

Localised coastal habitats have distinct underwater sound signatures

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ABSTRACT: There is evidence that ambient underwater sound is used by some pelagic larval reef fishes and decapods as a guide to direct them toward coastal areas. It would be advantageous to these organisms if they were also able to use sound to remotely identify suitable settlement habitats. However, it is unknown whether different coastal habitats produce different sounds that would be capable of providing distinctive cues for larvae. This study identified marked differences in the characteristics of ambient underwater sound at 3 distinct types of coastal habitat: a macroalgal-dominated reef, a sea urchin-dominated reef, and a sandy beach. The sea urchin-dominated reef habitat produced sound that was significantly more intense overall in a biologically important frequency band (800 to 2500 Hz), compared with that from macroalgal-dominated reefs and beach habitats. The sound produced by snapping shrimp also exhibited marked differences among habitat types, with the sea urchin-dominated reef having significantly more snaps than the macroalgal-dominated reef or beach habitat. Many of the differences in the sound produced by the 2 reef habitats became more apparent at dusk compared with noon. This study provides evidence that there are significant differences in the spectral and temporal composition of ambient sound associated with different coastal habitat types over relatively short spatial scales. An acoustic cue that conveys both directional and habitat quality information that is transmitted considerable distances offshore would have the potential to be of immense value to the pelagic larval stage of a coastal organism attempting to remotely locate a suitable habitat in which to settle.

KEY WORDS: Habitat type · Acoustic cue · Ambient underwater sound · Evening chorus · Larval orientation · Sea urchins · Snapping shrimp

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INTRODUCTION

Ambient sea noise is composed of a combination of acoustic sources (Acosta et al. 1997, Cato & McCauley 2002). Abiotic sources of ambient sea noise in the nearshore environment are mostly due to the effect of the wind and waves that produce noise of frequencies above 150 to 200 Hz. Biotic sound, which covers a very wide range of frequencies, is generated by a variety of marine life involved in reproductive displays, territorial defense, feeding and echolocation (Knudson et al. 1948, Tait 1962, Wenz 1962, Cato 1978, 1992, McCauley & Cato 2000, Radford et al. 2008a).

Ambient underwater noise varies from place to place (Urick 1983) and the vertical directionality of ambient

noise has been extensively studied (e.g. Sotorin & Hodgkiss 1990 and references therein). However, there is very little literature on the horizontal directionality of ambient noise and Urick (1983) reported 'few or no observations'. The horizontal directionality of noise due to surf and ice movement (Wilson et al. 1985, Yang et al. 1987, Deane 2000) has been described, but no reports of horizontal directionality due to different shore types in coastal waters appear to exist.

Ambient underwater sound is thought to be important in guiding some pelagic larval reef fishes and decapods to settlement habitats on coastal reefs (Tolimieri et al. 2000, 2002, 2004, Jeffs et al. 2003, 2005, Simpson et al. 2004, 2005, 2008a,b, Montgomery et al. 2006, Radford et al. 2007). For example, Simpson et al.

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(2005) showed that the settlement of different species of larval fish on experimental patch reefs were variously affected by the presence and frequency range of underwater sound broadcast from these reefs. While the overall extent to which reef sound influences the natural settlement of reef organisms is unknown, it is possible that spatial variation in ambient underwater sound could contribute to the large amount of spatial variability observed in larval settlement (Doherty 1991, Doherty & Fowler 1994, Caselle & Warner 1996). It would be advantageous for larval settlers to be able to remotely detect and respond to differences in underwater sound if the sound reliably represented differences in the coastal settlement habitat at the sound source. Currently, it is unknown whether different habitats that would be encountered over the active swimming distance (i.e. km's) of a larval settler (Stobutzki & Bellwood 1994, Stobutzki 1998, Dudley et al. 2000) are producing identifiably different sounds due to habitat related differences in the presence and abundance of sound-producing animals, such as snapping shrimp, fishes and sea urchins (Cato 1978, 1992, Radford et al. 2008a,b). While there have been a few previous studies of spatial variation in ambient underwater sound in shallow coastal waters, none to our knowledge have determined whether coastal habitats on the spatial scale encountered by a larval settler are producing distinct sound profiles.

The spatial extent to which larval settlers can use ambient underwater sound as an orientation cue is still controversial (e.g. Mann et al. 2007). Establishing a basis of the acoustic environment within which larval fish and decapods live is a prerequisite to defining the effective range of sound for orientation. Therefore, the aim of the present study was to describe differences in the gross character (temporal variation, spectral composition and spectrum level) of reef sound emanating from 3 types of habitat on a temperate coast (macroalgal-dominated rocky reef, sea urchin barren rocky reef and sandy beach) that were all located only a few kilometres apart. The results presented are selected from a comprehensive 1 yr study of underwater sound along about 50 km of varied coastline to investigate variations with shore type, season and time of day (Radford 2007).

Ambient underwater noise was defined by Urick (1983) as 'the residue noise background in the absence of individual identifiable sources that may be considered the natural noise environment of the hydrophone'. For the purposes of this study the main source of the sound energy is known to be sea urchins and snapping shrimp (Radford et al. 2008a,b). Even though the sound forms part of the ambient 'noise' it becomes the signal of interest when we consider its possible use for orientation and guidance and, hence, with appro-

prate qualification can be referred to as reef noise or reef sound.

MATERIALS AND METHODS

Radford et al. (2008b) showed that there was an intensity maximum in sounds produced by sea urchin and snapping shrimp during the new moon and a minimum during the full moon, with no difference between the 2 quarter moons. There was also a minimum (noon) and maximum (dusk) in sea urchin and shrimp sound activity during a 24 h period. Therefore, to assess spatial variation in reef sound recordings of ambient underwater noise were taken during October 2008 on the first and last quarter moon phases at 6 sites around the coast near Leigh in northeastern New Zealand (Fig. 1). There were 3 habitat types with 2 different sites for each habitat: macroalgal-dominated rocky reef (M1, M2), sea urchin-dominated rocky reef (U1, U2), open sandy beach, Pakiri Beach (B1, B2). These site selections were based on a previously created habitat map. Recordings were made using a floating hydrophone system to reduce extraneous noise. The system consisted of a sealed barrel that contained a Sound Devices 722 solid state recorder (48 kHz, 24 bit), which was connected to a calibrated HTI-96-MIN wideband omnidirectional hydrophone (High Tech). The hydrophone had a flat frequency response curve over the range of 10 Hz to 24 kHz and was weighted vertically to 10 m water depth from the outside of the floating barrel. Recordings of 5 min duration were made during 12:00 to 13:00 h (noon) and 17:00 to 18:00 h (dusk) at 10 to 20 m from the reef edge or 100 m from the shoreline of the sandy beach, which corresponded to 20 m water depth for the reef sites and 15 m for the beach sites.

The digital recordings were transferred to a personal computer and analysed using MATLAB software with codes specifically written for these recordings. Wind speed was recorded simultaneously every hour at the nearby climate station at the University of Auckland's Leigh Marine Laboratory.

Data analysis. No extraneous anthropogenic sources of noise, such as ships, power boats or nearby coastal activities were present in the recordings. All recordings were conducted in calm or near calm conditions (wind speed <5 knots [$\sim 9 \text{ km h}^{-1}$] and wave height <0.25 m). However, to ensure that variability in wind speeds did not exert an influence on the ambient underwater sound recordings, wind speeds were compared among all sites using ANOVA.

Each 5 min recording was examined for uniformity and acoustic power spectra were generated by analysis of 5 randomly selected 10 s samples. Data was high-pass filtered to 100 Hz to remove any effect of surface

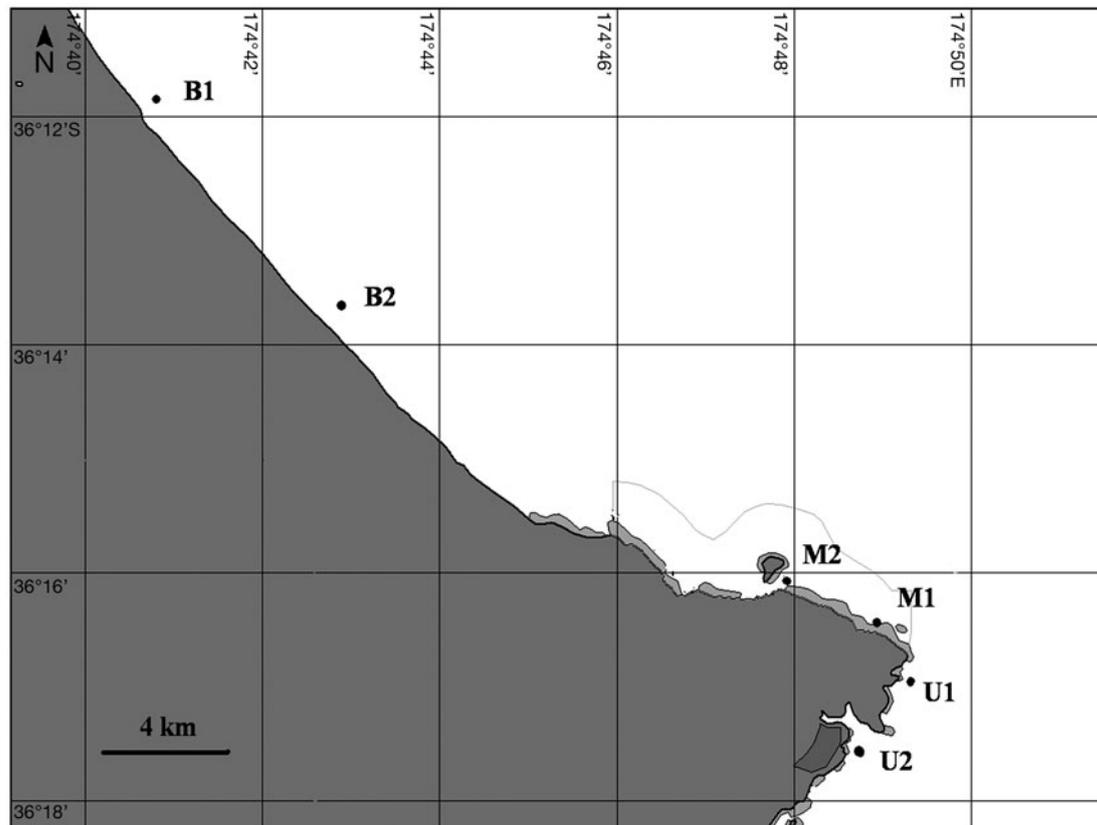


Fig. 1. Study sites off the northeastern coast of the North Island of New Zealand. U1: Rusty Ladder; U2: Nordic Reef; M1: One Spot Reef; M2: Waterfall Reef; B1 and B2: Pakiri Beach. Dark grey: land; light grey: intertidal; white: sea

waves and any 50 Hz interference. For each of the 5 randomly selected subsamples the total sound intensity (P_{rms}^2) was calculated. The subsamples were then band-pass filtered into 4 frequency bands 100 to 800 Hz, 800 to 2500 Hz (sea urchin feeding frequency; Radford et al. 2008a) 2500 to 20 000 Hz (dominant snapping shrimp frequency; Au & Banks 1998) and 20 000 to 24 000 Hz, and the overall proportion of total sound intensity in each frequency band was calculated. For each period (noon or dusk) the proportion of total sound intensity was analysed using a general linear mixed model, with Frequency Band, Habitat and Time (noon and dusk) as fixed factors. Habitat and Frequency Band were also nested within the random effect of Site. Significant differences between individual pairs of means were determined using Tukey's tests.

For each recording, the 5 randomly selected 10 s subsamples were taken and the number of snaps produced by snapping shrimp was estimated by setting a threshold level on the raw data and any transient spike that was <0.2 s duration and above a preset threshold level was counted as a snap by a shrimp. Preliminary manual analyses confirmed that this automated

method provided a reliable count of snapping shrimp snaps. The mean number of snaps for each recording site was compared with a general linear mixed model, which enabled comparisons to be made among Time (noon and dusk) and Habitat (fixed effects). Time and Habitat were also nested within Site (random effect) (Littell et al. 1996, McCullagh & Searle 2001). Significant differences between individual pairs of means were determined using Tukey's tests. All data were analysed using SAS and presented as the statistical mean + SE of the mean.

RESULTS

Wind speeds were similar among the times for which the underwater noise recordings were taken for each of the sites ($F_{5,160} = 1.0$, $p = 0.55$); therefore, wind was ruled out as the cause of any differences in the recorded ambient noise. Sea swell conditions were also not considered to have affected the recordings because all recordings were taken in conditions of <0.25 m swell (Climate Station, Leigh Marine Laboratory unpubl. data).

Spectra

The spectra for the 6 sites are shown in Fig. 2. There is a clear similarity between M1 and M2 and between B1 and B2. There is less similarity between U1 and U2 but both show an increase at dusk in the 800 to 2500 Hz band. In general the spectra divided naturally into the broad bands mentioned earlier. The 100 to 800 Hz band is due to small waves, some fish species and low frequency noise from distant

shipping and offshore storms. The 800 to 2500 Hz band is dominated by sea urchins with a peak around 1000 to 1200 Hz, and the 2.5 to 20 kHz band is dominated by snapping shrimp with a broad peak at 5 kHz. Overall, sea urchin noise shows a significant increase in spectrum level between noon and dusk and snapping shrimp noise shows a smaller increase. Spectra B1 and B2 show low levels of sea urchin and snapping shrimp noise at dusk, which is probably due to sound from distant reefs. The higher

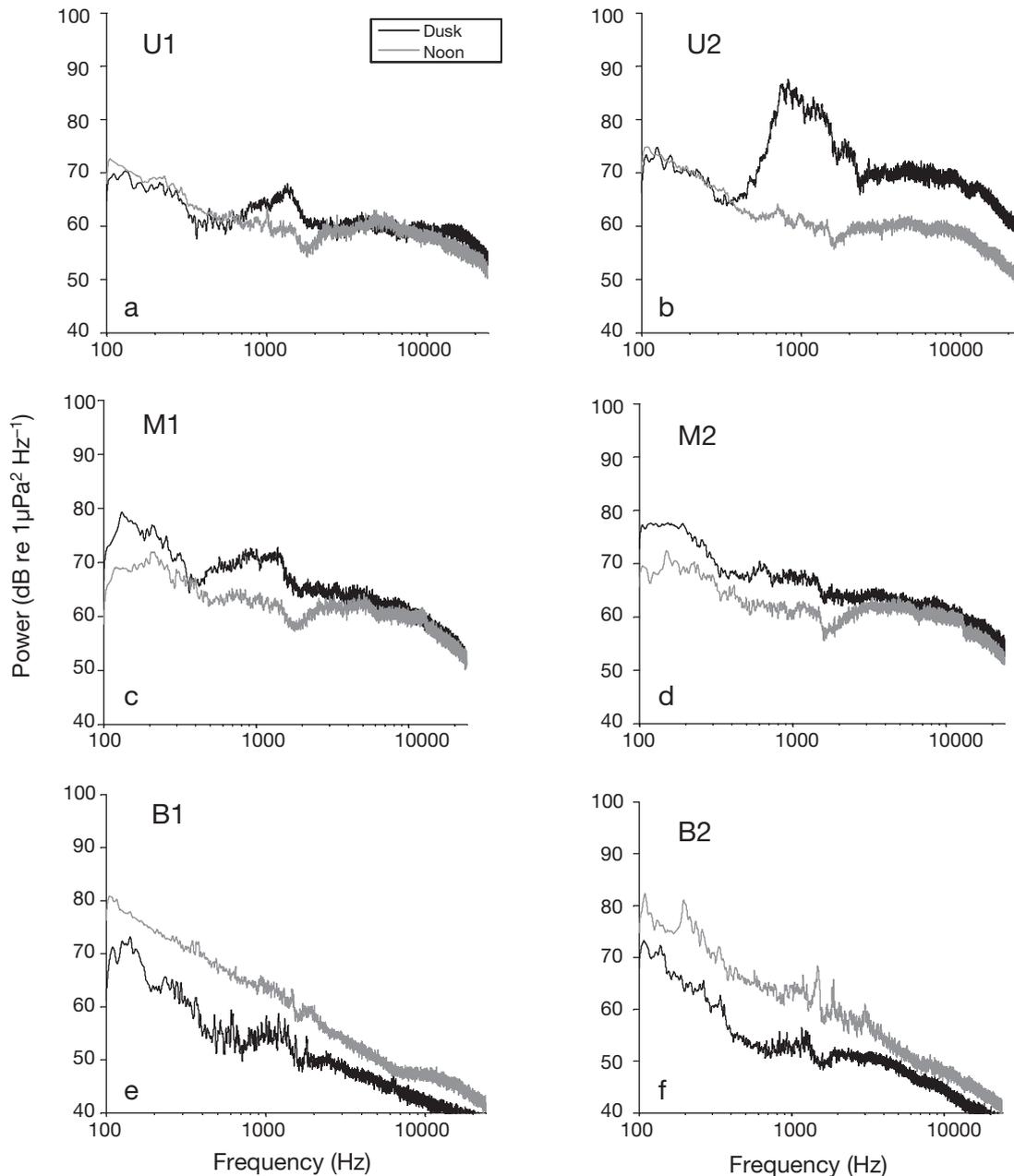


Fig. 2. Noon and dusk spectra: (a) U1: Rusty Ladder; (b) U2: Nordic Reef; (c) M1: One Spot Reef; (d) M2: Waterfall Reef; (e) B1: Pakiri Beach 1; (f) B2: Pakiri Beach 2

overall levels at noon are due to small waves at the shore from daytime sea breezes.

The spectra in Fig. 2 for different habitats are different in their overall appearance suggesting that acoustic characteristics vary over relatively small spatial scales, and within habitats, between noon and dusk. In general, all the reef sites (U1, U2, M1 and M2) had higher power level in the frequency band 2500 to 20 000 Hz, whereas the 2 beach sites (B1 and B2) did not. The 2 sites at sea urchin-dominated habitat had an additional large (10 to 20 dB) increase in power between 800 and 2500 Hz at dusk when compared

with noon, whereas the macroalgal-dominated habitat had smaller increases of about 5 dB. The 2 sites at the sandy beach habitat had higher power levels in the lower frequencies (100 to 300 Hz) compared with all of the 4 sites at reef habitats.

Proportion of total sound intensity

At noon the proportion of sound intensity in the different frequency bands (Fig. 3d-f) was significantly different for Frequency ($F_{3,9} = 74.20, p < 0.0001$) and

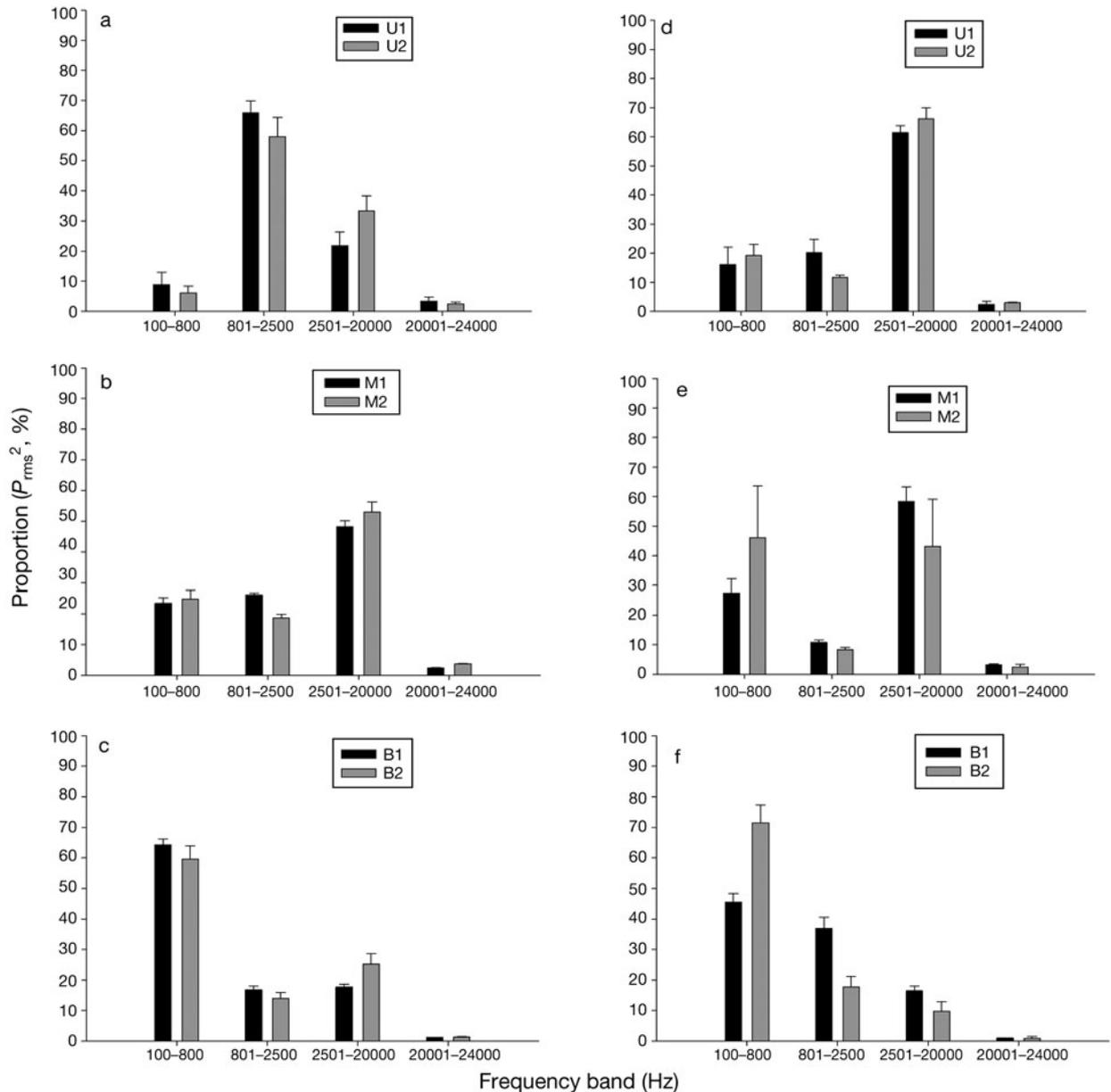


Fig. 3. Proportion of total noise intensity (P_{rms}^2 , mean + SE) occurring in the biologically dominant frequency bands at (a-c) dusk or (d-f) noon

the interaction Habitat \times Frequency ($F_{6,9} = 7.58$, $p < 0.01$), but was similar between Habitat ($F_{2,3} = 0.19$, $p = 0.83$). All sites were similar in the frequency band 800 to 2500 Hz, while at dusk (Fig. 3a–c) the sea urchin habitats had the greatest proportion of total sound intensity. At noon the macroalgal and sea urchin habitats were similar in the frequency band 2500 to 20 000 Hz, but these were significantly greater than for the beach habitat. For all other frequency bands the habitats were similar.

At dusk the proportion of total sound intensity in different frequency bands showed significant differences for Site (Habitat) ($F = 28.15$, $p < 0.01$), Site (Habitat \times Frequency) ($F = 38.96$, $p < 0.05$), Habitat ($F_{2,3} = 3.44$, $p < 0.05$), Frequency ($F_{3,9} = 197.97$, $p < 0.001$) and the interaction Habitat \times Frequency ($F_{6,9} = 32.52$, $p < 0.001$). The sea urchin-dominated habitat had a significantly higher proportion of total sound intensity (range, 55 to 65%) in the frequency band 800 to 2500 Hz at dusk compared with the other 2 habitat types, macroalgal reef (range, 15 to 25%) and sandy beach (range, 15 to 20%). However, the macroalgal reef sites had a significantly higher proportion of total sound intensity in the frequency bands 2500 to 20 000 Hz (range, 45 to 55%) than did the sea urchin reef (range, 20 to 30%) and sandy beach habitat (range, 15 to 25%) at dusk. At dusk the sandy beach habitat had the highest proportion (range, 58 to 63%) of total sound intensity in the frequency 100 to 800 Hz band ($p < 0.05$) and the urchin habitat had the lowest proportion (range, 8 to 10%) ($p < 0.05$). All of the habitats had a similar proportion of total sound intensity in the 20 000 to 24 000 Hz band ($p > 0.05$) at dusk.

Overall, the sea urchin-dominated reefs (U) at dusk had a significantly greater proportion of sound intensity in the frequency band 800 to 2500 Hz compared with those at noon ($p < 0.01$). In contrast, the proportion of sound intensity in the frequency band 2500 to 20 000 Hz for the sea urchin-dominated reefs was lower at dusk than at noon ($p < 0.01$). The macroalgae-dominated reefs (M) had a significant rise in the proportion of sound intensity in the 800 to 2500 Hz frequency band at dusk compared with that at noon ($p < 0.05$); whereas, the sandy beach habitats (B) were similar at dusk and noon.

Snapping shrimp

The number of snaps produced by snapping shrimp (Fig. 4) exhibited significant differences for Site (Habitat) ($F = 8713.2$, $p < 0.05$), Habitat ($F_{2,3} = 9.01$, $p < 0.05$), Time ($F_{1,3} = 43.46$, $p < 0.01$) and the interaction Time \times Habitat ($F_{2,3} = 9.19$, $p < 0.05$). Overall, the Nordic Reef site (U2) had significantly more snaps produced by

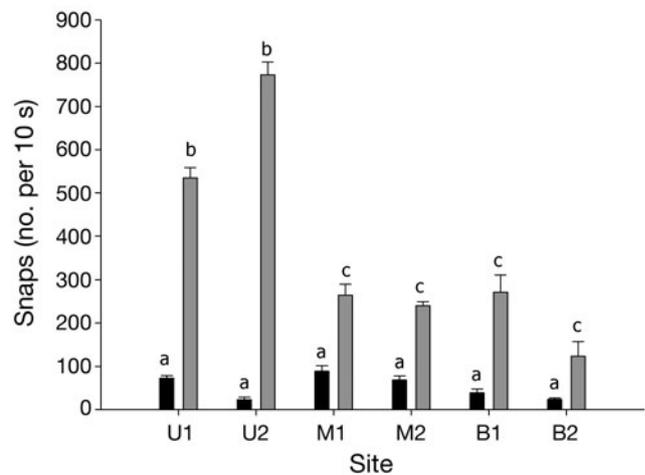


Fig. 4. *Alpheus* spp. and *Syalpheus* spp. Mean number (+SE) of snaps of snapping shrimp in 10 s for the 6 study sites at noon (grey) and dusk (black). See Fig. 1 for site locations

snapping shrimp than any other site, while Pakiri Beach 2 (B2) had the least. Both sea urchin-dominated reef sites (U1 and U2) had similar numbers of snaps, but had significantly more than the 2 macroalgal reef sites (M1 and M2). Significantly more snaps were recorded at the sea urchin habitat sites during dusk (ranging from 550 to 750 snaps per 10 s) than at the macroalgae habitat sites (240 to 280 snaps per 10 s) and the beach habitat sites (120 to 260 snaps per 10 s). There were significantly more snaps produced by snapping shrimp during dusk than at noon for every site; however, the number of snaps produced at noon was similar among all the sites (range, 20 to 100 snaps per 10 s).

DISCUSSION

The aim of the present study was to describe gross differences in the spectral composition and level of the ambient noise emanating from 3 distinct types of habitat on a temperate coast (macroalgal-dominated reef, sea urchin-dominated reef, and sandy beach) all within relatively close proximity (a few km apart). Analyses of representative samples of underwater noise revealed there were marked differences between the habitat types, especially in specific frequency bands. In particular, the frequency band associated with sea urchin feeding (800 to 2500 Hz) was significantly more intense at the sea urchin-dominated reef habitat sites (U1 and U2) than at the macroalgal-dominated reef and the sandy beach habitats. This is confirmed by the proportion of total sound intensity in the frequency band 800 to 2500 Hz being significantly greater at the sea urchin habitat sites than at either the

macroalgal reef or sandy beach habitat sites. In contrast, the sounds recorded at sites of the same gross habitat type (i.e. sandy beach, sea urchin barren reef, macroalgal reef) were similar in terms of their spectral composition and temporal changes in their spectra.

To our knowledge this is the first study to observe marked differences in underwater noise levels over such small geographical scales (a few km) and associated with localised differences in habitat type. The greatest differences in the acoustic output from 3 distinctive coastal habitats were observed among the recordings taken at dusk. This suggests that underwater sound recordings should be conducted at dusk to determine differences between habitat types. The 800 to 2500 Hz frequency band caused most of the variation among the habitats at dusk, with the likely cause of this associated with the feeding behaviour of grazing sea urchins, which resonate at frequencies between 800 to 2500 Hz depending on their size (Radford et al. 2008a). The presence of large numbers of sea urchins is an important characteristic of coastal reefs in New Zealand and their grazing activity is of major importance in maintaining the barren reef habitat (Shears & Babcock 2002, 2003).

Another source of variation within the data was due to one of the most ubiquitous sound-producing animals in marine temperate waters, the snapping shrimp (Fish 1964, Cato 1992, Au & Banks 1998, Cato & McCauley 2002). Snapping shrimp dwell in a range of habitats from shallow bays and estuaries to rocky and coral reefs (Au & Banks 1998). The total output of sound by snapping shrimp is influenced by the size of the shrimp bed and time of day (Fish 1964, Radford et al. 2008b). Assuming that the number of snaps estimated from sound recordings broadly indicates the number of snapping shrimp, i.e. *Alpheus* spp. and *Syalpheus* spp., present on and around the reef, the sea urchin-dominated reef type had significantly more shrimp than the macroalgal reef habitat. This suggests that habitat type is important in determining the abundance of resident snapping shrimp. In contrast, previous studies have shown that macroalgal habitats are more diverse and complex than sea urchin barren habitats (Simenstad et al. 1978, Behrens & Lafferty 2004, Graham 2004, Tuya et al. 2006). Watanabe et al. (2002) used the numbers of snaps produced by snapping shrimp as an environmental monitoring tool and showed that the number of snaps produced in an unpolluted habitat was significantly greater than at a polluted site. Therefore, the results of the present research also highlight the potential use of passive acoustics as a tool for monitoring habitat quality, remotely surveying habitat type and determining the abundance of some sound-producing organisms, such as snapping shrimp.

This study shows that different types of coastal habitat found over a relatively small spatial scale (km's) have marked differences in their spectral frequency and level composition of the ambient underwater sound they produce. The 2 types of reef habitat examined in this study both produced sound of sufficient intensity in frequency ranges that were likely to be transmitted some distance beyond the habitat (Radford et al. 2005). The sound output from both types of reef habitat was significantly higher at dusk than at noon. Dusk is also the time when the nocturnal settling stages of many coastal reef fishes and crustaceans become active in the water column. A number of studies have now produced evidence that the pelagic settling stages of some reef-dwelling fishes and crustaceans are capable of orienting toward ambient underwater sound produced by reefs (Tolimieri et al. 2000, 2002, 2004, Jeffs et al. 2003, 2005, Simpson et al. 2004, 2005, 2008a, Montgomery et al. 2006, Radford et al. 2007). This ability, combined with strong swimming capabilities identified in many of these settling stages (Stobutzki & Bellwood 1994, 1997, Shanks 1995, Leis & Carson-Ewart 1997, 1999, Stobutzki 1997, 1998, Jeffs & Holland 2000, Jeffs et al. 2005, Fisher et al. 2005), would theoretically provide increased capacity for settlers to reach suitable settlement habitat.

Acoustic cues that convey directional as well as habitat quality information would potentially be of immense value to the pelagic larval stage of a reef organism attempting to remotely locate a suitable habitat in which to settle. Three studies provide some limited support for this proposition. Divers in the field observed a clear difference in the swimming speed and directional movements of the settlement stage of the reef fish *Chromis atripectoralis* in the vicinity of underwater speakers broadcasting either natural reef sound or artificial pure tones, suggesting that settling-stage fishes have the ability to discriminate and respond to different underwater sounds (Leis et al. 2002). Simpson et al. (2005) showed that the settlement of different species of settlement-stage fish on experimental patch reefs were affected by differences in the frequency range of underwater sound broadcast from the reefs. The broadcast sound consisted of recordings of natural reef sound filtered into high frequency (>570 Hz) or low frequency (<570 Hz) components. The researchers found that pomacentrid fish species responded preferentially to the high frequency treatment, while other fishes, such as apogonids, showed no preference between the 2 different sound treatments. Simpson et al. (2008b) conducted a similar experiment by broadcasting high frequency (570 to 2000 Hz) and low frequency (<570 Hz) components of natural reef sound in conjunction with light traps, which are widely used for catching settlement-stage

reef fish. Of the 7 fish families represented in catches of >10 individuals, 4 were caught in significantly greater numbers in the high-frequency traps than in either the low-frequency or the silent traps (Pomacentridae, Apogonidae, Lethrinidae and Gobiidae). Only the family Siganidae showed no preference between any of the sound treatments.

Overall, these results suggest that settlement-stage fish are able to discriminate differences in acoustic cues, which may relate to possible differences in habitat. This ability appears to be retained after settlement as juvenile and adult fish. Simpson et al. (2008a) found that the highest diversity of both adult and juvenile reef fish was found in experimental patch reefs broadcasting the low frequency (<570 Hz) component of natural reef sound compared with those broadcasting high frequency component (>570 Hz). In addition, the adults from 2 fish families (Gobiidae and Blenniidae) preferred to relocate to patch reefs broadcasting the low frequency sound, while juvenile Acanthuridae preferred the patch reefs with higher frequency sound. These previous findings, together with our results, indicate that differences in underwater sound emanating from different types of habitat may play a significant role in settlement processes as well as in the orientation of juveniles and adults of some species. The results reported here show that statistically significant differences in sound occur over relatively short distances and could provide a basis for habitat selection by settling fish.

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