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Tidal migration and ecology of *Donax cuneatus* (Cuneate Wedge Shells/Pipis) on north Queensland beaches

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Abstract

Wedge Shells or Pipis (*Donax cuneatus*) are abundant on the Cairns Northern Beaches and are the dominant macrofauna present in the swash zone. They migrate up and down the beach to remain within the swash zone as tides of up to 3 m rise and fall. Waves are used to 'swash ride' to a new location. The ability to select waves suitable for swash riding appears to be critical to survival as errors in wave selection could be fatal. If Pipis are swept up the beach above the active swash zone or swept into deeper waters below the toe of the beach, as far as is known, they have no ability to move themselves back into suitable habitat. This paper records how Pipis swash ride in variety of wave conditions in order to reveal aspects of wave selection. In north Queensland, wind-driven, choppy wave conditions prevail and provide a contrast with previous studies of swash riding in *Donax* spp., which have taken place on beaches subject to ocean swells. Beaches exposed to wind-driven chop are steeper and are subject to very wide fluctuations in wave conditions. Pipis manage to swash ride in a variety of conditions including very still weather, long shore winds with waves striking the beach at low glancing angles and when multiple waves travelling in different directions are superimposed at the moment of encounter with the beach. Often Pipis can be seen ejecting from the sand *en masse* just prior to the arrival of a suitable wave. The variety of wave conditions and the localised responses of Pipis to approaching wave fronts allow investigation of swash riding behaviour at a high level of detail. Small groups of Pipis approximately a metre across will often eject to swash ride when elsewhere on the Pipi-loaded beach there is no visible Pipi activity. These localised responses suggest that Pipis can determine, with a spatial resolution of a metre, whether the incoming waves will combine in a way that provide the conditions they need for swash riding.

Reasons why Pipis may need to swash ride in such a difficult environment are also investigated. Being within the swash zone may provide shelter from predators and the ability of predators to obtain Pipis from within and adjacent to the swash zone is described. Beach geomorphology may also drive tidal migration in Pipis, as just below the swash zone is the beach step, a feature which also migrates up and down the beach with the tides. With each tide, waves impacting the beach step churn and rework the sand to a depth of tens of centimetres, probably making the beach step a very hostile environment for in-fauna, including Pipis.

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Introduction

Only one species of bivalve commonly occurs in the swash zone of the Cairns Northern Beaches, Far North Queensland, Australia (16°50′ S, 145°44′ E). The term Pipis will be used for *Donax cuneatus* in this paper as this seems to be the main name in local use; I also use it (as *pipis*) generically for other members of the genus. *Donax* are also called Wedge Shells or Beach Clams. Pipis come in a wide range of colours (Fig. 1).

On the rising tide Pipis are most visible when they have been deposited on wet sand by a retreating swash (Fig. 2). They rapidly burrow in by orienting their shells vertically with the narrow end down, then pulling the whole shell into the sand using their muscular foot. Many *Donax* species including *D. cuneatus* have shells that are truncated above the hinge, creating a wedge-like shape. This shape reduces the depth to which the pipis have to pull themselves down to be completely covered.

Figure 1. Pipis have a wide array of colours. All photos are by the author.

Figure 2. Pipis burrowing in after riding a swash.

Once the Pipis have moved they may remain hidden for many minutes before repeating the process. When they do move, they often move *en masse*, with many thousands of Pipis simultaneously ejecting and surfing the same wave.

Pipis migrate even in the calmest of conditions and will migrate to the very top of the beach even during a king tide. This is despite the great difficulty of migrating under such conditions and the high risk of being stranded above the swash zone.

Pipis are a major food item for Australian Pied Oystercatchers (*Haematopus longirostris*) in parts of their range (Taylor *et al*. 2014) including north Queensland (personal observations). A number of fish and crab species also feed on pipis (e.g. Manning & Lindquist 2003).

The primary objective of this study is to present evidence that Pipis are selective about how and when they swash ride. However it is also necessary to understand why Pipis might need to swash ride. Conditions that can result in mortality from predation, stranding and being removed from the swash zone and their relationship with tidal movements are investigated as possible reasons for tidal migration.

Previous research

There are more than 50 species of *Donax* and most species live in the swash zone of tropical beaches. Constraints imposed by this environment, result in many species of *Donax* being of very similar size and shape, which allows results from many studies to be compared. An extensive literature covering a wide range of species and all inhabited continents has developed covering many aspects of biology and behaviour

Most studies concentrate on population dynamics as the genus is targeted by subsistence fisheries throughout most of its range (Medeiros *et al.* 2014; Ocaña & Ocaña 2015; Hafsaoui *et al.* 2016). There is concern in many countries that fishing pressure could cause population declines. In Far North Queensland, pipis are a minor food item for people of mainly Asian and Pacific Island backgrounds.

A few studies cover the ecology of these species including their ability to move up and down the beach with the tides to remain in the swash zone, a topic that is the focus of this paper. A major study by Ellers (1995a) investigated how Coquina Clams (*D. variabilis*) use the flow of the swash to migrate up and down the beach face with the tides, a behaviour that he termed swash-riding. In a separate paper (Ellers 1995b), the shape and mass of the pipis was found to be highly adapted to swash riding in that the pipis have a higher density in comparison with other similar sized bivalves and had a shape that could pivot in response to flowing water to an orientation that resisted being picked up or tumbled by the backwash. Other authors have searched for the clues that trigger the mass ejection of pipis on the approach of a suitable wave. Turner and Belding (1957) concluded that the acoustic shock of breaking waves provided the trigger for pipis to emerge from the sand and be carried further up the beach.

The Ellers study was undertaken on an ocean beach in North Carolina, and reported approximately five waves per minute. Ocean beaches are exposed to surf from ocean swells and usually have fine sand and very low slopes. These beaches are referred to as dissipative beaches. Due to the very low slopes, swash usually arrives as a flow rather than as a breaking wave crashing directly into the swash zone. The fine sand and low slopes also result in the swash zone being almost always saturated as seawater only slowly drains into or out of the beach’s watertable. These characteristics almost certainly have a bearing on the morphology and behaviour of *Donax* spp. present in this environment.

Whilst Ellers studied the swash riding adaptations of *Donax* sp., De la Huz *et al*. (2002) investigated the ability of *Donax* sp. to burrow. De la Huz reported that *D. trunculus* on the Iberian Peninsula takes from 6 to 114 seconds to burrow into the sand. De la Huz determined that beaches with coarse sand provide more difficult burrowing conditions than beaches with fine sand and that pipis longer than 35 mm found burrowing significantly more difficult than individuals smaller than 25 mm. De la Huz also measured an increase in energy costs for burrowing into coarser sand and postulated that this cost created an ecological limitation on the distribution of larger members of this species. Research by de la Huz suggests that the speed of burrowing may be related to the need to burrow in before burrowing conditions become difficult when fluidised sand sets into a compact surface as the sand drains.

On many beaches in the Atlantic and Gulf of Mexico, pipis reach very high densities and crowding is believed to have an influence of swash riding behaviour and even on the shape of the shells, with pipis of species with narrower shells occurring in areas of higher density (*https://youtu.be/VpG8YIDSoW0*, viewed 28 July 2019).

Wade (1967) described the ecology and swash riding of *D. denticulatus* in the Caribbean where reflective beaches and wind-drive waves prevail. These conditions are similar to the conditions of the study area for this paper and, of all the papers reviewed, this study is also the closest in scope to the present study. However, Wade's research was on a Jamaican Beach with a tidal range of approximately 1 m, which is considerably smaller than the 3.5 m tidal range of the Far North Queensland coast. Even with this smaller tidal range, it was found that pipis migrated with the tides. Wade also undertook basic research into possible reasons for pipi migration. Additionally, Wade describes the exposure of pipis to predators and other forms of mortality.

Donax belongs to a family of bivalves (Donacidae) that includes many deposit feeders. Wade (1967) also undertook research to demonstrate that pipis in Jamaica (*D. denticulatus*) were suspension or filter feeders, rather than deposit feeders which ingest bottom sediment to separate out the small fraction of organic material.

Methods

There were two data collection processes, general observations and planned observations. General observations involved visiting the beach with a superzoom camera (Canon sx50 or sx70) and photographing or videoing any interesting events or species. Planned observations involved deliberately going to the beach during certain weather and tide conditions and attempting to observe the swash zone over a sufficient period of time to be reasonably sure that the typical behaviour of Pipis under those conditions had been observed. Planned observations were usually repeated to provide replication of observations.

A superzoom camera enables observations of animals from distance so that their behaviour is unlikely to be influenced by the act of making the observation. Standing in the swash zone causes large perturbations in flow both above and below the person and also out to a few metres on each side, which are potentially detected by the Pipis. For this reason, data collection has to be from a distance.

Selected photos from the large number taken in the field were dragged from a photo viewer into a custom built ms-access application for management. For significant photos, metadata including a line of text was added to provide contextual information. This system allowed hundreds of observations spanning several years to be organised and analysed. All observation reported here are backed by photographic evidence or notes from planned observations and have been repeated multiple times.

Study sites

On the Cairns Northern Beaches, waves breaks occurred at a rate of 15-20 per minute (Fig. 3). These beaches also had steep slopes and medium to coarse sand, which results in a very narrow swash zone. Known as reflective beaches (*https://ozcoasts.org.au/*, viewed 28 July 2019), they also differ from dissipative beaches by not having an off-shore break where waves tumble over a submerged sand bar. Whilst the waves that impact Far North Queensland beaches are smaller than ocean waves, all of the wave energy is expended in a very narrow band. Waves average 0.5 m in height and break directly on the beach. Beyond the beach, the sea surface can have many trains of waves moving in different directions, which is referred to as chop (Fig. 4).

Figure 3. Waves strike the beach with a very high frequency and often destructively or constructively interfere.

Figure 4. Complex sea surface with chop waves and swells seen from end of Palm Cove Jetty.

Observations were made at Holloways Beach (16°50'38.2"S, 145°44'39.4"E) in the south, then Yorkeys Knob Beach, Pretty Beach and Oak Beach at the northern end (16°36'28.7"S, 145°31'50.0"E). Pretty Beach lies behind a fringing coral reef and the swash zone has fine sand and a low angle similar to a dissipative beach. The other beaches were all typical reflective beaches. All of the beaches are subject to a tidal cycle which varies from approximately 3 m for spring tides to 1 m for neap tides. Occasional very small neap tides also occur when there is little difference between high and low tide height. Strong south east trade wind result in high chop pounding the beaches for most of the year. Weaker northeast trade winds are experienced in most summers. Cyclonic events are frequent and result in temporary beach erosion but do not change the swash zone characteristics.

The Cairns Northern Beaches are largely sheltered from the Pacific Ocean by the Great Barrier Reef which lies approximately 25 to 45 km from the coast. Ocean swells can move through the passages in the reef but are reduced to a several centimetres or a few tens of centimetres in height by the time they reach the coast. Trade winds, which create the high chop are held offshore by land breezes in the morning and in the afternoon are brought in and amplified by strong sea breezes. At approximately 5:30 PM, the chop reaches a peak with breaking waves ranging from approximately 0.5 to 1 m high. Refraction around distant reefs and headlands results in a criss-crossed wave pattern for most of the year as wave originating from different directions converge.

Results

Migration

At low tide, Pipis are often found only near the bottom of the beach face, suggesting that they migrate down the beach as the tide falls. Digging a series of holes higher up the beach face usually fails to produce any Pipis, suggesting that the Pipis don’t remain hidden where they were observed at higher tide levels waiting for the return of the sea.

The process of migration involves Pipis ejecting from the sand just before or just as the swash of an advancing wave passes over them. These events happen so quickly that video is usually required to make observations. Once the forward motion of the swash has stopped or the desired position has been reached, each Pipi will vigorously vibrate its long foot into the sand. When the foot has a purchase, the shell is righted and pulled down vertically into the sand. Usually the Pipis are almost fully buried by the arrival of the following swash and are resistant to being washed out. The full process from ejecting and burrowing back in takes place within a period of 3–4 seconds. When the following wave washes over them, the Pipis will extend their siphons up to the sand surface and filter-feed in the standard bivalve way by pumping water over their gills.

The Pipis do not seem have much control on how far they are carried up the beach. If they have been carried further than they wanted to go, they sometimes keep their foot within their shells and wait for another wave to carry them back down to their preferred level in the swash zone. Pipis seem to have more control over their movement down the face of the beach. Their streamlined shells are rotated by the swash to an orientation that presumably minimises drag (narrower end of shell facing up the beach). To arrest seaward movement, the Pipis foot is rapidly extended and forms a broad shield which prevents water flowing beneath the shell, which would create lift and result in the Pipi being washed down the beach (Fig. 5). As the sand mobilised by the swash starts to settle, the foot also wriggles into the loose sand to become an anchor. Siphons are extended from the opposite end of the shell and seem to be used like arms to push into the sand and perhaps angle the tip of the shell down to keep the tip pressed into the sand and out of the flow (Fig. 6). As the backwash thins, the white foot wriggles into the

Figure 5. A strong foot both directs retreating swash over the shell and vibrates vigorously into the sand.

Figure 6. Siphons seem to be used like arms to grab the sand and help stop the Pipi being carried down the beach by retreating swash. In this photo, the siphons are already being retracted.

sand vigorously and on obtaining purchase pulls down, which brings the shell to a vertical position. As soon as the foot has a hold in the sand, the siphons are retracted. Once the Pipi has risen to vertical, a few more pulls from the foot and the Pipi has disappeared into the sand. The siphons then rise to be flush with the surface and filter feeding takes place.

These actions are very quick and take place within a turbulent mix of sand and water, so observation during normal conditions is very difficult. Most recorded observations of individual Pipis were made on beaches with low angles where swash moves more slowly, the water is clearer and in calmer conditions when Pipis have more difficulty in swash riding. These conditions do affect swash riding behaviour with Pipis often allowing themselves to be moved around by a series of waves rather than burrowing in with urgency after surfing their selected wave. However, once they have decided to burrow in, the actual behaviour involved in arresting seaward motion and burrowing in would be similar.

Video viewed frame-by-frame also helped to make the sequence of events clearer. In normal conditions the commotion of turbulent swash means that it is difficult to see the Pipis ejecting and swash riding. Standing in the swash greatly changes the flow patterns so video has to be taken from a distance using a telephoto lens.

As Pipis depend on waves creating partial liquefaction of the sand to burrow in, they are often trapped on the surface or only partially buried when they ride small waves which lack the power to fluidise packed sand. It can take a few minutes for a wave to strike the beach with enough power to loosen the sand and allow the Pipis to fully disappear. Some bivalve species that live on nearby sand flats can liquefy sand by closing their valves quickly and directing a jet of water down into the sand which loosens the sand around their partially buried shells allowing them to burrow in fully. Pipis do not seem to be able to do this. The beaches they live in also tend to have coarse, free draining sand which requires very large volumes of flowing water to fluidise.

Beach morphology

In the study area, Pipis are found in both refractive beaches (mainly) and dissipative beaches. The geomorphological feature which probably has the most impact on survival of Pipis is the beach step. Fig. 7 below indicates the relationship between the beach step and the face of a refractive beach.

The beach step is a sudden transition from a sloping sandy surface to steep drop which varies locally from about 15 to 30 cm high (Wikipedia 2019). Below the beach step the seabed has tall parallel sand ripples (Fig. 8). The beach step is created when backswash from the previous wave runs at speed and into the base of the incoming wave, causing it to topple just as it reaches the beach. The resulting rumble excavates the toe of the beach and creates the beach step (Fig. 9). It is a very turbulent and violent place.

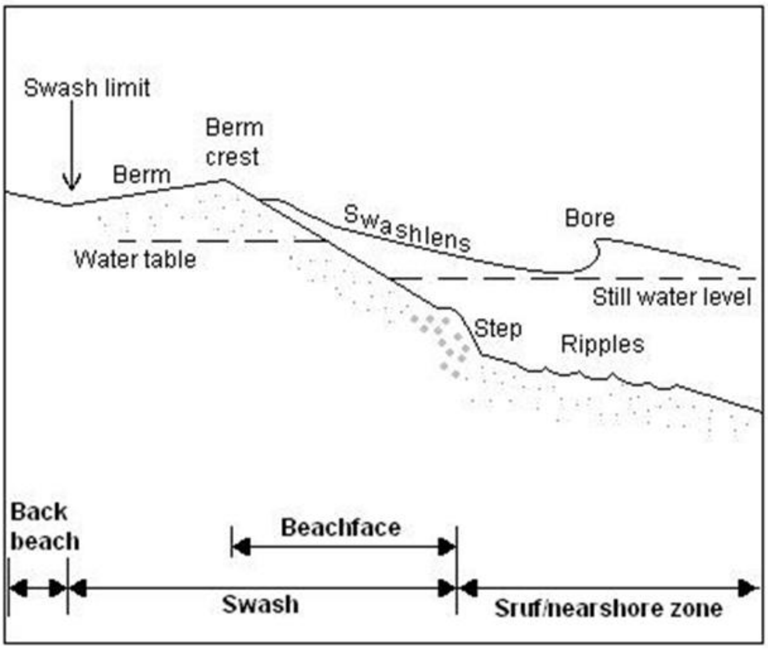

Figure 7. Swash zone and beachface morphology showing terminology and principal processes. Modified from Masselink & Hughes 1998.

Figure 8. Beach steps are present even on calm days. The sudden change in seabed morphology at the beach step is clearly visible on this day.

Figure 9. Usually conditions are rough and seas are so turbid that the beach step is not clearly visible. These conditions result in a large beach step.

Like the Pipis, the beach step migrates up and down the beach with the tides. When southeast trade winds raise a high chop, the beach step can rework the top 25 cm of sand across almost the full tidal range every day. The beach step is a formidable feature for an animal with the limited mobility of a Pipi to contend with. Pipis seem to do everything they can to avoid being swept over the beach step. Evidence for this aversion to crossing the beach step can be obtained by finding white Pipis and dropping them into the retreating swash and watching were they go. They grip the bottom to arrest their motion and try to swash-ride back up the beach. It can take a few minutes to succeed and the Pipis sometimes appear to be too exhausted to dig in, even when they reach their preferred zone.

The beach step is like a signal filter as it prevents waves that follow too close to the preceding wave, or which are too large for the shallow water of the swash zone, from surging up the beach. A wave can can only surge up the beach when there has been enough time for the preceding wave to fully retreat and for the water surface to rebound, covering the step. Small incoming waves may also cover the beach step, so following medium-sized waves can surge up the beach. Fig. 10 shows the shape of the beach step on a fairly calm day and Fig. 11 shows how the beach step can stop a wave.

Figure 10. The beach step is sometimes exposed with wave retreat, it is the steep convex slope at toe of the beach.

Figure 11. If the beach step is exposed, waves will crash into it and loose nearly all of their energy.

Wave selection and swash riding

On rising tides, the sudden mass emergence of Pipis prior to a suitable wave is a noteworthy phenomenon. Often no Pipis were visible for an interval of a few minutes, then thousands will synchronously eject from the sand. They push with their muscular foot until the full length of the shell stands vertically above the surface. On Cairns beaches, Pipis eject from the beach in one very rapid motion that can only be captured on video with a high frame rate (160 f/s). Pipis were observed ejecting into the leading edge of the swash, sometimes with enough energy to leap through the swash and a few centimetres into the air. This action occurs within a twentieth of a second and is almost impossible to observe by eye in the commotion of the swash zone. Pipis may also eject just before the swash arrives and a video taken by the author can be viewed at *https://youtu.be/qANuJiA1J8A*, with selected frames illustrated in Fig. 12. The intent of the video was to show that waves are selected prior to the swash reaching the buried Pipis.

As the Cairns Northern Beaches are dominated by wind-driven chop rather than swells, wave conditions can vary substantially over distances of even a few metres. Each lineal metre of beach can experience different wave and swash motion when waves strike the beach obliquely (Fig. 13). With a lot of practice, it is possible to identify which waves the Pipis will use for surfing before the waves arrive at the beach. The Pipis prefer larger waves, but in light conditions when larger waves are absent they make use of momentary wave peaks that result from the superposition of small waves

Figure 12. Video frames showing a Pipi ejecting into swash.
Left to right: Frame 1, Pipi is visible as a streak in front of the approaching swash; Frame 8, swash arrives; Frame 11, Pipi ejecting into swash 0.07 seconds after Frame 1.

(Fig. 14). Pipis appear to have the ability to sense localised areas of stronger swash arising from the juxtaposition of smaller waves travelling at different speeds and in different directions.

Pipis usually ride gentle surging waves and avoid dumping, beach-break waves. The mechanism they use for sensing the waves is not clear. There are a few possibilities. Emergence from the sand can be very localised, with groups occupying a space as small as one metre across synchronously ejecting. This suggests that the method they use for sensing incoming waves can separate signals about conditions in their immediate vicinity from signals that travel from further away. One possibility is that they sense the flow of swash across their siphons. This however mainly provides information about the previous wave and in a chaotic environment, when a promising retreating swash provides little information about the next wave, might be dangerous. Crossed sets of incoming waves can also destructively interfere so what appears to be a good wave a few metres from shore can often be reduced to an indecisive slosh as it reaches the beach. It is likely that there is some simple set of environmental clues that they can pick up, such as vibration caused by an incoming wave.

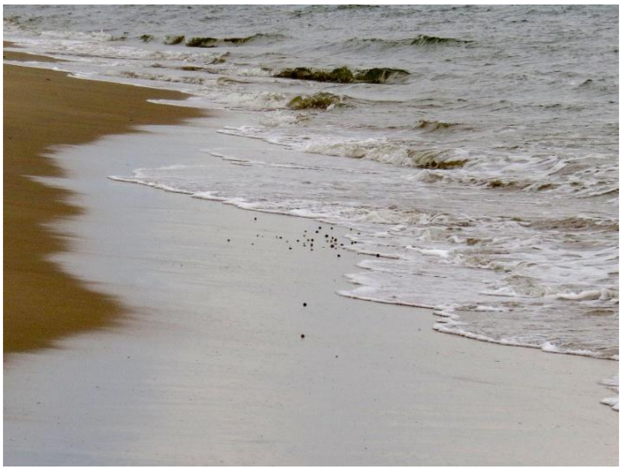

Figure 13. Waves striking the beach at an oblique angle and small group of Pipis that selected the same wave and moved in synchrony.

Figure 14. Three waves are about to merge into one swash. Pipis often ride swashing waves composed of juxtaposed chop waves.

Incoming waves are more defined and powerful than backwash. They are responsible for creating the ripples in the sea bed. Possibly movement of sand on the beach step can be heard when a suitable wave passes over, which would give the Pipis a fraction of a second to eject from the sand. Perhaps surging waves with the right velocity sound different to other waves. Pipis often eject from exposed sand approximately one metre in front of the approaching swash so they can sense waves over at least that distance and either ignore or cannot sense the presence of more distant waves.

Long-period waves have a gentle power (Fig. 15). They produce a non-turbulent flow that can smoothly sweep a Pipi along. In comparison to chop waves, swash from long period waves loses power and reverses more gradually. However, the backwash picks up a lot of speed on a steep beach and Pipis have to secure a grip very quickly if they are not to be swept away (Fig. 16). Interestingly at night, when the powerful sea breezes have died down, most of the waves are long-period waves of the type that Pipis ride during the day, yet on most nights, few Pipis can be observed migrating.

On the Cairns Northern Beaches, long-period waves occur at a rate of about 10 per minute, although most are spoiled by interference with chop. In choppy conditions, any given point on the beach will experience approximately 20 rolling waves per minute, although many will be small and overwashed by following waves.

Pipis only eject from fully drained wet sand surfaces on a rising tide. They do not jump into the retreating swash on a rising tide. On the falling tide, they eject into long-period gentle swash as the swash begins to change direction. Sometimes Pipis can be seen ejecting into the swash about

Figure 15. A large swashing wave on a still day.

Figure 16. The steep slope of the beach results in backwash that accelerates to a high speed.

0.5 m behind the edge of the swash at the point of reversal. Unfortunately, the Pipis are hidden from casual view by the swash and are visible only in unusual conditions.

Should the Pipis be washed away before they have pulled down into the sand, they appear to keep swash riding until they return to their preferred position in the swash zone. However, the energy required to pull down into the sand appears to be high and the Pipis that fail the second attempt at burrowing in seem to lack the stamina to try again and are then passively washed up and down the beach face in the swash. The very limited number of times an individual has the energy to burrow in makes wave selection a critical survival choice. Where the beach is steep, the retreating swash rapidly picks up velocity and the Pipis can only counter this excessive energy by gripping the substrate and beginning to burrow in before the retreating water has picked up too much speed. Pipis tend to move down the beach in small moves, rather than large ones, evidently due to this factor.

Pipis can also be stranded above the swash zone if the waves suddenly die down (Fig. 17). However they can survive for at least 15 hours out of water, such as on a desk at home. On release, most can burrow in on the first swash. In damp sand, they can potentially survive for longer periods and may be able to return to the swash zone on the high tide of the following day. Even most of the Pipis discarded by ghost crabs and left on their sides in the hot sun for quite long periods can recover on release into the swash.

When Pipis are feeding, their siphons are almost flush with the sand surface (Fig. 18). Ingestion of

Figure 17. Pipis exposed in new Ghost Crab hole above the high tide line.

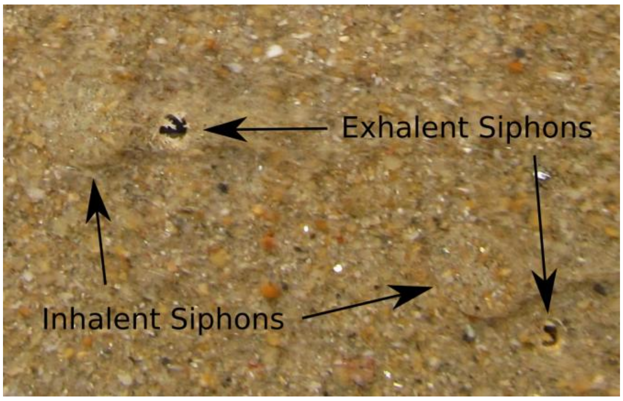

Figure 18. Two Pipis in the act of filter feeding.

sand is prevented by branched tentacles that act as a screen over the mouth of the inhalant siphon. A few much less branched tentacles are also present around the mouth of the exhalent siphon.

On a calm day, it is common for Pipis to become trapped by sand that solidifies before the Pipis can burrow in (Fig. 19, 20). It can take a few minutes before a wave with enough power arrives to loosen the sand and the Pipis can dig in. This situation only occurs on rising tides.

I have donned a snorkel to watch for Pipis being sucked down over the beach step (none were observed). Conversely, I have also placed Pipis on the seabed below the beach step to see if they would be washed back up. No Pipis were observed crossing from below the beach step from the swash zone above. Even digging around in the sand below the beach step with my fingers failed to locate any Pipis. For the Pipis placed in this zone and observed, there seemed to be little chance of being washed back into the swash zone.

Figure 19. A Pipi unable to burrow into tight wet sand.

Figure 20. Large number of Pipis can be trapped at the surface by fully drained, tight wet sand.

Habitat selection

Pipis prefer beaches which do not yield to sand flats on regular low tides. They also prefer steep beaches with coarse sand and where the vertical tidal migrations do not require long horizontal migrations (Fig. 21, 22). Beaches which support large populations of Pipis extend from Barr Creek north to Oak Beach. These beaches have relatively steep slopes and coarse sand. Redden Island and Ellie Point, at the mouth of the Barron River, have sand flats at low tide and Pipis have not been observed there. Four Mile Beach at Port Douglas

Figure 21. Many of the Cairns Northern Beaches are very steep. This area has 3 m tides, yet the intertidal beach face can be as narrow as 15-18 m.

Figure 22. The beach face of steep beaches has a thin layer of fine sand over deep, free draining deposits of coarse river sand.

has a very flat beach with fine sand and resembles a dissipative beach and also has few or no Pipis.

In Mackay, some 750 km further south, where the tides rise to 6.5 m and the intertidal extent of the beach is 150 m, the horizontal distance is too great for migration (Fig. 23). A few small Pipis were observed and these left tracks in the sand at low tide (Fig. 24). It seems they pull themselves along horizontally in a manner similar to the movement of freshwater mussels until they encountered a sheet of water draining from the beach and their trail disappears. Perhaps they can filter feed on the film of water draining from the beach.

Fine-grained sandy beaches tend to have very gentle slopes and these habitats tend to support tiny filter-feeding Siponid worms rather than Pipis. As the swash retreats, Siponids sweep with swash with a pair of 1 cm long tentacles, which makes small star patterns in the sand. In this habitat, incoming waves also swash gently up and down and Matutid crabs are freely able to forage within the underwater environment and possibly exert huge predation pressure on the Pipis. Pipis are present in these area in relatively low numbers

Figure 23. Very high tidal ranges also create very wide beaches such as Lamberts Beach in Mackay.

Figure 24. Small Pipis, which appear to be *Donax cuneatus*, move horizontally to create these streaks in the sand.

Population sinks

Creeks and river mouths, and associated beach areas seem to provide poor or unsuitable habitat for Pipis. Creek mouths are constantly narrowed by longshore drift of sand and have high current velocities through their restricted mouths that can create alluvial fans (Fig. 25) and mega ripples (Fig. 26) which are heavily reworked with each tide. No mobile bivalve species have been observed in this environment. Large predatory crab species

Figure 25. Outgoing tides create large alluvial fans which are washed away by longshore drift when tide returns.

Figure 26. Creek mouths have strong currents which rework the substrate to a high degree with each tide, creating conditions that are difficult for most filter-feeding animals.

including Mud Crabs (*Scylla* spp., *Thalamita* sp.) and specialised mollusc predators such as Thunder Crabs (*Myomenippe* sp.) are also present and exert enough predation pressure to almost eliminate oysters from rocks and mangroves at creek mouths.

Creek mouths also have beaches or berms with low crests that can be overtopped by swash (Fig. 27). Pipis have been observed being washed over the beach crest in large numbers and they burrow on the reverse slope, and become permanently stranded. Pipi shells are very uncommon in the washed up lines of seashells (mainly cockles) on beaches, which is probably related to the high specific gravity of the shells (Ellers 1995a). However, Pipi shells are sometimes moderately common around creek mouths, suggestive of high mortality at these locations (Fig. 28).

Figure 27. Swash over the beach crest creates a trap for Pipis, which cannot migrate down the beach once washed over the crest.

Figure 28. Pipi shells are not commonly found and are mainly found near creek mouths after bad weather.

Predation

Pipis are eaten by Ghost Crabs, mainly *Ocypode ceratophthalmus,* and occasionally *O. cordimana*. Only the larger crabs have the power to crush Pipis in their chelae. Pipis that are exposed on the surface are easily picked up by the crabs, which will often carry them above the swash zone to consume (Fig. 29, 30). Under normal conditions, Ghost Crabs are mainly nocturnal. However in still conditions, when the Pipis struggle to burrow in after a wave, *O. ceratophthalmus* can be active in bright sunlight and can consume several Pipis within an hour.

Judging by the number of crushed shells per 100 m of beach (typically about 3 per 100 m), the overall level of predation is quite low. However the potential level of predation is quite high as large Ghost Crabs are abundant.

Figure 29. Horn-eyed Ghost Crab (*Ocypode ceratophthalma*) crushing and feeding on small Pipis.

Figure 30. Outside a large Ghost Crab holes are broken shells and live Pipis that were too strong to crush.

Beach Stone-curlews (*Esacus magnirostris*) patrol the beach almost every night but seem to be exclusively targeting Ghost Crabs. Each morning, it is possible to follow the footprints of a Beach Stone-curlew and identify where prey captures had taken place. The remains of the prey are often present. No Pipi remains associated with footprints were observed. Beach Stone-curlews have also been observed on the faces of the beaches rich in Pipis during daylight hours and no predation of Pipis has been observed. Predation of crabs, including Sentinel, Soldier, small Mud and possibly Fiddler Crabs, was directly observed or implied from remains found.

Pipis lying on the beach unable to dig in are ignored by Australian Pied Oystercatchers, which are a major predator and perhaps the only significant predator of feeding Pipis. Oystercatchers spear the tips of their bills between the open valves of a feeding Pipi and it appears that the Pipis clamp shut on the bill allowing them to be picked up (Fig. 31). The Oystercatchers would require a very precise action, which appears to be something that even full-sized juveniles cannot do (Fig. 32). It appears that juvenile Oystercatchers serve a long apprenticeship under their parents as they learn to catch Pipis. A pair of Oystercatchers and a large chick are semi-permanent residents of the 300 m long beach extending north of Barr Creek and feed mainly on Pipis with *Matuta* crabs and Fiddler Crabs (in adjoining mangroves) being occasionally hunted.

Below the waves are more predators. *Matuta* or *Ashtoret* crabs (family Matutidae) are the most abundant and can have population densities similar to the Ghost Crabs above the swash zone, with perhaps one large crab per lineal metre of beach. Matutid crabs pop out of the sand under the cover of an advancing wave, scurry about for a few seconds, then quickly burrow back into the sand before the wave retreats (Fig. 33). Observing the behaviour of animals that live in the swash zone is very difficult and it is possible that Matutid crabs target juvenile Pipis and juvenile Mole Crabs (*Hippa* sp.) which are abundant at certain times. Fig. 34 shows Matutid crabs fighting over a Pipi-sized bivalve on a sand flat near Mowbray River.

Figure 31. A Pipi clamped onto the tip of an Australian Pied Oystercatcher's beak.

Figure 32. Juvenile Australian Pied Oystercatchers (grey legs) lack Pipi hunting skills and depend on a parent to catch and remove the Pipi from its shell.

In still weather conditions, Cow-tailed Rays (*Pastinachus sephen*) and Giant Shovel-nosed Rays (*Glaucostegus typus*) will patrol below the beach step and occasionally will swim through the swash zone (Fig. 35, 36). Both of these animals have mouths specialised for crushing molluscs.

It is often possible to tell which predator consumed a Pipi by examining the shells. Oystercatchers leave opened shells scattered along the beach (Fig. 37) and Ghost Crabs tend to leave solitary crushed shells on the beach at night (Fig. 38).

Spat

Rice-grain sized juvenile Pipis (spat, Fig. 39) occur on the same beaches as adult Pipis and also migrate with tides. They are most easily observed on beaches with fine sand. Their small size often leads to them being swept further up the beach than larger Pipis. Small Matutid crabs (1–2 cm carapaces, see Fig. 40) are often very active in the swash and potentially prey on juvenile Pipis.

Figure 33. Large Matutid crab in swash zone.

Figure 34. Matutid crabs on a sand flat predating another species of bivalve.

Figure 35. A juvenile Giant Shovel-nosed Ray (*Glaucostegus typus*) in the swash on a calm day.

Figure 36: Cow-tailed Rays (*Pastinachus sephen*) also feed in the swash zone on occasions.

Figure 37. Shells of Pipis predated by Oystercatchers are open and unbroken.

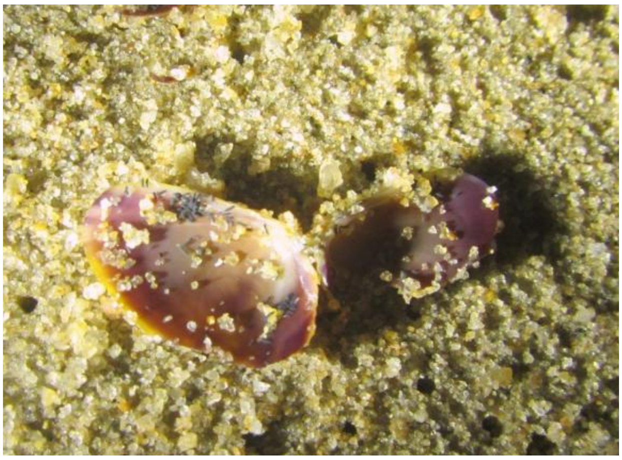

Figure 38. Shells of Pipis predated by crabs are broken. Inside this shell are tiny purple springtails which are feeding on traces of flesh left by the crab.

Figure 39. Spat (juvenile Pipis) – Oak Beach early April 2018.

Figure 40. Small Matutid crab – Yorkeys Knob Beach late March 2018.

Discussion

Pipis seem to possess considerable behavioural sophistication with regard to tidal migration. They are confronted with a need to follow the swash zone up and down with the tides, yet cannot move by themselves. They have to choose a wave of precisely the right energy and flow to carry them to a new position. On the coastline where they were observed, one of these waves may come only every few minutes. Between suitable waves can be dozens of unsuitable waves. Their active selection of waves is demonstrated by the mass migration of Pipis on the arrival of a suitable wave and no visible activity at other times.

Observations made during marginal conditions provide a wealth of information about the precision with which pipis sense their environment. In studies on the Atlantic Coast of the US (Turner & Belding 1957; Ellers 1995a), surf conditions on dissipative beaches were studied in a location with a 1 m tidal range. Ellers reported 5 swashes per minute for his study site, which compares with approximately 20 waves per minute for beaches in this study. On the Atlantic Coast, it is believed that the pipis sense the shock of an incoming wave, as they can be persuaded to eject from the sand by stomping on the ground to create a shock. This behaviour has not been noted in north Queensland. Indeed, in almost still conditions, there is no shock and the question is how do Pipis sense the small proportion of very slightly larger waves in such quiet conditions.

On the Cairns Northern Beaches, Pipis have been observed swash riding on momentary wave peaks resulting from the constructive interference between sets of waves travelling in different directions or at different speeds. These momentary wave peaks are bounded on both sides by smaller interfering waves. The sweet spots for migration created by these peaks are visible to the human eye and it is possible to decide moments before the peak arrives if Pipis will swash ride. These sweet spots may only be a metre wide; the observation of metre wide patches of ejecting Pipis suggests that Pipis are detecting them.

In rough conditions, the wave environment on the Cairns Northern Beaches may also promote differing swash-riding strategies to those observed in other studies. In north Queensland, larger breaking waves tend to tumble violently on encountering the beach step and are of no use for swash riding. Beach steps are a feature of reflective beaches and not dissipative beaches so are described in other papers. Video of pipis in Texas reveal dissipative waves slowly rolling up a very low slope and pipis having to preempt the flow by emerging several seconds before the arrival of the swash (*https://youtu.be/VpG8YIDSoW0*, viewed 28 July 2019). This strategy is not observed in north Queensland, where ejection and burrowing back in is completed between one wave and the next, usually in less than approximately four seconds. As larger waves tend to break on the beach step, it is medium-sized surging waves are the most useful for swash riding. Smaller waves that lack power to carry the Pipis up the beach are also rejected as are sets of waves or swashes which are destructively interfering. How Pipis select incoming waves of the correct size deserves more investigation. Additionally, it seems that avoiding the beach step is a major factor in Pipi migration. Pipis seem to have only enough energy for two attempts to burrow in. Rapidly burrowing in would reduce the risk of being swept down and across the beach step, which is potentially a greater source of mortality than predation.

In other studies, pipi migration may have been influenced by their population density. In the Atlantic, pipi populations reach more than 3000 animals per square metre and the ability to burrow in in such cramped conditions is a factor. Wade (1967) researched the impact of such high densities on pipis and concluded that shells became elongated in response and that damage to shells often occurred due to shells rubbing together. However, no discussion was provided on the potential impact of crowding on tidal migration strategies. High levels of crowding may be a very important reason why pipis eject from a few to several seconds in advance of a suitable wave, as seen in videos of pipis on Atlantic and Caribbean Beaches. In north Queensland, the population density appears to be much lower, hence Pipi swash riding is probably only related to wave characteristic rather than crowding and Pipis eject just fractions of a second before or after arrival of the swash front.

In other papers, the active migration process and responses to tidal states have been demonstrated. However, the consequences of choosing the wrong time to eject from the sand were not explicitly explored. Schlacher (2014) indicated that Ghost Crabs on the Atlantic Coast are highly efficient predators of *Donax faba* (58-89% of annual production) so it follows that tidal migration may be a predation avoidance mechanism. As local Pipis burrow in very quickly, their exposure to Ghost Crabs appears to be far less. The low abundance of crushed shells provides further evidence. Witmer (2011) noted that even after a hurricane affected a Texas beach, *Donax* sp. could only be found in the swash zone, whereas other members of the wash zone fauna could be found in near-shore subtidal areas. The implication is that the *Donax* sp., which is similar to local Pipis, cannot survive in subtidal areas or are rapidly predated. Predation by Portunid crabs (similar in size and appearance to local Matutid crabs) and fish including Whiting (*Menticirrhus* spp.) and Florida Pompano (*Trachinotus carolinus*) was noted for ocean beaches in North Carolina on the Atlantic Coast of the US (DNRSC 2005). However this predation often took the form of nipping off part of the foot of the pipi with the animal surviving the injury in most cases (Salas *et al.* 2001). This form of predation may be less prevalent on the Cairns Northern Beaches as the swash zone is a narrow, shallow, violent environment that is unsuitable for fish most of the time.

The level of precision required for selecting a wave to surf ride does not appear to have been previously researched. The sensory input and the rules for processing this input are currently unknown for reflective beaches. Waves that are suitable for migration are relatively uncommon. They are usually surging waves with a long period. These waves can be genuine long-period waves or can be a juxtaposition of smaller waves. It is, however, possible for a human observer to predict with a moderately high degree of reliability which incoming waves will be suitable for surfing before they reach the beach. The choice of waves is therefore highly non-random. For this ability alone, Pipis are interesting.

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