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Feeding by the sand crab *Portunus pelagicus* on material discarded from prawn trawlers in Moreton Bay, Australia

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Abstract

A field and laboratory study in 1984–1985 using the foregut contents of crabs caught in Moreton Bay, Queensland, when trawling was underway, showed that animals discarded from trawls constituted about 33% of the diet. *Portunus pelagicus* can fill its foregut in about 8 min and clear it completely of tissues in about 6 h, except for fish bone which requires about 24 h. *P. pelagicus* used a zigzag search pattern to find food and moved towards it at a mean point-to-point speed of 290 m h^{-1} (8 cm s^{-1}). Underwater still photography on the trawl grounds showed that *P. pelagicus* was the most common scavenger attracted to a bait that simulated trawl-discards, and that it was most active at dusk. Trawler-discards at periods of high food demand in summer may allow larger populations of *P. pelagicus* to exist than would otherwise occur.

Introduction

Nets used by otter trawlers for catching penaeid prawns also take considerable quantities of other species. Some of this by-catch is retained, but most, especially other invertebrates and small or inedible fish, is dumped back into the sea (Allsopp, 1982; Furnell, 1982; Saila, 1983). Little is known of the fate of discarded material that reaches the seabed, although it is thought to be eaten by benthic feeders such as certain crabs and fish (Paul, 1981).

In Moreton Bay, Queensland, an intensive otter-trawl fishery operates in an area that also supports a large fishery for the sand crab *Portunus pelagicus* (Thomson, 1951). This crab fishery involves about 50 full time fishermen (Williams, 1980). The crab is widely distributed through the Indo-Pacific region (Barnard, 1950). The diet of *P. pelagicus* consists of benthic invertebrates such as bivalves, polychaetes and crustaceans (Williams, 1982). Although Williams (1982) identified prawn and squid remains in the gut contents of *P. pelagicus* captured in trawls, she suggested that these relatively mobile animals were eaten while the crabs were in the cod-end of the trawl net. Since feeding by crabs in a cod-end during trawling would be difficult, we decided to investigate the possibility that *P. pelagicus* feeds on material discarded by trawlers.

Materials and methods

Identification of food items and measurement of foregut volume

Trawlers in Moreton Bay do not operate from 18.00 hrs on Friday to 18.00 hrs on the following Sunday. It was thus possible to collect specimens of *Portunus pelagicus* that had had no access to fresh trawl discards for up to 48 h. Samples of at least 50 *P. pelagicus* (81 to 162 mm carapace width) were collected from the catch of a commercial trawler in Moreton Bay, Queensland (27 °S; 135 °E) on two occasions, in September and in November 1984. On each occasion, specimens of *P. pelagicus* were collected from the first trawl on a Sunday evening (48 h since trawling ceased) and from a trawl 6 to 8 h after regular trawling had begun. Only crabs in Intermoult Stages 4 or 5 (Williams, 1982) were retained. They were killed by placing them in iced sea water, and were brought back to the laboratory, where they were kept frozen at –20 °C until they were examined.

In the laboratory, the sex and carapace width of each crab were recorded and an estimate made of the relative fullness of the foregut. Food items in the foregut were identified to class for molluscs, annelids and echinoderms and to order for crustaceans; the total number of food items in each taxonomic category was counted. The numerical composition was obtained by dividing the total number of each taxonomic food category by the sum of all food items. The material in each taxonomic category was dried to constant weight at 70 °C and expressed as a proportion of the total dry weight of food.

Nonparametric analyses were used to compare the diet items of the crab sample collected 48 h after the last trawl with the crabs collected during trawling as there were many missing data values. The Mann-Whitney *U* test (Zar, 1974) was used to compare the numbers and weights of each diet item in the two samples. Parametric analysis were used for all other statistical tests. The total volume of the foregut was measured using the method of Hill (1976).

Rate of uptake and clearance of food

Portunus pelagicus were kept in the laboratory in tanks (2.0×1.1×0.8 m) divided into six equal compartments and filled to 300 mm depth with continuously flowing sea water. Each crab was kept in a separate compartment and fed daily on fish, but starved for 24 h prior to experiments.

The rate of uptake of food by *Portunus pelagicus* was measured using a piece of whiting (*Sillago maculata*) as food. The fish was weighed and put into a compartment. The time at which the crab began feeding was noted. Ten crabs were each allowed to feed for a limited period, after which all uneaten fish were removed, blotted dry and reweighed. Weights were corrected for water uptake by the tissue. The difference gave an estimate of the quantity eaten. The experiment was repeated with ten crabs at each of the following feeding times: 2, 4, 8, 16 and 32 min.

The rate of clearance of the foregut of *Portunus pelagicus* was measured using the method described by Hill (1976). The technique involves measuring the quantity of food in the foregut of the crabs after varying times following a set feeding period. Clearance rates were measured for fish muscle, fish head bone and prawn tissue in three separate experiments. In the first experiment, *P. pelagicus* that had fed for 15 min on skinned, boneless fillets of winter whiting (*Sillago maculata*) were killed in batches of ten crabs after varying time periods (0, 2, 4 or 6 h). Their foregut contents were removed and oven-dried to constant weight at 70 °C. In the second experiment, 30 crabs that had fed for 15 min on the cephalothorax of *Metapenaeus bennettae* were killed in batches of ten after 1, 3 and 6 h and the weight of foregut contents measured. In the final experiment, 30 crabs that had fed for 20 min on whole heads of winter whiting were killed in batches of ten crabs after 0, 12, and 24 h and the weight of foregut contents measured. Ten pieces of each type of food were oven-dried to constant weight to obtain factors for converting wet weight to dry weight. The quantity of fish muscle and prawn cephalothorax in the foregut was expressed as a percentage of the quantity ingested. Since this could not be done for fish bone, the actual weight of bone remaining in the foregut is given.

Underwater photographic record of scavengers on trawl grounds

A 35 mm camera with a motor drive, data-back, a quartz timer set to take pictures at 2 min intervals, and a 28 mm lens, was enclosed in an aluminium alloy housing and placed on a tetrapod, 1 m above the substrate. Two electronic flashes were fastened onto the frame of the tetrapod, 300 mm below the camera and outside its field of view. Each flash was covered with a red filter giving about 90% transmittance above 600 nm. Two winter whiting, *Sillago maculata,* were attached to the midpoint of a cord tied diagonally across the base of the tetrapod.

The camera was lowered to the seabed on the trawl ground and left for 30 min (15 photographs). Three camera drops were made without a bait as a control. Camera drops were made around 14.30, 16.30, and 18.30 hrs and then hourly through the night to 06.30 hrs. This was done in four areas of Moreton Bay (Fig. 1) between January 1985 and November 1985 to give four replicates for each of the above times. The number of frames taken, the number and type of scavengers, the time taken for the scavengers to find the bait and the time spent at the bait were also noted. As the camera had to be switched on while it was on the boat, the starting time was taken from the time of the first photograph on the bottom. Because of the time interval between photographs, the recorded time spent by a scavenger at the bait was accurate to ± 2 min.

The average depth at which photographs were taken was 10 m (SD = 5.39). Sea water temperatures ranged from 19.0° to 27 °C (mean = 23.7 °C) and salinities from 30 to 37‰ (mean = 35.5‰).

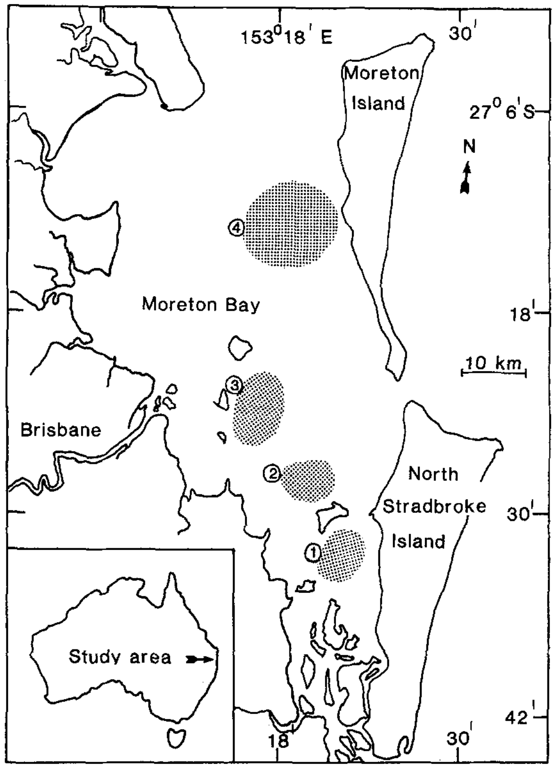

Fig. 1. Moreton Bay, Queensland, showing four locations where underwater camera was deployed. Individuals of *Portunus pelagicus* for foregut-content analysis were collected from Sites 1 and 2

Laboratory behaviour associated with feeding

The behavioural response of *Portunus pelagicus* to a bait was investigated in the tank (6 m diam, 0.6 m deep) described by Skinner and Hill (1986). A circulating pump created a current of about 4 m min^{-1} at the wall, decreasing to about 0.3 m min^{-1} near the centre. The tank was illuminated by eight 150 W white incandescent lights from 06.00 to 18.00 hrs each day, and by four 100 W red incandescent lights by night. A low-light-level television camera was placed centrally above the tank and connected to a time-lapse video-recorder that incorporated a time-date generator giving time accurate to one second.

The feeding behaviour of *Portunus pelagicus* was observed on 12 occasions with four crabs in the tank and 21 times with ten crabs. The crabs were fed on either *Sillago maculata* or the flounder *Pseudorhombus* sp. The baits were attached to a weight and put into the tank 1.5 m from the wall before 18.00 hrs. Television recording started shortly before the bait was introduced and continued overnight. As most activity occurred in the first hour after the bait was introduced, only the first 2 h of recording have been used in this analysis. Uneaten food was removed the following morning.

The following responses were recorded for each crab that fed: response time, speed of movement, angles turned, time at the bait and number of *Portunus pelagicus* simultaneously at the bait. Response time was the interval between introduction of the bait and arrival of the first crab at the bait. The track of crabs was traced from the 300×380 mm monitor screen onto a transparent plastic overlay. Speed of movement over the bottom was calculated from the length of the track and the time taken to move along it. Since the crabs tended to move in a zigzag path towards the food, speed over the bottom was not a good indication of the speed at which crabs move between two points. Measurement of point-to-point speed was complicated by the crabs having to follow a curved path in the circular pool. To overcome this problem, the path of a float on the water surface, over the bait, was traced on the television monitor screen for one circuit of the tank. The time at which a crab moving towards the food first crossed this path and the time of its arrival at the bait were noted. The time interval and the curved distance between the points were used to calculate the point-to-point speed. Speeds were calculated only for crabs that moved without stopping for more than 2 m (mean 7.0 m). When a crab changed direction or began moving again after stopping, the angle of the new track was measured relative to the old. If the crab's path curved, no angle was measured.

Results

Comparative diet analysis and foregut volume

The sizes of *Portunus pelagicus* in the two samples used for analysis of gut contents were not significantly different (123.9 mm average carapace width; Student's t-test = 1.52; degrees of freedom, DF = 131). In each sample, about 30% of crabs had no food in their foreguts. Bivalves predominated in the guts of both samples, which also contained gastropods, polychaetes, crustaceans, ophiuroids and unidentified material (Fig. 2). Small amounts of teleost fish bones but no penaeid prawns were found in crabs captured when no commercial trawling was underway (Fig. 2a). Fish and prawns were significantly higher ($P<0.01$ in both cases) in number and weight (33% by weight of all foregut contents) in the foreguts of crabs captured while trawling was occurring, while all other food items (except unidentified material) were lower (Fig. 2b). The foreguts of eight crabs contained the remains of penaeid prawns. *Penaeus plebejus* was identified in one crab and *Metapenaeus novaeguineae* in three. The teleost *Siphamia* sp. was found in the foreguts of three crabs.

The foregut volume (V in μl) of *Portunus pelagicus* was found to be a power function of carapace width (W) in mm:

$$V = 3.29 \times 10^{-3}\ W^{2.91} \quad (r=0.98,\ F=2241,\ DF=1{,}73).$$

Rate of uptake and foregut clearance of food

The mean quantity of fish eaten by *Portunus pelagicus* increased rapidly with time, reaching a maximum of 6 g within 8 min (Fig. 3). After that time they did not eat any more, even if the food was available for 32 min. In the experiment on foregut clearance, *P. pelagicus* (140.7 mm average carapace width, SD = 11.3) ate an average of 5.03 g (SD = 1.03, $n=40$) wet weight in 15 min. The amount of fish muscle found in the foregut immediately after the crabs had fed accounted for 93% of the amount estimated to have been eaten. About 50% of this muscle tissue was cleared within 1.5 h and more than 95% of the tissue ingested was cleared from the foregut within 6 h (Fig. 4a). The crabs consumed an average of 4.26 g (SD = 0.33, $n=30$) wet weight of *Metapenaeus bennettae* cephalothorax in 15 min. The clearance rate for this tissue was found to be similar to that for fish muscle (Fig. 4a), with 50% cleared from the foregut after 1.5 h and 95% cleared by 6 h. An average of 7.17 g (SD = 1.98, $n=30$) of fish-head bone was consumed by the crabs. The clearance rate of bone from the foregut was rapid. Only 450 mg of bone tissue remained after 6 h and less than 100 mg after 12 h, and it was virtually all gone after 24 h (Fig. 4b). The rate of clearance varied widely: four crabs had cleared their foregut completely by 12 h. These results indicate that foregut clearance rates are rapid for all tissues and that nearly all soft tissues are cleared within 6 h.

Underwater photography on trawl grounds

A total of 881 photographs was taken on the Moreton Bay trawl grounds. Forty five photographs, taken as controls with no bait, showed no scavengers, but scavengers were

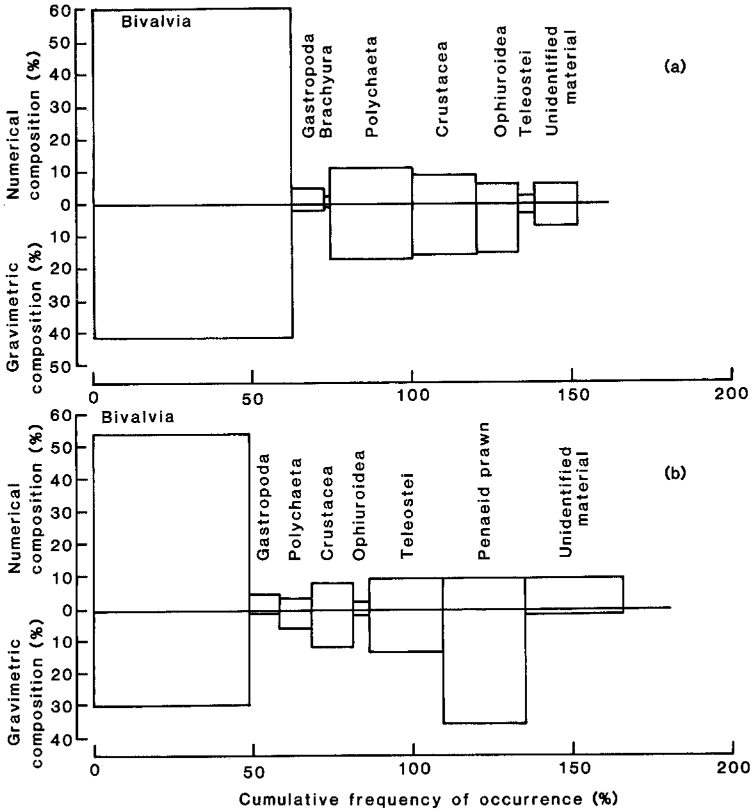

Fig. 2. *Portunus pelagicus.* Comparison of diet of crabs caught (a) a minimum of 12 h after trawling had ceased ($n = 83$), and (b) 6 to 8 h after trawling had begun ($n = 50$)

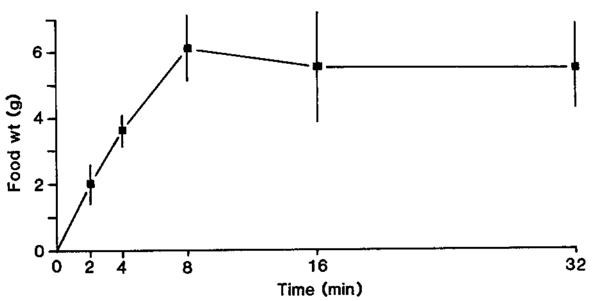

Fig. 3. *Portunus pelagicus.* Average weight of food eaten by crabs in 2, 4, 8, 16 and 32 min. Vertical bars are ±2 SE, $n = 10$ at each point

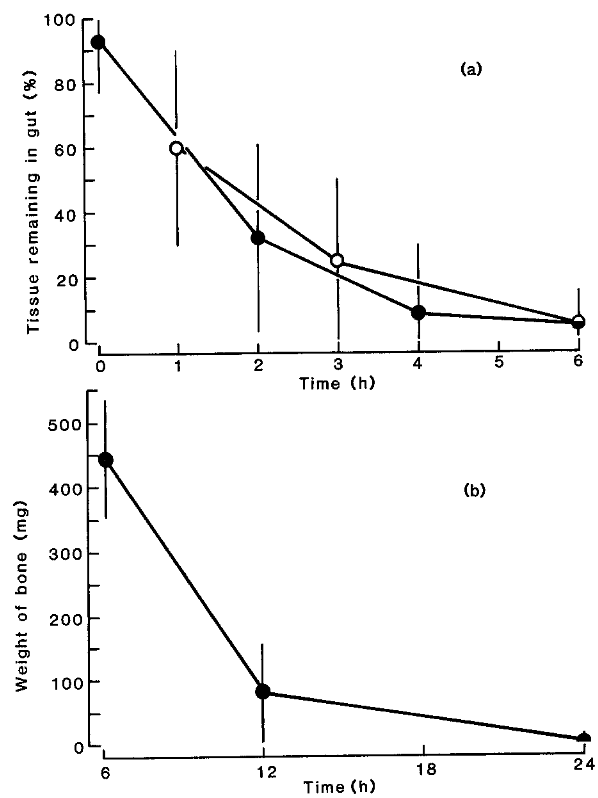

Fig. 4. *Portunus pelagicus.* Clearance rate for various tissues in foreguts of crabs ($n = 10$ at each point). (a) *Sillago maculata* muscle (●) and *Metapenaeus bennettae* cephalothorax (○); vertical bars are 95% confidence intervals for percentages. (b) *S. maculata* bone, average weight with standard deviations

observed in 45.7% of all baited exposures. *Portunus pelagicus* was the most frequently observed scavenger, appearing in 23% of photographs. It was also the most frequently photographed scavenger in each of the four areas in Moreton Bay. The next most frequent scavengers (11% of photographs) were small fish that could not be identified from the photographs. Two other species of crab were observed in 4% of photographs: *Galene bispinosa* and *Thalamita sima.* Crabs were the first scavengers to arrive at the bait in 73.5% of baited camera drops, taking an average of 9.3 min to do so. In 16% of all photographs, the fish came later than the crabs; in only 6% of cases did they precede crabs. Seastars, stomatopods and one penaeid prawn were also observed. The prawn was not seen at the

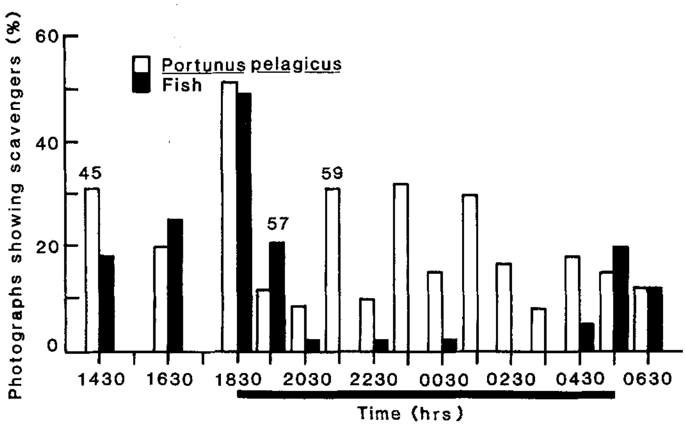

Fig. 5. Percentage of photographs showing scavengers (*Portunus pelagicus* or fish) attracted to baited camera set on seabed in Moreton May. At each time $n=60$, except where indicated. Dark horizontal bar indicates night

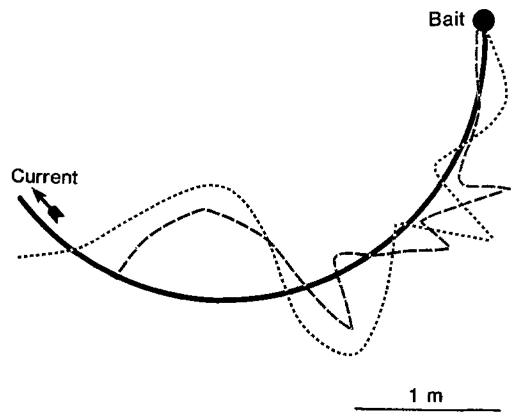

Fig. 6. *Portunus pelagicus.* Tracks (broken lines) of crabs moving towards bait in a tank. Bold line indicates current shown by path of a float that passed over bait

bait but swimming over it. Only two baited camera drops did not attract scavengers.

An average of 12.0 photographs were recorded of *Portunus pelagicus* at the bait each time the camera was deployed (Fig. 5). A chi-square analysis of frequency of photographs with crabs showed that attraction of crabs to the baited camera was not uniform throughout the night ($P<0.01$). Subsequent analysis showed that the difference was due to a significant peak ($P<0.01$) in the number of photographs of *P. pelagicus* at 18.30 hrs. The average time a single crab spent at the bait was 3.4 min (SD = 1.7, $n=17$). If more than one crab was observed at the bait during 30 min, the length of time spent at the bait by the first crab to arrive was 3.9 min (SD = 2.2, $n=32$). These times were not significantly different (Student's $t=-0.84$, DF = 47), and suggests that the arrival of a second crab at the bait did not reduce the length of time spent by a single crab at the bait. Fish were attracted to the bait during the day; this activity declined after dusk but recommenced just before dawn (Fig. 5).

Laboratory behaviour associated with feeding

Crabs moved towards the bait in a zigzag path in the 6 m tank (Fig. 6). The mean time interval between introduction of the bait and the arrival of the first *Portunus pelagicus* was 5.5 min ($n=24$). When there was no food in the tank, the crabs moved at a speed of 300 to 399 m h^{-1} with little movement over 700 m h^{-1} (Fig. 7a). With food in the tank, the crabs travelled more rapidly over the bottom: from 400 to 499 m h^{-1}, and 40% of movement exceed 700 m h^{-1} (Fig. 7b). *P. pelagicus* moved more rapidly in the presence of food (mean speed 559 m h^{-1}) than when food was absent (mean 387 m h^{-1}) However, the point-to-point speed towards food was low (mean 290 m h^{-1}, Fig. 7c).

When there was no food in the tank, 85% of the angles of change in direction by *Portunus pelagicus* were less than 90° (Fig. 8a). If food was present, over half (56%) of the angles turned were between 90° and 180° (Fig. 8b). This resulted in the crab crossing and recrossing the probable scent trail coming from the bait.

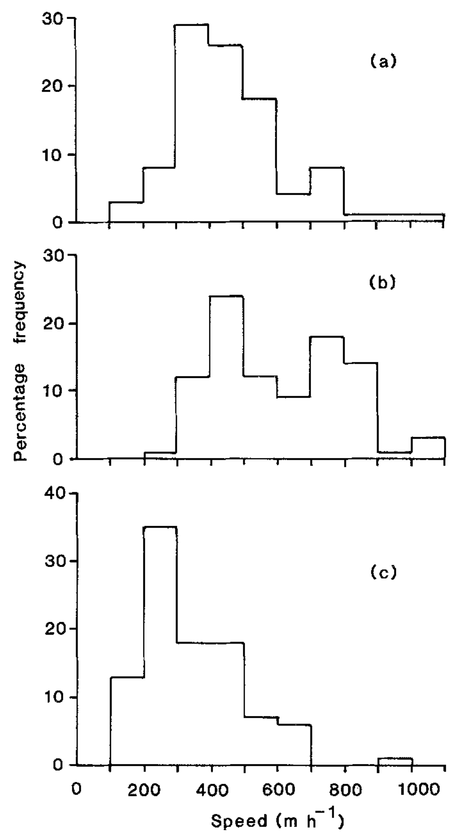

Fig. 7. *Portunus pelagicus.* Speed of movement of crabs in a 6 m diam tank showing (a) speed over bottom when no food was in tank ($n=73$), (b) speed over bottom when moving towards food ($n=74$), and (c) point-to-point speed when moving towards food ($n=71$)

Since the number of *Portunus pelagicus* present at the bait at one time was identical with either four or ten crabs in the tank, the two sets of data have been combined. A

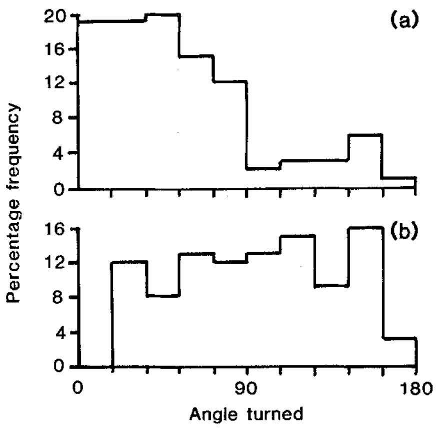

Fig. 8. *Portunus pelagicus.* Frequency of angles (degrees) turned by crabs when (a) no food was in tank ($n = 115$), and (b) when moving towards food ($n = 109$)

total of 554 min of feeding activity was recorded; for 96.6% of this time, only one crab was present at the bait. As a second crab arrived at the bait, it spread its chelae wide, the first crab then either left the bait or displayed similar agonistic behaviour until one of the crabs left. Thus, when two crabs were at the bait, they were usually displaying to each other rather than feeding simultaneously. The period for which two crabs were at the bait (mean 0.4 min, SD = 0.58, $n = 54$) was much shorter than that for a single individual (3.2 min, SD = 3.3, $n = 177$). The mean time spent at the bait when a crab left voluntarily (3.9 min, SD = 3.6, $n = 98$) was not significantly longer (Student's $t = 1.40$, 112 DF, $P > 0.05$) than when it left after being challenged by a newcomer (3.1 min, SD = 3.3, $n = 22$).

Discussion

Crabs have often been regarded as important scavengers of dead fish. Bernard (1979) found carrion, apparently from a dogfish (*Squalus acanthias*) fishery, in the diet of *Cancer magister.* Jewett and Feder (1982, 1983) attributed fish found in crab foreguts to deadfall from seabirds and sealions feeding on schools of fish. Paul (1981) suggested that fish remains found in *Callinectes arcuatus* resulted from scavenging on dead fish discarded by fishermen. None of these claims has been supported by direct evidence.

Portunus pelagicus consumes a wide variety of sessile or slow-moving organisms but rarely feeds on more mobile prey such as fish and prawns (Patel *et al.,* 1979; Williams, 1982). In the present study, neither recently ingested fish nor prawns were found in the foreguts of crabs captured when trawling was not taking place. During trawling times, however, when by-products were being discarded, both food items were found in the foreguts. The undigested appearance of this material and the rapid foregut clearance rate indicate that it had been recently ingested.

Underwater photographs in Moreton Bay showed that *Portunus pelagicus* was the most common scavenger attracted to a fish bait in the trawl grounds. Photographs also showed that *P. pelagicus* was common in all areas of Moreton Bay investigated and that it was attracted to, and fed on, the bait throughout the night. A peak in the occurrence of *P. pelagicus* in photographs taken around 18.00 hrs coincides with reported peak catches of *P. pelagicus* by trawlers (Stephenson *et al.,* 1982), which supports the suggestion that activity is greater at dusk. Crabs caught at dusk also had more food in their guts. In over 70% of cases, *P. pelagicus* was the first scavenger to arrive at the baited camera, and did so on average within 9.3 min of the bait reaching the bottom. Experimentally, we found that *P. pelagicus* could travel between two points at a speed of around 290 m h^{-1}. Thus, crabs arriving at the bait within 10 min of its reaching the bottom could have come from up to 40 to 50 m away, assuming that the response by the crabs to the bait was instantaneous. Thus, discarded material from trawlers is likely to be found by scavengers shortly after it reaches the seabed.

Laboratory observations on the behaviour of *Portunus pelagicus* showed that they responded to a bait by emerging from the substrate, moving upcurrent and zigzagging, crossing and recrossing the probable scent trail. Chemosensory location of food has advantages over visual detection where visibility is hampered by low light at night or high turbidity. The speed at which scavengers arrive at food will in part depend on foraging strategies (Lampitt *et al.,* 1983), current speed and direction, rate of attractant diffusion and the continuing emission properties of the bait (Morrissy, 1975). Chemosensory responses to attractants by scavengers have been reported for many crustaceans (McLeese, 1970; Hamner and Hamner; 1977; Lampitt *et al.,* 1983; Wilson and Smith, 1984). Feeding and walking responses in *Homarus americanus* were elicited by 13 amino acids; freshly prepared extracts of cod, shrimp and lobster muscles brought the quickest response (McLeese, 1970). Thus, damaged, freshly killed and discarded material from trawlers could be expected to act as a strong food stimulus to crabs.

The time spent by *Portunus pelagicus* at the bait both in the field and in laboratory tanks, was less than the time required to fill the foregut. Although the crabs in the field may have had food in their foregut when they arrived at the bait, the experimental crabs had been starved for about 20 h and thus their foreguts would have been empty. In both the field and the laboratory, the bait was attached so that it could not be removed by crabs. Under these conditions, the crabs fed briefly and then in many cases broke off a piece of bait and moved away with it. This strategy could reduce conflicts with conspecifics and other competitors and could reduce the element of risk to scavengers by predators that might be attracted to aggregations of food falls (Lampitt *et al.,* 1983). Competition between *P. pelagicus* at a bait was rarely observed in the field, and laboratory observations showed that, for 97% of the time when feeding was taking place, there was only one crab at the bait even though there were ten crabs in the tank. Where there was a conflict between crabs, the first crab to have fed often left the bait if challenged even if the second crab was smaller.

Portunus pelagicus in Australian waters extrude eggs between September and April (Thomson, 1951; Penn, 1977; Smith, 1982; Potter *et al.*, 1983; Campbell and Fielder, 1986). In Moreton Bay this period overlaps with the prawn trawling season (September to May), when discards would be available as a supplementary food source. Fusaro (1978) showed that an increased food supply to the crab *Hippa pacifica* nearly doubled the percentage of ovigerous females relative to control populations. It is possible that the food available to *P. pelagicus* from prawn trawlers in Moreton Bay may enable higher population densities of these crabs to be maintained than there would be without trawling.

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