information about zoantharians from the East Atlantic, especially from the Canary Islands, the aim of this PhD thesis was to provide knowledge about some aspects of the biodiversity and ecology of these species in current expansion in subtropical algae-dominated ecosystems, as well as infer some of their population trends in a future climate

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change scenario. The present dissertation would be crucial as a baseline reference for any future assessments aiming at interpreting trajectories of change in local ecosystems in the current global change framework. In this sense, the specific aims of this PhD thesis were included within the three following chapters:

Chapter 1: Diversity of zoantharian species and their symbionts from the Macaronesian and Cape Verde ecoregions demonstrates their widespread distribution in the Atlantic Ocean.

Zoantharia Brachycnemina biodiversity around the Macaronesia and Cape Verde ecoregions is addressed by using molecular, morphological and ecological approaches. We initially identified all the specimens with the broadly used gross morphological features to delimitate Brachycnemina species. Subsequently, we checked and supported the results with phylogenetic analyses based on molecular sequences of the cytochrome oxidase subunit I (COI-mtDNA), 16S ribosomal DNA (16S-rDNA) and the internal transcribed spacer region of ribosomal DNA (ITS-rDNA). Because a specific species of symbiont can partially determine the viability of Anthozoa to adapt to environmental conditions, symbiont species inhabiting within zoantharian hosts were also addressed by phylogenetic analyses of the 23S ribosomal DNA region (23S-rDNA) and ITS-rDNA.

The results of this manuscript are published in the journal *Coral Reefs* (DOI <https://doi.org/10.1007/s00338-019-01773-0>).

Chapter 2: Distribution of zooxanthellate zoantharians in the Canary Islands: Potential indicators of ocean warming.

Relationships between brachycnemic zoantharian distributions and the east-to-west gradient of temperature that naturally exists throughout the Canarian Archipelago were addressed by extensive surveys of their populations in El Hierro, Tenerife and Lanzarote-La Graciosa islands, from warmer to colder islands, respectively. Data collection included abundances and composition of zoantharian communities in both intertidal and subtidal zones of the four islands. In order to detect differences among

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island orientations, further surveys were carried out around Tenerife, where the island mass effect is more evident, with sea surface temperature reaching lower values within the northern coast than in the south-eastern and south-western coasts.

This manuscript is in press in the journal *Estuarine, Coastal and Shelf Science* (DOI: 10.1016/j.ecss.2019.106519)

Chapter 3: Effects of low pH and high temperature on two *Palythoa* spp. and their predator-prey interactions

The results of a long-term laboratory experiment in *Palythoa* aff. *clavata* and *P. caribaeorum* are presented in order to assess potential effects of climate change over these structuring species in the near future. Colonies were kept under low pH and high temperature values forecasted for the year 2100 within the Canary Islands region (IPCC 2013). After 62 days under experimental conditions, health status of the colonies and their symbionts were evaluated, as well as changes in the vulnerability of colonies to predation by the clown crab *Platypodiella picta*. A discussion of potential ecological success of *P. aff. clavata* and *P. caribaeorum* populations in a climate change scenario is presented.

This manuscript is under review in the journal *Aquatic Conservation: Marine and Freshwater Ecosystems*

Finally, this thesis closes with a general discussion, dealing with the implications of our findings for the future dynamics of the zoantharians populations and discussing their potential to impact shallow rocky communities in the Canary Islands.

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Chapter 1

Diversity of zoantharian species and their symbionts from the Macaronesian and Cape Verde ecoregions demonstrates their widespread distribution in the Atlantic Ocean

In this chapter, zoantharians from the suborder Brachycnemina collected in the Macaronesia and Cape Verde ecoregions were studied combining morphological, molecular and ecological data, in order to comprehensively assess the species diversity of the region. Moreover, molecular analyses of their endosymbiotic zooxanthellae were also performed to provide more information on each holobiont. Our integrative results demonstrated that Brachycnemina species diversity increases as seawater temperature rises toward the tropics with a total of nine species recorded: one from waters around northern Madeira, five in the Canary Islands and seven in the southernmost Cape Verde Archipelago. All species were seen to host either Symbiodiniaceae of the genera *Symbiodinium* or *Cladocopium*. Finally, this study recorded for the first time the presence of *Palythoa grandis*, *P. aff. clavata*, *P. grandiflora*, an unknown *Zoanthus* species and *Z. pulchellus* in the East Atlantic Ocean. These results show no endemic zooxanthellate zoantharians in the East Atlantic, with all species shared with the West Atlantic.

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Introduction

Macaronesia is the name given to a group of five archipelagos in the east Atlantic Ocean; from north to south composed of the Azores, Madeira, the Selvagens Islands, the Canary Islands, and Cape Verde (Fernández-Palacios et al. 2011). Although these islands share many characteristics, the more tropical climate and biota of Cape Verde places this archipelago into its own ecoregion (Spalding et al. 2007). The Macaronesian biogeographic region thus includes the Azores, Madeira, Selvagens Islands and the Canary Islands, is within the Lusitanian province of the Temperate Northern Atlantic realm, while Cape Verde is an ecoregion within the West African Transition province of the Tropical Atlantic realm (Spalding et al. 2007). In this sense, Macaronesia is a collection of 30 oceanic islands that differ in latitude, altitude, area and distance from the Africa continent (Fernández-Palacios et al. 2011), and the group is located in the western branch of the Gulf Stream, the Canary Current (Barton et al. 1998). The biodiversity and unique marine fauna of the Macaronesian ecoregion, included within the Mediterranean biodiversity hotspot, has long been noted as one of the most important areas for conservation worldwide (Myers et al. 2000). Additionally, the Cape Verde Islands are often regarded as a 'laboratory of evolution' due to their high levels of endemism and as an important hotspot of tropical biodiversity (Roberts et al. 2002; Peters et al. 2016).

The total diversity of species of most marine taxa from the eastern Atlantic Islands is far from being known. Such is the case of the Zoantharia, an order of hexacorals (Cnidaria: Anthozoa: Hexacorallia), whose study is still somewhat limited in this region. Previous reports have noted the presence of some zoantharian species in these two ecoregions (i.e. Haddon and Duerden 1896; Brito 1984; Morri et al. 2000; Villar et al. 2003; Ocaña and Brito 2004; Ocaña et al. 2007; Monteiro et al. 2008; Reimer et al. 2010; Cen-Pacheco et al. 2014). However, only two recent studies have examined the shallow zooxanthellate zoantharians of the Cape Verde Islands utilizing molecular methods combined with morphological analyses, and these studies are somewhat limited in specimen numbers and scope (Reimer et al. 2010; López et al. 2018).

Zoantharians are commonly found in intertidal rocky platforms and from shallow waters to the deep sea. As with many other anthozoans, most shallow tropical and

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subtropical zoantharians live in symbioses with photosynthetic dinoflagellate zooxanthellae of the family Symbiodiniaceae (Burnett et al. 1995, 1997; Burnett 2002; Reimer et al. 2007a; Costa et al. 2013; LaJeunesse et al. 2018). Despite being very common benthic organisms, zoantharian species remain taxonomically problematic due to high levels of intraspecific variation, resulting from phenotypic plasticity in polyp shape, colony shape, size, and oral disk color (Burnett et al. 1995, 1997; Ryland and Lancaster 2003; Ong et al. 2013). For these reasons, much recent research has combined morphological, molecular and ecological data to more successfully identify as well as revise zoantharian taxa (e.g. Reimer et al. 2006b, c; Sinniger et al. 2008; Koupaei et al. 2014; Irei et al. 2015). Additionally, characterizing the Symbiodiniaceae of zoantharians may aid in understanding the ecology and biogeographic of holobionts (Reimer and Todd 2009). Given these difficulties, species diversity of zoantharians, particularly shallow-water *Zoanthus* and *Palythoa* spp., may be overestimated at the present time (Burnett et al. 1997; Reimer et al. 2004). Moreover, high larval dispersal abilities support this hypothesis (Ryland et al. 2000; Polak et al. 2011), despite recent examinations from insular and isolated oceanic regions that have confirmed the presence of potentially endemic or rare zoantharian species (Irei et al. 2015).

Most recent knowledge about the molecular systematics of zoantharians is from Indo-Pacific species. However, some studies have also been performed in the Atlantic Ocean, such as in the Caribbean Sea (Swain and Wulff 2007; Reimer et al. 2012a), Ascension Island (Reimer et al. 2017a), Brazil (Santos et al. 2016), the Azores (Carreiro-Silva 2017), the Canary Islands (Ocaña and Brito 2004; Ocaña et al. 2007), and the Cape Verde Islands (Reimer et al. 2010; López et al. 2018), reporting potentially unknown species and increasing the distribution ranges of many others.

This study focuses on zoantharians from the suborder Brachycnemina, including the families Sphenopidae (*Palythoa*) and Zoanthidae (*Zoanthus*, *Isaurus*). Six zooxanthellate zoantharian species have previously been recorded from the two ecoregions examined in this study, two belonging to the genus *Palythoa*: *P. caribaeorum* Duchassaing and Michelotti, 1864 (Morri and Bianchi 1995; Morri et al. 2000; Monteiro et al. 2008; Reimer et al. 2010a) and *P. canariensis* Haddon and Duerden, 1896 (Pax 1908; Brito et al. 1984; Araújo and Freitas 2003); three to *Zoanthus*: *Z. aff. pulchellus sensu* Reimer et al. (2010a), *Z. sociatus*, Ellis, 1768 and *Z. solanderi* LeSueur, 1818 *sensu*

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Karlson (1980) (López et al. 2018); and one to the genus *Isaurus*: *I. tuberculatus* Gray, 1828 (Reimer et al. 2010a). However, these previous studies generally reported on small numbers of specimens from limited locations, and no ecoregion-wide assessment of species diversity has been performed as of yet. Additionally, no molecular phylogenetic assessment of *P. canariensis* has been performed.

Because of the general lack of information about brachynermic zoantharians from the Canary Islands, our aim was to confirm the identity of specimens from this region, and to add information on additional new specimens and morphotypes recently collected from the Cape Verde and Madeira Islands. We combined morphological, ecological and molecular analyses for host species, and also examined their Symbiodiniaceae flora, in order to better understand the biogeography of the ecologically important suborder Brachynerminia.

Material and Methods

1. Study sites and initial identification

Collection of specimens was carried out between 2014 to 2016 from 20 sites in the Canarian and Cape Verde Archipelagos, as well as from Madeira Island (Fig. 1). Zoantharians of the genus *Palythoa*, *Zoanthus* and *Isaurus* were collected on intertidal rocky platforms by walking or snorkeling, and in the subtidal zone by scuba diving. We collected all different morphotypes observed. A total of 67 specimens; 34 from the Canary Islands, 31 from Cape Verde, and two from Madeira, were collected and stored in 99.5% ethanol for subsequent molecular analyses (Appendix). Specimens were given initials according to the geographic location where they were collected from (MA: Madeira, CN: Canary Islands and CV: Cape Verde), followed by a sample number (Appendix).

Preliminary morphological analyses were performed utilizing *in situ* photographs. We examined the numbers of tentacles, polyp shape and colony size, following published literature (see Reimer et al. 2012a for details).

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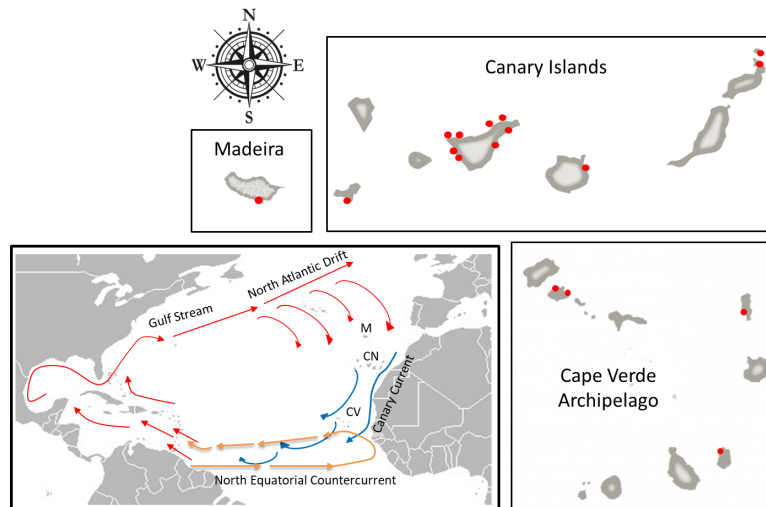


Fig. 1. Study sites around Macaronesian and Cape Verde Islands where zoantharian specimens were collected. Course of the main currents in the North Atlantic Ocean are shown.

2. Molecular analyses

2.1 DNA extraction, PCR amplification and sequencing

50 mg of tissue from polyps of each specimen were used to extract DNA following the procedures outlined in López et al. (2015). For mitochondrial DNA (mtDNA) analyses, fragments of the mitochondrial cytochrome oxidase subunit I (COI) gene and 16S ribosomal DNA (16S) were amplified by polymerase chain reaction (PCR) using the zoantharian-specific primers designed by López et al. (2018) and Sinniger et al. (2005), respectively. Additionally, the 23S ribosomal DNA region (23S) of their Symbiodiniaceae was amplified using primers designed by Santos et al. (2002) for a subset of samples that were selected taking into account location and habitat. Moreover, because of its less conservative nature, the Internal Transcribed Spacer region of ribosomal DNA (ITS-rDNA) of both zoantharians and their symbionts were amplified. The ITS-rDNA of zoantharians was amplified using primers designed by Swain (2009) and by Reimer et al. (2007b). For Symbiodiniaceae, zooxanthellae-specific primers by Rowan and Powers (1992) and Hunter et al. (1997) were used.

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PCR amplifications from template genomic DNA were performed using AmpONE Taq DNA polymerase (GeneAll Biotechnology, South Korea), following the manufacturer's instructions. PCR cycle conditions consisted of an initial step at 94 °C for 2 min, followed by 40 cycles of denaturation at 94 °C for 10 s, annealing at 52 °C for 16S, 57 °C for COI, 48 °C for ITS (zoantharians), and 53 °C for 23S and 50 °C for ITS (Symbiodiniaceae) for 20 s, extension at 72 °C for 30 s and a final extension at 72 °C for 10 min. The amplifications were carried out in a Veriti 96-well thermocycler (Applied Biosystems, USA). Aliquots of amplified products were electrophoresed on 1.7% agarose gel to verify DNA amplification. Subsequently, PCR products were enzymatically purified with ExoSAP-IT kit (GE Healthcare, Illustra) according to the manufacturer's instructions, and the samples sequenced at the Genomic Service (SEGAI) of the University of La Laguna.

2.2 Phylogenetic analyses

DNA sequences were edited and assembled using MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 (Kumar, Stecher, and Tamura 2016). Sequence alignment was performed using CLUSTAL W (Thompson et al. 1994) as implemented in MEGA7.

The best-fitting model of nucleotide substitution for each data set was selected in jModelTest (Darriba et al. 2012) according to the Bayesian Information Criterion (Schwarz 1978). Phylogenetic trees of zoantharians and their symbionts were inferred from each single gene and from the concatenated COI and 16S-rDNA sequences (zoantharians) by maximum likelihood (ML) and Bayesian inference (BI), using the previously determined models of nucleotide evolution (K80, K80+I, TrN+G for COI, 16S and ITS of zoantharians, respectively; F81 and K80+G for 23S and ITS of Symbiodiniaceae, respectively).

All phylogenetic analyses were performed through the Mobylye SNAP Workbench (Monacell and Carbone 2014). ML analyses were conducted using RAxML software (Stamatakis 2014) with 1,000 replicates of bootstrap. When concatenated sequences were

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analysed, the GTR+CAT approximation was used to accommodate heterogeneity rate among partitions. For BI we used MrBayes software (Huelsenbeck and Ronquist 2001). In this case, two independent runs were performed with defaults prior values, running 10 million generations and sampling each 100 generations. All parameters were unlinked across partitions when concatenated sequences were used. Convergence of all parameters in the two independent runs was assessed using Tracer 1.5 software (Rambaut and Drummond 2007). After removing 25% of samples as a burn-in, the remaining trees were used to obtain a majority consensus tree. Posterior probabilities higher than 0.95 were considered significant (Huelsenbeck et al. 2001). Finally, trees were visualized and edited with Figtree v1.4.3 (Rambaut 2016).

Results

1. Morphological analyses

A preliminary identification by means of morphological analyses recognized two general types of zoantharian specimens (Fig. 2). Specimens with sand in their body wall were grouped into the family Sphenopidae (*Palythoa*), while specimens with no sand encrustation were members of the family Zoanthidae (*Zoanthus*, *Isaurus*) (Ryland and Lancaster 2003; Reimer 2010).

1.1 Family Sphenopidae

Specimens of *Palythoa canariensis* were found in colonies formed by hundreds of ‘liberae’ polyps (Pax 1910), with a poorly developed coenenchyme. However, we also frequently observed smaller *P. canariensis* colonies with 10-20 polyps (Fig. 2c). Mean oral disk diameter of expanded polyps was 8.50 ± 0.18 mm (n=20) with a maximum of 11.9 mm. Number of tentacles of its brown-green polyps ranged 44-66 with a mean value of 52 ± 5 mm (n= 20 polyps examined).

P. caribaeorum had embedded ‘immersae’ polyps (Pax 1910) with a well-developed coenenchyme (Fig. 2e-f, Table 1), forming colonies composed of thousands of polyps that covered huge extensions in the subtidal zone. In this species, mean oral disk

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diameter of expanded polyps was 6.00 ± 0.08 mm (n=20) with a maximum of 9.3 mm (Table 1). All polyps had yellow-green appearance, showing fewer numbers of tentacles than *P. canariensis*, ranging 24-34 with a mean value of 29.24 ± 2 tentacles (Table 1; n=20 polyps examined).

Although specimens CN30 and CN86 - CN89 (Appendix) collected in Alcalá site (west Tenerife Island) were initially identified as *P. canariensis*, they had much larger polyps, reaching up to 21.97 mm for expanded oral disk diameter (mean value: 14 ± 0.34 mm; n=20 polyps examined) (Table 1). In addition, the overall colony sizes were also larger (maximum colony area found: 2784.23 cm² compared to 603.27 cm² for *P. canariensis*). Although the ranges of number of tentacles greatly overlapped (42-70 for *Palythoa* specimens from Alcalá and 44-66 for *P. canariensis* specimens), mean numbers were also higher in Alcalá samples than in specimens from the other collection sites (54 ± 6). Therefore, we considered these specimens as a different *Palythoa* species (Table 1).

Finally, specimens CV18, MA95 and MA96 (Appendix) were initially identified as *P. canariensis* due to their similar morphology to *P. canariensis* from the Canaries.

1.2 Family Zoanthidae

Regarding family Zoanthidae, specimen CN131 was easily identified as *Isaurus tuberculatus* due to its large polyp size with external tubercles (Fig.2a) (Muirhead and Ryland 1984; Reimer et al. 2008). All other non-sand-encrusted specimens were members of the genus *Zoanthus*.

On the other hand, three *Zoanthus* morphotypes were observed (Fig. 2). All colonies found in the intertidal zone of the Canary Islands and specimens CV15 and CV52 (Appendix) from the subtidal zone of Cape Verde were classified as morphotype 1 (MP1), having a poorly developed coenenchyme (Pax 1910) with white-grey oral disk and tentacles (Table 1; Fig. 2g-h). We found a wide range of variation within the oral disk diameter of morphotype 1, from 0.3 to 1.4 cm (Table 1). However, these *Zoanthus* specimens could not be identified to species level by morphological characteristics alone as they did not exactly fit with any described species.

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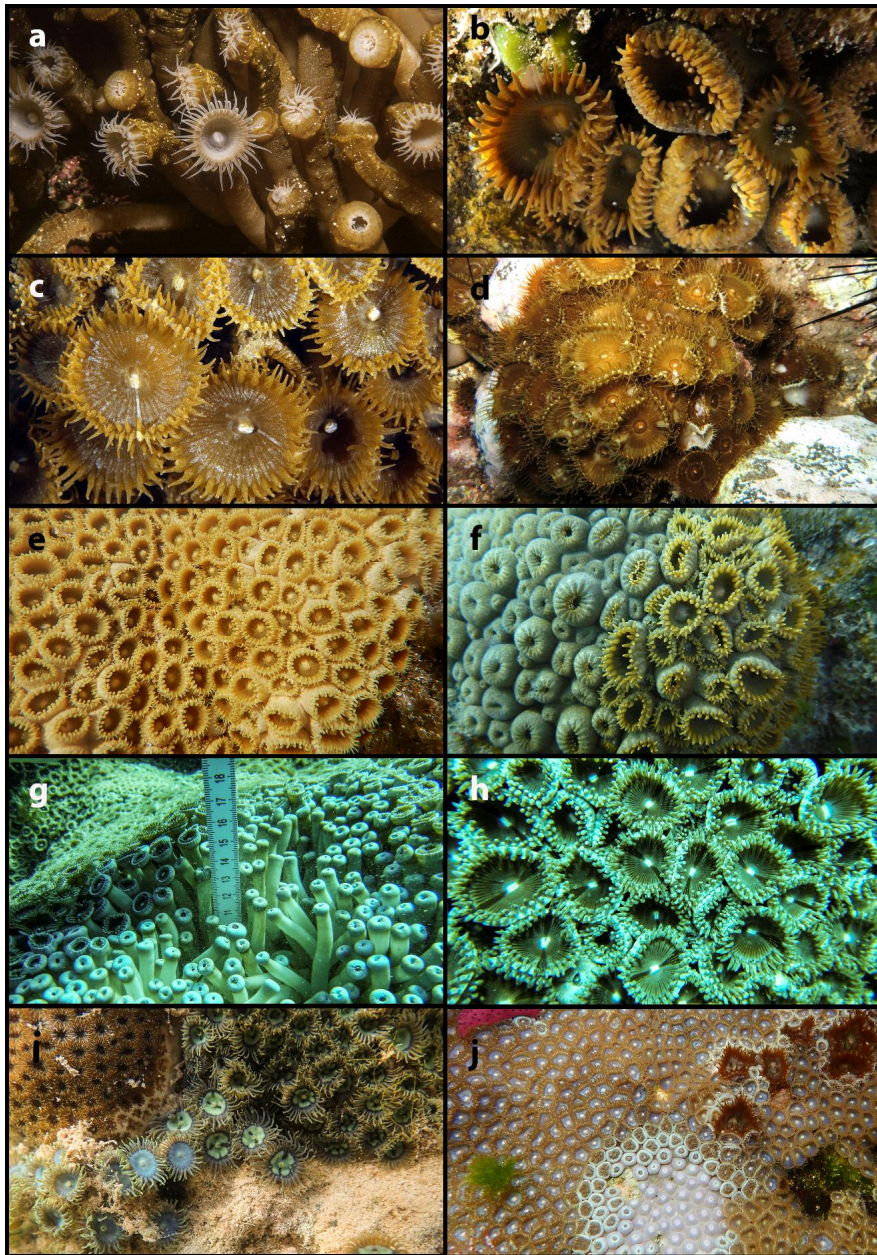


Fig. 2. Zoantharian species examined in this study. (a) *Isaurus tuberculatus*, (b) *Palythoa grandiflora*, (c) *Palythoa* aff. *clavata*, (d) *Palythoa grandis*, (e-f) *Palythoa caribaeorum*, (g-h) *Zoanthus pulchellus*, (i) *Zoanthus sociatus* and (j) *Zoanthus* aff. *pulchellus*.

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The other two morphotypes (MP2 and MP3) were found exclusively in Cape Verde and could be easily distinguished from each other by coenenchyme development. Specimens belonging to MP2 had a well-developed coenenchyme with “immersae” polyps (Pax 1910) with an external greyish coloration, brown tentacles and blue or green oral disk. These characteristics match with *Z. aff. pulchellus* previously reported from Cape Verde (Reimer et al. 2010). It was not possible to measure the oral disk diameter of MP2 as most of the polyps were partially closed, and other polyps were so close one to the other that it was very difficult to distinguish between them with the tentacles expanded (Fig. 2f).

On the other hand, the characteristics of MP3 were similar to *Z. sociatus* found in Maio Island (Cape Verde) (López et al. 2018). Polyps were ‘liberae’ in form with a poorly developed coenenchyme (Pax 1910), and included a wide variation in oral disk colors; from yellow or green fluorescent in the middle to the entire oral disk bluish (Fig. 2i). Mean oral disk diameter (0.47 ± 0.1 mm) and number of tentacles (48-62) were higher in MP3 than the values recorded in Maio (n = 20 polyps) (Table 1).

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Table 1. Distribution and morphological characteristics of the species analyzed in this study. Numbers in brackets are the number of samples analyzed of each location.

	<i>Palythoa</i> aff. <i>clavata</i>	<i>Palythoa grandiflora</i>	<i>Palythoa caribaeorum</i>	<i>Zoanithus pulchellus</i> (MP1)	<i>Zoanithus aff. pulchellus</i> (MP2)	<i>Zoanithus sociatus</i> (MP3)
Distribution	Canary Islands (13), Cape Verde (2)	Alcalá (5) (Tenerife, Canary Islands)	Canary Islands (10), Cape Verde (10)	Canary Islands (5), Cape Verde (2)	Cape Verde (9)	Cape Verde (5)
Deep (m)	Intertidal to 10 m	Intertidal to 2 m	Intertidal to 15 m	Low intertidal to 10 m	Intertidal	Intertidal to 3 m
External oral disk color	brown-green	brown-green	yellow-green	white or grayish and green	brown-green	mint green, fluorescent green, yellow
Coenenchyme development	Not well developed	Not well developed	Well-developed	Not well developed	Well-developed	Not well developed
Polyp structure	Liberae	Liberae	Immersae	Liberae	Immersae	Liberae
Number of tentacles	44-66	42-70	24-34	40-56	44-54	40-50
Oral disk diameter (mm)	8.5 ± 0.18	14 ± 0.34	6 ± 0.08	5.5 ± 0.26	-	26.5 ± 0.53
Max oral disk diameter (mm)	11.9	19.7	9.3	14	-	3.54

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2. Molecular analyses

New sequences obtained in this study were deposited in GenBank (accession numbers MH612382 - MH612581) (Appendix).

2.1. Zoantharian phylogenetics analyses

A matrix of 962 nucleotide positions was obtained after concatenation of partial fragments of COI and 16S-rDNA for 55 samples. Among the 962 nucleotide sites utilized for the phylogenetic analyses, 56 were variable and 55 were phylogenetically informative. Seventeen additional sequences from GenBank corresponding to different zoantharian species were included to perform the phylogenetic analyses. One specimen of *Parazoanthus swifitii* from the suborder Macrocnemina was added to the analyses as outgroup.

Phylogenetic trees using BI and ML approaches from concatenated mitochondrial fragments recovered the same topology (Fig. 3) with two very strongly supported clades corresponding to the families Sphenopidae (BI posterior probability/ML bootstrap % = 1.0/100%) and Zoanthidae (1.0/100%), both clearly differentiated from outgroup *Parazoanthus* (Fig. 3). Identical topologies with lower supports were obtained for each fragment separately (data not shown).

Within the family Sphenopidae four subclades were recovered. One moderately supported subclade included sequences from all specimens previously identified as *P. caribaeorum* (0.77/90%), and also included identical sequences to its Indo-Pacific sister species *P. tuberculosa* Esper, 1805 (Fig. 3). It has been shown that Zoantharia species from the Atlantic and their sister species from the Indian/Pacific Oceans have highly similar or identical mtDNA and ITS-rDNA sequences (Reimer et al. 2010, 2012a). Sequences of the unidentified *Palythoa* sp. specimens from Alcalá (CN30, CN86, CN87 and CN89) formed a subclade derived from *P. caribaeorum* and closely related to *P. grandiflora* Verril, 1900 from Brazil (0.85/83%) (Fig. 3).

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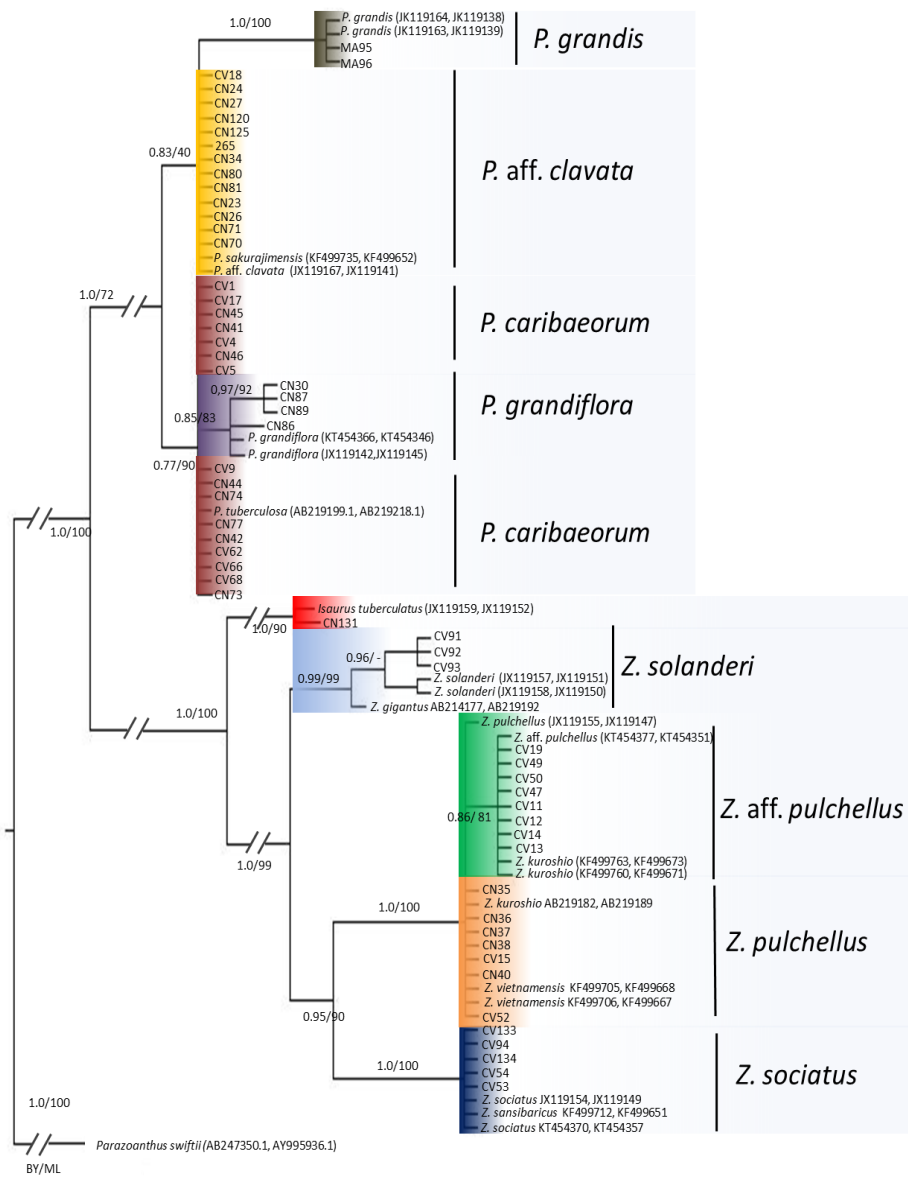


Fig. 3. Phylogenetic tree of concatenated mitochondrial COI and 16S-rDNA genes obtained by Bayesian inference (BI). Numbers above branches represent Bayesian posterior probabilities and Maximum Likelihood bootstraps, respectively. Sequences with names and GenBank Accession Number from previous studies.

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Concatenated phylogenetic analyses confirmed that specimens MA95 and MA96 from Madeira belonged to a different clade, similar to previously reported sequences of *P. grandis* Verrill, 1900 from Florida and *P. cf. grandis* from Dominica. All sequences morphologically identified as *P. canariensis* had exactly the same sequences for both COI and 16S-rDNA fragments (Fig. 3), including the specimens from the Canary and Cape Verde Islands. All of these formed a well-supported subclade (1.0/100%) including the previously reported sequences from *P. aff. clavata sensu* Reimer et al. (2012) from Florida and its sister species in the Pacific Ocean, *P. sp. 'sakurajimensis' sensu* Reimer et al. (2007b).

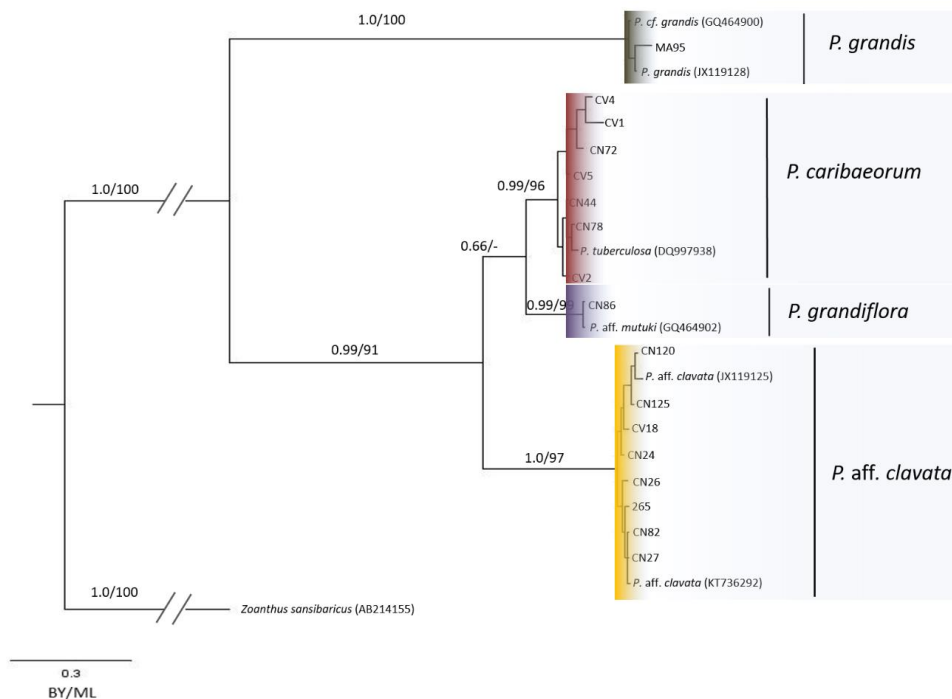


Fig. 4. Phylogenetic tree of the internal transcribed spacer of ribosomal DNA (ITS-rDNA) sequences for *Palythoa* species included in this study. Numbers above branches represent Bayesian posterior probabilities and Maximum Likelihood bootstraps, respectively. Sequences with names and GenBank Accession Number from previous studies.

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Because the bootstrap supports of *Palythoa* species clades were low, a subset of samples representing all locations and habitats was selected to amplify ITS-rDNA due to its higher levels of divergence within Brachycnemina (Reimer et al. 2007b), and its ability to more clearly delineate *Palythoa* spp. (Reimer et al. 2007c). The alignment included 24 sequences of 743 nucleotides with 242 positions variable and 223 phylogenetically informative. The relationships observed in the phylogenetic tree based on concatenated sequences of COI and 16S-rDNA to *Palythoa* spp. were confirmed with the ITS-rDNA phylogenetic analyses. Four well-supported clades were obtained and differentiated from the outgroup *Zoanthus sansibaricus* Carlgren, 1900 (Fig. 4). Specimen MA95 matched with sequences of *P. cf. grandis* and *P. grandis* from Dominica and Florida respectively (1.0/100%). All specimens identified as *P. caribaeorum* were similar to previously reported sequences of its sister species *P. tuberculosa* from Japan (0.99/96%). In the same way as in the concatenated tree, specimen CN86 from Alcalá formed a subclade derived from *P. caribaeorum* and had exactly the same sequences as *P. aff. mutuki sensu* Swain (2010) from the Caribbean (0.99/99%). All sequences belonged to *P. canariensis* formed a well-supported clade (1.0/97%) with previously reported sequences from *P. aff. clavata* from Florida.

Regarding the family Zoanthidae, the phylogenetic tree for concatenated sequences of COI and 16S-rDNA showed two clearly separated clades (Fig. 3). One well-supported clade was composed of the sequence from specimen CN131 and an *I. tuberculatus* sequence from Florida (1.0/90%), and the other clade included three well-supported subclades including the rest of the *Zoanthus* sp. sequences. One subclade included sequences of CV91, CV92 and CV93 along with sequences of *Z. solanderi* from Florida and its sister species *Z. gigantus* Reimer and Tsukahara, 2006 from Japan (0.99/99%). On the other hand, sequences from specimens CV53, CV54, CV94, CV133 and CV134 morphologically identified as MP3, clustered with sequences from *Z. sociatus* from Florida and Brazil, and together with sequences of sister species *Z. sansibaricus* from Taiwan, they formed a highly supported clade (1/100%). Finally, sequences of CV11-14, CV19, CV47, CV49 and CV50 were closely related to sequences from *Z. aff. pulchellus* from Florida and its sister species from the Pacific, *Z. kuroshio* Reimer and Ono, 2006. These sequences formed a moderately supported group (0.86/81%), which included all specimens in this study identified as MP2. Sequences from specimens

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identified as MP1 from the Canary Islands and Cape Verde were basal to the *Z. aff. pulchellus* and related sequences, and were identical to one previously reported sequence from *Z. kuroshio* from Japan and two sequences from the related species *Z. vietnamensis* Pax and Müller, 1957 from Taiwan.

2.2 Symbiodiniaceae alignments

A total of 620 nucleotide positions for chloroplast 23S rDNA gene and 717 for nuclear ITS-rDNA gene were analyzed for 41 and 24 samples of Symbiodiniaceae, respectively. Although 23S rDNA is more conservative than ITS-rDNA (16% and 30% variable sites, respectively), phylogenetic trees obtained with both ML and BI approaches showed similar topologies (Fig. 5 and 6). Symbiodiniaceae sequences generated in this study belonged to two genera, *Symbiodinium* (former *Symbiodinium* 'Clade A') and *Cladocopium* (former *Symbiodinium* 'Clade C') (Fig. 5 and 6). All zoantharian specimens

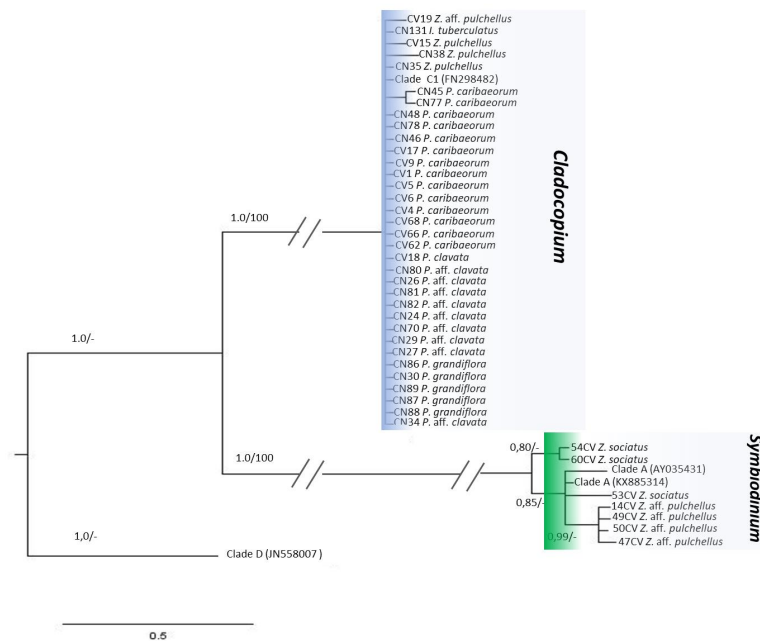


Fig. 5. Bayesian inference tree of 23S rDNA from Symbiodiniaceae hosted by zoantharian specimens analyzed in this study. Numbers above branches represent Bayesian posterior probabilities and Maximum Likelihood bootstraps, respectively. Sequences with GenBank Accession Number from previous studies.

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collected in the Canary Islands hosted *Cladocopium*, forming a well-supported clade (1.0/100%) (Fig. 5 and 6). However, specimens from Cape Verde included both *Symbiodinium* and *Cladocopium* (Fig. 5 and 6).

All *Palythoa* species from Cape Verde hosted *Cladocopium* together with specimens of *Z. pulchellus*, *Z. aff. pulchellus* and *Z. solanderi* (Fig. 5 and 6). The other well-supported clade (1/100%) was composed of sequences belonging to *Symbiodinium* and included *Z. sociatus*, *Z. solanderi* and *Z. aff. pulchellus* hosts (Fig. 5 and 6).

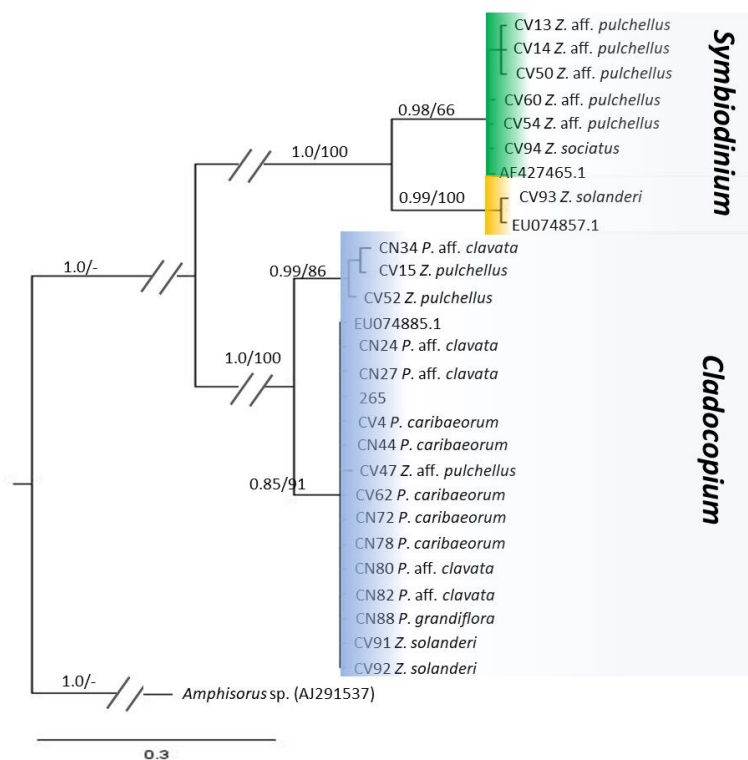


Fig. 6. Bayesian inference tree of internal transcribed spacer ribosomal DNA from Symbiodiniaceae hosted by zoantharian specimens analyzed in this study. Numbers above branches represent Bayesian posterior probabilities and Maximum Likelihood bootstraps, respectively. Sequences with GenBank Accession Number from previous studies.

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Discussion

The results of this study highlight the amphi-Atlantic distribution of Brachycnemina. A total of nine species of shallow water zoantharians were recorded within the Macaronesian and Cape Verde ecoregions, according to molecular, morphological and ecological data: four *Palythoa* spp, four *Zoanthus* spp. and one *Isaurus* sp. All specimens analyzed belonged to species commonly found in the West Atlantic, as well as in other archipelagos in the open Atlantic Ocean such as Ascension Islands (Hartog and Türkay 1991; Reimer et al. 2012a, 2017a; Santos et al. 2016). Long-distances and oceanographic patterns are important biogeographic barriers between both East and West Atlantic Ocean (Souza et al. 2017). However, these barriers may be permeable by natural or artificial ways depending on the ecology and life history of the organism involved (Nunes et al. 2011; Hoeksema et al. 2012, 2018; López et al. 2015; de Souza et al. 2017; Santos and Reimer 2018). Zoanthellae (Sphenopidae) and zoanthinae (Zoanthidae) larvae have long planktonic lifespan, up to 190 days (Polak et al. 2011), being commonly found around the Atlantic and explaining the amphi-Atlantic distribution of some Brachycnemina species whose larvae are able to cross the open ocean (Ryland et al. 2000). However, zoanthellae and zoanthinae larvae have not been found in the 20–24°C water band of the Gulf Stream that flows easterly to the Azores (Ryland et al. 2000). The presence of zooxanthellate zoantharian species has not been recorded in this archipelago, but the larvae become more frequent as temperature increases in the islands to the south, which are immersed in a descending branch of the Gulf Stream, the Canary Current (Fig. 1 and 6) (Barton et al. 1998). Supporting this theory, one Brachycnemina species was found in northern Madeira, five in the Canary Islands, and seven in southern Cape Verde Archipelago.

1. Sphenophidae species identification

All the specimens from the Canary and Cape Verde Islands identified by morphological characteristics as *P. caribaeorum* were clustered together as one group in the molecular analyses (Fig. 4). *P. caribaeorum* is an amphi-Atlantic tropical species with the Canaries as its northern distribution limit in the East Atlantic Ocean. This species inhabits habitats ranging from intertidal rocky platforms to depths of at least 17 m in

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specific locations in the Canary Islands archipelago, especially in the western islands, where the sea water temperature is warmer than in the rest of the Archipelago (Barton et al. 1998, Fig. 7). In Cape Verde, *P. caribaeorum* is frequently found dominating rocky platforms and bedrocks at 4-10 m depth, especially around Sal Island, where it dominates the subtidal zone and overgrows scleractinian coral species such as *Porites astreoides* and *Siderastrea radians* (Morri et al. 2000; Monteiro et al. 2008).

A few specimens previously catalogued as *P. canariensis* were initially misidentified due to difficulty distinguishing between this species and other ‘liberae’ *Palythoa* species in the field. Surprisingly, our molecular analyses showed the existence of three species groups within specimens initially identified as *P. canariensis*. Most specimens collected around the Canary Archipelago and specimens CV18 and 265 from Cape Verde in Reimer et al. (2010) were closely related to *P. aff. clavata* from Florida (Reimer et al. 2012a) in both phylogenetic trees, and the closest match in the taxonomic literature to this morphotype is *P. clavata* from St. Thomas (Duchassaing 1850). The original description is also identical to our morphological results with the exception of oral disk color, as our specimens were brown with green and white oral disks (Fig. 2c), while *P. clavata* was originally described as having violet or purple oral disk and tentacles (Duerden 1898). Some authors have suggested that color variation can be informative for distinguishing between species (West 1976; Swain 2009). However, intraspecific color variation is very common in both Macrocnemina (e.g. Herberts 1972) and Brachycnemina (e.g. Duerden 1898; Burnett et al. 1995, 1997; Reimer et al. 2004), and color variation occurs even within a single species, as is the case of *Zoanthus sansibaricus*, which can change color depending on depth (Kamezaki et al. 2013). The results of the present study showed that in the case of *Palythoa* species, characters such as polyp color need to be taken with care as in some cases color may depend on the color of the sand/particles available at each location (Reimer et al. 2006b, c). For instance, specimens CN74 and CN73 of *P. caribaeorum* collected from Órzola (Lanzarote, Canary Islands), where the sand is composed of white shell fragments, are completely white in coloration (Fig. 2e-f) and in contrast to the usual yellow-green color of the species. *P. canariensis* frequently inhabits intertidal rocky shores around the Canary Islands and colonies can be found in the subtidal zone down to 10 m depths in well-lit areas. If *P. aff. clavata* and *P. canariensis* are in fact the same species, this case can demonstrate how zoantharian intraspecific morphological plasticity can cause taxonomic confusion. Clearly, thorough

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systematic research on *Zoanthus* and *Palythoa* spp. are needed to clarify the potentially very large numbers of synonyms in the groups (Burnett et al. 1997; Reimer et al. 2004, 2012; Low and Reimer 2016).

In this study, two species were recorded in the Macaronesian ecoregion for the first time, *P. grandiflora* and *P. grandis* (Fig. 2b and d respectively) based on morphological and molecular analyses. Colonies of *P. grandiflora* were found in the low intertidal rocky platform up to 1 m depth in the subtidal of just one specific location, Alcalá, on the warmest side of Tenerife Island (Fig. 1; Brito 2010) and the colonies are found in an area where cropland irrigation waters flow directly into the sea. It is known that these colonies have inhabited this location since at least 1980 (A. Brito pers. com.); further research is needed to understand why this species inhabits just this one location in the region.

Our phylogenetic analyses showed that specimens MA95 and MA96 collected in Madeira belong to the *P. grandis*-*P. cf. grandis* complex. Until now *P. canariensis* (= *P. aff. clavata*), was the only zoantharian species known from the southern coast of Madeira and around Porto Santo Island, representing the northernmost record of the species (Wirtz 1995; Araújo and Freitas 2003).

2. Zoanthidae species identification

Zoanthidae specimens in this study all belonged to either the *Isaurus* or *Zoanthus*. *I. tuberculatus* is a pan-tropical species easily identifiable due to its unique tubular polyps (Muirhead and Ryland 1984). Our results confirmed its presence in the Canary Islands where this species reaches its northernmost distribution in the East Atlantic.

Although there are large amounts of phenotypic plasticity found in *Zoanthus* spp., particularly concerning oral disk color and polyp height (Fig. 2; Ong et al. 2013), the morphological characteristics used in the current study were successful in separating species. Moreover, our morphological species delimitations are in agreement with the phylogenetic results obtained with the concatenated COI and 16S rRNA sequences, as has previously been reported for other members of the genus *Zoanthus* (Sinniger et al.

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2008). Specimens CV15, CV52 as well as all *Zoanthus* specimens collected in the Canaries had COI and 16S-rDNA sequences identical to those previously reported from *Z. kuroshio* and *Z. vietnamensis* in the Pacific, two species phylogenetically closely related to each other (Reimer et al. 2013), and to *Z. pulchellus* from Florida (Reimer et al. 2012a). We identified these specimens as *Z. pulchellus* (Duerden 1898; Pax 1910) since morphological analyses fit well with the description given to this species. It has been shown that polyp height can be misleading in identifying *Zoanthus* species, as sites with low hydrodynamic energy may have colonies with taller polyps than those from the same species inhabiting sites with stronger currents and wave action (Reimer et al. 2006b; Ong et al. 2013). We also found a great variety of polyp height within *Z. pulchellus* colonies depending on the hydrodynamics of the study location. In rocky platforms of northern Tenerife (Canary Islands), characterized by high hydrodynamic levels (Yanes et al. 2006) such as the Punta del Hidalgo and Los Silos sites, colonies had polyps which reached only a few millimeters in height. However, in sheltered sites, for example inside the fishing port in La Restinga (El Hierro, Canary Islands), a large colony with polyps up to 13.5 cm in height (Fig. 2g) was found. This study recorded *Z. pulchellus* for the first time in the East Atlantic, inhabiting from intertidal rocky platforms to up to 20 m deep in the sublitoral of the western islands of the Canarian Archipelago. From its wide distribution in this study it appears that *Z. pulchellus* has the highest thermal tolerance within the zoantharian species analyzed.

Cape Verde specimens CV11-14 and CV19 from Sal and CV47, CV49 and CV50 from São Vicente matched molecularly and morphologically with *Z. aff. pulchellus* previously reported from the Archipelago (Reimer et al. 2010), and also with *Z. kuroshio* from Japan. Although phylogenetically closely related, *Z. pulchellus* and *Z. aff. pulchellus* are morphologically well distinguished from each other, similar to what has been seen with their sister species *Z. kuroshio* and *Z. vietnamensis* from the Indo-Pacific Ocean (Reimer et al. 2006b). *Z. pulchellus* has polyps free of the coenenchyme with a great variety of polyp heights and pale greenish-yellowish colors in the oral disk and tentacles (Fig. 2 g-h), while *Z. aff. pulchellus* has polyps immersed in the coenenchyme, limiting polyp height to a few mm, and a general whitish appearance with a characteristic white ring around dark brown tentacles (Fig. 2f). Therefore, and despite of their close molecular relationships, it seems appropriate to considerer *Z. aff. pulchellus* as a unique *Zoanthus* species, as in the case of their sister species *Z. kuroshio* and *Z. vietnamensis* in

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the Pacific (Reimer et al. 2006a). Our results show that the distribution range of this species reaches to Sal Island in Cape Verde, indicating that it is widely distributed around the Archipelago as it has previously been reported from Santiago and São Vicente Islands (Reimer et al. 2010). Most specimens were found in the rocky intertidal zone, including some of them completely exposed to the open air at low tides, showing the species' tolerance to desiccation.

Morphotype 3 was identified as *Z. sociatus*, previously known from the western tropical Atlantic and also reported from Maio Island, as it matched with the morphological and molecular analyses of the samples described in the 'Zoanthus zone' found in Maio Island (López et al. 2018). This species is able to co-inhabit with *Z. solanderi*, and can cover huge areas in the subtidal zone as has been previously observed in Jamaica (Karlson 1981; López et al. 2018). Specimens of *Z. sociatus* (Fig. 2i) collected in São Vicente extend the distribution of the species within the Cape Verde archipelago, where it can inhabit intertidal rocky platforms, forming small colonies.

3. Symbiodiniaceae

The zoantharian species recorded in this study were collected across several archipelagos that have great differences in sea surface temperatures (Fig. 7). From Madeira (32°N) to Cape Verde (14°N), specimens of shallow-water zoantharians were collected from tidepools, in which seawater can experience both relatively extreme low and high temperatures and salinity values (Legrand et al. 2018), and also from depths to 10 m or more, where seawater conditions are more stable. Mean sea surface temperatures in Madeira, Canary and Cape Verde Islands during winters months (March) are approximately 18°C, 20°C and 22°C, respectively, while in late summer (October), they reach 22.5°C, 24°C and 26°C, respectively, showing a significant latitudinal gradient (Fig. 7; Brito 2010). Moreover, a pronounced longitudinal temperature gradient exists due to the Saharian upwelling influence (Barton et al. 1998; Vélez et al. 2015). Therefore, there is a decreasing gradient of sea water temperature from the warmer western islands to the eastern islands of the Canaries, with temperatures 3°C lower in the eastern islands, and more tropical species inhabit the western islands (Fig. 7; Brito et al. 2005). However,

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in this study, we did not notice any specific Symbiodiniaceae shifts due to temperature as has been seen in some recent studies on zoantharians (Reimer et al. 2017b).

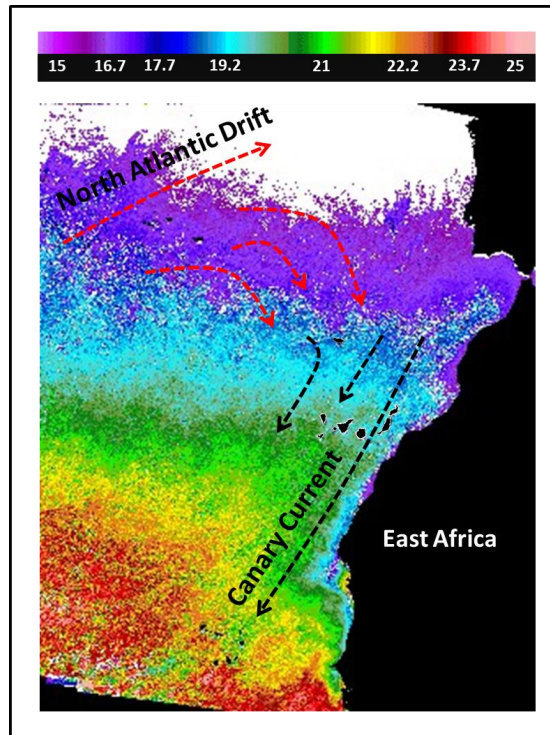


Fig. 7. Sea water temperature around Macaronesia and Cape Verde ecoregions corresponding to winter months (March average) (SAT Union System, ULPGC) and course of the Canary Current which branches south from the North Atlantic Drift and flows parallel to the east Africa coast to Senegal (red warm water current, black cool water current). Figure modified from Brito et al. (2010).

All *Palythoa* specimens examined from the Canarian and Cape Verde Archipelagos hosted *Cladocopium*, regardless of site or depth, while most *Zoanthus* specimens hosted *Symbiodinium* in Cape Verde. Many *Symbiodinium* are speculated to be adapted to high levels of UV light and usually appears in hosts that inhabit the shallowest zones in tropical areas (LaJeunesse 2002; Finney et al. 2010) as seen in our specimens from Cape Verde. The fact that all *Palythoa* spp. hosted *Cladocopium*, even in the samples collected in the intertidal zone of tropical regions of Cape Verde, may be related to the occurrence of sand and detritus incrustations in their body wall, which can

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reach the 65% of wet tissue weight (Mueller and Haywick 1995), which would give symbionts some protection against UV light. The fact that one colony of *Z. solanderi* from Maio (Cape Verde) had *Symbiodinium* (CV93) and the others *Cladocopium* (CV91 and CV92) (Fig. 5) in the same environment may be due to the fact that many host species commonly host several types of Symbiodiniaceae within the same colony, such as the case of *Millepora alcicornis* in the Caribbean (Grajales and Sanchez 2016). It is expected that host species at shallower depths exhibit a marked shift in symbiont type due to higher light intensities and radiation that could exclude some symbiont types (LaJeunesse 2002; Finney et al. 2010). However, our results are based on ITS-rDNA sequences and there it is likely that there are different species present within these specimens, based on results from higher resolution markers (LaJeunesse and Thornhill 2011) in *Palythoa* in the Pacific Ocean (Noda et al. 2017) and the Red Sea (Reimer et al. 2017b).

In conclusion, our study showed an increase in the number of Brachycnemina zoantharian species as sea water temperature rises towards the tropics; at least one species inhabits the waters of Madeira (*Palythoa grandis*), five in the Canary Islands (*P. caribaeorum*, *P. aff. clavata*, *P. grandiflora*, *I. tuberculatus*, *Zoanthus pulchellus*) and seven in the Cape Verde Archipelago (*P. caribaeorum*, *P. aff. clavata*, *Z. pulchellus*, *Z. sp.*, *Z. sociatus*, *Z. solanderi*, *I. tuberculatus*). Although acceptable for discerning most species (Sinniger et al. 2008), the standard DNA markers for Zoantharia remain problematic in detecting closely related species (Mizuyama et al. 2018). Future application of next-generation sequencing data and analytical methods (e.g. Toonen et al. 2013) may help better solve such issues, and provide higher phylogenetic support for relationships currently less well supported. Our results also confirm that in the case of the Macaronesian region and Cape Verde Islands, zoantharians host two Symbiodiniaceae genera; *Symbiodinium* and *Cladocopium*. Under global warming, formerly low ocean temperatures may no longer act as effective barriers in the distribution of shallow-water zooxanthellate zoantharians, and these already widespread species may extend their distribution ranges, causing shifts in high latitudes ecosystems (Reimer et al. 2018).

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Appendix

Identity of zoantharian specimens from the Macaronesian region and Cape Verde islands analyzed in this study, their collection information and associated GenBank Accession Numbers. n/a = not acquired.

Specimen number	Site	Island	Depth (m)	16S	COI	ITS	ZITS	23S	Identity
CV1	Baia de Murdeira	Sal	intertidal	MH612384	MH612484	MH612550	n/a	MH612477	<i>P. caribaeorum</i>
CV2	Baia de Murdeira	Sal	intertidal	n/a	n/a	MH612554	n/a	n/a	<i>P. caribaeorum</i>
CV4	Baia de Murdeira	Sal	intertidal	MH612393	MH612493	MH612549	MH612561	MH612457	<i>P. caribaeorum</i>
CV5	Baia de Murdeira	Sal	intertidal	MH612396	MH612496	MH612551	n/a	MH612458	<i>P. caribaeorum</i>
CV6	Baia de Murdeira	Sal	intertidal	n/a	n/a	n/a	n/a	MH612453	<i>P. caribaeorum</i>
CV9	Baia de Murdeira	Sal	intertidal	MH612406	MH612506	n/a	n/a	MH612442	<i>P. caribaeorum</i>
CV11	Baia de Murdeira	Sal	intertidal	MH612433	MH612533	n/a	n/a	n/a	<i>Z. aff. pulchellus</i>
CV12	Baia de Murdeira	Sal	intertidal	MH612434	MH612534	n/a	n/a	n/a	<i>Z. aff. pulchellus</i>
CV13	Baia de Murdeira	Sal	intertidal	MH612435	MH612535	n/a	MH612575	n/a	<i>Z. aff. pulchellus</i>
CV14	Baia de Murdeira	Sal	intertidal	MH612436	MH612536	n/a	MH612576	MH612465	<i>Z. aff. pulchellus</i>
CV15	Baia de Murdeira	Sal	unknown	MH612437	MH612537	n/a	MH612565	n/a	<i>Z. pulchellus</i>
CV17	Baia de Murdeira	Sal	intertidal	MH612385	MH612485	n/a	n/a	MH612480	<i>P. caribaeorum</i>
CV18	Baia de Murdeira	Sal	intertidal	MH612386	MH612486	MH612548	n/a	MH612479	<i>P. aff. clavata</i>
CV19	Baia de Murdeira	Sal	intertidal	MH612421	MH612521	n/a	n/a	MH612478	<i>Z. aff. pulchellus</i>
CN23	Punta del Hidalgo	Tenerife	intertidal	MH612407	MH612507	n/a	n/a	MH612481	<i>P. aff. clavata</i>
CN24	BuenaVista	Tenerife	intertidal	MH612387	MH612487	MH612547	n/a	MH612476	<i>P. aff. clavata</i>
CN26	Güímar	Tenerife	intertidal	MH612408	MH612508	MH612544	n/a	MH612475	<i>P. aff. clavata</i>

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CN29	Alcalá	Tenerife	intertidal	n/a	n/a	n/a	MH612473	<i>P. aff. clavata</i>
CN27	Alcalá	Tenerife	intertidal	MH612388	MH612488	MH612543	MH612559	<i>P. aff. clavata</i>
CN30	Alcalá	Tenerife	intertidal	MH612397	MH612497	n/a	MH612472	<i>P. grandiflora</i>
CN34	Los Silos	Tenerife	intertidal	MH612416	MH612516	n/a	MH612471	<i>P. aff. clavata</i>
CN35	Punta del Hidalgo	Tenerife	intertidal	MH612422	MH612522	n/a	MH612470	<i>Z. pulchellus</i>
CN36	Punta del Hidalgo	Tenerife	intertidal	MH612423	MH612523	n/a	n/a	<i>Z. pulchellus</i>
CN37	Punta del Hidalgo	Tenerife	intertidal	MH612424	MH612524	n/a	n/a	<i>Z. pulchellus</i>
CN38	Punta del Hidalgo	Tenerife	intertidal	MH612425	MH612525	n/a	MH612469	<i>Z. pulchellus</i>
CN40	Punta del Hidalgo	Tenerife	intertidal	MH612426	MH612526	n/a	n/a	<i>Z. pulchellus</i>
CN41	Playa San Juan	Tenerife	intertidal	MH612392	MH612492	n/a	n/a	<i>P. caribaeorum</i>
CN42	Playa San Juan	Tenerife	intertidal	MH612409	MH612509	n/a	n/a	<i>P. caribaeorum</i>
CN44	Playa San Juan	Tenerife	intertidal	MH612410	MH612510	MH612552	MH612468	<i>P. caribaeorum</i>
CN45	Alcalá	Tenerife	intertidal	MH612391	MH612491	n/a	MH612467	<i>P. caribaeorum</i>
CN46	Igueste	Tenerife	unknown	MH612395	MH612495	n/a	MH612466	<i>P. caribaeorum</i>
CV47	Calhau	Sao Vicente	intertidal	MH612427	MH612527	n/a	MH612563	<i>Z. aff. pulchellus</i>
CV49	Baia das Gatas	Sao Vicente	intertidal	MH612428	MH612528	n/a	MH612461	<i>Z. aff. pulchellus</i>
CV50	Baia das Gatas	Sao Vicente	intertidal	MH612429	MH612529	n/a	MH612577	<i>Z. aff. pulchellus</i>
CV52	Calhau	Sao Vicente	2 intertidal	MH612430	MH612530	n/a	MH612566	<i>Z. pulchellus</i>
CV53	Baia das Gatas	Sao Vicente	intertidal	MH612431	MH612531	n/a	MH612462	<i>Z. sociatus</i>
CV54	Baia das Gatas	Sao Vicente	intertidal	MH612432	MH612532	n/a	MH612460	<i>Z. sociatus</i>
CV60	Baia das Gatas	Sao Vicente	intertidal	n/a	n/a	n/a	MH612579	<i>Z. aff. pulchellus</i>
CV62	Garé	Sao Vicente	intertidal	MH612411	MH612511	n/a	MH612459	<i>P. caribaeorum</i>
CV66	Calhau	Sao Vicente	intertidal	MH612412	MH612512	n/a	MH612456	<i>P. caribaeorum</i>
CV68	Calhau	Sao Vicente	intertidal	MH612415	MH612515	n/a	MH612455	<i>P. caribaeorum</i>
CN70	Finca del Apio	Tenerife	intertidal	MH612413	MH612513	n/a	MH612454	<i>P. caribaeorum</i>
CN71	Finca del Apio	Tenerife	intertidal	MH612414	MH612514	n/a	n/a	<i>P. aff. clavata</i>
CN72	Orzola	Lanzarote	intertidal	n/a	n/a	MH612553	MH612568	<i>P. caribaeorum</i>

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CN73	Órzola	Lanzarote	intertidal	MH612398	MH612498	n/a	n/a	n/a	<i>P. caribaeorum</i>
CN74	Órzola	Lanzarote	intertidal	MH612399	MH612499	n/a	n/a	n/a	<i>P. caribaeorum</i>
CN77	La Restinga	El Hierro	8	MH612400	MH612500	n/a	n/a	MH612451	<i>P. caribaeorum</i>
CN78	La Restinga	El Hierro	8	n/a	n/a	MH612555	MH612569	MH612450	<i>P. caribaeorum</i>
CN80	La Laja	Gran Canaria	intertidal	MH612401	MH612501	n/a	MH612570	MH612449	<i>P. aff. clavata</i>
CN81	La Laja	Gran Canaria	intertidal	MH612402	MH612502	n/a	n/a	MH612448	<i>P. aff. clavata</i>
CN82	La Laja	Gran Canaria	intertidal	n/a	n/a	MH612541	MH612571	MH612447	<i>P. aff. clavata</i>
CN86	Alcalá	Tenerife	intertidal	MH612403	MH612503	MH612556	n/a	MH612446	<i>P. grandiflora</i>
CN87	Alcalá	Tenerife	intertidal	MH612404	MH612504	n/a	n/a	MH612445	<i>P. grandiflora</i>
CN88	Alcalá	Tenerife	intertidal	n/a	n/a	n/a	MH612572	MH612444	<i>P. grandiflora</i>
CN89	Alcalá	Tenerife	intertidal	MH612405	MH612505	n/a	n/a	MH612443	<i>P. grandiflora</i>
CV91	Porto Cais	Maio	1	MH612417	MH612517	n/a	MH612573	n/a	<i>Z. solanderi</i>
CV92	Porto Cais	Maio	1	MH612418	MH612518	n/a	MH612574	n/a	<i>Z. solanderi</i>
CV93	Porto Cais	Maio	1	MH612419	MH612519	n/a	MH612581	n/a	<i>Z. solanderi</i>
CV94	Porto Cais	Maio	1	MH612420	MH612520	n/a	MH612580	n/a	<i>Z. sociatus</i>
MA95	Caníço	Madeira	14	MH612382	MH612482	MH612557	n/a	n/a	<i>P. grandis</i>
MA96	Caníço	Madeira	14	MH612383	MH612483	n/a	n/a	n/a	<i>P. grandis</i>
CN120	Mala	Lanzarote	3	MH612389	MH612489	MH612545	n/a	n/a	<i>P. aff. clavata</i>
CN125	Caleta de Sebo	La Graciosa	intertidal	MH612390	MH612490	MH612546	n/a	n/a	<i>P. aff. clavata</i>
CN131	Los Silos	Tenerife	intertidal	MH612440	MH612540	n/a	n/a	MH612441	<i>Isaurus tuberculatus</i>
CV133	Baia das gatas	Sao Vicente	0.5	MH612438	MH612538	n/a	n/a	n/a	<i>Z. sociatus</i>
CV134	Baia das gatas	Sao Vicente	0.5	MH612439	MH612539	n/a	n/a	n/a	<i>Z. sociatus</i>
265	Tarrafal	Santiago	intertidal	MH612394	MH612494	MH612542	MH612560	n/a	<i>P. aff. clavata</i>

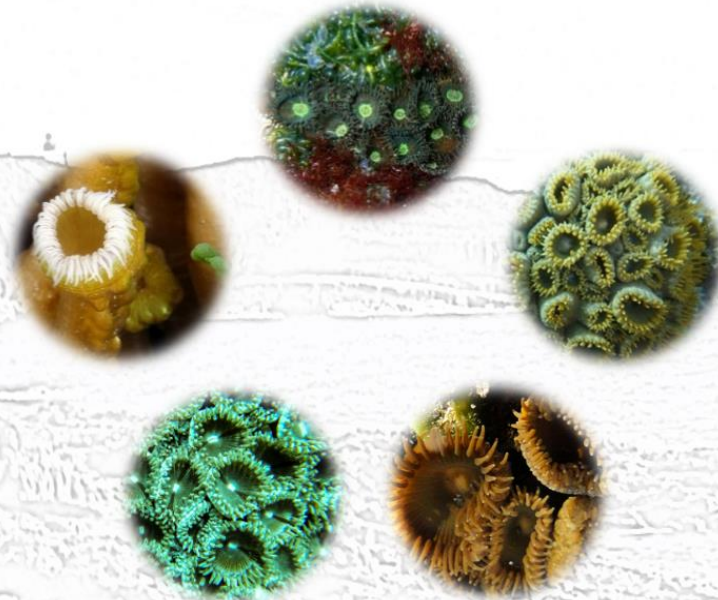
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Distribution of zooxanthellate zoantharians in the Canary Islands: Potential indicators of ocean warming

In this chapter, a baseline of the distribution and abundance of zoantharians brachycnemid populations at the Canary Islands region was established. In order to elucidate whether these species are potential bioindicators of ocean warming processes, patterns of species distribution and their relation with the gradient of temperature that naturally exist throughout the Archipelago were also evaluated. Results of this study highlighted a wide variability in distribution patterns of zoantharians along the Canary Islands, which greatly depended on the species studied. We have demonstrated that only intertidal and subtidal populations of *Palythoa* aff. *clavata* and *P. caribaeorum* respectively, followed a distribution pattern related to ranges of temperature recorded *in situ* by data loggers. The species showed extensive populations in the western islands where sea water temperature is warmer than in the eastern ones. We determined that *P.* aff. *clavata* and *P. caribaeorum* are potential indicators of ocean warming and then, effective monitoring programs should be established.

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Introduction

The Canary Archipelago consists of seven main islands distributed around 28°N of latitude, where the Saharian upwelling, the cold Canary Current and the trade winds give rise to a variety of mesoscale phenomena (Barton et al. 1998, 2004). These oceanographic and climatic characteristics generate a longitudinal sea water temperature (SST) gradient that can exceed 3°C among the coldest easternmost island (Lanzarote) and the warmest westernmost islands (El Hierro-La Palma islands) (Braun and Molina 1984; Barton et al. 1998) (Fig. 1a). In this context, the marine biota of the eastern islands of Lanzarote and Fuerteventura show many species of temperate affinities shared with the Mediterranean region and higher latitudes, while in the western islands of El Hierro and La Palma there are more elements with tropical affinities (Sangil et al. 2011; Falcón et al. 2015). Moreover, the disturbance of the oceanic flow by an island, called “island mass effect” (Doty and Oguri 1956; Hernández-León et al. 2007), leaves wakes of warm sea water in the leeward sides of the islands, especially during summer, when the intensity of trade winds is higher (Van Camp and Nykjaer 1988; Aristegui et al. 1994). Because of this island mass effect, eddies or vortices are also formed in the lee side depending on the shape of the island and the fluid speed that pass through it (Simpson and Tett 1986; Aristegui et al. 1994). This mesoscale variability combined with the influence of upwelling filaments from the African Coast, result in a complex pattern of regional oceanographic variability (Barton et al. 1998; Aristegui et al. 2009), with lower SST in the northern and north-eastern coasts than in the western coasts at each island (Fig. 1a). This spatial heterogeneity is more evident in the highest islands (Tenerife, La Palma and Gran Canaria), which show clearly differentiated coastal orientations in terms of temperature regimens related to main current and wind directions (Fig. 1a). Because of these complex environmental conditions, marine biota of the Canary Islands is characterized by a mixture of tropical, subtropical and temperate species distributed in a relative small region (Falcón et al. 1996; Brito and Ocaña 2004; Brito 2010; Sangil et al. 2011; González et al. 2016).

In the last decades the biota of the Canary Islands has been modified by the effects of ocean warming, especially in the warmer westernmost islands, where several tropical

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species are now frequently found (Brito et al. 2005; Falcón et al. 2015; González et al. 2017). Most of them appear sporadically, but some already have stable populations within the Archipelago, e.g. the ocean triggerfish *Canthidermis sufflamen*, the goldspot goby *Gnatholepis thompsoni* or the gorean blenny *Parablennius goreensis* (Brito et al. 2005; Falcón et al. 2015; Brito et al. 2017). Not only vagile but also sessile organisms have been able to settle down in this new environment, such as the fire coral *Millepora alcicornis* (Clemente et al. 2011) or the algae *Penicillus capitatus* (Sangil et al. 2010). These recent colonizations are closely associated with the increase in ocean and air temperatures (+0.28 °C and +0.09 °C per decade, respectively) detected in this region during the last few decades (Martín-Esquivel et al. 2012; Vélez et al. 2015) (Fig. 1b). These changing conditions facilitate tropical species to establish new populations towards highest latitudes (tropicalization process) (Perry et al. 2005; Brito et al. 2005; Bañón and Mucientes 2009; e Costa et al. 2014), while native species with warm-water affinities are able to expand their populations within their native biogeographic region (meridionalization process) (Sangil et al. 2012; Brito et al. 2014; Yapici et al. 2016). The impact of this biota reorganization has been widely recognized, resulting in modified patterns of distributions of many species around the world. It causes changes in biodiversity and/or in ecological processes (Done 1999), modifying local ecosystems (Bellwood et al. 2004; Caralt and Cebrián 2013; Vergés et al. 2014; Piazzini et al. 2016). Reef building coral species are among the most affected organisms by the increase in ocean temperature, mainly because of their sensitive association with symbiotic dinoflagellates of the family Symbiodiniaceae, which are greatly affected by changes in temperature (Muscatine 1990). This association might break under several stressful conditions. For instance, when sea water heats up, corals expel their zooxanthellae (bleaching), losing their main source of food (Baker et al. 2008; Davy et al. 2012).

Zoantharia of the order Brachycnemina (Anthozoa, Hexacorallia) are a group of benthic cnidarian found in most marine environments in tropical and subtropical areas around the world (Ryland and Lancaster 2003). Currently, five Brachycnemina zooxanthellate species are known in the Canary Islands: *Palythoa* aff. *clavata*, *P. caribaeorum* and *P. grandiflora* belonging to the family Sphenopidae, and *Zoanthus pulchellus* and *Isaurus tuberculatus* to the family Zoanthidae (López et al. 2019 – chapter 1). All of them are amphi-atlantic tropical and subtropical species that have in the Canary Islands their northern limit of distribution within the eastern Atlantic Ocean, with the

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exception of two isolated colonies of *P. aff. clavata* recorded further north at one site in the south of Madeira Island (Araújo and Freitas 2003; López et al. 2019 – chapter 1). *P. aff. clavata* and *P. caribaeorum* are currently catalogued as species of special interest in Canarian ecosystems (BOE-A-2010-9772), as they were known to only show discrete populations around the intertidal and subtidal zone of the Archipelago (Arechavaleta 2009). In fact, despite zoantharians are common worldwide sessile organisms, few studies have paid attention to the group in the Canarian Archipelago, and some of them focused only in their toxins (Villar et al. 2003; Cen-Pacheco et al. 2014; Fraga et al. 2017) or taxonomy (López et al. 2019 – chapter 1), but ecological studies are still scarce.

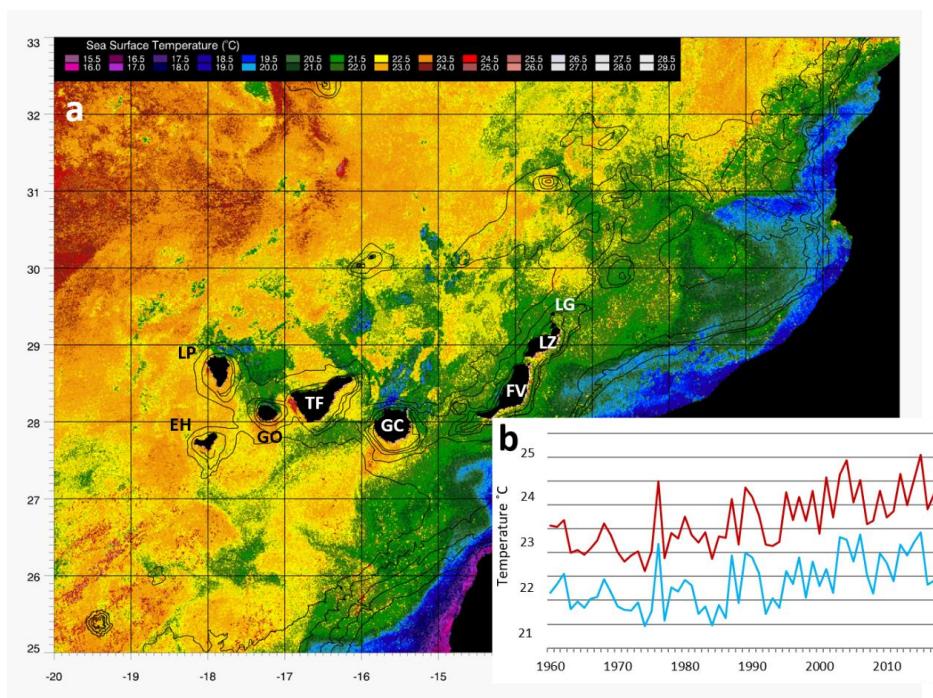


Fig. 1. Image generated by satellites AVHRR/NOAA of sea water temperature (SST) around the Canary Islands region in summer time, showing the east-west gradient due to the influence of the Saharian upwelling (a). Differences in SST originated by the Canary Current and trade winds are also noticed, especially in westerns islands which are the highest of the Archipelago (a). Long-term trend of mean SST in summer months from 1960 to 2018 at El Hierro (red line) and La Graciosa (blue line) islands (b) (Kalnay et al. 1996). La Palma (LP), El Hierro (EH), La Gomera (GO), Tenerife (TF), Gran Canaria (GC), Fuerteventura (FV), Lanzarote (LZ) and La Graciosa (LG).

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Recent studies have shown how some zoantharian species can cover extensive areas and cause changes in local biota composition due to their substrate dominance (Cruz et al. 2015; González et al. 2018), even replacing hard coral ecosystems (Cruz et al. 2016a, b). Because of their warm water affinities, it would be expected that the actual increase in SST favour the expansion of zooxanthellate *Brachygnemina* species, especially at the periphery of their distribution ranges (Durante et al. 2018; Reimer et al. 2018). In this context, the purpose of this study was to create a baseline of the distribution and abundance of zooxanthellate zoantharian populations at their northern limit of distribution, and to assess their relation with the temperature gradient that exists within the Canarian Archipelago. Our aim was to determine whether populations of these species are appropriate bioindicators of ocean warming and, therefore, monitoring programs have to be considered. We hypothesized that, if these species respond to changes in ocean temperature, zoantharian populations should be more abundant in the western island of El Hierro, where SST is the warmest within the Archipelago, than in Lanzarote which is closer to the Saharian upwelling (Fig. 1a). We also evaluated populations of *P. aff. clavata* and *P. caribaeorum* since they are considered by law species of special interest in Canarian ecosystems and therefore periodically monitoring of population status and progression is highly recommended.

Material and Methods

1. Environmental data

Temperature data loggers (HOBO Water Temp Pro v1) were deployed in September 2016 in two intertidal and subtidal sites of the three surveyed islands (Lanzarote, Tenerife and El Hierro) (Fig. 2). Subtidal loggers were placed among 1 to 7 meter depth (Fig. 2), in order to *in situ* register the east-to-west temperature gradient that exists within the Archipelago in coastal waters. In addition, intertidal HOBO loggers were deployed in order to record data in intertidal sites where large zoantharian populations were found, giving accurate information about oscillations in temperature experienced by the species during tidal cycles. All tide pools chosen to deploy loggers were similar in size and depth and avoided loggers' exposition to air during low tide. In all cases temperature data was recorded at hourly intervals during 12 months.

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2. Distribution of zooxanthellate zoantharians in the intertidal zone

In order to detect any regional variability in zooxanthellate zoantharian populations, sampling surveys were conducted during 2015 and 2016 at the Canary Islands (Fig. 2), covering intertidal rocky platforms where zoantharian species could inhabit. Because Zoantharia populations are not tentatively very abundant in the Archipelago, these surveys consisted in exhaustively searching through the entire study area during monthly spring low tides by at least two people, in order to detect every single colony that could indicate an expansion of populations. Each location was visited as many times as needed to cover the whole intertidal platform, recording the number of colonies of all zooxanthellate species observed. Due to the complexity of the substrate that makes difficult to delimitate clones in the field, we recognized colonies as all clustered polyps connected by the same coenenchyma, including polyps within a 5 cm radius (Irei et al. 2011). Species were identified by means of morphological characteristics and, when necessary, genetic analyses were performed (López et al. 2019 – chapter 1).

The effect of the east-to-west ocean temperature gradient in zoantharian populations was evaluated by means of comparing the number of colonies found in the westernmost (El Hierro) and easternmost islands (Lanzarote and La Graciosa) of the Archipelago (Fig. 2). In order to do so, six intertidal rocky platforms of El Hierro were sampled as locations with warm conditions, and six sites and one site of Lanzarote and La Graciosa, respectively, were sampled as temperate conditions (Fig. 2). Given that the complex oceanographic conditions of the Archipelago lead to differences in SST among orientations of the highest islands -northern, south-western and south-eastern coasts-, exhaustive surveys were conducted and 20 sites around Tenerife island were visited.

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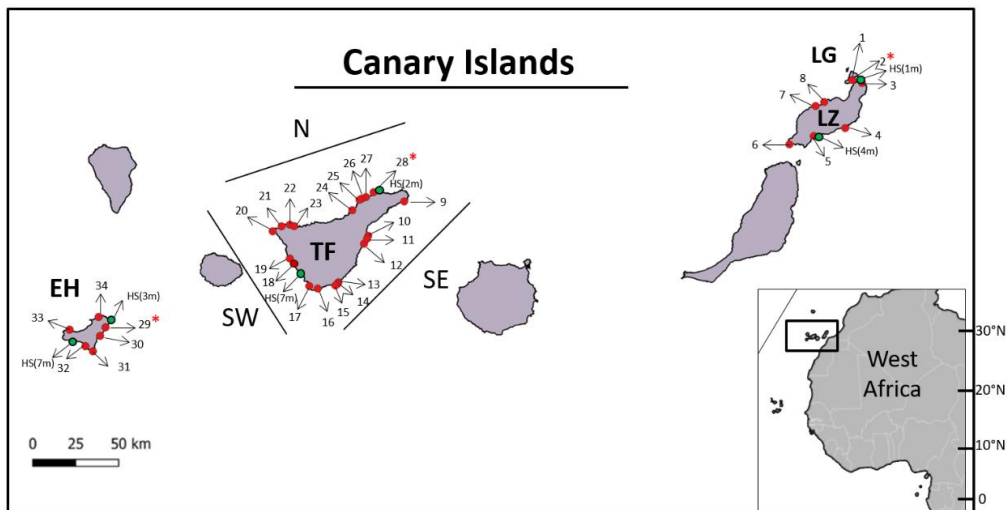


Fig. 2. Sampling sites throughout the Canary Islands visited during the course of the study. In La Graciosa island (LG): Caleta de Sebo north (1) and Caleta de Sebo south (2) sites. In Lanzarote island (LZ): Órzola (3), Arrecife (4), Playa Quemada (5), Faro Pechiguera (6), Tenesar (7) and La Santa (8) sites. In Tenerife island (TF): Iguete de San Andrés (9), El Socorro (10), Güímar (11), La Caleta-Punta Prieta (12), El Médano (13), Montaña Roja (14), La Tejita (15), Las Galletas (16), El Palm-Mar (17), Alcalá (18), Playa Blanca (19), Teno (20), Buena Vista (21), Los Silos (22), La Caleta de Interián (23), El Sauzal (24), Finca del Apio (25), La Barranquera (26), Jover (27) and La Punta del Hidalgo (28) sites. In El Hierro island (EH): Timijiraque (29), Roque de Bonanza (30), La Restinga (31), Tacorón (32), Arenas Blancas (33) and Pozo de las Calcosas (34). *Locations where intertidal temperature data loggers (HOBO Water Temp Pro v1) were deployed. Green circles show locations where subtidal temperature HOB0 (HS) loggers were deployed and their depth is also included.

3. Distribution of zooxanthellate zoantharians in the subtidal zone

Subtidal surveys were conducted in six sites, up to 20 m depth, by means of scuba diving in El Hierro, Tenerife and Lanzarote. Whenever zoantharian species were found, their depth range was also recorded. Because some zoantharians are able to cover huge extensions in the subtidal zone, size frequency distributions of the species were also recorded. In order to do so, photographs with a metric scale were taken and used to count the number of polyps using Image J-software and assign each colony to one of the following 5 size categories: < 50 polyps (XS), 50-100 polyps (S), 100-500 polyps (M), 500-1000 polyps (L) and > 1000 polyps (XL). Due to inherent characteristics of *P. caribaeorum* growth, with polyps embedded in a well-developed coenenchyma, size

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classes were defined according to the colony coverage area, which was estimated *in situ* with the aid of a ruler in the following categories: < 0.5 m² (XS), 0.5-1 m² (S), 1-2 m² (M), 2-4 m² (L) and > 4 m² (XL).

4. Statistical Analyses

Geographic Information System QGIS open source software (QGIS Development Team 2018) was used to grid the coastline of the islands into 500 x 500 m. The biological information recorded during surveys was referred to the corresponding grid and mapped as points. Likewise, all available information about zoantharian populations around the Canary Islands, including references as well as presence sites where species have been sighted were also mapped using the same software but not incorporated in further statistical analyses.

4.1 Environmental data

In order to assess whether there are differences in SST among the studied islands, data collected by the HOBO loggers in the subtidal habitat were analysed by one-way permutational ANOVAs (Anderson 2001) with the factor “Island” treated as fixed factor with 2 levels (El Hierro and Lanzarote). Data from Tenerife was excluded from analyses given that the two HOBO located in the subtidal were lost and information of just a 7-month period from the data logger located in the south-western coast could be retrieved. The daily mean SST during the year, summer and winter SST average and higher and lower records of summer months (from July to October) and of winter months (from January to April) were specifically compared. Because SST of the intertidal zone greatly depends on air and rocky platform conditions, only the data collected by subtidal loggers were used to perform the statistical analyses. We used Euclidean distances and all *p*-values were obtained using 9999 permutations of the appropriate exchangeable units, considering significant all *p*-values <0.05.

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4.2. Distribution of zooxanthellate zoantharians in the intertidal zone

Differences in zoantharian assemblages recorded at each 500 x 500 m grid sampled within the different surveyed islands, in relation to the east to west ocean temperature gradient of the Archipelago, was assessed by means of a distance-based permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001). Moreover, species-specific analyses were performed separately to contrast species abundances with distance-based permutational ANOVAs (Anderson 2001). Analyses were conducted using Euclidean distances for both PERMANOVA and ANOVAs, with log (X+1) transformed and raw data respectively. We used one-way designs in which factor “Island” was treated as a fixed factor (4 levels: El Hierro, Tenerife, Lanzarote and La Graciosa islands).

Patterns of distribution of zoantharian species at the different coastal orientations -northern, south-western and south-eastern coasts- were assessed using comparisons of the number of colonies of all species recorded in Tenerife (Fig. 2) by means of PERMANOVA and ANOVAs procedures, as previously mentioned above. In this case we used one-way designs in which “Orientation” was treated as a fixed factor with 3 levels (north, south-west and south-east).

In all previous analyses, the size of intertidal rocky platforms surveyed was included as a covariable. The area of each intertidal platform (m²) was calculated using aerial ortho-photographs of study sites during low tide and an image processing software (Image J). All *p*-values were obtained using 9999 permutations of the appropriate exchangeable units and significant terms were examined individually using appropriate *a posteriori* pairwise comparisons, also conducted by permutations (Anderson 2001). Hypothesis-driven test were accepted as significant with *p*-values ≤0.05 and as marginally significant with *p*-values between 0.05-0.09. Principal coordinates analyses (PCO) were performed to visualize the basic community structure and groups obtained for the zoantharian distributions along the Archipelago, as well as at different coastal orientations around Tenerife island. The statistical software PRIMER 7 & PERMANOVA+ (www.primers-e.com) was used to conduct all analyses of variance.

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4. 3 Distribution of zooxanthellate zoantharians in the subtidal zone

Species-specific analyses for the most abundant species found in the subtidal zone, i.e. *Palythoa* aff. *clavata*, *P. caribaeorum* and *Zoanthus pulchellus*, were conducted in order to compare the number of colonies of each species found at the different islands surveyed within the temperature gradient of the Archipelago. One-way distance-based permutational ANOVAs (Anderson 2001) with factor “Island” treated as a fixed factor (3 levels: El Hierro, Tenerife and Lanzarote) were conducted. We used Euclidean distances and all *p*-values were obtained using 9999 permutations of the appropriate exchangeable units, considering significant all *p*-values <0.05. Significant terms were further examined using *a posteriori* pairwise comparisons, also conducted by permutations (Anderson 2001).

Size frequency distribution data of *P. caribaeorum* colonies was compared among Islands by means of a Kolmogorov-Smirnov test using SPSS software (version 25). Numbers of recorded colonies of *P. aff. clavata* and *Zoanthus pulchellus* were not enough to performed size distribution analyses.

Results

1. Environmental data

Data collected by the three temperature data loggers recovered, out of the six deployed at first in intertidal platforms, was very heterogeneous. In Lanzarote island the data logger was deployed in Órzola site (site 3 in Fig. 2) (Fig. 3a), in a tide pool completely covered by *Palythoa caribaeorum* with few discrete colonies of *P. aff. clavata*. The range of temperature recorded varied between 14.098 - 30.722°C, constituting the lowest mean temperature (20.36 ±2.28°C) recorded in the studied intertidal habitats of the Canary Islands (Fig. 3a). In Tenerife, the HOBO logger was placed in the northern site of Punta del Hidalgo (site 28 in Fig. 2) in an area where *Zoanthus pulchellus* has one of its largest populations known for the Archipelago, cohabiting with several colonies of *P. aff. clavata*. This location experienced the most extreme ranges of temperature variation, recording the minimum and the maximum

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values of the whole archipelago (11.832 - 31.077°C). However, the mean temperature during the whole study period (21.15 ±2.24°C) was slightly higher than that recorded in Lanzarote (Fig. 3a). In El Hierro, the HOBO data logger was deployed in the south-eastern coast of Timijiraque (site 29 in Fig. 2) where a large population of *P. aff. clavata* was found. In this site the range of temperature variation recorded during the study period was the shortest (15.557 - 29.715°C) (Fig. 3a), but the highest mean temperatures were recorded (21.23 ±1.77°C) in comparison with the other two islands.

Regarding temperature data recorded in the subtidal habitat, the loggers deployed at each studied island clearly showed the east-to-west temperature gradient of the Canarian Archipelago. The warmest mean SST was recorded in El Hierro (21.79°C ±0.06 °C), with an annual range of variation from 18.937 to 24.388°C in La Caleta (north site in El Hierro, Fig. 2) and from 18.771–25.501°C in Los Mozos site (south-eastern site in El Hierro, Fig. 2) (Fig. 3b). In contrast, the coldest mean SST was recorded in Lanzarote (20.80°C ±0.09 °C) with a range of temperature variation from 17.534 – 24.436°C and from 17.201- 25.065 °C in Playa Quemada and Órzola, respectively (north and south sites in Lanzarote in Fig. 2, respectively) (Fig. 3b). In fact, there were statistical differences in the daily average throughout the year (F= 119.58; p=0.001), the summer and winter months' average (F= 210.1; p=0.015 and F= 177.93; p=0.001, respectively) and the minimum SST record during the winter (F= 177.93; p=0.001) between the two extremes of the archipelago, El Hierro and Lanzarote. The higher records of temperature registered during summer months revealed not significant differences between the two islands (F= 3.17; p(MC)=0.101). Despite lack of year-around SST data in Tenerife, the information gathered was enough to highlight the importance of the island mass effect in south-western coast of Tenerife, as temperature started to increase in this location even above levels recorded within El Hierro (Fig. 3b), oscillating from 23.136°C in November 2016 to 18.628 °C in June 2017 (Fig. 3b).

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Fig. 3. Oscillations of sea water temperature (°C) recorded during an annual cycle by HOBO data loggers deployed in a) intertidal tidepools inhabited by zoantharians and b) subtidal locations of El Hierro, Tenerife and Lanzarote islands.

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2. Distribution of zooxanthellate zoantharians in the intertidal zone

A total of 1534 colonies of Zoantharia, Suborder Brachycnemina, were recorded within the sixty-five grids of 500 x 500 meters visited in 34 localities throughout the Canary Islands, comprising a surveyed area of $\approx 616,000 \text{ m}^2$. *Palythoa* aff. *clavata* was the dominant species with 1109 colonies observed around the Archipelago (Fig. 9).

2.1 Zoantharia populations across the Canarian Archipelago

Results of the PERMANOVA analysing the abundance and composition of zoantharian populations within the Canarian Archipelago showed a significant interaction of factor "Island" and covariable "Platform size" (Table 1). *A posteriori* pairwise analyses only revealed significant differences in species distribution between Lanzarote and the rest of the surveyed islands (Table 1). La Graciosa, Tenerife and El Hierro showed similar abundances and compositions of species, with no significant differences detected among these islands (Table 1). The PCO, explaining 82% of total data variability, showed greater dispersion of data corresponding to Tenerife and the highest densities of *Z. pulchellus* recorded in sites within this Island (Fig. 4). Data from Lanzarote and El Hierro were less dispersed, with populations of *P. aff. clavata* more frequently found in surveys conducted in the latter island (Fig. 4). La Graciosa showed the highest abundances of *P. aff. clavata*, along with a few sites of Tenerife Island (Fig. 4).

Table 1. Results of the one-way PERMANOVA analysing the variation in the number of colonies of zooxanthellate zoantharians in different Islands of the Canarian Archipelago (LG: La Graciosa, LZ: Lanzarote, TF: Tenerife and EH: El Hierro). Intertidal platforms size (m^2) was included as a covariable in the analysis. Results of pairwise tests examining the significant factor 'Island' are shown. * $p < 0.05$ and ** $p < 0.01$.

PERMANOVA						Pairwise test		
Source	df	SS	MS	Pseudo-F	p	Groups	t	p (perm)
Platform size	1	7.80	7.18	2.40	0.098	LG vs. LZ	3.19	0.001**
Island	3	40.97	13.66	4.57	0.002**	LG vs. TF	0.79	0.468
Ps x Island	3	27.35	9.12	3.05	0.021*	LG vs. EH	0.58	0.563
Res	58	173.47	299			LZ vs. TF	3.56	0.001**
Total	65	248.98				LZ vs. EH	2.61	0.006**
						TF vs. EH	0.27	0.983

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P. aff. clavata, *P. caribaeorum* and *Z. pulchellus* were the most abundant species recorded along the Archipelago with densities that varied between islands (Fig. 5). Species-specific analyses showed a significant effect of the interaction of factor 'Island' and covariable "Platform size" for *P. aff. clavata* (Table 2). Significantly higher densities of this species were found in one location of La Graciosa in comparison with the other studied islands, while abundances recorded within Lanzarote were significantly lower than in the rest of islands (Table 2, Fig. 5). Differences in the number of colonies of *P. aff. clavata* were not significant between Tenerife and El Hierro, with intermediate species abundances (Table 2, Fig. 5). In the case of abundances of *P. caribaeorum*, there was a significant interaction of the size of the intertidal platform with factor 'Island' (Table 2). Large population abundances of the species were recorded in the largest intertidal rocky platform of Lanzarote, in Órzola site (site 3 in Fig. 2) (Fig. 5 and 9).

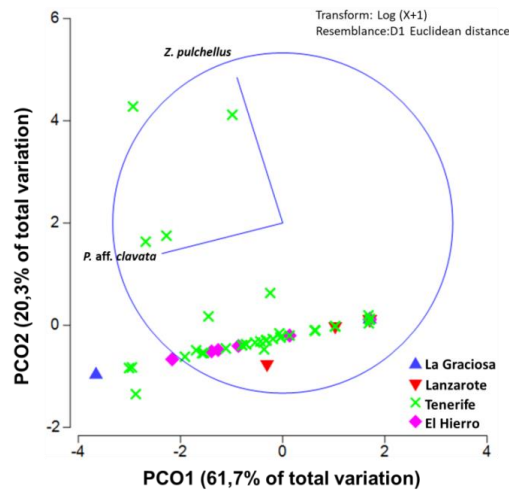


Fig. 4: Principal coordinate analysis (PCO) showing the first two axes (82% of variability), based on Euclidean distances of Log (X + 1) transformed data of intertidal zoanthellate zoantharian population densities at the islands studied in the Archipelago.

No significant differences in the abundance of *Z. pulchellus* among islands and not significant effect of the area of the intertidal platform were found (Table 2). However, despite the lack of statistical significance, data showed that intertidal populations of *Z. pulchellus* only occurred in Tenerife (Fig. 5 and 9).

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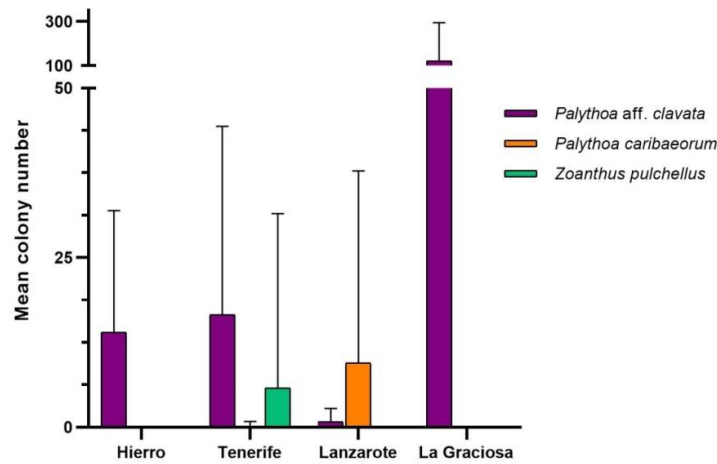


Fig. 5. Number of colonies (mean \pm SD) of the three most abundant zooxanthellate zoantharian species, *Palythoa aff. clavata*, *P. caribaeorum* and *Zoanthus pulchellus*, in four islands of the Canarian Archipelago.

2.2 Zoantharia populations in Tenerife Island

The PERMANOVA analysing densities and composition of zoantharian populations recorded in Tenerife revealed significant differences among orientations of the island and the covariable ‘Platform Size’ (Table 3). *A posteriori* pairwise analyses showed that the differences in species distribution were found between the south-western and northern sides of the island, while differences in population between the south-western and south-eastern coasts were marginally significant, and non-significant differences were obtained when comparing the northern and south-eastern parts of the island (Table 3). The PCO analysis, explaining $\approx 85\%$ of total data variability, showed that overall surveys conducted on Tenerife displayed high data variability, especially within the northern coast where populations of *Z. pulchellus* were more frequent and reached higher abundances (Fig. 6 and 9). Data from the south-eastern and south-western sides of the island were less dispersed and varied mainly according to the abundance of *P. aff. clavata* and *P. grandiflora*, with surveys from the south-eastern coast frequently showing less abundance of colonies of the studied species (Fig. 6 and 9).

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Table 2. Results of one-way permutational analyses of variance (ANOVAs) assessing the variability of the density of the most abundant zoantharian species (*Palythoa* aff. *clavata*, *P. caribaeorum* and *Zoanthus pulchellus*) in different islands of the Canary Islands (LG: La Graciosa, LZ: Lanzarote, TF: Tenerife and EH: El Hierro). Intertidal platforms size (m²) was included as a covariable in the analysis. Results of pairwise tests examining the effect of factor 'Island' whenever significant are shown. **p*<0.05 and ***p*<0.01.

<i>P. aff. clavata</i>						<i>Pairwise</i>		
Source	df	SS	MS	Pseudo-F	P (perm)	Groups	t	P (perm)
Platform size	1	201.28	201.28	0.34	0.520	LG vs. TF	112.86	0.001**
Island	3	25713.00	8570.90	14.39	0.001**	LG vs. LZ	5.49	0.001**
Ps x Island	3	30609.00	10203.00	17.13	0.001**	LG vs. EH	6.75	0.001**
Res	58	31544.00	595.58			LZ vs. TF	2.17	0.040*
Total	65	91066.00				LZ vs. EH	2.10	0.037*
						TF vs. EH	0.14	0.904

<i>P. caribaeorum</i>					
Source	df	SS	MS	Pseudo-F	P (perm)
Platform size	1	2345.00	2345.00	36.09	0.001**
Island	3	59.96	19.98	0.30	0.612
Ps x Island	3	944.48	314.83	4.85	0.053*
Res	58	3768.30	64.97		
Total	65	7117.80			

<i>Zoanthus pulchellus</i>					
Source	df	SS	MS	Pseudo-F	P (perm)
Platform size	1	987.81	987.81	2.52	0.108
Island	3	1499.70	499.90	1.28	0.224
Ps x Island	3	4295.90	1432.00	3.65	0.103
Res	58	22735.00	391.99		
Total	65	29519.00			

Table 3. Results of the one-way PERMANOVA analyzing the variation in the number of colonies of zooxanthellate zoantharians around sites located in different orientations of Tenerife island. Intertidal platforms size (m²) was included as a covariable in the analysis. Results of pairwise tests examining the significant factor 'Orientation' obtained in the analysis are shown. **p*<0.05 and ***p*<0.01. Underlined *p*-values were accepted as marginally significant.

PERMANOVA					<i>Pairwise tests</i>			
Source	df	SS	MS	Pseudo-F	p(perm)	Groups	t	p(perm)
Platform size	1	11.15	11.15	3.45	0.029*	N vs. SE	1.26	0.204
Orientation	2	17.33	8.67	2.68	0.027*	N vs. SW	2.11	0.009**
Ps x Or	2	6.83	3.42	1.06	0.380	SE vs. SW	1.57	<u>0.081</u>
Res	39	126.00	3.23					
Total	44	161.30						

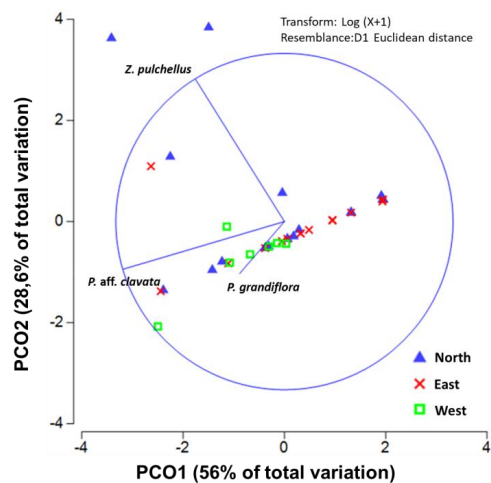
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Species-specific analyses only showed significant differences among orientations of Tenerife in the case of *P. caribaeorum* ($F= 5.53$; $p=0.015$), which was more abundant in the south-western side than in the south-eastern and northern coasts, with no occurrence of the species recorded in the latter orientation (Fig. 7 and 9). In the case of *P. aff. clavata*, the most abundant zoantharian species across Tenerife, not significant differences in the number of colonies recorded among island's orientations were obtained ($F= 1.06$; $p= 0.334$). However, the highest mean number of colonies of the species were also found in the south-western coast, followed by the northern and the south-eastern sides (Fig. 7 and 9). *P. grandiflora* showed marginally significant differences among orientations ($F= 3.04$; $p= 0.084$) since this species was just located in one site in the western coast of Tenerife (Alcalá site number 18 in Fig. 2), in high population densities (72 colonies in 250 m²) (Fig. 7 and 9).

Species belonging to the family Zoanthidae were significantly influenced by platform size (*Zoanthus pulchellus*: $F= 4.32$, $p=0.039$; *Isaurus tuberculatus*: $F=4.21$, $p=0.049$), but not by island orientations or the interaction of the factor and covariable. The greatest populations of both species were found in the two largest rocky platforms of northern Tenerife, Los Silos (site 22 in Fig. 2) and Punta del Hidalgo sites (site 28 in Fig. 2) (93 and 157 colonies of *Z. pulchellus*, respectively; 5 and 6 colonies of *I. tuberculatus*, respectively, Fig. 9).

Fig. 6: Principal coordinate analysis (PCO) showing the first two axes (84.6% of variability), based on Euclidean distances of Log (X + 1) transformed data of abundances (number of colonies) of populations of zooxanthellate zoantharians around Tenerife island.



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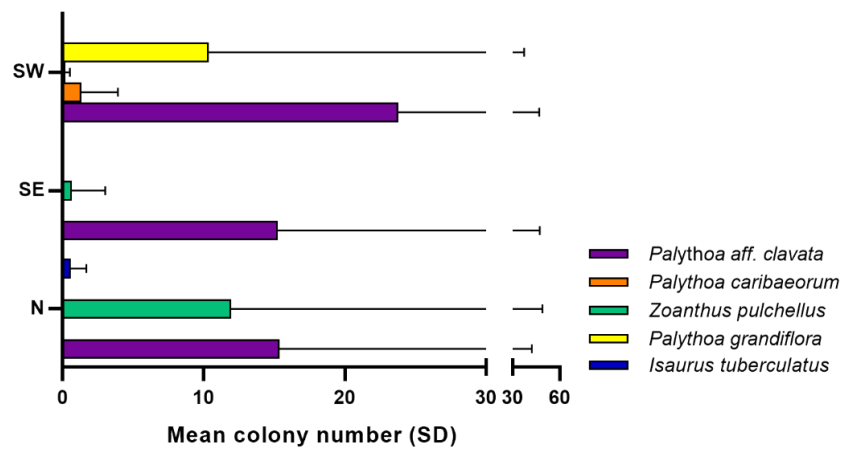


Fig. 7: Number of colonies (mean \pm SD) of all zooxanthellate zoantharian recorded around different sites located in the northern (N), south-eastern (SE) and south-western (SW) coast Tenerife island.

3. Distribution of zooxanthellate zoantharians in the subtidal zone

Only three zoantharian species were found in the subtidal zone of the Canary Islands -*Palythoa* aff. *clavata*, *P. caribaeorum* and *Zoanthus pulchellus*- with only two colonies of the latter species registered in Tenerife and El Hierro (Table 4, Fig. 10). Species-specific analyses of the most abundant species, including *Palythoa* aff. *clavata* and *P. caribaeorum*, showed contrasting effects of the factor island. Marginally non-significant differences in the abundance of *P. aff. clavata* were recorded among studied islands ($F= 3.21$; $p=0.067$), with higher mean numbers of colonies in Tenerife than in El Hierro ($t= 2.04$; $p= 0.064$) while no differences within the lowest abundances of Lanzarote and El Hierro ($t= 0.15$; $p= 0.888$) was observed (Table 4). Discrete colonies of this species were found in some subtidal locations of Tenerife and El Hierro, within a depth range of 1 to 10 m (Table 4). The two colonies recorded in Lanzarote in the shallower subtidal, at a maximum depth of 3 m, were the largest found in the whole study, considering both the subtidal and intertidal zones (Table 4).

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Table 4: Summary of population features recorded for zoantharian species *Palythoa* aff. *clavata* and *Zoanthus pulchellus* at the different islands surveyed throughout the Canarian Archipelago. Total number, mean abundance, depth range, and size frequency distribution (measured by the number of polyps) of colonies at each island are reported.

	Total number of colonies	Mean abundance (\pm SD)	Depth range (m)	Size frequency distribution of colonies (%)				
				XS	S	M	L	XL
<i>P. aff. clavata</i>								
Lanzarote	2	0.29 \pm 0.49	1.5 - 3					100
Tenerife	7	1.4 \pm 1.14	1 - 6	71	29			
Hierro	2	0.25 \pm 0.46	10 - 11	50	50			
<i>Z. pulchellus</i>								
Lanzarote	0	-	-					
Tenerife	1	0.2 \pm 0.44	3					100
Hierro	1	0.125 \pm 0.35	4					100

P. caribaeorum was only found in the subtidal of the western islands (Fig. 10), being especially abundant in both El Hierro and in Tenerife (19.75 \pm 24.11 and 26.00 \pm 50.75 colonies, respectively). However, the analyses of variance did not detect statistical differences in population abundances between studied islands ($F=0.37$, $p=0.488$). In the south-eastern coast of Tenerife, the species locally covered large extensions (> 100 m²), constituting the largest subtidal area occupied up to the moment by the species in the Archipelago, between 2-7 m depth. Despite size frequency distribution analysis showed no significant differences between islands ($Z=0.63$; $p=0.819$), a trend of higher occurrence of the largest size categories of colonies (2-4 m² and > 4 m²) in Tenerife than in El Hierro can be observed, accounting for >26% of the surveyed colonies in the former, while in El Hierro only \approx 14% of the colonies reached large sizes (Fig. 8). Smaller size categories of the species were more frequent in El Hierro (74% of occurrence) than in Tenerife (\approx 58%) (Fig. 8). Despite the largest areas occupied by *P. caribaeorum* in Tenerife, the species was more widespread in El Hierro, where it reached up to 17 m, as the deepest record of the species.

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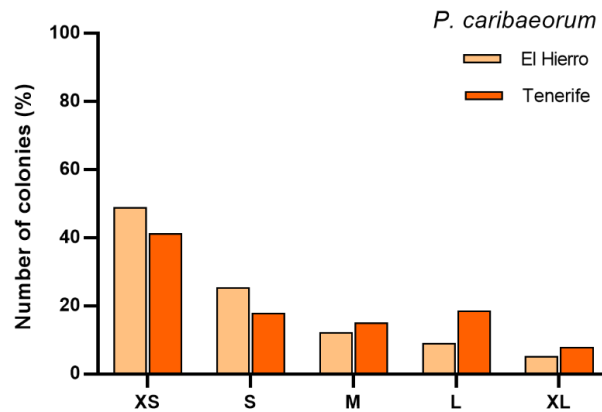


Fig. 8. Size frequency distribution (%) of subtidal populations of *Palythoa caribaeorum* found in El Hierro and Tenerife islands. Size categories of the colonies are given considering colony coverage area. XS: < 0.5 m², S: 0.5-1 m², M: 1-2 m², L: 2-4 m², and XL: > 4 m².

Discussion

Results of this study highlighted a wide variability in distribution patterns of zooxanthellate zoantharians along the Canary Islands. The distribution of intertidal and subtidal populations of *Palythoa* aff. *clavata* and *P. caribaeorum* respectively, followed patterns related to contrasting sea water temperatures regimens recorded at benthic habitats of different islands. In contrast, species such as *Zoanthus pulchellus* were more influenced by platform size. Intertidal *P. aff. clavata* was most abundant in the western coast of Tenerife while its smallest populations were seen in Lanzarote. In the subtidal, *P. caribaeorum* was only recorded in the western islands where SST are warmer throughout the year. Despite results showed that *P. aff. clavata* is more influenced by extreme environmental conditions of the intertidal zone, we consider both *Palythoa* species populations as potential indicators of tropicalization processes in the Canary Islands, showing their value for monitoring programs. Furthermore, since *P. aff. clavata* and *P. caribaeorum* are in fact common species found throughout the whole Archipelago, the two species should no longer be catalogued as species of special interest in Canarian ecosystems, according to species conservation criteria of endemism, level of endangerment, etc.

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Distribution of zooxanthellate zoantharians in the intertidal zone

The two recorded species of the family Zoanthidae, *Isaurus tuberculatus* and *Zoanthus pulchellus*, were only found in the intertidal zone of Tenerife, showing preference for large rocky platforms of the north coast (Fig. 9). Few discrete colonies of *I. tuberculatus* were found in the low intertidal of Los Silos and Punta del Hidalgo (sites 22 and 28 in Fig. 2, respectively), locations that are characterised by high hydrodynamic levels (Yanes et al. 2006) and more constant sea water parameters, given the proximity to the subtidal and smaller exposure times during low tides. Although *I. tuberculatus* has a pan-tropical distribution, it has been claimed as an uncommon species mainly due to its cryptic appearance and habitat preferences, which usually hinder the detection of colonies (Reimer et al. 2008a). On the contrary, *Z. pulchellus* showed high population densities that were able to cover extensive areas in rocky tidepools of the same northern locations of Tenerife (Fig. 9). The species showed great tolerance to the low SST recorded in tidepools of Punta del Hidalgo site, where winter temperatures reached minimum values as low as 11.8°C. Such surprisingly low temperature range for the subtropical location of the islands is probably related to the wet and fresh air of trade winds that blow mainly against the north sides of the islands (Font 1956; García-Herrera et al. 2001). These conditions affect *Z. pulchellus* the most, given the location of the species in tidepools that keep disconnected from the sea during large periods. However, despite this great tolerance to low temperatures, *Z. pulchellus* has not been recorded in the eastern island of Lanzarote, characterized by the coldest waters of the Archipelago, not even in the wide rocky intertidal platform of Órzola (site 3 in Fig. 2). In general, we have not found a clear longitudinal distribution pattern of the species related to SST in members of the family Zoanthidae, and other factors such as specific habitat features or interspecific interactions, may be responsible for the abundance of the species.

Regarding the family Sphenopidae, *Palythoa grandiflora* showed high densities only in one location in the warmest coast of south-western Tenerife Island (Fig. 9), where cropland irrigation waters flow directly into the sea. It is known that *P. grandiflora* can be locally dominant by taking advantage in degraded coral reefs, being able to cause communities' phase shifts (Cruz et al. 2016a). Future studies focusing both in biotic and abiotic parameters are needed to clarify the environmental and ecological requirements

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of this species, in order to early detect any potential ecosystem effects in the Canary Islands.

P. aff. clavata is an amphi-Atlantic tropical species that inhabits from Cape Verde to Madeira in the East Atlantic (Araújo and Freitas 2003; Reimer et al. 2012a; López et al. 2019 – chapter 1). Despite previous studies had only described a few dispersed colonies of the species in the whole Canarian Archipelago (López-Pérez 2014; Riera et al. 2014), our results showed that *P. aff. clavata* has turned into a very common element in the Archipelago, with colonies recorded in all surveyed islands (Fig. 9). The fact that the largest population densities were found in the western islands of El Hierro and Tenerife, especially in the warmest locations within each island (Barton et al. 1998), highlights the tropical affinities of the species. What is more, despite reduced habitat availability due to the narrower intertidal rocky platforms of the more tropical island of El Hierro compared to Tenerife, densities of *P. aff. clavata* were similar in both islands. Unexpectedly, one of the largest populations of *P. aff. clavata* was recorded in the eastern side of the Archipelago, in La Graciosa island (Fig. 9), in which appears to be a recent population expansion as only one colony was previously recorded in the year 2000 at the same location (A. Brito pers. comment.). Colonies were found concentrated in a specific location and species abundance might be related to the topographic conditions of a very flat intertidal rocky platform with shallow tide pools (5-10 cm depth), in which SST easily warms up and reaches high values during low tide. However, futures studies should consider other parameters that could be determining the high abundances of *P. aff. clavata* in this specific location, such as nutrients availability or type of substrate.

P. caribaeorum is known to show high tolerance to changes in temperature and water conditions in tropical tide pool environments (Bastidas and Bone 1996; Bouzon et al. 2012). However, few populations of the species were found in intertidal coasts of the subtropical region of the Canary Islands (Fig. 9). One of the most extensive populations was in Lanzarote (~50 m²), in an intertidal habitat very similar to that of the other large population of the species previously known in the nearby island of Fuerteventura (~90 m², previous unpublished data). In both cases, extensive marine abrasion platforms occur (Carracedo and Rodríguez Badiola 1993; Meco et al. 1997) in the eastern side of the islands.

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The large size and height of the rocky platforms combined with the wide tidal amplitude experienced in these islands that constitutes the widest within the Archipelago (maximum low tide of 1.8 m in comparison to a maximum of 1.1 m in the western islands; source: <https://puertoscanarios.es/>), leave many tidepools separated from the open ocean for several hours. This explains the huge variation in temperature ranges recorded *in situ* by the temperature data logger (14.098 - 30.722°C), and the heating experienced during low tide might be the reason why the thermophilic *P. caribaeorum* is able to inhabit in the intertidal zone of the eastern colder islands. Moreover, a distribution pattern related to sea water temperature variability within a single island was detected for this species. Colonies of *P. caribaeorum* are known to inhabit in the western intertidal coast of Tenerife since 1980 (Arechavaleta 2009), where air and sea water temperatures are warmer than in other orientations of the island (Barton et al. 1998). This study constitutes the first intertidal record of *P. caribaeorum* in the eastern coast of Tenerife (Fig. 9), which suggests a recent expansion at the island scale. However, the species has not yet been able to settle in the northern coast of the island, neither in Madeira Island, despite the high dispersion abilities of its larvae (Ryland et al. 2000). This is probably related to the low temperatures reached during winter and the sensitivity of Sphenopidae larvae to cold SST (Ryland et al. 2000), or processes of spatial competition with other components of intertidal habitats at northern locations, where algae stand are more developed than in southern coasts (Sangil et al. 2011).

Distribution of zooxanthellate zoantharians in the subtidal zone

Palythoa caribaeorum, *P. aff. clavata* and *Zoanthus pulchellus* resulted more common in subtidal locations of the western warmer islands of the Canary Islands (Fig. 10). On the other hand, *P. grandiflora* and *Isaurus tuberculatus* were not found in subtidal sites surveyed within this study, probably as a result of the low abundances of colonies in the case of the latter species. In fact, some observations of disperse colonies of *I. tuberculatus* are known for different islands of the Archipelago (Tenerife, El Hierro and Fuerteventura), up to 30 m depth (L. Martín and R. Herrera pers. comment).

Members of the family Zoanthidae have shown to be more tolerant than other zoantharians to low temperatures in the Pacific Ocean (Reimer et al. 2008b) and species

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such as *Z. sansibaricus* can be found up to 36°N (Reimer et al. 2018). On the other hand, distribution of their planktonic larvae around the Atlantic Ocean also supports that Zoanthidae species present higher tolerance than Sphenopidae species (in waters up to 18°C and 22°C, respectively) (Ryland et al. 2000). However, the results of this study showed that *Zoanthus pulchellus* was absent in subtidal locations of the eastern archipelago while *P. aff. clavata* was the most widespread zoantharian. In fact, the latter species was the only zoantharian able to inhabit subtidal locations of Lanzarote, where SST reached the minimum values recorded (17.53°C) due to the influence of the Saharian up-welling (Barton et al. 1998; Vélez et al. 2015). Moreover, only *Palythoa* spp. have been so far recorded at 32°N in Madeira Island, constituting the northernmost limit of distribution for Brachycnemina zoantharian in the East Atlantic (Araújo and Freitas 2003; López et al. 2019 – chapter 1). Therefore, our data showed species-specific temperatures affinities along the temperature gradient of the Canary Archipelago, being *P. aff. clavata* more tolerant to cold water than *Z. pulchellus*. Nevertheless, other factors such as habitat availability, incidence of currents or simply stochastic features, might be determining the distribution of these species throughout the Archipelago.

Results of our extensive surveys and previous literature revised showed that all subtidal populations of *P. caribaeorum* were found in the western islands of La Palma, El Hierro and Tenerife and, in fact, a large population of >100 m² has been recently recorded in the south eastern coast of La Gomera island (Fig. 10). *P. caribaeorum* distribution clearly showed a relationship with warmer environments, but also occurring in association with high densities of the frequent echinoid *Diadema africanum*, that leaves unvegetated spaces available for *P. caribaeorum* growth (pers. comment). These wide extensions of bare rocky substrate were completely covered by this species that leaves few free spaces available for other important benthic organisms, such as macroalgae and other sessile invertebrates, greatly modifying the underwater landscapes. *P. caribaeorum* has been reported as a widespread tropical species with great tolerance to environmental conditions (Sebens 1982), being locally dominant in hard bottom substrates of tropical and subtropical reefs (Sebens 1982; Acosta 2001; Silva et al. 2015). Given the potential of *P. caribaeorum* to completely modify benthic ecosystems, further ecological studies are needed to better understand processes of habitat and communities' transformation mediated by the proliferation of this zoantharian in the Canary Islands.

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The restricted subtidal distribution of *P. caribaeorum* to the western islands shows that the temperature gradient throughout the Archipelago, which has been proven to cause significant differences in temperature regimens in nearshore environments, is an important factor to consider in the species distribution within the region. Although in Lanzarote SST reached similar maximum values recorded in subtidal benthic habitats than in El Hierro, minimum temperature records during winter months greatly contrasted among the two extremes of the Archipelago. These differences could be hindering the settlement of this species in the eastern islands. Indeed, the species' strong competitive ability (Sebens 1982) and antipredator mechanisms (Bastidas and Bone 1996; Tubaro et al. 2011; Cen-Pacheco et al. 2014) limit the number of factors that can determine its distribution. In an ocean warming scenario, it is expected that this species will become dominant in subtidal zones, expanding their populations to the eastern islands as temperature rises. Following this regional expansion of the species' distribution range, important changes in subtidal landscapes and potential alterations in natural ecosystems can be expected for the Archipelago.

Brachynemina species as indicators of ocean warming

Zoantharians have shown to be more resistant than hermatypic corals to current habitat degradation, pollution and the increase of ocean temperature related to climate change (Dubinsky and Stambler 1996; Hoegh-Guldberg et al. 2007; Vermeij et al. 2011). In fact, some species are currently expanding their populations, becoming locally abundant under these conditions (Karlson 1981; Sebens 1982; Acosta 2001; Silva et al. 2015; López et al. 2018) and even causing phase-shifts in coral reef ecosystems (Cruz et al. 2016a, b). Intrinsic characteristics of Zoantharia species, such as colony plasticity (Karlson 1983; Costa et al. 2011) and fast growth combined with an effective asexual reproduction (Suchanek and Green 1981; Fadlallah et al. 1984; Acosta and Asbahr 2000; Acosta et al. 2001; Rabelo et al. 2013) and the production of powerful palytoxin (Tubaro et al. 2011) are probably involved in such colonization success. This study constitutes an example of such population spread outside tropical regions and, up to our knowledge, one of the few cases occurring in macroalgae-dominated systems.

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Biological indicators that react to a given impact may allow the evaluation of the whole ecosystem condition. However, the selection of an appropriate indicator is a difficult task as the organisms or populations of organisms selected depend on the final goal and the studied region (Gerhardt 2002). In general, they should specifically respond to a single pressure, being easy to identify and sample, as well as show high abundances and widespread distributions (Gerhardt 2002; Rice and Rochet 2005; Dulvy et al. 2008). Considering these characteristics, Brachycnemina populations appear to be ideal indicators of ocean warming in the Canary Islands, especially *P. aff. clavata* and *P. caribaeorum*, which showed a clearer pattern of distribution related to SST. In these matters, monitoring programs of subtidal populations of *P. caribaeorum* should be specially considered as its tropical affinity is causing a current outbreak and expansion of the species with a great potential to modify local ecosystems. Because their populations are easy to sample, individuals are long-lived and without many predators, these species are ideal for developing long-term monitoring actions aiming to compare changes in ecosystems not only in the Canary Islands, but also at other locations as they are worldwide widespread species, both including coral reefs and macroalgae-dominated systems. The present study would be crucial as a baseline reference of the status of these zoantharian populations for any future assessments aiming for interpreting trajectories of change in local ecosystems in the current global change context.

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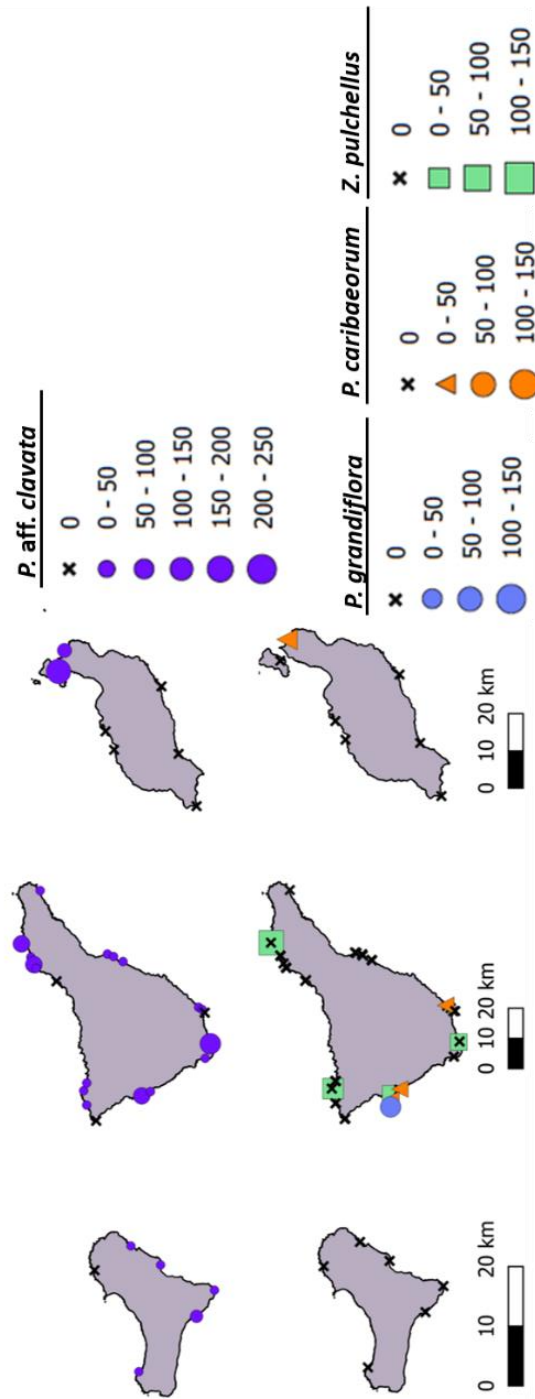


Fig 9. Distribution and abundances of Zoantharia Brachyneremina species around intertidal habitats throughout the Canary Islands

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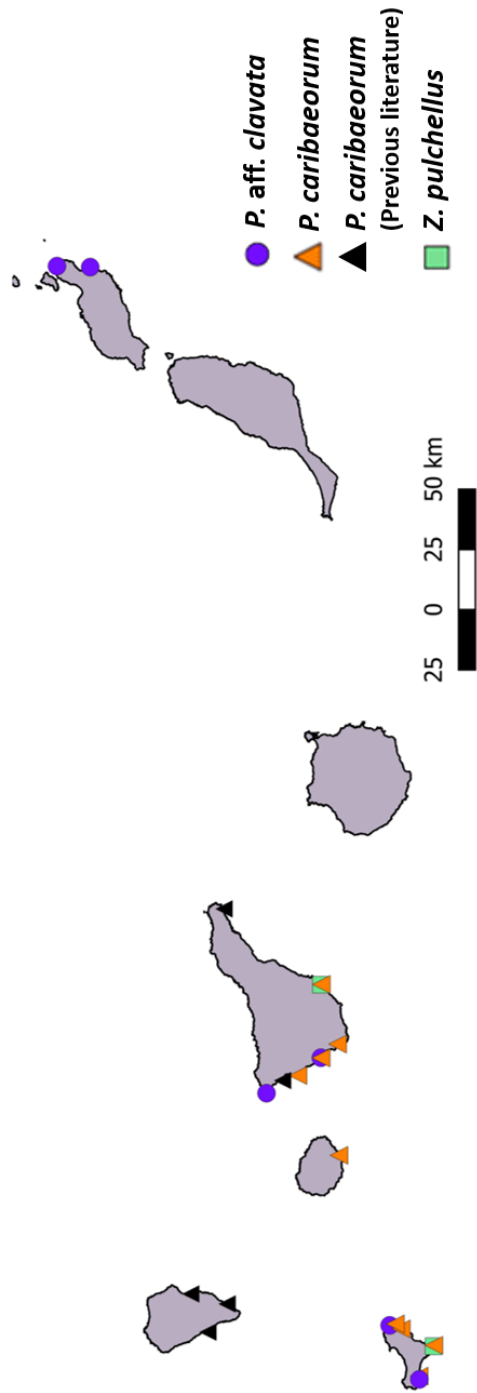
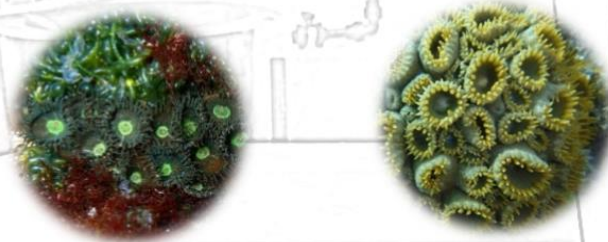


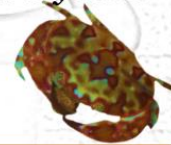
Fig 10. Distribution and abundances of Zoantharia Brachynemina species in subtidal habitats throughout the Canary Islands, including previous data from the literature (Arechavaleta M 2009; Martín-García 2013).

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Effects of low pH and high temperature on two *Palythoa* spp. and predator-prey interactions



In this chapter, the effects of low pH and high temperature regimens predicted for the Canary Islands region was evaluated in two *Palythoa* species. Experimental long-term exposure to low pH resulted in detrimental effects on colonies of *P. aff. clavata* and *P. caribaeorum* that significantly decreased in weight and size, probably related to a reduction in the chlorophyll content. Moreover, predation by the crab *Platypodiella picta* also decreased over *P. aff. clavata* exposed to acidic conditions, which may compensate ecological performance of the species in climate change conditions. Oceans worldwide are facing the effects of climate change and consequences for many marine species are already noticeable. Despite being suggested as winner species in a climate change scenario, our study demonstrated that long-term exposures to low pH negatively impact *Palythoa* spp. survival, although consequences in their populations could be ameliorated with a decrease in predation rates.

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Introduction

The increase of human population is causing alterations in climate primarily through fossil-fuel, industrial, agricultural, and other land-use emissions that alter atmospheric composition (Doney et al. 2009). Rising concentrations of atmospheric carbon dioxide (CO₂) is one of the most critical problems of climate change because its effects are globally pervasive and irreversible on ecological timescales. Oceans are able to mitigate the effects of climate change through absorption of ≈30% of the total CO₂ emissions from human activities (Feely et al. 2004; Sabine et al. 2004). However, such accumulation of CO₂ is causing dramatic deviations in sea water chemistry, a process called ocean acidification, which includes a decrease in pH and carbonate ions (CO₃²⁻) as well as an increase in bicarbonate ions (HCO₃⁻¹) (Gattuso and Buddemeier 2000). The main effect of ocean acidification is a decrease in calcification rates of many marine organisms with calcareous structures such as algae (Feely et al. 2004), molluscs (Michaelidis et al. 2005), echinoderms (Shirayama and Thornton 2005), and corals (Langdon et al. 2003). However, not only calcareous organisms are affected by lowered pH conditions. For instance, some species of non-calcareous macroalgae are favoured by elevated CO₂ that promote photosynthesis and growth rates (Gao et al. 1993; Kübler et al. 1999; Riebesell et al. 2007), while others are disadvantaged (Israel et al. 1999; Rodríguez et al. 2018) or suffer no observable effect (Israel and Hophy 2002; Jokiel et al. 2008) depending on their ability to use dissolved inorganic carbon (DIC) (Cornwall et al. 2015, 2017). Recent models estimate a reduction in surface ocean pH ranging from 0.3 to 0.5 units over the next 100 years, depending on the CO₂ emission scenario used (Caldeira and Wickett 2005; Lüthi et al. 2008). Under these conditions, it is expected that morphological, physiological and ecological modifications in marine organisms will become more frequent.

Another consequence of the increase of greenhouse gases concentrations is that global air and sea surface temperatures (SST) have risen considerably (Bindoff et al. 2007). This trend is expected to accelerate in the current century (IPCC 2013), causing modifications in ecosystems worldwide. Most evident effects of ocean warming are changes in patterns of species distributions, which are leading to global tropicalization (Perry et al. 2005; Bañón and Mucientes 2009; Horta and Gonçalves 2013; López et al. 2015) and meridionalization (Yapici et al. 2016) of the marine biota. Furthermore, an

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increase in ocean temperatures would negatively impact in the survival of marine species that already live in their limit of distribution (Somero 2002; Hughes et al. 2003; Harley et al. 2006). Organisms most affected by the rise in ocean temperature are those who live in association with dinoflagellates (zooxanthellae). It is known that symbioses between zooxanthellae of the family Symbiodiniaceae and hermatypic corals are very sensitive to changes in temperature. As sea water temperatures reach higher levels, this association breaks and corals expel their dinoflagellates (coral bleaching) (Winter et al. 1998; Michalek-Wagner and Willis 2001), thus losing their main source of energy (Baker et al. 2008). In hermatypic corals, up to 143% of the host daily energy requirements are provided by symbiotic dinoflagellates through photosynthesis (Muscatine et al. 1984; Davies 1991). Such coral bleaching events have already led to extensive mortality in both hard (Glynn et al. 2001; Loya et al. 2001; Depczynski et al. 2013) and soft corals around the world (Harvell et al. 2001; Goldberg and Wilkinson 2004; Prada et al. 2010; Dias and Gondim 2015).

There are many effects of both ocean warming and acidification at the individual level, e.g. changes in morphology, physiology and behaviour (Pörtner and Knust 2007; García et al. 2015; Nagelkerken and Munday 2016). Additionally, indirect effects of such alterations can be detected at community levels, e.g. modifications of the outcomes of species interactions such as competition for space or resources, or predatory interactions (Rodríguez et al. 2017; Ullah et al. 2018). Most experimental studies have only explored the effects of these factors in isolation (Dupont et al. 2012; Luz et al. 2018), but the number of studies combining both factors is starting to increase (e.g. Holcomb et al. 2012; Kroeker et al. 2013; Heuer et al. 2014; Cole et al. 2018; Ullah et al. 2018). However, there is still a lack of long-term experiments, despite that it has been suggested that maintaining climate change conditions during longer periods may result in acclimation and could considerably change the conclusions obtained (Kroeker et al. 2013). Moreover, there is also a need for experiments focusing on assessing not only direct effects of climate change conditions on single species but also indirect effects such as predator-prey interactions (Dixson et al. 2010; Ferrari et al. 2011; Ghedini et al. 2015).

Zoantharian species of the genus *Palythoa* (Cnidaria: Anthozoa) are zooxanthellae benthic cnidarians widely distributed in tropical and subtropical regions around the world (Acosta et al. 2005; Ong et al. 2013; Santos et al. 2016). Because of the lack of carbonate

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in their body wall, it has been suggested that zoantharians are robust to changes in ocean pH (Reimer et al. 2008b). What is more, species of the genus *Palythoa* have been considered as early-indicators of *bleaching* events (Williams Jr and Bunkely-Williams 1990; Goldberg and Wilkinson 2004) due to their sensitivity to thermal stress (Parkinson et al. 2016). However, due to their mixotrophic condition (Reimer 1971; Santana et al. 2015) *Palythoa* rarely died during such *bleaching* events (Jimenez 2001), being able to survive only by heterotrophic plankton feeding (Tanner et al. 2002). These intrinsic features combined with their fast growth rates (Karlson 1988; Rabelo et al. 2013), efficient sexual and asexual reproduction strategies (Acosta et al. 2001, 2005; Hirose et al. 2011; Polak et al. 2011), and their antipredator mechanisms through synthesis of toxic chemicals (Sebens 1982; Tubaro et al. 2011), make zoantharians especially resilient to different sources of environmental stress. In a climate change context, they may become ecologically dominant species to the detriment of other sessile organisms (Reimer et al. 2008b; Durante et al. 2018).

The Canary Islands constitute the northern limit of the distribution ranges of *Palythoa caribaeorum* and *P. aff. clavata* in the East Atlantic, except for some isolated colonies of *P. aff. clavata* found in the southern coast of Madeira (Araujo and Freitas 2003; López et al. 2019-chapter 1). Populations of both species are widely extended in the Canarian Archipelago with some evidence of recent expansions, which might be related to current increases in ocean temperatures (Vélez et al. 2015; chapter 2). In fact, actual patterns of distribution of the species seem to be related to the temperature gradient over the regional geographic range off the Canary Islands (chapter 2), located between the cool and nutrient-rich waters from the northwest African coastal upwelling and the warmer and nutrient-poor open ocean waters (Barton et al. 1998; chapter 2). *P. caribaeorum* is extensively distributed in subtidal habitats of the western warmest islands within the Archipelago, where it can cover large extensions of rocky platforms. Conversely, *P. aff. clavata* is more abundant in intertidal habitats but also more frequent in the western islands (chapter 2).

The aim of this study was to evaluate the combined effects of ocean warming and acidification levels expected for a future scenario of climate change, in these two zooxanthellate zoantharian species located at their northern limits of distribution and showing two different habitat affinities (subtidal and intertidal). Because the direct

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responses of marine organisms to climate change greatly determine many others biotic interactions, we also evaluated the effects of high temperature and low pH regimens on the susceptibility of both *Palythoa* species to predation by one of their few known predators, the crab *Platypodiella picta* (Hartog and Holthuis 1984; Hartog and Türkay 1991).

Material and Methods

1. Specimens collection and acclimatization to laboratory conditions

Collection of specimens of *Palythoa* aff. *clavata* and *P. caribaeorum* from the field was performed in November 2016, when SST is within its highest values in Tenerife Island (22°C) (Canary Islands, Spain), in order to minimize any potential temperature shock experienced by the colonies during laboratory experiments. Approximately 70 fragments of different colonies of *P. aff. clavata* were collected in the intertidal zone of La Barranquera, north of Tenerife (28°32'17.98"N, 16°23'50.87"W). Likewise, 70 fragments of *P. caribaeorum* belonging to different colonies were collected at 3-6 m depth in the subtidal zone of Tajao, south-eastern coast of Tenerife (28°6'46.95"N, 16°27'48.04"W). Specimens were immediately transported to the laboratory in dark and wet conditions.

Fragments of *P. aff. clavata* (9-16 polyps) and *P. caribaeorum* (6-9 cm²) were glued in artificial substrates and placed in tanks with running filtered sea water and 12 h light/12 h dark cycle under LED lighting (Leddy Tube, 6W) (Fig. 1). Specimens were maintained during 53 days for acclimatization to laboratory conditions at control temperature and pH levels that corresponded to the natural values of sea water in the Canary Islands (22.132°C ± 0.36 and pH 8.1 ± 0.08). Only colonies with open polyps and without any external signal of damage were selected to perform further experiments of responses to climate change conditions. Previously, the colonies were acclimated progressively from 22°C and pH 8.1 to the experimental conditions during one week.

In both acclimatization and experimental periods, salinity and temperature (WTW Cond 3110), and pH (Hanna HI 98919) parameters were monitored twice a day. Given their mixotrophic condition, colonies were fed weekly with a mix of Phyto and

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Zooplankton (AF Phyto Mix, Aquaforest). After 4 h colonies feeding, the sea water with excess of nutrients was eliminated to avoid eutrophication and replaced by fresh sea water (approximately 1/3 of each tank). In addition, sea water at each tank was completely replaced once a week.

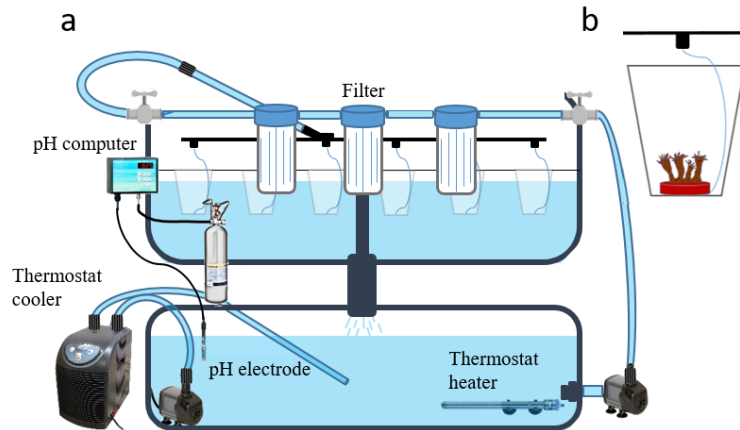


Fig. 1: (a) Scheme of the experimental tanks and sea water circuit in which laboratory experiments were carried out. Thermostat coolers and heaters, and computerized pH systems were used to control sea water parameters. (b) Beakers and artificial substrates for experimental colonies are also shown.

2. Experimental design and sea water chemistry

Sixty colonies of each species, *Palythoa* aff. *clavata* and *P. caribaeorum*, were placed into 1 L beakers and distributed in four tanks 300 L, in which sea water temperature was controlled using thermostat coolers (ECHEIM AQUATIC, 50W, with a precision $\pm 0.5^{\circ}\text{C}$) and heaters (Tetra HT200) and pH using computerized pH systems (AquaMedic) (Fig. 1). The experiment consisted on four treatments that combined contrasting levels of SST and pH (NBS scale) corresponding to the natural sea water conditions at the Canary Islands, and SST and pH predicted for the region for the year 2100 (IPCC 2013): a first tank at 22°C (control SST in early autumn in the Canary Islands) and pH 8.1 units (average current sea water pH) as a control treatment, a second tank with 26°C (SST predicted to be reached during the warmest season for the year 2100) and pH 8.1 as a temperature condition treatment, a third tank at 22°C and pH 7.5

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(predicted pH for the year 2100) as a pH condition treatment, and a fourth tank combining both high temperature and low pH (26°C and pH 7.5) which represented the climate change scenario for the year 2100 in the sampling region. Low pH treatments were maintained with a computerized system (AquaMedic) that regulated pH by injecting pure CO₂ directly into the sea water, to a resolution of ± 0.01 pH units. Both temperature and pH conditions were manipulated in an adjacent tank and, through a hosepipe circuit provided with filters, sea water was continuously renovating in each beaker while experimental conditions for each colony were kept isolated at each beaker (Fig. 1).

Water quality parameters for marine aquariums (NO₃, NO₂, NH₃/NH₄ and PO₄) were checked weekly using the Marine Care Test Kits (Red Sea). Total alkalinity (TA) for each treatment was also measured weekly by titration (Methrom, 665 Dosimar, Switzerland), using an open cell titration system and following the Standard Operation Procedure 3b (Dickson et al. 2007). Other sea water carbonate chemistry parameters (pCO₂, calcite saturation state (Ω_c) and aragonite saturation state (Ω_a) were calculated from TA and pH results, using CO₂sys software (Lewis and Wallace 1998). Calculations for pCO₂, Ω_c and Ω_a, were based on a set of constants K1 and K2 from Mehrbach et al. (1973), refitted by Dickson and Millero (1987).

3. Survival, growth and health status of coral species

A total of fifteen replicates per species and per combination of temperature and pH treatments were maintained during 62 days of experiment.

Coral growth rates were measured by differences in weight between the beginning and end of the experiment using a laboratory scale with a precision ± 0.001 g. In the case of *P. caribaeorum*, growth in terms of colony surface area was also measured by means of analysing photographs with ImageJ 1.50 software. Because zoantharian survival also depends on their symbiotic dinoflagellates, their health status was evaluated by means of measuring the content of chlorophyll a (Chla), pigment used for photosynthesis in all photosynthetic species and whose concentrations can give information about colonies health condition (Iglesias-Prieto et al. 1992). Concentration of Chla was obtained through fluorometry following the procedure by Costa et al. (2008) and the results were

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normalized using the weight of each colony sample. To assess any potential effect of colonies' manipulation and laboratory conditions on the status of the symbiont, extraction of dinoflagellates was also performed with colonies at the moment of collection from the field and compared with colonies kept at control treatment conditions after 115 days under laboratory conditions (53 days of acclimatization plus 62 days of experiment). In order to evaluate whether experimental treatments affected zooxanthellae status, and considering that Chla concentration method was destructive, only two colony replicates per species and per combination of temperature and pH condition were used to extract dinoflagellates at the middle of the experiment (after 31 days of exposure) and three at the end of the experiment (after 62 days). Additionally, in order to detect any potential bleaching event in relation to experimental conditions, changes in the color of experimental colonies were estimated every two weeks using a "CoralWatch Coral Health Chart" (Siebeck et al. 2006), which has been proved to be a useful complementary technique in assessing *Palythoa* zooxanthellae condition (Parkinson et al. 2016). This non-invasive method allowed us to indirectly evaluate the symbiosis quality of all colony replicates throughout the experiment.

4. Predation experiments

After 62 days under the experimental conditions, six colonies of *P. aff. clavata* and six of *P. caribaeorum* of each combination of temperature and pH treatments were used in a predation experiment. We evaluated potential indirect effects of such sea water conditions on colonies' susceptibility to the predatory crab *Platypodiella picta*. Specimens of *P. picta* were collected in Tajao site (28°6'46.95"N, 16°27'48.04"W), in Tenerife Island, two days prior to the starting of the experiment. During these two days the crabs were maintained in the laboratory without feeding, to acclimatize specimens to experimental conditions in each tank and standardize their feeding status (Scheibling and Robinson 2008). Then, one individual of *P. picta* was placed into each replicate beaker containing an experimental colony of *P. aff. clavata* or *P. caribaeorum*. Respective controls without predatory crabs were also established using another set of six colonies per species and combination of temperature and pH conditions. All experimental and control colonies were weighted just before the commencement of predatory essays, and then

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daily up to 6 days (when some experimental colonies showed ≈90% of their biomass predated) to assess changes in colony weight due to crab feeding activity.

5. Statistical analyses

Colony survival of *Palythoa* aff. *clavata* and *P. caribaeorum* was evaluated throughout the course of the experiment by means of distance-based permutational analyses of variance (ANOVAs) (Anderson 2001). Two-way designs were performed with two fixed factors, “pH” (2 levels: 8.1 and 7.5 units) and “Temperature” (2 levels: 22 and 26 °C). For each species, growth rates of experimental colonies, both in terms of weight or surface cover increments, were also analysed by means of distance-based permutational ANOVAs (Anderson 2001) using the previous design.

To evaluate whether symbiotic Symbiodiniaceae were affected by laboratory conditions, distance-based permutational ANOVAs (Anderson 2001) of the concentration of chlorophyll a (Chla) of samples of the two zoantharia species at control conditions (pH 8.1 and 22°C) was performed. A one-way design was carried out with “Time” treated as a fixed factor with 2 levels (1: at the moment of specimens’ collection and 2: at the end of the experiment, after 115 days under laboratory conditions). A second set of analyses was performed in order to check for any changes in zooxanthellae condition due to experimental treatments. In this model, Chla concentration was compared using a three-way design in which factors “pH” (2 levels: 8.1 and 7.5 units), “Temperature” (2 levels: 22 and 26°C) and “Time” (2 levels: at 31 days of the experiment and at end of the experiment, 62 days) were treated as fixed. Data with the “CoralWatch Coral Health Chart” were collected as a measure of bleaching experienced by colonies under contrasting treatments of pH and temperature. Color score of experimental colonies, ranging from 1 (completely bleached) to 6 (healthy colonies), were examined by means of frequency analyses (χ^2) using the SPSS 15.0 statistical software.

Susceptibility of zoantharians to the predatory crab *Platypodiella picta* was assessed by means of calculating predation rates upon experimental specimens as the difference in the weight of colonies between the commencement and end of the experiment (6 days). A distance-based permutational ANOVA (Anderson 2001) for each

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Palythoa species was used to evaluate differences in predation rates due to the experimental conditions. A three-way design was carried out with factors “Experimental vs. control” (2 levels: with and without predatory crab, respectively), “pH” (2 levels: 8.1 and 7.5 units) and “Temperature” (2 levels: 22 and 26 °C) treated as fixed factors.

In all ANOVA analyses Euclidean distances of raw data and 9999 permutations of the appropriate exchangeable units were used (Anderson 2001). Whenever enough permutations were not obtained for a valid test, the p-values were corrected with Monte Carlo method (Anderson and Robinson 2003). Significant terms in the full models were examined using *a posteriori* pairwise comparisons by permutations (Anderson 2001). All statistical analyses were carried out using PRIMER 7 & PERMANOVA+ v. 1.0.1 software.

Results

1. Sea water chemistry

Physicochemical parameters of sea water during the course of the experiment are given in Table 1. Target temperatures and pH were achieved in each replicated treatment (Table 1). The partial pressure of CO₂ (pCO₂) increased at low pH levels in all temperature treatments and saturation levels of calcite (Ω_C) and aragonite (Ω_A) decreased in low pH conditions (Table 1). Sea water only approached subsaturation values with respect to aragonite ($\Omega_A < 1$) under conditions of acidic pH (Table 1).

2. Survival, growth and health status of coral species

All colonies of *P. aff. clavata* survived to the 62 days of experiment, regardless of the experimental conditions. However, survival of *P. caribaeorum* varied significantly between treatments with a marginally significant two-way interaction of “pH x Temperature” (F= 3.62; p= 0.059). *A posteriori* pairwise analyses only showed significant differences between temperatures (22 vs. 26°C) at pH 7.5 units (t= 3.54; p(MC)= 0.001), with all colonies surviving at high pH conditions in contrast to the 66.6% of colonies that survived at climate change conditions.

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Table 1: Mean values (\pm SD) of the physicochemical parameters of sea water measured in each experimental treatment during 62 days of experiment. Total alkalinity (AT), partial pressure of CO₂ (pCO₂), carbonic acid (H₂CO₃), carbonate (CO₃²⁻) and saturation levels of calcite (Ω_c) and aragonite (Ω_A) were calculated by means of CO2SYS (Lewis and Wallace 1998). Control treatment: 22°C and pH=8.1, temperature treatment: 26°C and pH=8.1, pH treatment: 22°C and pH=7.5 and climate change treatment: 26°C and pH 7.5.

	Control treatment	Temperature treatment	pH treatment	Climate change treatment
Temperature (°C)	22.060 \pm 0.170	25.660 \pm 0.160	22.100 \pm 0.370	25.720 \pm 0.470
pHT	8.090 \pm 0.085	8.094 \pm 0.077	7.529 \pm 0.069	7.504 \pm 0.072
AT (mmol Kg-1)	2.547 \pm 0.062	2.620 \pm 0.056	2.768 \pm 0.138	2.918 \pm 0.164
pCO ₂ (μ atm)	364.160 \pm 9.110	367.420 \pm 8.230	1925.330 \pm 95.620	2046.880 \pm 115.760
H ₂ CO ₃ (mmol Kg-1)	1.932 \pm 0.048	1.911 \pm 0.043	2.565 \pm 0.129	2.674 \pm 0.152
CO ₃ ²⁻ (mmol Kg-1)	0.253 \pm 0.007	0.293 \pm 0.007	0.085 \pm 0.005	0.103 \pm 0.006
Ω_c	5.971 \pm 0.154	6.869 \pm 0.154	1.994 \pm 0.107	2.416 \pm 0.139
Ω_A	3.912 \pm 0.101	4.554 \pm 0.102	1.306 \pm 0.070	1.602 \pm 0.093

The results of the permutational ANOVA analysing the growth rate of *Palythoa* spp. under experimental conditions, measured as variation in colony weight, showed significant differences at low pH for both species, whereas no differences were found between temperature treatments or within the interaction of factors (Table 2). Both *Palythoa* species experienced the greatest decrease in colony weight under the combined effects of low pH and high temperature (Fig. 2). In general, *P. aff. clavata* showed a decrease in colony weight in all experimental treatments (Fig. 2) but being more evident at pH 7.5 (-3.30 ± 0.71 g, Fig. 2). *P. caribaeorum* specimens that were kept at control pH (8.1 units) experienced an increase in colony weight regardless of the temperature (Fig. 2). Low pH showed to affect *P. caribaeorum* as colonies experienced a decrease in colony weight that was more severe at high temperature (-1.042 ± 0.29 g, Fig. 2).

Table 2: Results of the two-way permutational ANOVAs analysing differences in colony weight of *P. aff. clavata* (a) and *P. caribaeorum* (b) during the laboratory experiment at two different pH levels (7.5 and 8.1) and temperatures (22 and 26°C).

PERMANOVA					
Source	df	SS	MS	Pseudo-F	p (perm)
<i>(a) P. aff. clavata</i>					
Temperature (Te)	1	2.61	2.61	1.94	0.174
pH	1	70.08	70.08	52.09	0.001
Te x pH	1	3.98	3.98	2.96	0.100
Total	51	141.25			

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Table (Continued)

Source	df	SS	MS	Pseudo-F	p (perm)
<i>(b) P. caribaeorum</i>					
Temperature (Te)	1	17.14	17.14	1.33	0.279
pH	1	87.14	87.14	6.76	0.005
Te x pH	1	2.55	2.55	0.20	0.719
Total	40	571.12			

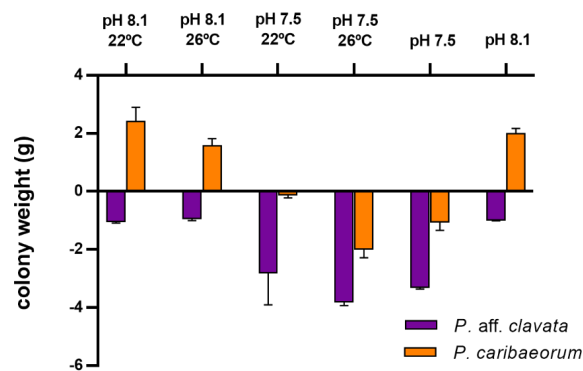


Fig. 2: Mean difference in colony weight (\pm SD) at each combined treatment of temperature (22 and 26°C) and pH (7.5 and 8.1 units) for *P. aff. clavata* and *P. caribaeorum* at laboratory experiments. Statistically different ($p < 0.01$) overall differences in colony weight at pH 7.5 and 8.1 for each species are also included.

Although measurements of *P. caribaeorum* colony area also showed a noticeable decrease in size at low pH ($-4.49 \pm 2.38 \text{ mm}^2$, Fig. 3), specimens appeared to be affected also by high temperature as only the colonies that grew at control conditions showed a slight increment in area ($0.29 \pm 1.78 \text{ mm}^2$, Fig. 3). However, the ANOVA assessing differences in *P. caribaeorum* coverage area at different environmental conditions only showed a significant effect of pH, while no effect of temperature or of the interaction of both factors was observed (Table 3).

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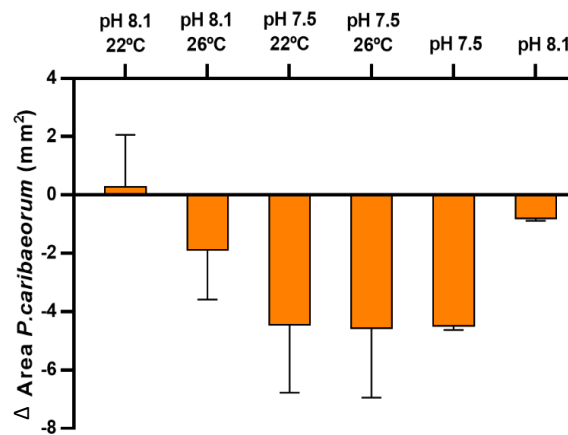


Fig. 3: Mean difference in colony coverage area (\pm SD) of *P. caribaeorum* at each combined treatment of temperature (22 and 26°C) and pH (7.5 and 8.1 units) at laboratory experiments. Statistically different ($p < 0.001$) overall differences in colony area at pH 7.5 and 8.1 are also included.

Table 3: Results of the two-way permutational ANOVAs analysing differences in colony coverage area of *P. caribaeorum* during the laboratory experiment at two different pH levels (7.5 and 8.1) and temperatures (22 and 26°C).

PERMANOVA					
Source	df	SS	MS	Pseudo-F	p (perm)
Temperature (Te)	1	11.68	11.68	2.86	0.099
pH	1	125.60	125.60	30.79	0.001
Te x pH	1	9.60	9.60	2.35	0.131
Total	38	299.69			

Experimental colonies of *P. aff. clavata* showed a slight decrease in chlorophyll a concentration (Chla) after 115 days under laboratory control condition. Values ranged from 99.99 ± 26.80 mg/m³ of Chla at specimen collection vs. 71.80 ± 48.93 mg/m³ at the end of the experiment, however these results were not significant ($F = 3.12$; $p = 0.107$). *P. caribaeorum* experienced an increase in Chla content, with 2.50 ± 3.76 mg/m³ at specimen collection vs. 6.92 ± 4.89 mg/m³ at the end of the experiment, but this increase was not significant ($F = 3.12$; $p = 0.107$).

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Results of the ANOVA analysing the differences in concentrations of Chla under experimental conditions showed a significant three-way interaction of factors “pH x Temperature x Time” for *P. aff. clavata* (Table 4). This result indicates that the effects of pH and temperature in the Chla content varied significantly across the course of the experiment. *A posteriori* pairwise analyses showed that after 31 days under experimental conditions, significant differences in Chla concentration between temperature treatments were found at pH 7.5, while no differences among temperature regimes were obtained at pH 8.1 (Table 5). There was an increase in Chla at pH 7.5 when colonies were kept at 26°C compared to 22°C (Fig. 4). Despite marginally non-significant differences, a trend towards higher Chla content was detected with increasing temperature at pH 8.1 at the end of the experimental conditions (Table 5, Fig. 4). Non-significant differences were obtained between temperatures at both pH treatments after 62 days of experiment (Table 5), although the lowest concentrations of Chla was registered in the combined effect of low pH and high temperature (Table 5, Fig. 4).

In the case of *P. caribaeorum*, ANOVA analysing differences in Chla concentration revealed significant differences in pH treatments, while no effects of temperature, time or the interaction between them were found (Table 4, Fig. 4).

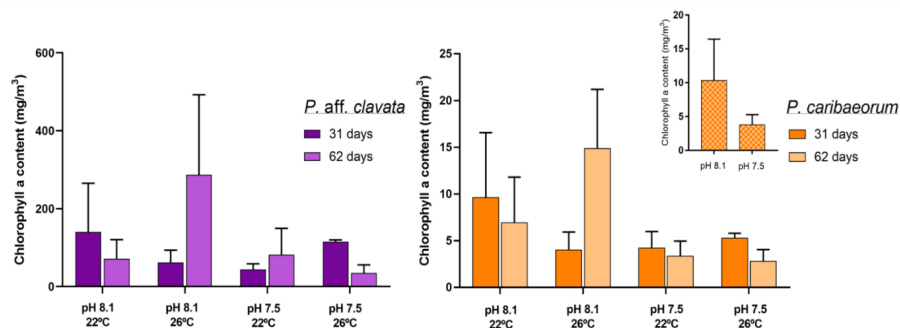


Fig. 4: Mean concentration of chlorophyll a (\pm SD) in *P. aff. clavata* (left) and *P. caribaeorum* (right) at each combined treatment of temperature (22 and 26°C) and pH (7.5 and 8.1 units) at laboratory experiments. Overall mean concentrations of chlorophyll a at pH 7.5 and 8.1 (upper right) are also included (statistically different only for *P. caribaeorum*, $p < 0.05$).

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Table 4: Results of the three-way permutational ANOVAs analysing differences in zooxanthellae chlorophyll a concentration of *P. aff. clavata* (a) and *P. caribaeorum* (b) at two different pH levels (7.5 and 8.1 units) and temperatures (22 and 26°C), considering two periods of time during the course of the laboratory experiment (at 31 and 62 days of experimental conditions commencement).

PERMANOVA					
Source	df	SS	MS	Pseudo-F	p (perm)
<i>(a) P. aff. clavata</i>					
Time (Ti)	1	4224.80	4224.80	0.51	0.490
pH	1	26493.00	26493.00	3.21	0.092
Temperature (Te)	1	8502.70	8502.70	1.03	0.342
Ti x pH	1	12757.00	12757.00	1.55	0.239
Ti x Te	1	9954.00	9954.00	1.21	0.302
pH x Te	1	4101.50	4101.50	0.50	0.503
Ti x pH x Te	1	55031.00	55031.00	6.67	0.023
Total	22	2.6296E+05			
<i>(b) P. caribaeorum</i>					
Time (Ti)	1	7.06	7.06	0.42	0.526
pH	1	117.41	117.41	7.06	0.023
Temperature (Te)	1	2.43	2.43	0.15	0.711
Ti x pH	1	39.76	39.76	2.39	0.148
Ti x Te	1	43.13	43.13	2.59	0.127
pH x Te	1	0.97	0.97	0.06	0.805
Ti x pH x Te	1	69.02	69.02	4.15	0.067
Total	20	540.09			

Table 5: Results of pairwise tests examining the significant interaction of factors “Time x pH x Temperature” obtained in the permutational ANOVA on chlorophyll a content of *P. aff. clavata* zooxanthellae during laboratory experiments.

	31 days				62 days			
	pH 7.5		pH 8.1		pH 7.5		pH 8.1	
<i>Pairwise tests</i>	t	p (perm)	t	p (perm)	t	p (perm)	t	p (perm)
22°C vs 26°C	6.48	0.021	0.87	0.480	1.32	0.238	2.08	0.09
	22°C		26°C		22°C		26°C	
<i>Pairwise tests</i>	t	p (perm)	t	p (perm)	t	p (perm)	t	p (perm)
pH 7.5 vs pH 8.1	1.08	0.399	2.36	0.137	0.24	0.814	2.52	0.052

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Bleaching status of the colonies, evaluated by frequency analyses of their color score, showed significant differences between the combination of pH and temperature treatments for both *P. aff. clavata* ($\chi^2= 51.95$; $p<0.01$) and *P. caribaeorum* ($\chi^2=47.83$; $p<0.01$). *P. aff. clavata* exhibited low values of card score, representing loss of color, in colonies that were kept at the low pH treatment and under the combined treatment of low pH and high temperature (Fig. 5). On the contrary, colonies kept at control pH and high temperature conditions showed values ranging from 4 to 6, which is associated with healthy colonies (Siebeck et al. 2006; Siebeck, Logan and Marshall 2008) (Fig. 5). *P. caribaeorum* specimens also showed low color scores at the pH treatment, while the highest values were obtained in colonies maintained at control pH and high temperature (Fig. 5). All colonies of *P. caribaeorum* that were kept at the combination of low pH and high temperature exhibited the lowest values of the color card after 62 days (Fig. 5).

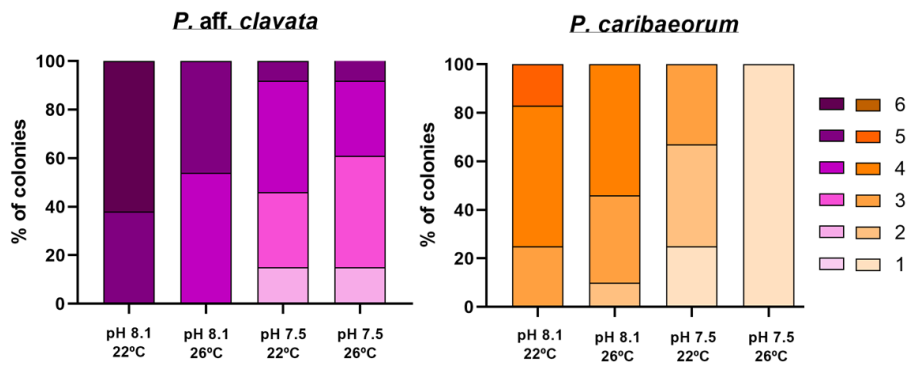


Fig. 5: Cumulative percentage of colonies of *P. aff. clavata* (left) and *P. caribaeorum* (right) at each color category (“CoralWatch Coral Health Chart” method) within each combined treatment of temperature (22 and 26°C) and pH (7.5 and 8.1), after 62 days under laboratory experiments. Color score categories: from 6 to 1 increasing bleaching of colonies, associated to a loss of health.

3. Predation experiments

Colonies of both *Palythoa* species showed an overall decrease in colony weight at experimental conditions with the predator *Platypodiella picta*, regardless the experimental treatment of temperature and pH applied. Specimens at control conditions without the predatory crab showed rather stable colony weights throughout the experimental period.

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Results of the permutational ANOVA analysing predation of *P. picta* upon *P. aff. clavata* showed a significant interaction of factors “*P. picta* vs. control x pH” (Table 6), meaning that colonies’ weight varied differently between conditions with and without the predator depending on the pH treatment (Fig. 6). *A posteriori* pairwise analyses showed a significant lower weight loss of colonies with crabs at pH 7.5 ($-1.64 \text{ g} \pm 0.56$) compared to those that were kept at pH 8.1 ($-4.26 \text{ g} \pm 1.80$) (Fig. 6, Table 7).

In general, colonies of *P. caribaeorum* suffered a loss of weigh in all experimental treatment analysed when *P. picta* were present ($-2.50 \pm 1.44 \text{ g}$) compared with colonies without the crab, whose weight remained relatively stable ($-0.73 \pm 0.93 \text{ g}$) (Fig. 6). Results of the 3-way permutational ANOVA analysing the susceptibility of *P. caribaeorum* to be predated by *P. picta* at different combination of pH and temperature confirmed these results as only the factor “*P. picta* vs. control” showed significant differences, while no effects of factor temperature or pH or any interaction of these factors was detected (Table 6).

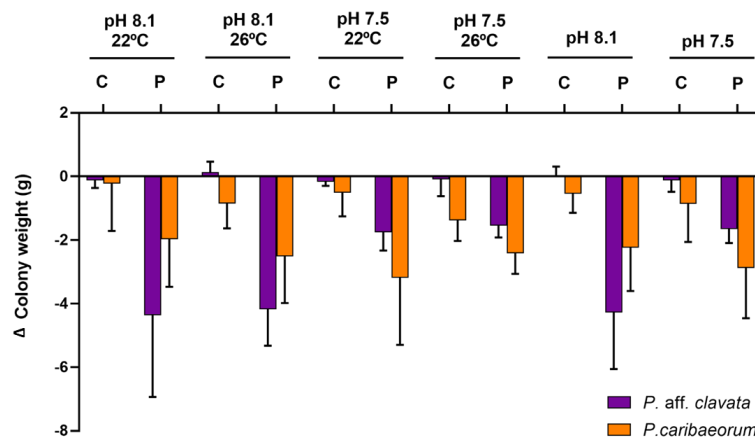


Fig. 6: Results of predation experiments with *P. aff. clavata* and *P. caribaeorum*, showing mean differences in colony weight (\pm SD) after 6 days of exposure to the crab *Platypodiella picta* (P: experimental colonies) and to control conditions without crab (C: control colonies), at each combined treatments of temperature (22 and 26°C) and pH levels (7.5 and 8.1 units). Overall mean differences in colony weight at pH 7.5 and 8.1 for both species at each predation treatment are also included (statistically significant interaction of factors only for *P. aff. clavata*, $p < 0.001$).

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Table 6. Results of the three-way permutational ANOVA analysing differences in colony weight of (a) *P. aff. clavata* and (b) *P. caribaeorum* at predation experiments with the predatory crab *Platypodiella picta* (“*P. picta* 1 vs. control”, 2 levels), conducted at different pH levels (7.5 and 8.1 units) and temperature conditions (22 and 26°C) during 6 days.

<i>PERMANOVA</i>					
(a) <i>P. aff. clavata</i>					
Source	df	SS	MS	Pseudo-F	p (perm)
<i>P. picta</i> vs. Control	1	57.34	57.34	62.06	0.001
pH	1	10.78	10.78	11.66	0.002
Temperature	1	0.21	0.21	0.22	0.659
Pp vs. C x pH	1	12.88	12.88	13.94	0.001
Pp vs. C x Te	1	0.03	0.03	0.01	0.951
pH x Te	1	0.01	0.01	0.01	0.920
Pp vs. C x pH x Te	1	0.02	0.02	0.01	0.910
Total	27	96.77			
(b) <i>P. caribaeorum</i>					
<i>P. picta</i> vs. Control	1	16.87	16.87	11.16	0.005
pH	1	1.24	1.24	0.82	0.386
Temperature	1	0.53	0.53	0.35	0.569
Pp vs. C x pH	1	0.03	0.03	0.02	0.887
Pp vs. C x Te	1	1.01	1.01	0.67	0.434
pH x Te	1	0.40	0.38	0.25	0.628
Pp vs. C x pH x Te	1	0.79	0.79	0.52	0.477
Total	21	43.94			

Table 7. Pairwise tests examining the significant interaction of factors “*P. picta* vs. control x pH” at predation experiments with the predatory crab *Platypodiella picta* in *P. aff. clavata*.

Pairwise tests	pH 7.5		pH 8.1		
	t	p (MC)	t	p (MC)	
<i>P. picta</i> vs. Control	6.42	0.003	6.13	0.001	
		<i>P. picta</i>		Control	
pH 8.1 vs. 7.5	t	p (MC)	t	p (MC)	
	3.12	0.014	0.66	0.526	

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Discussion

Results of this study revealed species specific responses of corals of the genus *Palythoa* to the combined effects of temperature and pH ranges expected for a future climate change scenario within a subtropical region. High temperature and low pH seemed to affect host and their symbiont in different ways. Contrary to what was expected for coral species without carbonate in their body wall, low pH had greater effect than temperature in both organisms' fitness. In general, *Palythoa caribaeorum* was shown to be less resistant than *P. aff. clavata* considering both survival rates of colonies in laboratory conditions and effects over its Symbiodiniaceae.

We generally found high survival rates (>66 %) of both *Palythoa aff. clavata* and *P. caribaeorum* to the climate change stressors set in the laboratory. While survival of *P. aff. clavata* showed no effect of environmental conditions, the survival of *P. caribaeorum* was found to be lower at the combined conditions of low pH and ocean warming. Five colonies of the latter species died during the course of the experiment, showing species-specific responses. Intertidal habitats are one of the most stressful environments for marine organisms due to the severe daily and seasonal fluctuations of abiotic conditions such as temperature, salinity and pH (Truchot 1988; Helmuth et al. 2006). Despite *P. aff. clavata* is common and abundant in the intertidal zone (chapter 2) and then, it experiences such drastic changes in environmental conditions, our results showed that after a long term exposure to constant low sea water pH levels, colonies showed detrimental effects in their growth rates. Negative effects of pH in growth rates were also evident in the case of subtidal colonies of *P. caribaeorum*, which also displayed a reduction in colony area. Such effects were seen at both temperatures considered, control and sea water warming conditions, while just increases in sea water temperature (temperature treatment) did not render consequences to any of the coral host species. In contrast to *P. caribaeorum*, experimental colonies of *P. aff. clavata* experienced weight loss both at control and temperature treatments, suggesting suboptimal conditions during the experiment.

It has been found that colonies of *Zoanthus sociatus* that inhabit intertidal habitats show lower photochemical efficiencies (F_v/F_m) than colonies of the subtidal zone and despite the higher chlorophyll a content (Leal et al. 2015). In the same way, in *P. caribaeorum* F_v/F_m was lower in cyclically emerged polyps than polyps of the same

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colony that were always immersed (Rosa et al. 2016). Main carbon supplier of healthy cnidarians are their symbionts but under environmental stress the host can change main feeding source from autotrophy to heterotrophy (Gustafsson et al. 2013). Taking this in consideration, intertidal colonies of *P. aff. clavata* that experience daily exposure during low tide may need more energetic resources provided by heterotrophy compared to subtidal colonies of *P. caribaeorum*. Future studies should consider such habitat differences and heterotrophic conditions in order to achieve optimal laboratory settings. Despite this likely deficit in energetic requirements, colonies of *P. aff. clavata* kept at control and temperature treatments not only showed active polyps and the common coloration of the species, but also weight loss was three and four times lower than colonies kept at low pH and climate change conditions, respectively. This demonstrated that colonies were in healthy conditions despite the slight decrease in growth rate.

The main effect of ocean acidification on biological components of marine systems is related to the loss of carbonate available in sea water for calcifying organisms, including hard corals (McCulloch et al. 2012), and many other organisms (Andersson et al. 2008; Agostini et al. 2018). Despite *Palythoa* spp. do not have calcareous skeletons, growth rates of both species were strongly affected by the decrease in pH to levels of 7.5 units. It has been shown that changes in pH conditions not only reduce calcifications rates but it also alters many physiological mechanisms in marine species (Arnold et al. 2012; Li and Gao 2012). In fact, predicted models based on habitat suitability of *P. caribaeorum* suggested that 7.85 units of pH might be a barrier to the distribution pattern of this species in the West Atlantic (Durante et al. 2018). Biological performance of zooxanthellate zoantharians is highly mediated by the status of their symbiont, since species sustenance strongly depends on nutrients photosynthesized by Symbiodiniaceae. Then, reduction in growth induced by low pH levels in *Palythoa* spp. could be related to detrimental effects over densities and/or photosynthetic activity of symbiotic dinoflagellates, as it has been previously found in both soft (Michalek-Wagner and Willis 2001) and hard corals (Porter et al. 1989). *Palythoa* spp. in the Canary Islands have been shown to host symbionts belonging to *Cladocopium* (formerly clade C, LaJeunesse et al. 2018), regardless depth or location (López et al. 2019 - chapter 1). Although we did not examine the symbiont type, due to the fact that all *Palythoa* species inhabiting in the Macaronesia and Cape Verde ecoregions have *Cladocopium* (López et al. 2019 – chapter 1), we may assume that experimental colonies also hosted this genus of symbiont. *Cladocopium* members are the

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most abundant and widely distributed genus within the family Symbiodiniaceae and are adapted to a wide range of temperatures and irradiances (LaJeunesse et al. 2005, 2018). This is in concordance with results of our study, in which symbionts of the experimental colonies of both *Palythoa* species were more vulnerable to low pH than to high temperatures and, in fact, the highest concentrations of Chla were reached at 26°C and control pH levels. Despite the general vulnerability of Symbiodiniaceae to changes in temperature beyond thermal tolerance limits (Glynn 1996; IPCC 2007), intrinsic characteristics and differences in abundance and heterogeneity of dinoflagellates types play a crucial role to overcome these effects (Fay and Weber 2012; Yorifuji et al. 2017).

It has been found that some autotrophic organisms are able to utilize both CO₂ and HCO₃⁻ by means of carbon-concentrating mechanisms (CCMs) catalysed by the enzyme carbonic anhydrase (CA) (Sültemeyer 1998; Kaplan and Reinhold 1999; Leggat et al. 1999) as an offset against low level of dissolved CO₂ available for photosynthesis (Badger and Price 2003; Giordano et al. 2005). CCMs vary in their efficiency depending on the taxonomic group (Tortell 2000; Giordano et al. 2005), even among different genera of Symbiodiniaceae (Brading et al. 2011). Previous studies have shown that the activity of the CA of *P. aff. clavata* and their symbiont, which also belong to *Cladocopium* genus (formerly clade C), was not affected by high temperature and enzyme activity decreased at low pH in the dinoflagellate but not in host tissues (Graham et al. 2015). In some cases, it has been shown that acidification reduces algal cell densities (Graham and Sanders 2015; Graham et al. 2015; Manson 2018) and may explain the decreased Chla content recorded at low pH in the present study for *P. caribaeorum*. In *P. aff. clavata*, increased levels of Chla were observed at the combined conditions of low pH and high temperatures compared to control temperature only after 31 days of experimental conditions. These results show that higher temperatures compensate the negative effects of lowered pH in Chla content, as high temperatures can lead to a proliferation in cell numbers (Dimond and Carrington 2007, 2008; Graham and Sanders 2015; Graham et al. 2015). However, after 62 days of maintaining *P. aff. clavata* colonies at predicted climate change conditions for the Canary Islands, no such effect persisted and a detrimental effect was observed at a longer term, with a drop in Chla. Despite both *Palythoa* spp. hosted *Cladocopium* spp., it seems that symbiotic dinoflagellates hosted by *P. aff. clavata* were able to adapt to these drastic changes in sea water conditions at least during short periods of time. In the case of *P. caribaeorum*, the effect of pH was more severe and regardless

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of time no effect of temperature regimes on Chla concentrations was observed during the experiment, despite the tropical affinities of the species. It has been demonstrated that different species of *Cladocopium* (formerly subclades) can be greatly adapted to different environmental conditions (LaJeunesse et al. 2018). For example, subclade C15 is more tolerant to high levels of temperature and irradiance than C1, which is considered as generalist (LaJeunesse et al. 2003, 2005). The stable conditions of the subtidal zone might lead to *P. caribaeorum* hosting a symbiont subtype less adapted to drastic changes in abiotic conditions in comparison to *P. aff. clavata* inhabiting intertidal changing environments, explaining the differences among species.

The negative effect of low pH in experimental colonies was also confirmed with color health chart results, in which the color of a colony is correlated to its zooxanthellae density and/or chlorophyll content (Siebeck et al. 2006; Siebeck, Logan and Marshall 2008). Colonies of both *Palythoa* species that were kept at 7.5 pH units experienced loss of color but being more severe in *P. caribaeorum*. The effect of low pH was aggravated with the combined effect of high temperature and colonies exhibited loss of color of more than 2 units of the scale. Once again *P. caribaeorum* demonstrated to be less resistant as all the experimental colonies that grew under climate change stressors showed the lowest values of color score registered. On the other hand, colonies kept at control pH and high temperature conditions showed higher color score, which are related to higher concentrations in Chla (Reimer et al. 2007a). Coral color chart has been demonstrated to be an effective method for distinguishing between bleached colonies and colonies in a good health status in scleractinian corals (Siebeck et al. 2006). In zoantharians color variation is much more common (Burnett et al. 1995; Reimer et al. 2004; López et al. 2019 – chapter 1), which could make the monitoring of populations with this method difficult (Parkinson et al. 2016). However, in this study color chart revealed to be a useful tool to track changes of individual colonies through time.

Many sessile marine invertebrates produce toxic metabolites to avoid predation and outcompete other species, especially soft-bodied organisms which lack of structural protection (Tanner 1995; Marty and Pawlik 2015). The fact that few predators are able to feed on zoantharian species might be related to the efficiency of their chemical defences that include nematocyst and highly potent toxins known as palytoxin (Chanas and Pawlik 1995; O’Neal and Pawlik 2002; Hines and Pawlik 2012). However, coevolutionary

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processes may lead to certain predators that are highly adapted to feeding from specific preys despite their high toxin contents, such as some nudibranch slugs that eat specific sponges (Proksch 1994; Cheney et al. 2016) or obligate coral-feeding fish species (McIlwain and Jones 1997; Rotjan and Lewis 2008) or the *P. picta*-zoantharia association described here. Results of this study support these previous findings (Den Hartog and Holtuis 1984) since *P. picta* was able to actively feed on both *Palythoa* spp., which showed significant decrease in colonies' weight in short periods of 6 days. Moreover, we have shown that simulated low pH conditions decreased the rate of consumption on *P. aff. clavata* by the crab. Given that the species lacks structural defences that could be damaged by acid conditions, this is probably a result of changes in palatability of colonies mediated by alteration in chemical defences. The large variability in the concentration of palytoxin found in zoantharians suggest that the toxin is produced only under specific environmental or genetic conditions (Seemann et al. 2009). In fact, it has already been demonstrated that high concentrations of CO₂ promote chemical changes in carbon-based secondary metabolites both in terrestrial (Peñuelas and Estiarte 1998) and marine plants (Arnold et al. 2012). Because palytoxin is a non-protein molecule composed of a long carbon chain, variations in CO₂ content might also contribute to changes in its biosynthesis (Peñuelas and Estiarte 1998). The biogenetic origin of palytoxin is still unclear. Some authors have suggested a bacterial source (Moore et al. 1982; Seemann et al. 2009) while other supported the production of palytoxin by symbiotic dinoflagellates (Nakamura et al. 1993; Onodera et al. 2004). Results of this study do not agree with the latter since lower pigment concentration, as a proxy of dinoflagellates abundances, was obtained at low pH. Similar mismatch between Chl_a and palytoxin production has been previously found (Gleibs et al. 1995), although more accurate analyses need to be performed in order to shed light into the source of toxin production. In fact, previous studies have shown that *P. aff. clavata* is 90% more toxic than *P. caribaeorum* (Béress et al. 1983; Sawelew et al. 2018), which could explain the active consumption upon *P. caribaeorum* by the crab regardless the experimental environmental conditions.

In the last years, land and sea water temperature have been increasing due to the effects of climate change. In the tropics, temperature is predicted to exceed the thermal threshold for many coral species and, if they are not able to acclimate, changes in species and coral reefs distribution will probably occur (Hoegh-Guldberg 1999). In this context of biota reorganization, zoantharian species have demonstrated to be more resistant and,

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in fact, they are increasing their populations causing phase-shifts in many coral reef ecosystems (Cruz et al. 2016a, b). Even in the case of the subtropical region of the Canary Islands, *Palythoa* spp. are in current population expansions and some populations of *P. caribaeorum* are able to cover huge extensions in the subtidal zone (chapter 2). However, results of this study have shown that temperature and pH values forecasted by IPCC 2013 may affect the viability of *Palythoa* populations in the Canary Islands in terms of survival and growth rates. However, this detrimental effect over *Palythoa* populations could be compensated, in some way, with a reduction in predation rates. Predicting the response to combined climate-change stressors not only of a single species but also through indirect processes that can lead to cascading effects (Brook et al. 2008; Bellard et al. 2012) has become an urgent field of research to properly establish protection management decisions. However, the results of this study highlight the difficulty of making accurate predictions due to the fact that warming ameliorates or aggravates the effects of acidification at different levels and at different time scales. What is more, many other factors should be simultaneously considered, such as salinity, turbidity or nutrient concentration that could also interplay in the outcomes of climate change processes.

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Studies within this thesis contribute to a better understanding of the diversity, biology and ecology of Zoantharia Suborder Brachycnemina in the Canary Islands, which are very common organisms that had been previously understudied in this subtropical location. Additionally, the potential of *Palythoa* aff. *clavata* and *P. caribaeorum* (López et al. 2019 – chapter 1) as bioindicators of ocean warming in the subtropical region of the Canary Islands is demonstrated (chapter 2 and 3). Species' patterns of distribution along the thermal gradient of the Archipelago, as well as results of our long-term combined experiment, showed their affinities for warmer waters and the potential of their populations to increase in a future ocean warming scenario (chapters 2 and 3). Furthermore, the results of this thesis can be extrapolated to other regions around the world as the combined phylogenetic and morphological analyses have clarified that Zoantharia species inhabiting the Canary Islands are, in fact, common species in the Atlantic Ocean (López et al. 2019 – chapter 1). This is crucial in the current context of climate change and human impacts over marine communities, in which key species can aid to early detect alterations in their structure and mitigate loss of ecosystem functions.

The western and eastern basins of the Atlantic Ocean are well connected by the Gulf Stream that branches into the Canary Current and the North Equatorial Countercurrent, which act as potential dispersal routes for marine organisms (Boekschoten and Best 1988; Nunes et al. 2011; Freitas et al. 2013; López et al. 2015). All Zoantharia Brachycnemina species found in the East Atlantic are shared with the West Atlantic (Reimer et al. 2010, 2012a; López et al. 2019 – chapter 1), showing the Caribbean region the highest richness of species (Santos et al. 2019). Then, we might presume a west-to-east colonization process from the Caribbean to the East Atlantic, as found in many other organisms (Boekschoten and Best 1988; Muss et al. 2001; Reimer et al. 2010; López et al. 2019 – chapter 1). Additionally, since the Pacific Ocean shows the highest level of brachycnemic zoantharian diversity in terms of both genera and species numbers, we might consider it as the biodiversity source of zoantharians. This biogeographic pattern has been previously described in many other marine taxa such as hard corals (Veron et al. 1995, 2009) and tropical fishes (Floeter et al. 2008). However, and in contrast to other taxonomic groups, species from the Atlantic and the Pacific are still morphologically and molecularly closely related, with sister species shared among both oceans (Reimer et al. 2010, 2012a; López et al. 2019 – chapter 1). This may be related to the high intrinsic dispersion abilities of members of the group (Ryland et al.

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2000; Polak et al. 2011) and to biogeographical processes such as the emergence of the Isthmus of Panama that isolated widely distributed zoantharian species into two separated populations (Coates and Obando 1996; Reimer et al. 2012a).

Based on morphological features, previous studies had suggested the occurrence of nine Zoantharia, Suborder Brachycnemina, species in the Canary Islands, with four endemic species (Brito 1984). However, results of the extensive surveys conducted within this study confirmed at least five brachycnemic species inhabiting the Archipelago, all of them shared with the West Atlantic: *Isaurus tuberculatus*, *Zoanthus pulchellus*, *Palythoa caribaeorum*, *P. aff. clavata* and *P. grandiflora* (López et al. 2019 – chapter 1). Their distributions in the intertidal zone of the Canary Islands were very variable and species-specific, and only populations of *P. aff. clavata* and *P. caribaeorum* seemed to be temperature dependent (chapter 2). In the case of *P. caribaeorum*, apart from the three intertidal populations already known in the Archipelago since 1980 (Arechavaleta 2009), throughout the course of this study a new colony was found in El Médano, south-eastern coast of Tenerife (chapter 2). Furthermore, repeated surveys showed that the population at the south-western coast of Tenerife is currently increasing, with four new colonies recorded during the last years (2017-2019) (pers. comm.). Fluctuations in the abundance and distribution of intertidal organisms from accessible shorelines are useful to monitor the effects of changes in climate, as these communities are easy to observe at long-term (Mieszkowska et al. 2019). The restricted intertidal distribution of *P. caribaeorum* in the Canary Islands, always related to locations that experience local increases in sea water temperature (chapter 2), and the fact that *P. aff. clavata* prevail in warmer environments of the western islands (chapter 2), suggest that these species might become more abundant in a future ocean warming scenario (Fig. 1). In fact, results of our long-term experiment controlling sea water temperature and pH demonstrated that both species are favoured by the increase in sea water temperature expected to be reached in 2100 for the Canary Islands region (chapter 3).

Ecological implications of the increased population success of zoantharians still need to be disentangled, but available information and biological characteristics of the species support the idea of a significant alteration of marine communities (Cruz et al. 2015; Cruz et al. 2016a). It has been demonstrated that the replacement of macroalgae

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communities by colonies of *P. aff. clavata* is able to modify the composition of associated mesofauna (González-Delgado et al. 2018). However, given the specific growth strategy of the species, showing discrete colonies usually covering areas less than 2 m² (chapter 2), we expect that expansions of *P. aff. clavata* populations will help us to early detect the effects of ocean warming without *a priori* compromising the whole structure of the Canary Islands' ecosystems. However, this does not seem to be the case of *Palythoa caribaeorum*. This species is able to cover huge extensions of rocky substrates, of even more than 100 m² in subtidal locations, where it completely modifies macroalgae dominated landscapes of the Islands (chapter 2) (Fig. 1).

The Canarian Archipelago constitutes one of the few examples in the world in which proliferations of *P. caribaeorum* populations to the detriment of macroalgae-dominated systems have been reported. This is specially worrying in the current context in which the intense overfishing lead to the expansions of herbivore sea urchins' populations that promote the establishment of barren grounds due to their intense grazing (Hernández et al. 2008; Clemente et al. 2010). These barrens could be facilitating the settlement of *P. caribaeorum* as they leave space free of erect macroalgae, main benthic competitors for space and resources (Tanner 1995; Rabelo et al. 2007; McClanahan et al. 2012) (Fig. 1). Similar processes facilitating scleractinian corals settlement by sea urchin grazing has been extensively documented within coral reefs ecosystems (Edmunds et al. 2001; Idjadi et al. 2010). Under decreased herbivorous pressure, phase-shifts processes that transform coral reefs to algal dominance have been widely studied (Vergés et al. 2014), but studies analysing phase-shifts to zoantharian species are still scarce despite emerging during the last years (Yang et al. 2013; Cruz et al. 2015). Specifically, nothing is known about their relevance at temperate and subtropical regions where macroalgae are the main structuring components of marine communities. We could assume that phase-shifts from macroalgae to *P. caribaeorum* communities, mediated by climate change, overfishing that promotes proliferation of grazers, and other human impacts (Fig. 1), would cause a loss of biodiversity due to the reduction of free space (Fig. 1). The ability of mat-forming colonial zoanthids, such as *P. caribaeorum*, to reduce the complexity of the substrata decreasing the space and number of refuges available for other benthic organisms (Fig. 1) has been already reported, with severe declines of some associated species (Mendoza-Neto 2008; Cruz et al. 2015, 2016a). However, future

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studies are necessary to assess the effect of *P. caribaeorum* on the Canary ecosystems as well as its potential to compete against main macroalgae species.

Predicting the fate of zooxanthellate organisms requires taking in consideration both members of the holobiont. Symbionts of *P. aff. clavata* and *P. caribaeorum* kept at 26°C, temperature expected to be reached in the Canary region by 2100 (IPCC 2013), showed an increment of chlorophyll a content (chapter 3) that can potentially enhance photosynthetic rates, resulting in increased nutrient supply for the host (Joyce et al. 2003). Recent phylogenetic analyses have demonstrated that *Palythoa* spp. from Madeira to Cape Verde, regardless depth or location of origin, hosted subclade C1 of the symbiont (López et al. 2019 – chapter 1), which belongs to the genus *Cladocopium* (LaJeunesse et al. 2018). Subclade C1 has been described as generalist, living in a variety of environments and hosts, and less adapted to high temperatures and irradiance regimes (LaJeunesse et al. 2005; Reimer et al. 2006a).

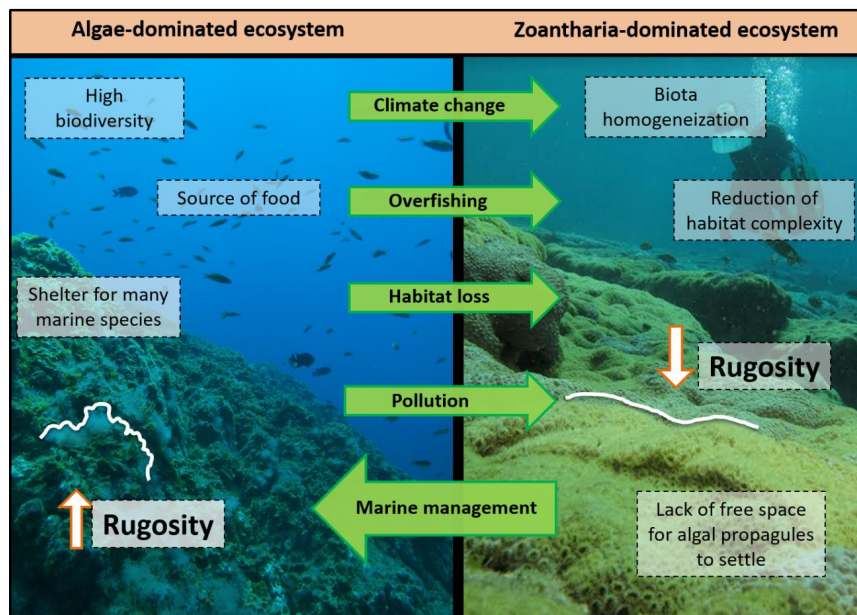


Fig. 1: Conceptual model of the phase-shift from macroalgae to Zoantharia dominated ecosystems under a climate change and human impacts scenario.

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However, even intertidal *Palythoa* spp. from the tropical area of Cape Verde hosted C1, indicating a great tolerance to wide environmental conditions of the holobiont. This could be related to the ability of members of the family Sphenopidae to incorporate sand and detritus in their body walls (Mueller and Haywick 1995), which might decrease the intensity of UV light that impinge the symbionts. This physical mechanism against UV light has already been reported for anemones and sea urchins, which are able to regulate irradiance levels by covering themselves with fragments of rocks and shells (Dykens et al. 1984; Kehas et al. 2005). Additionally, the great tolerance to changes in environmental conditions along the latitudinal gradient of the Canary Islands (López et al. 2019 – chapter 1), and even under experimental ocean warming conditions (chapter 3), could be related to the species' mixotrophic feeding strategies that may act as an alternative mechanism to increase the source of energy obtained by heterotrophy under adverse situations (Baird et al. 2009). However, we demonstrated that low pH levels affected both *Palythoa* aff. *clavata* and *P. caribaeorum*, showing a significant bleaching and weight loss in their colonies after long exposures (chapter 3), despite being traditionally considered robust to acidification given the lack of carbonate in their body walls (Reimer et al. 2008b). In this sense, the long-term combined effects of high temperature and low pH levels expected for the year 2100 could negatively affect the survival of *Palythoa* spp. if species are not able to adapt. Despite acidification levels forecasted for next century would probably have severe impacts in marine systems, nowadays the most evident effect of climate change is increasing ocean temperatures, which are already triggering changes in marine communities (Harley et al. 2006). In this sense, *Palythoa* spp. in the Canary Islands are good indicator species of ocean warming in the upcoming years. Monitoring the status and local spread of their populations throughout the Archipelago could give important insights about the effects of this climate change process.

Predicting species distribution is becoming imperative for marine biodiversity management that lead to environmental conservation (Austin 2002; D'heygere et al. 2003; Liu et al 2005; Acosta et al. 2016; Durante et al 2018). Distributions of Zoantharia brachycnemic species in the East Atlantic follow the general latitudinal gradient of increasing biodiversity towards the equator (Allen et al 2002; Willig et al. 2003), with at least one species inhabiting Madeira, five in the Canary Islands and seven in Cape Verde (López et al. 2019 – chapter 1). In the actual context of a general tropicalization of the

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General Discussion

marine biota, we can expect that zoantharian species that are currently restricted to Cape Verde would be able to settle populations in the Canary Islands, favoured by an increase in sea water temperature. Similar range expansions have been recently recorded with other species, such as the fire coral *Millepora alcicornis* (López et al. 2015). The species distribution modelling confirmed its potential expansion to higher subtropical and temperate latitudes of minimal temperatures $>16^{\circ}\text{C}$ (Rodríguez et al. 2018). Similar species distributions models have been applied to *Palythoa caribaeorum* from the West Atlantic, which is currently distributed between 30°N to 30°S but is expected to northward expand its populations under mild climate change scenarios (Durante et al. 2018). It has been suggested that temperate regions such as the Canaries would act as potential refuges for tropical species from the effect of ocean warming (Kumagai et al. 2017). In this sense, we might expect a future biota in the Archipelago similar to that nowadays found in Cape Verde, where hard corals and zoantharians cohabit (Morri and Bianchi 1995; Morri et al. 2000). However, intrinsic characteristics of zoantharians, such as the long-lived pelagic larvae (Ryland et al. 2000), could facilitate them to early arrive and proliferate instead of scleractinian species, which otherwise might efficiently compete with zoantharians for space and resources (Rabelo et al. 2013). In fact, only one location where zoantharians species dominate the rocky bottom in Cape Verde has been found until now (López et al. 2018), in contrast to seven subtidal locations already known in the Canary Islands (Martín-García et al. 2013; chapter 2).

Local conservation efforts can greatly enhance the resilience of marine communities helping to mitigate the global issue of climate change (Fig. 1). Results provided by this thesis reinforce the idea that any future monitoring program should include broad exploratory surveys even in locations where *P. aff. clavata* and *P. caribaeorum* have not been found yet. Recording the establishment of new colonies of these species could reveal degraded areas due to climate change or human impacts. Given that *P. aff. clavata* and *P. caribaeorum* are widespread species, easy to find and long-lived, joint monitoring programs are easy to establish among different regions in order to compare trends in biodiversity changes. In our study region, surveys might include Madeira Island, as the northernmost site of indicator species distributions, where only two intertidal colonies of *P. aff. clavata* have been recorded until now. In fact, we believe that the Macaronesia and Cape Verde ecoregions, considered as a whole, constitute an

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General Discussion

ideal emplacement to establish a network for monitoring these bioindicator species, in order to trace the effects of climate change on marine communities.

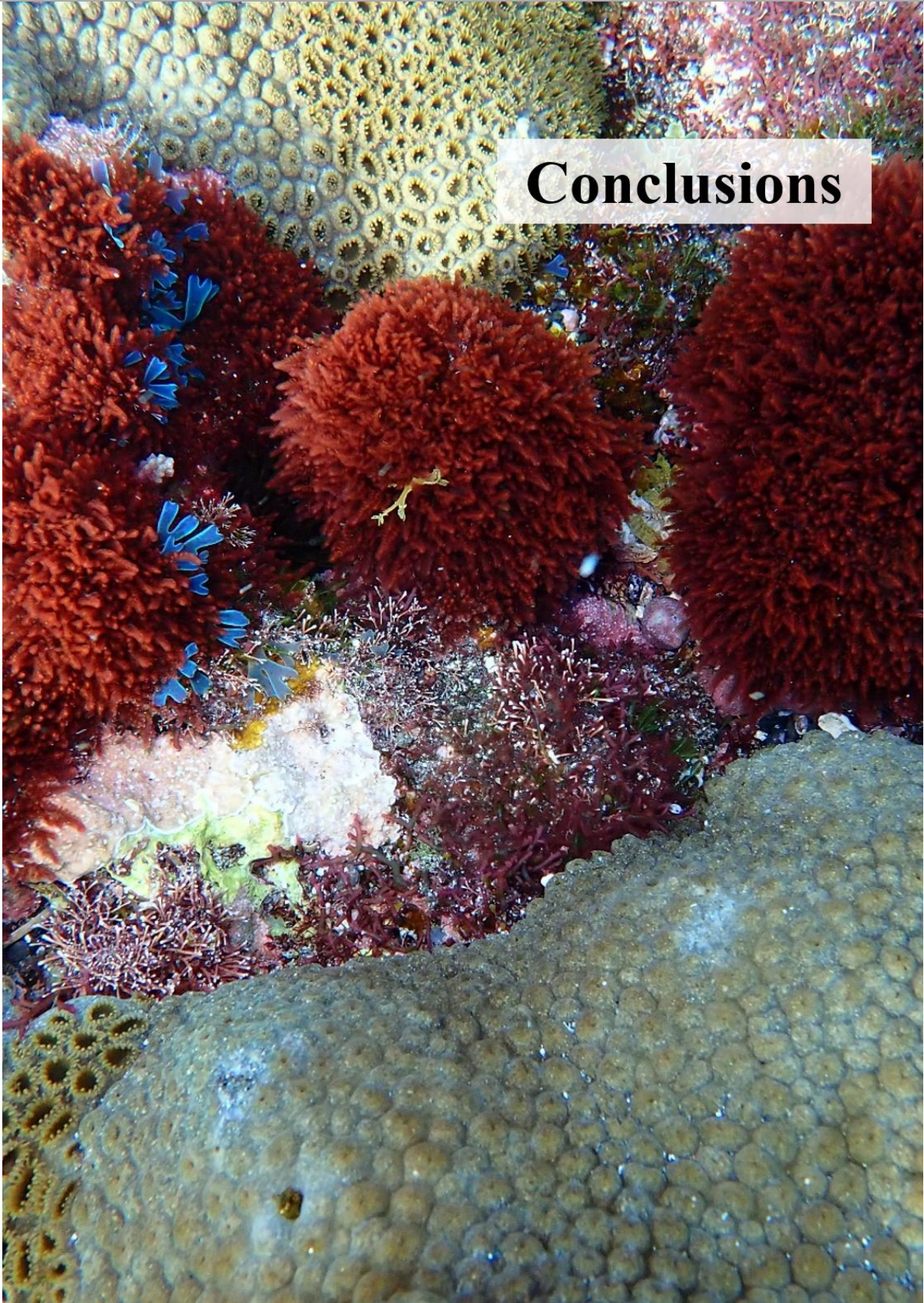
Future monitoring

Results from this thesis provide new insight into many aspects of Zoantharia communities within the Canary Islands, however it also highlights the need for many other investigations, specially in terms of their potential to act as key structuring species under the on-going climate change context. Studying fauna and flora components found within Zoantharia-dominated systems, and comparing them with different native macroalgae-dominated ecosystems, could help elucidate the consequences of expected zoantharian blooms in upcoming years for whole marine communities. Furthermore, space competition experiments could help determine which macroalgae communities are more susceptible to be replaced by zoantharians in order to set appropriate conservation actions and mitigate the projected changes. Detecting most vulnerable species and communities will undoubtedly help in any conservation decision making. Apart from assessing biotic interactions, there is a need to explore the effects of abiotic factors upon Zoantharia populations and their influence in species distributions, such as salinity, nutrients and oxygen concentrations. These abiotic parameters, combined with the information gathered by visual surveys of populations, could be used to generate species distribution models to accurately forecast changes in zoantharians populations under a climate change scenario.

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Conclusions

1. Morphological features combined with genetic analyses showed that the biodiversity of Zoantharia from the East Atlantic increases as sea water temperature rises towards the tropics, with one species inhabiting in Madeira, five in the Canary Islands and seven in the Cape Verde Archipelago. The species *Palythoa grandis*, *P. aff. clavata*, *P. grandiflora*, an unknown *Zoanthus* species and *Z. pulchellus* were recorded for the first time in the East Atlantic Ocean.

2. Despite the large phenotypic plasticity within Zoantharia species, oral disk diameter, number of tentacles and colony and polyp shape have demonstrated to be useful characters to delimitate Brachycnemina species from the Macaronesia and Cape Verde ecoregions. However, phylogenetic analyses confirmed that other features such as color or polyp height do not have taxonomic value, showing high phenotypic variation depending on environmental conditions.

3. The concatenated phylogenetic tree of mitochondrial cytochrome oxidase subunit I (COI) and 16S ribosomal DNA (16S-rDNA) genes had enough resolution to delineate members of the family Zoanthidae (*Zoanthus* and *Isaurus*). All representatives of the same species showed the same sequences for both genes (COI and 16S-rDNA) and grouped into well-supported clades that included members from the Atlantic and the Pacific Oceans.

4. Delimitation of species within the family Sphenopidae (*Palythoa*) required less conservative molecular markers such as the internal transcribed spacer rDNA (ITS-rDNA). For this fragment, the individuals belonging to the same species formed a well-supported clade that included specimens collected in both Eastern and Western Atlantic and their sister species from the Pacific Ocean, highlighting the low genetic variability of zoantharian species even for molecular markers with high mutational rates.

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5. All colonies of zoantharians analyzed around the Macaronesia hosted a generalist algal symbiont belonging to the genus *Cladocopium* (family Symbiodiniaceae) regardless the species, depth of collection and sampling location, with no effect of the marked gradient of sea water temperature among and within regions of the Macaronesia.

6. Most zoantharian specimens from Cape Verde Islands hosted *Cladocopium* sp. but *Symbiodinium* sp. also occurred within colonies of *Zoanthus* spp., which could be an adaptation for living under high UV conditions.

7. Field surveys showed species-specific distribution patterns of zoantharian brachycnemic species along the Canary Islands, greatly depending on environmental conditions recorded in more variable intertidal habitats or in more stable subtidal habitats.

8. Zooxanthellate zoantharians in the intertidal zone of the Canary Islands showed a huge variability both in distributions patterns and populations densities, being *Palythoa* aff. *clavata* the most common species. On the contrary, *P. caribaeorum*, *P. grandiflora*, *Isaurus tuberculatus* and *Zoanthus pulchellus* showed isolated populations at specific locations.

9. Intertidal populations of *Palythoa* aff. *clavata* followed patterns of distribution related to oscillations of sea water temperature throughout the Canary Islands, being more widespread in Tenerife and El Hierro than in the coldest island of Lanzarote. On the contrary, populations of *P. caribaeorum*, *Zoanthus pulchellus* and *Isaurus tuberculatus* were more influenced by the size of intertidal rocky platforms.

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Conclusions

10. In Tenerife, *Palythoa caribaeorum* showed larger population sizes in the intertidal zone of the western coast, where sea water temperature reaches maximum values within the island. Furthermore, a new colony was recorded for the first time in the south-eastern coast of this Island, which may had been facilitated by the current ocean warming of the region.

11. In the subtidal zone of Lanzarote only colonies of *Palythoa* aff. *clavata* were found, demonstrating the tolerance of the species to the minimum values of sea surface temperature reached during winter months in this Island.

12. Subtidal populations of *Palythoa caribaeorum* inhabited only the western islands of La Palma, El Hierro, La Gomera and Tenerife, showing a clearly relationship with warmer environments. The species completely covered large extensions of rocky substrates, potentially compromising the viability of macroalgal benthic communities. The documented Zoantharia population spread constitutes one of the few cases occurring outside tropical regions and in macroalgae-dominated systems.

13. Results of the experimental study controlling sea water conditions demonstrated that *Palythoa* aff. *clavata* and *P. caribaeorum* will be favoured by the increase in ocean temperature forecasted for the year 2100 for the subtropical region of the Canary Islands. The baseline of the status of zoantharian populations established in this study will then allow future assessments aiming for interpreting trajectories of change in local ecosystems.

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Conclusions

14. Intertidal colonies of *Palythoa* aff. *clavata* resulted to be tolerant to changes in environmental conditions without compromising its survival, despite some detrimental effects such as bleaching, lower growth rates or reduction in chlorophyll contents. However, contrary to what was expected for a species without carbonate in their body wall, sea water acidification could have negative consequences for populations success.

15. Holobionts of *Palythoa caribaeorum* that are used to stable abiotic conditions of the subtidal zone, showed a lower resistance to combined climate change stressors, significantly reducing colonies' survival.

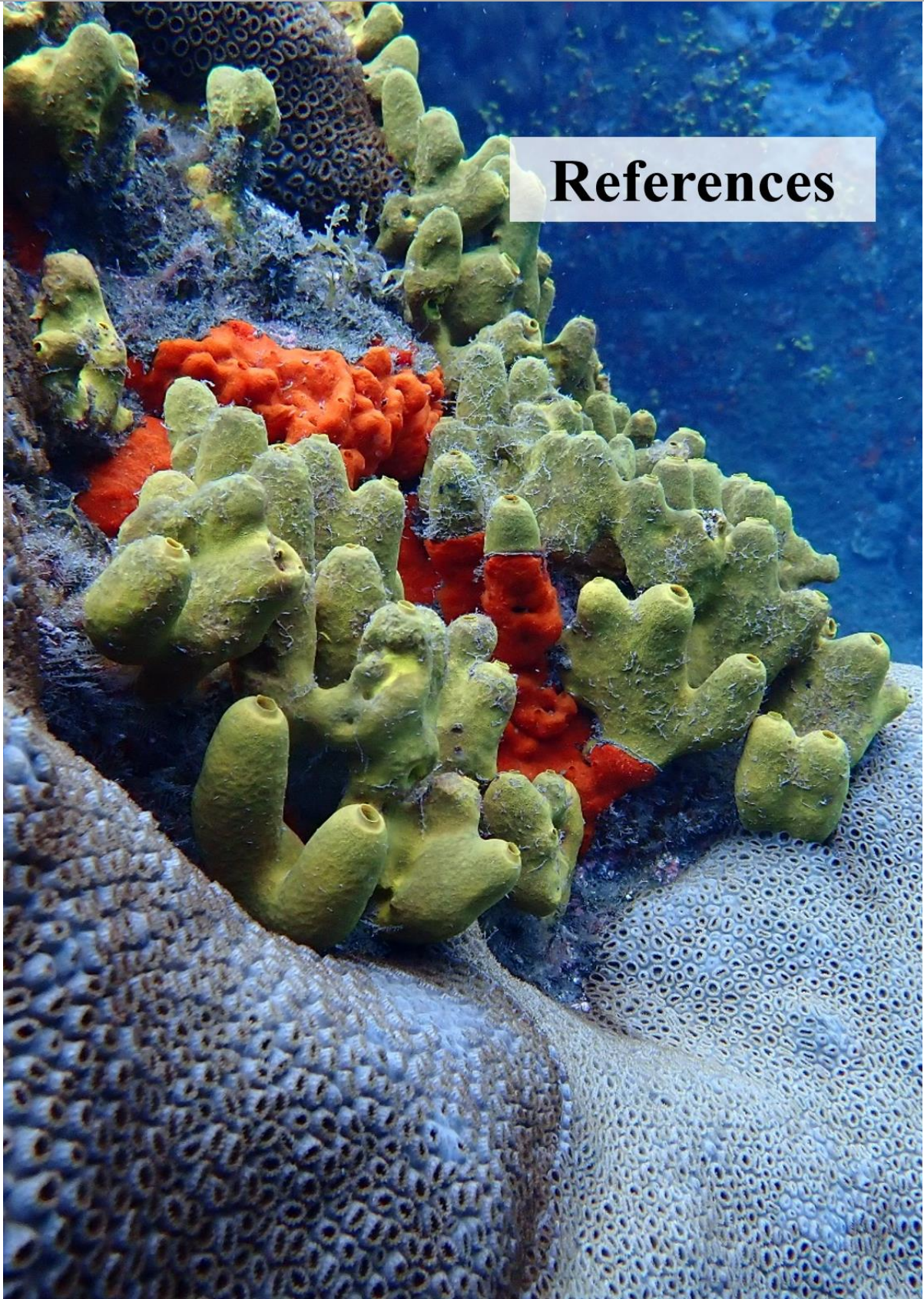
16. Increased sea water temperature of 26°C compensated the negative effect of low pH in *Palythoa* aff. *clavata* and *P. caribaeorum* at short-term exposures (31 days), highlighting the tropical affinities of these species. However, longer-term experimental exposures (62 days) at 26 °C and 7.5 units of pH had negative effects in species' growth, probably associated to the detrimental effects detected over chlorophyll content of their symbiotic dinoflagellates.

17. Feeding experiments demonstrated that coevolutionary processes have led to the ability of the crab *Platypodiella picta* to actively prey on *Palythoa caribaeorum* and *P. aff. clavata*, despite their high toxicity. Simulated low sea water pH decreased the rate of consumption of *P. aff. clavata* by the crab. Therefore, the detrimental effect of low pH over *Palythoa* populations could be compensated, to some extent, with a reduction in predation rates at least in the case of *P. aff. clavata*.

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References

- Acosta A (2001) Disease in Zoanthids: dynamics in space and time. *Hydrobiologia* 460:113-130
- Acosta A, Asbahr M (2000) Reproductive effort in *Palythoa caribaeorum*. Proc 8th Int Coral Reef Symp 295
- Acosta A, Casas M, Vargas CA, Camacho JE (2005) Lista de Zoantharia (Cnidaria: Anthozoa) del Caribe y de Colombia. *Biota Colombiana* 6:(2)147-162
- Acosta AL, Giannini TC, Imperatriz-Fonseca VL, Saraiva AM (2016) Worldwide alien invasion: a methodological approach to forecast the potential spread of a highly invasive pollinator. *PLOS ONE* 11(2): e0148295
- Agostini S, Harvey BP, Wada S, Kon K, Milazzo M, Inaba J, Hall-Spencer JM (2018) Ocean acidification drives community shifts towards simplified non-calcified habitats in a subtropical-temperate transition zone. *Sci Rep-UK* 8: 11354
- Allen AP, Brown JH, Gillooly JF (2002) Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science* 297(5586): 1545-1548
- Alongi DM (2008) Mangrove forests: Resilience, protection from tsunamis, and responses to global climate change. *Estuar Coast Shelf S* 76: 1-13
- Anderson MJ (2001) Permutation tests for univariate or multivariate analysis of variance and regression. *Can J Fish Aquat Sci* 58: 626-639
- Anderson MJ, Robinson J (2003) Generalized discriminant analysis based on distances. *Aust N Z J Stat* 45 (3): 301–318
- Andersson AJ, Mackenzie FT, Bates NR (2008) Life on the margin: implications of ocean acidification on Mg-calcite, high latitude and cold-water marine calcifiers. *Mar Ecol Prog Ser* 373: 265–73
- Araújo R, Freitas M (2003) A new crab record *Platypodiella picta* (A. Milne-Edwards, 1869) (Crustacea: Decapoda: Xanthidae) from Madeira Islands waters. In: Natural History Museum of Funchal ISSN: 0523-7904
- Arechavaleta M (2009) Evaluación de especies catalogadas de Canarias: *Palythoa caribaea*. Expte. Palcar 08/2009. Dirección General del Medio Natural. Consejería de Medio Ambiente y Ordenación Territorial. Gobierno de Canarias
- Aristegui J, Sangra P, Hernández-León S, Canton M, Hernandez-Guerra A, Kerling JL (1994) Island-induced eddies in the Canary Islands. *Deep-Sea Res* 41(10): 1509-1525
- Aristegui J, Barto ED, Álvarez-Salgado XA, Santos AMP, Figueiras FG, Kifani S, Hernández-León S, Mason E, Machú E, Demarcq H (2009) Sub-regional ecosystem variability in the Canary Current upwelling. *Prog Oceanogr* 83: 33-48
- Arnold T, Mealey C, Leahey H, Miller WA, Hall- Spencer JM, Milazzo M, Maers K (2012) Ocean acidification and the loss of phenolic substances in marine plants. *PIOS ONE* 7(4): e35107
- Austin MP (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modeling. *Ecol Modell* 157: 101-118

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References

- Ayres RU, Simonis UE (1994) Industrial metabolism: Restructuring for sustainable development. In Ayres and Simonis (eds) United Nations University Press, Tokyo, New York, Paris. ISBN 92-808-0841-9
- Badger MR, Price GD (2003) CO₂ concentrating mechanisms in cyanobacteria: molecular components, their diversity and evolution. *J Exp Bot* 54: 609–622
- Baird AH, Bhagooli R, Ralph PJ, Takahashi S (2009) Coral bleaching: the role of the host. *Trends Ecol Evol* 24(1): 16-20
- Baker AC, Glynn PW, Riegl B (2008) Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. *Estuar Coast Mar Sci* 80: 435-471
- Bañón R, Mucientes G (2009) First record of *Seriola fasciata* (Carangidae) from Galician waters (NW Spain). A new northernmost occurrence in the NE Atlantic. *Cybium* 33(3): 247-248
- Barton ED, Arístegui J, Tett P, Canton M, García-Braun J, et al. (1998) The transition zone of the Canary Current upwelling region. *Prog Oceanogr* 41: 455–504
- Barton ED, Arístegui J, Tett P, Navarro-Pérez E (2004) Variability in the Canary Islands area of filament-eddy exchanges. *Prog Oceanogr* 62: 71–94
- Bastidas C, Bone D (1996) Competitive strategies between *Palythoa caribaeorum* and *Zoanthus sociatus* (Cnidaria: Anthozoa) at a reef flat environment in Venezuela. *B Mar Sci* 59: 543-555
- Behrenfeld MJ, O'Malley RT, Siegel DA, McClain CR, Sarmiento JL, et al. (2006) Climate-driven trends in contemporary ocean productivity. *Nature* 444: 752–755
- Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012) Impacts of climate change on the future of biodiversity. *Ecol Lett* 15(4): 365-377
- Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. *Nature* 429: 827–833
- Béress L, Zwick J, Kolkenbrock HJ, Kaul PN, Wassermann O (1983) A method for the isolation of the caribbean palytoxin (C-PTX) from the coelenterate (zooanthid) *Palythoa caribaeorum*. *Toxicon* 21: 285-290
- Bindoff NL, Willebrand J, Artale V, Cazenave A, Gregory JM, et al. (2007) Observations: Oceanic climate change and sea level, climate change 2007: The physical science basis. Contribution of working group I to the fourth assessment report of the Intergovernmental Panel on Climate Change, Cambridge University Press. In: S Solomon, D Qin, M Manning, M Marquis, KB Averyt, M Tignor, HL Miller and Z Chen (eds) Cambridge, UK and NY, USA, pp 385-432. ISBN 978-0-521-70596-7
- BOE (2010) Ley 4/2010, de 4 de junio, del Catálogo Canario de Especies Protegidas. <https://www.boe.es/buscar/pdf/2010/BOE-A-2010-9772-consolidado.pdf>
- Boekschoten GJ, Borel Best M (1988) Fossil and recent shallow water corals from the Atlantic islands off Western Africa. *Zoologische Mededelingen, Leiden* 62: 99-112
- Borges PAV, Costa A, Cunha R, Gabriel R, Gonçalves V, Martins AF, Melo I, Parente M, Raposeiro P, Rodrigues P, Santos RS, Silva L, Vieira P, Vieira V (eds) (2010) A list of the terrestrial and marine biota from the Azores. *Principia, Cascais* ISBN 978-989-8131-75-1

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References

- Bouzon JL, Brandini FP, Rocha RM (2012) Biodiversity of sessile fauna on rocky shores of coastal islands in Santa Catarina, Southern Brazil. *Mar Sci* 2: 39-47
- Brading P, Warner ME, Davey P, Smith DJ, Achterberg EP, Suggett DJ (2011) Differential effects of ocean acidification on growth and photosynthesis among phylotypes of *Symbiodinium* (Dinophyceae). *Limnol Oceanogr* 56(3): 927-938
- Braun JG, Molina R (1984) El mar. El Atlántico en el área de Canarias. In: Editorial Interinsular Canaria (eds) Geografía de Canarias. Geografía Física. Santa Cruz de Tenerife ISSN 84-505-5165-X
- Brito A (1984) Zoogeografía marina de las Islas Canarias. In: Edirca SL (ed) Fauna marina y terrestre del Archipiélago Canario. Las Palmas de Gran Canaria
- Brito A (2010) Biogeografía y conservación de la biodiversidad marina en la Macaronesia. *Rev Acad Canar Cienc* XXII 4: 161-175
- Brito A, Ocaña O (2004) Corales de las Islas Canarias. In: Lemus, Francisco (eds) La Laguna, 477 pp. ISBN 978-84-87931-67-3
- Brito A, Falcón JM, Herrera R (2005) Sobre la tropicalización reciente de la ictiofauna litoral de las islas Canarias y su relación con cambios ambientales y actividades antrópicas. *Vieraea* 33: 515-526
- Brito A, Clemente S, Herrera R (2011) On the occurrence of the African hind, *Cephalopholis taeniops*, in the Canary Islands (eastern subtropical Atlantic): introduction of large-sized demersal littoral fishes in ballast water of oil platforms? *Biol Invasions* 13: 2185
- Brito A, Dorta C, Falcón JM (2014) First valid record of *Gymnothorax vicinus* (Pisces: Muraenidae) for Macaronesian ecoregion (Canary Islands): A process of tropicalization? *Rev Acad Canar Cienc* 26: 71-78
- Brito A, Moreno-Borges S, Escáñez A, Falcón JM, Herrera R (2017) New records of Actinopterygian fishes from the Canary Islands: tropicalization as the most important driving force increasing fish diversity. *Rev Acad Canar Cienc* 29: 31-44
- Brook BW, Sodhi NS, Bradshaw CJA (2008) Synergies among extinction drivers under global change. *Trends Ecol Evol* 23(8): 453-460
- Burnett WJ (2002) Longitudinal variation in algal symbionts (zooxanthellae) from the Indian Ocean zoanthid *Palythoa caesia*. *Mar Ecol Prog Ser* 234:105-109
- Burnett WJ, Benzie JAH, Beardmore JA, Ryland JS (1995) Patterns of genetic subdivision in populations of a clonal cnidarian, *Zoanthus coppingeri*, from the Great Barrier Reef. *Mar Biol* 122: 665-673
- 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
- Caldeira K, Wickett ME (2003) Anthropogenic carbon and ocean pH. *Nature* 425: 365
- Caldeira K, Wickett ME (2005) Ocean model predictions of chemistry changes from carbon dioxide emissions to the atmosphere and ocean. *J Geophys Res* 110:C09S04

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References

- Caralt S, Cebrián E (2013) Impact of an invasive alga (*Womersleyella setacea*) on sponge assemblages: compromising the viability of future populations. *Biol Invasions* 15: 1591-1600
- Carine MA, Schaefer (2009) The Azores diversity enigma: why are there so few Azorean endemic flowering plants and why are they so widespread? *J Biogeogr* 37: 77-89
- Carracedo JC, Rodríguez BE (1993) Evolución geológica y magmática de la isla de Lanzarote Islas Canarias. *Rev Acad Canar Cienc* 4: 25-58
- Carreiro-Silva M, Ocaña O, Stanković D, Sampaio I, Porteiro FM, Fabri MC, Stefanni S (2017) Zoantharians (Hexacorallia: Zoantharia) associated with cold-water corals in the Azores Region: new species and associations in the deep sea. *Front Mar Sci* 4: 88
- Cen-Pacheco F, Martín MN, Fernández JJ, Hernández-Daranas A (2014) New oxidized zoanthamines from a Canary Islands *Zoanthus* sp. *Mar Drugs* 12: 5188-5196
- Chanas B, Pawlik JR (1995) Defenses of caribbean sponges against predatory reef fish II. Spicules, tissue toughness, and nutritional quality. *Mar Ecol Prog Ser* 127: 195-211
- Cheney KL, White A, Mudianta IW, Winters AE, Quezada M, et al. (2016) Choose your weaponry: Selective storage of a single toxic compound, Latrunculin A, by closely related nudibranch molluscs. *PLOS ONE* 11(1): e0145134
- Clemente S, Hernández JC, Rodríguez A, Brito A (2010) Identifying keystone predators and importance of preserving functional diversity in sublittoral rocky-bottom areas. *Mar Ecol Prog Ser* 413: 55-67
- Clemente S, Rodríguez A, Brito A, Ramos A, Monterroso Ó, Hernández JC (2011) On the occurrence of the hydrocoral *Millepora* (Hydrozoa: Milleporidae) in the subtropical eastern Atlantic (Canary Islands): is the colonization related to climatic events? *Coral Reefs* 30: 237-240
- Coates AG, Obando JA (1996) The geological evolution of the Central American Isthmus. In: *Evolution and environment in tropical America*, Jackson JBC, Budd AF, Coates AG (eds) pp 21-56, University of Chicago Press, Chicago, Ill, USA
- Cole C, Finch AA, Hintz C, Hintz K, Allison N (2018) Effects of seawater pCO₂ and temperature on calcification and productivity in the coral genus *Porites* spp.: an exploration of potential interaction mechanisms. *Coral Reefs* 37: 471-481
- Cornwall CE, Pilditch CA, Hepburn CD, Hurd CL (2015) Canopy macroalgae influence understory corallines' metabolic control of near-surface pH and oxygen concentration. *Mar Ecol Prog Ser* 525: 81-95
- Cornwall CE, Revill AT, Hall-Spencer JM, Milazzo M, Raven JA, Hurd CL (2017) Inorganic carbon physiology underpins macroalgal responses to elevated CO₂. *Sci Rep* 7
- Costa CF, Sassi R, Gorch-Lira K (2008) Uma abordagem metodológica para o estudo das zooxantelas de corais do brasil. *Boletim do Laboratório de Hidrobiologia* 21: 83-94
- Costa CF, Sassi R, Gorch-Lira K, LaJeunesse TC, Fitt WK (2013) Seasonal changes in zooxanthellae harbored by zoanthids (Cnidaria, Zoanthidea) from coastal reefs in northeastern Brazil. *Pan-Am J Aquat Sci* 8: 253-264
- Costa DL, Gomes PB, Santos AM, Valenca NS, Vieira NA, Perez CD (2011) Morphological plasticity in the reef zoanthid *Palythoa caribaeorum* as an adaptive strategy. *Ann Zool Fennici* 48: 349-358

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References

- Cruz ICS, Loiola M, Albuquerque T, Reis R, De Anchieta CC, et al. (2015) Effect of phase shift from corals to Zoantharia on reef fish assemblages. PLOS ONE 10(1): e0116944
- Cruz ICS, Kikuchi RK, Creed JC (2016a) Ecological processes of phase shift to *Palythoa grandiflora* dominance on reefs of Todos-os-Santos Bay, Brazil. Front Mar Sci Conference Abstract: XIX Iberian Symposium on Marine Biology Studies. doi: 10.3389/conf.FMARS.2016.05.00050
- Cruz ICS, Meira VH, Kikuchi RKP, Creed JC (2016b) The role of competition in the phase shift to dominance of the zoanthid *Palythoa cf. variabilis* on coral reefs. Mar Environ Res 115: 28–35
- Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. Nat Methods doi:10.1038/nmeth.2109
- Davies PS (1991) Effect of daylight variations on the energy budgets of shallow-water corals. Mar Biol 108: 137-144
- Davy SK, Allemand D, Weis VM (2012) Cell biology of cnidarian-dinoflagellate symbiosis. Microbiol Mol Biol Rev 76: 229–261
- Depczynski M, Gilmour JP, Ridgway T, Barnes H, Heyward AJ, et al. (2013) Bleaching, coral mortality and subsequent survivorship on a West Australian fringing reef. Coral Reefs 32: 233-238
- de Souza JN, Nunes FLD, Zilberberg C, Sanchez JA, Migotto AE, et al. (2017) Contrasting patterns of connectivity among endemic and widespread fire coral species (*Millepora* spp.) in the tropical South western Atlantic. Coral Reefs 36: 701-716
- D'heygere T, Gorthals PLM, De Pauw N (2003) Use of genetic algorithms to select input variables in decision tree models for the prediction of benthic macroinvertebrates. Ecol Modell 160: 291-300
- Dias TLP, Gondim AI (2015) Bleaching in scleractinians, hydrocorals, and octocorals during thermal stress in a northeastern Brazilian reef. Mar Biodivers 6: 303-307
- Dickson AG, Millero FJ (1987) A comparison of the equilibrium constants for the dissociation of carbonic acid in seawater media. Deep-Sea Res 34: 1733–1743
- Dickson AG, Sabine CL, Christian JR (eds) (2007) Guide to best practices for ocean CO₂ measurement. Sidney, British Columbia, North Pacific Marine Science Organization, 191pp. ISBN 1-897176-07-4
- Dimond J, Carrington E (2007) Temporal variation in the symbiosis and growth of the temperate scleractinian coral *Astrangia poculata*. Mar Ecol Prog Ser 348: 161–172
- Dimond J, Carrington E (2008) Symbiosis regulation in a facultatively symbiotic temperate coral: zooxanthellae division and expulsion. Coral Reefs 27: 601–604
- Dixon DL, Munday PL, Jones GP (2010) Ocean acidification disrupts the innate ability of fish to detect predator olfactory cues. Ecol Lett 13: 68–75
- Domingues VS (2007) Phylogeography and historical demography of the warm water costal fish of the Azores in the context of the recent evolution of the Atlantic and Mediterranean. Ph. Doctoral Thesis, Universidade dos Açores, Horta
- Done TJ (1999) Coral community adaptability to environmental change at the scales of regions, reefs and reef zones. Am Zool 39: 66–79

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References

- Doney SC, Fabry VJ, Feely RA, Kleypas JA (2009) Ocean acidification: The other CO₂ problem. *Annu Rev Mar Sci* 1: 169–92
- Doney SC, Ruckelshaus M, Duffy JE, Barry JP, Chan F, et al. (2012) Climate Change impacts on marine ecosystems. *Annu Rev Mar Sci* 4: 11–37
- Doty MS, Oguri M (1956) The island mass effect *Journal du Conseil, Conseil International pour l'Exploration de la Mer* 22: 33-37
- Dubinsky Z, Stambler N (1996) Marine pollution and coral reefs. *Glob Change Biol* 2: 511–526
- Duchassaing PF (1850) *Animaux Radiaires des Antilles*, Plon Frères, Paris, France
- Duerden JE (1898) Jamaican Actiniaria. Part I. Zoantheae. *Sci Proc R Dublin Soc* 6: 329–385
- Dulvy NK, Rogers SI, Jennings S, Stelzenmüller V, Dye SR, Skjoldal HR (2008) Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *J Appl Ecol* 45: 1029–1039
- Dupont S, Dorey N, Stumpp M, Melzner F, Thorndyke M (2012) Long-term and trans-life-cycle effects of exposure to ocean acidification in the green sea urchin *Strongylocentrotus droebachiensis*. *Mar Biol* 160: 1835–1843
- Durante LM, Cruz ICS, Lotufo TMC (2018) The effect of climate change on the distribution of a tropical zoanthid (*Palythoa caribaeorum*) and its ecological implications. *PeerJ* doi10.7717/peerj.4777
- Dykens JA, Shick JM (1984) Photobiology of the symbiotic sea anemone, *Anthopleura elegantissima*: defenses against photodynamic effects, and seasonal photo acclimatization. *Biol Bull* 167: 683–697
- e Costa BH, Assis J, Franco G, Erzini K, Henriques M, Gonçalves EJ, Caselle JE (2014) Tropicalization of fish assemblages in temperate biogeographic transition zones. *Mar Ecol Prog Ser* 504: 241-252
- Edmunds PJ, Carpenter RC (2001) Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. *PNAS* 98(9): 5067-5071
- Enochs IC, Manzello DP, Donham EM, Kolodziej G, Okano R, et al. (2015) Shift from coral to macroalgae dominance on a volcanically acidified reef. *Nat Clim Change* 5: 1083–1088
- Fadlallah YH, Karlson RH, Sebens KP (1984) A comparative study of sexual reproduction in three species of Panamanian zoanths (Coelenterata: Anthozoa). *Bull Mar Sci* 35: 80-89
- Falcón JM, Bortone SA, Brito A, Bundrick CM (1996) Structure and relationships within and between the littoral, rock-substrate fish communities off four islands in the Canarian Archipelago. *Mar Biol* 125 (2): 215-231
- Falcón JM, Herrera R, Ayza O, Brito A (2015) New species of tropical litoral fish found in Canarian waters. Oil platforms as a central introduction vector. *Rev Acad Canar Cienc* 27: 67-82
- Fay SA, Weber MX (2012) The occurrence of mixed infections of *Symbiodinium* (Dinoflagellata) within individual hosts. *J Phycol* 48: 1306–1316
- Feely RA, Sabine CL, Lee K, Berelson W, Kleypas J, Fabry VJ, Millero FJ (2004) Impact of anthropogenic CO₂ on the CaCO₃ system in the oceans. *Science* 305: 362-366

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References

- Feely RA, Doney SC, Cooley SR (2009) Ocean acidification: present conditions and future changes in a high-CO₂ world. *Oceanography* 22: 37–47
- Fernández-Palacios JM, Nascimento L, Otto R, Delgado JD, García-del-Rey E, Arévalo JR, Whittaker RJ (2011) A reconstruction of Palaeo-Macaronesia, with particular reference to the long-term biogeography of the Atlantic island laurel forests. *J Biogeogr* 38: 226-246
- Ferrari MCO, Mc Cormick MI, Munday PL, Meekan MG, Dixson DL, Lonnstedt O, Chivers DP (2011) Putting prey and predator into the CO₂ equation—qualitative and quantitative effects of ocean acidification on predator–prey interactions. *Ecol Lett* 14: 1143–1148
- Filbee-Dexter K, Scheibling RE (2014) Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. *Mar Ecol Prog Ser* 495: 1-25
- Finney JC, Pettay DT, Sampayo EM, Warner ME, Oxenford H, LaJeunesse TC (2010) The relative significance of host-habitat, depth, and geography on the ecology, endemism, and speciation of coral endosymbionts in the genus *Symbiodinium*. *Microb Ecol* 60: 250–263
- Fischer-Kowalski M, Haberl H (2007) Socioecological transitions and global change. Trajectories of social metabolism and land use. In: Fischer-Kowalski M, Haberl H (eds) Edward Elgar, Cheltenham and Northampton, 288pp. ISBN 978184720340
- Floeter SR, Rocha LA, Robertson DR, Joyeux JC, Smithvaniz WF, et al. (2008) Atlantic reef fish biogeography and evolution. *J Biogeogr* 35: 22-47
- Font I (1956) El tiempo atmosférico en las Islas Canarias. Servicio Meteorológico Nacional (eds) Madrid, España, 96pp.
- Fraga M, Vilarinho N, Louzano MC, Molina L, López Y, Poli M, Botana LM (2017) First identification of palytoxin-like molecules in the Atlantic coral species *Palythoa canariensis*. *Anal Chem* 89:(14) 7438–7446
- Freitas R, Luiz OJ, Silva PN, Floeter SR, Bernardi G, Ferreira CEL (2013) The occurrence of *Sparisoma frondosum* (Teloestei: Labridae) in the Cape Verde Archipelago, with a summary of expatriated Brazilian endemic reef fishes. *Mar Biodivers* 44: 173–179
- Friedlander AM, Ballesteros E, Clemente S, Gonçalves EJ, Estep A, Rose P, Sala E (2017) Contrasts in the marine ecosystem of two Macaronesian islands: A comparison between the remote Selvagens Reserve and Madeira Island. *PLOS ONE* 12(11): e0187935
- Fujii T, Reimer JD (2013) A new family of diminutive zooxanthellate zoanthids (Hexacorallia: Zoantharia). *Zool J Linn Soc* 169: 509–522
- Gao K, Aruga Y, Asada K, Kiyohara M (1993) Influence of enhanced CO₂ on growth and photosynthesis of the red algae *Gracilaria* sp. and *G. chilensis*. *J Appl Phycol* 5: 563–571
- García E, Clemente S, López C, McAlister J, Hernández JC (2015) Ocean warming modulates the effects of limited food availability on *Paracentrotus lividus* larval development. *Mar Biol* 162: 1463-1472
- García-Herrera R, Gallego-Puyol G, Hernández-Martín E (2001) Influence of the North Atlantic oscillation on the Canary Island precipitation. *J Climate* 14: 3889-3903
- Gattuso JP, Buddemeier RW (2000) Ocean biogeochemistry: calcification and CO₂. *Nature* 407: 311-313

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References

- Gattuso JP, Hansson L (2011) Ocean acidification: background and history. In: Gattuso JP, Hansson L (eds) Ocean acidification. Oxford: Oxford University Press, pp 1-20
- Gazeau F, Quiblier C, Jansen JM, Gattuso JP, Middelburg JJ, Heip CHR (2007) Impact of elevated CO₂ on shellfish calcification. *Geophys Res Lett* 34: L07603
- Gerhardt A (2002) Bioindicator species and their use in biomonitoring. Environmental monitoring. Encyclopedia of Life Support Systems (EOLSS) Vol. I
- Ghedini J, Russell BD, Connell SD (2015) Trophic compensation reinforces resistance: herbivory absorbs the increasing effects of multiple disturbances. *Ecol Lett* 18: 182–187
- Giordano M, Beardall J, Raven JA (2005) CO₂ concentrating mechanisms in algae: mechanisms, environmental modulation, and evolution. *Annu Rev Plant Biol* 56: 99–131
- Gleibs S, Mebs D, Werding (1995) Studies on the origin and distribution of palytoxin in a Caribbean coral reef. *Toxicon* 33(11): 1531-1537
- Glynn PW (1996) Coral reef bleaching: Facts, hypotheses and implications. *Glob Change Biol* 2: 495–509
- Glynn PW, Maté JL, Baker AC, Calderón MO (2001) Coral bleaching and mortality in Panamá and Ecuador during the 1997–1998 El Niño–Southern Oscillation Event: spatial/temporal patterns and comparisons with the 1982–1983 event. *Bull Mar Sci* 69: 79-109
- Goldberg J, Wilkinson C (2004) Global threats to coral reefs: coral bleaching, global climate change, disease, predator plagues and invasive species. Status of coral reefs of the world. Wilkinson, C. Townsville, Australia, 67-92 pp
- González-Delgado S, López C, Brito A, Clemente S (2018) Marine community effects of two colonial zoanths in intertidal habitats of the Canary Islands. *Reg Stud Mar Sci* 23: 23-31
- González JA (2016) Brachyuran crabs (crustacean: Decapoda) from the Canary Islands (eastern Atlantic): checklist zoogeographic considerations and conservation. *Sci Mar* 80(1): 89-102
- González JA, Triay-Portella Raül, Escribano A, Cuesta JA (2017) Northernmost record of the pantropical portunid crab *Cronius ruber* in the eastern Atlantic (Canary Islands): natural range extension or human-mediated introduction? *Sci Mar* 81: 81-89
- Graham ER, Sanders RW (2015) Species-specific photosynthetic responses of symbiotic zoanths to thermal stress and ocean acidification. *Mar Ecol* 37: 442-458
- Graham ER, Parekh A, Devassy RK, Sanders RW (2015) Carbonic anhydrase activity changes in response to increased temperature and pCO₂ in *Symbiodinium*–zoanthid associations. *J Exp Mar Biol Ecol* 473: 218–226
- Grajales A, Sanchez JA (2016) Holobiont assemblages of dominant coral species (*Symbiodinium* types and coral species) shape Caribbean reef community structure. *Rev Acad Colomb Cienc Exact Fis Nat* 40: 300–311
- Gustafsson MSM, Baird ME, Ralph PJ (2013) The interchangeability of autotrophic and heterotrophic nitrogen sources in scleractinian coral symbiotic relationships: a numerical study. *Ecol Model* 250: 183–194
- Haddon AC, Shackleton AM (1891) Reports on the zoological collections made in Torres Straits by Professor AC. Haddon, 1888–1889. Actiniae: I. Zoantheae. *Sci Trans R Dublin Soc* 4: 673–701

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References

- Haddon AC, Duerden JE (1896) On some Actiniaria from Australia and other districts. *Sci Proc R Dublin Soc* 2(6): 139-164
- Harley CDG, Hughes AR, Hultgren KM, Miner BG, Sorte JBC, et al. (2006) The impacts of climate change in coastal marine systems. *Ecol lett* 9: 228-241
- Hartog JC, Holthuis LB (1984) A note on an interesting association of the crab *Platypodiella picta* (A. Milne Edwards, 1869) and species of Zoantharia. *Courier Forschungsinstitut Senckenberg* 68: 21-29
- Hartog JC, Türkay M (1991) *Platypodiella georgei* spec. nov. (Brachyura: Xanthidae), a new crab from the island of St. Helena, South Atlantic Ocean, with notes on the genus *Platypodiella* Guinot, 1967. *Zool Meded* 65: 209-220
- Harvell D, Kim K, Quirolo C, Weir J, Smith G (2001) Coral bleaching and disease: contributors to 1998 mass mortality in *Briareum asbestinum* (Octocorallia, Gorgonacea). *Hydrobiologia* 450: 97-104
- Haywick DW, Mueller EM (1997) Sediment retention in incrusting *Palythoa* spp. - a biological twist to a geological process. *Coral Reefs* 16: 39-46
- Helmuth B, Mieszkowska N, Moore P, Hawkins SJ (2006) Living on the edge of two changing worlds: forecasting the responses of rocky intertidal ecosystems to climate change. *Annu Rev Ecol Evol Syst* 37: 373-404
- Herberts C (1972) Etude systématique de quelques zoanthaires tempérés et tropicaux. *Tethys Suppl* 3: 69-156
- Hernández-León S, Gómez M, Arístegui J (2007) Mesozooplankton in the Canary Current System: the coastal-ocean transition zone. *Progr Oceanogr* 74: 397-421
- Hernández JC, Clemente S, Sangil C, Brito A (2008) The key role of *Diadema* aff. *antillarum* (Echinoidea: Diadematidae) throughout the Canary Islands (eastern subtropical Atlantic) in controlling macroalgae assemblages: an spatio-temporal approach. *Mar Environ Res* 66: 259-270
- Heuer RM, Grosell M (2014) Physiological impacts of elevated carbon dioxide and ocean acidification on fish. *Am J Physiol Integr Comp Physiol* 307: R1061-R1084
- Hiddink JG, ter Hofstede R (2008) Climate induced increases in species richness of marine fishes. *Glob Change Biol* 14: 453-460
- Hines DE, Pawlik JR (2012) Assessing the antipredatory defensive strategies of Caribbean non-scleractinian zoantharians (Cnidaria): is the sting the only thing? *Mar Biol* 159: 389-398
- Hirose M, Obuchi M, Hirose E, Reimer JD (2011) Timing of spawning and early development of *Palythoa tuberculosa* (Anthozoa, Zoantharia, Sphenopidae) in Okinawa, Japan. *Biol Bull* 220: 23-31
- Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Mar Freshwater Res* 50: 839-866
- Hoegh-Guldberg O, Bruno JF (2010) The impact of climate change on the world's marine ecosystems. *Science* 328: 1523-8
- Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, et al. (2007) Coral reefs under rapid climate change and ocean acidification. *Science* 318: 1737-1742

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References

- Hoeksema BW, Roos PJ, Cadee GC (2012) Trans-Atlantic rafting by the brooding reef coral *Favia fragum* on man-made flotsam. *Mar Ecol Prog Ser* 445: 209–218
- Hoeksema BW, Pedoja K, Poprawski (2018) Long-distance transport of a West Atlantic stony coral on a plastic raft. *Ecology* 2402-2404
- Hofmann GE, Barry JP, Edmunds PJ, Gates RD, Hutchins DA, Klinger T, Sewell MA (2010) The effect of ocean acidification on calcifying organisms in marine ecosystems: An organism-to-ecosystem perspective. *Annu Rev Ecol Evol S* 41(1): 127-147
- Holcomb M, Cohen AL, McCorkle DC (2012) An investigation of the calcification response of the scleractinian coral *Astrangia poculata* to elevated pCO₂ and the effects of nutrients, zooxanthellae and gender. *Biogeosciences* 9: 29–39
- Horta e Costa B, Gonçalves EJ (2013) First occurrence of the monrovia doctorfish *Acanthurus monroviae* (Perciformes: Acanthuridae) in European Atlantic waters. *Mar Biodivers Rec* 6: 1-4
- Huang D, Meier R, Todd PA, Chou LM (2008) Slow mitochondrial COI sequence evolution at the base of the metazoan tree and its implications for DNA barcoding. *J Mol Evol* 66: 167–174
- Huelsenbeck JP, Ronquist F (2001) MrBayes: Bayesian inference of phylogeny. *Bioinformatics* 17: 754-755
- Huelsenbeck JP, Ronquist F, Nielsen R, Bollback JP (2001) Bayesian inference of phylogeny and its impact on evolutionary biology. *Science* 294: 2310-2314
- Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, et al. (2003) Climate change, human impacts, and the resilience of coral reefs. *Science* 301: 929–933
- Hunter C, Morden C, Smith C (1997) The utility of ITS sequences in assessing relationships among zooxanthellae and corals. *Proc 8th Int Coral Reef Symp* 2: 1599–1602
- Idjadi JA, Haring RN, Precht WF (2010) Recovery of the sea urchin *Diadema antillarum* promotes scleractinian coral growth and survivorship on shallow Jamaican reefs. *Mar Ecol Prog Ser* 403: 91-100
- Iglesias-Prieto R, Matta JL, Robins WA, Trench RK (1992) Photosynthetic response to elevated temperature in the symbiotic dinoflagellate *Symbiodinium microadriaticum* in culture. *Proc Biol Sci* 89: 10302-10305
- Iglesias-Rodriguez MD, Halloran PR, Rickaby REM, Hall IR, Colmenero-Hidalgo E, et al. (2008) Phytoplankton calcification in a high-CO₂ world. *Science* 320 (5874): 336-340
- Inglis GJ, Hayden BJ, Nelson WA (2006) Are the marine biotas of island ecosystems more vulnerable to invasion? In: Allen RB, Lee WG (eds) *Biological invasions in New Zealand. Ecological Studies (Analysis and Synthesis)* Springer, Berlin, Heidelberg vol 186 119-135pp. ISBN 978-3-540-30023-6
- IPCC (2007) *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of working group II to the fourth assessment report of the Intergovernmental Panel on Climate Change.* In: ML Parry, OF Canziani, JP Palutikof, PJ van der Linden, CE Hanson (eds) Cambridge University Press, Cambridge, UK, 976pp
- IPCC (2013) *Climate change 2013: the physical science basis. Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change.* In: Stocker TF, Qin D, Plattner GK, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (eds)

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References

- Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp 255–316
- Irei Y, Nozawa Y, Reimer JD (2011) Distribution patterns of five zoanthid species at Okinawa Island, Japan. *Zool Stud* 20(4): 426-233
- Irei Y, Sinniger F, Reimer JD (2015) Descriptions of two azooxanthellate *Palythoa* species (Subclass Hexacorallia, Order Zoantharia) from the Ryukyu Archipelago, southern Japan. *ZooKeys* 478: 1-26
- Israel A, Hophy M (2002) Growth, photosynthetic properties and rubisco activities and amounts of marine macroalgae grown under current and elevated seawater CO₂ concentrations. *Glob Change Biol* 8: 831–840
- Israel A, Shlomit K, Dubinsky Z, Merrill JE, Friedlander M (1999) Photosynthetic inorganic carbon utilization and growth of *Pophrhya linearis* (Rhodophyta). *J Appl Phycol* 11: 447-453
- Jevrejeva S, Moore JC, Grinsted A, Woodworth PL (2008) Recent global sea level acceleration started over 200 years ago? *Geophys Res Lett* 35: 8–11
- Jiménez C (2001) Bleaching and mortality of reef organisms during a warming event in 1995 on the Caribbean coast of Costa Rica. *Rev Biol Trop* 49: 233–238
- Jokiel PL, Rodgers KS, Kuffner IB, Andersson AJ, Cox EF, Mackenzie FT (2008) Ocean acidification and calcifying reef organisms: a mesocosm investigation. *Coral Reefs* 27: 473–483
- Joyce KE, Phinn SR (2003) Hyperspectral analysis of chlorophyll content and photosynthetic capacity of coral reef substrates. *Limnol Oceanogr* 48: 489-496
- Kalnay E, Kanamitsu N, Kistler R, Collins W, Deaven D, et al. (1996) The NCEP/NCAR Reanalysis 40-year Project. *Bull Amer Meteor Soc* 77: 437-471
- Kamezaki M, Higa M, Hirose M, Suda S, Reimer JD (2013) Different zooxanthellae types in populations of the zoanthid *Zoanthus sansibaricus* along depth gradients in Okinawa, Japan. *Mar Biodivers* 43: 61–70
- Kaplan A, Reinhold L (1999) CO₂ concentrating mechanisms in photosynthetic microorganisms. *Annu Rev Plant Biol* 50: 539–570
- Karlson RH (1981) Reproductive patterns in *Zoanthus* sp. from Discovery Bay, Jamaica. *Proc 4th Int Coral Reef Symp* 2: 699–704
- Karlson RH (1983) Disturbance and monopolization of a spatial resource by *Zoanthus sociatus* (Coelenterata, Anthozoa). *B Mar Sci* 33: 118-131
- Karlson RH (1988) Growth and survivorship of clonal fragments in *Zoanthus solanderi*, Lesueur. *J Exp Mar Biol Ecol* 123(1): 31–39
- Kayanne H, Hata H, Kudo S, Yamano H, Watanabe A, et al. (2005) Seasonal and bleaching-induced changes in coral reef metabolism and CO₂ flux. *Glob Biogeochem Cycles* 19: GB3015
- Kehas AJ, Theoharides KA, Gilbert JJ (2005) Effect of sunlight intensity and albinism on the covering response of the Caribbean sea urchin *Tripneustes ventricosus*. *Mar Biol* 146(6): 1111-1117

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References

- Kise H, Maeda T, Reimer JD (2018) A phylogeny and the evolution of epizooism within the family Hydrozoanthidae with description of a new genus and two new species. *Mol Phylogenet Evol* 130: 304-314
- Koupaei AN, Mostafavi PG, Mehrabadi JF, Fatemi SMR (2014) Molecular diversity of coral reef-associated zoanthids off Qeshm Island, northern Persian Gulf. *Int Aquat Res* 6: 64
- Krausmann F, Gingrich S, Eisenmenger N, Erb HK, Haberl H, Fischer-Kowalski M (2009) Growth in global materials use, GDP and population during the 20th century. *Ecol Econ* 68(10): 2696-2705
- Kroeker KJ, Kordas RL, Crim R, Hendriks IE, Ramajo L, et al. (2013) Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. *Glob Change Biol* 19: 1884–1896
- Kübler JE, Johnston AM, Raven JA (1999) The effects of reduced and elevated CO₂ and O₂ on the seaweed *Lomentaria articulata*. *Plant Cell Environ* 2: 1303–1310
- Kuffner IB, Andersson AJ, Jokiel PL, Rodgers KS, Mackenzie FT (2008) Decreased abundance of crustose coralline algae due to ocean acidification. *Nat Geosci* 1: 77–140
- Kumagai NH, Molinos JG, Yamano H, Takao S, Fujii M, Yamanaka Y (2018) Ocean currents and herbivory drive macroalgae-to-coral community shift under climate warming. *PNAS* 115(36): 8990-8995
- Kumar S, Stecher G, Tamura K (2016) MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for Bigger Datasets. *Mol Biol Evol* 33: 1870–1874
- LaJeunesse TC (2002) Diversity and community structure of symbiotic dinoflagellates from Caribbean coral reefs. *Mar Biol* 141: 387–400
- LaJeunesse TC (2005) ‘Species’ radiations of symbiotic dinoflagellates in the Atlantic and Indo-Pacific since the Miocene-Pliocene transition. *Mol Biol Evol* 22: 570–81
- LaJeunesse TC, Thornhill DJ (2011) Improved resolution of reef-coral endosymbiont (*Symbiodinium*) species diversity, ecology, and evolution through psbA non-coding region genotyping. *PLOS ONE* 6(12): e29013
- LaJeunesse TC, Loh W, van Woesik R, Hoegh-Guldberg O, Schmidt GW, Fitt WK (2003) Low symbiont diversity in southern Great Barrier Reef corals, relative to those of the Caribbean. *Limnol Oceanogr* 48: 2046-2054
- LaJeunesse TC, Parkinson JE, Gabrielson PW, Jeong HJ, Reimer JD, Voolstra CR, Santos SS (2018) Systematic revision of Symbiodiniaceae highlights the antiquity and diversity of coral endosymbionts. *Curr Biol* 28: 2570-2580
- Langdon C, Broecker WS, Hammond DE, Glenn E, Fitzsimmons K, et al. (2003) Effect of elevated CO₂ on the community metabolism of an experimental coral reef. *Global Biogeochem Cy* 17(1): 1011
- Leal MC, Cruz IC, Mendes CR, Calado R, Kikuchi RKP, et al. (2015) Photobiology of the zoanthid *Zoanthus sociatus* in intertidal and subtidal habitats. *Mar Freshwater Res* 67 (12): 1991-1997
- Leggat W, Badger M, Yellowlees D (1999) Evidence for an inorganic carbon-concentrating mechanism in the symbiotic dinoflagellate *Symbiodinium* sp. *Plant Physiol* 121: 1247–1255

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References

- Legrand E, Riera P, Pouliquen L, Bohner O, Cariou T, Martin S (2018) Ecological characterization of intertidal rockpools: Seasonal and diurnal monitoring of physico-chemical parameters. *Reg Stud Mar Sci* 17: 1-10
- Levitus S, Antonov JI, Boyer TP, Locarnini RA, Garcia HE, Mishonov AV (2009) Global ocean heat content 1955–2008 in light of recently revealed instrumentation problems. *Geophys Res Lett* 36: L07608
- Lewis E, Wallace D (1998) Program developed for CO₂ system calculation. In: ORNL/CDIAC-105 de América. Carbon Dioxide Information Analysis Center, Oak Ridge, Tennessee
- Li W, Gao K (2012) A marine secondary producer respire and feeds more in a high CO₂ ocean. *Mar Pollut Bull* 64: 699-703
- Liu C, Berry PM, Dawson TP, Pearson RG (2005) Selecting thresholds of occurrence in the prediction of species distributions. *Ecography* 28: 385-393
- López C, Clemente S, Almeida C, Hernández JC, Brito A, Hernández M (2015) A genetic approach to the origin of *Millepora* sp. in the eastern Atlantic. *Coral Reefs* 34: 631-638
- López C, Freitas R, Magileviciute E, Ratão SS, Reimer JD (2018) Report of a *Zoanthus* zone from the Cape Verde Islands (Central Eastern Atlantic). *Thalassas* 34(2): 409-413
- López C, Reimer JD, Brito A, Simón D, Clemente S, Hernández M (2019) Diversity of zoantharian species and their symbionts from the Macaronesian and Cape Verde ecoregions demonstrates their widespread distribution in the Atlantic Ocean. *Coral Reefs* 38(2): 269–283
- López-Pérez Y (2014) *Palythoa canariensis*: ecología, ensayos preliminares de cultivo y detección de palitoxina. PhD thesis, Instituto Agronómico Mediterráneo de Zaragoza (Spain)
- Losos JB, Ricklefs RE (2009) Adaptation and diversification on islands. *Nature* 457: 830–836
- Low MEY, Reimer JD (2016) *Palythoa heideri* Carlgren, 1954, objective synonym and valid name for the zoantharian currently known as *Palythoa singaporensis* Pax & Müller, 1956 (Cnidaria: Hexacorallia: Zoantharia: Sphenopidae). *Nature in Singapore* 9: 47-48
- Loya Y, Sakai K, Yamazato Y, Nakano Y, Sambali H, Van Woesik R (2001) Coral bleaching: the winners and the losers. *Ecol Lett* 4:122-131
- Lüthi D, Le Floch M, Bereiter B, Blunier T, Barnola JM, et al. (2008) High-resolution carbon dioxide concentration record 650,000–800,000 years before present. *Nature* 453: 379–382
- Luz DC, Zebal YD, Klein RD, Marques JA, Marangoni LFB, et al. (2018) Oxidative stress in the hydrocoral *Millepora alcicornis* exposed to CO₂-driven seawater acidification. *Coral Reefs* 37(2): 571–579
- MacArthur RH, Wilson EO (1963) An equilibrium theory of insular zoogeography. *Evolution* 17: 373-387
- MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton, NJ
- Manson RAB (2018) Decline in symbiont densities of tropical and subtropical. *Coral Reefs* 37: 945–953

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References

- Martín Esquivel JL, Bethencourt J, Cuevas-Agulló E (2012) Assessment of global warming on the island of Tenerife, Canary Islands (Spain). Trends in minimum, maximum and mean temperatures since 1944. *Climatic Change* 114: 343-355
- Martín-García (2013) La distribución espacial de las comunidades bentónicas infralitorales de canarias y su importancia en la gestión del medio marino. PhD thesis, Universidad de La Laguna (Spain)
- Marty MJ, Pawlik JR (2015) A fish-feeding laboratory bioassay to assess the antipredatory activity of secondary metabolites from the tissues of marine organisms. *Jove-J Vis Exp* 95: 1-6
- McCarty JP (2001) Ecological consequences of recent climate change. *Conserv Biol* 15: 320–331
- McClanahan TR, Donner SD, Maynard JA, MacNeil MA, Graham N (2012) Prioritizing key resilience indicators to support coral reef management in a changing climate. *PLOS ONE* 7(8): e42884
- McCulloch M, Falter J, Trotter J, Montagna P (2012) Coral resilience to ocean acidification and global warming through pH upregulation. *Nat Clim Change* 2:623–627
- McIlwain JL, Jones GP (1997) Prey selection by an obligate coral-feeding wrasse and its response to small-scale disturbance. *Mar Ecol Prog Ser* 155: 189-198
- Meco J, Petit-Mairte N, Fontugne M, Shimmield G, Ramos AJ (1997) The Quaternary deposits in Lanzarote and Fuerteventura eastern Canary Islands, Spain: an overview. In: Meco J, Petit-Maire N (eds) *Climates of the Past Proc Pub*, Universidad de Las Palmas de Gran Canaria
- Mehrbach C, Culberson CH, Hawley JE, Pytkowicz RM (1973) Measurement of the apparent dissociation constants of carbonic acid in sea water at atmospheric pressure. *Limnol Oceanogr* 18: 897–907
- Mendoça-Neto JP (2009) The native *Palythoa caribaeorum* overgrows on invasive species in the intertidal zone. *Coral Reefs* 28: 497–497
- Michaelidis B, Ouzounis C, Palaras A, Pörtner HO (2005) Effects of long-term moderate hypercapnia on acid–base balance and growth in marine mussels *Mytilus galloprovincialis*. *Mar Ecol Prog Ser* 293: 109–118
- Michalek-Wagner K, Willis BL (2001) Impacts of bleaching on the soft coral *Lobophytum compactum*. II Biochemical changes in adults and their eggs. *Coral Reefs* 19: 240-246
- Mieszkowska N, Benedetti-Cecchi L, Burrows MT, Cristina Mangano M, Queirós A, Seuront L, Sarà G (2019) Multinational, integrated approaches to forecasting and managing the impacts of climate change on intertidal species. *Mar Ecol Prog Ser* 613: 247–252
- 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* 4(6): e5132
- Molnar JL, Gamboa RL, Revenga C, Spalding MD (2008) Assessing the global threat of invasive species to marine biodiversity. *Front Ecol Environ* 6(9): 485-492
- Monacell JT, Carbone I (2014) Moby SNAPP Workbench: A web-based analysis portal for population genetics and evolutionary genomics. *Bioinformatics* 30: 1488-1490
- Monteiro J, Almeida C, Freitas R, Delgado A, Porteiro F, Santos RS (2008) Coral assemblages of Cape Verde: preliminary assessment and description. *Proc 11th Int Coral Reef Symp* 1416-1419

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References

- Montenegro J, Sinniger F, Reimer JD (2015) Unexpected diversity and new species in the sponge-Parazoanthidae association in southern Japan. *Mol Phylog Evol* 8: 73-90
- Moore RE, Helfrich P, Patterson GML (1982) The deadly seaweed of Hana. *Oceanus* 25: 54-63
- Morri C, Bianchi CN (1995) Cnidarian zonation at Ilha do Sal (Arquipelago de Cape Verde). *Beitr Paläontol* 20: 41-49
- Morri CR, Cattaeno-Vietti R, Sartori G, Bianchi CN (2000) Shallow epibenthic communities of Ilha do Sal (Cape Verde Archipelago, eastern Atlantic). *Arquipel Life Mar Sci Suppl* 2: 157-165
- Mueller E, Haywick DW (1995) Sediment assimilation and calcification by the Western Atlantic reef zoanthid, *Palythoa caribaeorum*. *Bull Inst Ocean Monaco* 14: 89-100
- Muirhead A, Ryland JS (1984) A review of the genus *Isaurus* Gray, 1828 (Zoanthidea), including new records from Fiji. *J Nat Hist* 19: 323-335
- Mumby PJ, Hastings A, Edwards HJ (2007) Thresholds and the resilience of Caribbean coral reefs. *Nature* 450: 98-101
- Muscatine L, Falkowski PG, Porter JW, Dubinsky Z (1984) Fate of photosynthetic fixed carbon in light- and shade-adapted colonies of the symbiotic coral *Stylophora pistillata*. *Proc R Soc Lond B* 222: 181-202
- Muscatine L (1990) The role of symbiotic algae in carbon and energy flux in reef corals. In: Dubinsky Z (eds) *Coral reefs*. Elsevier, Amsterdam
- Muss A, Robertson R, Wirtz P, Bowen B, Stepien CA (2001) Phylogeography of the genus *Ophioblennius*: the role of ocean currents and geography in reef fish evolution. *Evolution* 55: 561-572
- Myers N, Mittermeier RA, Mittermeier CG, Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403: 853-858
- Nagelkerken I, Munday PL (2016) Animal behaviour shapes the ecological effects of ocean acidification and warming: moving from individual to community-level responses. *Glob Change Biol* 22: 974-989
- Nakamura H, Asari T, Ohizumi Y, Kobayashi J, Yamasu T, Murai A (1993) Isolation of zooxanthella toxins, novel vasoconstrictive substances from the zooxanthella *Symbiodinium* sp. *Toxicon* 31: 371-376
- National Research Council (2011) *Climate stabilization targets: Emissions, concentrations and impacts over decades to millennia*. Washington, DC: Natl Res Counc ISBN 978-0-309-15176-4
- Neigel J, Domingo A, Stake J (2007) DNA barcoding as a tool for coral reef conservation. *Coral Reefs* 26: 487-499
- Noda H, Parkinson JE, Yang SY, Reimer JD (2017) A preliminary survey of zoantharian endosymbionts shows high genetic variation over small geographic scales on Okinawa-Jima Island, Japan. *PeerJ* 5: e3740
- Nunes FLD, Norris RD, Knowlton N (2011) Long distance dispersal and connectivity in amphiatlantic corals at regional and basin scales. *PLOS ONE* 6(7): e22298

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References

- Ocaña O, Brito A (2004) A review of Gerardiidae (Anthozoa: Zoantharia) from the Macaronesian Islands and the Mediterranean Sea with the description of a new species. *Rev Acad Canar Cienc* 15: 159-189
- Ocaña O, Brito A (2018) Zoanths parasitizing Anthozoa: Taxonomy, ecology and morphological evolution by genomes acquisition. *Rev Acad Canar Cienc* 30(1): 103-134
- Ocaña O, Brito A, González G (2005) The genus *Actinia* in the Macaronesian archipelagos: a general perspective of the North-oriental Atlantic and the Mediterranean species (Actiniaria: Actiniidae). *Vieraea* 33: 477-494
- Ocaña O, Brito A, González G, Herrera R (2007) Additions in relation to Gerardiidae from the Macaronesian waters and the Mediterranean Sea (Anthozoa: Zoantharia) *Vieraea* 35: 163-168
- O'Neal W, Pawlik JR (2002) A reappraisal of the chemical and physical defenses of caribbean gorgonian corals against predatory fishes. *Mar Ecol Prog Ser* 240: 117-126
- Ong CW, Reimer JD, Todd PA (2013) Morphologically plastic responses to shading in the zoanths *Zoanthus sansibaricus* and *Palythoa tuberculosa*. *Mar Biol* 160: 1053-1064
- Onodera K, Nakamura H, Oba Y, Ojika M (2004) Zooxanthellamide B, a novel large polyhydroxy metabolite from a marine dinoflagellate of *Symbiodinium* sp. *Biosci Biotechnol Biochem* 68: 4 955-958
- Orr JC, Fabry VJ, Aumont O, Bopp L, Doney SC, et al. (2005) Anthropogenic decline in high-latitude ocean carbonate by 2100. *Nature* 437(7059): 681-686
- Pajuelo JG, González JA, Triay-Portella R, Martín JA, Ruiz-Díaz R, Lorenzo JM, Luque Á (2016) Introduction of non-native marine fish species to the Canary Islands waters through oil platforms as vectors. *J Marine Syst* 163: 23-30
- Parkinson JE, Yang SY, Kawamura I, Byron G, Todd PA, Reimer JD (2016) A citizen science approach to monitoring bleaching in the zoantharian *Palythoa tuberculosa*. *PeerJ* 4:1815
- Parry ML, Canziani OF, Palutikof JP, van der Linden PJ, Hanson CE (2007) *Climate Change 2007: Impacts, adaptation and vulnerability. Contribution of working group II to the fourth assessment report of the Intergovernmental Panel on Climate Change*, Cambridge University Press, Cambridge, UK, 982pp
- Pax F (1908) Die Aktinienfauna Westafrikas. *Denks Med Naturw Gesselsch Jena* 13
- Pax F (1910) Studien an westindischen Actinien. *Zool Jahrb Suppl* 11: 157-330
- Peñuelas J, Estiarte M (1998) Can elevated CO₂ affect secondary metabolism and ecosystem function? *Trends Ecol Evol* 13: 20-24
- Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. *Science* 308: 1912-1915
- Peters H, O'Leary BC, Hawkins JP, Callum MR (2016) The cone snails of Cape Verde: Marine endemism at a terrestrial scale. *Glob Ecol Conserv* 7: 201-213
- Petit JR, Raynaud D, Basile I, Chappellaz J, Davisk M, et al. (1999) Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature* 399: 429-36

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References

- Piazzì L, Balata D, Bulleri F, Gennaro P, Ceccherelli G (2016) The invasion of *Caulerpa cylindracea* in the Mediterranean: the known, the unknown and the knowable. *Mar Biol* 163:161
- Pinheiro HT, Bernardi G, Simon T, Joyeux JC, Macieira RM, et al. (2017) Island biogeography of marine organisms. *Nature* 549: 82–85
- Polak O, Loya Y, Brickner I, Kramarski-Winter E, Benayahu Y (2011) The widely-distributed Indo-Pacific zoanthid *Palythoa tuberculosa*: a sexually conservative strategist. *Bull Mar Sci* 87: 605–621
- Poloczanska ES, Brown CJ, Sydeman WJ, Kiessling W, Schoeman DS, et al. (2013) Global imprint of climate change on marine life. *Nat Clim Change* 3: 919-925
- Porter JW, Fitt WK, Spero HJ, Rogers CS (1989) Bleaching in reef corals, physiological and stable isotopic responses. *Proc Natl Acad Sci USA* 86: 9342-9346
- Pörtner HO, Knust R (2007) Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* 315: 95-97
- Prada C, Weil E, Yoshioka PM (2010) Octocoral bleaching during unusual thermal stress. *Coral Reefs* 29: 41-45
- Proksch P (1994) Defensive roles for secondary metabolites from marine sponges and sponge-feeding nudibranchs. *Toxicon* 32(6): 639-655
- QGIS Development Team (2018) QGIS Geographic Information System. Open Source Geospatial Foundation Project. <http://qgis.osgeo.org>
- Rabelo EF, Soares MO, Matthews-Cascos H (2013) Competitive interactions among zoanthids (Cnidaria: Zoanthidae) in an intertidal zone of northeastern Brazil. *Braz J Oceanogr* 61: 35-42
- Rabelo EF, Rabay SG, Matthews-Cascon H, Fortes-Xavier ACM (2016) Distribuição de zoantídeos (Cnidaria: Zoanthidea) em recifes de arenito: influencia da competição com macroalgas. XII Congresso Latino-Americano de Ciências do Mar
- Rambaut A, Drummond AJ (2007) Tracer v1.4.
- Rambaut A (2016) <http://tree.bio.ed.ac.uk/software/figtree/>
- Rayner NA, Brohan P, Parker DE, Folland CK, Kennedy JJ, et al. (2006) Improved analyses of changes and uncertainties in sea surface temperature measured in situ since the mid-nineteenth century: the HadSST2 dataset. *J Clim* 19: 446–69
- Reimer AA (1971) Observations on the relationships between several species of tropical zoanthids (Zoanthidea, Coelenterata) and their zooxanthellae. *J Exp Mar Biol Ecol* 7: 207–214
- Reimer JD (2010) Key to field identification of shallow water brachycnemid zoanthids (Order Zoantharia: Suborder Brachycnemina) present in Okinawa. *Galaxea J Coral Reef Stud* 12: 23-29
- Reimer JD, Fujii T (2017) Zoantharia (Cnidaria: Anthozoa: Hexacorallia) Diversity research in Japan: Current state and future trends. In: Motokawa M, Kajihara H (eds) *Species diversity of animals in Japan*. Springer Japan, Tokyo, 383–399pp
- Reimer JD, Sinniger F (2010) Discovery and description of a new species of *Abyssoanthus* (Zoantharia: Hexacorallia) at the Japan Trench: the world's deepest known zoanthid. *Cah Biol Mar* 51: 451–457

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References

- Reimer JD, Todd PA (2009) Preliminary molecular examination of zooxanthellate zoanthids (Hexacorallia: Zoantharia) and associated zooxanthellae (*Symbiodinium* spp.) diversity in Singapore. *Raffles Bull Zool* 22: 103–120
- Reimer JD, Ono S, Fujiwara Y, Takishita K, Tsukahara J (2004) Reconsidering *Zoanthus* spp. diversity: molecular evidence of conspecificity within four previously presumed species. *Zool Sci* 21: 517–525
- Reimer JD, Takishita K, Maruyama T (2006a) Molecular identification of symbiotic dinoflagellates (*Symbiodinium* spp.) from *Palythoa* spp. (Anthozoa: Hexacorallia) in Japan. *Coral Reefs* 25: 521–527
- Reimer JD, Ono S, Iwama A, Tsukahara J, Maruyama T (2006b) High levels of morphological variation despite close genetic relatedness between *Zoanthus* aff. *vietnamensis* and *Zoanthus kuroshio* (Anthozoa: Hexacorallia). *Zool Sci* 23: 755–761
- Reimer JD, Ono S, Takishita K, Tsukahara J, Maruyama T (2006c) Molecular evidence suggesting species in the zoanthid genera *Palythoa* and *Protopalythoa* (Anthozoa: Hexacorallia) are congeneric. *Zool Sci* 23: 87–94
- Reimer JD, Takishita K, Ono S, Maruyama T, Tsukahara J (2006d) Latitudinal and intracolony ITS-rDNA sequence variation in the symbiotic dinoflagellate genus *Symbiodinium* (Dinophyceae) in *Zoanthus sansibaricus* (Anthozoa: Hexacorallia). *Phycol Res* 54 (2): 122–132
- Reimer JD, Shusuke O, Yasuo F, Junzo T (2007a) Seasonal changes in morphological condition of symbiotic dinoflagellates (*Symbiodinium* spp.) in *Zoanthus sansibaricus* (Anthozoa: Hexacorallia) in Southern Japan. *South Pac Stud* 27: n2
- Reimer JD, Takishita K, Ono S, Tsukahara J, Maruyama T (2007b) Molecular evidence suggesting interspecific hybridization in *Zoanthus* spp. (Anthozoa: Hexacorallia). *Zool Sci* 24: 346–359
- Reimer JD, Takishita K, Ono S, Maruyama T (2007c) Diversity and evolution in the zoanthid genus *Palythoa* (Cnidaria: Hexacorallia) based on nuclear ITS-rDNA. *Coral Reefs* 26: 399–410
- Reimer JD, Shusuke O, Tsukahara J, Fumihito I (2008a) Molecular characterization of the zoanthid genus *Isaurus* (Anthozoa: Hexacorallia) and associated zooxanthellae (*Symbiodinium* spp.) from Japan *Mar Biol* 153: 351–363
- Reimer JD, Ono S, Sinniger F, Tsukahara J (2008b) Distribution of zooxanthellate zoanthid species (Zoantharia: Anthozoa: Hexacorallia) in southern Japan limited by cold temperatures. *Galaxea J Coral Reef Stud* 10: 57–67
- Reimer JD, Hirose M, Wirtz P (2010) Zoanthids of the Cape Verde Islands and their symbionts: previously unexamined diversity in the Northeastern Atlantic. *Contrib Zool* 79: 147–163
- Reimer JD, Hirose M, Irei Y, Obuchi M, Sinniger F (2011) The sands of time: rediscovery of the genus *Neozoanthus* (Cnidaria: Hexacorallia) and evolutionary aspects of sand incrustation in brachyencemic zoanthids. *Mar Biol* 158: 983–993
- Reimer JD, Foord C, Irei Y (2012a) Species diversity of shallow water zoanthids (Cnidaria: Anthozoa: Hexacorallia) in Florida. *J Mar Biol* doi: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

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References

- Reimer JD, Lorion J, Irei Y, Hoeksema BW, Wirtz P (2017a) Ascension Island shallow-water Zoantharia (Hexacorallia: Cnidaria) and their zooxanthellae (*Symbiodinium*). *J Mar Biol Assoc UK* 97: 695-703
- Reimer JD, Herrera M, Gatins R, Roberts MB, Parkinson JE, Berumen ML (2017b) Latitudinal variation in the symbiotic dinoflagellate *Symbiodinium* of the common reef zoantharian *Palythoa tuberculosa* on the Saudi Arabian coast of the Red Sea. *J Biogeogr* 44: 661–673
- Reimer JD, Kim S, Arai S, Keshavmurthy S, Choi K (2018) First record of zooxanthellate *Zoanthus* (Anthozoa: Hexacorallia: Zoantharia) from Korea and Japan (East) Sea. *Mar Biodivers* 48: 1269-1273
- Rice J, Rochet MJ (2005) A framework for selecting a suite of indicators for fisheries management. *J Mar Sci* 62: 516–527
- Riebesell U, Schulz KG, Bellerby RGJ, Botros M, Fritsche P, et al. (2007) Enhanced biological carbon consumption in a high CO₂ ocean. *Nature* 450: 545–548
- Riera R, Becerro MA, Stuart-Smith RDS, Delgado JD, Graham JE (2014) Out of sight, out of mind: Threats to the marine biodiversity of the Canary Islands (NE Atlantic Ocean). *Mar Pollut Bull* 15: 9-18
- Ries JB, Cohen AL, McCorkle DC (2008) Marine biocalcifiers exhibit mixed responses to CO₂-induced ocean acidification. 11th Int Coral Reef Symp Ft. Lauderdale
- Roberts C, McClean CJ, Veron JEN, Hawkins JP, Allen GR, et al. (2002) Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science* 295: 1280-1284
- Rodríguez A, Hernández JC, Brito A, Clemente S (2017) Effects of ocean acidification on juveniles sea urchins: Predatos-prey interactions. *J Exp Mar Biol Ecol* 493: 31-40
- Rodríguez A, Clemente S, Brito A, Hernández JC (2018) Effects of ocean acidification on algae growth and feeding rates of juvenile sea urchins. *Mar Environ Res* 140: 382-389
- Rodríguez L, García JJ, Carreño, Brezo Martínez (2019) Integration of physiological knowledge into hybrid species distribution modelling to improve forecast of distributional shifts of tropical corals. *Divers Distrib* 25: 1-14
- Rosa I, Rocha RJM, Lopes A, Cruz ICS, Calado R, et al. (2016) Impact of air exposure on the photobiology and biochemical profile of an aggressive intertidal competitor, the zoanthid *Palythoa caribaeorum*. *Mar Biol* 163:222
- Rotjan RD, Lewis SM (2008) The impact of coral predators in tropical reefs. *Mar Ecol Prog Ser* 367: 73–91
- Rowan R, Powers DA (1992) Ribosomal RNA sequences and the diversity of symbiotic dinoflagellates (zooxanthellae). *Proc Natl Acad Sci USA* 89: 3639–3643
- 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
- Ryland JS, Lancaster JE (2003) Revision of methods for separating species of *Protopalythoa* (Hexacorallia: Zoanthidea) in the tropical West Pacific. *Invertebr Syst* 17: 407–428
- Sabine CL, Feely RA, Gruber N, Key RM, Lee K, et al. (2004) The oceanic sink for anthropogenic CO₂. *Science* 305: 367-371

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References

- Sangil C, Sansón M, Afonso-Carrillo J, Martín-García L (2010) Extensive off-shore meadows of *Penicillus capitatus* (Udoteaceae, Chlorophyta) in the Canary Islands (eastern Atlantic Ocean). *Bot Mar* 53: 183-187
- Sangil C, Sansón M, Afonso-Carrillo J (2011) Spatial variation patterns of subtidal seaweed assemblages along a subtropical oceanic archipelago: thermal gradient vs herbivore pressure. *Estuar Coast Shelf S* 94: 322-333
- Sangil C, Sansón M, Afonso-Carrillo J, Herrera R, Rodríguez A, Martín-García L, Díaz-Villa T (2012) Changes in subtidal assemblages in a scenario of warming: Proliferations of ephemeral benthic algae in the Canary Islands (eastern Atlantic Ocean) *Mar Environ Res* 77: 120-128
- Santana EFC, Alves AL, Santos ADM, Cunha MDGGS, Perez CD, Gomes APB (2015) Trophic ecology of the zoanthid *Palythoa caribaeorum* (Cnidaria: Anthozoa) on tropical reefs. *J Mar Biol Assoc UK* 95: 301-309
- Santos MEA, Reimer JD (2018) Rafting in Zoantharia: a hitchhiker's guide to dispersal? *Mar Pollut Bull* 130: 307–310
- Santos MEA, Kitahara MV, Lindner A, Reimer JD (2016) Overview of the order Zoantharia (Cnidaria:Anthozoa) in Brazil. *Mar Biodivers* 46: 547-559
- 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. *Syst Biodiv* 17: 165-178
- Santos SR, Taylor DJ, Kinzie R, Hidaka M, Sakai K, Coffroth MA (2002) Molecular phylogeny of symbiotic dinoflagellates inferred from partial chloroplast large subunit (23S)-rDNA sequences. *Mol Phylogenet Evol* 23: 97–111
- Sawelew L, Gault F, Nuccio C, Perez Y, Lorquin J (2018) Characterization of palytoxin from an undescribed *Palythoa* (Anthozoa: Zoantharia: Sphenopidae) with significant in vitro cytotoxic effects on cancer cells at picomolar doses. *BioRxiv* doi: <http://dx.doi.org/10.1101/292219>
- Sax DF, Gaines SD, Brown JH (2002) Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. *Am Nat* 160: 766–783
- Scheibling RE, Robinson MC (2008) Settlement behavior and early post-settlement predation of the sea urchin *Strongylocentrotus droebachiensis*. *J Exp Mar Biol Ecol* 365: 59–66
- Schwarz G (1978) Estimating the dimension of a model. *Ann Stat* 6: 461–464
- Sebens KP (1982) Intertidal distribution of zoanths on the Caribbean coast of Panama: effects of predation and desiccation. *Bull Mar Sci* 32: 316–335
- Seebens H, Gastner MT, Blasius B (2013) The risk of marine bioinvasion caused by global shipping. *Ecol Lett* 16: 782-790
- Seeman P, Gernert C, Schmitt S, Mebs D, Hentschel U (2009) Detection of hemolytic bacteria from *Palythoa caribaeorum* (Cnidaria, Zoantharia) using a novel palytoxin-screening assay. *Antonie van Leeuwenhoek* 96: 405–411
- Shearer TL, Van Oppen MJH, Romano SL, Wörheide G (2002) Slow mitochondrial DNA sequence evolution in the Anthozoa (Cnidaria). *Mol Ecol* 11: 2475-2487

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References

- Shirayama Y, Thornton H (2005) Effect of increased atmospheric CO₂ on shallow water marine benthos. *J Geophys Res* 110: C09S08
- Siebeck U, Marshall N, Klüter A, Hoegh-Guldberg O (2006) Monitoring coral bleaching using a colour reference card. *Coral Reefs* 25: 453-460
- Siebeck U, Logan D, Marshall N (2008) CoralWatch: a flexible coral bleaching monitoring tool for you and your group. *Proc 11th Int Coral Reef Symp* 1: 54-553
- Silva JF, Gomes PB, Santana EC, Silva JM, Lima ÉP, Santos AMM, Pérez CD (2015) Growth of the tropical zoanthid *Palythoa caribaeorum* (Cnidaria: Anthozoa) on reefs in northeastern Brazil. *An Acad Bras Ciênc* 87(2): 985-996
- Simpson JH, Tett PB (1986) Island stirring effects on phytoplankton growth. In: Bowman MJ, Yentsch CM, Peterson WT (eds) *Tidal Mixing and Plankton Dynamics*. New York ISBN 978-1-4612-4966-5
- Sinniger F, Montoya-Burgess JI, Chevallon P, Pawlowski J (2005) Phylogeny of the order Zoantharia (Anthozoa, Hexacorallia) based on mitochondrial ribosomal genes. *Mar Biol* 147: 1121-1128
- Sinniger F, Reimer JD, Pawlowski J (2008) Potential of DNA sequences to identify zoanthids (Cnidaria: Zoantharia). *Zool Sci* 25: 1253-1260
- Sinniger F, Reimer JD, Pawlowski J (2010) The Parazoanthidae (Hexacorallia: Zoantharia) DNA taxonomy: description of two new genera. *Mar Bio* 40(1): 57-70
- Somero GN (2002) Thermal physiology and vertical zonation of intertidal animals: optima, limits, and costs of living. *Integ Comp Biol* 42: 780-789
- Southward AJ, Hawkins SJ, Burrows MT (1995) Seventy years` observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. *J Therm Biol* 20: 127-155
- Spalding MD, Fox HE, Gerald GR, Davidson N, Ferdaña ZA, et al. (2007) Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *Bio Sci* 57: 573-583
- Spiridonov VA, Neretina TV, Schepetov D (2014) Morphological characterization and molecular phylogeny of *Portunoidea* Rafinesque, 1815 (Crustacea Brachyura): Implications for understanding evolution of swimming capacity and revision of the family-level classification. *Zool Anz* 253: 404-429
- Stamatakis A (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies *Bioinformatics* 30 (9): 1312-1313
- Stramma L, Siedler G (1988) Seasonal changes in the North Atlantic Subtropical Gyre. *J Geoph Res* 93: 8111-8118
- Suchanek TH, Green DJ (1981) Interspecific competition between *Palythoa caribaeorum* and other sessile invertebrates on St. Croix reefs, U.S. Virgin Islands. *Proc 4th Int Coral Reef Symp* 679-684
- Sültemeyer D (1998) Carbonic anhydrase in eukaryotic algae: characterization, regulation, and possible function during photosynthesis. *Can J Bot* 76: 962-972

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References

- Swain TD (2009) Phylogeny-based species delimitations and the evolution of host associations in symbiotic zoanthids (Anthozoa, Zoanthidea) of the wider Caribbean region. *Zool J Linn Soc Lond* 156: 223–238
- Swain TD (2010) Evolutionary transitions in symbioses: dramatic reductions in bathymetric and geographic ranges of Zoanthidea coincide with loss of symbioses with invertebrates. *Mol Ecol* 19: 2587–2598
- Swain TD, Wulff JL (2007) Diversity and specificity of Caribbean sponge–zoanthid symbioses: a foundation for understanding the adaptive significance of symbioses and generating hypotheses about higher-order systematics. *Biol J Linn Soc* 92: 695–711
- Tanner JE (1995) Competition between scleractinian corals and macroalgae: An experimental investigation of coral growth, survival and reproduction. *J Exp Mar Biol Ecol* 190(2): 151-168
- Tanner JE (2002) Consequences of density-dependent heterotrophic feeding for a partial autotroph. *Mar Ecol Prog Ser* 227: 293-304
- Telesca L, Belluscio A, Criscoli A, Ardizzone G, Apostolaki ET, et al. (2015) Seagrass meadows (*Posidonia oceanica*) distribution and trajectories of change. *Sci Rep-UK* 5: 12505
- Thompson JD, Higgins DG, Gibson TJ (1994) CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Res* 22:4673–4680
- Thomsen MS, Byers JE, Schiel DR, Bruno JF, Olden JD, Wernberg T, Silliman BR (2014) Impacts of marine invaders on biodiversity depend on trophic position and functional similarity. *Mar Ecol Prog Ser* 495: 39–47
- Toonen RJ, Puritz JB, Forsman ZH, Whitney JL, Fernandez-Silva I, Andrews KR, Bird CE (2013) ezRAD: a simplified method for genomic genotyping in non-model organisms. *PeerJ* 19(1):e203
- Tortell P (2000) Evolutionary and ecological perspectives on carbon acquisition in hytoplankton. *Limnol Oceanogr* 45: 744–750
- Truchot JP (1988) Problems of acid–base balance in rapidly changing intertidal environments. *Am Zool* 28: 55–64
- Tubaro A, Durando P, Del Favero G, Ansaldi F, Icardi G, Deeds JR, Sosa S (2011) Case definitions for human poisoning postulated to palytoxins exposure. *Toxicol* 57: 478–495
- Ullah H, Nagelkerken I, Goldenberg SU, Fordham DA (2018) Climate change could drive marine food web collapse through altered trophic flows and cyanobacterial proliferation. *Plos Biology* 16(1): e2003446
- Van Camp L, Nykjaer L (1988) Remote sensing of the Northwest Africa upwelling area: Vol. 1. Final technical description of the AVHRR and meteorological data processing software. Report of the Commission of the European Communities Joint Research Centre, Ispra, Italy
- Vélez P, González M, Pérez MD, Hernández A (2015) Open ocean temperature and salinity trends in the Canary Current large marine ecosystem. In: Valdés JL, Déniz GI (eds) Oceanographic and biological features in the Canary Current large marine ecosystem. IOC-UNESCO IOC Technical Series, Paris

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References

- Vergés A, Steinberg PD, Hay ME, Poor AGB, Campbell AH, et al. (2014) The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. *Proc R Soc* 281: 20140846
- Vermeij MJA, Bakker J, van der Hal N, Bak RPM (2011) Juvenile coral abundance has decreased by more than 50% in only three decades on a small Caribbean island. *Diversity* 3(3): 296-307
- Veron JEN (1995) Corals in space and time. Cornell University Press, Ithaca, NY
- Veron JEN, DeVantier LM, Turak E, Green AL, Kininmonth S, Stafford-Smith M, Peterson N (2009) Delineating the Coral Triangle. *Galaxea* 11: 91–100
- Villar RM, Gil-Longo J, Daranas AH, Souto ML, Fernández JJ, et al. (2003) Evaluation of the effects of several zoonthamine-type alkaloids on the aggregation of human platelets. *Bioorg Med Chem* 11: 2301–2306
- Walther GR, Roques A, Hulme PE, Sykes MT, Pusek P, et al. (2009) Alien species in a warmer world: risk and opportunities. *Trends Ecol Evol* 24(12): 686-693
- Welladsen HM, Southgate PC, Heimann K (2010) The effects of exposure to near-future levels of ocean acidification on shell characteristics of *Pinctada fucata* (Bivalvia: Pteriidae). *Molluscan Res* 30(3): 125-130
- West DA (1976) Aposematic coloration and mutualism in sponge-dwelling tropical zoanths. In: Mackie GO (ed) *Coelenterate ecology and behavior*. New York
- Williams JEH, Bunkley-Williams L (1990) The world-wide coral reef bleaching cycle and related sources of coral mortality. *Atoll Research Bulletin* 335: 1-71
- Willig MR, Kaufman DM, Stevens RD (2003) Latitudinal gradients of biodiversity: pattern, process, and synthesis. *Annu Rev Ecol Evol S* 34: 273-309
- Winter A, Appeldoorn RS, Bruckner A, Williams EH, Goenaga C (1998) Sea surface temperatures and coral reef bleaching of La Parguera, Puerto Rico (northeastern Caribbean Sea). *Coral Reefs* 17: 377-382
- Wirtz P (1995) One vascular plant and ten invertebrate species new to the marine flora and fauna of Madeira. *Arquipel Life Mar Sci Suppl* 13: 119-123
- Whittaker RJ, Fernández-Palacios JM (2007) *Island biogeography: ecology, evolution, and conservation*, 2nd edn. Oxford University Press, Oxford
- Whittaker RJ, Triantis KA, Ladle RJ (2008) A general dynamic theory of oceanic island biogeography. *J Biogeogr* 35: 977–994
- Wood HL, Spicer JI, Widdicombe S (2008) Ocean acidification may increase calcification rates, but at a cost. *Proc R Soc London Ser B* 275: 1767–73
- Yanes A, Marzol MV, Romero C (2006) Characterization of sea storms along the coast of Tenerife, the Canary Islands. *J Coast Res* 48: 124-128
- Yang S, Bourgeois C, Ashworth CD, Reimer JD (2013) *Palythoa* zoanthid ‘barrens’ in Okinawa: examination of possible environmental causes. *Zool Stud* 52(1): 39-49
- Yapici S, Filiz H, Bilge G (2016) Northwards range expansion of *Sparisoma cretense* (Linnaeus, 1758) in the Turkish Aegean Sea. *J Aquacult Eng Fish Res* 2(4): 201-207

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References

Yorifuji M, Harii S, Nakamura R, Fudo M (2017) Shift of symbiont communities in *Acropora tenuis* juveniles under heat stress. PeerJ 5: e4055

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