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How many fish could be vocal? An estimation from a coral reef (Moorea Island)

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Abstract. A recurrent question arising in fish bioacoustics research concerns the number of vocal fish species that may exist. Although it is not possible to provide a precise globally valid number, an estimation based on recordings already collected at coral reefs (Moorea) and on morphological approaches indicates that approximately half of the fish families of this particular environment has at least one known sound-producing species. In light of this, acoustic behaviour should be fully considered in biology, ecology and management plans as it may provide information on a consistent portion of fish biodiversity. Fish bioacoustics has switched from anecdotal reports to long-term, large-scale monitoring studies, capable of providing high resolution information on fish populations' composition and dynamics. This information is vital for successful management plans in our quickly changing seas.

Keywords. Acoustic, biodiversity, monitoring, sonic, teleost.

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Introduction

In the last decades, increasing human pressure on marine ecosystems and resources, driven by demographic and economic growth, as well as by the diversification and intensification of maritime activities, poses unprecedented threats to global biodiversity and to the overall health of our seas. Fishing has always represented a central economic activity that has provided livelihood opportunities to hundreds of thousands of people while shaping the cultural fabric of coastal towns and communities. Today, the sea plays a central role, being increasingly pivotal for the sustainable development of many regions. The main challenge is

to find new monitoring approaches capable of quickly providing high-resolution information on marine ecosystems and communities' status and health.

All teleost species may produce sounds if we include feeding, swimming, splashing and jumping noises (Rountree *et al*. 2018). However, these sounds can be considered as incidental or as by-products of fish activities and are not species- or family-specific. In order to monitor fish species in the wild, based on the sounds they naturally emit, the sampling effort should focus only on sounds which are species-specific. This is the case for communicative sounds, i.e., sounds which are intentionally made by fish during social interactions to elicit a behavioural response in the receiver that is advantageous (at least) for the sender (Bradbury & Vehrencamp 1998). Fish sound production was first mentioned by Aristotle and it has been known and exploited by fishermen for centuries (Lobel *et al*. 2010). Fishermen from different regions worldwide locate fish aggregations by listening to their sounds. For example, in the Gironde estuary, the long-standing knowledge about the meagre (*Argyrosomus regius*) vocal abilities has been used by fishermen to locate large aggregations of this species during its spawning period (Lagardère & Mariani 2006). However, the idea that most underwater organisms (except whales and dolphins) would be unable to produce sounds and live in a silent environment is still very popular, maybe aided by a misapprehension derived from the documentary "The Silent World" (Cousteau & Dumas 1953). Some decades ago, only few fish species were considered to rely on acoustic communication (Moulton 1958, 1963; Fish & Mowbray 1970; Lobel *et al*. 2010). Today, fish acoustic communication should be considered as an important aspect of teleost social behaviour across a wider taxonomic spectrum; fish sounds have indeed been reported in several, unrelated taxa inhabiting different aquatic habitats. Fish sounds have been recorded in freshwater streams, rivers and lakes, as well as in temperate and tropical coastal areas and also in the deep-sea (Fine & Parmentier 2015). Acoustic signals mediate fish social interactions in a wide range of activities which are crucial for their survival, such as competitive feeding, distress or alarm situations, conspecific identification, courtship and agonistic interactions, mate choice, mate quality assessment and coordination of gamete release (Amorim *et al*. 2015). Collectively, the increasing number of studies describing the vocal abilities of marine fish points to acoustic communication as an important aspect of teleost biology, which mediates social interactions during pivotal activities for fish survival and fitness. Reliance on acoustic communication may be of even greater importance for nocturnal species or for species living in deep sea habitats (Ruppé *et al*. 2015; Desideràt *et al*. 2019).

The Actinopterygii comprises 488 families (Van der Laan & Fricke 2019) and around 34200 species (Froese & Pauly 2019). In some taxa, all or almost all species have the ability to produce sounds for social purposes (Fine & Parmentier 2015). Conversely, large fish families may be mostly mute since none, one or only a few species have been reported to produce socially relevant sounds (Fine & Parmentier 2015). However, cycles of sound-producing muscle hypertrophy during mating seasons (Connaughton *et al*. 1997) imply that some species are unlikely to be vocal throughout the rest of the year, making the adage "absence of evidence is not evidence of absence" particularly relevant.

The assessment of the total number of vocal fish species could be achieved by counting the number of species for which sounds have been effectively recorded. This number should be updated each time a new study on the subject is published. Moreover, this number could be further improved by using morphological data, which allow to confidently infer the ability to emit sounds even in species that have not yet been recorded, as long as they have been shown either to possess the required mechanisms or be closely related to a vocal species (Frédérich *et al*. 2014; Raick *et al*. 2018). The estimation of an exact globally valid number of vocal fish species would be extremely time consuming and likely ineffective if all fish taxa present worldwide are surveyed by using the above-mentioned approach. A more effective strategy would be to apply this approach to specific habitats first. Here, we focus on one of the most acoustically and taxonomically diverse, as well as most studied, aquatic environments, i.e., coral reefs. To provide a first response to the question "how many fish are vocal?", we calculated the ratio of calling teleost species to

the total number of species in the coral reefs of Moorea Island (French Polynesia), where fish acoustic communication has been investigated for more than 20 years. We postulate that our approach to estimate the ratio of vocal species, which we calculated for a localised, well-known fish vocal community, can be applied to other marine habitats and eventually be upscaled to estimate a global ratio of vocalising fish species. Under the assumption that environmental pressures and taxonomic composition have acted similarly on acoustic diversity in different biotopes, we would expect that ratios being precisely calculated for a selected number of different biotopes with our approach could approximate the ratio of other different environments and provide a rough but coherent estimation of the total number of potential vocal fish species.

In coral reefs, fish acoustic behaviours are prominent as many species produce sounds during agonistic interactions with competitors, responses to predators or threats, and during courtship and spawning. Worldwide, 179 fish families occupy coral reefs and adjacent marine habitats. Sounds were first reported in species of 48 (27%) of these families (Lobel *et al*. 2010). However, these authors considered all sounds, including swimming and feeding sounds that could be by-products of movement and food processing. Boyle and Tricas conducted a pioneering study to estimate the ratio of vocal species in Hawaiian reefs (Tricas & Boyle 2014). They estimated that 45 species out of 96 (from 12 families out of 24) produced sounds in several behavioural contexts. This means that half of the detected families were represented by at least one vocal species. However, Boyle and Tricas' methodology was based on scuba diving performed during daytime, which therefore excludes many species that are mostly vocally active during night time hours and/or that are behaviourally cryptic (Ruppé *et al*. 2015; Picciulin *et al*. 2019). This approach also overlooked small and cryptic species such as gobies or blennies, which have sonic representatives (De Jong *et al*. 2007; Malavasi *et al*. 2012). In fact, a total of 481 species (not 96) can be found in Hawaiian reefs (Froese & Pauly 2019) and hence it is likely that the number of vocal species was underestimated.

The recently published complete list of shore fishes from French Polynesia (Siu *et al*. 2017) was used here to estimate the ratio of calling species, genera and families (Table 1). In Moorea, 18 of the 66 fish families (27%) possess species for which sound production for communication purposes has been demonstrated (Table 1). Obviously, many species living in this area have not yet been recorded, i.e., they have not been investigated yet in terms of vocal abilities. This implies that the number of calling species is most probably larger than estimated. Species from French Polynesia that belong to genera such as *Platax sp.* (Ephippididae), *Hyporhamphus sp.* (Hemiramphidae), *Polydactylus sp.* (Polynemidae) and *Caranx sp.* (Carangidae) possess vocal co-generics in other parts of the world (Fish & Mowbray 1970; Lobel *et al*. 2010) supporting the possibility that species from Moorea are also capable of sound production. If we include these four additional taxa, the ratio of families having at least one vocal species would be up to 33%.

Moreover, it is interesting to consider nine additional fish families from French Polynesia (Aulostomidae, Bythidae, Blenniidae, Diodontidae, Gobiidae, Hemiramphidae, Ophidiidae, Scorpaenidae, Syngnathidae) which hold species that are potentially vocal for two reasons. First, some of them possess anatomical features supporting sound production (Hallacher 1974; Parmentier *et al*. 2010; 2013; Fine & Parmentier 2015) and second, acoustic communication has been proven in species (Moulton 1958, 1963; Lobel *et al*. 2010; Tricas & Boyle 2014) being from the family but not from the same genus. Based on these assumptions, we can reasonably suggest that these nine families (Table 1) should also be added to the list of soniferous fish families from Moorea. In this case, the ratio of vocal families further increases to 47% (32 out of 66). Additional data are obviously needed to identify and validate calling species identity within these families and in others. At the current state of art, we know that there are more calling species than those currently identified, because most of the sounds recorded in the wild using passive acoustics have not yet been attributed to a species (Jublier *et al*. 2019; Bertucci *et al*. 2020).

Considering the lower taxonomic genus level, 22% of the 241 fish genera inhabiting Moorea's reef include species known to use acoustic communication (Table 1). Although one fifth is already an important ratio, we suspect that this number is probably still an underestimation if we follow the same reasoning that was applied for the families. Fish species from ten genera which are present in Moorea have been recorded in other parts of the world (Table 1). Adding these genera to our assessment increases the ratio of fish genera having vocal species to 26%.

We can try to tackle this argument also in another way. The 31 (or 47%) fish families of Moorea that possess calling fish altogether contain 161 genera (Table 1). If all genera that belong to the 31 aforementioned families have sonic species, 67% of the genera found in Moorea could then have at least one representative vocal species. However, acoustic abilities have not yet been indicated in all genera within these families and it is not always easy to make predictions. For example, many if not all Carapidae, Holocentridae and Pomacentridae species probably make sounds because they all possess the required acoustic sonic mechanisms (Fine & Parmentier 2015). In other families, such as Blenniidae or Gobiidae, the sonic ability has been shown in certain genera only (De Jong *et al*. 2007; Malavasi *et al*. 2012) and further studies still have to be conducted to investigate other genera. This comparison highlights the need of additional tests to better assess the number of fish genera having calling species.

Coral reefs are characterised by rich habitat complexity and biodiversity; here, fishes have evolved amazing colour patterns. Although environmental conditions of coral reefs should favour visual communication, the ratio of calling species to not calling species is quite significant. Importantly, fish acoustic diversity peaks during night-time hours, i.e., when visual communication is not possible (Ruppé *et al*. 2015; Bertucci *et al*. 2020). This suggests that acoustic communication should be important also under other conditions in which dependence on visual communication is impaired, such as murky and dark environments as well as the deep-sea. Although many deep-sea fish species are likely to emit sounds as they possess the required anatomical structures, empirical data for this biotope are still too scattered to provide robust estimations on the ratio of vocal to not vocal fish species (Bolgan & Parmentier 2020).

Conclusion

Providing a precise number of vocal fish species is currently impossible as it would require an alienating and time-consuming effort to collect, identify, and record all worldwide distributed species that have not yet been recorded. We here humbly attempted to estimate a first ratio of vocal species by taking advantage of a unique combination of extensive recordings and monitoring of the ichthyologic community of the coral reef of Moorea. Half of the families and around a third of the genera in Moorea have been estimated to contain species being able to produce communicative sounds. Even if approximated and limited to a single habitat, these ratios emphasise the importance that calling behaviour may have in the biology of many more fishes than previously thought. Biodiversity assessments remain as one of the most difficult challenges encountered by ecologists and conservation biologists. This growing need for biodiversity assessments raises questions of whether current monitoring techniques are appropriate and efficient. Indeed, biodiversity assessment tools should effectively detect the highest possible number of species, including cryptic ones, in order to provide high resolution information on fish diversity. By taking advantage of the sounds produced by fish species, passive acoustic monitoring has demonstrated its potential to evaluate the diversity of coral reef fish, based on the vocal activities of their numerous inhabitants. The present study clearly supports that fish bioacoustics should be considered as an important tool in marine conservation and monitoring studies. Acoustic behaviour should be fully included in the biology and ecology of teleosts and in future conservation studies of marine ecosystems. However, additional studies are still required to confirm the same ratio in other habitats. Although at present risky, extrapolation of our observations to all teleost species would indicate that up to half of the world's fish families (i.e., 244 out of 448) could possibly possess vocal species.

TABLE 1

List of the fishes present in Moorea waters (French Polynesia) with information related to acoustic communication. VSM: identified vocal species from Moorea. VG: genus of coral reef family having at least one identified vocal species. PVG: genus of coral reef having potentially (based on literature) one vocal species. Family in yellow: at least one identified and recorded calling species. Families in green: family known to host at least one vocal species but not yet recorded in French Polynesia. Families in blue: no information concerning acoustic communication. Numbers after each family refer to the number of genera found in Moorea. The Table has been built on the basis of different studies (Fish *et al.* 1952; Moulton 1958, 1963; Fish & Mowbray 1970; Lobel *et al.* 2010; Malavasi *et al.* 2012; Tricas & Boyle 2014; Fine & Parmentier 2015; Parmentier *et al.* 2016).

FAMILY	GENUS-SPECIES	VSM	VG	PVG
Megalopidae	**1**			
	Megalops			
	Megalops cyprinoides			
Albulidae	**1**			
	Albula			
	Albula glossodonta			
Chanidae	**1**			
	Chanos			
	Chanos chanos			
Moringuidae	**1**			
	Moringua			
	Moringua javanica			
Chlopsidae	**2**			
	Chilorhinus			
	Chilorhinus platyrhynchus			
	Kaupichthys			
	Kaupichthys brachychirus			
	Kaupichthys diodontus			
Muraenidae	**8**			
	Anarchias			
	Anarchias seychellensis			
	Echidna			
	Echidna leucotaenia			
	Echidna nebulosa			
	Echidna polyzona			
	Enchelycore			
	Enchelycore bayeri			
	Enchelynassa			
	Enchelynassa canina			
	Gymnomuraena			
	Gymnomuraena zebra			

FAMILY	GENUS-SPECIES	VSM	VG	PVG
	Gymnothorax			
	Gymnothorax buroensis			
	Gymnothorax chilospilus			
	Gymnothorax eurostus			
	Gymnothorax fimbriatus			
	Gymnothorax formosus			
	Gymnothorax gracilicauda			
	Gymnothorax javanicus			
	Gymnothorax kontodontos			
	Gymnothorax margaritophorus			
	Gymnothorax melatremus			
	Gymnothorax meleagris			
	Gymnothorax pictus			
	Gymnothorax reevesii			
	Gymnothorax richardsonii			
	Gymnothorax rueppelliae			
	Gymnothorax undulatus			
	Gymnothorax zonipectis			
	Scuticaria			
	Scuticaria tigrina			
	Uropterygius			
	Uropterygius alboguttatus			
	Uropterygius fuscoguttatus			
	Uropterygius inornatus			
	Uropterygius kamar			
	Uropterygius supraforatus			
Congridae	**4**			
	Ariosoma			
	Ariosoma fasciatum			
	Ariosoma scheelei			
	Conger			
	Conger cinereus			
	Gorgasia			
	Gorgasia galzini			
	Heteroconger			
	Heteroconger lentiginosus			
Ophichthidae	**6**			
	Callechelys			
	Callechelys marmorata			

FAMILY	GENUS-SPECIES	VSM	VG	PVG
	Leiuranus			
	Leiuranus semicinctus			
	Myrophis			
	Myrophis microchir			
	Schismorhynchus			
	Schismorhynchus labialis			
	Schultzidia			
	Schultzidia johnstonensis			
	Scolecenchelys			
	Scolecenchelys gymnota			
	Scolecenchelys laticaudata			
Synodontidae	**2**			
	Saurida			
	Saurida gracilis			
	Synodus			
	Synodus binotatus			
	Synodus dermatogenys			
	Synodus jaculum			
	Synodus variegatus			
Antennariidae	**2**			
	Antennarius			
	Antennarius randalli			
	Antennatus			
	Antennatus coccineus			
	Antennatus tuberosus			
Ophidiidae	**1**			
	Brotula			X
	Brotula multibarbata			
Bythitidae	**3**			
	Alionematichthys			X
	Alionematichthys piger			
	Diancistrus			X
	Diancistrus katrineae			
	Dinematichthys			X
	Dinematichthys iluocoeteoides			
Carapidae	**3**			
	Carapus		X	
	Carapus boraborensis	X		
	Carapus homei	X		

FAMILY	GENUS-SPECIES	VSM	VG	PVG
	Carapus mourlani	X		
	Encheliophis		X	
	Encheliophis chardewalli	X		
	Encheliophis gracilis	X		
	Onuxodon		X	
	Onuxodon fowleri	X		
Hemiramphidae	**2**			
	Hemiramphus			
	Hemiramphus depauperatus			
	Hyporhamphus		X	
	Hyporhamphus affinis			
Belonidae	**3**			
	Ablennes			
	Ablennes hians			
	Platybelone			
	Platybelone argalus			
	Tylosurus			
	Tylosurus crocodilus			
Holocentridae	**4**			
	Myripristis		X	
	Myripristis adusta			
	Myripristis amaena	X		
	Myripristis berndti	X		
	Myripristis kuntee	X		
	Myripristis murdjan			
	Myripristis pralinia	X		
	Myripristis violacea	X		
	Myripristis woodsi			
	Neoniphon		X	
	Neoniphon argenteus			
	Neoniphon opercularis			
	Neoniphon sammara	X		
	Plectrypops			X
	Plectrypops lima			
	Sargocentron		X	
	Sargocentron caudimaculatum			
	Sargocentron diadema			
	Sargocentron microstoma			
	Sargocentron punctatissimum			

FAMILY	GENUS-SPECIES	VSM	VG	PVG
	Sargocentron spiniferum	X		
	Sargocentron tiere	X		
	Sargocentron tiereoides			
Aulostomidae	**1**			
	Aulostomus			
	Aulostomus chinensis			
Fistulariidae	**1**			
	Fistularia			
	Fistularia commersonii			
Syngnathidae	**4**			
	Choeroichthys			
	Choeroichthys brachysoma			
	Corythoichthys			
	Corythoichthys flavofasciatus			
	Doryrhamphus			
	Doryrhamphus excisus			
	Minyichthys			
	Minyichthys myersi			
Scorpaenidae	**7**			
	Caracanthus			
	Caracanthus maculatus			
	Caracanthus unipinna			
	Dendrochirus			
	Dendrochirus biocellatus			
	Pterois			X
	Pterois antennata			
	Pterois radiata			
	Pterois volitans			
	Scorpaenodes			
	Scorpaenodes guamensis			
	Scorpaenodes hirsutus			
	Scorpaenodes minor			
	Scorpaenodes parvipinnis			
	Scorpaenopsis diabolus			
	Scorpaenopsis			
	Scorpaenopsis macrochir			
	Scorpaenopsis papuensis			
	Scorpaenopsis possi			

FAMILY	GENUS-SPECIES	VSM	VG	PVG
	Sebastapistes			
	Sebastapistes fowleri			
	Sebastapistes strongia			
	Sebastapistes tinkhami			
	Taenianotus			
	Taenianotus triacanthus			
Synanceiidae	**1**			
	Synanceia			
	Synanceia verrucosa			
Platycephalidae	**1**			
	Sunagocia			
	Sunagocia otaitensis			
Dactylopteridae	**1**			
	Dactyloptena		X	
	Dactyloptena orientalis	X		
Serranidae	**11**			
	Aporops			
	Aporops bilinearis			
	Cephalopholis		X	
	Cephalopholis argus	X		
	Cephalopholis aurantia			
	Cephalopholis leopardus			
	Cephalopholis urodeta			
	Epinephelus		X	
	Epinephelus fasciatus			
	Epinephelus merra			
	Epinephelus polyphekadion			
	Epinephelus socialis			
	Epinephelus tauvina			
	Gracila			
	Gracila albomarginata			
	Grammistes			
	Grammistes sexlineatus			
	Grammistops ocellatus			
	Liopropoma			
	Liopropoma mitratum			
	Liopropoma pallidum			
	Liopropoma tonstrinum			

FAMILY	GENUS-SPECIES	VSM	VG	PVG
	Plectranthias			
	Plectranthias cf. *winniensis*			
	Plectranthias longimanus			
	Plectranthias nanus			
	Pseudanthias		X	
	Pseudanthias bicolor	X		
	Pseudanthias lori			
	Pseudanthias mooreanus			
	Pseudanthias olivaceus			
	Pseudanthias pascalus			
	Pseudogramma			
	Pseudogramma polyacantha			
	Suttonia			
	Suttonia lineata			
	Variola			
	Variola louti			
Pseudochromidae	**1**			
	Pseudoplesiops			
	Pseudoplesiops revellei			
Priacanthidae	**2**			
	Heteropriacanthus		X	
	Heteropriacanthus cruentatus	X		
	Priacanthus		X	
	Priacanthus hamrur			
Cirrhitidae	**5**			
	Amblycirrhitus			
	Amblycirrhitus bimacula			
	Cirrhitichthys			
	Cirrhitichthys oxycephalus			
	Cirrhitus			
	Cirrhitus pinnulatus			
	Neocirrhites			
	Neocirrhites armatus			
	Paracirrhites			
	Paracirrhites arcatus			
	Paracirrhites forsteri			
	Paracirrhites hemistictus			

FAMILY	GENUS-SPECIES	VSM	VG	PVG
Apogonidae	**10**			
	Apogon			
	Apogon coccineus			
	Apogon crassiceps			
	Apogon doryssa			
	Apogonichthys			
	Apogonichthys ocellatus			
	Apogonichthys perdix			
	Cheilodipterus			
	Cheilodipterus artus			
	Cheilodipterus macrodon			
	Cheilodipterus quinquelineatus			
	Fowleria			
	Fowleria vaiulae			
	Gymnapogon			
	Gymnapogon urospilotus			
	Nectamia			
	Nectamia fusca			
	Nectamia luxuria			
	Nectamia savayensis			
	Ostorhinchus			
	Ostorhinchus angustatus			
	Ostorhinchus apogonoides			
	Ostorhinchus nigrofasciatus			
	Ostorhinchus novemfasciatus			
	Ostorhinchus taeniophorus			
	Pristiapogon			
	Pristiapogon exostigma			
	Pristiapogon fraenatus			
	Pristiapogon kallopterus			
	Pseudamiops			
	Pseudamiops gracilicauda			
	Siphamia			
	Siphamia randalli			
Mugilidae	**4**			
	Crenimugil			
	Crenimugil crenilabis			
	Liza			
	Liza vaigiensis			

FAMILY	GENUS-SPECIES	VSM	VG	PVG
	Mugil			
	Mugil cephalus			
	Osteomugil			
	Osteomugil engeli			
Sphyraenidae	**1**			
	Sphyraena			
	Sphyraena barracuda			
	Sphyraena forsteri			
	Sphyraena helleri			
	Sphyraena qenie			
Polynemidae	**1**	**X**		
	Polydactylus		X	
	Polydactylus plebeius			
	Polydactylus sexfilis			
Malacanthidae	**1**			
	Malacanthus			
	Malacanthus brevirostris			
Echeneididae	**1**			
	Echeneis			
	Echeneis naucrates			
Carangidae	**8**	**X**		
	Carangoides			
	Carangoides ferdau			
	Carangoides orthogrammus			
	Caranx		X	
	Caranx ignobilis			
	Caranx lugubris			
	Caranx melampygus			
	Caranx papuensis			
	Caranx sexfasciatus			
	Decapterus			
	Decapterus macarellus			
	Decapterus macrosoma			
	Elagatis			
	Elagatis bipinnulata			
	Scomberoides			
	Scomberoides lysan			
	Selar			
	Selar crumenophthalmus			

FAMILY	GENUS-SPECIES	VSM	VG	PVG
	Seriola			
	Seriola rivoliana			
	Trachinotus		X	
	Trachinotus baillonii			
Lutjanidae	**4**			
	Aphareus			
	Aphareus furca			
	Aprion			
	Aprion virescens			
	Lutjanus		X	
	Lutjanus bohar			
	Lutjanus fulvus			
	Lutjanus gibbus			
	Lutjanus kasmira	X		
	Lutjanus monostigma			
	Lutjanus rivulatus			
	Paracaesio			
	Paracaesio xanthura			
Caesionidae	**1**	**X**		
	Pterocaesio		X	
	Pterocaesio tile			
Lethrinidae	**3**			
	Gnathodentex			
	Gnathodentex aureolineatus			
	Lethrinus			
	Lethrinus olivaceus			
	Lethrinus xanthochilus			
	Monotaxis			
	Monotaxis grandoculis			
Mullidae	**3**			
	Mulloidichthys		X	
	Mulloidichthys flavolineatus	X		
	Mulloidichthys vanicolensis			
	Parupeneus		X	
	Parupeneus barberinus			
	Parupeneus ciliatus			
	Parupeneus cyclostomus			
	Parupeneus insularis	X		
	Parupeneus multifasciatus	X		
	Parupeneus pleurostigma			

FAMILY	GENUS-SPECIES	VSM	VG	PVG
	Upeneus			
	Upeneus vittatus			
Pempheridídae	**1**			
	Pempheris		X	
	Pempheris oualensis	X		
Kyphosidae	**1**	**X**		
	Kyphosus		X	
	Kyphosus cinerascens			
	Kyphosus vaigiensis			
Chaetodontidae	**4**			
	Chaetodon		X	
	Chaetodon auriga	X		
	Chaetodon bennetti			
	Chaetodon citrinellus			
	Chaetodon ephippium			
	Chaetodon lineolatus			
	Chaetodon lunula			
	Chaetodon lunulatus			
	Chaetodon mertensii			
	Chaetodon ornatissimus	X		
	Chaetodon pelewensis			
	Chaetodon quadrimaculatus			
	Chaetodon reticulatus			
	Chaetodon semeion			
	Chaetodon trichrous			
	Chaetodon trifascialis			
	Chaetodon ulietensis			
	Chaetodon unimaculatus			
	Chaetodon vagabundus			
	Forcipiger		X	
	Forcipiger flavissimus	X		
	Forcipiger longirostris	X		
	Hemitaurichthys		X	
	Hemitaurichthys polylepis	X		
	Hemitaurichthys thompsoni	X		
	Heniochus		X	
	Heniochus acuminatus			
	Heniochus chrysostomus	x		
	Heniochus monoceros			

FAMILY	GENUS-SPECIES	VSM	VG	PVG
Ephippididae	**1**	**X**		
	Platax		X	
	Platax orbicularis			
Pomacanthidae	**5**			
	Centropyge		X	
	Centropyge bispinosa			
	Centropyge fisheri			
	Centropyge flavissima			
	Centropyge heraldi			
	Centropyge loricula	X		
	Centropyge multicolor			
	Genicanthus			
	Genicanthus bellus			
	Genicanthus watanabei			
	Paracentropyge			
	Paracentropyge multifasciata			
	Pomacanthus		X	
	Pomacanthus imperator	X		
	Pygoplites			
	Pygoplites diacanthus			
Pomacentridae	**10**			
	Abudefduf	X	X	
	Abudefduf septemfasciatus			
	Abudefduf sexfasciatus			
	Abudefduf sordidus			
	Abudefduf vaigiensis	X		
	Amphiprion		X	
	Amphiprion cf. *chrysopterus*			
	Chromis		X	
	Chromis acares			
	Chromis agilis	X		
	Chromis alpha			
	Chromis atripectoralis			
	Chromis iomelas			
	Chromis margaritifer			
	Chromis vanderbilti	X		
	Chromis viridis			
	Chromis xanthura			

FAMILY	GENUS-SPECIES	VSM	VG	PVG
	Chrysiptera			X
	Chrysiptera glauca			
	Chrysiptera leucopoma			
	Dascyllus		X	
	Dascyllus aruanus			
	Dascyllus flavicaudus			
	Dascyllus trimaculatus			
	Lepidozygus			X
	Lepidozygus tapeinosoma			
	Plectroglyphidodon		X	
	Plectroglyphidodon dickii			
	Plectroglyphidodon flaviventris			
	Plectroglyphidodon imparipennis			
	Plectroglyphidodon johnstonianus	X		
	Plectroglyphidodon lacrymatus			
	Plectroglyphidodon leucozonus			
	Plectroglyphidodon phoenixensis			
	Pomacentrus		X	
	Pomacentrus coelestis			
	Pomacentrus pavo			
	Pomachromis			X
	Pomachromis fuscidorsalis			
	Stegastes		X	
	Stegastes albifasciatus			
	Stegastes cf. *fasciolatus*			
	Stegastes nigricans			
	Stegastes punctatus			
Labridae	**24**			
	Anampses			
	Anampses caeruleopunctatus			
	Anampses melanurus			
	Anampses meleagrides			
	Anampses twistii			
	Bodianus			
	Bodianus axillaris			
	Bodianus loxozonus			
	Cheilinus			
	Cheilinus chlorourus			
	Cheilinus oxycephalus			

FAMILY	GENUS-SPECIES	VSM	VG	PVG
	Cheilinus trilobatus			
	Cheilinus undulatus			
	Cheilio inermis			
	Cirrhilabrus			
	Cirrhilabrus exquisitus			
	Cirrhilabrus scottorum			
	Coris			
	Coris aygula			
	Coris gaimard			
	Cymolutes			
	Cymolutes praetextatus			
	Epibulus			
	Epibulus insidiator			
	Gomphosus		X	
	Gomphosus varius	X		
	Halichoeres			
	Halichoeres claudia			
	Halichoeres hortulanus			
	Halichoeres margaritaceus			
	Halichoeres marginatus			
	Halichoeres melasmapomus			
	Halichoeres trimaculatus			
	Hemigymnus			
	Hemigymnus fasciatus			
	Hologymnosus			
	Hologymnosus annulatus			
	Hologymnosus doliatus			
	Iniistius			
	Iniistius pavo			
	Labroides			
	Labroides bicolor			
	Labroides dimidiatus			
	Labroides rubrolabiatus			
	Labropsis			
	Labropsis polynesica			
	Macropharyngodon			
	Macropharyngodon meleagris			
	Novaculichthys			
	Novaculichthys taeniourus			

FAMILY	GENUS-SPECIES	VSM	VG	PVG
	Oxycheilinus			
	Oxycheilinus bimaculatus			
	Oxycheilinus digramma			
	Oxycheilinus unifasciatus			
	Pseudocheilinus			
	Pseudocheilinus evanidus			
	Pseudocheilinus hexataenia			
	Pseudocheilinus ocellatus			
	Pseudocheilinus octotaenia			
	Pseudocheilinus tetrataenia			
	Pseudocoris			
	Pseudocoris aurantiofasciata			
	Pseudodax			
	Pseudodax moluccanus			
	Pseudojuloides			
	Pseudojuloides atavai			
	Pseudojuloides cerasinus			
	Stethojulis			
	Stethojulis bandanensis			
	Stethojulis strigiventer			
	Thalassoma		X	
	Thalassoma amblycephalum			
	Thalassoma hardwicke			
	Thalassoma lutescens			
	Thalassoma purpureum			
	Thalassoma quinquevittatum			
	Thalassoma trilobatum			
	Wetmorella			
	Wetmorella albofasciata			
	Wetmorella nigropinnata			
Scaridae	**6**			
	Calotomus			
	Calotomus carolinus			
	Cetoscarus			
	Cetoscarus ocellatus			
	Chlorurus		X	
	Chlorurus frontalis			
	Chlorurus microrhinos			
	Chlorurus spilurus	X		

FAMILY	GENUS-SPECIES	VSM	VG	PVG
	Hipposcarus			
	Hipposcarus longiceps			
	Leptoscarus			
	Leptoscarus vaigiensis			
	Scarus		X	
	Scarus altipinnis			
	Scarus chameleon			
	Scarus festivus			
	Scarus forsteni			
	Scarus frenatus			
	Scarus ghobban			
	Scarus globiceps			
	Scarus longipinnis			
	Scarus niger			
	Scarus oviceps			
	Scarus psittacus			
	Scarus rubroviolaceus			
	Scarus schlegeli			
Pinguipedidae	**1**			
	Parapercis			
	Parapercis millepunctata			
	Parapercis schauinslandii			
Creediidae	**2**			
	Chalixodytes			
	Chalixodytes tauensis			
	Limnichthys			
	Limnichthys nitidus			
Trypterygiidae	**2**			
	Enneapterygius			
	Enneapterygius fuscoventer			
	Enneapterygius hemimelas			
	Enneapterygius pyramis			
	Helcogramma			
	Helcogramma capidata			
Blenniidae	**13**			
	Aspidontus			
	Aspidontus dussumieri			
	Aspidontus taeniatus			
	Atrosalarias			
	Atrosalarias fuscus			

FAMILY	GENUS-SPECIES	VSM	VG	PVG
	Blenniella			
	Blenniella gibbifrons			
	Cirripectes			
	Cirripectes fuscoguttatus			
	Cirripectes quagga			
	Cirripectes variolosus			
	Enchelyurus			
	Enchelyurus ater			
	Entomacrodus			
	Entomacrodus cymatobiotus			
	Entomacrodus thalassinus			
	Exallias			
	Exallias brevis			
	Glyptoparus			
	Glyptoparus delicatulus			
	Istiblennius			
	Istiblennius edentulus			
	Nannosalarias			
	Nannosalarias nativitatis			
	Petroscirtes			
	Petroscirtes xestus			
	Plagiotremus			
	Plagiotremus tapeinosoma			
	Stanulus			
	Stanulus seychellensis			
Callionymidae	**2**			
	Callionymus			
	Callionymus filamentosus			
	Callionymus simplicicornis			
	Diplogrammus			
	Diplogrammus goramensis			
Gobiidae	**22**			
	Amblyeleotris			
	Amblyeleotris fasciata			
	Amblygobius			
	Amblygobius nocturnus			
	Amblygobius phalaena			
	Asterropteryx			
	Asterropteryx ensifera			
	Asterropteryx semipunctata			

FAMILY	GENUS-SPECIES	VSM	VG	PVG
	Bathygobius			
	Bathygobius coalitus			
	Bathygobius cotticeps			
	Bryaninops			
	Bryaninops tigris			
	Bryaninops yongei			
	Cabillus			
	Cabillus tongarevae			
	Callogobius			
	Callogobius sclateri			
	Ctenogobiops			
	Ctenogobiops feroculus			
	Eviota			
	Eviota afelei			
	Eviota albolineata			
	Eviota disrupta			
	Eviota infulata			
	Eviota prasites			
	Fusigobius			
	Fusigobius duospilus			
	Fusigobius humeralis			
	Fusigobius neophytus			
	Gnatholepis			
	Gnatholepis anjerensis			
	Gnatholepis cauerensis			
	Gobiodon			
	Gobiodon quinquestrigatus			
	Gobiopsis			
	Gobiopsis exigua			
	Oligolepis			
	Oligolepis cf. pacificus (Moorea Is.)			
	Oplopomus			
	Oplopomus caninoides			
	Oplopomus oplopomus			
	Paragobiodon			
	Paragobiodon echinocephalus			
	Paragobiodon lacunicolus			
	Paragobiodon modestus			

FAMILY	GENUS-SPECIES	VSM	VG	PVG
	Pleurosicya			
	Pleurosicya labiata			
	Pleurosicya micheli			
	Pleurosicya mossambica			
	Priolepis			
	Priolepis ailina			
	Priolepis cincta			
	Priolepis compita			
	Priolepis inhaca			
	Priolepis semidoliata			
	Priolepis squamogena			
	Priolepis triops			
	Trimma			
	Trimma emeryi			
	Trimma milta			
	Trimmatom			
	Trimmatom nanus			
	Valenciennea			
	Valenciennea strigata			
	Vanderhorstia			
	Vanderhorstia ornatissima			
	Vanderhorstia steelei			
Eleotridae	**1**			
	Calumia			
	Calumia godeffroyi			
Microdesmidae	**3**			
	Gunnellichthys			
	Gunnellichthys curiosus			
	Gunnellichthys monostigma			
	Nemateleotris			
	Nemateleotris helfrichi			
	Nemateleotris magnifica			
	Ptereleotris			
	Ptereleotris evides			
	Ptereleotris hanae			
	Ptereleotris heteroptera			
	Ptereleotris microlepis			
	Ptereleotris monoptera			
	Ptereleotris zebra			

FAMILY	GENUS-SPECIES	VSM	VG	PVG
Scombridae	**1**			
	Gymnosarda			
	Gymnosarda unicolor			
Zanclidae	**1**			
	Zanclus		X	
	Zanclus cornutus	X		
Acanthuridae	**4**			
	Acanthurus		X	
	Acanthurus achilles			
	Acanthurus blochii			
	Acanthurus guttatus			
	Acanthurus leucopareius			
	Acanthurus lineatus			
	Acanthurus mata			
	Acanthurus nigricans			
	Acanthurus nigricauda			
	Acanthurus nigrofuscus			
	Acanthurus nigros			
	Acanthurus nubilus			
	Acanthurus olivaceus	X		
	Acanthurus pyroferus			
	Acanthurus thompsoni			
	Acanthurus triostegus			
	Acanthurus xanthopterus			
	Ctenochaetus		X	
	Ctenochaetus binotatus			
	Ctenochaetus flavicauda			
	Ctenochaetus hawaiiensis	X		
	Ctenochaetus striatus			
	Naso			
	Naso annulatus			
	Naso brachycentron			
	Naso brevirostris			
	Naso hexacanthus			
	Naso lituratus			
	Naso unicornis			
	Naso vlamingii			
	Zebrasoma		X	
	Zebrasoma rostratum			

FAMILY	GENUS-SPECIES	VSM	VG	PVG
	Zebrasoma scopas			
	Zebrasoma velifer			
Siganidae	**1**			
	Siganus			
	Siganus argenteus			
	Siganus spinus			
Bothidae	**2**			
	Asterorhombus			
	Asterorhombus filifer			
	Bothus			
	Bothus mancus			
	Bothus pantherinus			
Samaridae	**1**			
	Samariscus			
	Samariscus triocellatus			
Soleidae	**1**			
	Aseraggodes			
	Aseraggodes melanostictus			
Balistidae	**8**			
	Balistapus		X	
	Balistapus undulatus	X		
	Balistoides			
	Balistoides viridescens			
	Melichthys		X	
	Melichthys niger	X		
	Melichthys vidua	X		
	Odonus		X	
	Odonus niger	X		
	Pseudobalistes			
	Pseudobalistes flavimarginatus			
	Pseudobalistes fuscus			
	Rhinecanthus		X	
	Rhinecanthus aculeatus	X		
	Rhinecanthus lunula			
	Rhinecanthus rectangulus	X		
	Sufflamen		X	
	Sufflamen bursa	X		
	Sufflamen fraenatum	X		
	Xanthichthys		X	
	Xanthichthys auromarginatus	X		

FAMILY	GENUS-SPECIES	VSM	VG	PVG
Monacanthidae	**4**			
	Aluterus		X	
	Aluterus scriptus	X		
	Amanses			
	Amanses scopas			
	Cantherhines		X	
	Cantherhines dumerilii			
	Cantherhines sandwichiensis			
	Pervagor			
	Pervagor aspricaudus			
Ostraciidae	**2**			
	Lactoria		X	
	Lactoria cornuta	X		
	Ostracion		X	
	Ostracion cubicus	x		
	Ostracion meleagris	X		
Tetraodontidae	**2**			
	Arothron			
	Arothron hispidus			
	Arothron meleagris			
	Arothron stellatus			
	Canthigaster			
	Canthigaster amboinensis			
	Canthigaster bennetti			
	Canthigaster janthinoptera			
	Canthigaster solandri			
	Canthigaster valentini			
Diodontidae	**1**	X		
	Diodon			X
	Diodon hystrix			
	Diodon liturosus			

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Conflict of interest

The authors have declared no conflicts of interests.

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