Dietary composition of the blue swimmer crab *Portunus pelagicus* L.
Does it vary with body size and shell state and between estuaries?

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**Abstract**

The aim of this study was to determine the diets of *Portunus pelagicus* in the large Peel–Harvey and Leschenault estuaries in south-western Australia in order to ascertain whether the dietary composition of this crab changes with body size during two different moult stages and differs between the two estuaries. *Portunus pelagicus*, ranging in age and carapace width from ca. 2 months and 12 mm to ca. 1 1/2 years and 159 mm, were collected from the shallow basins of the Peel–Harvey and Leschenault estuaries. Examination of the cardiac stomachs of these crabs showed that *P. pelagicus* does not feed just before or immediately after moulting and that the stomachs of recently-moulted crabs contained significantly more food than those of intermoult crabs. Although the volumetric contribution made by calcareous material to the stomach contents was similarly high in all size classes of recently-moulted crabs, i.e. 47 to 55%, the volumetric contributions made by small bivalves decreased with body size, whereas the reverse occurred with shell fragments of large decapods and, to a lesser extent, polychaetes. The dietary compositions of intermoult crabs were shown by classification and multi-dimensional scaling ordination to differ markedly from those of recently-moulted crabs and to undergo similar progressive ontogenetic changes in both the Peel–Harvey and Leschenault estuaries. Thus, the contribution made by small benthic and epibenthic crustaceans, such as amphipods and tanaids, declined with increasing body size, whereas the reverse occurred with larger prey, such as nereid polychaetes, small decapods and teleosts. The dietary composition of *P. pelagicus* was influenced more by moult stage, i.e. recently moulted vs. intermoult, than by body size. Although the dietary compositions of *P. pelagicus* in the two estuaries were not significantly different, they did differ from those recorded from coastal marine waters in the same region, thereby reflecting differences in the potential prey in those two environments. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

The blue swimmer crab *Portunus pelagicus* Linnaeus is found in coastal marine and estuarine waters throughout the Indo-West Pacific (Stephenson, 1962). This species forms the basis of substantial recreational and/or commercial fisheries in certain embayments and estuaries, such as the Peel–Harvey and Leschenault estuaries in south-western Australia (Potter et al., 1983; Kailola et al., 1993; Potter and de Lestang, 2000). In south-western Australia, *P. pelagicus* spawns in mid spring and early summer and small crabs are recruited into the estuaries of that region in late summer and more particularly the following spring (Potter et al., 1983; Potter and de Lestang, 2000). *Portunus pelagicus* reaches maturity in the Peel–Harvey and Leschenault estuaries at the end of its first year of life, with the ovigerous females migrating into coastal marine waters where their eggs are then released. Some of these crabs subsequently return to the estuary. Although 1 + crabs are found in these estuaries in summer and autumn, they tend to leave the estuary during winter when freshwater discharge increases markedly and, as a consequence, salinity declines precipitously (Potter et al., 1983; Potter and de Lestang, 2000).

Previous studies have shown that, in marine waters, *P. pelagicus* consumes a wide range of benthic invertebrates and, to a lesser extent, teleosts and plant material (Patel et al., 1979; Williams, 1982; Wassenberg and Hill, 1987; Edgar, 1990a; Sukumaran and Neelakantan, 1997; Wu and Shin, 1998). Edgar (1990a) found that the compositions of the diets of small and large *P. pelagicus* in coastal marine environments differed, a feature he attributed to variations in the potential prey in the nearshore, shallow and offshore, deeper waters where small and large crabs, respectively, typically occur. On the basis of work carried out on *P. pelagicus* in a large coastal embayment, Williams (1982) concluded that the dietary compositions of this species did not change with increasing body size in either intertidal or subtidal waters. However, her analyses of the dietary compositions of different-sized crabs were based on pooled data for different shell states and thus did not take into account any differences in the type of material ingested by crabs at different stages in the moult cycle.

We have determined the dietary composition of the full size range of *P. pelagicus* in the confines of the shallow Peel–Harvey Estuary. The resultant data have been used first to examine whether, irrespective of their size, recently-moulted crabs ingest a large amount of calcium-rich material, which would thereby facilitate a rapid subsequent calcification of their new shell. The data were next used firstly to determine whether sequential size groups of intermoult (hard-shelled) *P. pelagicus* ingest far smaller amounts of calcium-rich material than recently-moulted crabs, and secondly to ascertain whether, with increasing body size, the diet of this portunid shifts progressively from small invertebrate prey to larger invertebrates and teleosts. Although the dominant species of benthic macroinvertebrate and fish in the shallow basins of the Peel–Harvey and Leschenault estuaries are essentially the same, several of the less abundant species
are restricted to one or the other of those two systems (cf. Loneragan et al., 1986; Rose, 1994; Potter et al., 1997; Dürr and Semeniuk, 2000; Semeniuk, 2000; Semeniuk and Wurm, 2000). We have thus compared the dietary compositions of *P. pelagicus* in these two estuaries to ascertain whether any of the latter differences in potential prey are reflected in a significant difference between the compositions of the food ingested by crabs in those two systems. Comparisons between the dietary compositions of crabs of different size and shell state and in the two estuaries were facilitated by the use of non-metric ordination, which is particularly well suited for analysing dietary data (Platell et al., 1998).

2. Materials and methods

2.1. Sampling regime in the Peel–Harvey and Leschenault estuaries

*Portunus pelagicus* was collected from numerous sites throughout the basins of the Peel–Harvey (32°40′S and 115°40′E) and Leschenault estuaries (33°12′S and 115°40′E). In both estuaries, the water depth is usually < 2.5 m and the substratum is relatively homogeneous, comprising mainly sand and silt, with aquatic macrophytes sometimes being present. Although most crabs were caught by seine netting, some were collected by otter trawling. The size compositions of crabs caught by these two methods were similar. The seine nets used in the Peel–Harvey and Leschenault estuaries, which were 10.5 and 21.5 m long, respectively, and consisted of 3 mm mesh in the bunt, fished upwards to a height of 1.5 m. The otter trawl net, which contained 25 mm mesh in the bunt, was towed by boat at a speed of ca. 3–4 km/h for ca. 250 m.

*Portunus pelagicus* were removed from samples collected in each of the two estuaries at four or six-weekly intervals between November and April of 1995/1996 and 1996/1997, during which months of the year this portunid is most abundant in these systems (Potter et al., 1983; Potter and de Lestang, 2000). Up to 20 crabs, that covered a wide size range, were collected for dietary analysis on each sampling occasion in each estuary. Every attempt was made to ensure that each shell state (for definitions, see below) was well represented in the total sample of crabs collected from the Peel–Harvey Estuary. Since the catches of particularly the small *P. pelagicus* were far lower in the Leschenault Estuary, the crabs used for examining the dietary compositions of this species in this estuary were restricted to the intermoult stage, which was the most abundant shell state. The crabs were frozen immediately after capture.

Prior to examining the contents of its stomach, each crab was sexed and its carapace width (CW) measured to the nearest 1 mm and a record kept of its shell state. The criteria of Warner (1977) and Williams (1982) were used to identify the following shell states: premoult (old shell splitting, brittle sutures), newly moulted (soft shell with minimal calcification), recently moulted (flexible shell with some calcification) and intermoult (hard shell with calcification essentially complete).

The foregut of each crab was removed and the fullness of its cardiac stomach (sensu Warner, 1977) recorded using a scale of 0 (empty) to 10 (fully distended with food). N.B. The contents of the cardiac stomach had not yet undergone extensive grinding by
the gastric mill and were thus usually readily identifiable. Food was never found in the stomachs of any newly-moulted crab. The stomach contents of crabs of each of the other three shell states in the Peel–Harvey Estuary and of intermoult crabs in the Leschenault Estuary were stored in 70% ethanol. They were subsequently examined under a binocular microscope and each dietary item identified to the lowest possible taxon. For dietary analyses, each of the various dietary items was allocated to one of a number of broader dietary categories. The number of times that each dietary category was found in the stomach contents of premoult, recently-moulted and intermoult crabs was used to calculate its percentage frequency of occurrence (%F) in the diets of crabs in each of those three shell states. The percentage volumetric contributions of each dietary category to the total volume of the diet (%V) of each crab in these shell states was expressed using the points method, which takes into account stomach fullness (Hynes, 1950; Hyslop, 1980). The volumetric data for dietary categories were calculated separately for sequential size classes, i.e. < 30, 30–59, 60–89 mm CW etc., of recently-moulted and intermoult crabs in the Peel–Harvey Estuary and of intermoult crabs in the Leschenault Estuary. N.B. Since premoult crabs had not apparently been recently feeding (see Results), they were not subjected to the same detailed dietary analyses. Sediment and unidentifiable material contributed 12.0 and 2.8%, respectively, to the volume of the stomachs of recently-moulted crabs in the Peel–Harvey Estuary and 12.1 and 4.6%, respectively, to those of intermoult crabs in the Peel–Harvey and Leschenault estuaries collectively. These two dietary categories were not included in the dietary analyses.

2.2. Data analyses

One-way analysis of variance (ANOVA) was used to test whether the stomach fullness of crabs in the Peel–Harvey Estuary varied significantly amongst shell states, i.e. premoult, recently moulted and intermoult. Because Cochran’s C test showed that these data were heteroscedastic, they were log transformed, which resulted in homoscedasticity and therefore satisfied the assumptions of ANOVA. In those cases where ANOVA detected significant differences, Scheffe’s a posteriori test was used to determine which means were significantly different at \( P < 0.05 \). Since the stomachs of all newly-moulted crabs were empty and thus yielded zero values for fullness, the crabs of this shell state were not included in the ANOVA.

The mean percentage volumetric contributions of each dietary category to the diets of recently-moulted and intermoult crabs of sequential size classes in the Peel–Harvey Estuary was root-transformed and a similarity matrix constructed using the Bray–Curtis similarity coefficient. A Bray–Curtis similarity matrix was also constructed in the same manner, using a combination of data for the diets of intermoult crabs of sequential size classes in both the Peel–Harvey and Leschenault estuaries. Classification, involving hierarchical agglomerative cluster analysis with group-average linking, and ordination, employing non-metric multi-dimensional scaling (MDS), were performed on each of the two similarity matrices using the PRIMER package (Clarke and Warwick, 1994). One-way analyses of similarities (ANOSIM) were carried out to determine whether the dietary compositions of recently-moulted and intermoult crabs in the Peel–Harvey Estuary and of intermoult crabs in the Leschenault Estuary changed significantly with
body size (Clarke, 1993). One-way ANOSIM and two-way crossed ANOSIM were used to compare the dietary data for the corresponding size classes of intermoult crabs in the Peel–Harvey and Leschenault estuaries, in order to determine whether the dietary compositions of intermoult crabs in these two estuaries were significantly different. N.B. Although Clarke and Warwick (1994) recommend using replicates for tests employing ANOSIM, the contents of each crab stomach (replicate) often comprise only three or four of the 14 dietary categories recorded overall in stomachs. Thus, to reduce the number of zero values and thereby construct a more appropriate similarity matrix for testing with ANOSIM, the dietary data for up to six groups of three randomly-selected stomachs in each size class of each shell state in each estuary were pooled. It should be noted that, when different trios of randomly-selected stomachs were subjected to ANOSIM, they always yielded the same results. In those cases where significant differences were detected with ANOSIM, similarity percentages (SIMPER) were employed to identify those dietary categories which made the greatest contribution to those differences (Clarke, 1993). Multivariate dispersion (MVDISP) was used to determine the degree of dispersion of the dietary samples of crabs representing different size classes and shell states and occupying different estuaries (Somerfield and Clarke, 1997).

3. Results

3.1. Stomach fullness and overall dietary compositions in the Peel–Harvey Estuary

Since ANOVA showed that the values for the stomach fullness of females and males in neither the premoult, nor recently moulted, nor intermoult shell states differed significantly, the data on fullness for the two sexes in each of these shell states have been pooled. Food was found in the stomachs of 396 of the 455 Portunus pelagicus collected from the Peel–Harvey Estuary and, in the case of stomachs that contained food, the mean fullness ±1 S.E. was 4.7±0.1. However, ANOVA demonstrated that stomach fullness varied significantly among shell states (F = 4.11, P < 0.05). Scheffé’s a posteriori test showed that the stomach fullness of recently-moulted crabs (x = 5.9±0.3) was significantly greater than that of intermoult crabs (x = 4.5±0.1), which in turn was significantly greater than that of premoult crabs (x = 2.0±0.5).

ANOSIM demonstrated that the dietary compositions of neither recently-moulted nor intermoult crabs in the Peel–Harvey Estuary, nor of intermoult crabs in the Leschenault Estuary, differed significantly (P > 0.05) between the two sexes. For this reason, the dietary data for the females and males of each size class of both recently-moulted crabs and intermoult crabs in the Peel–Harvey Estuary and of intermoult crabs in the Leschenault Estuary were pooled.

Calcareous material was found in the stomachs of over 50% of premoult and over 70% of recently-moulted crabs in the Peel–Harvey Estuary and contributed over 50% to the volume of the diets of the crabs representing those two shell states (Table 1). This material, which comprised fragments of the shells of bivalve and gastropod molluscs, was more weathered and broken up in the stomach contents of recently-moulted than
Table 1

<table>
<thead>
<tr>
<th>Dietary categories</th>
<th>Peel–Harvey Estuary</th>
<th>Leschenault Estuary</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Premoult</td>
<td>Recently moulted</td>
</tr>
<tr>
<td>Number of stomachs</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small bivalves</td>
<td>13.3</td>
<td>58.5</td>
</tr>
<tr>
<td>Large bivalves</td>
<td></td>
<td>1.5</td>
</tr>
<tr>
<td>Small gastropods</td>
<td></td>
<td>15.4</td>
</tr>
<tr>
<td>Cephalopods</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gammarid amphipods</td>
<td></td>
<td>10.8</td>
</tr>
<tr>
<td>Small decapods</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Decapod shell fragments</td>
<td>21.5</td>
<td>9.4</td>
</tr>
<tr>
<td>Tanaids</td>
<td>26.7</td>
<td>21.5</td>
</tr>
<tr>
<td>Polychaetes</td>
<td>26.7</td>
<td>21.5</td>
</tr>
<tr>
<td>Echinoderms</td>
<td></td>
<td>1.5</td>
</tr>
<tr>
<td>Teleosts</td>
<td>6.7</td>
<td>1.5</td>
</tr>
<tr>
<td>Calcereous material</td>
<td>53.3</td>
<td>73.8</td>
</tr>
<tr>
<td>Plant material</td>
<td>6.7</td>
<td>26.2</td>
</tr>
</tbody>
</table>

premoult crabs. Polychaetes, especially the nereid Ceratoneiris aequisetis (Augener), and small bivalve molluscs, particularly the galeommatid Arthritica semen (Menke), were often consumed by crabs of these two shell states. However, the frequency with which polychaetes occurred in stomachs and their volumetric contributions were greater in premoult than recently-moulted crabs, while the reverse was true for small bivalves. Shell fragments of large decapods, especially Portunus pelagicus and Ovalipes australiensis (Stephenson and Rees), gammarid amphipods and small gastropods, mainly Tatea spp., which were each consumed by more than 10% of recently-moulted crabs and contributed 9.4, 3.4 and 2.6% to the dietary volume of these crabs, respectively, were never found in the stomachs of premoult crabs (Table 1).

Small bivalves, represented almost exclusively by A. semen, and polychaetes, especially C. aequisetis, were the dietary categories most frequently consumed by far by intermoult P. pelagicus in the Peel–Harvey Estuary, each being found in ca. 47% of stomachs and contributing 20.9 and 25.1% to the total dietary volume, respectively (Table 1). Gammarid amphipods were consumed by nearly one third of intermoult crabs and comprised nearly 20% of their dietary volume. No other category contributed more than 7% to the total dietary volume (Table 1).

3.2. Ontogenetic changes in diet in the Peel–Harvey Estuary

In recently-moulted crabs in the Peel–Harvey Estuary, calcereous material contributed between 47 and 55% to the total dietary volume of each of the four size classes in which the carapace widths lay between 30 and 159 mm (Fig. 1). Although crabs <90 mm CW
Fig. 1. Percentage volumetric composition of different dietary categories in sequential 30 mm carapace width classes of recently-moulted and intermoult *Portunus pelagicus* in the Peel–Harvey Estuary and of intermoult *P. pelagicus* in the Leschenault Estuary. Numbers above columns denote the number of crabs that contained identifiable dietary categories in their stomachs.
also consumed considerable amounts of small bivalves, i.e. ca. 30%, this category made only a small contribution to the diets of crabs >120 mm CW. In contrast, the contributions made by both polychaetes and the shell fragments of large decapods increased progressively as crabs of this shell state increased in size (Fig. 1).

The diets of small intermoult crabs in the Peel–Harvey Estuary, i.e. <30 mm, contained large amounts of crustaceans, such as amphipods and tanaids, particularly *Tanais dulongii* Thomson, and also small bivalve molluscs, which collectively contributed just over 90% to the total volume of the diet (Fig. 1). As *P. pelagicus* increased in size, the contribution of amphipods and, to a lesser extent, that of tanaids, declined progressively, while particularly those of polychaetes and teleosts (*Favonigobius lateralis* (Macleay)) and also small decapods (*Penaeus latisulcatus* Kishinouye) and calcareous and plant material increased.

Classification, using dietary data for the different size classes of recently-moulted and intermoult crabs in the Peel–Harvey Estuary, separated the dietary samples into two large groups, i.e. A and B (Fig. 2a). Group A contained all of the samples from recently-moulted crabs, while group B comprised all of those from intermoult crabs. Within groups A and B, the dietary samples from the two smallest size classes, i.e. groups D and F, respectively, were separated from those of the larger size classes of that shell state, i.e. groups C and E, respectively (Fig. 2a).

The results of ordination paralleled those of classification, with all of the points corresponding to the samples of recently-moulted crabs forming a discrete group, lying on the left of the plot and well separated from the discrete group of intermoult crabs, which lay on the right side of the plot (Fig. 2a and b). The samples for intermoult crabs followed a downwards progression on the plot according to the size of the crabs, with those representing the smaller crabs at the top and those of the largest crabs at the bottom (Fig. 2b). ANOSIM showed that the dietary compositions of intermoult crabs differed significantly with body size (*P* <0.001). SIMPER showed that the dietary differences in intermoult crabs were mainly attributable to the consumption of greater volumes of amphipods and tanaids by small crabs and of far larger amounts of polychaetes and teleosts by larger crabs. Although the trend exhibited on the ordination plot by the samples for recently-moulted crabs was less pronounced than with intermoult crabs, the samples for the two largest size classes of recently-moulted crabs still likewise lay below those for the two smallest size categories (Fig. 2b). However, ANOSIM failed to detect a significant difference in the dietary compositions of the different size classes of recently-moulted crabs, which is presumably due to the similar and consistently high contributions made by calcareous material to the diets of each size class. The latter view is consistent with the fact that, when this dietary category was excluded from the ANOSIM test, the dietary compositions of the different size classes became significantly different (*P* <0.01). The more pronounced variation in the dietary compositions of the different size groups of intermoult crabs than recently-moulted crabs is reflected in the greater multivariate dispersion values, i.e. 1.02 vs. 0.55.

### 3.3. Comparisons between diets in the Peel–Harvey and Leschenault estuaries

The three dietary categories most frequently preyed upon by intermoult *P. pelagicus*
in the Peel–Harvey Estuary, i.e. small bivalves, gammarid amphipods and polychaetes, were also those that were most frequently ingested by intermoult crabs in the Leschenault Estuary (Table 1). Furthermore, gammarid amphipods and polychaetes both contributed between ca. 20 and 33% to the dietary volume of intermoult crabs in both
estuaries. The volume of calcareous material made greater contributions to the diets of intermoult crabs in the Leschenault than Peel–Harvey estuaries, i.e. 9.9 vs. 3.1%. Each of the other nine dietary categories ingested by intermoult crabs in the Peel–Harvey Estuary were also consumed by intermoult crabs in the Leschenault Estuary (Table 1).

The diet of intermoult *Portunus pelagicus* underwent the same types of ontogenetic changes in the Leschenault Estuary as in the Peel–Harvey Estuary (Fig. 1). Thus, for example, the contributions made by polychaetes increased markedly with body size, whereas the reverse occurred with amphipods. However, calcareous material tended to be consumed in slightly greater volumes by the larger size classes of crabs in the Leschenault than Peel–Harvey estuaries, whereas the reverse applied to small decapods (Fig. 1).

Classification, using dietary data for the different size classes of intermoult crabs in the Peel–Harvey and Leschenault estuaries, separated the samples of the smallest size class of crabs in the Leschenault Estuary from those of all other dietary samples (Fig. 3a). Within the latter large group, i.e. A, the samples were separated into two main groups (B and C), with the former containing only samples from large crabs (CW ≥ 90 mm). In group C, which contained all but one of the samples of the smaller crabs (CW < 90 mm), the samples were separated according to the body size of the crab rather than the estuary in which the crab had been caught (Fig. 3a).

Ordination of the mean percentage volumetric contributions of the dietary categories for the five successive size classes of intermoult crabs in each of the two estuaries resulted in the points for samples representing the smallest size classes from each estuary lying towards the top of the plot (Fig. 3b). In contrast, those for the next two size classes, i.e. 30–59 and 60–89 mm CW, lay in the middle of the plot and those of the two larger size classes lay towards the bottom. There was no consistent trend for the samples of corresponding size classes from one estuary to lie either above or below or to the left or right of those from the other estuary (Fig. 3b). The dispersion values recorded for the dietary samples of crabs from the Peel–Harvey and Leschenault estuaries were very similar, i.e. 1.02 vs. 1.00. ANOSIM showed that, as with crabs from the Peel–Harvey Estuary, there was a significant size-related difference in intermoult crabs in the Leschenault Estuary \( (P < 0.05) \). SIMPER likewise demonstrated that the size-related differences in dietary compositions in the Leschenault Estuary were attributable to differences in the greater contributions made by amphipods and tanaids to the diets of smaller crabs and by polychaetes and teleosts to those of larger crabs. A two-way crossed ANOSIM, which took the size of crabs into account, showed that the dietary compositions of intermoult crabs in the two estuaries were not significantly different \( (P > 0.05) \) and a series of one-way ANOSIMs showed that the dietary compositions of each size class in the Peel–Harvey Estuary did not differ significantly from that of its corresponding size class in the Leschenault Estuary \( (P > 0.05) \).

4. Discussion

The intensive sampling carried out in the Peel–Harvey Estuary during the present study enabled *Portunus pelagicus* to be caught with carapace widths ranging from as low as 12 mm to as high as 159 mm. Furthermore, the crabs ranged in age from
approximately 2 months old to nearly one and a half years old and thus from little more than megalopas to those which greatly exceeded the size at which 50% of the population reach sexual maturity in south-western Australia, i.e. ca. 95 mm for females and 85 mm for males (Potter and de Lestang, 2000). Moreover, substantial numbers of premoult,
newly-moulted, recently-moulted and intermoult crabs were represented in these samples. It is also important to recognise that, because the assemblage of crabs being investigated was restricted to waters within the shallow basins of an estuary, all size classes were found in the same general region and were thus presented with the same potential prey. The above features therefore provided an ideal set of circumstances for examining whether, given the same opportunities, *P. pelagicus* does change its diet as it increases in size and, if so, whether any such changes occur with both recently-moulted and intermoult crabs. Thus, in these respects, our dietary study has the advantage over those of Edgar (1990a) and Williams (1982), which were carried out in marine waters where the small crabs occur in nearshore, shallow waters and are thus some distance from the large crabs which are found in offshore, deeper waters where the composition of the potential prey is different. Furthermore, we had the opportunity of employing contemporary multivariate and statistical methods for analysing whether the dietary compositions of different groups were significantly different and, if so, thereby determining statistically which taxa were contributing most to these differences.

4.1. Data used for determining dietary compositions of Portunus pelagicus

Williams (1981) claimed that the points method was not suitable for determining the volumetric contributions made by the different components of the diets of portunid crabs. She based this conclusion on the fact that the diet of portunids contains some soft-bodied organisms, such as polychaetes, which become so thoroughly masticated in the gastric mill that only a small part of their body remains recognisable. This would presumably account for the very high prevalence of unidentified organic material in the stomachs of the crabs she examined. However, such unidentifiable material contributed less than 5% to the total volume of the stomach contents of all intermoult crabs in the Peel–Harvey and Leschenault estuaries. Indeed, large volumes of the polychaete *Ceratonereis aequisetis*, which was the main soft-bodied organism ingested by *P. pelagicus* in the Peel–Harvey and Leschenault estuaries, were easily distinguishable in the stomachs of this portunid in these two estuaries. The very low volumetric contribution made by unidentifiable material to the dietary compositions during our study can be attributed to the use of samples that were obtained from the cardiac stomach and which, as a consequence, had not yet thus been subjected to extreme mastication in the gastric mill. For the above reasons, we feel fully justified in using the points method to estimate the volumetric contributions of the individual components of the diet in our study. While other workers, such as Wu and Shin (1998), have followed Williams in restricting their analyses to percentage frequency of occurrence of dietary categories in their studies on portunids, the use of volumetric data for determining dietary compositions was adopted by Edgar (1990a) and Sukumaran and Neelakantan (1997) for *P. pelagicus* and by other workers for other portunid species (Choy, 1986; Wear and Hadden, 1987; Norman and Jones, 1992; Friere and González-Gurriarán, 1995; Cannicci et al., 1996; Friere, 1996).

The ranking of each dietary category, in terms of relative importance, was found by Williams (1981) to be the same, irrespective of whether she used the points method to estimate its volume or the frequency with which it occurred in the stomachs. Although
our data followed similar trends, the ratios of the percentage volumetric data to the percentage frequency data for the different dietary categories varied. For example, in intermoult crabs from the Peel–Harvey Estuary, this ratio ranged from as low as 1:1.3 for small decapods to as high as 1:12.6 for echinoderms. Thus, the frequency of occurrence of a dietary category cannot be used as a direct substitute for its volumetric contribution (see also Choy, 1986). The two types of measurement supply complementary rather than the same data (see also Cortés, 1997; Marshall and Elliott, 1997) and should thus ideally be used in conjunction to interpret dietary data.

4.2. Food and feeding of different moult stages of Portunus pelagicus

Although the stomachs of premoult crabs in the Peel–Harvey Estuary sometimes contained material, this never constituted a large volume and was restricted to the relatively indigestible remains of prey, such as the jaws of nereid polychaetes and the remains of bivalves. Furthermore, irrespective of their size, newly-moulted crabs in the Peel–Harvey Estuary did not ingest food. These results are consistent with the conclusions drawn by Williams (1982) that *P. pelagicus* does not feed immediately prior to or just after mouling.

The importance of calcareous material to the diets of recently-moulted crabs is emphasised by the fact that it was found in nearly 75% of stomachs and contributed ca. 50% to the volume of the stomach contents of each size class of such crabs in the Peel–Harvey Estuary. The high contribution made by this material to the diet of crabs of this shell state parallels the situation recorded by Williams (1982) for *P. pelagicus* in a marine embayment and for other portunids, such as *Liocarcinus holsatus*, *Necora puber*, *Scylla serrata* and *Thalamita crenata*, which were likewise located in marine environments (Hill, 1976; Choy, 1986; Norman and Jones, 1992; Cannicci et al., 1996). Williams (1982) pointed out that crabs would not have the mechanical strength to break up living or fresh shell at this stage. However, the calcareous material ingested by the representatives of this shell state was more highly weathered and fragmented than that of intermoult *P. pelagicus*, which implies that this material was already represented by fragments at the time of its ingestion. Focussing on the ingestion of calcareous material at this stage would be highly advantageous as it would provide the crab with the substantial amounts of calcium that are required to calcify the new cuticle (Warner, 1977; Stevenson, 1985).

The diet of intermoult crabs in the Peel–Harvey Estuary, which was more diverse than that of recently-moulted crabs in that estuary, was dominated, both in terms of frequency of occurrence and volumetric contributions, by amphipod crustaceans, polychaetes and small bivalves. The wider diversity of prey ingested by intermoult than recently-moulted crabs is presumably related to the fact that, since their mouthparts and chelipeds are fully calcified, their prey-handling ability is greatly enhanced, and they are also not constrained by a requirement to ingest large amounts of calcium-rich material.

The food ingested by recently-moulted crabs comprises large amounts of substrate and includes prey such as the small bivalve *Arthritica semen* and the polychaete *C. aequisetis*, which live either on the substrate surface or protrude from their burrows above that surface. Intermoult crabs also consume the two latter prey species and other
prey, such as the amphipods *Corophium* spp. and *Grandidierella* spp., and the small
teleost *Favonigobius lateralis*, which likewise live on or just below the substrate surface.
The above implications that *P. pelagicus* obtains most of its food from on or directly
below the substrate surface is consistent with the observations of the senior author that,
while feeding, *P. pelagicus* sometimes uses its chelipeds and first pair of walking legs to
scoop up sediment and prey towards its mouth.

4.3. **Ontogenetic changes in the diets of recently-moulted and intermoult crabs**

The contributions made by individual dietary categories to the diets of sequential size
classes of intermoult crabs in the Peel–Harvey and Leschenault estuaries and the
progressive trends exhibited by the points for the dietary samples for each of these size
classes on the ordination plot both clearly demonstrate that the composition of the diet of
crabs at this moult stage undergoes conspicuous ontogenetic changes. Thus, the
contributions made by small benthic and epibenthic crustaceans, such as amphipods and
tanaids, declined with increasing body size, while the reverse trend occurred with larger
prey, such as nereid polychaetes, small decapods and teleosts. Although Edgar (1990a)
also found that the contribution made particularly by polychaetes rose as *P. pelagicus*
increased in size in a marine coastal environment, he attributed this to the fact that small
and large crabs were feeding in locations that differed in potential prey. However, since
the full size range of crabs were collected from the same general location in both the
Peel–Harvey and Leschenault estuaries and they would thus have had access to the same
potential prey, such dietary changes in these two estuaries represent true ontogenetic
changes.

The ingestion of small amphipods and tanaids by the small representatives of *P.
pelagicus* may be facilitated by the close interlocking of the fine teeth on their chelae.
The marked ontogenetic changes in the diets of intermoult *P. pelagicus*, with the volume
of polychaetes, teleosts and decapods increasing with body size, implies that larger crabs
are more efficient in capturing larger and more mobile prey. Although the above
ontogenetic changes can be attributed in part to an increase in the size and strength of
the mandibles and chelipeds, it is relevant that, in another species of portunid
(*Liocarcinus depurator*) in which the larger members likewise ingest fish, the rapidity
with which the chelipeds can be used to capture prey has been shown to increase with
body size (Friere, 1996; Friere et al., 1996).

Although the extent of ontogenetic changes in the diet of recently-moulted crabs was
not as great as that in intermoult crabs, due to the similar and very high contribution
made by calcareous material to the diets of all size classes, the dietary composition did
still change with body size. Thus, the contribution of small bivalves to the diet of
recently-moulted crabs declined with increasing body size, whereas the reverse trend
occurred with the shell fragments of large decapods and, to a lesser extent, polychaetes.
In comparison with the situation with intermoult crabs, the large representatives of
recently-moulted crabs consumed either far less or none of the larger and more mobile
prey, i.e. errant polychaetes and teleosts. This can be attributed to a combination of the
reduced muscle mass in their chelipeds and the greater vulnerability of the developing
shell of these structures to damage (Skinner, 1985).
4.4. Comparisons of diets in the Peel–Harvey and Leschenault estuaries and in coastal marine waters

The similarities in the dietary compositions of intermoult *P. pelagicus* in the Peel–Harvey and Leschenault estuaries presumably reflect the fact that the main dietary categories of this portunid in these two estuaries, i.e. *A. semen*, *C. aequisetis* and different species of amphipods, are abundant in both systems (Rose, 1994; Dürr and Semeniuk, 2000; Semeniuk, 2000; Semeniuk and Wurm, 2000). Although the *P. pelagicus* found in coastal marine waters along the lower west coast of Australia also ingest substantial volumes of polychaetes, they consume far greater volumes of the gastropod *Cantharidus lepidus* and far lower volumes of crustaceans than was the case in either the Peel–Harvey or Leschenault estuaries (cf. Edgar, 1990a and Fig. 1). The pronounced differences between the diet in that coastal region and the two estuaries can be related to differences in the potential prey in those environments (cf. Wells and Bryce, 1984; Edgar, 1990b; Rose, 1994; Dürr and Semeniuk, 2000; Semeniuk, 2000; Semeniuk and Wurm, 2000). For example, gastropods are relatively far more abundant in coastal marine waters and *A. semen* is confined to estuaries. Moreover, in marine environments elsewhere in the world, ophiuroids and anomuran crabs make substantial contributions to the diet (Williams, 1982; Wassenberg and Hill, 1987; Wu and Shin, 1998). However, these prey were ingested in only very small amounts by *P. pelagicus* in the Peel–Harvey and Leschenault estuaries and were likewise either not recorded or recorded in only very low abundances in the Peel–Harvey and Leschenault estuaries (Rose, 1994; Dürr and Semeniuk, 2000; Semeniuk, 2000; Semeniuk and Wurm, 2000). The ability of *P. pelagicus* to feed opportunistically on the most abundant benthic macroinvertebrates in their habitat helps account for the success of this species in different environments.

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References


