Biodiversity and distribution of sea anemones (Cnidaria, Anthozoa, Actiniaria) in the Northern Humboldt Current System

Allison Durand
Universidad Nacional Mayor de San Marcos
Deysi Valdivia-Chávez
Instituto del Mar del Perú: Instituto del Mar del Peru
Víctor Aramayo (varamayon@unmsm.edu.pe)
Universidad Nacional Mayor de San Marcos https://orcid.org/0000-0003-2026-4487

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Abstract

Diverse and abundant sea anemones are common in shallow marine areas. Detailed biodiversity analyses in the Northern Humboldt Current System (NHCS) are comparatively scarce. To contribute to the biodiversity inventory and distribution information of this taxa, we analyzed exhaustively the available literature in this region. A total of 23 anemone species were identified, distributed in 68 localities, and grouped into 1 order (Actiniaria), 6 families (Actiniidae, Actinostolidae, Aiptasiidae, Isanthidae, Phelliidae and Sagartiidae), and 20 genera. The most reported species are *Anthothoe chilensis* (37 references), *Phymactis clematis* (28), *Phymanthea pluvia* (27), *Oulactis concinnata* (18), and *Antholoba achates* (15). Lima is the region with the highest number of publications, followed by La Libertad, Piura, Lambayeque, and Ancash. *Anthothoe chilensis* occurs in almost all Peruvian coastal regions. On the contrary, *O. concinnata* has been primarily observed in Lima, while *A. achates* occurred only in the southern regions (Ica, Arequipa, and Moquegua). Rocky substrates (~ 55% records) seem to be the most suitable habitat for sea anemones in Peru, corresponding to exposed (e.g. vertical walls) and sheltered zones (e.g. rocky crevices, caves, under rock areas). Although most species in the NHCS exhibit a relatively wide spatial distribution, our results suggest there are several regions with little or no research efforts. Despite a growing study effort over the past 30 years (> 50% of biodiversity reported), the current biodiversity status for this group is still unclear. Significant effort is needed to better analyze occurrence patterns and unveil new species amid human-induced environmental changes.

Introduction

Actiniaria is currently classified into two suborders (Rodríguez et al. 2014): Anenthemonae and Enthemonae. Major differences lie in anatomical structures; in the first suborder, a unique arrangement of mesenteries is characteristic; while the second suborder possesses a typical body scheme, mostly hexamerous cycles, in which pairs of mesenteries arise in the exocoels (Rodríguez et al. 2014). To the untrained eye, actiniarians look very similar; however, the so-called true anemones account for approximately 1200 species grouped in 46 families and are represented within the subclass Hexacorallia, class Anthozoa (Brusca 1980; Daly et al. 2007).

Sea anemones constitute a conspicuous and diverse group in marine environments across all depths and latitudes (Daly et al. 2007; Fautin 2013; Rodríguez et al. 2014). These organisms survive mostly adhered to hard substrates, but several species exhibit both a commensalism strategy (e.g. epibiosis on hermit crabs) (Ruppert and Barnes 1996) and burial behavior (sand and/or mud) (Häussermann and Försterra 2009). A large number of polypoid-shaped species grow in colonial or solitary stages of surviving, yet clonal aggregations stand out as a notoriously efficient and successful strategy for rapid growth, space competition, and dispersal of individuals (Fautin 2013).

Physical factors modulating the distribution and aggregation patterns of sea anemones are substrate availability and local oceanographic conditions (e.g. transparency, turbulence, and ocean currents). Nevertheless, intra- and interspecific competition for food and space has largely been known as equally crucial for these organisms (Chintiroglou and Koukouras 1992). Early-life survival and ecological connectivity also play a critical role in the success of the settlement of sea anemones species and their distribution among marine regions (Ocaña et al. 2007; Watson et al. 2018). Because of their high metabolic sensitivity along their life cycle, some species have been proposed as key bioindicators of pervasive changes in the chemistry of surrounding waters and the overall marine environment health (Linton and Warner 2003; Duckworth et al. 2017).

Although frequently observed living at rocky and sandy shores substrates, exhibiting both patchy and highly dense distributions along depth gradients, thorough studies addressing the sea anemone biodiversity and ecology remain scarce in the Northern Humboldt Current System (NHCS), corresponding to the Peruvian waters in the southeastern Pacific. Most of the available information derivate from sporadic reports for specific sites as a result of compilatory efforts (e.g. Novoa et al. 2010; Hooker et al. 2011) or general benthic inventories (e.g. Paredes et al. 1999; Uribe et al. 2013). There is no specific research aiming the sea anemones as a target group in the NHCS. As such, specific information for these organisms is scant and scattered, limiting our opportunities to assess the ecological relevance of these populations and analyze their prevailing status. To contribute to the study of this benthic group, in this paper we perform an exhaustive bibliographic review to document the biodiversity and distribution of sea anemone species reported in the NHCS.

Methods

Study area

Information and data published on sea anemones from 68 localities (most representatives in Fig. 1) in 10 specific Peruvian coastal regions were used. Our geographic range included data from both the equatorially influenced sector in Northern Peru (approximately from the Peruvian northern border to ~ 5°S) and the cold sector from part of Northern, Central and Southern Peru (Chaigneau et al. 2013), also named the Humboldtian region off Peru or the NHCS. The Peruvian waters are recurrently affected by interannual events such as El Niño (EN), along with an intense oxygen minimum zone (OMZ, dissolved oxygen < 0.5 $ml.l^{-1}$) from shallow to deeper areas that modulate the abundance and development of both pelagic and benthic communities (Tarazona et al. 2003; Bertrand et al. 2011).

For practical purposes, this article will use 'the NHCS' to refer to all localities studied, although our spatial scale covers a study area comprising the entire Peruvian coast, including both cold and tropical marine ecosystems and several types of coastal habitats (beaches, islets, islands).

Data sources and criteria employed

An exhaustive literature review was performed to list the sea anemone species reported in different benthic habitats of the NHCS. We focused on the true anemones only. The Ceriantharia and Hexacorallia subclasses (tube anemones and colonial anemones, respectively) were excluded since these groups are critically less documented for this ocean region.

Overall, we reviewed 110 scientific references that analyze several topics of sea anemones, including peer-reviewed papers, official bulletins and reports (from national institutions), theses and dissertations, and even seminal reports (e.g. Verrill 1867). Grey literature was explicitly excluded in this work (conference abstracts, nonreferenced technical reports, unsourced or poorly documented online material, etc.) Authoritative online resources (i.e. databases) were used to confirm local references in some cases and verify the global incidence of some species; for instance, the World Register of Marine Species (WoRMS: http://www.marinespecies.org/), the Ocean Biodiversity Information System (OBIS: https://obis.org/), the Global Biodiversity Information Facility (GBIF: https://www.gbif.org/) and the Biodiversity Heritage Library database (BHL: https://www.biodiversitylibrary.org/).

When the geographic coordinates range and/or specific sampling locality were not indicated, we used the local name of the city reported in the document as the main reference. Our list includes the region name followed by the specific locality (in parentheses). Due to missing data regarding the bathymetric range of some species, our discussion of the bathymetric distribution was based only on reliably known information. Finally, to avoid confusion when indicating scientific names, we decided not to use abbreviations for the species *Anthothoe chilensis* and *Actinostola chilensis*.

Results

Sea anemone biodiversity and latitudinal distribution

A total of 23 species have been reported for the Peruvian coast, grouped into 1 order (Actiniaria), 1 superfamily with a temporary name (Actiniaria *incertae sedis*), 6 families (Actiniidae, Actinostolidae, Aiptasiidae, Isanthidae, Phelliidae and Sagartiidae) and 20 genera (Table 1; Fig. 2a). The most diverse families were Actiniidae (11 spp., 50% of total), Actinostolidae, and Sagartiidae (both with 3 spp., 13.6%). The species *Anactis picta* and *Paractis peruviana* are not currently assigned to a specific family (Table 1); instead, they have been temporally placed under the superfamily category Actiniaria *incertae sedis*. Precisely, these two species have been mentioned in early bibliographic references only (Verrill 1867; Pax 1912). Contemporaneously, Fautin (2013, 2016) cited the same authors when referring to these species.

Out of 23 species identified, the top five exhaustively reported are *Anthothoe chilensis* (37 references), *Phymactis clematis* (28), *Phymanthea pluvia* (27), *Oulactis concinnata* (18), and *Antholoba achates* (15) (Fig. 2a). Major contributions to the scientific references of these and other species have been authored by Häussermann & Försterra (2009) and Fautin (2013, 2016). Moreover, our time series for reported species in Peruvian waters (1860–2020) revealed very low progress, with long periods of research inactivity in terms of new species discoveries or new records, with slight changes every 50 years approximately, and a clear shift over the last 30 years only (Fig. 2b).

Our findings indicate that the top five reported species (~ 22%) have a broad spatial distribution (Fig. 2c; Table 1). For instance, studies concerning *Anthothoe chilensis*, *Phymactis papillosa*, *O. concinnata*, *P. clematis*, and *P. pluvia* reveal the extensive distribution of these species, especially in intertidal zones throughout the Peruvian coast. Conversely, about 50% of identified species for Peru, namely *A. picta*, *P. peruviana*, *Anthopleura dowii*, *Parantheopsis ocellata*, *Actinostola chilensis*, *Paranthus niveus*, *Bartholomea peruviana*, *Phellia rubens*, *Actinothoe gravieri*, *Sagartia lessonii*, and *Bunodosoma grande* exhibit a latitudinal distribution restricted to the northern regions. Less-studied species such as *Anemonia alicemartinae*, *Bunodactis octoradiata*, *Anthopleura radians*, *A. achates* and *Cnidanthea maculata* seem to be constrained to the southern coast (~ 23% of spp.). Likewise, *Nemactis primula* has been exclusively reported for the central region (Lima, ~ 5%). Recent reports indicate that *Oulactis coliumensis* inhabit the central and southern coasts (Spano et al. 2022).

The highest number of scientific publications (18) corresponds to the Lima region, which possesses more than twice the studies developed for other regions (Fig. 2d) such as La Libertad (9) as well as Piura, Lambayeque, and Ancash (7). However, the number of localities studied in each region is unevenly distributed, since some north-central regions (La Libertad, Ancash, and Lima) exhibit a high number of localities surveyed, compared to the southern regions such as Arequipa, Moquegua, and Tacna (Fig. 2d). Consequently, the research effort (indicated by the number of publications) does not seem to have targeted those regions with a rather scarce number of studies.

Table 1 Sea anemones species from Peru, considering taxonomic information, geographic distribution, the total number of localities, and bathymetric range. UD: undetermined. Symbol (*) indicates doubtful information.

Family	Nº	Species	Geographic area	Localities in Peru	Bathymetric range (m)	Main references
N/A	1	*Anactis picta* (Lesson, 1830)	Peru	Piura (Paita)	UD	Verrill 1867; Pax 1912; Fautin 2013,2016
	2	*Paractis peruviana* (Lesson, 1830)	Peru	Piura (Paita)	UD	Fautin 2013, 2016
Actiniidae	3	Anemonia alicemartinae (Häussermann and Försterra, 2001)	Coasts of the Humboldt Current ecosystem. Peru, Ecuador (Gulf of Guayaquil*) and Chile.	Moquegua (Puerto Inglés; Punta Coles, Ilo); Tacna (Boca del Rio)*	0 - 15	Häussermann and Försterra 2001; Canales-Aguirre et al. 2015; Baldarrago et al. 2019; Pinochet et al. 2019; Zuñiga 2019; OBIS 2021*
	4	*Anthopleura dowii* (Verrill, 1869)	Mexico, El Salvador, Nicaragua, Panama, Ecuador, Peru	Piura (Isla Foca)	UD	Novoa et al. 2010
	5	Anthopleura radians (Spano and Häussermann, 2017)	Chile (Pan de Azúcar (26° 11'S ; 70° 39'W) to Puerto Aldea (30° 17 S; 71° 36'W)), Mexico (Punta Eugenia - Baja California Sur), Peru, New Zealand*.	Moquegua (Puerto Inglés)	0 - 1	Spano and Häussermann 2017; Zuñiga 2019; Vassallo-Avalos et al. 2020
	6	*Bunodactis octoradiata* (Carlgren, 1899)	South Atlantic (Falkland Islands, Beagle Channel, Strait of Magellan, Santa Cruz Province and Argentina); SE Pacific (Strait of Magellan, Tierra del Fuego, Chile (53°S-55°S) and Peru) and Antarctica.	Arequipa (La Metalera, Albizuri)	UD	Häussermann 2006; Häussermann and Försterra 2009; Zanabria 2013; Carrizo 2014; Garese et al. 2014
	7	*Bunodosoma grande* (Verril, 1869)	Pacific Ocean. Mexico, Nicaragua, Costa Rica*, Panama, Ecuador, Peru.	Tumbes (Zorritos); Piura (Paita)	UD	Verrill 1867; Garese et al. 2009; Fautin 2013, 2016; Barragán et al. 2019
	8	*Nemactis primula* (Drayton in Dana, 1846)	Peru	Lima (Isla San Lorenzo; Callao)	UD	Verrill 1867; Fautin 2013, 2016
	9	*Oulactis concinnata* (Drayton in Dana, 1846)	Peru and Chile (up to Valparaiso)	La Libertad (Puerto Malabrigo, Isla Guañape, Paiján, Pacasmayo, Trujillo); Áncash (Bahía Ferrol, Bahía Samanco, Playa Las Salinas, Casma); Lima (Barranca, Chancayllo, Chancay, Ancón, Callao, Isla San Lorenzo, Punta Negra, Pampa Melchorita, Pucusana, Asia); Ica (Bahía de Pisco, Paracas, Playa Mendieta, Yumaque); Arequipa (La Metalera)	0 - 8	Verrill 1867; Paredes et al. 1988; Carter 1965; Tokeshi and Romero 1995; Paredes et al. 1999; Häussermann 2003, 2006; Guzmán 2012; Uribe et al. 2013; Zanabria 2013; Fautin 2013, 2016; Flores 2014; Atoche 2017; Tasso et al. 2018; De Lucio 2020; Uribe et al. 2020; A. Ramirez et al. 2022
	10	Oulactis coliumensis (Riemann-Zürneck and Gallardo, 1990)	Central Peru and Chile (up to Coliumo bay)	Lima (Isla San Lorenzo); Ica (Islas Chincha, Paracas)	3 - 25	Spano et al. 2022
	11	*Parantheopsis ocellata* (Lesson, 1830)	Peru and Chile	Piura (Paita)	UD	Carter 1965; Häussermann and Försterra 2009; Fautin 2013, 2016
	12	*Phymactis clematis* (Drayton in Dana, 1846)	California, El Salvador, Nicaragua, Panama, Peru, Chile (up to Tierra del Fuego, Juan Fernández and Easter Island)	Lambayeque (Isla Lobos de Tierra, Islas Lobos de Afuera); La Libertad (Puerto Malabrigo, Isla Guañape, Islote Cantores, Isla Macabí, Punta Uripe, Paiján); Lima (Barranca, Carquín, Chancaillo, Chancay, Ancón, Callao, Isla San Lorenzo, Isla Palomino, Punta Negra, Pucusana, Asia, Cerro Azul); Ica (Bahía de Pisco, Punta San Juan); Arequipa (La Metalera, Albizuri); Moquegua (Puerto Inglés; Punta Coles); Tacna (Playa Chasqui, Cerro Cortado)	0 - 15; 25; 28	Carter 1965; Paredes and Tarazona 1980; Paredes et al. 1988; Tokeshi and Romero 1995; Paredes et al. 1999; Rivadeneira and Oliva 2001; Guzmán 2012; Zanabria 2013; Fautin 2013, 2016; Flores 2014; Coronado 2015; Alfaro et al. 2016; Alegre 2017; Atoche 2017; Gonzáles and Pastor 2017; P. Ramírez et al. 2017a, 2017b, 2019a, 2019b, 2019c, 2020; Baldarrago et al. 2019; Zuñiga 2019; De Lucio 2020; A. Ramírez et al. 2022; Aramayo et al. 2022

Table 1 Cont.

	13	*Phymactis papillosa* (Lesson, 1830)	Mexico (Gulf of California and northern coast of Mexico), Peru (Playa Tantalean) to Chile (Chonos Archipelago)	Piura (Playa Tantalean, Paita); La Libertad (Isla Guañape, Trujillo, Paiján, Pacasmayo); Áncash (Playa Las Salinas, Isla Santa, Bahía Ferrol, Bahía Samanco, Bahía Tortugas, Casma, Huarmey); Lima (Playa San Francisco, Callao, Isla San Lorenzo, Pucusana); Ica (Bahía Independencia, Paracas, Islas Ballestas, Playa Mendieta); Arequipa (Matarani)	0 - 8	Häussermann, 2004b; Häussermann and Försterra 2009; Uribe et al. 2013; Fautin 2016; Atoche 2017; Cuya and Escobar 2017; Pastor et al. 2017; Alfaro et al. 2019; Uribe et al. 2020
	14	*Phymanthea pluvia* (Drayton in Dana, 1846)	Peru (Paita) to Chile (Valparaiso)	Piura (Isla Foca, Caleta Yacila, Playa Tantalean, Paita); Lambayeque (Islas Lobos de Afuera); La Libertad (Puerto Malabrigo, Isla Guañape, Isla Corcovado, Isla Chao, Islote Cantores, Isla Macabi, Punta Uripe, La Ramada); Áncash (Isla La Viuda, Hueco de la Vela, La Boquita, Playa Las Salinas, Isla Santa, Bahía Tortugas, Casma, Huarmey); Lima (Barranca, Carquin, Chancaillo, Ancón, Callao, Isla San Lorenzo, Isla Palomino, Punta Negra, San Bartolo, Pucusana, Asia, Cerro Azul); Ica (Bahía de Pisco, Bahía Independencia, Paracas, Islas Ballestas, Playa Mendieta, Punta San Juan, San Juanito); Arequipa (Caraveli, Matarani, La Metalera, Albizuri); Moquegua (Puerto Inglés, Punta Coles, Ilo)	0 - 15	Carter 1965; Paredes et al. 1988; Paredes et al. 1999; Häussermann 2004b; Novoa et al. 2010; Guzmán 2012; Uribe et al. 2013; Zanabria 2013; Fautin 2013, 2016; Flores 2014; Coronado 2015; Alfaro et al. 2016; Alegre 2017; Alfaro et al. 2017; Atoche 2017; Gonzáles and Pastor 2017; Pastor et al. 2017; Baldarrago et al. 2019; P. Ramirez et al. 2019c; Uribe et al. 2019; Zuñiga 2019; Monroy et al. 2020; Yafac-Piedra and Garcia-Alayo 2020; Donayre 2021
Actinostolidae	15	*Antholoba achates* (Drayton in Dana, 1846)	Peru, Chile, Argentina, Uruguay, Brazil and New Zealand	Ica (Islas Ballestas); Arequipa (La Metalera, Albizuri); Moquegua (Puerto Inglés, Punta Coles, Leonas)	0 - 10	Carter 1965; Häussermann and Försterra 2009; Zanabria 2013; Fautin 2013, 2016; Tejada and Baldarrago 2016; Pastor et al. 2017; Baldarrago et al. 2019; Zuñiga 2019
	16	*Actinostola chilensis* (McMurrich, 1904)	SE Pacific. Central and northern part of the fjords, from Seno de Reloncaví (41°35'35"S, 72°53'W) to Puyuhuapi (44°31,608'S; 72°32,107'W), Chile.	La Libertad (Isla Guañape, Isla Chao, Islote Cantores)	0 - 5	Häussermann 2004c, 2006; Häussermann and Försterra 2009; Alfaro et al. 2016; Atoche 2017
	17	*Paranthus niveus* (Lesson, 1830)	South Pacific East, Peru and Chile	Piura (Paita)	UD	Häussermann and Försterra 2009; Fautin 2013, 2016
Aiptasiidae	18	*Bartholomea peruviana* (Pax, 1912)	Peru	Piura (Paita)	UD	Pax 1912; Fautin 2013, 2016; Grajales 2014; Grajales and Rodriguez 2014
Isanthidae	19	*Cnidanthea maculata* (Carlgren, 1959)	Peru	Ica (Bahía de Pisco)	UD	Fautin 2013, 2016
Phelliidae	20	*Phellia rubens* (Verrill, 1869)	Peru	Tumbes (Zorritos)	UD	Andres 1884; Pax 1912; Fautin 2013, 2016
Sagartiidae	21	*Anthothoe chilensis* (Lesson, 1830)	E Pacific (Peru and Chile); SW Atlantic (Rio de Janeiro - Brazil, Mar del Plata - Argentina); Subantarctic Islands (South Georgia Island); South Atlantic (Namibia and South Africa).	Piura (Isla Foca); Áncash (Isla La Viuda, Isla Blanca, Isla Santa, Bahía Ferrol, El Dorado, La Boquita, Samanco, Bahía Tortugas); Lambayeque (Islas Lobos de Afuera, Isla Lobos de Tierra); La Libertad (Isla Guañape, Chérrepe); Lima (Ancón, Isla San Lorenzo, Isla Cabinza, Isla Palomino, Pampa Melchorita, Pucusana); Ica (Paracas, Bahía Independencia, Bahía de Pisco, Punta San Juan); Arequipa (La Metalera, Albizuri, Caleta La Ballenita); Moquegua (Puerto Inglés, Punta Coles)	0 - 15	Paredes et al. 1988; Excoffon et al. 1997; Paredes et al. 1999; Zanabria 2004; Quiroz-Garrido 2005; Retuerto et al. 2007; Häussermann and Försterra 2009; Firstater et al. 2010; Novoa et al. 2010; Hooker et al. 2011; Guzmán 2012; Uribe et al. 2013; Zanabria 2013; Galán 2015; Berrú and Nizama 2016; Alegre 2017; Atoche 2017; Gonzáles and Pastor 2017; Pastor et al. 2017; Tasso et al. 2018; Alfaro et al. 2019; Baldarrago et al. 2019; Berrú and Perea de la Matta 2019; P. Ramirez et al. 2019b, 2019c, 2020; Uribe et al. 2019; Zuñiga 2019; Donayre 2021
	22	*Actinothoe gravieri* (Pax, 1912)	Peru	Piura (Paita)	UD	Pax 1912; Fautin 2013, 2016
	23	*Sagartia lessonii* (Verrill, 1869)	Peru	Piura (Paita)	UD	Pax 1912; Fautin 2013, 2016

N/A: Not Applicable; UD: Undetermined

*doubtful

Habitats range

The description of habitat features (i.e. chemical and physical properties or the influence of gradients) is little analyzed, or it is absent, regarding sea anemone reports. Only 15 species (65%) have studies roughly offering habitat descriptions, while the other 8 (35%) have no specific data to discuss. Rocky substrates, like exposed (e.g. vertical walls) or sheltered zones (e.g. rock crevices, caves, intertidal pools), were the most frequently reported type of habitat (~ 55% records). Several species live indistinctively along the depth gradients inside the intertidal zone, whereas only a few permanently inhabit the subtidal shallow zone. It is worth noting the lack of bathymetric data for Peruvian waters, as we found information for 10 species only, from the Actiniidae, Actinostolidae, and Sagartiidae families (Table 1), inhabiting shallow environments (between 0 and 28 m). Notoriously, the vertical distribution of 13 species remains undescribed.

Several observations for the Peruvian regions of Ancash, Lima, Moquegua, and Ica suggest a shallow distribution for *Anthothoe chilensis* (Fig. 3a), with a bathymetric range fluctuating from the intertidal down to 15 m depth (Table 1). Indeed, this species often inhabits the littoral and sublittoral zones forming small aggregations; tidepools, crevices, and exposed areas have been reported as its common shallow habitats. Even so, these organisms can also be found on mixed and biogenic substrates as well as living in kelp forests.

Overall, *P. pluvia* (Fig. 3b) lives on rocky shores, shallow waters, and hard bottoms. Individuals are present in the lower intertidal and subtidal zone, in small caves, or attached to vertical walls. Observations from the regions of La Libertad, Ancash, and Moquegua reveal that the bathymetric distribution of this species extends from the intertidal zone down to 15 m depth (Table 1); although also reported in other regions (Fig. 2c), its vertical distribution is still poorly described. In the same sense, samples from the region of Moquegua indicate that individuals of *A. alicemartinae* (Fig. 3c) live down to 15 m depth (Table 1), inhabiting both the intertidal and shallow subtidal zones, attached to bare rock surfaces, half-buried under the sand or even on floating macroalgae.

Despite being one of the most reported sea anemone species, *A. achates* (Fig. 3d) remains insufficiently documented, with several local observations (D. Baldarrago, pers comm) and scarce registers of its occurrence derived from the southern coast only (Fig. 2c). However, a study in the Moquegua region has reported its presence down to 10 m depth (Table 1). Other dwellers such as *O. concinnata* (Fig. 3e) live among substrates like crevices or under the rocks of shallow hard bottoms from the intertidal to the shallow subtidal zones. Its occurrence in the Ancash region suggests a restricted vertical distribution ranging from the intertidal down to 8 m depth (Table 1). Unfortunately, despite having been reported in other regions, site-specific data is not available, and most information is addressed roughly indicating rocky habitats and exposed zones as representative coastal environments.

As for the bathymetric data available for *P. clematis* (Fig. 3f), individuals have been observed down to shallow subtidal zones (15 m depth) in the Moquegua region; while specimens have been found in samples collected from sandy and muddy bottoms at 25 and 28 m depth in the Tacna region (see references in Table 1). Occurrences in other regions have also been registered but lack precise bathymetric data.

Furthermore, the unique bathymetric distribution data available for *Actinostola chilensis* derives from samples obtained from vertical walls in Guañape Island (between 0 and 5 m depth) in the La Libertad region (Table 1). Likewise, *P. papillosa* has been reported throughout the Peruvian coast, but its bathymetric range (between 0 and 8 m depth) is known only for the Ancash region (Table 1). Finally, just a narrow bathymetric range was attributed for *A. radians* (0–1 m, Table 1) with occurrences on rocky shores of the Moquegua region.

The superfamily Actiniaria *incertae sedis* involves two species (*A. picta* and *P. peruviana*) with an unknown bathymetric range for Peru. Unfortunately, over the last two decades, there is no new data to resolve this uncertain status regarding the spatial distribution of these species and back up the original findings (see Fautin 2013, 2016).

Discussion

Species occurrence and biodiversity status

Sea anemone specific information for the Peruvian coast is scarce. Most of the data available derives from monitoring reports carried out only once in a particular locality (Hooker et al. 2011; Uribe et al. 2013; Gonzáles and Pastor 2017; Pastor et al. 2017). Diversity and distribution research targeting sea anemones in Peru has not yet been conducted, in contrast to other efforts in the region (Lancellotti and Vasquez 2000; Häussermann and Försterra 2005; Häussermann 2006). In fact, most occurrence reports, including taxonomy and ecological knowledge originate from overseas studies (e.g. Carter 1965; Stotz 1979; Excoffon et al. 1997; Häussermann and Försterra 2001; Häussermann 2003, 2006, 2004b, 2004c; Fautin 2016; Spano and Häussermann 2017; Pinochet et al. 2019). Nevertheless, our analysis suggests a gradual increase in interest in sea anemone biodiversity over time (Fig. 2b). Certainly, this is relatively recent, as representative species *Phymactis clematis* and *Anthothoe chilensis* were reported for the first time in the 1980s (Paredes and Tarazona 1980; Paredes et al. 1988). Since then, their occurrence in reports for the Peruvian coast has augmented considerably. Similar cases could follow a comparable pattern; for instance, species such as *Anemonia alicemartinae* reported for the first time in 2015 (Canales-Aguirre et al. 2015) and *Oulactis coliumensis*, whose northward spatial extension was recently confirmed (Spano et al. 2022).

Species like *Anthothoe chilensis*, *P. clematis*, *Phymanthea pluvia*, and *Oulactis concinnata* have been regularly mentioned in recent benthic diversity inventories and monitoring reports (Uribe et al. 2013, 2019; Alfaro et al. 2016, 2019; Gonzáles and Pastor 2017; Pastor et al. 2017; Tasso et al. 2018; Baldarrago et al. 2019; Berrú and Perea de la Matta 2019; A. Ramírez et al. 2022; P. Ramírez et al. 2019a, 2019b, 2019c, 2020). It is likely that their high occurrence in reports is due to the abundance of their populations in intertidal and shallow subtidal habitats. However, the lack of detailed registers in previous years providing information on this issue questions this explanation. It is possible that specimens were either reported as "Cnidaria", “Actiniaria indet.”, “actiniarian”, "anemone", not detected, or simply confused with other species. This situation is common with local observations for some indeterminate, but frequently observed species that cohabit in the intertidal and shallow subtidal (~ 25 m). For instance, sea anemones still unidentified have been found in southern Peru attached to rhizoids or fronds of *Lessonia trabeculata* (Fig. 4a, c) or even adhered to crevices in intertidal rocky shores (Fig. 4d). These findings highlight the necessity of increasing taxonomic identification efforts to expand the actual insights of sea anemones' diversity in southern regions.

The restricted information on qualitative and especially quantitative data (e.g. bathymetry), is another bottleneck for dimensioning the distribution of sea anemone communities in shallow waters. Habitat data has been the most critical point hindering better descriptions, this is common in monitoring reports. For instance, punctual depth values of the occurrence of *P. clematis* (Table 1) in the subtidal were obtained as individuals were found casually in samples collected to study the soft-bottom macrobenthos in southern Peru (Aramayo et al. 2022). Additionally, inaccurate bathymetric data has been found throughout our literature review. Among the scant information available, imprecise descriptions of the depth at which sea anemones have been found or sighted are unfortunately recurrent (e.g. Paredes and Tarazona 1980; Paredes et al. 1999; A. Ramírez et al. 2019; P. Ramírez 2019a, 2019b, 2019c; De Lucio 2020). Thus, we possess a relatively high degree of uncertainty regarding the bathymetric distribution of several species, limiting our capacity to analyze the influence of depth on biodiversity.

As an example, sea anemone species from the family Actinostolidae previously reported in deep areas in Chile have been registered on the Peruvian coastline, but only in the shallow subtidal (Table 1, Alfaro et al. 2016; Baldarrago et al. 2019). The species *Antholoba achates*, *Actinostola chilensis*, and *Paranthus niveus* have been found in Chile down to 327, 278, and 108 meters respectively (Carlgren 1899, as cited in Häussermann and Försterra 2009; McMurrich 1904, as cited in Häussermann and Försterra 2009; Carlgren 1959, as cited in Häussermann 2004c; Stotz 1977, as cited in Häussermann and Försterra 2009). Conversely, in Peru, a unique register of *P. niveus* is available for the locality of Paita (Piura region) without any bathymetric information (Fautin 2016). In the case of *Actinostola chilensis*, these individuals have been reported inhabiting the same areas as the commercially important sea cucumber *Pattalus mollis* (Alfaro et al. 2016). Therefore, a depth range for *Actinostola chilensis* has been obtained as a result of a casual report in the locality of Guañape Island (La Libertad region), yet this information remains unverified in this region, needing further efforts in future research initiatives.

The uneven research effort in the study of sea anemone diversity along the Peruvian coast (Fig. 2c, d) may be explained by different factors. The Lima region possesses the highest number of publications referring to sea anemones (Verrill 1867; Paredes and Tarazona 1980; Tokeshi and Romero 1995; Paredes et al. 1999; Häussermann 2003, 2004b; Quiroz-Garrido 2005; Retuerto et al. 2007; Firstater et al. 2010; Guzmán 2012; Fautin 2013, 2016; Galán 2015; Alegre 2017; Cuya and Escobar 2017; Tasso et al. 2018; Yafac-Piedra and Garcia-Alayo 2020; A. Ramírez et al. 2022). One explanation for this is the high research effort produced by several institutions from Lima, where private and public universities, as well as governmental establishments, are involved. Therefore, the Lima region does not only possess ecological studies (e.g. monitoring reports), as specific research has also targeted sea anemone species to investigate the toxins of their venom (Quiroz-Garrido 2005) and even its biochemical and biological activity (Retuerto et al. 2007; Cuya and Escobar 2017; Yafac-Piedra and Garcia-Alayo 2020) to consider it for future pharmaceutical and medical applications. On the other hand, the high number of occurrence registers in the north-central coast (La Libertad and Ancash regions) may be essentially a result of monitoring reports performed as there are determined sites where the intensive culture of Peruvian calico scallop *Argopecten purpuratus* takes place (Uribe et al. 2019). Unfortunately, most of the studies consulted do not correspond to a sustained research program of benthic biodiversity but rather episodic or unconnected initiatives. Biodiversity biases associated with the lack of data and information have frequently occurred in the marine environment affecting our ability to analyze specific taxa patterns and dimension ecological responses (Miloslavich et al. 2011).

Taxonomic Issues, Knowledge Gaps And Implications For Conservation Studies

Cnidarian taxonomy in Peru has often been neglected in the past. More specifically, in-depth taxonomy of sea anemones has been overlooked in most studies of marine benthos, paradoxically those of intertidal benthos where this group is a common item. Morphological identification is perhaps the most common limiting factor because of the high intra- and interspecific variability in morphotypes (González-Muñoz et al. 2015). But even problematic synonyms have fueled confusion among experts; for instance, *Isoulactis chilensis* has been catalogued as a synonym of *O. concinnata*, though they were formerly considered two different species with identical morphological features, color, habitat, and behavior (Häussermann 2003). Additionally, the challenge to differentiate *Actinostola* species even among individuals from the same species has been pointed out as an issue (Häussermann and Försterra 2009).

Alternative methods such as examining internal morphology through histology (cnidocites) and genetic analyses are needed to perform an accurate taxonomic identification in such cases (Barragán 2018; Häussermann 2004a, 2004c). Due to these obstacles, multiple sea anemone species are first registered as *Actinia* sp., like *A. alicemartinae* in Chilean reports from the ’70s (Häussermann and Försterra 2001). Similar cases hamper the understanding of sea anemones biodiversity in Peru. Indeed, recent monitoring reports registering anemone species by referring to their genus only demonstrate that classifying actiniarians at the species level is still demanding (Pastor et al. 2017; De Lucio 2020).

The identification of sea anemones is essentially based on preserved organisms and old, scattered literature (Häussermann and Försterra 2009). As an example, the species *Anactis picta* is still catalogued with an uncertain scientific name (Rodríguez et al. 2023). Issues such as an imprecise original description, doubtful species characters, and biological material (e.g. tentacles) in poor conditions (Verrill 1867; Andres 1884) are yet hindering an accurate classification of this species. Future studies in Peru should include detailed *in situ* observations following protocols that encourage observing external characteristics before preservation, as this provides crucial information for the identification (Häussermann 2004a).

Complementary methods such as metabarcoding may significantly favor our perspective on sea anemone biodiversity. It would give us the potential to identify new species and solve taxonomic doubts for cryptic ones (e.g. *Anthothoe chilensis*, Häussermann and Försterra 2009), which can affect the quantification of local biodiversity and the assessment of the environment's status.

The relevance of gathering abiotic and biotic data while collecting the individuals has also been highlighted, as this kind of input is still insufficient or unknown for most species inhabiting the Peruvian coast. Accurate information concerning the depth at which organisms have been collected is not unfortunately supplied by the sea anemone literature (Fautin 2016). Certainly, the actual bathymetric range of most sea anemone species recorded in Peru is still unclear, partially due to the methods used to collect data. The existing studies have mostly used autonomous diving, a method useful for exploring coastal benthic habitats but limited to the diver's experience, and therefore, with a potential bias on the real bathymetric range.

Comprehensive sampling campaigns targeting sea anemones could positively address the uncertainty existing regarding the habitat range of these specimens, and substantially favor the determination of spatial patterns of biodiversity and abundance. This is especially crucial when analyzing casual (unverified) reports of sea anemones about which virtually nothing is known. For example, the anemone *Anthopleura mariscali* (Daly & Fautin, 2004) is supposedly inhabiting hard bottoms in the locality of Las Pocitas (Piura region), according to popular websites like iNaturalist. However, these records are the only ones registered for the Peruvian coast and do not have complementary scientific information to corroborate them, revealing further sampling needs and a peer-review analysis. Only after this verification, species such as *A. mariscali* could be officially included in the species list of sea anemones reported in Peru. Similarly, a report of *A. alicemartinae* in the locality of Boca del Río (Tacna region) on the OBIS database requires as well both taxonomic reconfirmation and future *in situ* collection campaigns to validate this observation.

Preliminary reports for species such as *Anthopleura radians* indicate a rocky habitat (Puerto Inglés, Moquegua region) as a sporadic distribution (Zuñiga 2019). Nevertheless, it has been recently indicated this species is abundant in protected and semi-protected areas of rocky intertidal ecosystems on the northern Chilean coast (Spano and Häussermann 2017), suggesting both a southernmost distribution and an insufficient sampling effort in some Peruvian localities. Additionally, the possible influence of biological habitats (e.g. kelp forests) on the biodiversity of sea anemones and their distribution patterns is unknown. For instance, *A. alicemartinae* has been found frequently inhabiting *Macrocystis integrifolia* kelp beds (Villegas et al. 2008) and even attached to floating macroalgae in Chilean offshore waters (Thiel and Gutow 2005), suggesting that this flora is a suitable substrate for anemones, but further analyses are needed to elucidate adaptability and habitat range in this group.

Particular cases highlight episodic and disconnected research activity on sea anemones, providing remarkable opportunities to analyze new data. For example, specimens of *Actinia* sp. and *Paranthus* sp. have been reported as prey items of the green turtle *Chelonia mydas* in both Piura and Ica regions

(Paredes 2015; Quiñones et al. 2017, 2021). Patches of *Paranthus* sp. and algae have also been described as part of important feeding areas of *C. mydas* in the Ica region (Paredes et al. 2020). However, there are cases when some species have not reappeared since their first reports (Verrill 1867; Andres 1884; Pax 1912). Precisely, Pax (1912) suggested considering the sea anemone species *A. picta, Phellia rubens, Actinothoe gravieri* (*Sagartia gravieri* before), and *Sagartia lessonii* as endemic to Peru due to their apparent restricted distribution to this ecosystem. As the present revision has not hitherto found any register of the occurrence of these species in other countries, neither in databases (e.g. GBIF; OBIS) nor in articles, they could be considered as such. Forthcoming research should focus on these species to understand why they have not been spotted again, as we may have ignored these potentially native sea anemone species for decades.

The sea anemone species *A. alicemartinae* may be native to the Peruvian coast. To date, *A. alicemartinae* has only been reported on the Peruvian and Chilean coasts (GBIF; OBIS; Häussermann and Försterra 2001; Castilla et al. 2005; Canales-Aguirre et al. 2015; Fautin 2016; Baldarrago et al. 2019; Pinochet et al. 2019; Brante et al. 2019). Canales-Aguirre et al. (2015) suggested that the population present in southern Peru would be the ancestral one that gave rise to the current distribution of *A. alicemartinae* in Chile. Recently, Pinochet et al. (2019) concluded this species seems to be invasive to the Chilean coast, coming from the northern Humboldt ecosystem. Until now, the only records of *A. alicemartinae* occurring in Peru are those from the southern coast (Canales-Aguirre et al. 2015; Baldarrago et al. 2019). Potential studies should be carried out on our coasts to confirm this theory on the origin and distribution of *A. alicemartinae* in the South Pacific. Other sources of bias must be considered, namely the difference in the sampling efforts at regional level (i.e. considering Peru and Chile localities) and its potential influence when analyzing latitudinal distribution patterns and promoting conservation initiatives.

Critically less documented, the potential effects of large-scale ocean-atmosphere fluctuations such as EN are poorly known in Peru, despite being a recurrent event. Recent results suggest diverse ecological responses associated with a significant reduction in the latitudinal distribution range in *P. pluvia* during the 2015 and 2017 EN events, whereas *P. clematis* exhibited an expansion southward (Valqui et al. 2021). However, intrinsic biological responses are complex and depend on the degree of adaptability, thermal tolerance, and feeding habits, among other physiological and ecological aspects. Sea temperature variability, for example, is a pervasive driver for survival and can influence the permanence of local populations. Species such as *A. alicemartinae* tend to be more resistant to thermal stress when compared with *Anthothoe chilensis*, which adaptatively responds by increasing its detachment rate to evade higher temperatures (Suárez et al. 2020). With both species also reported in Peru, it is likely to observe a similar population response in *A. alicemartinae*, expecting a greater tolerance than *Anthothoe chilensis* amid EN events. In addition, the establishment of *P. clematis* in the lower intertidal zones as a co-dominant species after EN events (1982/83 and 1997/98) has been documented along the northern Chilean coast (Rivadeneira 1998, as cited in Rivadeneira and Oliva 2001). The anemone *P. clematis* seems to be a resistant and opportunistic species amidst disturbances in its environment, as there is evidence of being ubiquitous along the Peruvian coast during EN conditions (Valqui et al. 2021). Nevertheless, long-term records of benthic rocky intertidal communities are needed to observe changes attributed to EN events and to have accurate insights concerning benthic responses.

A chronic, shallow, and intense OMZ spans to most part of the Peruvian waters. However, knowledge regarding the response of sea anemones communities to this stressor is scant. Central Peru holds several representative localities influenced by the presence of OMZ (e.g. San Lorenzo Island) where sea anemones have been observed (see Table 1). Spatially near findings indicate that local soft-bottom benthic communities are highly adapted to reduced conditions, but it is unclear the ecological threshold of these responses over time (Aramayo et al. 2021). In fact, future climate change scenarios for the Peruvian sea highlight that even commercially important benthic species are more threatened than others in this complex marine ecosystem (Ramos et al. 2022), consequently producing more uncertainty in other poorly studied species inhabiting this area.

Sea anemone species living in extreme or impacted environments, are certainly not rare. Riemann-Zürneck and Gallardo (1990) described a new sea anemone species *Saccactis coliumensis* (now *Oulactis coliumensis*), from samples collected between 40 and 55 m depth in eutrophicated sediments exposed to deoxygenated waters on the central Chilean shelf. As the Eastern South Pacific OMZ comprises the regions of Ecuador, Peru, and Chile (Paulmier et al. 2006), it is expected to encounter *O. coliumensis* and perhaps other sea anemone species integrating the Peruvian OMZ benthic fauna.

This first review on sea anemone biodiversity in Peruvian waters provides a baseline analysis for future research. It is noteworthy that most species reported here do not appear in frequent monitoring reports or in few *ad hoc* studies on this benthic group. Despite the progressive, albeit slow, growing interest in this group of benthic invertebrates in recent decades, several knowledge gaps on some species have yet to be addressed, and adequately identify the potential biases in this existing data, especially the lacking environmental information.

A significant development in the study of actiniarians requires a relevant effort to analyze their ecological importance and responses regarding multiple sources of impact, especially large-scale ones such as EN events and regional stressors like OMZ. In the context of future climate change scenarios, an increasing frequency of these phenomena is likely. However, studies addressing this panorama are insufficient, rare, or do not exist. Sea anemones are highly adaptive, although more than one of the species reported here may be already exposed to some degree and sort of population pressure, either due to natural causes or anthropic impacts (pollution, habitat loss, etc.) resulting in increased uncertainty concerning an accurate biodiversity status of this taxa.

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Competing interests

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Authors contributions

All the authors contributed to the study conception and design. Literature review, data collection, and analysis were performed by AD, DVC, and VA. The first draft of the manuscript was written by all authors. All the authors read and approved the final manuscript.

Data availability

The datasets generated during the current study are not publicly available but are available from the corresponding author on reasonable request.

Ethical approval

No ethical approval was required for this study. Authors declare no conflict of interest.

Consent to participate

Not applicable.

Consent to publish

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Figures

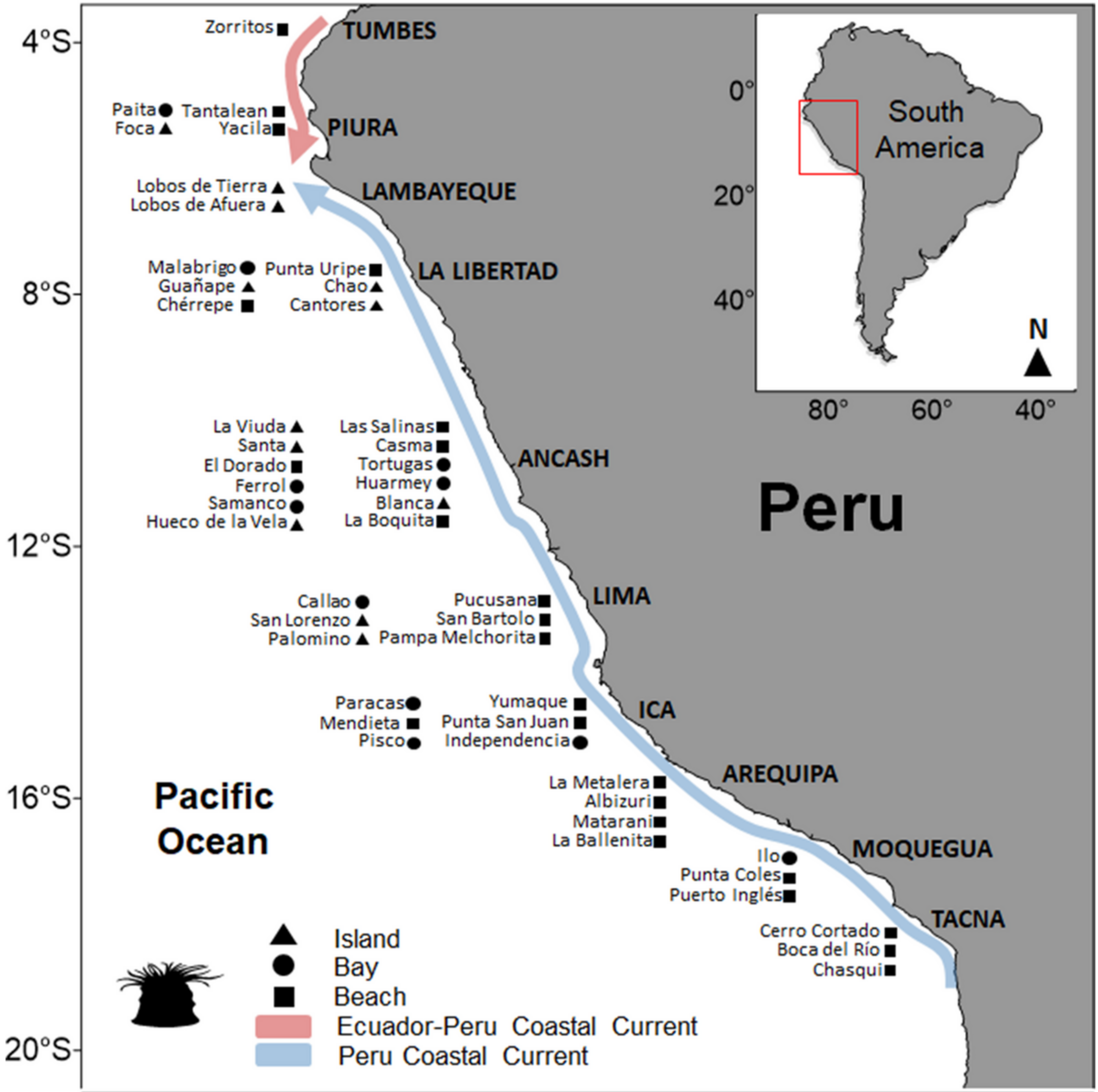

Figure 1

Study area and most representative localities of sea anemones in Peru. Symbols accompanying each locality describe the type of site (island, bay, or beach) in which sea anemones have been reported. Though indicated as an island, Cantores and Hueco de la Vela are inlets.

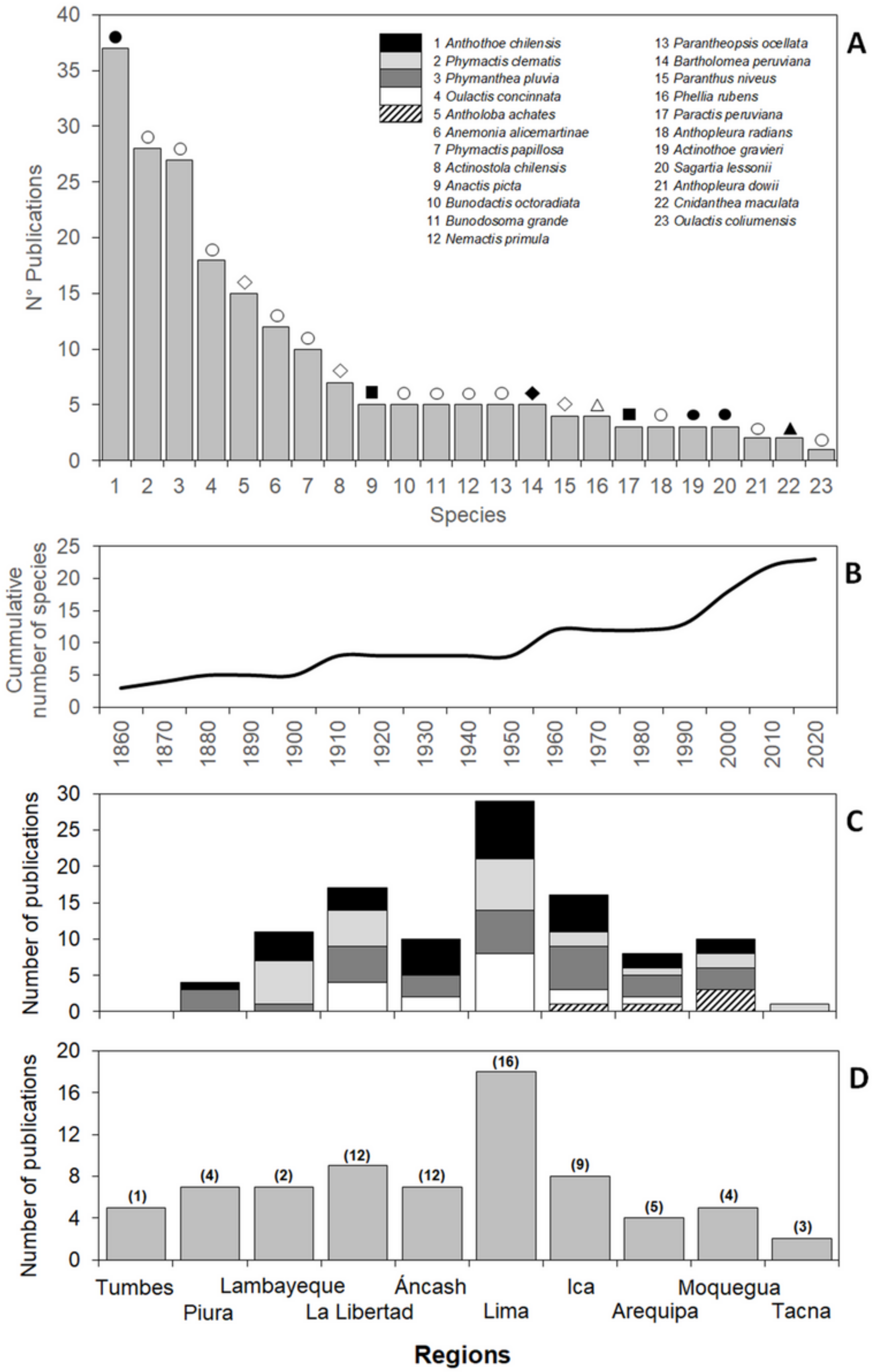

Figure 2

a Number of publications by species of sea anemones reported in Peru. Symbols indicate the families Sagartiidae (black circle), Actiniidae (white circle), Actinostolidae (white rhombus), Aiptasiidae (black rhombus), Actiniaria *incertae sedis* (black square), Phelliidae (white triangle) and Isanthidae (black triangle). **b** The cumulative number of species over time from 1860 to 2020. **c** Regional variability of the number of publications for the top five most studied sea anemones species. **d** The sampling effort (No. publications) along the Peruvian coast, number of localities between parenthesis.

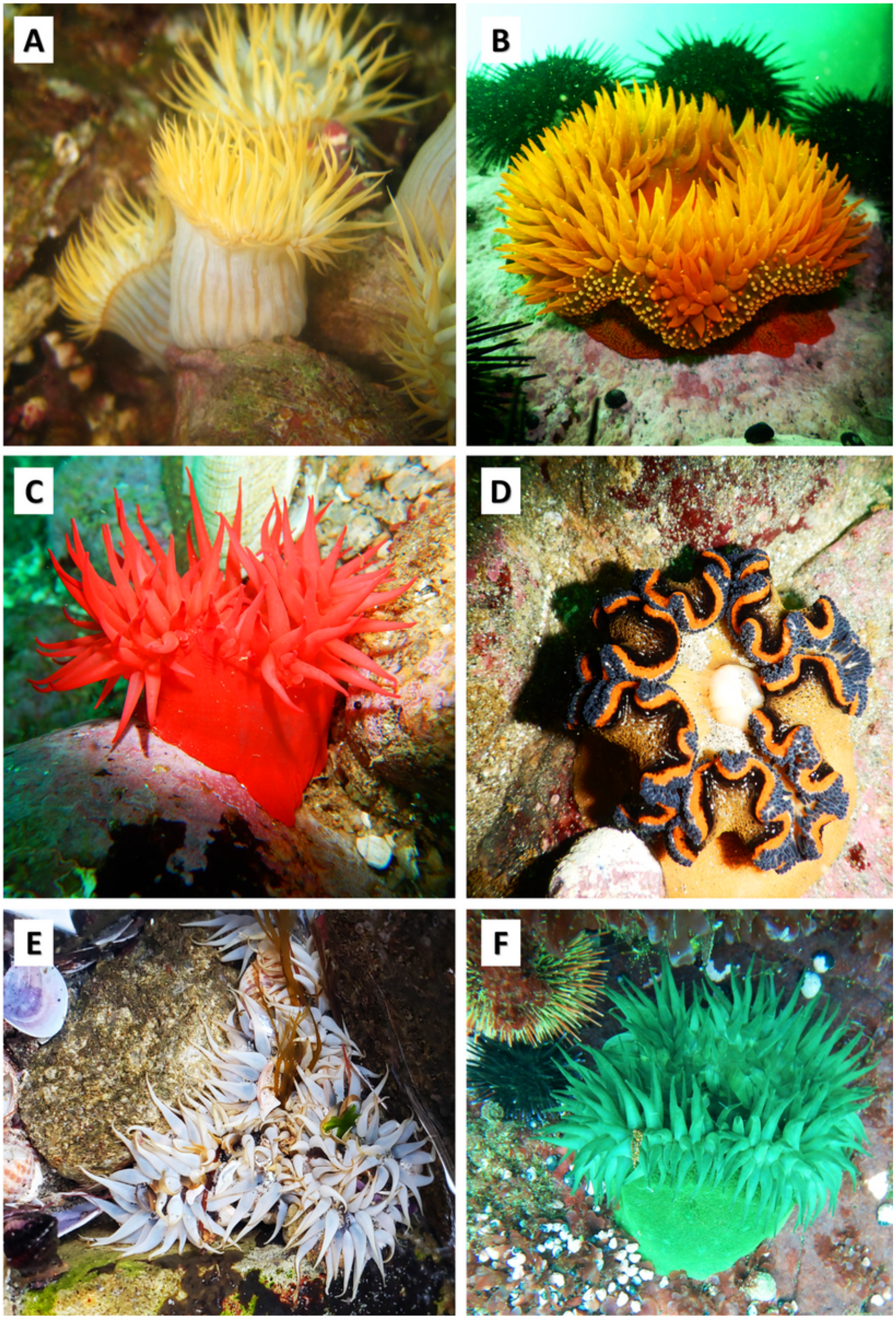

Figure 3

Representative sea anemones species inhabiting coastal areas in Peru. **a** *Anthothoe chilensis*, **b** *Phymanthea pluvia*, **c** *Anemonia alicemartinae*, **d** *Antholoba achates*, **e** *Oulactis concinnata*, **f** *Phymactis* *clematis*. Photo credits: a-d (R. Uribe), e (V. Aramayo), f (D. Baldarrago).

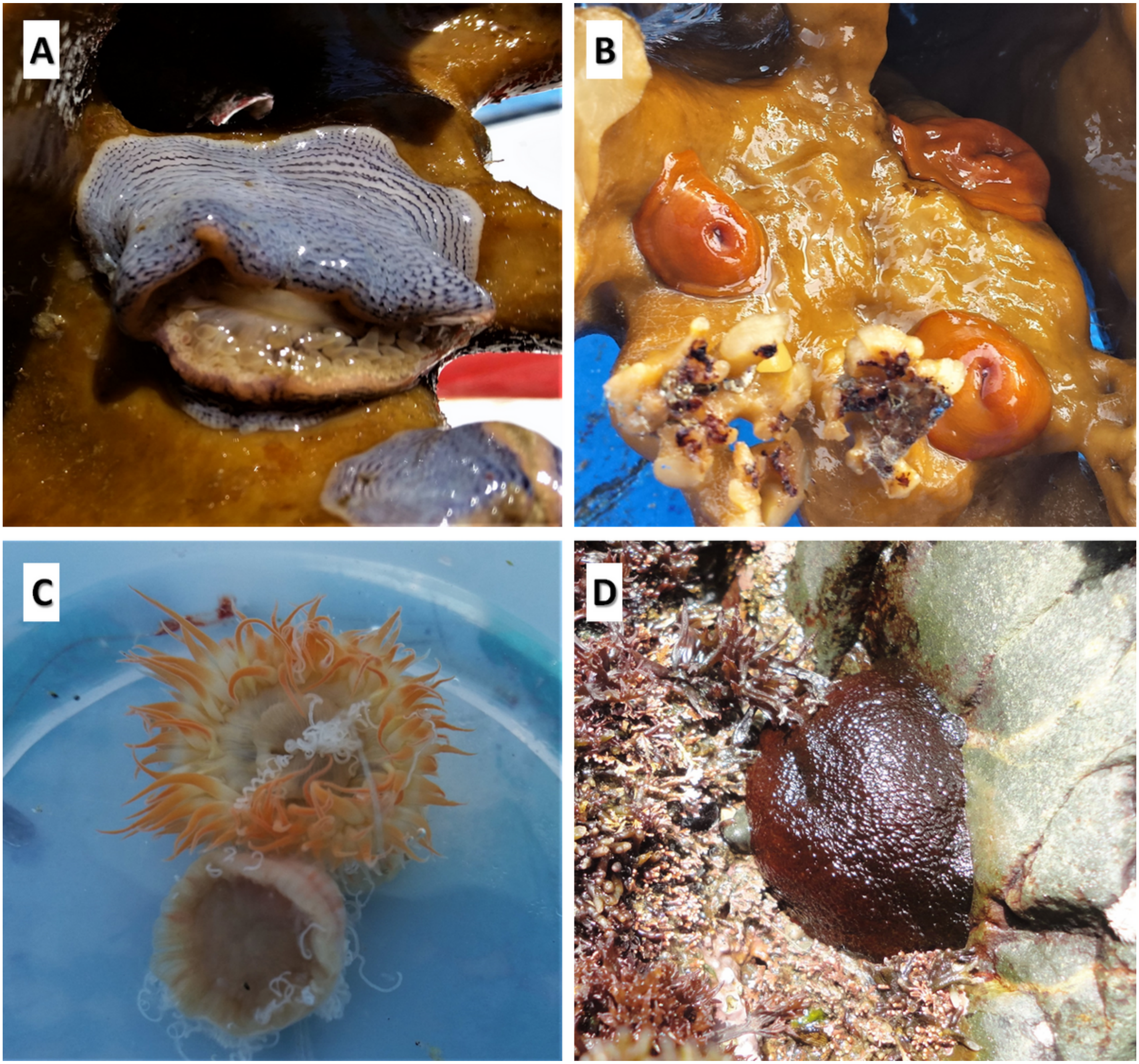

Figure 4

Unidentified species of sea anemones in southern Peru. Photo credits: a-d (D. Valdivia).