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How do spiny lobster post-larvae find the coast?

ANDREW G. JEFFS
National Institute of Water and Atmospheric Research Limited
P.O. Box 109695
Auckland, New Zealand
and
School of Biological Sciences
University of Auckland
Private Bag 92019
Auckland, New Zealand
email: a.jeffs@niwa.co.nz

JOHN C. MONTGOMERY
School of Biological Sciences
University of Auckland
Private Bag 92019
Auckland, New Zealand

CHRIS T. TINDLE
Physics Department
University of Auckland
Private Bag 92019
Auckland, New Zealand

Abstract The larvae or phyllosomes of many species of spiny lobsters (Palinuridae) are known to complete their development in offshore oceanic waters. Phyllosomes metamorphose to non-feeding, nektonic post-larvae or pueruli, which move into shallow coastal waters where they settle to become benthic dwelling juveniles. There is growing evidence that the movement of pueruli is directed toward the coast rather than a process of random dispersal. The migration inshore by the non-feeding pueruli is likely to be one of the more extreme examples of onshore orientation among marine organisms, but is still poorly understood. This article provides a synthesis of the current state of knowledge of the possible cues and sensory mechanisms that might be used by pueruli of spiny lobsters for orienting toward the coast from offshore waters. The review is used to identify the potential cues that would benefit from future research efforts.

Keywords Palinurid; post-larvae; puerulus; underwater sound; magnetic sense; onshore movement

INTRODUCTION

Spiny lobsters of the family Palinuridae are found throughout tropical and temperate seas, where they are of considerable ecological and economic importance (Lipcius & Eggleston 2000). The life cycle of these lobsters includes a transition from an oceanic planktonic larval phase (phyllosome) through a single-stage nektonic post-larva (puerulus) that moves inshore to settle in shallow coastal waters and then moults to become a benthic dwelling first-instar juvenile. The biology of lobsters during this period of their life cycle is poorly understood, especially the ecology of the puerulus stage (Butler & Herrnkind 2000). The larval phase in spiny lobsters is extensive, lasting up to 18 months in some species, and usually involving 7–13 distinct phyllosome stages, with each stage represented by one or more instars (Phillips & Sastry 1980). This long larval period is unusual among marine invertebrates as only c. 5% of benthic invertebrates have a larval phase that lasts more than 12 weeks (Thorson 1950). The early phyllosome developmental stages that follow from the hatching of eggs have limited swimming abilities and consequently, they are eventually dispersed widely offshore by currents (Phillips & Sastry 1980; Bruce et al. 2000). As a result, the later phyllosome stages in most palinurid species are most commonly found inhabiting oceanic waters beyond the continental shelf, as much as 1500 km from the coast (Berry 1974; Serfling & Ford 1975; Phillips et al. 1979; Booth et al. 1998).

The location and trigger for the metamorphosis from the final stage phyllosome to the puerulus is uncertain because of difficulties obtaining direct

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observational or experimental evidence. An early review of the available evidence for the Western Australian lobster, *Panulirus cygnus*, suggested that salinity changes near the continental shelf edge were likely to be responsible for triggering the metamorphosis for the pueruli that were encountered in this area of the ocean (Phillips & McWilliam 1986). A subsequent review concluded that metamorphosis in the final stage larva only occurred after it had reached a critical, specific, level of stored energy reserves (McWilliam & Phillips 1997). However, only three studies provide any firm evidence of the location of metamorphosis for pueruli and hence the starting point for the onshore migration. Ritz (1972) inferred the location of metamorphosis from 19 cast exuviae of final stage phyllosomes of *P. cygnus*, all caught more than 161 km (ranging from 215 to 400 km) from the shore of Western Australia. Yoshimura et al. (1999) caught three metamorphosing final stage phyllosomes of *Panulirus japonicas* in the Kuroshio Current at 54 and 63 km from the nearest land. Jeffs et al. (2001) inferred the location of metamorphosis for pueruli of *Jasus edwardsii* based on the presence of soft carapaces in 33 out of 260 pueruli caught in an extensive offshore survey east of New Zealand. These recently metamorphosed pueruli were captured between 24 and 216 km offshore (mean of 92.4 km ± 7.8 SE), and had widely varying energy stores (total lipid of 21–39.5% of dry body mass), suggesting that a specific critical level of stored energy was not required for triggering metamorphosis (Jeffs et al. 2001). The locations where newly metamorphosed pueruli were caught were not reliably associated with any of the variables that have previously been suggested as the trigger for metamorphosis, i.e., sea surface temperature, salinity, depth, distance offshore, ocean primary productivity.

Once final stage phyllosomes have metamorphosed to non-feeding pueruli, the mechanisms by which they move inshore into shallow waters to settle is also unclear, but it is likely to involve a combination of active onshore swimming and the use of natural onshore advection or passive processes, such as wind-driven surface currents (Butler & Herrnkind 2000). However, the evidence supporting mechanisms of onshore movement is mostly circumstantial. For example, evidence for active onshore swimming is largely inferred from measured short-distance swimming speeds and rates of energy consumption (Lemmens 1994; Jeffs et al. 1999, 2001; Jeffs & Holland 2000). Likewise, the only evidence for passive onshore transport comes from correlations between the timing of arrivals of settling pueruli and natural phenomenon such as onshore winds, rainfall, and current patterns (Phillips & Pearce 1991; Caputi & Brown 1993; Caputi et al. 1995a,b; Acosta et al. 1997; Eggleston et al. 1998; Yoshimura et al. 1999). These studies have consistently shown relatively weak correlations between onshore advective physical processes and the arrival of settling pueruli on the coast, or have produced conflicting results. For example, the abundance of *Panulirus argus* pueruli arriving in the Florida Keys over an 8-year period were only marginally correlated with onshore windforcing of surface waters (Acosta et al. 1997). Wind speed and direction only explained around half of the variation in *P. argus* pueruli arrivals at three sites at Lee Stocking Island in the Bahamas during a 6-year study (Eggleston et al. 1998). A subsequent 2-year study found pueruli abundance at two sites in the Florida Keys was not correlated with wind patterns (Yeung et al. 2001). However, pueruli abundance was correlated with either the magnitude or frequency of onshore and long shore currents (accounting for c. 60% of variation) which in turn tended to be generated by the presence of mesoscale eddies offshore. However, it was not clear if pueruli were being transported onto the coast directly by these currents, or if the increased pueruli abundance was a result of the presence of the mesoscale eddies which had transported water masses containing pueruli from the Gulf of Mexico to offshore of the Florida Keys. Correlations between the abundance of pueruli on the coast and weather and/or current patterns have been found in other Palinurid species, but in all instances they fail to provide the high level of correlation that would be expected should pueruli be behaving as purely passive particles in the ocean environment (Pearce & Phillips 1988; Hayakawa et al. 1990; Caputi & Brown 1993; Caputi et al. 1995b; Booth et al. 2000).

The distribution of pueruli in a number of offshore surveys strongly suggests that their movement is directed onshore rather than dispersing at random (Ritz 1972; Chiswell & Booth 1999). For example, in the most common species of spiny lobster in New Zealand, *J. edwardsii*, late-stage phyllosomes are most often caught beyond the edge of the continental shelf (>44 km offshore), whereas pueruli prefer to settle in coastal waters of less than 15 m depth (Booth et al. 1991; Bruce et al. 2000). Comparisons among the distributions of mid- and late-stage phyllosomes, and pueruli of *J. edwardsii* sampled over a series of offshore transects from New Zealand demonstrated that the distribution of mid-stage phyllosomes was consistent with passive drift via measured ambient ocean currents (Chiswell & Booth 1999). In comparison, the distribution of late stage phyllosomes was significantly displaced inshore, consistent with shoreward directed movement of 4–6 cm s^{-1}, which was inconsistent with the ocean gyre which dominates this ocean region. Pueruli were found significantly more inshore again than late stage phyllosomes, consistent with shoreward directed movement of 8–10 cm s^{-1}. These findings suggest that both pueruli and late stage phyllosomes are capable of orienting shoreward from considerable distances offshore (>50 km).

Orientation cues used by late stage phyllosomes and pueruli during this shoreward movement from offshore waters are unknown. Unfortunately, there are no useful parallels to be drawn from fishes, as there has been very little research on the larval movement of the very few groups of fishes which have extended offshore larval development, such as the Cheilodactylids, Bovichthyids, and Anguillidae (B. Bruce, CSIRO, Hobart pers. comm.). The aim of this article is to review the possible cues and sensory mechanisms that might be used by early life stages of spiny lobsters for orienting toward the coast from offshore waters. This review serves to identify those potential orientation cues and methodologies that will be most useful for directing future research endeavours.

UNDERWATER SOUND

Underwater sound has long been recognised as one of the strongest candidates for onshore orientation by pelagic organisms because it is conducted long distances offshore and it can also carry biologically significant information about distant coastal locations, such as reefs (Myrberg 1978; Hawkins & Myrberg 1983; Kingsford et al. 2002). A number of researchers have suggested that underwater sound, such as waves breaking on the coast, may provide a shoreward orientation cue for the pueruli of spiny lobsters (Phillips & Penrose 1985; Phillips & Macmillan 1987; Macmillan et al. 1992).

Coastal reefs of New Zealand and Australia where pueruli are known to settle have ambient underwater noise with high amplitude sound between 1200 and 1600 Hz (Tait 1962; Cato 1978). This noise originates from rocky coastlines and increases markedly for c. 3 h after sunset. Tait (1962) measured a 7–10 dB directional increase in ambient noise at a point 5 km off shore and a 6 dB fall-off with distance doubled. Attenuation is only 0.1 dB km^{-1} at these frequencies, so the directional noise would be detectable at least 10 km offshore. Cato (1978) reported detecting reef noise that would be louder than surface wind noise at up to 25 km in Australian waters. Based on assumptions of the sensory modality of mechanoreceptors observed on the antennae of pueruli of *P. cygnus*, Phillips & Penrose (1985) concluded that pueruli of this species would only be able to effectively detect directionality of reef noise above 1750 kHz. Furthermore, they estimated that the attenuation of reef noise at this frequency would prevent it from being detected beyond 40 km away from the source. Although 1750 Hz is slightly beyond the band of high intensity reef noise described by Tait (1962), the estimate of 40 km could provide a useful indication of the maximum range for reef noise to be a directional cue. However, if pueruli are capable of detecting lower frequencies, then it is possible that this estimated range could be extended considerably because of greatly reduced attenuation at lower frequencies.

Underwater sound was implicated as a possible cause for more than 4000 pueruli of *J. edwardsii* being caught in the seawater intake of a power station on the west coast of New Zealand where pueruli collectors placed on the adjacent coast failed to collect any individuals (Booth 1989). Subsequent underwater sound recordings indicated that the power station generates a sound signature that can be detected above background ambient noise for some considerable distance offshore and is in the same frequency range as natural reef underwater sound sources (Jeffs unpubl. data).

To date, no behavioural experiments with orientation to underwater sound by pueruli or phyllosomes have been reported, although experiments to test if pueruli of *J. edwardsii* can be attracted to collectors associated with artificial sources of underwater sound have been attempted (Jeffs unpubl. data). The results of these field experiments were inconclusive because of low catches of pueruli in the experimental collectors. However, a number of recent field studies have used a range of techniques to confirm underwater sound as an important orientation cue in larval and post-larval crabs and fishes (Tolimieri et al. 2000, 2004; Leis et al. 2002; Jeffs et al. 2003; Simpson et al. 2004). Diver observations suggested that the swimming behaviour of larval fishes changed in response to the presence of some artificial sources of underwater sound (Leis et al. 2002). Floating light traps associated with and without artificial sound sources produced significantly different catches of crab and fish larvae and post-larvae (Tolimieri et al. 2000; Jeffs et al. 2003; Simpson et al. 2004). Larval reef fish placed in experimental choice chambers in the sea demonstrated a choice toward artificial sources of pre-recorded reef sound (Tolimieri et al. 2004).

There is, however, some debate over the sensory mechanisms that might be used by larval fishes and especially decapod crustaceans (Budelmann 1992; Popper et al. 2001). In general, the sensory structures found in fishes can be compared and related to those well described in many other vertebrate species. However, such comparisons are not possible for crustaceans because the presence of an exoskeleton necessitates different sensory arrangements. Decapods have a wide variety of sensory structures which have attracted considerable research interest, but their sensory and behavioural functions are often still poorly understood (Popper et al. 2001). A variety of receptors have been identified that may have the ability to respond to parameters of underwater sound such as particle motion, pressure changes, and hydrodynamic movement, but their operation, sensory thresholds, range of sensitivity, and especially their behavioural significance is not well defined (Popper et al. 2001).

Investigations of the antennal sensory structures of the early lifecycle stages of several species of spiny lobster found an almost continuous array of pinnate setae along the flagella of the antennae of both pueruli and early juveniles, but absent from late stage phyllosomes (Phillips & Penrose 1985; Phillips & Macmillan 1987; Macmillan et al. 1992; Jeffs et al. 1997). Similar arrays of sensory setae are seen in other decapods without a shoreward migrating lifecycle phase, but it has been speculated that they may also be used for detecting low frequency water vibrations (Ball & Cowan 1977; Denton & Gray 1985). Electrophysiological recordings from such setae have produced conflicting results. Pinnate setae of the antennae of both *Palinurus elephas* and *P. japonicus* are known to have only limited sensitivity, and can only detect gross water movement or act as proprioceptors (Tazaki & Ohnishi 1974; Vedel 1985). However, the pinnate setae on the antennae of some freshwater crayfish are coupled with neighbouring sensory setae and consequently are highly sensitive to low frequency vibrations (Tautz et al. 1981; Masters et al. 1982; Bender et al. 1984). Regardless, the absence of an array of pinnate setae from late stage phyllosomes would prevent them from sensing and responding to underwater sound via this mechanism (Nishida & Kittaka 1992) despite their apparent ability to orient shoreward from offshore (Chiswell & Booth 1999). It has also been suggested that statocysts and chordotonal organs associated with joints of flexible body appendages may also play a role in sound reception in crustaceans. However, there is very limited information on these structures in the early life history stages of Palinurids (Budelmann 1992; Popper et al. 2001). The statocyst of pueruli of *J. edwardsii* are different to the highly developed statocysts of other decapods because they lacked sensory hairs, secretory pores, and fluid within the statocyst cavity (Sekiguchi & Terazawa 1997). Overall, these studies would suggest that although aquatic crustaceans in general appear to have some capacity to detect water-borne sound and vibration, the role of underwater sound in the orientation of the early stages of Palinurids remains unclear. Further work is required to identify the sensory mechanisms, sensitivities, and behavioural importance of this sensory modality for natural sound cues in these early life history stages.

WATER CHEMISTRY

Crustaceans have highly developed chemosensory abilities which have been shown to play a key role in the settlement behaviour of a number of species, especially crabs (O'Connor & Gregg 1998; Forward et al. 2003; Keller et al. 2003). Consequently, it has been suggested that subtle changes in water chemistry may be instrumental in triggering metamorphosis in final stage phyllosomes and provide some guide to subsequent inshore movement (Phillips & McWilliam 1986). There is limited evidence for chemotaxis to be a mechanism for onshore orientation in early Palinurids. Post-larvae of the American lobster *Homarus americanus* can swim toward odours from adult conspecifics and organisms typically found in settlement habitat, whilst avoiding odours from a fish predator (Boudreau et al. 1993). Post-larvae did not orientate in response to inshore or offshore water, but did toward water conditioned by a rocky substratum versus a sandy substratum. Boudreau et al. (1993) concluded from Y-maze trials that distance chemoreception may play a role in locating settlement habitat by clawed lobster post-larvae. Observations of the post-larvae "zigzagging" through the zone of mixing in the flume, as well as the active movements of the chemosensory antennules and chelipeds would support the role of chemotaxis in these experiments.

Despite these encouraging results, the experimental flume was under a metre in length and it remains unclear on what ecological scale this behaviour may take place.

Among fish there is good evidence that chemical signals can be used over long distances, e.g., the olfactory homing of salmonids (Dittman et al. 1996). Pre-settlement coral reef fishes orient toward lagoon water versus ocean water in a Y-maze apparatus inferring that these settling stages may be orienting to plumes of lagoon water that were present over much larger scales (up to 4 km from the reef) (Atema et al. 2002). Orientation to reefs over these larger scales could help to be achieved by the larvae being guided by directional information contained in the fine scale eddy structure of lagoon-flavoured water carried beyond the lagoon by tidal currents. This sensory modality is known as eddychemotaxis (Atema 1996)

An extensive number and range of chemosensory sensilla are found in various locations on the exoskeleton in the early lifecycle stages of spiny lobsters, especially associated with the antennae and antennules of phyllosomes and pueruli (Nishida & Kittaka 1992; Jeffs et al. 1997; Cox & Bruce 2002). The exact chemosensory and behavioural roles of these structures, however, are yet to be determined. Mechanoreceptor sensilla on the antennae of adults of the spiny lobster *P. japonicus* have also been implicated in osmoreception, which may also provide another source of water-borne chemical information about coastal locations (Tazaki & Tanino 1973; Tazaki 1975). Newly hatched larvae of the Caribbean spiny lobster, *P. argus*, can detect and avoid low salinity waters (Scarratt & Raine 1967). More recently there is evidence that pueruli of this species will actively move toward coastal water versus oceanic water in an experimental choice chamber (J. Goldstein, Old Dominion University, Virginia pers. comm.).

Clearly, further work is required to identify the sensory mechanisms, sensitivities, and behavioural importance of the sensory modality for natural olfactory cues in these stages.

MAGNETIC FIELDS

Magnetic orientation abilities have been reported in a wide range of animal groups, including spiny lobsters (Wiltschko & Wiltschko 1995). Benthic juvenile spiny lobsters posses an ability to detect and orient using magnetic fields, and parts of their bodies retain ferromagnetic material (Lohmann 1984, 1985; Lohmann et al. 1995; Boles & Lohmann 2003). Early experiments demonstrated that *P. argus* was sensitive to, and used magnetic field polarity, for some direction-setting behaviour (Lohmann 1985; Lohmann et al. 1995). A magnetic sense is thought to be involved in true navigation in this species, i.e., can determine their position relative to a goal without relying on familiar surroundings, cues emanating from the destination, or information collected on the outward journey (Boles & Lohmann 2003). This was based on a series of experiments where heading direction of tethered juvenile lobsters was measured after they had been displaced considerable distances from their home territory (>5 km) whilst deprived of external cues in transit. Artificial magnetic fields were also used to experimentally “displace” captive juvenile lobsters and a significant proportion responded by adjusting their heading direction appropriately.

Despite these intriguing initial experiments it is unclear which features of the Earth’s magnetic field spiny lobsters are able to detect; inclination, direction, and/or localised variation in field intensity. The use of some of these features of magnetic fields, such as localised variation in field intensity, for orientation at an ecologically meaningful scale requires a high level of magnetic sensitivity and specific behavioural algorithms that rely on a previous and detailed knowledge of the arrangement of the magnetic field.

We are not aware of any research on the orientation of pueruli or phyllosomes of Palinurids in relation to magnetic cues, or to any attempts to identify a magnetic receptor in these earlier life stages. Such research is likely to be logistically difficult given that actively swimming pueruli require large experimental arenas and tethering pueruli has been found to markedly alter their behaviour (Jeffs & Holland 2000).

CELESTIAL CUES

A wide variety of arthropod species have been shown to make very effective use of celestial cues for long distance orientation (Giroud & Balvay 1999; Horváth & Wehner 1999; Ugolini 2003). In particular, a number of insect species make extensive use of tracking the movements of celestial bodies, as well as the spectral, intensity, and polarisation gradients of celestial light sources for deriving directional information (Rossel & Wehner 1984; Horváth & Varjù 1997). For some crustacean and insect species the eye structure has become highly developed for detecting positional information from light fields. For example, in some species of stomatopods, cladocerans, desert ants, and bees the morphology of the compound eye has become highly specialised for discriminating the polarisation angles of sky-light so that it can be used for orientation (Mote & Wehner 1980; Wehner 1997; Marshall et al. 1999; Flamarique & Browman 2000).

Given the importance of celestial cues in other arthropods, it would be reasonable to assume that celestial cues could play a significant role as a cue for shoreward orientation in phyllosomes and pueruli. However, there is no evidence to support the use of celestial cues for onshore orientation in the early stages of the lifecycle of Palinurids, although there are indications that ambient light levels may help to determine the scale of vertical movements in the water column and that this in turn may affect passive offshore and onshore movement by oceanographic water movements (Rimmer & Phillips 1979). Among the pelagic stages of other crustaceans only the megalopae of several crab species swim in the direction of the sun's bearing. However, it was unclear how this orientation behaviour might assist with onshore migration (Shanks 1995).

The eyes of adults and pueruli of *P. cygnus* show a very marked change from an apposition- to a clear-zone type of compound eye (Meyer-Rochow 1975a,b) and the overall structure of the eyes of pueruli indicated they are very efficient for the perception of polarised light. Excellent abilities to detect polarised light have been confirmed from electrophysiology recordings from other decapod crustaceans with similar eyes (see Meyer-Rochow 1975a,b). However, the atypical arrangement of the axons of the retinula cells found in the pueruli eye may interfere with this level of sensitivity to polarised light. Meyer-Rochow (1975a) concluded that behavioural assays would be required to determine the true functioning of eyes in pueruli. Regardless, an ability to detect the angle of polarisation of sky-light could provide a useful basis for setting a consistent swimming orientation for pueruli, but would provide no information about the direction of the coast in offshore waters.

HYDRODYNAMIC CUES

In crustaceans, a wide variety of external sensilla as well as internal sensory organs such as statocysts and proprioreceptors have been identified as potentially important in detecting hydrodynamic stimuli and body movements created by hydrodynamic forces such as waves (Sekiguchi & Terazawa 1997; Popper et al. 2001). A small number of studies have investigated hydrodynamic behaviour in juvenile and adult spiny lobsters, but very little has been reported for pueruli or phyllosomes. Spiny lobsters can localise discrete hydrodynamic stimuli around their bodies (Vedel & Clarac 1976; Wilkens et al. 1996). It was thought this sensitivity was important for the detection and defence against swimming predators rather than for any long distance orientation behaviour. However, hydrodynamic cues, especially wave surge, have been implicated in longer distance orientation behaviour of *P. argus* and *Panulirus guttatus* moving around benthic reef habitats (Herrnkind & McLean 1971; Walton & Herrnkind 1977; Nevitt et al. 1995; Lozano-Álvarez et al. 2002). The direction of ocean swells is a potentially useful orientation cue for pueruli. Because large waves require fetch to develop, they are less likely to be heading shoreward than offshore (Lewis 1994; Kingsland & Macky 1999; Montgomery et al. 2001). Rheotaxis, the orientation and movement in relation to water currents, may also be important in long distance orientation of benthic spiny lobsters (Walton & Herrnkind 1977). However, rheotaxis behaviour was not observed for the pueruli of *J. edwardsii* in small seawater flume trials (Jeffs & Holland 2000). Attempts to establish whether pueruli orient to orbital accelerations associated with wave motion using tethered animals in experimental chambers also failed (Jeffs & Holland 2000; Jeffs unpubl. data).

ELECTROSENSE

Ocean currents and animals moving through the Earth's magnetic field generate electrical fields that have the potential to be detected and used for orientation by aquatic animals. A relatively small number of fishes are known to be able to detect weak electric fields which for some may provide directional information (Kalmijn 1987; Paulin 1995). However, there is no corresponding evidence for marine invertebrates.

BEHAVIOURAL OBSERVATIONS

Although there has been little direct experimentation on the orientation cues in spiny lobster phyllosomes and pueruli, it is possible that some of their behaviours that have been observed might provide clues about their orientation. Pueruli have only been observed active at night at or near the surface, most often actively swimming in straight lines (Phillips & Olsen 1975; Serfling & Ford 1975; Calinski & Lyons 1983; Jeffs & Holland 2000). Pueruli of most species have been observed at times swimming within centimetres of the surface or on occasions with their antennae emergent. Likewise, zooplankton net studies have caught pueruli in their greatest abundance near the surface at night and they appear to be in deeper waters or absent from the water column during the day (Phillips et al. 1978; Phillips & Pearce 1997; Yoshimura et al. 1999). However in *P. cygnus*, there is an indication for zooplankton net data that the initial onshore movement of pueruli is undertaken at greater depths, later moving to surface waters once well within shelf waters (Ritz 1972; Phillips et al. 1978). During periods of rough sea conditions the pueruli of some species are more concentrated in surface waters (Ritz 1972; Phillips et al. 1978). The pueruli of a number of species are almost exclusively found during the dark new moon period probably to avoid detection by predators (Acosta et al. 1997; Acosta & Butler 1999), whereas the pueruli of other species have no lunar periodicity to their activity (Hayakawa et al. 1990). Returning to surface waters at night would be required for establishing a compass bearing that was reliant on celestial cues, because the key features of light with the potential to be used for orientation are lost with depth because of absorption and scattering (Lythgoe 1987; Nilsson 1997). However, it is unlikely that those species that are active only during the new moon phase would be able to access any celestial orientation cues given the absence of moonlight. Visiting the surface at night may also allow for better use of wave orientation cues because orbital acceleration from waves is more intense closer to the surface, and dominates the upper 30 m of the ocean (Cook 1984). Some of the behavioural observations of wild pueruli indicate that they are highly sensitive to water movements and are capable of detecting the difference between turbulence and reflected waves (Calinski & Lyons 1983). If pueruli are highly sensitive to wave motion as this observation would suggest, it should be possible for them to discriminate wave interference caused by reflected and refracted waves emanating from coastal and reef features. Reflected waves from the coast may be capable of travelling up to a few kilometres offshore and the direction of these reflected waves when taken in relation to the direction of prevailing onshore waves would provide a very reliable directional heading toward the coast. Again, this may help to explain the numerous observations of pueruli travelling close to the surface of the ocean. In this location pueruli would be well placed to detect waves reflected and refracted from the coast or shallow reefs. In contrast, surface waters are unlikely to be an ideal position in the water column for detecting and orienting toward underwater sound sources. Reflection and scattering of sound from the air/water interface and bubble noise from any breaking waves would potentially obscure the ability to detect more distant acoustic sources.

DISCUSSION

Overall, there is very little evidence for any long distance orientation cue playing a role in the directed shoreward movement of the pueruli of Palinurids (Table 1). Reliable compass bearings could be derived by magnetic sense and the use of celestial cues, but this is insufficient for pueruli of many species seeking the coastal water from a complete range of compass bearings. It could be that these omnipotent cues are used to provide an ongoing compass bearing that is set in conjunction with a more reliable shoreward cue such as underwater sound. Ambient underwater sound does have the potential to provide an onshore orientation cue for pueruli. However, the potentially effective range for this cue may be limited to less than 40 km offshore (Phillips & Penrose 1985). Other known potential shoreward orientation cues generally have major limitations, particularly in relation to their potential to provide a reliable cue over the longer distances traversed by pueruli (>50 km). Water-borne chemical cues are unlikely to provide a reliably direct shoreward orientation cue from offshore locations, especially for a post-larval stage with limited energy reserves to expend on circuitous routes. However, chemical cues may play a role in locating suitable settlement habitats in the coastal zone, as they have been found to do in other crustaceans such as crabs (Boudreau et al. 1993; Welch et al. 1997; Forward et al. 2003; Keller et al. 2003). Hydrodynamic cues such as wave and current directions would be unreliable sources of information for locating the coast from offshore, although in shallower waters wave direction, including the direction of reflected and refracted waves, could help to locate key coastal features such as reefs.

It is likely that the pueruli of spiny lobsters use an integrated mix of orientation cues that may change in importance with increasing proximity towards inshore settlement areas or with changing circumstances. A similar model for the use of multiple orientation cues has recently been proposed for hatchling turtles and is well established in migratory birds (Avens & Lohmann 2003). A mix of cues is illustrated in the way that lunar phase modulates the orientation behaviour of larval crab stages toward underwater sound (Jeffs et al. 2003). The behavioural significance of this may be to make use of onshore tidal movements, or to avoid times of strong tidal currents.

Research progress in identifying the important shoreward orientation cues in late stage phyllosomes and pueruli are unlikely to come from conventional laboratory experimental approaches because these pelagic stages are extremely difficult to manipulate without modifying their behaviour (Jeffs & Holland 2000). Field research is also problematic given the highly cryptic behaviour and the relatively low abundance of these life history stages in most locations. Large-scale tank experiments or contained field experiments may be sufficient to yield useful results. Additionally, detailed examination of the morphology and sensory capabilities of these stages may also provide useful clues to understanding their full orientation capabilities. Although it will be difficult to reveal the basis and extent of the

Table 1 Estimated effective ranges for various shoreward orientation cues in pueruli of Palinurids and closely related taxa.

Shoreward orientation cue	Potential range of operation	Limitations	Existing evidence
Acoustic	<100 km	Effectiveness reduced in rough sea conditions	No evidence in Palinurid pueruli. Crab larvae and post-larvae moved toward reef sounds—Jeffs et al. (2003).
Chemical	<100 km	Poor directional resolution over long distances	Pueruli of *Panulirus argus* observed to move toward coastal water—Goldstein (unpubl. data). Post-larvae of *Homarus americanus* chemically mediated behaviour in Y-maze—Boudreau et al. (1993). Chemically mediated behaviour in post-larvae of decapod crab species, e.g., Welch et al. (1997); Forward et al. (2003); Keller et al. (2003).
Magnetic field	>100 km	Requires prior knowledge of location of the coast, or magnetic field	No evidence in Palinurid pueruli. Juvenile and adult *P. argus* shown to have magnetic sensitivity and magnetic navigation—Lohmann (1984, 1985); Lohmann et al. (1995); Wiltschko & Wiltschko (1995); Boles & Lohmann (2003).
Celestial	>100 km	Requires prior knowledge of location of the coast	No evidence in Palinurid pueruli. Crab post-larvae shown to orient in relation to the sun position—Shanks (1995). Evidence from a variety of other crustaceans, e.g., Giroud & Balvay (1999); Ugolini (2003).
Hydrodynamic —waves	<100 km	Wave direction unreliable, unless using reflected or refracted waves	No evidence in Palinurid pueruli. Adult *P. argus* and *P. guttatus* shown to orient in relation to waves—Herrnkind & McLean (1971); Walton & Herrnkind (1977); Nevitt et al. (1995); Lozano-Álvarez et al. (2002). Evidence from other crustaceans and marine arthropods, e.g., Nishimoto & Herrnkind (1978); Rudloe & Herrnkind (1980).
—current	>100 km	Requires prior knowledge of location of the coast	No evidence in Palinurid pueruli. Adult *P. argus* shown to use water current direction in orientation—Walton & Herrnkind (1977).
Electrosense	>100 km	Requires prior knowledge of location of the coast	No evidence in Palinurid pueruli. No evidence in any crustacean.

orientation behaviour of late stage phyllosomes and pueruli, a greater understanding of this most extreme example of onshore orientation among marine invertebrates is of wide biological significance.

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