Ocean and Coastal Management 276 (2026) 108111

Contents lists available at ScienceDirect

Ocean and Coastal Management

journal homepage: www.elsevier.com/locate/ocecoaman

An unseen threat to coral reef biodiversity: the international trade of live corals for the aquarium industry as reflected by CITES records (1990–2021)

Bert W. Hoeksema[a,b,*]

[a] Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA, Leiden, the Netherlands
[b] Groningen Institute for Evolutionary Life Sciences, University of Groningen, P.O. Box 11103, 9700 CC, Groningen, the Netherlands

ARTICLE INFO

Keywords:
Biodiversity threat
CITES trade database
Coral cultivation
Coral fisheries
Coral harvesting

ABSTRACT

The Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) has been keeping annual trade records of live stony corals (Scleractinia) since 1990. On a global scale, CITES data can be used as indicators for trends in the popularity of particular species. A maximum global trade record of $3.1{\cdot}10^6$ wild-caught corals was reported for the year 2007, which declined to less than 50% ($1.4{\cdot}10^6$) in 2021. Indonesia was the leading exporting country until 2018, being replaced by Fiji in 1996–1998 and 2000–2001. Australia has been the dominant exporter of wild-sourced corals since 2018, which was facilitated by Indonesia's declining export quotas and by temporary export bans by Indonesia and Fiji. Indonesia has been the main exporter of cultivated corals since 2005 with an annual global trade record of nearly $0.6{\cdot}10^6$ specimens for 2017. The USA always had the highest import records. *Acropora*, consisting of branched colonies with small polyps, was the most-traded coral genus worldwide ($3.4{\cdot}10^9$ specimens from 1990 to 2021). Corals with large fleshy polyps, such as *Trachyphyllia geoffroyi* ($1.5{\cdot}10^6$ specimens), *Catalaphyllia jardinae* ($1.0{\cdot}10^6$), *Euphyllia glabresens* ($0.9{\cdot}10^6$), *Fimbriaphyllia ancora* ($0.7{\cdot}10^6$), and *Heliofungia actiniformis* ($0.7{\cdot}10^6$) were the most-traded species in that period. Harvesting of corals rich in associated fauna may affect coral reef diversity at a larger scale, particularly if these corals are inhabited by host specialists. Since not much research has been done on the impact of selective fisheries on wild coral populations, there is a risk of overfishing popular species, especially those that are not much cultivated. Therefore, better monitoring of coral harvesting is needed and coral cultivation should be stimulated. Stricter trade quotas and bans may be needed as precautionary measures to counteract negative impacts of coral fisheries on reef biodiversity.

1. Introduction

Despite continuing conservation efforts, coral species are globally threatened owing to the worldwide decline of coral reefs (Carpenter et al., 2008; Riegl et al., 2009). Various publications report on large-scale coral mortality and its causes, such as rising seawater temperatures (Hughes et al., 2018; McManus et al., 2020), strong tropical storms (Harmelin-Vivien, 1994; White et al., 2013; Hernández-Delgado et al., 2024), coral diseases (Morais et al., 2022; Burke et al., 2023), coral predators (Scott et al., 2017; Miller et al., 2025), sedimentation (Erftemeijer et al., 2012; Duckworth et al., 2017), pollution (Dubinsky and Stambler, 1996; Ouédraogo et al., 2023), lost fishing gear (Ballesteros et al., 2018; Mehrotra et al., 2024a), and destructive fisheries (Edinger et al., 1998; Fox et al., 2003). The long-term effects of these threats are clearly visible by the increasing presence of dead coral skeletons and fragments, quantifiable as dead coral cover. Such coral loss not only affects corals themselves but also other reef organisms that depend on them (Munday, 2004).

There is one threat to reef corals that has not received much attention in the recent scientific literature, i.e., the marine ornamental trade in the international aquarium industry (Pavitt et al., 2021). This trade was discussed more frequently in older studies (Wood and Wells, 1988; Green and Shirley, 1999; Bruckner, 2001; Jones, 2008; Tissot et al., 2010; Wood et al., 2012) and was valued at hundreds of millions of US dollars over 20 years ago (Green and Hendry, 1999; Bruckner, 2000; Wabnitz et al., 2003). The general public and most scientists in source countries may not be aware of coral fisheries because coral harvesting does not happen in plain sight. Also, not many people may visit aquarium shops and companies that export corals to see what is offered for sale. They may not be interested to know more about the aquarium trade

* Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA, Leiden, the Netherlands.
E-mail address: bert.hoeksema@naturalis.nl.

https://doi.org/10.1016/j.ocecoaman.2026.108111
Received 18 June 2025; Received in revised form 24 January 2026; Accepted 26 January 2026
Available online 11 February 2026

because keeping a tropical seawater aquarium is complex and requires much money, dedication, knowledge and skill from the owner or care taker (Delbeek and Sprung, 1994, 1997). Only a small portion of wild-sourced corals is intended for domestic markets while the majority will be exported to other countries.

Besides, in contrast to the threats mentioned earlier, harvesting of corals for the aquarium industry does not leave dead skeletons behind. Since most reef corals live attached to dead coral rock (Sheppard, 1981), collecting them will be forceful and may result in reef damage (Harriott, 2003; Bruckner, 2003) without leaving any evidence of its cause. Coral harvesting will result in the loss of live coral cover and the vacant spots will just contribute to the overall dead coral cover. Reef-health surveys in which live and dead coral cover are compared (e.g. Mumby et al., 2004; Cleary et al., 2008; 2014; Polónia et al., 2015) are not species-specific and therefore not useful as indicator of coral harvesting and biodiversity loss. Ideally, areas were coral harvesting takes place should be monitored annually for its effects on coral populations, but this rarely happens (Harriott, 2003). A time-efficient way to estimate changing densities of fished coral species would be the application of video transects (Carleton and Done, 1995; Kayal et al., 2023; Akmal et al., 2025), which allows storage and reanalyzing of raw data by scientists not personally involved in the *in situ* recording. Another way to look for possible effects of overharvesting in coral fisheries would be to determine size-class frequencies of exploited coral populations (Knittweis and Wolff, 2010), but this would require time-consuming coral-size measurements.

An indirect way to study developments and trends in live-coral harvesting is by analyzing international trade records that report on the annual import and export numbers of coral species by countries. These records are reported by Parties to the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) of taxa listed in the CITES Appendices and published in the CITES Trade Database (CITES Secretariat and UNEP-WCMC, 2022). The purpose of CITES is to help in the prevention of overexploitation of natural populations of species in the international trade in order to ensure their survival in the wild. Starting with 17 genera in 1985 and the addition of all other genera in 1989, stony corals of the order Scleractinia have been listed in CITES Appendix II (Wells and Barzdo, 1991), which concerns “species that are not necessarily presently threatened with extinction but may become so unless trade is closely controlled” (CITES Secretariat, 2025a). At present 184 parties have joined CITES, consisting of 183 countries plus the European Union (EU) (CITES Secretariat, 2025b).

CITES is used as a legal instrument in the international trade of wildlife through the requirement of export and import permits. Although, it is logistically challenging and expensive to ship live corals by airfreight over long distances (Sosnowski et al., 2020), merchants still import corals illegally with the risk of confiscation and becoming fined. In the USA, over 90% of seized corals appeared to come from the four most important source countries: Indonesia, Tonga, Australia, and Fiji (Petrossian et al., 2020). Illegal imports may lack appropriate permits or may contain coral specimens that were misidentified, possibly without the importer being aware of that.

CITES also has the task of monitoring international trade of wildlife (Bruckner, 2001; Foster et al., 2016). Effective reporting of coral trade data started in 1990 (Pavitt et al., 2021). Other popular groups of marine aquarium species that have been listed in CITES Appendix II are giant clams since 1985 (Mies et al., 2017; Vogel and Hoeksema, 2024) and seahorses since 2004 (Foster et al., 2016, 2022; Koning and Hoeksema, 2021).

The aim of the present study is to use CITES’ international trade data from 1990 to 2021 to obtain quantitative information as an indicator of how much the international aquarium industry poses a potential threat to particular reef coral species that are popular among aquarists and which are the possible consequences for reef coral biodiversity in the countries where these corals are exploited. The data are also used to find out which exporting and importing countries have been playing dominant roles in the coral trade over this period. This information is important for seeing which part they take in the aquarium industry and how this can be relevant in policy-making, like the establishment of quotas and trade bans. A study in Singapore revealed that consumers and retail sellers have limited knowledge of the provenance of the corals available in the trade (Tan et al., 2025). The present study may help to create awareness among consumers, retailers, marine park managers, and other stakeholders about the possible ecological impact of coral harvesting in the absence of reliable field assessments.

A distinction is made between corals that are reported as wild-caught and corals that have been cultivated. This may show whether coral cultivation could serve as an alternative to coral fishing, and which coral species are most suitable for this. Finally, an overview is presented of much-traded species and their role as hosts for associated species, in order to demonstrate their importance for coral reef biodiversity and how the loss of these particular host-coral species may lead to the loss of additional fauna. This mainly concerns corals with large, fleshy polyps, which are particular popular in the coral trade (Green and Shirley, 1999; Delbeek, 2001a). In the aquarium industry such coral are termed LPS (large-polyp scleractinians) with a polyp diameter over 5 mm, as opposed to small-polyp scleractinians (SPS) with smaller sizes (Bradley et al., 2022).

Previous studies that partly or entirely dealt with the international trade of live corals are not up-to-date anymore, covering much shorter time spans and a limited number of taxa (Green and Shirley, 1999; Bruckner, 2001; Wabnitz et al., 2003; Jones, 2008; Tissot et al., 2010; Wood et al., 2012; Pavitt et al., 2021). Others only focused on one major exporting country, such as Indonesia (Raymakers, 2001, 2002), or an important importing country, such as the USA (Blundell and Mascia, 2005; Rhyne et al., 2012; 2017; Petrossian et al., 2020) or the relationship between one exporting country, such as Indonesia, and one importing country, the Netherlands (Janssen and Blanken, 2016).

The purpose of the present study is to present for the first time an overview of changes in the international trade of live corals over three decades, highlighting the most important taxa, most dominant exporting countries and major importing countries. It also serves to give insight in the magnitude of coral harvesting in the absence of first-hand knowledge on its threat to coral reef biodiversity.

The present study is unique because:

1) it presents data covering from the year 1990, when trade in scleractinian corals started to be reported by CITES, until the last year, 2021, for which all species reports were completed at the time of the analysis;
2) it compares data on wild-caught and cultivated corals in this period;
3) it presents trade trends of the most prominent importing and exporting countries;
4) it discusses the ecological importance of popular coral taxa in coral reef biodiversity;
5) it highlights popular coral taxa in need of conservation management.

2. Material and methods

All scleractinian corals are CITES-listed. Since their taxonomy is traditionally based on skeleton morphology, species distinction of live corals may be difficult (Bruckner, 2001). Therefore, most live corals are allowed to be reported at genus level in export documents with the exception of the genera *Euphyllia*, *Physogyra*, and *Plerogyra*. These have to be reported at species level because supposedly they can more easily be distinguished by a combination of their skeleton and polyp morphologies (CITES SecretariatUNEP, 2002; 2013; Bradley et al., 2022).

At present, the CITES nomenclature of scleractinian corals (UNEP-WCMC, 2012; 2025a; 2025b; UNEP-WCMCa and CITES Secretariat, 2025b) is about 25 years out of date in comparison with the science-based and continuously updated World List of Scleractinia of WoRMS, the World Register of Marine Species (Hoeksema and Cairns, 2025). Both systems mention taxonomic synonyms, which enables cross-referencing between the two databases when taxonomic names differ for certain genera and species. Thus, mismatches in reporting between importing and exporting countries can be compensated by linking synonyms. For example, when the CITES-listed species name *Scolymia australis* is entered in WoRMS, it shows that this name is a superseded combination because it moved to another genus and should now be named *Homophyllia australis*. On the other hand, when the valid name *Homophyllia australis* is entered in search windows of CITES websites, the outdated combination name *Scolymia australis* is also shown. The effects of altered genus names may become less transparent when coral taxa are reported at genus level, involving genera consisting of a number species that are popular in the aquarium trade.

Trade data of scleractinian taxa was obtained from the CITES Trade Database (CITES Secretariat and UNEP-WCMC, 2022; UNEP-WCMC and CITES Secretariat, 2025c), which was facilitated by use of the tool CITES Wildlife TradeView (UNEP-WCMC and CITES Secretariat, 2025a). CITES trade data are reported on an annual basis with number of specimens as unit. The year range 1990–2021 has been selected because before 1990 reporting of the trade in live corals was not substantial and for after 2021 the data was not yet completely available during the study. In analyses comparing exporting countries, importer-reported numbers were used, coming from many countries, rather than exporter-reported numbers, which are from only one country and risk more bias. Importer-reported numbers and exporter-reported numbers can show large differences, depending on the exporting country (Pavitt et al., 2021; EMS Figs. S2.1–S2.2).

An overview is presented of the reporting of wild-caught corals (source code "W") by the six most important exporting countries (Australia, Fiji, Haiti, Indonesia, Tonga, Solomon islands) and 13 most important importing countries. Data on cultivated corals was added for Indonesia only, which was by far their most important producer for this category. Depending on the importing country, the source of cultivated corals was reported as "captive-bred" (source code "C") or "born in captivity" (source code "F"), whereas they are actually maricultured by asexual reproduction through fragmentation or cutting (Bradley et al., 2022). Since, cultivated corals are mostly reported as "F" (Wood et al., 2012), this code is used in the rest of this study, also for the less than 2% that were reported as "C". For convenience, wild-caught corals are also referred to as "W-corals", and cultivated corals as "F-corals".

Thus, trade data through CITES Wildlife TradeView was accessed by filtering the following variable entries: taxon name, year range, source (either code "W" or codes "C" + "F"), and exporter-reported/importer-reported. The following fixed filters were used: unit (as numbers of specimens), origin (direct), trade term (live, coded "LIV"), purpose (commercial, code "T"). The output presented the numbers for the top exporting and top importing numbers. By entering taxon name "Scleractinia", a ranking of top-traded species and genera was given. To analyze trade of species and genera over the whole period of 1990–2021, only importer-reported data were used as these proved to be more reliable by covering many different sources instead of one. Information in graphs is presented as accurate data in ESM Tables S1.1–S1.12.

3. Results

3.1. Decadal trade records with popularity ranking

Nearly 50 million scleractinian coral specimens have been traded worldwide in the period 1990–2021 (Table 1). Most of them were sold in the 2nd decade, 2001–2010. A large majority of the exported coral taxa are from Indo-Pacific countries. Since trade in species is easier to discuss than trade in multi-specific genera, because species within a genus may differ in geographic range and ecological trait, both taxon levels are evaluated separately.

Acropora is by far the most-traded coral genus, with import records over three million. Live *Acropora* corals are sold as small-polyp scleractinians (SPS), like *Montipora* (#4), *Porites* (#10), and some species of *Turbinaria* (#7). The other multi-specific genera consist of species with large polyps. *Goniopora* is the second-most popular coral genus, with over 2 million imports in 32 years (1990–2021). All genera represent attached colonial species, with the exception of *Fungia* (#6) and *Scolymia* (#8), which consist of free-living solitary species.

Table 1
Import records of all live wild-caught scleractinians (numbers in millions) and 15 most-traded taxa reported at genus level (numbers in thousands), following CITES nomenclature, over the period 1990–2021 and by decade. Bold-printed numbers indicate maximum decadal records.

		1990–2021	1991–2000	2001–2010	2011–2020
	All Scleractinia	Imports 10^6	Imports 10^6	Imports 10^6	Imports 10^6
		49.4	13.4	**19.9**	14.7
	Coral genus	Imports 10^3	Imports 10^3	Imports 10^3	Imports 10^3
1.	*Acropora*	3440.8	342.6	**1843.3**	1174.6
2.	*Goniopora*	2290.0	403.2	**1094.3**	694.4
3.	*Lobophyllia*	895.6	103.3	338.6	**400.6**
4.	*Montipora*	787.6	40.8	**573.5**	155.8
5.	*Acanthastrea*	733.4	0	80.2	**556.4**
6.	*Fungia*	695.8	47.7	253.8	**344.8**
7.	*Turbinaria*	601.1	102.3	**320.4**	170.3
8.	*Scolymia*	561.0	19.9	80.8	**394.7**
9.	*Favites*	521.9	41.3	**253.8**	200.5
10.	*Porites*	517.5	85.5	**293.6**	129.7
11.	*Caulastraea*	487.2	52.6	**228.4**	192.8
12.	*Favia*	369.6	41.4	105.4	**188.9**
13.	*Tubastraea*	304.5	77.1	104.2	**108.9**
14.	*Echinophyllia*	223.3	0	23.2	**172.4**
15.	*Platygyra*	197.9	11.8	64.1	**104.6**

Taxonomic updates not yet accepted in the CITES nomenclature of Table 1 are: #3: *Lobophyllia* now contains species of *Symphyllia*, with which it was merged (Huang et al., 2016); #5: *Acanthastrea* including *A. bowerbanki*, now *Homophyllia bowerbanki*, and *A. lordhowensis*, now *Micromussa lordhowensis* (Arrigoni et al., 2016); #6: most *Fungia* species moved to the genera *Cycloseris*, *Danafungia*, *Lithophyllon*, *Lobactis*, and *Pleuractis* (Gittenberger et al., 2011); #7: *Turbinaria* including *T. peltata*, now *Duncanopsammia peltata* (Baird and Thomson, 2018); #8: *Scolymia* including *Scolymia australis*, now *Homophyllia australis* (Huang et al., 2016); #11: some *Caulastraea* species moved to *Astraeosmilia* (Arrigoni et al., 2021); #12: most Indo-Pacific species of *Favia* moved to *Dipsastraea* (Huang et al., 2014).

All popular taxa reported at species level have large, fleshy polyps (Table 2). *Trachyphyllia geoffroyi* and *Catalaphyllia jardinae* have over one million specimens sold within the period 1990–2021. The other species with single, large polyps are *Heliofungia actiniformis* (#5), *Homophyllia australis* (#10), and *Cynarina lacrymalis* (#13). The other species are colonial.

Examples of genera sold predominantly in the second decade (2001–2010) are *Heliofungia actiniformis*, *Goniopora stokesi*, *G. lobata*, and *Euphyllia cristata*. These were mostly exported from Fiji and Indonesia. Typical species showing maximum trade records during the last decade (2011–2020), more than twice as much than in the previous decade, are *Homophyllia australis*, *Micromussa lordhowensis*, *Duncanopsammia axifuga*, *Fimbriaphyllia paraancora*, and *Blastomussa wellsi.* These species were mostly exported from Australia and were traded much less during the first decade or not at all, thus showing large raises in import records and reaching the top 15 of most-traded species despite their later and shorter availability.

Taxonomic updates not yet accepted in the CITES nomenclature but presented in Table 2 are: #4: *Euphyllia ancora* is now *Fimbriaphyllia ancora* (Luzon et al., 2017; Arrigoni et al., 2023); #10: *Scolymia australis* is now *Homophyllia australis* (Huang et al., 2016); #11: *Acanthastrea lordhowensis* is now *Micromussa lordhowensis* (Arrigoni et al., 2016); #14:

Table 2
Import records of live wild-caught corals of the 15 most-traded scleractinian taxa reported at species level (numbers in thousands) over the period 1990–2021 and by decade. Bold-printed numbers indicate maximum decadal records. Genera with only one species in the trade are also included.

	Coral species	1990–2021	1991–2000	2001–2010	2011–2020
		Imports 10^3	Imports 10^3	Imports 10^3	Imports 10^3
1.	*Trachyphyllia geoffroyi*	1476.9	279.2	559.8	**566.7**
2.	*Catalaphyllia jardinei*	1037.4	269.8	286.3	**425.7**
3.	*Euphyllia glabrescens*	857.8	13.6	314.3	**442.3**
4.	*Fimbriaphyllia ancora*	709.9	6.8	262.1	**379.3**
5.	*Heliofungia actiniformis*	693.7	167.9	**329.0**	175.2
6.	*Plerogyra sinuosa*	474.2	3.1	**224.6**	223.9
7.	*Goniopora stokesi*	456.2	18.5	**262.3**	165.3
8.	*Goniopora lobata*	405.4	37.4	**230.2**	131.5
9.	*Euphyllia cristata*	382.8	7.5	**237.1**	128.1
10.	*Homophyllia australis*	345.6	0	23.4	**279.3**
11.	*Micromussa lordhowensis*	312.2	0	28.7	**246.4**
12.	*Duncanopsammia axifuga*	265.7	0	26.1	**207.9**
13.	*Cynarina lacrymalis*	215.7	2.7	70.4	**119.3**
14.	*Fimbriaphyllia paraancora*	215.2	0	6.6	**146.8**
15.	*Blastomussa wellsi*	199.8	0.4	45.9	**131.5**

Euphyllia paraancora is now *Fimbriaphyllia paraancora (*Luzon et al., 2017; Arrigoni et al., 2023); #15: *Blastomussa wellsi* now includes the new species *B. vivida* (Benzoni et al., 2014).

3.2. Annual trade records

Annual global trade numbers over the years 1990–2021 are presented for all scleractinians together, comparing wild-sourced corals with cultivated ones. All small-polyp scleractinians (SPS) are reported at genus level, and most large-polyp scleractinians (LPS) are reported at species level. If a popular species belongs to a multi-specific genus and is not reported at species level, trade in this particular species may strongly determine the import numbers of this genus. In the following paragraphs detailed analyses are presented of taxa that are popular in the trade, representing either SPS or LPS corals.

3.2.1. All scleractinians

The global trade in wild-sourced corals had its first strong increase in sales between 1993 and 1998, after which its decreased and showed two more peaks, with a maximum record of over $3{\cdot}10^6$ in 2007 (Fig. 1). Since then the numbers started to drop, although with fluctuations, and more or less stabilized under $1.5{\cdot}10^6$. This decline coincided with a raise of trade in cultivated corals, which peaked in 2017, just above $0.5{\cdot}10^6$. In 2019, there was a dip for both wild-sourced corals and cultivated corals, when Indonesia had an export ban.

The most prominent export countries over the period 1990–2021 showed successions in ranking (Fig. 2). Most countries exported corals from the Indo-Pacific. For wild-sourced corals (Fig. 2A), Indonesia started as most important exporter and was succeeded by Fiji, which was replaced by Indonesia again, and finally by Australia. Fiji showed a peak of nearly $1.85{\cdot}10^6$ in 1998 and Indonesia a maximum of about $1.72{\cdot}10^6$ in 2007. Australia started exports in 2005 and dominated the exports after 2017 by a strong rise, while the other countries moderated their exports. Australia's maximum export of $1.14{\cdot}10^6$ corals was reached in 2020. Tonga and Solomon Islands were less important exporters with annual trade records remaining below $0.20{\cdot}10^6$. Haiti was the only major exporter of Caribbean corals, mainly from 2000 until 2014, with a maximum of $0.64{\cdot}10^6$ in 2004.

The export of cultivated corals was always less (Fig. 2B), with a short-lasting important role by Fiji in 2008, showing a maximum of $0.50{\cdot}10^6$, and in 2009. Indonesia started exports in 2008 and dominated the export market since 2009, with a peak of $0.57{\cdot}10^6$ in 2017, except when it had an export ban in 2019. Haiti was again the most important exporter in the Caribbean, mainly from 2003 to 2011, with a small peak of $40.6{\cdot}10^3$ in 2005.

In the world market, the decreasing trade in Indonesian W-corals

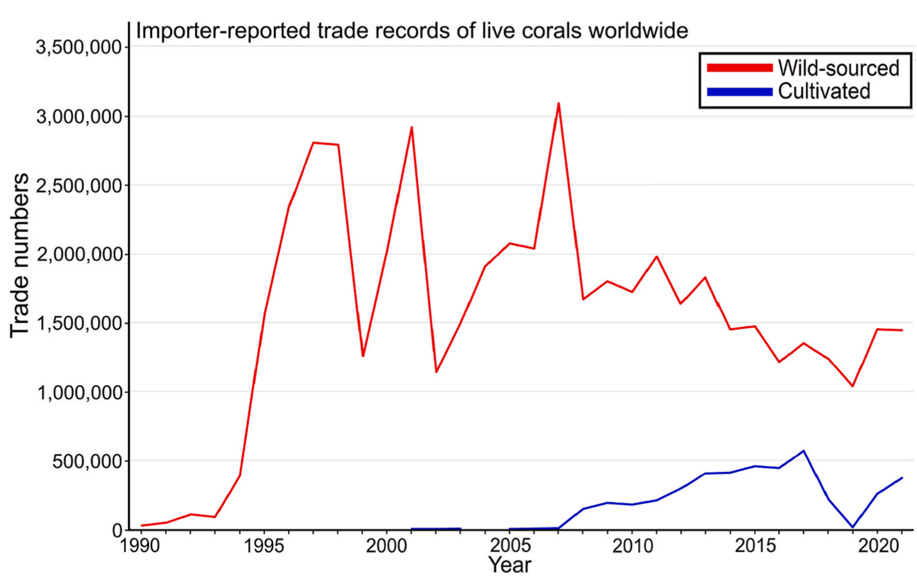

Fig. 1. Annual global import records of wild-sourced and cultivated corals over the period 1990–2021 (data from ESM Table S1.1).

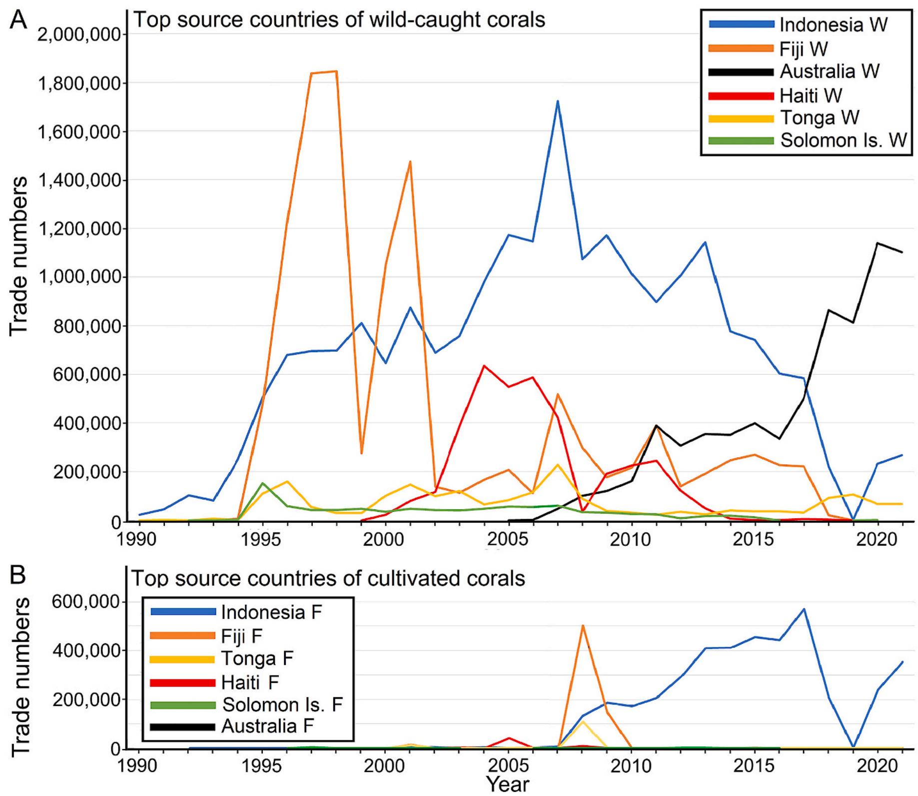

Fig. 2. Annual importer-reported records for wild-sourced (A) and cultivated scleractinian corals (B) over the period 1990–2021 by main exporting countries ranked in order of importance in the legends (data from ESM Table S1.2). W = wild-sourced; F = cultivated. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

since 2007 appeared to have been compensated by an increase of Indonesian exports of F-corals until 2017 (Fig. 2B), and Australian exports of W-corals (Fig. 2A) until at least 2021. Since 2019 the exports of Indonesian W-corals and F-corals have both been growing again.

The annual import data of wild sourced corals show large inconsistencies between trade numbers issued by exporters and importers (Fig. 3). The much higher numbers reported by exporters are largely determined by over-reporting by Fiji (ESM Fig. S2.1). This also influenced the ranking of importing countries over the whole period (1990–2021). The USA was always the dominant importer, Since 2019, Denmark has become the second-most important importing country of wild-sourced corals (Fig. 3B).

The annual import data of cultivated corals also show large discrepancies between trade numbers reported by exporters and importers (Fig. 4). The much higher numbers reported by exporters are largely determined by over-reporting by Indonesia (ESM Fig. S2.1), which dominated the market since 2007. There are no striking differences in the ranking of importing countries over the whole period (1990–2021) when export data and import data are compared. The USA was always the dominant importer of F-corals.

3.2.2. *Small-polyp scleractinians (SPS corals)*

Coral colonies of *Acropora* (family Acroporidae) are characterized by a branching growth form with small polyps (Bradley et al., 2022).

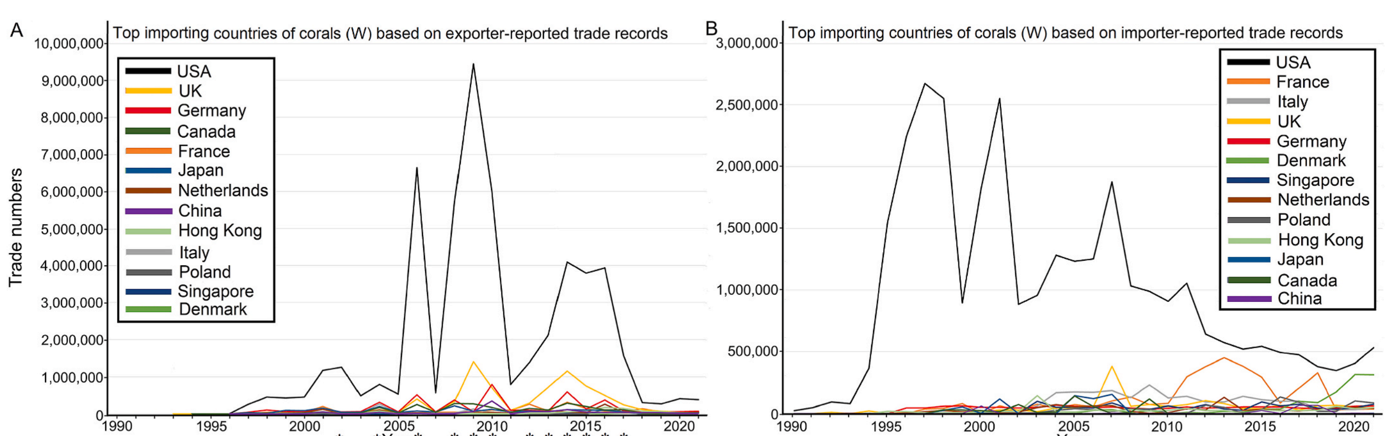

Fig. 3. Annual exporter- (A) and importer- (B) reported records for wild-sourced scleractinian corals over the period 1990–2021 by 13 main importing countries ranked in order of importance in the legends (data from ESM Table S1.3). Peak years marked by an asterisk (A: *) correspond with over-reporting by Fiji (ESM Fig. S2.1). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

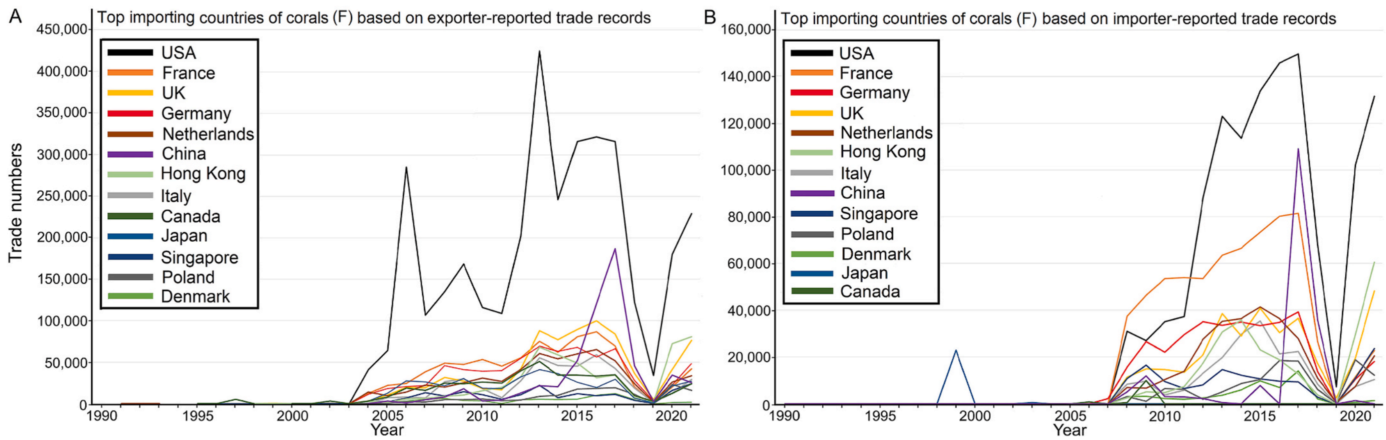

Fig. 4. Annual exporter- (A) and importer- (B) reported records for wild-sourced scleractinian corals over the period 1990–2021 by 13 main importing countries ranked in order of importance in the legends (data from ESM Table S1.4). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Despite being SPS instead of LPS, *Acropora* was the most-traded coral genus (Table 1). The export of W-corals was dominated by Fiji, Indonesia and Australia (Fig. 5A), showing peaks of $54.0{\cdot}10^3$ in 2004, $155.0{\cdot}10^3$ in 2007, and $151.7{\cdot}10^3$ in 2019, respectively. Most years since 2009, F-corals from Indonesia were sold more than W, showing a peak of $202.4{\cdot}10^3$ in 2013.

Coral colonies of *Montipora* (family Acroporidae) also have small polyps. They start as encrusting corals and later become predominantly plate-shaped or branched (Veron, 2000; Bradley et al., 2022). Trade in *Montipora* (W) (Fig. 5B) showed a similar pattern as that of *Acropora* (W) with the exception that Tonga was more important than Fiji as exporting country. Indonesia as first dominant exporter of W-corals showed a peak of $23.2{\cdot}10^3$ in 2007; it was succeeded by Australia, which showed a peak of $14.3{\cdot}10^3$ in 2021. Proportion-wise, the difference between F- and W-corals was higher than in *Acropora*. Indonesia exported most F-corals ($39.9{\cdot}10^3$) in 2013.

Porites colonies (family Poritidae) have small polyps and can be predominantly massive or branching, starting as crusts (Bradley et al., 2022). Their trade was always dominated by Indonesia, with the exception of 2019, when this country had an export ban and Australia sold more (Fig. 5C). In 2020, Indonesia was the most important exporter again with peaks of $35.7{\cdot}10^3$ (W) in 2005 and $8.4{\cdot}10^3$ (F) in 2017.

Pocillopora colonies (family Pocilloporidae) are branching and have small polyps (Bradley et al., 2022). Their exports (Fig. 5D) resembled those of *Acropora* in pattern but in much lower quantities, and with a more important role for Fiji and a less important one for Australia.

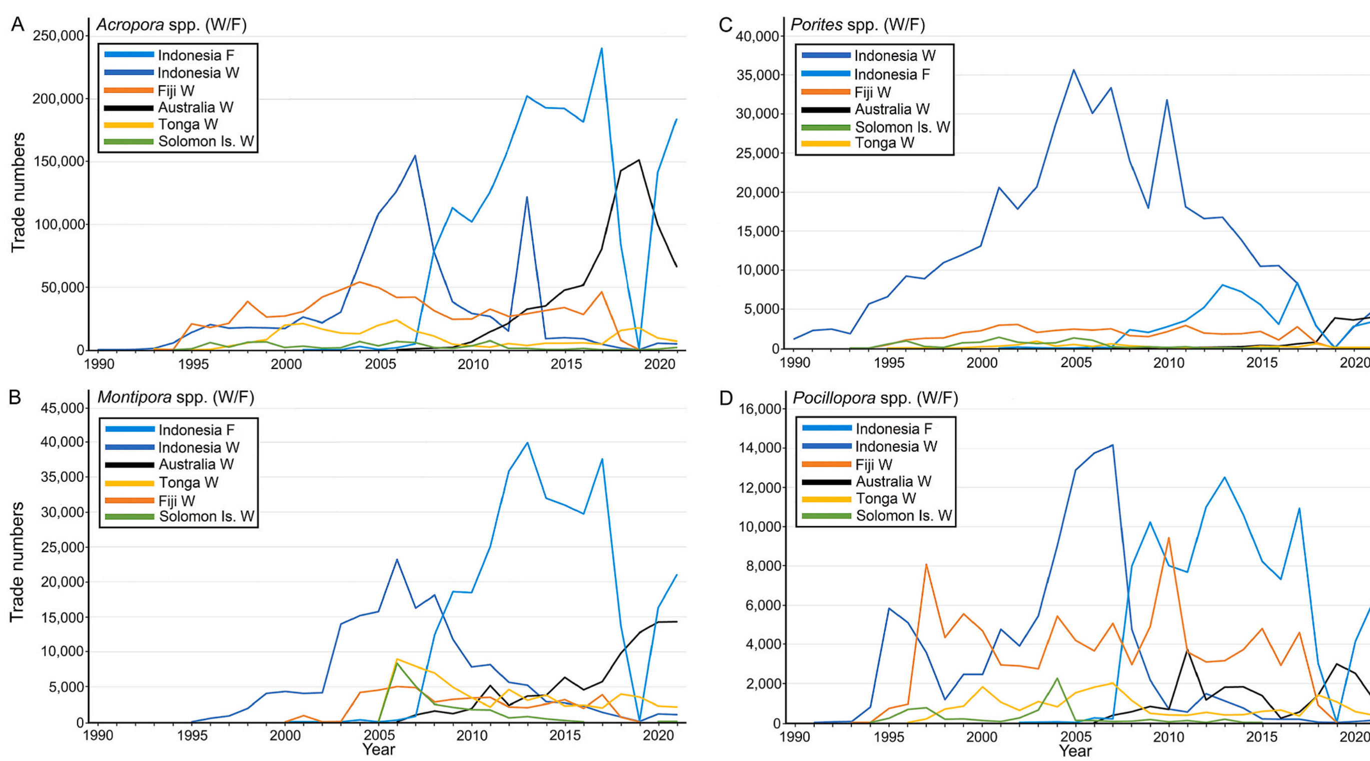

Fig. 5. Scleractinian corals with small polyps (SPS) (data from ESM Table S1.5). Annual importer-reported records over the period 1990–2021 for five main exporting countries ranked in order of importance in the legends. (A) *Acropora* spp. (family Acroporidae); (B) *Montipora* spp. (family Acroporidae); (C) *Porites* spp. (family Poritidae); (D) *Pocillopora* (family Pocilloporidae). W = wild-sourced; F = cultivated. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Regarding W-corals, Indonesia showed a maximum export of $14.2 \cdot 10^3$ in 2007 and Fiji one of $9.4 \cdot 10^3$ in 2010. Indonesia sold most of its F-corals ($12.5 \cdot 10^3$) in 2013.

3.2.3. Scleractinians with long-stalked polyps

Corals of the genera *Goniopora* (family Poritidae) and *Alveopora* (family Acroporidae) look very similar (Bradley et al., 2022), but belong to different families (Hoeksema and Cairns, 2025). Therefore, they are considered as look-alike taxa. Corals of both genera are massive or columnar in shape and have polyps on long, retractable stalks, but in *Goniopora* they have 24 tentacles and in *Alveopora* only 12. Corals of *Alveopora* are less dense in structure and less heavy-weight than those of *Goniopora* and are therefore more fragile.

Trade in *Goniopora* spp. (W) was mostly dominated by Indonesia with a peak of $0.2 \cdot 10^6$ in 2010 (Fig. 6A). In 2018, Indonesia was replaced by Australia as dominant exporter, with a maximum of $65.6 \cdot 10^3$ in 2021. *Alveopora* spp. (W) were traded in lower quantities and Fiji did not export (Fig. 6B). Most Indonesian specimens were F, with a maximum of $5.1 \cdot 10^3$ in 2015. Australia has been the most important exporter of W-corals since 2012 and exceeded the trade in Indonesia's F-corals since 2018, with a maximum of $26.2 \cdot 10^3$ in 2021. Other countries played minor roles (Fig. 6).

3.2.4. Family Euphylliidae

Species that are CITES-listed as *Euphyllia* (family Euphylliidae) are popular in the aquarium industry because of their fleshy polyps with large tentacles (Bradley et al., 2022). Five of them have recently been moved to the genus *Fimbriaphyllia* (Hoeksema and Cairns, 2025), but are still traded as *Euphyllia*. Two species show annual trade numbers over 50,000: *E. glabrescens* and *F. ancora* (Fig. 7A and B). Three have numbers exceeding 20,000: *E. cristata*, *F. paraancora*, and *F. divisa* (Fig. 7C–E). Two have records below 10,000: *F. yaeyamaensis* and *F. paradivisa* (Fig. 7F and G).

The species varied in trade patterns. The two most-traded species, *E. glabrescens* and *F. ancora*, were initially predominantly exported from Indonesia, at first as W- and then as F-corals, but since 2018 the market became dominated by W-corals from Australia (Fig. 7A and B). *Euphyllia glabrescens* showed maximum records from Indonesia (W) of $31.6 \cdot 10^3$ in 2005, Indonesia (F) of $38.4 \cdot 10^3$ in 2017, and Australia (W) of $73.3 \cdot 10^3$ in 2021 (Fig. 7A). For *F. ancora* the peaks were as follows: Indonesia (W) of $30.5 \cdot 10^3$ in 2005, Indonesia (F) of $27.1 \cdot 10^3$ in 2017, and Australia (W) of $53.6 \cdot 10^3$ in 2021 (Fig. 7B). *Euphyllia cristata* (W) was always sold most from Indonesia, but after a peak of $30.5 \cdot 10^3$ in 2005, the trade numbers dropped and remained below $10.0 \cdot 10^3$ since 2017 (Fig. 7C). *Fimbriaphyllia paraancora* (W) and *F. divisa* (W) were predominantly exported by Australia, with steeply increasing numbers in the last decade, while corals from Indonesia as second-most important exporter, mainly concerned specimens of *F. paraancora* (F) and *F. divisa* (W) over the whole period (Fig. 7D and G). The maximum numbers from Australia for these two species were $29.4 \cdot 10^3$ in 2018 and $23.4 \cdot 10^3$ in 2020, respectively (Fig. 7D and E). The market of *F. yaeyamaensis* and *F. paradivisa* (Fig. 7F and G) was dominated by F-corals from Indonesia, showing peaks of $9.8 \cdot 10^3$ in 2017 and $5.1 \cdot 10^3$ in 2016, respectively (Fig. 7F and G). Of the other countries, Solomon Islands was temporarily an important exporter of *E. glabrescens* and *F. paradivisa* (Fig. 7A and G), whereas Fiji and Tonga played minor roles. Australia did not export *F. yaeyamaensis* and Fiji did not export *F. paradivisa*.

3.2.5. Family Lobophylliidae

Some Lobophylliidae species are popular in the aquarium trade

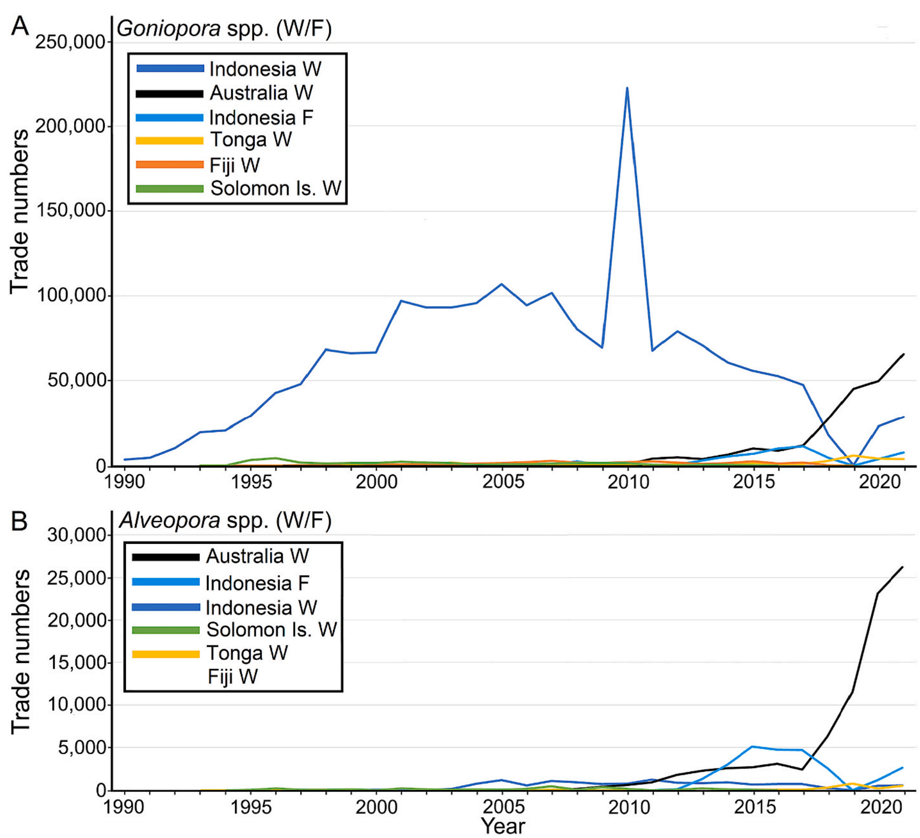

Fig. 6. Scleractinian corals with long-stalked polyps (data from ESM Table S1.6). Annual importer-reported records over the period 1990–2021 for five main exporting countries ranked in order of importance in the legends (no colour = no exports). (A) *Goniopora* spp. (family Poritidae); (B) *Alveopora* spp. (family Acroporidae). W = wild-sourced; F = cultivated. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

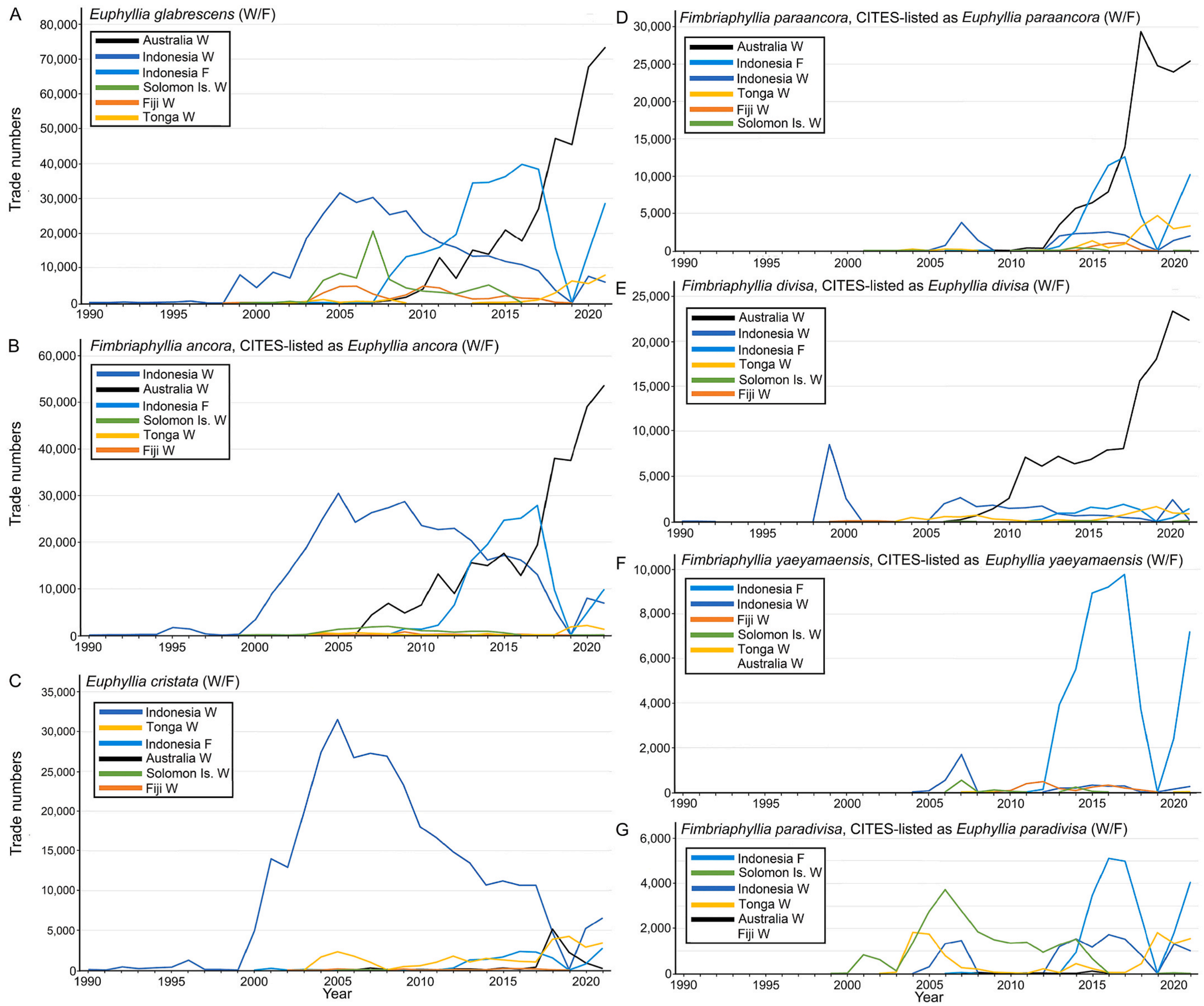

Fig. 7. Family Euphylliidae: corals of the genera *Euphyllia* and *Fimbriaphyllia*, traded as separate *Euphyllia* species (data from ESM Table S1.7). Annual importer-reported records over the period 1990–2021 for five main exporting countries ranked in order of importance in the legends (no colour = no exports). (A) *E. glabrescens*; (B) *F. ancora*; (C) *E. cristata*; (D) *F. paraancora*; (E) *F. divisa*; (F) *F. yaeyamaensis*; (G) *F. paradivisa*. W = wild-sourced; F = cultivated. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

because of their large, fleshy and colourful polyps (Bradley et al., 2022). There have been several recent changes in the taxonomy of this family, concerning the shifts of species between genera (Hoeksema and Cairns, 2025). Species that are CITES-listed as *Acanthastrea* spp. (Fig. 8A) showed very high annual trade numbers, which were largely contributed by two species that were moved to other genera, *Micromussa lordhowensis* and *Homophyllia bowerbanki* (Fig. 8B and C). The first one of these two species was the most commonly traded of the whole family, while the last one showed the opposite (Fig. 8B and C). *Homophyllia australis* showed the highest trade records of the family, mainly from Australia (Fig. 8D).

CITES records of *Scolymia* spp. were almost entirely represented by exports of *H. australis*, which is CITES-listed as *Scolymia* spp. (ESM Table S1.8J). Similar to *H. bowerbanki*, records of *Moseleya latistellata* remained below $10.0{\cdot}10^3$ (Fig. 8E). Among *Lobophyllia* species that are CITES-listed as either *Lobophyllia* spp. or *Symphyllia* spp., the first category was nearly traded thrice as much as the second (Fig. 8F and G). Trade in *Lobophyllia rowleyensis*, CITES-listed as *Australomussa rowleyensis*, has not been analyzed because of its low trade records. *Cynarina lacrymalis* and *Acanthophyllia deshayesiana* are look-alike species but the first one has more records than the second (Fig. 8H and I). Exports of *A. deshayesiana* from before 2009 were nearly non-existent (Fig. 8I).

Most Lobophylliidae showed a strong increase in trade after 2005, mostly owing to the exports by Australia, which dominated the market of this coral family since then. All maximum trade records concern Australia: *Acanthastrea* spp. had a record of $93.0{\cdot}10^3$ in 2021, *M. lordhowensis* $47.2{\cdot}10^3$ in 2018, *H. bowerbanki* $5.2{\cdot}10^3$ in 2021, *H. australis* $72.4{\cdot}10^3$ in 2018, *M. latistellata* $8.6{\cdot}10^3$ in 2011, *Lobophyllia* spp. $41.2{\cdot}10^3$ in 2020, *Lobophyllia* spp. (ex-*Symphyllia* spp.) $15.2{\cdot}10^3$ in 2021, *C. lacrymalis* $18.6{\cdot}10^3$ in 2021, and *A. deshayesiana* $6.8{\cdot}10^3$ in 2019 (Fig. 8). *Acanthastrea* spp. showed some participation by Tonga (W) and Indonesia (F) (Fig. 8A). Australia had near-monopolies for the export of *Homophyllia bowerbanki* and *Homophyllia australis*, and a complete monopoly for *Moseleya lastistellata* (Fig. 8B–D). *Lobophyllia* spp. were exported much by Indonesia, both as W and F (Fig. 8F and G). Despite a strong drop in the trade of *Lobophyllia* spp. (W) from Indonesia, it did not become entirely replaced by the trade in F-corals. *Cynarina lacrymalis* (W) and *Acanthophyllia deshayesiana* (W) were predominantly exported

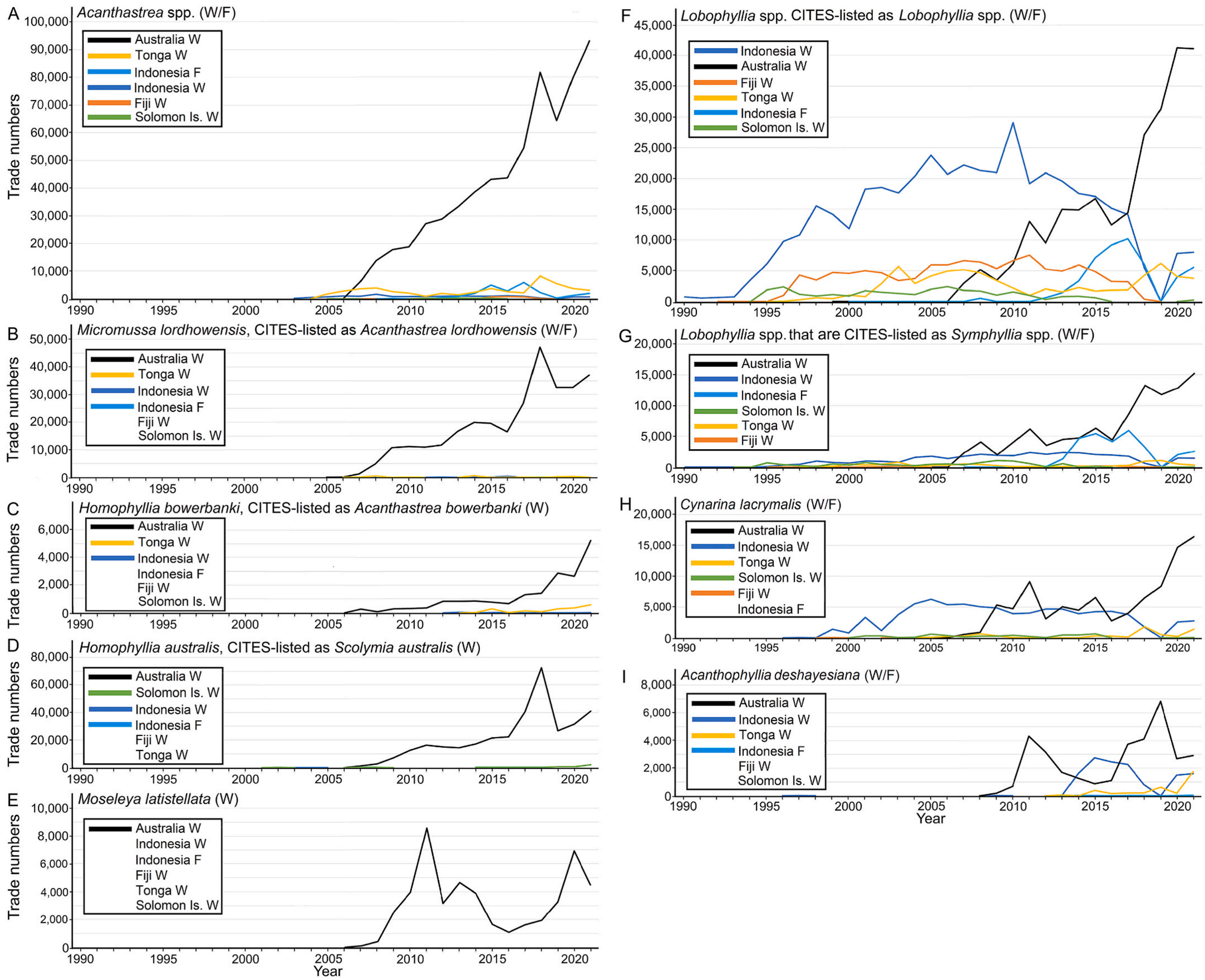

Fig. 8. Much-traded taxa of family Lobophylliidae (data from ESM Table S1.8). Annual importer-reported records over the period 1990–2021 for five main exporting countries ranked in order of importance in the legends (no colour = no exports). (A) *Acanthastrea* spp.; (B) *Micromussa lordhowensis*; (C) *Homophyllia bowerbanki*; (D) *Homophyllia australis*; (E) *Moseleya lastistellata*; (F, G) *Lobophyllia* spp.; (H) *Cynarina lacrymalis*; (I) *Acanthophyllia deshayesiana*. W = wild-sourced; F = cultivated. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

from Indonesia and Australia, but the maximum records concerned imports from Australia (Fig. 8H and I). The other major exporting countries only played important roles in the export of *Lobophyllia* spp. (Fig. 8F). Fiji did not participate in exports of several Lobophylliidae, only of *Acanthastrea* spp., *Lobophyllia* spp. and *C. lacrymalis* (Fig. 8A and F–H). Solomon Islands did not join in the export of four species and Tonga not of two species.

3.2.6. Family Merulinidae

The most-traded taxa of the family Merulinidae are *Trachyphyllia geoffroyi*, *Catalaphyllia jardinae* and *Caulastraea* spp. (Fig. 9). All of these taxa have large fleshy polyps, while *C. jardinei* also has long, retractable tentacles (Bradley et al., 2022). Four species of the genus *Caulastraea* were moved to the resurrected look-alike genus *Astraeosmilia*, while two species remained behind as *Caulastraea* spp. (Hoeksema and Cairns, 2025). All of them are still CITES-listed as *Caulastraea* spp.

Trachyphyllia geoffroyi and *Catalaphyllia jardinae* showed peak trade records that were slightly higher for Indonesia than for Australia: *T. geoffroyi* had a maximum record of $58.6{\cdot}10^3$ from Indonesia in 2005 and one of $55.4{\cdot}10^3$ from Australia in 2021 (Fig. 9A); for *C. jardinae* these were $57.7{\cdot}10^3$ from Indonesia in 1998 and $50.1{\cdot}10^3$ from Australia in 2021 (Fig. 9B). These corals are solitary LPS and therefore not suitable for reproduction by fragmentation, which is reflected in the low numbers of F-corals from Indonesia and high numbers of W-corals, first from Indonesia and later from Australia (Fig. 9A and B). In contrast, corals of *Caulastraea* spp. and *Astraeosmilia* spp. are attached and their polyps are slender and branched, which makes them suitable for reproduction by fragmentation, which is shown by a large proportion of F-corals from Indonesia in the trade (Fig. 9C). They showed maximum records of $22.0{\cdot}10^3$ from Indonesia (W) in 2007, $11.5{\cdot}10^3$ from Indonesia (F) in 2013, and $10.0{\cdot}10^3$ from Australia (W) in 2020 (Fig. 9C). Among the other countries, Fiji was the third-most important exporter of *T. geoffroyi* and *Caulastraea* spp./*Astraeosmilia* spp. (Fig. 9A and C).

3.2.7. Family Fungiidae

Most mushroom coral species (family Fungiidae) are solitary, free-living corals, consisting of one large polyp (Bradley et al., 2022). Most of them are CITES-listed as *Fungia* spp. (Fig. 10A), although this genus was split up in various separate genera (Hoeksema and Cairns, 2025). Similar-looking species belong to the genus *Cycloseris*, which was not

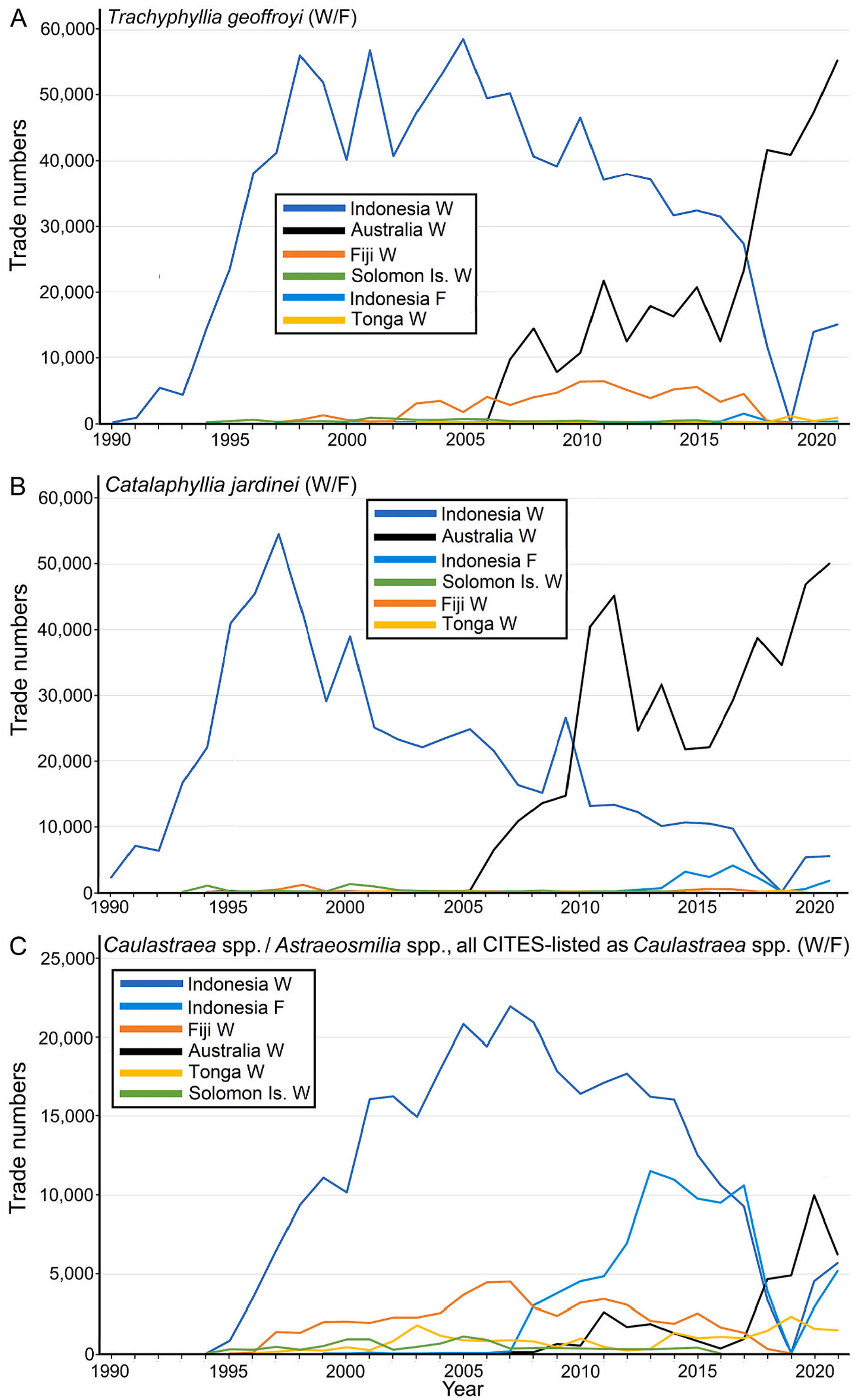

Fig. 9. Much-traded taxa of family Merulinidae (data from ESM Table S1.9). Annual importer-reported records over the period 1990–2021 for five main exporting countries ranked in order of importance in the legends. (A) *Trachyphyllia geoffroyi*; (B) *Catalaphyllia jardinei*; (C) *Caulastraea* spp. and *Astraeosmilia* spp. W = wild-sourced; F = cultivated. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

analyzed due to relatively low trade numbers. *Heliofungia actiniformis* is also a free-living coral with a single mouth but it differs from *Fungia* spp. by its fleshy polyp with large tentacles, resembling those of *Euphyllia glabrescens* (Bradley et al., 2022). *Polyphyllia talpina* is also free-living but it has numerous small mouths, hidden by a dense cover of short tentacles (Bradley et al., 2022).

Most *Fungia* spp. (W) were imported from Indonesia, with a peak of $23.3{\cdot}10^3$ in 2007. Since 2018 much of this market was taken over by Australia, showing a maximum number of $41.1{\cdot}10^3$ in 2021 (Fig. 10A). Since 1990, *H. actiniformis* (W) used to be the most-traded fungiid, predominantly from Indonesia, peaking at $40.5{\cdot}10^3$ in 2005, but since 2018 most specimens came from Australia, showing a peak of $15.3{\cdot}10^3$ in 2020 (Fig. 10B). With the exception of 2019, most W-corals of *Polyphyllia talpina* came from Indonesia, peaking at $7.7{\cdot}10^3$ in 2005 with a

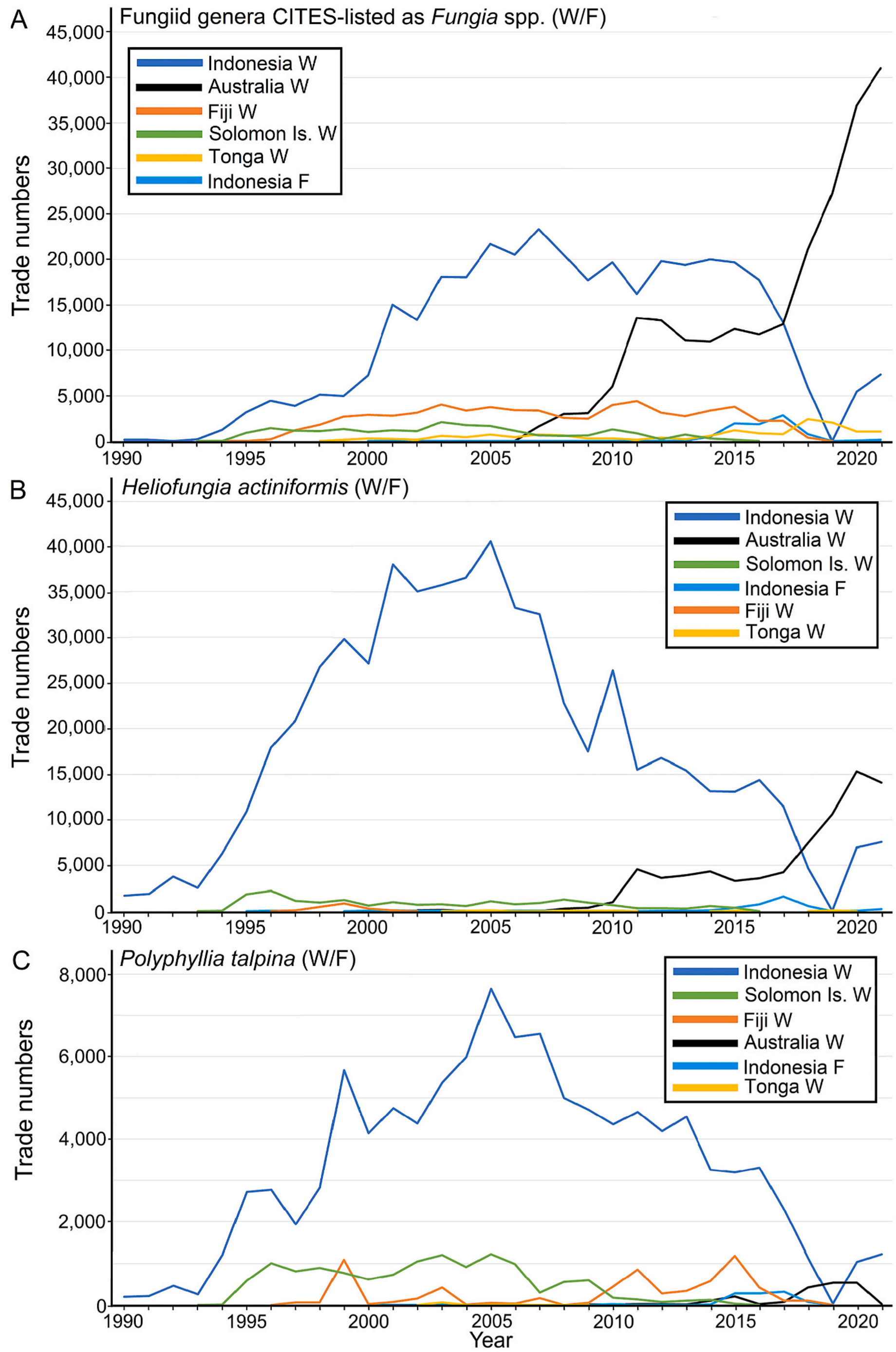

Fig. 10. Much-traded free-living corals of family Fungiidae (data from ESM Table S1.10). Annual importer-reported records over the period 1990–2021 for five main exporting countries ranked in order of importance (see legends). (A) Genera traded as *Fungia* spp.; (B) *Heliofungia actiniformis*; (C) *Polyphyllia talpina*. W = wild-sourced; F = cultivated. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

strong decline afterward (Fig. 10C). In all cases, F-corals from Indonesia did not compensate for the decline of trade in W-corals (Fig. 10).

3.2.8. Family Plerogyridae

Plerogyridae was established in 2020 (Hoeksema and Cairns, 2025) and consists of LPS-corals (Bradley et al., 2022). *Blastomussa* spp. were the most-traded species, followed by *Plerogyra sinuosa*, *Physogyra lichtensteini*, and *Nemenzophyllia turbida* (Fig. 11). *Plerogyra simplex* is the least important (Fig. 11D).

During many years, Indonesia was the main exporter of most species. *Blastomussa* spp. (W) was an exception with a peak of only 6.0·10^3 in 1998 by Indonesia, whereas Australia became the dominant exporter in 2008 and scored 40.6·10^3 in 2020 (Fig. 11A). Indonesia was the main exporter of *P. sinuosa* (W) until 2018, with a peak of 27.7·10^3 in 2005, after which it was replaced by Australia, which scored 17.5·10^3 in 2021 (Fig. 11B). *Physogyra lichtensteini* (W) had a maximum record of 10.2·10^3 in 2005 by Indonesia, which was replaced by Australia as dominant exporter in 2019 and 2020 (Fig. 11C). *Plerogyra simplex* (W) from Indonesia showed a small peak of 3.9·10^3 in 1999, after which Fiji and Tonga became main exporters, but with lower numbers (Fig. 11D). Indonesia had a near-monopoly of *N. turbida* (W) exports, peaking 9.0·10^3 in 2004 (Fig. 11E). Australia did not participate in exports of

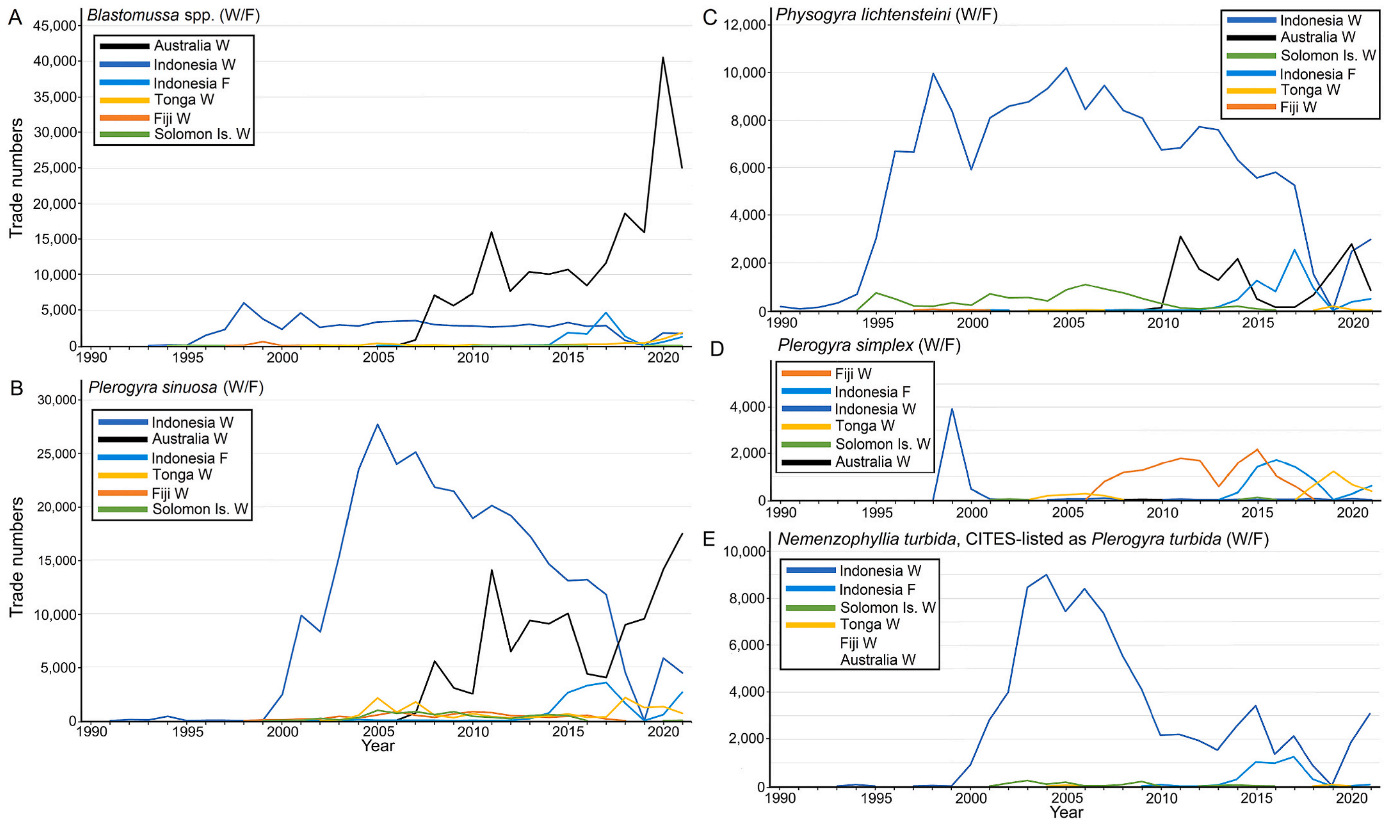

Fig. 11. Much-traded taxa of family Plerogyridae (data from ESM Table S1.11). Annual importer-reported records over the period 1990–2021 for five main exporting countries ranked in order of importance (see legends; no colour = no exports). (A) *Blastomussa* spp.; (B) *Plerogyra sinuosa*; (C) *Physogyra lichtensteini*; (D) *Plerogyra simplex*; (E) *Nemenzophyllia turbida*. W = wild-sourced; F = cultivated. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

P. simplex and neither of *N. turbida* together with Fiji (Fig. 11D and E). F-corals from Indonesia did not constitute a large part of the trade, except for *P. simplex* in 2016–2018, succeeding W-corals from Fiji and preceding W-corals from Tonga (Fig. 11D).

3.2.9. *Family Dendrophylliidae*

Many Dendrophyllidae species have medium-large polyps with brightly coloured tentacles (Arrigoni et al., 2014; Bradley et al., 2022). Corals of some genera look alike and may easily be confused in the trade, such as *Dendrophyllia* spp., *Eguchipsammia* spp., and *Tubastraea* spp. (Bradley et al., 2022). *Turbinaria* spp. were the most-traded species of the family, followed by *Duncanopsammia axifuga* and *Tubastraea* spp. (Fig. 12B, F, and E). Indonesia had near-monopolies in the export of all taxa, except for *D. axifuga* (Fig. 12).

Trade in *Dendrophyllia* spp. (W) showed a maximum record of $5.1{\cdot}10^3$ by Indonesia in 2000, and of $3.1{\cdot}10^3$ and $2.6{\cdot}10^3$ by Australia and Tonga in 2019, respectively, during Indonesia's export ban (Fig. 12A). *Turbinaria* spp. (W) were mainly exported by Indonesia, with a peak of $36.2{\cdot}10^3$ in 2010, but not during Indonesia's export ban, when Australia became leading exporter until 2020 (Fig. 12B). *Duncanopsammia peltata* (W) was mainly exported from Indonesia, with a peak of $12.5{\cdot}10^3$ in 2007 (Fig. 12C). *Eguchipsammia* spp. (W) were mainly exported from Indonesia, peaking at $11.4{\cdot}10^3$ in 2005, with the exception of 2019 and 2020, during Indonesia's export ban (Fig. 12D). *Tubastraea* spp. (W) were exported from a mix of countries, in many years dominated by Indonesia with a peak of $18.6{\cdot}10^3$ in 1998, temporarily succeeded by the Solomon Islands, with a peak of $6.1{\cdot}10^3$ in 2005, and eventually by Australia, with a peak of $12.8{\cdot}10^3$ in 2020 (Fig. 12E). Australia had a monopoly in the export of *D. axifuga* (W), with a maximum record of $32.1{\cdot}10^3$ in 2020 (Fig. 12F). F-corals from Indonesia consisted of foliaceous corals that could easily be fragmented or sawn, such as *Turbinaria* spp. and *D. peltata* (Fig. 12B and C).

4. Discussion

International trade data of live corals can be used as a proxy for coral harvesting and as an indicator for damage inflicted on coral reef ecosystems in countries that export live corals for the aquarium industry. Unlike threats causing coral mortality *in situ*, which leave dead coral skeletons behind, coral harvesting does not leave traces that can be used to measure loss of coral diversity and live cover. Ideally, local harvesting data should be used, but obtaining these data would require strict and consistent monitoring of coral harvesters. Not all landings of live corals may be reported since illegal imports may still occur, as found in the USA (2003–2012) from Indonesia (26.8% of imports), Tonga (16.3%), Australia (15,9%) and Fiji (13.4%) (Petrossian et al., 2020).

International trade data of live corals could present an underestimation of what is being caught because of (1) illegal harvesting and unregistered legal harvesting (Harriott, 2003; Gurjão and Lotufo, 2018; Sosnowski et al., 2020); (2) collecting for the souvenir and curio trade (Wood and Wells, 1988; Best, 1997); (3) use for domestic markets (Larkin and Degner, 2001); (4) illegal trade (Best, 1997; Petrossian et al., 2020), and (5) post-collection mortality (Delbeek, 2001b; Borneman, 2005; Sheridan et al., 2013; Intyas et al., 2023, Fig. 13). However, even though CITES trade data are undervaluing coral loss, they are useful in showing trends in trade over three decades and enabling comparisons between species, countries, and source codes (W and F+C).

4.1. *Major coral-exporting countries of wild-caught corals*

Worldwide, there is a need for more information on the impact of harvesting on the natural populations (Smith et al., 2011; Dee et al.,

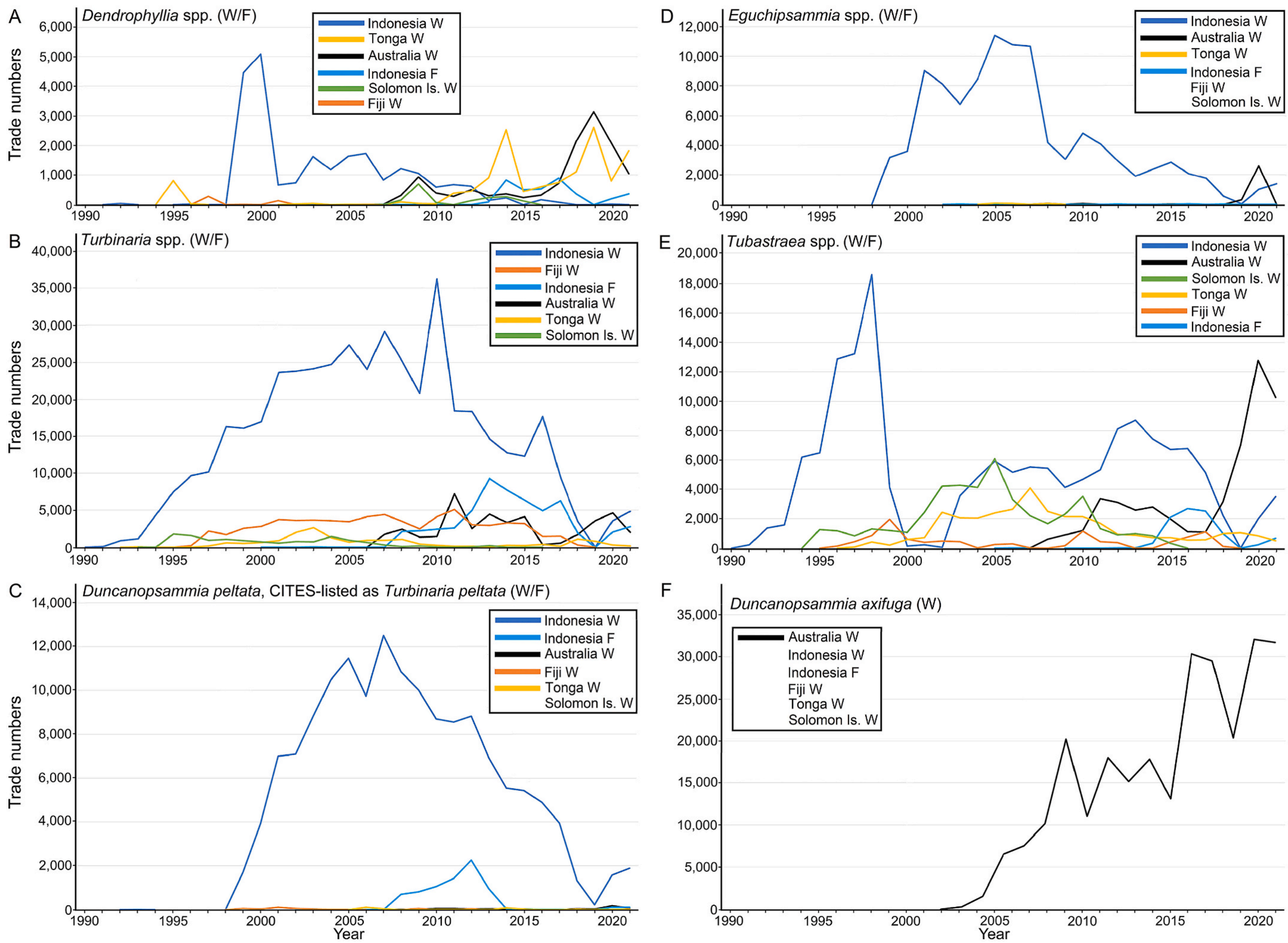

Fig. 12. Much-traded taxa of family Dendrophylliidae (data from ESM Table S1.12). Annual importer-reported records over the period 1990–2021 for five main exporting countries ranked in order of importance (see legends: no colour = no exports). (A) *Dendrophyllia* spp.; (B) *Turbinaria* spp.; (C) *Duncanopsammia peltata*; (D) *Eguchipsammia* spp.; (E) *Tubastraea* spp.; (F) *Duncanopsammia axifuga*. W = wild-sourced; F = cultivated. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2014). According to importer-reported records, Indonesia was the main exporting country of W-corals in the years 1990–1995, 1999, and 2002–2017. It was succeeded by Fiji in 1996–1998 and 2000–2001, and by Australia since 2018. Australia's sudden rise in exports was facilitated by temporary export bans by Indonesia and Fiji, and Indonesia's declining export quotas. Indonesia has been the main exporter of F-corals since 2005, which compensated for its declining sales of W-corals. Haiti, Tonga and Solomon Islands were less important export countries. Haiti was the only major exporting country for the Caribbean. All other countries exported corals from the Indo-Pacific. Indonesia has been the main exporter of cultivated corals since 2005.

Indonesia and Fiji have export quotas for corals, while Australia uses harvest quotas. Quotas are only effective when they regulate harvesting (Bruckner, 2003), which appears to be the case for Indonesia's export quotas because they have decreased much over the years (CITES Secretariat, 2025a). The advantage of export quotas is that they enable analyses of trade data more easily because of the best available compatibility over long time spans and because they allow comparing trade trends between coral taxa and between countries involved in the trade. However, harvest records are expected to be higher than trade records because of domestic trade and pre-export mortality (Fig. 13B).

4.1.1. Indonesia

Indonesia is able to export many corals because it is a large tropical island nation with long coastlines and much reef surface area, and because it is located in the Coral Triangle, where the highest concentration of coral species can be found (Veron, 2000; Hoeksema, 2007; Razak et al., 2024), Furthermore, this country has a large population of low-income fishermen, many of whom are involved in coral fisheries (Knittweis and Wolff, 2010; Ferse et al., 2012, 2014). It also has good aviation connections for the shipping of live corals, which is a critical factor in the global aquarium industry (Rhyne and Tlusty, 2012). Indonesia has published export quotas for wild-caught corals since 2000 (CITES Secretariat, 2025b). These are divided over nine collecting areas, each with their own catch quota per species or genus (Kusumo et al., 2023; KLHK, 2024), which have the same effect as harvest quotas. Indonesia had a self-imposed 20-month export ban from May 2018 until January 2020 (Chalias, 2020), resulting in a strong dip in the trade (Fig. 2). Recently, this country published a stock assessment (Hadi et al., 2020) and a non-detriment finding (NDF) for its coral harvesting (Kusumo et al., 2023). Indonesia has increased sales of cultivated corals, replacing the export of wild-caught corals (Intyas et al., 2023b; Johan et al., 2023, Fig. 2). It issues annual cultivation licenses to mariculture companies, most of which are based in Bali and East Java. They are regularly controlled by the government to check on which coral species they are capable of cultivating with minimal use of wild stock.

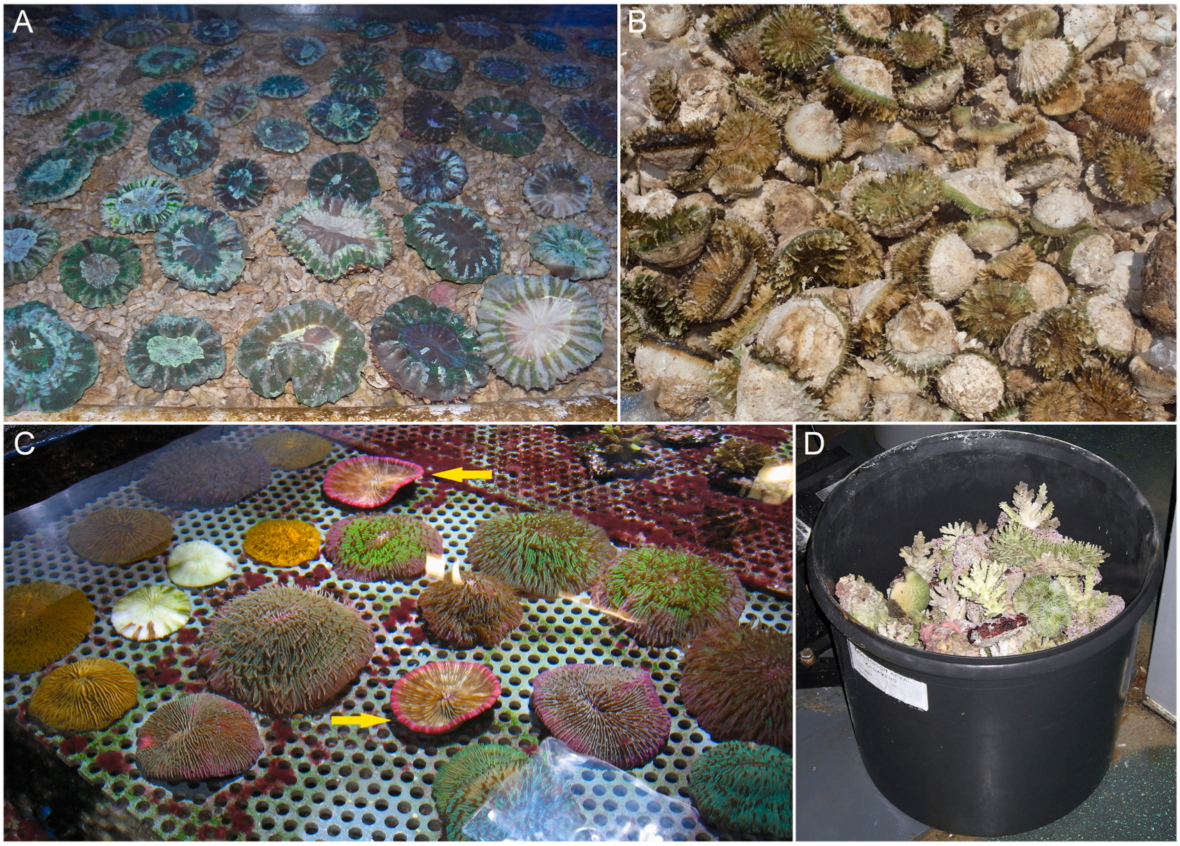

Fig. 13. Corals lost in the international aquarium trade. A. Live specimens of *Cynarina lacrymalis* kept in a concrete basin of a wholesaler in South Sulawesi, Indonesia (photo taken in 2015). B. A heap of dead *C. lacrymalis* in the backyard of the same coral wholesaler. C. Indonesian mushroom corals confiscated by customs in 2012; the corals were wild-caught (W) but exported as cultivated (F). Corals with a pink margin (arrows) are *Lithophyllon spinifer*, traded as either *Cycloseris* spp. or *Fungia* spp. White corals were dying. D. Dead corals confiscated when alive but died in storage. Photo credits: the author. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4.1.2. Fiji

Fiji is a small island nation for which the coral trade has been considered of major economic importance and of potential concern for the conservation of reef resources (Vunisea, 2003; UNEP-WCMC, 2015). The fluctuating trade patterns of Fiji since 1990 (Fig. 2A) reflect a strategy of intensive-fishing periods followed by bans, a concept also known as periodically harvested closures (PHCs), which is commonly practised in the West Pacific (Mills et al., 2011; Goetze et al., 2018). At present, it is not clear whether there is a national management plan with regard to coral fisheries. In the past, coral reef management was performed at community level and the status of Fiji's coral reefs was surveyed over several years, but not much recently (Lovell, 2001; Cumming et al., 2002; Sykes, 2007; Lovell and Mclardy, 2008; Bruckner et al., 2016). A non-detriment finding (NDF) was published in 2009, in which Fiji's export numbers of 27 coral taxa were compared with estimated population sizes in the collecting areas (Lovell and Whippy-Morris, 2009). However, some scientists were critical about the unknown state of Fijian coral reef fisheries due to the lack of long-term monitoring (Teh et al., 2009). It appears that a monitoring plan was set up (Sykes and Lovell, 2009) but it does not specifically address coral taxa collected for the aquarium industry but only those that are common on Fijian reefs (WCS, 2010). It is unclear whether monitoring of coral populations actually happened. Anyway, long-term management of Fiji's coral resources was performed through annual export quotas (Fiji CITES Management Authority, 2007; CITES Secretariat, 2025c) and an export ban from 2018 to 2024 (Pederson, 2024, Fig. 2A). In contrast to the earlier NDF (Lovell and Whippy-Morris, 2009), Fiji's most recent NDF does not present species-specific estimations of population sizes in the catch areas (Lovell and Sykes, 2025). Fiji did not engage much in coral cultivation, because producers did not consider it economically viable (Lal and Cerelala, 2005).

4.1.3. Australia

Australia showed a strong growth in the export of corals since 2018, which was facilitated by the self-imposed export bans by Fiji and Indonesia (Fig. 2A). The year 2021 showed a drop, which could be caused by growing exports of corals from Indonesia (Fig. 2). Australia's coral fisheries are managed by the state government fisheries management authorities of Western Australia, Northern Territories, and Queensland, while the Australian Government is overseeing the conservation and CITES-related matters of corals (Pratchett et al., 2020b). In addition, there is coral harvesting in the Coral Sea, which is limited to species of the family Acroporidae (in particular the genus *Acropora*) and managed by the Coral Sea Aquarium Fishery (Pratchett et al., 2020b; D'Alberto and Timmiss, 2025). The Queensland coral fishery is by far the largest of these four (Pratchett et al., 2020b). Although there are risk assessments for the four coral harvesting areas (Pratchett et al., 2020a, 2021a, 2021b, 2022; D'Alberto and Timmiss, 2025), the real effect of fisheries on the natural coral populations is unclear, also because there are several other threats, such as coral bleaching, tropical cyclones, coral diseases and coral predators (De'ath et al., 2012; Emslie et al., 2024), which all together require species-specific monitoring in the areas where corals are being harvested (Pratchett et al., 2020a; Pratchett, 2024).

In contrast to Fiji and Indonesia, Australia does not have annual nation-wide trade quotas per coral taxon. Instead, there are harvesting quotas per state, which may either cover calendar years, January 1 – December 31 (Western Australia) or financial years, July 1 – June 30 (Northern Territories and Queensland). Furthermore, Australia's coral harvests are usually expressed in weight instead of numbers of specimens reported by other countries. Many small individuals of popular species, such as *Trachyphyllia geoffroyi* and *Catalaphyllia jardinei* (Fig. 9A and B), would weigh as much as a few large ones, which could stimulate overfishing of these species. While harvest data are regulated per state, exporting companies can be located in other states, including those that have no coral reefs. These discrepancies, plus post-harvesting mortality and demand by the domestic market could cause differences between harvest data and export data.

4.2. Major coral-importing countries

The USA always had the highest import records of W-corals (Fig. 3). Tissot et al. (2010) suggested that it should use its economic influence on coral-exporting countries to stimulate more sustainable trade. This may have happened because the US showed a decline in the import of wild-caught corals after 2010, and a growth in the import of cultivated corals (Figs. 3 and 4). France was the major importing country of cultivated corals until 2012, after which it was succeeded by the USA (Fig. 4B).

In the Americas, Canada was the second-most important importer but it stopped reporting import records (ESM Fig. S2.3), causing underestimations of global import records. In Europe, various countries succeeded each other as most dominant importer (ESM Fig. S2.4). Overall, France was the most important importer, followed by Italy, the UK, Germany, Denmark, the Netherlands, and Poland. Among Asian countries, Singapore had the highest importer-reported trade records (ESM Fig. S2.5). It t is possible that Japan imported more corals but since it did not report imports anymore since 2008, this cannot be verified.). Hong Kong and China may serve as a single market because of unrestricted cross-border transport of corals (UNEP-WCMC and CITES Secretariat, 2025c).

4.3. Discrepancies in reporting by exporting and importing countries

There are various general explanations for the differences between importer- and exporter-reported trade records, which may also be applicable to the trade in live corals: 1) inconsistencies in the use of trade terms, for example confusing dead and live animals (Foster et al., 2016); 2) illegal trade (Best, 1997; Nijman, 2010; Petrossian et al., 2020); 3) exports reported at the end of one year and the corresponding imports reported in the next year (Janssen and Blanken, 2016); 4) exports being based on numbers on permits and imports on customs-declared numbers (Blundell and Mascia, 2005; Janssen and Blanken, 2016); 5) mortality during shipping (Delbeek, 2001b; Borneman, 2005); 6) corals breaking during transport, increasing the number of specimens; 7) reporting at different taxonomic levels, like genus and species (Section 4.7); 8) misidentifications by either exporter or importer (Section 4.8); 9) differences in the reported destination, like China and Hong Kong (Section 4.2); 10) inconsistent trade units, like exports expressed as weight and imports as number of specimens (Pavitt et al., 2021, Section 4.1) or unknown trade units (Foster et al., 2016); 11) countries not reporting imports (Pavitt et al., 2021, Section 4.2); 12) imports that are re-exported to third countries but not reported as such; 13) species permitted for export, but not for import due to trade suspensions (Janssen and Blanken, 2016); 14) quantities traded lower than permitted because of insufficient stock or other reasons (Robinson and Sinovas, 2018); 15) specimens reported for export but refused by the destination country (Janssen and Blanken, 2016).

For example, in the period 1990–2021, Indonesia reported the export of 314,000 wild-caught specimens of *Eguchipsammia* while importers reported 107,000 corals of that species (UNEP-WCMC and CITES Secretariat, 2025a), which can partly be explained by an EU-import ban for Indonesian *Eguchipsammia* since July 2015 (UNEP-WCMC, 2025a), implying that records from export permits had no follow-up in import records. Regardless these differences and assuming that countries are consistent in the way they report, it appears that importer-reported records are the most reliable tool to study trends over long periods of time.

4.4. Most-traded coral taxa

4.4.1. Taxa reported at genus level

Among the top-15 most-traded coral genera (W), *Acropora* was by far the most popular (Table 1). Together with *Montipora* and *Porites* it has small polyps, which allow fast growth and easy regeneration (Hughes, 1983). Corals of these genera are commonly observed in high densities at shallow reef flats and upper reef slopes (Done, 1982; Moll, 1983; 1986; Veron, 2000). They are often used in reef restoration programs, which rely much on coral fragmentation of branching and foliaceous species (Boström-Einarsson et al., 2020).

The capacity to SPS corals to break easily is convenient in coral cultivation (Delbeek and Sprung, 1994). Among four SPS genera, three were traded more as F-corals than as W-corals (Fig. 5). These three taxa (i.e., *Acropora*, *Montipora* and *Pocillopora*) consist of branching and foliaceous corals, whereas the fourth one, *Porites*, also has several massive coral species in addition to branching and foliaceous ones (Veron, 2000). Massive *Porites* W-corals are also sold as substrate when they contain Christmas tree worms of the genus *Spirobranchus* (Delbeek and Sprung, 1994). These corals are common as hosts and offer protection to the worms, which live in tubes that are embedded deep inside the coral skeletons (Nishi and Nishihira, 1999; Hoeksema et al., 2019b). Trade in wild-caught *Porites* declined strongly after its last peak year in 2010 (Fig. 5C), for which no explanation can be given. Export quotas were not a limiting factor herein, since they were much higher than the trade data (CITES Secretariat, 2025c). It is also not clear why *Pocillopora* corals were much less popular in the aquarium trade than the other SPS corals (Fig. 5), but it is noteworthy that in the 1990s they were the most-sold genus of dead corals in the curio trade (Bruckner, 2001, 2002b).

Popular coral genera characterized by large, fleshy polyps, such as *Goniopora*, *Lobophyllia*, *Acanthastrea*, *Scolymia*, and *Caulastraea* (Table 1) are usually scattered on reef slopes (Best et al., 1989; Veron, 2000). Trade in *Goniopora* corals declined strongly after a peak year in 2010 (Fig. 6A), even though it was not restricted by export quotas (CITES Secretariat, 2025c). In contrast, trade of W-corals of its look-alike *Alveopora* (Fig. 6B) was very much restricted by Indonesia's export quotas (CITES Secretariat, 2025c), which since around 2012 became substituted by the export of F-corals from that country and much more by the export of W-corals from Australia. *Goniopora* and *Alveopora* corals have a reputation of being difficult to keep in aquariums for periods longer than 6–18 months (Delbeek and Sprung, 1994; Bruckner, 2002b), which may negatively affect their popularity.

The export market of *Lobophyllia* W-corals was first dominated by Indonesia (Fig. 8F and G) and since 2018 by Australia, whereas *Acanthastrea* was predominantly exported by Australia since 2007 (Fig. 8A) owing to popular species like *A. lordhowensis* (= *Micromussa lorhowensis*) and *A. bowerbanki* (= *Homophyllia bowerbanki*) (Fig. 8B and C; Table 2). *Lobophyllia* corals are easy to keep in aquariums (Delbeek and Sprung, 1994) and those of *Acanthastrea* slightly less so (Sprung, 1999), which implies that hardiness does not likely impact their popularity. Although *Scolymia* corals are more difficult to keep in aquariums (Sprung, 1999), this does not prevent them from being popular in the trade, in particular the very colourful *S. australis* (= *Homophyllia australis*) from Australia (Fig. 8D; Table 2).

Caulastraea corals are easy to keep in aquariums (Delbeek and Sprung, 1994). They can live on sand and form large patches of over 5 m across (Delbeek and Sprung, 1994; Veron, 2000). Because of their phaceloid colony shape, often with bifurcating polyps, they can easily be broken or sawn in pieces, which make them suitable for cultivation as shown by the trade data (Fig. 9C).

Free-living, solitary mushroom corals of the genus *Fungia* consist of large polyps, which may occur in large, dense multi-species aggregations in the company of other free-living fungiid corals (Hoeksema and Matthews, 2011; Hoeksema and Benzoni, 2013). Live wild-caught *Fungia* corals were predominantly exported from Indonesia until 2017, after which Australia took over with maximum trade numbers that were two times higher (Fig. 10A). Owing to their remarkable shape, fungiids are also popular as dead coral skeletons in the curio trade (Bruckner, 2001).

The remaining genera of the top-15 are also common in shallow waters (Best et al., 1989; Veron, 2000). Some of them consist of foliaceous corals, such as *Turbinaria* (Fig. 12B) and *Echinophyllia*, whereas the other ones are mostly Indo-Pacific *Favia* (presently known as *Dipsastraea*) and *Platygyra*.

4.4.2. Taxa reported at species level

Coral trade reported at species level pertains to species that have to be reported at species level instead of genus, or may concern monospecific genera, or genera with only one commercial species (Table 2). Some exporting countries issue permits with names at species level, which may be copied in trade records by the importing country, while reporting at genus level suffices.

Trachyphyllia geoffreyi and *Catalaphyllia jardinae* were the most-traded coral species, both mainly wild-sourced with a very small proportion of cultivation specimens, and both first predominantly exported from Indonesia and later from Australia (Fig. 9A and B). Large specimens are colourful, free-living and flabello-meandroid, with their tapering base buried in sandy substrate below reef slopes and their top covered by thick fleshy tissue (Hoeksema, 1993; Bruckner, 2002a). They are difficult to cultivate, although *C. jardinae* has been reported to reproduce asexually in captivity (Delbeek and Sprung, 1994). Both species are hardy when kept in aquariums (Delbeek and Sprung, 1994), implying that they may be long-lived and do not need to be replaced frequently.

Two *Euphyllia* species (*E. glabrescens* and *E. cristata*) and two *Fimbriaphyllia* species (*F. ancora* and *F. paraancora*) are among the 15-most traded species (Table 2). First Indonesia and later Australia were the most dominant exporting countries of W-corals (Fig. 7A–D). Only one of these four species (i.e., *E. cristata*) is rarely cultivated (Fig. 7C), similar to *E. divisa* (Fig. 7E), but in contrast to *F. yaeyamaensis* and *F. paradivisa,* which are mostly traded as F-corals but not in large quantities (Fig. 7F and G). This variation may be related to Indonesia's export quotas for W-corals, which were, for example, relatively high for *E. cristata* in 2021 (n = 12,000) and much lower for *E. divisa* (n = 600), *F. yaeyamaensis* (n = 0) and *F. paradivisa* (n = 1800) (Kusumo et al., 2023). Some euphyllids may be relatively easy to cultivate because of their morphology, such as *E. glabrescens* (Fig. 7A), which has thin phaseloid corallites that can easily be cut, whereas *F. divisa* with little trade in F-corals (Fig. 7E) has wide flabello-meandroid corallites (Veron, 2000). In addition, cultivated *E. glabrescens* is known to be very fast-growing (Johan et al., 2023), which may also explain why it much cultivated. All these euphylliid species are popular because of their fleshy polyps and large tentacles extending during daytime and darkness (Delbeek and Sprung, 1994; Sprung, 1999). They are generally found in shallow reef environments but considered uncommon (Veron, 2000; Waheed et al., 2015). *Euphyllia* and *Fimbriaphyllia* corals are hardy when kept in aquariums (Delbeek and Sprung, 1994).

Heliofungia actiniformis is exceptional among mushroom corals because of its very long tentacles. This feature may explain why it is popular in the aquarium trade (Knittweis et al., 2009a, 2009b, Table 2). This species was predominantly exported from Indonesia with a peak of over 40,000 specimens in 2005 (Fig. 10B). It is unclear whether the declining trade numbers after that year were caused by overfishing or by decreasing export quotas. Indonesia's position as major exporter of wild-sourced specimens was taken over by Australia. There was little trade in cultivated specimens, which may be related to the fact that specimens of *H. actiniformis* do not regenerate as their original, circular shape after being cut in pieces. Asexual reproduction by budding may have better results (Hoeksema, 1989; Sayco et al., 2024), but this may not yet be applied much in the aquarium industry. *Polyphyllia talpina* is an elongate coral covered by many small tentacles, also in daytime. Its trade pattern is similar to that of *H. actiniformis*, except that numbers were about 80% less and that Australia did not play a major role herein (Fig. 10C). Both species are moderately common on reef flats and slopes but *H. actiniformis* has a more restricted distribution range (Hoeksema, 1989, 2012). In contrast to *P. talpina*, *H. actiniformis* cannot easily be kept in aquariums, which may cause a large turnover as long as it remains popular in demand (Delbeek and Sprung, 1994).

Plerogyra sinuosa and *Blastomussa wellsi* (mostly reported as *Blastomussa* spp.) were initially predominantly exported from Indonesia and later from Australia (Table 2; Fig. 11A and B). Both species have large, fleshy polyps. They are not common and usually occur on reef slopes (Veron, 2000) and are moderately easy to keep in aquariums (Delbeek and Sprung, 1994). This implies that they may not be replaced frequently once they are established. *Physogyra liechtensteini* and *Nemenzophyllia turbida* were almost exclusively exported from Indonesia and showed an important decline is sales (Fig. 11C and E), whereas *Plerogyra simplex* is less popular (Fig. 11D). *Physogyra lichtensteini* has a similar ecology and aquarium care as *Plerogyra sinuosa*. *Nemenzophyllia turbida* is common on lower, muddy reef slopes (Bruckner and Borneman, 2006; Waheed and Hoeksema, 2013) and is difficult to keep in aquariums (Delbeek and Sprung, 1994).

Goniopora stokesi is an uncommon species that usually can be found as free-living individuals on patches of sandy substrates within its large distribution range (Hoeksema and Waheed, 2011a; Reimer et al., 2020; Samimi-Namin et al., 2025). *Goniopora lobata* is more common and usually occurs on reef slopes (Veron, 2000). Both species are difficult to keep in aquariums (Delbeek and Sprung, 1994), which implies that they may need to be replaced frequently.

Micromussa lordhowensis, *Homophyllia australis*, and *H. bowerbanki* are popular coral species, which were nearly exclusively exported from Australia (Fig. 8B–D; Table 2), where they are locally common in shallow subtropical areas (Veron, 2000). *Homophyllia australis* is difficult to keep alive in aquariums (Sprung, 1999). *Moseleya latistellata* was only exported from Australia (Fig. 8E), where it occurs as an uncommon species on muddy seafloors exposed to low tides (Veron, 2000).

Cynarina lacrymalis and *Acanthophyllia deshayesiana* were mainly exported from Indonesia and recently particularly from Australia (Fig. 8G and H). They can be found as free-living corals on sandy reef bases (Best and Hoeksema, 1987) and are relatively easy to keep in aquariums (Delbeek and Sprung, 1994; Sprung, 1999).

Among dendrophylliids, most species were predominantly exported from Indonesia, with the exception of *Duncannopsamia peltata*, which was almost exclusively exported from Indonesia (Fig. 12C) and *D. axifuga*, which was entirely exported from Australia (Fig. 12F). Both species may occur in turbid water, the first one as a common species in shallow water and the latter one as rare species in water deeper than 20 m (Veron, 2000). Both species are easy to maintain in aquariums (Delbeek and Sprung, 1994).

4.5. Extinction risks of the most-traded coral taxa

4.5.1. The IUCN Red List of threatened species

CITES-listed species can be evaluated according to their threat status (Challender et al., 2023). Scleractinian corals have been assessed by the IUCN in 2006 and in 2022/2023, and were officially red-listed in 2008 and 2024 (Carpenter et al., 2008; Gutierrez et al., 2024). Among the 15 most-traded taxa reported at species level (Table 3), *Micromussa lordhowensis* was listed as EN (Endangered), *Homophyllia australis* as VU (Vulnerable), and the rest as LC (Least Concern) (IUCN, 2025).

Although biological resource use was mentioned as a threat to 691 of the 874 evaluated species, apparently no distinction was made between species that are popular in the aquarium trade and those that were not (IUCN, 2025). Since coral fisheries is done by hand-picking, allowing it to selectively target popular species, it is recommended that future Red List assessments could take a more species-specific approach with regard

Table 3
IUCN Red list categories expressing threat status for the 15 most-traded coral species (Table 2) according to assessments in 2006 (Carpenter et al., 2008) and 2022/2023 with upgrading (↑) or downgrading (↓) (IUCN, 2025): LC = Least Concern; NT = Nearly Threatened; VU = Vulnerable; EN = Endangered.

	Coral species	2006	2022/2023
1.	*Trachyphyllia geoffroyi*	NT	LC ↓
2.	*Catalaphyllia jardinei*	VU	LC ↓
3.	*Euphyllia glabrescens*	NT	LC ↓
4.	*Fimbriaphyllia ancora*	VU	LC ↓
5.	*Heliofungia actiniformis*	VU	LC ↓
6.	*Plerogyra sinuosa*	NT	LC ↓
7.	*Goniopora stokesi*	NT	LC ↓
8.	*Goniopora lobata*	NT	LC ↓
9.	*Euphyllia cristata*	VU	LC ↓
10.	*Homophyllia australis*	LC	VU ↑
11.	*Micromussa lordhowensis*	NT	EN ↑
12.	*Duncanopsammia axifuga*	NT	LC ↓
13.	*Cynarina lacrymalis*	NT	LC ↓
14.	*Fimbriaphyllia paraancora*	VU	LC ↓
15.	*Blastomussa wellsi*	NT	LC ↓

to coral exploitation, as done in the assessment of 2006.

During the 2006-assessment, 13 of the 15 most-traded coral species had higher conservation priorities, either NT or VU. For example, *Trachyphyllia jardinae* was considered NT (Nearly Threatened) and *Catalaphyllia jardinae* was considered VU in 2006 (Carpenter et al., 2008), whereas both of them were downgraded to LC in 2023 IUCN, 2025). In contrast, *Homophyllia australis* was considered the only coral marked as LC in 2006, but became upgraded to EN in 2022, and *Micromussa lordhowensis* was upgraded from NT to EN (Carpenter et al., 2008; IUCN, 2025). *Acanthophyllia deshayesiana* (Fig. 8I) has not yet been evaluated (IUCN, 2025) after it became separated from *Cynarina lacrymalis* in 2016 (Darus et al., 2016; Hoeksema and Cairns, 2025). The role of coral fisheries was also not considered (IUCN, 2025) for many species reported by CITES at genus level (Table 1). Since it appears that selective coral harvesting received less priority during the last IUCN evaluation, the Red List may have become a less useful tool in assessing the threat status of corals in the aquarium trade (Lovell and Sykes, 2025).

4.5.2. *The EDGE score (Evolutionarily distinct and globally Endangered)*

In addition to IUCN Red List criteria, the EDGE score applies phylogenetics to express the evolutionary distinctiveness and uniqueness to the threat status of taxa (Redding et al., 2010; Gumbs et al., 2023). The more isolated the phylogenetic position of a species, the greater the loss if it becomes extinct. By taking this aspect into account, more attention is given to the preservation of evolutionary lineages that contain unusual life-history and morphological traits (Redding and Mooers, 2006; Redding et al., 2010; Huang, 2012). When applied to scleractinians and based on the IUCN Red List of 2008, the two most-traded coral species, *Catalaphyllia jardinei* and *Heliofungia actiniformis* (Table 3), received the highest rank: whereas *Trachyphylliia geoffroyi* and *Blastomussa wellsi* were also highly ranked but received less priority (Curnick et al., 2015). These results indicate that EDGE scores could be useful in expressing the urgency of conservation needs in coral fisheries, although they are only applied to a selected number of species.

4.6. *Coral cultivation*

Although aquaculture is promoted as the best alternative to the fishing of marine ornamental species, not all species are suitable for this (Calado, 2017). Trade in cultivated coral specimens is rather new, starting to become successful after 2007 (Fig. 1). Indonesia has been the only country relying much on the export of cultivated corals. The increase of Indonesian exports of F-corals since 2007 coincided with the decline of trade in its W-corals until 2017, after which both of them decreased until 2019 (Fig. 2). It appears that the low export quotas of Indonesian W-corals (CITES Secretariat, 2025c) have been compensated by the exports of F-corals. Growing exports of both W-corals and F-corals since 2020 indicate that the quotas still left space for some additional export of W-corals, but not as much as the export of F-corals. For many Indonesian coral species in the aquarium trade, cultivation of has become more a replacement than a supplement to harvesting.

Coral cultivation in the aquarium industry is performed by means of fragmentation, for which a mother stock from natural populations is required. The fragments are cemented to a solid substrate, usually a piece of concrete or plastic, which is better for their survival (Leal et al., 2017). Cultivation by sexual reproduction is possible for some species (Leal et al., 2017), but this method has not yet been employed in the aquarium industry.

4.6.1. *Artificial fragmentation*

Fragmentation success is species-dependent because some species are fast-growing and can be fragmented continuously without fresh supply from natural populations, whereas others are slow-growing and not healing quickly. When demand is high, it is tempting to add newly collected specimens to replenish the mother stock. This can be demonstrated in offspring fragments of LPS species that still have their original, large primary polyp in place, since offspring fragments should only have smaller secondary polyps. The best cultivation success is achieved with SPS species, which usually are fast-growing and generating many new polyps while their fragmentation scars heal well. In contrast, most LPS species do not grow new polyps easily and their regeneration scars may remain visible, decreasing their attractiveness. In single-polyp species the polyp shape may become damaged by fragmentation. Branched and foliaceous corals can more easily be fragmented than massive ones. Massive corals can be sawed into pieces but the shape of the regenerating fragment may still not look natural.

There are opportunities for fraud by selling W-corals as F-corals (Janssen and Blanken, 2016). Fragmented corals are placed on an artificial base made of concrete or another substance, which is marked by a tag with coded information. By attaching fragments of wild-harvested corals or entire coral colonies to an artificial substrate, they are supposed to pass as cultivated corals (Bradley et al., 2022).

Because of an unsuitable coral shape, slow regeneration process, imperfect scar-healing, and an unnatural look, some coral species may not be successfully traded as cultivated specimens. For example, in the aquarium industry fragments of free-living mushroom corals are cemented to a piece of concrete (Fig. 14), whereas naturally fragmenting mushroom corals live unattached on sand or rubble (Hoeksema and Gittenberger, 2010; Heintz and Laboute, 2020). This may explain why cultivated mushroom corals are not in high demand (Fig. 10). Among SPS corals from Indonesia, species with a fragile branched and plate-formed shape, such as *Acropora*, *Montipora* and *Pocillopora*, are more easy to cut and more popular as F-corals than those of *Porites*, which are either massive or have strong branches (Fig. 5).

LPS corals of the family Lobophyliidae can be sawn in pieces, such as *Acanthastrea* spp. (Fig. 8A), or have their large vase-shaped polyps broken off, such as *Lobophyllia* spp. *sensu stricto* (Fig. 8F), but they are not popular as cultivated specimens. The same accounts for Plerogyridae (Fig. 11), which has species with the same colony morphologies as Lobophylllidae (Fig. 8).

Corals consisting of single, large free-living polyps are also not commonly sold as cultivated specimens, such as *Trachyphyllia geoffroyi* (Fig. 9A), *Catalaphyllia jardinei* (Fig. 9B), and *Duncanopsammia axifuga* (Fig. 12F) which are very popular as W-corals. Indonesian *Caulastraea* corals have smaller polyps that branch and can easily be cultivated but they are equally popular as wild-caught specimens (Fig. 9C).

It is unclear why cultivated Dendrophylliidae corals are not popular in the trade (Fig. 12), because plate-shaped specimens with small polyps (e.g., *Turbinaria* spp.) and corals with larger polyps and branching or massive skeletons (e.g., *Dendrophyllia* spp., *Duncanopsammia axifuga*, *Eguchipsammia* spp., *Tubastastraea* spp.) can easily be broken or cut.

Fig. 14. False mariculture of the mushroom coral *Polyphyllia talpina* from Indonesia. (A, B) A piece of live-harvested coral glued to an artificial substrate seen from above (A) and aside (B). The fragment was part of a complete individual and has an unnatural appearance, only identifiable by its tentacles. (C) For comparison, an undamaged free-living specimen on rubble in its natural habitat.

4.6.2. Potential role of natural fragmentation and budding

Apart from *Acropora* spp. (Fig. 5A) and some other branching coral species (Arvedlund et al., 2003), there appears to be little interest in the specific use of fragile corals in coral cultivation, in particular those that can easily become fragmented in natural conditions. Some *Acropora* corals are known to have branches that break easily during turbulence and attach themselves to substrates (Guest et al., 2011; Lewis et al., 2022, 2025; Huang et al., 2023), which may be one of the reasons why they are so common on coral reefs (Highsmith, 1982; Wallace, 1985). Corals of other species also break easily but they do not need to attach themselves because they can survive easily as free-living fragments on unconsolidated substrates, such as sand and rubble. Other examples of natural fragmentation have been observed in corals with branching polyps of the family Dendrophylliidae (Mehrotra et al., 2023). Well-known examples of fragile dendrophylliid corals are *Eguchipsammia* spp. (Tempera et al., 2015) and *Duncanopsammia axifuga* (Subhan et al., 2022), both showing high trade numbers (Fig. 12D and F).

Various species of free-living mushroom corals are good examples, since they are known to be very successful in asexual reproduction, resulting in large, densely covered fields of one or two species. They can achieve this by four different mechanisms: 1) Species with thin, fragile skeletons, such as *Halomitra* spp., *Polyphyllia hiberniae* and *Zoopilus echinatus* break easily by external force and form high concentrations of large individuals (Littler et al., 1997; Hoeksema and Gittenberger, 2010; Heintz and Laboute, 2020); 2) *Cycloseris* species, previously known as *Diaseris* spp., can apply repetitive self-fragmentation, also known as autotomy (Yamashiro and Nishihira, 1998; Hoeksema and Waheed, 2011a), resulting in high concentrations of small, regenerating specimens (Hoeksema et al., 2018, 2019a); 3) budding from a post-detachment settlement stalk (Hoeksema and Yeemin, 2011); 4) budding from a mother coral (Gilmour, 2004; Hoeksema, 2004). The second example of budding is also used by the poritid *Goniopora stokesi* (Hoeksema and Waheed, 2011b; Reimer et al., 2020), which is popular in the aquarium industry (Fig. 6A).

4.7. Taxonomic discrepancies in trade reporting

The CITES nomenclature of stony corals as presented in Species+ (UNEP-WCMC, 2025a) is over 25 years old (UNEP-WCMC, 2012). It is almost entirely based on works by Cairns et al. (1999) and Veron (2000). In that time, scleractinian classification was only based on morphological characters, but with the recent developments of molecular techniques in scleractinian phylogeny reconstructions, there have been many taxonomic changes (Kitahara et al., 2016; Quek et al., 2023; Cowman et al., 2026). These changes are continuously updated in the World List of Scleractinia of WoRMS (World Register of Marine Species) (Hoeksema and Cairns, 2025), which also keeps track of invalidated synonyms. It is understandable that in the aquarium industry, names are not continuously updated, but it may be confusing if export reports on corals in the international aquarium trade do not use similar names for the same species, like Indonesia using the CITES nomenclature of Species+ (Hadi et al., 2020) and Australia using WoRMS (Pratchett et al., 2020a). These inconsistencies may become more problematic if exporting countries and importing countries use different nomenclatures for the same transaction. It is also more difficult to compare CITES trade data with scientific field data relevant for the managaement of coral populations. This inconsistency is surmountable since Species+ and WoRMS both mention taxonomic synonyms enabling cross-referencing. The trade data for the present study were based on Species + nomenclature and translated to WoRMS nomenclature if necessary. Thus, the disadvantage of an outdated coral taxonomy in trade reports, making comparisons with scientific data more complicated, is compensated by linking synonyms. Nevertheless, since most coral taxa are reported at genus level, the effects of altered genus names of coral taxa moving from one genus to another have become less transparent.

For example, some species moved from one genus to another, like the split-up of *Caulastraea* with the resurrection or *Astraeosmilia* (Fig. 9C; Arrigoni et al., 2021). Or, when many former *Fungia* spp. (Fig. 10A), became divided over *Fungia* and five other genera (Gittenberger et al., 2011). Species names also changed after genus mergers, like when *Symphyllia* spp. merged with *Lobophyllia* spp. (Fig. 8G; Huang et al., 2016). Some species also just moved from one genus to another without splits or mergers, like *Nemenzophyllia turbida* (Fig. 11E) becoming *Plerogyra turbida* and then *N. turbida* again (Hodgson and Ross, 1982; Veron and Hodgson, 1989; Veron, 2000).

Name changes may become more problematic when threatened coral species are allowed to be reported at genus level, which concerns almost all Scleractinia except those of the genera *Euphyllia*, *Plerogyra*, and *Physogyra* (CITES Secretariat and UNEP, 2002; 2013), and monospecific genera, like *Cynarina lacrymalis* (Fig. 8H) and *Acanthophyllia deshayesiana* (Fig. 8I). When a country exports the popular species *Micromussa lordhowensis* (Fig. 8A), the importing country may report it as *Acanthastrea* spp. because its CITES-listed name is *A. lordhowensis*. Reporting as *Acanthastrea* spp. will conceal the popularity of this species and the possible threats caused by coral harvesting. In this case, it would be better to report the species by its own name, as in *Euphyllia*. Five of ten *Euphyllia* spp. became *Fimbriaphyllia* spp. (Fig. 7), after a taxonomic vision of *Euphyllia* (Luzon et al., 2017). This does not cause a problem because all species concerned have to reported at species level in permits. A similar problem arises when a new coral species is described, which appears to be popular in the trade but with a wrong name. For example, *Blastomussa vivida* was described recently (Benzoni et al., 2014) and is reported either as *Blastomussa* spp. (Fig. 11A) or *B. welssi*, which indicates that its own correct name should be added to Species+ (UNEP-WCMC, 2025a) and that its trade should be reported at species level since the few known *Blastomussa* species can be distinguished relatively easily.

Because of recent taxonomic revisions, corals also became classified under different family names. In several studies, entire genera moved to other families, such as *Alveopora* from Poritidae to Acroporidae, *Blastomussa* from Mussidae to Plerogyridae, *Galaxea* from Oculinidae to Euphylliidae, *Physogyra*, and *Plerogyra* from Caryophylliidae to Plerogyridae, *Catalaphyllia* from Caryophylliidae to Merulinidae, and *Euphyllia* from Caryophylliidae to Euphylliidae (UNEP-WCMC, 2012; Hoeksema and Cairns, 2025). Also, some species moved to other genera and other families at the same time, like *Coscinarea wellsi*, of the family Coscinariidae (Benzoni et al., 2012a), and *Psammocora explanulata*, of the family Psammocoridae (Benzoni et al., 2010), which both moved to *Cycloseris* of the family Fungiidae (Benzoni et al., 2012b). These taxonomic changes make it difficult to identify traded corals based on morphological characters, which is the basis of the CITES nomenclature, instead of the one presently used by WoRMS, which is based on phylogeny.

4.8. Look-alikes

Species identification is an important problem in reporting trade data, especially when it concerns species of large genera, such as *Acropora* (Quek et al., 2024), which has about 140 valid species (Hoeksema and Cairns, 2025). At genus level there are also several coral taxa that strongly resemble other ones, so-called “look-alikes”, which could result in the misidentification of traded specimens (Alfino and Roberts, 2019; Bradley et al., 2022; Challender et al., 2023).

A clear example of look-alikes in the coral trade is the morphological similarity of the genera *Alveopora* (family Acroporidae) and *Goniopora* (family Poritidae). They resemble each other because of their stalked, inflatable polyps, but differ in the number of tentacles per polyp (Bruckner, 2002a; Bradley et al., 2022). *Goniopora* is much more popular in the aquarium industry (Fig. 6), but it is possible that its trade numbers also include *Alveopora* and vice versa.

Acanthophyllia deshayesiana and *Cynarina lacrymalis* (family Lobophylliidae) were considered synonyms for a while because of their morphological similarity, both of them being free-living, solitary corals with fleshy polyps of equal size (Best and Hoeksema, 1987), but application of morphometrics revealed detailed differences in skeleton morphology (Darus et al., 2016). No molecular studies are known that corroborate their distinction at genus level. Both species show high trade numbers, but it is unclear whether *C. lacrymalis* (Fig. 8H) has higher numbers because it is more abundant and easier to collect than *A. deshayesiana* (Fig. 8I) or because its name is more commonly known and used in misidentifications.

A similar misidentification problem consists of species traded as *Cycloseris* spp. (Fungiidae) but belonging to other mushroom coral genera. For example, *Lithophyllon spinifer* (Fig. 13D) was originally known *as Fungia spinifer* (see Gittenberger et al., 2011) and should be CITES-listed under *Fungia* spp. (Fig. 10A). In the trade it is identified as *Cycloseris* sp. because it is also known as *Cycloseris colini*, following Veron (2000), which is an invalid synonym (Hoeksema and Cairns, 2025). Because of its colourful appearance it is popular in the aquarium trade but reported as *Cycloseris* spp. it may not be noticed in the trade records. On photographs, the mushroom coral *Heliofungia actiniformis* can easily be confused with the euphylliid *Euphyllia glabrescens* because of their almost-identical, large tentacles, but both species can easily be separated when their tentacles are retracted, revealing the very different skeleton shapes (Bradley et al., 2022).

Species of the genera *Dendrophyllia*, *Eguchipsammia*, and *Tubastraea*, all of the family Dendrophylliidae (Arrigoni et al., 2014), are moderately common in CITES trade records (Fig. 12A, D, and E), but can easily be confused with one another (Bruckner, 2002a; Bradley et al., 2022). Because these species are azooxanthellate, they are not considered reef-building (hermatypic) and receive little or no attention in many reef-coral fauna lists (Best et al., 1989; Veron and Hodgson, 1989; Veron, 1993; Huang et al., 2015) and identification guides (Nishihira, 1991; Veron, 2000; Claereboudt, 2006; Turak and DeVantier, 2011). In an Indonesian publication on coral cultivation (Suharsono et al., 2013), an illustration of a *Tubastraea* species is shown, wrongly identified as *Dendrophyllia fistula*, a superseded combination name for *Eguchipsammia fistula* (Hoeksema and Cairns, 2025). Over the period 1990–2021, Indonesia reported the export of 314,000 wild-caught specimens of *Eguchipsammia* and no *Dendrophyllia*, while importers reported 107,000 and 13,353, respectively (UNEP-WCMC and CITES Secretariat, 2025a, Fig. 12A and D). Part of this difference can be explained by an EU-import ban for Indonesian *Eguchipsammia* since July 2015 (UNEP-WCMC, 2025a), implying that records from export permits did not result in import records. The absence of *Dendrophyllia* export records vs. 13,353 import records, suggests, that they could have been exported as misidentified *Eguchipsammia*. This possibility is supported by a recent paper on Indonesian coral harvesting, which mentions export quotas issued for *Eguchipsammia* and *Tubastraea* but none for *Dendrophyllia* (Kusumo et al., 2023).

4.9. The unknown impact of coral fisheries on coral reef biodiversity

Coral harvesting is not only a threat to reef coral diversity but also to coral reef biodiversity in a wider sense. Coral species that are popular in the aquarium industry are threatened by overfishing (Knittweis et al., 2009b; Knittweis and Wolff, 2010; Ferse et al., 2014). Many associated reef species use corals as a substrate or as shelter and therefore contribute to the entire coral reef species richness; if their hosts are threatened, this associated fauna is also at risk (Stella et al., 2011; Hoeksema, 2017; Montano, 2020, 2022).

These relationships can be very specialized, with one coral associate depending on one or a few host species (van der Schoot and Hoeksema, 2024). For example, the mushroom coral *Heliofungia actiniformis*, which is popular in the coral trade (Knittweis et al., 2009a, 2009b; Knittweis and Wolff, 2010, Fig. 10B) because of its long tentacles, enabling it to act as a the only host for a couple of animals, including a pipefish and some shrimps (Hoeksema and Fransen, 2011; Hoeksema et al., 2012). Thus, the need to manage coral fisheries as a conservation strategy is also important to protect unique coral-associated fauna, even if they are considered parasitic, because the ecological role in their environment is usually not well understood (Carlson et al., 2020; Mehrotra et al., 2024b).

It is also worth noting that some coral-associated species are considered pests in the aquarium industry, causing the death of corals kept in storage, such as some barnacles, flatworms, sea slugs, and sea spiders (Barton et al., 2020, 2021; Cabrito et al., 2022; Krol et al., 2023). They are also considered a risk to natural coral reefs if released by accident, which is why the aquarium industry is considered a possible vector in the introduction of non-native, invasive species and a risk to biosecurity (Padilla and Williams, 2004; Morrisey et al., 2011; Akmal et al., 2020).

5. Conclusions and recommendations

Coral harvesting is a unique threat to coral reef biodiversity because it targets specific taxa, risking overfishing (Tables 1 and 2). To understand the effect of harvesting on these targeted species, their fished populations need to be monitored. If this is not done, no effective non-detriment-finding can be made and trade restrictions may be necessary, like strict export quotas or import bans.

Coral cultivation appears to be an effective alternative to the fishing of wild corals, but cannot be applied easily to all species. It requires a strict control on the use of mother stock instead of wild-caught corals in order to prevent white-washing.

Based on the analyses of the present study, in particular the taxa with large and fleshy polyps are in need of better management in the fisheries of wild-sourced corals because of strong recent increases in trade records and their ecological role as host species for associated fauna (see Table 2): Corals with stalked polyps: *Alveopora* spp. and *Goniopora* spp.; Euphylliidae: *Euphyllia glabrescens*, *Fimbriaphyllia ancora*, *F. divisa*, and *F. paraancora*; Lobophylliidae: *Acanthastrea* spp., *Acanthophyllia deshayesiana*, *Cynarina lacrymalis*, *Homophyllia australis*, *H. bowerbanki*, *Lobophyllia* spp., *Micromussa lordhowensis*, and *Moseleya lastistellata*; Merulinidae: *Catalaphyllia jardinei* and *Trachyphyllia geoffroyi*; Fungiidae: *Heliofungia actiniformis* and various genera that are CITES-listed as *Fungia*; Plerogyridae: *Blastomussa* spp. and *Plerogyra sinuosa*; Dendrophylliidae: *Duncanopsammia axifuga*.

Tubastraea spp. (Dendrophyllidae) also show a large increase in exports, but they are locally abundant, particularly on artificial substrates, which also explains why they are successful as invasive species in the West Atlantic (Creed et al., 2017). Other coral taxa do not show steep increases in trade, or are widespread and locally very common, and therefore are less urgently in need of trade management.

In the future, CITES may consider to report additional coral taxa at species level instead of genus level if this does not hamper their identification. Australia in particular has started to report more corals at species level instead of genus level, which can be useful because (1) some species within a genus are more distinct than their congeners, (2) they can move taxonomically from one genus to another, and (3) some rare or popular species in a genus may need more conservation focus.

Some research could be applied to support the development of conservation policies. For example, more attention should be given to species that are difficult to keep and short-lived in captivity (see Delbeek and Sprung, 1994; Sprung, 1999). When aquarists keep on buying short-lived coral species without knowing about their vulnerability or short lifespan, this may affect fishing pressure. It would also be interesting to study the effects of changing retail prices on coral trade and the role of aquarium hobbyists in cultivating corals (Muka, 2022).

In the light of the present study, there should be an analysis of the effectiveness of export quota and trade bans, and whether these cause shifts towards the trade in other, less popular species, imports from alternative source countries, or more substitution by cultivated corals. More research is needed on the relationship between harvest data and trade data to see how much is lost by mortality, how much is sold at domestic markets, and how much is exported. This may also show how effectively trends in CITES trade data can reflect trends in harvesting data. Finally, it is recommended that selective harvesting of corals for the aquarium trade will be used again as criterion to differentiate among coral species during future assessments for IUCN red-listings.

Finally, as long as the long-term effects of coral harvesting on coral populations remain unknown, the management of the aquarium industry should be more cautious. This paper should act as a wake-up call, making managers aware of the need of annual monitoring and reporting of size/density fluctuations in harvested coral populations. We need to understand if sudden drops in trade data are related to environmental causes, such as overfishing and other stressors (e.g., coral bleaching, diseases, predators), or if these drops are caused by management and economic policies, such as trade quotas, bans, and tariffs. In this regard we also need to remember that CITES trade data do not take illegal exports into account. Long-term, invariably repeated trade quotas are not helpful in the management of harvested coral populations; they should be adapted annually, based on the present condition of the harvested populations. Coral cultivation may help to decrease the fishing pressure, but its success depends on the species concerned since small-polyped, fast-growing corals can be cultivated more easily than slow-growing, large-polyped corals. This requires species-specific control of allegedly cultivated corals by CITES authorities before these become exported.

Funding

This study did not receive any external funding

Declaration of competing interest

The author declares that he has no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The author is grateful to members of the Scientific Advisory board of CITES Netherlands for support and to two anonymous reviewers for their constructive comments, which helped to improve the manuscript.

Appendix A. Electronic Supplementary Material (ESM)

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ocecoaman.2026.108111.

Data availability

All data has been added as Electronic Supplementary Material.

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