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Aquaculture of marine ornamental fish: overview of the production trends and the role of academia in research progress

Simon Pouil[1], Michael F. Tlusty[2], Andrew L. Rhyne[3] and Marc Metian[4]

1 ISEM, Université de Montpellier, CNRS, IRD, EPHE, Montpellier, France
2 University of Massachusetts Boston, Boston, Massachusetts, USA
3 Roger Williams University, Bristol, Rhode Island, USA
4 Environment Laboratories, International Atomic Energy Agency, Principality of Monaco

Correspondence
Simon Pouil, ISEM, Institut de Recherche pour le Développement (IRD), Université de Montpellier, Place Eugène Bataillon, Montpellier Cedex 05, France. Email: simon.pouil1@gmail.com

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Abstract

The marine ornamental fish trade is expanding and still largely relies on wild fish from tropical coral reef ecosystems. There are unknowns in the wild harvest so that the sustainability of marine ornamental fish trade can therefore be questioned with aquaculture being perceived as a responsible alternative for the procurement of these ornamental marine fish. However, there are still many technical constraints that hinder its development. These blocks require additional coordination with the outcome being an accelerated development of ornamental marine fish production. The main objective of this review was to better identify, understand and discuss the role and the impacts of academic research in the production of marine ornamental fish through qualitative and quantitative approaches. To do so, 222 selected scientific publications (including peer-reviewed articles, conferences articles, thesis and reports) from the literature available to date were analysed and outcomes were framed in perspective of the total number of captive-bred species. Results of the meta-analyses indicate that academic research has led to significant advances in the breeding of some of the more difficult to breed species. While it has a leading role in conservation, its advance of techniques still lags behind private companies and hobbyists. Partnerships promoting synergistic activities between academic research institutes and the private sector (aquaculture farms and public aquariums) are important to optimize future ornamental marine fish production.

Key words: academic research, aquaculture, captive breeding, fishkeeping, research and development, sustainable production.

Introduction

In 2003, Disney and Pixar released a hit movie, ‘Finding Nemo’ with the two main protagonists being Nemo, a clown anemone fish *Amphiprion ocellaris* and Dory, a Pacific blue tang *Paracanthurus hepatus*. Although the influence of the movie (called the ‘Nemo Effect’; Militz & Foale 2017) on purchases of wild-caught fish could not be rigorously demonstrated (D. Veríssimo, S. Anderson, M.F. Tlusty, unpublished data), some news media papers and pet stores reported increasing clownfish sales following the release of this film (Prosek 2010). Notwithstanding, some authors argue that such movies based on an emotive but scientifically incorrect approach, driven by popular media to promote coral reef ecosystems protection can be damaging because it could unintentionally contribute to impulsive purchase of coral marine species by uninformed people (Militz & Foale 2017; Olivotto *et al*. 2017).

The threats for coral reefs related to the collection of ornamental fish include the reduction in biodiversity from over-extraction and habitat destruction in some source countries (Dammannagoda 2018). The large number of species in the trade (over 2500, Rhyne *et al*. 2017b) from a large number of countries with many species being collected at number <1000 individuals per year (Rhyne *et al*. 2017b) make any fisheries management plan onerous.

Furthermore, destructive methods are still used illegally such as cyanide in Southeast Asia (Vagelli 2011; Cohen *et al.* 2013) although some efforts have been made to adopt friendly collecting methods such as nets and traps (Lecchini *et al.* 2006). Destructive methods are non-selective, cause considerable and long-term damages to coral reefs, risky for collectors and resulted in very high mortality of wild-caught fish. For instance cyanide fishing has been reported to result in >80% mortality of marine aquarium fish being exported to other countries (Rubec *et al.* 2001). Taking account all the steps from the catches to the final buyer, it is usually estimated that only 30–40% caught marine ornamental fish survive (Wabnitz *et al.* 2003). All these figures demonstrate a high degree of unknowns regarding the sustainability of wild fish collection for the marine ornament market.

The marine aquarium trade is a global multimillion industry that started in the 1930s and experienced a significant increase over the last decades (Wabnitz *et al.* 2003; Murray *et al.* 2012; Rhyne *et al.* 2012; Leal *et al.* 2015). Thus, marine ornamental fish trade increased from US$24-40 million annually in the 1980s (Wood 1985) to currently exceed US$300 million (Palmtag 2017). Approximately 20–30 million marine reef fish are commercialized every year worldwide (Wabnitz *et al.* 2003; Rhyne *et al.* 2012; Leal *et al.* 2015). The pressure on wild stocks is increasing, to the point of endangering certain species. One of the famous examples of the direct impacts of fisheries for aquarium trade is the Banggai cardinalfish *Pterapogon kauderni* natives to Sulawesi. As described by Rhyne *et al.* (2012), once *P. kauderni* entered the marine aquarium trade it quickly became heavily traded and overexploited. Import prices of *Banggai cardinalfish* dropped as supplies increased and wild population suffered a reduction in population fitness. The Banggai cardinalfish is now included in the IUCN Red List of Threatened Species under the ‘Endangered’ status (IUCN 2019).

The captive breeding of marine ornamental fish species (i.e. spawning, hatching, settling and growth to the juvenile or adult stage in enclosed system) is a way to support marine fish aquarium trade (Olivotto *et al.* 2017). However, there are still numerous critical steps to widely produce ornamental marine fish (Moorhead & Zeng 2010; Olivotto *et al.* 2011, 2017). One of the bottlenecks in marine ornamental fish production is the larval rearing: many species produce larvae virtually impossible to maintain under appropriate conditions, including adequate feeding based on our current knowledge (DiMaggio *et al.* 2017; Olivotto *et al.* 2017; Rhyne *et al.* 2017a; Callan *et al.* 2018). Increase the research effort on marine ornamental fish aquaculture is one of the ways to overcome the current brakes to increase the availability of captive-bred (CB) species.

Previous literature reviews on this topic have examined the state-of-the-art marine ornamental fish production advances from academic research, at different points of time, including developments in breeding methods as well as larval rearing (see Moorhead & Zeng 2010). The present review is looking at the historical status of marine ornamental fish aquaculture with an emphasis on the advances of academic research. It also provides a qualitative and quantitative analysis on the field of research to highlight, understand and discuss the impacts of academic research in the marine ornamental fish aquaculture. Although this study was focused on marine ornamental fish aquaculture, most of the issues addressed apply also to invertebrates.

Methods

Captive-bred species list

Captive-bred species list from the CORAL Magazine

The starting point of this study was collection of the data from the annually updated CORAL Magazine (https://www.coralmagazine.com). This magazine is known for reporting all existing captive-bred marine fish species in a list (after called CORAL list) since January 2013. More precisely, this list is an annual project, carried out by CORAL Magazine and the Marine Breeding Initiative (MBI), and correspond to an annual accounting of first-time tropical marine fish breeding accomplishments as well as accessibility of CB marine fishes within the marine aquarium hobby and industry (CORAL 2018). This list was drawn from previous inventories such as the Frank Baensch’s CB species list established for Reef Culture Technologies (https://www.frankbaensch.com/marine-aquarium-fish-culture/my-research) last updated in 2011.

To be listed, breeding successes of new species must be supported by documentation to attest to the veracity of the information and/or confirmed by third-party sources (see CORAL 2018 for details regarding methodology). The list included species bred in captivity as well as their relative availability in the US market. Thus, listed species can be:

(1) Unavailable: Authors and consulted parties were unaware of any availability of these species.
(2) Scarce: Only one source or breeder identified for these species, limited number of individuals have been commercially available.
(3) Moderate: Limited availability for these species, but several sources identified.
(4) Common: Commonly available on the market, easy to find as CB species, and available from several sources.

Before the publication of a new list, the authors and editors of the list once again reach out to commercial aquaculturists, public aquarists and academic researchers, in an attempt to compile the most comprehensive list possible (CORAL 2018).

Checking and updating the CB species list

In order to check and update the CORAL list content, all the lists established for the years 2012 to 2017, available online (CORAL 2018), have been downloaded and sorted by year. In all cases, species names were verified using the World Register of Marine Species (WoRMS) (Appeltans *et al*. 2012) and FishBase (Froese & Pauly 2019) and corrected when species names were misspelled or species listed under a former synonym. A sorting was then made to remove species mainly raised for human consumption. As a result of this sorting, 20 species from six families were removed from the list (Table 1). Although seahorses are used in traditional medicine, Koldewey and Martin-Smith (2010) have shown that sale of live seahorses for aquariums was the dominant market for CB seahorses, and why these species were included in our analysis. Data on each reported breeding success were collected from general online public articles, reports and discussion forums. In order to evaluate the availability of CB species on the world market, availability from e-commerce websites (n = 9) from different countries were recorded from September to December 2018 as well as the product list on aquaculture company and wholesaler websites (n = 8). In parallel, surveys were sent to the marine ornamental aquaculture stakeholders (consultants and wholesalers, n = 4 replies) from Asia and Europe to determine the availability of species recorded in the CORAL list established for 2017 in non-US markets. Global Marine Aquarium Database (GMAD, Wabnitz *et al*. 2003) was one more source of information used to evaluate the availability of CB species in the aquarium trade.

The entire data collection process led to the construction of a database (Data S1) for the year 2017 where the identified ornamental marine fish species already CB were reported and sorted by family. Aceepted scientific names, vernacular name, IUCN Red List status (IUCN 2019) and commercial availability were also provided.

Table 1 List of the CB marine fish species for human consumption and fishkeeping that have been excluded from our analysis

Family	Scientific name	Vernacular name
Batrachoididae	*Opsanus tau*	Oyster toadfish
Ephippidae	*Chaetodipterus faber*	Atlantic spadefish
	Platax batavianus	Humpback batfish
	Platax orbicularis	Orbicular batfish
	Platax pinnatus	Dusky batfish
Lutjanidae	*Lutjanus sebae*	Emperor red snapper
Serranidae	*Cromileptes altivelis*	Humpback grouper
	Plectropomus leopardus	Leopard coralgrouper
	Epinephelus lanceolatus	Giant grouper
	Epinephelus marginatus	Dusky grouper
	Plectropomus areolatus	Squaretail coralgrouper
	Plectropomus leopardus	Leopard coralgrouper
Siganidae	*Siganus canaliculatus*	White-spotted spinefoot
	Siganus fuscescens	Mottled spinefoot
	Siganus guttatus	Orange-spotted spinefoot
	Siganus lineatus	Golden-lined spinefoot
	Siganus rivulatus	Marbled spinefoot
	Siganus vermiculatus	Vermiculated spinefoot
Tetraodontidae	*Sphoeroides annulatus*	Bullseye puffer
	Sphoeroides maculatus	Northern puffer

Academic literature search

Searches were performed individually for each identified captive bred fish species fish (see section Checking and updating the CB species list) using two commonly used databases: Google Scholar and Web of Science (WOS). In addition, the proceedings from the World Aquaculture Society (WAS) were also considered. Searches included peer-reviewed articles, conferences articles, thesis and scientific reports over the time span from 1950 to present (2018, December 31). Following searches, non-relevant records (i.e. studies that did not address aquaculture and captive breeding) and review articles were removed. The completeness of the results obtained was considered as satisfactory based on (i) comparison with previous reviews (Koldewey & Martin-Smith 2010; Moorhead & Zeng 2010; Olivotto *et al*. 2011; Domínguez & Botella 2014; Cohen *et al*. 2017) and (ii) using 'snowballing' references (i.e. checking citations on reference lists of relevant articles until no further relevant articles could be found; Sayers 2007).

Advances in academic research

We are aware that improvements made in the cultivation of more suitable live prey such as copepods (e.g. Alajmi *et al*. 2015) were among the most important advances achieved in academic research on marine ornamental fish production. Nevertheless, this review is only focusing on research directly related to fish. From the list of final list of selected papers, each record was then categorised on the basis of the study content and the method used. The different categories are mainly resulting from the key stages of fish biological development (from egg to adult) and main aquaculture production steps. The selected categories are the following:

(1) *Broodstock management*: studies addressing basic aspects of maintenance and maturation in captivity of adult fish used as broodstock.

(2) *Spawning*: studies reporting spawning in captivity from already CB or wild broodstock, matured or not in captivity.

(3) *Egg/Embryonic development*: studies quantifying egg quality from captive spawning and/or describing incubation phase and embryonic development.

(4) *Larval rearing*: studies addressing main aspects of larval rearing such the influence of first exogenous food, food enrichment, prey density or/and physical and chemical conditions on zootechnical performances.

(5) *Metamorphosis*: studies in which larval rearing has been accomplished until larvae metamorphosis. This category includes both studies reporting complete larval rearing (from hatching to metamorphosis) or partial larval rearing resulting, for example from purchased hatched larvae.

(6) *Juvenile rearing*: studies investigating juvenile rearing from juveniles obtained from larvae or purchased from Aquaculture Company.

Results

Captive bred species reported from 2012 to 2017

There are currently 338 marine ornamental fish species belonging to 37 families reported as Captive bred (CB) species (Fig. 1 and Table 2; excluding species that may be intended for human consumption). Among these species, 134 are commercially available but only 18% of them are regularly available on the market (Table 2). These are mainly species of clownfish (Pomacentridae), dottyback (Pseudochromidae), blenny (Blennidae) and cardinalfish (Apogonidae).

Since 2012, when the first CORAL list was published, the number of marine ornamental CB fish species has linearly increased from 225 to 338 in 2017 (Fig. 1a). However, the trends observed are not the same depending on the families considered. Among the six most represented families (i.e. 69% of the studied species in 2017; Fig. 1a), the number of CB species has been constant since 2012 for Blennidae, Pomacentridae and Pseudochromidae (Fig. 1b). Conversely, for the lesser studied species, the number of Gobiidae, Pomacanthidae and Syngnatidae increased over the last 2–3 years (Fig. 1c).

Academic research effort

Summary of scientific database searches

From the initial aquaculture-related studies within the bibliographic survey, 222 relevant records were identified (according to the criteria described in the section Advances in academic research). These studies were composed of 184 peer-reviewed research articles, seven scientific reports, three theses and 28 conference abstracts and articles. These indicated that academic research effort focused on 117 species from 23 families (Table 3).

The bibliometric analysis revealed that academic research effort on reproduction, growth and/or production of

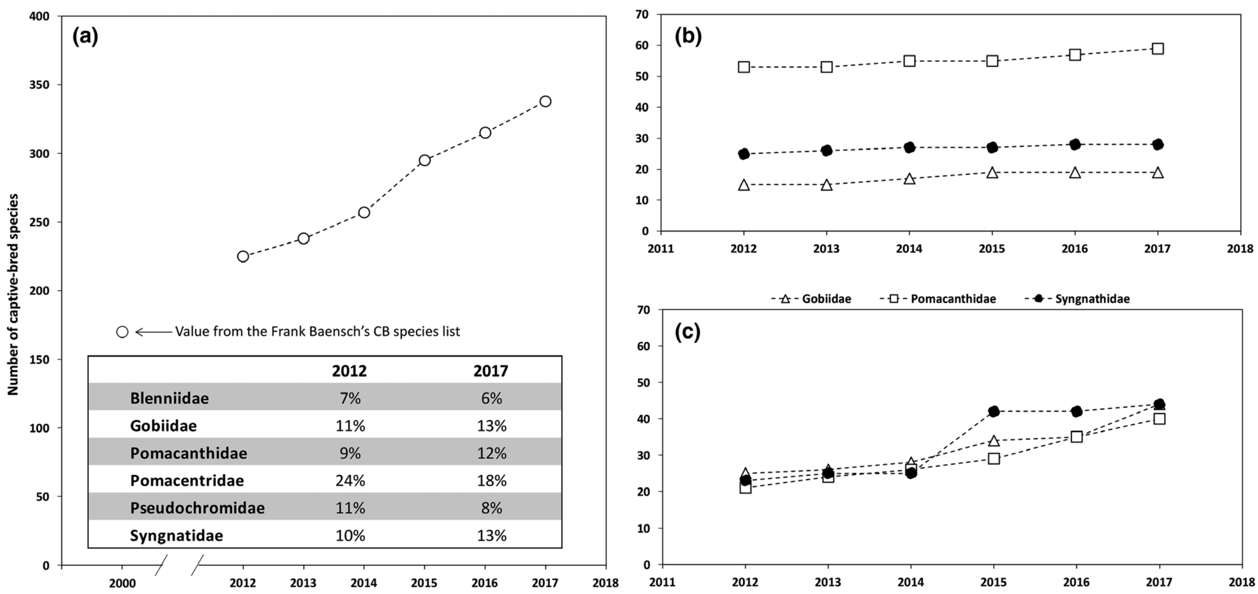

Figure 1 (a) Overview of CB marine ornamental fish species listed from 2012 to 2017. The proportions (in number of species) for the 6-main CB families are indicated in the table, (-○-) all species (b) Stagnation of the number of species CB in 3 of the main families: -△- Blennidae, -□- Pomacentridae and -●- Pseudochromidae over the period 2012–2017: and (c) Increase in species produced in the -△- Gobiidae, -□- Pomacanthidae and -●- Syngnathidae in the period 2012–2017. For a baseline, the number of CB species reared in 2000 from Frank Baench's list is provided.

Table 2 Summary of the CB species reported at the end of 2017

Family	Number of species	Availability on the market (%)				IUCN status (%)					
		Unavailable	Scarce	Moderate	Common	NE	DD	LC	NT	VU	EN
Acanthuridae	2	50	50					100			
Antennariidae	1	100				100					
Apogonidae	16	38	38	12	12	75		19			6
Balistidae	3	67	33			34		33	34		
Batrachoididae	1	100				100					
Blennidae	19	47	16	21	16			100			
Callionymidae	7	43	14	43		86		14			
Carangidae	2			100				100			
Centriscidae	1	100					100				
Chaetodontidae	5	80	20					100			
Dasyatidae	1	100							100		
Diodontidae	2	100						100			
Gobiesocidae	2	50		50				100			
Gobiidae	44	57	23	20		38	2	55		5	
Grammatidae	3	67	33					100			
Haemulidae	3	33	67					100			
Hemiscylliidae	5	40	20	40				20	60	20	
Heterodontidae	1		100				100				
Kuhliidae	1	100						100			
Labridae	8	100				12		75			13
Labrisomidae	1	100						100			
Monacanthidae	5	40	20		40	20		60		20	
Opistognathidae	3	100						100			
Ostraciidae	1	100						100			
Pholidichthyidae	1	100				100					
Plesiopidae	6	17	33	50		100					
Plotosidae	1	100				100					
Pomacanthidae	40	53	47			3	2	93		3	
Pomacentridae	59	53	20	8	19	90		10			
Pseudochromidae	28	61	18	7	14	64	4	32			
Ptereleotridae	2	100				50		50			
Scianidae	4	75	25					100			
Scyliorhinidae	1	100							100		
Serranidae	11	91	9					100			
Syngnathidae	44	77	9	9	5	9	36	25	5	23	2
Tetraodontidae	3	100						67		33	
Tripterygiidae	1	100						100			
TOTAL (% total species)	338 (100)	204 (60)	73 (22)	37 (11)	24 (7)	125 (37)	21 (6)	165 (49)	8 (2)	16 (5)	3 (1)

For the International Union for Conservation of Nature (IUCN) status: DD, Data Deficient; EN, Endangered; LC, Least Concern; NE, Not Evaluated; NT, Near Threatened; VU, Vulnerable.

marine ornamental fish species increased exponentially from the 1960s until the 2000s with one publication published during the 1960s against 85 publications by the end of the 2000s (Fig. 2). After 2009, the research effort continued to increase, with 120 publications published between 2010 and December 2018. A similar trend was observed for the number of species considered (Fig. 2). Globally, 26 countries contributed, 20 with more than one study (Fig. 3). The largest contributor was the USA, represented by 51 studies on 46 species, followed by India with 34 studies on 26 species and Australia represented by 23 studies on 22 species. The remaining countries were represented by 1 to 15 studies each on 1 to 14 species (Fig. 3).

Academic research from a zootechnical point of view

In addition to the reports on the studied species, information on the main zootechnical advances led by academic research was collected. For this purpose, the selected publications were analysed in order to determine which production phases were considered keeping in mind that some studies may investigate more than one phase. Results shows that more than 70% of the published academic research

Table 3 Summary of the marine ornamental fish species studied in academic research

Family	Number of studies	Number of species	IUCN status (%)						Captive-bred (%)
			NE	DD	LC	NT	VU	EN	
Acanthuridae	7	2			100				100
Apogonidae	5	7	72		14			14	71
Blenniidae	3	1			100				100
Callionymidae	6	2	100						100
Carangidae	1	1			100				100
Chaetodontidae	5	3			100			33	77
Dasyatidae	1	1				100			100
Diodontidae	2	3	67	33					
Gobiesocidae	1	1			100				100
Gobiidae	13	8	14		86				57
Grammatidae	2	2	50		50				50
Haemulidae	3	3			100				100
Hemiscylliidae	3	2			50	50			100
Labridae	4	4			100				
Microdesmidae	1	1			100				100
Opistognathidae	1	1			100				
Pomacanthidae	19	15	7		93				86
Pomacentridae	75	30	93		7				90
Pseudochromidae	5	8	88		12				100
Sciaenidae	1	3			100				100
Scyliorhinidae	1	1				100			100
Serranidae	1	1	100						
Syngnatidae	73	17	6	53			35	6	94
TOTAL (% total species)	222	117	49 (42)	10 (9)	46 (39)	3 (3)	6 (5)	2 (2)	96 (80)

For the International Union for Conservation of Nature (IUCN) status: DD, Data Deficient; EN, Endangered; LC, Least Concern; NE, Not Evaluated; NT, Near Threatened; VU, Vulnerable.

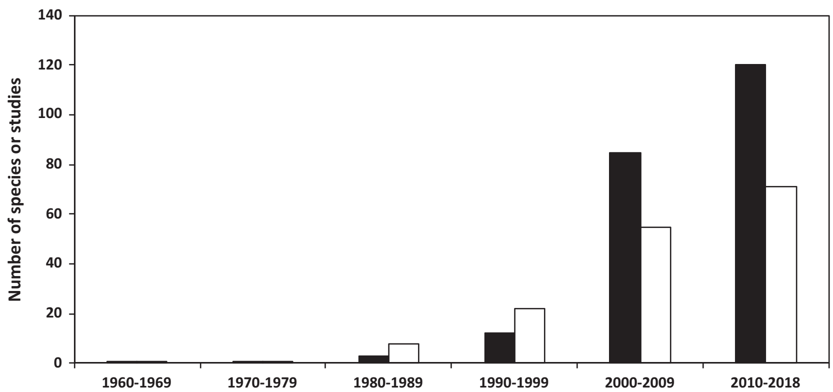

Figure 2 Historical trends in the academic research performed on reproduction and rearing of marine ornamental fish expressed as number of published works and number of species studied since the 1960s to present. (■) Studies; (□) Species.

was focused on the first production steps (i.e. from the broodstock management to the eggs), whereas only 46% were performed on larval rearing, while 32% carried out experiments until metamorphosis (Fig. 4). Furthermore, there was disparity between the families studied (Fig. 4). Indeed, the production of species from certain families such as Apogonidae, Blennidae, Gobiidae or Pomacentridae were the focus of research on all life stages. This was also true for other species without free-larval stage such as the Hemiscylliidae, Scyliorhinidae or Syngnathidae. On the other hand, full coverage of each life stage was not researched for other families. This is particularly true for the species of Pomacanthidae family: although academic research effort was important on this family with 19 studies on the breeding of different species from this family (e.g. Olivotto *et al*. 2006; Baensch & Tamaru 2009; Callan *et al*.

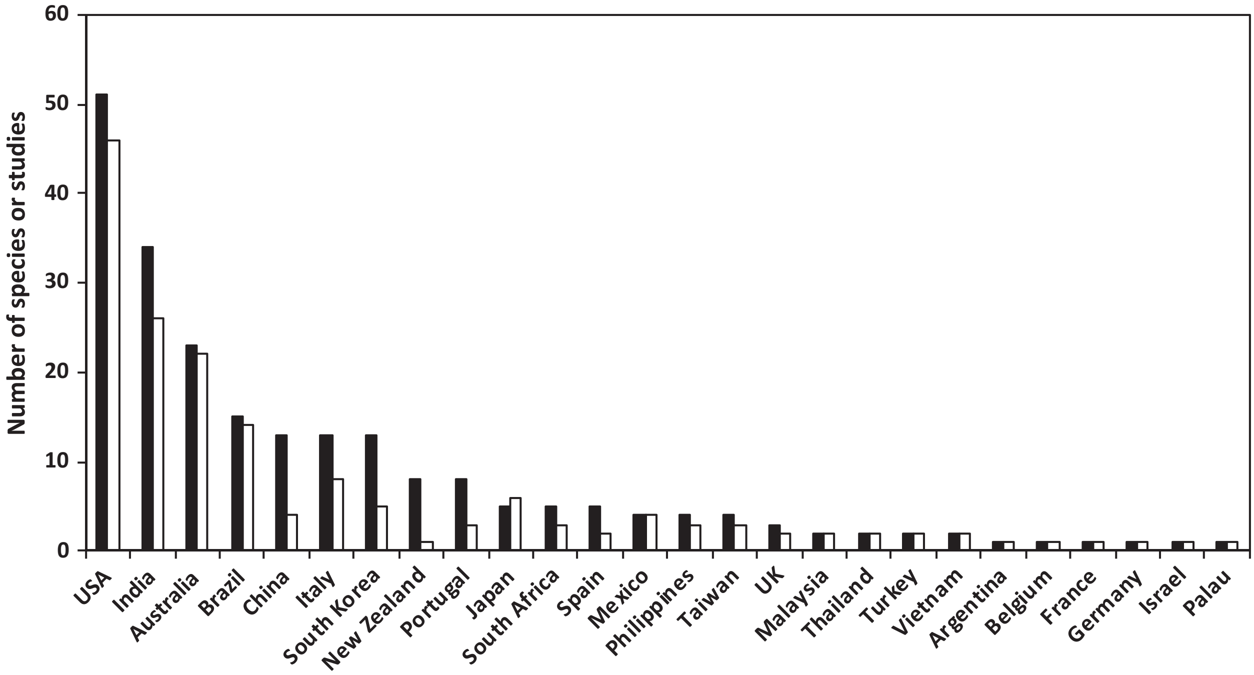

Figure 3 Overview of research on reproduction and rearing of marine ornamental fish by country expressed by total number of published studies and species studied from 1960s to present. (■) Studies; (□) Species.

2014; Rajeswari *et al.* 2017; Fig. 3), metamorphosis was almost never achieved. This observation was also true for other less studied families such as Acanthuridae and Chaetodontidae.

Total CB species vs. species studied in academic research

Sections Captive bred species reported from 2012 to 2017 and Summary of scientific database searches revealed that, 338 species from 37 different families were CB and 117 species from 23 families studied by research scientists from academia respectively (Fig. 5). The two families most represented were Pomacentridae (with 59 CB and 30 studied species), and Syngnathidae (with 44 CB and 17 studied species). For these families, there were at least twofold more CB species than species studied at the academic research side. Interestingly, Gobiidae were also among the most CB families with 44 species but their occurrence was limited in scientific literature (eight species, Fig. 5). With the exception of Microdesmidae (no recorded as CB but one species studied by academists, Madhu & Madhu 2014), there was always a greater number of CB species than species studied by academic researchers. This trend was particularly true for Gobiidae because they were also among the most studies CB families with 44 species, but their occurrence was limited in scientific literature (eight species, Fig. 5).

Discussion

Overview of marine ornamental fish aquaculture

Based on the CORAL list analysis, to date, 338 species of marine ornamental fish have been successfully captive bred with much of this success driven by private companies and enlightened hobbyists. Although this number has increased by an average percentage rate of 8% since 2012, it only represents 19% of the marine ornamental fish species traded for the aquarium hobby (i.e. a minimum of 1800 species traded annually; Palmtag 2017; Rhyne *et al.* 2017b). Moreover, our results shown that only a minor fraction of these CB species (7%) are commonly available on the market such as blenny, clownfish and dottyback (Table 2). Other species have a limited availability on the market (i.e. releases not constant throughout the year and/or in small quantities) such as cardinalfish, goby and some seahorses (Table 2), while others are on the verge of being commercialized with very first releases in the last 2 years, such as CB surgeonfish (Acanthuridae). This meta-analysis confirms a vast majority of marine ornamental fish are still wild-caught to date. Research in aquaculture of marine ornamental species is therefore crucial to allow a move towards greater sustainability of the marine fishkeeping practice.

One of the primary benefits of aquaculture research is that the species' biology is thoroughly investigated. This often leads to improvements of cultivation methods (e.g.

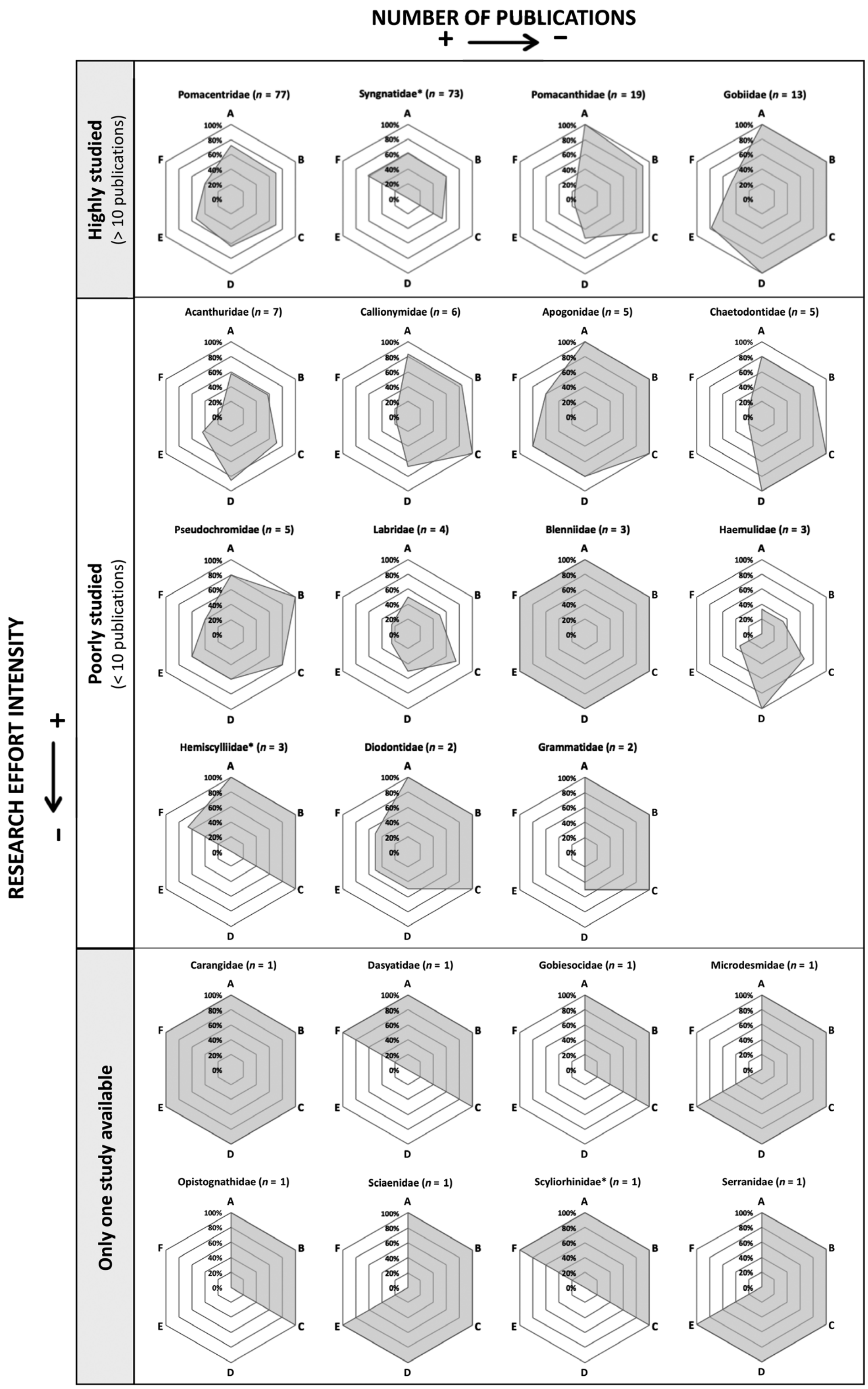

Figure 4 Advances in academic research for the different families studied. For each family, the proportion of published studies that have reached a given breeding stage (i.e. broodstock management, spawning, egg/embryonic development, larval rearing, metamorphosis and juvenile rearing) is indicated. The number of studies per family is indicated in brackets. (a) broodstock management, (b) Spawning, (c) Egg/Embryonic development, (d) Larval rearing, (e) Metamorphosis, (f) Juvenile rearing.

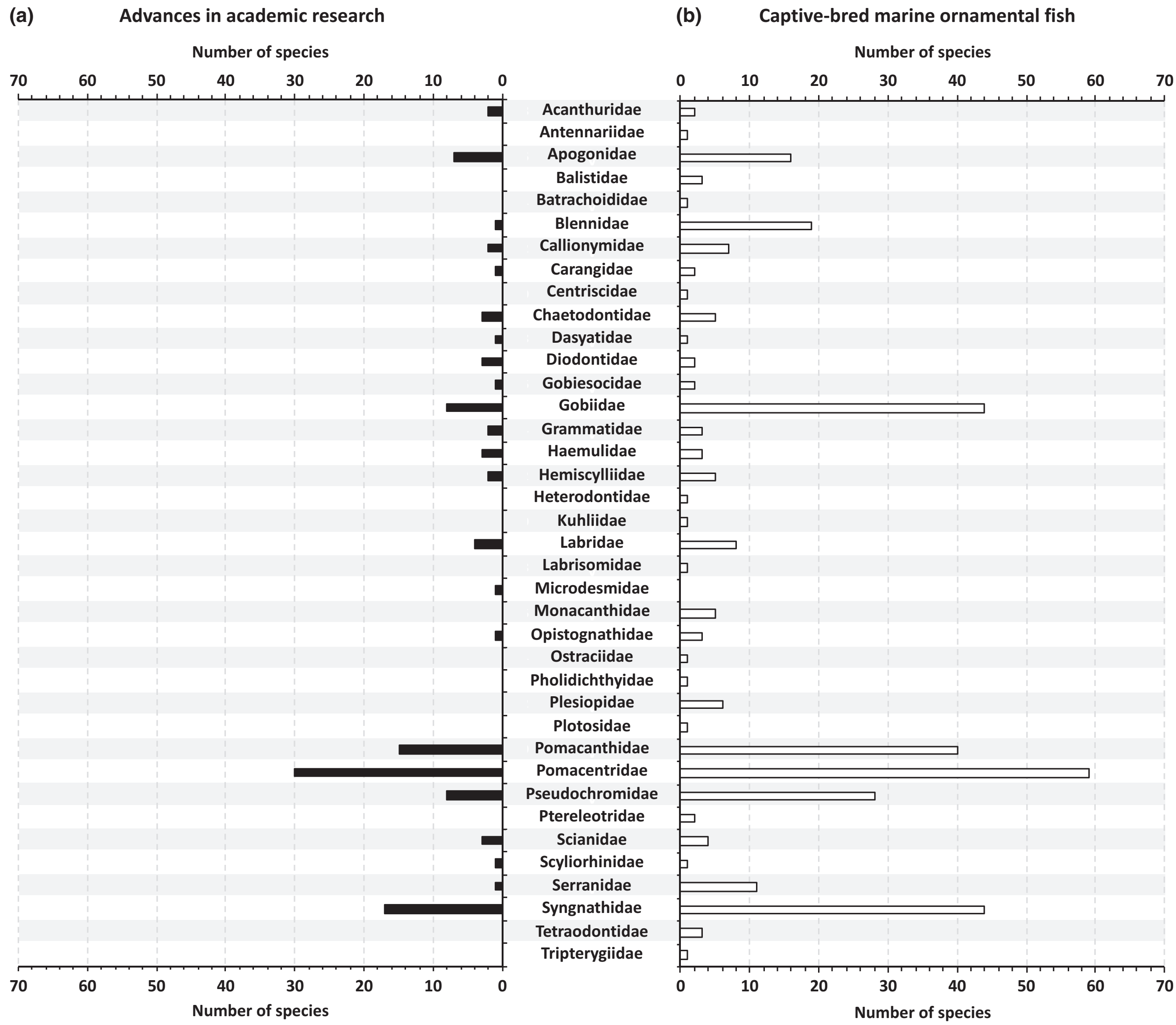

Figure 5 (a) Number of marine ornamental fish species studied in academic research and (b) CB species.

broodstock management, larval rearing and nutrition), which can then be transferred to other species (Tlusty 2002). For now, there are still numerous technical critical factors limiting captive propagation (see Olivotto *et al.* 2017; Rhyne *et al.* 2017a). Nevertheless, the main challenge encountered in marine ornamental production remains the larval rearing: larvae are small and they need very small, living foods for first feeding such as copepods (Olivotto *et al.* 2017; Rhyne *et al.* 2017a). However, mass-scale production of adequate copepod species remains challenging (Dhont *et al.* 2013), and thus, streghtening research effort on first exogenous feeding of new species' early life-stage is necessary. In addition, one last benefit is that information on the general biology of species can further assist wildlife biologists in the management of the species on their natural environment (Nicosia & Lavalli 1999; Tlusty 2002).

Current state of the marine ornamental fish academic research

Academic research regarding marine ornamental fish aquaculture is most common in North America, Asia and Europe. Three countries (USA, India and in a lesser extent Australia) are responsible for ~50% of the worldwide publications. Among these countries, it is not surprising to find the USA in the foreground of research effort in marine ornamental fish aquaculture since it is the main importer country of coral reef organisms (Rhyne *et al.* 2012, 2017b). In India, the marine ornamental fish trade has been a more recent development and research is largely focused on hatchery production methods to sustain this trade (Gopakumar *et al.* 2009). In the meantime, we have to acknowledge the potential bias (Morrison *et al.* 2012) in

Table 4 Top 5 families of marine ornamental fish in terms of (A) volume of fish imported on the world, the USA and the Switzerland markets, (B) number of species studied by academia and (C) number of species captive bred by private companies and hobbyists

Rank	A - Markets			B - Academic research	C - Private companies and hobbyists
	World	USA	Switzerland		
1	Pomacentridae	Pomacentridae	Pomacentridae	Pomacentridae	Pomacentridae
2	Labridae	Labridae	Labridae	Syngnatidae	Syngnatidae
3	Gobiidae	Pomacanthidae	Gobiidae	Pomacanthidae	Gobiidae
4	Pomacanthidae	Gobiidae	Acanthuridae	Gobiidae	Pomacanthidae
5	Acanthuridae	Acanthuridae	Pomacanthidae	Pseudochromidae	Pseudochromidae

our analyses in academic research on ornamental marine fish. Indeed, our selection methodology is restrictited to English-language articles and it can result in an underestimation of the reality. A necessary follow-up would be to address academic marine ornamental research publications from important producer countries (e.g. China, Thailand, Philippines, Czech Republic) that are published in their native language.

The evolution of the number of studies published per decade (Fig. 2) indicates that the research effort is growing. However, the information published in this research area to date is limited to 117 species, and only 13 were among the top 20 species imported into the US (Rhyne *et al.* 2017b). Nevertheless, we found no relationship between the volume of fish imported and the intensity of academic research (i.e. number of publications).

Currently, less than 50% of the studies have been focused on first-exogenous feeding, the most critical phase in marine fish aquaculture. Furthermore, academic research results have been published on all breeding stages (i.e. from the broodstock management to the juvenile rearing) for only 58 species (i.e. 50% of the studied species). These results suggest that advances in the captive breeding of ornamental marine fish are mainly attributable to private companies through their research and development activities and advanced hobbyists. This finding contrasts with the aquaculture of marine fish for human consumption. Indeed, marine food-fish aquaculture developed in the 70–80s, and the bottlenecks regarding captive breeding and nutrition were solved by intense academic research efforts (Nicolaisen 2018). For example aquaculture of European seabass *Dicentrarchus labrax* and gilthead seabream *Sparus aurata* was initiated on the basis of an important mostly public research effort (UK, France) which started in the 1970s. Then, private entrepreneurship and international cooperation joined the effort and expanded aquaculture all around the Mediterranean Sea (Harache & Paquotte 1996). Some authors suggest that the achievements in marine foodfish culture may be applicable to techniques for marine ornamental fish aquaculture, however, concerted scientific research efforts are lacking (Ostrowski & Laidley 2001). Furthermore, as indicated in the Table 1, some species can be used both for ornamental purpose or as food resource (usually depending on their life-stage). In this case, academic research performed is beneficial to both production sectors (food or ornamental). Batfish (*Platax* sp.) juveniles are attractive for the ornamental market while adults are marketed for human consumption in Asian and South Pacific regions (e.g., Masanet 1995; Barros *et al.* 2011; Leu *et al.* 2018).

Interestingly, three of the five most important families on the market: Pomacentridae, Gobiidae and Pomacanthidae are among the most studied families with the highest number of CB species (Table 4). The Pomacentridae largely dominate the aquarium market and 80% of the 10 best-selling species belong to this family (Rhyne *et al.* 2017b). Like Gobiidae, Pomacentridae are generally low value (per individual) species (Biondo 2017; Rhyne *et al.* 2017b) unlike Pomacanthidae, which are among the most valuable species (Wood 2001; Balboa 2003). The values of one species has been shown to be closely related to his availability on the market (Green 2003). Considering that, we assume that similarities and differences between the patterns observed for academic research and private sector (Fig. 5) can be explained by the following three different strategies:

(1) Private companies would be focused on mass production of easy-to-trade and easy-to-breed species such as Pomacentridae and dedicate their R&D for very valuable species such as Pomacanthidae.
(2) Academists would work on a variety of species depending on the need: species easy to breed in order to work on specific research topics in replicated experiments or challenging species to work on a new species (like, e.g. Chaetodontidae or Pomacanthidae species).
(3) Advanced hobbyists would be less interested in the captive breeding of common species, and work on original species that not yet captive bred on a large scale without any economic objective.

Academic research and private sectors can be linked. Obviously, the publication of scientific results and extension papers makes information accessible to companies. Other interactions exist between academic research and the private sector such as funding or graduate students working for private companies that may assist in more effective technology transfer than publications. A non negligible part of the academic studies included in this review (approx. 10%) were carried out, at least partially, in collaboration with production companies (e.g. da Hora & Joyeux 2009; Leis *et al.* 2011) or public aquaria (e.g. Tlusty *et al.* 2013, 2017; Doi *et al.* 2015a,b). This can be explained by the availability of infrastructures better adapted to maintain some species with special needs (e.g. pelagic spawners such as Acanthuridae and Pomacanthidae; Leu *et al.* 2009, 2010; Cassiano *et al.* 2015; Leu *et al.* 2015) or large specimens such as sharks (Harahush *et al.* 2007; Hövel *et al.* 2010; Payne 2012). Furthermore, public aquaria are also involved in the conservation programs of some species in collaboration with academists (Maitland 1995; Tlusty *et al.* 2013).

Some species can be challenging to captive bred due to their specific requirements, the investment in time and money needed and/or their high production costs, which are inconsistent with profitability objectives from private companies. In this context, academic research can lead to significant advances. For instance some species of Acanthuridae and Chaetodontidae required many years of intensive research and for which the first successes of breeding in captivity up to the production of juveniles were recently published by academic teams (DiMaggio *et al.* 2017; Callan *et al.* 2018; Ohs *et al.* 2018). Although survival rates (<1%) are still incompatible with large-scale commercial production, this research has unlocked certain barriers in the production of pelagic spawner species (Olivotto *et al.* 2017) such as the Pacific blue tang *Paracanthurus hepatus*, reef butterflyfish *Chaetodon sedentarius* and yellow tang *Zebrasoma flavescens*. These success stories illustrate the benefits of interactions between research institutes and private sector in the production of marine ornamental fish.

Drivers of marine ornamental fish aquaculture research

To understand how the dynamic of marine ornamental fish aquaculture research is influenced, it is important to consider all the potential drivers. The trade of marine ornamental organisms is the main obvious one. Indeed, as a consequence of the growing demand for marine ornamental fish, the pressure on wild stocks is increasing. Although, most of the species currently traded are abundant and occur over wide geographical areas and are generally not endemic or 'rare' (Rhyne *et al.* 2012), current knowledge regarding the real status of wild populations is limited. Indeed, we found in our analysis, that among the 338 CB species, 37% were not evaluated by IUCN (Table 2). Furthermore, the negative impacts of fisheries for aquarium trade have been demonstrated for some species. One of the most striking example is the Banggai cardinalfish, an endemic species of the Banggai Islands (Central Sulawesi, Indonesia). Indeed, several subpopulations of this species were strongly affected by the aquarium fishery and exhibited dramatic declines (Yahya *et al.* 2012; Talbot *et al.* 2013; Conant 2015). Therefore, another driver that could be identified is policy: restricting or banning the harvest of some marine ornamental fish from the wild to supply the marine aquarium trade is becoming a growing option when advocating reef conservation (Dee *et al.* 2014). In the near future, the collection of several banned species in the trade will be severely restricted, or even prohibited (Calado 2017). In this context, academic research plays also important role in marine fish conservation as evidenced by the 8 threatened species that have been studied by academics (seven Syngnathidae et one Apogonidae, see Table 3). An increasing demand on the market combined with increasingly constrained wild-catches are factors that may favour research on marine ornamental fish aquaculture, whether academic, conducted by private companies or by hobbyists. Nevertheless, there are other limiting factors that restrain the research done on marine ornamental fish in addition to the zootechnical brakes well detailed in literature (e.g. Olivotto *et al.* 2017) that may eventually be overcome.

One of the aims of this research is to be able to supply the market with marine ornamental fish produced through closed-cycle aquaculture. Despite significant progress, production of CB fish is unfortunately not cost-effective yet compared to their wild-caught counterparts. The selling prices of CB fish, can be at least 25% higher than those of their wild equivalents (Fotedar & Philips 2011). For example aquaculture of mandarin dragonets *Synchiropus* sp. is feasible but faces a large supply of cheaper wild fish (25 USD per wild fish *vs.* 60 USD per CB fish; Rhyne *et al.* 2017a). Thus, the marketplace need to appreciate fully the advantages of cultured species over wild-caught species to accept the higher prices charged (Corbin *et al.* 2003).

In this context, successful large-scale production of ornamental marine CB fish is mainly dependent on consumer (i.e. hobbyist) choice and thus the risk on the market is the non-sustainability of the demand in the long run. The bright side for future of farming of ornamental fish is that the current fishkeepers are becoming more and more sensitive to the sustainability of ornamental fish production and price does not seems to be the determining factor in their purchase (Militz *et al.* 2017). The context for the marine fish aquaculture is thus positive, which could consequently stimulate the future research undertaken in this field. Moreover, it should be emphasized that the role of hobbyists is and will remain predominant because they can act on both the trade, by favouring CB fish, as well as through their own research, often freely shared, mainly motivated by the challenge of successful reproduction of difficult to captive-bred species.

Conclusion

This review highlighted that, regarding advances in captive breeding of marine ornamental fish, academic research is only the tip of the iceberg. Many advances have come through private companies and enlightened hobbyists. However, academic research plays a key role for developing captive reproductive success of certain species requiring many years of development, and for marine species conservation especially in the current context where more and more drastic measures are being taken by the governments concerned to protect coral ecosystems (Dee *et al.* 2014). Unfortunately, from a realistic point of view and despite all the progress made, the research effort in this domain remains to date very expensive and time consuming. It is unlikely that in the near future the majority of marine ornamental fish will be CB as seen freshwater ornamental fish, of which an increasing number of species are now domesticated (Teletchea 2016). In this context, it is crucial to first act in favour of sustainable fishing methods (i.e. with proper stock management and avoiding habitat destruction), then to promote CB fish production (Rhyne *et al.* 2014). Consumer awareness is a necessary component to drive the development of alternatives to ornamental fish collected from the wild.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1. List of ornamental marine fish species studied in academic research.