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Tracked mangrove horseshoe crab *Carcinoscorpius rotundicauda* remain resident in a tropical estuary

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ABSTRACT: Mangrove horseshoe crab *Carcinoscorpius rotundicauda* were tracked for 6 mo in the tropics using acoustic telemetry to determine whether they either show homing behaviour, remain near the site of capture, or travel to the open sea. Twelve adult horseshoe crabs were caught on the Mandai mudflats at Kranji and acoustic telemetry transmitters attached. Six acoustic receivers were deployed suspended from floating fish farm platforms ~1 km apart along the Strait of Johor, an estuary off the north coast of Singapore. Four individuals, 2 of each sex, were used in each of 3 tests: 4 crabs were released at the site of capture, 4 were released at a second site ~5.7 km away to determine if they exhibited homing, and 4 were caught along the muddy beach at the second site, tagged and released into deep water under one of the receivers. Although there were gaps in detection, 11 of 12 crabs were located intermittently within ~6 km of the point of release. One crab disappeared after 5 d. Homing was not exhibited, and the crabs were detected within the estuary for 6 mo. We concluded that the crabs in the tropical estuary, where there are no seasons or marked changes in water temperature, showed no tendency to travel out to sea and did not exhibit homing behaviour or any synchronized movement pattern to deeper waters.

KEY WORDS: Mangrove horseshoe crab · Telemetry · Homing · Movement · Tropics

INTRODUCTION

All 3 Asian species of horseshoe crab (*Carcinoscorpius rotundicauda*, *Tachypleus gigas*, *Tachypleus tridentatus*) are under threat, and a pattern of decline throughout the region is apparent. Reports from Hong Kong (Chiu & Morton, 1999, 2003, Shin et al. 2009), Taiwan (Chen et al. 2004), Japan (Itow 1993) and Malaysia (Christianus & Saad 2007) all indicate that populations are diminishing, mainly due to coastal development and habitat destruction. A warning of possible extinction was issued 2 decades ago (Earle 1991), yet these species are still not protected, and the IUCN Red List (IUCN 2010) still lists them as 'data deficient' despite the amount of information currently available. Protection of even small or individual sites or populations would be effective in preventing global extinction of the Asian species. However, if conservation or management measures are to be implemented, knowledge of the biology and behaviour of the species is essential. This includes migratory or seasonal movement patterns, especially where such movement may cross national boundaries or lead to large congregations of individuals that can then easily be captured. With increasing fragmentation of habitats, horseshoe crab conservation, research and management efforts need to be applied at the local level, taking account of the movement patterns of a specific population. In Japan, studies of the movement patterns of the Asian horseshoe crab *Tachypleus tridentatus* have contributed to the establishment of a marine protected area (O'Dor et al. 2001). The present study provides important information on the movement patterns of the mangrove horseshoe crab *Carcinoscorpius rotundicauda* in Singapore, classified as 'vulnerable' in the Singapore Red Data Book (Davidson et al. 2008).

Acoustic telemetry has proved an important technique for monitoring the movements of horseshoe

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crabs. Most work on horseshoe crabs has been done on the American horseshoe crab *Limulus polyphemus* (Brousseau et al. 2004, Moore & Perrin 2007, Watson et al. 2009, Schaller et al. 2010, Watson & Chabot 2010), but an increasing body of work is now emerging from Asia on the other species, particularly in Japan (Seino et al. 1995, 1999, Seino & Uda 1999). However, there have been no studies on the movements and travel range of the Asian species in tropical waters, where there are no seasonal changes in water temperature, and the present work is the first study to track mangrove horseshoe crabs.

Work on *Limulus polyphemus* using acoustic telemetry in 2 sub-embayments in Maine indicated that horseshoe crabs remained loyal to their own bay and did not travel to a neighbouring bay <4 km away (Moore & Perrin 2007). However, they exhibit a seasonal pattern in their movement, remaining during spring near the spawning beaches, while in winter, as the sea temperature drops, the crabs move to the deeper parts of the bay, where they over-winter, moving very little (Watson et al. 2009, James-Pirri 2010, Schaller et al. 2010).

In northern latitudes, where the sea temperature changes seasonally, horseshoe crabs in Asia also move to deeper water in winter (Chiu & Morton 2003, Shin et al. 2009). In areas where the sea temperature remains high and the same year round, there is no imperative for horseshoe crabs to move to deeper waters, so movement patterns may be different from those described from more northern latitudes. In addition, *Limulus polyphemus*, a species that inhabits sandy substrates, moves out with the daily tide into moderately deep water (Watson et al. 2009), whereas *Carcinoscorpius rotundicauda*, which lives on muddy shores, does not necessarily move out with the receding tide but sinks into the wet mud and can be found on the inter-tidal mudflat at low tide. So, movement patterns of *C. rotundicauda* on both a daily and seasonal level may be very different from those of other species in higher latitudes and different habitats.

The Strait of Johor, just 1° north of the equator, is an estuary between the north coast of Singapore and the south coast of Malaysia. It is the habitat of the last substantial breeding population of *Carcinoscorpius rotundicauda* on the main Singapore island (see Fig. 1). This part of Singapore is the only remaining stretch of coastline not yet subjected to development or land reclamation. In a recent survey of accessible shoreline around the rest of the main island of Singapore, very few horseshoe crabs were found in other sites (Cartwright-Taylor et al. 2011). So although mangrove horseshoe crabs are abundant at the mudflats along the northwest coast of Singapore, their habitat area is a tiny proportion of the total Singapore coastline.

It is not clear whether the horseshoe crabs remain near the mudflats, move to the deeper water in the strait or move outside the strait into the open sea. Although the crabs are quiescent while they settle into the mud when the tide is out, they are active when covered by water and can move well using large jumps across the seabed, probably with a speed similar to a human walking pace. It is important for any conservation strategy to know if the individuals stay close to the mudflats and spawn there or in the nearby mangroves or whether they travel out to sea and are only sporadic or transient visitors to the site.

Tracking studies of *Limulus polyphemus* indicate that adults travel further if the access to the site is not restricted by a narrow entrance (James-Pirri et al. 2005) or if the site is in a large embayment with a shoreline of >100 km (Smith et al. 2010), but where the embayment is small, movement is restricted (Watson et al. 2009). The Strait of Johor is small and has a restricted and distant entrance to the west, which would suggest that *Carcinoscorpius rotundicauda* does not travel out to sea. However, in deep waters, American horseshoe crabs move in the direction of benthic currents, burrowing into the seabed on the slack tide and moving on when the current flows in their direction (Anderson & Shuster 2003). Currents move along the Strait of Johor and back with the tidal flow, which, according to local fish farmers, can be up to 1.5 knots. So it is conceivable that the mangrove horseshoe crabs in the strait could ride out to the open sea and back.

The present study was undertaken in the Strait of Johor to track the movement of adult *Carcinoscorpius rotundicauda* labeled with acoustic transmitters for a period of 6 mo, the approximate lifetime of the transmitters, which included a change in monsoon when there was a reversal in the prevailing wind direction. This reversal itself takes ~2 mo. There are no seasons in the region and no change in ambient or sea temperature during the year, as there is in temperate climates, to precipitate a migration of the horseshoe crabs. Therefore, the objectives of the present study were, first, to determine if the mangrove horseshoe crabs remain within the local area over an extended period, and, secondly, to determine whether they show homing behaviour when removed from the site of capture. Using methods described by Brousseau et al. (2004) and James-Pirri (2010), we attached acoustic tags to adult horseshoe crabs and monitored their movements using stationary passive receivers deployed in the Strait of Johor for as long as the batteries in the tags lasted.

MATERIALS AND METHODS

Study site

The study was conducted in the Strait of Johor off the north coast of Singapore (approx. 1° N, 103° E), from the Mandai mudflats at Kranji to the west of Lim Chu Kang (see Fig. 1). The strait is an estuary ~2 km wide with large rivers and terrestrial runoff draining into it from both sides. To the west, the strait continues ~20 km to the open sea in the Strait of Malacca southwest of the main island. To the east is the causeway, a stone embankment, across the strait to Johor Bahru in Malaysia. Although there is flushing of the sea through it at surface level, the causeway acts as a barrier to the free movement of benthic dwellers like horseshoe crabs. Outside these boundaries, the Singapore shoreline is highly developed with reclaimed land and removal of the mangrove fringes, where man-made beaches are unsuitable for horseshoe crabs.

Near the causeway, the depth of water in the middle of the strait is ~7 m, increasing to ~15 m further west. Near the causeway, the coastline on both sides is built up with sea walls, but toward the west, the shoreline on both sides is undeveloped. Along the Singapore shore, this coastline supports a population of *Carcinoscorpius rotundicauda* in the mangrove forest, on the Mandai mudflats, in the wetlands of the Sungei Buloh Nature Reserve, in the west along the muddy shore and mangrove fringes of an undeveloped and restricted area and in the deeper waters of the strait (all contiguous or connected sites).

Along the strait there are several floating fish farms that probably provide good foraging for horseshoe crabs on the seabed below. With the permission of the fish farmers, we used the fish farm platforms as attachments for the acoustic receivers suspended in the water.

Zone of detection

A pilot study was first conducted to test the acoustic equipment and software and to determine the zone of detection of the passive receivers in sites along the area of interest in the Strait of Johor, using a Sonotronics stationary submersible acoustic receiver (SUR) and an acoustic transmitter (Sonotronics; www.sonotronics.com). We estimated the depth of the water using a marked plumb line. The zone of detection was ~500 m in water ~12 m deep. This is consistent with findings at other sites in the world using the same acoustic tracking systems (Brousseau et al. 2004, M.-J. James-Pirri pers. comm.). This information was used to determine the optimum position for the receivers to be fixed during the tracking study, such that most of the area of interest in the strait was covered by an SUR without overlap, and to give the best chance of receiving signals from transmitters attached to the horseshoe crabs.

Acoustic SUR only work in seawater and not on land, and reception is best in deep water. The zone of detection shrinks substantially as the depth of water decreases below ~4 m. Thus, a major limitation of this equipment is that the SUR do not detect signals from horseshoe crabs on the mudflats or in shallow water. This meant that if the tagged crabs remained in the shallows or buried in the mud, they would not be detected.

Sites of the receivers

Once the zone of detection was established, we surveyed the area of interest by boat, identified a possible site for each of 6 receivers and noted the co-ordinates using a GPS. Before the receivers were deployed, we tested each with activated transmitters and set the local time and date. In November 2010, we suspended 6 activated stationary receivers from floating fish farms ~1 km apart at a depth of 2 m in the water column with a weight to maintain each receiver in position and to counteract any strong currents that might lift the receiver. As the platform was floating, it rose and fell with the tide so that the SUR remained at the same depth below the water surface. Each receiver was covered by a nylon stocking because of the rapid build up of marine life that might otherwise have blocked good reception of the signal. This stocking was removed with the attached marine life and replaced as necessary each time the site was visited and data were downloaded. The positions of the receivers with zones of detection and geographic coordinates are shown in Fig. 1.

There were no points to attach a receiver close to the first release site (Site A), so this area was to be surveyed monthly using a manual hydrophone from a boat. However, the hydrophone malfunctioned after the first month. Nevertheless, we felt that if the crabs travelled west along the strait, they would be detected by one of the other receivers.

The SURs scanned all frequencies of the transmitters such that a scan was completed every 3 min. The data recorded by the receiver included the receiver identity, the unique signal of each transmitter within range

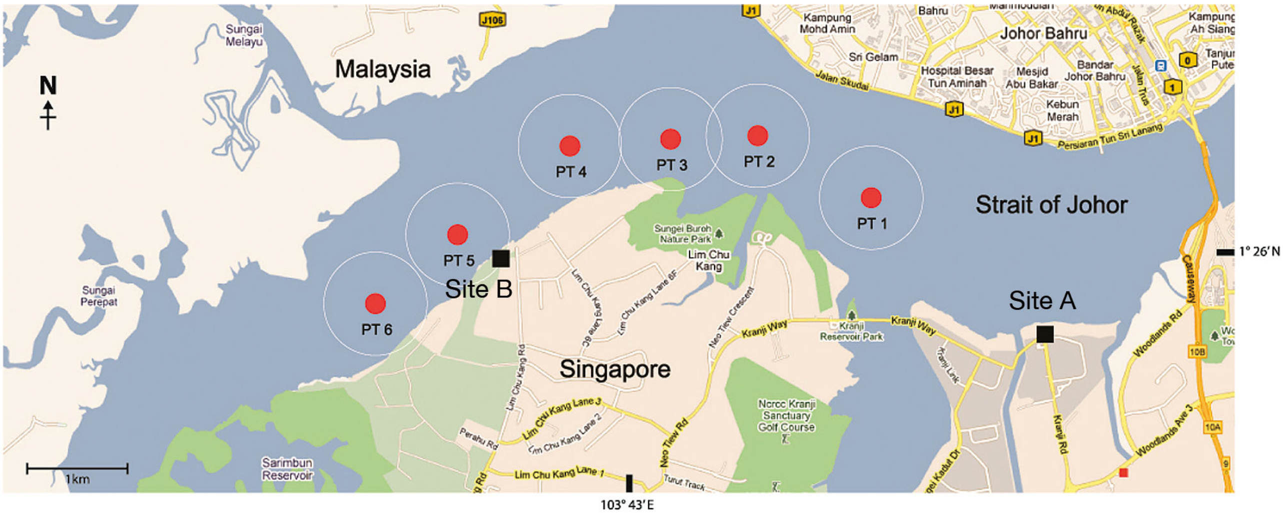

Fig. 1. Position of submersible ultrasonic receivers (SURs) in the Strait of Johor. Point (PT) refers to the SUR attachment site and the circles indicate the zone of detection. Site A is Kranji, the first capture and release site. Site B is Lim Chu Kang, the second capture site. Point 1: 1.44952° N, 103.73939° E; Point 2: 1.45457° N, 103.72835° E; Point 3: 1.45429° N, 103.72134° E; Point 4: 1.45398° N, 103.71252° E; Point 5: 1.44671° N, 103.70406° E; Point 6: 1.44126° N, 103.69640° E

(kHz and millisecond intervals) and the time and date of the signal. All detections were stored in the receiver's memory and downloaded every 3 to 6 wk. One of the fish farm owners was recruited to look after the receivers and check their attachments regularly.

Transmitters

Before being used in the field, all of the transmitters were activated and tested using an active tracking hydrophone. We prepared the transmitters following a method described by James-Pirri (2010) and Brousseau et al. (2004). The tags were first attached to a suitably sized piece of Velcro using cable ties and CA25 cyanoacrylate glue. An accelerator was used to speed up the bonding process. Then, the back of the crab between the eyes was cleaned with ethanol, and the other part of the Velcro was attached to the crab using glue. One of the 2 parts of the Velcro with the transmitter was coated with glue, and the other part was coated with accelerator. The 2 parts of Velcro were then pressed together, and some glue was added round the edges to ensure a secure attachment.

Horseshoe crab collection

During the ebb tide in late November 2010, we collected 8 horseshoe crabs from the population at the Mandai mudflat at Kranji and 4 at Lim Chu Kang, a site ~5.7 km to the west of Kranji. Large adult *Carcinoscorpius rotundicauda*, 6 males and 6 females, >10 cm in prosoma width, were captured. The prosomal width of the females varied from 11.4 to 15.5 cm and that of the males from 10.5 to 12.2 cm. Only crabs free of barnacles were selected to ensure the attachment of the transmitters and as a precaution against the tagged crabs moulting during the study period as few or no barnacles suggests the crab may have recently moulted. Large female moults, the size of sexually mature adults, have been found at the site by the authors, suggesting that at least 1 moult may occur after the crabs reach sexual maturity. The sex and transmitter code of each individual horseshoe crab were recorded, and the transmitters were attached as described.

Group A

To determine if crabs remained in the Strait of Johor near the site of capture, 2 males and 2 females were caught at low tide on the Mandai mudflats at Kranji, tagged and released back onto the mudflat at the capture site while the tide was out (Site A; Fig. 1). The nearest receiver was Point 1. We felt that although we may not detect them if they remained in shallow water close to shore, if they travelled west more than 2 km away to the open sea, they may be detected by one or more of the receivers positioned along the route.

Group B

To determine if the crabs showed any homing tendency, 2 males and 2 females were caught at low tide on the Mandai mudflats at Kranji, tagged and taken to Lim Chu Kang, a site ~5.7 km to the west of the capture site (Site B; Fig. 1), where they were released into shallow water on the shore at mid-tide. The nearest receiver was Point 5. As the causeway to the east of the capture site acts as a barrier, any crabs collected at Site A would not be passing through, so we felt any homing tendency would be revealed if the crabs seemed to make an effort to return to this site.

Group C

To guarantee that tagged crabs would be detected from the time they were released, 2 males and 2 females were caught at low tide along the muddy shore at Lim Chu Kang, tagged and released directly under Point 3 in the deep waters of the strait (Fig. 1). Reception of the acoustic SURs is optimum in seawater, there is no reception on land, and reception is best in deep water. The zone of detection shrinks substantially as the depth of water decreases below ~4 m. Thus, a major limitation of this equipment is that the SURs do not detect signals from horseshoe crabs on the mudflats or in shallow water.

Data collection

From December 2010 to June 2011, we visited the site every 3 to 4 wk to check the receivers, remove marine growth and download the data. SURsoft DPC v6.8.1 2010 (Sonotronics) was used to process the data using a tolerance of 4 kHz to filter out background frequencies. The data were then exported to a spreadsheet and displayed graphically. As there were numerous consecutive hits at the same point over several weeks, the data were collapsed to show weekly hits when an individual moved position from one receiver to another. This gave an indication of how long an individual remained in the same detection zone and how rapidly it moved from place to place. In addition, points of movement were shown on a map to demonstrate the route travelled by an individual, but this did not show how fast it travelled.

RESULTS

None of the receivers was lost. In total, 9968 reliable detections were recorded from 5 of the 6 receivers over the 6 mo period. The receiver at Point 1 had no reliable detections from any of the crabs during the study, although it was functioning properly. The numbers of reliable detections from each crab varied from only 2 from the group released where there was no coverage for 2 km (i.e. Group A) to 5051 detections for a crab released directly under a receiver (i.e. Group C).

The change in monsoon started from approximately mid-March, Weeks 16 or 17, to approximately Weeks 24 to 25 of the study. Although most of the detections (90%) occurred before the start of the monsoon change, this does not indicate a move away from the site due to the change in monsoon. Most signals were detected immediately after release, 53% within 1 mo and 82% by the end of December, well before the start of the monsoon change, and crabs could still be detected sporadically in the strait after the start of the monsoon change.

Group A

The area close to Site A was not covered by an SUR as there was no secure attachment for a receiver. Within the first month, we attempted to locate a signal using manual tracking with a directional hydrophone held 2 m deep in the water from a boat, but detected only 1 signal. Unfortunately, the hydrophone malfunctioned and could not be used again. As a result, there were only 14 detections in total from this group.

Two crabs in this group were picked up only 5 times and the other 2 only twice by the stationary receivers. One crab was detected with the manual hydrophone ~1.5 km from the site of release at Kranji 4 wk after release and then was detected 10 wk later at Point 4, but not at any of the intervening points. It was then detected 3 more times at Points 4 and 6 over 9 wk (Fig. 2). After 3 mo, 2 of the crabs were detected only 2 or 5 times at Point 6 over 4 to 6 wk until the signals died. They were not detected at any intervening points, suggesting that they must have moved along the shore in shallow water rather than travelling in deep water where they would have been detected earlier. The fourth crab was detected only twice, once at Point 4 a total of 15 wk after release at Site A and again at Point 6 a total of 9 wk after the first detection.

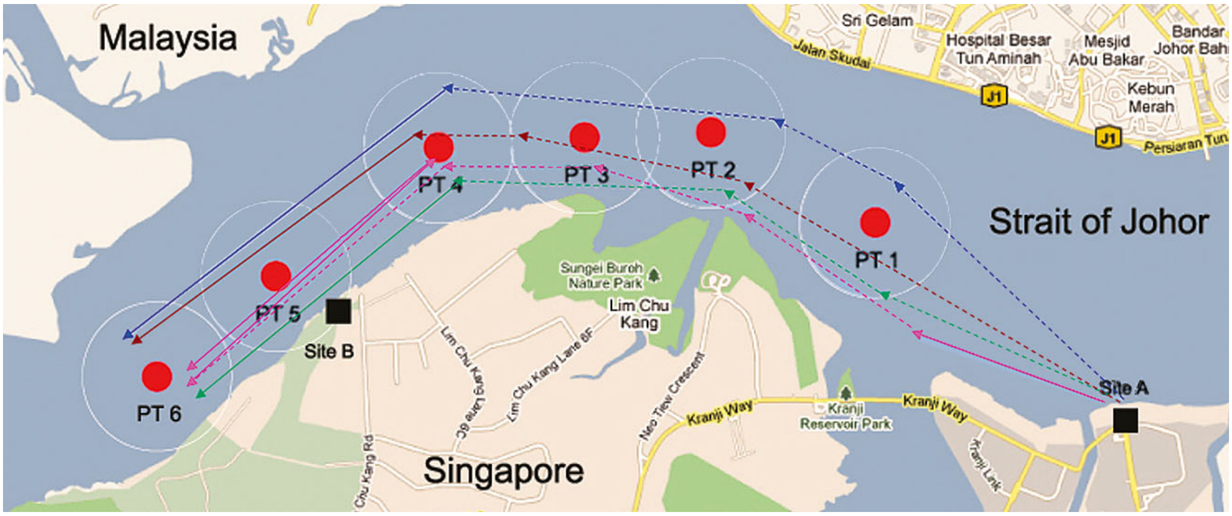

Fig. 2. *Carcinoscorpius rotundicauda*. Travel paths of the 4 horseshoe crabs in Group A over 6 mo in the Strait of Johor, Singapore. A = capture and release site. Dotted lines indicate presumptive route

All of the crabs in this group were eventually detected west of their release point after 14 wk, but they escaped detection by the 3 receivers nearest to the release site. Signals would not have been detected if the crabs were travelling in shallow water over the mudflats.

Group B

There were 2268 detections from this group. All 4 crabs captured at Site A in the east and released on the mudflats at Site B, 5.7 km to the west, were first detected 4 to 7 d after release at Point 4 or 5 and then between Points 3 to 6 for the next 4 mo. They were never detected by the SUR at Point 2 or nearest the point of capture (Point 1). There was no sign of either males or females making their way back eastward to the site of their capture.

These crabs were released on the mudflat at low tide, so the fact that they were detected by receivers 4 to 7 d after release indicates movement perpendicular to the shore into deeper water where they could be detected. The movements of these crabs and the periods spent at each detection point are shown in Figs. 3 & 4, respectively.

In all cases, there were periods when the crabs were not detected for a few weeks, but these periods were not synchronized.

Crab 11 seemed to make rapid excursions from Point 3 to Point 6 and back, a distance of 3.25 km, sometimes in the space of 2 h. Either the crab was taking advantage of the prevailing benthic currents, or these detections were interference on the same frequency.

Group C

Crabs in this group, captured at Site B and released directly under Point 3, moved back and forth between Points 2 and 6 (Fig. 5). The periods spent at each detection point are presented in Fig. 6.

Of these 4 crabs, released directly under the Point 3 receiver, 3 were detected many times in the first 2 to 3 wk before they moved on. Two individuals, Crabs 56 and 69, were detected every hour for 7 and 13 d respectively, including over a full moon period, suggesting there is no synchronized daily or monthly movement up the shore linked with the tide or the moon cycle. The exception was Crab 99, which was detected for 11 h at the release point and then 5 d later at Point 4 for 6 h, at which point it disappeared. It may have been captured or entangled in nets. Crabs 69 and 86 showed gaps in detection from about Week 3 to about Week 11 or 12. Both were male. The female, Crab 56, remained under or close to Point 3 for most of the study period, with a short excursion of 2 wk to Point 6, but it returned and stayed at Point 3.

Movement pattern by sex

There were 6735 (67%) detections of males and 3233 (32%) of females at all receivers except Point 1. The numbers of detections at each point by sex are shown in Table 1.

Most of the detections were at the receivers closest to the site of release. All but one of the detections of

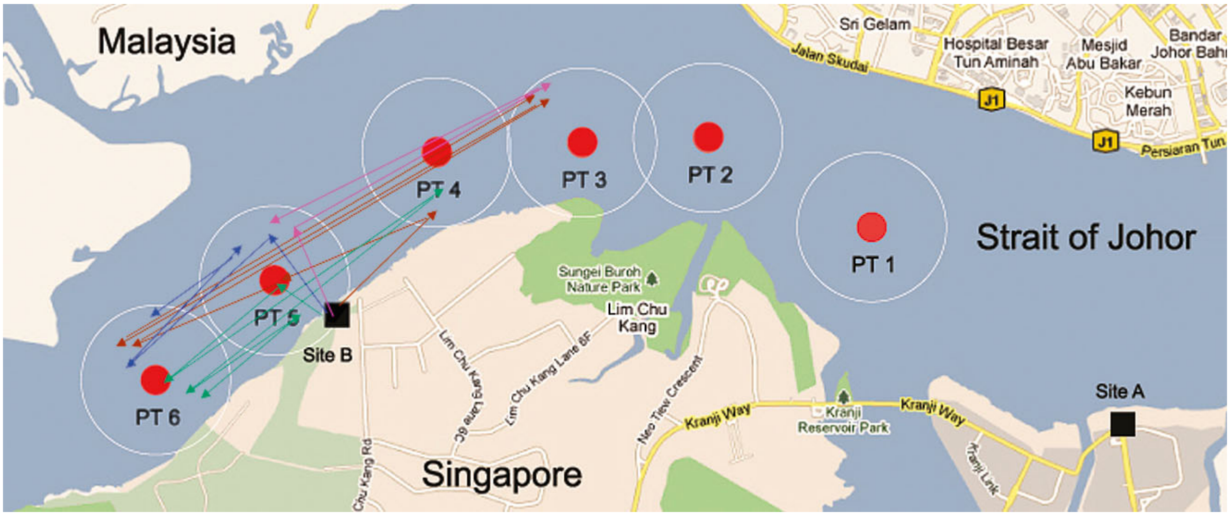

Fig. 3. *Carcinoscorpius rotundicauda*. Travel paths of 4 horseshoe crabs in Group B captured at Site A and released at Site B, ~5.7 km from the capture site. The points at which each crab was detected over time after release are presented in Fig. 4, showing the length of time the crabs spent away from the site of capture

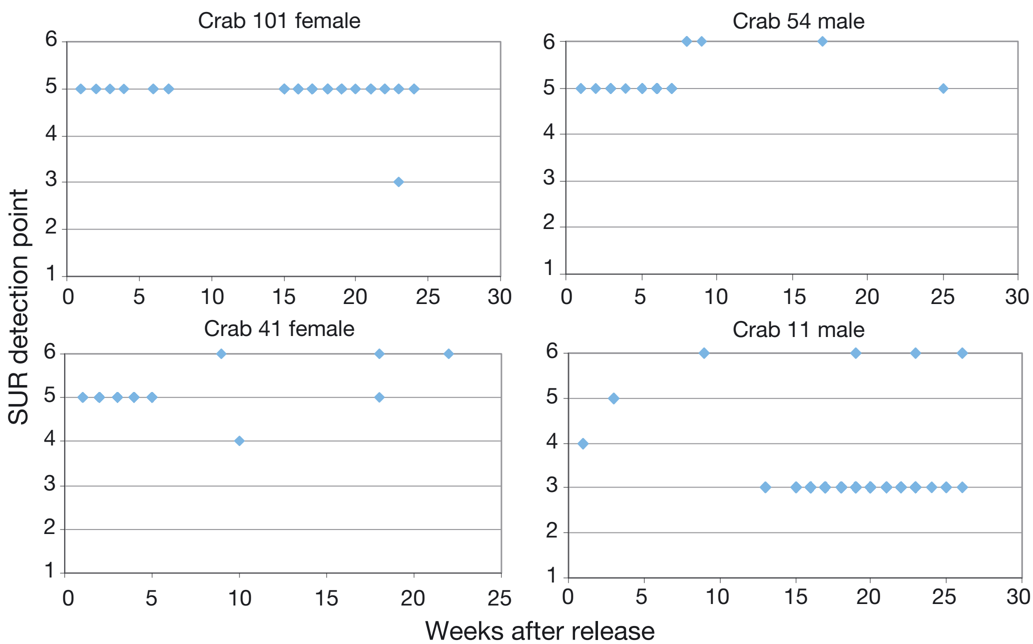

Fig. 4. *Carcinoscorpius rotundicauda*. Movement of crabs in Group B captured at Site A and released at Site B ~5.7 km away, nearest to Point 5, on 20 Nov 2010 and tracked until 4 June 2011

the males in Group B at Point 3 was due to a single male, Crab 11, that took 13 wk to move within the area of detection and then stayed. The greater number of detections of males than females suggests that males remain longer in deeper water, but it is not possible to determine any differences between movement patterns of the sexes. The numbers of each sex in each group (2) were too small for any meaningful analysis, and the number of detections was too variable (5051 and 91 in the males of Group C), but the detections do suggest that both sexes remained in the vicinity most of the time.

DISCUSSION

One aim of the present study was to determine if the mangrove horseshoe crabs are transient visitors

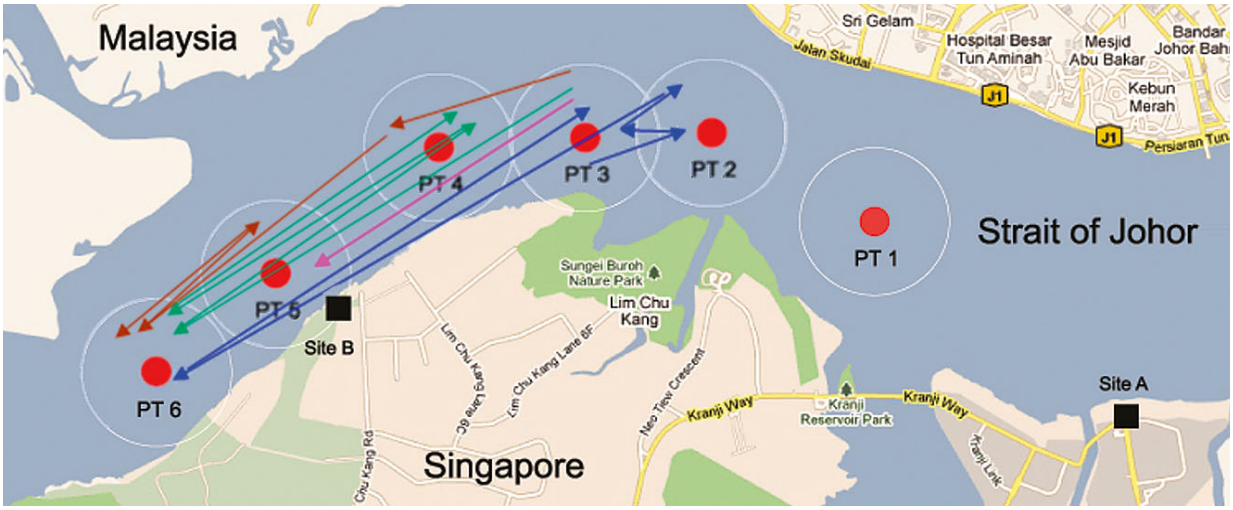

Fig. 5. *Carcinoscorpius rotundicauda*. Travel paths of 4 horseshoe crabs in Group C captured at Site B and released under Point 3

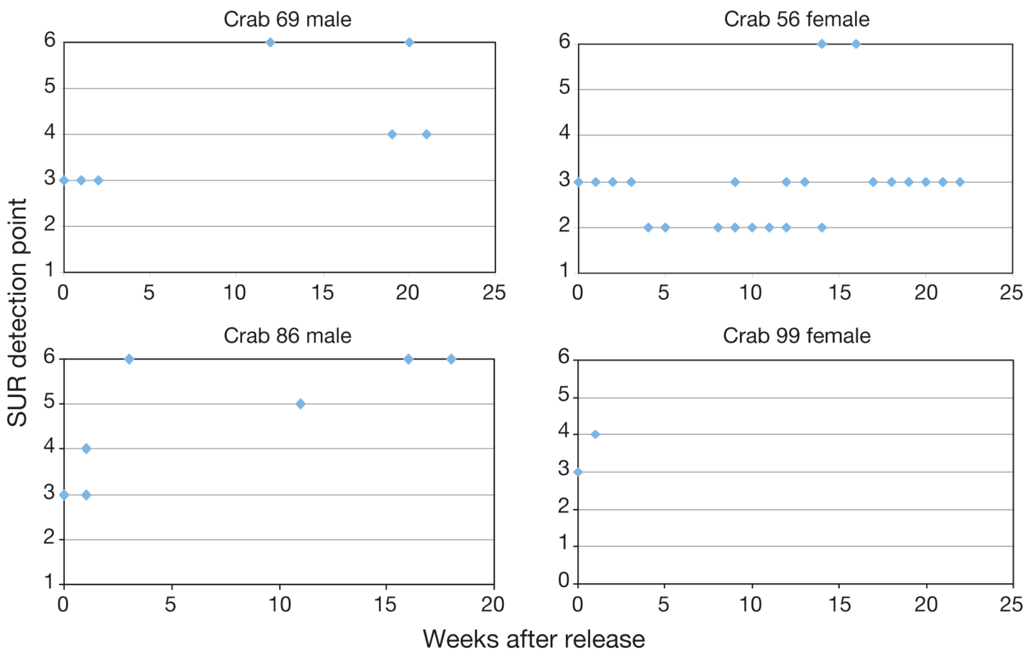

Fig. 6. *Carcinoscorpius rotundicauda*: Movement of crabs in Group C captured at Site B and released directly under Point 3 on 14 Dec 2010 and tracked until 4 June 2011

to the study site or more permanent residents. The acoustic telemetry indicated that crabs probably remained within the Strait of Johor for the 6 mo study period and made no attempt to reach the open sea, >16 km away. Males and females alike were detected within a few kilometers of the release site for most of the present study, suggesting that *Carcinoscorpius rotundicauda* does not travel far and that there was no apparent difference in movement between the sexes. Of the 12 tagged crabs, 11 were detected intermittently for 5 to 6 mo after release, the expected lifetime of the transmitter batteries. The one exception was detected for only 5 d even though it was released directly beneath one of the receivers, suggesting it may have become trapped on shore or in the shallows out of detection range. Entrapment in illegally deployed fishing nets is a major hazard for the crabs in the Strait of Johor, even though fishing is not conducted at a commercial scale. The other tagged crabs released under the receiver were

Table 1. *Carcinoscorpius rotundicauda*. Numbers of detection for males and females at each receiver point. –: no detections

	Point 1	Point 2	Point 3	Point 4	Point 5	Point 6
Group A						
Males	–	–	–	–	–	7
Females	–	–	–	3	–	3
Group B						
Males	–	–	1017	1	560	10
Females	–	–	1	1	675	3
Group C						
Males	–	–	5075	57	1	7
Females	–	62	2463	20	–	2

detected almost constantly at the same point for the first 2 or 3 wk, including over a full moon period, before they moved on to be picked up by another receiver, suggesting that not all individuals move up the beach daily with the tide or monthly at the high spring tide. Good foraging on the seabed under the fish farms from the unused fish food and dead fish that sink to the bottom in addition to the normal benthic life of the strait may have provided all of the food requirements of the crabs or attracted other species that the crabs feed on. Although there is little published work on the feeding preferences of *C. rotundicauda* in the wild, the larval stage is thought to scavenge on small fish, oligochaetes, small crabs and thin-shelled bivalves (Zhou & Morton 2004). In captivity, adults at Singapore Zoo are fed fish, squid and prawns (J. Kee pers. comm.).

The second aim of the present study was to determine if the horseshoe crabs showed any homing tendencies when removed from the capture site. The group of crabs released far from the capture site showed no inclination to return home. There was no evidence of a concerted move by either the females or males back east along the strait to where they were caught. This lack of homing may be useful if individuals are relocated to restock areas where a degraded habitat has been restored as part of a conservation scheme, even if the site is not far from the capture site.

The present work is the first study to track the movement of mangrove horseshoe crabs in the tropics, and it indicates major differences from movement patterns of other species in temperate climates, including Hong Kong. There are no distinct seasons in Singapore, only a reversal in wind direction occurring around October–November and then again about late March through to May, with the latter change falling toward the end of the study period. Although most of the detections occurred before the start of the monsoon change, crabs could still be detected intermittently at the site after the change in monsoon. There was no evidence of synchronised movement of the tagged crabs to any particular part of the strait or to deeper waters, as occurs with horseshoe crab species in temperate climates in the USA or Asia during seasonal spawning or as the water temperature drops (Chiu & Morton 2003, Brousseau et al. 2004, Shin et al. 2009, James-Pirri 2010). Unlike temperate populations, no migration pattern was detected in this tropical population of mangrove horseshoe crabs. The water temperature of the Strait hardly varies from ~28 to 30°C year round, and even with the monsoon, a change in wind direction, all but one of the tagged crabs could still be detected in the strait before, during and after the monsoon. In addition, spawning occurs year round although with periods of high and low reproductive activity (Cartwright-Taylor et al. 2009), so there is no pressing reason for the horseshoe crabs to move. Studies of *Limulus polyphemus* in the warmer waters off the Yucatan peninsula indicate that spawning is also a year-round activity there (Zaldivar-Rae et al. 2009), and in India, spawning of both *Carcinoscorpius rotudicauda* and *Tachypleus gigas* has been reported throughout the year (Chatterji & Abidi 1993), suggesting that in warmer climes there is no periodic or seasonal migration to deeper waters.

Crabs from Groups B and C were detected most frequently near the sites of release where the water is deeper than it is further east and where there is a concentration of fish farms that provide suitable forage. There were no reliable hits at Point 1, suggesting that the crabs in Group A also remained near the release site for most of the study period. The many intermittent gaps in detection of all of the crabs may have been for any of several reasons. As the tide ebbed or if the crabs moved close inshore, perhaps for spawning, they would not have been detected in shallow water. In addition, unlike the species that live on sandy substrates and move out with the ebb tide, many mangrove horseshoe crabs remain immobile on the mudflats and sink into the mud as the tide recedes, making constant detection more difficult. Even radio transmitters would not pick up signals from buried crabs, making it difficult to detect any patterns of daily or monthly movement up the beach. Crabs can always be found on the mudflat at low tide at all times of the month and year, and only a low percentage of these are in amplexus (Cartwright-Taylor & Hsu 2012), so mating is clearly not the reason. It is not clear why some individuals remain on the flats as the tide recedes and others remain in deep water.

The present study indicates that the mangrove horseshoe crabs are not merely transient visitors to the Strait of Johor but remain there for several months, possibly permanently. Thus, any development along this shore will seriously threaten this population. Coastal development projects are threatening the survival of all 3 Asian species of horseshoe crabs. However, it should be possible to allow development in such a way as to preserve the mudflats and their inhabitants. A landmark decision was made in Japan to alter plans for proposed flood control modifications to 2 river systems flowing into Moriye Bay, Oita Prefecture in NE Kyushu Island, Japan, a horseshoe crab spawning and nursery habitat, after tracking studies using radio-acoustic telemetry demonstrated that crabs return to the site outside the breeding season (Seino & Uda 1999). These findings have resulted in the preservation of critical mudflats and the creation of a marine protected area (O'Dor et al. 2001). It is time for countries throughout the Asia-Pacific region to follow the example of Japan and demonstrate that environmental considerations can be successfully incorporated into development plans before it is too late for these endangered species.

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