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The role of aquaculture in the international trade of giant clams (Tridacninae) for the aquarium industry (2001–2019)

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ABSTRACT

An overview over the international trade in live giant clams (Bivalvia: Tridacninae) from 2001 to 2019 was made based on worldwide import data from the CITES Trade Database. A distinction was made between trade records of wild-caught clams and maricultured ones. A general decline in the trade of wild giant clams was observed. Since these bivalves naturally live attached to rocky substrate in coral reefs and their forceful removal is harmful to surrounding corals, this trend helped to prevent damage to their natural environment. Possible reasons behind this decline are lower population numbers, trade restrictions, and a decrease in demand. Trade in wild-caught *Tridacna crocea* decreased, whereas that of *T. maxima* increased, taking over the former's position as most popular species. From 2015 onwards, over 50% of the source was made up by aquaculture, up to 2019. Aquaculture of live giant clams can be profitable, but there are still obstacles to overcome in order to ensure stable production numbers and long-term profit. With more research and support from governments, aquaculture can help to take pressure off wild populations of giant clams that are already suffering from exploitation for the seafood market and souvenir industry, and also from habitat degradation due to climate change and other anthropogenic disturbances.

1. Introduction

Giant clams (Tridacninae) are important ecological engineers in coral reef regions, which supply food, shelter, and substrate to other organisms and contribute to the general reef complexity (Vicentuan-Cabaitan et al., 2014; Neo et al., 2015, 2017; van der Schoot et al., 2016; van Wynsberge et al., 2017; Mehrotra et al., 2022; de Guzman et al., 2023). They form a monophyletic group in the family Cardiidae (Herrera et al., 2015; Ma et al., 2022). Most species are found on coral reefs throughout the Indo-West Pacific, but a few species have more limited ranges (Wells, 1997; Tan et al., 2022a; Neo, 2023). They are restricted to shallow depths as they depend on symbiotic unicellular algae (Symbiodiniaceae dinoflagellates) as major source of carbon, which need sun light to photosynthesise (LaJeunesse et al., 2018; Rossbach et al., 2019). Consequently, most species can be found at depths down to 20 m (Tiavouane and Fauvelot, 2017; Neo et al., 2017; Liu et al., 2020b), whereas there are two (*T. crocea* and *T. mbalavuana*) that may also occur just below 30 m (Braley, 1992a; Jantzen et al., 2008; Mies, 2019). The symbiodiniaceans live within the mantle of the giant clams, which are fully exposed when the valves are open (Yonge, 1975). It also allows the mantle to show its strikingly vivid colours caused by 'iridocytes' (or 'iridophores') and the clam's pigmentation (Griffiths et al., 1992; Rossbach et al., 2020; Wang et al., 2021; Ip et al., 2022; Li et al., 2022), which make them attractive as ornamental invertebrates in the aquarium industry (Wabnitz et al., 2003; Fartherree, 2023). As the name 'giant clams' already entails, some species can grow to considerable sizes, with *T. gigas* reaching lengths over 1 m, although they are taxonomically more related to cockles than clams in the strict sense of the word (Schneider and Foighil, 1999; Schneider, 2002).

Giant clams are hermaphrodites and reach sexual maturity relatively late (Yamaguchi, 1977; Hesslinga and Fitt, 1987; Lucas, 1994; Ellis, 1998; Soo and Todd, 2014). Depending on the species, male maturity is reached between two to three years and female maturity later, between three to four years (Lucas, 1994). Their reproduction strategy is broadcast spawning events where spawning of one individual triggers others to join (Gilbert et al., 2006b; Soo and Todd, 2014). The exact spawning stimulus is however not clearly identified, with the lunar cycle, changes in water temperature and water flow, and phytoplankton blooms debated as possible triggers (Braley, 1984; Soo and Todd, 2014; van Wynsberge et al., 2016).

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Because of their sessile nature, large adult size and striking colouration as well as their occurrence in shallow waters, giant clams are easy to collect by fishermen (Beckvar, 1981; Hardy and Hardy, 1969; Gilbert et al., 2006b; Ullmann, 2013). Traditionally, they are mainly harvested for their meat as a food source and their shells as decorative material (Beckvar, 1981; Heslinga et al., 1984; Lucas, 1994; Wells, 1997; Lachapelle, 2020; Moore, 2022). The demand for giant-clam meat mostly affects the larger species, such as *T. gigas* and *T. derasa*, which are most endangered and in urgent need of conservation measures (Beckvar, 1981; Gilbert et al., 2006b; Neo et al., 2017). In the last three decades giant clams have also been used as living ornamentals in the aquarium trade (Hart et al., 1998; Wabnitz et al., 2003; Lachapelle, 2020). Since the 1980s, species with the most colourful mantles, *T. crocea* and *T. maxima,* are the most popular in the aquarium trade (Hart et al., 1998; Mies et al., 2017; Zhou et al., 2021).

Aquaculture of giant clams is often listed as an option to reduce fishing pressure on wild giant clams and additionally give an alternative for local fishermen to generate income (Bell et al., 1997; Lucas, 1997; Hart et al., 1998; Hean and Cacho, 2002). Aquaculture is also reported as being simple since the clams are nearly autotrophic by depending on their symbionts for growth and do not need much additional feeding (Heslinga et al., 1984; Crawford et al., 1987; Lucas, 1997; LaChapelle, 2020). Depending on ownership and management, *Tridacna* farms may have different objectives. Those that are government-owned usually focus on food production, the restocking of wild populations, and supply for the aquarium trade; those managed by NGOs mainly focus on restocking wild populations; and privately owned aquafarms aim at generating profit through the aquarium trade (Davila et al., 2017; Mies et al., 2017; Moorhead, 2018; Moore, 2022).

Consumption of *Tridacna* meat is a tradition that mainly happens within the countries where they are harvested (Neo, 2023), but demand for the aquarium international trade has become an additional threat (Mies et al., 2017). According to the IUCN Red List of Threatened Species, the conservation status of four species is considered "vulnerable" (VU), of one "of least concern" (LC), and of the rest is lower risk (conservation dependent) or not evaluated (Wells, 1997), but this evaluation was made in 1996 and needs updating (IUCN, 2023). Category LC means that a species is threated, but at a low level, whereas VU means that a species is facing a high risk of extinction in the wild and has a higher need for conservation (Rodrigues et al., 2006).

At present, there are 12 accepted tridacnine species (Fauvelot et al., 2020; MolluscaBase eds, 2023; Neo, 2023), although the application of novel molecular techniques has revealed that taxonomic species richness does not fully represent phylogenetic richness (Tan et al., 2022a). Some of the ten species were previously synonymized but have been resurrected and are now widely accepted, such as *T. noae* (Su et al., 2014; Borsa et al., 2015b, 2015a; Neo et al., 2018; Fauvelot et al., 2019; Marra-Biggs et al., 2022) and *T. elongatissima* (Fauvelot et al., 2020; Tan et al., 2022b; Velkeneers et al., 2022). In addition, there are potential other cryptic species that need further investigation (Huelsken et al., 2013; Hui et al., 2016; Liu et al., 2020b). Within single species, populations can be composed of various lineages, depending on gene flows that vary in their isolation from each other, which is partly determined by distance and the course of currents (Pappas et al., 2017; Keyse et al., 2018; Fauvelot et al., 2020). Such a genetic structure may be relevant for species that are popular in the aquarium industry because of their colour variation, such as *T. crocea*, which has a phylogeography that is well studied (Ravago-Gotanco et al., 2007; DeBoer et al., 2008, 2014; Kochzius and Nuryanto, 2008; Hui et al., 2017; Waheed et al., 2023).

The international trade of giant clams is regulated by CITES, short for Convention on International Trade in Endangered Species of Wild Fauna and Flora (Wells, 1997; CITES, 2023a). CITES was established in 1973 and defined all giant clams in 1985 as "vulnerable to exploitation but not yet at risk of extinction" (UNEP-WCMC and CITES Secretariat, 2023a). The species are listed in CITES Appendix II, concerning "species that are not necessarily now threatened with extinction but that may become so unless trade is closely controlled. It also includes so-called look-alike species, i.e. species whose specimens in trade look like those of species listed for conservation reasons" (https://cites.org/eng/app/index.php). Currently 184 parties have joined the convention, consisting of 183 countries plus the EU (CITES, 2023b). They report their exports and imports of the different giant clam species to the CITES Secretariat, which publish them in the CITES Trade Database (CITES Secretariat and UNEP-WCMC, 2022). Other groups of marine aquarium species that are listed in CITES are corals (Hoeksema and Arrigoni, 2020; Petrossian et al., 2020), seahorses (Koning and Hoeksema, 2021; Foster et al., 2022), and sharks (da Silva et al., 2019; Shiffman et al., 2021). Like giant clams, these animals and other traded marine ornamentals do not only suffer from exploitation for the aquarium industry but also for other markets (Dee, 2014; Pavitt et al., 2021).

The present study compares international trade numbers of both wild-caught and maricultured live giant clams registered via the CITES data base from 2001 to 2019. Its main objectives are to identify trends over time regarding the main target species and the main exporting and importing countries, looking at the exploitation of wild populations as well as aquaculture stock. An earlier study that used CITES data (Wabnitz et al., 2003) showed a general increase in the international trade of live Tridacninae from 1993 to 2001 and predicted a continuation of this trend. The expectation of a continuing trade increase is not supported by Rhyne and Tlusty (2012), who observed fluctuations in the international aquarium trade, eventually resulting in a declining trade, which they ascribed to changes in the global economy and to technological developments concerning cultivation in importing countries.

In the last decade, the EU has implemented suspensions and negative opinions on the import of several *Tridacna* species for a number of source countries (Cambodia, Cook Islands, Fiji, Marshall Islands, Micronesia, Mozambique, Palau, Solomon Islands, Tonga, Vanuatu, Vietnam) with regard to wild-caught animals (https://speciesplus.net/). This could have caused a decline in the trade of wild-caught giant clams, and favoured trade in cultivated animals. Mies et al. (2017) compiled data over 2012–2014 and noted that already in those three years approximately 50% of traded clams are aquacultured. So, there are reasons to hypothesize that the international trade in wild-caught Tridacninae will show declines due to trade restrictions. This can be replaced by more trade in acquacultured animals, but that may decrease again if traditional import countries start to cultivate themselves. The most likely scenario is that there may have been a general decline in the international trade in giant clams and a larger proportion of the remainder will consist of cultivated animals.

2. Material and methods

The currently accepted extant species within the subfamily Tridacninae are divided over two genera: *Tridacna* with ten species and *Hippopus* with two (Table 1; Fauvelot et al., 2020; Liu et al., 2020b; Tan et al., 2022b; MolluscaBase eds, 2023).

To assess the international trade in giant clams for the period from 2001 to 2019 a search was made in the CITES Trade Database (https://trade.cites.org/) for species listed with the family Tridacnidae (UNEP-WCMC and CITES Secretariat, 2023b), now considered subfamily Tridacninae within the family Cardiidae (MolluscaBase eds, 2023). Trade numbers are usually available from at least two years before the current year (CITES Secretariat and UNEP-WCMC, 2022), but it appeared that data for 2020 were also incomplete and therefore this year was excluded from the assessment.

The search of the CITES Trade Database was filtered by only including live specimens (LIV) regarding all sources and purposes. Annual import numbers were extracted by species, by export country, and by import country; then entered in a spreadsheet for calculating totals. To avoid double counts, re-exports were excluded in the analyses of source (wild and aquaculture). Although, trade numbers are usually reported in numbers of specimens, quantities were rarely reported in

Table 1
Giant clam species (*Tridacninae*) with their threat status based on the IUCN Red List of Threatened Species (Wells, 1997) and their trade status in the CITES Trade Database (CITES Secretariat and UNEP-WCMC, 2022).

Species	Conservation status (last assessed)	Trade status
Hippopus hippopus (Linnaeus, 1758)	Lower risk/conservation dependent (1996)	Traded
H. porcellanus Rosewater, 1982	Lower risk/conservation dependent (1996)	Not traded
Tridacna crocea Lamarck, 1819	Least concern (1996)	Traded
T. derasa (Röding, 1798)	Vulnerable (1996)	Traded
T. elongatissima Bianconi, 1856	Not evaluated	Not traded
T. gigas (Linnaeus, 1758)	Vulnerable (1996)	Traded
T. maxima (Röding, 1798)	Lower risk/conservation dependent (1996)	Traded
T. mbalavuana Ladd, 1934	Vulnerable (1996)	Negligible
T. noae (Röding, 1798)	Not evaluated	Negligible
T. rosewateri Sirenko & Scariato, 1991	Vulnerable (1996)	Not traded
T. squamosa Lamarck, 1819	Lower risk/conservation dependent (1996)	Traded
T. squamosina Sturany, 1899	Not evaluated	Not traded

weight unit (kg). These weight entries (25 out of 4881 = 0.5%) were excluded, as they were neglectable and incompatible with the other data. The trade numbers reported by importing and exporting countries usually differed substantially. There are two reasons for this. Firstly, some countries do not list their actual export numbers but those indicated on the export permits, which are usually higher than the numbers shipped abroad (Bruckner, 2001; Blundell and Mascia, 2005; Mies et al., 2017; Koning and Hoeksema, 2021). Countries are not obliged to report imports, but in case they do so, they register the usually lower import numbers. Secondly, some nations that export tridacnines are not parties of CITES and do not submit export numbers (CITES, 2023b). The data selected for the present study are therefore from countries that report actual import numbers to CITES. The data was split into live clams with purpose code "commercial" (T) and trade code "live" (LIV) that were either harvested from the wild (source code W) or produced through aquaculture. The latter consist of animals that are categorised as source codes "captive-bred" (C), "born in captivity" (F), or "ranched" (R) (UNEP-WCMC and CITES Secretariat, 2023b). Source code "unknown" (U) was excluded from the study. Source code R was considered aquaculture and not a separate category because its trade number for all species together was very low (n = 7367) over the period 2001–2019 (UNEP-WCMC and CITES Secretariat, 2023b). Ranching is distinct from captive-breeding in aquaculture because the stock is obtained from spat caught in the wild and reared in hatcheries for growth (Wells and Barzdo, 1991).

R-Studio (RStudio Team, 2022) was used to analyse the data. Raw data is presented in an Appendix as Electronic Supplementary Material).

3. Importance and trends of live animals in the international trade of giant clams

3.1. Live clams vs dead shells; import data vs export data

To understand the role of live giant clams (trade code LIV) in the international trade, it is important to compare their trade numbers with those of dead shells (trade code SHE). In this context, it is also relevant to compare how their import data differ with their export data. Most species show much higher importer-reported numbers than exporter-reported numbers for both live animals and shells over the years 2001–2019 (Table 2). Export records for live animals are 1.43 times higher than import records and import records for shells are 2.54 times higher. Based on import records of live animals and shells together (n = 2,413,245), trade in live clams constitutes 96%.

Table 2
Recorded numbers of Tridacninae spp. (*Hippopus* and *Tridacna*) from all sources in the international aquarium trade. Totals of importer-recorded and exporter-recorded numbers are divided over live animals (LIV) and shells (SHE) over the years 2001–2019 (UNEP-WCMC and CITES Secretariat, 2023b).

Species	Live animals		Shells	
	Import	Export	Import	Export
H. hippopus	20,503	5487	587	1737
H. porcelanus	–	–	14	1
T. crocea	708,390	703,433	3317	2666
T. derasa	283,379	67,754	14,593	5124
T. elongatissima	–	–	–	–
T. gigas	19,340	7911	66,702	8575
T. maxima	1,050,103	624,325	13,565	20,125
T. mbavavuana	1	–	–	6
T. noae	2	64	–	–
T. rosewateri	–	–	–	–
T. squamosa	224,346	201,702	8403	4039
T. squamosina	–	–	–	–
Total	2,306,064	1,610,674	107,181	42,273

3.2. Aquaculture: Captive bred vs born in captivity; import data vs export data

Aquaculture of giant clams mainly happens in two ways: (C) by captive breeding, in which animals are kept alive in a human-controlled environment during their entire live spans, and (F) by using mother stock that is taken from the wild for propagation in a human-controlled environment. The latter is expected to have more impact on the natural populations than the former.

The trade numbers show much variation among the six important cultivated giant clam species, and also differences between import and export records (Table 3). The higher importer-recorded numbers show slightly >40% C and nearly 60% F, and the exporter-recorded numbers show the opposite, 60% C and 40% F. Since the importer-recorded numbers are higher, they appear to be more complete and captive breeding could be more important than the use of wild-caught mother stock.

3.3. Trends: All giant clam species

Contrary to the historical trend (Wabnitz et al., 2003), the reported trade of giant clams decreased overall from 2001 until 2019 (Fig. 1A). The present peak in 2007 was higher than the previous one in 2001 (Wabnitz et al., 2003). The decreasing trade was demonstrated by a significant negative correlation (Fig. 1A). This trend appeared to be determined by lower imports of wild-caught individuals since the number from aquaculture remained relatively stable, shown by an insignificant rise. In 2012–2018, wild-caught clams subceeded aquacultured ones (Fig. 1A), but this ended in 2019 with a strong increase. Nevertheless, the balance over the entire period shows a negative correlation of the difference between wild-caught and aquaculture numbers in the import records (Fig. 1B).

3.4. Species trends: Wild-sourced specimens

In both decades, *Tridacna crocea* was the most imported wild-sourced species in the trade records, showing a peak in 2007 and a drop in 2009 (Fig. 2A). After 2012, imports decreased to low levels, showing the most dramatic decline of all species. *Tridacna maxima* was initially the second-most traded species but started to become dominant in 2013, after the decline in *T. crocea* trade. *Tridacna squamosa* (Fig. 2A) and *T. derasa* (Fig. 2B) were the third- and fourth-most imported wild-sourced species, but both of them showed a decrease in the trade after 2012 and 2009, respectively. The other species, *T. gigas* and *H. hippopus*, were traded in relatively low and shrinking numbers (Fig. 2B). The three most traded species (*T. crocea*, *T. maxima*, and *T. squamosa*) showed a

Table 3

Recorded numbers of Tridacninae spp. (*Hippopus* and *Tridacna*) from aquaculture, which were important in the international aquarium trade (Table 2). Totals of importer-recorded and exporter-recorded numbers are divided over captive-bred (C) and born in captivity (F), with their proportions (%) over the years 2001–2019 (UNEP-WCMC and CITES Secretariat, 2023b).

Species	Import				Export			
	C		F		C		F	
H. hippopus	5110	30%	11,958	70%	743	15%	4313	85%
T. crocea	42,092	39%	66,570	61%	16,327	28%	42,950	72%
T. derasa	77,553	44%	98,603	56%	72,693	68%	33,786	32%
T. gigas	5196	67%	2504	33%	6145	98%	100	2%
T. maxima	193,581	40%	286,547	60%	196,302	68%	91,561	32%
T. squamosa	39,876	45%	48,767	55%	20,856	35%	38,198	65%
Total	363,408	41%	514,949	59%	313,066	60%	210,908	40%

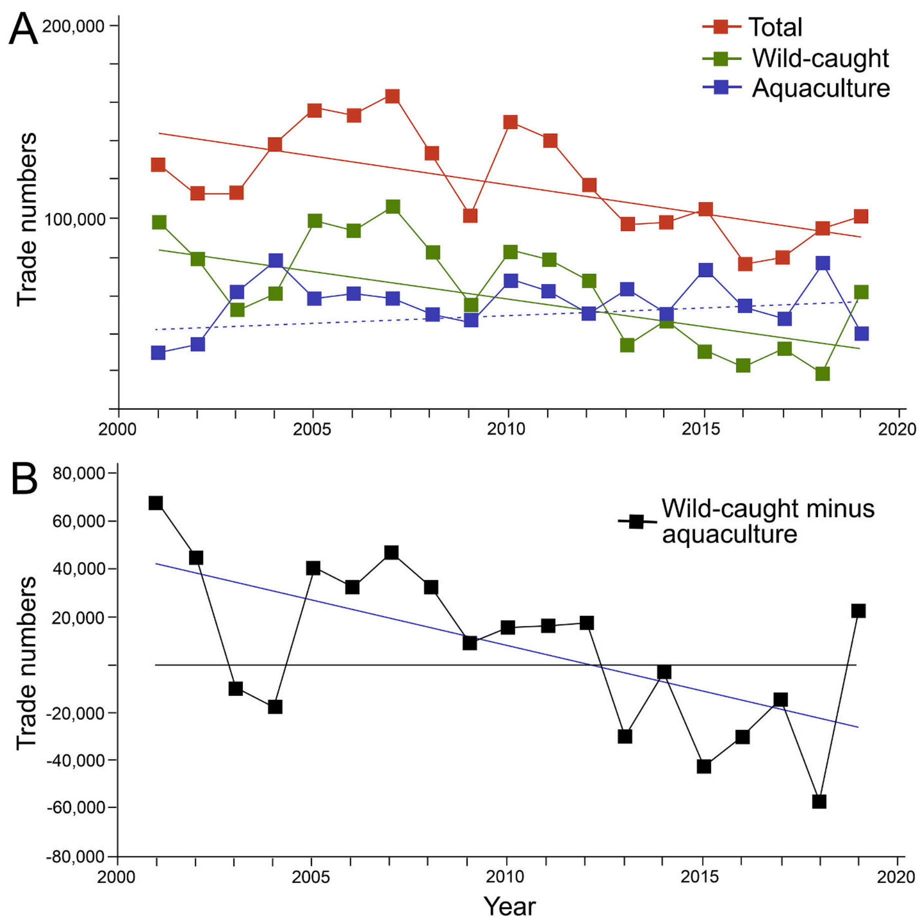

Fig. 1. Annual import numbers of giant clams (all species) from 2001 to 2019. Correlations (Pearson): Total $R = -0.622$, $p = 0.004$; Wild-caught R = -0.692, $p = 0.001$; Aquaculture $R = 0.176$, $p = 0.472$; Wild-caught minus Aquaculture $R = -0.627$, $p = 0.004$. Raw data in ESM Table S1.

rise in reported trade in 2019 (Fig. 2A).

3.5. Species trends: Cultivated specimens

Tridacna maxima was overall the most imported species from aquaculture from 2001 to 2019 in the records, as well as the most traded on an annual basis, peaking in 2015 (Fig. 3A). The second and third most-imported species were *T. derasa* and *T. crocea*, respectively. *Tridacna squamosa* showed slightly lower overall trade numbers (Fig. 3A)., whereas the remainder of the species were traded in comparably low numbers (Fig. 3B). In 2019, the four most-traded species (*T. crocea*, *T. derasa, T. maxima*, and *T. squamosa*) showed a decrease in the reported trade (Fig. 3A).

3.6. Major exporting countries: Wild-sourced giant clams

Seven countries were responsible for the export records of >90% of all wild giant clams from 2001 to 2019 (Fig. 4). Vietnam dominated this market (over 50%) until 2010, when it became succeeded by Cambodia and French Polynesia (Fig. 4A). Cambodia was the second-largest exporter. The third-largest exporter was French Polynesia, which started exports in 2009 (Fig. 4A). Annual exports from the other four countries remained lower than 10.000 most of the time (Fig. 4B).

3.7. Major exporting countries: Cultivated giant clams

Nine countries reported exports of >90% of all traded cultivated giant clams, although in highly fluctuating numbers (Fig. 5). The

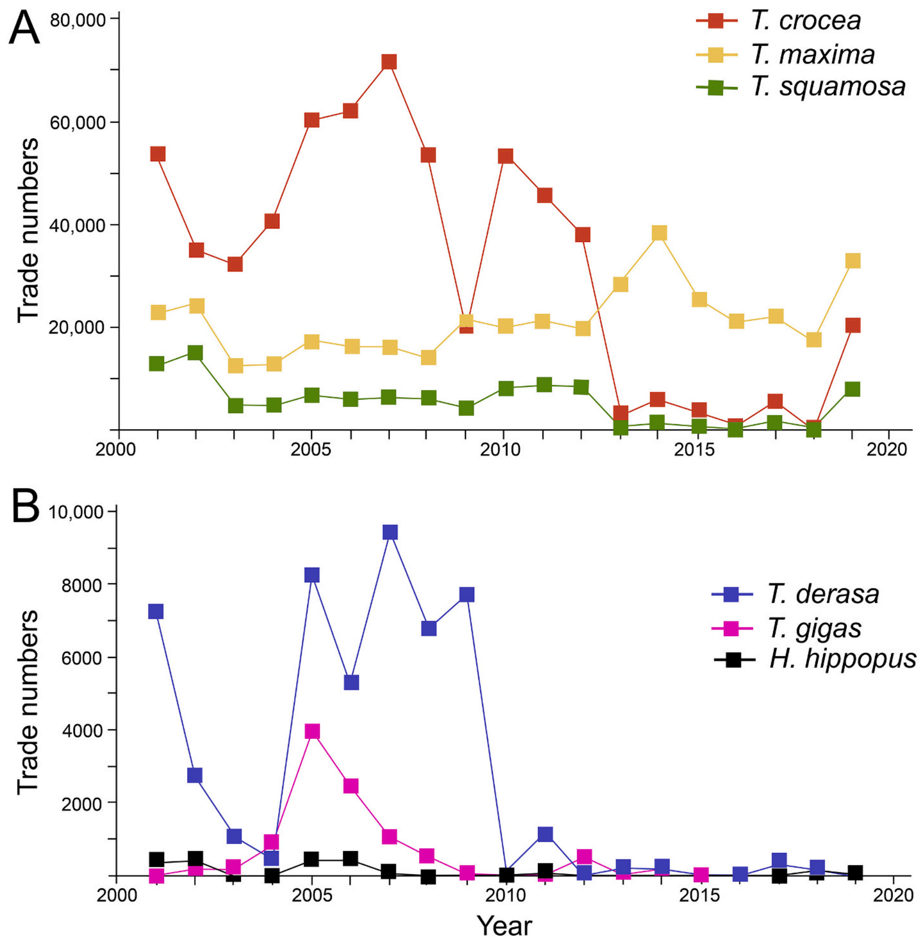

Fig. 2. Annual import numbers of six wild-sourced giant clam species from 2001 to 2019. Species are ranked by decreasing annual trade numbers. (A) Three species with the highest trade numbers. (B) Three species with the lowest trade numbers (n < 10,000). Raw data in ESM Table S2.

Marshall Islands was the largest exporter, followed by the Federated States of Micronesia, Australia, and Palau (Fig. 5A). Tonga and Kiribati continued to export during most of the years, whereas three countries stopped to report exports: Solomon Islands in 2011, Vanuatu in 2015, and Cook Islands in 2016 (Fig. 5B). Reported exports of other countries (e.g., Egypt, Fiji and Malaysia) were the lowest (not shown).

3.8. *Major importing countries: Wild-sourced giant clams*

Five countries were responsible for >90% of the of import records of wild giant clams from 2001 to 2019, all of them showing large fluctuations (Fig. 6). The USA was the largest importer. A small portion of its imports were re-exported, predominantly to other countries on the American continents, such as Brazil, Canada, Mexico, and Venezuela. The proportions of re-exports from the USA were very small and insignificant compared to its imports: *T. crocea* (1.1%), *T. derasa* (1.4%), *T. gigas* (0.3%), *T. maxima* (1.8%), *T. squamosa* (0.5%), and *H. hippopus* (1.0%). Vietnam and France were the second and third largest, respectively (Fig. 6A). Most Vietnamese imports came from Cambodia, but in a limited number of years, starting in 2010 (Fig. 6A). Germany and France showed relatively low numbers during the entire period (Fig. 6B).

3.9. *Major importing countries: Cultivated giant clams*

Five countries imported over 90% of all captive-bred giant clams from 2001 to 2019, all of them showing strong fluctuations (Fig. 7). The USA was the largest importer, followed by Germany (Fig. 7A). Germany showed a strong decline over the years. Great Britain, France and the Netherlands were the third, fourth, an fifth largest importers over the entire period (Fig. 7B). Imports of other countries (e.g., Denmark, Japan, Singapore, and Hong Kong) were the lowest (not shown).

3.10. *Export numbers per species and per country*

3.10.1. *Tridacna crocea*

This species was exported by eight countries (Table 4). Most specimens were wild-sourced during the first decade by Vietnam and the second decade by Cambodia. Most cultured clams came from Vietnam in the first decade and from Palau in the second. For many countries the market was dominated by cultured animals with major differences between the two decades: Indonesia, Marshall Islands, Micronesia, Palau, and Solomon Islands. Cambodia had no mariculture.

3.10.2. *Tridacna maxima*

This clam was exported by 18 countries (Table 5), which is more than any other. The market of wild-sourced animals was dominated by Vietnam in the first decade and by French Polynesia in the second. Australia, Marshall Islands and Micronesia were the most important producers of cultured animals. Cambodia, France and Sudan only exported animals from the wild. Kiribati and Cocos (Keeling) only traded cultured clams.

3.10.3. *Tridacna squamosa*

This clam species was exported by 11 countries (Table 6). The market of wild-sourced animals was dominated by Vietnam in the first decade and by Cambodia in the second. Marshall Islands was the most

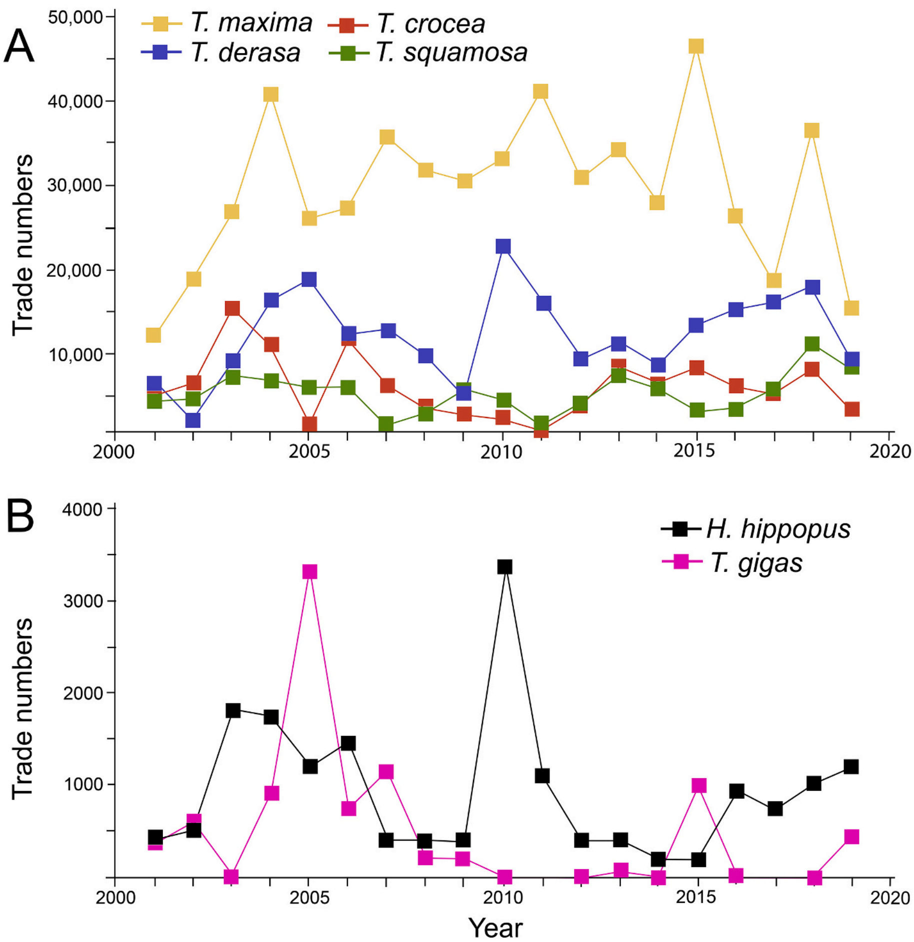

Fig. 3. Annual import numbers of six cultivated giant clams species from 2001 to 2019. Species are ranked by decreasing annual trade numbers. (A) Four species with the highest trade numbers. (B) Two species with the lowest trade numbers ($n < 4000$). Raw data in ESM Table S3.

important country producing cultured animals, followed by Tonga, Indonesia, and Palau. Cambodia only exported animals from the wild. Egypt and Micronesia only traded cultured clams.

3.10.4. Tridacna derasa

This clam species was exported by 10 countries (Table 7). The market of wild-sourced animals was dominated by Solomon Islands, followed by Micronesia. Cook Islands and Micronesia dominated the export market of maricultured animals in the first decade. Marshall Islands, Micronesia and Palau were major exporters of cultured clams in the second decade. Vietnam only exported animals from the wild and Australia only cultured clams.

3.10.5. Hippopus hippopus

This clam species was exported by five countries (Table 8). Most clams were cultured. Most exports occurred in the first decade. Marshall Islands dominated the market of both wild-sourced and cultured animals in the first decade. Micronesia was the major exporter of cultured animals in the second decade.

3.10.6. Tridacna gigas

This species was predominantly exported by Tonga in the first decade, pertaining to both wild-sourced and cultured animals (Table 9).

4. Discussion

4.1. Trade in live animals and dead shells

Since the international trade in giant clams over the years 2001–2019 has been reported to be dominated (96:4) by live animals over dead shells according to the import data, commercial trade in these animals can almost entirely be attributed to the aquarium industry. A similar relationship was found for exporter-reported data for 2007–2016 (Pavitt et al., 2021). However, thanks to reports on seizures by customs, we know of substantial quantities of dead *Tridacna* shells that are illegally traded (Nijman et al., 2015; Tittensor et al., 2020).

Although it is clear that the international trade in dead shells is underreported, this cannot explain such a large difference between the two categories. Possible underreporting by countries (export/import) could be caused by large traded quantities expressed by weight instead of numbers of individuals. Such records are rare but illustrative. For example, Vietnam reported exports of in total 68,000 kg of *T. squamosa* shells to the USA over the years 2001–2006, as opposed to only 24,000 kg reported by the importing country (UNEP-WCMC and CITES Secretariat, 2023b). An export of *T. maxima* shells from Mozambique to Spain in 2001 was stated as 11,000 individuals by the exporting country and as 22,000 kg by the importing country (UNEP-WCMC and CITES Secretariat, 2023b), causing an underestimation of 11,000 individuals in the import data. All these numbers are not sufficient to compensate for the difference in numbers for live clams, but show that there are inconsistencies in the reporting. Export and import records of live clams expressed by weight are rare and would not make much difference if

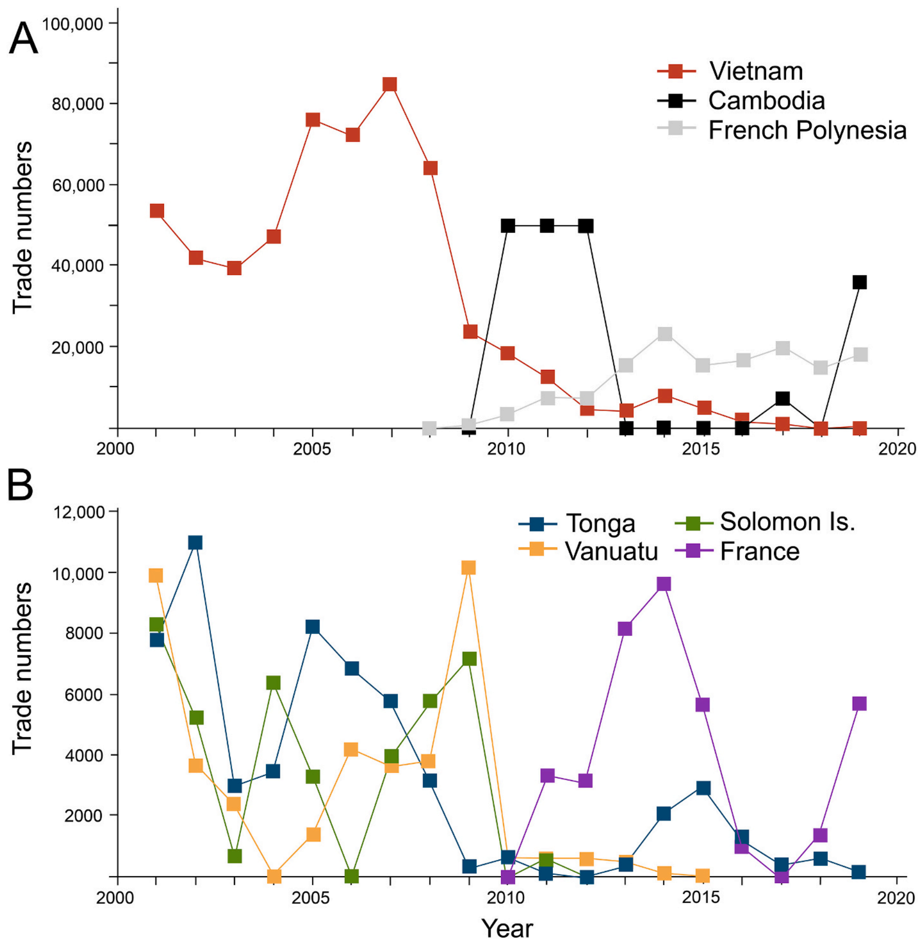

Fig. 4. Top seven exporting countries of wild-sourced giant clams from 2001 to 2019. Countries are ranked by decreasing annual trade numbers. (A) Three countries with the highest trade numbers. (B) Four countries with the lowest trade numbers (n ⟨12,000). Raw data in ESM Table S4.

they would be expressed by numbers.

Most shells were harvested from the wild, but it is not clear if they were taken from living animals that were fished for meat (Planes et al., 1993; Lucas, 1994; Hean and Cacho, 2002) or whether they were collected as leftover from earlier harvesting (Ullmann, 2013). Empty shells are used for the production of tools, household items, and ornaments (Moir, 1990; Heslinga, 1996; Neo and Todd, 2012), but also as a resource for the production of building materials (Salm, 1981; Brown and Muskanofola, 1985; di Piazza, 1998). *Tridacna* shells are also used as souvenirs in the tourism industry, ornaments in houses and churches, shellcraft and tools by fishermen, and as collector's items (Gössling et al., 2004; Duncan and Ghys, 2019; Neo, 2023; Simard et al., 2023). Some of these usages may explain the presence of *Tridacna* shells in the international trade. Although these shells are extracted from the wild, their part in the international trade is modest and therefore they are not expected to affect the relative importance of cultivated giant clams herein.

Interestingly, the dominance of live giant clams in the international trade as opposed to dead shells, is in contrast with that of seahorses, where dead bodies are traded at least 15 times more than live individuals (Pavitt et al., 2021). This is caused by the use of dried seahorses in the traditional medicine market, but because much of this trade is not reported the real difference is expected to be much larger (Foster et al., 2016, 2019).

4.2. Importer-recorded data vs exporter-recorded data

There are various explanations for differences in importer-recorded data and exporter-recorded data. Most species showed higher import data, but shells of *T. maxima* had much lower imports than exports (Table 2). This can be attributed to a single transaction in which the importing country counted by weight and the exporting country by numbers (Section 4.1). Otherwise, one would expect the total import numbers to be lower than export numbers because the former are usually based on numbers requested for export permits (“permits used”) and the latter on the imports themselves (“actual trade”), which can be lower than ordered if the exporting company cannot meet the demand (CITES Secretariat and UNEP-WCMC, 2022). On the other hand, there can be deficiencies in export data because clam-exporting countries that are not CITES parties (Fig. 5) are not obliged to report them to CITES (Pavitt et al., 2021). Overall, it appears that importing countries are stricter in reporting trade in giant clams than exporting countries.

4.3. Aquaculture: Captive bred vs born in captivity

Based on import records, captive breeding (C) is reported to be less common than the use of wild-caught mother stock (F), while export data indicate the opposite. If wild-caught giant clams are able to survive for many years and if they are highly reproductive, the mother stock does not need to be replenished and the negative impact on natural populations could be nil, depending on the reproduction rate per parent. Depending on the species, giant clams are fast-growing, reaching maturity after 4–10 years, and produce much annual offspring (Heslinga et al., 1984; Lucas, 1994; Gomez et al., 2000). Since, it is estimated that giant clams may reach life spans of 30 years (Munro, 1993) and because it is easy to use new generations for further reproduction (F1, F2, etc.) the distinction between C and F is small and does not make much

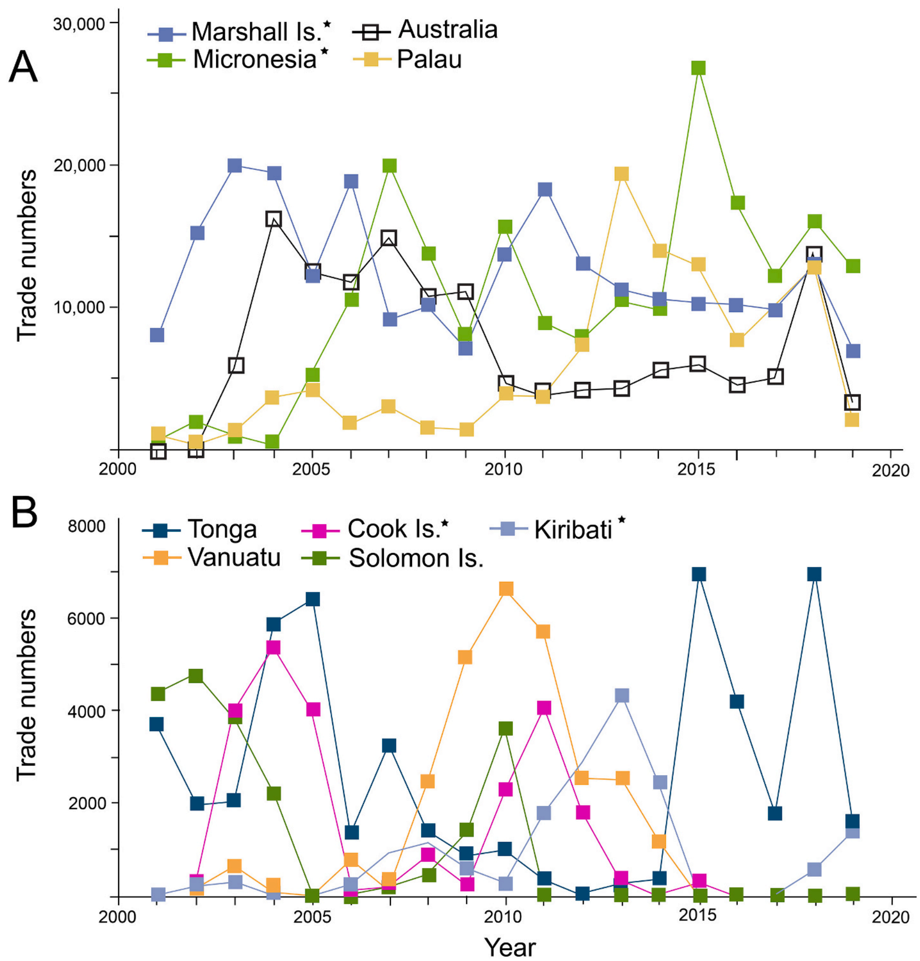

Fig. 5. Top nine exporting countries of aquacultured giant clams from 2001 to 2019. Countries are ranked by decreasing annual trade numbers. (A) Four countries with the highest trade numbers. (B) Five countries with the lowest trade numbers ($n < 8000$). * = Country is not a CITES party. Raw data in ESM Table S5.

difference for the conservation of the natural populations, especially if cultivation is used for restocking. Since juvenile clams have thinner shells and are more susceptible to predation than larger ones, keeping the clams in captivity may help them to survive and grow thick shells that can resist attacks by predators (Govan et al., 1992; Johnson et al., 2017).

There are few reports of captive breeding of giant clams in which the parent stock has been self-sustaining over many years. In the Seychelles, giant clams (*T. maxima*) were taken from the wild in the 1980s and have been used for the aquarium trade and restocking of wild populations at least until 2014 (Frias-Torres, 2017). Other examples of restoration by use of captive-bred giant clams have been reported from the Philippines (Lebata-Ramos et al., 2010), Singapore (Neo and Todd, 2012), and various areas in the West Pacific (Moorhead, 2018). Captive breeding may be more common in aquaculture than can be assumed based on trade data, because most examples of giant clam cultivation mentioned in the literature refer to restocking instead of aquarium industry and whether this is done by C or F is usually not specifically mentioned.

4.4. Overall trends

Some trends in the trade numbers of giant clams were clear, but many of them, either by species or by country, showed much fluctuation during the examined time period, The overall negative trend in the trade of giant clams in 2001–2019 was mostly determined by lower imports of wild-caught animals because the trade in cultivated specimens showed no significant change. Eventually, the imports of wild clams became lower than those of cultivated animals. While in 2001 only 23% of the traded giant clams were cultured (Wabnitz et al., 2003), this was observed to be 50% in the years 2012–2014 (Mies et al., 2017). The present study indicates that cultivated clams have showed a growing majority in the exports since 2012. In 2019, there appeared to be a turnaround with the most-traded species showing a rise in the reported imports of wild-caught clams (Fig. 2A) and a decline for maricultured ones (Fig. 3A). There is no clear explanation for this. Since traded numbers show much fluctuations over the whole period and this turnaround occurred only in the last year of the observation period, it could be the start of a new trend or become succeeded by a reverse change.

There are various possible explanations for the decline in the market of wild-sourced clams, one of which is that there could have been a decrease in the densities of natural populations, leading to smaller available stocks for exploitation (Andréfouët et al., 2005; van Wynsberge et al., 2016, 2017; Neo et al., 2018; Ramah et al., 2019). There are various reports on the overexploitation causing strong population declines (Neo et al., 2019; Mecha and Dolorosa, 2020; Mehrotra et al., 2021) and on the negative effects of elevated sea water temperatures (Zhou et al., 2019; Sayco et al., 2023). However, in the last 4500 years fluctuations in *Tridacna* populations have also been common without human impact and can perhaps be linked to climate change (Liu et al., 2020a).

Another explanation for reduced trade numbers is that there were trade suspensions of wild-sourced clams, such as import restrictions imposed by the EU (UNEP, 2023. The international marine aquarium industry also depends on the global economy. Declines in imports can

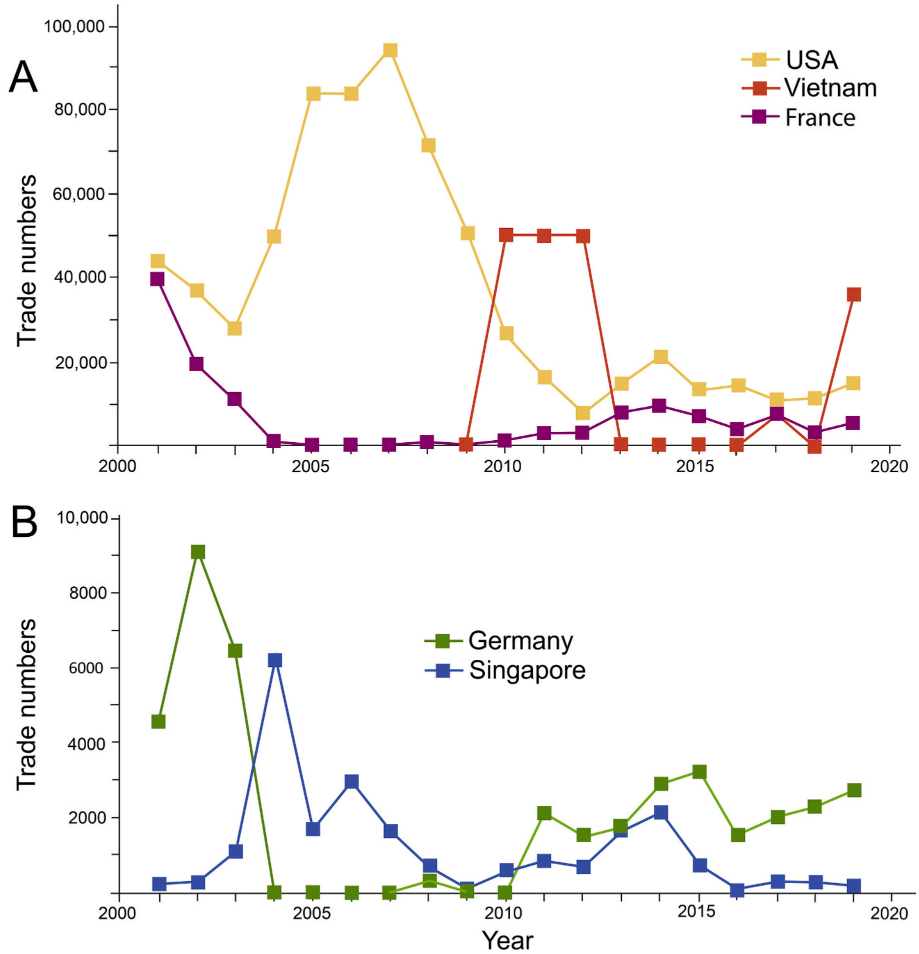

Fig. 6. Top five importing countries of wild-sourced giant clams from 2001 to 2019. Countries are ranked by decreasing annual trade numbers. (A) Three countries with the highest trade numbers. (B) Two countries with the lowest trade numbers (n < 10,000). Raw data in ESM Table S6.

also be explained by technological developments in importing countries that make it easy to cultivate giant clams outside their native ranges (Rhyne and Tlusty, 2012).

Another factor to be considered is that demand in consumer countries may be decreasing when companies here will be able to cultivate clams by themselves. At present, all giant clam aquaculture farms are based in countries inside their native range (Mies et al., 2017). Adult tridacnines rely very much on symbiodiniacean zooxanthellae and this may be problematic outside their natural range.

4.5. Species trends: Wild-sourced specimens

Tridacna crocea and *T. maxima* were the most exploited species in the wild, with *T. crocea* initially dominating the market until it was replaced by *T. maxima* since 2013. Both species may be popular in the aquarium industry because of their colourful mantles (Hart et al., 1998; Mies et al., 2017).

As a small giant clam species, *T. crocea* typically occurs in high densities, which facilitates finding many individuals in a short time (Hardy and Hardy, 1969; Neo et al., 2017, 2019; Zhang et al., 2020; Rehm et al., 2022). Harvesting would, however, be time-consuming and destructive to the environment, because the animals naturally live embedded in coral rock (Todd et al., 2009; Collins et al., 2023). There is a low demand from the seafood market because the animals are relatively small and more difficult to harvest than other *Tridacna* species (van Wynsberge et al., 2016; Neo et al., 2017). The main threats are therefore habitat degradation and the aquarium trade (van Wynsberge et al., 2016; Liu et al., 2020a; Neo, 2023).

Population numbers of *T. maxima* remained relatively stable at high levels, but harvesting needs to remain low in order to be sustainable (Adams et al., 1988). It is possible that *T. maxima* numbers include *T. noae* because the two resemble each other and the latter was only re-established in 2014, after which it appeared to be widely distributed in the central Indo-West pacific (Su et al., 2014; Borsa et al., 2015a, 2015b; Fauvelot et al., 2019, 2020).

4.6. Species trends: Cultivated specimens

Tridacna maxima and *T. derasa* were the most commonly traded species from mariculture, followed by *T. crocea* and *T. squamosa*. Successful aquaculture depends on access to large, healthy brood stocks (Mies et al., 2017). Because *T. maxima* is still sufficiently common in the wild, it is easy to obtain adults for breeding purposes. Both *T. maxima* and *T. crocea* used to have low survival rates in aquaculture, with juveniles of the latter being most vulnerable to predation (Hart et al., 1998), but at present they are successfully used in restocking projects (Neo et al., 2019). Breeding trials in laboratory conditions have shown that selective breeding in *T. crocea* can intensify mantle colour and that crossbreeding generates higher growth and survival rates (Zhang et al., 2020), but this technology has not yet been applied for the market.

4.7. Major exporting countries: Wild-sourced giant clams

Vietnam used to be the dominant exporting country until 2010, but since then it was succeeded by Cambodia and French Polynesia. Vietnam experienced a large decline in exports since 2007, which was

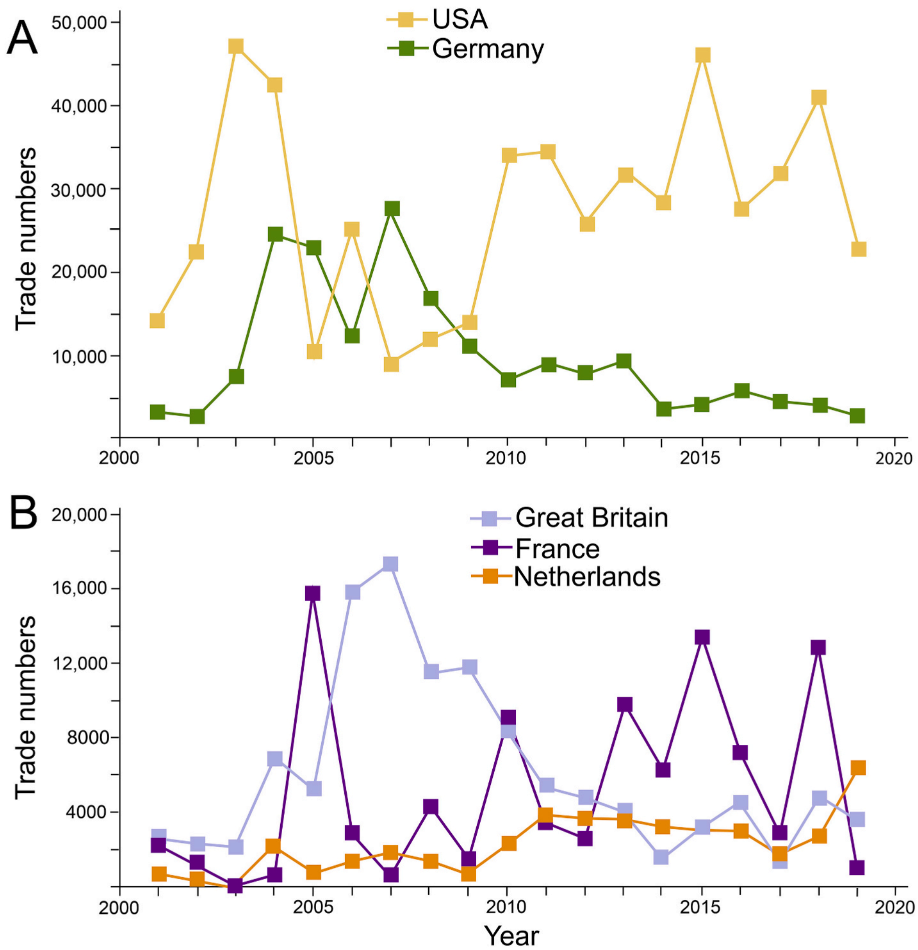

Fig. 7. Top five importing countries of aquacultered giant clams from 2001 to 2019. Countries are ranked by decreasing annual trade numbers. (A) Two countries with the highest trade numbers. (B) Three countries with the lowest trade numbers (n < 20,000). Raw data in ESM Table S7.

Table 4
Tridacna crocea. Importer-recorded trade numbers (rounded to hundreds) of live animals by major exporting countries (totals over 1000) divided over Wild and Cultured and per decade, 2001–2010 and 2011–2019 (UNEP-WCMC and CITES Secretariat, 2023c).

	Wild		Cultured	
	2001–2010	2011–2019	2001–2010	2011–2019
Cambodia	39,000	95,300	–	–
Indonesia	600	200	2000	9000
Marshall Is.	100	–	3100	–
Micronesia	300	100	9000	4600
Palau	400	300	6300	37,800
Solomon Is.	14,000	–	18,200	–
Vanuatu	7700	–	300	–
Vietnam	418,600	27,000	26,700	400

Table 5
Tridacna maxima. Importer-recorded trade numbers (rounded to hundreds) of live animals by major exporting countries (totals over 1000) divided over Wild and Cultured and per decade, 2001–2010 and 2011–2019 (UNEP-WCMC and CITES Secretariat, 2023c).

	Wild		Cultured	
	2001–2010	2011–2019	2001–2010	2011–2019
Australia	18,400	3400	82,000	46,300
Cambodia	5500	24,100	–	–
Cocos (Keeling) Is.	–	–	300	1400
Cook Is.	3000	400	4900	12,200
Fiji	6700	–	1400	–
France	–	38,100	–	–
French Polynesia	4100	139,600	–	900
Indonesia	500	–	100	3800
Kiribati	–	–	2800	25,700
Marshall Is.	10,800	–	81,700	42,200
Micronesia	13,600	1800	36,100	74,100
Palau	900	200	3500	12,600
Seychelles	200	–	2800	–
Solomon Is.	5100	–	3700	–
Sudan	–	4000	–	–
Tonga	29,300	7300	28,200	35,800
Vanuatu	28,500	1800	25,900	22,200
Vietnam	51,100	5200	3300	–

predominantly determined by trade restrictions that were imposed by importing countries (UNEP, 2023). This import ban was caused by the detection of the chromist *Perkinsus* in Vietnamese clams, which is an important pathogen of mollusks (Sheppard and Phillips, 2008). Trade in *T. crocea* was most dramatically affected by this ban.

Exports from Cambodia were only high in a few years and mostly to Vietnam for re-export. French Polynesia was the largest exporter of wild giant clams from 2013 until 2018, all consisting of *T. maxima* (Andréfouët et al., 2013). There are minimum size requirements for harvested clams and no-take areas (Gilbert et al., 2006a, 2006b; Andréfouët et al., 2013). Spat collection of this species, where larvae are collected from wild populations and reared in a protected environment, is allowed and regulated (Andréfouët et al., 2018). This method of giant clam production can be considered ranching (Wells and Barzdo, 1991) but is labelled as wild-harvesting, which is reflected in the increasingly

Table 6
Tridacna squamosa. Importer-recorded trade numbers (rounded to hundreds) of live animals by major exporting countries (totals over 1000) divided over Wild and Cultured and per decade, 2001–2010 and 2011–2019 (UNEP-WCMC and CITES Secretariat, 2023c).

	Wild		Cultured	
	2001–2010	2011–2019	2001–2010	2011–2019
Australia	–	1500	–	3700
Cambodia	5500	24,300	–	–
Egypt	–	–	–	4600
Indonesia	600	200	1000	13,300
Marshall Is.	4800	–	22,000	12,600
Micronesia	–	–	–	1600
Palau	500	100	1700	10,800
Solomon Is.	2200	–	4100	–
Tonga	8000	300	12,500	3500
Vanuatu	4000	–	5900	1500
Vietnam	49,500	5300	1300	–

Table 7
Tridacna derasa. Importer-recorded trade numbers (rounded to hundreds) of live animals by major exporting countries (totals over 1000) divided over Wild and Cultured and per decade, 2001–2010 and 2011–2019 (UNEP-WCMC and CITES Secretariat, 2023c).

	Wild		Cultured	
	2001–2010	2011–2019	2001–2010	2011–2019
Australia	–	–	5600	–
Cook Is.	2100	300	29,700	700
Fiji	1100	–	600	–
Indonesia	800	–	1000	600
Marshall Is.	600	–	18,600	48,100
Micronesia	12,000	400	29,400	35,500
Palau	6100	200	8600	27,100
Solomon Is.	18,800	600	13,600	–
Tonga	4700	400	8200	5500
Vietnam	2600	–	–	–

Table 8
Hippopus hippopus. Importer-recorded trade numbers (rounded to hundreds) of live animals by major exporting countries (totals over 1000) divided over Wild and Cultured and per decade, 2001–2010 and 2011–2019 (UNEP-WCMC and CITES Secretariat, 2023c).

	Wild		Cultured	
	2001–2010	2011–2019	2001–2010	2011–2019
Indonesia	100	–	800	600
Marshall Is.	1000	–	5700	100
Micronesia	100	100	2400	3700
Palau	100	–	1500	1400
Solomon Is.	500	–	1200	–

Table 9
Tridacna gigas. Importer-recorded trade numbers (rounded to hundreds) of live animals by major exporting countries (totals over 1000) divided over Wild and Cultured and per decade, 2001–2010 and 2011–2019 (UNEP-WCMC and CITES Secretariat, 2023c).

	Wild		Cultured	
	2001–2010	2011–2019	2001–2010	2011–2019
Philippines	500	700	–	100
Tonga	8300	–	5400	–

large numbers of wild *T. maxima* from French Polynesia (Neo et al., 2017). There have been several natural massive die-off events in French Polynesia (van Wynsberge et al., 2017), with one in 2009 during which 83% of one population died (Andréfouët et al., 2013). Harvesting for the aquarium trade could reduce the recruitment potential of the remaining populations.

4.8. Major exporting countries: Cultivated giant clams

A relatively large number of countries was involved in the market of cultivated giant clams. The most important ones were Marshall Islands, Micronesia, Australia, and Palau. Marshall Islands dominated the market of cultivated clams during several years, mostly by exports of *T. maxima* to the US and Japan, which supplied technical support (Neo et al., 2017). Overall, production per country depends on the species in which it is most specialized (Mies et al., 2017). Export countries varied in the species they could supply most (Tables 3–8), such as Marshall Islands, Australia and Micronesia mainly exporting *T. maxima*., Cook Islands mostly *T. derasa*, Palau mostly *T. crocea*, and Indonesia most. *T. squamosa*. Three species showed more trade in cultivated specimens than wild ones during the examined period: *T. maxima*, *T. derasa* and *H. hippopus* (Tables 3–8). Perhaps the natural stocks of these species have been depleted too much already, not necessarily because of the aquarium trade alone. Aquaculture farms face many challenges, such as insufficient healthy brood stock, lack of funding and high costs for infrastructure and logistics, and competition with wild-caught clams from other countries (Mies et al., 2017; Moorhead, 2018). Production in the Solomon Islands was stopped because of high costs for infrastructure and logistics, as they are remote from importing countries (Mies et al., 2017). More cooperation between farms, governments and the scientific community is needed to remove or lessen the current challenges in the aquaculture of giant clams (Mies et al., 2017).

4.9. Major importing countries

The USA was the major importing county for wild-sourced giant clams in the first decade (Fig. 6), but these trade numbers declined after 2007, when imports of cultivated individuals started to grow (Fig. 7). It is important to consider that the USA re-exports giant clams to other countries on the North and South American continent, but these numbers were relatively negligible. Vietnam was a major importer of wild-soured clams in 2010–2012 and 2019 but did not import cultivated animals (Figs. 6, 7). Initially, its imports were mostly intended for re-export (Wabnitz et al., 2003). This is obvious when Cambodia's export data (Fig. 4A) are compared with Vietnam's import data (Fig. 6A). The third largest importer of wild giant clams was France, which showed a decline in wild-sourced clams since 2001, and growing (but fluctuating) import numbers of cultivated individuals in 2005 and in the second decade. French imports can be re-exported to other EU countries without CITES permits. Four European countries were important importers of giant clams (Fig. 6,7) despite import suspensions of wild-sourced species from certain countries (UNEP, 2023). The latter could have been replaced by imports of captive-bred giant clams. Although Germany and Great Britain imported most captive-bred giant clams in the beginning of the observed period. The decline afterwards could be explained by increasing prices for giant clams from aquaculture and unstable production levels (Mies et al., 2017).

4.10. Data accuracy

When production numbers of giant clams given by aquaculture farms are compared with numbers given by CITES, there are some large differences, with farms reporting higher numbers than CITES (Mies et al., 2017). Since CITES only covers international trade, domestic markets are not included and animals may become lost due to diseases and other causes of death after harvesting. The database has been criticized for a lack of traceability, due to wrong entries for countries of origin and whether clams were wild-sourced or captive-bred (Mies et al., 2017). Some data can be erroneous due to wrong species identifications (Huelsken et al., 2013; Su et al., 2014; Liu et al., 2020b) and when trade numbers are taken from trade permits instead of actual transactions (Mies et al., 2017). Finally, as not all countries that export giant clams are parties of CITES it is difficult to enforce and implement the regulations of CITES (Wabnitz et al., 2003; Mies et al., 2017; Pavitt et al., 2021).

4.11. Aquaculture and restocking giant clam populations

With the capacity to cultivate large quantities of giant clams in aquafarms, it has become possible to use aquaculture for the restocking of wild populations, which has been practiced in countries such as Fiji (Adams et al., 1988), Australia (Lucas et al., 1989), Japan (Murakoshi et al., 2002; Neo et al., 2019), Singapore (Guest et al., 2008; Yong et al., 2022), and the Philippines (Gomez et al., 2000; Cabaitan and Conaco, 2017; Requilme et al., 2021). This is important because wild populations are needed to support aquaculture (Mies et al., 2017). *Tridacna* mariculture for restocking can be mixed with mariculture for the aquarium trade, as seen in the Marshall Islands (Neo et al., 2017). Restocking from aquaculture can also be used for populations that have been overfished for the aquarium industry. Thus, maricultured stock and natural populations cannot always be seen as independent of each other.

Partly owing to the aquarium industry, transport of cultivated live giant clams over large distances by air freight has become a routine (Braley, 1992b; Bell et al., 1997; Hart et al., 1998; Teitelbaum et al., 2010; Yong et al., 2022). In 1986 and 1987, ca. 2500 cultivated specimens of *T. gigas* were transported from eastern Australia to Fiji, for a reintroduction of this species after Fiji's native population appeared to have become extinct (Ledua and Adams, 1988). The transport of non-native clams may have consequences for species distributions and may perhaps even result in the introduction of non-native cryptic species. From a conservation perspective, restocking of giant clam populations should therefore be carried out with individuals that match genetically. Under CITES, such international shipments should not have the purpose code "T" for commercial transactions but "N" for reintroduction or introduction into the wild (CITES Secretariat and UNEP-WCMC, 2022). It is recommended that all restocking operations of giant clam populations follow the best practice guidelines for reintroductions and translocations, which have been published for this purpose (IUCN/SSC, 2013).

5. Conclusions

Our study shows that according to the CITES Trade Database, there was a world-wide decrease in the trade of live wild giant clams during the years 2001–2019, whereas the trade in cultivated animals has not changed significantly in that period. Both source categories showed much fluctuation, indicating that the international trade in giant clams is not stable. The trade in dead shells was insignificant in comparison. Trade restrictions of certain giant clam species from particular countries could be a helpful strategy to reduce pressure on wild populations, but information on harvesting is still incomplete or lacking (Pavitt et al., 2021). Such restrictions are not always based on information on population sizes in the exporting countries, which would be needed for making non-detriment findings (Nijman et al., 2015). Such NDFs are extremely difficult to find for giant clams, with one example known from Palau (Isamu, 2008). NDFs are important because giant clams are not only fished for the aquarium industry. Furthermore, they may undergo other threats, such as excessively elevated sea-water temperatures. There is a need for more research on giant clam populations in countries with high export rates. The main focus should be on the most popular species, *T. crocea* and *T. maxima*. Additional research may help to improve the success of aquaculture farms and stabilize production rates, which may help decrease the trade in wild giant clams.

CRediT authorship contribution statement

Maite L. Vogel: Conceptualization, Formal analysis, Investigation, Visualization, Writing – original draft, Writing – review & editing. **Bert W. Hoeksema:** Conceptualization, Formal analysis, Investigation, Supervision, Writing – original draft, Writing – review & editing.

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Declaration of competing interest

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

Data availability

All data has been added as Electronic Supplementary Material

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.aquaculture.2024.740563.

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