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Animal behaviour

First evidence of fish larvae producing sounds

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The acoustic ecology of marine fishes has traditionally focused on adults, while overlooking the early life-history stages. Here, we document the first acoustic recordings of pre-settlement stage grey snapper larvae (*Lutjanus griseus*). Through a combination of *in situ* and unprovoked laboratory recordings, we found that *L. griseus* larvae are acoustically active during the night, producing 'knock' and 'growl' sounds that are spectrally and temporally similar to those of adults. While the exact function and physiological mechanisms of sound production in fish larvae are unknown, we suggest that these sounds may enable snapper larvae to maintain group cohesion at night when visual cues are reduced.

1. Introduction

The acoustic ecology of coral reef fishes has received considerable attention in recent years. Adult fishes are able to produce and receive sounds, and acoustic signals are used to attract mates, defend territories and startle predators [1–3]. Sounds can provide information from abiotic and biotic sources in the surrounding environment, even for fish that can only receive but not produce sounds [4]. Recent studies have examined the hypothesis that larval reef fish use acoustic signals to orient towards reefs through field-based playback experiments and laboratory-based measurements of hearing thresholds [5–8]. Previous research in the acoustic ecology of coral reef fishes has established that juveniles and adults of many species of fish are sound-producers [1,3] but has overlooked the possibility that larvae emit sounds. Here, we ask whether a larval fish could also be soniferous.

Our focal species was the grey snapper, *Lutjanus griseus* (Linnaeus 1758), a commercially and recreationally harvested fish in Florida waters [9] (figure 1a), which occupies different habitats throughout its lifetime. Spawning activity peaks between July and August [9]. Larvae undergo flexion at 4–7 mm notochord length (NL) [10] and settle to shallow seagrass beds at 10–15 mm standard length (SL), after a 33–39-day pelagic phase (figure 1b [9,11]). Small adults gather in reef channels and larger adults move from inshore areas to waters farther offshore (depths of 30–180 m), where they form large schools [9]. The only documentation of sound production in this species was in captive adult *L. griseus*, which produced 'knocks', 'thumps' and 'growls' in response to manual or electrical stimulation in the laboratory [12]. The function of these sounds is unknown [12].

2. Material and methods

We recorded *L. griseus* larvae in their pelagic environment using a Lagrangian observation platform (moving with the current, see below), verified these results in the laboratory, and compared larval recordings to historical recordings of adults.

Field experiments took place between 13 and 19 August 2012, near the Fowey Rocks lighthouse (25°35'26" N, 80°5'49" W) in the northern Florida Keys Reef Tract. Late-stage *L. griseus* larvae (figure 1b) were collected (University of Miami Protocol no. 11–160, FWC permit no. SAL-11–1331-SR) with Action CARE and

Table 1. Acoustic characteristics of *L. griseus* sounds; larval sounds were recorded in the field in the DISC, and in a tank in the laboratory; adult sounds were recorded in tanks by Fish & Mowbray [12], data are from the Macaulay Library [15]. In the field, larvae were placed inside an acoustically transparent cylindrical mesh chamber (38 cm diameter, 10 cm height) located 70 cm above the hydrophone. Therefore, the amplitude can be considered the approximate 'source level', because source level is typically measured at 1 m distance.

	dominant frequency (Hz)		duration (ms)		amplitude (dB re: 1 μ Pa)	
	mean \pm s.d.	range	mean \pm s.d.	range	mean \pm s.d.	range
field knocks ($n = 679$)	363.8 \pm 56.9	234.4–507.8	23.8 \pm 4.2	11.1–42.2	122.0 \pm 2.65	121.7–142.4
field growls ($n = 172$)	291.6 \pm 45.0	102.5–395.5	107.0 \pm 71.0	22.6–140.0	119.5 \pm 6.6	111.9–145.9
tank knocks ($n = 162$)	287.2 \pm 76.4	239.6–582.7	18.9 \pm 8.1	5.7–73.0		
tank growls ($n = 14$)	294.6 \pm 12.4	259.7–309.5	220.2 \pm 85.5	74.0–360.0		
adult knocks ($n = 12$)	247.0 \pm 40.9	129.2–273.4	31.5 \pm 9.0	22.0–49.1		

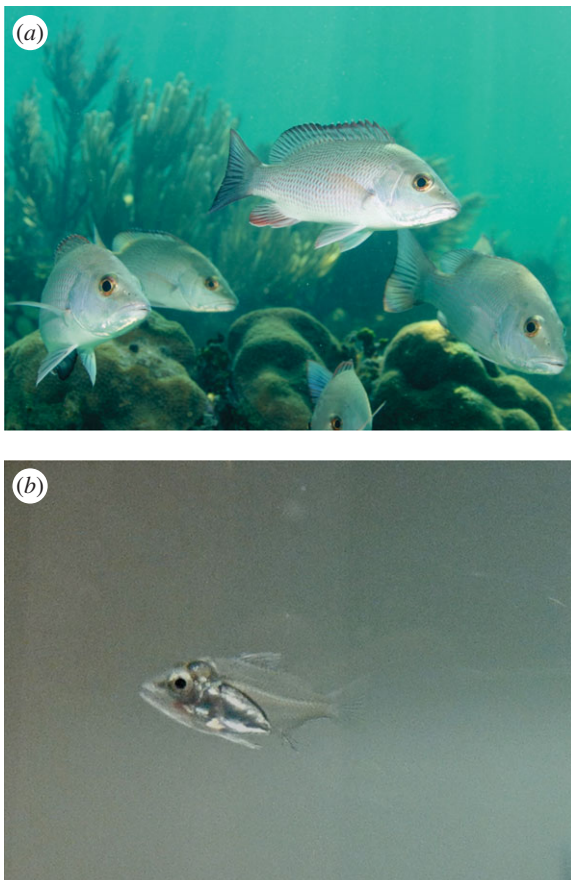


Figure 1. Grey snapper (*L. griseus*): (a) school of adults on the reef (photo: E. D'Alessandro); (b) unpigmented pre-settlement larva (photo: E. Staaterman). (Online version in colour.)

BellaMare light-traps moored near Fowey Rocks in 18 and 10 m of water, respectively. Seventy per cent of the 99 individuals collected were obtained on the night of the new moon, the peak arrival time for *L. griseus* [13]. The larvae ranged in size from *ca* 9 to 12 mm SL (figure 1b), were used in experiments within 24 h and were released at sea after testing.

Individual larvae were observed at sea in the behavioural arena of the drifting *in situ* chamber (DISC [14]). The DISC was equipped with a camera (Hero2, GoPro), GPS (GT-120, IgotU), spot lights with infrared LEDs (Tektite, 850 nm) and a DSG-Ocean (Loggerhead Instruments), which included a numerical compass, calibrated hydrophone and acoustic recording system (HTI-96, High-Tech, Inc., sensitivity: -170 dBV μ Pa $^{-1}$, sample rate: 20 kHz). The DISC's cylindrical arena (38 cm diameter,

10 cm height and transparent to odour, light and sound) was mounted 70 cm above the hydrophone. The DISC was set adrift, 3 m below the water's surface, and *ca* 500–1000 m from the fore-reef for 15 min deployments, during which time the boat engine was shut off and the DISC was undisturbed. A total of 58 behavioural deployments were conducted: 27 during the day (15.45–20.00) and 31 at night (20.00–02.00). These trials tested 42 individuals, as 16 were repeated during the day and at night.

The audio files were scrutinized aurally and visually using RAVENPRO 1.4 (Cornell Laboratory of Ornithology; fast Fourier transform (FFT) size: 512 samples). We observed two types of sounds: short-duration 'knocks', which resembled those produced by adults [12,15], as well as longer-duration 'growls'. Individuals that produced at least one knock or growl (22 of the 42 individuals) were subjected to a second round of analysis, in which we measured the following acoustic parameters: duration (ms), dominant frequency (the frequency with the greatest amplitude) and amplitude (RMS pressure, converted to dB re: 1 μ Pa using the calibration of the recording system). Knocks occurred either in isolation or in sets of two or three; acoustic parameters were measured for individual knocks and for the inter-knock interval. We performed the second round of analysis for trials that lacked high background noise from passing ships, which narrowed our analysis to 16 of the 22 sound-producing larvae.

To verify that the sounds we observed in the field were indeed produced by *L. griseus* larvae, we also recorded larvae during the night in acoustically isolated laboratory conditions. None of the individuals from the field trials were used in the laboratory trials, and none of the laboratory individuals were recorded repeatedly. A small audio recorder (Microtrack II, M-Audio; same hydrophone as above, 44.1 kHz sample rate) continuously recorded sounds in a rectangular tank (122 \times 32 \times 53 cm). Three larvae were recorded individually, each for 15 min, and we also recorded 15 individuals together in the tank for an 8-h period. Finally, we obtained laboratory recordings of *L. griseus* from the Macaulay Library [15]. Larval recordings in the laboratory and adult recordings from the Macaulay Library were subjected to the same analyses as described above, with two exceptions: (i) acoustic energy (less than 200 Hz) from the air conditioning system was excluded, and (ii) amplitude measurements were omitted as the distance between the animals and the hydrophone was unknown.

3. Results

All sound production occurred at night. Knocks from larvae in the field and knocks from adults in the tank were often

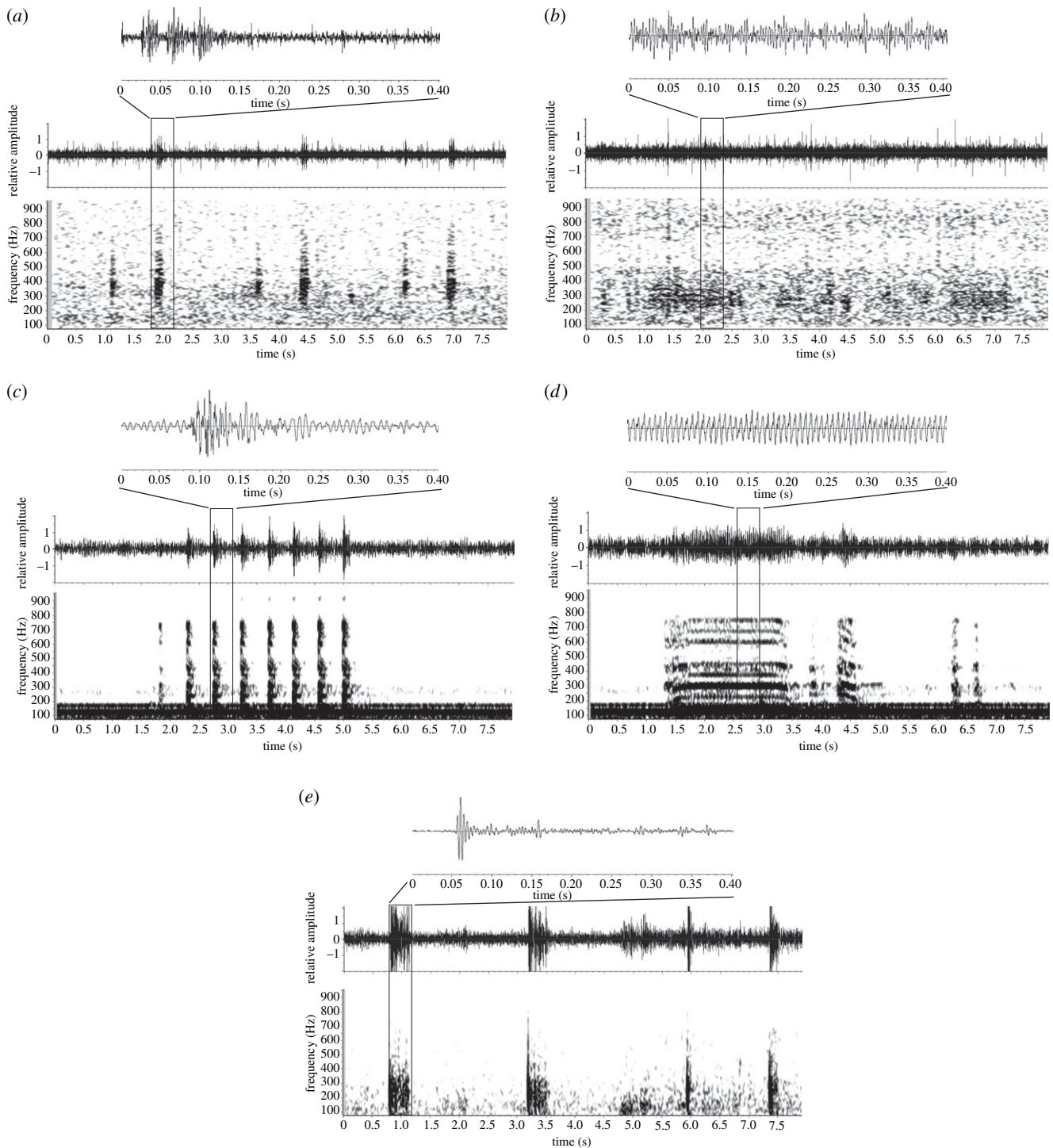


Figure 2. Visual representations of *L. griseus* sounds, corresponding to supplementary audio files. Larval knocks (a) and growls (b) in the field; larval knocks (c) and growls (d) in the tank, and adult knocks in the tank (e). (c,d) Acoustic energy (less than 200 Hz) from the laboratory's air conditioning system was excluded from analysis. (e) Adult recordings were obtained from the Macaulay Library [15]. Spectrogram parameters: 8 s duration, discrete Fourier transform (DFT) size: 4096 samples.

produced in short groups of twos or threes (mean inter-knock interval: 17.9 ± 4.1 ms, table 1 and figure 2), whereas larvae in the laboratory emitted series of 6–10 knocks with longer inter-knock intervals (mean duration: 221.0 ± 83.0 ms, table 1 and figure 2). Growls were not as common: they were not present in the adult recordings, although Fish & Mowbray [12] did note that knocks were 'sometimes followed by growls of low pitch and amplitude lasting up to 0.5 s'. In the field, larval growls were produced intermittently, but in the tank, they often occurred immediately following a series of knocks. This pattern was observed when animals

were alone in the tank, as well as when there were 15 individuals together.

4. Discussion

For the first time, we recorded pre-settlement stage fish larvae while adrift at sea and discovered that they emit sounds. These sounds are spectrally and temporally similar to those produced by adult *L. griseus* (table 1 and figure 2). Adult 'knocks' appeared to be lower in dominant frequency than

larval knocks, which was consistent with the finding that large fish produce lower-frequency sounds than small fish [16–18]. These ontogenetic differences are likely explained by the change in size of the sonic muscles surrounding the swimbladder [17,19]. Although their sound-producing mechanism has not been described, sonic muscles are likely, given the similarities to the drumming sounds produced by other marine fishes with a sonic muscle–swimbladder complex [2]. There was also a considerable difference between the behavioural context of sound production for adults and larvae in this study (manual stimulation in tanks [12] versus free-field *in situ* recordings). Future research should use comparable experimental conditions to examine the physiology and ontogeny of the sound-producing apparatus of *L. griseus*.

Through the use of the Lagrangian recordings at sea, we were able to observe and document acoustic qualities of snapper sounds in free-field, unprovoked conditions. The DISC provided a unique advantage compared to classical bioacoustic studies conducted in tanks, which can distort acoustic qualities [20]. Larval snapper sounds recorded in the field versus those produced in the laboratory had different acoustic parameters: field knocks were higher in dominant frequency than tank knocks. While the duration of growls was generally greater in the tank than in the field, duration was highly variable even within individuals, suggesting some degree of behavioural plasticity (table 1 and figure 2 [16]). Several tank-based studies have demonstrated sound production in juvenile fish (e.g. grey gurnard (*Eutrigla gurnardus*) at less than 1 year: [16], croaking gourami (*Trichopsis vittata*) at eight weeks [18], squirrelfish (Holocentridae) at settlement-stage [21]). Our results provide the first evidence for sound production during the pre-settlement stage of marine fishes and highlight the importance of *in situ* Lagrangian recording systems for future studies.

Our findings raise intriguing questions about the function of the knocks and growls. Many fish produce sounds in the same frequency range that they are able to detect [22], in the context of territory defense, feeding, predator avoidance or mating and courtship [1,2]. The only documented case of sound production in adult *L. griseus* was from Fish & Mowbray [12], where the investigators used manual or

electrical stimulation to elicit sound production. Here, without provocation, larvae produced sounds in the range of 200–800 Hz, which is within the hearing range of most adult fishes [2,22]. By late in the pelagic phase, the auditory and lateral-line systems have developed sufficiently and would likely allow larvae to detect very near-field vibrations from their neighbours [22], although the hearing thresholds in most larvae, including this species, remain to be tested.

We observed larval sound production during 70% of the night-time trials, and none of the daytime trials, implying that the sounds offer a function that is not attainable by other means in the dark. While in the pelagic environment, fishes can remain in mixed or sibling groups [23], form schools [24] and recruit in large assemblages [25]. Indeed, most of the snapper collected in this study arrived in large numbers over the span of only a few hours. We suggest that acoustic signals provide a mechanism for *L. griseus* larvae to maintain group cohesion during their pelagic journey. Further research into the acoustic ecology of *L. griseus* is required to better understand the behavioural context of sound production in both adults and larvae.

Fish larvae are not just listeners. Even without understanding the function of the sounds they emit, their mere existence prompts exciting research questions. How important is the contribution of planktonic organisms to pelagic soundscapes? Larval fish orient towards sounds of settlement habitat [5–7], but will they also orient towards sounds of conspecifics? Acoustic masking from boats occurred in this study, and anthropogenic noise in the ocean is on the rise. What are the consequences if larval fish sounds become undetectable? Our results reveal that the acoustic ecology of larval fishes is a research area rich in opportunity and discovery. Finally, *in situ* platforms such as the DISC are very promising for acoustic recordings of other small pelagic organisms.

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