

Exploring potential fish sound producers in Polynesian lower mesophotic coral reefs

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Abstract

Mesophotic coral reefs host unique fish assemblages and highly diverse biological sounds. However, many of the sources of these sounds remain unknown. The objectives of this study are to identify, based on the literature, the soniferous fish species present in the deep part of mesophotic coral ecosystems (MCEs) in French Polynesia; and to infer the sounds produced by the species present to link them with previously recorded sounds. A total of 39 fish families through to produce sounds were found to be possibly present at 120 m depth. This list includes well-known families such as Serranidae and Ophidiidae. The most abundant sound recorded in Polynesian mesophotic reefs exhibits similarities to sounds produced by Mediterranean *Scorpaena* species (Scorpaenidae), a genus also present in Polynesian MCEs. This study provides initial insights into which soniferous fish taxa are present in Polynesian MCEs.

Keywords

Fish sounds, mesophotic coral ecosystems, French Polynesia, reef fish, sonic morphology, biophony

Statements and Declarations

The authors declare no competing interests.

1. Introduction

Sound production is currently documented in 24 to 37% of fish families (Looby et al. 2022; Rice et al. 2022) with an estimated independent evolution of sound production occurring approximately 33 times among Actinopterygii. In contrast to tetrapods, fish use a wide variety of mechanisms to produce sounds, including for example intrinsic swim bladder muscles (Tower 1908; Connaughton 2004; Rice and Bass 2009), fast extrinsic swim bladder muscles (Sørensen 1895; Ono and Poss 1982; Lagardère and Mariani 2006; Parmentier and Diogo 2006; Kaatz and Stewart 2012; Mélotte et al. 2016, 2019), slow extrinsic swim bladder muscles (Parmentier et al. 2006a), muscles not attached to the swim bladder (Barber and Mowbray 1956; Lugli et al. 1995; Malavasi et al. 2008; Longrie et al. 2009; Parmentier et al. 2011a; Mélotte et al. 2019), buckling of modified scales (Raick 2015; Parmentier et al. 2017; Raick et al. 2018), sonic-ligament causing jaw-snapping (Parmentier et al. 2007; Colley and Parmentier 2012), or stridulation (Burkenroad 1931; Tavalga 1971). Fish can hear and gain signaling information in various communication contexts. Sounds emitted by fish are primarily used in agonistic and reproductive behaviors (Ladich 1997).

In French Polynesia, fish diversity (Pinheiro et al. 2016; Kahng et al. 2017) and its corresponding call composition have been shown to vary with depth (Raick et al. 2023b), with differences between altiphotic (from the surface to 30–40 m depth) and mesophotic (below 30–40 m depth) compartments of coral reefs. The recorded sound types were diverse, including both pulse series and frequency-modulated sounds (Raick et al. 2023b). Frequency-modulated sounds were in higher proportion in mesophotic coral reefs than in altiphotic reefs, but the majority of fish species responsible for producing these sound types remains unknown (Raick et al. 2023a, 2023b). Associating species with sounds has been conducted for shallow temperate species and species from altiphotic reefs, mainly through aquarium-based (Parmentier et al. 2017, 2022; Raick et al. 2018), mesocosm-based (Bolgan et al. 2019), and field-based methods

using cameras (Mann and Lobel 1997; Bradbury and Vehrencamp 1998; Kasumyan 2008; Amorim et al. 2013) or hydrophones held by rebreathing divers (Tricas and Boyle 2014). However, using these techniques in lower mesophotic reefs is impractical, primarily due to challenges such as the difficulty of prolonged dives at significant depths (Kahng et al. 2010) and the disturbance caused to nocturnal fish by artificial lighting. Furthermore, bringing these fish to the surface alive for study is highly challenging, given that the pressure differential induces irreversible damage to their swim bladders (Rummer and Bennett 2005).

Our study focuses on lower mesophotic coral reefs, found between 60 and 150 m deep, that host unique fish communities (Pineiro et al. 2016; Kahng et al. 2017), which are reflected in their biological sounds (Raick et al. 2023b). More precisely, we focused on the diversity of sounds previously reported at 120 m in French Polynesia (Raick et al. 2023a, 2023b), with the ultimate aim of helping future research that seeks to identify the fish species responsible for some of these sounds. The depth of 120 m was chosen because it has been studied in previous acoustic research (Raick et al. 2023a, 2023b, 2024). This study has been conducted in two phases. *(I)* Initially, a literature review was performed to identify teleost species inhabiting the deep regions (at 120 m) of mesophotic coral reefs in the Society and Tuamotu Archipelagos in French Polynesia, with the specific goal of pinpointing taxa believed to be soniferous. *(2)* Subsequently, we investigated the sounds by comparing them with the literature to identify, at best, the types of species that could produce them.

2. Materials and methods

2.1. Soniferous species present

Bibliographic research was conducted in four steps as detailed below (Fig. 1), resulting in a categorized list of species: *(I)* species certainly present (listed as ‘1’ in Table 1), *(II)* species probably present (listed as 2a if excluded at Step 3 and as 2b if excluded at Step 1), and *(III)*

species considered unlikely to be present and therefore excluded from consideration. In addition, the occurrence in the Society and Tuamotu Archipelagos was assessed.

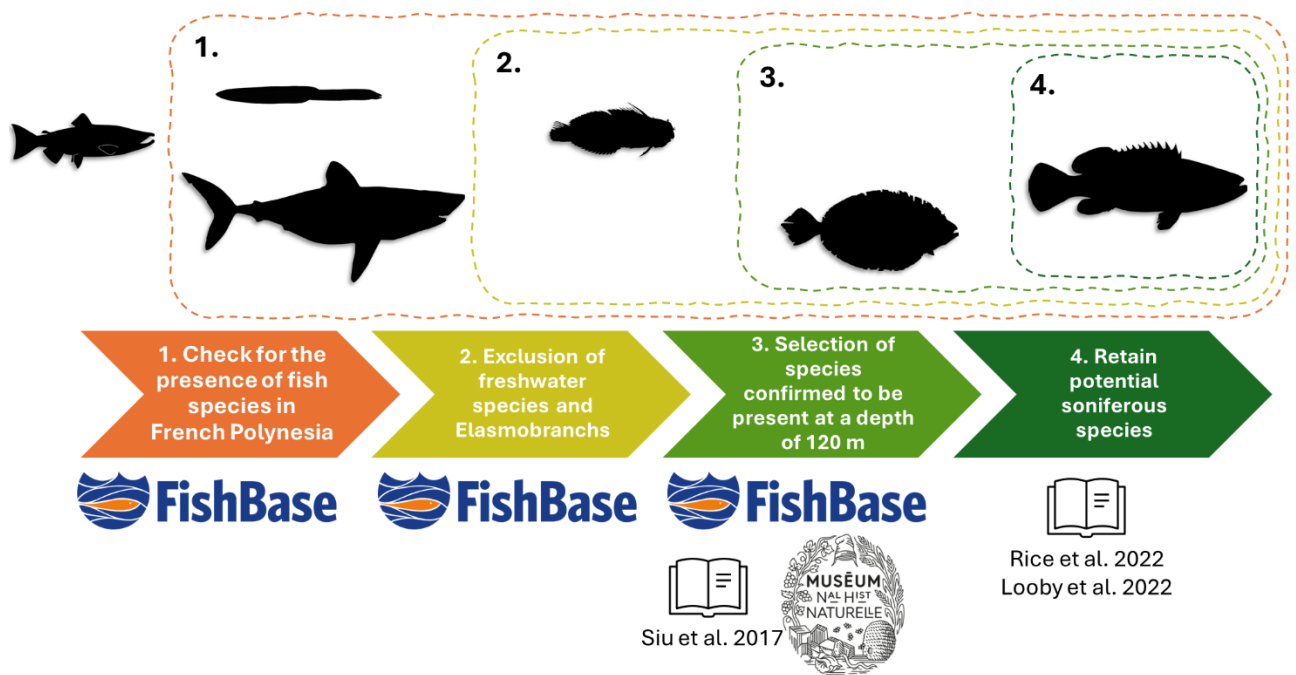


Figure 1 Summary of the four steps illustrating the survey and literature data combined for this study.

Step 1: Check for the presence of fish species in French Polynesia by using the Fishbase database (a globally recognized online database that provides detailed information on over 34,000 fish species, including their taxonomy, distribution, biology, ecology, and conservation status; <https://www.fishbase.de>) (Froese and Daully 2023) and Siu et al.'s (2017) updated list of Polynesian fish (Siu et al. 2017). This list includes 1,301 fish species known to occur in French Polynesia, limited to those with a reliably verifiable presence. The search criteria for Fishbase were set as *count_native\$Country=="French Polynesia" OR "Marquesas Is." OR "Tahiti" OR "Tuamotu Is."*. Any species found in Fishbase but not included in Siu et al.'s (2017) list were noted as '2b' in the table.

Step 2: Exclusion of freshwater species and Elasmobranchs based on Fishbase.

Step 3: Selection of species confirmed to be only present at a depth of 120 m. Species with a depth range shallower than 60 m (based on the minimum occurrence depth in Fishbase) or deeper than 200 m (based on the maximum occurrence depth in Fishbase) were omitted. Species indicated as ‘not present below 60 m’ in Siu et al. (2017) were also removed. Species known to occur at 120 m were retained, while those found shallower or deeper were noted as ‘2a’ in the table. Species with conflicting data (i.e., species not reported to occur deeper than 60 m according to Siu et al. (2017) but with records at greater depths in Fishbase) were cross-referenced with the literature. If these species were confirmed to be present at 120 m, they were included. Species with incomplete information were retained and also noted as ‘2a’ in the table.

In addition, all fish species from French Polynesia were automatically extracted from the French National Museum of Natural History’s list. Specimens captured between 60 and 200 m, belonging to soniferous families and not already present in our list, were included. Specimens captured within a depth range overlapping the ‘60 – 200 m range’ (e.g., 42 – 70 m range), belonging to soniferous families, and not yet on our list, were classified as ‘probably present’. Larval specimens were excluded. Additionally, the depth of all specimens was cross-referenced with Fishbase to identify any potential new species for inclusion.

Step 4: Retain potential soniferous species by selecting species belonging to known soniferous families (identified from scientific literature or qualitative descriptions) or families with a described sound-producing mechanism (Rice et al. 2022). The article by Rice et al. (2022) presents a mapping of sound production onto a family-level phylogeny of Actinopterygians, based on acoustic recordings, morphological specializations, and qualitative descriptions. The presence of these species in the soniferous fish inventory from Looby et al. (2022) was verified. The article by Looby et al. (2022) provides an inventory of known soniferous fishes, based on information extracted from 834 references. Four species with uncertain vocalization status (for example, considered ‘Doubt Species Did or Did Not Produce

Sounds' in Looby et al. 2022), namely *Aphareus furca* (Tricas and Boyle 2014), *Decapterus macarellus* (Fish et al. 1952; Fish 1954), *Mulloidichthys vanicolensis*, and *Naso hexacanthus* (Tricas and Boyle 2014), were excluded from the list. Within the output list, we specified whether the studies referred to the exact species or to other species within the same genus, or to species from another genus within the same family. Looby et al.'s list is a static resource fixed in time, but for future research, a dynamic version is now available on the FishSounds.net website (Looby et al. 2024). This version allows for species selection, research by geographical region, and includes validated acoustic recordings.

2.2. Connection between present taxa and recorded sounds

The sound types previously recorded at a depth of 120 m in Polynesian mesophotic reefs (Raick et al. 2023b) were compared to the sounds of the species from the literature. For each retained species, a literature review was conducted to determine their sonic morphology and/or the types of sounds they produce. If information was unavailable for a species, we examined other species within the same genus. In cases where information was lacking for a genus, we investigated other genera within the same family. The lists provided by Rice et al. (2022) and Looby et al. (2022) were used as starting points to locate references for family-level and species-level information, respectively. Additional literature was consulted for families with conflicting information (not designated as sonic families according to Looby et al. (2022) but identified as sonic by Rice et al. (2022): Apogonidae, Caesionidae, Leiognathidae, Lethrinidae, Myctophidae, and Uranoscopidae). The differences between the two datasets primarily arise from one being extrapolated to create an estimate, while the other quantifies the fish species known to produce sounds.

3. Results

3.1. Presence of soniferous species

In total, species from 39 vocal families were identified as potentially present at a depth of 120 m (Table 1; 118–123 species, 87–89 genera; when considering known soniferous species, and species likely soniferous but with references known only at the genus or family level), with the highest number of species found in Serranidae (18%), followed by Lutjanidae (13%), Gobiidae (6%), Scorpaenidae (5%), and Carangidae (5%, Fig. 2). This number decreases to 23 families when sonic abilities were identified at the genus level only.

Based on knowledge from altophotic reefs, the probability of recording their sounds using Passive Acoustic Monitoring (PAM) studies is not uniform. For example, although numerous species of Gobiidae are known to produce sounds (Lugli et al. 2003), these sounds are typically very faint and can only be heard within a few centimeters, making them infrequently used in PAM studies. Other taxa such as Carangidae, are fast-swimming predators found in the waters above the reef and in the open sea. The two soniferous genera found in the area (*Alectis* and *Selar*) are known to produce scratchy bursts (*Alectis* genus (Fish 1954; Fish and Mowbray 1970)) and sustained or irregular series of toothy grating sounds (*Selar* genus (Fish and Mowbray 1970)). These sounds are not easy to distinguish in PAM studies and are typically not considered during manual scrolling processes (Desiderà et al. 2019; Raick et al. 2023b). In contrast, other families (e.g., Carapidae, Ophidiidae, Scorpaenidae, Pomacentridae, or Serranidae) appear to be highly soniferous (Mann et al. 1997; Parmentier et al. 2006a; Bertucci et al. 2015; Di Iorio et al. 2018; Bolgan et al. 2019) and would be more easily found in recorded soundscapes (Table 1).

Table 1 State of the art of the soniferous species present in the study area. The column ‘Type’ separates species certainly present (1) and species probably present (2a and 2b). The column ‘Level’ separates known soniferous species (species), species likely soniferous but with references known only at the genus level (genus) and species likely soniferous but with references known only at the family level (i.e., in another genus from the family). Additionally, genera for which the exact species present in MCEs is uncertain are also indicated as ‘genus’. Families for which the exact genus present in MCEs is uncertain are also indicated as ‘family’. Similarly, references concern the exact species when ‘Type = species,’ another species of the same genus when ‘Type = genus,’ and another genus within the same family when ‘Type = family.’ The ‘Level’ column may be considered a metric of confidence (species > genus > family), but it mainly varies between taxa. In a taxon where all species produce sound using the same sonic mechanism, the confidence is higher, as all species with this mechanism could theoretically produce sounds. Conversely, confidence is lower when the mechanism is present in only a subset of the taxon. The four species that were not considered due to uncertainty regarding their sound production (*Aphareus furca*, *Decapterus macarellus*, *Mulloidichthys vanicolensis*, and *Naso hexacanthus*; see Methods) are not included at the species level (Type = ‘Species’ in the list). However, since other species from the same genus or family are known to be vocal (Type = ‘Genus’ or Type = ‘Family’), they appear in the final list with this lesser degree of confidence. * = families with conflicting information (non-sonic families according to (Looby et al. 2022) but sonic according to (Rice et al. 2022)), ** = only morphological evidence, S = Society Archipelago, T = Tuamotu Archipelago, Y = Yes, N = Not present.

| Family | Species | S | T | Type | Level | Reference |
|--------------|--------------------------------------|---|---|------|---------|--|
| Acanthuridae | <i>Naso hexacanthus</i> | Y | Y | 2a | family | (Tricas and Boyle 2014) |
| Apogonidae* | <i>Foa fo</i> | Y | N | 2b | family | (Moulton 1958; Tricas and Boyle 2014) |
| Balistidae | <i>Xanthichthys auromarginatus</i> | Y | Y | 1 | species | (Tricas and Boyle 2014) |
| Balistidae | <i>Xanthichthys caeruleolineatus</i> | Y | Y | 2a | genus | |
| Blenniidae | <i>Petroscirtes xestus</i> | Y | N | 2a | family | (Tavolga 1958; De Jong et al. 2007; Coers et al. 2008) |
| Bythitidae | <i>Tuamotuichthys bispinosus</i> | N | Y | 2b | family | (Marshall 1967) |
| Caesionidae* | <i>Caesionidae</i> | N | N | 2b | family | (Yokoyama et al. 1994) |
| Caesionidae* | <i>Pterocaesio</i> sp. | N | N | 1 | family | |
| Caproidae | <i>Antigonia capros</i> | Y | N | 1 | family | (Fish 1948) |
| Carangidae | <i>Alectis indica</i> | Y | Y | 2b | genus | (Fish 1954; Fish and Mowbray 1970) |
| Carangidae | <i>Atule mate</i> | Y | N | 2b | family | (Burkenroad 1931; Uchida 1934; Fish 1948, 1954; Fish et al. 1952; Moulton 1960; Shishkova 1958; Moulton 1958; Taylor and Mansueti 1960; Cummings et al. 1964; Steinberg et al. 1965; Tavolga 1968a; Fish and Mowbray 1970; Savchenko et al. 1981; Fujieda and Fujieda, Shigeru; Matsuno, Yasuhisa; Yamanaka, Yuichi; Chung, Yong-jin; Kishimoto 1993; Kaparang et al. 1998; Carriço et al. 2019) |
| Carangidae | <i>Selar boops</i> | Y | N | 2b | genus | (Fish and Mowbray 1970) |
| Carangidae | <i>Uraspis helvola</i> | N | N | 2b | family | (Burkenroad 1931; Uchida 1934; Fish 1948, 1954; Fish et al. 1952; Moulton 1960; Shishkova 1958; Moulton 1958; Taylor and Mansueti 1960; Cummings et al. 1964; Steinberg et al. 1965; Tavolga 1968a; Fish and Mowbray 1970; Savchenko et al. 1981; Fujieda and Fujieda, Shigeru; Matsuno, Yasuhisa; Yamanaka, Yuichi; Chung, Yong-jin; Kishimoto 1993; Kaparang et al. 1998; Carriço et al. 2019) |
| Carapidae | <i>Carapus mourlani</i> | Y | Y | 2a | species | (Parmentier et al. 2006a, 2016) |

| | | | | | | |
|-----------------|--|---|---|----|---------|---|
| Chaetodontidae | <i>Chaetodon</i> sp. | N | N | 1 | genus | (Moulton 1958; Fish and Mowbray 1970; Tricas et al. 2006; Tricas and Boyle 2014, 2015) |
| Chaetodontidae | <i>Heniochus singularius</i> | N | N | 2b | genus | (Parmentier et al. 2011a) |
| Congridae | <i>Ariosoma scheelei</i> | Y | N | 2a | family | (Fish et al. 1952; Fish 1954) |
| Congridae | <i>Ariosoma sereti</i> | N | N | 1 | family | |
| Congridae | <i>Bathyuconger vicinus</i> | N | N | 1 | family | |
| Congridae | <i>Congriscus marquesaensis</i> | N | N | 1 | family | |
| Congridae | <i>Uroconger</i> sp. | | | 1 | family | |
| Dactylopteridae | <i>Dactyloptena</i> sp. | N | N | 1 | family | (Dufossé 1874; Fish and Mowbray 1970; Carriço et al. 2019) |
| Diodontidae | <i>Diodontidae</i> | N | N | 1 | family | (Burkenroad 1931; Fish et al. 1952; Fish 1954; Moulton 1958; Fish and Mowbray 1970; Tricas and Boyle 2014; Carriço et al. 2019) |
| Gobiidae | <i>Gnatholepis anjerensis</i> | Y | Y | 2a | family | (Amorim and Neves 2007; Amorim et al. 2013) |
| Gobiidae | <i>Gunnellichthys monostigma</i> | Y | N | 2a | family | |
| Gobiidae | <i>Kraemeria bryani</i> | Y | N | 2b | family | |
| Gobiidae | <i>Oxyurichthys notonema</i> | Y | N | 2a | family | |
| Gobiidae | <i>Priolepis farcimen</i> | Y | Y | 2b | family | |
| Gobiidae | <i>Priolepis</i> sp. | N | N | 1 | family | |
| Gobiidae | <i>Valenciennea strigata</i> | Y | Y | 2a | family | |
| Holocentridae | <i>Myripristis chryseres</i> | Y | Y | 1 | genus | (Salmon 1967; Fish and Mowbray 1970; Horch and Salmon 1973; Parmentier et al. 2011b; Tricas and Boyle 2014) |
| Holocentridae | <i>Ostichthys archiepiscopus</i> | Y | N | 1 | family | (Moulton 1958; Winn and Marshall 1963; Gainer et al. 1965; Salmon 1967; Tavalga 1968a; Fish and Mowbray 1970; Horch and Salmon 1973; Carlson and Bass 2000; Parmentier et al. 2011b; Tricas and Boyle 2014; Locascio and Burton 2016) |
| Holocentridae | <i>Ostichthys ovaloculus</i> | Y | N | 1 | family | |
| Holocentridae | <i>Pristilepis</i> sp. | | | 2b | family | |
| Labridae | <i>Bodianus bilunulatus</i> | N | N | 2b | genus | (Fish and Mowbray 1970; Tricas and Boyle 2014) |
| Labridae | <i>Bodianus paraleucosticticus</i> | Y | N | 2a | genus | |
| Labridae | <i>Cirrhilabrus claire</i> | Y | N | 2a | family | (Fish et al. 1952; Fish 1954; Moulton 1958; Shishkova 1958; Protasov and Romanenko 1962; Steinberg et al. 1965; Fish and Mowbray 1970; Bordeau 1982; Boyle and Cox 2009; Tricas and Boyle 2014) |
| Labridae | <i>Oxycheilinus lineatus</i> | Y | N | 2a | family | |
| Labridae | <i>Polylepion russelli</i> | Y | N | 1 | family | |
| Leiognathidae* | <i>Deveximentum insidiator</i> | Y | N | 2b | family | (Uchida 1934; Yamada 1941) |
| Leiognathidae* | <i>Gazza minuta</i> | Y | N | 2b | family | |
| Lethrinidae* | <i>Gymnocranius confer grandoculis</i> | N | Y | 1 | family | (Moulton 1964) |
| Lethrinidae* | <i>Lethrinus rubrioperculatus</i> | Y | N | 1 | family | |
| Lutjanidae | <i>Aphareus furca</i> | Y | Y | 1 | family | (Fish and Mowbray 1970; Tricas and Boyle 2014) |
| Lutjanidae | <i>Aphareus rutilans</i> | Y | N | 1 | family | |
| Lutjanidae | <i>Etelis carbunculus</i> | Y | Y | 1 | family | |
| Lutjanidae | <i>Etelis coruscans</i> | Y | Y | 1 | family | |
| Lutjanidae | <i>Etelis radiosus</i> | Y | N | 1 | family | |
| Lutjanidae | <i>Lutjanus kasmira</i> | Y | Y | 1 | species | (Tricas and Boyle 2014) |

| | | | | | | |
|----------------|--|---|---|----|---------|---|
| Lutjanidae | <i>Lutjanus argentimaculatus</i> | | | 2b | genus | (Moulton 1958; Fish and Mowbray 1970; Staatterman et al. 2014; Tricas and Boyle 2014) |
| Lutjanidae | <i>Lutjanus</i> sp. | N | N | 1 | genus | |
| Lutjanidae | <i>Parapristipomoides squamimaxillaris</i> | N | N | 2a | family | (Fish and Mowbray 1970; Tricas and Boyle 2014) |
| Lutjanidae | <i>Pristipomoides argyrogrammicus</i> | Y | Y | 1 | family | |
| Lutjanidae | <i>Pristipomoides auricilla</i> | Y | N | 1 | family | |
| Lutjanidae | <i>Pristipomoides filamentosus</i> | Y | Y | 1 | family | |
| Lutjanidae | <i>Pristipomoides flavipinnis</i> | Y | N | 1 | family | |
| Lutjanidae | <i>Pristipomoides sieboldii</i> | N | N | 1 | family | |
| Lutjanidae | <i>Pristipomoides zonatus</i> | Y | Y | 1 | family | |
| Lutjanidae | <i>Randallichthys filamentosus</i> | Y | N | 2a | family | |
| Macrouridae | <i>Malacocephalus laevis**</i> | N | N | 2a | species | (Marshall 1965) |
| Macrouridae | <i>Malacocephalus nipponensis</i> | Y | N | 1 | genus | |
| Macrouridae | <i>Malacocephalus</i> sp. | Y | N | 1 | genus | |
| Mullidae | <i>Mulloidichthys pfluegeri</i> | Y | N | 2a | genus | (Fish and Mowbray 1970; Tricas and Boyle 2014) |
| Mullidae | <i>Mulloidichthys</i> sp. | N | N | 1 | genus | |
| Mullidae | <i>Mulloidichthys vanicolensis</i> | Y | Y | 1 | genus | (Tricas and Boyle 2014) |
| Mullidae | <i>Parupeneus</i> sp. | N | N | 1 | genus | |
| Myctophidae* | <i>Benthoosema fibulatum</i> | N | N | 2b | family | (McCauley and Cato 2016) |
| Myctophidae* | <i>Diaphus splendidus</i> | Y | N | 1 | family | |
| Myctophidae* | <i>Lampadena luminosa</i> | Y | N | 1 | family | |
| Myctophidae* | <i>Symbolophorus evermanni</i> | N | N | 2b | family | |
| Ophidiidae | <i>Brotula multibarbata</i> | Y | Y | 2a | family | (Wielsen 1965; Marshall 1967; Courtenay 1971; Carter and Musick 1985; Mann et al. 1997; Sprague and Luczkovich 2001; Rountree and Bowers-Altman 2002; Parmentier et al. 2006b, 2010, 2018b, 2018a; Fine et al. 2007; Anderson et al. 2008; Nguyen et al. 2008; Mann and Grothues 2009a, 2009b; Kéver et al. 2012, 2014b, 2014a, 2016; Wall et al. 2013; Ali et al. 2016; Picciulin et al. 2018; Desiderà et al. 2019) |
| Ophidiidae | <i>Ophidion muraenolepis</i> | N | N | 1 | genus | (Mann et al. 1997; Rountree and Bowers-Altman 2002; Parmentier et al. 2006b; Kéver et al. 2012, 2016) |
| Ostraciidae | <i>Lactoria</i> sp. | N | N | 1 | genus | (Parmentier et al. 2021) |
| Ostraciidae | <i>Ostracion</i> sp. | N | N | 1 | genus | (Lobel 1996; Tricas and Boyle 2014; Parmentier et al. 2019) |
| Ostraciidae | <i>Tetrosomus</i> sp. | N | N | 1 | family | (Steinberg et al. 1965; Fish and Mowbray 1970; Moyer 1979; Lobel 1996; Parmentier et al. 2019, 2021) |
| Peristediidae | <i>Satyrichthys</i> sp. | | | 1 | genus | (Fish 1948) |
| Pleuronectidae | <i>Nematops nanosquama</i> | N | N | 1 | family | (Fish et al. 1952; Fish 1954; Fish and Mowbray 1970) |
| Pomacanthidae | <i>Centropyge boylei</i> | N | N | 1 | genus | (Tricas and Boyle 2014) |
| Pomacanthidae | <i>Centropyge narcosis</i> | Y | Y | 1 | genus | |
| Pomacanthidae | <i>Genicanthus bellus</i> | Y | Y | 1 | family | (Moulton 1958; Fish and Mowbray 1970; Tricas and Boyle 2014) |

| | | | | | | |
|----------------|--------------------------------------|---|---|----|---------|---|
| Pomacentridae | <i>Chromis</i> sp. 2 (Tahiti Island) | Y | N | 1 | genus | (Picciulin et al. 2001; Frédéricich et al. 2014; Tricas and Boyle 2014) |
| Pomacentridae | <i>Pomacentridae</i> sp. (Rapa Is.) | N | N | 1 | family | |
| Priacanthidae | <i>Cookeolus japonicus</i> | N | N | 1 | family | (Moulton 1962; Walls 1964; Salmon and Winn 1966) |
| Priacanthidae | <i>Priacanthus hamrur</i> | Y | Y | 1 | genus | (Salmon and Winn 1966) |
| Scombridae | <i>Thunnus maccoyii</i> | N | N | 1 | genus | (Allen and Demer 2003) |
| Scombridae | <i>Thunnus obesus</i> | Y | Y | 1 | genus | |
| Scorpaenidae | <i>Neomerinthe naevosa</i> | N | N | 1 | genus | (Hallacher 1974) |
| Scorpaenidae | <i>Pontinus macrocephalus</i> | Y | Y | 2a | genus | |
| Scorpaenidae | <i>Pteroidichthys amboinensis</i> | N | N | 1 | family | (Fish and Mowbray 1970; Hallacher 1974; Beattie et al. 2017; Bolgan et al. 2019) |
| Scorpaenidae | <i>Pteroidichthys causseii</i> | N | N | 1 | family | |
| Scorpaenidae | <i>Scorpaena lacrimata</i> | Y | N | 2b | genus | (Moulton 1958; Fish and Mowbray 1970; Hallacher 1974; Bolgan et al. 2019) |
| Scorpaenidae | <i>Scorpaenopsis pusilla</i> | N | N | 1 | genus | (Fish 1948; Fish and Mowbray 1970) |
| Serranidae | <i>Cephalopholis aurantia</i> | Y | Y | 2a | genus | (Fish and Mowbray 1970; Tricas and Boyle 2014; Laxminarsimha Chary et al. 2020) |
| Serranidae | <i>Cephalopholis igarashiensis</i> | Y | Y | 1 | genus | |
| Serranidae | <i>Cephalopholis polleni</i> | Y | Y | 2a | genus | |
| Serranidae | <i>Cephalopholis sexmaculata</i> | Y | Y | 1 | genus | |
| Serranidae | <i>Epinephelus morrhua</i> | N | N | 1 | genus | (Moulton 1958; Hazlett and Winn 1962; Fish and Mowbray 1970; Mann et al. 2010; Nelson et al. 2011; Rowell et al. 2012; Schärer et al. 2012a; Locascio and Burton 2016; Ibrahim et al. 2018) |
| Serranidae | <i>Epinephelus retouti</i> | Y | Y | 1 | genus | |
| Serranidae | <i>Epinephelus tuamotuensis</i> | Y | Y | 1 | genus | |
| Serranidae | <i>Hyporthodus octofasciatus</i> | Y | N | 2a | genus | (Fish and Mowbray 1970) |
| Serranidae | <i>Belonoperca pylei</i> | N | Y | 1 | family | (Fish et al. 1952; Fish 1954; Moulton 1958; Hazlett and Winn 1962; Steinberg et al. 1965; Tavolga 1968a; Fish and Mowbray 1970; Lobel 1992; Mann et al. 2009, 2010; Nelson et al. 2011; Rowell et al. 2012, 2015, 2019, 2020; Schärer et al. 2012b, 2012a, 2014; Wall et al. 2012a, 2012b, 2014b, 2014a; Tricas and Boyle 2014; Bertucci et al. 2015; Locascio and Burton 2016; Sanchez et al. 2017; Koenig et al. 2017; Carriço et al. 2019; Malinowski et al. 2019; Desiderà et al. 2019; Laxminarsimha Chary et al. 2020; Chérubin et al. 2020; Wilson et al. 2020; Jublier et al. 2020) |
| Serranidae | <i>Gracila albomarginata</i> | Y | Y | 2a | family | |
| Serranidae | <i>Liopropoma erythraeum</i> | Y | N | 1 | family | |
| Serranidae | <i>Liopropoma lunulatum</i> | Y | N | 1 | family | |
| Serranidae | <i>Odontanthias tapui</i> | Y | N | 1 | family | |
| Serranidae | <i>Plectranthias bennetti</i> | Y | N | 2a | family | |
| Serranidae | <i>Plectranthias kamii</i> | Y | N | 2a | family | |
| Serranidae | <i>Plectranthias rubrifasciatus</i> | N | Y | 1 | family | |
| Serranidae | <i>Plectranthias</i> sp. | Y | Y | 1 | family | |
| Serranidae | <i>Plectranthias taylori</i> | Y | Y | 1 | family | |
| Serranidae | <i>Pogonoperca punctata</i> | Y | Y | 1 | family | |
| Serranidae | <i>Saloptia powelli</i> | Y | Y | 1 | family | |
| Serranidae | <i>Pseudanthias privitera</i> | Y | N | 2a | genus | (Tricas and Boyle 2014) |
| Serranidae | <i>Pseudanthias ventralis</i> | Y | Y | 1 | genus | |
| Setarchidae | <i>Setarches guentheri</i> ** | | | 2a | species | (Hallacher 1974) |
| Sphyraenidae | <i>Sphyraena acutipinnis</i> | | | 2b | genus | (Moulton 1958; Fish and Mowbray 1970; Tricas and Boyle 2014) |
| Syngnathidae | <i>Hippocampus kuda</i> | Y | N | 2b | genus | (Fish 1953; Colson et al. 1996) |
| Syngnathidae | <i>Hippocampus</i> sp. | N | N | 1 | genus | |
| Tetraodontidae | <i>Sphoeroides pachygaster</i> | Y | N | 1 | genus | (Burkenroad 1931; Fish et al. 1952; Fish 1954; Moulton 1958; Fish and Mowbray 1970) |
| Uranoscopidae* | <i>Genyagnus monoptyerygius</i> | Y | N | 2b | family | (Fish and Mowbray 1970) |
| Zanclidae | <i>Zanclus cornutus</i> | Y | Y | 2a | species | (Tricas and Boyle 2014) |

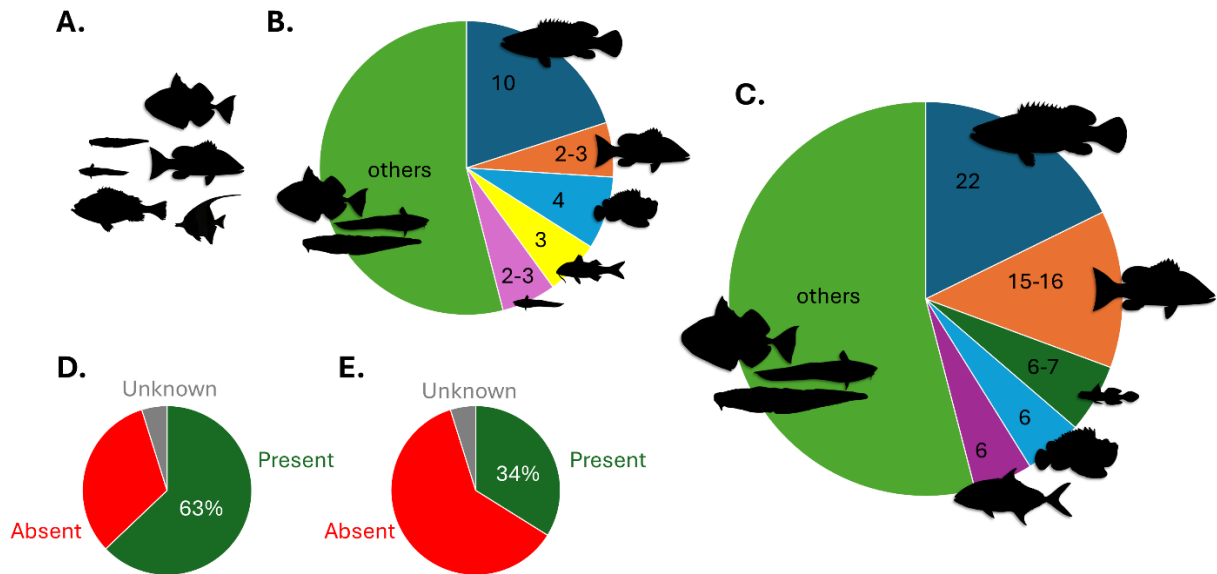


Figure 2 Graphical abstract of Table 1. (A) Known soniferous species present in the study area. (B) Species likely soniferous but with references known only at the genus level. (C) Species likely soniferous but with references known only at the family level (i.e., in another genus from the family). (D) Percentage of species found in the Society Archipelago. (E) Percentage of species found in the Tuamotu Archipelago. Fish shapes represent: (A) Balistidae, Carapidae, Lutjanidae, Macrouridae, Setarchidae, and Zanclidae. (B) From most to less abundant: Serranidae, Lutjanidae, Scorpaenidae, Mullidae, and Macrouridae. (C) From most to less abundant: Serranidae, Lutjanidae, Gobiidae, Scorpaenidae, and Carangidae.

3.2. Link between present taxa and recorded sounds

More than 65 fish sound types are known from Polynesian mesophotic reefs (Raick et al. 2023b). Each category of sound was analyzed and compared with sounds emitted by species documented in the literature (see Table SP1) in the subsequent sub-sections.

3.2.1. Frequency-modulated sounds

In Polynesian mesophotic reefs, several frequency-modulated (FM) sounds have been recorded (Raick et al. 2023b). Frequency-modulated sounds are present in diverse clades of marine fish, such as two families found in French Polynesia: Gobiidae (Lugli et al. 1997) and Serranidae (Lobel 1992; Bertucci et al. 2015; Desiderà et al. 2019). These FM sounds can be

categorized as downsweeps (DS), upsweeps (US), and complex sounds (CS; a combination of DS and US). Each category will now be examined in more detail.

3.2.1.1. Downsweeps

Some of the low-frequency DS sounds recorded in Polynesian MCEs (Fig. 3) exhibit similarities to sounds produced by certain species of groupers such as in *E. marginatus*, a temperate grouper species (Bertucci et al. 2015; Desiderà et al. 2019). In the area of study, eleven genera of Serranidae are present: *Belanoperca*, *Cephalopholis*, *Epinephelus*, *Gracila*, *Hyporthodus*, *Liopropoma*, *Odontanthias*, *Plectranthias*, *Pogonoperca*, *Pseudanthias*, and *Saloptia*.

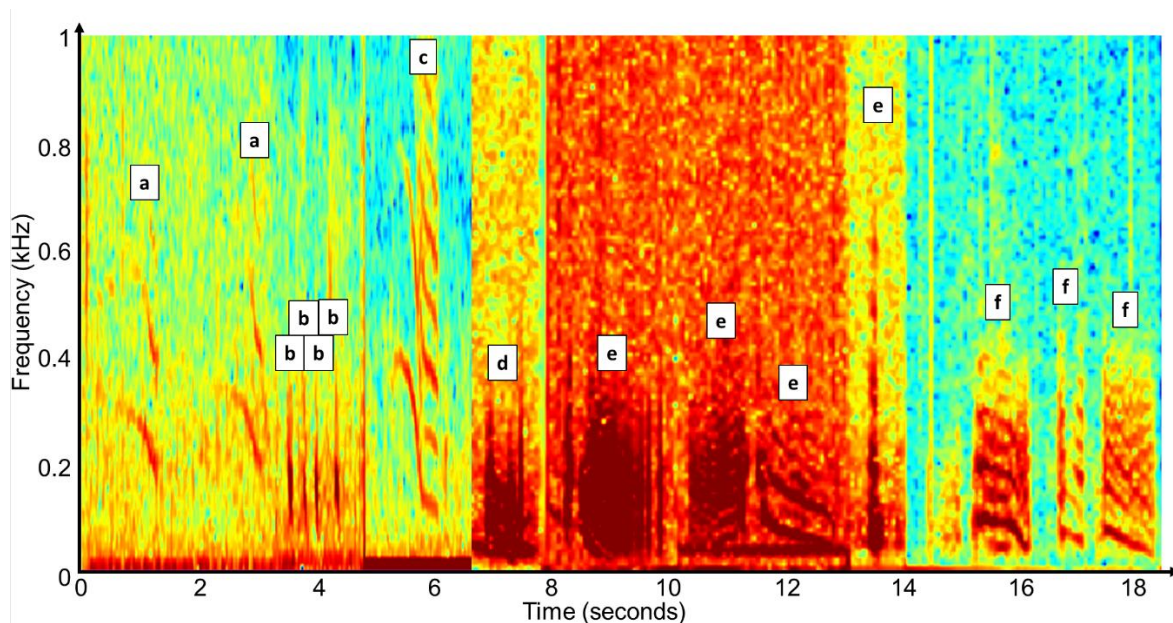


Figure 3 Comparison of fish downsweeping sounds recorded in Polynesian altiphotic and mesophotic reefs. (a) DS5, (b) rare series of low DS, and (c) CS6 (Raick et al. 2023b) and downsweeping sounds from three groupers species from the literature: (d) *Epinephelus adscensionis*, (e) *Epinephelus guttatus*, and (f) *Epinephelus striatus*. CS6 is a complex sound, mainly characterized by a downweep following a very short upsweep at the beginning. The figure is a compilation of several spectrograms visualized in Raven (FFT = 256, sampling frequency: 4 kHz). Sounds a, b, and c are from Raick et al. (2023b) while sounds d, e, and f were downloaded from FishBase. The color code is relative to the amplitude: the hotter the color, the louder the sound (to be considered separately for each sound).

3.2.1.2. Upsweeps

Upsweep sounds are known to occur in Batrachoididae and Triglidae (Fish and Mowbray 1970; Amorim and Vasconcelos 2008). However, these two families are not known to inhabit Polynesian mesophotic reefs. Some Ophidiidae, such as *Genypterus maculatus*, are also known

to produce US growls but with a less pronounced FM pattern and at much lower frequencies than the US observed in Polynesian MCEs (Parmentier et al. 2018a).

3.2.1.3. Complex sounds

The CS2 sounds recorded in Polynesia share similarities with those recorded offshore in the Atlantic Ocean (40 – 200 m depth), referred to as the ‘300 Hz FM harmonic single’ (Wall et al. 2013). CS3 from French Polynesia is identical to the ‘sound #46’ from the Indian Ocean (Puebla-Aparicio et al. 2024). French Polynesian’s CS1 (Raick et al. 2023b) is identical to the ‘whoot’ described in Society Islands (Bertucci et al. 2020) and highly similar to the ‘sound #13’ described in Mozambique (Puebla-Aparicio et al. 2024). In both studies, it is a non-abundant sound. There is currently no valid scientific identification on the emitter of this peculiar sound type (Raick et al. 2023a).

3.2.2. ‘kwa-like’ sounds

In French Polynesian MCEs, the most abundant sound is a sound named AS4 (Raick et al. 2023b) (Fig. 4a) and shares similarities with a sound described in the Mediterranean Sea and named ‘/kwa/’ (Di Iorio et al. 2018) (Fig. 4b). Both sounds are pulse train characterized by a similar number of pulses (/kwa/: 13 ± 6 vs. AS4: 12.3 ± 1.2). On the spectrograms, they appear as pseudo-harmonics around a 800 Hz contour (/kwa/: 747 ± 136 Hz vs. AS4: 846.9 ± 147.6 Hz). Their contour is characterized by a similar initial and final frequency giving them a generally arch-shaped contour. For both sound types, the peak sound emission occurs at the beginning of the night (Di Iorio et al. 2018). In the Mediterranean Sea, /kwa/ are attributed to *Scorpaena* species (Scorpaenidae). MCEs from Society and Tuamotu Islands seems to inhabit several genera of Scorpaenidae such as *Pontinus*, *Scorpaena*, and *Scorpaenopsis*. In addition to AS4, a second ‘kwa-like’, named AS5 (Raick et al. 2023b), is found in MCEs, with its peak sound production following that of AS4 (Raick et al. in review). This sound is 72 ms shorter, has 5 fewer peaks, and its peak frequency is 203 Hz lower than that of AS4.

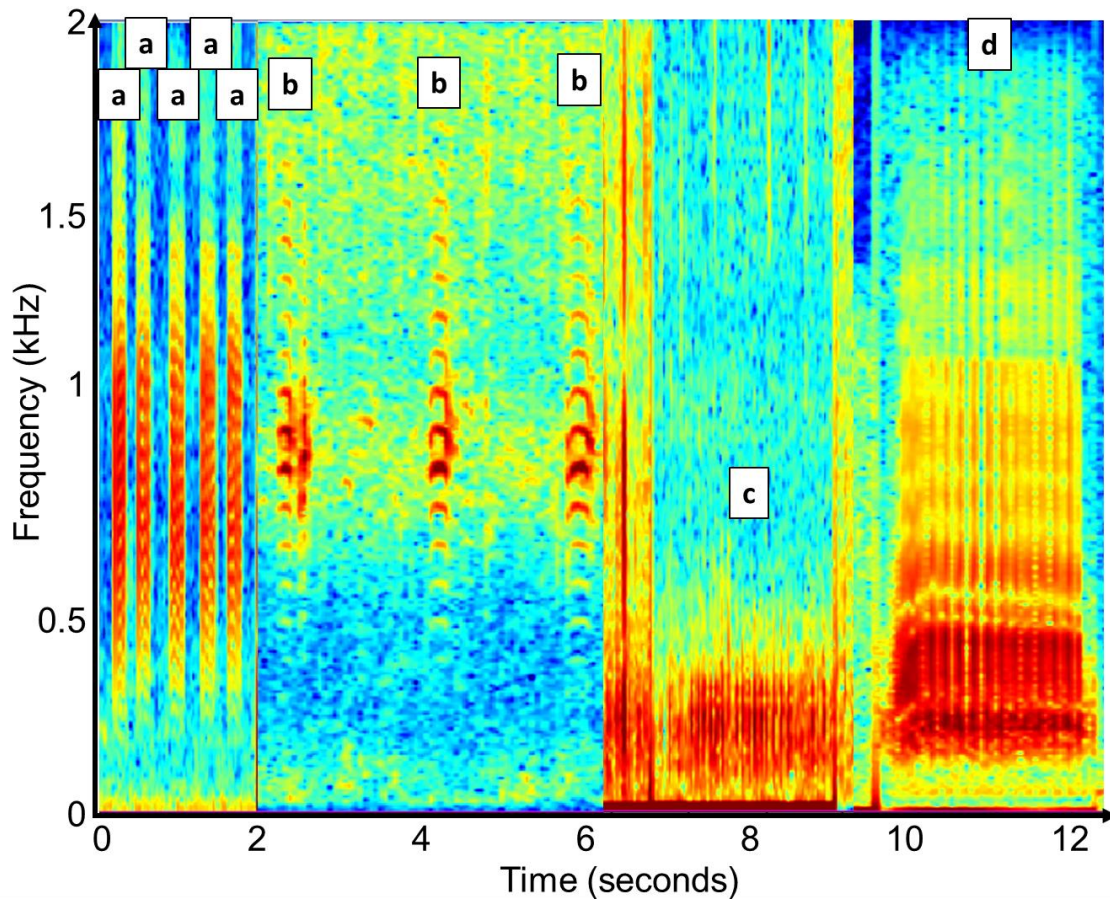


Figure 4 Comparison of fish complex, arched, and pulse series sounds. (a and b) arched sounds, and (c and d) and pulse series recorded in Polynesian altiphotic and mesophotic reefs (a) AS4, and (c) PS10 and similar sounds from the literature: (b) ‘/kwa/’ (Di Iorio et al. 2018), and (d) *Ophidion rochei* male. The figure is a compilation of several spectrograms visualized in Raven (FFT = 256, sampling frequency: 4 kHz). Sounds a and c are from Raick et al. (2023b), sound b is from Di Iorio et al. (2018a), and sound d is from Picciulin et al. (2019). The color code is relative to the amplitude: the hotter the color, the louder the sound (to be considered separately for each sound).

3.2.3. Pulse series and fast pulse trains

Some PS recorded in Polynesian MCEs exhibit similarities with sounds described in Carapidae. Sounds produced by *Carapus boraborensis* (duration: 3–14 s, 10–83 pulses, pulse period: 180–212 ms, (Lagardère et al. 2005)) share temporal similarities with PS6 sounds from MCEs (duration: 5.7 ± 7.7 s, 26 ± 24 pulses, pulse period: 185 ± 69 ms; mean \pm SD) but not in terms of peak frequency (200 Hz vs. 640 ± 438 Hz).

Carapus mourlani, a species present in Polynesian MCEs, is able to produce double-pulse sounds highly similar to a sound observed in MCEs and named ‘2P’. This sound was not considered in (Raick et al. 2023b) because of its rarity but was examined in (Raick et al. in review), where it represented 1.26% of sounds recorded in MCEs. In the literature, some *C.*

mourlani sounds are described as having two pulses, with the second one being lower in amplitude (Parmentier et al. 2006a). 2P was also composed of 2 ± 0 pulses, with the second one being generally lower in amplitude by $1,08 \pm 1,14$ dB re 1 μ Pa. However, the pulse period ($67,77 \pm 10,04$ ms) was higher than in *C. mourlani* sounds (theoretically around 31.3 ms by summing a described pulse duration of 22 ± 4.2 ms and an interpulse interval: 9.26 ± 2.2 ms (Parmentier et al. 2006a)). The peak frequency is higher in *C. mourlani* (765 ± 124 Hz, (Parmentier et al. 2006a)) than in 2P (471 ± 224 Hz).

PS10 (duration: 1.5 ± 0.5 s, 18 ± 6 pulses, pulse period: 85 ± 21 ms, peak frequency: 221 ± 25 Hz, Fig. 4c) recorded in Polynesian MCEs exhibits similarities with sounds described in shallower species of Ophidiidae (Mann et al. 1997; Sprague and Luczkovich 2001; Parmentier et al. 2010; Raick et al. 2023b) (Fig. 4d). A close zoom on the oscillograms of PS10 reveals a series of pulses dominated by a high-amplitude peak. In the inter-pulse interval, smaller peaks can be observed. This configuration is similar to the one observed in some species from genus *Ophidion*. However, the main difference between PS10 and sounds from *Ophidion* species is the difference in frequency range, with a lower frequency for PS10. On the contrary, PS10 exhibits a higher frequency compared to *Genypterus*, a larger species of Ophidiidae from the Southern Hemisphere. In MCEs from the Society and Tuamotu Islands, the literature review highlighted only one species of Ophidiidae (*Brotula multibarbata*) but the National Museum of Natural History (Paris) possesses different undescribed species from upper MCEs (50 m) and the rariphotic zone (below 283 m), so it would not be surprising if more species occur in the lower MCEs.

4. Discussion

The literature review reports the presence of 74 to 124 potentially soniferous species (i.e., known soniferous species, and species likely soniferous but with references known only at the

genus or family level) potentially present in Polynesian lower MCEs while the analysis of sounds from PAM has identified 69 distinct fish sounds in the same habitat (Raick et al. in review). Correlating these two types of data proves to be particularly challenging (Staaterman et al. 2017; Desiderà et al. 2019; Mooney et al. 2020; Raick et al. 2023b), mainly because the recorded sounds can vary according to several factors, such as water temperature (Ladich and Maiditsch 2020), the size of the individuals (Colleye et al. 2009; Parmentier et al. 2017), motivational state (Ladich 1997), or behavioral context (Tricas and Boyle 2014). Furthermore, a single species may be capable of producing different types of sounds (Salmon 1967; Fish and Mowbray 1970; Amorim et al. 2008; Raick 2015), adding complexity to the analysis. This is well exemplified in Serranidae. For example, *Mycteroperca bonaci* is known to produce single booms, sustained thundering rolls, bursts of several pulses, or short pulses followed by a longer tonal portion (Tavolga 1968b; Fish and Mowbray 1970; Schärer et al. 2014). In addition, difficulties arise from the reliance on available literature and the potential subjectivity of sound comparisons. A significant portion of the data from the literature comes from studies conducted in aquaria or with hand-held fish, which may further complicate comparisons. Finally, while many species have had their sounds described, a large number of species expected to have sonic abilities (depending on the taxon, with varying degrees of confidence for an unknown species within a sonic genus or family) still lack documented descriptions of their exact sounds.

The two main sonic families encountered at a depth around 120 m in the Society and Tuamotu Islands were Serranidae and Lutjanidae, collectively constituting 31% of all fish species present. However, the most abundant and diverse taxa in terms of species richness are not the most prominent contributors to the underwater biophony (see (Bolgan et al. 2019) for an example). While Serranidae are well-studied for their vocalizations (Mann et al. 2009; Schärer et al. 2012a; Bertucci et al. 2015; Koenig et al. 2017; Rowell et al. 2019; Desiderà et al. 2024), there is limited understanding of sound production in Lutjanidae, with current

research predominantly centered on the Lutjaninae subfamily (Fish and Mowbray 1970; Tricas and Boyle 2014). Their sounds have been described as ‘low-pitched’, ‘feeble’, or ‘possible’ (Fish and Mowbray 1970), and these descriptions are limited to non-FM non-harmonic pulse(s)-like sounds (Fish and Mowbray 1970; Tricas and Boyle 2014). Nevertheless, little is known about the mechanism underlying their sound production, and it has only been suggested that the swim bladder may be involved (Fish and Mowbray 1970).

In MCEs, AS4 accounts for 40% to 66% of all sound types (measured at 120 m during sunset, (Raick et al. 2023b)). This pseudoharmonic sound closely resembles the /kwa/ vocalizations produced by *Scorpaena* spp. in the Mediterranean Sea in terms of frequential and temporal patterns. Moreover, as in the Mediterranean Sea, these Polynesian AS4 have similar diel cycles. *Scorpaena* would not be a monophyletic taxon and also include *Scorpaenopsis* species in a monophyletic group (Rabosky et al. 2018). These two genera are known to inhabit lower MCEs in Polynesian waters (Siu et al. 2017). The occurrence of similar sounds produced at the same time of day in both habitats, which also share species from the same genera, strongly suggests that the sound producers in French Polynesia belong to the genera *Scorpaena* and *Scorpaenopsis*. This reasoning can similarly be applied to AS5.

Within Serranidae, a wide array of species have been documented as producing non-FM non-harmonic pulsed-like sounds, which have been described using various terms such as thumps, knocks, single pulses, pulse series, single booms, serial booms, loud booms, deep booms, low-frequency pulse sequences, pulse train calls, hollow knocks (Tavolga 1968a; Fish and Mowbray 1970; Mann et al. 2009, 2010; Nelson et al. 2011; Schärer et al. 2012a; Tricas and Boyle 2014; Bertucci et al. 2015; Desiderà et al. 2019), or a combination of PS and tonal elements (Schärer et al. 2014; Rowell et al. 2019, 2020). Additionally, tonal and downsweeps (DS) sounds have been identified in several serranid genera, including *Epinephelus* (Mann et al. 2010; Schärer et al. 2012a; Bertucci et al. 2015; Desiderà et al. 2019), *Hypoplectrus* (Lobel

1992), and *Mycteroperca* (Schärer et al. 2012b, 2014; Rowell et al. 2019, 2020). At least one of them, the long tonal call of *E. adscensionis* (Fish and Mowbray 1970), resembles a low-frequency tonal AS sound recorded in MCEs (Raick et al. 2023b). These genera are not clustered together in the phylogeny tree but are distributed across both the Anthiinae/Serraninae and Epinephelinae taxa (Rabosky et al. 2018). High-frequency DS from MCEs do not resemble grouper sounds but are highly similar to an unknown sound previously documented in the Atlantic Ocean and referred to as ‘unknown sound 365 Hz harmonic’ (Wall et al. 2013). More investigation is needed to know which low-frequency DS and certain tonal calls from MCEs (Raick et al. 2023b) are produced by which species of Serranidae. Given the substantial number of groupers found at greater depths than MCEs (Service de la pêche 2004), it is highly probable that similar sound types still exist in the rariphotic zone.

Ophidiidae taxon is well-known for its sonic capabilities, exhibiting a high diversity of mechanisms and distinct sounds not only between related species but also between males and females of the same species (Courtenay 1971; Howes 1978; Carter and Musick 1985; Casadevall et al. 1996; Parmentier et al. 2006b). *Brotula multibarbata* is a species known to inhabit Polynesian MCEs. Further investigation is needed to determine whether this species produces low-frequency, long, fast pulse trains or other types of sounds.

In conclusion, this study offers preliminary insights into which soniferous fish taxa are present in Polynesian MCEs. However, further research, particularly focusing on morphological aspects, is imperative to deepen our understanding and complement these initial findings.

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Author contributions

X.R.: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data Curation, Writing – Original Draft, Writing – Review & Editing, Visualization, Supervision, Project administration, and Funding acquisition. D.L.: Funding acquisition. E.P.: Validation, Writing – Review and Editing.

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