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A decade of population genetics studies of scleractinian corals: A systematic review

Viridiana Alvarado-Cerón [a,***], Aarón Israel Muñiz-Castillo [a], María Geovana León-Pech [b], Carlos Prada [b,**,1], Jesús Ernesto Arias-González [a,*,1]

[a] Departamento de Recursos del Mar, Centro de Investigación y de Estudios Avanzados del I.P.N., Unidad Mérida. Km. 6 Antigua carretera a Progreso, Cordemex, 97310, Mérida, Yucatán, Mexico
[b] Department of Biological Science, University of Rhode Island, 120 Flag Road, Kingston, RI, 02881, USA

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ABSTRACT

Coral reefs are the most diverse marine ecosystems. However, coral cover has decreased worldwide due to natural disturbances, climate change, and local anthropogenic drivers. In recent decades, various genetic methods and molecular markers have been developed to assess genetic diversity, structure, and connectivity in different coral species to determine the vulnerability of their populations. This review aims to identify population genetic studies of scleractinian corals in the last decade (2010–2020), and the techniques and molecular markers used. Bibliometric analysis was conducted to identify journals and authors working in this field. We then calculated the number of genetic studies by species and ecoregion based on data obtained from 178 studies found in Scopus and Web of Science. *Coral Reefs* and *Molecular Ecology* were the main journals published population genetics studies, and microsatellites are the most widely used molecular markers. The Caribbean, Australian Barrier Reef, and South Kuroshio in Japan are among the ecoregions with the most population genetics data. In contrast, we found limited information about the Coral Triangle, a region with the highest biodiversity and key to coral reef conservation. Notably, only 117 (out of 1500 described) scleractinian coral species have genetic studies. This review emphasizes which coral species have been studied and highlights remaining gaps and locations where such data is critical for coral conservation.

1. Introduction

Coral reefs support almost 30 percent of the marine species (Nakabayashi et al., 2019), provide food, habitat, and economic value to millions of people on Earth, and are among the most value ecological, social, and cultural resources in the world (Costanza et al., 1997; de Groot et al., 2012; Spalding and Ravilious, 2002). However, coral reefs cover have been shrinking as a result of natural disturbances, including infectious disease outbreaks, habitat degradation, storm damage, coral bleaching, and predator outbreaks (Kitchen et al., 2019), as well as anthropogenic factors, including ocean acidification and increasing sea levels due to climate change (Shinzato et al., 2014; Quigley et al., 2020; Underwood et al., 2020). Adaptation to these stressors may allow coral species to remain resilient in natural populations; if genetic variation within local populations is maintained and genetic exchanges among populations are facilitated (Matz et al., 2018). Even today, two factors could facilitate rapid adaptation: i) high genetic variation that corals still harbor and, ii) conservation efforts that incorporate an evolutionary approach to coral conservation (Baums et al., 2019). Adding an evolutionary approach using genetic variation during coral conservation and especially restoration facilitates rapid adaptation, allows self-sustaining populations, enhance sexually reproducing, and produce genetically diverse and viable offspring that would allow populations to cope with future unknown environmental variation (Baums et al., 2019).

Extensive conservation efforts are ongoing worldwide, which will be considerably facilitated by the acquisition of genomic data (Kitchen

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[*] Corresponding author.
[**] Corresponding author.
[***] Corresponding author.

E-mail addresses: viridiana.alvarado@cinvestav.mx (V. Alvarado-Cerón), aaron.muniz@cinvestav.mx (A.I. Muñiz-Castillo), mleonpech@uri.edu (M.G. León-Pech), prada@uri.edu (C. Prada), earias@cinvestav.mx (J.E. Arias-González).

[1] These authors contributed equally.

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et al., 2019). One of the advantages of investigating genomic markers further is that many studies have already identified putative markers associated with adaptive traits and critical to the maintenance of natural populations (e.g., Lundgren et al., 2013; Bay and Palumbi, 2014, 2017; Dixon et al., 2015; Kirk et al., 2018; Kitchen et al., 2019). By integrating population genomics and climate change science, predictions can be made using species distribution models (SDMs) and detect the vulnerability of populations to climate change. This integration is done by studying evolutionary processes, such as gene flow, population dispersal, and genomic load (Aguirre-Liguori et al., 2021).

In recent decades, different tools and molecular markers have been developed to assess genetic diversity, genetic structure, and connectivity of a wide range of species and provide powerful tools for population genetics studies (Shinzato et al., 2014). Different molecular techniques have been used in population genetics studies of corals (Vignal et al., 2002; van Oppen et al., 2002; Matz et al., 2018; Parkinson et al., 2019). Genetic markers are used to track DNA variation among or within individuals, populations, or species (Parkinson et al., 2019). The methods used to identify such variations include ranging from Allozyme electrophoresis (Paz-García et al., 2012) to high-throughput sequencing (Cros et al., 2016) and low coverage whole-genome sequencing (lc-WGS) (Fuller et al., 2020). Allozyme identification by electrophoresis (Bonnell and Selander, 1974) was one of the earliest methods in scleractinian corals population genetics (Baums, 2008). In the 1980s, Kary Mullis developed the Polymerase Chain Reaction (PCR), a revolutionary method that measured genetic variation at the DNA level, principally with microsatellites (Hamada et al., 1982) and amplified fragment length polymorphism (AFLP) (Vos et al., 1995; Zabeau and Vos, 1993). Population genetic studies on corals were still few due to the scarcity of population genetic markers (Concepcion et al., 2010). However, in the last decade, the ability to quantify genetic variation in Scleractinia corals has improved enormously with Second generation sequencing technologies (Drury et al., 2016) that include methods of reduced representation of the whole genome sequencing (WGS) such as genotyping by sequencing (GBS), restriction-site associated DNA (RAD) sequencing, and amplicon sequencing (Matz, 2018). With the use of these technologies, genetic variability can be assessed for hundreds, or even thousands, of markers and loci that are highly polymorphic (Williams et al., 2014), e.g., single nucleotide polymorphisms (SNPs). Sequencing of entire genomes of scleractinian corals using Next-Generation Sequencing (NGS) tools enabled us to identify an enormous number of SNPs to study genetic variation among a wide variety of corals species (Fuller et al., 2020; Prada et al., 2016; Shinzato et al., 2011; Ying et al., 2019). It is necessary to identify and recognize the use of different methods, and the state-of-the-art of population genetics in corals. Therefore, a systematic review and bibliographic analysis of existing work on the subject can help us understand the patterns in the knowledge and the areas of opportunity.

The present review is a bibliometric analysis of the scientific journal articles published from 2010 to 2020 related to genetic populations of scleractinian corals. The analysis was based on the Web of Science (WoS) and Scopus data sources. There are four aims of this review: i) identify journals with the most papers focusing on the study of population genetics of scleractinian corals; ii) determine the most studied species and functional groups in this field; iii) identify the molecular techniques and markers used in genetic research for scleractinian corals; and iv) determine the number of population genetics studies by ecoregion, to identify the most studied locations.

2. Materials and methods

2.1. Search strategy

An exhaustive literature search was performed in Web of Science (WOS) and Scopus to track down population genetic studies in scleractinian corals species from 2010 to 2020. The purpose of our study was to collect information since the complete genome of corals was published (Shinzato et al., 2011), at the same time that NGS techniques were developed (Miller et al., 2011a; Concepcion et al., 2010; Ball et al., 2021; Drury et al., 2016; Narum et al., 2013) that enhanced our ability to quantify genetic variation in scleractinian corals (Drury et al., 2016). Previously, genetic studies of corals were rare due to the lack of genetic markers (Concepcion et al., 2010). It is also important to note that genetic advances in population genetics had been described before 2010 (Baums, 2008; Miller et al., 2011a). Therefore, we decided to describe starting in 2010. The following codes were used to the advanced search:

2.1.1. Scopus

TITLE-ABS-KEY (“genotypic diversity” OR “genetic connectivity” OR “genetic differentiation” OR “″genetic variability” OR “population structure” OR “gene flow” OR “Next Generation Sequencing” OR “microsatellite” OR “SNP” OR “microarrays” OR “RadSeq” OR “GBS” OR “LPGS” AND “coral” OR “coral reef” OR “scleractinia”) AND DOCTYPE (ar OR re) AND PUBYEAR >2010 AND EXCLUDE (DOCTYPE, “cp”) OR EXCLUDE (DOCTYPE, “ip”) OR EXCLUDE (DOCTYE,“ed”) OR EXCLUDE (DOCTYPE, “le”)) AND (LIMIT-TO (LANGUAGE, “English”)).

2.1.2. Web of Science

(TS = (“genotypic diversity” OR “genetic connectivity” OR “genetic differentiation” OR “genetic variability”" OR “population structure” OR “gene flow” OR “Next Generation Sequencing” OR “microsatellite” OR “SNP” OR “microarrays” OR “Rad-Seq” OR “GBS” OR “WGS”) AND TS= (“coral” OR “coral reef” OR “scleractinia”))AND LANGUAGE: (English) AND TYPES OF DOCUMENTS: (Article).

2.2. Data management

The articles list extracted from Web of Science and Scopus were exported in BibTex format to identify and eliminate duplicate records using the package Bibliometrix (Aria and Cuccurullo, 2017) in R v 4.0.3 (R Core Team, 2020.). The final list was exported to an Excel database (Microsoft 365, v 2204).

2.3. Selection and data collection process

Two authors carried out a data selection process as follows, only studies performed specifically with scleractinian corals were included. Subsequently, only population genetics studies were selected. The articles without data on diversity index and gene flow into full text were discarded. Disagreements were resolved by discussion with the authors and the reasons for excluding the articles were recorded. We used a guide to extract the data from articles (Table S1).

2.4. Bibliometric analysis

Bibliometrix R-package (Aria and Cuccurullo, 2017) in R v 4.0.3 (R Core Team, 2020) was used to analyze scientific research of population genetics of scleractinian corals from 2010 to 2020. We measured the citation impact of authors, the number of published academic papers, and key journals for the publications in this area.

We also identify the frequency of the keywords used by authors, we choose the most frequent keywords, considering only terms consisting of at least two words, because compound terms offer greater search precision and represent more specifically different terms (Grames et al., 2019). Furthermore, we create a matrix of co-occurrences. To this, it was used the *litsearchr* library functions of R, in which it is possible to extract terms from different automated algorithms.

An analysis was performed to extract the most relevant keywords to identify and analyze the relationship between the most frequent terms present in the keywords used by the authors (Grames et al., 2019). First, terms related to geographic regions or specific reefs areas, species, and taxonomic terms were eliminated to focus on methods and concepts.

Other obvious terms, such as coral reefs, reefs, and corals, were also eliminated. In addition, terms that were synonymous such as Microsatellite, Microsatellites, Microsatellite markers, etc. were standardized using the same terms. To extract keywords and create a matrix of co-occurrences between the identified terms, we used the functions present in the *litsearchr* library of R, in which it is possible to extract terms from different automated algorithms. The network analysis chose only the terms with at least three occurrences and the nodes that represent at least 75% cumulatively of the node strength. According to the recommendations and algorithms described in Grames et al. (2019), these procedures were performed.

2.5. Marine ecoregions

Population genetics studies of scleractinian corals were located in The Marine Ecoregions of the World (MEOW) proposed by Spalding et al. (2007). We created a biogeographic system of population genetic studies of scleractinian corals from this database. This information was represented on a map produced with the QGIS version 3.2.0 (QGIS Development Team, 2018).

2.6. Life-history strategies

We used the classification of Darling et al. (2012) to select life-history strategies of scleractinian corals that have to do with four groups: competitive, weedy, stress-tolerant, and generalist taxa, which are primarily separated by colony morphology, growth rate, and reproductive mode.

We consulted The Coral Trait Database Species website (https://www.coraltraits.org/species) to classify the species studied for each paper. The Coral Trait Database is a compilation of scleractinian coral life-history trait, phylogenetic and biogeographic data (Madin et al., 2016).

3. Results and discussion

3.1. Bibliometric analysis

In the Scopus and Web of Science (WOS) databases screening from 2010 to 2020, 1681 and 1582 studies were found, respectively, for a total of 3263. The results indicate that the databases have different journal coverage, Scopus discovered 99 more studies. Scopus covers a broader range of journals than WOS (Mongeon and Paul-Hus, 2016). About 99.11% of journals listed on the WOS are also listed in Scopus (Singh et al., 2021).

Subsequently, duplicates were eliminated from both databases, that account for a total of 1473 studies remaining. The WOS is among the most complete, reliable, and comprehensive databases for bibliometric analyses and hosts a wide range of quality and high-impact scientific international journals (Ekundayo and Okoh, 2018; Zyoud et al., 2017). In the first screening, 299 studies corresponded only to scleractinian corals, and 178 corresponded to scleractinian corals and population genetics subjects (genetic diversity and gene flow) (Table S2). Hereafter, we only present results of these 178 studies.

It is worth mentioning that other types of documents such as meeting abstracts, theses, proceeding papers, among others, were excluded from this review. The selection of different sources is complex and requires strict procedures (Wang et al., 2014). Nevertheless, this is the first bibliometric study in the last decade about population genetics on scleractinian corals and a baseline in this area for future research. Also, the WOS and Scopus databases have a larger coverage, reliable indexing technology and are well accepted among scientific communities (Ekundayo and Okoh, 2018).

The number of publications each year ranges from 11 to 22 with a mean total of 15 (2.948 SD) articles per year (Table S2). In the last decade, publications on population genetics of the scleractinian corals have remained relatively constant, with no clear trend of increase or decrease in the number of publications (Fig. S1). The papers with the highest number of citations range from 59 (Baums et al., 2010) to 127 (Barshis et al., 2010), with an average per year from 4.92 to 10.58, respectively (Table 1). *Coral Reefs* and *Molecular Ecology* were the main journals that published population genetics studies of scleractinian corals in the last decade (Table 2). *Coral Reefs Journal* is a specialized journal within the International Coral Reef Society that promotes interdisciplinary research, understanding, and management of coral reef systems, experimentation, modeling, quantitative analysis, and applied sciences (https://www.springer.com). *Molecular ecology Journal* includes evolutionary, population genomics, population structure, phylogeography, and conservation studies (https://onlinelibrary.wiley.com). Besides, some of the most recognized Open Access generalist journals, including *PlosOne*, *Scientific Reports,* and *PeerJ*. Other journals specialized in the study of molecular ecology and conservation of resources based on genetic studies were also identified (Table 2).

Keyword analysis showed that *microsatellite, population genetics, gene flow,* and *connectivity* are the terms most frequent in the references considered in this work (Fig. 1a). The terms *microsatellite* and *population genetics* are the centers of the keyword network (Fig. 1b). Network centrality measures the relative importance of nodes within networks and could be viewed as an indicator of their importance and frequency within the keywords used by authors. This centrality is because microsatellites are the most frequently used markers in population genetics studies. Among the most closely related terms in *population genetics* and *microsatellite* are *gene flow* (e.g., Polato et al., 2010; van Oppen et al., 2011; Richards and van Oppen, 2012; Richards et al., 2016; Tisthammer et al., 2020), *connectivity* (e.g., Concepcion et al., 2010; Foster et al., 2012; Ulmo-Díaz et al., 2018), and *conservation* (e.g., Davies et al., 2013; Devlin-Durante and Baums 2017; Drury et al., 2017). Other terms related to *microsatellite* and *population genetics* are *genetic diversity* (e.g., Souter 2010; van Oppen et al., 2015; Huang et al., 2018) and *genetic structure* (e.g., Saavedra-Sotelo et al., 2011; Ladner and Palumbi 2012; Sammarco et al., 2017; Drury et al., 2018; Martinez-Castillo et al., 2018). Also, we have observed that some terms focused on the study of *conservation* are closely related to terms such as *climate change* (e.g., Souter et al., 2010; Serrano et al., 2014; Rose et al., 2018) and *restoration* (e.g., Drury et al., 2016; Devlin-Durante and Baums 2017; Miller et al., 2019). *Connectivity* studies are closely related to the terms *gene flow* and *dispersal* (e.g., Starger et al., 2010; Bongaerts et al., 2011; Lirman et al., 2014; Davies et al., 2015; Rosser et al., 2020; Thomas et al., 2020).

Our results show that molecular markers and population genetics have only been studied in 117 scleractinian coral species. These species represent just the eight percent of 1500 scleractinian coral species (800 zooxanthellate and 700 azooxanthellate) (Kitahara et al., 2016). The branching corals *Acropora* spp. and *Pocillopora* spp., the dominant shallow reef-building corals globally (Veron, 2000), are the most studied

Table 1
Top cited articles in the field of population genetics on scleractinian coral 2010–2020.

Author	Year	Journal	Total citations	Average citations per year
Barshis et al.	2010	Molecular Ecology	127	10.58
Foster et al.	2012	Molecular Ecology	120	12.00
Bongaerts et al.	2010	PlosOne	117	09.75
Pinzón et al.	2011	Molecular Ecology	112	10.18
Bay and Palumbi	2014	Current Biology	94	11.75
Ladner and Palumbi	2012	Molecular Ecology	92	09.20
Pinzón et al.	2013	Journal of Biogeography	82	09.11
Serrano et al.	2014	Molecular Ecology	66	08.25
Baums et al.	2012	Molecular Ecology	64	06.40
Baums et al.	2010	Coral Reefs	59	04.92

Table 2
Key journals for the publications of population genetic on Scleractinian coral.

Journals	Number of articles	Impact factor	H-Index
Coral Reefs	25	3.90	109
Molecular Ecology	22	6.18	225
Plos One	17	3.24	332
Scientific Reports	12	4.13	213
Ecology and Evolution	9	2.91	63
Marine Biology	9	2.57	119
PeerJ	8	2.98	70
Molecular Phylogenetics and Evolution	5	4.28	159
Conservation Genetics	4	2.53	73

genera. *Pocillopora damicornis* has the highest number of studies on population genetics (18 studies) (Fig. 2a), followed by *A. cervicornis* (16 studies), *A. palmata* (14 studies), *A. hyacinthus* (13 studies) and *Montastraea cavernosa* (11 studies) (Table S3). Consequently, the most studied families are Acroporidae, and Pocilloporidae (Fig. 2b). We found that studies per species are based on their role in reefs, abundance, and ecology. *Pocillopora damicornis*, *Acropora cervicornis*, and *Acropora palmata* are the most studied species, the most important hermatypic species in their distribution area, and they are all listed by the IUCN (ABRT, 2005; Aronson et al., 2008; Hoeksema et al., 2014). Furthermore, *A. cervicornis* and *A. palmata* do not represent ecological redundancy, and they contribute significantly to coral reef building and functioning (Baums et al., 2019; Kuffner and Toth, 2016). The most studied species in all coral reefs are found in the Caribbean and the Australian Great Barrier Reef.

The studies in this review include *Cladocora caespitosa*, *Orbicella annularis,* and *Orbicella faveolata*, which are listed as Evolutionarily Distinct and Globally Endangered (EDGE), hence are considered species that contribute significantly to the phylogenetic diversity of the regions and are vulnerable or threatened. EDGE species have few close relatives on the tree of life and are often extremely unusual in how they look, live, and behave, as well as in their genetic make-up (https://www.edgeofexistence.org). *C. caespitosa, O. annularis,* and *O. faveolata* are important reef-building corals and have recently experienced severe population reductions (Casado-Amezúa et al. 2011, 2014; Miller et al., 2018). The pillow coral (*Cladocora caespitosa*), endemic and

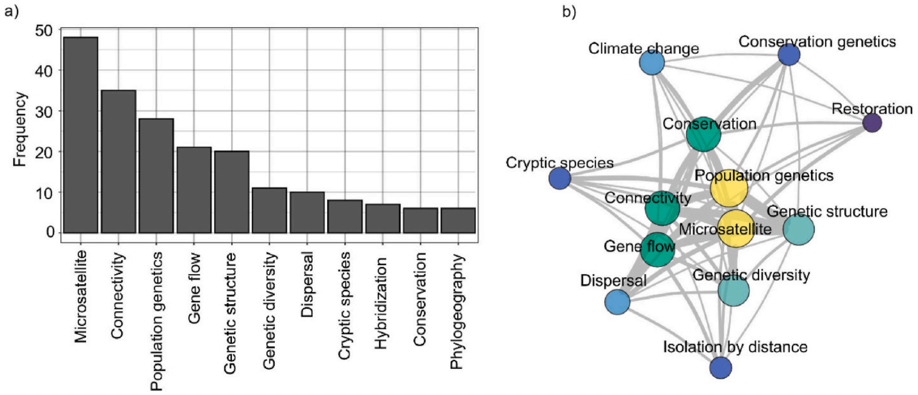

Fig. 1. Keyword analysis. a) The graph shows the terms most frequently used by the authors as keywords in population genetic studies of Scleractinia corals. b) The keyword co-occurrence network shows the most frequent terms associated with each other (the thickness of the links represents the strength of the relationship between the terms, and the size of the modes and their frequency of occurrence in the studies).

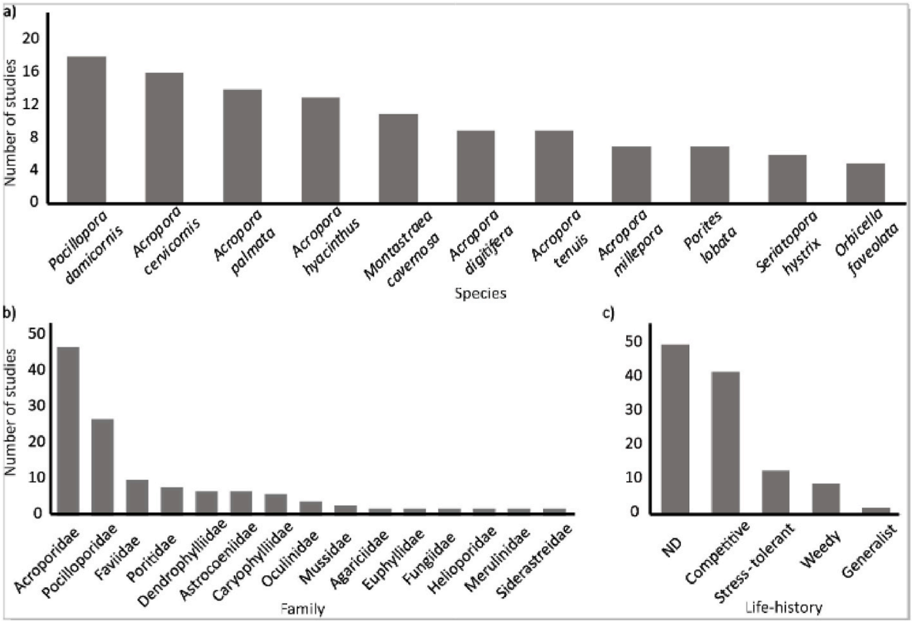

Fig. 2. a) Number of studies per species, only the most frequent species with at least four studies are shown. b) Number of studies per family and c) Number of studies per life-history strategies. Unclassified species were assigned as ND (Not Determined).

endangered, present a regional genetic differentiation among four populations in the Western Mediterranean Sea: Cape Palos (SE Spain), Cala Galdana (Balearic Islands), Columbretes Islands, and L'Ametlla (NE Spain) (Casado-Amezúa et al., 2014). Furthermore, this coral has a relatively low genetic differentiation probably due to a potential barrier to gene flow between the northern and central-southern in the Adriatic Sea (López-Márquez et al., 2019).

Population genetic studies of *O. faveolata* found a local restriction of gene flow in the Caribbean region (Ulmo-Díaz et al., 2018); and exist a strong genetic break around the Mona Passage and within the Mesoamerican Barrier Reef System (MBRS) (Rippe et al., 2017). In the MBRS, *O. faveolata* presents high genetic diversity, low clonality, and low to moderate population structure (Porto-Hannes et al., 2015). Additionally, the genetic diversity signature at Flower Garden Banks suggests its possible function as a downstream genetic sink (Rippe et al., 2017).

In the field of population genetics, we could only find one paper on *Dendrogyra cylindrus* (Chan et al., 2019), a rare species that has become highly threatened in recent years. The most recent stressor on Florida's *D. cylindrus* population is "stony coral tissue loss disease" (SCTLD). Unrecoverable losses of tissue and massive mortality that occurred within the *D. cylindrus,* at the end of 2020 have led to functional extinction of *D. cylindrus* on the Florida Reef Tract (Neely et al., 2021). However, it is important to know the status of this species in other Caribbean regions and it is imperative to include these species in genetic studies. By 2020, the estimated number of surviving genotypes had declined from 181 to 51 with the remaining population assumed to be reproductively extinct and at high risk for regional extinction (Miller et al., 2020).

3.2. Life-history strategies

Among 117 of the scleractinian corals reported in this review, only 67 species (57.26%) were classified using Darling's classification (Darling et al., 2012) and The Coral Trait Database (Madin et al., 2016) systems. Forty-three species were classified as competitive (64.17%), 13 (19.4%) stress-tolerant, 9 (13.4%) weedy, and 2 (3%) generalists (Fig. 2c). Of the 67 classified species, most belong to the genus *Acropora* (47.76%), other four *Acropora* species (*A. muricata*, *A. nasuta*, *A. prolifera,* and *A. sp. 1* (Nakajima et al., 2012)) have not been classified in any life history category.

We found that most studies are done on competitive species. These are species of fast growth, with branching mainly in *Acropora*. Stress-tolerant species are the second most studied. Identifying more stress-tolerant species and studying their population genetics could be of great importance for current coral reef restoration programs, which seek to transplant tolerant species capable of adapting to and surviving climate change. Study weedy corals have a special place in climate change scenarios because they may also survive better than non-weedy corals due to their wide range of traits. Hence, they may be able to colonize a variety of disturbed habitats, such as heavily fished reefs or shallow back reef lagoons (Darling et al., 2012). Generalist species have been poorly studied, despite being important reef builders, such as *Orbicella faveolata*. *Orbicella* species are disease-susceptible, becoming less abundant as disease rates increase, negatively affecting their physical protection. More disease-resistant species might colonize these lost reef spaces but are less efficient reef builders, which makes disease susceptibility an important predictor of the changing ecological function of Caribbean reefs (MacKnight et al., 2021).

Life history traits would promote genetic differentiation and demographic independence among populations or stablish connectivity on large scales (León-Pech et al., 2015). For example, in sessile species, the earliest stages of life larval dispersal capability affect genetic connections (Costantini et al., 2017; Nunes et al., 2011). Genetic studies allow investigating larval processes when direct observations cannot be used (Costantini et al., 2017). In genetic population studies, incorporating life histories provides information on the distribution of alleles among marine populations. These studies are crucial to determine the extent of genetic connectivity and genetic diversity among populations which are vital for monitoring their health and resilience (Afiq-Rosli et al., 2021; Costantini et al., 2017). In addition, life history also influences susceptibility to diseases, such as white plague disease (MacKnight et al., 2021). For optimizing these studies, molecular markers with a particular emphasis on the "next-generation" DNA sequencing technologies are essential. Hence, we emphasized that fifty species (42.73%) are not included in Darling's classification and Coral Trait Database (Table S3). We highlight the importance of incorporating more species into Coral traits life history classifications.

3.3. Molecular markers and techniques

Fourteen molecular techniques and twenty night markers (16 nuclear markers, 11 mitochondrial markers, and 2 Enzyme systems) were identified in the population genetics studies of scleractinian corals (Tables 3 and 4). Parkinson et al. (2019) identified 127 papers on the topics of "coral" and "biomarker" from 1997 to 2019, it showed that citations exceeded growth in publications, suggesting that interest is outpacing research on developing these tools.

At least 120 (67.41%) population genetic studies in scleractinian corals have been carried out with microsatellite markers in the last decade, compared to 22 studies (12.35%) with single nucleotide polymorphisms (SNPs) markers recorded in this review (Table 4). Despite the advantages of SNPs and recent advances in whole-genome sequencing, microsatellites continue to excel in the study of population genetics of scleractinian corals (e.g., Liu et al., 2020; Oury et al., 2020; Parker et al., 2020; Rosser et al., 2020; Sturm et al., 2020; Torres et al., 2020; Yetsko et al., 2020). Microsatellites were discovered in the '80s, and they became popular in the scientific community. They are relatively simple tools to develop highly reproducible (de Amezúa Ayala 2012), and still, many researchers use them.

Unlike SNP's markers, microsatellites have been developed extensively since their discovery (Litt and Luty, 1989; Weber & May 1989). Because of their high mutation rate and polymorphism, these regions of the genome have been widely used to estimate population connectivity, clonal structure and genetic diversity at different biogeographical scales (Adjeroud et al., 2014; Nakajima et al., 2016; van der Ven et al., 2016; Liu et al., 2020). In the first decade of the 2000s, research efforts focused on developing microsatellites for several species of scleractinian corals. Maier et al. (2001) developed the first microsatellite markers in the coral *Seriatopora hystrix* (Pocilloporidae). Since then, the number of studies,

Table 3
Molecular techniques used for the study of population genetics in scleractinian corals.

Molecular technique and DNA sequencing	Year	Autor
Restriction site-associated 2b-RAD	2012	Wang et al.
Genotyping by sequencing (GBS)	2011	Elshire et al.
Diversity Arrays Technology (DArT)	2010	Diversity Arrays Technology
Low coverage whole-genome sequence (lc-WGS)	2009	Kulathinal et al.
Restriction site Associated DNA sequencing (RADseq)	2007	Miller et al.
Pyrosequencing	1993	Nyren, Petersson and Uhlen
Amplified Fragment Length Polymorphisms (AFLPs)	1993	Zabeau and Vos
Paired-end shotgun sequencing	1991	Caskey
Microarray	1983	Chang
Microsatellite	1982	Hamada et al.
Restriction Fragment Length Polymorphism (RFLP)	1978	Sir Alec Jeffreys
Beginning of DNA sequencing	1977	Sanger
Shotgun sequencing	1979	Staden
Allozyme electrophoresis	1974	Bonnell and Selander

Table 4
Molecular markers used for the study of population genetics in scleractinian corals.

Molecular marker type	Marker	Number of studies
Nuclear (16)	Microsatellite	120
	ITS (Internal transcribed spacer)	25
	SNPs (Single Nucleotide Polymorphisms)	22
	β-tubulin (gen)	5
	Pax-C (intron)	4
	CaM (Calmodulin)	3
	Mini-collagen (intron)	3
	ATPsα (adenine triphosphate synthesis-α intron)	2
	Exons	2
	ATPsβ (adenine triphosphate synthesis-β intron)	1
	CAH 3/550	1
	H2 (histone)	1
	SRP54 (intron)	1
	r28S	1
	SNV (Single Nucleotide Variant)	1
	RAD-Tag	1
Mitochondrial (11)	CR (Control Region)	14
	ORF (open reading frame region)	12
	COI (cytochrome oxidase)	8
	D-loop	3
	IGR (noncoding intergenic region)	3
	NAD5	3
	r16S	2
	CYB (Cytochrome B)	1
	HSP70 (heat shock protein 70 gene)	1
	NAD3	1
	COX1 (cyclooxygenase)	1
Enzyme systems (2)	EST (esterase)	1
	GDH (glutamate dehydrogenase)	1

including microsatellite markers, has increased (Table S4). A technical inconvenience with microsatellites is their isolation and development costly; they are not transferable to other species outside the genus level (de Amezúa Ayala 2012). Also, it is not always possible to compare data produced by different laboratories due to the eventuality of inconsistencies in allele size calling (Vignal et al., 2002).

After microsatellites, SNPs became the most popular markers and were considered the markers “of the future” (Liu 2007). SNPs have been noticed since DNA was sequenced back in 1977; but they were not used as markers for two decades because of inefficient genotyping technologies (Liu 2007). Therefore, its application boomed with the advent of Next-Generation Sequencing (NGS) tools. NGS molecular tools for SNPs identification have allowed to obtain complete genomes or loci from different species in many samples and more detailed analyses in population genetics studies (Eguiarte et al., 2013; Narum et al., 2013; Prada et al., 2016). An important advantage of SNPs markers is that they have a high resolution to detect differentiation within and between populations, also the genetic diversity of threatened populations of scleractinian corals (Devlin-Durante and Baums, 2017; Drury et al., 2016; Elshire et al., 2011). An example is the study of *A. cervicornis*, using SNPs markers to identify population structure within the Florida Reef System (Willing et al., 2012) where microsatellite markers did not detect it (Baums et al., 2010).

Kitchen et al. (2020) developed a high-resolution hybridization-based genotype array to co-analyze host and symbionts of two Caribbean *Acropora* species, based on bi-allelic single nucleotide polymorphisms (SNPs) markers (~30k SNPs). Analytic tools to produce multi-locus genotypes of hosts were combined in a workflow called the Standard Tools for Acroporid Genotyping (STAG). The STAG workflow and database are contained within a customized Galaxy environment (https://coralsnp.science.psu.edu/galaxy/). Acroporids can be genotyped using a subset of the SNPs loci and additional markers enable the detection of symbionts. However, this type of tool does not allow the identification of new variants.

Unlike microsatellites, for which genotyping is standardized with PCR amplification and sizing, many approaches have been considered for SNPs genotyping (Liu 2007; Vignal et al., 2002). SNPs can be genotyped with a wide range of techniques and instrumentations, from small-scale, low-budget to expensive high-throughput systems (Liu 2007).

Several Second-generation sequencing techniques have been used for the development of microsatellites in scleractinian corals, including the 454 sequencing technique (Dubé et al., 2017), 454 GS-FLX Titanium pyrosequencing platform (Addamo et al., 2015), Illumina MiSeq (Liu and Cheng 2018; Nakajima et al., 2017; Shinzato et al., 2014), Illumina TruSeq (Yang et al., 2018), ABI PRISM 3730 DNA Sequencer, and Applied Biosystems (Davies et al., 2013; Liu and Cheng 2018; Serrano et al., 2014). The 3730 line was developed to meet the demands of high-throughput sequencing and genotyping projects. High-throughput sequencing techniques are powerful tools for isolating new markers in genomes that had not been sequenced before (Addamo et al., 2015; Martin et al., 2010).

Second-generation sequencing techniques stand out in recent years, including methods of reduced representation of the whole genome such as RAD-seq (Baird et al., 2008), ddRAD-seq (Peterson et al., 2012), 2b-RAD (Wang et al., 2012), and GBS (Elshire et al., 2011). Hundreds to thousands of SNPs representing 1–5% of the genome can be found using these techniques (Mahler 2018). Restriction site associated DNA markers sequencing (RAD-seq) combines the use of re-striction enzymes to cut DNA into fragments (as for RFLPs and AFLPs), and the use of molecular identifiers (MID) to associate sequence reads to particular individuals (Davey and Blaxter 2010). RAD-seq is a genetic analysis method for detecting single nucleotide polymorphisms (SNPs) and it is particularly useful for genotyping when a reference genome is not available. (Andrews et al., 2016; Baird et al., 2008). Several species have been studied using this approach including *Porites lobata* and *Porites compressa* (Forsman et al., 2017), *Oculina patagonica* (Leydet et al., 2018), *Pocillopora damicornis, P. eydouxi* and *P. elegans* (Combosch and Vollmer 2015).

Scleractinian corals have been studied using the following techniques that are modifications of the original RAD-seq technique: 2b-RAD y GBS. 2b-restriction site-associated DNA (2b-RAD) is a streamlined restriction site-associated DNA (RAD) genotyping method based on sequencing the uniform fragments produced by type IIB restriction endonucleases (*Bsa*XI or *Alf*I) (Wang et al., 2012). This technique has been used for the study of *Montastraea cavernosa* (Sturm et al., 2020), *Leptopsammia pruvoti* (Boscari et al., 2019) and *Acropora palmata* (Devlin-Durante and Baums 2017).

Genotyping-by-sequencing (GBS) is a variation of RAD-seq that modulates the barcode composition using degenerate nucleotides and methylation-resistant restriction endonucleases to avoid repetitive regions of the genome, thus increasing the depth of the sequencing in low copy number regions (López de Heredia 2016). *Isopora brueggemanni*, *Acropora digitifera* (Thomas et al., 2020); *Acropora cervicornis* (Drury et al., 2016, 2017, 2018), *Montastraea cavernosa* (Drury et al., 2020) were studied with this technique.

Diversity Arrays Technology (Kilian et al., 2012) is similar to RADseq and is a widely applied approach for exploring population genetic structure in species that lack genome assemblies (Thomas et al., 2017; Underwood et al., 2020). DArT is assaying for the presence (or amount) of a specific DNA fragment in a representation that is derived from the total genomic DNA of an organism or a population of organisms (Jaccoud et al., 2001). This technique has been used for the study of *Acropora spathulata* (Quigley et al., 2020), *Acropora aspera* and *Isopora brueggemanni* (Underwood et al., 2020), and *Pocillopora damicornis* (Thomas et al., 2017).

Low-coverage whole genome sequencing (lc-WGS; for example, 0.5–6x coverage) has emerged as a powerful and cost-effective approach for population genomic studies in both model and non-model species (Lou et al., 2021). Lc-WGS has higher power in detecting single nucleotide polymorphisms (SNPs) than sequencing a smaller number of individuals at high coverage depth (Cheng et al., 2014). This technique has been used to sequence the complete genome of *Acropora millepora* (Fuller et al., 2020) and *Orbicella faveolata* (Prada et al., 2016).

Third and Fourth-generation technologies have already been applied to studying coral-associated microbiomes. PacBio sequencing, also referred to as SMRT (Single Molecule Real Time) sequencing, has been used to assess the population structure and diversity of bacterial populations associated with *Porites lutea* (Pootakham et al., 2019). In several families of scleractinian corals, Oxford Nanopore Technologies (Fourth-generation) has been used for molecular characterization of coral hosts and associated microbial assemblages (Carradec et al., 2020).

Cooke et al. (2020) used shallow whole-genome resequencing to identify genomic signatures. Additionally, they generated the complete genome reference for *Acropora tenuis* based on PacBio long-read sequencing (Third-generation). We did not find studies using fourth-generation sequencing methods on the genetics of scleractinian coral populations. This gap opens a window to explore genetic studies of scleractinian corals with these new techniques.

In addition to these markers, several other markers are historically used in studies of scleractinian coral population genetics. The ITS region of the nuclear ribosomal DNA and the 5.8S gene are the most extensively used in phylogenetic studies of scleractinian coral species (Fukami et al., 2004; de Amezúa Ayala 2012). Considering the existing hybridization between species of corals (van Oppen et al., 2001; Vollmer and Palumbi 2004; de Amezúa Ayala 2012) and the extremely high levels of intra and inter-individual diversity of these multi-locus markers complicate their interpretation in a population genetic context (Márquez et al., 2003). However, population studies with these markers are still being developed in scleractinian corals. In this review, we found twenty-five studies performed with the ITS region. The most recent were done in *Goniocorella dumosa, Madrepora oculata, Solenosmilia variabilis* (Zeng et al., 2020), *Porites lobata* (Tisthammer et al., 2020), *Porites lutea* (Huang et al., 2018), *Porites sverdrupi* (Martinez-Castillo et al., 2018), *Seriatopora* (Sinniger et al., 2017).

As for mitochondrial markers, the Control Region (CR) has been used to assess *Pocillopora acuta* (Torres et al., 2020), *Orbicella faveolata* (Ulmo-Díaz et al., 2018), *Seriatopora hystrix* (Underwood et al., 2018). Open reading frame region (ORF) has been widely used in scleractinian corals as *Pocillopora acuta* (Nakajima et al., 2018) and *Seriatopora* (Sinniger et al., 2017) (Table 4). Other mitochondrial markers that have been highly relevant in this field are 16S in *Desmophyllum dianthus* (Miller et al., 2011b; Addamo et al., 2012), cytochrome *b* in *Acropora* spp. (Robert et al., 2019; van Oppen et al., 1999) and cytochrome oxidase subunit I (COI) in *Oculina patagonica* (Leydet and Hellberg 2015), *Porites lobata* (Hellberg et al., 2016) and *Platygyra verweyi* (Keshavmurthy et al., 2012).

Also, sequences from a limited number of introns have been used to address speciation and hybridization questions like mini-collagen in *Acropora* spp. (Hatta et al., 1999); *Acropora prolifera* (Vollmer and Palumbi, 2002) and *Acropora solitaryensis* (Suzuki and Fukami, 2012) Molecular relationships between several species of *Acropora* have been evaluated using the PaxC intron (Rosser, 2016; van Oppen et al., 2001). The calmodulin (CALM) gene and the alpha subunit of the ATP synthase complex (ATPSα) have been used to analyze of genetic diversity and differentiation of *Acropora austera* and *Platygyra daedalea (*Montoya-Maya et al., 2016). However, some of these markers (mini-collagen, PaxC, calmodulin and CR) have low intrapopulation variability, making them impractical for studying gene flow and clonal structure (Baums et al., 2005).

In the last decade, early sequencing techniques such as Alloenzymes are still being used in some species such as *Pocillopora damicornis* and *Porites panamensis* (Paz-García et al., 2012). This technique has been widely used since the 1980s and 1990s to study the population structure and connectivity of reef-building corals in Indo-Pacific species as *Pocillopora damicornis* (Stoddart 1984; Ayre et al., 1997); *Seriatophora hystrix*, (Ayre and Dufty 1994), *Mycedium elephantotus* (Yu et al., 1999); *Goniastrea aspera* (Nishikawa and Sakai 2003), *Acropra millepora* (Smith-Keune and van Oppen 2006); Caribbean corals *Acropora palmata*, (Zubillaga et al., 2008), and some coral species in South Africa as *Pocillopora verrucosa* (Ridgway et al., 2001). This technique does not require a priori knowledge of the species' genome under study since metabolic enzymes common to most organisms are used, which makes the method cost-effective (de Amezúa Ayala 2012; van Oppen et al., 2002). However, the need for preserving fresh tissue in liquid nitrogen makes its use impractical, considering the often-remote settings of coral reefs. Hense, a single copy, variable, DNA-based, nuclear markers is required (Baums et al., 2005).

3.4. *Marine ecoregions*

The 178 studies on scleractinian coral population genetics were in 97 of the 232 ecoregions proposed by Spalding et al. (2007) (Fig. 3a; Table S5). Although, coral species are distributed only in 150 marine ecoregions (Veron et al., 2015). The ecoregions with the highest number of studies were Florida (25 studies), South Kuroshio (23 studies), and Greater Antilles (22 studies) (Fig. 3b). The Caribbean Sea was the most genetically studied region (Fig. 3). Other regions have been historically studied in coral taxonomy and biogeography like Australia and the Indo-Pacific (Veron 1986; Veron and Marsh 1988; Veron and Science, 1993; Veron 2008), the Philippines (Veron and Hodgson 1989) and Japan (Veron et al., 1992). However, these regions did not show the highest density of genetic studies (Fig. 3).

Coral Triangle (CT), the region with the highest diversity of coral species in the world (Hoegh-Guldberg et al., 2009), with 627 coral species in total (Veron et al., 2009), comprised 17 studies in 9 ecoregions, each with one to four population genetics studies (Fig. 3; Table S5). Within the Western Coral Triangle, the Sulawesi Sea/Makassar Strait is the most studied ecoregion (e.g., Umar et al., 2019a; 2019b; Jompa et al., 2020; Rosser et al., 2020). The early coral biogeography focused on the Indian Ocean, presumably because knowledge of the existence of the Coral Triangle was revealed in the 1990s, a relatively recent development. (Veron et al., 2015). This may explain the few studies in the world center of coral diversity. There is also a general concern about the quality of data in biogeographic publications. Therefore, they do not include most studies relevant to the Coral Triangle, any species revealed by molecular techniques, or any fieldwork undertaken within the past 15 years (Veron et al., 2015). Additionally, the Sulu Sea, Sunda Shelf, and Java Sea have recently been added to the TC, which contain several unidentified species (Veron et al., 2015). It is worth noting that, being the region with the greatest diversity of corals in the world, this has not been addressed in terms of genetic diversity, highlighting the importance of future genetic research in this area.

Veron (2013) divides the historical study of corals into faces: 1) museum-based studies of coral collections, 2) in-situ studies using scuba, and 3) currently, genetic and molecular studies. The latter is related to climate change (e.g., Souter et al., 2010; Serrano et al., 2014; Rose et al., 2018; Nakabayashi et al., 2019; Parker et al., 2020) and phylogeny studies (e.g., Addamo et al., 2012; Palumbi et al., 2012; Suzuki and Nomura 2013; Johnston et al., 2017; Mao et al., 2018; Colín-García et al., 2020). Genetic approaches are currently used to provide useful or even necessary information to support efforts to conserve aquatic organisms (Umar et al., 2019b). Future developments in coral biogeography will increasingly take in the molecular determination of species (Veron et al., 2015). Molecular studies will therefore be particularly informative about the diversity of ecoregions, especially those of high latitudes (Veron et al., 2015). For example, among the species studied in the Mediterranean region are *Oculina patagonica*, *Cladocora caespitosa* and *Astroides calycularis*, although coral reefs do not characterize the region. *Oculina patagonica* had been considered an invasive species from

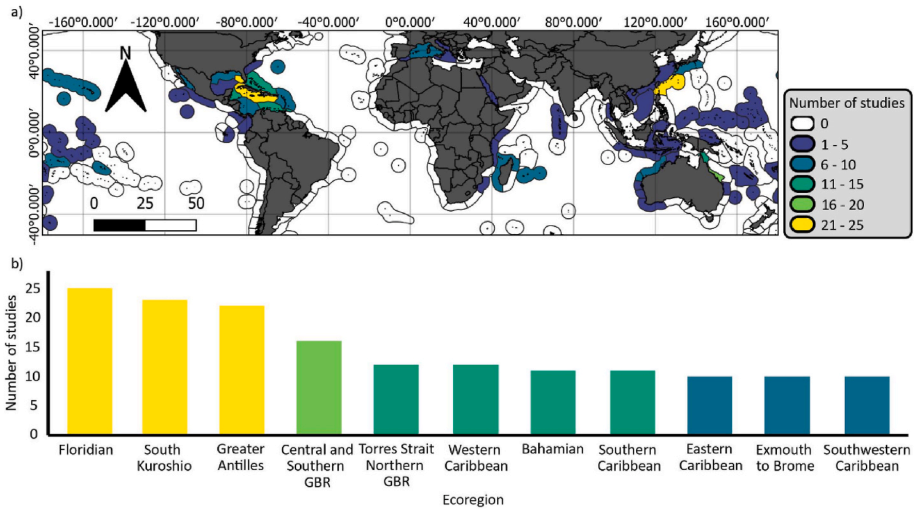

Fig. 3. a) Population genetics studies are shown, based on a color scale, in the different ecoregions. Coral reef regions in yellow have the most genetic studies, while coral reef regions in purple have less than five studies. b) The graph shows the 11 ecoregions with the highest number of population genetics studies (10–25 studies).

the Atlantic. However, RAD-seq revealed genetic changes in the coral *Oculina patagonica* associated with range expansion along the Spanish Mediterranean coast (Leydet and Hellberg 2015).

4. Conclusions

Our results suggest that microsatellites continue to be the most widely used markers, although there has been a significant increase in NGS studies. In addition, of the 1500 species of scleractinian corals, only 117 have been studied for population genetics. The two most studied ecoregions are those in the Caribbean Sea and the Great Barrier Reef. Critically, the Coral Triangle, a region with high diversity and relevance for conserving coral reefs, has very few genetic studies.

We also found that the most studied aspects are genetic structure, gene flow, connectivity, and genetic diversity. Genetics has also been addressed in connection with conservation and climate change. From 2010 to 2020, the knowledge contribution to the subject has been constant, although no increase has been observed. We found that the most studied species are those of the genus *Acropora* and *Pocillopora,* with a marked dominance. These two genera are important shallow reef builders in the Caribbean and Pacific, respectively. Many of the species studied have not been catalogued within any functional group. Finally, we also observed that there is a need for information on rare species that may be at high risk of extinction, such as *Dendrogyra cylindrus*. Hence, scientists will have to work on genetic/genomic research and multidisciplinary research to continue contributing to our understanding of coral reefs, their ecology, and their conservation.

4.1. Population genetics of coral species: a decade of advances and future directions

Our study highlighted the lack of population genetics studies on the 90% species of the scleractinian corals, life-history strategies, and biogeography. There is a notable gap in information at the Coral Triangle, despite being the epicenter of marine biodiversity. There are other marine ecoregions with little or no genetic research on Scleractinia corals, such as the Eastern Philippines, Northeastern New Zealand, the Gulf of Thailand, and Cocos Islands. Population genetics supports biogeography studies in terms of diversity, allowing biogeographic characterization and ecoregion delimitation. Further, genetic variation can contribute to the knowledge of life history strategies and is important in adaptive potential information. Even so, sequencing technologies have increased, and very few species are studied with second-generation technologies, particularly with SNP markers. There are currently 3rd and 4th technologies being developed that we did not have in 2010. In addition, genetic studies must be conducted with other species, especially endangered species that have a significant role in the ecosystem, to ensure their conservation. Due to coral reef degradation worldwide, genomic information is crucial to conservation programs. Moreover, it is crucial to overcome the biggest challenge of communication between geneticists, bioinformatics and stakeholders in the conservation and restoration of coral reefs to achieve self-sustainability from a genomic and evolutionary perspective.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2022.105781.

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