

Resonating sea urchin skeletons create coastal choruses

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ABSTRACT: Ambient sound intensity in coastal waters typically increases by as much as 2 to 3 orders of magnitude (20 to 30 dB) immediately after sunset and before sunrise in what is known as a dawn and evening chorus. The dominant feature of the chorus is most often a dramatic increase in spectrum level usually in a narrow frequency range of around 400 to 4000 Hz. While the sources of some choruses have been identified, the sources of many choruses remain unidentified. Here we confirm that in New Zealand, the sound is the feeding noises of sea urchins for which frequencies in the range of 800 to 2800 Hz are amplified by the ovoid calcareous skeleton, or 'test', of urchins acting as a Helmholtz resonator. Furthermore, the timing of the dawn and dusk choruses is related to the crepuscular feeding activity of sea urchins. Underwater sound recordings from individual sea urchins of a range of sizes confirm earlier speculation that the urchin test acts as a Helmholtz resonance chamber capable of generating sufficient acoustic power to create these choruses. These results indicate the potential importance of coastal urchin populations as a major contributor to the underwater choruses, which appear to be important in assisting the larvae of key reef species, such as fishes, crabs, and lobsters, to locate suitable settlement sites.

KEY WORDS: Sea urchins · Dusk chorus · Helmholtz resonator · Ambient underwater sound · Orientation cue · *Evechinus chloroticus*

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INTRODUCTION

There is growing evidence of the ecological importance of underwater sound in structuring marine communities through its use in communication and by providing vital orientation and warning cues for animals (McCauley & Cato 2000, Stocker 2002, Simpson et al. 2005, Montgomery et al. 2006). For example, recent research has demonstrated that underwater sound emanating from reefs provides a key orientation cue for the recruiting stages of many types of reef fishes and crabs swimming toward settlement habitats (Stobutzki & Bellwood 1998, Tolimieri et al. 2000, 2002, 2004, Leis et al. 2002, Jeffs et al. 2003, 2005, Simpson et al. 2004, 2005, 2008, Leis & Lockett 2005, Radford et al. 2007). While many of the biological sources of underwater sound and choruses have been identified (Fish 1964, Tait 1964, D'Spain & Batchelor 2006), there

remain many choruses for which the sound sources are unknown. It is very difficult to use field recordings of animals in open waters to confirm the target animals as the source of any ambient noise. The tremendous acoustic conductivity of seawater means that sound recorded in the field could have come from any noise-producing animal or abiotic source, both near or far. There are several ways in which source organisms can be reliably determined. Noise-generating organisms can be recorded and their sounds characterized in isolation from all other potential acoustic sources. Alternatively, they can be studied *in situ* with video recorders in association with recording devices to determine behavioral events associated with noise production (Tricas et al. 2006), or the animals can be observed directly while recording their sounds by divers using closed-circuit rebreathers to limit extraneous noise (Lobel 2001, 2005, Radford et al. 2005).

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Many of the organisms responsible for the dramatic increase in ambient underwater sound immediately after dusk and before dawn, which is a feature of coastal reef ecosystems in many parts of the world (Fish 1964), remain unidentified. For example, the source of underwater dusk choruses, which increase ambient sound levels by as much as 20 to 30 dB re 1 μ Pa in temperate waters such as in Australia and New Zealand, has never been reliably confirmed, although responsibility has been assigned to a range of potential candidate species, including fishes and urchins (Cummings et al. 1964, Fish 1964, Cato 1978). The feeding activities of sea urchins have been suggested as a possible source of the major component of the chorus due to their ubiquitous presence in most temperate reef systems (Tait 1964, Cato 1978). In addition, the possibility of the feeding noises being amplified by the ovoid calcareous skeleton (or 'test') of urchins acting as a resonance chamber was invoked in an attempt to reconcile the large overall intensity level of the dusk chorus versus the relatively small size of the urchins (Castle 1974, Castle & Kibblewhite 1975, Cato 1977). Although an urchin test would appear to have suitable attributes to operate as a Helmholtz resonator, i.e. an enclosed volume of fluid with an external aperture allowing oscillations of fluid through the aperture to entrain the enclosed fluid to oscillate in sympathy (Cato 1977), there is no experimental evidence to support this proposition.

We therefore set out to determine the biological source of this important phenomenon by recording the ambient underwater sound near a temperate reef and then analyzing the frequency components that characterized the choruses. The spectral composition of ambient sound was then compared to feeding noises recorded from sea urchins over a range of sizes isolated in tanks. The frequency components of sound generated by individual urchins over a range of test sizes were compared to theoretical predictions for Helmholtz resonators to establish if the frequencies of the acoustic output from the urchin skeletons were consistent with ideal resonant Helmholtz chambers.

MATERIALS AND METHODS

The study was undertaken at the Leigh Marine Laboratory, located in northern New Zealand (36° 15' S, 174° 47' E) next to a marine reserve encompassing 6.5 km of rocky reef coastline typical of a temperate marine environment. Sixty urchins of a range of sizes (31 to 90 mm test diameter) were collected using SCUBA from a nearby reef (North Reef, Leigh, 36° 15' 45" S, 174° 47' 33" E) and transferred to the lab-

oratory where they were held in flow-through aquaria (1500 L; 1.8 m diameter, 0.65 m deep) containing ambient seawater (temperature 15°C; salinity 33‰). The experiment ran from 10 July to 12 August 2006. To stimulate urchin feeding, an artificial diet (Hay et al. 1998) was painted onto weathered cobble stones (210 × 210 mm) and set in a refrigerator. The external diameters of urchin tests were measured with pointed Vernier calipers squeezed tightly between the spines down to the exterior of the test. Measured urchins were then sorted into 10 mm size classes (31–40 mm, 41–50 mm, 51–60 mm, 61–70 mm, 71–80 mm, and 81–90 mm) and held in separate aquaria without food for 2 nights before being used for experimental recordings. The night before being recorded, the urchins were removed from the aquaria and placed into separate aquaria (5 urchins per night) and allowed to recover from the disturbance. The urchins were then placed onto the cobble stones 30 min before dusk, when the first recording started. Five 2 min recordings were made of each urchin grazing. It was possible to record up to 5 urchins each night, and in total, 30 urchins were recorded (5 urchins in each of the 6 size classes). Control recordings were taken in empty aquaria before urchins were placed into them, and there was no extraneous noise that could have influenced the results.

Urchin grazing noises were recorded with a calibrated SQ03 wideband omnidirectional hydrophone (Sensor Technology), with a flat frequency-response curve from 10 to 60 kHz. This enabled the hydrophone to be calibrated by recording a single frequency acoustic pinger (NetMark™ 1000, source level 130 dB re 1 μ Pa at 1 m, 10 kHz signal, 300 ms pulse length, 4 s repetition rate). The hydrophone was suspended in the tanks and maintained at a distance of 10 cm away from the feeding urchin and 1 cm above the cobble stone. The hydrophone signal was recorded on a Sony TCD-D8 digital recorder with a sampling rate of 48 kHz. The digital recordings were transferred to a PC and analyzed using Matlab software with codes specifically written for these recordings. Resonant frequencies were obtained by analyzing 1 randomly selected grazing event out of each of the 2 min recordings from each urchin.

Urchins have a hard test in the shape of a flattened sphere with a circular opening on the ventral surface for the mouthparts. It is likely that this test behaves acoustically as a neckless Helmholtz resonator with a resonant frequency given by $f = [c/(2\pi)] \times \sqrt{(2R/V)}$, where c is the speed of sound in water, R is the radius of the neck and V is the volume of the resonator (Stephen & Bate 1966). Assuming that urchins maintain the same proportions as they grow, the neck radius (R) will be proportional to the diameter (D) of the urchin, and

the volume (V) will be proportional to D^3 , giving a resonant frequency proportional to $1/D$. The hypothesis that the urchins behave as Helmholtz resonators was tested by regression analysis of the resonant frequency as a function of the reciprocal ($1/D$) of the urchin diameter. An adequacy of fit test was conducted on the regression due to the repeated-measure nature of the data. To test whether the theoretical model fitted the experimental data, a Student's t -test was conducted to compare the slopes of the regression lines (Zar 1999).

To assess temporal variation in ambient noise at the North Reef study site, ambient noise was recorded over the new moon (which was considered to be 3 d either side of the astronomical event) during the austral spring (September to November). A hydrophone-recorder unit was placed 1 m off the seafloor in 21 to 23 m of water depending on the tide, and 80 m away from the margin of the coastal fringing reef. The hydrophone-recorder consisted of a calibrated Sonatech BM 216 omnidirectional hydrophone (10 Hz to 60 kHz flat response) connected to an automated recording system contained in an underwater housing. The system consisted of a Unidata Micrologger timing and relay unit operating a Sony TCD-D8 digital recorder with a sampling rate of 48 kHz, which took a 5 min recording hourly, on the hour. The hydrophone was calibrated by recording a NetMark 1000 acoustic pinger (specifications: source level 130 dB re 1 μ Pa at 1 m, 10 kHz signal, 300 ms pulse length, 4 s repetition rate). The recordings were transferred to a PC and analyzed using Matlab software with codes specifically written for these recordings. Spectrum levels were obtained by taking a Fourier transform of 1 s of data and smoothing the result with a triangular window.

RESULTS

We observed a 100-fold increase (20 dB re 1 μ Pa² Hz⁻¹) in the overall intensity of ambient underwater sound between recordings taken from North Reef at midday (12:00 h) compared to early evening (18:00 h). Over 82% of this dramatic increase in acoustic intensity was in the range of 700 to 2000 Hz (Fig. 1). The daily pattern of timing of these choruses is entirely consistent with the crepuscular feeding behavior that is common among sea urchins, including the urchin species most common at our study site, *Evechinus chloroticus*.

Analyses of underwater sound recordings of the feeding of isolated individual urchins demonstrated that the spectral band of the sound output for the 30 urchins recorded over a wide range of sizes was entirely consistent with the dominant component of the ambient chorus recorded near a reef, i.e. in the range

of 700 to 2000 Hz. One example is shown of the typical waveform of a single scrape for an urchin with a test diameter of 83 mm (Fig. 2A). Six oscillations in 0.007 s equates to 1 oscillation in 0.00116 s or a frequency of 860 Hz. This corresponds to the spectrograms, with the resonant frequency close to 900 Hz (Fig. 2B), and is consistent with the presence of resonance amplification of base feeding noises in these specific frequency ranges. The corresponding sonogram of this scrape also shows that the majority of the noise was produced at 900 Hz (Fig. 3). A second example shows that a 42 mm test diameter urchin produced 7 oscillations in 0.004 s (Fig. 4A), which equates to a single oscillation in 0.00057 s or a frequency of 1754 Hz (Fig. 4B) in a single feeding scrape. Furthermore, there was a very close inverse relationship between urchin test diameter and the dominant frequency (Fig. 5). Regression analysis of 150 feeding events (5 from each of 30 individuals) showed a positive and significant correlation ($r^2 = 0.85$, $y = 106\,297x - 319.71$) between the dominant frequencies produced by feeding urchins and the reciprocal of the test diameter ($1/D$) (Fig. 5). The adequacy of fit test showed that the regression was also a linear fit to the data ($F = 1.2$, $p > 0.05$). The largest urchin recorded (88 mm test diameter) had a dominant frequency output of 822 ± 70 Hz, and the smallest urchin recorded (31 mm) had a dominant frequency output of 2800 ± 140 Hz. These observed frequencies are entirely consistent with resonant frequencies calculated for theoretical Helmholtz resonators of the same dimensions ($t_{0.05(2),31} = 0.9$, $p > 0.05$; Cato 1977; Fig. 5).

DISCUSSION

Our results strongly suggest that the feeding sound resonating in the calcareous skeletons of sea urchins accounts for the evening chorus in the frequency range 700 to 2000 Hz in New Zealand waters. It also suggests that sea urchins could be responsible for evening choruses with a similar frequency bandwidth that have been observed in other parts of the world, e.g. the Bahamas (Fish 1964), San Diego, California, USA (D'Spain & Batchelor 2006), and Australia (Cato 1978). The unique frequency signature and the intensity of the sound produced by urchins during the chorus has the potential to be an important source of habitat information for marine organisms listening to this sound from more distant locations. However, only 2 studies have indicated that larval fish can respond to different frequencies (Simpson et al. 2005, 2008). Using patch reefs and replaying either high (>570 Hz) or low (<570 Hz) frequency sound, Simpson et al. (2005) showed that pomacentrid fish settled in higher numbers in response to low frequency sound, apogonid fish

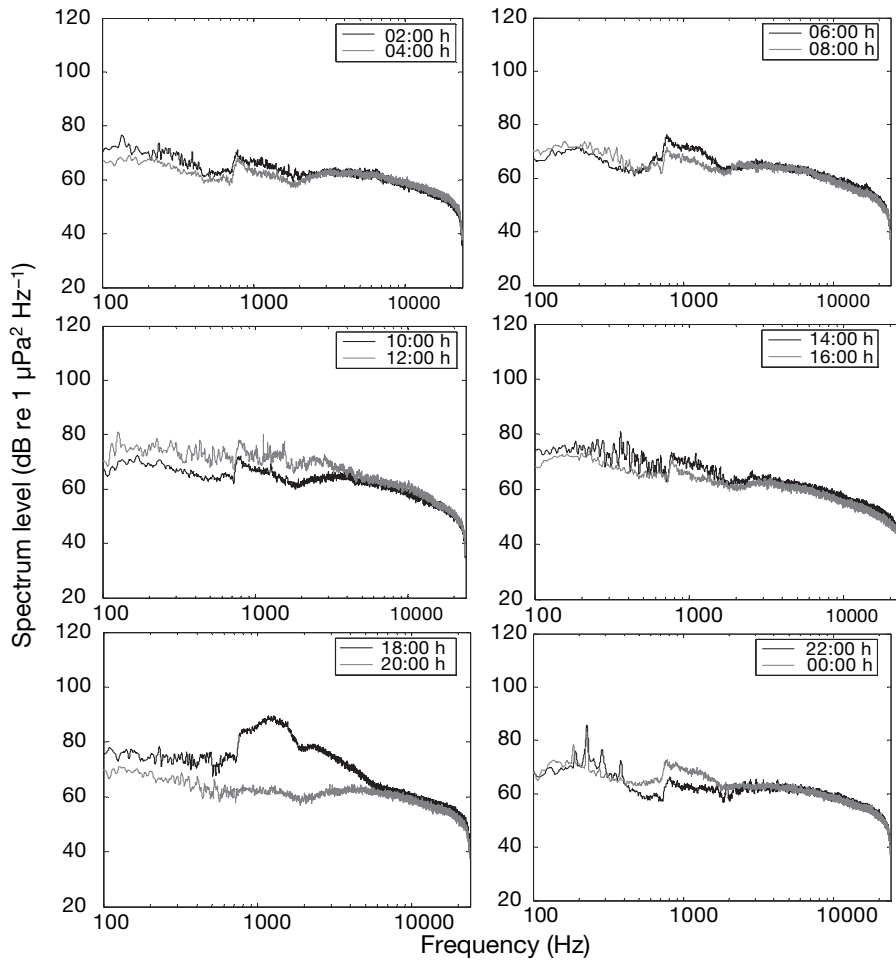


Fig. 1. *Evechinus chloroticus*. Spectrum levels taken during the new moon period in the austral spring. Each plot represents 2 recordings separated by a 2 h period (times are indicated in the legends)

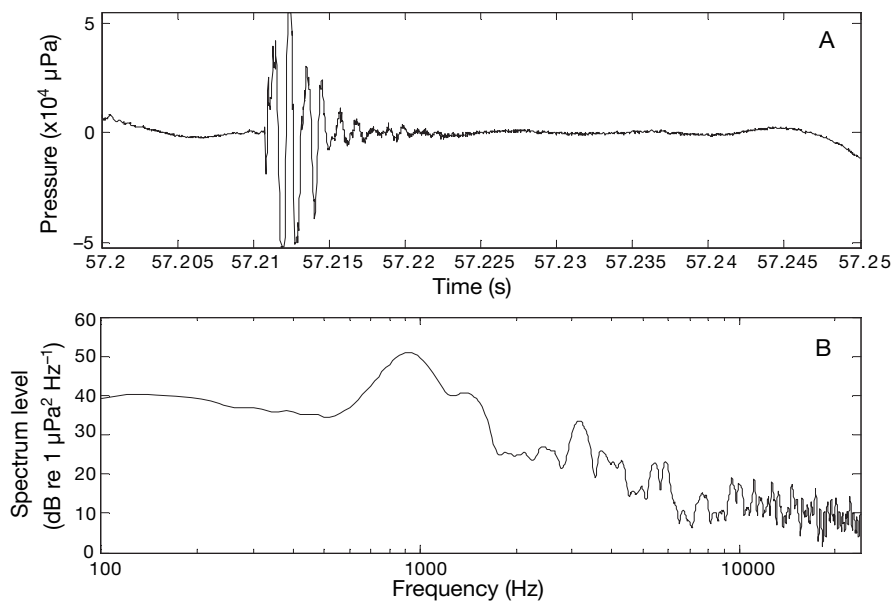


Fig. 2. *Evechinus chloroticus*. (A) Wave form of a typical scrape by an urchin with an 83 mm diameter test grazing on the cobble stone; (B) corresponding spectrum of the wave form showing the resonant frequency 900 Hz

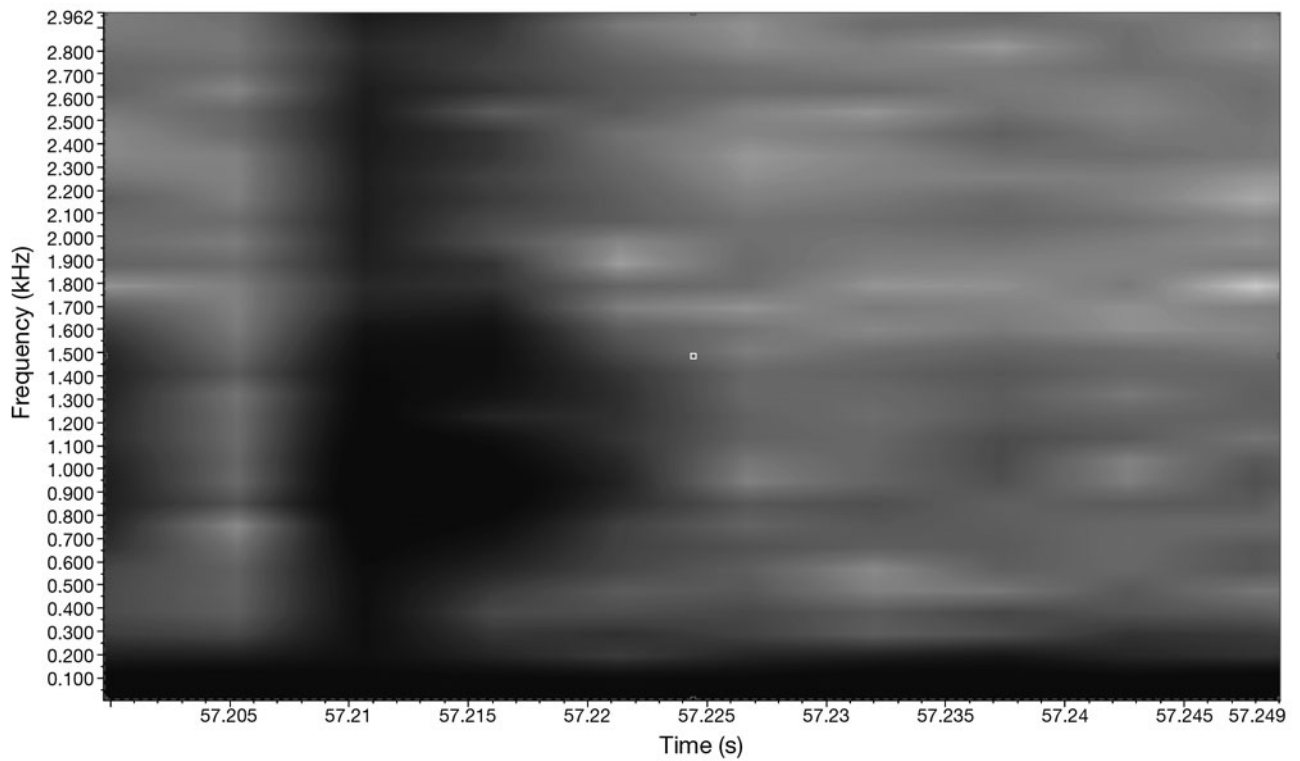


Fig. 3. *Evechinus chloroticus*. Sonogram of a typical scrape by an urchin with an 83 mm diameter test (Fast Fourier Transformation = 512 with a Hann Window)

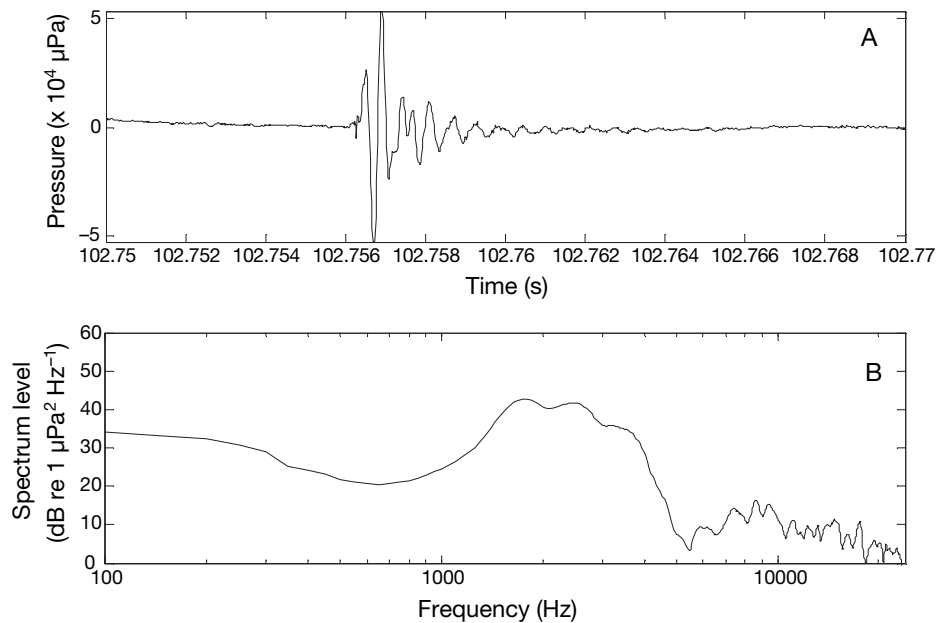


Fig. 4. *Evechinus chloroticus*. (A) Wave form of a typical scrape by an urchin with a 42 mm diameter test grazing on the cobble stone; (B) corresponding spectrum of the wave form showing the resonant frequency (1754 Hz)

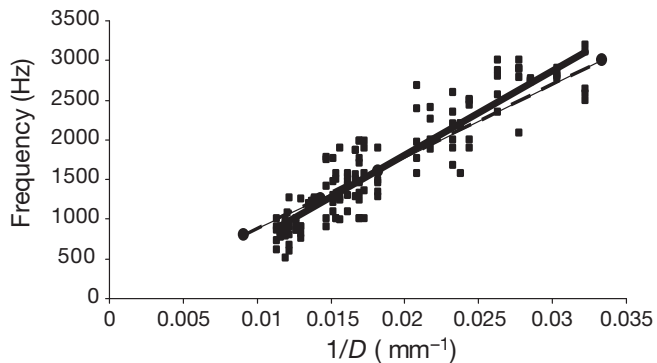


Fig. 5. *Evechinus chloroticus*. Resonant frequencies of 150 urchin feeding events (30 urchins) of different test diameters (D). Squares: measured resonant frequency from urchins; circles: theoretical Helmholtz resonant frequency (Cato 1977); solid line: regression line for the present study; dashed line: regression line for theoretical values

showed no preference, and acanthurids preferred high frequency sound. Simpson et al. (2008) also showed a higher diversity of adult species moving toward reefs broadcasting low frequency sound compared to reefs broadcasting high frequency sound. Our study highlights the possible importance of the urchin chorus in New Zealand and possibly other locations in providing fish and decapod larvae with a distinctive reef cue for onshore orientation. Furthermore, understanding what frequencies these animals are listening and responding to is crucial for determining the ranges at which they can detect underwater sound, because the attenuation of underwater sound is strongly dependent on frequency.

In many coastal ecosystems around the world, urchins are keystone species that have experienced significant harvesting pressure in recent years for their roe (Andrew et al. 2002). In addition to direct fishing pressure, coastal urchin populations have been dramatically affected by trophic cascades resulting from harvesting of predators in some locations (Shears & Babcock 2003, Guidetti 2006). Based on our evidence, these changes in urchin populations could result in changes in the sound levels and frequency composition of ambient underwater sound, which could have a knock-on effect on larval fish and decapod settlement. These results in conjunction with the evidence that larval fishes and decapods orientate with respect to the 'soundscape' raises important issues for management, conservation, and the protection of sound cues in natural behavior.

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LITERATURE CITED

- Andrew NL, Agatsuma Y, Ballesteros E, Bazhin AG and others (2002) Status and management of world sea urchin fisheries. *Oceanogr Mar Biol* 40:343–425
- Castle MJ (1974) A study of ambient sea noise. PhD thesis, University of Auckland
- Castle MJ, Kibblewhite AC (1975) The contribution of the sea urchin to ambient noise. *J Acoust Soc Am* 58:S122
- Cato DH (1977) Marine biological noise in tropical waters near Australia. PhD thesis, University of Sydney
- Cato DH (1978) Marine biological choruses observed in tropical waters near Australia. *J Acoust Soc Am* 64: 736–744
- Cummings WC, Brahy BD, Hernkind WF (1964) The occurrence of underwater sounds of biological origin of the west coast of Bimini, Bahamas. In: Tavolga WN (ed) *Marine bioacoustics*. Pergamon Press, New York, p 27–43
- D'Spain GL, Batchelor HH (2006) Observations of biological choruses in the Southern California Bight: a chorus at mid-frequencies. *J Acoust Soc Am* 120:1942–1955
- Fish MP (1964) Biological sources of sustained ambient sea noise. In: Tavolga WN (ed) *Marine bio-acoustics*. Pergamon Press, New York, p 175–194
- Guidetti P (2006) Marine reserves reestablish lost predator interactions and cause community changes in rocky reefs. *Ecol Appl* 16:963–976
- Hay EH, Stachowicz JJ, Cruz-Rivera E, Bullard S, Deal MS, Lindquist N (1998) Bioassays with marine and freshwater macroorganisms. In: Haynes KF, Miller JG (eds) *Methods in chemical ecology*. Chapman & Hall, New York, p 39–141
- Jeffs AG, Tolomieri N, Montgomery JC, Tindle CT (2003) Crabs on cue to the coast: the use of underwater sound 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? *N Z J Mar Freshw Res* 39:605–617
- Leis JM, Lockett MM (2005) Localization of reef sounds by settlement-stage larvae of coral reef fishes. *Bull Mar Sci* 76:715–724
- Leis JM, Carson-Ewart BM, Cato DH (2002) Sound detection *in situ* by the larvae of coral reef damselfish (Pomacentridae). *Mar Ecol Prog Ser* 232:259–268
- Lobel PS (2001) Fish bioacoustics and behavior: passive acoustic detection and the application of closed-circuit rebreathers for study. *Mar Technol Soc J* 35:19–28
- Lobel PS (2005) Scuba bubble noise and fish behavior: a rationale for silent diving technology. In: Godfrey JM, Shumway SE (eds) *Diving for science 2005: Proc Am Acad Underwater Sci 24 Annu Symp*, p 1–8
- McCauley RD, Cato DH (2000) Patterns of fish calling in a nearshore environment in the Great Barrier Reef. *Phil Trans R Soc Lond B* 355:1289–1293
- Montgomery JC, Jeffs AG, Simpson SD, Meekan MG, Tindle CT (2006) Sound as an orientation cue for the pelagic larvae of reef fishes and decapod crustaceans. *Adv Mar Biol* 51:143–199
- Radford CA, Jeffs AG, Tindle CT, Cole RG, Montgomery JC (2005) Bubbled waters: the noise produced by underwater breathing apparatus. *Mar Freshw Behav Physiol* 38: 259–268
- Radford CA, Jeffs AG, Montgomery JC (2007) The directional swimming behaviour of five species of crab postlarvae in response to reef sound. *Bull Mar Sci* 80:369–378
- Shears NT, Babcock RC (2003) Continuing trophic cascade effects after 25 years of no-take marine reserve protection.

- Mar Ecol Prog Ser 246:1–16
- Simpson SD, Meekan MG, McCauley RD, Jeffs A (2004) Attraction of settlement stage coral reef fishes to reef noise. *Mar Ecol Prog Ser* 276:263–268
- Simpson SD, Meekan MG, Montgomery JC, McCauley RD, Jeffs AG (2005) Homeward sound. *Science* 308:221
- Simpson SD, Jeffs AG, Montgomery JC, McCauley RD, Meekan MG (2008) Nocturnal relocation of adult and juvenile coral reef fishes in response to reef noise. *Coral Reefs* 27:97–104
- Stephens RWB, Bate AE (1966) *Acoustics and vibrational physics*, 2nd edn. Edward Arnold, London
- Stobutzki IC, Bellwood DR (1998) Nocturnal orientation to reefs by late pelagic stage coral reef fishes. *Coral Reefs* 17:103–110
- Stocker M (2002) Sounding the alarm on underwater noise. *Nature* 420:740
- Tait RI (1964) The evening chorus: a biological noise investigation. NRL Report, Naval Research Laboratory, HMNZ Dockyard, Auckland
- Tolimieri N, Jeffs A, Montgomery JC (2000) Ambient sound as a cue for navigation by the pelagic larvae of reef fishes. *Mar Ecol Prog Ser* 207:219–224
- Tolimieri N, Haine O, Montgomery JC, Jeffs A (2002) Ambient sound as a navigational cue for larval reef fish. *Bioacoustics* 12:214–217
- Tolimieri N, Haine O, Jeffs A, McCauley RD, Montgomery JC (2004) Directional orientation of pomacentrid larvae to ambient reef sound. *Coral Reefs* 23:184–191
- Tricas TC, Kajiura SM, Kosaki RK (2006) Acoustic communication in territorial butterflyfish: test of the sound production hypothesis. *J Exp Biol* 209:4994–5004
- Zar JH (1999) *Biostatistical analysis*, 4th edn. Prentice Hall, Upper Saddle River, NJ

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