

Research article

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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 & VEHCAMP 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; DESIDERÀ *et al.* 2019).

The Actinopterygii comprises 488 families (VAN DER LAAN & FRICKE 2019) and around 34 200 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.* (Ephippidae), *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 <i>Megalops</i> <i>Megalops cyprinoides</i>			
Albulidae	1 <i>Albula</i> <i>Albula glossodonta</i>			
Chanidae	1 <i>Chanos</i> <i>Chanos chanos</i>			
Moringuidae	1 <i>Moringua</i> <i>Moringua javanica</i>			
Chlopsidae	2 <i>Chilorhinus</i> <i>Chilorhinus platyrhynchus</i> <i>Kaupichthys</i> <i>Kaupichthys brachychirus</i> <i>Kaupichthys diodontus</i>			
Muraenidae	8 <i>Anarchias</i> <i>Anarchias seychellensis</i> <i>Echidna</i> <i>Echidna leucotaenia</i> <i>Echidna nebulosa</i> <i>Echidna polyzona</i> <i>Enchelycore</i> <i>Enchelycore bayeri</i> <i>Enchelynassa</i> <i>Enchelynassa canina</i> <i>Gymnomuraena</i> <i>Gymnomuraena zebra</i>			

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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