Journal of Zoology

Journal of Zoology. Print ISSN 0952-8369

ORIGINAL RESEARCH

Acoustic repertoire and anatomical features of the flying gurnard from the Adriatic Sea

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Keywords
grunt; marine bioacoustics; action camera; micro-CT; multimodal; sonic muscles; *Dactylopterus volitans*; sound production in fish.

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Editor: Andrew Kitchener
Associate Editor: Francesca Raffini

Received 17 June 2025; revised 6 November 2025; accepted 30 December 2025

doi:10.1111/jzo.70101

Abstract

Ray-finned fish communicate by emitting acoustic signals; however, many species have not yet been investigated for their ability to produce sound. *Dactylopterus volitans* is a marine bottom-dwelling fish occurring throughout the Atlantic Ocean and Mediterranean Sea, including the Adriatic Sea. In this study, we explored the vocal repertoire of *D. volitans* by analysing sounds opportunistically acquired by an action camera during a field survey in the south Adriatic Sea (Croatia). The acoustic repertoire was composed of two distinct sound types (Grunt A and Grunt B) produced in an alternating order. Grunt A was a harmonic sound composed of two to nine pulses that lasted around 30 ms. They were produced singly or in trains (bursts), and we could differentiate short- and long-intervals between the sounds within the bursts. Grunt A was harmonic and possessed up to six harmonics, with the peak frequency of around 225 Hz. Grunt B, composed of two to four pulses and lasting around 110 ms, had overlapping peak and fundamental frequencies (~170 Hz). In addition, we recorded several sounds of juvenile *D. volitans*. By examining the anatomy, we provide insights into the swim bladder mechanism and other anatomical features of the skull and vertebral column. The large swim bladder was separated along the midline into two rostrocaudal chambers, and the walls of each chamber were surrounded by highly vascularized intrinsic sonic muscles. The skull of *D. volitans* possessed two large openings situated posteriorly; the anterior extensions from the swim bladder fitted into these openings, hence shortening the distance between the bladder and inner ear. Our study establishes *D. volitans* as a sonic species, paving the way for future bioacoustic surveys to provide valuable insights into its status and distribution in the Adriatic Sea.

Introduction

Soniferous behaviour is ancient in vertebrates including Actinopterygii (Chen & Wiens, 2020; Rice et al., 2022). It evolved independently in multiple fish groups, and it is significantly linked to life-history traits such as territoriality and benthic lifestyle (Chen & Wiens, 2020; Ladich, 2014; Looby, Cox, et al., 2022; Rice et al., 2022). Recently, a database of sound-producing fish was created (FishSounds; fishsounds.net), highlighting that demersal and reef-associated groups contain the highest proportion of soniferous species (Looby, Cox, et al., 2022; Looby, Vela, et al., 2022). Around 1000 fish species are recognized as actively soniferous (Looby, Cox, et al., 2022; Rice et al., 2022). Interestingly, of the 169 fish families that have been examined for sound production, actively soniferous species were observed in 133 (or 78%) of them (Looby, Cox, et al., 2022). This supports the hypothesis that active sound production is a taxonomically prevalent behavioural trait among fishes (see Looby, Cox, et al., 2022).

Similarly to other soniferous animal groups, actinopterygian fish utilize sounds to acquire and transmit relevant social and biological information (Ladich, 2000, 2015; Parmentier & Fine, 2016; Raick et al., 2023; Simmons, 2003). They often produce different, sometimes species-specific, sounds for intraand interspecific communication, mainly by modifying acoustic spectro-temporal features (Amorim, 2006; Banse, Bertimes, et al., 2024; Ladich, 2014, 2015; Parmentier & Fine, 2016). Fish sound production can be associated with different behaviours such as disturbance, aggression, reproduction, or other contexts such as mobbing or cleaning mutualisms (Amorim, 2006; Banse, Lecchini, et al., 2024; Banse, Minier, et al., 2024; Fish & Mowbray, 1970; Looby et al., 2023). Indeed, fish frequently produce sounds when predators approach or during capture. These sounds can be labelled as alarm, startling, warning, distress, or disturbance sounds. From the behavioural standpoint, disturbance is the most reported context for sound production in marine subtropical fish species, as it is the easiest method to elicit sound production (Looby et al., 2023).

Dactylopteridae is a small fish family composed of marine benthic species that morphologically resemble triglids (Nelson et al., 2016). Despite similar appearance, dactylopterids are more related to seahorses and pipefishes (Betancur-R et al., 2013, 2017; Nelson et al., 2016; Song et al., 2014, 2019; Stiller et al., 2022). *Dactylopterus volitans* (Linnaeus, 1758) or flying gurnard, is a bottom-dwelling species that employs its large and vividly coloured pectoral fins to glide and to forage (Davenport & Wirtz, 2019; Fish & Mowbray, 1970; Randall, 1967). This species occurs throughout the Atlantic Ocean and Mediterranean Sea on sandy and muddy bottoms, seagrass beds, rocky areas, and coral reefs (Dulčić & Kovačić, 2020; Nelson et al., 2016). In the Croatian part of the Adriatic Sea, it was considered an uncommon species, occasionally captured as bycatch (Dulčić & Kovačić, 2020; Jardas, 1996). Nonetheless, *D. volitans* began to spread northward in recent years (Dragičević et al., 2017), and it has started to appear in fishermen's catches more frequently, even in the colder northern Adriatic (Dragičević, unpublished data). Although *D. volitans* is not a commercially significant or targeted species for fisheries, it is important from the faunistic and biological aspects of the fish community, as it inhabits threatened coastal sandy habitats and seaweed meadows, such as those formed by the endemic Neptune grass *Posidonia oceanica*.

Currently, there is a lack of descriptions of acoustic activity and sound features of *D. volitans*, except for two studies carried out by Dufossé (1874) and Fish and Mowbray (1970), which only briefly mentioned the soniferous ability of this species. Hence, this study aims to: (1) describe the sound production of *D. volitans* in the wild, (2) characterize the spectral and temporal acoustic parameters of the sounds, (3) outline the observed soniferous behaviour, and (4) provide descriptions of the swim bladder sonic mechanism and anatomical features of the cranium and vertebral column.

Materials and methods

Study area and field recordings

Diving sessions complemented by audio-video recordings were conducted in the morning hours (09:00–10:00 a.m.) of July 2021, during underwater visual censuses (UVC) in the south Adriatic Sea, at Pasjača (42°30′48.5″ N, 18°19′13.6″ E) in the Konavle region (Croatia). The UVC was part of a monitoring program aimed at detection of non-native fish species in Croatian waters (MSFD descriptor 2). The sea surface temperature was low for the period of the year (19°C; measured with Mares Pro Puck diving computer). Opportunistic recordings of *D. volitans* sounds were obtained by three divers snorkelling at depths of 3–6 m, covering *c.* 800 m^2 (40 × 20 m). *c.* 20 individuals of *D. volitans* were observed during four recordings; however, the precise number of individuals that produced sounds is unknown. The recording period falls within *D. volitans* reproductive season, which extends from late spring to early summer (Dulčić & Kovačić, 2020; Jardas, 1996). The UVC site featured a sandy bottom with scattered boulders sparsely covered by photophilic algae and patches of *Posidonia oceanica* (a few m^2 to ca. 0.4 ha). Additional recording of a juvenile fish (total length < 10 cm) was made during a SCUBA dive near Komiža, Vis Island (43°2′23.87″N, 16°5′24.99″ E; 5 m depth) on the evening of 1 October 2021, in a similar habitat.

The acoustic behaviour of *D. volitans* was recorded by actively chasing the fish. Each individual chase lasted from 20 s to 1 min, depending on how quickly the fish would flee. The chases were performed repeatedly. The distance to the fish varied between several centimetres to one meter. Sound-producing adult fish measured 25–30 cm total length (TL), and the sex of emitter was unknown. Recordings were made *in situ* using a handheld GoPro5 Black (GoPro™, San Mateo, CA, USA; 48 kHz, 16-bit; three internal microphones) in its waterproof housing. Recording ended when the fish moved beyond visual and acoustic range. Note that a recent study suggested that GoPro cameras could be useful for several underwater bioacoustics applications (Chapuis et al., 2021). The audio tracks were extracted (as .wav files) from the audio-video (mp4) recordings and used for the subsequent acoustic analysis. Recording at sea (depths >2 m) minimized issues such as reverberation, resonance or degradation compared to laboratory and tank settings (Akamatsu et al., 2002).

Sound analysis and acoustic features

The audio recordings were subsampled at 4 kHz (16-bits) and band-pass filtered (0.05–2 kHz) to improve S/N ratio. The audio recordings were aurally and visually inspected, and the detected sounds were manually analysed using Avisoft-SASLab Pro 5.2 software (Avisoft Bioacoustics, Glienicke, Germany) (1024-point FFT, FlatTop window; 100% frame). The temporal features were measured from oscillograms, while frequency features were obtained from logarithmic power spectra (FlatTop window, 512-points FFT, 96.87% overlap; frequency resolution 8 Hz). For each recorded sound, we measured the following acoustic variables: (1) sound duration (DUR, duration of the sound, in ms); (2) number of pulses (NP); (3) pulse repetition rate (PRR; NP divided by DUR and multiplied by 1000, Hz); (4) pulse duration (PD; measured from the start to the end of the pulse, ms); (5) pulse period (PP; average peak-to-peak interval of consecutive pulses, ms); (6) peak frequency (PF, the peak with the highest energy from the logarithmic power spectrum, Hz). For each harmonic (range: 1–6), we measured the frequency in Hz (variables 7–12; H_1 – H_6). (13) The number of visible harmonics (NH) within the sound was also counted. The fundamental frequency was measured (in Hz) as the lowest peak on the power spectrum.

As some sounds were produced in sequences, that is, in sound bursts, we also calculated the following: burst duration (BDUR, duration of the sound train, in ms); and number of sounds per burst (BNS). Furthermore, to characterize the rhythmicity of all the sounds produced (14), inter-onset interval (IOI, time between the onsets of consecutive sounds in ms) and the normalized pairwise Variability Index (nPVI) values were measured. The nPVI is a measure that quantifies the variability of inter-onset intervals; it ranges from 0 to 200, decreasing with more regular intervals and reaches zero with a perfect isochronous rhythm (Vieira et al., 2021).

Sound types produced by the adults were compared statistically for six acoustic variables (DUR, NP, PP, PF, H_1 and NH) by using a non-parametric Wilcoxon–Mann–Whitney test. Due to the small sample size and large discrepancies in the number of sounds per sound type, we implemented a subsampling and bootstrap (10 000 permutations) procedure to validate the significance of the results. The significance level was $\alpha = 0.05$. Statistical analyses were conducted in R, ver. 4.4.0 (R Core team, 2021).

Context of sound production

We described the ethological context associated with sound production, specifically focusing on certain body parts (head, fins, tail), by re-watching the audio-video recordings (frame by frame, five frames per sec) and annotating the exhibited behavioural events in Solomon Coder (ver. 17.0, Péter, A.).

Fish dissection and micro-CT imaging

Three individuals were studied at the Institute of Oceanography and Fisheries (Split, Croatia) and Faculty of Science (Zagreb, Croatia). An anatomical dissection was performed on one fresh specimen obtained directly from a fisherman (♀, TL = 30.7 cm, weight W = 287 g) caught in December 2021 by a beach seine near Rogoznica (Croatia) and on two additional specimens kept frozen (♀, TL = 37.2 cm, W = 518.8 g, and ♂, 28 cm, W = 241.3 g) both caught in April 2023 by a trammel net near the Island of Brač (Croatia). In each specimen, the morphology of the swim bladder was described. In addition, we cleaned the neurocranium of all three specimens by immersing it in a 10% hydrogen peroxide solution for 24 h.

Furthermore, we performed micro-computed tomography (μCT) on a single specimen of *D. volitans* (♀, TL = 30.0 cm, W = 288 g) caught near Savudrija (Istria, North Adriatic). The specimen was fixed in 10% formaldehyde for 2 months before scanning. μCT imaging was conducted using a SkyScan 1076 scanner (Bruker, Kontich, Belgium) at 36 μm voxel size, 70 kV voltage, and 140 μA current, with a 0.1 mm aluminium filter to reduce beam hardening. The sample was rotated 198° in 0.7° steps, yielding 495 projection images, and data were reconstructed with NRecon software (Bruker, Massachusetts, USA). The same individual (stored in formalin) was subsequently stained with a phospho-tungstic acid-ethanol solution (EPTA), following the manufacturer's protocol (Bruker, 2017). Phospho-tungstic acid is a soft tissue contrast agent used widely for staining coupled with high-resolution micro-CT imaging. The individual was immersed for 2 weeks, and the efficiency of staining was verified after 7 and 14 days. The 400 ml of EPTA solution was prepared by using 3 g of PTA dissolved in 100 ml of H_2O, and then mixed into 300 ml of 96% ethanol. As the fish was caught by a professional fisherman, no sampling permission was required.

No apparent sexual dimorphism was observed in the shape or size of the swim bladder or associated musculature among the dissected individuals (3♀:1♂). Because the male specimen was unsuitable for scanning and males are less abundant in the wild (sex ratio F:M ≈ 4:1; N'zi et al., 2023), μCT imaging was performed on a single well-preserved female representative of the general morphology.

Results

D. volitans produced 148 sounds during recording sessions, while exhibiting distress/disturbance behaviour during diver chase. After an initial aural inspection, we used 132 sounds presenting appropriate spectro-temporal quality and S/N ratio for characterization and acoustic analysis. We recognized two different sound types produced by *D. volitans*: 105 Grunt A sounds, which constitute the majority of the observed acoustic activity (72.9%), and 17 Grunt B sounds, which were less common (11.8%) (Fig. 1). Additionally, we recorded 22 sounds (produced singly) from one *D. volitans* juvenile (Fig. 2).

Sound diversity and acoustic features

Grunt A are drumming and harmonic sounds lasting 31 ± 6.9 ms, composed of two to nine pulses (Fig. 1, Table 1). The amplitude of the pulses gradually increased during the first two or three pulses, after which it reached a maximum and then slowly decreased. Pulse repetition rate was 127.9 ± 24.3 Hz. The pulse period ranged from 3.4 to 8.2 ms. Grunt A presented a fundamental frequency (FF, which was also H_1) of 159.5 ± 31.7 Hz and a peak frequency of 221.9 ± 83 Hz (Table 1). In several cases, the fundamental frequency was also the peak frequency, but this was not a strict rule. The bandwidth of Grunt A extended up to 1200 Hz, although most of the energy was concentrated within the 50–800 Hz frequency band (Table 1). The harmonic nature of Grunt A is evident in spectrograms; the number of harmonics varied from one to six, with frequencies of the harmonics presented in Table 1.

Grunt B are low-frequency sounds composed of two to four pulses (further divided on cycles) and lasted 108.8 ± 28.6 ms (Fig. 1, Table 1). Pulse duration was 22.0 ± 6.2 ms, and pulse period varied from 23.9 to 63.1 ms. Each pulse had 3.2 ± 0.9 cycles and had cycle repetition rates (which indicate

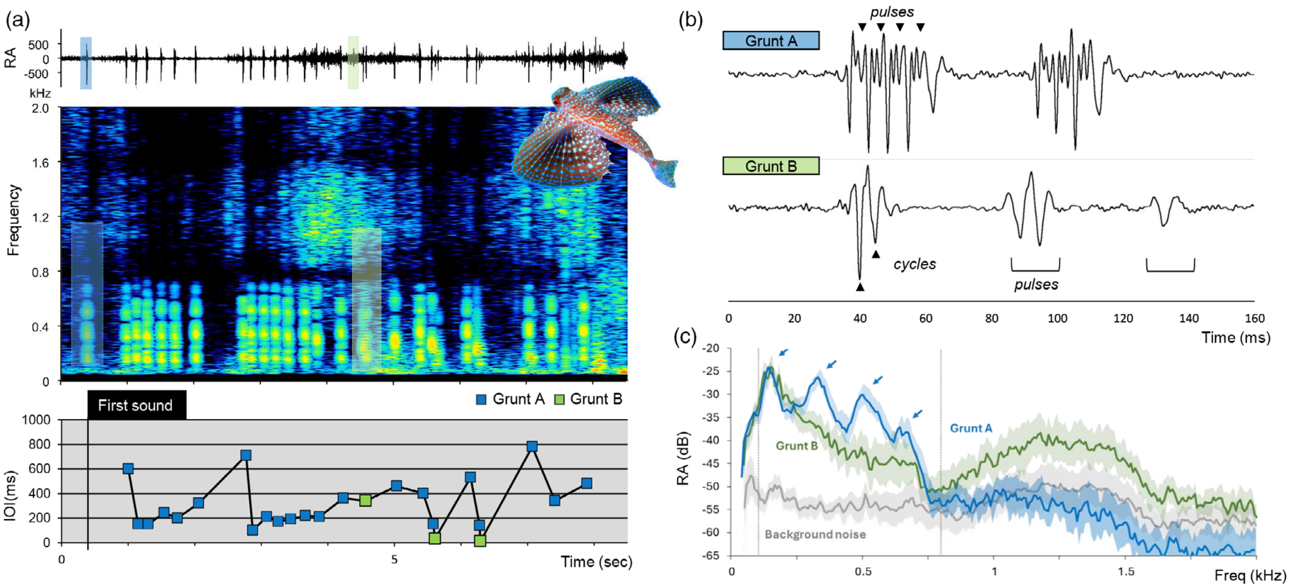

Figure 1 Acoustic activity in *Dactylopterus volitans*. (a) Sound production of *D. volitans* recorded at the Adriatic Sea. The oscillogram (upper part) and spectrogram (middle part) highlight the repeated pattern sound production. In the lower part, the sound inter-onset intervals (IOI) are presented for this short clip of the recording (lasting around 8 s). On the spectrogram, acoustic components below 800 Hz consist of fish sounds (here displayed as multi-harmonic sounds, blue rectangle – Grunt A; green – Grunt B), and everything above the 800 Hz relates to underwater noise. Warmer colours indicate higher sound pressure level. Spectrogram parameters: FFT 512 points, Hamming window; 100% frame size; 96.87% overlap; resolution: 4 Hz. Fish photo: Luis Perez Berrocal (source: iNaturalist). (b) Expanded oscillograms of two sound types: Grunt A (two sounds composed of five and four pulses, respectively) and single Grunt B composed of three pulses (further composed of several cycles), highlighting the temporal variability and pulsed structure of the sounds. (c) Averaged power spectra of Grunt A (blue line, $n = 15$) and Grunt B (green line, $n = 10$) produced by *D. volitans* and of the underwater background noise (grey line, $n = 15$) measured on the recordings. Thin lines represent the 95% confidence interval. Two dashed grey lines indicate the low-frequency region (from 0.1 to 0.8 kHz) dominated by the fish sounds, with sound level above the background. Notice how the sound level of the spectra increases between ca. 0.8 and 1.5 kHz, which seems to be related to the diver breathing sound. Arrows indicate the most important frequency peaks of Grunt A. RA, relative amplitude.

the pattern of cycle production within pulse) of 158.4 ± 41.1 Hz. Cycle duration within each pulse was 6.7 ± 2.2 ms, while the cycle period was 6.9 ± 3.9 ms. Grunt B was lower in frequency, with peak frequency ranging from 74.5 to 258.1 Hz. Peak frequency overlapped with the values of fundamental frequency (FF or $H_1 = 167.7 \pm 40.4$ Hz). Grunt B had one to three harmonics (Table 1).

We recorded 22 sounds from a single juvenile, but extracted spectro-temporal features only from ten signals. Sounds lasted 149.6 ± 33.9 ms, were composed of 4–9 pulses, having the pulse duration of 12.0 ± 1.7 ms and pulse period of 26.1 ± 2.3 ms. Peak frequency was 283.9 ± 14.4 Hz and the sounds were also harmonic in nature, with 3–5 harmonics (Fig. 2; Table 1).

Grunt A and Grunt B differed significantly in five acoustic variables (DUR, NP, PP, H_1 and NH; Mann–Whitney-Wilcoxon test, W = 0–1702; $P < 0.05$; $n_{\text{gruntA}} = 102$; $n_{\text{gruntB}} = 17$; Fig. 3), but not in PF ($W = 1049$, $P > 0.16$; Fig. 3). However, after subsampling the dataset and permutation-based test (10 000 randomizations), it turns out that NP and NH differ significantly ($P < 0.05$), while the remaining variables were not significant ($P > 0.05$). Juvenile sounds were not included in the statistical analyses due to the availability of only a single individual.

Calling activity and rhythmicity

Sounds were produced with a variable sound rate (from 0.1 to 5.8 sounds per sec), which usually increased when the diver approached the fish at close distance. Grunt A was more common, often with sounds being produced in trains or bursts (Fig. 4). Grunt A bursts ($n = 45$) lasted on average 204.8 ± 245.3 ms and were composed of two to seven grunt sounds (Table 1). Occasionally, single grunts were observed; 10 grunts were considered isolated when the IOI, relative to the previous and subsequent sounds, was greater than *c.* 250 ms (Fig. 4). Within a Grunt A burst, it was possible to distinguish shorter (IOI below ca. 100 ms; the most common) and longer intervals (Fig. 4). The suggested thresholds for the classification of Grunts A into isolated, short-interval, and long-interval categories was based on visual inspection of the histogram and cumulative IOI curve, following Lindström and Lugli (2000). Globally, the IOI of Grunt A ranged from 30 ms to 5.7 s (Table 1). Grunt B occurred mostly within the burst of Grunt A and usually with a higher IOI (Table 1, Fig. S1). Taking into account all Grunt A and B sounds, the IOI between consecutive sounds ranged 10 ms – 5.7 s (Table 1) (Fig. 4). Rhythms varied between individuals (Fig. S1), but it was possible to observe some alternation between

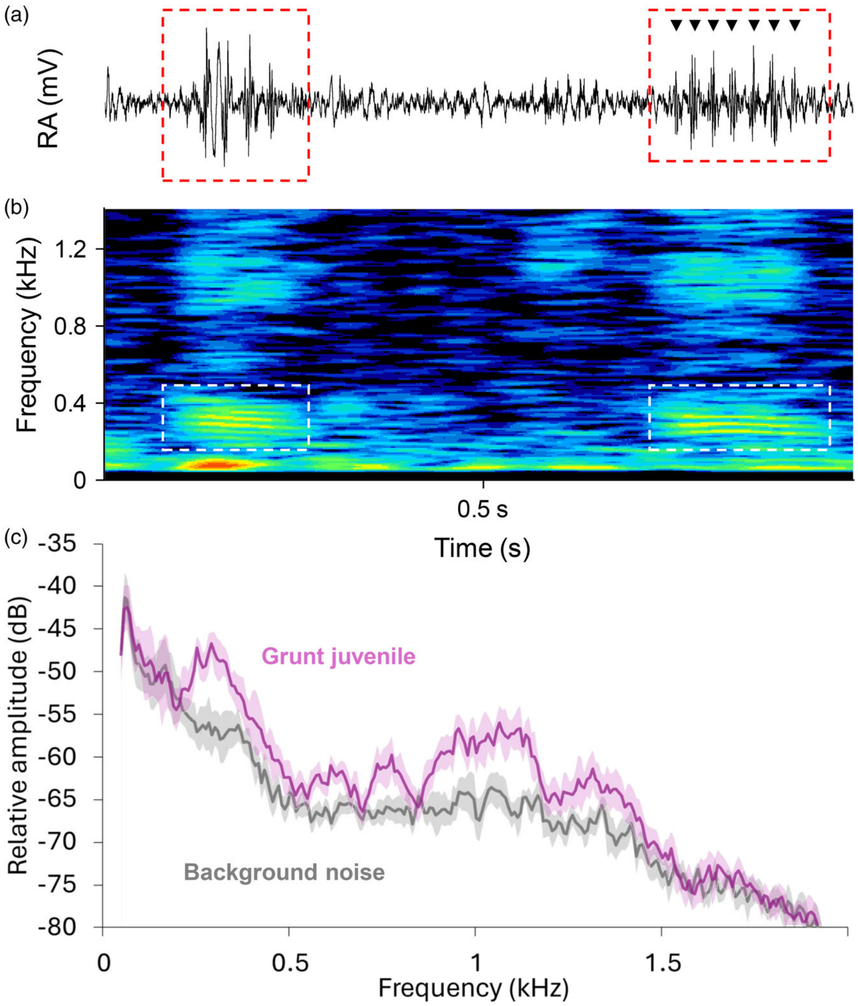

Figure 2 Sound production of a juvenile *Dactylopterus volitans* recorded at the Adriatic Sea. (a) Oscillogram of two representative sounds with their corresponding spectrograms in (b). Averaged power spectrum (c) of juvenile sounds (purple line, $n = 10$) and of the underwater background noise (grey line, $n = 10$) measured on the recording. Thin lines represent the 95% confidence intervals. Spectrogram parameters: FFT 512 points; Hamming window; 100% frame size; 96.87% overlap; resolution: 8 Hz. On the spectrogram, warmer colours indicate higher sound pressure level. In (c), the sound level of the grunts is above the background noise, particularly between 0.25 and 0.5 kHz, but remains mostly elevated in the 0.2–1.3 kHz frequency range. Red and white dotted rectangles in (a) and (b) indicate the beginning and the end of the sound. Black arrowheads indicate pulses within the second sounds. RA, relative amplitude (mV).

sounds with higher period and with lower IOI (example in Fig. 4). In terms of nPVI, overall values considering all sound types ranged from 70.1 to 118.6.

Behaviour during acoustic signalling

The sounds were actively produced when the fish were chased, but no sound emission was observed when fish were at rest laying on the bottom, prior to disturbance. During sound emission, the fish displayed distressed related behaviour (spreading the large pectoral fins while fleeing; Video S1). At distances more than 1 m, fish slowly orientated in the opposite direction and started to swim away by undulating the tail region and caudal fin. In these situations, large pectoral fins were never fully expanded. At distances less than 1 m, fish rapidly expanded the posterior part of the pectoral fins (i.e. larger part of the fin with membranes and vivid pattern of blue spots on the sides) and simultaneously produced loud audible sounds while fleeing. When pairs of *D. volitans* were approached (during 2 sessions), they would split and a single individual was chased. The chased fish was always the one actively producing sounds. The sound emission was not related to any observable rhythmic movements.

Anatomy and sonic mechanism

The swim bladder is situated laterally and dorsally to the vertebral column occupying the space between the skull and epaxial musculature, leaving only the ventral surface of the bladder

Table 1 Summary of the acoustic variables (mean ± standard deviation and minimum and maximum values in brackets) related to three sound types produced by flying gurnard *Dactylopterus volitans*.

Variable	Grunt A (*n* = 102)	Grunt B (*n* = 17)	Juvenile (*n* = 10)
DUR (ms)	31.0 ± 6.9 (18.2–67.6)	108.8 ± 28.6 (56.3–160.7)	149.6 ± 33.6 (94.2–201.5)
NP	3.9 ± 0.9 (2–9)	3.4 ± 0.6 (2–4)	6.1 ± 1.5 (4–9)
PRR (Hz)	127.9 ± 24.3 (50.3–219.8)	158.4 ± 41.1 (68.0–269.9)[a]	40.7 ± 2.8 (37.4–45.7)
PD (ms)		22.0 ± 6.2 (10.4–48.7)	12.0 ± 1.7 (8.8–14.1)
PP (ms)	6.2 ± 0.7 (3.4–8.2)	38.9 ± 7.5 (24.0–63.1)	26.1 ± 2.3 (22.6–29.5)
PF (Hz)	221.9 ± 83.0 (94.9–351)	167.1 ± 40.9 (74.5–258.1)	283.9 ± 14.4 (261.0–310.9)
H_1 (Hz)	159.5 ± 31.7 (62.0–329.6)[b]	167.7 ± 40.4 (74.5–258.1)[b]	238.5 ± 23.9 (211.0–278.2)
H_2 (Hz)	322.8 ± 57.3 (156–590)	473.2 ± 122.3 (257.3–696.8)	282.9 ± 36.38 (248.0–347.7)
H_3 (Hz)	491.9 ± 55.1 (285–709)	606.5 ± 110.9 (415.7–706.5)	335.5 ± 58.9 (285.0–444.4)
H_4 (Hz)	638.1 ± 55.0 (476–858)	/	341.69 ± 16.7 (316.0–367.0)
H_5 (Hz)	777.6 ± 163.0 (629.5–1171)	/	386.4 ± 17.0 (374.9–398.0)
H_6 (Hz)	859 (*n* = 1)	/	/
NH	3.9 ± 0.7 (1–6)	1.7 ± 0.6 (1–3)	3.8 ± 0.9 (3–5)
IOI (ms)	393.8 ± 587.2 (10–5770)		7188.1 ± 10479.8 (535–34 659)
IOI (ms)[c]	350.6 ± 614.5 (30–5770)	634.7 ± 317.3 (10–1320)	

n indicates to the number of sounds analysed for each sound type. Grunt A lacks PD due to temporal irregularities in the start and end times of pulses. From the total number of Grunt A sounds (105), three sounds were removed due to the inability to extract spectral values.

Abbreviations: DUR, sound duration; H1 – H6, frequency of the harmonics; IOI, inter-onset interval; NH, number of harmonics; NP, number of pulses; PD, pulse duration; PF, peak frequency; PP, pulse period; PRR, pulse repetition rate.

[a] PRR in Grunt B represents CRR, that is, the cycle production rate within pulse.

[b] For Grunt A and Grunt B the first visible harmonic (H1) represents the fundamental frequency.

[c] IOI measured only within Grunt A or Grunt B sounds.

below the column (Fig. 5). The swim bladder is separated along the midline into two lateral rostrocaudal chambers (i.e. having a bilobed shape), with anterior (AP) and posterior (PP) protrusions present on each chamber (Fig. 5). The swim bladder extends from first to fourth (I.–IV.) modified vertebrae (Fig. 5). A small transverse duct connecting the two lateral chambers was observed. This transverse duct is built from connective tissue, possesses inner membranes, and has a wider opening on the lateral side leading to the chambers and narrows to the midline below the vertebrae. The duct is situated approximately below the third modified vertebrae (Fig. S2). Each chamber holds a broad band of intrinsic sonic muscle on the dorsal and lateral region of the swim bladder wall. The sonic muscles are highly vascularized, leaving only the ventral surface of the bladder exposed. The muscle fibres were arranged obliquely but perpendicular to the midline body axis. On the bladder, conical/triangular anterior extensions (AE) are present on each anterior side (Figs 5 and 6).

On the posterior side of the cranium (Figs 5 and 6), two large openings/cavities (termed lateral occipital foramens, or LOF) were noticed (arrow in Figs 5 and 6). Located medially, directly above the rigid vertebral tube, these openings constitute a section where the two conical anterior extensions from each lateral chamber of the bladder terminate, hence forming the tight connection between the bladder and the neurocranium. The neural spines are transformed into vertical plates, and they separate two openings medially.

The swim bladder is positioned right above the modified section of the vertebral column. Calderwood (1891) named this modified section of the vertebral column a ‘rigid tube’, which does morphologically resemble a merged ossified structure. Anatomically, the first four vertebrae build this section of the vertebral column, but they were altered in comparison to the trunk vertebrae by becoming elongated and thinner, lacking transverse processes or rudimentary ribs (Fig. 5). Typical trunk vertebrae (with neural spines and transverse processes) follow four modified vertebrae. Additionally, the articulation points of the first four vertebrae were not clearly visible on unstained specimens under μCT, while on EPTA-stained individuals, contact points were easily observable (Fig. S2).

Discussion

This study documents, for the first time, natural sounds of the flying gurnard *D. volitans* from the Adriatic Sea. Notably, the recordings were obtained within *Posidonia oceanica* seagrass meadows, a protected and ecologically important habitat. Fish sounds are an essential part of underwater marine soundscape biophony, especially within the 100–1000 Hz frequency range (Duarte et al., 2021; La Manna et al., 2021; Looby, Cox, et al., 2022; Muñoz-Duque et al., 2024). The identification of the distinct sound types produced by *D. volitans* expands current knowledge of Mediterranean fish biophony and provides new insights into the acoustic repertoire of this demersal species. Accurate identification and characterization of soniferous fishes such as *D. volitans* are essential for understanding the composition and ecological relevance of marine soundscapes.

Sound repertoire and acoustic characteristics

Adult *D. volitans* produced Grunt A and Grunt B sounds. Although we could not recognize the sex of soniferous individuals, our

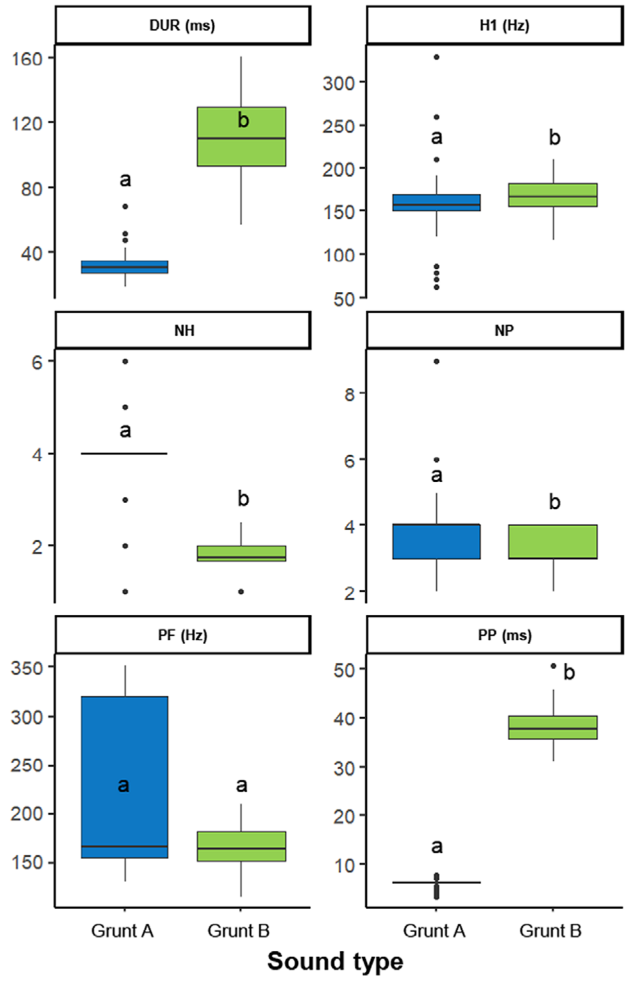

Figure 3 Boxplots of six acoustic variables used to compare two sound types of *Dactylopterus volitans*. Significance was tested with Wilcoxon signed-rank tests, before the subsampling and permutations. Lowercase letters above boxplots indicate pairwise differences obtained by Wilcoxon *post hoc* tests. Abbreviations of the variables: DUR, duration (ms); NP, number of pulses; PF, peak frequency (Hz); PP, pulse period (ms); H_1 – fundamental frequency in grunts A and B, but first harmonic in juvenile sounds (Hz); and NH – number of visible harmonics. Thick black middle line represents the median; whiskers represent minimum and maximum values, while the box highlights the 25th–75th percentile range. Outliers are represented with black points.

findings strongly suggest that the two distinct sound types can be produced in an alternating order. Grunt B was produced less often than Grunt A, while Grunt A was higher in frequency and presented four pronounced harmonics. Furthermore, we recorded sounds of juvenile fish, indicating that the sound production ability is already present in this species at lengths below 10 cm. Although the sounds of *D. volitans* had been recorded in the past (Dufossé, 1874; Fish & Mowbray, 1970), neither a quantitative description of the sound parameters nor details of the acoustic activity were provided in these studies. However, in the audio recordings of disturbance sounds from a hand-held specimen of *D. volitans* reported by Fish and Mowbray (1970), it is possible to detect disturbance grunt-like sounds, similar to the ones recorded in our study (Fig. S3).

Temporal patterns of fish sounds, particularly their rhythm (i.e. IOI and its variation, calling rate but also variations in pulse period and duration), are critical for species recognition (Amorim & Neves, 2008; Myrberg et al., 1978; Parmentier et al., 2017). Rhythms can code for individual or context-related information (Burchardt et al., 2021; Picciulin et al., 2024; Vieira et al., 2021). Here, we report rhythms quite distinct from an isochronous rhythm (all nPVI >70), but with some alternation between long and short IOI (Fig. S1). This type of alternation was also observed in the Lusitanian toadfish (Vieira et al., 2021) and may provide the receiver with additional information about the intended messages and the sound source. Furthermore, Grunt A was produced singly or in grunt trains. We distinguished short and long interval grunts, differentiating them according to the variability of the period between consecutive sounds. Grunt B was usually produced within Grunt A bursts and with higher IOI. Our findings thus suggest that rhythms are specific to each sound type that perhaps can alter rhythmic behaviour, underscoring the need for further investigation. Changes in rhythm may be influenced by species (Burchardt et al., 2021), context (Vieira et al., 2021), and fitness-related conditions (Picciulin et al., 2024).

Acoustic similarities with Triglidae and Syngnathiformes

Due to the morphological resemblance and similar ecology (benthic lifestyle, habitat preference and feeding behaviour), dactylopterids were previously considered a sister taxon to triglids. Results of the present study indicate the convergence in temporal and spectral characteristics of *D. volitans* sounds with those of triglids, which are also aurally similar. According to Amorim (2006), the acoustic signals produced by European Triglidae are mainly made up of pulses; they generate three types of sounds (known as knocks, grunts, and growls), which present interspecific variability in pulse pattern, periodicity, duration, and frequency (10–3000 ms; 250–600 Hz; Amorim, 2006).

The number of different sound types emitted by European gurnards varies with species (Amorim, 1996; Amorim et al., 2004; Amorim & Hawkins, 2000). The grey *Eutrigla gurnardus* and red *Chelidonichthys cuculus* gurnards produce three different sounds (i.e. knocks, grunts, and growls) whereas the streaked *Chelidonichthys lastoviza* and tub *Chelidonichthys lucerna* gurnards emit a single type of sound, growls and grunts respectively (Amorim, 2006). Radford et al. (2016) recognized four different sound types in Bluefin gurnard (*Chelidonichthys kumu*), and separated them into two aural categories, grunts and growls. These authors described grunts as harmonic sounds, while growls lacked harmonic components. Notably, the two sound types produced by *D. volitans*, Grunt A and Grunt B, resemble *gru2* and *gru1* sounds of *C. kumu*, respectively (Radford et al., 2016), especially considering the harmonic nature of Grunt A sounds.

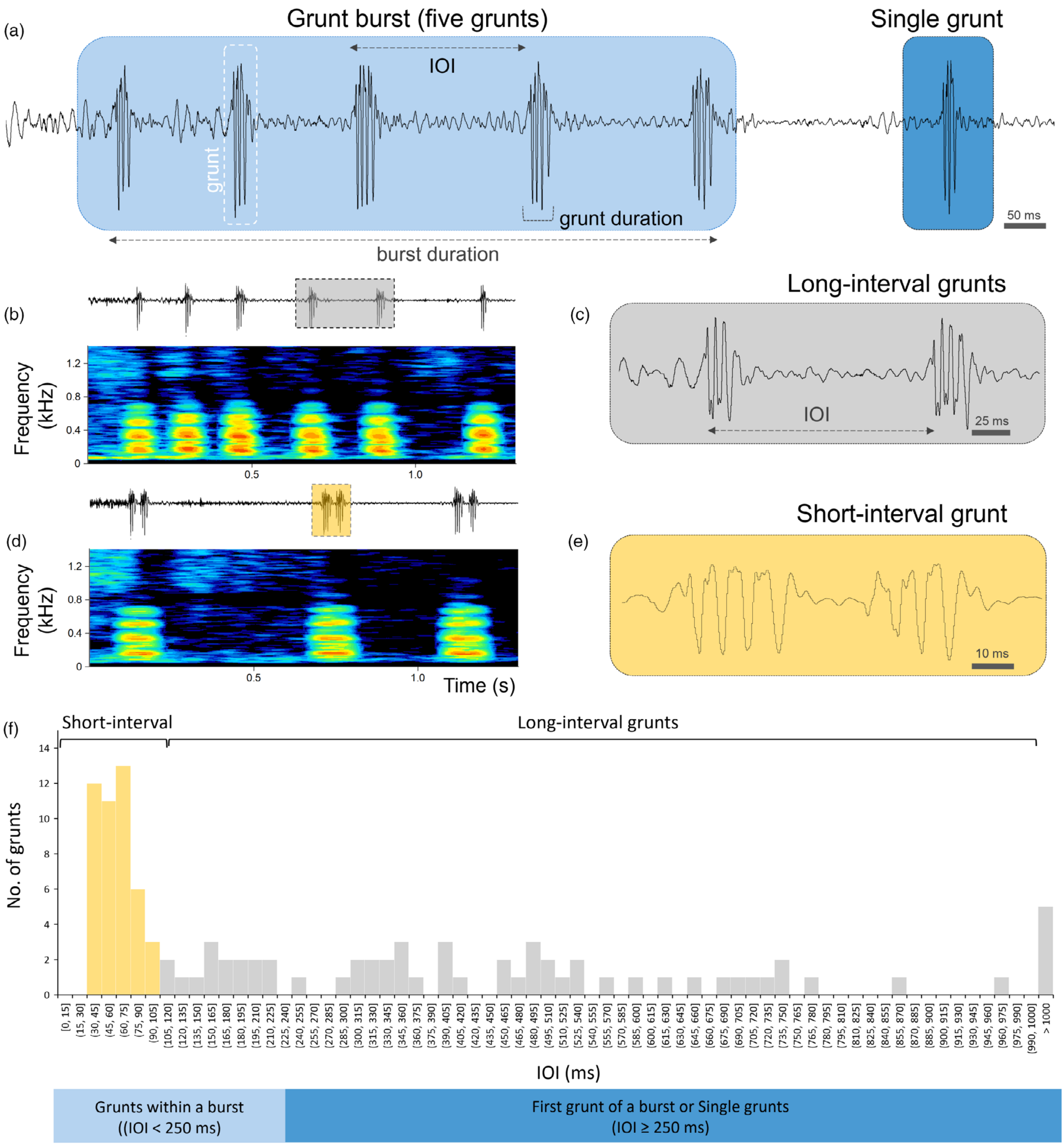

Figure 4 Acoustic structure and temporal patterning of the Grunt A. In (a) Grunt A is produced in either a train or burst of sounds (darker blue), or as a single grunt (light blue). The dashed horizontal lines and arrows highlight the corresponding parameters which were calculated from these sounds. In (b and c), temporal parameters of the long-interval Grunt A (grey) are highlighted, while in (d and e) a short-interval burst (orange) is shown. The histogram in (f) depicts the temporal separation between short- and long-interval bursts, and Grunt A bursts and single grunts, according to the inter-onset interval (IOI, in ms). Spectrogram parameters: FFT 512 points; Hamming window; 100% frame size; 98.43% overlap; resolution: 8 Hz.

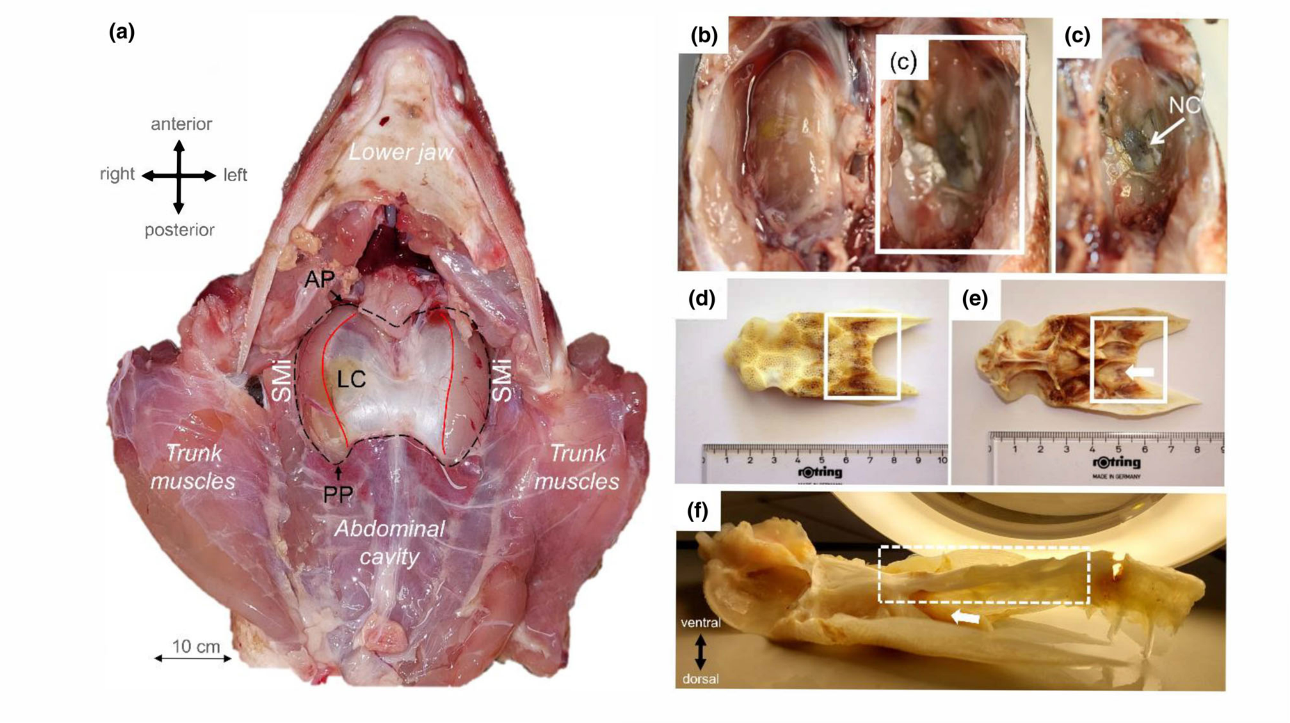

Figure 5 Swim bladder morphology and anatomical peculiarities of the cranium and vertebral column in female *D. volitans*. (a) Ventral view of the dissected abdominal cavity. The swim bladder is encircled by a black dashed line indicating its contour, while the intrinsic sonic muscles (SMi, encircled with the red curved lines) and lateral chambers (LC) are also highlighted. (b) Abdomen after extraction of the left swim bladder lateral section, while the right was kept intact. (c) Exposed part of the neurocranium (NC). (d) and (e) are dorsal and ventral view of a cleaned cranium, respectively. The white rectangle indicates the position of the extracted swim bladder. (f) The cranium (situated flat on its dorsal side) with the first four vertebrae fused into a rigid tube (dashed rectangle). AP, anterior protrusion; NC, neurocranium; PP, posterior protrusion; SMi, swim bladder intrinsic muscle. (a), (b), and (c) are dissections performed on a fresh specimen. White arrows in (e) and (f) indicate the openings on the cranium.

From the taxonomic perspective, the database of soniferous fish (fishsounds.net) indicates 16 soniferous taxa within Syngnathiformes (excluding *D. volitans*), and our study broadens the acoustic repertoire of syngnathiforms by indicating that harmonic and pulsatile sounds are also part of their acoustic diversity.

Context of sound production

Multimodal signals contain components that are transmitted through multiple sensory channels (Otovic & Partan, 2009). The sound production by *D. volitans* was followed by the spreading of pectoral fins and exposing the pectoral fin membranes with vividly coloured markings. This suggests that during disturbance (e.g. diver harassment), *D. volitans* emits multimodal signals combining visual and acoustic components. Multiple components could enhance the efficacy of a signal; in this way, warning coloration would play a clear strategic role of warning the predator (i.e. increasing the detectability of the signal), and the sounds would have a purely tactical function (i.e. increasing the signal efficiency; Rowe, 2013). Interestingly, the spreading of large, vividly coloured pectoral fins during sound production is also a hallmark of agonistic displays in triglids (Amorim, 2006), further highlighting convergence with dactylopterids.

Fish may attempt to dissuade predators by displaying threatening behaviours, such as emitting loud sounds (Ladich, 2021). Vocal fish have been reported to emit sounds when approached by predators, or when caught, chased, or being hand-held (Banse, Lecchini, et al., 2024; Bertucci et al., 2021; Ladich, 2021; Parmentier et al., 2019).

Sound production mechanism

Sound producing mechanisms have evolved independently in various fish groups, making them the most diverse vertebrate group in this regard (Ladich, 2014; Ladich & Fine, 2006; Parmentier & Fine, 2016). The swim bladder mechanism is certainly one of the most studied models of sonic mechanism and involves the contractions of specialized sonic muscles that vibrate the swim bladder (Ladich, 2014; Ladich & Fine, 2006; Parmentier & Fine, 2016). These muscles can be intrinsic (attached exclusively to the swim bladder walls) or extrinsic (originating on other skeletal structures; Ladich, 2014;

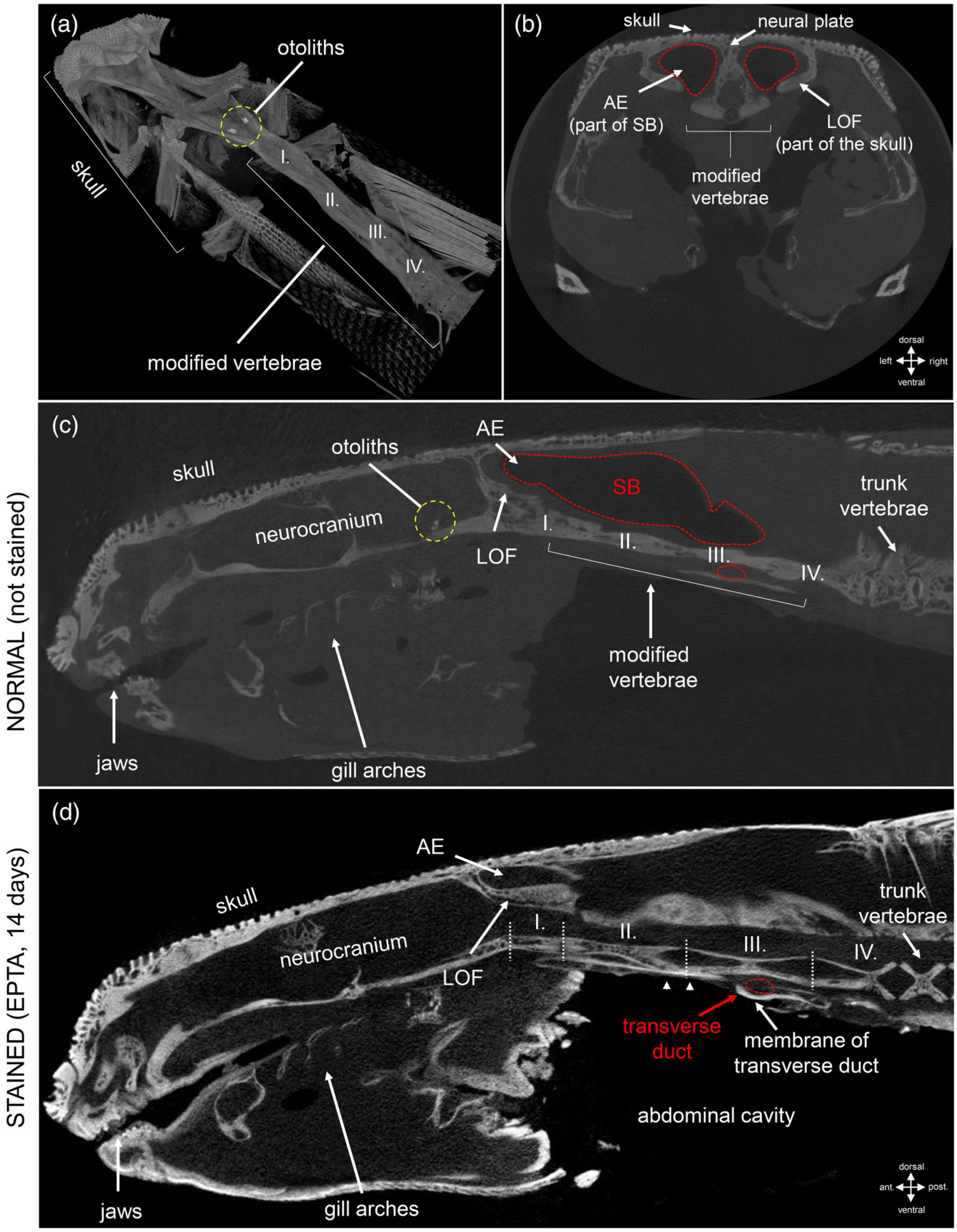

Figure 6 Microcomputed tomography (micro-CT) scans of female *D. volitans* (TL = 30 cm) sonic mechanism. (a) Dorsal view of the osseous structures corresponding to the skull and modified first four (I.–IV.) vertebrae. Otoliths are circled with yellow dashed lines, while the modified vertebrae are highlighted. Keep in mind that two post-temporal bones that form a spine were excluded to get better resolution of the vertebral column. (b) Transverse section showing the posterior margin of the cranium with two lateral occipital foramens (LOF) and the swim bladder anterior extensions (AE, red dashed lines) which terminate within these foramens. The neural plate is composed of dorsal processes of the vertebrae and is formed by corresponding membranes that fuse together to form continuous vertical neural plates. (c) Left lateral view of unstained micro-CT scanned specimens, highlighting the skull and the dorsal position of the swim bladder (red dashed line) in relation to the vertebral column. (d) Left lateral view of EPTA stained and micro-CT scanned specimens of *D. volitans*. Specimen was left for 14 days in EPTA solution, then scanned with micro-CT. The swim bladder with its anterior extensions is situated between fused first (I.) and fourth (IV.) modified vertebrae, and its anterior extensions fit into lateral occipital foramens within the skull. The ventral side of the body was dissected and cleared of organs, and therefore, no structures and organs are visible. Osseous structures are represented with light grey, while soft tissues with dark grey colour. Transverse duct connecting two lateral chambers of the bladder is highlighted with dashed red line. In (d), due to the staining, osseous and connective structures are scanned with high contrast.

Parmentier & Diogo, 2006). Acoustic characteristics and anatomical dissections suggest that *D. volitans* produces sounds via intrinsic sonic muscles acting on the swim bladder. Calderwood (1891) suggested that one-half of the anterior (triangular) swim bladder extension, composed of an extremely thin membrane, is situated within the rigid bone cup within the skull, a feature we also observed. In addition, we observed that each lateral chamber of the swim bladder is divided into three portions: anterior (the one within the cranium), medium (largest), and posterior (smaller than the previous, Fig. 6). This is also in accordance with Calderwood (1891).

Furthermore, the shape of the bladder in *D. volitans* is interesting, since it possesses anterior and posterior protrusions, and it is similar in morphology to the one described for Lusitanian toadfish (Dos Santos et al., 2000). Except for sound production, modified swim bladder shapes may be linked to audition or gas secretion (Fine & Parmentier, 2022). In oyster toadfish (*Opsanus tau*), the pattern of sound radiation measured in the wild was not omnidirectional but followed the morphology of the heart-shaped swim bladder (Barimo & Fine, 1998). According to Fine and Parmentier (2022), the protrusions of a swim bladder in oyster toadfish could enhance hearing by directing sound detected by the swim bladder toward the inner ear. Alternatively, they aid in under-stimulation of the ears when the fish emits sounds, by directing them away from the hearing organs due to the absence of sonic muscles on the anterior bladder and the thick column connecting the two protrusions (Fine & Parmentier, 2022). In non-otophysan fishes, anterior extensions of the swim bladder directly contacting the auditory region (bullae) of the skull represent a direct connection between the bladder and the inner ear (Schulz-Mirbach & Ladich, 2016). However, the direct morphological relationship between swim bladder and third end organ, lagena, was not observed here. So far, this was only observed in Asian cichlid *Etroplus maculatus*, where the direct and complex connection between the swim bladder and auditory end organ (lagena) was corroborated by µCT imaging and histological serial semithin sectioning (Schulz-Mirbach et al., 2013). Interestingly, in plainfin midshipman (*Porichthys notatus*), sexually dimorphic rostral swim bladder extensions (similar to our anterior extensions) in females and type II males function to enhance sound pressure auditory sensitivity and broaden the upper hearing range (Colleye et al., 2019; Mohr et al., 2017). Furthermore, Schulz-Mirbach et al. (2012) demonstrated that in cichlids, larger swim bladders enable detection of higher frequencies, and rostral swim bladder extensions increased sensitivity to sounds between 500 and 1000 Hz. Therefore, in the future, auditory sensitivity experiments and comparative examination of the anterior protrusions and anterior extensions of males and females of *D. volitans* should be carried out. On µCT scanned specimen (♀, TL = 30 cm), the distance from the visible otolith to the anterior extensions was *c.* 8–10 mm.

Finally, the modified section of the vertebral column is directly associated with the swim bladder. In several soniferous Ophidiidae (*Parophidion vassal*, *Ophidion rochei*, and *O. barbatum*), the sound-producing mechanism comprises modified vertebrae, three pairs of sonic muscles, and a highly modified swim bladder, functioning as a rebound system involving a rapid backward snap of the bladder's anterior part (Fine & Parmentier, 2016; Parmentier et al., 2022). In *D. volitans*, the first four vertebrae lack any specific skeletal features that could aid in sound production (e.g. neural rocker or wing-like process) but may provide stiffness and rigidity to the bladder during emission. In addition, the thin and elongated bodies of these vertebrae could have been modified due to the specific position of the swim bladder, freeing up the space for the bladder. Alternatively, it could partially serve in vibration transmission from the bladder to the inner ear. If a modified vertebral column indeed acts as a transmitter, this may represent a specialization for enhanced hearing in *D. volitans*.

Acknowledgments

The authors would like to thank the Croatian Ministry of Environment and Green Transition for funding the project 'Monitoring and Observation System for the Continuous Assessment of the State of the Adriatic Sea (JADMON) 2021–2026. – Work Area 1 RC-MORE' during which the video material was recorded. This research was funded in part by the grant of the Croatian Science Foundation under the project IP-2022-10-7542 (LinkFish), and in part by the project PRIMOS funded by NextGenerationEU.

Author contributions

BD, NS, and MP performed the field sampling. SH and BD conceived the ideas and designed the methodology. IE performed CT scans. SH and MV led the curation and analysis of data, and the writing of the initial version paper. Review and editing of the paper was performed by SM, MCPA, PJF, DZ, NS, IE, and MP. All authors contributed critically to the drafts and gave final approval for publication.

Conflict of interest statement

The authors declare no conflicts of interest.

Data availability statement

Raw data from this study are deposited in *Figshare* public repository https://figshare.com/s/b264c831f5645a10e6eb.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Variation of IOI (inter-onset interval) throughout each recording (four recordings, a–d), and respective phase plots. IOI was not measured on the first sound of each recording. Note that in first recording there were a pair of individuals.

Figure S2. Differences between micro-CT scanned (unstained, left) and EPTA-stained (right) specimens of *D. volitans*. Specimen was left for 14 day in EPTA solution, then scanned with micro-CT. (a) and (c) display the dorsal perspective of abdominal cavity with swim bladder lobes, while (b) and (d) highlights the dorsal perspective of transverse duct connecting two lateral chambers of the bladder. (e) Highlights the freshly dissected transverse duct connecting two lateral chambers of the bladder (eliminated here), situated ventrally to the vertebral column. Red colour indicates the structures related to swim bladder. m.—modified.

Figure S3. Comparison between power spectrums of grunts recorded on the present study and sounds recorded by Fish and Mowbray (1970). Both recordings down-sampled to 4 kHz.

Video S1. Video showing the sound production of wild *Dactylopterus volitans* recorded during diving activities in southern Adriatic Sea (Croatia). Video made by Branko Dragičević.