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Zootaxa 20 years: Phylum Porifera

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Abstract

The peer-reviewed journal *Zootaxa* has accelerated the rate of sponge (Porifera) species discoveries in 289 peer-reviewed papers published between 2002 up until the end of 2020, describing 725 new species, six new subspecies, 27 new genera, four new subgenera, and 123 new species and genus names needed to resolve existing homonyms. *Zootaxa* has been the most prolific of all taxonomic journals in its contributions to describing new taxa of Porifera in modern times. This present article analyses these taxonomic contributions over the past 20 years of *Zootaxa*, including their trends and highlights pertaining to sponge publications.

Introduction

Sponges (Phylum Porifera) are animals with Precambian origins (e.g. Dohrmann & Wörheide 2017) and a continuous fossil record since the Cambrian (~500 Ma, e.g. Antcliffe *et al*. 2014, Schuster *et al.* 2018). They are accepted as monophyletic (e.g. Wörheide *et al.* 2012) and considered by most researchers the sister group to all other metazoans (e.g. Telford *et al.* 2016).

Sponges are all aquatic, widely distributed from ephemeral freshwater habitats to hadal depths in all ocean basins, and extending from polar to tropical regions (e.g. Van Soest *et al.* 2012). They are major components of benthic communities although their patterns of abundance can be highly variable, ranging from highly dense and extensive populations in some communities to sparse and rare in others (e.g. Bell *et al.* 2020).

Most sponges are sessile (although some are capable of limited locomotion, e.g. Bond & Harris 1988, Morganti *et al.* 2021) and suspension feeders, having many important functional environmental values associated with their ability to filter large quantities of water (e.g. Weisz *et al*. 2007). Using their unique flagellated collar cells (choanocytes, or anucleate collar bodies in the Hexactinellida) they actively create water currents to filter and consume both particulate (POM) and dissolved organic matter (DOM), thus producing a strong link between benthic and pelagic ecosystems 'the sponge loop', also referred to as benthic–pelagic coupling (e.g. de Goeij *et al.* 2013). Some deep sea species of the Family Cladorhizidae have lost these choanocytes and have evolved carnivorous

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feeding strategies (e.g. Vacelet & Boury-Esnault 1995). Sponges are also primary bioeroders of coralline substrates. Recycling $CaCO_3$ back to the reef system, which is vital to the formation and maintenance of coral reefs (e.g. Webb *et al.* 2019), they furthermore contribute to reef consolidation by binding unconsolidated coral rubble, increasing rates of carbonate accretion (Wulff & Buss 1979).

Economically, marine demosponges in particular have proven to be the richest source of diverse and novel chemical compounds, some of which have bioactive properties of interest to the medical and marine natural products industries (e.g. Leal *et al.* 2012). Nearly 5,000 new compounds were discovered between 1970–2010, representing about 30% of all marine natural products discoveries so far (Mehbub *et al.* 2014), with bioactivities including anticancer, antiviral, antibacterial, antifungal, antiprotozoal, anthelmintic, anti-inflammatory, immunosuppressive, neurosuppressive, neuroprotective and antifouling efficacies. For example, since 2014, of the 39 marine-derived potential anticancer agents, 18 compounds were from sponges, of the 16 marine natural products under preclinical trials as new drug candidates, six were from sponges, and of these, four commercial drugs from sponge compounds (Adcetris®, Cytosar®, Halaven®, and Yondelis®) are so far approved for use in humans (Newman & Cragg 2014). The source of these compounds is increasingly shown to be a complex range of interactions between the sponge host and its diverse microbiota (the 'sponge holobiont') (e.g. Pita *et al.* 2018), with their metabolic collaborations having coevolved over the millennia, whereby microbial symbionts can interact with host cells through production and degradation of metabolic compounds (O'Brien *et al*. 2019).

Consequently, our ability to differentiate and enumerate these sponge host species through the processes of taxonomy and systematics is critical to the continued need for discovery of novel bioactive compounds as infectious microorganisms evolve and develop resistance to existing pharmaceuticals (Mehbub *et al.* 2014)—in addition to the myriad aquatic ecosystem services sponges provide (see Folkers & Rombouts 2019 for an overview).

Over the past three decades there has been a significant surge in the collection and discovery of new species and genera of sponges, with the number of described Porifera currently standing at 9,366 valid (accepted) species (of nearly 24,000 nominal species names), in 852 accepted genera (Van Soest *et al.* 2021). Undoubtedly, however, these known species represent only a small proportion of all sponge species—estimated at about only 33% of the extant sponge fauna—with the remainder already collected but still undescribed, or not yet discovered (e.g. Appeltans *et al.* 2012).

The higher systematics of Porifera, however, has had a more unstable history (see an overview of the history of the phylum in Hooper, Van Soest & Debrenne 2002), reaching some level of consensus with a single unified classification proposed with the publication of the *Systema Porifera*, based largely on cladistic analysis of morphological data (Hooper & Van Soest (Eds) 2002). At that time three recent classes were recognised (Demospongiae, Calcarea and Hexactinellida), with seven subclasses, 25 orders, 127 families and 682 accepted genera. This consensus higher classification built on the earlier works of Lévi–Bergquist–Hartman during the 1960-1970s (see summary in Morrow & Cárdenas 2015).

The last decade saw an acceleration of molecular systematics and many clashes between the prevailing classification and phylogenetic relationships emerging from these molecular studies. This was particularly true for the Demospongiae, and in 2013 two new orders were proposed, Biemnida and Chondrillida (Redmond *et al.* 2013) based on molecular evidence. Subsequently, in 2015 a substantial revision of the higher classification of Class Demospongiae was proposed, based on the increasing number of molecular phylogenetic studies that revealed or confirmed numerous polyphyletic groups and new clades discovered (Morrow & Cárdenas 2015), resulting in a widening gap in the phylogeny and higher classification of demosponges. They proposed three subclasses (Verongimorpha, Keratosa and Heteroscleromorpha), retained seven of the 13 orders from the *Systema Porifera* (Agelasida, Chondros(i)ida, Dendroceratida, Dictyoceratida, Haplosclerida, Poecilosclerida, Verong(i)ida), abandoned seven orders (Astrophorida, Hadromerida, Halichondrida, Halisarcida, 'lithistids', Spirophorida, Verticillitida), resurrected or upgraded six orders (Axinellida, Merliida, Spongillida, Sphaerocladina, Suberitida, Tetractinellida), created seven new orders (Bubarida, Desmacellida, Polymastiida, Scopalinida, Clionaida, Tethyida, Trachycladida), resulting in a total of 22 orders in the revised classification of Demospongiae post *Systema Porifera*, which constitutes by far the largest sponge class with about 85% of all species.

Another major recent change in Porifera's systematics was the recognition of Class Homoscleromorpha. In the *Systema Porifera* Homoscleromorpha was still a subclass of Demospongiae. This group was then raised to the full class rank thanks to molecular studies that retrieved it as the sister group of Class Calcarea and not as part of the Class Demospongiae (Gazave *et al*. 2010, 2012). Currently, one order (Homosclerophorida) and two families (Oscarellidae and Plakinidae) are recognised in this class, which comprises about 1% of all sponge species.

For the other two sponge classes, which contain about 8% of sponge species each, only minor changes occurred with the support of molecular phylogenies. The monophyly of the two subclasses of Hexactinellida (Amphidiscophora and Hexasterophora) was confirmed and the position of some internal taxa has been revealed (Dohrmann *et al*. 2008, 2012). They form the sister group to Demospongiae as "Silicea *sensu stricto*" (Philippe *et al.* 2009). For Calcarea, which form a yet unnamed clade with Homoscleromorpha, several works confirmed the monophyly of this class and their subclasses, Calcinea and Calcaronea (Manuel 2003), and showed several less inclusive polyphyletic taxa (Dohrmann *et al*. 2006, Voigt *et al*. 2012). Using both morphological and molecular approaches, some new genera were proposed but higher taxa still await resolution (Klautau *et al*. 2013, Cóndor-Luján & Klautau 2016, Lopes *et al*. 2018).

In 2008 the World Porifera Database (WPD, part of the World Register of Marine Species, WoRMS, http://www.marinespecies.org) commenced in earnest to database the sponge taxonomic literature (predominantly containing living species, but including some fossil representatives), together with access to the literature that underpin those taxonomic decisions, and the consortium of WPD Editors continue to track and revise sponge species and their higher systematics as new discoveries are published and taxonomic revisions are proposed (Van Soest *et al.* 2021).

The WPD higher taxonomic structure was extensively revised following the publication of Morrow & Cárdenas (2015), and therefore currently recognises four extant classes: Demospongiae (7,506 species in three subclasses), Calcarea (792 species in two subclasses), Hexactinellida (687 species in two subclasses) and Homoscleromorpha (the least diverse, with only 127 species known so far in a single order), and one exclusively extinct class: †Archaeocyatha that lived during the Early to Late Cambrian, with 304 genera considered valid (Debrenne *et al*. 2002) and yet with still unresolved relationships to the extant taxa (see Botting & Muir 2019).

Zootaxa (https://www.mapress.com/j/zt/), which commenced in 2001 with the first sponge paper published in 2002 (Boury-Esnault *et al*. 2002), has accelerated the rate of sponge species discoveries up until the end of 2020, and also revised the higher systematics of many sponge taxa since the *Systema Porifera* was published in 2002.

As for many other animal phyla published in the special volume of *Zootaxa* celebrating its 20th anniversary, it has been the most prolific of all taxonomic journals in its contributions to describing new species of Porifera in modern times. This present article analyses these taxonomic contributions over the past 20 years of *Zootaxa*, including their trends and highlights.

Methods

All sponge papers published in *Zootaxa* up until December 2020 were surveyed by the current Porifera Subject Editors, gathering the following data:

- Number of papers published each year, their authors, and their countries of affiliation at the time of publication
- Number of new species, subspecies, genera and subgenera, and known species redescribed each year
- Number of species and papers published each year for the major ocean basins (and also including freshwater habitats)
- Number of new species by country of collection
- Number of papers published each year for each marine province (following the *Marine Ecoregions of the World* (MEOWs) system of Spalding *et al.* (2007), and the Global Open Ocean and Deep Sea (GOODS) classification of Watling *et al.* (2013))
- Number of papers published each year with *in situ* species photographs, papers illustrated with scanning electron micrographs (SEMs), and the various collection methods used
- Number of papers each year that described species using only morphological traits, or those also using molecular and integrative methodologies
- Number of new species and papers published each year classified according to water depth zones: Intertidal-sublittoral/ photic (0–30m depth), Mesophotic (31–200m), Upper bathyal (201-800m), Lower bathyal (801-3,500), Abyssal (3,501-6,500), Hadal (below 6,501m depth)
- Number of citations of papers published each year based on the 'Cited Reference Count' and 'Times Cited All Databases' metrics from the Clarivate Analytics Web of Science database (Clarivate *Web of Science*. © Copyright Clarivate 2021)

- Proportion of papers published each year with open access based on the *Zootaxa* online search feature (http://mapress.com/j/zt/search) for "Porifera"
- Proportion of manuscripts rejected each year, and on average between 2011 and 2020, based on records kept by the Porifera Subject Editors commencing in 2011.

Data were analysed in tabular format and yearly trends are illustrated for each of the 19 years of Porifera publications in *Zootaxa* (which commenced in 2002 and analysed up to the end of 2020). Data trends were tested for their statistical significance using the Analysis ToolPack of Microsoft Office® Excel (2006). The linear regression trendline using the 'least squares' method to calculate a straight line that best fits the data calculating a statistic (R^2) that describes that trendline. An analysis of variance (ANOVA, F statistic) tested the significance of the regression, with the null hypothesis (H_0) being that there were no statistically significant differences between papers published on Porifera in *Zootaxa* during the period of analyses ($P \geq 0.05$), against the alternate hypothesis (H_1) that there were statistically significant differences in yearly trends for the various metrics analysed here ($P<0.05$).

Results & Discussion

Between 2002 and December 2020 there were 289 *Zootaxa* publications on sponges describing 725 new species, six new subspecies, 27 new genera, four new subgenera, and 123 new names for sponges that were discovered to be homonyms of other unrelated taxa published earlier (Fig.1).

Unsurprisingly, the number of papers published each year has accelerated significantly (Fig. 2), as has the number of (unique) authors publishing each year reflecting the rise of multi-authored papers over the two decades (Fig. 3), but there was no statistically significant difference in any trend observed for the mean number of authors per publication (on multi-authored papers) compared each year over the 20 years of *Zootaxa* (Fig. 4). Authors publishing on sponges during this period had affiliations to a total of 45 different countries (Fig. 5), with the trendline in the number of authors from different countries each year accelerating significantly (Fig. 6).

The number of new species of sponges described each year and redescriptions of previously described species from new collections showed a highly significant statistical increase in the trendline over the 20 years, an increased but less significant number of new records of previously known species published each year (Fig. 7), but no obvious yearly trends were observed in the numbers of other taxa (new genera, subgenera or subspecies) published each year. There were no significant trends in the number of new species described between the different ocean basins (or freshwater bodies), but the trendline is dominated by new species described from the Atlantic Ocean in 2017 and 2018 (Fig. 8), and the number of new species from Brazilian waters in particular (Fig. 9).

The nature of sponge publications—methodology and technology—has also evolved over the 20 years, with the number of *in situ* illustrations (species and their habitats) (Fig. 10), the use of scanning and transmission electron microscopy, and molecular systematics all showing significant increases over this period (Fig. 11), although the number of papers published based solely on phenotypic (morphological) attributes continue to simultaneously rise over the decades until the present—presumably due to authors' limited access to institutional facilities to undertake molecular analyses and/or the preservation history of samples collected. 'Papers of significance' (monographs, special issues) increased slightly over this period but their trendlines were not conclusively different (Fig. 12). The number of papers published showed significant trendlines for some of the methods used to collect specimens, with SCUBA and Remotely Operated Vehicles (ROVs) showing increases in the period analyzed (Fig. 13).

Over the two decades, publications of species from the Atlantic and Pacific Oceans were predominant (Fig. 14 A, B), the sponge fauna of the *Tropical Southwestern Atlantic* province having the largest number of publications (Fig. 15).

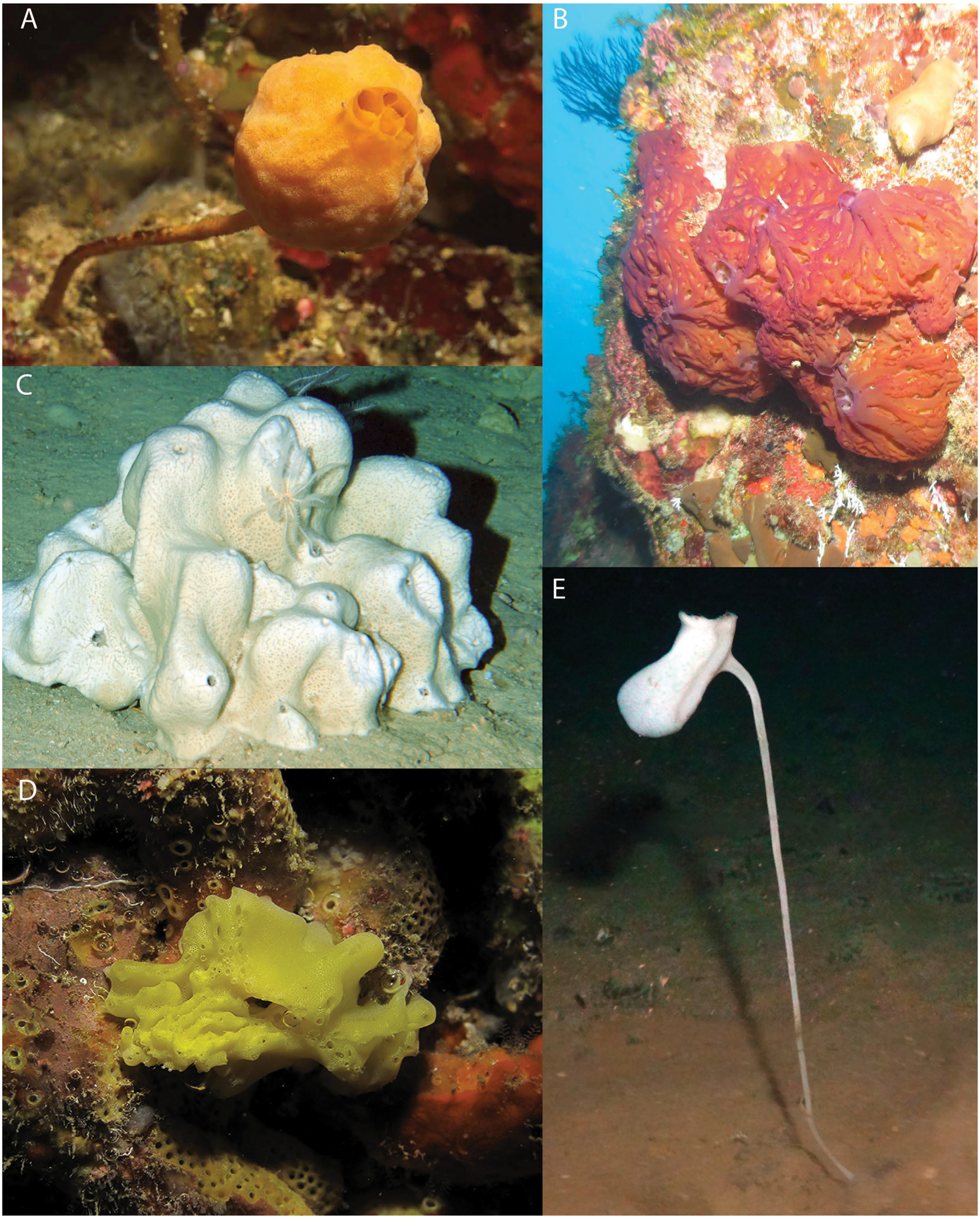

FIGURE 1. Some images of sponge species described in *Zootaxa* between 2011 and 2018. (A) *Podospongia colini* Sim-Smith & Kelly, 2011 (Class Demospongiae, Order Poecilosclerida). (B) *Oscarella filipoi* Pérez & Ruiz, 2018 (Class Homoscleromorpha, Order Homosclerophorida). (C) *Neopetrosia dutchi* van Soest, Meesters & Becking, 2014 (Class Demospongiae, Order Haplosclerida). (D) *Bidderia bicolora* Lopes, Cóndor-Luján, Azevedo, Pérez & Klautau, 2018 (Class Calcarea, Order Clathrinida). (E) *Sympagella clippertonae* Herzog, Amon, Smith & Janussen, 2018 (Class Hexactinellida, Order Lyssacinosida).

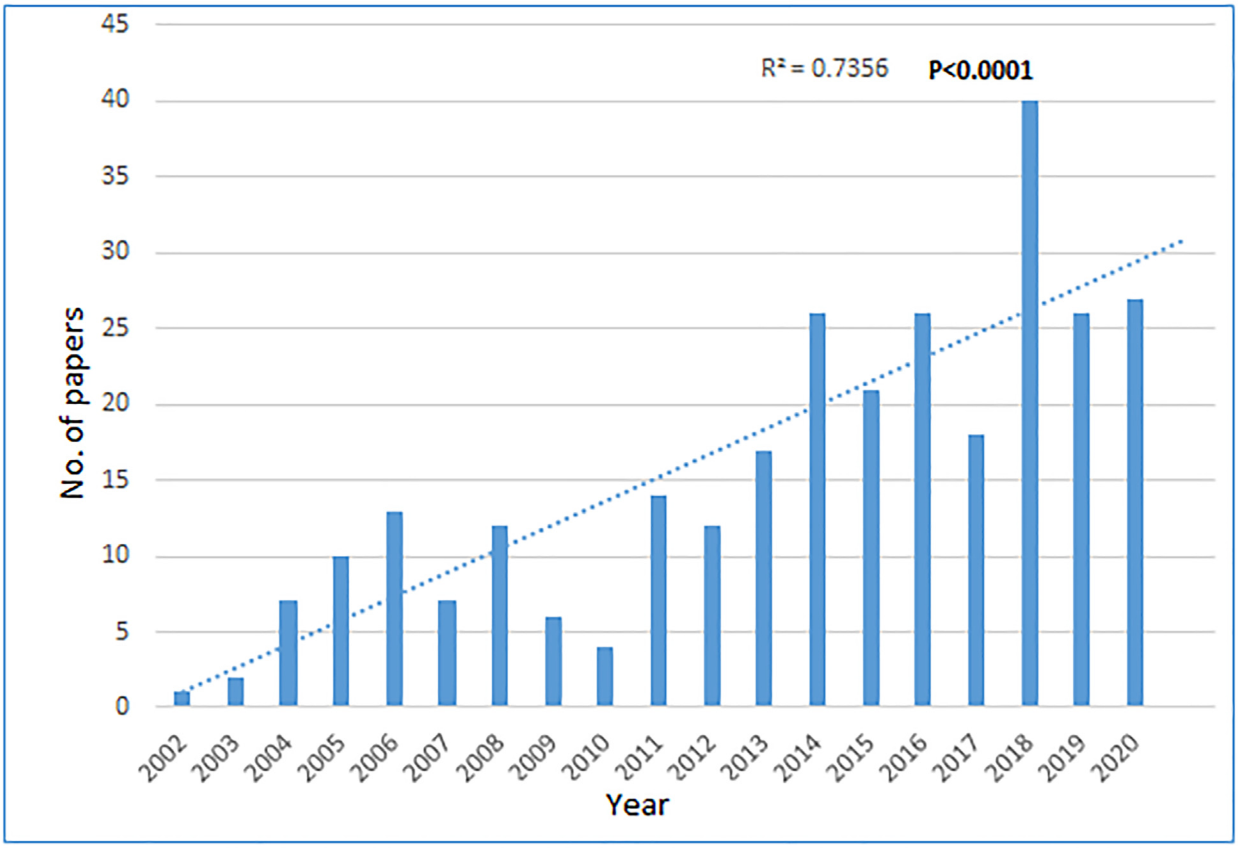

FIGURE 2. Number of taxonomic and systematics papers on Porifera published in *Zootaxa* between 2002 and 2020, with a linear regression trendline and analysis of the statistical significance of the observed data.

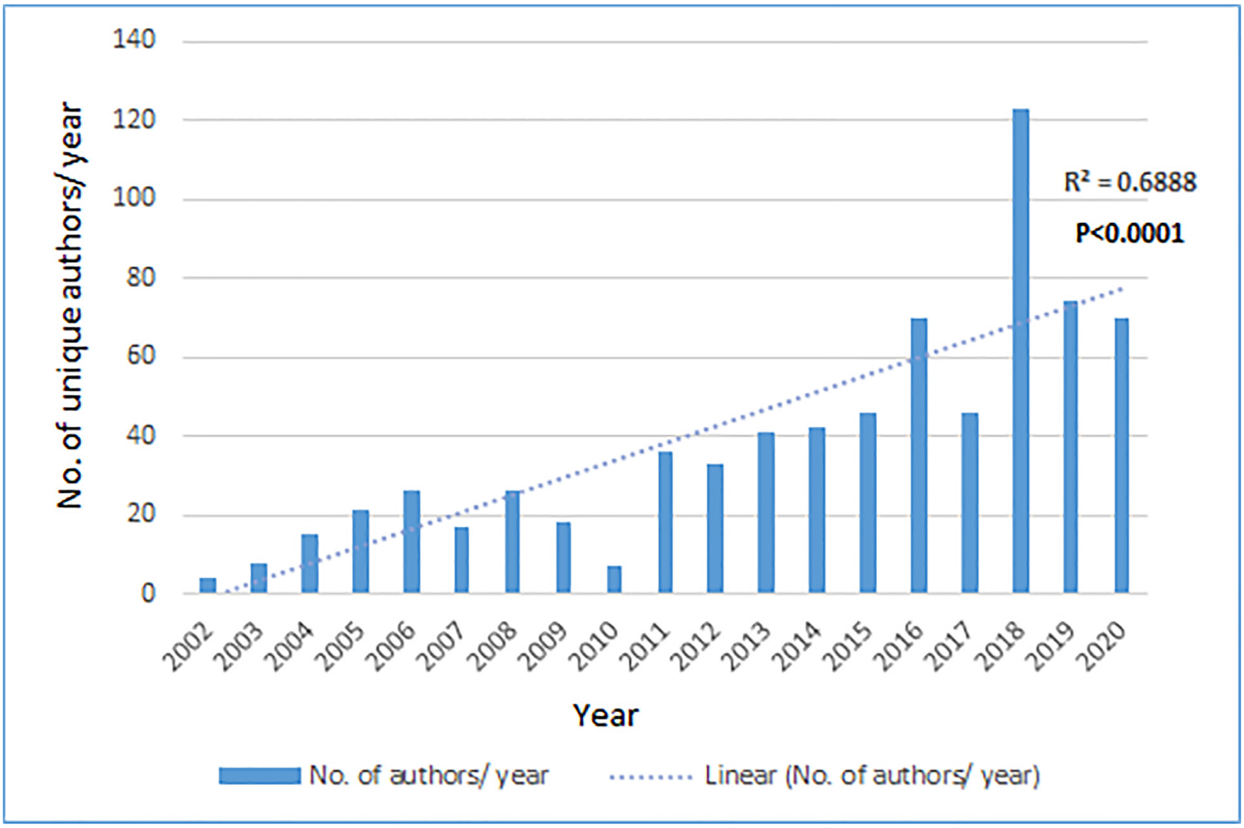

FIGURE 3. Number of unique authors publishing on Porifera in *Zootaxa* between 2002 and 2020, with a linear regression trendline and analysis of the statistical significance of the observed data.

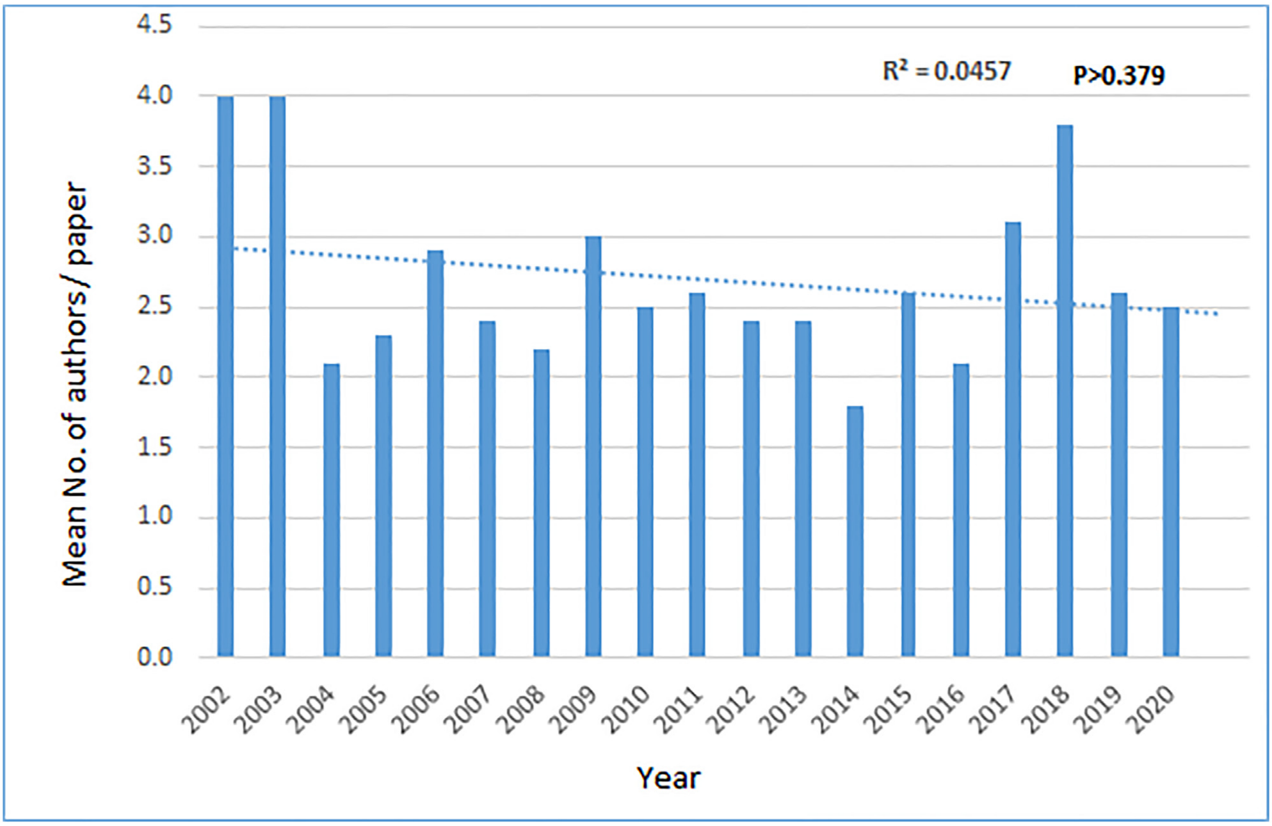

FIGURE 4. Mean number of authors/ paper publishing on Porifera in *Zootaxa* each year between 2002 and 2020, with a linear regression trendline and analysis of the statistical significance of the observed data.

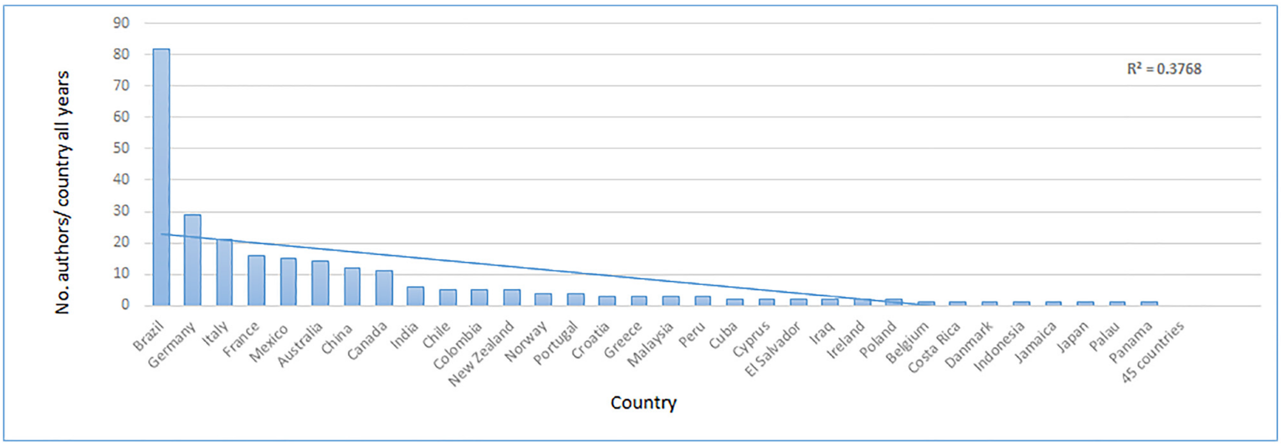

FIGURE 5. Number of authors in each country publishing on Porifera in *Zootaxa* each year between 2002 and 2020, with a linear trendline of the observed data.

Publications of collections from the intertidal-sublittoral photic zone (0–30m depth), mesophotic zone (31–200m depth) and upper bathyal zone (201–800m depth) showed moderately consistent rises in their trendlines over the two decades, with the number of papers on the fauna of the lower bathyal zone (801–3,500m depth) rising significantly over the past seven years (Fig. 16), presumably due to better technological access to the deep sea over the past decade. This trend is reflected in the number of new species discovered and described in *Zootaxa* each year from those depth profiles (Fig. 17). Of the two Clarivate Analytics© metrics used to examine yearly trends in citations of *Zootaxa* Porifera publications, the trendline for 'Cited References' showed a statistically significant strong increase over the two decades, whereas the 'Times Cited' trendline was not statistically significant in demonstrating either annual growth or any decreases in citations (Fig. 18).

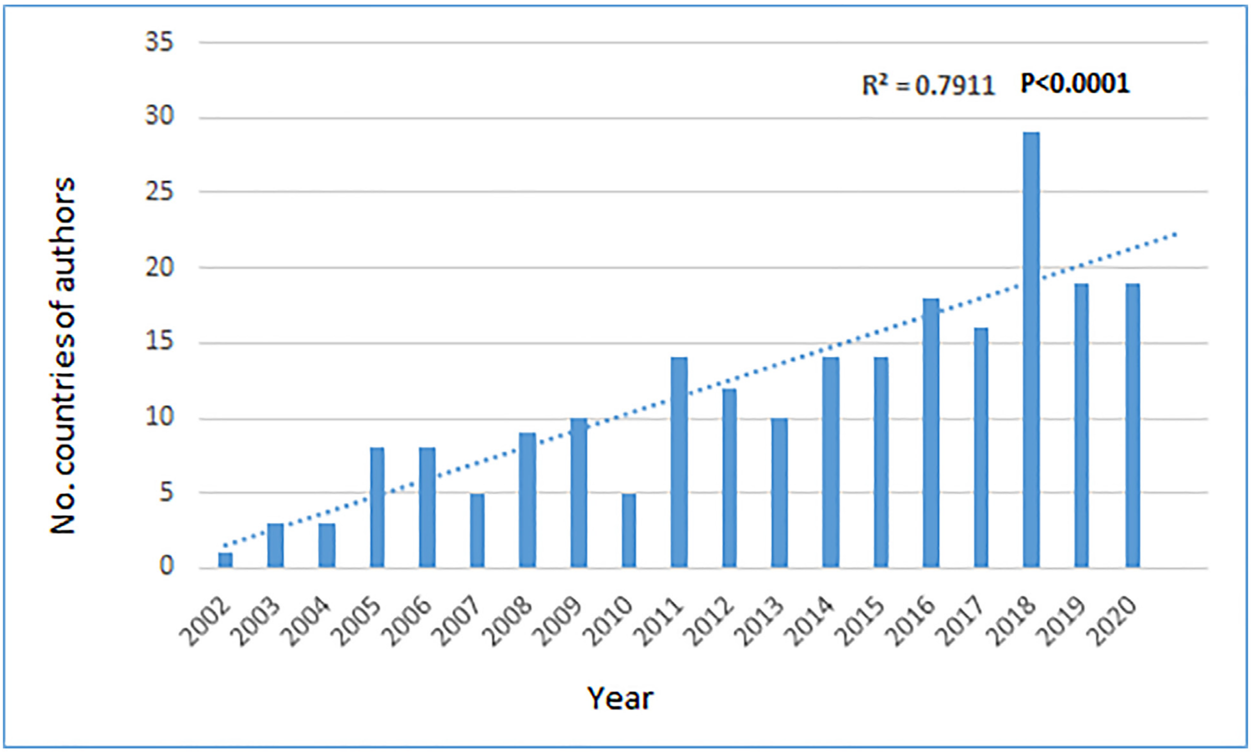

FIGURE 6. Number of countries of authors publishing on Porifera in *Zootaxa* each year between 2002 and 2020, with a linear regression trendline and analysis of the statistical significance of the observed data.

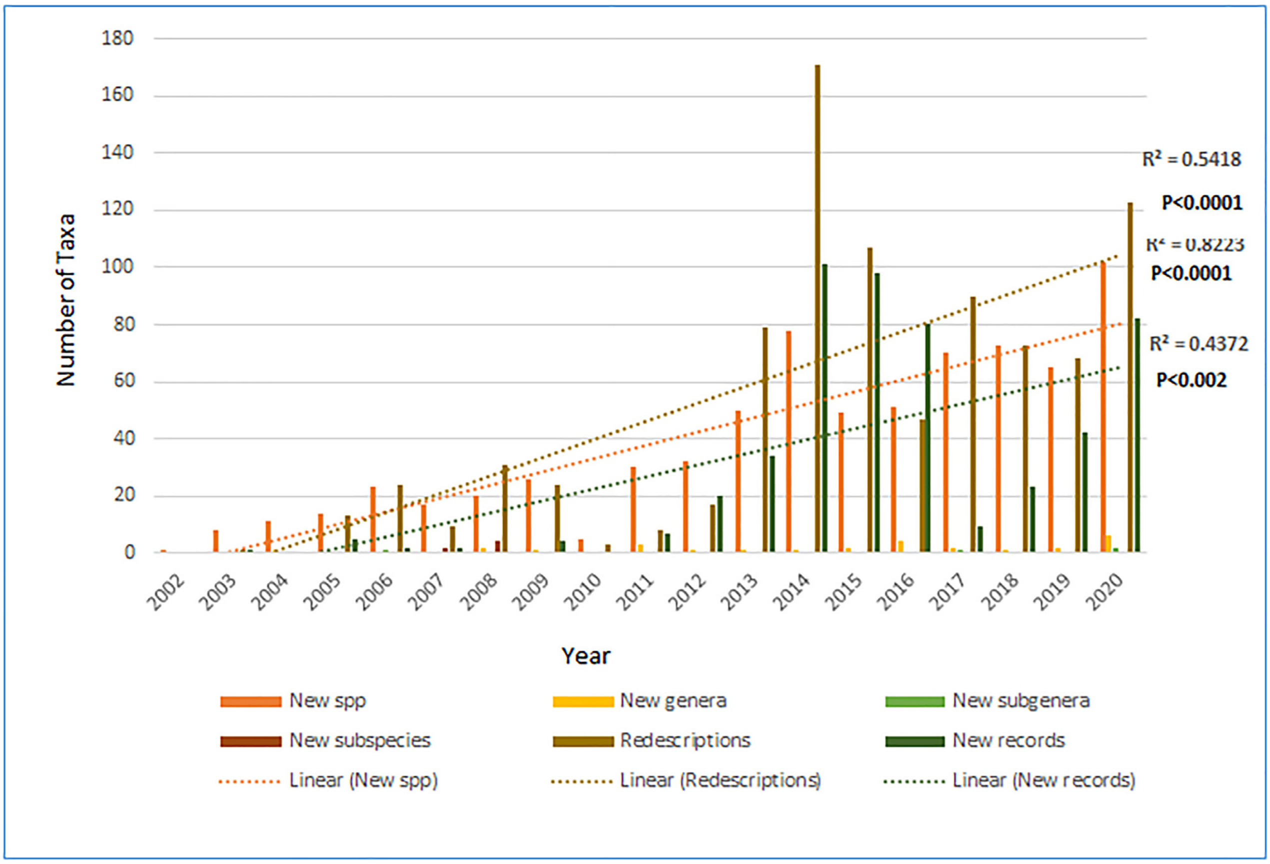

FIGURE 7. Number of taxa published on Porifera in *Zootaxa* each year between 2002 and 2020, with linear regression trendlines and analysis of the statistical significance of the observed data for new species (orange trendline), redescriptions of existing taxa (brown trendline), and new taxonomic records for countries or provinces (green trendline).

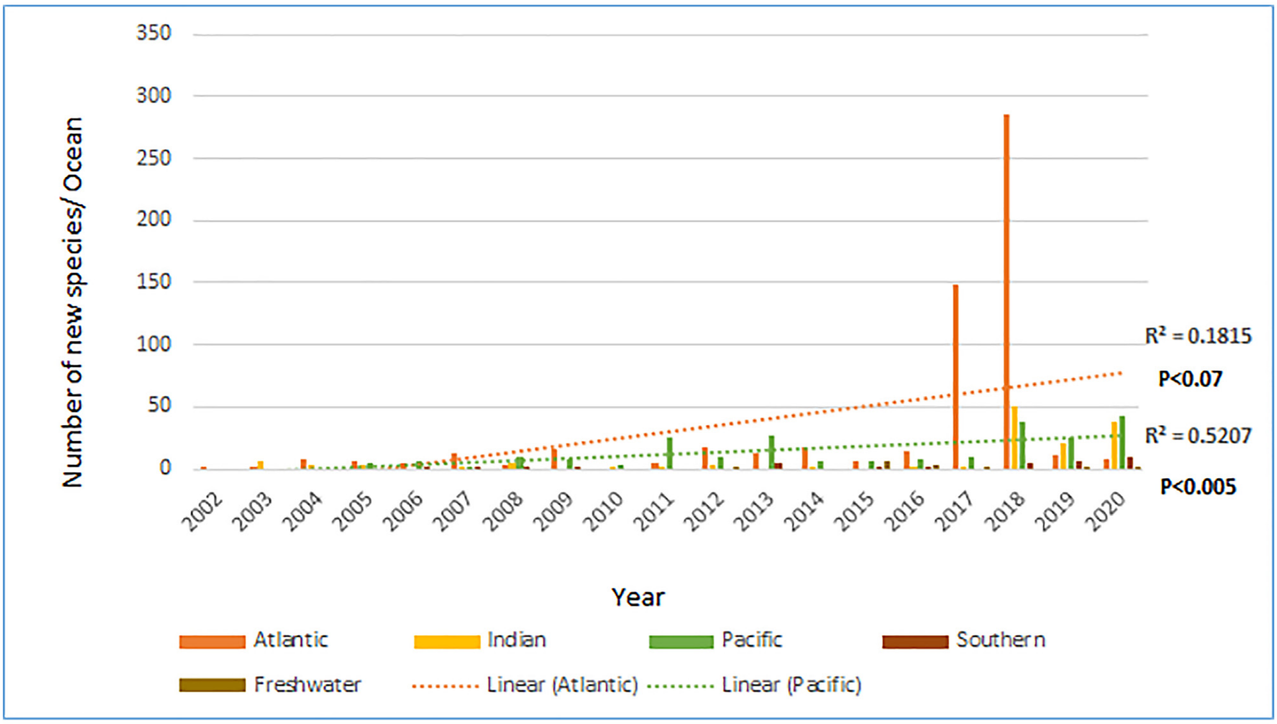

FIGURE 8. Number of new species per ocean basin (and freshwater bodies) published on Porifera in *Zootaxa* each year between 2002 and 2020, with linear regression trendlines and analysis of the statistical significance of the observed data for new species from the Atlantic Ocean (orange trendline) and new species from the Pacific Ocean (green trendline).

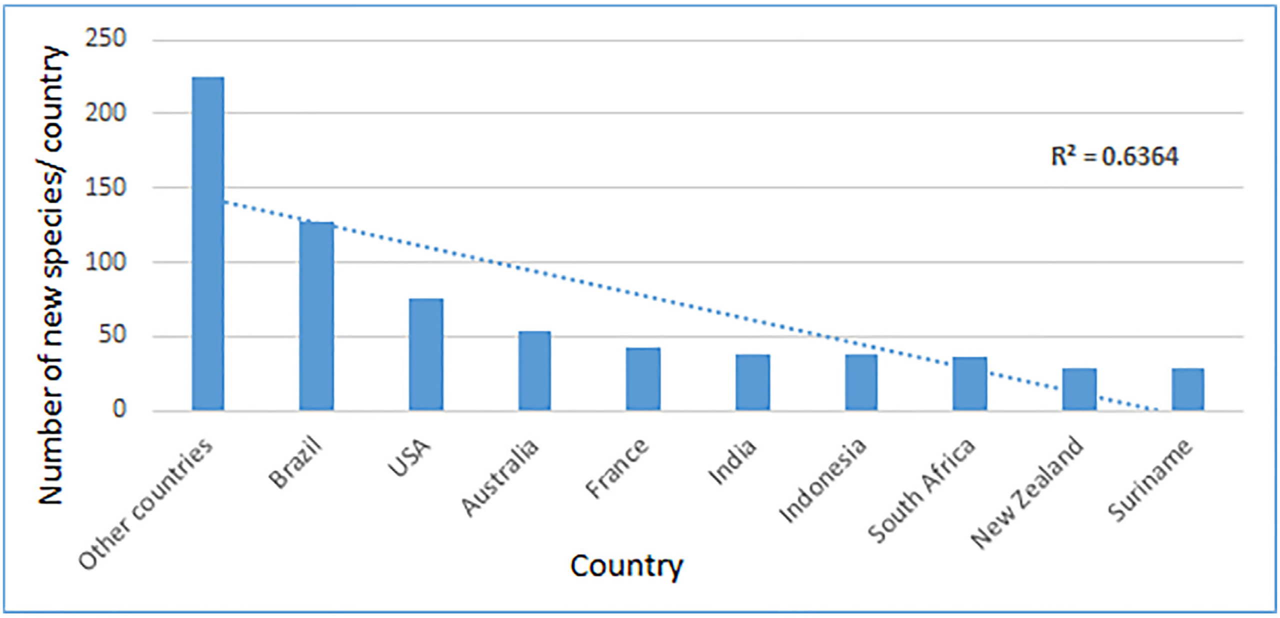

FIGURE 9. Number of new species per country published on Porifera in *Zootaxa* each year between 2002 and 2020, with a linear regression trendline of the observed data.

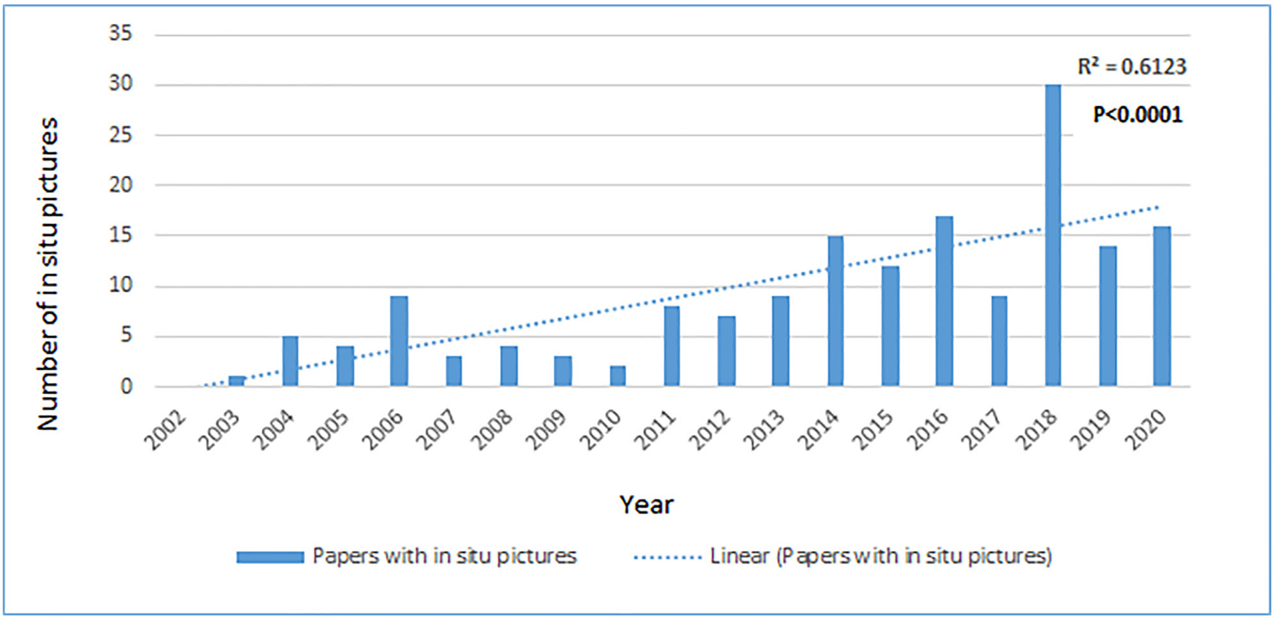

FIGURE 10. Number of papers with *in situ* illustrations of species of Porifera or their habitats published in *Zootaxa* each year between 2002 and 2020, with a linear regression trendline and analysis of the statistical significance of the observed data.

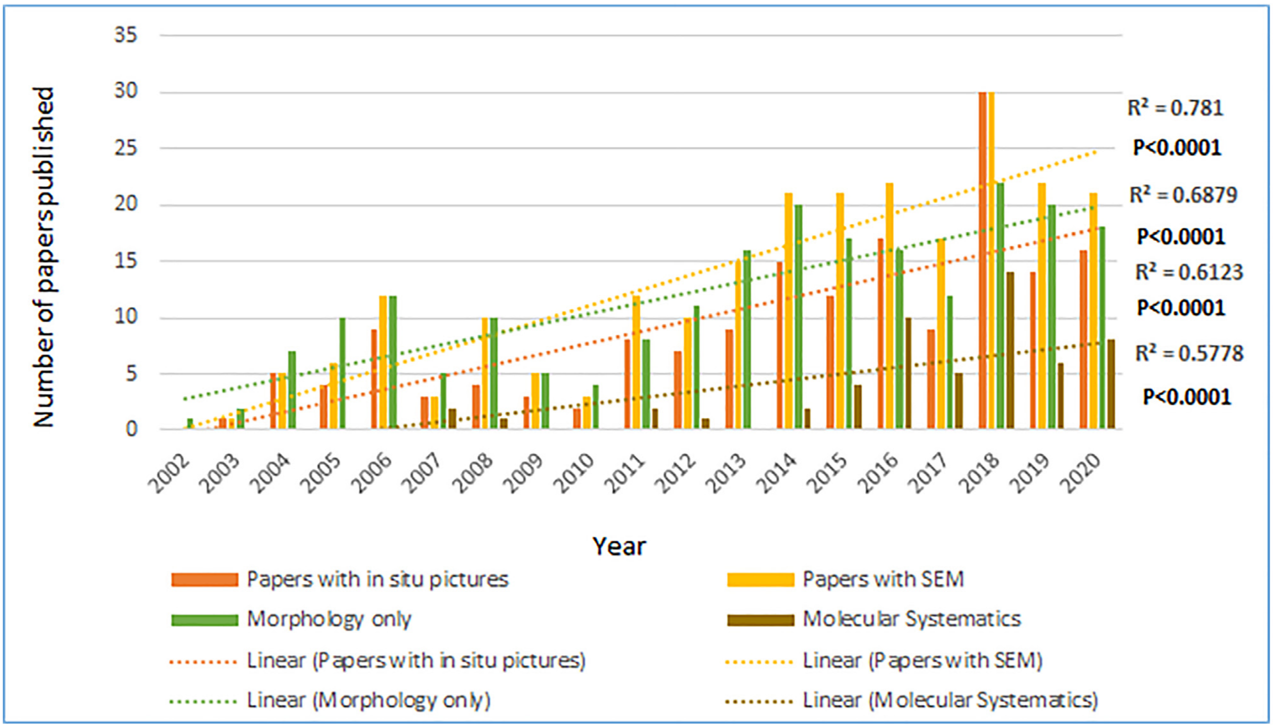

FIGURE 11. Number of papers with *in situ* illustrations of species or habitats (orange bars), scanning electron micrographs (SEMs, yellow bars), and including molecular systematics (brown bars), or based on morphology only (green bars), published on Porifera in *Zootaxa* each year between 2002 and 2020, with linear regression trendlines and analysis of the statistical significance of some of the observed data.

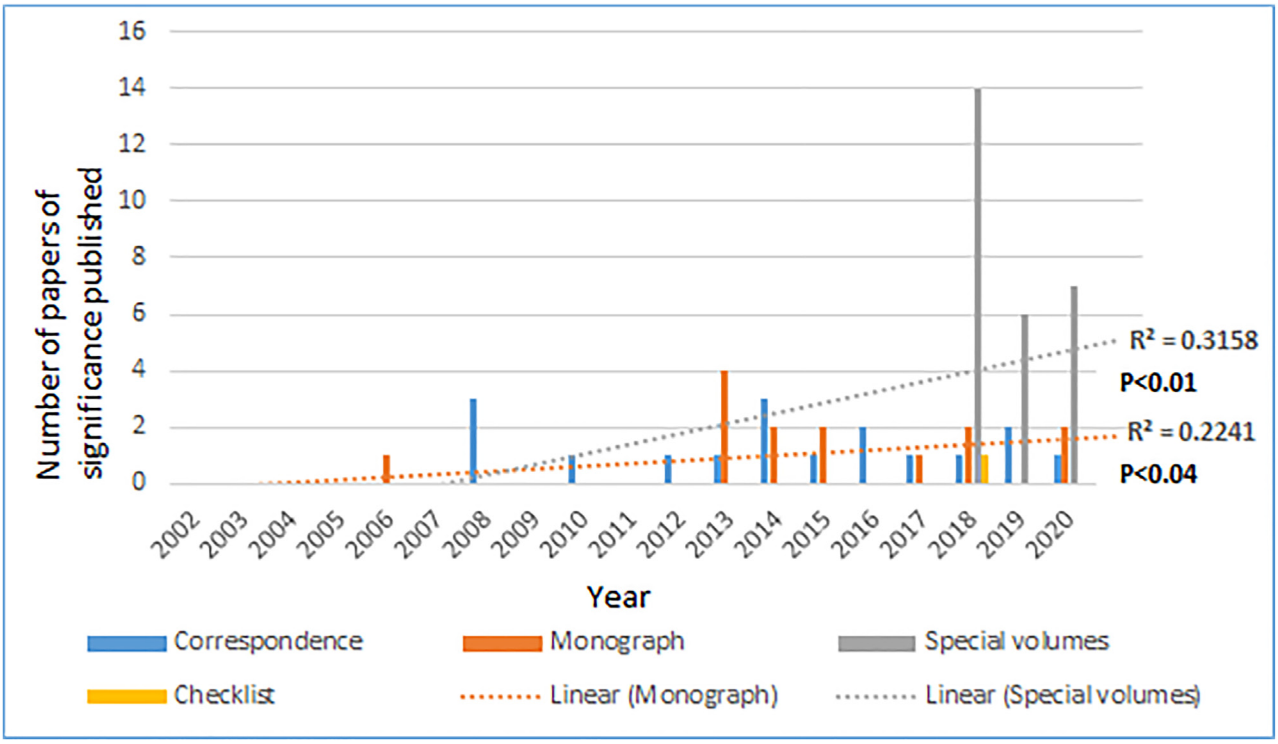

FIGURE 12. Number of 'papers of significance' published on Porifera in *Zootaxa* each year between 2002 and 2020, with linear regression trendlines and analysis of the statistical significance of some of the observed data.

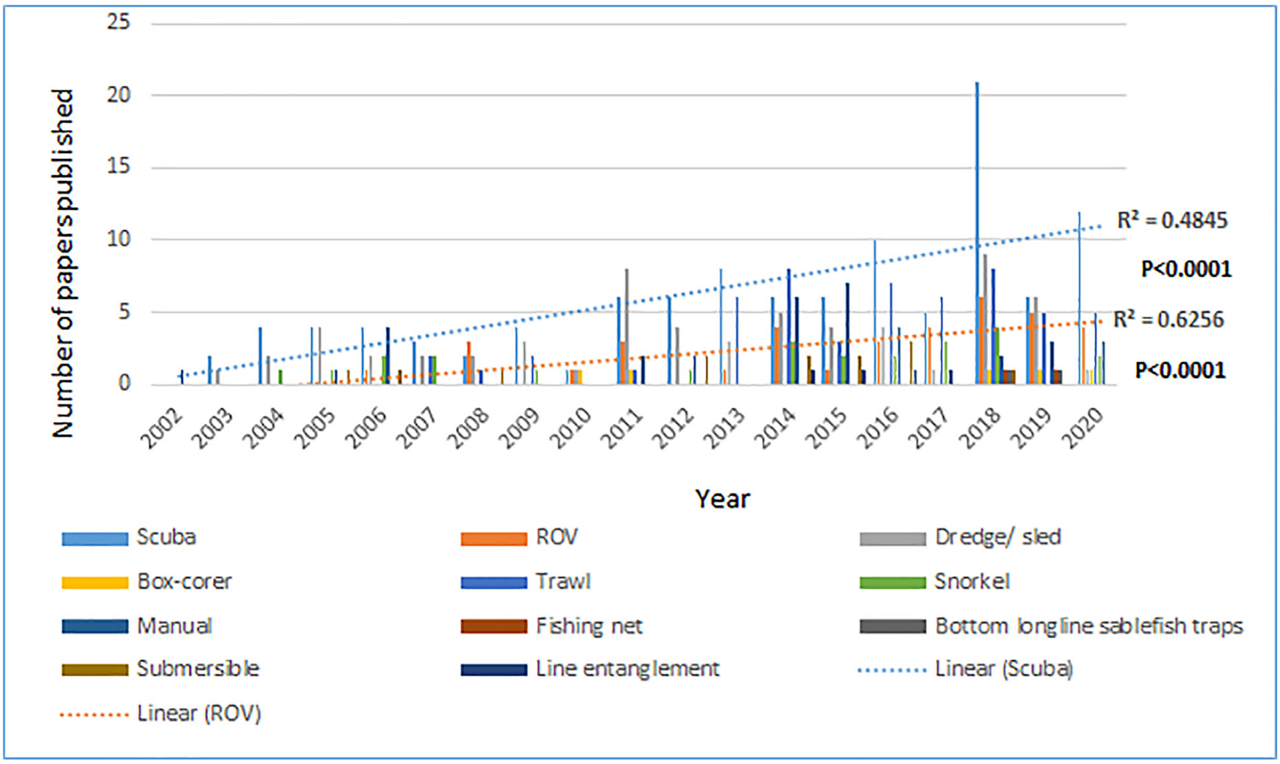

FIGURE 13. Number of papers published on Porifera in *Zootaxa* each year between 2002 and 2020, for each type of collection methods, with linear regression trendlines and analysis of the statistical significance of some of the observed data.

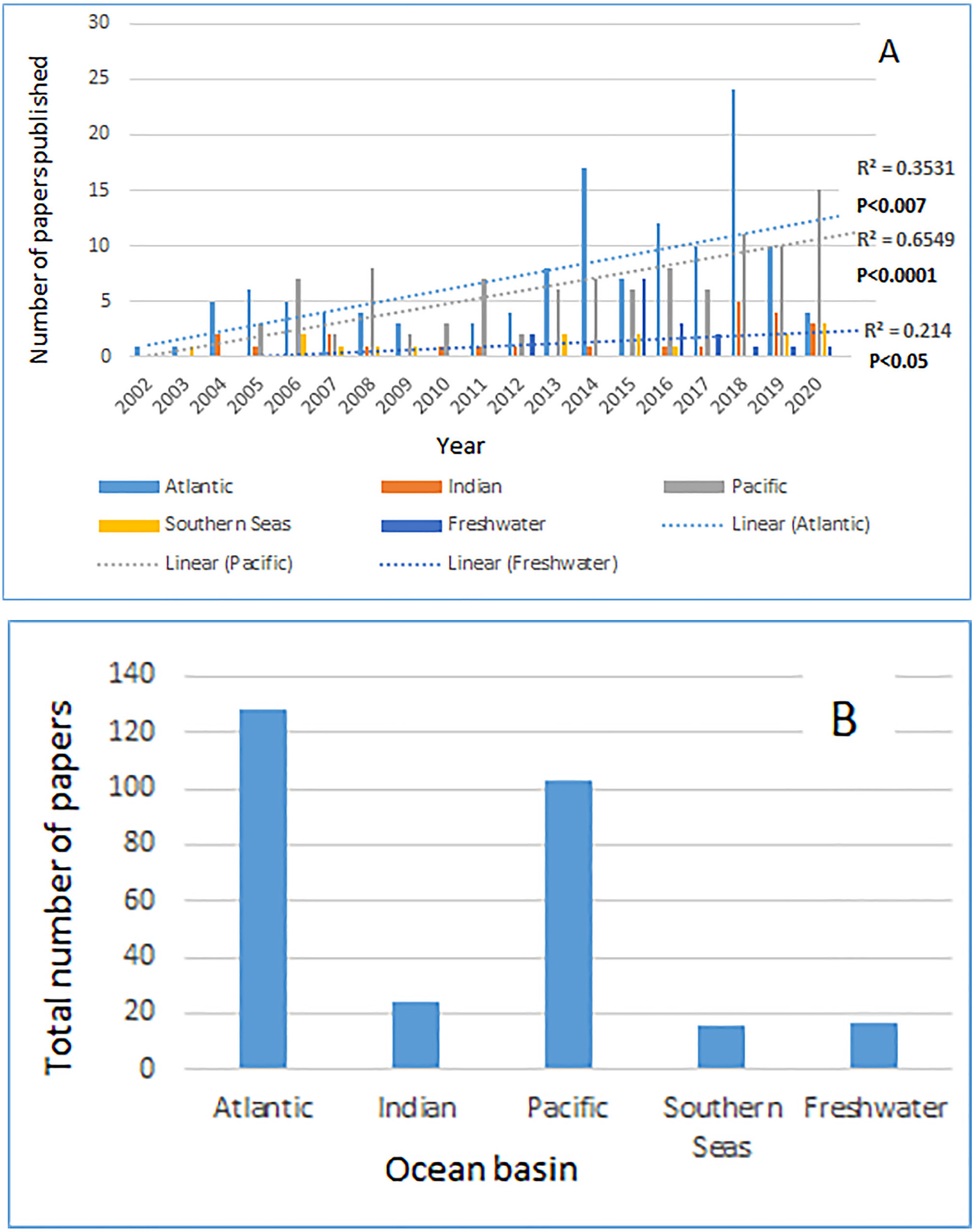

FIGURE 14. Number of papers (A) published for each ocean basin (and freshwater bodies), and (B) total number of papers published on Porifera in *Zootaxa* each year between 2002 and 2020, with linear regression trendlines and analysis of the statistical significance of some of the observed data.

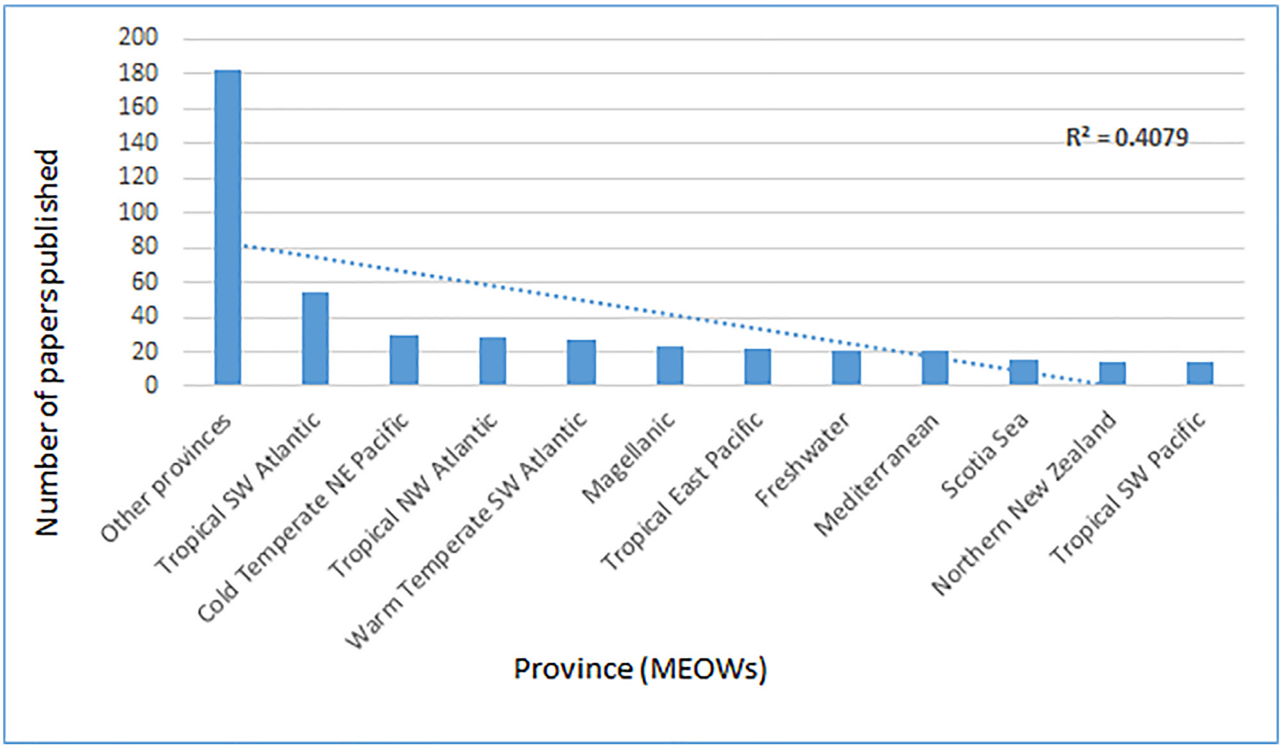

FIGURE 15. Number of papers published on Porifera in *Zootaxa* each year between 2002 and 2020 for the 12 most studied MEOW Provinces, with a linear regression trendline of the observed data.

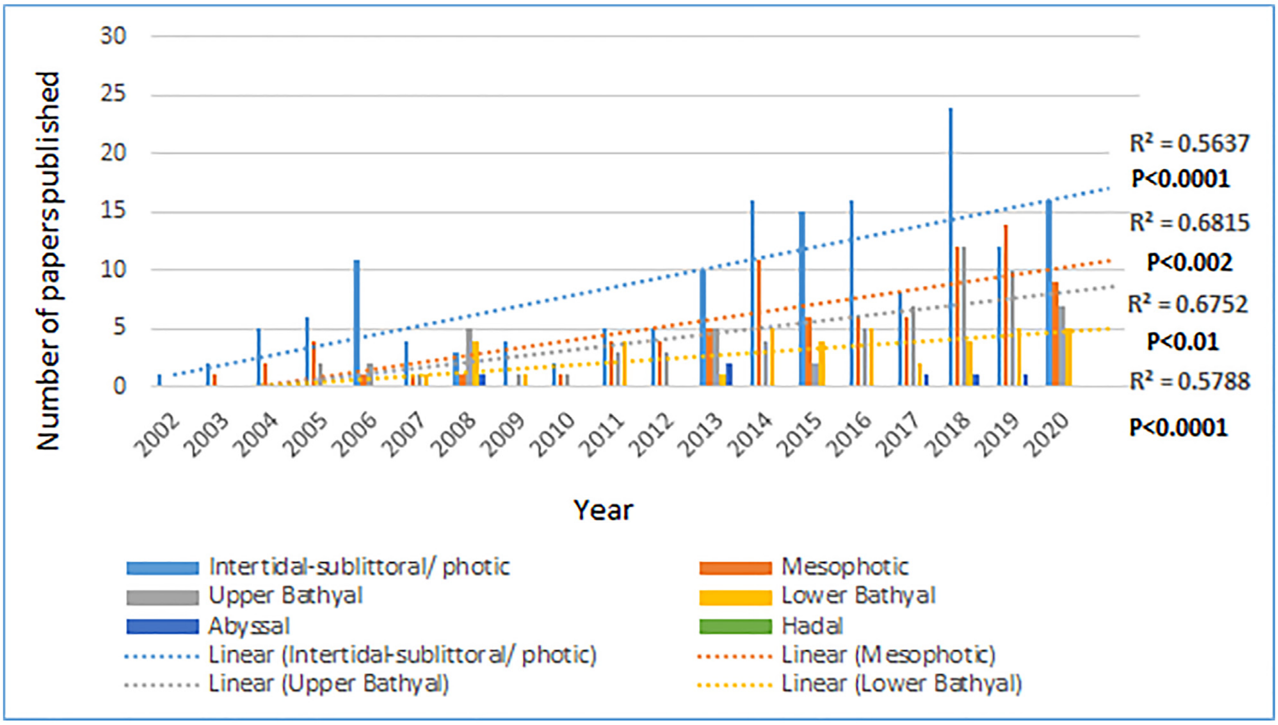

FIGURE 16. Number of papers published on Porifera in *Zootaxa* each year between 2002 and 2020 for each depth zone, with linear regression trendlines and analysis of the statistical significance of some of the observed data.

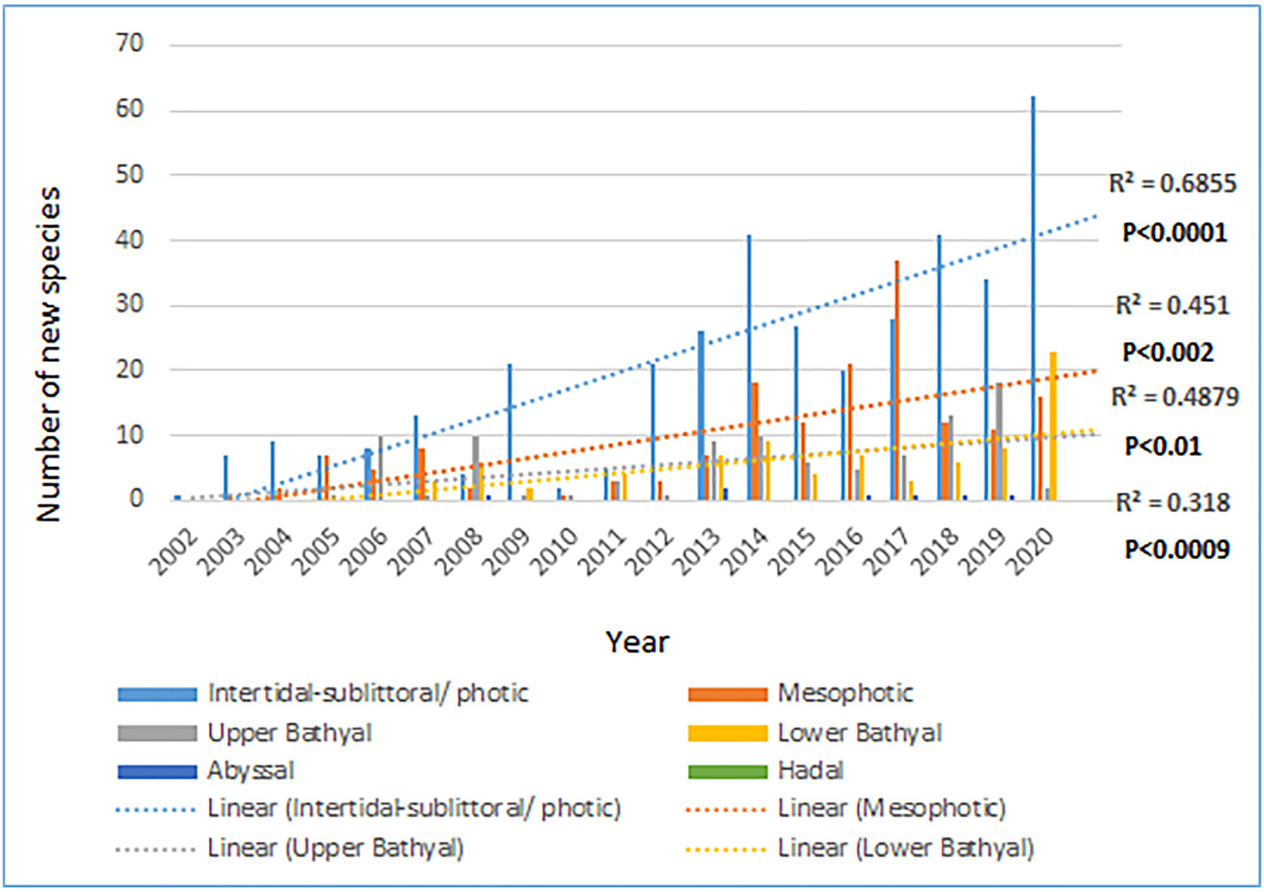

FIGURE 17. Number of new species for each depth zone published on Porifera in *Zootaxa* each year between 2002 and 2020, with linear regression trendlines and analysis of the statistical significance of some of the observed data.

The number of papers published in *Zootaxa* under open access each year remained consistently low (with an average of only 17% of all papers published between 2002 and 2020; Fig. 19). This low number likely relates to the funding situation for authors and their institutions, and is one reason why *Zootaxa* has become the choice for authors without funding for their taxonomic publications. Data on rejection rates of manuscripts submitted to the Porifera Subject Editors was only kept from 2011 up until the present, with an average of 13% of all manuscripts submitted during that period rejected by the Editors, showing a fairly consistent trend over the 10 years of data (Fig. 20).

Our results show the importance of *Zootaxa* for the knowledge on the diversity and distribution of Porifera with significantly increasing output every year. The number of multi-authored papers has also been increasing each year as has the scientific users of these (as demonstrated by the cited 'Clarivate Reference Count' metric), reinforcing that there continues to be an escalated uptake of taxonomic information on sponges published in *Zootaxa* by the scientific community over this period, such as the World Porifera Database, with predictions that this trend will continue to escalate in the future due to rapid electronic publications like *Zootaxa*.

Brazil was the country with the greatest number of authors, papers and description of new species. This is explained by the establishment of several taxonomy oriented research groups over two decades ago and their continued support, which allowed the formation of additional taxonomy groups led by younger scientists.

The greatest number of new species from Brazil also influenced the highest number of new species from the Tropical SW Atlantic. On the other hand, German authors were responsible for the second highest number of publications, but these publications were not related to the number of new species from Germany, showing that they are working on the description of species abroad - spanning from Antarctica, Indo-West Pacific, Northeast and Northwest Pacific, the Red Sea and Gulf of Oman amongst others. The USA was the third country with more authors and the second one with more new species described, followed by Australia. It is clear that more and more countries are contributing to *Zootaxa* every year, which indicates that the number of sponge taxonomists actively publishing seems to be increasing.

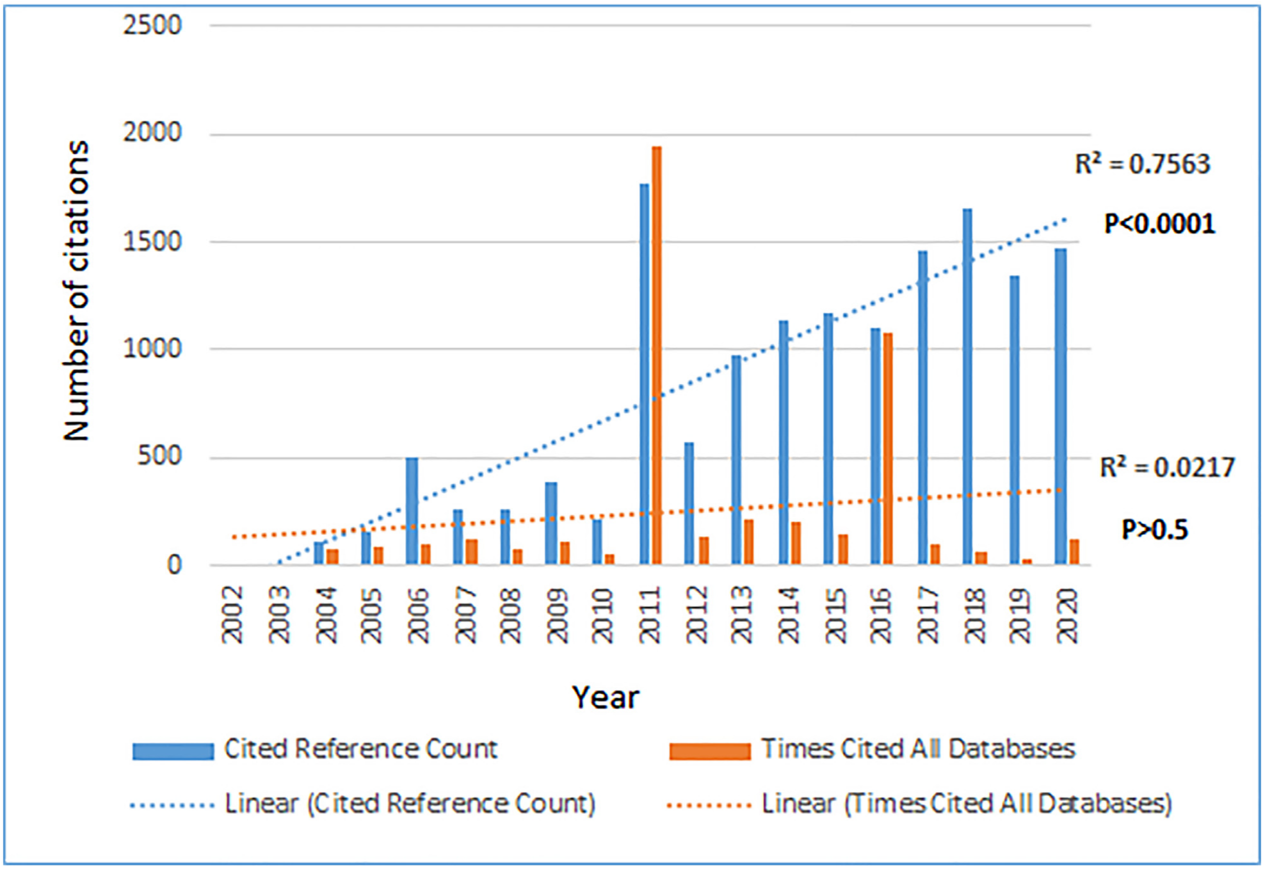

FIGURE 18. Number of citations of papers published on Porifera in *Zootaxa* each year between 2002 and 2020 (based on the 'Cited Reference Count' and 'Times Cited All Databases' metrics from the Clarivate Analytics Web of Science database), with linear regression trendlines and analysis of the statistical significance of the observed data.

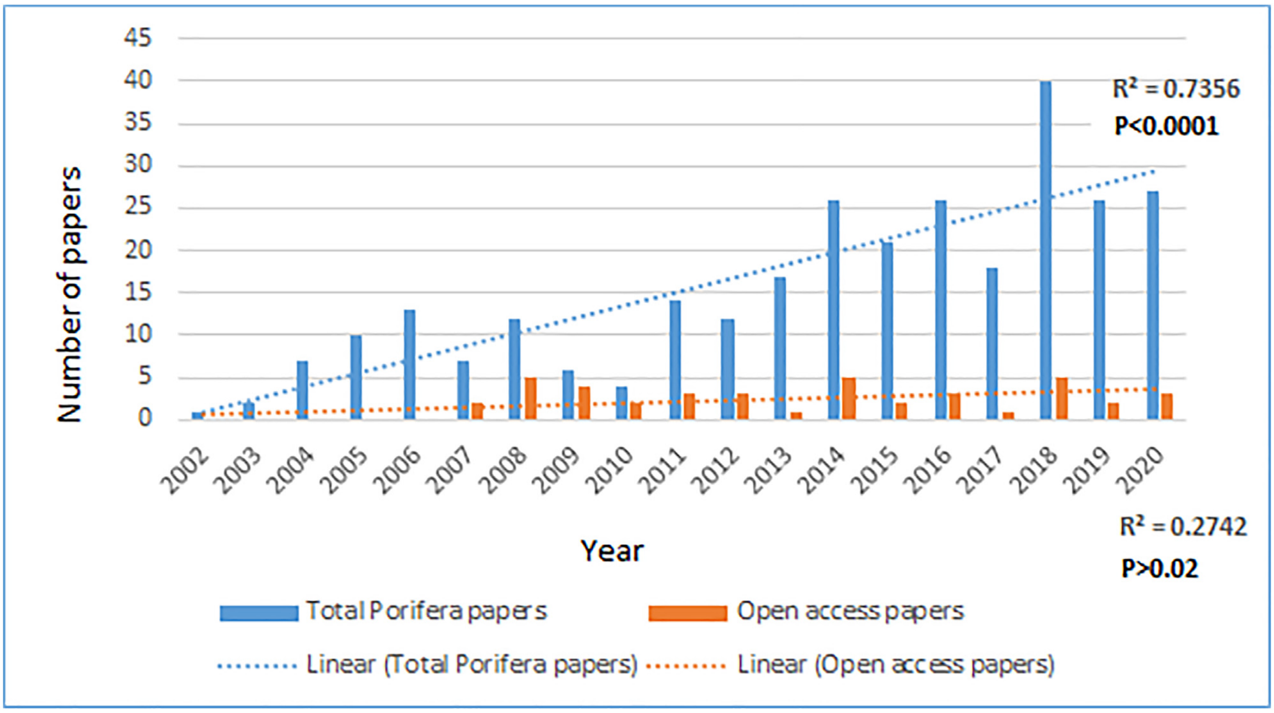

FIGURE 19. Number of all papers published on Porifera in *Zootaxa* each year between 2002 and 2020 compared to the number of these published under open access, with linear regression trendlines and analysis of the statistical significance of the observed data.

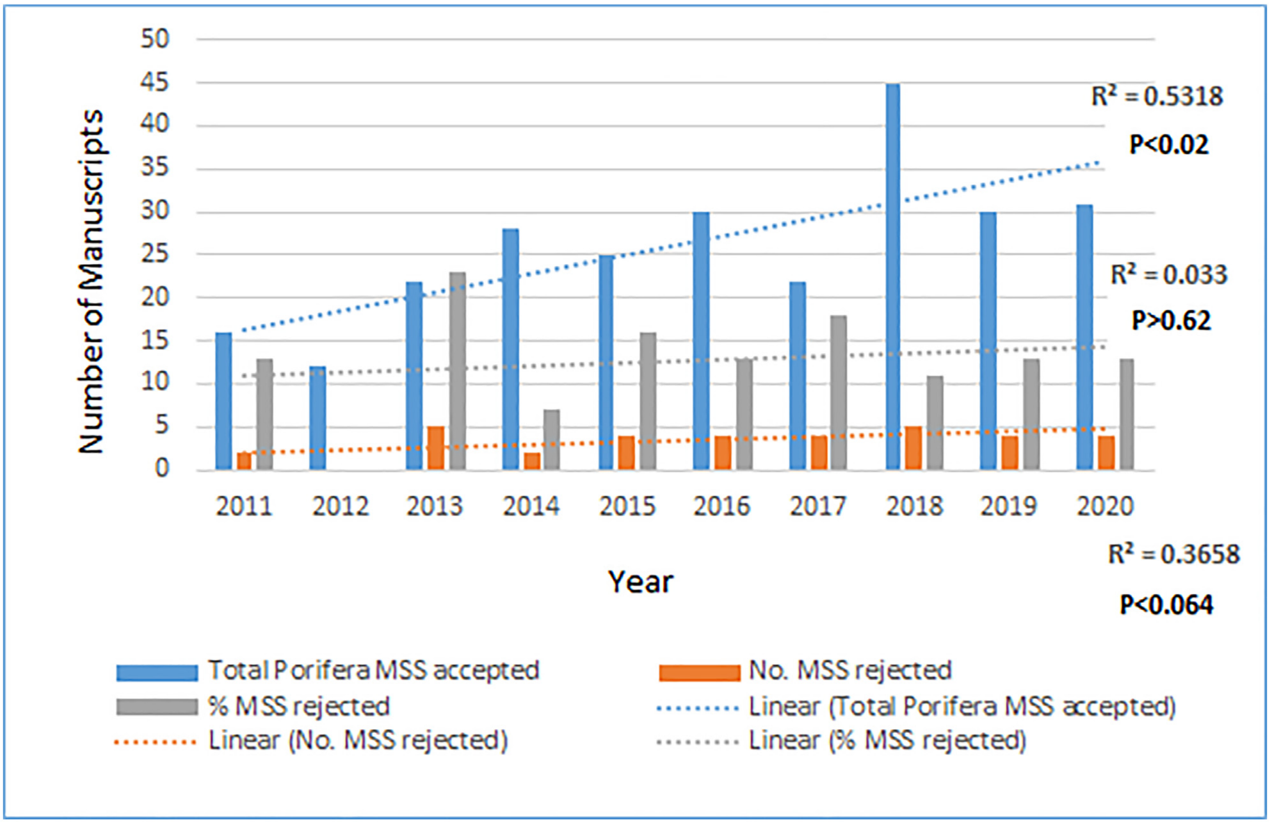

FIGURE 20. Number of manuscripts on Porifera submitted to *Zootaxa* each year between 2011 and 2020 compared to the number and percentage of manuscripts rejected by the Subject Editors, with linear regression trendlines and analysis of the statistical significance of the observed data.

The evolution of taxonomy is clearly observed by the increase over time of better quality papers, i.e. papers with *in situ* and SEM images and molecular phylogenies, with the former metric possibly linked to the rise in the increase of SCUBA and ROVs being used for collections over the decades. The continuous growing number of papers with molecular systematics also shows a trend in Porifera taxonomy as our technologies rapidly evolve to better sample the benthos.

Our results also show the importance of the role of special volumes for *Zootaxa*. Special volumes organised in 2018, 2019 and 2020 were associated with more authors, countries and papers (although they were not necessarily responsible for the description of the highest number of new species, but moreso focussed on special ecosystems etc). In this case, taxonomic monographs seem to be more effective.

All in all, our results indicate that *Zootaxa* has been, and will continue to be, one of the most important vehicles to the description of new species and redescription of already known sponge species. As such it provides an unrivalled platform for the dissemination of taxonomic knowledge. Although taxonomy has unfortunately experienced a decreasing attention over the last decades from academia and its various funding sources, reliable taxonomy remains pivotal for the understanding of biodiversity, evolution, phylogeny and most other aspects of life sciences. Accurate taxonomic knowledge underpins the accurate understanding of biodiversity knowledge, globally.

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