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# Biodiversity and distribution of sea anemones (Cnidaria, Anthozoa, Actiniaria) in Peru

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**Research Article**

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## Abstract

Sea anemones represent a highly abundant and diverse group within marine ecosystems, yet biodiversity analyses in Peru remain comparatively scarce. To enhance the inventory of biodiversity and its distribution, a comprehensive review of the available literature on species from Peruvian waters was performed. Only seven well-documented species (i.e. verified records) were found representing 31.8% of the total species reported in Peru (22 spp.) These seven species are *Anthothoe chilensis*, *Phymactis papillosa* (formerly reported as *P. clematis*), *Phymanthea pluvia*, *Oulactis concinnata*, *Antholoba achates*, *Anemonia alicemartinae* and *Oulactis coliumensis*. Overall, specimens were identified in 68 localities, the Actiniidae family exhibited the highest diversity with five species (71.4% of the total), whereas Actinostolidae and Sagartiidae each contributed one species (14.3%). The highest number of scientific publications (18) corresponds to the Lima region, with over twice as many studies as other regions, it is followed by Ica (8), Áncash (7), La Libertad (6), Tumbes (5), Piura (4), Arequipa (3), Tacna (2), Moquegua (1) and Lambayeque (1). However, the studied localities are unevenly distributed across regions. Rocky substrata (~55% of records) are the most reported habitat for sea anemones in Peru, including exposed vertical walls and sheltered crevices, caves and areas under rocks. Despite wide spatial distribution, our results indicate several under-researched regions. The growing interest in these benthic invertebrates over recent decades has revealed over 50% of reported biodiversity, yet many doubts about species described long ago remain. Potential biases in existing data require identification along with further analysis of environmental information.

## Introduction

Sea anemones constitute a conspicuous and diverse group in marine environments and thrive in a wide range of underwater habitats, spanning all depths and latitudes (Daly *et al*., 2007; Fautin, 2013; Rodríguez *et al*., 2014). The distribution and aggregation patterns of sea anemones are modulated by a complex interplay between physical factors and biological interactions. While substratum availability and local oceanographic conditions (e.g. water transparency, turbulence and current patterns) are recognized as key physical determinants, intra- and interspecific competition for food and space are equally important biological drivers (Chintiroglou and Koukouras, 1992). Their high metabolic sensitivity throughout their life cycle makes certain sea anemone species valuable bioindicators of pervasive changes in surrounding water chemistry and overall marine environmental health (Linton and Warner, 2003; Duckworth *et al*., 2017).

Early-life survival influences the settlement of sea anemone species and their subsequent distribution across marine regions (Ocaña *et al*., 2007; Watson *et al*., 2018). Beyond these primary factors, several species exhibit additional behavioural adaptations to enhance their survival and distribution. Some engage in commensalism, such as epibiosis on hermit crabs (Ruppert and Barnes, 1996), while others display a burial behaviour in sandy or muddy substrata (Häussermann and Försterra, 2009). Most species live solitary, but clonal aggregations stand out as a notoriously efficient and successful strategy for rapid growth, space competition and dispersal of individuals (Fautin, 2013).

Despite their frequent occurrence on both rocky and mixed shores of Peru, with patchy and dense distributions observed along depth gradients, a comprehensive understanding of sea anemone biodiversity and ecology remains elusive. Most existing information comes from sporadic reports on specific sites (e.g. Novoa *et al*., 2010; Hooker *et al*., 2011) or broader benthic surveys (e.g., Paredes *et al*., 1999; Uribe *et al*., 2013). These studies, while valuable, primarily emphasize the importance of monitoring efforts to assess the effectiveness of conservation tools and the ecological status of coastal bays, rather than providing a comprehensive understanding of sea anemone diversity and ecological roles. Likewise, specific collections in national museums lack material on this group or have poorly preserved specimens that are unsuitable for taxonomic identification purposes. Consequently, a critical gap in the literature remains, highlighting the need for further research to understand the biodiversity status of this group, species-level responses linked to key phenology changes, and emerging conservation needs of sea anemones in this region. To contribute to the study of this benthic group, we performed an exhaustive bibliographic review to document the biodiversity and distribution of sea anemone species reported from Peru.

## Material and methods

### *Study area*

Information and data published on sea anemones from 68 localities were utilized (Figure 1) across 10 specific coastal regions in Peru. The geographic range encompassed both the tropical region in Northern Peru (from the Peruvian northern border to approximately 5°S) and the cold region spanning parts of Northern, Central, and Southern Peru (Chaigneau *et al.*, 2013), also known as the Humboldtian region. This spatial scale also covers the main types of substrata (rocky, mixed) inhabited by sea anemones. The Peruvian waters are regularly affected by interannual events such as El Niño (EN), along with the presence of an intense oxygen minimum zone (OMZ, dissolved oxygen $< 0.5$ ml.l$^{-1}$) that extends from shallow (~50 m) to deeper areas (Graco *et al.*, 2019, 2021). These factors play a role in shaping the abundance and development of both pelagic and benthic communities (Tarazona *et al.*, 2003; Bertrand *et al.*, 2011).

### *Data sources and criteria employed*

An exhaustive literature review was performed to list the sea anemone species (Actiniaria) reported in different benthic habitats in Peruvian waters. Overall, 112 scientific publications were reviewed, including peer-reviewed papers, official (governmental) reports and seminal reports (e.g. Verrill, 1869). Grey literature was excluded in this work (conference abstracts, non-referenced technical reports, theses, unsourced or poorly documented online material, etc.). Authoritative online resources/databases were used to confirm local references in some cases and verify the global incidence of some species; for instance, the World List of Actiniaria (part of the World Register of Marine Species: https://www.marinespecies.org/actiniaria), 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/).

For the purpose of this review, we considered well-documented species of sea anemones those specimens that have been peer-verified, exhibit continuous records in the time series, and have a consensual acceptance of their occurrence and distribution in a given locality. However, in order to offer a broader perspective, the total number of species reported in Peruvian

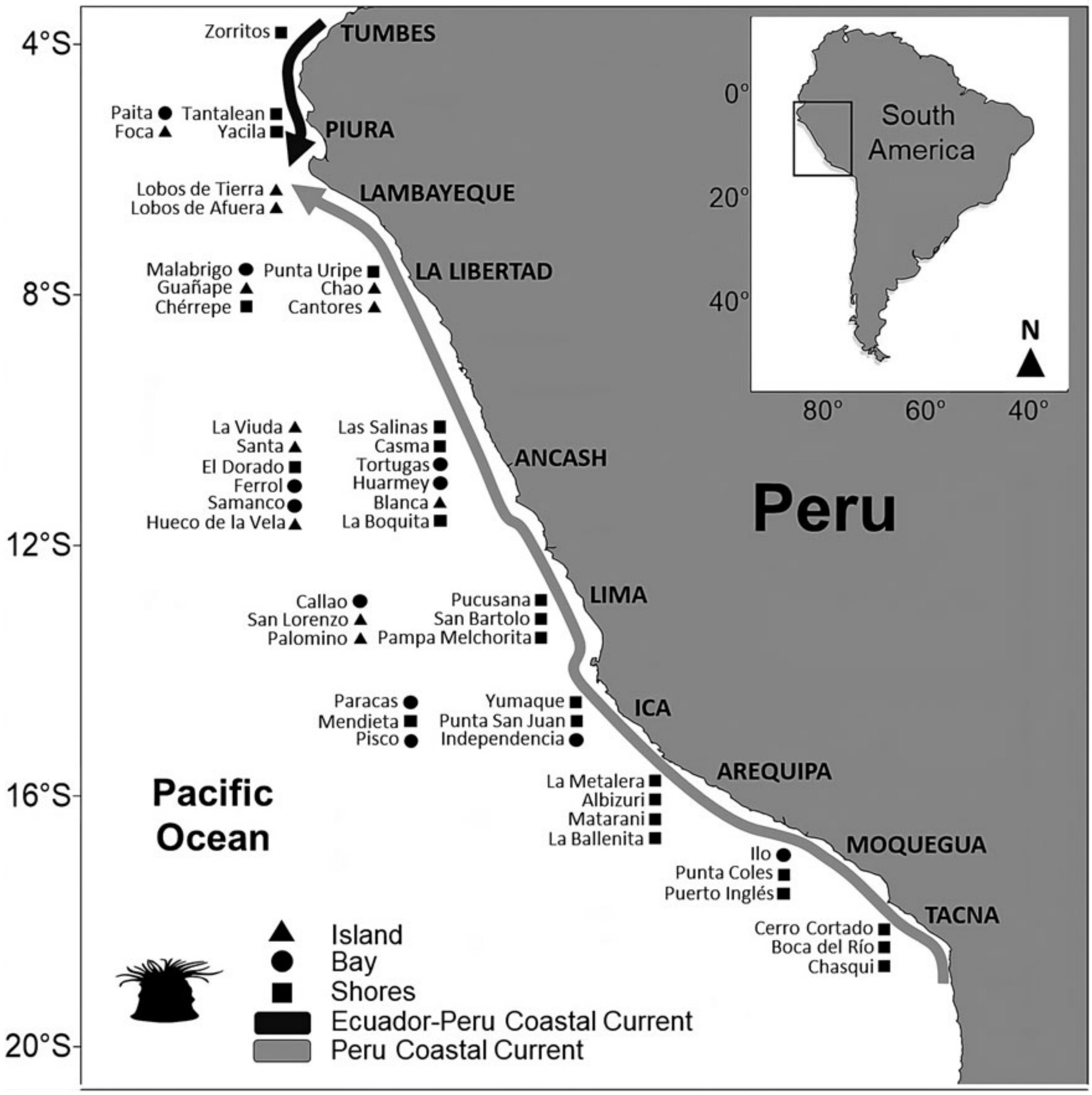

**Figure 1.** Study area and most representative localities of sea anemones reports in Peru. Symbols accompanying each locality describe general (bay) to specific rocky and mixed sites (island, and shores). Though referred to as islands, Cantores and Hueco de la Vela are inlets.

waters, including the well-documented ones and those from dubious sources and unfrequent records, is also mentioned.

When geographic coordinates or specific sampling locations were not provided, we used the city name reported in the document as the primary reference. Our list included the region name followed by the specific locality (in parentheses, Table 1). The bathymetric distribution analysis was limited to species with well-documented depth ranges, due to gaps in the available data for certain taxa. Localities in the bibliography exhibited different typologies; we considered the specificity of data/information to indicate general (bays), and specific rocky and mixed sites (*sensu* Bally *et al.*, 1984), namely, island and shores (Figure 1).

## Results

### Sea anemone biodiversity and latitudinal distribution

Sea anemone biodiversity was predominantly documented through official governmental reports (52%), primarily derived from monitoring studies rather than *ad hoc* research efforts. However, many of the reports on sea anemones in Peru present information on taxonomy that may need further verification. Peer-reviewed scientific articles made up 37% of the 112 documents resulting from collaborative research efforts that provided specific data inputs. Foreign expeditions contributed 11% of all reports, containing many species records not subsequently rediscovered.

Only seven well-documented species (i.e. verified records) were found, representing 31.8% of the total species reported in Peru (22 spp.), classified into three families: Actiniidae, Actinostolidae and Sagartiidae, spanning six genera (Figure 2A, Table 1). The family Actiniidae exhibited the highest diversity with five species (71.4% of the total), whereas Actinostolidae and Sagartiidae each contributed one species (14.3%). These seven most common species are *Anthothoe chilensis* (Lesson, 1830) (36 references), *Phymactis papillosa* (formerly reported as *P. clematis*) (Lesson, 1830) (35), *Phymanthea pluvia* (Drayton in Dana, 1846) (26), *Oulactis concinnata* (Drayton in Dana, 1846) (18), *Antholoba achates* (Drayton in Dana, 1846) (15), *Anemonia alicemartinae* Häussermann and Försterra, 2001 (12) and *Oulactis coliumensis* (Riemann-Zürneck and Gallardo, 1990) (1) (Figure 2A).

Major contributions to the scientific literature of these and other species come from a few researchers (e.g. Häussermann, Paredes, compilations by Fautin). Moreover, the time series for well-documented species in Peruvian waters (1950–2022) revealed slow progress, with long periods of research inactivity in terms of new species discoveries or new records, with a clear shift in 1965 and only slight changes in the last 20 years (Figure 2B). On the other hand, the temporal variability of the total species reported indicates a higher number of species but with highly uncertain data supporting those records.

Well-documented species such as *A. chilensis*, *P. pluvia* and *P. papillosa* exhibit a broad spatial distribution (Figure 2C, Table 1). Studies concerning especially intertidal zones reveal the extensive distribution of these species throughout the Peruvian coast. Less-studied species such as *A. achates* and *A. alicemartinae* seem to be restricted to the southern coast. The species *O. concinnata* has mostly been found on the central coast. Recent reports (Spano *et al.*, 2022) indicate that *O. coliumensis* inhabits the central and southern coasts.

The highest number of scientific publications (18) corresponds to the Lima region, with more than twice the studies developed for other regions (Figure 2D). It is followed by Ica (8), Áncash (7), La Libertad (6), Tumbes (85), Piura (4), Arequipa (3), Tacna (2), Moquegua (1) and Lambayeque (1). However, the number of localities studied in each region is unevenly distributed, since some northern-central regions (La Libertad, Áncash and Lima) exhibit a high number of localities surveyed, compared to the northern (Tumbes, Lambayeque) and southern (Moquegua, Tacna) regions (Figure 2D). Consequently, the research effort (indicated by the number of publications) seems to be undeveloped in those regions with a rather scarce number of studies.

### Habitat ranges

Rocky substrata, such as exposed (e.g. vertical walls) or sheltered zones (e.g. rock crevices, caves, intertidal pools) were the most frequently reported type of habitat (~55% of records). Six species from the Actiniidae, Actinostolidae and Sagartiidae families have been found in the intertidal and subtidal zones down to 28 m depth (i.e. *A. alicemartinae*, *O. concinnata*, *P. papillosa*, *P. pluvia*, *A. achates*, *A. chilensis*), whereas only one of these seven species is known to permanently inhabit the subtidal zone (i.e. *O. coliumensis*) between 3 and 25 m depth (Table 1).

Several observations from the Peruvian regions of Áncash, Lima, Moquegua and Ica suggest a shallow distribution for *A. chilensis* (Figure 3A), with a bathymetric range fluctuating from the intertidal (mostly tidepools, crevices and exposed areas) down to 15 m depth (Table 1). These organisms have been also found on mixed and biogenic substrata as well as in kelp forests.

Overall, *P. pluvia* (Figure 3B) inhabits shallow 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, Áncash and Moquegua reveal that the bathymetric distribution of this species extends from the intertidal zone down to 15 m depth (Table 1). While this species has also been reported in other regions (Figure 2C), its vertical distribution is still poorly described.

In the same sense, samples from the region of Moquegua indicate that individuals of *A. alicemartinae* (Figure 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. In Chile, *P. pluvia* and *A. alicemartinae* are found in the same bathymetric range, from the intertidal zone down to 16 m depth (Häussermann, 2006).

Despite being one of the most reported sea anemones species in Peru, *A. achates* (Figure 3D) remains insufficiently documented, with several local observations (D. Baldarrago, per. com.), and scarce registers of its occurrence derived from the southern coast only (Figure 2C). A study in the Moquegua region has reported its presence down to 10 m depth (Table 1), while Häussermann (2006) mentioned that *A. achates* is distributed from the intertidal to 100 m depth in Chile. This species is also known to host symbiotic amphipods (Krapp-Schickel and Vader, 2009). Other anemones such as *O. concinnata* (Figure 3E) live on hard substrata such as crevices or under boulders from the intertidal to the shallow subtidal zones. Its occurrence in the Áncash region suggests a restricted vertical distribution ranging from the intertidal down to 8 m depth (Table 1). Unfortunately, despite having been reported in other locations, site-specific data are not available. Häussermann (2006) indicated *O. concinnata* is distributed from the intertidal to 15 m depth along the Chilean coast.

As for the bathymetric data available for *P. papillosa* (Figure 3F), individuals have been observed down to shallow subtidal zones (8 and 15 m depth) in the Áncash and Moquegua regions, respectively; while specimens have been found in samples collected from mixed sandy and fine-gravel soft bottoms at 25 and 28 m depth in the Tacna region. Individuals of *P. papillosa* have also been reported in other locations throughout the Peruvian

**Table 1.** Total species reported of sea anemones in Peru, considering taxonomic information, geographic distribution, the total number of localities, and bathymetric range

| Family | No | Species | Distribution | Localities in Peru | Bathymetric range (m) | References for Peruvian localities |
|---|---|---|---|---|---|---|
| N/A | 1 | *Anactis picta* (Lesson, 1830) (*) | Peru | Piura (Paita) | UD | Lesson (1830); Verrill (1869); Pax (1912) |
| | 2 | *Paractis peruviana* (Lesson, 1830) (*) | Peru | Piura (Paita) | UD | Lesson (1830); Pax (1912) |
| Actiniidae | 3 | *Anemonia alicemartinae* Häussermann and Försterra, 2001 | Coasts of the Humboldt Current ecosystem. Peru and Chile | Moquegua (Puerto Inglés; Punta Coles, Ilo); Tacna (Mesas, Chero) | 0–15 | Canales-Aguirre *et al.* (2015); Baldarrago *et al.* (2019); Pinochet *et al.* (2019) |
| | 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 | Zuñiga (2019) |
| | 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 | Zanabria (2013) |
| | 7 | *Bunodosoma grande* (Verrill, 1869) (*) | Pacific Ocean. Mexico, Nicaragua, Costa Rica*, Panama, Ecuador, Peru. | Tumbes (Zorritos); Piura (Paita) | UD | Verrill (1869) |
| | 8 | *Nemactis primula* (Drayton in Dana, 1846) (*) | Peru | Lima (Isla San Lorenzo; Callao) | UD | Dana (1846) |
| | 9 | *Oulactis concinnata* (Drayton in Dana, 1846) | Peru and Chile (up to Valparaíso) | 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) | 0–8 | Dana (1846); Verrill (1869); Carter (1965); Paredes *et al.* (1988); Tokeshi and Romero (1995); Paredes *et al.* (1999); Häussermann (2003, 2006); Guzmán (2012); Uribe *et al.* (2013); Tasso *et al.* (2018); Uribe *et al.* (2020); Valqui *et al.* (2021); Ramírez *et al.* (2022) |
| | 10 | *Oulactis coliumensis* (Riemann-Zürneck and Gallardo, 1990) | Central Peru and Chile (off Coliumo bay, 36°30′S) | 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 | Lesson (1830); Verrill (1869) |
| | 12 | *Phymactis papillosa* (Lesson, 1830) | California, El Salvador, Nicaragua, Panama, Mexico (Gulf of California and northern coast of Mexico), Peru (Playa Tantalean) to Chile (up to Tierra del Fuego, Juan Fernández, Easter Island and Chonos Archipelago) | Piura (Playa Tantalean, Paita); Lambayeque (Isla Lobos de Tierra, Islas Lobos de Afuera); La Libertad (Puerto Malabrigo , Islote Cantores, Isla Macabí, Punta Uripe, Isla Guañape, Trujillo, Paiján, Pacasmayo); Áncash (Playa Las Salinas, Isla Santa, Bahía Ferrol, Bahía Samanco, Bahía Tortugas, Casma, Huarmey); Lima (Barranca, Carquín, Chancaíllo, Chancay, Ancón, Playa San Francisco, Callao, Isla Palomino, Isla San | 0–28 | Dana (1846); Verrill (1869); Pax (1912); Carter (1965); Paredes and Tarazona (1980); Paredes *et al.* (1988); Tokeshi and Romero (1995); Paredes *et al.* (1999); Häussermann (2004b); Guzmán (2012); Uribe *et al.* (2013); Alfaro *et al.* (2016); Cuya and Escobar (2017); Gonzáles and Pastor (2017); Pastor *et al.* (2017); Ramírez *et al.* (2017a, 2017b, 2019a, 2019b, 2019c, 2020); Alfaro *et al.* (2019); Baldarrago *et al.* (2019); Uribe *et al.* (2020); |

| | | | | | | |
|---|---|---|---|---|---|---|
| | | | | Lorenzo, Punta Negra, Asia, Pucusana, Cerro Azul); Ica (Bahía de Pisco, Bahía Independencia, Paracas, Islas Ballestas, Playa Mendieta, Punta San Juan); Arequipa (Matarani); Moquegua (Puerto Inglés; Punta Coles); Tacna (Playa Chasqui, Cerro Cortado) | | Valqui *et al.* (2021); Ramírez *et al.* (2022); Aramayo *et al.* (2022) |
| | 13 | *Phymanthea pluvia* (Drayton in Dana, 1846) | Peru (Paita) to Chile (Valparaíso) | 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 Macabí, 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, Carquín, Chancaíllo, 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); Arequipa (Caravelí, Matarani); Moquegua (Puerto Inglés, Punta Coles, Ilo) | 0–15 | Dana (1846); Verrill (1869); Carlgren (1959); Carter (1965); Paredes *et al.* (1988); Paredes *et al.* (1999); Häussermann (2004b); Guzmán (2012); Uribe *et al.* (2013); Alfaro *et al.* (2016); Alfaro *et al.* (2017); Gonzáles and Pastor (2017); Pastor *et al.* (2017); Baldarrago *et al.* (2019); Ramírez *et al.* (2019c); Uribe *et al.* (2019); Monroy *et al.* (2020); Yafac-Piedra and García-Alayo (2020); Valqui *et al.* (2021) |
| Actinostolidae | 14 | *Antholoba achates* (Drayton in Dana, 1846) | Peru, Chile, Argentina, Uruguay, Brazil and New Zealand | Ica (Islas Ballestas); Moquegua (Punta Coles, Leonas) | 0–10 | Carter (1965); Tejada and Baldarrago (2016); Pastor *et al.* (2017); Baldarrago *et al.* (2019) |
| | 15 | *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 | Alfaro *et al.* (2016) |
| | 16 | *Paranthus niveus* (Lesson, 1830) (*) | South East Pacific, Peru and Chile | Piura (Paita); Lima (Callao) | UD | Lesson (1830); Verrill (1869) |
| Aiptasiidae | 17 | *Bartholomea peruviana* (Pax, 1912) (*) | Peru | Piura (Paita) | UD | Pax (1912) |
| Isanthidae | 18 | *Cnidanthea maculata* Carlgren, 1959 (*) | Peru | Ica (Bahía de Pisco) | UD | Carlgren (1959) |
| Phelliidae | 19 | *Phellia rubens* Verrill, 1869 (*) | Peru | Tumbes (Zorritos) | UD | Verrill (1869); Pax (1912) |
| Sagartiidae | 20 | *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); Moquegua (Puerto Inglés, Punta Coles) | 0–15 | Paredes *et al.* (1988, 1999); Retuerto *et al.* (2007); Firstater *et al.* (2010); Guzmán (2012); Uribe *et al.* (2013); 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); Ramírez *et al.* (2019b, 2019c, 2020); Uribe *et al.* (2019) |
| | 21 | *Actinothoe gravieri* (Pax, 1912) (*) | Peru | Piura (Paita) | UD | Pax (1912) |
| | 22 | *Cylista lessonii* (Verrill, 1869) (*) | Peru | Piura (Paita) | UD | Verrill (1869); Pax (1912) |

UD, undetermined. Symbol (*) indicates doubtful information/reports. N/A, Not Applicable.

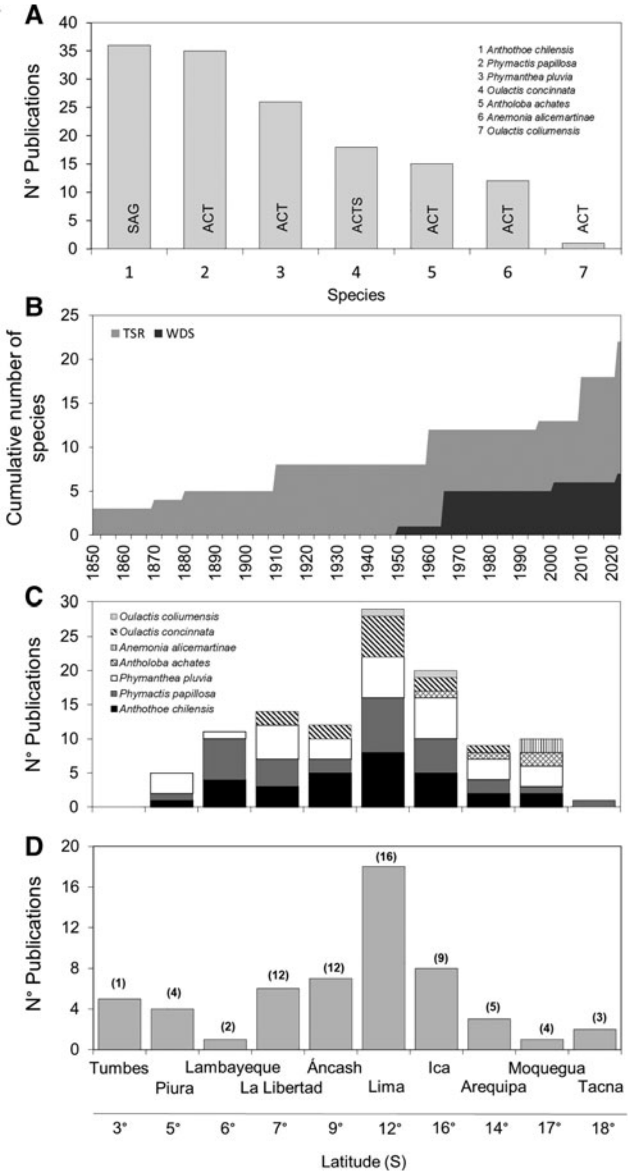

**Figure 2.** (A) Number of publications of the seven well-documented species (WDS) of sea anemones, (B) cumulative number (1850–2022) of the WDS and the total species reported (TSR) of sea anemones. Spatial variability in (C) number of publications by region of the seven WDS, and (D) number of publications by region for the TSR in Peru (number of localities indicated between parentheses). Acronyms indicate the following categories: Sagartiidae (SAG), Actiniidae (ACT) and Actinostolidae (ACTS).

coast but lack precise bathymetric data. Häussermann (2006) mentioned *P. papillosa* is distributed from the intertidal to 16 m depth in Chile. *Phymactis papillosa* also frequently harbours symbiotic porcellanid crabs (Baeza and Stotz, 2003).

Aside from the confirmed reports, doubtful sea anemone species reports for the Peruvian coast have also been identified (see Discussion). Occurrence reports of 15 sea anemone species along the Peruvian coast derive exclusively from old literature including their original descriptions, seminal and expedition reports (e.g. Lesson, 1830; Dana, 1846; Verrill, 1869; Pax, 1912; Carlgren, 1959). This is the case of *Anactis picta*, *Paractis peruviana*, *Bunodosoma grande*, *Nemactis primula*, *Parantheopsis ocellata*, *Paranthus niveus*, *Bartholomea peruviana*, *Cnidanthea maculata*, *Phellia rubens*, *Actinothoe gravieri* and *Cylista lessonii* (Table 1). Doubtful reports due to the scarcity of enough supporting scientific literature have also been identified, such as the case of *Anthopleura dowii*, *Anthopleura radians*, *Bunodactis octoradiata* and *Actinostola chilensis* (Table 1). Records of *B. octoradiata* and *A. chilensis* would imply an expansion of their known latitudinal and bathymetric distribution.

## Discussion

### *Species occurrence and biodiversity status*

A high number of the documents consulted correspond to 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 adjacent regions (Zamponi and Excoffon, 1995; Lancellotti and Vasquez, 2000; Häussermann and Försterra, 2005; Häussermann, 2006). However, foreign studies on taxonomy and ecological knowledge have brought valuable information (e.g. Carter, 1965; Stotz, 1979; Excoffon *et al.*, 1997; Häussermann and Försterra, 2001; Häussermann, 2003, 2006, 2004b, 2004c; Spano and Häussermann, 2017; Pinochet *et al.*, 2019). Despite this situation, our analysis suggests a gradually growing interest in sea anemone biodiversity over time; however, when comparing the total species count to well-documented species (see Figure 2B), a significant portion of the data requires reconfirmation or further taxonomic analysis.

Local research efforts have played a crucial role in improving the biodiversity inventory of anemones. For example, some species such as *P. papillosa* and *A. chilensis* became highly reported in the 1980s (Paredes and Tarazona, 1980; Paredes *et al.*, 1988). Similar instances are observed with species like *A. alicemartinae*, documented for the first time in 2015 (Canales-Aguirre *et al.*, 2015), and *O. coliumensis*, whose northward spatial expansion was recently verified (Spano *et al.*, 2022). However, the limited availability of qualitative and particularly quantitative data, such as bathymetry, poses a significant challenge in accurately assessing the distribution of sea anemone communities in shallow waters.

Habitat data have been the most critical point in the literature, hindering better complementary ecological descriptions. For instance, the current bathymetric range known for *A. chilensis* on the Peruvian coast is from the intertidal zone down to 15 m depth (Tasso *et al.*, 2018; Baldarrago *et al.*, 2019), whereas in Chile this species has been found inhabiting sublittoral zones down to 60 m depth (Häussermann, 2006). Recently, *P. papillosa* was reported in the subtidal zone beyond 15 m, in samples collected at depths of 25 and 28 m during a study of soft-bottom macrobenthos in southern Peru (Aramayo *et al.*, 2022). Additionally, unclear bathymetric records have been found throughout this literature review (e.g. Paredes and Tarazona, 1980; Paredes *et al.*, 1999; Ramírez *et al.*, 2019a, 2019b, 2019c, 2019d).

A meticulous screening has enabled the detection of several dubious reports of sea anemones on the Peruvian coast. For example, records of *A. picta*, *P. peruviana*, *B. grande*, *N. primula*, *P. niveus*, *B. peruviana*, *C. maculata*, *P. rubens*, *A. gravieri* and *C. lessonii* may not be reliable as they are exclusively based on old literature (Lesson, 1830; Dana, 1846; Verrill, 1869; Pax, 1912; Carlgren, 1959), but particularly because these specimens have not been found again. Unfortunately, no subsequent work provides additional information for *A. picta*, *P. peruviana*, *N. primula*, *C. maculata*, *P. rubens*, *A. gravieri* and *C. lessonii* to compare these original records.

In the case of *P. niveus*, Lesson (1830) and Verrill (1869) described it as an abundant benthic species in the localities of Callao and Paita; however, there have been no new records since then, even though Callao and Paita are among the most frequently and moderately monitored areas in Peru, respectively. Records of *B. peruviana* could also be considered as dubious as

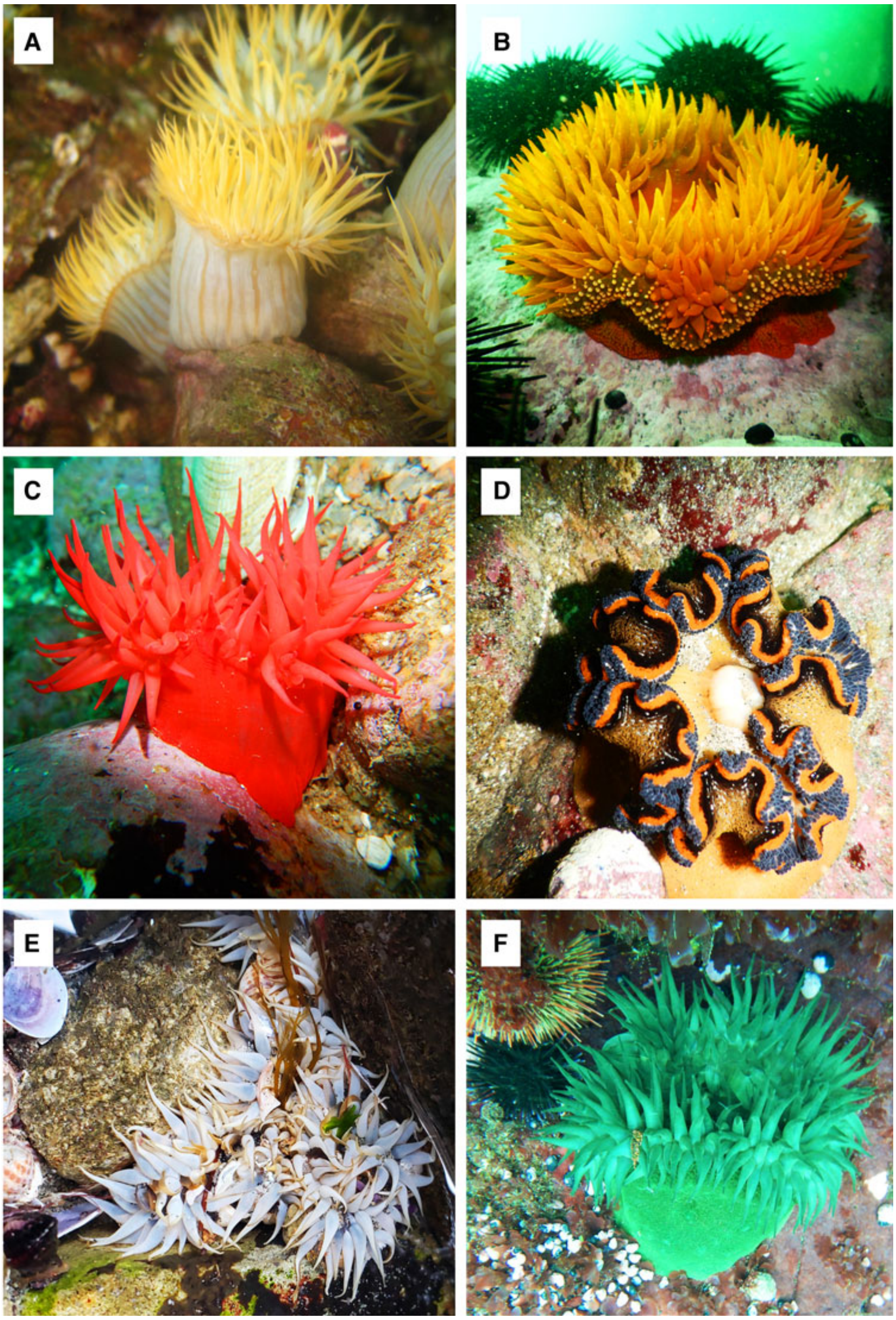

**Figure 3.** Representative sea anemone species inhabiting coastal areas in Peru. (A) *Anthothoe chilensis*; (B) *Phymanthea pluvia*; (C) *Anemonia alicemartinae*; (D) *Antholoba achates*; (E) *Oulactis concinnata*; (F) *Phymactis papillosa*. Pedal disc diameter, A: 1.5 cm, B: 10 cm, C: 2.5 cm, D: 6.5 cm, E: 5.5 cm, F: 9.5 cm. Photo credits: A–D (R. Uribe), E (V. Aramayo), F (D. Baldarrago).

this species has been reported only once. Although recent studies indicate its distribution on the Peruvian coast (Grajales and Rodríguez, 2014), this species lacks type material to confirm that claim. The same uncertainty applies to *B. grande*, as Fautin *et al.* (2007) and Barragán *et al.* (2019) report its distribution along the northern coast of Peru, but they cite previous dubious references.

Reports suggesting a possible expansion of the known latitudinal and bathymetric distribution of certain sea anemone species is another issue. The occurrence of *P. ocellata* in Peru has only been registered for the northern coast by Verrill (1869), which may be strange as this species is also known to be distributed along the Chilean coast (Carter, 1965; Häussermann and Försterra, 2005; Häussermann, 2006). Additional surveys throughout the Peruvian coast, including the southernmost localities adjacent to Chile, plus a taxonomic verification of the species are needed to validate this *P. ocellata* report.

Similarly, it is known that *B. octoradiata* is part of the benthic invertebrate communities along the Strait of Magellan in Chile (Häussermann and Försterra, 2005; Andrade *et al.*, 2016) and in southern Patagonia, Argentina (Garese *et al.*, 2014; Friedlander *et al.*, 2020, 2023). As *B. octoradiata* has not been found further north along the Chilean coast, the record by Zanabria (2013) for the southern Peruvian coast seems dubious.

Morphological descriptions, by observing the internal and external anatomy as well as the characterization of cnidae are essential to confirm the presence of this species.

The record of *A. chilensis* from Alfaro *et al.* (2016) on the northern Peruvian coast has to be confirmed with reliable data and taxonomic verification by experts because it would imply a latitudinal and bathymetric range expansion for the species. It does not seem likely to find individuals of *A. chilensis* in the shallow subtidal zone along the exposed coast, as Häussermann (2006) has reported this species between 6 and 278 m depth. Regarding its latitudinal distribution, the occurrence of *A. chilensis* has been recorded in the northern and central parts of the Chilean fjord region (Häussermann, 2004c, 2006; Häussermann and Försterra, 2005).

The uneven research effort in the study of sea anemone diversity along the Peruvian coast (Figure 2C, D) may be explained by different factors. The Lima region possesses the highest number of publications referring to sea anemones (e.g. Dana, 1846; Verrill, 1869; Carlgren, 1959; Paredes and Tarazona, 1980; Tokeshi and Romero, 1995; Paredes *et al.*, 1999; Häussermann, 2003, 2004b; Retuerto *et al.*, 2007; Firstater *et al.*, 2010; Guzmán, 2012; Cuya and Escobar, 2017; Tasso *et al.*, 2018; Yafac-Piedra and Garcia-Alayo, 2020; 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 institutes, are involved. Therefore, the Lima region does not only possess ecological studies (e.g. monitoring reports), as specific research has been conducted to investigate toxins and even their 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 records on the northern-central coast (La Libertad and Áncash regions) may be a result of monitoring studies performed at determined sites where the intensive culture of Peruvian calico scallop *Argopecten purpuratus* takes place (Uribe *et al.*, 2019). Most of the consulted studies, however, do not correspond to a sustained research programme of benthic biodiversity but rather are episodic or unconnected research initiatives. Particular cases illustrate this situation, such as research conducted by industries as part of assessment programmes (Tasso *et al.*, 2018), and surveys carried out to study the population status of threatened species. For example, specimens of *Actinia* sp. and *Paranthus* sp. have been reported as prey items of the green turtle *Chelonia mydas* in northern and southern Peru (Quiñones *et al.*, 2017, 2021). Despite being occasional, these studies contribute new information and ideas for sustained research on sea anemone biodiversity and their distribution. Sea anemones are also well-known hosts for other organisms, primarily crustaceans (Baeza and Stotz, 2003; Krapp-Schickel and Vader, 2009), and therefore also deserve attention in future research.

Species like *A. chilensis*, *P. papillosa*, *P. pluvia* and *O. concinnata* have been regularly mentioned in recent benthic diversity inventories and monitoring reports (Uribe *et al.*, 2013; 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; Uribe *et al.*, 2019; Ramírez *et al.*, 2019a, 2019b, 2019c, 2020, 2022; Valqui *et al.*, 2021). The most plausible explanation for these records is the high abundance of their populations in intertidal and shallow subtidal habitats. Zúñiga (2019) reported the occurrence of *A. radians* inhabiting rocky intertidal and shallow subtidal areas in southern Peru (Moquegua region). The southernmost extent of *A. radians*, encompassing the Tacna region adjacent to Chile, is suggested by Spano and Häussermann (2017) to be abundant in protected and semi-protected rocky intertidal ecosystems along the northern Chilean coast, however, a potentially broader global distribution is suspected for this species (Spano *et al.*, 2022).

## *Taxonomic issues, knowledge gaps and implications for conservation studies*

In-depth taxonomic analysis of sea anemones has not been included in most studies of marine benthos, paradoxically including those of intertidal benthos where this group is abundant. Synonymy, a recurring issue in the identification of benthic species, is not an exception for sea anemone taxonomy and is always a topic addressed by experts (Häussermann, 2004c, 2006; Häussermann and Försterra, 2005; Fautin *et al.*, 2007; Hancock *et al.*, 2017). For instance, *Isoulactis chilensis* (Carlgren, 1959) has been catalogued as a synonym of *O. concinnata*, although they were formerly considered two different species with identical morphological features, colour, habitat and behaviour (Häussermann, 2003). Morphological identification is a common limiting factor because of the high intra- and interspecific variability in morphotypes (González-Muñoz *et al.*, 2015). Häussermann and Försterra (2005) highlighted the challenge of differentiating *Actinostola* species even among individuals from the same species.

However, the main challenge lies in the preservation of the soft bodies of sea anemones, which complicates their taxonomy as accurate identification requires detailed morphological and histological analysis. Häussermann (2004a) produced a protocol for the examination of sea anemones, detailing methods to perform histological studies to observe the muscle and tissue anatomy, as well as to obtain cnidae data. These approaches have been included in multiple research projects by examining the external (e.g. pedal disc, column, tentacles, protuberances) and internal anatomy (e.g. actinopharynx, arrangement of mesenteries, marginal sphincter muscle, size and types of cnidae) looking for important features to identify species accurately (Häussermann, 2004c; Fautin *et al.*, 2007; Garese *et al.*, 2014; Barragán *et al.*, 2019). Thus, sea anemone taxonomy is arduous and complicated, but is a needed step to improve biodiversity analysis.

Due to these difficulties, multiple sea anemone species are first registered as *Actinia* sp., like *A. alicemartinae* in Chilean reports from the 1970s (Häussermann and Försterra, 2001). In Peru, there is an increasing effort in identifying common actiniarians in contrast to previous years where specimens were often reported as 'Cnidaria', 'Actiniaria indet.', 'actiniarian' or 'anemone'. However, this nomenclature is still utilized in local observations for some indeterminate, but frequently observed species that cohabit in the intertidal and shallow subtidal (~25 m).

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 collection depth is often not given in the 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 diving depth and therefore, with a potential bias on the real bathymetric range. Biodiversity biases associated with the lack of data and information have frequently occurred in the marine environment affecting our ability to analyse specific taxa patterns and dimension ecological responses (Miloslavich *et al.*, 2011).

Pax (1912) suggested considering the sea anemone species *A. picta*, *P. rubens*, *A. gravieri* (formerly *Sagartia gravieri*) and *C. lessonii* (formerly *Sagartia lessonii*) as endemic to Peru because their distribution appears to be restricted to this ecosystem.

Nevertheless, species that have not reappeared since their first reports (i.e. Lesson, 1830; Dana, 1846; Verrill, 1869; Pax, 1912; Carlgren, 1959) should not be considered until more specimens are found and contrasted with museum collections, identified by modern protocols, and comparing their external and internal morphological features with the ones mentioned in their original descriptions (Spano and Häussermann, 2017). Due to vague original descriptions and the absence of type material, future research should prioritize an extensive exploration of habitats and apply fine taxonomy and anatomy analysis for a better taxonomic diagnosis.

Recently reported species for the Peruvian coast may be due to their invasive nature. For instance, *A. alicemartinae* has only been found occurring on the southern coast (Canales-Aguirre *et al.*, 2015; Baldarrago *et al.*, 2019; Pinochet *et al.*, 2019). Previous studies from Chile hypothesized the *A. alicemartinae* population present in southern Peru would be the ancestral one giving rise to the current distribution of *A. alicemartinae* along the Chilean coast (Canales-Aguirre *et al.*, 2015; Pinochet *et al.*, 2019). However, Glon *et al.* (2020) suggested that *A. alicemartinae* has been introduced to the Eastern Pacific Ocean from either the Indo-West Pacific or the Atlantic Ocean, based on the absence of this species in historical literature and on the lack of reports of any other species of *Anemonia* in this region. The authors also mentioned the native range of this species is still unknown possibly due to the scarcity of studies in these matters or the early stage of its invasion.

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. papillosa* exhibited higher abundances 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 (Aramayo *et al.*, 2021).

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 *A. 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 *A. chilensis* to EN events. In addition, the establishment of *P. papillosa* in the lower intertidal zones as a co-dominant species after EN events (1982/83 and 1997/98) has been documented along the Chilean coast (Rivadeneira and Oliva, 2001). The anemone *P. papillosa* seems to be a resistant and opportunistic species amidst disturbances in its environment, as there is also 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 (30–40 m depth) and intense OMZ spans most of the Peruvian waters (Tarazona and Arntz, 2001; Helly and Levin, 2004), but almost nothing is known regarding the response of sea anemone communities to this stressor. 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). Studies in neighbouring areas reveal that, although local soft-bottom benthic communities seem to be adapted to low-oxygen conditions, the ecological threshold of these responses over time is unclear (Aramayo *et al.*, 2021); indeed, future climate change scenarios for the Peruvian sea emphasize oxygen deficiency as a critical tipping point, primarily posing a significant threat to commercially important benthic species, as well as to other, less studied benthic species inhabiting the same region (Ramos *et al.*, 2022).

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 *O. 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.

## Conclusions

The data analysed in this review represent an integrative synthesis, and it is particularly noteworthy that most of the species reported here do not appear in the usual monitoring reports or the few *ad hoc* studies on actiniarians in Peru. Although there has been a progressive increase, albeit slow, in interest in this benthic group over recent decades, it is also true that we need to clarify many doubts about species described long ago, and adequately identify potential biases in existing data, especially the lack of environmental information.

A significant advance in the study of this group also requires an important effort to analyse its ecological importance and responses concerning the many existing sources of impact, especially the large-scale ones such as EN and regional stressors like OMZ. The increasing frequency of these phenomena in future climate change scenarios (e.g. warmer waters and widespread deoxygenation) is highly probable, studies addressing this panorama are rather insufficient, rare or simply do not exist. Although sea anemones are highly adaptive, more than one of the species reported here may be currently subject to some degree of population pressure, either due to natural causes or anthropogenic impacts (pollution, habitat loss, etc.) resulting in increasing uncertainty about the true biodiversity status of this group.

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