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BEHAVIORAL ECOLOGY - ORIGINAL RESEARCH

Inducers of settlement and moulting in post-larval spiny lobster

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Abstract The rapid and often remote location of suitable habitats used by migrating organisms is often critical to their subsequent recruitment, fitness and survival, and this includes in the marine environment. However, for the non-feeding post-larval stage of spiny lobsters, effective settlement cues for habitat selection are critical to their success but are poorly described. Therefore, the current study examined whether acoustic and substrate cues have the potential to shorten the time to moulting and affect their subsequent nutritional condition in the pueruli of the southern spiny lobster, *Jasus edwardsii*. Individuals moulted to first instar juveniles up to 38 % faster when exposed to the underwater sound from two types of typical settlement habitat (coastal kelp- and urchin-dominated reefs) compared to those with no underwater sound. The settlement delay in the post-larvae without underwater sound also resulted in juveniles in poorer survival and nutritional condition as measured by their protein and lipid contents. In a separate experiment, post-larvae presented with seaweed and rock substrates were found to complete settlement and moult to juvenile by as much as 20 % faster compared to those on the sand and control treatments. Overall, the results are the first to demonstrate that the pueruli of *J. edwardsii* have the ability to detect and respond to underwater sound, as well as determining that both acoustic and substrate cues play a role in modulating physiological development during settlement.

Keywords Underwater sound · Spiny lobster · Settlement cues · Moulting · Puerulus

Introduction

The pelagic larval phase of the lifecycle of most benthic marine organisms typically involves dispersal away from parental habitats, ending with the larvae selecting a suitable benthic habitat in which to settle (O'Connor and Gregg 1998). An extreme example is the lifecycle of spiny lobsters which have a complex and extended pelagic larval phase (i.e., phyllosoma) lasting 12–22 months, and passing through up to 11 distinct developmental stages, the majority of which occur while the larvae are in oceanic waters tens to hundreds of kilometres offshore (Phillips and Sastry 1980; Booth 2006). The pelagic larval phase of spiny lobsters ends at metamorphosis from an oceanic planktonic larva, or phyllosoma, to a nektonic post-larva, known as a puerulus, which migrates onshore into coastal waters, settling and moulting to become a benthic dwelling first-instar juvenile (Jeffs et al. 2005; Wahle and Fogarty 2006). Settlement of the pueruli has been described to occur in structurally complex habitats in shallow coastal waters, such as crevices and small holes in reefs, or in some species of spiny lobster among macroalgae and mangrove roots (Acosta and Butler 1997; Jeffs and Davis 2003; Booth 2006).

The mechanisms by which the pueruli of the Australasian southern spiny lobster, *Jasus edwardsii*, move inshore to settle is unclear, but is thought to involve a combination of active onshore swimming and the passive use of natural

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onshore advection processes that are guided by a range of environmental directional cues (Phillips and Macmillan 1987; Butler and Herrnkind 2000; Booth 2001; Jeffs et al. 2005; Wilkin and Jeffs 2011). The potential onshore orientation cues that might be used by pueruli include underwater sound, magnetic fields, water chemistry, physical cues, celestial cues, and hydrodynamic cues; however, there is little evidence in support of the use of any particular one of these orientation cues (Jeffs et al. 2005). After migrating into shallow coastal water, the pueruli must locate suitable settlement habitat, usually consisting of crevices in rocky reefs or among boulders, usually in <15 m water depth (Booth and Stewart 1993).

This process is poorly understood in this lobster species, despite the mechanisms of selection of settlement habitats in marine invertebrates being extensively reported, with a wide range of potential sensory information being used to identify and guide settlers to preferred settlement habitats (Pawlik 1992; Rodriguez et al. 1993). For example, the larvae of many reef-dwelling animals appear to use chemical, visual, and physical cues when settling, including specific cues such as salinity, depth, substrate rugosity, and chemicals emanating from conspecifics and prey items, as well as underwater sound (Forward et al. 2001; Leis et al. 2003; Radford et al. 2007; Simpson et al. 2005, 2008a, b; Stanley et al. 2010, 2012; Stobutzki and Bellwood 1998). For spiny lobsters, finding an appropriate settlement habitat is critical to their subsequent survival and recruitment into the adult population, with consistently high estimates of juvenile mortality in the first year after settlement, exceeding 80 % and likely to be in the order of 97 % (Marx 1986; Herrnkind and Butler 1994; Phillips 2003).

The puerulus stage of spiny lobsters is lecithotrophic, relying solely on endogenous energy reserves accumulated during the extensive preceding phyllosoma phase, and consisting mostly of lipid and protein (Jeffs et al. 1999, 2001b). The duration of the puerulus stage in *J. edwardsii* is ~20–40 days, but may extend to as much as 70 days (Lesser 1978; Hayakawa et al. 1990; Kittaka 1990; Booth and Stewart 1992). The pueruli can migrate from hundreds of kilometres offshore to the coast where they settle (Jeffs et al. 2001a, 2005). With the highly active and the extensive period of the pueruli placing huge demands on their endogenous energy reserves, and with strong evidence that delayed settlement leads to depletion of these reserves, it is likely to compromise subsequent survival (Jeffs et al. 2001a; Wilkin and Jeffs 2011; Fitzgibbon et al. 2013). The rapid location and establishment of a puerulus on a suitable settlement habitat is of vital importance, and will determine its subsequent chances of survival. Therefore, it could be expected that the puerulus would make good use of environmental cues that could expedite settlement.

The remote recognition of ambient habitat-specific acoustic cues are known to be important in long-distance migration of many terrestrial animals, especially birds. For example, migrating birds can reliably assess the suitability of possible stopover habitats during landfall from a distance, using both visual (Hutto 1985; Moore and Aborn 2000) and acoustic cues (Mukhin et al. 2008). Acoustic cues become especially important during twilight landfall when visual cues are reduced or absent. Migrant birds can also remotely assess the qualities of habitats, using acoustic information such as vocalisations made by conspecifics and/or heterospecifics inhabiting the area (Herremans 1990; Schaub et al. 1999; Mukhin et al. 2008). Recent research has shown that underwater sound emanating from coastal habitats assists in the settlement of post-larval decapod crabs by influencing swimming direction and advancing physiological changes at settlement (Radford et al. 2007; Stanley et al. 2010, 2011, 2012). Although underwater sound has been suggested as a potential orientation and settlement cue for the pueruli of spiny lobsters for many years, evidence for the use of this cue remains circumstantial at best (Phillips and Penrose 1985; Jeffs et al. 1997). Likewise, relatively little is known about physical and chemical settlement cues in spiny lobsters, although they are known to be very important in the post-larvae of decapod crabs (Forward et al. 2001; Gebauer et al. 2003). The most extensive experimental study in spiny lobsters showed that the development of puerulus to juvenile was advanced by 20–30 % in the Caribbean spiny lobster, *Panulirus argus*, in the presence of red macroalgae *Laurencia* spp. a preferred settlement habitat (Goldstein and Butler 2009). Therefore, the aim of this study was to determine whether underwater sound from coastal habitats and physical/chemical properties of common settlement substrates are involved in expediting the settlement and moult from puerulus to first instar juvenile of the spiny lobster, *J. edwardsii*, and if so, whether this may impact the nutritional condition of the resulting settled juvenile.

Materials and methods

Ethics statement

The work was conducted under University of Auckland Animal Ethics Committee approval number R930.

Source of pueruli

Crevice collectors were used to capture newly settling Stage 1 pueruli for the experiments, and characterised by resembling a juvenile in shape and almost completely transparent (Booth 1979; Booth and Tarring 1986). Dependent upon the location of the experiment, 15 crevice collectors were deployed approximately 5–8 m apart in shallow water (<15 m depth) by suspending them beneath the wharf in the Port of Gisborne, or 25 crevice collectors were deployed haphazardly, on the seabed in shallow water at low tide (<3 m depth) at Castle Point on the east coast of North Island of New Zealand. In both circumstances, the collectors were recovered the following day and pueruli that had arrived within the last 12 h (Stage 1 pueruli; sensu Booth 1979) were retained for experiments. For the Castle Point individuals, experiments were carried out in a temporary laboratory approximately 5 min from the capture location. For the Gisborne-caught individuals, they were held in low light conditions in thermally insulated containers filled with ambient seawater with a low flow air supply to limit noise and to maintain a constant ambient temperature ±1.5 °C, dependant on the ambient temperature at their source (17 and 22 °C for Gisborne and Castle Point, respectively), and transported immediately to the Leigh Marine Laboratory, taking approximately 6 h. There was no mortality during transport from either of the locations.

Sound recordings for laboratory-based experiments

Recordings of ambient underwater sound were made at the two most common types of shallow water reef habitats in north-eastern New Zealand into which *J. edwardsii* pueruli are known to settle, i.e., a kelp-dominated rocky reef and urchin-dominated rocky reef (Radford et al. 2008a, 2010). Each habitat recording was only taken at one representative location, as a previous study has indicated that habitat sounds are characteristic and consistent among different locations on this coast (Radford et al. 2010). Sound recordings were taken during the summer at dusk on a new moon as this time has been previously determined as the intensity maximum for underwater sound (Radford et al. 2008b); Waterfall Reef (36°16′2.46″S, 174°48′3.05″E), a kelp-dominated rocky reef, and Nordic Reef (36°17′35.46″S, 174°48′37.48″E), an urchin-dominated rocky reef, commonly described as an urchin barren reef, due to the absence of kelp caused by grazing of the common sea urchin, *Evechinus chloroticus*. In situ habitat sounds were recorded using a remote underwater recording system which consisted of a calibrated HTI 96-MIN omnidirectional hydrophone (flat frequency response over the range of 10–24,000 Hz; High Tech, MI, USA) connected to a digital recorder Roland Edirol R09HR, contained in an underwater housing. There was no anthropogenic sources of noise such as large vessels or recreational boats present in the visible area at the time of recording. All recordings were conducted in near calm conditions (<0.5 m wave height and <2.6 m s^{-1} wind speed) (Climate Station, Leigh Marine Laboratory). Digital recordings were downloaded to PC and the spectral composition and sound pressure level determined using MATLAB software (MathWorks) with codes written specifically for the analysis for underwater sound recording. Power spectra were generated using fast Fourier transformation analysis of ten 10-s samples randomly selected from the original recording and smoothed using an 11-point triangular window. Sound pressure levels were determined for between 100 and 24,000 Hz from each of the ten samples and the mean used for the treatment levels. Three typical 4-min sequences from each habitat recording were randomly selected and transferred to MP3 players and used for playback in the sound treatment replicates. The three different sequences used in each of the replicates was to avoid pseudoreplication that would have occurred by using the same recording for each replicate (Kroodsma et al. 2001).

Laboratory-based experiments (acoustic and substrate)

Acoustic

The behavioural assay used in the experiments was taken and modified from Stanley et al. (2012).

The experiment consisted of three sound treatments (two rocky reef habitat sounds, i.e., kelp-dominated rocky reef and urchin-dominated rocky reef, and a silent control). Each treatment was contained within three replicate water baths (experimental tanks), used to maintain a constant water temperature at ambient levels from their source for the duration of the experiment (17 °C). Thick foam rubber matting was used to prevent transfer of acoustic energy from the environment into the experimental treatments, and this was verified using a hydrophone prior to the commencement of the experiment.

All replicates for both the sound and silent treatment had a waterproofed Phillips loudspeaker (4 Ω, 5 W) submerged in the experimental tank. The sound replicates only had a DSE MP3 player which was connected to the speaker and used to continually play a 4-min loop of the recorded ambient underwater reef sound into the tank. A calibrated hydrophone (HTI 96-MIN; High Tech) and recorder (722 recorder; Sound Devices, WI, USA) were used to adjust the sound level produced by the loudspeakers in each sound treatment tank so that it was equivalent to the sound level of the natural habitat as earlier recorded in the field, i.e., 109 and 116 dB re 1 μPa RMS level in the 100–24,000 Hz for the kelp-dominated and urchin-dominated rocky reef treatments, respectively. The broadcast sounds in the experimental tanks were recorded for comparison with the source signals recorded from the natural habitats, and to confirm the absence of significant sound in the silent treatment.

In each of the nine experimental tanks, five replicate acoustically transparent 750-ml plastic containers (n = 45

Table 1 Statistical comparisons among median TTMs and moulting rates for each treatment

Type of experiment	Total number of individuals (n)	Treatment	Median TTM (h)	Difference in median TTMs (h)	P value	H statistic	Moulting rate
Acoustic	15	Reef	192	24	<0.001*	23.9	7.8
	15	Urchin	216				8.8
	15	Silent	312	96			9.5
Substrate	5	Rocks	144	0	0.003*	14.1	8.7
	5	Algae	144				9
	5	Sand	180	36			7.3
	5	Control	180	0			11.4

* Significant difference in TTM among treatments ($P \leq 0.05$, Kruskal–Wallis test)

total; Table 1) each held a single randomly assigned Stage 1 puerulus in 700 ml of filtered (1 μm) and UV-treated seawater together with a 200 × 90 mm piece of plastic mesh acting as a chemically inert settlement surface.

Substrate

The experiment consisted of four treatments each with a different settlement substrate (rocks, sand, algae and control) to individually test physical and chemical settlement cues, and within each treatment were five replicate 1-l plastic containers, each containing a single randomly assigned Stage 1 puerulus and 800 ml of filtered (5 μm) seawater ($n = 20$; Table 1). The containers were held in a water bath at ambient seawater temperature from where the pueruli were collected (22 ± 0.5 °C). Replicate containers in the rocks treatment contained six similarly sized rocks (~4 cm^2) taken from a subtidal reef and scrubbed clean of all foreign material and then boiled. The sand treatment contained 250 ml of subtidal sand which was boiled and thoroughly rinsed to remove any biological material. The algae substrate treatment contained an 80-mm length of thallus of the kelp, *Carpophyllum maschalocarpum*, which had been thoroughly cleaned of all other associated organisms.

Experimental protocol

The tank experiments were commenced when the minimum number of Stage 1 pueruli (≥45 for the acoustic and ≥20 for the substrate experiments) were collected from the crevice collectors in one morning. The Stage 1 pueruli were randomly allocated to replicates within the experimental treatments at 1000 hours on the day following their capture and, for the acoustic experiments, the MP3 player was switched on to initiate sound in the sound treatments. Subsequently, every 6 h, an observational period occurred, to determine whether individual Stage 1 puerulus had moulted to the first instar juvenile stage. The time from establishing the experiment to the first observation of a first instar juvenile was termed the time to moulting (TTM). Each period of observation lasted not more than 40 min for all treatments. When the observational period occurred at night, weak red light was used to observe the behaviour and developmental status of the pueruli (Cronin 1986). The experimental tanks were kept at ambient temperatures (17 and 22 ± 1.0 °C; DST CTD mini logger; StarODDI, Iceland) and under natural light period for that time of the year (Gisborne 11 h light:13 h dark and Castle Point 14 h light:10 h dark) for the duration of the experiment in a quiet concrete laboratory with restricted access. Each individual plastic container holding a puerulus had a daily water change during the daylight observational period. The experiment was concluded when all pueruli in all treatments had moulted. In the acoustic experiments, the juvenile pueruli were removed from the experiment and immediately frozen at −80 °C for biochemical analyses at the time of the first observation that they had moulted to a juvenile. In the substrate experiments, all juvenile pueruli were returned to the place of capture at the conclusion of the experiment.

Biochemical analyses

For each individual in each treatment, the lipid and protein contents were measured ($n = 15$ for each treatment). For each individual, the lipid content of the individual puerulus was measured gravimetrically with a modified Bligh and Dyer (1959) one-phase methanol/chloroform/water extraction (Jeffs et al. 2004) from individual lyophilised pueruli, and using a XS205 DualRange precision balance (Mettler Toledo). Total lipid of the pueruli was then calculated as a percentage of dry weight to standardise for initial weight differences among individuals. After lipid extraction, individual puerulus were lyophilised again and homogenised with a micropestle, re-weighed, and then used for protein analysis. Protein content of individual pueruli was measured using the bicinchoninic acid (BCA) method using a Micro BCA protein assay kit (Thermo Scientific Pierce), using bovine serum albumin as the reference protein. For this, a pre-weighed sample of the lyophilised pueruli were digested for 12 h in 0.1 m NaOH at 50 °C to release bound protein. Total protein content of the pueruli was then calculated as a percentage of original dry weight to standardise for initial weight differences among individuals.

To estimate the energy density of the pueruli, the protein and lipid masses for each individual were converted to calorific energy equivalents using the estimated combustion coefficients of Gnaiger (1983): 23.9 kJ g^{-1} for protein and 39.5 kJ g^{-1} for lipid, such that total energy from protein and lipid (kJ) = (protein mass × 23.9) + (lipid mass × 39.5). Energy equivalents of the pueruli was then calculated as a percentage of dry weight to standardise for initial weight differences among individuals.

Data analyses

The non-parametric Kruskal–Wallis comparison of ranks was used to test for a difference in the median TTMs among the replicates within the same treatment (i.e., each treatment analysed separately, $n = 15$ for each treatment in sound experiments) (Zar 1999). If there was no difference found among the three replicates within a treatment, the data from the three replicates were pooled for an experiment-wide comparison. The Kruskal–Wallis test was then used to compare the distribution of median TTMs for pueruli among the treatments using the data pooled for the three replicates within each of the three treatments ($n = 45$). For all statistical tests, P values ≤ 0.05 were considered to be significant. To isolate differences among individual treatments a Tukey's test pairwise multiple comparison procedure was used. Sen's slope analysis was used to calculate a moulting rate for each treatment; this is a non-parametric alternative which estimates the value for slope for the time series of time to moulting.

Analyses of biochemical data

The non-parametric Kruskal–Wallis comparison of ranks was used to test for a difference in the total lipid and protein as a percentage of dry weight among treatments because the data were not from a normal distribution (Zar 1999). To isolate differences among individual treatments a Tukey's test pairwise multiple comparison procedure was used. All analyses were performed using Sigma Stat 4.0 (Systat Software) and Minitab 16.1.0 (Minitab) software.

Results

Sound analyses

The broadcast sound within the experimental tanks was reasonably consistent with the sound level and overall spectral composition of the original sounds recorded from the natural habitats in situ, with a small reduction in sound level in the middle and higher frequencies (i.e., 800–2,000 and 7,000–20,000 Hz) (Fig. 1b). The field recording of the kelp-dominated rocky reef habitat had a peak in the spectra around 200–10,000 Hz, which is produced by the high frequency snaps of snapping shrimp (Fig. 1a), while in the recordings of the urchin-dominated rocky reef, there was a peak in the spectra around 600–1,500 Hz, which is produced by the feeding of the sea urchin, *E. chloroticus* (Fig. 1b).

The silent treatments had no sound transfer from any external sources, with the flat response seen at approximately 40 dB, representing the lower recording limit of the recording system (Fig. 1c).

Laboratory-based experiments

Acoustic

For all treatments, there was no significant difference in the median TTM among the three replicates within each treatment ($P > 0.1$); therefore, the TTM data for the replicates within each treatment were pooled to test for an overall effect. Overall, the median TTM for the pueruli differed significantly among the three treatments (Kruskal–Wallis test; Table 1; Fig. 2a). The median TTM of pueruli in the silent treatment was significantly longer (Tukey's test, $P < 0.05$) to those in both the kelp-dominated rocky reef and the urchin-dominated rocky reef treatments; however, there was no significant difference in the median TTM between the two types of reef treatment. The kelp-dominated rocky reef treatment had the shortest median TTM among the three treatments of 192 h, followed by urchin-dominated rocky reef of 216 h, and silent of 312 h.

The time from the onset of the experiment to the time of the first puerulus to complete moulting varied among the treatments, with the first puerulus moulting in the kelp-dominated rocky reef and urchin-dominated rocky reef treatments, both occurring on average at 168 ± 8 h SE for the three replicates (Table 2). In comparison, the first puerulus to complete moulting in the silent treatment occurred 72 h later, after 240 ± 7.2 h on average for the three replicates. The mean times it took for all pueruli in each replicate to complete moulting within the kelp-dominated rocky reef and urchin-dominated rocky reef treatments

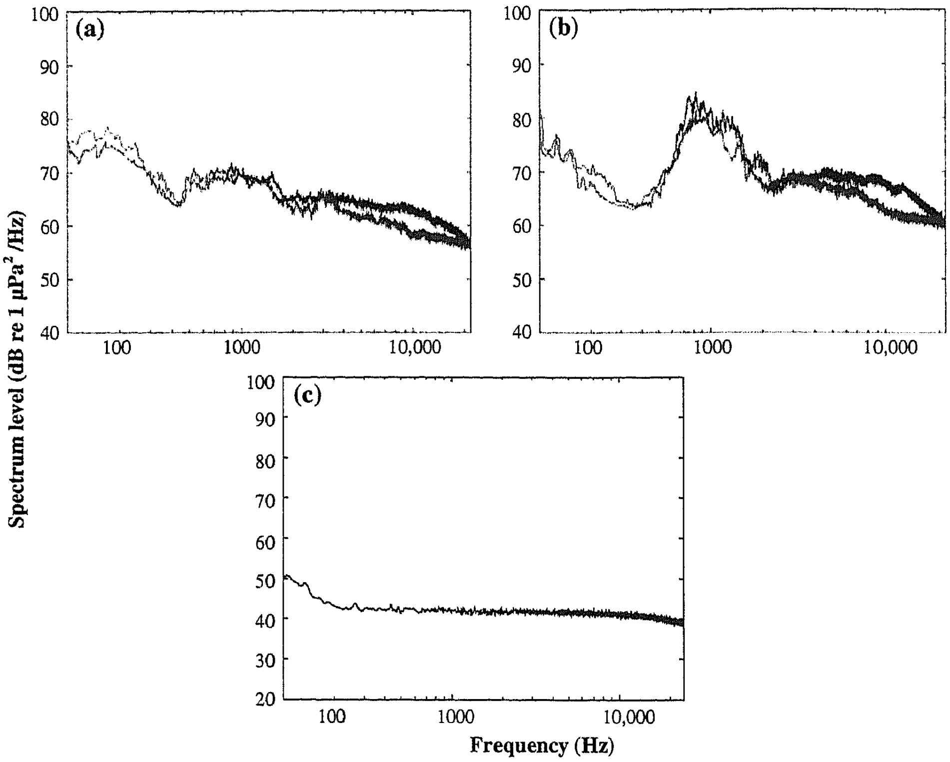

Fig. 1 Spectral plots showing composition and sound level of ambient underwater sound when recorded at coastal reefs and when replayed in experimental tanks. **a** Kelp-dominated rocky reef (Waterfall Reef), **b** urchin-dominated rocky reef (Nordic Reef) and, **c** silent treatment. *Black lines* original natural ambient sound and *blue lines* experimentally replayed sound (colour figure online)

were 288 ± 16 and 288 ± 21 h, respectively, compared to 348 ± 4 h in the silent treatment, a 60-h difference.

Three of the individual pueruli in the silent treatment died shortly after moulting, with two at 336 h and another at 348 h, which was well beyond the completion of moulting for all pueruli in the two reef sound treatments.

Biochemical analyses

Total lipid

In all treatments in the acoustic experiment, the total lipid content (percentage of dry weight) of first instar juvenile lobsters tended to decrease with increasing TTM. The lipid content per puerulus differed significantly among acoustic treatments (Kruskal–Wallis test, $H = 7.4$, $P = 0.025$; Fig. 3). Pueruli in the kelp-dominated rocky reef treatment had significantly more lipid (7.7 % of dry weight, 25 % quartile–7.1, 75 % quartile–8.2) than either the urchin-dominated rocky reef or silent treatments (6.2 %, 25 %–9, 75 %–7.5, and 6.1 %, 25 %–4.3, 75 %–7, respectively) (Tukey's test, $P \leq 0.05$). There was no significant difference in the median lipid content of pueruli between the urchin-dominated rocky reef and silent treatments ($P > 0.05$).

Total protein

The total protein content (percentage of dry weight) of first instar juvenile lobsters tended to decrease with increasing TTM over all of the treatments. The median total protein content of pueruli differed significantly among treatments (Kruskal–Wallis test, $H = 14.8$, $P \leq 0.001$; Fig. 4). Pueruli in the kelp-dominated rocky reef treatment and urchin-dominated rocky reef treatments both had significantly more protein (35.7 %; 25 % quartile–34.4, 75 % quartile–36.5 and 35 %; 25 %–32.3, 75 %–36.5 of dry weight, respectively) than the silent treatment (31.1 %; 25 %–28.7, 75 %–33.1) (Tukey's test, $P \leq 0.05$). There was no significant difference between the median protein content of pueruli in the kelp-dominated rocky reef and urchin-dominated rocky reef treatments ($P > 0.05$).

Total energy

Over all treatments, the total energy from both protein and lipid values of first instar juvenile lobsters tended to decrease with increasing TTM. The median total energy from the lipid and protein masses of pueruli differed significantly among treatments (Kruskal–Wallis

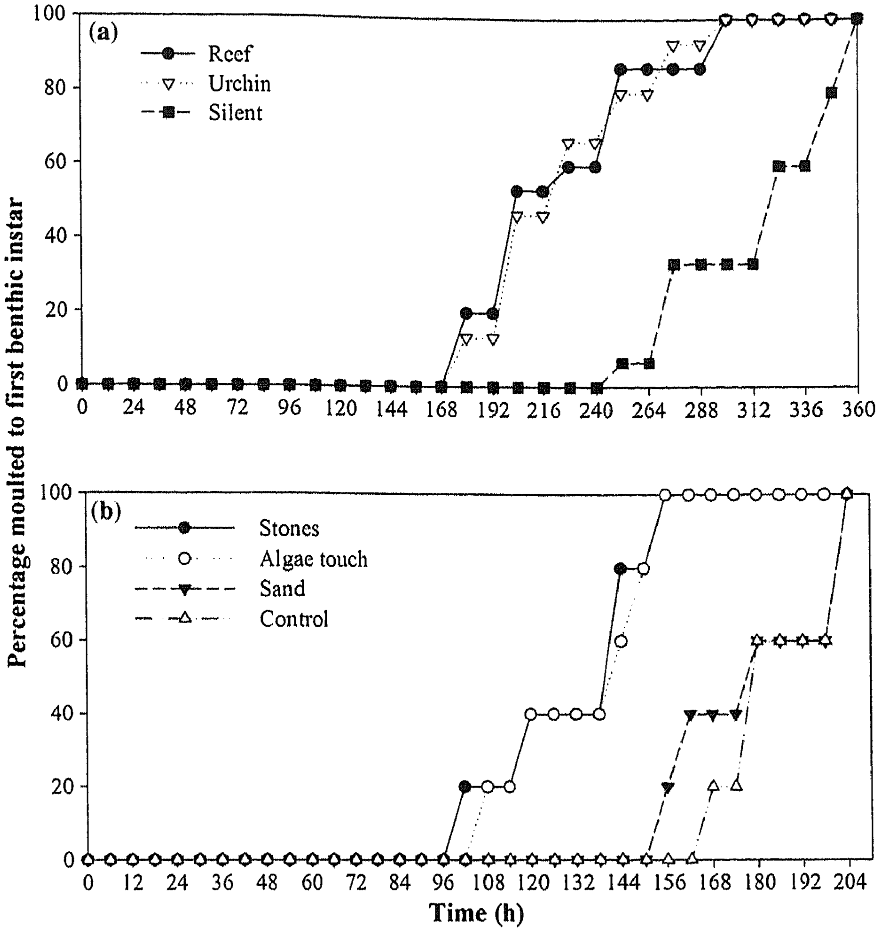

Fig. 2 Settlement response plot showing percentage of all pueruli moulted over time (h), **a** in each of the three experimental sound treatments, i.e., silent, kelp-dominated rocky reef ($n = 15$), and urchin-dominated rocky reef ($n = 15$), and **b** in each of the four chemical/physical experimental treatments ($n = 5$ each)

Table 2 Summary of comparisons among first moult, completed moult and the difference among each treatment

Type of experiment	Treatment	First moult (h)	Difference (h)	Completed metamorphosis (h)	Difference (h)
Acoustic	Reef	168	0	288	0
	Urchin	168	72	288	60
	Silent	240		348	
Substrate	Rocks	102	6	156	6
	Algae	108	48	156	42
	Sand	156		204	0
	Control	168	12	204	

test, $H = 13.4$, $P = 0.001$; Fig. 5). Pueruli in the kelp-dominated rocky reef treatment and urchin-dominated rock reef treatment both had significantly more total energy (5 %; 25 % quartile–4.5, 75 % quartile–5.3 and 4.8 %; 25 %–4, 75 % quartile–5.1 of dry weight) than the silent treatment (3.9 %; 25 %–3.6, 75 %–4.4) (Tukey's test, $P \leq 0.05$). There was also no significant difference between the median energy content of pueruli in the kelp-dominated rocky reef and urchin-dominated rocky reef treatments ($P > 0.05$).

Substrate

Overall, the median TTM for the pueruli differed significantly among the four settlement substrate treatments (Kruskal–Wallis test; Table 1; Fig. 2b), with significant differences in TTM (Tukey's test, $P < 0.05$) among all pairwise comparisons among the four treatments except rocks versus algae substrate and sand versus control.

The rocks and algae substrate treatments had the equal shortest median TTM among the four treatments of 144 h,

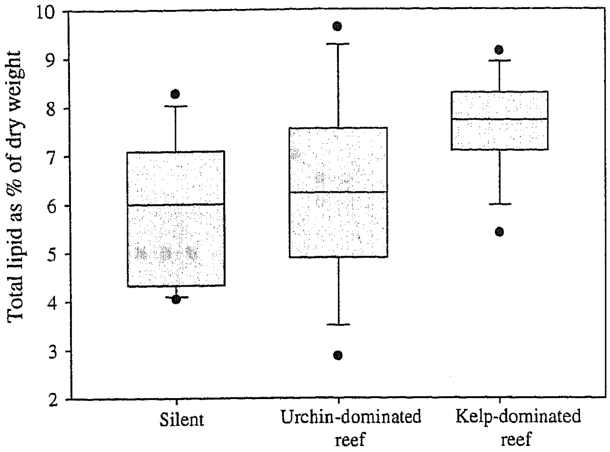

Fig. 3 Median levels and quartiles of lipid as a percentage of dry weight for puerulus in each treatment

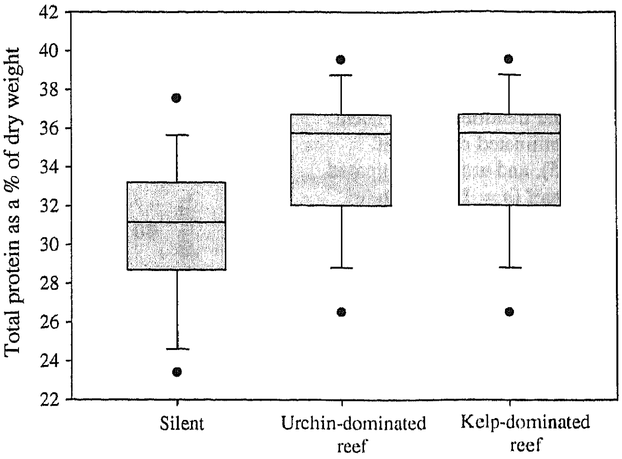

Fig. 4 Median levels and quartiles of protein as a percentage of dry weight for puerulus from each treatment

followed by the sand and control treatments both with a median TTM of 180 h. The time from the outset of the experiment to the first puerulus to complete moulting varied among the treatments, with the first puerulus in the rocks treatment completing moulting at 102 h, compared to 108 h in the algae substrate treatment, 156 h in the sand treatment, and 168 in the control treatment (Table 2). The time it took for all pueruli in each treatment to complete moulting also differed among treatments, with the rocks and algae substrate treatments completing moulting at 156 h, while sand and control completed moulting at 204 h, a 50-h difference. The temperature of the tanks throughout the experiment varied by <0.5 °C (median ± SD: day 1: 22.2 ± 0.22; day 2: 22.2 ± 0.15; day 3: 22.5 ± 0.10; day 4: 22.4 ± 0.05; day 5: 22.4 ± 0.09; day 6: 22.5 ± 0.1; day 7: 22.5 ± 0.05).

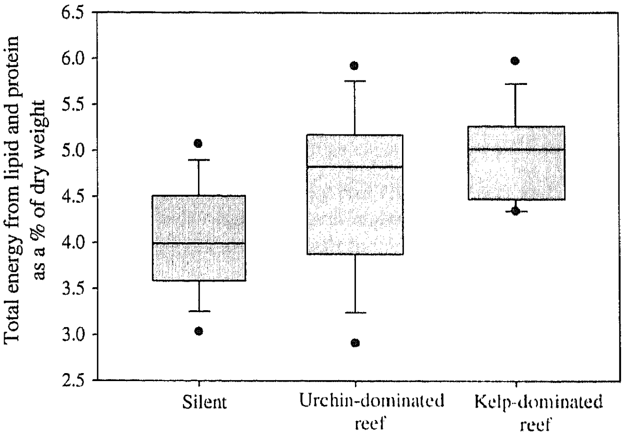

Fig. 5 Median levels and quartiles of energy from lipid and protein as a percentage of dry weight for puerulus from each treatment

Discussion

This study is the first to demonstrate that Stage 1 pueruli of *J. edwardsii* respond to natural sources of underwater sound associated with settlement habitats, by advancing the development of pueruli to first instar juveniles by as much as 38 % compared to a control. In the substrate settlement experiments, the development was reduced by 20 % in the presence of a rock or algal substrate when compared to the sand and control treatments.

These results are consistent with the preferred settlement habitat of this species with most pueruli and first-instar juveniles of *J. edwardsii* found in rocky substrate in holes and crevices 10–20 mm in diameter and 20–30 mm deep, where light levels are low (Booth and Forman 1995; Edmunds 1995). The reduction in TTM of the pueruli of *J. edwardsii* due to underwater sound is in support of those previously reported for settlement-stage brachyuran crabs (33–47 %) (Stanley et al. 2011, 2012) and mussels (40 %) (Wilkens et al. 2012), and suggests that underwater sound plays a role in modulating physiological development prior to settlement in *J. edwardsii*. For example, in a study by Stanley et al. (2011), which examined the behavioural threshold responses to optimal habitat sound in several species of brachyuran crabs, the results suggested that there may be different larval settlement strategies among species. Crab species with a high acoustic threshold (lower sensitivity) would rely on a much more rapid settlement once in the immediate vicinity of a suitable habitat, whereas species with a lower threshold (higher sensitivity) may detect a suitable habitat from greater distances, but not accelerate their settlement response to the same degree in order to have sufficient time to swim towards and locate a suitable settlement habitat (Stanley et al. 2011).

To date, only one study has experimentally combined testing for the interaction of both acoustic and chemical or substrate cues for any marine larvae (Huijbers et al. 2012). This previous study identified that, during a specific life phase, larval French grunt (*Haemulon flavolineatum*) exhibited receptivity to multiple sensory cues and found that different cues induced different behaviours towards the same habitat. It is clear that larval settlers are relying on multiple settlement cues when searching for and selecting a suitable habitat; however, how these cues interact is still largely unknown, and is likely to be important in terms of operating over different spatial scales, especially for pueruli migrating to the coast from great distances offshore (Jeffs et al. 2005).

The rate of development (number of days until moulting) from Stage 1 puerulus to first instar juvenile varied between the two experiments in the current study (acoustic and substrate) due to differences in the ambient water temperatures at the time of the experiment. This is consistent with development timing in previous studies on *J. edwardsii* in which the rate of development varied with season, with the period between Stage 1 to the moult ranging from 9 days in summer water temperatures to 20 days in winter temperatures (Booth and Stewart 1993).

There was no difference in median TTM between the two sound treatments, and both the first and last pueruli to moult to first instar juvenile occurred after the same time period for both reef habitats, despite marked differences in the intensity and spectra of these habitat sounds in this experiment. In contrast, the ability to discriminate among habitat sounds and respond to differences in sound intensity have been found in previous studies on the settlement behaviour of the megalopae of a number of coastal reef-dwelling brachyuran crab species (Stanley et al. 2011, 2012). These behavioural differences between the postlarval stages of crustacean taxa suggest that, while using underwater sound to discriminate between different types of rocky reef habitat is possible, that for *J. edwardsii* pueruli it is not of critical importance. Underwater sound may be used by pueruli migrating from offshore waters to distinguish their arrival in shallow coastal waters rather than for fine scale selection of habitats. This result is also consistent with observations of the behaviour of pueruli of *J. edwardsii* upon arrival in coastal habitats, whereby they remain highly mobile at night, moving among localised habitats via swimming and walking, for which they may be using chemical and physical substrate cues for selecting ultimate settlement sites (Hayakawa et al. 1990; Booth and Stewart 1993).

To date, only experimental increases in water temperature of 3–5 °C above ambient sea temperature have been found to decrease the TTM in *J. edwardsii* pueruli, which is likely as a direct result of a poikilothermic metabolic response (Booth and Stewart 1993). The presence or absence of conspecific pueruli, food, cover, and differing substrate types (rocks, algae and sand) has previously been found not to influence TTM (Booth and Stewart 1993). However, in the current study, TTM was also observed to be significantly shortened when pueruli were in contact with clean rock and macroalgae material (*C. maschalocarpum*) as a settlement substrate compared to sand and a control, providing evidence for the likely use of these substrate cues in fine-scale habitat selection. Reductions in the TTM in pueruli of around 25 % have also been reported for *P. argus* in response to the presence of chemical cues from red macroalgae (*Laurencia* spp.) which dominates their preferred settlement habitat (Goldstein and Butler 2009).

The pueruli of *J. edwardsii* typically migrate from beyond the continental shelf into shallow coastal waters of <15 m depth where they settle, an overall distance of around 200 km on average (Booth 2001; Jeffs et al. 2001b). The migration of pueruli is thought to make substantial use of active swimming in order to reduce transit time and uncertainty associated with relying solely on passive transport mechanisms, such as riding ocean currents (Wilkin and Jeffs 2011). The energetic task is made more difficult as pueruli are lecithotrophic, relying solely on the endogenously stored lipid and protein gathered during the extensive phyllosomal phase which is largely undertaken in oligotrophic waters with low prey availability (Fitzgibbon et al. 2013). These stores are crucial for fuelling this migration and the subsequent development and moult into a benthic-dwelling juvenile (Jeffs et al. 1999; Limbourn et al. 2008). There is evidence that delays in migration to reach suitable settlement habitats will result in depletion of the stored biochemical reserves, and that this is likely to compromise the future survival of pueruli or subsequent early benthic juveniles (Jeffs et al. 2001b; Wilkin and Jeffs 2011; Fitzgibbon et al. 2013). The current study compared the quantity of total lipid and protein as a percentage of dry weight remaining in the resulting juveniles at the completion of the acoustic portion of the experiment. The results showed that the lipid content of newly moulted first instar juvenile lobsters was significantly lower in the silent treatments compared to the kelp-dominated rocky reef and urchin-dominated rocky reef sound treatments. This was likely related to the significantly longer TTM in this treatment, as the lipid content of pueruli tended to decrease with increased time to moulting. The protein content of pueruli in the silent treatment had significantly lower levels than those in both the kelp-dominated rocky reef and urchin-barren rocky reef treatments. Extending the TTM in the lecithotrophic pueruli results in increased depletion of energy reserves by the pueruli with the potential to compromise subsequent survival (Limbourn et al. 2008; Fitzgibbon et al. 2013). In the current study, the last three pueruli to moult (i.e., 336 and 338 h TTM) also had the lowest lipid stores (4.0, 4.1 and 4.3 %), and all died shortly after moulting. These individuals may have been energetically compromised at capture and, since subsequent moulting was delayed, had insufficient endogenous nutritional reserves to survive beyond the moult.

Delayed metamorphosis has been considered a selective advantage for some benthic marine species as it should theoretically improve the likelihood of finding an optimal habitat in which to settle (Thorson 1950); however, in lecithotrophic larvae such as spiny lobster pueruli, any delays in metamorphosis can affect the survival prospects for the following stages due to an extended period of metabolic losses (Pechenik 1990, 1999). For example, enhanced mortality and reduction in size after extending the larval phase due to the absence of cues to trigger metamorphosis have been demonstrated in the first benthic juvenile of the estuarine crab, *Neohelice granulata*, an effect that was thought to be due to the additional utilisation of internal reserves (Anger 1987). There is some evidence that lecithotrophic larvae and post-larvae of marine organisms may be less discriminatory and therefore less reliant on settlement habitat cues as a result of their constrained duration of competency (Bishop et al. 2006). However, for the lecithotrophic pueruli of *J. edwardsii*, it appears as though a variety of settlement cues may be involved in contributing to improving the overall outcome of settlement into suitable habitats.

The results produced from this study demonstrating settlement responses to ambient underwater sound could also suggest that anthropogenic underwater noise, especially of a continuous nature, has the potential to interfere with critical settlement processes of lobsters reliant on ambient underwater sounds to locate and settle into suitable coastal habitats. Some sources of anthropogenic underwater noise in coastal environments have high peak pressure levels that may mask natural levels of ambient reef sound used in natural larval settlement responses (Montgomery et al. 2006; Radford et al. 2007; Pine et al. 2012). For lobster pueruli, auditory masking is the most likely effect, and this occurs when biologically irrelevant anthropogenic sound prevents animals from hearing biologically relevant sound (Popper et al. 2003).

Within the natural range of *J. edwardsii*, examples have been observed of wholesale habitat change, which are reported to be due to fishing pressures and practices, climate change or other environmental factors (Shears and Babcock 2002; Johnson et al. 2011; Flukes et al. 2012; Strain and Johnson 2012). For example, in eastern Tasmania over the past 8–9 years, there have been reports of reductions in recruitment of *J. edwardsii* and subsequent legal-sized rock lobsters (Pecl et al. 2009; Linnane et al. 2010; Gardner et al. 2011; Hartmann et al. 2012). These reductions are suggested to be associated with large-scale environmental change, ocean warming off the east coast of Tasmania, and compounded with the overfishing of large predators (e.g. large individuals of *J. edwardsii*) (Ling et al. 2009; Caputi et al. 2013). One recognised impact of climate change in eastern Tasmania is the shift from the dense and productive kelp beds (*Macrocystis pyrifera*) to areas of bare rock (Pecl et al. 2009; Johnson et al. 2011). This dramatic habitat change is largely due to the southern penetration of the warm and nutrient-poor East Australian Current (EAC) and range expansion of other warmer water species such as the sea urchin *Centrostephanus rodgersii* (among other northern species). Over-grazing of kelp beds by the recently established *C. rodgersii* has caused major changes in the structure and dynamics of rocky reef systems in eastern Tasmania, with the formation of 'urchin barren' habitats (Pecl et al. 2009; Johnson et al. 2011). This change from kelp beds to barrens may affect the local productivity and is thus of concern in the context of recruitment of this valuable fishery resource (Ling and Johnson 2009; Johnson et al. 2011; Hinojosa et al. 2014).

The current study provides a first step towards investigating whether the change from productive kelp-dominated reef to areas of bare rock and the subsequent trophic cascades may be resulting in the loss of habitat-specific cues (e.g. acoustic and substrate cues) which may be impacting the recruitment of *J. edwardsii*. The results suggest that differences in auditory and substrate associated habitat cues between kelp-dominated rocky reef and urchin-dominated rocky reef do not produce significant differences in TTM in the pueruli of *J. edwardsii* in New Zealand waters, and therefore other factors leading to this decline in recruitment need to be further investigated. Climate change is noted to have had an observable effect on the water temperature, zooplankton and phytoplankton off south-eastern Australia (Lough 2009; Richardson et al. 2009; Hallegraeff et al. 2012). Moreover, these changes have great potential to compromise survival rates and successful recruitment in spiny lobsters which have long pelagic larval durations (Fitzgibbon et al. 2013).

Furthermore, there are also other biological factors which differ between kelp-dominated rocky reef and urchin-dominated rocky reef habitats which could have an effect on the subsequent post-settlement fitness and survival of *J. edwardsii* recruits, such as prey availability (Stanley et al., unpublished data), complex physical structures (Andrew 1993), and predation risks (Hinojosa et al. 2014). The results of the present study provide strong evidence that the pueruli of *J. edwardsii* have the ability to detect and respond to large-scale acoustic and substrate habitat cues by significantly decreasing time to moulting. However, they do not appear to distinguish between kelp-dominated and urchin-dominated rocky habitats using these cues, suggesting that the ultimate habitat is likely to be encountered and selected on a finer scale via post-settlement movement.

Author contribution statement JS, AJ and JH conceived and designed the study. JS and JH performed the experiments. JS, JH, IH and AJ conducted field work. JS and AJ wrote the manuscript; other authors provided experimentaland editorial advice to the final manuscript.

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