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Induction of settlement in crab megalopae by ambient underwater reef sound

Jenni A. Stanley, Craig A. Radford, and Andrew G. Jeffs
Leigh Marine Laboratory, University of Auckland, PO Box 349, 160 Goat Island Rd, Leigh, Warkworth 0941, New Zealand

The larvae of a number of crab species have been found to orientate and swim toward ambient underwater sound emanating from coastal settlement habitats. This current study examined whether ambient underwater sound also has the potential to trigger settlement responses in crab larvae. The effect of exposure to reef sound on the settlement behavior and time to metamorphosis (TTM) was examined in the megalopae of 5 common crab species, 3 from temperate waters and 2 from tropical waters. The megalopae of all 5 crab species showed marked changes in swimming behavior and a significant decrease in TTM when exposed to replayed ambient underwater reef sound compared with a silent (control) treatment. Megalopae exposed to sound decreased swimming activity earlier and displayed crawling behavior that was a precursor to both settlement and metamorphosis. Sound exposure decreased the median TTM by 33 h in *Hemigrapsus sexdentatus* and by 75 h in Grapsidae sp. 2. The consistent results among all species examined indicate that ambient underwater sound is likely to be an important settlement cue for the megalopae of many crab species. The wider ecological significance of acoustic settlement cues in crab larvae, in relation to other settlement cues and processes, now needs to be determined. *Key words:* crab, megalopae, metamorphosis, settlement cue, underwater sound. *[Behav Ecol 21:113–120 (2010)]*

A pelagic larval phase in the life cycle of many benthic marine organisms typically involves dispersal away from parental habitat with the final stage of larval development selecting a suitable benthic habitat in which to settle (O'Connor and Gregg 1998). Settlement and metamorphosis often involves a specific cue or a combination of physical and/or chemical settlement cues (Gebauer et al. 2004). These cues include salinity, depth, substrate rugosity, as well as a wide range of chemical cues from sources such as conspecifics, settlement substrates, aquatic vegetation, estuarine water, and potential prey. These cues can be both general and apply to many species, such as the specific chemical cues associated with conspecific adults (*Uca pugilator, Uca pugnax, Pagurus maclaughlinae, Paguristes tortugae, Chasmagnathus granulata, Panopeus herbstii*, and *Sesarma curacaoence*) (Gebauer et al. 2003) and species specific, such as the presence of certain macroalgae species for the blue crab, *Callinectes sapidus* (Forward et al. 1996).

The majority of studies on marine invertebrate larval settlement and metamorphosis have concentrated on species that are sedentary as adults, especially commercially important biofouling and aquaculture organisms, such as barnacles and oysters (Forward et al. 2001). By comparison, relatively little is known about settlement cues in mobile marine invertebrates, such as brachyuran crabs which are common and important inhabitants of coastal habitats around the world (Wear and Fielder 1985).

The larvae of many marine organisms are known to be capable of extending their larval phase, often for considerable periods, until suitable settlement cues or habitats are encountered. For example, polychaetes (Wilson 1977), gastropods (Paige 1988), echinoderms (Strathmann 1978), and coral reef fish (Victor 1986) have all been shown to delay metamorphosis until appropriate settlement cues are encountered. Some larvae will metamorphose spontaneously or even die without metamorphosing in the absence of specific settlement cues (Pechenik 1990; Zimmerman and Pechenik 1991; Gebauer et al. 2003).

Brachyuran crabs seem to lack the ability to delay metamorphosis indefinitely as they appear to have a temporal threshold beyond which settlement and metamorphosis occurs even in the absence of settlement cues (Weber and Epifanio 1996). To determine maximum time to metamorphosis (TTM), megalopae are typically reared in the laboratory and exposed to a control treatment of untainted seawater. The mean TTM in previous studies of brachyuran crabs has varied from 5 to 20 days depending on the species (Forward et al. 2001). In brachyuran crabs, the TTM can often be shortened by 15–25% on exposure to chemical cues that serve as indicators of potentially suitable settlement habitat. These chemical cues can be sourced from the presence of adults, aquatic vegetation, biofilms, conspecifics, estuarine water, humic acids, related crab species, and potential prey (Forward et al. 2001). The majority of these past studies have been carried out in laboratory aquaria or compartmentalized containers. Consequently, the spatial range over which these settlement cues operate in nature is largely unknown, and it is assumed that other physical processes, such as tidal currents, serve to initially position the megalopae in the vicinity of these chemical cues. Therefore, the current evidence suggests chemical settlement cues are being used over small distances (m) and do not appear to acting as an orientation cue over larger distances such as on the scale of kilometers (Butman 1987; Boudreau et al. 1993; Forward et al. 1994).

A number of experimental studies have concluded that ambient underwater sound emanating from coastal habitats may act as a long-distance orientation cue for settlement stage crabs and fishes attempting to locate suitable habitats (Stobutzki and Bellwood 1998; Tolimieri et al. 2000; Jeffs et al. 2003, 2005; Leis and Lockett 2005; Simpson et al. 2005;

Address correspondence to J.A. Stanley. E-mail: ja.stanley@auckland.ac.nz.

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Montgomery et al. 2006; Radford et al. 2007). However, previously the role of underwater sound as a settlement cue has not been investigated. Therefore, the aim of this present research was to investigate the potential for underwater sound to trigger settlement behavior and/or shorten TTM in settlement stage larvae (megalopae) of common species of brachyuran crabs from both temperate and tropical waters.

MATERIALS AND METHODS

The study was undertaken in temperate waters near the Leigh Marine Laboratory, located in northern New Zealand (36°15′S, 174°47′E) and in tropical waters near the Lizard Island Research Station, north-eastern Australia (14°39.5′S, 145°26′E) during October to December 2008.

Source of megalopae

Light traps were used to capture megalopae for behavioral experiments (Hickford and Schiel 1999). Up to 2 light traps were deployed at night within 500 m of the shoreline, 15 m apart and submerged 2 m in water of 5–7 m depth. The traps were recovered within 2 h of sunrise the following morning. When large planktivorous fishes were found in a light trap, megalopae were not used in the experiments as they may have altered behavior due to stress from being in the presence of a predator (Forward and Rittschof 2000). The megalopae were transported in seawater to a nearby laboratory where they were counted, sorted into settlement stage, and identified to lowest taxonomic level possible given the available taxonomic descriptions (Wear and Fielder 1985; McLay 1988). Only intermolt presettlement (i.e., natant and active swimming) megalopae of a similar size were selected for use in the experiments. The megalopae were held in a flowing filtered (40 μm) seawater system with natural light period and ambient temperature (14–31.0 °C, dependent on timing and location) until experiments begun the evening after capture. Five species of brachyuran megalopae were used for this research. The reptant phase in the life cycle of these 3 temperate species, *Hemigrapsus sexdentatus*, *Cyclograpsus lavauxi*, and *Macrophthalmus hirtipes* are all known to be associated with nearshore subtidal and intertidal habitats. The 2 tropical species were both identified to be members of the Grapsidae family, however, more detailed taxonomic placement was not possible due to the lack of taxonomic descriptions of megalopae and first instar juveniles of crab species in this region. The researchers observed early juvenile crabs with similar taxonomic characters to both experimental species settled in nearshore subtidal reef habitats. For the purposes of this work the species have been referred to as Grapsidae sp. 1 and Grapsidae sp. 2.

Behavioral assay

Each treatment (i.e., sound and silent) consisted of 3 replicate water baths that were used to maintain a constant water temperature for megalopae throughout the experiment. Each replicate water bath contained one Perspex container housing a group of megalopae (up to 5 megalopae) and one plastic vial housing a single megalopa. Individually housed megalopa were included in the experiment as a comparison with communally housed megalopae to test for any interactive effects on settlement behavior that may exist among individuals.

Grouped megalopae were housed in a clear Perspex container (160 × 160 × 140.5 mm deep) with a square piece of Perspex sheet (100 × 100 × 15 mm) on the bottom imitating a settlement surface. The upper surface of the sheet had been roughened with coarse sandpaper to provide a chemically inert settlement substrate for settling megalopae. Each individually held megalopa was in a plastic vial (250 ml) with a roughened base, within the same water bath as the container holding the group-housed megalopae. Each replicate for both the sound and silent treatments had a weighted Sony loudspeaker inside a watertight plastic bag, which was submerged in the water bath. For the sound replicates only, a Sony CD Walkman D–EJ815 was used to continually play a 4-min loop of recorded ambient underwater reef sound into the water bath and through the acoustically transparent plastic containers holding the crabs (Gerber 1978) (Figure 1).

When sufficient (>30) megalopae of the same species were collected from the light traps to conduct the experiments, they were randomly allocated to the experimental treatments and replicates. Both grouped megalopae and the individuals in each treatment were kept in filtered (1 μm) and UV-treated seawater under natural light period and ambient water temperature (14–31.0 °C, depending on local temperature) for the duration of the experiment. Sound and silent (control) treatments were randomly allocated to water baths for each experiment. Both sound and silent treatments were located in the same laboratory but were acoustically isolated using foam rubber mats beneath all water baths to prevent any transfer of acoustic energy to the silent treatment. The absence of any significant acoustic signal in the silent treatment tanks was confirmed by recording with a calibrated hydrophone (High Tech Inc. Gulfport, Mississippi).

The megalopae were added to the experiment at 1700 h on the day of their capture, and the CD Walkman was switched on to initiate sound in the sound treatment. Every 6 h, the

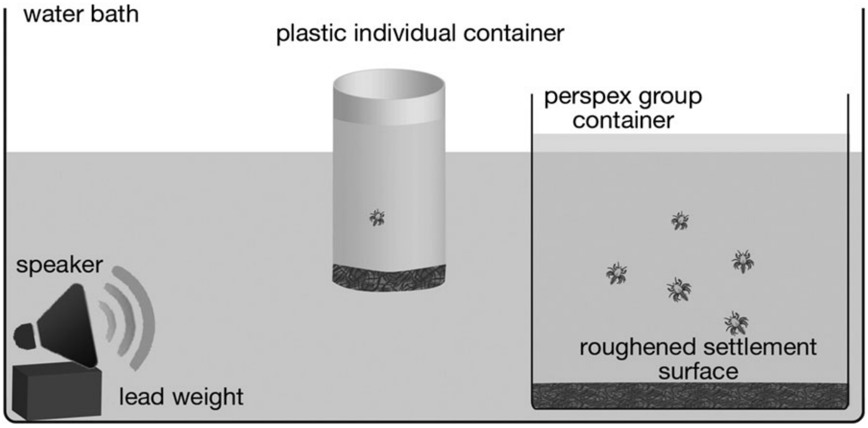

Figure 1
Schematic diagram of a side view of one experimental replicate showing the layout of the water bath, speaker, container holding an individual megalopa, and a container holding a group of megalopae. Shaded lines indicate water level.

behavior of the megalopae were observed and counts made of the number of individuals that had settled to the substrate and metamorphosed into the first instar benthic juvenile stage. The period of observation lasted no more than 20 min for both treatments. In this study, “settlement” is defined as the transition from a planktonic (continual swimming) to a benthic existence (crawling) and “metamorphosis” as the transformation to the adult body form, which no longer has the extended abdomen, characteristic of the megalopa, held posteriorly (Wear and Fielder 1985). During each 6 hourly observational period descriptions of behavior of each megalopa was categorized in the following manner. 1) “Normal” presettlement swimming behavior, that is, highly active swimming, low number of downward swimming events, no exploratory crawling behavior; 2) medium swimming activity, medium number of downward swimming events, small amount of exploratory crawling behavior; 3) low swimming activity, high number of downward swimming events, extensive exploratory crawling behavior; 4) complete settlement and metamorphosis, that is, no swimming activity.

The experiment was terminated when all experimental megalopae in both treatments had metamorphosed. The settled juvenile crabs were kept for 10 days after the experiment in flowing seawater and fed and were monitored for mortality.

Sound treatment

Recordings of typical reef noise in the vicinity of the study locations were collected using 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 hydrophone was calibrated by recording a NetMark 1000 acoustic pinger (specifications: source level 130 dB re 1 μPa at 1 m, 10 kHz signal, 300 ms pulse length, 4 s repetition rate). Digital recordings were transferred to a PC, and the spectral composition analyzed using MATLAB software with codes specifically written for these recordings. A typical 4-min sequence of each recording was randomly selected and transferred to a CD for playback in the sound treatments of the settlement experiments.

For the experiments using the 3 temperate crab species a recording of North Reef in north-eastern New Zealand (36°15′S, 174°47′E) during the summer at dusk on a new moon was used. A calibrated hydrophone (High Tech, Inc. HTI–96–MIN) was used to adjust the sound level produced by the Sony speakers in each experimental sound treatment tank to 114 dB re 1 μPa at 1 m, which was within the typical range of ambient sound level for evening chorus at reefs such as North Reef in New Zealand’s coastal waters (Tolimieri et al. 2000; Radford, Jeffs, and Montgomery 2008). There was a peak in the spectra around 1.2 kHz, which is thought to be produced by feeding of the sea urchin, *Evechinus chloroticus*, whereas the higher frequency pulses were the snaps of snapping shrimp (Tait 1962; Castle 1974; Radford, Jeffs, Tindle, and Montgomery 2008).

The 2 tropical crab species were exposed to a recording of the reef immediately offshore of Coconut Beach at Lizard Island on the Great Barrier Reef (GBR) (14°39.5′S, 145°26′E) during the summer at dusk on a new moon. A calibrated hydrophone (High Tech, Inc. HTI–96–MIN) was used to adjust the sound level produced by the Sony speakers in each experimental sound treatment tank to 109 dB re 1 μPa at 1 m, which is within the typical range of ambient sound level of evening chorus on the GBR in Australia (Cato and McCauley 2002). This recording consisted of a chorus of pops made by nocturnal fishes together with a higher frequency crackle produced by snapping shrimp, as well as other feeding and calling sounds typical of a coral reef (Cato and McCauley 2002; Simpson et al. 2004).

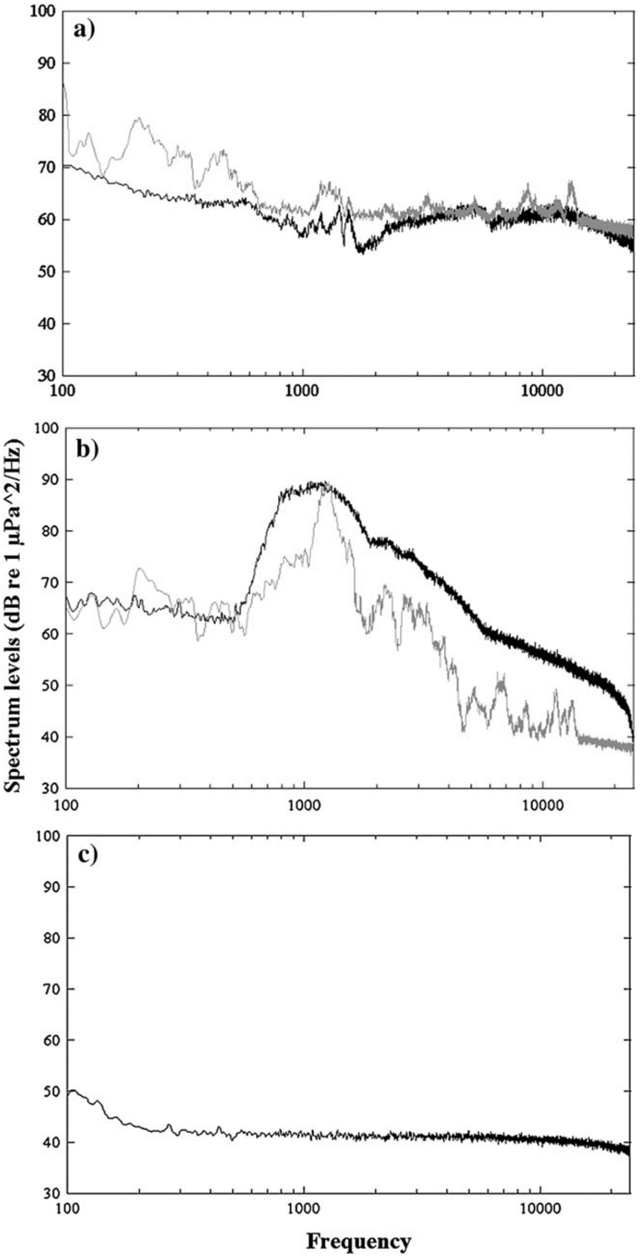

Figure 2
Spectral composition of underwater sound when recorded at coastal reefs and when replayed in experimental tanks. (a) Coconut Beach Reef, Lizard Island—tropical waters. (b) North Reef, north-eastern New Zealand—temperate waters. Black lines represent natural reef sound in situ and gray lines represent replayed sound in experimental sound treatments. (c) Sound in silent treatment tank.

Data analyses

Nonparametric statistical methods were used to analyze differences in the number of crabs that had settled every 6 h because the data were not continuous. The following analytical steps were repeated for the experiment for each crab species. First, a Kruskall–Wallis test was used to test for a difference in the median TTMs among the replicate group-housed megalopae within the same treatment (i.e., sound and silent analyzed separately). If this test found no difference, the data from the replicates were pooled. Second, the Mann–Whitney *U* test

Table 1

Summary of comparisons among median TTM among the group replicates and between the group and individually housed megalopae for each treatment (i.e., sound vs. silent) for 5 crab species

		Test statistic		Test statistic	
Species	Treatment	Group replicates[a]	Chi square	Group versus individual[b]	*U* value
Hemigrapsus sexdentatus	Sound	0.658	0.836	0.275	2.000
	Silent	0.337	2.174	0.822	4.000
Cyclograpsus lavauxi	Sound	0.984	0.032	0.817	4.000
	Silent	0.453	1.584	0.184	1.500
Macrophthalmus hirtipes	Sound	0.706	0.697	0.050	0.000
	Silent	0.455	1.576	0.822	4.000
Grapsidae sp. 1	Sound	0.639	0.895	0.102	0.000
	Silent	0.722	0.651	0.121	1.000
Grapsidae sp. 2	Sound	0.860	0.303	0.121	1.000
	Silent	0.784	0.486	0.121	1.000

[a] Kruskall–Wallis test showing no significance (>0.05).

[b] Mann–Whitney *U* test showing no significance (>0.05).

was used to test for a difference in median TTM between the individually and group-housed megalopae within the same treatment (i.e., sound and silent analyzed separately). If this test found no difference in the median TTMs the individual and group settlement data were also pooled for each treatment. Lastly, the Mann–Whitney *U* test was used to compare the median TTMs for megalopae in the sound treatment versus the silent (control) treatment. For all statistical tests, *P* values ≤0.05 were considered to be significant. A metamorphosis rate for each treatment within each species was also calculated as the slope of the linear line of best fit for the data points between the last sample prior to the first megalopa metamorphosing and the last megalopa to metamorphose for each treatment. All analyses were performed using the software Statistica (Version 6), SPSS 16.0 and Microsoft Excel 2007.

RESULTS

Sound analyses

In the experiments for both temperate and tropical crab species the broadcast sound within the experimental tanks had a similar overall spectral composition and sound level to the source signals recorded from the natural reef habitats (Figure 2). Hydrophone recordings taken in the silent treatments confirmed the absence of sound transfer from the sound treatments or other external sources (Figure 2).

Pooling

In all 5 crab species there were no significant differences in the median TTMs among the group replicates for both the sound and silent treatments (Kruskall–Wallis test) (Table 1). Therefore, for each crab species the settlement data for group-housed megalopae from the replicate tanks within each treatment were pooled and compared with corresponding data for individually housed megalopa for each treatment. There were also no significant differences in the median TTMs between individually and group-housed megalopae in either the silent or sound treatments for all species examined (Mann–Whitney *U* test, Table 1) (Figure 3), indicating there were no interactive effects on TTM between individuals in the group experiments.

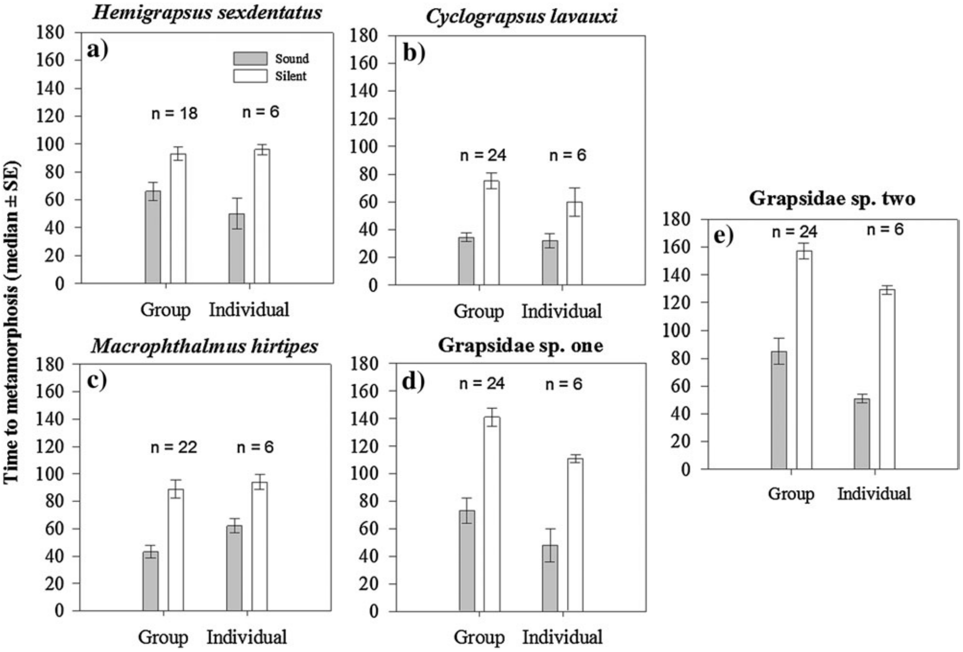

Figure 3
Median TTM in group and individual replicates. (a) *Hemigrapsus sexdentatus*, (b) *Cyclograpsus lavauxi*, (c) *Macrophthalmus hirtipes*, (d) Grapsidae sp. 1, and (e) Grapsidae sp. 2. Gray bars represent sound treatment and white bars represent silent treatment.

Therefore, for all crab species the group and individual data were pooled within treatments to test for the overall treatment effect, that is, sound versus silent.

Behavioral observations

A general description of changes in behavior was compiled using a set preset scale. Prior to metamorphosis, swimming activity of larval crabs was present in both the dark and light periods. However, swimming activity appeared to be greater during the dark periods than during the light periods. The behavior of megalopae that were approaching metamorphosis changed noticeably including reduced swimming activity, more frequent downward swimming to the settlement substrate followed by "exploratory crawling" whereby the megalopae would slowly crawl around on the artificial settlement substrate (Figure 4). This behavior is consistent with presettlement behavior previously observed in other crab species (Forward et al. 2001) and was consistent among the megalopae of all 5 species and preceded settlement and metamorphosis. There were no observed differences in the settlement behavior of megalopae between the sound and silent treatments except for timing of the onset of this behavior. In the sound treatment this behavior was consistently observed well in advance of the silent (control) treatment for every species examined (Figure 4).

Across all treatments and species the megalopae did not settle and metamorphose to the first instar benthic juvenile until at least 24 h after the start of the experiment, with some taking up to 114 h. Mortality was absent during these experiments, and all first instar crabs that were kept for up to 10 days after the conclusion of the experiment survived (Table 2, Figure 5).

Sound effect on TTM

In all 5 species of crabs the megalopae in the sound treatment had a significantly shorter median TTM than those in the silent treatment.

The tropical species Grapsidae sp. 2 had the largest difference in median TTMs between the 2 treatments, with a median TTM of 69 h in the sound treatment and 114 h in the silent treatment, that is, a 75 h difference (Mann–Whitney *U* test, $P = 0.004$, Table 2). This was followed by Grapsidae sp. 1 with a median TTM of 72 h in the sound treatment and 123 h in the silent treatment, that is, 51 h difference (Mann–Whitney *U* test, $P = 0.004$, Table 2).

The same trend was also present in the crab species from temperate waters, where megalopae of *M. hirtipes*, *C. lavauxi*, and *H. sexdentatus* in the sound treatment had a significantly shorter median TTM than those in the silent treatment, 72 and 108 h (48 h difference) (Mann–Whitney *U* test, $P = 0.004$, Table 2), 30 and 75 h (45 h difference) (Mann–Whitney

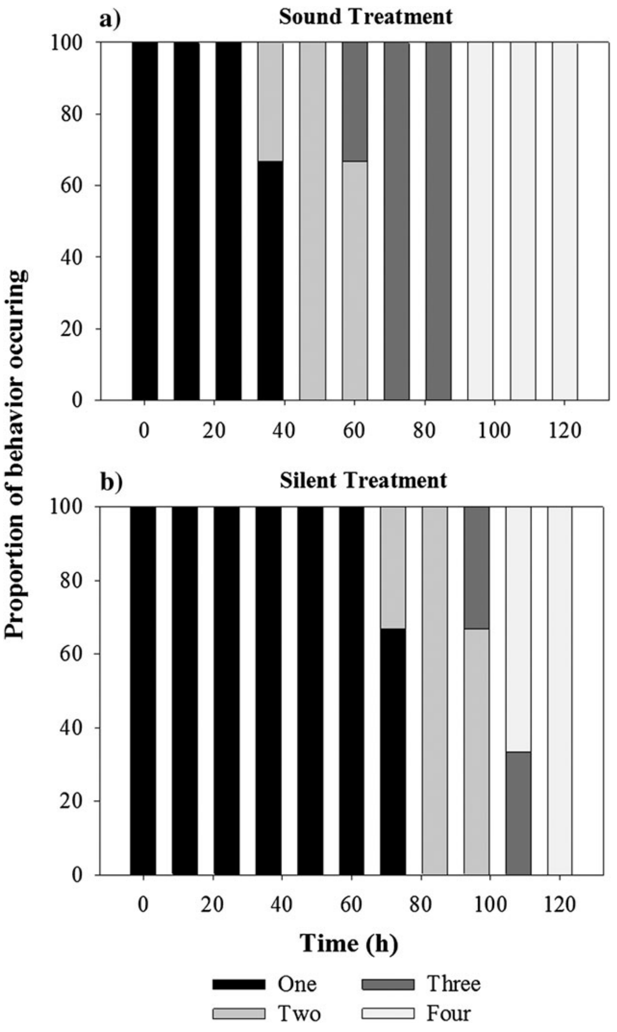

Figure 4
Proportions of categorized behaviors during the course of the experiment for *Hemigrapsus sexdentatus.* (a) Sound treatment and (b) Silent treatment.

Table 2
Summary of comparisons among median TTMs and settlement rates for each treatment (i.e., sound vs. silent) for 5 crab species

Species	Total number of individuals (n)	Treatment	Median TTM (h)	Difference in median TTMs (h)	Test statistic	*U* value	Metamorphosis rate
Hemigrapsus sexdentatus	12	Sound	63	33	*** (0.005)	0.500	9
	12	Silent	96				13.7
Cyclograpsus lavauxi	15	Sound	30	45	*** (0.005)	0.500	15
	15	Silent	75				8.3
Macrophthalmus hirtipes	14	Sound	72	48	*** (0.004)	0.000	11
	14	Silent	108				8.4
Grapsidae sp. 1	15	Sound	72	51	*** (0.004)	0.000	6.3
	15	Silent	123				8.3
Grapsidae sp. 2	15	Sound	69	75	*** (0.004)	0.000	5.5
	15	Silent	144				9.2

Asterisks indicate a significant difference in TTMs between treatments (significant at $P < 0.05$, Mann–Whitney *U* test). Test statistic rounded to 3 decimal places.

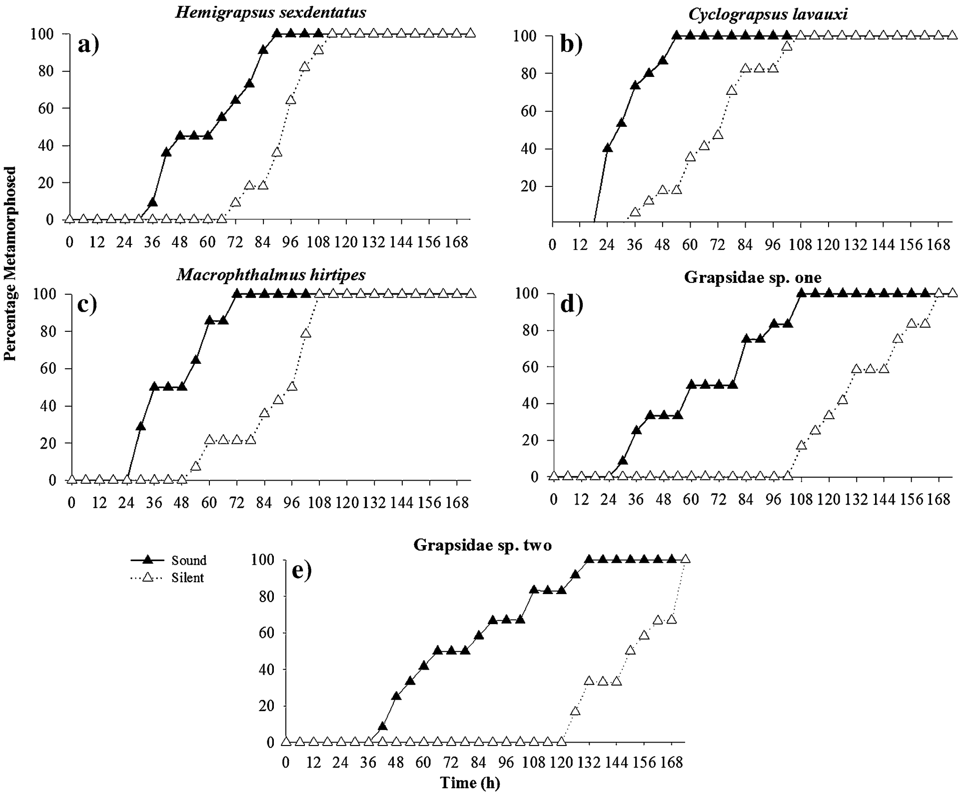

Figure 5
Percentage of total number of megalopae metamorphosed against time (h). (a) *Hemigrapsus sexdentatus*, (b) *Cyclograpsus lavauxi*, (c) *Macrophthalmus hirtipes*, (d) Grapsidae sp. 1, and (e) Grapsidae sp. 2. Solid lines represent sound treatment and broken lines represent silent treatment.

U test, $P = 0.005$, Table 2), and 63 and 96 h (33 h difference) for each species, respectively (Mann–Whitney *U* test, $P = 0.005$, Table 2).

Difference in time to the first metamorphosis between the 2 treatments varied substantially among the 5 species (Table 3), with *C. lavauxi* exhibiting the smallest difference of 12 h and Grapsidae sp. 2 exhibiting the greatest difference of 84 h. Grapsidae sp. 2 also had the greatest difference in time to completed metamorphosis between the 2 treatments, with all the megalopae completing metamorphosis in 108 h in the sound treatment and 168 h in the silent treatment (Table 3). *Hemigrapsus sexdentatus* had the smallest difference in time to completed metamorphosis between the 2 treatments (24 h).

Rates of metamorphosis

The metamorphosis rate of the silent treatment was 1.5 times faster than that of the sound treatment in *H. sexdentatus* (13.7 and 9, respectively). However, both *C. lavauxi* and *M. hirtipies* had faster metamorphosis rates in the sound treatment, 1.8 times and 1.3 times faster, respectively (Table 2).

The metamorphosis rates of the silent treatments were faster than the sound treatments in both tropical species. Grapsidae sp. 1 had a metamorphosis rate that was 1.3 times faster than in the silent treatment compared with the sound treatment with rates of 8.3 and 6.3, respectively. Grapsidae sp. 2 had a metamorphosis rate 1.6 times faster in the silent treatment (9.2) compared with the sound treatment (5.6) (Table 2).

DISCUSSION

There have been a number of laboratory and field studies in the last decade investigating specific physical and chemical cues such as temperature, salinity, and adult odor that shorten or lengthen the TTM in the megalopae of crabs (O'Connor 1991; Harvey and Colasurdo 1993; Lim 1997; O'Connor and

Table 3
Summary of comparisons among first metamorphosis, completed metamorphosis, and the difference between each treatment (i.e., sound vs. silent) for 5 crab species

Species	Treatment	First metamorphosis (h)	Difference (h)	Completed metamorphosis (h)	Difference (h)
Hemigrapsus sexdentatus	Sound	42	30	90	24
	Silent	72		114	
Cyclograpsus lavauxi	Sound	24	12	54	54
	Silent	36		108	
Macrophthalmus hirtipes	Sound	30	24	72	63
	Silent	54		108	
Grapsidae sp. 1	Sound	30	78	108	60
	Silent	108		168	
Grapsidae sp. 2	Sound	42	84	132	42
	Silent	126		174	

Gregg 1998; Gebauer et al. 2002, 2004). Cues that were found to shorten the TTM were most often chemical cues associated with sources from settlement habitats, adult habitats, or nursery areas, (i.e., adult habitat substrate, conspecific odor, related species odor and estuarine water) (Forward et al. 2001). For example, the effect of water-soluble conspecific odor on metamorphosis was tested by exposing megalopae to water in which adults had been held. It was found that the TTM for megalopae of the Atlantic mud crab, *P. herbstii*, decreased with higher concentrations of adult water and was not affected by odors from fishes and other crab species (Rodriguez and Epifanio 2000).

This current study provides the first evidence that underwater sound consistently shortens the TTM in a range of tropical and temperate crab megalopae, by between 34% and 60%. The response was also found to be consistent whether the experimental megalopae were housed individually or in groups. In contrast, some previous studies have found that increased TTM can be the result of decreased experimental density (Fernandez et al. 1994; Forward et al. 1996). For the blue crab, *C. sapidus*, reduced TTM was due to physical interactions between the megalopae and mortalities due to vulnerability to cannibalism during metamorphosis (Fernandez et al. 1994).

Recent research has shown that the pelagic stages of some marine organisms such as decapod crustaceans and fish can orientate and actively swim toward underwater reef sound (Tolimieri et al. 2002, 2004; Jeffs et al. 2003; Leis and Lockett 2005; Radford et al. 2007; Simpson et al. 2008). For example, 5 species of coastal crab megalopae consistently oriented and swum toward an artificial source of underwater reef sound (Radford et al. 2007). The results of these previous studies indicate that underwater reef sound may be used as a long-distance orientation cue for locating coastal settlement habitat in some crab species, including 2 of the species examined in the current study. Despite the increasing evidence for the use of ambient underwater sound as an orientation cue for pelagic stages of coastal crustaceans, no studies to date have examined the role of underwater sound as a short distance settlement cue for these stages (Jeffs et al. 2003; Radford et al. 2007). The current study provides the first evidence of ambient underwater sound decreasing the TTM of megalopae of both temperate and tropical coastal crab species, by as much as a half in some species such as, *C. lavauxi* and Grapsidae spp. 2. This reduction of time in the water column is likely to reduce the risk of predation, which is often very high during the pelagic megalopal phase of the life cycle and improve the ability to settle into suitable habitats for the reptant phase of the life cycle (O'Connor 1991; O'Connor and Gregg 1998). Early settlement can also improve initial growth or survival after metamorphosis (Pechenik 1990; O'Connor and Gregg 1998).

Crab megalopae are thought to possess a temporal threshold beyond which metamorphosis occurs even in the absence of suitable settlement cues (Weber and Epifanio 1996). From our results it would appear that there is perhaps a longer temporal threshold in the 2 tropical Australian species or that sound is a more dominant cue for initiating metamorphosis in these species. Compared with the temperate New Zealand crab species, the initiation of metamorphosis among megalopae of the 2 tropical Australian Grapsid species was delayed for much longer in the absence of a sound cue (102 and 120 h for Grapsidae sp. 1 and 2, respectively). However, once metamorphosis was initiated in the silent treatment it was rapid, with the rate of metamorphosis being higher in the silent treatment than the sound treatment for both species.

Overall, there was no consistent pattern in the rates of metamorphosis between sound and silent treatments among all 5 species even though it might be expected that megalopae that were consistently responding to a sound cue would also produce a higher metamorphosis rate. The variability in metamorphosis rates may be due to the absence of secondary metamorphosis cues which are known to be important in some crab species (Gebauer et al. 2004) or may be related to the delayed metamorphosis culminating in a spontaneous metamorphosis once a threshold has been reached (Gebauer et al. 2003).

The results of this study appear to greatly extend the role that ambient underwater sound may play in triggering behavioral and physiological changes in presettlement animals looking for suitable settlement habitats. The consistent behavioral response to acoustic cues found in 5 crab species from both temperate and tropical waters suggests the phenomenon has the potential to be widespread geographically and among crab species. If this is the case, then underwater acoustic cues may play a very significant role in the settlement and recruitment processes of many important coastal crab species.

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