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Effect of biological and anthropogenic sound on the orientation behavior of four species of brachyuran crabs

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ABSTRACT: The settlement phase of crustaceans is critical and can ultimately affect their population structure. Underwater sound has been proposed as one of the most important sensory cues used by these animals during this phase because it can provide direction and habitat quality information. Here, we evaluated the effect of different acoustic signals (biological and anthropogenic) on the orientation response of different stages (megalopae and juveniles) of 4 brachyuran crabs (*Cyrtograpsus angulatus*, *C. altimanus*, *Neohelice granulata*, *Leptuca uruguayensis*) from Mar Chiquita coastal lagoon in Argentina. A binary choice chamber system was used, and different sound sources (crustacean, fish and motorboat signals) selected from recordings of the lagoon soundscape were reproduced. *C. angulatus* megalopae and juveniles responded positively towards crustacean signals, while juveniles responded negatively towards fish sounds. *N. granulata* juveniles orientated negatively towards crustacean, motorboat and fish signals. *C. altimanus* and *L. uruguayensis* juveniles did not respond to fish signals. The results support the idea that invertebrates can discriminate among conspecific signals and highlight the role of sound on prey–predator relationships. The behavioral orientation response to the motorboat sound evidences a presumably negative effect of anthropogenic sound on the biological interactions of species. This information is important, given the urgent need to increase knowledge about coastal marine lagoons to enhance their protection, especially considering the role of the key species of crabs in this habitat.

KEY WORDS: Acoustic cues · Habitat selection · Decapoda · Megalopae · Coastal lagoon

1. INTRODUCTION

In crustaceans, the pelagic larval phase is an important part of the life cycle to facilitate dispersal. For estuarine species, adults are typically restricted to the confines of the estuary, and they have evolved 2 larval dispersal strategies: retention of larval stages within the estuary or export of larval stages from the estuary (Hovel & Morgan 1997, Giménez & Torres 2020). The latter strategy involves the dispersal of the first larval stage from the parental estuarine habitat (where adult reproduction, fecundation and egg incubation occur) towards the open coast, where the last larval stage (i.e. megalopa) migrates back to the estuary for recruitment. The megalopa stage is a sensitive part of the life cycle. Individuals in this larval stage have to find and select a suitable habitat that enables successful recruitment and survival as juve-

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niles (e.g. Luppi et al. 2002a, Moksnes 2002). In decapods, habitat selection has been considered an important process influencing population distributions since settlers actively select complex habitats (e.g. Botero & Atema 1982, Herrnkind & Butler IV 1986, Fernandez et al. 1993).

Several sensory cues are involved in the orienting and settlement behaviors of marine pelagic larvae, including physical oceanographic features (e.g. Jeffs et al. 2005, Pineda et al. 2010, Ospina-Alvarez et al. 2018), chemical signals (Kingsford et al. 2002, Jeffs et al. 2005, Gebauer & Paschke 2020) and ambient underwater sound, the latter of which has been emphasized as the most important (e.g. Popper et al. 2001, Hinojosa et al. 2016, Lecchini et al. 2018). The underwater sound of a particular habitat, i.e. the soundscape, is characterized by a combination of geophony (produced by physical agents like wind, rain, waves), biophony (produced by animals) and anthropophony (produced by human activities) (Pijanowski et al. 2011). Sound has been highlighted as a potentially important orientation and settlement cue because it propagates over large distances, is directional and can carry important habitat information (e.g. Hawkins & Myrberg 1983, Radford et al. 2011). In a number of decapod crustaceans, specific underwater sounds can play an important role in the orientation and settlement behaviors of their pelagic larvae (Jeffs et al. 2003, Radford et al. 2007, Stanley et al. 2012, Hinojosa et al. 2016).

Underwater habitat soundscapes are becoming homogenized due to increasing human activities, with many generating noise, such as shipping, wind and wave turbines, pile driving and seismic survey (e.g. Payne et al. 2008, Pine et al. 2012, Solan et al. 2016, Buscaino et al. 2019). Such anthropogenic sounds affect soundscapes of aquatic habitats by masking natural sounds (Clark et al. 2009, Ceraulo et al. 2018). Anthropogenic sounds in coastal areas have important negative effects on the behavior (antipredator, foraging, parental, agonistic) and physiology (ventilation and metabolic rates) of many vertebrate and invertebrate marine species (e.g. Wale et al. 2013, Blom et al. 2019, Mauro et al. 2020). Specifically, larval settlement behavior of fish, crabs and coral was reported to be altered by anthropogenic sound (Pine et al. 2012, Simpson et al. 2016, Lecchini et al. 2018).

Among coastal marine ecosystems, coastal lagoons are important ecosystems that play a key role in concentrating a significant proportion of biodiversity and offer important services (Bedford et al. 2001). The Mar Chiquita coastal lagoon (Buenos Aires, Argentina) is a wetland declared as a Man and Biosphere Reserve by UNESCO (Iribarne 2001), conforming to the World Network of Biosphere Reserves, which establishes a balanced relationship between the social–economic development and the conservation of nature (Strategies of Sevilla; Reserves 1996). Thus, the lagoon is an important area for tourism and recreation (fishing and aquatic sports) and provides important ecosystem services (Isacch et al. 2010). A recent study characterized the soundscape of the lagoon and showed clear spatial and temporal patterns of the biological sounds produced by fish and crustaceans; the physical sounds produced by waves, wind and tide; and the anthropogenic sound produced by motorboat passages (Ceraulo et al. 2020).

Grapsid (*Neohelice granulata*, *Cyrtograpsus angulatus* and *C. altimanus*) and ocypodid (*Leptuca uruguayensis*) crabs are dominant inhabitants of the lagoon (Spivak et al. 1994). In all 4 species, reproduction occurs from September/October to March/May, with many egg clutches produced during each season (Spivak et al. 1991, 1996). Peaks of larval density are synchronized during the beginning and end of the reproductive season (Anger et al. 1994, Bas et al. 2009). Zoeae hatch within the lagoon and are transported rapidly towards coastal marine waters at nocturnal high tides (taking approximately 6 h, i.e. the duration of the high tide), using the outflowing ebb currents for transportation and avoiding pelagic predation (Anger et al. 2008, Bas et al. 2009). Megalopae then reinvade the lagoon, also at nocturnal high tides, and select and settle in adult habitat (Anger et al. 1994). Megalopae recruitment may depend on environmental factors, such as currents, wind direction and chemical cues (Bas et al. 2009, Gebauer & Paschke 2020), and on biological factors, such as developmental stage, larval swimming ability and predator avoidance behavior (Valero et al. 1999, Luppi et al. 2002a). However, the effect of the lagoon sound sources on the orientation of crab megalopae and first juvenile stages remains unknown. Thus, we aimed to test the effect of single isolated biological and anthropogenic sound sources of the Mar Chiquita coastal lagoon on the orientation of megalopae and first juvenile stages of 4 different crab species that inhabit it.

2. MATERIALS AND METHODS

2.1. Study area and species

The Mar Chiquita coastal lagoon (37° 45′ S, 57° 19′ W), Argentina, is a body of brackish water (46 km^2) of low tidal amplitude (ca. 1 m) permanently

connected to the sea (Reta et al. 2001), with wide ranges of salinity (2–35 PSU; Schwindt et al. 2004) and temperature (1.4–27.3°C; Luppi et al. 2013).

We studied the 4 dominant crab species of the lagoon. *Neohelice granulata* is found inside the lagoon, from the mouth to its northern limit (Fig. 1A,B). Adults construct burrows in the upper intertidal on mudflats or in saltmarshes of *Sporobolus densiflora* grassland, although errant individuals can be found in the subtidal (Fig. 1C) (Spivak et al. 1994). The principal megalopae recruitment habitat is in conspecific adult burrows, where they molt and remain until they reach an approximate size of 7 mm carapace width, after which they construct their own burrows (Luppi et al. 2002a).

Cyrtograpsus angulatus is primarily distributed in rocky open seashores and secondarily in coastal lagoons (Spivak et al. 1994). In Mar Chiquita, this species is present in the whole lagoon and the adjacent sea (Fig. 1A). Adults inhabit the subtidal, but can also be found in the intertidal following the diel tidal movements of the water (Fig. 1C) (Spivak et al. 1994). Megalopae mainly recruit in reefs constructed by the invading tube-building polychaetae *Ficopomatus enigmaticus* (Serpulidae), where settlers and early juvenile crabs live colonially within the tubes, which grow together and form large stacks (Fig. 1C) (Luppi et al. 2002a,b). Other recruit areas are the bivalve beds and the rocky shore (Fig. 1C) (Luppi et al. 2002a,b)

C. altimanus is a euryhaline marine species predominantly inhabiting the intertidal area of open rocky seashores (Spivak et al. 1994). In Mar Chiquita, this species is principally found in the lower intertidal rocky area from the mouth to approximately 2.5 km inside the lagoon (Fig. 1A,C). Megalopae settle in the adult habitat (Fig. 1C) (Luppi et al. 2002a).

Leptuca uruguayensis is a semi-terrestrial burrowing species restricted to the upper intertidal of tidal mudflats, usually associated with salt marshes. In Mar Chiquita, it is distributed from the mouth to approximately 3 km inside the lagoon (Fig. 1A) (Spivak et al. 1991). Adults live in burrows where megalopae also recruit and, immediately after molting, first juvenile crabs construct their own burrows (Fig. 1C) (Spivak et al. 1991).

2.2. Collection and maintenance

Megalopae were collected in the mouth (inner side) of Mar Chiquita lagoon using artificial collectors during the reproductive season 2018–2019 (from October 2018 to April 2019). Collectors were constructed from plastic bags containing 8 pieces of 20 × 20 cm window screens (0.2 cm size mesh) (Valero et al. 1999), secured 10 cm above the seafloor and inspected every 2 d. When megalopae were found, collectors were carried to the shore and replaced by new ones. Collectors containing larvae were placed in containers filled with seawater and immediately transported to the laboratory. In the laboratory, megalopae were removed, separated and differentiated by species (*N. granulata* and *C. angulatus*), following Boschi et al. (1967) and Rieger & Vieira (1997), respectively. Different species were held separately in aquaria and maintained under laboratory acclimation conditions (14:10 h light:dark cycle, temperature 24 ± 3°C, salinity 23 PSU and continuous aeration) for 24 h. Experiments were conducted during the daytime.

N. granulata and *L. uruguayensis* stage 1 juveniles (hereafter 'crab-1') were captured manually from adult conspecific burrows and their own burrows, respectively, while *C. angulatus* and *C. altimanus* were obtained from the collectors when megalopae of this species metamorphosed to crab-1 inside the collectors. The different species were identified following Luppi et al. (2002b). Crab-1 individuals were maintained under the same laboratory conditions described for megalopae and used in the experiments after 24 h of acclimation.

2.3. Acquisition of acoustic stimuli

Acoustic recordings were obtained from a previous study of the lagoon soundscape using 5 autonomous recorders (equipped with an omnidirectional calibrated hydrophone, model Benthowave Low Noise Broadband Hydrophone BII 7016 T6), with a flat sensitivity response of −174.5 ± 2 dB re V/µPa from 0.1 to 100 kHz and a Digital Signal Processor, model C5535 DSP-TMS320C5535, coupled with an AIC3204 audio codec; Texas Instruments), deployed in 5 locations from the mouth to the inner side of the lagoon (Ceraulo et al. 2020). From the description of the area soundscape, biophony and anthropophony were composed of 3 main sources: sounds produced by fish (black drum *Pogonias courbina*; 'fish': Audio S1 in the Supplement at www.int-res.com/articles/suppl/m669p107_supp/), impulsive broadband signals produced by crustaceans ('crustacean': Audio S2) and motorboat sounds ('motorboat': Audio S3).

To test if the isolated sounds could affect the orientation of megalopae or crab-1 stages, the different sound signals were selected from recordings col-

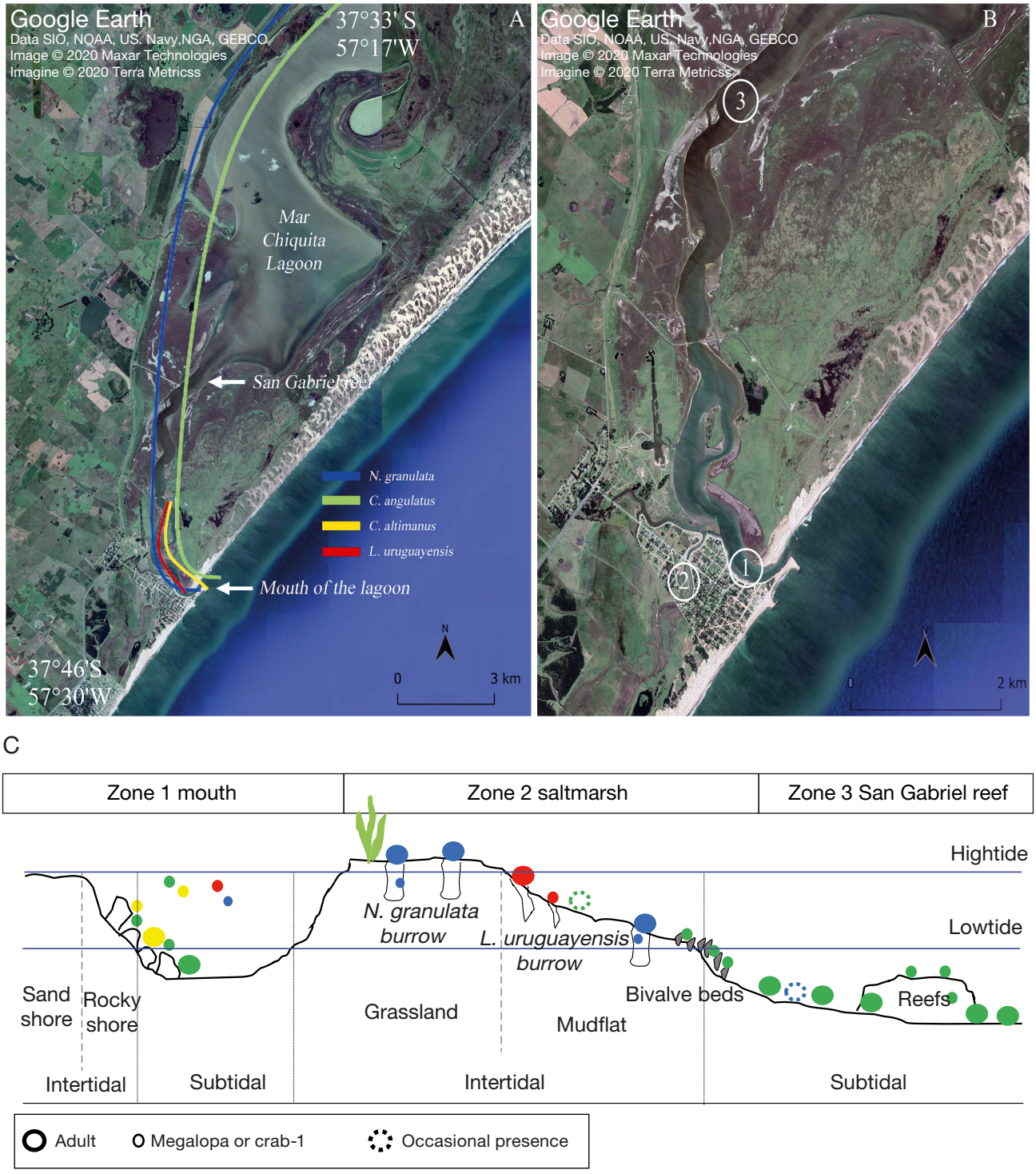


Fig. 1. (A) Mar Chiquita coastal lagoon, showing the distribution of 4 crab species (*Cyrtograpsus angulatus*, *C. altimanus*, *Neohelice granulata*, *Leptuca uruguayensis*) along the entire lagoon. (B) Detailed view of the south area of the lagoon, showing the site where megalopae collectors were placed (this study) and the area where sounds were recorded (Ceraulo et al. 2020) in the mouth of the lagoon (zone 1); the location of *N. granulata* and *L. uruguayensis* burrows where megalopae and juvenile crabs of stage 1 ('crab-1') were collected (zone 2); and the San Gabriel reef (zone 3) where the impulsive sound signals were recorded (Ceraulo et al. 2020). (C) Schematic of zones 1–3, showing the diverse habitat/microhabitat of the different crab species (color-coded as in panel A). Vertical lines divide different habitats (intertidal, subtidal) by their intersection with the low tide line and the schematic relief line. Dashed vertical lines divide different microhabitats

lected during spring (November) when crabs reproduce and megalopae re-enter the lagoon. Following Ceraulo et al. (2020), the crustacean sounds used here belong to recordings obtained in the *Ficopomatus* reef (in San Gabriel, an area located 7 km away from the mouth), the main recruitment site of *C. angulatus*, in which impulsive crustacean signals are abundant in terms of numbers and are constant during the whole day; the fish sounds used were recorded in the mouth of the lagoon at sunset hours when choruses of *P. courbina* start and are synchronized (Ceraulo et al. 2021); and the motorboat passages were obtained from the lagoon mouth during daylight hours when fishing activity is intense.

To reduce pseudo-replication problems (see Slabbekoorn & Bouton 2008) and generalize the experimental results, files containing only 1 source of fish, crustacean and broadband motorboat sounds were randomly selected from the entire spring dataset recorded in the lagoon mouth and San Gabriel reef. For each stimulus, a generalized additive model (with a smooth function) was conducted using the normalized power spectral density (PSD) of the different randomly selected stimuli (n = 7), and the 95% confidence interval (CI) was calculated. For fish and crustacean signals, comparisons showed low variability in the frequency distribution (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m669p107_supp/). Thus, 2 wave files of 7 s containing crustacean or fish signals were randomly selected and used as stimuli in the experiment. For motorboat signals, one of the selected stimuli showed a high-intensity peak below 1 kHz compared to others, and all stimuli showed a low variability over these frequencies (see Fig. S1). Considering that the shallow depth of the experimental tank would act as a high-band pass filter during the playback stimuli, the low-frequency intense motorboat stimulus was considered suitable in the experimental system to represent the motorboat noise recorded in the lagoon.

To isolate the different biological signals and avoid possible co-presence of different sources of soundscape components, i.e. different geophonic conditions, specific filters were applied to the original selected files: 500 Hz high-pass filter for the crustacean signals and 1000 Hz low-pass filter for fish signals. No filters were applied to the motorboat signals.

2.4. Experimental system

Individuals were exposed to different sound sources in a binary choice chamber I-maze system (Fig. 2). The I-maze structure was constructed with phenolic wood boards and consisted of a rectangular box (180 cm length, 60 cm depth, 30 cm width) open at the top with a chamber at each terminal end. This structure was housed in the center of a larger rectangular PVC tank (3 m length × 2 m width × 1 m depth). To diminish the area available for individual movements inside the I-maze and to track them easily by an observer during the experiment, a white PVC gutter (15 cm diameter, 10 cm depth) was housed inside. The gutter was placed in the center of the I-maze, immediately below the water surface level (55 cm total water depth) by tying it to the walls of the I-maze to maintain it in a fixed position throughout the experiment. At both ends of the gutter, a net (0.2 cm size mesh) was placed to prevent the individuals from escaping the gutter. A red LED tube light was used to illuminate the system for animal observation.

A submersible transductor (Model UW30, Lubell Labs) was placed in one end of the I-maze (suspended in a central position, 40 cm from the bottom, without touching any wall of the system), called the 'source chamber' (Fig. 2). The playback system was composed of the transductor , connected to a power amplifier (type APXII-300, American Pro, 230 V, 50 Hz) plugged into the stereo output of the PC (HP model TPN C129, Realteck sound controller, 1.0.704.1 version). The 7 s '.wav' files (n = 3) containing each stim-

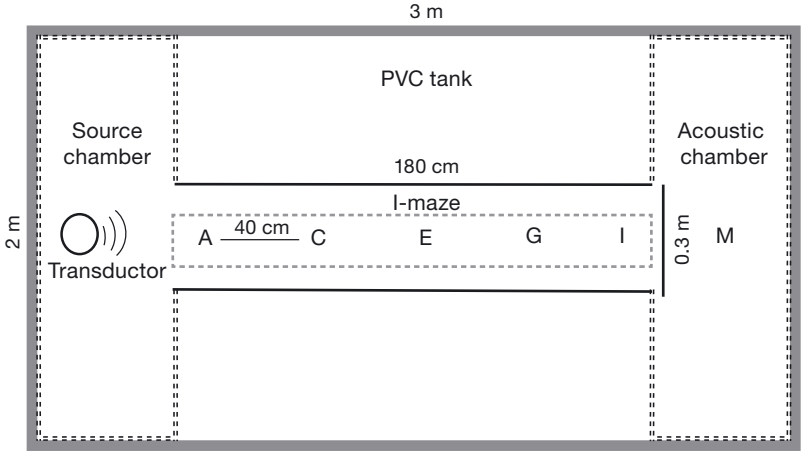
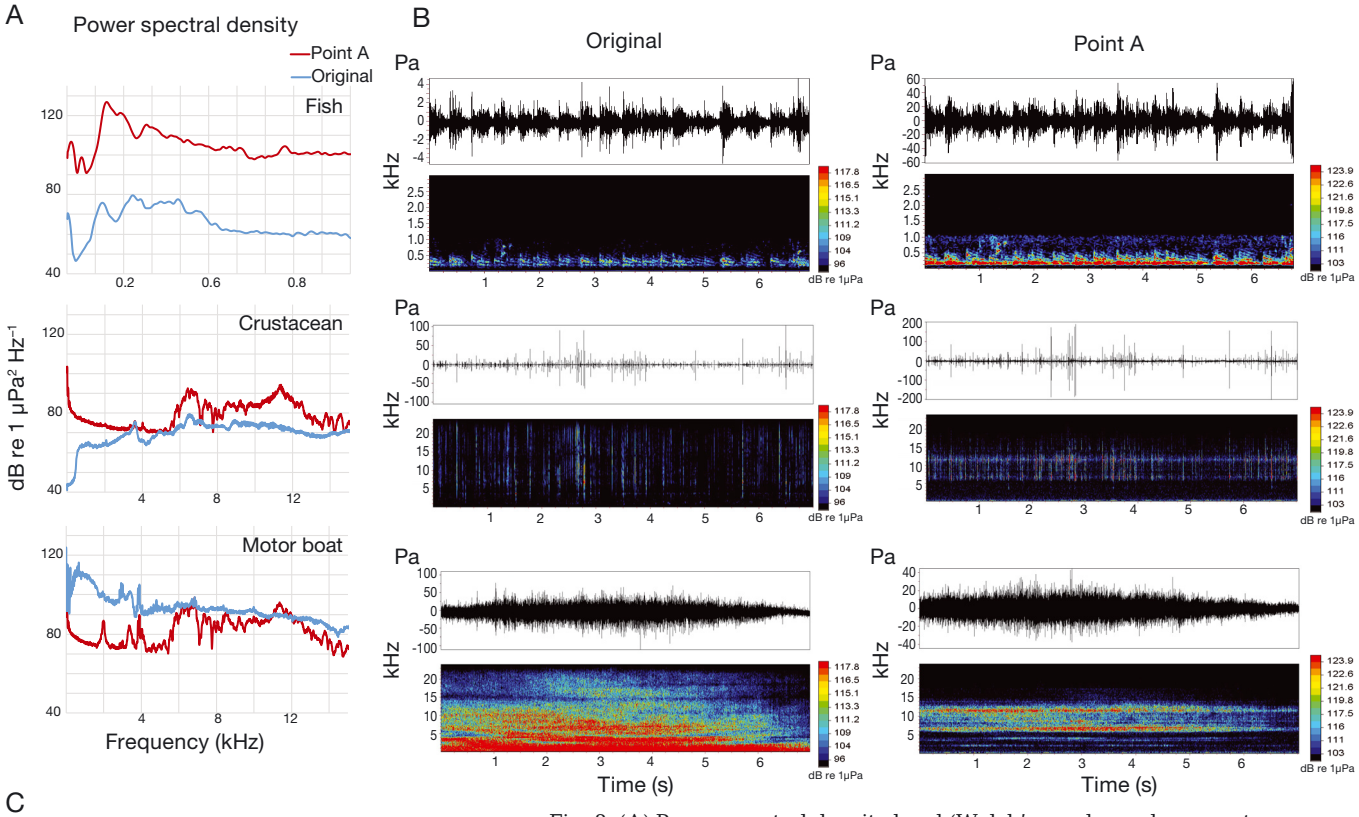


Fig. 2. Top-down view of the experimental system built: the PVC tank (thick gray lines) containing the I-maze (thin black lines) with a chamber at each end (black dashed lines): the source chamber holding the transductor and the acoustic chamber. Inside the I-maze is the gutter (grey dashed rectangle). Points A, C, E, G, I and M represent the decreasing gradient of sound obtained inside the I-maze from the source to the acoustic chamber. E represents the central point of the I-maze

ulus (fish, crustacean or motorboat passage) were played back using the 'loop mode' function of the Avisoft-SASLab recorder software (Avisoft Bioacoustics).

A calibrated hydrophone (model Reson TC4013, with a sensitivity response of –211 ± 3 dB re 1V/µPa between a wide frequency range of 1 Hz and 150 kHz) was used to determine sound intensity at locations A, C, E, G, I and M in the I-maze (Fig. 2). The hydrophone was coupled with a preamplifier (1 MHz bandwidth single-ended voltage and a high-pass filter set at 10 Hz, 20 dB gain, Avisoft Bioacoustics), connected to a digital acquisition card (Avisoft UltraSoundGate 116 h) managed by the Avisoft Recorder USGH software (Avisoft Bioacoustics). The 3 acoustic stimuli and tank background noise were acquired at a sampling frequency of 300 kHz with 16-bit resolution and analyzed with Avisoft-SASLab Pro software (Avisoft Bioacoustics).

The frequency and temporal variations of the 3 acoustic stimuli (fish, crustacean, motorboat) emitted in the tank were measured (Fig. 3). The power spectral density over 7 s of the stimuli recorded in the Mar Chiquita lagoon and at point A of the I-maze are shown in Fig. 3A. Different energy levels among the emitted signals were chosen to obtain a decreasing energy gradient from point A to point M in the I-maze system (see below). For this reason, to allow the frequency comparison among the single event stimuli, Fig. 3C also shows a linear normalized power spectrum of a single pulse event of fish (Hamming window, duration 0.1 s, bandwidth 13 Hz, resolution 6 Hz) and crustacean (Hamming window, duration 0.01 s, bandwidth 130 Hz, resolution 94 Hz), and 0.01 s of motorboat stimulus (Hamming window, bandwidth 130 Hz, resolution 94 Hz). The playback stimuli in the controlled environment were subject to a frequency distortion and a high-band



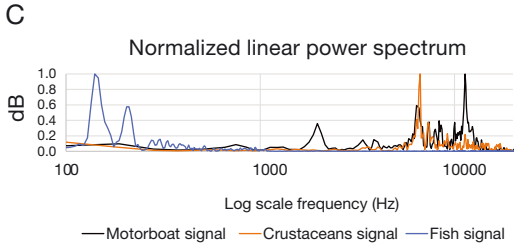


Fig. 3. (A) Power spectral density level (Welch's overlapped segment averaging estimator in Hann windows of 1 s and signal superposition of 50 %) of the 7 s stimuli (fish, crustacean and motorboat passage) selected from Mar Chiquita lagoon soundscape recorded in the lagoon and at point A in the I-maze (see Fig. 2). (B) Spectrogram and oscillogram of 7 s of the original stimuli and the recorded stimuli at point A in the I-maze (FFT size 512 samples and signal superposition of 50 %). (C) Normalized linear power spectrum of single reproduced stimuli recorded at point A in the I-maze (for motorboat and crustacean: duration 0.01 s, bandwidth 130 Hz, resolution 93.750 Hz; for fish: duration 0.1 s, bandwidth 12.729 Hz, resolution 5.859 Hz)

pass filter due to the low depth of the experimental tank condition (Akamatsu et al. 2002), but for the signals that had low-frequency components (fish and motorboat), energy peaks below 5 kHz were present (Fig. 3A,C). The spectrogram and oscillogram showed that the 3 acoustic playback stimuli maintained the original temporal structure (Fig. 3B).

Based on the calibrated recordings in the I-maze system, the root mean-square sound pressure levels (SPL_{rms}) of playback stimuli were calculated by averaging every 100 ms (Fig. 4). In order to investigate if a decreasing gradient of sound intensity from the source chamber towards the opposite extreme of the I-maze (from point A to point M, see Fig. 4A) was created, a generalized linear model analysis was conducted for each stimulus using 10 SPL_{rms} values for each point randomly selected in the subset. This analysis demonstrated that the SPL_{rms} decreased significantly between the different points A–M (fish: pseudo-R = 0.794, df = 1, $p < 0.0001$; crustacean: pseudo-R = 0.49, df = 1, $p < 0.0001$; motorboat: pseudo-R = 0.775, df = 1, $p < 0.0001$). However, for the fish stimulus, the energy registered at point I was higher than at point G (Fig. 4A). Based on these data, we conducted 2 different experiments (see Section 2.5). The experimental tank background noise had lower SPL_{rms} than the acoustic stimuli, with a maximum SPL_{rms} of 120.2 dB re 1 µPa. Fig. 4B shows the SPL_{rms} of the different stimuli at the selected points (A–M) and demonstrates that the frequency compositions and differences in PSD among the stimuli were maintained along with the system.

2.5. Experimental setup

Based on the different acoustic gradients recorded along the I-maze system for the 3 acoustic stimuli, 2 different experimental systems were designed

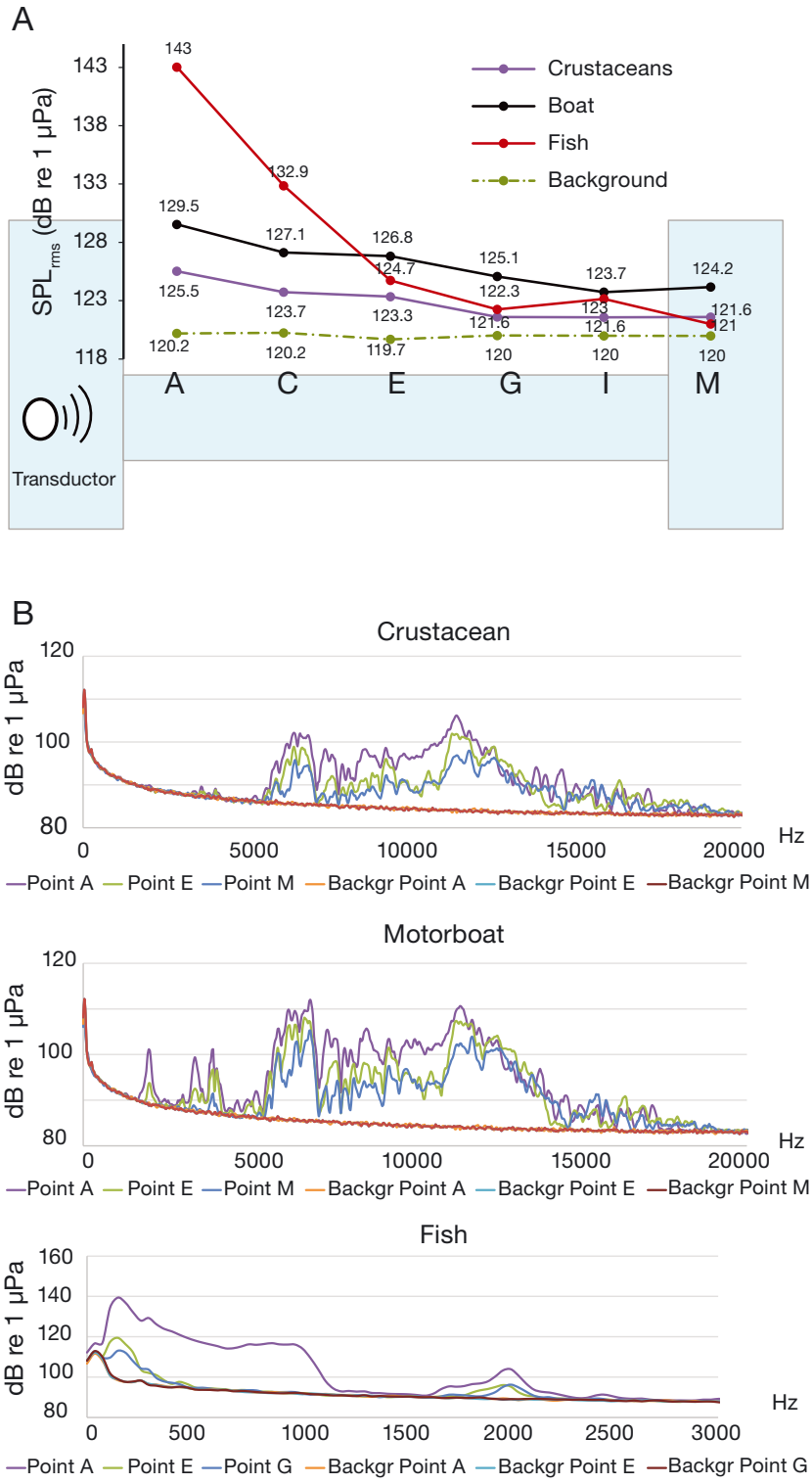


Fig. 4. (A) Averaged root mean-square sound pressure level (SPL_{rms}, dB re 1µ Pa) gradient of the different stimuli (crustacean, motorboat and fish) and the background noise recorded at points A–M in the I-maze. Note the higher energy at point I compared to G for the fish stimulus. (B) Different stimuli showing the averaged power spectrum in the different selected points (FFT size 8192, Hamming window, bandwidth 48 Hz)

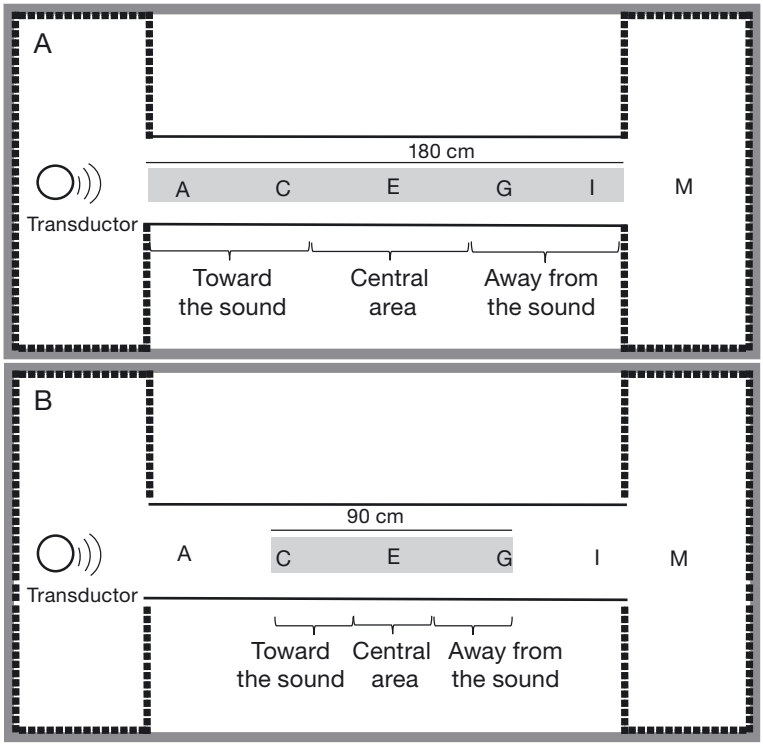


Fig. 5. Experimental system built showing the (A) long (for crustacean and motorboat stimuli) and (B) short (for fish stimulus) gutter (gray rectangles), and the 3 equally sized areas in which the position of the individuals was registered at the end of the experiment: toward the sound, central area and away from the sound

by using a long gutter (180 cm length) for crustacean and motorboat stimuli (Fig. 5A), and a short gutter (90 cm length) for the fish stimulus (Fig. 5B). To quantify the behavioral response of the individuals to the different acoustic signals, the system was divided into 3 equally sized zones named: 'toward the sound', 'central area' and 'away from the sound' (Fig. 5).

Considering the different systems, we conducted 2 experiments: Expt 1 (long gutter) consisted of 3 trials testing the effects of 2 acoustic signals, i.e. crustacean and motorboat, and a control with no sound; while Expt 2 (short gutter) consisted of 2 trials testing the effects of the fish acoustic signal and a control with no sound. In both experiments, we used megalopae and crab-1 individuals of *N. granulata* and *C. angulatus*. However, given the limited number of *C. altimanus* and *L. uruguayensis* individuals, we only included the crab-1 stage of these species in Expt 2.

In each trial, one individual, either a megalopa or a crab-1, was placed in the center of the gutter (point E) by using a plastic pipette. After 30 s of acclimation, the playbacks began and finished 5 min later. During each experimental trial, individuals were allowed to move freely, either towards (points A–C) or away from the sound source (points G–M; Fig. 2). The position of the individual was registered by an operator who was standing close to the tank (10 cm) in a central position without moving. After 5 min, when the experiment ended, the operator registered the position of the individual: toward the sound, in the central area or away from the sound. If the individual reached any terminal net of the gutter before the end of the experiment (i.e. before 5 min), the experiment was ended at this time and the position registered. The duration of the experiment was determined after conducting preliminary observations on megalopae behavior in the I-maze, which demonstrated that immediately after being placed in the system, they showed a swimming behavior (Valero et al. 1999).

2.6. Statistical analyses

An analysis to test for a difference in proportions (expected versus observed) was applied to investigate whether the individuals preferred to orientate to a particular acoustic stimulus: the observed frequencies were compared with expected frequencies of individuals in each area (toward the sound, central area, away from the sound) at the end of the experiment for each trial, considering the null hypothesis of independence between the acoustic stimulus and individuals' preferences. Significant differences between the observed and expected frequencies were examined using a chi-squared test of independence. When the chi-squared test detected differences, we calculated the contribution of each area selected by the individuals based on the contribution of absolute standardized residuals with the 'round' function in R. Analyses were performed using R version 3.3.1 (R Core Team 2016).

3. RESULTS

In Expt 1, megalopae and crab-1 individuals of *Cyrtograpsus angulatus* exhibited a significant positive response towards the crustacean sound ($p < 0.01$ for both crab stages), while they showed no significant orientation response to the motorboat stimulus, although the data for crab-1 individuals showed a ten-

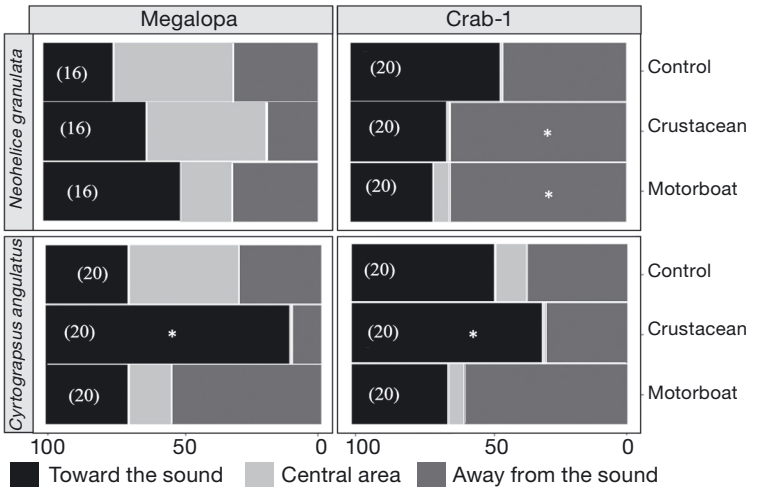


Fig. 6. Proportion of *Cyrtograpsus angulatus* and *Neohelice granulata* individuals (megalopa or stage 1 juvenile ['crab-1']) in the different areas (toward the sound, central area, away from the sound) at the end of the experiment for each trial (motorboat and crustacean stimuli and a control without sound stimulus). The N of each trial is shown in brackets. *Significant differences in pairwise comparisons between the toward the sound and away from the sound areas

Table 1. Results of the test for differences in proportions per species, crab stage (megalopa or stage 1 juvenile ['crab-1']) and trial: using the different acoustic stimuli (motorboat, crustacean, fish) and the control (without sound stimulus). Pairwise comparisons (difference between observed and expected values) are shown: Ts: toward sound area; Afs: away from sound area; Ca: central area. **Bold** indicates significant differences at $p < 0.01$; (–) no significant differences

Species	Stage	Trial	df	χ^2	Pairwise
Neohelice granulata	Megalopa	Motorboat	2	2.37	–
		Crustacean	2	1.56	–
		Control	2	1.31	–
		Fish	2	0.12	–
		Control	2	3.56	–
	Crab-1	Motorboat	2	**10.9**	Afs > Ts > Ca
		Crustacean	2	**11.7**	Afs > Ts > Ca
		Control	2	**10.3**	Ts = Afs > Ca
		Fish	2	**19.9**	Afs > Ts = Ca
		Control	2	**10.3**	Ts = Afs > Ca
Cyrtograpsus angulatus	Megalopa	Motorboat	2	0.6	–
		Crustacean	2	**29.2**	Ts > Afs > Ca
		Control	2	0.4	–
		Fish	2	2.43	–
		Control	2	1.19	–
	Crab-1	Motorboat	2	13.65	–
		Crustacean	2	**14.8**	Ts > Afs > Ca
		Control	2	**7.54**	Ts = Afs > Ca
		Fish	2	**19.17**	Afs > Ts > Ca
		Control	2	**15.5**	Ts = Afs > Ca
Cyrtograpsus altimanus	Crab-1	Fish	2	0.4	–
		Control	2	0.4	–
Leptuca uruguayensis	Crab-1	Fish	2	0.7	–
		Control	2	1.3	–

dency towards avoidance (Fig. 6, Table 1). *Neohelice granulata* megalopae showed no significant orientation to any sound sources, while *N. granulata* crab-1 showed a negative orientation response to both the crustacean and motorboat sound sources ($p < 0.01$ in both cases; Fig. 6, Table 1).

In Expt 2, the megalopae of *N. granulata* and *C. angulatus* did not show a significant response to the fish acoustic stimulus (Fig. 7, Table 1). In contrast, crab-1 individuals of both species showed a negative orientation response to the fish sound source ($p < 0.01$; Fig. 7). *Leptuca uruguayensis* and *C. altimanus* crab-1 juveniles showed no response to the fish sound stimulus (Fig. 7, Table 1).

In both Expts 1 and 2, although significant differences were found in control trials for crab-1 individuals of both *N. granulata* and *C. angulatus* (see p-values in Table 1), the pairwise test indicated that these differences were mainly due to the lower proportion of animals in the central area than to differences in the proportion of individuals moving towards or away from sound areas (Table 1). This suggests that crab-1 juveniles without a sound stimulus randomly chose between areas towards and away from the sound. For this reason, Figs. 6 & 7 only show when significant differences were found after pairwise comparisons in the proportion of individuals towards and away from sound areas.

4. DISCUSSION

The results of our experiment suggest that habitat-specific sounds could be used by megalopae and first juvenile crab stages to orient towards conspecific sound signals (*Cyrtograpsus angulatus* megalopae and crab-1 juveniles to crustacean stimulus) and away from predation sound signals (*Neohelice granulata* crab-1 individuals to fish and crustacean stimuli and *C. angulatus* to fish stimulus) or anthropogenic sound (*N. granulata* crab-1 juveniles to motorboat stimulus).

Reefs constructed by the invasive tube-building polychaete *Ficopomatus enigma-*

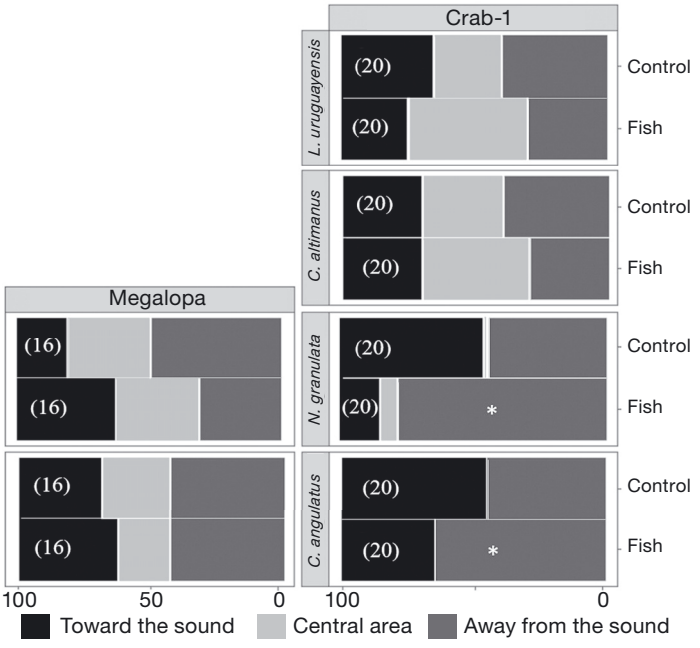


Fig. 7. Proportion of *Cyrtograpsus angulatus, Neohelice granulata, Cyrtograpsus altimanus* and *Leptuca uruguayensis* individuals (megalopa or stage 1 juvenile ['crab-1']) in the different areas (toward the sound, central area, away from the sound) at the end of the experiment for each trial (fish stimulus and a control without sound stimulus). The N of each trial is shown in brackets. *Significant differences in pairwise comparisons between the toward the sound and away from the sound areas

ticus play an important ecological role within this system by providing a source of nutrients and refuge for macrofaunal species (Bazterrica et al. 2012). Megalopae, juveniles and adults of *C. angulatus* preferentially settle inside reef crevices (Anger et al. 1994, Luppi et al. 2002a). Specifically, the *F. enigmaticus* reefs significantly impact the population biology of *C. angulatus* by increasing refuge availability and recruitment success and reducing intraspecific cannibalism (Spivak et al. 1994, Luppi et al. 2002a). The crustacean sound reproduced in the present study was recorded in a specific lagoon area, San Gabriel, with a high abundance of reefs (Ceraulo et al. 2020). Therefore, it was not surprising that megalopae and the first juvenile stage of *C. angulatus* responded positively toward the crustacean impulsive acoustic stimulus. Even though San Gabriel reef is an area located in the inner part of the lagoon, 7 km away from the mouth, sound emanating from the reef might orient *C. angulatus* megalopae as they return from the sea to reinvade the parental habitat. Several studies have proposed that the behavioral response towards the sound to settle and metamorphose cue could be extended to many kilometers (up to 40 km) (Radford et al. 2011, Stanley et al. 2011).

Moreover, impulsive crustacean acoustic signals were recorded in different parts of the lagoon, such as the mouth (connected to the sea) and Celpa (located approximately at 3.5 km from the mouth) (Ceraulo et al. 2020). These signals increased during the warm months (spring) and showed a clear circadian pattern in the mouth, being more frequently recorded after sunset (19:30 h) and before sunrise (05:30 h) (Ceraulo et al. 2020). The mouth is an important area where adults of *C. angulatus* congregate at high densities in spring for reproductive activities (Spivak et al. 1994). Two processes, i.e. (1) zoea hatching and their transport from the lagoon to the sea, and (2) megalopae reinvading the lagoon, are restricted and occur synchronously at extreme high tides (allowing rapid transport towards coastal marine waters) and during the night (diminishing predation risk by avoiding being seen), coinciding with the high-density larval peaks and the warm months when crabs reproduce (Anger et al. 1994, Bas et al. 2009). Consequently, *C. angulatus* megalopae may be using the impulsive crustacean signals of the different parts of the lagoon. Similarly, Stanley et al. (2012) reported the preference of different crab species for the high-frequency sounds associated with the high abundance of soniferous invertebrates inhabiting reefs, the primary adult habitat. These sound signals show a circadian pattern: the underwater sound made by several invertebrates of coastal reefs in New Zealand and Australia increase in intensity after sunset, coinciding with times when larvae are recruiting (Booth 2001, Radford et al. 2010). The orientation response towards a sound source was demonstrated in postlarvae of 5 New Zealand crab species, highlighting that this mechanism may be widespread among crab species (Radford et al. 2007). However, other factors mentioned previously, such as directional flow and megalopae swimming capacity, may be acting jointly with acoustic cues.

In contrast to *C. angulatus*, the megalopae of *N. granulata* did not show a positive response towards the crustacean acoustic stimulus. This could be explained by the recruitment process of this species, which occurs in a different habitat inside the lagoon. *N. granulata* megalopae settle within the adult burrows constructed in the mudflat and *Sporobolus densiflora* marsh of the lagoon, where different crab stages of this species (newly settled recruits, juveniles and adults) are found in high densities (Spivak et al. 1994). Given that the crustacean sound used as

stimuli in this experiment was recorded in San Gabriel reef, an area preferentially occupied by *C. angulatus*, and not in the mudflat or saltmarsh where *N. granulata* recruits, it was expected that megalopae would not show a positive orientation response. Similarly, megalopae of the mud crab *Austrohelice crassa* settled in soft sediment habitats and exhibited no response to underwater reef sound, demonstrating a discriminating capacity among suitable settlement habitats based on the habitat sound signature (Stanley et al. 2011). Furthermore, the negative response of *N. granulata* juveniles toward the crustacean stimulus may be related to avoiding predation risk, given that laboratory experiments have demonstrated that juveniles of *C. angulatus* prey heavily on *N. granulata* settlers (Luppi et al. 2001).

Sound-production capacity has been demonstrated in *N. granulata* (Filiciotto et al. 2019) and is associated with mating behavior (Sal Moyano et al. 2019). Thus, future studies testing the role of specific *N. granulata* acoustic signals recorded from its settlement/adult habitat could help to elucidate their importance to megalopae orientation. However, *N. granulata* megalopae could be using multiple factors for orientation; for example, they are capable of actively swimming to select suitable substrate (Valero et al. 1999), and can detect suitable settlement habitats following chemical cues from conspecifics and substrate (Gebauer & Paschke 2020). Postlarvae of the lobster *Jasus edwardsii* likely orient by using multiple cues: waves and wind when they are far from the coast and chemical signals when they are close to the coast, which could then trigger the use of acoustic cues (Hinojosa et al. 2018).

When testing the effect of the motorboat acoustic stimulus, megalopae of both *N. granulata* and *C. angulatus* did not show a preference, either positively or negatively, to the played back sound. In contrast, the first juvenile stage of *N. granulata* showed a negative response to the motorboat stimulus. *C. angulatus* crab-1 juveniles exhibited no statistically significant response to motorboat sound, although a tendency toward a negative effect was observed in the data. The different behavioral responses of both species between the 2 developmental stages, megalopae and crab-1, to the motorboat sound could be due to the temporal occurrence of megalopae. Motorboat activity is more frequent during the spring and summer in the lagoon because fishing and recreational boating activities occur mostly in those seasons, which coincide with peaks in larval abundance. However, the noise associated with motorboat activity inside the lagoon is restricted to daylight and sunset hours (Ceraulo et al. 2021), while megalopae enter the lagoon mostly at night. Therefore, it is suggested that motorboat activity might not affect megalopae orientation and settlement behavior, given that larvae may not be greatly exposed to this noise type under natural ambient conditions.

As an alternative explanation, sensory organs in megalopae may not be similarly developed as those in juveniles, thus causing an impaired ability to detect the anthropogenic sound. Sensory abilities are expected to increase between hatching and settlement, being more limited earlier in the life of crustacean larvae (Kingsford et al. 2002). The controlled environment condition of our experiment resulted in a reduction of stimuli energy in the low-frequency band. This could have reduced the perception of the motorboat noise, which has a higher energy component in the low-frequency band (Kaplan & Mooney 2015), probably making it perceivable only by juveniles. The auditory system of decapod crustaceans is poorly understood, even less so in early life history stages, although sensory structures such as receptors have been described to respond to hydrodynamic flows, particle motion and pressure changes (Popper et al. 2001). No information about acoustic capacities of our studied species has been published. Thus, further studies are needed to understand the mechanisms underlying the perception of positive or negative acoustic stimuli.

The results of our study suggest that in the Mar Chiquita lagoon, multiple factors influence megalopae habitat selection, including ocean physical factors, natural acoustic signals and swimming behavior of larvae, while others, such as anthropogenic sound, might not have such an important effect on their orientation response. In contrast, previous studies have demonstrated that motorboat noise can increase the median time to metamorphosis of crab megalopae (Pine et al. 2012), reduce the successful development of embryos and increase mortality of recently hatched sea hare larvae (Nedelec et al. 2014), and disrupt the settlement behaviors of coral planulae (Lecchini et al. 2018). Thus, the effect of the anthropogenic sound on other biological activities of crab larvae in the lagoon should not be disregarded.

Juvenile *N. granulata* and *C. angulatus* are restricted to their respective microhabitats inside the lagoon and, although the motorboat passages are mostly concentrated in the mouth, other areas of the lagoon are also exposed to this anthropogenic sound (Ceraulo et al. 2020). Consequently, the motorboat noise could affect the diverse biological activities of the crabs, such as reproductive or trophic activities,

which are also higher during spring and summer. Anthropogenic sound might have a negative effect on the physiology and/or behavior of crustaceans (e.g. Wale et al. 2013, Edmonds et al. 2016, Filiciotto et al. 2016). Specifically, in *N. granulata*, exposure to a sweep-tone noise had negative effects on the behavioral and biochemical responses of adults (Filiciotto et al. 2018).

In our study, megalopae of both *C. angulatus* and *N. granulata* exhibited no response to the fish acoustic stimulus, which might be related to the fact that we used recordings of *Pogonias courbina*. This species does not feed on megalopae; thus, it is not a predator of megalopae of either species tested here. By contrast, *P. courbina* largely feeds on benthic invertebrates, including juvenile and adult crabs of *C. angulatus* and *N. granulata* (Blasina et al. 2010). As expected, therefore, juveniles (crab-1) of both species exhibited a negative response to the fish acoustic stimulus. Lower-frequency fish vocalizations associated with a predatory threat to crabs were previously reported (Connaughton 2004). *C. altimanus* and *L. uruguayensis* showed no response to the fish acoustic sound. A possible explanation for this is that these species occupy habitats rarely reached by *P. courbina*: *C. altimanus* is restricted to the rocky intertidal area of the lagoon mouth (Spivak et al. 1994), while *L. uruguayensis* is a burrowing crab of the upper intertidal and, when burrows are covered with water during high tide, crabs remain inside them and close the entrance with sediment (Spivak et al. 1991, Ribeiro et al. 2003).

5. CONCLUSION

This study shows how isolating different sound components of the overall soundscape and testing them in a controlled laboratory experiment can determine diverse effects on different crab species and life stages based on their ecological role. The diverse orientation response of megalopae and crab-1 stages of the different species to the acoustic cues seems to depend on specific temporal and spatial sound patterns. It is highly likely that sound signals do not work in isolation but rather act in combination with other factors, such as physical cues (tide, salinity, wind), chemical cues, swimming capacity and biological interactions (predation, cannibalism). However, acoustic signals may be very important, given that in our controlled experiment, no effect of physical or chemical factors occurred, but both megalopae and crab-1 juveniles of the different species showed diverse positive/negative responses towards the acoustic cues. The results support the idea that invertebrates can discriminate among sound signals and also emphasize the role of sound on prey–predator relationships. Moreover, the negative response of juveniles towards the motorboat noise may reflect an effect of anthropogenic sound on behavior, possibly affecting intra- and interspecific biological interactions. This is very important, given the role of the key crab species inside the lagoon, and especially considering the importance of this habitat in terms of productivity, biodiversity and its function as an important source of ecosystem services. However, conducting acoustic experiments in laboratory tanks produces limitations given that animals in the natural habitat are usually exposed to multiple sound sources simultaneously, rather than individually and in isolation. This should probably be addressed in future studies. Also, future investigations measuring the particle motion sound propagation in this type of tank experiment are needed to better understand the results obtained and the sensory abilities of the different crab stages to respond positively or negatively to the different sound sources.

Dedication: We dedicate this article to Salvo Mazzola (28 July 1953 – 17 January 2021). This work is the expression of a collaboration that would have been impossible without his acuity, determination and imagination, and for this we feel deeply the great loss that his passing represents.

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LITERATURE CITED

Akamatsu T, Okumura T, Novarini N, Yan HY (2002) Empirical refinements applicable to the recording of fish sounds in small tanks. J Acoust Soc Am 112:3073–3082

Anger K, Spivak E, Bas C, Ismael D, Luppi T (1994) Hatching rhythms and dispersion of decapod crustacean larvae in a brackish coastal lagoon in Argentina. Helgol Meeresunters 48:445–466

Anger K, Spivak E, Luppi T, Bas C, Ismael D (2008) Larval salinity tolerance of the South American salt-marsh crab, *Neohelice* (*Chasmagnathus*) *granulata*: physiological

constraints to estuarine retention, export and reimmigration. Helgol Mar Res 62:93–102
Bas C, Luppi T, Spivak E, Schejter L (2009) Larval dispersion of the estuarine crab *Neohelice granulata* in coastal marine waters of the Southwest Atlantic. Estuar Coast Shelf Sci 83:569–576
Bazterrica MC, Botto F, Iribarne O (2012) Effects of an invasive reef-building polychaete on the biomass and composition of estuarine macroalgal assemblages. Biol Invasions 14:765–777
Bedford BL, Leopold DJ, Gibbs JP (2001) Wetlands ecosystems. In: Levin SA (ed) Encyclopedia of biodiversity, Vol 5. Academic Press, Orlando, FL, p 781–804
Blasina GE, Barbini SA, Díaz de Astarloa JM (2010) Trophic ecology of the black drum, *Pogonias cromis* (Sciaenidae), in Mar Chiquita coastal lagoon (Argentina). J Appl Ichthyol 26:528–534
Blom EL, Kvarnemo C, Dekhla I, Schöld S, Andersson MH, Svensson O, Amorim MCP (2019) Continuous but not intermittent noise has a negative impact on mating success in a marine fish with paternal care. Sci Rep 9:5494
Booth JD (2001) Habitat preferences and behaviour of newly settled *Jasus edwardsii* (Palinuridae). Mar Freshw Res 52:1055–1065
Boschi EE, Scelzo MA, Goldstein B (1967) Desarrollo larval de dos especies de Crustáceos Decápodos en el laboratorio, *Pachycheles haigae* Rodrigues da Costa (Porcellanidae) y *Chasmagnathus granulata* Dana (Grapsidae). Bol Inst Biol Mar 12:1–46
Botero L, Atema J (1982) Behavior and substrate selection during larval settling in the lobster *Homarus americanus*. J Crustac Biol 2:59–69
Buscaino G, Mattiazzo G, Sannino G, Papale E and others (2019) Acoustic impact of a wave energy converter in Mediterranean shallow waters. Sci Rep 9:9586
Ceraulo M, Papale E, Caruso F, Filiciotto F and others (2018) Acoustic comparison of a patchy Mediterranean shallow water seascape: *Posidonia oceanica* meadow and sandy bottom habitats. Ecol Indic 85:1030–1043
Ceraulo M, Sal Moyano MP, Bazterrica MC, Hidalgo FJ and others (2020) Spatial and temporal variability of the soundscape in a Southwestern Atlantic coastal lagoon. Hydrobiologia 847:2255–2277
Ceraulo M, Sal Moyano MP, Hidalgo FJ, Bazterrica MC, Mazzola S, Gavio MA, Buscaino G (2021) Boat noise and black drum vocalizations in Mar Chiquita coastal lagoon (Argentina). J Mar Sci Eng 9:44
Clark CW, Ellison WT, Southall BL, Hatch L, Van Parijs SM, Frankel A, Ponirakis D (2009) Acoustic masking in marine ecosystems: intuitions, analysis, and implication. Mar Ecol Prog Ser 395:201–222
Connaughton MA (2004) Sound generation in the searobin (*Prionotus carolinus*), a fish with alternate sonic muscle contraction. J Exp Biol 207:1643–1654
Edmonds NJ, Firmin CJ, Goldsmith D, Faulkner RC, Wood DT (2016) A review of crustacean sensitivity to high amplitude underwater noise: data needs for effective risk assessment in relation to UK commercial species. Mar Pollut Bull 108:5–11
Fernandez M, Iribarne O, Armstrong D (1993) Habitat selection by young-of-the-year Dungeness crab *Cancer magister* and predation risk in intertidal habitats. Mar Ecol Prog Ser 92:171–177
Filiciotto F, Vazzana M, Celi M, Maccarrone V and others (2016) Underwater noise from boats: measurement of its influence on the behaviour and biochemistry of the common prawn (*Palaemon serratus*, Pennant 1777). J Exp Mar Biol Ecol 478:24–33
Filiciotto F, Sal Moyano MP, de Vincenzi G, Hidalgo F and others (2018) Are semi-terrestrial crabs threatened by human noise? Assessment of behavioural and biochemical responses of *Neohelice granulata* (Brachyura, Varunidae) in tank. Mar Pollut Bull 137:24–34
Filiciotto F, Sal Moyano MP, Hidalgo F, de Vincenzi G and others (2019) Underwater acoustic communication during the mating behaviour of the semi-terrestrial crab *Neohelice granulata*. Sci Nat 106:35
Gebauer P, Paschke K (2020) Cues for metamorphosis and implications. In: Rodriguez EM, Luppi TA (eds) *Neohelice granulata*, a model species for studies on crustaceans. Vol 1, Life history and ecology. Cambridge Scholars Publishing, Newcastle upon Tyne, p 105–116
Giménez L, Torres G (2020) Phenotypic plasticity. In: Rodriguez EM, Luppi TA (eds) *Neohelice granulata*, a model species for studies on crustaceans. Vol 1, Life history and ecology. Cambridge Scholars Publishing, Newcastle upon Tyne, p 45–64
Hawkins AD, Myrberg AA (1983) Hearing and sound communication under water. In: Lewis B (ed) Bioacoustics, a comparative approach. Academic Press, London, p 347–405
Herrnkind WF, Butler MJ IV (1986) Factors regulating postlarval settlement and juvenile microhabitat use by spiny lobsters *Panulirus argus*. Mar Ecol Prog Ser 34:23–30
Hinojosa IA, Green BS, Gardner C, Hesse J, Stanley JA, Jeffs AG (2016) Reef sound as an orientation cue for shoreward migration by pueruli of the rock lobster, *Jasus edwardsii*. PLOS ONE 11:e0157862
Hinojosa IA, Gardner C, Green BS, Jeffs A (2018) Coastal chemical cues for settlement of the southern rock lobster, *Jasus edwardsii*. Bull Mar Sci 94:619–633
Hovel KA, Morgan SG (1997) Planktivory as a selective force for reproductive synchrony and larval migration. Mar Ecol Prog Ser 157:79–95
Iribarne O (ed) (2001) Reserva de Biosfera Mar Chiquita: características físicas, biológicas y ecológicas. Editorial Martin, Mar del Plata
Isacch J, Escapa M, Fanjul E, Iribarne O (2010) Valoración ecológica de bienes y servicios ecosistémicos en marismas del Atlántico Sudoccidental. In: Laterra P, Jobaggy E, Paruelo J (eds) Valoración de servicios ecosistémicos: conceptos, herramientas y aplicaciones para el ordenamento territorial. INTA, Buenos Aires, p 529–551
Jeffs A, Tolimieri N, Montgomery JC (2003) Crabs on cue for the coast: the use of underwater sound for orientation by pelagic crab stages. Mar Freshw Res 54:841–845
Jeffs AG, Montgomery JC, Tindle CT (2005) How do spiny lobster post-larvae find the coast? NZ J Mar Freshw Res 39:605–617
Kaplan MB, Mooney TA (2015) Ambient noise and temporal patterns of boat activity in the US Virgin Islands National Park. Mar Pollut Bull 98:221–228
Kingsford MJ, Leis JM, Shanks A, Lindeman KC, Morgan SG, Pineda J (2002) Sensory environments, larval abilities and local self-recruitment. Bull Mar Sci 70:309–340
Lecchini D, Bertucci F, Gache C, Khalife A and others (2018) Boat noise prevents soundscape-based habitat selection by coral planulae. Sci Rep 8:9283
Luppi TA, Spivak ED, Anger K (2001) Experimental studies on predation and cannibalism of the settlers of *Chasma-*

gnathus granulata and *Cyrtograpsus angulatus* (Brachyura: Grapsidae). J Exp Mar Biol Ecol 265:29–48

Luppi TA, Spivak ED, Anger K, Valero JL (2002a) Patterns and processes of *Chasmagnathus granulata* and *Cyrtograpsus angulatus* (Brachyura: Grapsidae) recruitment in Mar Chiquita coastal lagoon, Argentina. Estuar Coast Shelf Sci 55:287–297

Luppi T, Spivak E, Anger K (2002b) Postsettlement growth of two estuarine crab species, *Chasmagnathus granulata* and *Cyrtograpsus angulatus* (Crustacea, Decapoda, Grapsidae): laboratory and field investigations. Helgol Mar Res 55:293–305

Luppi T, Bas C, Méndez Casariego A, Albano M and others (2013) The influence of habitat, season and tidal regime in the activity of the intertidal crab *Neohelice* (= *Chasmagnathus*) *granulata.* Helgol Mar Res 67:1–15

Mauro M, Pérez-Arjona I, Perez EJB, Ceraulo M and others (2020) The effect of low frequency noise on the behaviour of juvenile *Sparus aurata.* J Acoust Soc Am 147:3795–3807

Moksnes PO (2002) The relative importance of habitat-specific settlement, predation and juvenile dispersal for distribution and abundance of young juvenile shore crabs *Carcinus maenas* L. J Exp Mar Biol Ecol 271:41–73

Nedelec SL, Radford AN, Simpson SD, Nedelec B, Lecchini D, Mills SC (2014) Anthropogenic noise playback impairs embryonic development and increases mortality in a marine invertebrate. Sci Rep 4:5891

Ospina-Alvarez A, Weidberg N, Aiken CM, Navarrete SA (2018) Larval transport in the upwelling ecosystem of central Chile: the effects of vertical migration, developmental time and coastal topography on recruitment. Prog Oceanogr 168:82–99

Payne JF, Andrews CD, Fancey LL, Guiney J, Cook A, Christian JR (2008) Are seismic surveys an important risk factor for fish and shellfish? Bioacoustics 17:262–265

Pijanowski BC, Villanueva-Rivera LJ, Dumyahn SL, Farina A and others (2011) Soundscape ecology: the science of sound in the landscape. Bioscience 61:203–216

Pine MK, Jeffs AG, Radford CA (2012) Turbine sound may influence the metamorphosis behaviour of estuarine crab megalopae. PLOS ONE 7:e51790

Pineda J, Porri F, Starczak V, Blythe J (2010) Causes of decoupling between larval supply and settlement and consequences for understanding recruitment and population connectivity. J Exp Mar Biol Ecol 392:9–21

Popper AN, Salmon M, Horch KW (2001) Acoustic detection and communication by decapod crustaceans. J Comp Physiol A Neuroethol Sens Neural Behav Physiol 187: 83–89

R Core Team (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Radford CA, Jeffs AG, Montgomery JC (2007) Directional swimming behavior by five species of crab postlarvae in response to reef sound. Bull Mar Sci 80:369–378

Radford CA, Stanley JA, Tindle CT, Montgomery JC, Jeffs AG (2010) Localised coastal habitats have distinct underwater sound signatures. Mar Ecol Prog Ser 401:21–29

Radford CA, Tindle CT, Montgomery JC, Jeffs AG (2011) Modelling a reef as an extended sound source increases the predicted range at which reef noise may be heard by fish larvae. Mar Ecol Prog Ser 438:167–174

Reserves B (1996) The Seville strategy and the statutory framework of the world network. UNESCO, Paris

Reta R, Martos P, Perillo GME, Piccolo MC, Ferrante A (2001) Características hidrográficas del estuario de la laguna Mar Chiquita. In: Iribarne O (ed) Reserva de Biósfera Mar Chiquita: características físicas, biológicas y ecológicas. Editorial Martin, Mar del Plata, p 31–52

Ribeiro PD, Iribarne OO, Jaureguy L, Navarro D, Bogazzi E (2003) Variable sex-specific mortality due to shorebird predation on a fiddler crab. Can J Zool 81:1209–1221

Rieger PJ, Vieira RRR (1997) Desenvolvimento larval de *Cyrtograpsus angulatus* Dana (Crustacea, Decapoda, Grapsidae) em laboratorio. Rev Bras Zool 14:601–623

Sal Moyano MP, Ceraulo M, Mazzola S, Buscaino G, Gavio MA (2019) Sound production mechanism in the semiterrestrial crab *Neohelice granulata* (Brachyura, Varunidae). J Acoust Soc Am 146:3466–3474

Schwindt E, Iribarne OO, Isla FI (2004) Physical effects of an invading reef-building polychaete on an Argentinean estuarine environment. Estuar Coast Shelf Sci 59: 109–120

Simpson SD, Radford AN, Holles S, Ferarri MCO, Chivers DP, McCormick MI, Meekan MG (2016) Small-boat noise impacts natural settlement behavior of coral reef fish larvae. In: Popper AN, Hawkins A (eds) The effects of noise on aquatic life II. Springer, New York, NY, p 1041–1048

Slabbekoorn H, Bouton N (2008) Soundscape orientation: a new field in need of sound investigation. Anim Behav 76: e5–e8

Solan M, Hauton C, Godbold JA, Wood CL, Leighton TG, White P (2016) Anthropogenic sources of underwater sound can modify how sediment-dwelling invertebrates mediate ecosystem properties. Sci Rep 6:20540

Spivak ED, Gavio MA, Navarro CE (1991) Life history and structure of the world's southernmost *Uca* population: *Uca uruguayensis* (Crustacea, Brachyura) in Mar Chiquita Lagoon (Argentina). Bull Mar Sci 48:679–688

Spivak E, Anger K, Luppi T, Bas C, Ismael D (1994) Distribution and habitat preferences of two grapsid crab species in Mar Chiquita Lagoon (Province of Buenos Aires, Argentina). Helgol Meeresunters 48:59–78

Spivak ED, Anger K, Bas CC, Luppi TA, Ismael D (1996) Size structure, sex ratio, and breeding season in two intertidal grapsid crab species from Mar Chiquita lagoon, Argentina. Neritica 10:7–26

Stanley JA, Radford CA, Jeffs AG (2011) Behavioural response thresholds in New Zealand crab megalopae to ambient underwater sound. PLOS ONE 6:e28572

Stanley JA, Radford CA, Jeffs AG (2012) Location, location, location: finding a suitable home among the noise. Proc R Soc B 279:3622–3631

Valero J, Luppi T, Iribarne O (1999) Size as indicator of swimming speed in crab megalopae. J Shellfish Res 18: 663–666

Wale MA, Simpson SD, Radford AN (2013) Noise negatively affects foraging and antipredator behaviour in shore crabs. Anim Behav 86:111–118

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