

Acoustic Communication in Butterflyfishes: Anatomical Novelties, Physiology, Evolution, and Behavioral Ecology

Timothy C. Tricas and Jacqueline F. Webb

Abstract Coral reef fishes live in noisy environments that may challenge their capacity for acoustic communication. Butterflyfishes (Family Chaetodontidae) are prominent and ecologically diverse members of coral reef communities worldwide. The discovery of a novel association of anterior swim bladder horns with the lateral line canal system in the genus *Chaetodon* (the laterophysic connection) revealed a putative adaptation for enhancement of sound reception by the lateral line system and/or the ear. Behavioral studies show that acoustic communication is an important component of butterflyfish social behavior. All bannerfish (*Forcipiger*, *Heniochus*, and *Hemitaurichthys*) and *Chaetodon* species studied thus far produce several sound types at frequencies of <1 to >1000 Hz. Ancestral character state analyses predict the existence of both shared (head bob) and divergent (tail slap) acoustic behaviors in these two clades. Experimental auditory physiology shows that butterflyfishes are primarily sensitive to stimuli associated with hydrodynamic particle accelerations of ≤ 500 Hz. In addition, the gas-filled swim bladder horns in *Chaetodon* are stimulated by sound pressure, which enhances and extends their auditory sensitivity to 1700–2000 Hz. The broadband spectrum of ambient noise present on coral reefs overlaps with the frequency characteristics of their sounds, thus both the close social affiliations common among butterflyfishes and the evolution of the swim bladder horns in *Chaetodon* facilitate their short-range acoustic communication. Butterflyfishes provide a unique and unexpected opportunity to carry out studies of fish bioacoustics in the lab and the field that integrate the study of sensory anatomy, physiology, evolution, and behavioral ecology.

Keywords Acoustic behavior • Coral reef fish • Communication • Evolution • Hearing • Lateral line • Laterophysic connection • Soundscape

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1 Introduction

The butterflyfishes (Family Chaetodontidae) are a conspicuous, speciose, and highly social family of coral reef fishes. The family includes four genera of coralfishes (*Amphichaetodon*, *Chelmon*, *Chelmonops*, *Coradion*), four genera of bannerfishes (*Forcipiger*, *Hemitaurichthys*, *Heniochus*, *Johnrandallia*), and a clade composed of the genera *Prognathodes* and *Chaetodon*, the latter of which represents approximately 70 % of the species in the family (Blum 1988; Smith et al. 2003; Fessler and Westneat 2007; Bellwood et al. 2010). The butterflyfishes are diverse in their feeding habits and they include species that are planktivores, obligate and facultative coral-ivores, benthic invertebrate predators, and omnivores (reviewed by Cole and Pratchett 2014). Individuals are rarely solitary and several types of social relationships are found among species (Hourigan 1989; Yabuta and Berumen 2014). Many species form monogamous pairs that are maintained for several years (or for life) in which the same two individuals carry out all of their daytime activities in close proximity to one another (separated by only a few body lengths) while foraging over large home ranges, or defending a feeding territory (Reese 1975; Fricke 1986; Tricas 1989; Roberts and Ormond 1992). Other species form long-term harem associations that consist of a single male and multiple females. During daylight hours some species form larger groups, shoals, or schools that feed on plankton in the water column above the reef. Their highly conspicuous species-specific color patterns and behavioral displays are used to visually mediate many social interactions such as the recognition of conspecifics (Zumpe 1965; Boyle and Tricas 2014), identification of mates (Reese 1975; Yabuta 2002), defense of territories (Tricas 1985, 1989; Roberts 1992; Wrathall et al. 1992; Kosaki 1999), avoidance of predators (Motta 1984; Neudecker 1989), and determination of behavioral state (Hamilton and Peterman 1971). However, the more recent discoveries of novel anatomical features associated with the lateral line system and the discovery of sound production have refocused attention on butterflyfish bioacoustic behavior in relation to their behavioral ecology and evolution, which is the focus of this chapter.

The laterophysic connection (LC; Figs. 1 and 2) is a unique anatomical feature in the genus *Chaetodon* that is defined by the presence of cylindrical, anterior swim bladder horns in proximity to a medial opening in the lateral line canal in the supracleithral bone, located at the posterior margin of the skull. This unique feature was proposed to facilitate the transmission of sound pressure stimuli to the lateral line canal system and to the ear (Webb 1998; Webb et al. 2006). Behavioral studies in the lab and field demonstrate that sound is produced in all *Chaetodon* species and in representatives of other butterflyfish genera studied thus far (summarized in Tricas and Boyle 2015a). The tendency for *Chaetodon* species to form monogamous pairs and other close social associations is consistent with their use of both the auditory and lateral line systems for the perception of acoustic signals at short distances. This may be especially important on coral reefs in which the soundscape is characterized by high intensity, broadband, ambient noise levels that

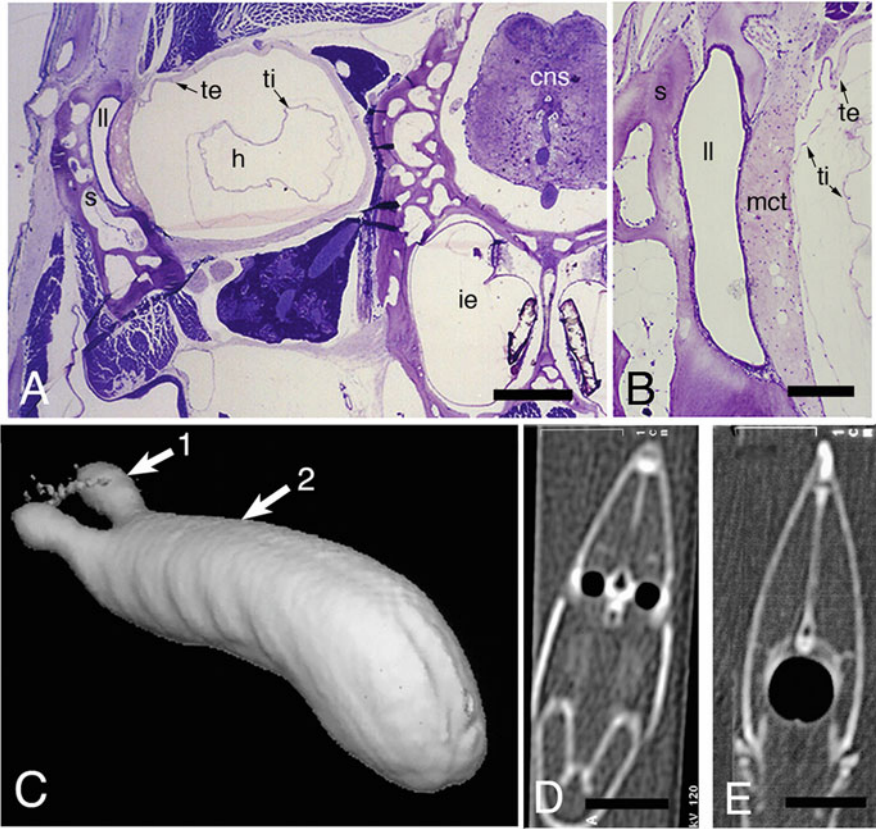


Fig. 1 Histological sections and CT images of the laterophysic connection (LC) and swim bladder in *Chaetodon* species. (a) Transverse section through LC in *C. octofasciatus*. Scale bar=500 μ m (modified from Webb 1998). (b) Close-up of laterophysic tympanum in *C. octofasciatus*. Scale bar=200 μ m. (c) 3-D reconstruction (CT) of the air volume in the swim bladder and swim bladder horns in *C. ephippium*. (d) Transverse CT slice at level of arrow 1 (swim bladder horns) in c. (e) Transverse CT slice at level of arrow 2 (body of swim bladder) in c. In d and e white represents high density bone (cranium, vertebral column, fin supports), and scales covering body. Soft tissue is grey, like the water surrounding the fish. Scale bar in d and e=10 mm. *cns* central nervous system, *h* horn, *ie* inner ear, *ll* lateral line canal, *mct* mucoid connective tissue, *s* supracleithrum, *te* tunica externa, *ti* tunica interna (from Smith et al. 2003, Reproduced with permission by John Wiley & Sons)

overlap the frequency range for both hearing and sound production and may present a challenge for the extraction of biologically relevant acoustic information. In this chapter we review the comparative anatomy of the laterophysic connection (in *Chaetodon* species), ear, and swim bladder, which may all be involved in the reception of acoustic field stimuli (Sect. 2). We review the current (but still limited) knowledge of the diversity of butterflyfish sounds and sound production mechanisms, and examine the evolution of their acoustic behaviors (Sect. 3). We describe

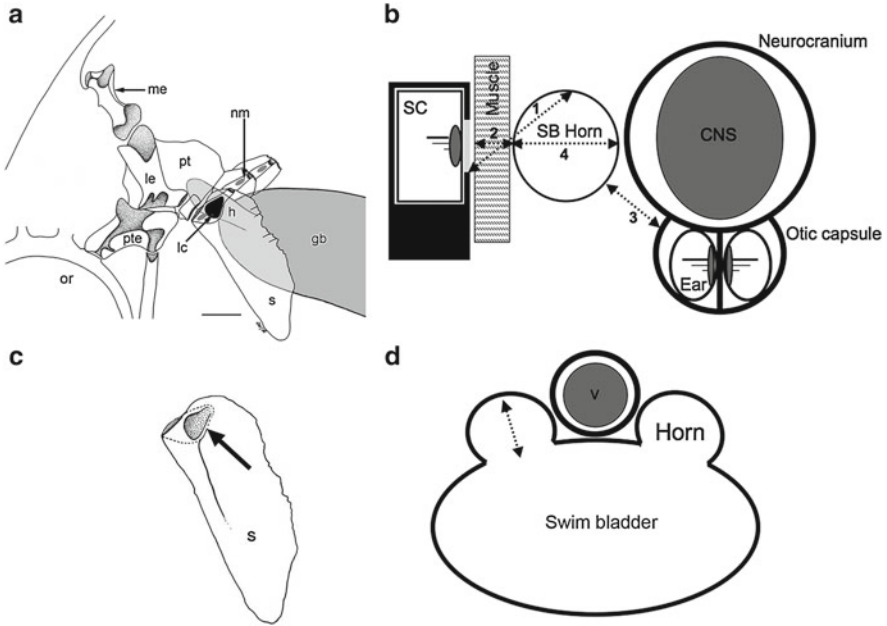


Fig. 2 Laterophysic connection in *Chaetodon*. (a) Drawing (lateral view, rostral to right) of the bones just behind the left orbit in *C. octofasciatus*. The anterior swim bladder horn (shaded) sits deep to the medial opening in the lateral line (LL) canal in the supraclathrum (black teardrop, = site of the laterophysic connection), and in the vicinity of several canal neuromasts within the LL canals (grey ovals). (b) Medial view of the right supraclathrum (in same orientation as a). Arrow points to the posterior terminal pore of the short LL canal (lumen is shaded), which is illustrated as a black oval in a. gb gas bladder (swim bladder), h swim bladder horn, lc site of laterophysic connection (black teardrop), le lateral extrascapular, me medial extrascapular, nm neuromast (grey oval), or orbit, pt post-temporal, pte pterotic, s supraclathrum. Scale bar = 1 mm. (c) Schematic representation (in transverse view) of the spatial relationships of the LL canal in the supraclathrum, the swim bladder horn and the otolith organs of the ear in *C. ocellatus*. The left LL canal is in the supraclathrum (sc), the medial opening in the canal (light grey gap in canal wall) and the neuromast that sits on the tissue filling the opening, muscle tissue that sits deep to the opening, the cylindrical swim bladder horn, and the skull containing the central nervous system (CNS) and beneath it, the ear, with the sensory macula of the sacculus on the medial wall in the midline (see also Fig. 7). “1–4” indicate distances measured to describe spatial relationships of ear and horns in Webb et al. (2012). (d) Transverse view of the relationship of the body of the swim bladder, and the bilateral swim bladder horns (in *C. ocellatus*) showing that the horns are outpocketings of the swim bladder that emerge dorsally (arrow) on either side of the vertebral column (v) (from Webb et al. 2006, 2012, reprinted with permission of John Wiley & Sons)

butterflyfish hearing capabilities and the likely importance of both the auditory and lateral line systems in acoustic communication (Sect. 4). We also consider how acoustic communication during social behaviors may enhance individual fitness (Sect. 5), and discuss the ecological implications for acoustic communication by different butterflyfish species on noisy coral reefs (Sect. 6).

2 Anatomy Associated with the Reception of Acoustic Stimuli

Butterflyfishes have a well-developed lateral line canal system on the head and trunk and have an ear that is typical of those teleost fishes that lack otophysic connections (a swim bladder-ear connection). The laterophysic connection, a unique feature of the genus *Chaetodon*, demonstrates a considerable degree of variation among species, and the morphology of the swim bladder is correlated with that of the laterophysic connection.

2.1 The Laterophysic Connection

The “laterophysic connection” (LC), the association of anterior swim bladder horns with an opening in the lateral line canal contained within the supracleithral bone, was named to draw attention to its apparent structural and putative functional similarity to otophysic connections found in other fishes. Webb (1998) suggested that the LC is the site of transduction of pressure oscillations generated by sound pressure waves in the air-filled swim bladder and swim bladder horns into fluid movements in the lateral line canal in the supracleithral bone, which are capable of stimulating canal neuromasts just rostral and caudal to the LC. It was hypothesized that the presence of an LC in *Chaetodon* would thus make the lateral line system, in addition to the inner ear (by virtue of the proximity of the swim bladder horns to the otic capsule), sensitive to sound pressure, thus expanding its functional repertoire. It was further suggested that novel interactions of lateral line and auditory input would enhance the interpretation of acoustic stimuli (Webb 1998; Webb et al. 2006), and the reception of acoustic communication stimuli produced by *Chaetodon* in their natural coral reef habitats (Tricas et al. 2006; see Sect. 3).

LC morphology varies interspecifically but, like the external body features of butterflyfishes, is not sexually dimorphic (Webb and Smith 2000). Two LC types are found among *Chaetodon* species (Figs. 3 and 4): (1) a Direct LC, characterized by direct contact of the lateral wall of the cylindrical anterior swim bladder horns with the medial opening in the supracleithrum, and (2) an Indirect LC, defined by the presence of muscle or kidney tissue between the lateral wall of the anterior swim bladder horn and the medial opening in the supracleithrum (Webb and Smith 2000). Two variants on a direct LC (Dir1 and Dir2) and four variants on an indirect LC (Ind1–Ind4) were found among 22 *Chaetodon* species in the 11 *Chaetodon* subgenera (Smith et al. 2003; Webb et al. 2006, Figs. 3 and 4; Table 1). These variants are defined by the type(s) of tissues found between the swim bladder horns and the supracleithrum (presence or absence of mucoid connective tissue in the medial opening), the length and diameter of the swim bladder horns (long [~1.5–3.5 mm] vs. short [<1 mm] horns, wide [~1–3 mm] vs. narrow [<1 mm] horns; Fig. 4), and the presence or absence of an external constriction (*ductus communicans*) of the

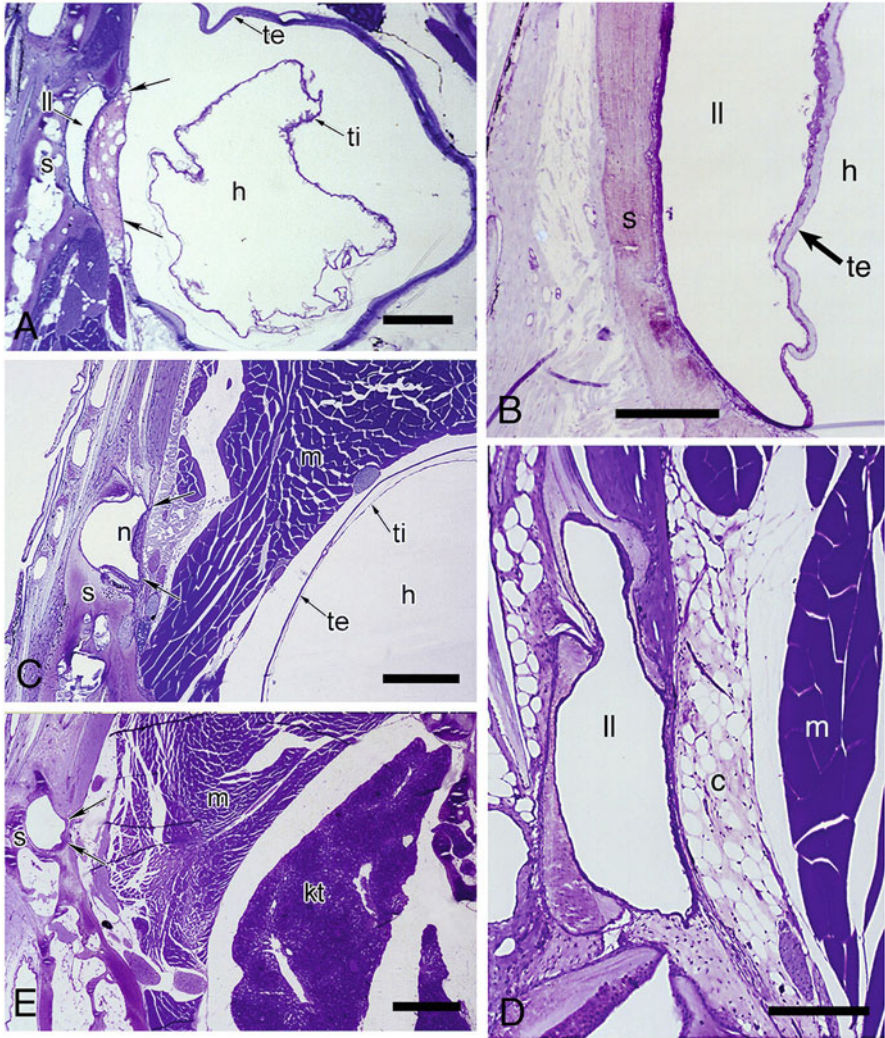


Fig. 3 Laterophysic connection (LC) variants among *Chaetodon* species represented schematically in Fig. 4. (a) *Dir1*—direct LC with mucoid connective tissue (arrows) in *Chaetodon octofasciatus*. Scale bar=500 μ m. (b) *Dir2*—direct LC without mucoid connective tissue in *Chaetodon plebeius*. Scale bar=200 μ m. (c) *Ind2*—indirect LC with no mucoid connective tissue in *Chaetodon multicinctus*. Scale bar=500 μ m. (d) *Ind1*—indirect LC (arrows) with mucoid connective tissue in *Chaetodon kleinii*. Scale bar=200 μ m. (e) *Ind3*—indirect LC with short horns in *Chaetodon ornatissimus*. Note that the swim bladder horns are not present in this section (at the level of the LC), and instead the space occupied by long horns in other species is filled by muscle (m) and kidney tissue (kt). Scale bar=500 μ m. Arrows indicate the dorsal and ventral extent of the tissues that separate the LL canal from the swim bladder horn in a, c, and e. c mucoid connective tissue (as in d), h swim bladder horn, kt kidney tissue, ll lateral-line canal, m muscle, n neuromast, s supracleithrum, te tunica externa, ti tunica interna (from Smith et al. 2003, reprinted with permission of John Wiley & Sons)

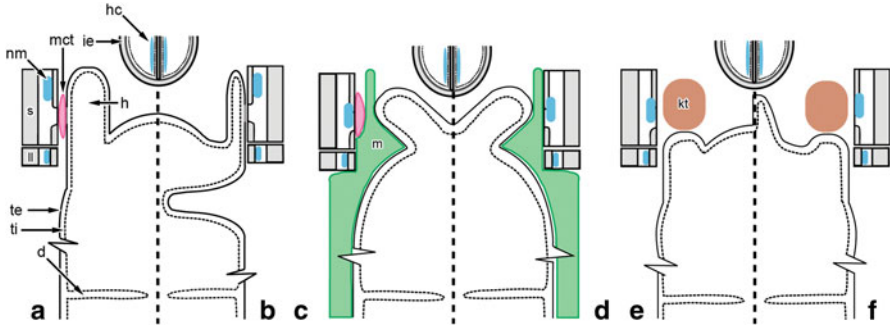


Fig. 4 Schematic representation of the six LC variants in dorsal view (rostral to top) among *Chaetodon* species (see Table 2 for more information). (a) *Dir1*—direct LC with mucoid connective tissue (pink) deep to opening in supracleithral lateral line canal containing neuromast (blue), wide horns, and one-chambered swim bladder (e.g., *Chaetodon auriga*). (b) *Dir2*—direct LC without mucoid connective tissue, with narrow horns, and a two-chambered swim bladder (e.g., *C. plebeius*). (c) *Ind1*—indirect LC with mucoid connective tissue (pink) deep to opening in supracleithral lateral line canal, with muscle (green) lateral to wide horns, and one-chambered swim bladder (e.g., *C. kleinii*). (d) *Ind2*—indirect LC without mucoid connective tissue, with muscle (green) lateral to wide horns, and one-chambered swim bladder (e.g., *C. multicinctus*). (e) *Ind3*—indirect LC with short horns (which do not reach the level of the opening in the supracleithral canal), and a one-chambered swim bladder (e.g., *C. ornatissimus*). (f) *Ind4*—indirect LC with short horns, a one-chambered swim bladder, and a medial anterior extension of swim bladder (e.g., *C. meyeri*). *d* diaphragm (transverse) in tunica interna, *h* swim bladder horn, *hc* sensory macula, *e* ear in otic capsule, *kt* kidney tissue, *ll* 1st lateral-line scale, *m* muscle, *mct* mucoid connective tissue, *nm* neuromast, *s* supracleithrum, *te* tunica externa of swim bladder (solid line), *ti* tunica interna of swim bladder (dotted line). (From Webb et al. 2006, reprinted with permission of John Wiley & Sons)

external wall (tunica externa) of the swim bladder (Webb et al. 2006; Fig. 4). Only one LC variant is found in each of the 11 *Chaetodon* subgenera, with the exception of the subgenus *Citharoedus* in which two short horn variants (*Ind3* and *Ind4*) are found.

2.2 The Swim Bladder

Butterflyfishes have a euphysoclitous swim bladder that sits just below the vertebral column and is typically 30 % of the length of the body. The swim bladder wall is composed of a thicker collagenous tunica externa and a thinner, epithelial tunica interna (Woods 2006; Woods et al. 2006). The gas exchange structures in the tunica interna (the secretory *rete mirabile* and resorptive oval) are well developed. A transverse diaphragm pierced by a central opening is formed by the infolding of the tunica interna and divides the swim bladder into anterior and posterior chambers (in *Chaetodon* and *Forcipiger*, and presumably other chaetodontid genera). The morphology of the diaphragm tissue suggests that the size of the opening can be changed, perhaps in order to control relative gas pressure in the two compartments

Table 1 Taxonomic placement of butterflyfishes, morphology of the Laterophysic Connection (LC variants, see Sect. 2.1), and feeding habit of *Chaetodon* species

	Species ^a	Subgenus ^b	LC Var. ^c	Feeding habit
Clade 1	<i>C. robustus</i>			
Clade 2	<i>C. tinkeri</i>	<i>Roaops</i>	Ind3	
	<i>C. argentatus</i>	<i>Exornator</i>	?	Omnivore ^d
	<i>C. fremblii</i>	<i>Exornator</i>	Ind2	Omnivore ^d
	<i>C. blackburnii</i>	<i>Exornator</i>	?	
	<i>C. citrinellus</i>	<i>Exornator</i>	Ind2	Corallivore ^d Omnivore ^d
	<i>C. quadrimaculatus</i>	<i>Exornator</i>	Ind2	Corallivore ^c Omnivore ^d
	<i>C. miliaris</i>	<i>Exornator</i>	Ind2	Planktivore ^d
	<i>C. santaehelenae</i>	<i>Exornator</i>	?	
	<i>C. sedentarius</i>	<i>Exornator</i>	Ind2	
	<i>C. multinctus</i>	<i>Exornator</i>	Ind2	Corallivore ^c
	<i>C. interruptus</i>	<i>Lepidochaetodon</i>	?	Corallivore ^c
	<i>C. unimaculatus</i>	<i>Lepidochaetodon</i>	Ind1	Corallivore ^c
	<i>C. kleinii</i>	<i>Lepidochaetodon</i>	Ind1	Planktivore ^d
Clade 3	<i>C. aureofasciatus</i>	<i>Discochaetodon</i>	Dir1	Corallivore ^c
	<i>C. rainfordi</i>	<i>Discochaetodon</i>	Dir1	Corallivore ^c
	<i>Parach-aetodon ocellatus</i>	<i>Megaprototon</i> ^f	?	
	<i>C. baronessa</i>	<i>Gonochaetodon</i>	Dir1	Corallivore ^c
	<i>C. bennetti</i>	<i>Tetrachaetodon</i>	Dir2	Corallivore ^c
	<i>C. plebeius</i>	<i>Tetrachaetodon</i>	Dir2	Corallivore ^c
	<i>C. tricinctus</i>	<i>Discochaetodon</i>	?	Corallivore ^d
	<i>C. trifascialis</i>	<i>Megachaetodon</i>	Dir2	Corallivore ^c
	<i>C. lunulatus</i>	<i>Corallochaetodon</i>	?	Corallivore ^c
	<i>C. trifasciatus</i>	<i>Corallochaetodon</i>	Ind2	Corallivore ^c
	<i>C. meyeri</i>	<i>Citharoedus</i>	Ind4	Corallivore ^c
	<i>C. ornatissimus</i>	<i>Citharoedus</i>	Ind3	Corallivore ^c
	<i>C. reticulatus</i>	<i>Citharoedus</i>	?	Corallivore ^c
Clade 4	<i>C. auriga</i>	<i>Rhabdophorus</i>	Dir1	Omnivore ^d
	<i>C. auripes</i>	<i>Rhabdophorus</i>	?	Corallivore ^d
	<i>C. collare</i>	<i>Rhabdophorus</i>	?	Corallivore ^d
	<i>C. lunula</i>	<i>Rhabdophorus</i>	?	Omnivore ^d
	<i>C. lineolatus</i>	<i>Rhabdophorus</i>	?	Omnivore ^d
	<i>C. ulietensis</i>	<i>Rhabdophorus</i>	?	Omnivore ^d
	<i>C. ephippium</i>	<i>Rhabdophorus</i>	Dir1	Omnivore ^d
	<i>C. capistratus</i>	<i>Chaetodon</i>	?	Corallivore ^d
	<i>C. striatus</i>	–	Dir1	Corallivore ^d Omnivore ^d
	<i>C. humeralis</i>	<i>Chaetodon</i>	?	Omnivore ^d
	<i>C. ocellatus</i>	<i>Chaetodon</i>	Ind2	
	<i>C. melannotus</i>	<i>Rhabdophorus</i>	–	Corallivore ^f

^aPlacement of species in *Chaetodon* clades (1–4) is based on Bellwood et al. (2010)

^bSubgeneric placement is from Smith et al. (2003)

^cLC type and variant is from Webb et al. (2006)

^dFrom Hourigan (1989)—in Hawaiian waters

^eCorallivore = obligate corallivore, from Bellwood et al. (2010)

^fObligate corallivore, feeds on soft corals (Bellwood et al. 2010)—in Australian waters

?LC variant not determined histologically, but LC type (Direct, Indirect) can be inferred from swim bladder morphology or subgeneric placement (Webb et al. 2006)

(Woods 2006; Woods et al. 2006; Webb et al. 2006). The swim bladder is bounded dorsally by the vertebral column, laterally by the ribs, and ventrally by the peritoneum that lines the abdominal cavity. This configuration limits the overall shape and volume of the swim bladder as indicated by the obvious indentations in the volume of air created by the ribs (Webb et al. 2006; Fig. 1c). Neither extrinsic nor intrinsic sonic muscles are found in association with the swim bladder, so the swim bladder likely functions as a sound resonator, which is stimulated by the physical motion of other adjacent sound production mechanisms (Sect. 3 below).

Variation in the morphology of the swim bladder may have implications for both bioacoustic reception and sound production. The gross morphology of the swim bladder varies among *Chaetodon* species (such variation within a genus is unusual and thus notable), and is correlated with LC type (Direct, Indirect; with a few minor exceptions; Webb 1998; Webb and Smith 2000; Smith et al. 2003; Fig. 4). *Chaetodon* species with a Direct LC (e.g., *C. auriga*, *C. octofasciatus*) have a swim bladder with a distinct “kink” in its long axis, such that the anterior half of the swim bladder and swim bladder horns is relatively horizontal, whereas the posterior half of the swim bladder is more vertical in orientation. The thick tunica externa is composed of multiple layers of collagen and is somewhat thicker dorsally than it is ventrally (Woods 2006). The ventral surface of the swim bladder is covered by a thin peritoneum (lining of the abdominal cavity) that wraps tightly around the swim bladder’s posterior end (a “free” swim bladder; Smith et al. 2003). The thickness of the lateral wall of the swim bladder horns decreases quite dramatically near the medial opening in the supracleithrum (Woods 2006), which may allow pressure-induced movement of the tissue covering the opening resulting in movements of fluids in the canal. Sound production by *Chaetodon* species with a direct LC is so far quantified only in *C. auriga* (very low frequency pulse sounds; Sect. 3). In addition, the enhanced auditory sensitivity of *C. auriga* appears to depend more on the swim bladder horns rather than on the body of the swim bladder (Sect. 4).

In contrast, *Chaetodon* species with an Indirect LC (e.g., *C. multicinctus*, *C. unimaculatus*, *C. kleinii*, *C. ornatissimus*), and species in non-*Chaetodon* genera (*Forcipiger*, *Heniochus* and *Hemitaurichthys*) have a swim bladder that is more smoothly contoured (lacking a “kink”). The tunica externa in these species is much thinner overall (and translucent) when compared to that in species with a direct LC. It is thinner dorsally than it is ventrally, but its thickness does not vary along the length of the swim bladder or along the horns as in species with a Direct LC (Woods 2006). In contrast to species with Direct LC, a thick, opaque peritoneum covers the ventral surface of the swim bladder and attaches laterally to the ribs (an “attached” swim bladder; Smith et al. 2003; Webb et al. 2006). In several *Chaetodon* species with an indirect LC, as well as several non-*Chaetodon* species, sound production includes both low and high frequency pulsed sounds with a stronger contribution of the body of the swim bladder for auditory sensitivity (see Sects. 3 and 4 below).

The swim bladder of teleost fishes is also quite important for the control of buoyancy, which makes the study of its adaptive evolution rather complex. The euphysoclistic swim bladder of chaetodontids (and other “advanced” teleosts) regulates its air volume physiologically (by active secretion and passive resorption of gases).

Chaetodon species are known to sometimes make quick excursions along reef walls from 2 to 8 m in only 5–15 s during which they experience rapid pressure changes close to 1 atm (Tricas, unpublished observations). The ability to precisely control gas pressure in the swim bladder would also enable fishes to consistently and accurately monitor sounds produced by mates, conspecifics, and competitors (see Sect. 3). The fine control of buoyancy may also facilitate precise maneuvers made with paired fins during paired swimming and interactions, which is when sounds are produced (Sect. 3). Finally, swim bladder shape and the presence of anterior swim bladder horns may alter the center of gravity or center of buoyancy in *Chaetodon*. This may help to control posture, especially when feeding on benthic invertebrate prey (Woods 2006), an ability also suggested in other fishes (Parmentier et al. 2011). Thus, the evolution of swim bladder morphology is likely the result of responses to a range of selective pressures involved with sound production, hearing, locomotion, and/or feeding behavior.

2.3 *The Ear and Its Proximity to the Swim Bladder*

Prior to the discovery of the LC, the structure and function of swim bladder horns defining the otophysic connection was explored to some extent in holocentrid fishes, which provide a useful context for interpreting the LC in *Chaetodon*. The holocentrid, *Myripristis kuntzei*, has robust anterior swim bladder horns that make contact with a thinned otic capsule wall, and a saccular macula (sensory epithelium) that is modified in shape relative to that in *Sargocentron* (another holocentrid) and in other percormorph fishes that lack an otophysic connection (Nelson 1955; Popper 1977; Fig. 5b). *Myripristis* also has higher sensitivity to sound stimuli over a broader frequency range, when compared to *Sargocentron* (Coombs and Popper 1979; Fig. 5a). In his analysis of the ears of Hawaiian fishes, Popper (1977) described the sensory epithelium of the sacculus and lagena in one chaetodontid, *C. miliaris*, and found that it was similar to that in other teleosts that lack an otophysic connection. However, we now know that *C. miliaris* has an indirect LC (see Sect. 2.1) and is not representative of all chaetodontid species. Thus, Webb et al. (2010) examined ear morphology in *Chaetodon* species with different LC types and in *Forcipiger flavissimus* in light of the hypothesized acoustic functions of the LC and the known correlation of swim bladder and LC morphology among *Chaetodon* species (Sect. 2.2). Ear morphology was found to be similar in all chaetodontid species examined. The otic capsule sits ventral to the hindbrain, the left and right ears share a common wall in the midline of the otic capsule (Figs. 1a and 2c), and the shape of the sensory maculae of the lagenar, saccular, and utricular otolithic organs was similar in *Chaetodon* and *Forcipiger*, and in other perciform fishes that lack swim bladder horns or an otophysic connection (discussed in Webb et al. 2010). Thus, swim bladder morphology in butterflyfishes is in direct contrast to that in holocentrids, which demonstrates a correlation between the presence of swim bladder horns, modified

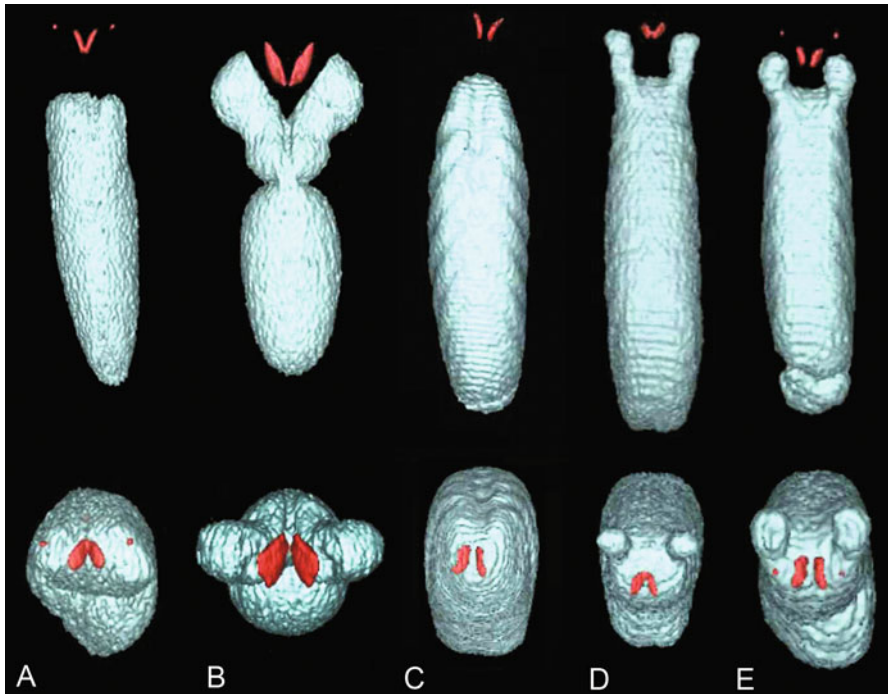


Fig. 5 3-D reconstruction of CT data illustrating the relationship of otoliths (red) to the volume of air within the swim bladder (white; swim bladder diameter ≈ 1 cm) in dorsal (top) and frontal (bottom) views of two species of holocentrids (a, b) and three species of chaetodontids (c–e). (a) *Sargocentron* sp. (Holocentridae: Holocentrinae)—no swim bladder horns, (b) *Myripristis* sp. (Holocentridae: Myripristinae)—swim bladder horns extend rostrally and wrap around the otic capsules containing the very large saccular otoliths, (c) *Forcipiger flavissimus*, (d) *Chaetodon auriga*, (e) *Chaetodon multicinctus*. In the two species of *Chaetodon* (d, e) the air-filled cylindrical horns extend rostrally, but are dorsal and lateral to the otic capsules that contain the otoliths. The large otoliths are the saccular otoliths and the smaller otoliths [visible in a, e] are the utricular otoliths. (From Webb et al. 2010, reprinted with permission of John Wiley & Sons)

otic capsule, and modified ear morphology (and enhanced hearing capabilities). It is apparent in *Chaetodon*, that the LC evolved and diversified among species without apparent morphological modification of the ear or otic capsule (Webb et al. 2010).

In adult *Chaetodon*, the swim bladder horns extend rostrally and approach the ear to within 1–2 mm (Webb et al. 2010; Fig. 5). In species with a direct LC (e.g., *C. auriga*; Fig. 5d) the swim bladder horns sit further from the otic capsule (and closer to the laterally placed supracleithral bones) than the swim bladder horns in species with an indirect LC (e.g., *C. multicinctus*; Fig. 5e). The anterior end of the swim bladder of *Forcipiger* (which has no horns or LC) sits at approximately the same distance from the ear as do the horns of *Chaetodon* species with a direct LC (Webb et al. 2010; Fig. 5c). This close juxtaposition of the volume of gas in the

swim bladder or swim bladder horns to the ear is now known to enhance the hearing sensitivity and frequency range during social communication in adult *Chaetodon* species (see Sect. 4.2). In the tholichthys larvae of *C. ocellatus* the distance between the swim bladder and the ear increases to about 1.2 mm as fish grow. This distance does not increase after transformation to the juvenile stage (with continuing increases in fish size) as the long swim bladder horns increase in length with no significant change in hearing sensitivity (Webb et al. 2012) suggesting that the distance between the air within the horns and the ear is of functional importance even in early life history stages.

2.4 Evolution of the Laterophysic Connection in *Chaetodon*

Blum (1988) determined that the medial opening in the supracleithrum is a synapomorphy that defines the genus *Chaetodon*. Webb (1998) then defined the LC as an association of swim bladder horns with the medial opening in the supracleithrum. Webb et al. (2006) defined two Direct LC variants (Fig. 4a, b) and four Indirect LC variants (Fig. 4c–f) among *Chaetodon* species. Smith et al. (2003) mapped LC characters on a new hypothesis of phylogenetic relationships based on morphological characters and suggested that *Chaetodon* ancestor had a Direct LC. This was surprising given the correlation of swim bladder morphology with LC type among *Chaetodon* species and because *Chaetodon* species with an Indirect LC have a swim bladder that is quite similar to those non-*Chaetodon* genera in lack an LC (e.g., *Forcipiger*, *Hemitaurichthys*; Fig. 5).

More recent phylogenetic analyses (using molecular evidence) identified four *Chaetodon* clades (Fessler and Westneat 2007; Bellwood et al. 2010). A Direct LC is found in Clades 3 and 4, but an Indirect LC is found in Clades 2, 3, and 4. Data are not available for any species in Clade 1 (Table 1). In contrast to the mapping of LC type in Smith et al. (2003), a mapping of LC variants on a molecular phylogeny (Fessler and Westneat 2007), in which Clade 2 is considered to be the sister group to Clades 3+4, suggests that an Indirect LC is the ancestral LC type in *Chaetodon*. Unfortunately, the mapping of LC variants on a more recent molecular phylogeny (Bellwood et al. 2010) sheds no light on the identity of the ancestral LC condition because it shows Clades 2, 3, and 4 as an unresolved trichotomy. Regardless, the occurrence of one LC variant in each of the *Chaetodon* subgenera, which are intact within the four clades, substantiates the value of the subgenera as taxonomic units that presumably evolved in response to different selective pressures associated with LC structure, and presumably function. The distribution of LC variants among subgenera reveals that most of the variants evolved at least two times within the genus *Chaetodon* (Table 1).

It was hypothesized that ecological correlates (e.g., feeding habit) might shed light on the functional significance of the evolution of LC morphology (Webb and Smith 2000). However, of the 15 *Chaetodon* species now known to be obligate corallivores that are monogamous and territorial (Table 1), seven have a Direct LC and

eight have an Indirect LC (Webb et al. 2006). Thus, LC type is not correlated with corallivory, which is thought to be a major ecological factor in the evolution of *Chaetodon* species. The drivers of the evolutionary diversification of the LC have yet to be identified, but it has been shown experimentally that the presence of long swim bladder horns enhances auditory capabilities (threshold, frequency range) in *Chaetodon* species regardless of other defining features of LC variation (Sect. 3).

3 Diversity and Evolution of Sound Production in Butterflyfishes

The discovery of the LC in *Chaetodon* led to the hypothesis that these highly social fishes produce sounds for acoustic communication during social interactions. Subsequent field and laboratory investigations on several species show that sound production is used by *Chaetodon* and representatives of other genera during their social interactions.

3.1 Acoustic Behavior and Sound Production Mechanisms

Sound production is now known for eight *Chaetodon* species and for all of the species of *Forcipiger*, *Heniochus*, and *Hemitaurichthys* studied so far. The names for most acoustic behaviors (and sound types) are derived from the most prominent observable motor pattern that occurs during the sound production event (Table 2). Lab and field studies show that as a group, these fishes produce a large repertoire of pulsed sounds and pulse trains that are generated by: (1) multiple sound production mechanisms associated with subtle movements of various body parts (e.g., head bob, jaw protrusion, body motion, buckling of the anterior body wall), and (2) hydrodynamic stimuli generated by movement of the whole body during a stereotyped locomotor tail slap in *Chaetodon*. Several sound production mechanisms appear to be shared among species studied, which generate sounds across a broad range of frequencies (Table 2).

Kinematic and electromyographic analyses indicate the presence of at least three sound production mechanisms in non-*Chaetodon* bannerfish species, which produce sounds with peak frequencies of 27–170 Hz (Table 2). The head bob sound is produced by the two known species of *Forcipiger* and is associated with a rapid and prominent vertical motion of the head (Fig. 6). The head bob acoustic behavior is driven by epaxial muscle action on the skull and a ventral linkage between the head and pectoral girdle, which is maintained by simultaneous activity of the adductor mandibulae and sternohyoideus muscles (Boyle and Tricas 2011). This results in the anterior motion of the pectoral girdle, ribs, and rostral swim bladder before the head is released and rotated dorsally (and also contributes to apparent passive motions of

Table 2 Sound production in butterflyfishes and their behavioral contexts

	Clade	Sound type	Single pulse or train	Pulse duration (ms)	Peak frequency (Hz)	6 dB bandwidth (Hz)	Behavioral context	References
<i>Forcipiger flavissimus</i>		Head bob	ST	29–74	62–254	287	CSI	4, 8
		Anal fin retraction	ST	54	27	64	CSI	8
<i>F. longirostris</i>		Head bob	S	98	100	–	CSI	4
<i>Hemitaenichthys polylepis</i>		Hypaxial buckling pulse	ST	38	116	126	A, C, V	3, 7
		Blended pulse	ST	186	147	69	A, C, V	7
<i>H. thompsoni</i>		Hypaxial pulse	ST	56	170	214	V	7
<i>Heniochus chrysostomus</i>		Hypaxial pulse	ST	57	140	–	A	6
<i>Chaetodon kleinii</i>	C2	Jaw protrusion	S	17	516	358	CSI	8
		High frequency pulse	S	7	3609	4219	A	7
<i>C. multincinctus</i>	C2	Body pulse	ST	25–50	137–184	350	CSI	2, 8
		Body shake	S	55	29	62	CSI	8
<i>C. unimaculatus</i>		Tail slap	ST	154–418	9–69	15	CSI	2, 8
	C2	Head bob + Jaw protrusion	S	10–16	2752–3415	708	CSI	2, 8
<i>C. ornatissimus</i>		Tail slap	S	52	1031	227	CSI	8
	C3	Body pulse	S	424	<1	6	CSI	8
<i>C. auriga</i>		Tail slap	S	36	346	19	A, C	7
	C4	Head bob + Jaw protrusion	S	366	6	14	A	8
<i>C. ocellatus</i>	C4	Pulse	ST	93	23	42	CSI	8
<i>C. striatus</i>	C4	Pulse	S	–	–	–	E	1
<i>C. ulietensis</i>	C4	–	S	–	–	–	E	1
		–	–	–	–	–	S	5

See Table 1 and Fig. 8 for phylogenetic placement of these species

Behaviors: A agonistic interactions, C courtship, CSI conspecific social interactions, E induced by electric stimulation, S schooling, V vigilance (approached by predator or diver)

References: 1 = Fish and Mowbray (1970), 2 = Tricas et al. (2006), 3 = Boyle and Tricas (2010), 4 = Boyle and Tricas (2011), 5 = Lobel et al. (2010), 6 = Parmentier et al. (2011), 7 = Tricas and Boyle (2014), 8 = Tricas and Boyle (2015a)

the jaws). These motions stimulate the adjacent swim bladder to produce a pulsed sound with peak frequency in the range of 100–200 Hz (Boyle and Tricas 2011; Boyle et al. 2013; Tricas and Boyle 2014, 2015a). The anal fin retract sound is also produced by *F. flavissimus* and has a much lower peak frequency (27 Hz) (Fig. 6; Tricas and Boyle 2015a). These two acoustic behaviors in *Forcipiger* are not yet reported for the other bannerfish genera studied so far.

In contrast, the bannerfishes *Hemitaurichthys polylepis* and *H. thompsoni* produce loud pulse sounds that do not involve a head bob motion, but instead produce sounds that are associated with a buckling of the anterior body wall caused by contraction of the hypaxial musculature lateral to the anterior portion of the swim bladder (Boyle and Tricas 2010; Tricas and Boyle 2014). This mechanism is similar to that demonstrated in *Heniochus chrysostomus*, which likely involves the contraction of the lateral subdivision of the hypaxial musculature (Parmentier et al. 2011). Thus the head bob sound in *Forcipiger* is produced by the action of the epaxial, adductor mandibula and sternohyoideus muscles, and their musculoskeletal linkages. The anal-fin spine-retraction sound is produced by the action of the anal fin erector and retractor muscles and their associated linkages. The pulsed sounds of *Heniochus* and *Hemitaurichthys* are driven primarily by the action of the hypaxial musculature.

Several acoustic behaviors of *Chaetodon* (including some for which the sound production mechanisms are not yet confirmed) clearly vary among species and clades, and span a wider range of frequencies than those produced by the bannerfishes (Table 2; Tricas and Boyle 2015a). A prominent head bob behavior that is similar to that seen in *Forcipiger* occurs in both *C. unimaculatus* (Clade 2) and *C. auriga* (Clade 4), but also includes a prominent and active protrusion of the jaws (Fig. 6). In comparison, pulsed sounds produced by the blacklip butterflyfish, *C. kleinii*, (Clade 2) involves jaw protrusion without a prominent head bob motion. The possibility that the jaw motion found among Clade 2 species causes the relatively high average peak frequency pulsed sounds (e.g., *C. kleinii*=516 Hz, *C. unimaculatus*=1031 Hz) needs to be tested and examined in more species. In addition, the causal factors for the head-bob jaw-protrusion sound in *C. auriga* and its lower peak frequency (23 Hz) need to be resolved. Furthermore, the common sound produced by *C. multinctus* (also in Clade 2) does not involve a visible head bob or jaw protrusion, but instead is a body motion pulse sound (average peak frequency=137 Hz) similar to that described for *Hemitaurichthys* and *Heniochus*. Additional detailed electromyographic studies are needed to confirm or reject the presence of similar internal kinematic patterns (see Tricas and Boyle 2015a). A similar body motion acoustic behavior occurs in *C. ornatissimus* (Clade 3), but that pulsed sound has a much lower peak frequency (10 Hz). Collectively, the head bob, jaw protrusion, and body motion sounds produced by *Chaetodon* species studied thus far span a greater frequency range than sounds produced by members of other butterflyfish genera, and involve several sound production mechanisms.

Several species of *Chaetodon* also produce a very low frequency hydrodynamic stimulus known as the tail slap, which has peak frequencies that range from <1 to 69 Hz and a significant component in the infrasound (<20 Hz) range (sensu Sand

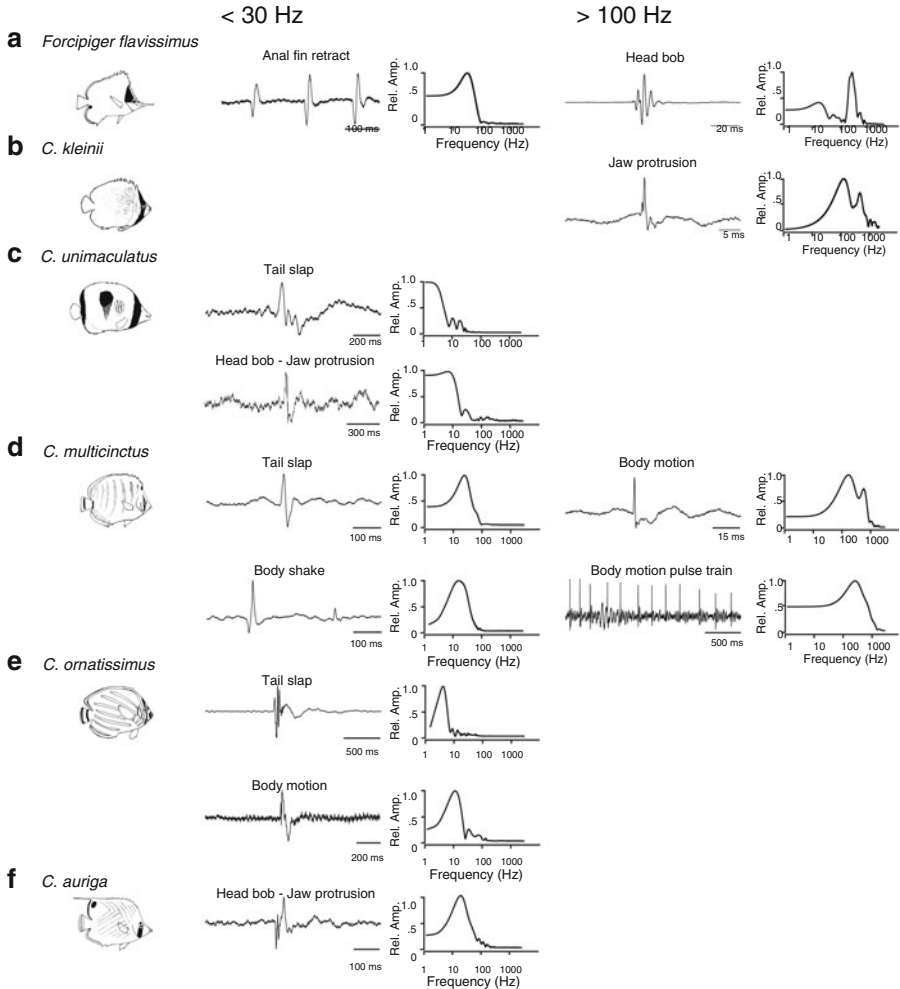


Fig. 6 Representative waveforms and spectra of sounds produced by five species of *Chaetodon* and by *Forcipiger flavissimus* during social interactions with conspecifics. Sounds are categorized as those with peak frequencies near infrasound (<30 Hz) and with peak frequencies >100 Hz. **(a)** *F. flavissimus* produced a low frequency pulse sound associated with erection of the anal fin and a higher frequency pulse sound associated with the head bob-jaw protrusion behavior. **(b)** *C. kleinii* produced a short pulse sound during protrusion of the jaw with average peak frequency near 500 Hz. **(c)** *C. unimaculatus* produced pulse sounds with peak frequency <10 Hz during slap behavior or protrusion of the jaw. **(d)** *C. multicinctus* produced low frequency pulse sounds from 10 to 30 Hz during tail slap and body shake acoustic behaviors. Single and trains of pulses were produced during the body motion sound and had a higher average peak frequency of 137 Hz. **(e)** *C. ornatissimus* produced low frequency pulse sounds near 10 Hz during both tail slap and body motion acoustic behaviors. **(f)** *C. auriga* produced the head bob-jaw protrusion sound which had a low average peak frequency near 20 Hz. Fast Fourier transforms of sound waveforms show relative amplitude (Rel. Amp.) of example peak frequencies. From Tricas and Boyle (2015a)

and Karlsen 2000). This sound is generated by a tail slap locomotor behavior during agonistic interactions with conspecifics (Fig. 6; Tricas et al. 2006; Tricas and Boyle 2015a). The tail slap is a stereotyped motion of the body that follows other aggressive movements, such as a rapid approach or intense lateral display, which is described in detail by Dewan and Tricas (2011). Swift movements of the lateral body surface and tail creates a hydrodynamic acceleration that may produce complex vortices that impinge on the lateral body surface of the receiver fish (Hanke et al. 2008), and at high intensities can displace a receiver's body (Tricas et al. 2006). Whole body acceleration directly stimulates the ear of the receiver, but the associated sound pressure wave is thought to produce only relatively small displacements of the wall of the swim bladder and swim bladder horns relative to hydrodynamic motions from the source at frequencies <10 Hz, as modeled in the cod swim bladder (Sand and Hawkins 1973). The tail slap behavior is most commonly observed in paired, monogamous, and territorial species such as *C. multicinctus* and *C. ornatissimus*, which aggressively defend food resources and mates. The tail slap behavior is not commonly observed in planktivorous species such as *C. miliaris* or *C. kleinii*, and is not yet described for other butterflyfish genera. These differences in aggressive behavior and the production of the tail slap sound among butterflyfish species are also associated with differential expression of arginine vasotocin neuropeptide by neurons that project to the forebrain (Dewan et al. 2008, 2011; Dewan and Tricas 2011, 2014). Further neuroanatomical and physiological investigations are required to determine the proximate mechanisms responsible for the central neural control of aggressive acoustic behaviors in butterflyfishes.

3.2 The Broad Palette of Butterflyfish Sound Characteristics

The acoustic stimuli produced by *Chaetodon* species during social interactions span a frequency range of at least four decades (<1 to >1000 Hz). Extreme low frequency sounds with an average peak frequency of <10 Hz and long duration (400 ms) are associated with the tail slap behavior in *C. ornatissimus*, *C. multicinctus*, and *C. unimaculatus* (Tricas and Boyle 2015a), and this sound is also produced by *C. auriga* in the field but is not yet quantified (Tricas and Boyle unpublished observations). Other low frequency pulse sounds in the ~10–30 Hz range are produced by *C. multicinctus*, *C. ornatissimus*, *C. auriga*, and *Forcipiger* via different mechanisms. Sounds with higher peak frequencies of 100–1000 Hz are also readily produced during social interactions in the lab by *C. kleinii*, *C. unimaculatus*, *C. multicinctus*, and *Forcipiger*. These have pulse durations of ≤ 50 ms and are similar with respect to frequency and bandwidth characteristics. There is also great variation in the frequency range of sounds produced by different species (Tricas and Boyle 2014, 2015a). For example, each *Chaetodon* species (with the exception of *C. kleinii*) produces at least one sound type with a peak frequency of 1–30 Hz and another sound type at 10–100 Hz. Sounds with peak frequency in the 10–100 Hz band can include several sound types, and the 6 or 10 dB bandwidth of these sounds often

extends to higher frequencies. These comparisons show that the sound characteristics of a single species may span a wide range of frequencies and are not made by a single sound production mechanism or behavior. Thus the acoustic repertoire for some species covers a wide range of frequencies as the result of the production of several sound types (as in *C. unimaculatus* and *C. multicinctus*), whereas the number and frequency range of sounds produced by other species may be more limited.

3.3 Evolution of Sound Production in Butterflyfishes

The evolutionary interpretations of the diversity of acoustic behaviors and sound production mechanisms in butterflyfishes are in the very early phases of analysis, but some patterns are beginning to emerge. Characters defined by acoustic behaviors that are mapped onto a molecular phylogeny of butterflyfishes shows that the head bob and body motion behaviors may be shared among some members of the bannerfish and *Chaetodon* clades, whereas the tail slap acoustic behavior may be a character only of *Chaetodon* (Fig. 7, Tricas and Boyle 2015a). The prominent head bob acoustic behavior in *Forcipiger*, which is driven by several muscles and a ventral linkage between the head and pectoral girdle (see Sect. 3.1), is not yet known in *Hemitaenichthys* or *Heniochus* (see Sect. 3.1). The head bob behavior in *C. unimaculatus* (Clade 2) and *C. auriga* (Clade 4) includes a prominent and active protrusion of the jaws, whereas *C. kleinii* (Clade 2) only demonstrates the prominent jaw protrusion and not the head bob. The apparent variation in the occurrence of the head bob and associated jaw actions among *Chaetodon* species leaves the question of the ancestral character state of the head bob behavior open to interpretation (Fig. 8a). The head bob behavior is apparently lacking in both *C. multicinctus* (also Clade 2) and in *C. ornatissimus* (Clade 3). In addition, preliminary EMG experiments on *C. multicinctus* demonstrate activity of the ventral portion of the anterior epaxial muscles lateral to the anterior swim bladder horns during the production of the body motion sound (Boyle and Tricas, unpublished data). This muscle activity pattern appears to be most similar to that observed for the nearby region of the hypaxial muscles in both *Hemitaenichthys* (Boyle and Tricas 2010) and *Heniochus* (Parmentier et al. 2011). Further kinematic, anatomical, and electromyographic analyses are needed to test the hypotheses that the head bob sound is a shared trait nested deep within the butterflyfish phylogeny, that it was lost at least once in the bannerfishes and twice in *Chaetodon*, or that it has evolved in parallel in these groups.

In contrast to the head bob behavior, the most distinctive acoustic behavior in *Chaetodon* is the tail slap, which is not yet reported in the bannerfishes. Statistical models that use currently available data to reconstruct the ancestral character states for the tail slap behavior show that this character may have existed in the ancestors of the *Chaetodon* clade (Tricas and Boyle 2015a). However, the existence of the tail slap behavior in the common ancestor of both the bannerfishes and *Chaetodon* can-

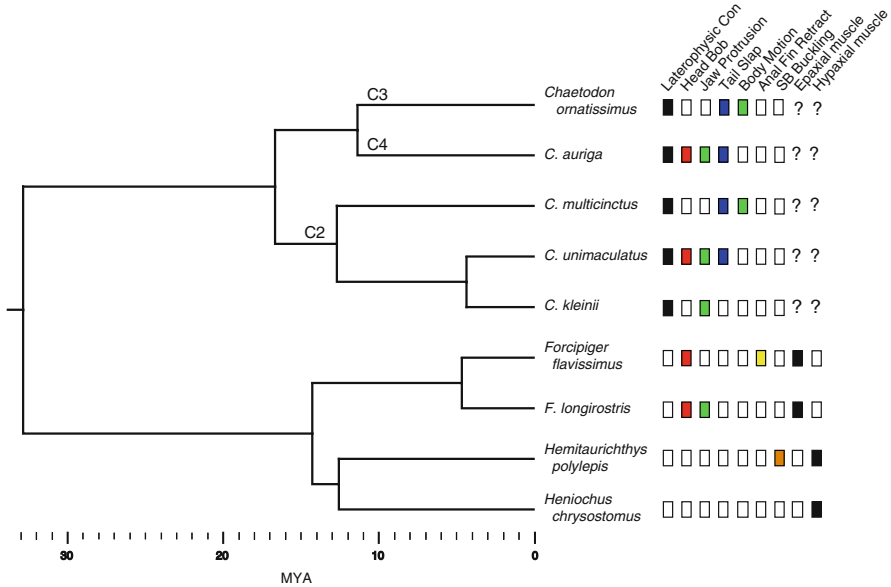


Fig. 7 Character states associated with sound production for nine species in the two major butterflyfish clades. In the bannerfish clade (*bottom*), the head bob sound is known so far only for *Forcipiger* and involves epaxial muscle activity. In contrast, sound production by *Heniochus* and *Hemitaurichthys* does not include the head bob motion and involves the hypaxial muscles. A pronounced head bob sound occurs in *Chaetodon* species (*top*), including clade 4, not clade 3, and was variable among species in clade 2. Note the frequent but not consistent linkage between the head bob and jaw protrusion movements. Of note, the tail slap behavior is found only in *Chaetodon* and is represented in clades 2–4. The box matrix below the sound character traits indicate the presence (*filled*) or lack (*open*) for each species. ? verification of muscle activity remains to be tested, *C* clade, *Con* Connection, *MYA* million years ago. Supplemental data from other sources are included for the laterophytic connection (Smith et al. 2003), *Forcipiger* (Boyle and Tricas 2011), *Hemitaurichthys* (Boyle and Tricas 2010), and *Heniochus* (Parmentier 2011). The phylogeny and clock estimates were taken from Bellwood et al. (2010). From Tricas and Boyle (2015a)

not be predicted without data from more species (Fig. 8b). This points to the need for studies on *Prognathodes* (the sister genus to *Chaetodon*), coralfishes (*Amphichaetodon*, *Coradion*, *Chemonops*, and *Chelmon*), and chaetodontid outgroups such as the pomacanthids (angelfishes) and ephippids (spadefishes).

4 The Butterflyfish Ear and Lateral Line in the Reception of Acoustic Stimuli

The discovery and characterization of natural sounds produced by chaetodontids make it possible to form and test hypotheses about how these stimuli are encoded by the ear and/or lateral line, and to evaluate the effect of the swim bladder horns on

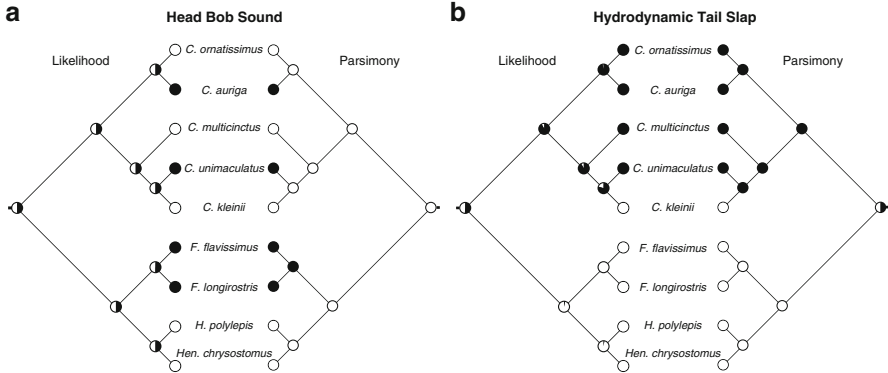


Fig. 8 Ancestral state reconstruction of two acoustic behaviors used during social interactions in butterflyfishes. **(a)** The head bob acoustic behavior occurs in both *Chaetodon* and *Forcipiger* with an equivocal likelihood for it as the ancestral state (*left*), and the possible independent evolution among clades in the parsimony model (*right*). **(b)** The tail slap behavior is so far observed during social interactions only by *Chaetodon* species and produces a very low frequency acoustic stimulus that is directed towards the receiver fish. It is not yet documented in the bannerfish clade and both the likelihood (*left*) and parsimony (*right*) models are equivocal on the presence of this trait in the common ancestor. The darkened portion of the circles indicates the probability that the trait is present at each node. *C* *Chaetodon*, *F*. *Forcipiger*, *H*. *Hemitaurichthys*, *Hen*. *Heniochus*. From Tricas and Boyle (2015a)

hearing sensitivity in *Chaetodon* species. Butterflyfishes are diurnally active in the clear waters of coral reefs and exhibit numerous forms of complex social and mating behaviors that include monogamous pairing, harem mating systems, solitary behavior, and aggregation or schooling (Reese 1975; Hourigan 1989; Yabuta and Berumen 2014). A recent field study shows that while visual signals are used for recognition of conspecifics and other behaviors in these colorful fishes (see Sect. 1), chemical cues are also required for the discrimination of mates from non-mates (Boyle and Tricas 2014). In this section, we first review the basic features of underwater acoustic fields and how they are likely encoded by the fish auditory and lateral line systems. We then interpret in more detail how the butterflyfish ear and lateral line systems likely encode their biologically relevant acoustic signals that they produce during social interactions.

4.1 The Acoustic Field: Hydrodynamic Particle Motion and Sound Pressure Stimuli

The acoustic field of an underwater sound includes a hydrodynamic flow component in close proximity to the source that can accelerate the body of a nearby receiver and directly stimulate the inner ear (Kalmijn 1988; Braun and Grande 2008). During the

production of sounds such as the tail slap, head bob or body pulse in *Chaetodon*, and the head bob or anal fin pulse in *Forcipiger* (see Sect. 3), a local hydrodynamic flow is generated by the displacement of the adjacent water mass. Directional motions of the body produce a polar hydrodynamic flow field that could generate a whole body acceleration of a nearby fish and thus stimulate its ear depending on the amplitude, direction, and distance of the acoustic source. At very short distances of a few body lengths, the hydrodynamic flow also produces a pressure gradient across the surface of the receiver fish that may stimulate the lateral line system to provide additional information about stimulus direction and intensity (Schellart and Popper 1992; Hawkins 1993; Webb 1998; Braun and Coombs 2010). At greater distances, sound pressure waves penetrate the body of a receiving fish and may set into motion the walls of the gas-filled swim bladder and swim bladder horns of *Chaetodon*, which secondarily induce local particle motions in the ear (Fletcher and Crawford 2001; Schellart and Popper 1992; Tricas and Boyle 2015b) and presumably in the lateral line canals in the vicinity of the LC (Webb et al. 2006).

4.2 Stimulation of the Ear in Chaetodon and the Effect of the Swim Bladder Horns

Several lines of evidence from data obtained in the laboratory by the auditory evoked potential (AEP) technique (which estimates hearing sensitivity thresholds to short tone stimuli) indicate that all butterflyfishes species tested to date are sensitive to the hydrodynamic flow component (particle acceleration) of an acoustic field, and that the auditory sensitivity of *Chaetodon* is enhanced by coincident sound pressure stimuli that are mediated by the gas-filled swim bladder horns (Tricas and Boyle 2015b). Sensitivity to hydrodynamic particle acceleration is indicated for *Forcipiger* (which lacks swim bladder horns) by higher stimulus thresholds at all frequencies compared to that for all tested *Chaetodon* species, and these curves converge at the lowest stimulus frequency of 100 Hz (Fig. 9). The best frequency sensitivity of *Forcipiger* to particle acceleration was at the lowest test frequency of 100 Hz (Fig. 9b), which is predicted for particle acceleration sensitive species (see Ladich and Fay 2013 for discussion). None of the hearing thresholds for *Forcipiger* increased (or changed) following deflation of its gas-filled swim bladder, which would be required for the transduction of sound pressure stimuli to stimulate the ear (Fig. 10a). A relatively low absolute sensitivity to sound pressure for all butterflyfishes is indicated by their apparently much higher AEP thresholds compared to species with anatomical specializations for reception of sound pressure stimuli such as the Weberian apparatus (Kenyon et al. 1998; Ladich 1999; Amoser and Ladich 2005; Lechner and Ladich 2008), anterior swim bladder horns and otic bullae, or a suprabranchial organ (Ladich and Yan 1998). Further, the lowest particle acceleration threshold levels in this low frequency band for butterflyfishes ranged from

about 70–85 dB re: $1 \mu\text{m s}^{-2}$ (Fig. 9b), which is similar to that reported for a marine damselfish (*Chromis*) and goby (*Gobius*) that lack auditory specializations for sound pressure sensitivity (Wysocki et al. 2009).

Comparison of butterflyfish audiograms also shows evidence for sensitivity to sound pressure and the resultant enhanced hearing capabilities in *Chaetodon*. The maximum response frequency of 1000 Hz for some *F. flavissimus* (which lacks swim bladder horns) is considerably less than the 1700–2000 Hz maximum observed for *Chaetodon* species (which have swim bladder horns and an LC, Fig. 9). An extended upper frequency range of hearing is common for pressure sensitive fishes (see Ladich and Fay 2013). Recent comparative AEP experiments on cichlid genera show that species with anterior swim bladder horns have improved auditory sensitivities of 20–40 dB (SPLs) at frequencies of 0.5 to 1 kHz (Schulz-Mirbach et al. 2012), which is higher than the improvement in hearing sensitivity for *Chaetodon* (10–15 dB) compared to *Forcipiger*. In addition, the frequency of lowest hearing thresholds (best frequency) in species sensitive to sound pressure is predicted to be greater than 100–200 Hz (Ladich and Fay 2013) and this is best seen at 600 Hz for *C. multinctus* (Figs. 9 and 10c). Experimental displacement of gas from the swim bladder horns (by the injection of gel) in both *C. multinctus* (LC variant Ind1) and *C. auriga* (LC variant Dir1) decreased auditory sensitivity (increased thresholds) in the low pass 200–600 Hz frequency range and variably among species at higher frequencies (Fig. 10c, d). Removal of gas from the swim bladder horns and body in *Chaetodon* species increases their hearing thresholds much closer to that of *Forcipiger* (Fig. 10b–d). Combined, these findings support the hypothesis that all butterflyfishes are primarily sensitive to hydrodynamic particle acceleration and that hearing sensitivity and frequency range are enhanced by the transduction of sound pressure stimuli mediated by the swim bladder horns in *Chaetodon* species with either Direct or Indirect LC's.

Enhanced frequency sensitivity in *Chaetodon* may facilitate acoustic communication. The frequency band of best sensitivity to sound pressure stimuli at 200–600 Hz overlaps the frequency spectrum of the body motion pulse in *C. multinctus* and *C. ornatissimus*, the head bob-jaw protrusion pulse of *C. unimaculatus*, and the jaw protrusion pulse sound of *C. kleinii* (Fig. 6, Table 2, Tricas and Boyle 2015b). This match provides evidence that the swim bladder horns can enhance the perception of biologically relevant acoustic signals used in social interactions. However, enhanced

Fig. 9 (continued) measured as total sound pressure level (SPL) are similar among *Chaetodon* species with lower thresholds and an extended response range to 1700 Hz for all species and to 2000 Hz for *C. ornatissimus*. (b) Thresholds measured as particle acceleration level (PAL) show similar curve shapes to SPL audiograms. The accelerometer was not calibrated at 2000 Hz, thus that data point is lacking for *C. ornatissimus*. N =sample size of fish tested at each frequency. Fractions indicate the proportion of tested fish that showed a response. Audiograms are means and SE for thresholds for all fish tested at a given frequency in that study in order to increase sample size, increase frequency resolution and to reduce variation for overlaying of the comparative audiogram plots. From Tricas and Boyle (2015b)

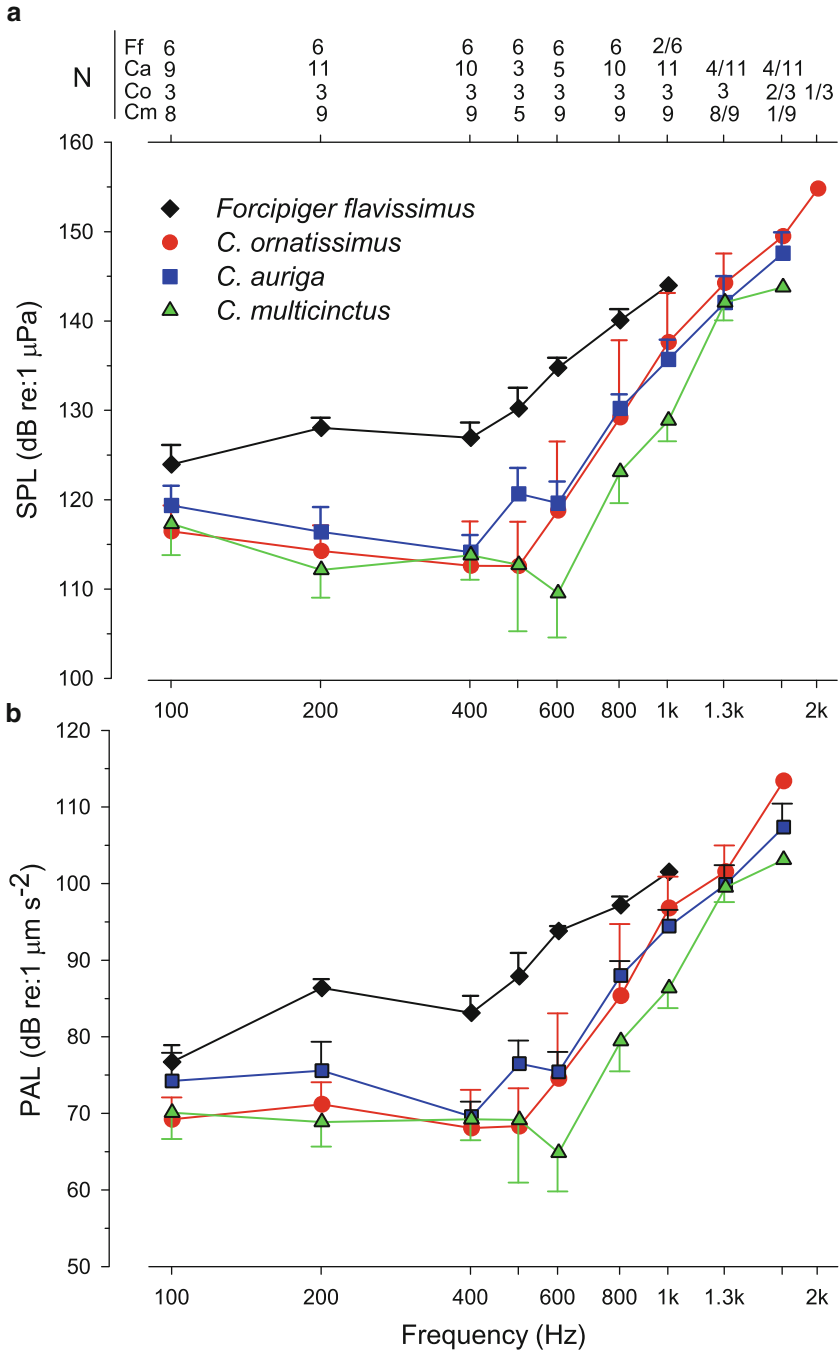


Fig. 9 Comparative hearing threshold audiograms for adult *Forcipiger flavissimus* and three *Chaetodon* species as measured by the auditory evoked potential technique. (a) Hearing thresholds

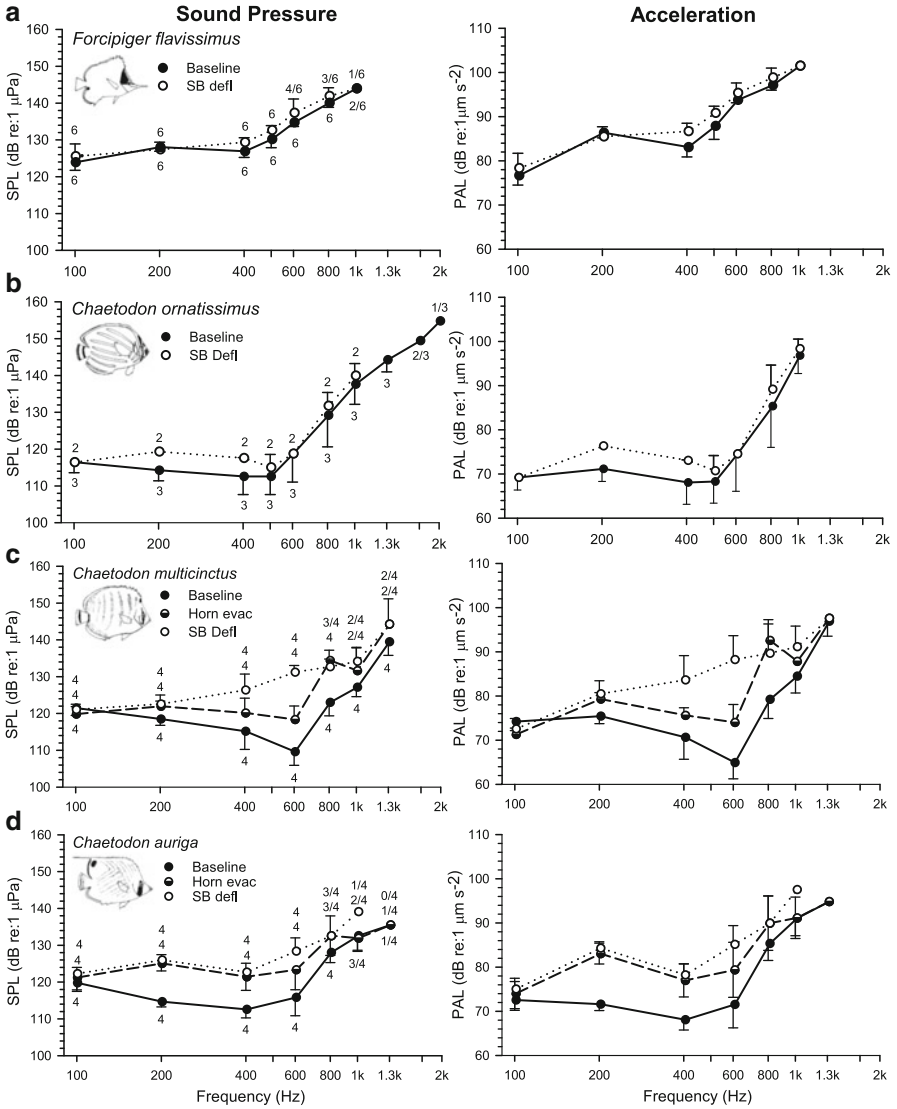


Fig. 10 The effect of the gas-filled swim bladder horns and chamber on hearing sensitivity in *Chaetodon* with different LC morphologies as determined by the auditory evoked potential (AEP) technique. (a) *Forcipiger flavissimus*, which lacks an LC and swim bladder horns (see Fig. 5c) shows little change in normal AEP threshold (solid circles) following deflation of the swim bladder (open circles). (b) *C. ornatissimus* has short swim bladder horns with an indirect connection to the LC (see Fig. 4c) that we were not able to manipulate. The baseline thresholds extended to 2000 Hz and appear to increase by approximately 5 dB in the 200–400 Hz band following deflation of the swim bladder. (c) *C. multinctus* has long swim bladder horns with an indirect connection to the LC (see Fig. 5e). Baseline thresholds increased in the 200–600 Hz band after gas was evacuated from the swim bladder horns (half-filled circles) with a maximum increase of 10 dB at 600 Hz.

hearing sensitivity in *C. auriga* does not match the lower frequency band of the only sound (head-bob jaw-protrusion) recorded to date for this species in the laboratory. It is possible that higher frequency sounds are produced in the field by *C. auriga* as observed in *C. ornatissimus* (Tricas and Boyle 2014). In addition, a biological function, if any, for the extended frequency range of hearing (up to 2 kHz) for some *Chaetodon* sound types remains to be demonstrated. In addition, the 200–300 Hz band of best sensitivity in late larval and juvenile spotfin butterflyfish, *C. ocellatus* (Webb et al. 2012), is also well below the upper 1–3 kHz range reported for species highly sensitive to sound pressure (reviewed by Ladich and Fay 2013), thus the potential use of sound pressure stimuli by larval butterflyfish may be more limited in bandwidth.

Detailed morphological studies of the ear in *Forcipiger flavissimus* and in several *Chaetodon* species with different LC variants confirm that there is no intimate association of the swim bladder horns with the otic capsule, or notable modification of the ear (Webb et al. 2010). However, the swim bladder horns of both *C. auriga* and *C. multicinctus* are long and have similar lengths when corrected for body size (Woods 2006). Further, the swim bladder horns of *C. multicinctus* are closer to the ear (1 mm) than those in *C. auriga* (2 mm). The proximity of the horns to the ear and the shape of the swim bladder horns in species with Indirect LC variants may explain the stronger effect of the horns on auditory sensitivity in *C. multicinctus* (and likely other species with Indirect LC variants) than in *C. auriga* (and other species with Direct LC variants, Woods 2006). Subsequent evacuation of gas from the swim bladder further reduced hearing sensitivity in *C. multicinctus*, but not in *C. auriga* (Fig. 10; Tricas and Boyle 2015b). Of particular interest is that the highest frequency sensitivity found among butterflyfishes (2 kHz) was observed in *C. ornatissimus*, a species with short swim bladder horns (LC variant Ind2) that approach the ear to within a distance of about 1 mm (Woods 2006). Further modeling and experiments are needed to demonstrate the frequency-dependent displacement amplitudes of the swim bladder horns in three axes that are caused by sound pressure stimuli, and to determine their physical contribution to the extended hearing sensitivity and frequency range of *Chaetodon*.

←
Fig. 10 (continued) Subsequent deflation of the swim bladder demonstrated further threshold increases most notable at 600 Hz. **(d)** *C. auriga* has long swim bladder horns with a direct connection to the LC. Baseline thresholds increased by about 10 dB at 200–600 Hz after gas was evacuated from the swim bladder horns and swim bladder. AEP threshold data are provided in relation to sound pressure (*left column*) and particle acceleration (*right column*). Data are means and SE among individuals. Numbers at circles indicate sample size at each test frequency, or fraction of test subjects for which an AEP response was recorded. From Tricas and Boyle (2015b)

4.3 Stimulation of the Lateral Line System in Chaetodon and the Potential Effect of the Swim Bladder Horns and LC

Body motions that generate sound produce dipole or higher order hydrodynamic flow fields that can be directed towards a receiver fish. Butterflyfishes have a well-developed set of cranial and trunk lateral line canals (and presumably superficial neuromasts on the head and trunk) that can respond to these hydrodynamic stimuli. In addition to stimulating the ear by whole body accelerations (as described above), such hydrodynamic flows generated by body motions produce steep pressure gradients across the skin of the receiver that can stimulate the lateral line system at distances within a few body lengths (Coombs and Montgomery 1999). Weak tail slaps by *Chaetodon multicinctus* create slow fluid vortices that impinge on the skin of the receiver fish (Hanke et al. 2008) and potentially provide information on the intensity and frequency components of water velocity via superficial neuromasts and acceleration via canal neuromasts (as defined by Kroese and Schellart 1992; Weeg and Bass 2002). The somatotopic organization of these hydrodynamic mechanoreceptors can potentially provide direction and distance information for social stimuli as demonstrated for the detection of stimuli generated by prey (Coombs et al. 1996). During territory border conflicts that occur among pairs in several butterflyfish species (Hourigan 1989; Tricas 1989; Tricas et al. 2006) such lateral-line mediated directional information may be complementary to visual and auditory cues and provide unambiguous directional information, as proposed by Braun et al. (2002) and Coffin et al. (2014). In addition, the mechanosensory lateral line system may also be activated by sound pressure that is transduced by the LC (see Sect. 2.1). Thus, coincident sound pressure information may be received by both the ear and a portion of the lateral line canal system in the vicinity of the LC, while different features of the hydrodynamic flow field are detected by the ear and the greater lateral line system. However, the transduction of sound pressure stimuli to the mechanosensory lateral line via the LC awaits experimental confirmation. Experiments that involve the pharmacological or physical ablation of neuromasts are also needed to determine the relative contribution of the lateral line and auditory systems to the perception of an acoustic field (Higgs and Radford 2013).

5 The Behavioral Ecology of Acoustic Communication in Butterflyfishes

Sound production provides important information for social interactions in a wide range of fish species (Myrberg and Lugli 2006, reviewed by Ladich and Myrberg 2006). Honest signals provide accurate information about the condition of the signaler (Fitch and Hauser 2002) and can contribute to a dependable assessment of the quality of an opponent. Evidence is accumulating that the acoustic stimuli generated by butterflyfishes contain reliable information about the size or motivation of the signaler, which may be important for decision-making in social contexts as reported

for other fishes (Ladich and Fine 2006; Amorim 2006). For instance, the low frequency (9–69 Hz) aggressive tail slap and body pulse (137–184 Hz) sounds produced by *C. multinctus* during social interactions increase in intensity with body size (Tricas and Boyle 2015a), and a similar relationship between sound intensity and body size was reported for the head bob sound in *F. flavissimus* (Boyle and Tricas 2011). A preliminary independent contrast analysis of the continuous variables that define sound characteristics (duration, peak frequency, median frequency, bandwidth, and intensity) produced by the tail slap in *Chaetodon* and other sound types in *Forcipiger* shows evidence for correlated changes between sound duration and sound pressure intensity (Tricas and Boyle 2015a). This indicates a possible evolutionary trend for the generation of loud and long pulse sounds by butterflyfishes, although data on additional species are needed. Members of both *Forcipiger* and *Chaetodon* engage in contests over territories to protect mates and food resources, so signals that convey information on body size may reduce the risk of injury (e.g., lacerations, lost scales, broken spines) that commonly occur during escalated disputes. Reinforcement of information on relative body size conveyed by visual and acoustic signals may also be used to maintain low levels of aggression, as commonly seen among neighbors in stable territories (Hourigan 1989; Tricas 1989; Roberts and Ormond 1992). In *C. multinctus*, acoustic information that is correlated with body size may also benefit individuals because body size is correlated with the size of a feeding territory (Tricas 1989). Thus, sounds and other sensory cues may be important indicators of resource-holding potential and be factors in the evolution of their social behavior.

In summary, sound production between mates and between conspecific competitors is common in *Chaetodon* and appears to be widespread among butterflyfishes. Single pulse or pulse train sounds are produced during non-aggressive interactions with mates, initial social interactions with unfamiliar conspecifics, aggressive interactions with competitors and during courtship. Several species produce multiple sound types with a frequency range from infrasound to >1 kHz. Analysis of kinematics correlated with sound production indicates that sound production mechanisms vary substantially among chaetodontid taxa. These sounds are likely to provide useful information about size or quality of the individual and have critical implications for butterflyfish ecology and fitness. Additional kinematic and electromyographic analyses of sound production in other butterflyfish genera (e.g., *Amphichaetodon*, *Coradion* and *Chelmon*) and angelfishes (family Pomacanthidae, a hypothesized sister group to Chaetodontidae) are needed to more completely address the origin and evolutionary diversification of sound production in butterflyfishes.

6 The Acoustic Soundscape of Coral Reefs and Implications for Butterflyfish Acoustic Communication

Ambient acoustic noise is common in both freshwater and marine habitats and can decrease the ability to detect biologically relevant sounds especially in taxa that possess anatomical specializations for enhancement of hearing sensitivity and frequency range (see review by Ladich 2013). The coral reef environment is replete

with acoustic noise from abiotic and biotic sources that spans the frequency range of butterflyfish sounds and their auditory sensitivity.

6.1 Sources of Ambient Noise

Low frequency background noise (<10–100 Hz) originates primarily from abiotic sources such as wind, waves, and tidal streaming (Wenz 1962; Urick 1983). The complex physical structure of a coral reef also contributes to multiple sources, forms and features of acoustic noise within the sub-habitats inhabited by different butterflyfish species. For example, wind-driven ocean swells with surface chop pass over the outer reef where planktivorous butterflyfishes feed in the water column during daylight hours, and where corallivores and other benthic invertebrate feeding butterflyfish species forage in long-term territories and in larger home ranges on the bottom. Onshore swells break onto the shallow outer reef crest and impact the substrate with severe broadband acoustic noise, substrate vibrations, and strong low frequency hydrodynamic turbulence that can affect resident butterflyfish species that inhabit shallower areas of the reef. Wave action and surge then flow over the reef flat into back reef lagoons where other butterflyfish species have long-term home ranges. Thus, ambient noise (from both hydrodynamic and sound pressure sources) is expected to vary considerably among different habitats and will have differential effects on the perception of sounds produced for social communication. In addition, ambient noise at the higher end of the hearing range of butterflyfishes (e.g., 100 to >1000 Hz) is generated by biological sources such as other reef fishes (Cato and McCauley 2002; McCauley and Cato 2000; Tricas and Boyle 2014), snapping shrimp, and other invertebrates (Cato 1978; Lammers et al. 2008). Seasonal ambient sounds generated by migratory marine mammals such as the humpback whale in offshore Hawaiian waters have intense fundamental frequencies (reviewed in Au and Hastings 2008) that are also in the hearing frequency range of butterflyfishes. Thus both abiotic and biotic sources of ambient noise are expected to vary across time in intensity and spectra among different habitats on a coral reef, and to have potential effects on butterflyfish acoustic communication.

6.2 Ambient Noise, Sound Production and Hearing in Butterflyfish Territories

Acoustic recordings on Hawaiian reefs show that the intensity of ambient noise near the substrate on the outer reef overlaps in the frequency domain with sounds used for communication by butterflyfishes (Tricas and Boyle 2015b). Field measurements of average ambient noise levels during an afternoon with modest onshore winds were 10–15 dB higher in shallow water territories of *C. multicinctus* (at <6 m

deep) compared to those in deeper waters (Fig. 11). This difference in total noise with depth was most notable at frequencies of 10–500 Hz, which overlaps with the low frequency spectra of representative tail slap, body shake, and body pulse sounds produced by *C. multicoloratus*, as well as with several low frequency sounds produced by other species (e.g., *C. ornatissimus* and *F. flavissimus*) that live on the same reef (see Fig. 5). Calculated sound pressure levels in the frequency band of the tail slap sound decrease with depth whereas ambient noise in the higher frequency band of the body pulse sound did not (Fig. 12a). Subsequent estimation of the signal to noise ratio (SNR) of each sound band at different territory sites showed an increase in SNR with increased territory depth for the tail slap sound, but not for the body

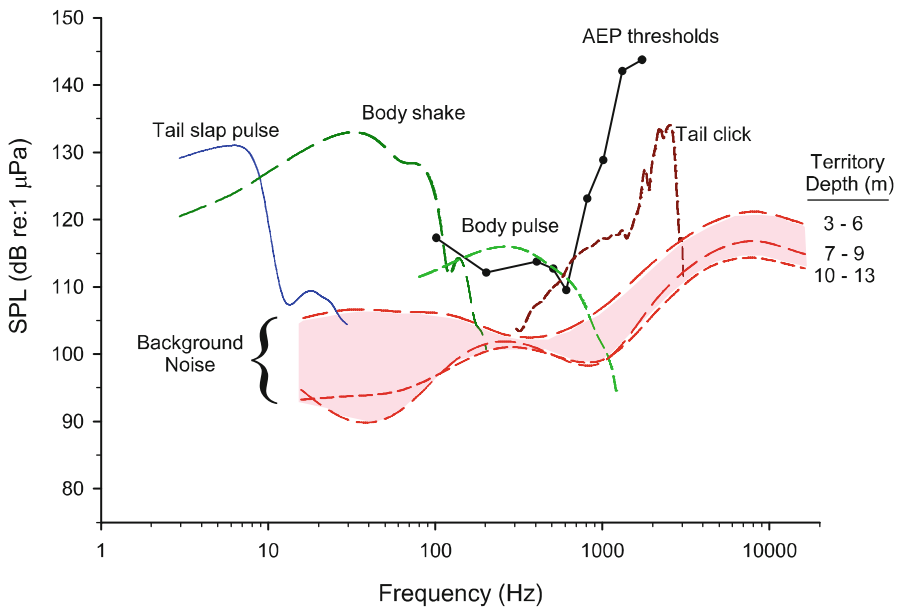


Fig. 11 Hearing thresholds, four representative vocalization intensities and the ambient background noise environment for acoustic social communication by *Chaetodon multicoloratus*, in coral reef territories at Puako Reef, Hawai‘i. Fish AEP thresholds to tone stimuli from 100 to 2000 Hz were determined in the lab and show a low pass sensitivity below 600 Hz (black solid dots). Curves for the power spectrum of four representative sounds (tail slap, body shake, body pulse, and tail click) were determined by fast Fourier transforms of sound waveforms. The low frequency band of best hearing sensitivity is nearest to the band of the body pulse sound used commonly in close social interactions (light green dashed curve). The infrasound tail slap (solid blue line curve) and body shake (dark green dashed curve) pulses are produced during agonistic interactions and have peak frequencies <100 Hz, but sensitivity to these low frequency stimuli remain to be experimentally determined. The high frequency tail click sound (dark red dashed curve) is likely beyond their hearing capabilities. The range of average ambient background octave noise band (red shaded area) is shown for 11 territories at depths from 2.5 to 12.8 m and illustrate the general higher background noise levels that occur within territories in shallow habitats ≤ 6 m deep. The background noise levels in the band <20 Hz remain to be characterized for most coral reef environments. From Tricas and Boyle (2015b)

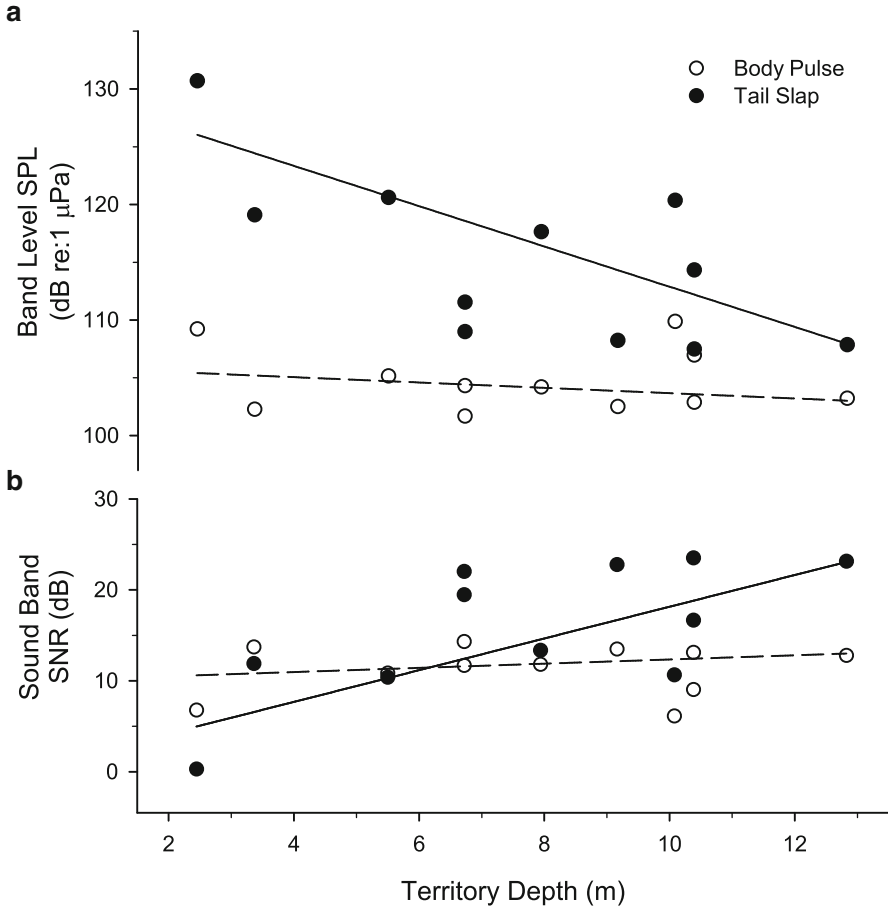


Fig. 12 The potential impact of sound-band-specific ambient noise on the transmission of communication sounds in coral reef territories of *Chaetodon multicinctus*, at Puako Reef, Hawai'i. **(a)** Background noise band level sound pressure within the predominate frequency range (top 6 dB of the power spectrum) of the body pulse (21–414 Hz) and tail slap sounds (2–18 Hz) indicate that the background noise levels change with territory depth for the tail slap but not for the body pulse sound. **(b)** Signal-to-noise ratio of signal sound amplitudes near the source to ambient noise levels for the frequency bands of the body pulse and tail slap sounds at different territory depths. Perception of the tail slap but not the body pulse sound should improve at deeper territory locations. From Tricas and Boyle (2015b)

motion sound (Fig. 12b). These estimations indicate that the tail slap sound, which is used in agonistic interactions with conspecifics, may be a more effective communication signal in deeper territories. Deeper areas of a reef may provide higher quality food (coral) resources and a quieter environment (with lower swell and wave action) that would benefit acoustic communication used in defense of food resources. It remains to be demonstrated how the distances required for effective acoustic communication among conspecifics may be affected by ambient noise, and whether any

masking effects occur given their apparent low absolute hearing sensitivity (see Sect. 3). Nonetheless, effective acoustic communication is degraded at large distances in a noisy reef environment and the signal to noise ratio is enhanced at the short distances of separation found among individuals of most butterflyfish species (Tricas and Boyle 2015b).

This analysis is founded on the interpretation of acoustic communication within the butterflyfish's natural habitat. However, more studies of sensory ecology are needed in which local ambient noise levels and frequency spectra are considered across different time scales (diel, lunar, season, annual), among sub-habitats, and with respect to natural acoustic signals and hearing capabilities of butterflyfishes in order to determine the nature of the constraints on acoustic communication. For example, higher signal-to-noise ratios at lower frequencies of <1–100 Hz are expected to occur on leeward reefs, which normally experience low wind velocity and wave conditions when compared to windward reefs, which are subject to stronger and continuous trade winds. Furthermore, recordings of ambient noise levels made on reefs (e.g., Simpson et al. 2005; Radford et al. 2014; Tricas and Boyle 2015b) have not yet distinguished between the hydrodynamic (surge/water turbulence) and sound pressure components of ambient sounds, which will also differ, respectively, with habitat and depth. In addition, distinct spectral and intensity signatures are found in different coastal habitats, and it is suggested that these may provide important navigational cues for larval reef fishes (Kennedy et al. 2010; Radford et al. 2014). However, it should be noted that the swim bladder horns of *C. ocellatus*, which impart sound pressure sensitivity in adult *Chaetodon*, do not develop until larvae have already moved into potential settlement areas. Thus, they do not likely play a role in interpreting acoustic stimuli that may be involved in finding suitable settlement sites (Webb et al. 2012).

7 Conclusions and Future Work

The study of the ecology and social behavior of butterflyfishes has provided an exciting context for the discovery and interpretation of auditory anatomy, auditory physiology, and the evolution of sound production and sensory systems. Some important questions that should guide future research are detailed below.

1. Sound production and hearing, in addition to vision and chemoreception, are important in the complex social behavior of butterflyfishes. The head bob acoustic behavior appears to be a shared character of several species in the bannerfish and *Chaetodon* clades, whereas the tail slap acoustic behavior appears to be a derived character in *Chaetodon*. The occurrence of sound production and sound communication in butterflyfish genera other than *Chaetodon* indicates that these capabilities evolved in the family prior to the evolutionary origin of *Chaetodon* and the LC, which is a defining character of that genus. Furthermore, the evolution of swim bladder horns and the laterophysic connection (LC) in *Chaetodon* was not

accompanied by modification of the ear or otic capsule. Thus, the evolution of acoustic anatomy, physiology, and behavior has a complex and interesting history that deserves more study. Future studies on sound production in other chaetodontid genera and outgroups are needed to better understand the evolution of butterflyfish acoustic behaviors.

2. The sounds produced by butterflyfishes are diverse in form, frequency and with respect to their correlated kinematic (motor) patterns. This indicates that a variety of sound production mechanisms are present that are open for more investigation. In addition, the production of very low frequency sounds (<1–30 Hz) requires that the role and reception of “infrasound” for social communication be further considered in butterflyfishes and other fish taxa.
3. All butterflyfishes are sensitive to the hydrodynamic flow component of an acoustic field. In *Chaetodon*, the swim bladder horns also respond to sound pressure stimuli that enhances their auditory sensitivity from 100 to 600 Hz and extends their absolute hearing range up to 2 kHz. Studies on sound pressure sensitivity are needed on more species to define the potential roles of LC types and variants in the enhancement of hearing.
4. The physical motion of the wall of the swim bladder horns at the medial opening of the supracleithrum (which defines the LC) and the resultant activation of adjacent canal neuromasts (hypothesized by Webb 1998; Webb et al. 2006) remain to be determined.
5. The importance of the swim bladder horns in affecting auditory sensitivity and frequency range in *Chaetodon* begs the question of what other groups of fishes, and coral reef fishes in particular, may have evolved adaptations for the enhancement of auditory capabilities in noisy reef habitats.
6. The coral reef environment is replete with abiotic and biotic noise that overlaps with the spectrum of butterflyfish sounds and their auditory sensitivity. The close affiliative social behaviors demonstrated by most butterflyfishes facilitate acoustic communication in these noisy coral reef environments and indicate that the non-visual sensory environment may influence the evolution of behavior in these fishes.
7. Studies are needed to determine the amplitude of sound pressure and hydrodynamic stimuli in the many sub-habitats of the coral reef, which are occupied by different butterflyfish species, in order to better understand the constraints on acoustic communication imposed by the soundscape.
8. The relative contributions of the ear and lateral line in the detection of different components of hydrodynamic and acoustic stimuli generated at close range (especially at low frequencies, <1–100 Hz) need to be determined. In addition, neuroanatomical and neurophysiological analyses of the central neural pathways that integrate diverse auditory (direct or via the swim bladder) and lateral line (direct or via the laterophysic connection) inputs will likely to provide novel insights into the function of these complementary acoustic modalities.

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