

Changes in hermit crab feeding patterns in response to trawling disturbance

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ABSTRACT: Bottom trawling leads to the death, injury or exposure of benthic fauna, thus creating a potential source of food for predators and scavengers. We examined the behaviour of 2 sympatric species of hermit crab, *Pagurus bernhardus* and *P. prideaux*, in response to beam trawl disturbance. Catch numbers, body size and stomach contents of the 2 species were analysed from a treatment wayline before and after it was fished with a 4 m commercial beam trawl and from 2 adjacent unfished control waylines. Catch numbers of *P. bernhardus* were significantly higher on the treatment wayline 2 and 3 d after fishing, whilst on the fourth day they were no longer significantly different. Numbers of *P. prideaux* did not vary significantly between control or treatment waylines or with time. After fishing, the size distribution of *P. bernhardus* on the treatment wayline became skewed towards larger size-classes of crabs. For 3 d after fishing, *P. bernhardus* collected from the treatment wayline had significantly higher stomach content weights per unit body mass than those from the control area. No such difference occurred for *P. prideaux*. The diets of the 2 species were similar, including crustaceans, polychaetes and molluscs, although the ranked importance of each type of prey differed between the 2 hermit crab species. There was an increase in the proportion of crustaceans and polychaetes found in the stomachs of *P. bernhardus* from the treatment wayline 1 d after fishing. These results suggest that *P. bernhardus* migrate into recently trawled areas because they are able to benefit from feeding on the damaged or disturbed fauna generated by beam trawling. *P. prideaux* apparently neither move into the trawled area nor respond to the additional food source if already there, even though they have similar dietary characteristics to *P. bernhardus*.

KEY WORDS: Hermit crabs · Feeding · Beam trawling · Fishing impact

INTRODUCTION

Demersal fishing methods, particularly beam trawling, have been shown to result in the mortality of some non-target benthic species (van Beek et al. 1990, Bergman & Santbrink 1994, Fonds 1994, Santbrink & Bergman 1994, Kaiser & Spencer 1995). A proportion of the non-commercial and undersized animals from the catch die, despite being returned to the sea (Kaiser & Spencer 1995) and many animals are also damaged by the trawl but remain on the seabed (Bergman & Santbrink 1994). This latter type of mortality has been

described as 'non-catch mortality' (Bergman & Santbrink 1994, Santbrink & Bergman 1994). The tickler chains of a beam trawl are designed to penetrate the surface of the sediment, thereby increasing the catch of the target species, sole *Solea solea* and plaice *Pleuronectes platessa*, but also disturbing and damaging infaunal animals, such as the burrowing heart urchin *Echinocardium cordatum* (Bergman & Hup 1992) and the tube dwelling amphipod *Ampelisca spinipes* (Kaiser & Spencer 1994). Other animals may be crushed by the beam shoes, chain mat or cod-end as the trawl passes over them. Small animals may enter the net and escape through the mesh but still be damaged during this process (Craeymeersch 1994, Fonds 1994, Kaiser & Spencer 1995).

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Various studies have investigated the consumption of fisheries discards by predatory or scavenging birds, fishes and crustacea (Wassenberg & Hill 1987, 1990, Furness et al. 1988, Hudson & Furness 1988, Blaber & Wassenberg 1989, Berghahn 1990) but fewer have examined the consumption of damaged fauna in the tracks of a trawl. Kaiser & Spencer (1994) found that the composition of the diets of gurnards and whiting altered in a fished area and suggested that these fish were feeding on fauna damaged by the trawl. More recent studies (Kaiser & Spencer 1996a, K. Ramsay unpubl. data), have found that other scavengers such as starfish *Asterias rubens* and hermit crabs *Pagurus* spp. are attracted to areas disturbed by trawling.

Pagurus bernhardus (L.) is widely distributed in European waters and occurs from the littoral zone to depths of 100 m (Pike & Williamson 1959). *P. bernhardus* apparently exhibits a variety of feeding methods including scavenging (Jackson 1913, Nickell & Moore 1992, Kaiser & Spencer 1996a), deposit feeding (Orton 1927) and filter feeding (Gerlach et al. 1976, Erri Babu 1988). Less is known about the biology of *Pagurus prideaux* Leach which is sympatric with *P. bernhardus* at the study site described in this paper. The most striking external difference between these species is that *P. bernhardus* occupies empty gastropod shells, whereas the abdomen of *P. prideaux* is usually cloaked by the anemone *Adamsia carciniopados* (Pike & Williamson 1959).

The present study investigated whether (1) these 2 hermit crab species migrate into trawled areas, (2) crabs in trawled areas consume more food than those in surrounding untrawled areas and (3) their diets change as a result of trawling.

METHODS

The experimental site used in this study was located ca 9 miles off the northeast coast of Anglesey, Irish Sea (Kaiser & Spencer 1996b) and has a water depth of ca 40 m. This site is rarely visited by commercial fishing vessels and no fishing other than our experimental fishing took place during the course of this study. In April 1995 a 2.8 m beam trawl designed to maximise epibenthic catch (Kaiser et al. 1994) was used to sample an epibenthic community at time intervals before and after fishing a 1.5 km wayline with a commercial 4 m beam trawl. The 2.8 m beam trawl had a square mesh cod-end with a knot to knot distance of 4 cm. Catch numbers of epibenthic species were recorded and 2 hermit crab species, *Pagurus bernhardus* and *P. prideaux*, were collected and stored frozen for later analysis in the laboratory.

To create a trawling disturbance, the treatment wayline was fished 10 times using a 4 m commercial beam trawl fitted with a chain matrix, flip-up ropes and an 80 mm diamond mesh cod-end. A Differential Global Positioning System (DGPS), which gives a position accurate to within 5 m, used in conjunction with a navigational package, Sextant[®], on board the ship ensured accurate trawling. Previous experience had shown that towing the 4 m beam trawl 10 times would ensure that on average a corridor with a width of 30 to 40 m was completely fished once (Kaiser & Spencer 1996b).

The experimental design was such that a treatment (fished) wayline and 2 control waylines were sampled, once before fishing the treatment wayline with the 4 m beam trawl, and then for 4 d after fishing at approximately 24 h intervals. The control waylines ran parallel to the treatment wayline at a distance of 250 m on either side. Six replicate tows were made with the 2.8 m beam trawl, each with a duration of 3.5 min, on each wayline on each sampling occasion (18 tows per day). The exception to this was the final day (28 April 1995) when, due to time constraints, only 1 control wayline and the treatment wayline were fished, each 5 times. To minimise temporal differences in sampling between waylines the following pattern of sampling was adopted: 2 tows were carried out on 1 wayline, then on a second wayline (the first 2 waylines to be sampled were chosen at random), and then on the remaining wayline. This pattern was repeated twice until 6 tows had been completed on each wayline. No attempt was made to sample at identical positions on consecutive days and therefore the sampling can be considered to have been at random points along each wayline. The times of each period of fishing are shown in Table 1. Catches from both the 2.8 m beam trawl and the 4 m beam trawl were discarded at a distance of ca 4 km away from the experimental area to avoid the possible confounding effects of discarded carrion landing on the seabed.

The start and finish position of each tow were recorded from the DGPS at the moment the trawl reached the seabed and the moment the winch began to retrieve the net. Distance towed over the seabed was then calculated and catch numbers standardised to numbers per 1000 m². Differences between mean catch numbers were analysed using analysis of variance on log(x+1)-transformed data. A few tows have been omitted from the analysis where problems with the DGPS meant that it was not possible to ascertain tow length.

Hermit crabs were collected from each 2.8 m beam trawl catch and stored frozen. In the laboratory, crabs were defrosted and, for each individual, thorax length was measured to ± 1 mm, sex was noted and

Table 1 Times and duration of sampling periods with the 2.8 m beam trawl and fishing with the 4 m beam trawl

Date (1995)	Fishing/sampling gear used	Waylines sampled	Time period (h GMT)
24 Apr	2.8 m beam trawl	1 treatment, 2 control	08:19–13:23
24 Apr	4 m beam trawl		22:01–03:57
25 Apr	2.8 m beam trawl	1 treatment, 2 control	05:23–10:38
26 Apr	2.8 m beam trawl	1 treatment, 2 control	05:12–11:04
27 Apr	2.8 m beam trawl	1 treatment, 2 control	05:02–13:07
28 Apr	2.8 m beam trawl	1 treatment, 1 control	05:03–08:03
27 Oct	2.8 m beam trawl	1 treatment, 1 control	11:41–18:49
27 Oct	4 m beam trawl		19:54–01:40
28 Oct	2.8 m beam trawl	1 treatment, 1 control	07:07–10:57
29 Oct	2.8 m beam trawl	1 treatment, 1 control	08:49–11:50
30 Oct	2.8 m beam trawl	1 treatment, 1 control	08:47–13:16

the stomach was dissected out. For crabs with undamaged legs and chelae, the height of the right cheliped was determined and the wet body weight (without the shell) was also recorded. The stomach contents were preserved in 70% alcohol and later examined under a low-power dissecting microscope. The points method (Hynes 1950, Williams 1981) was used to estimate volumetric abundance of different phyla in the stomach contents. Thus each phylum was given 1, 2, 4, 8, 16 or 32 points based on its estimated relative volume in the gut. Unidentifiable components of the stomach contents were grouped separately. Percentage points for each phylum were then calculated (see Freire et al. 1991):

$$\% \text{ points}_j = \frac{\sum_{i=1}^n a_{ji}}{\sum_{i=1}^n a_i} \times 100$$

where a_{ji} is the number of points assigned to phylum j in stomach i , n is the number of hermit crabs in a group and a_i is the total number of points for stomach i . Percentage points were calculated for each hermit crab species for the control samples and the treatment samples for each day. The stomach contents of 20 randomly chosen crabs were analysed per treatment (fished or unfished control) on each day. Data from these 20 crabs were pooled prior to further analyses. Cluster analysis and multidimensional scaling (MDS) were then carried out on $\ln(x+1)$ -transformed data using data for all phyla (including unidentified material). Similarity between samples was determined using the Bray-Curtis index of similarity and the group average linkage method. An *a priori* analysis of similarities test (ANOSIM) was performed to investigate whether the diets of the 2 species differed significantly. The PRIMER statistical software package was used for this analysis (Clarke & Warwick 1994). To give an indica-

tion of diversity of the diets, mean number of phyla per stomach and the Shannon diversity index were calculated for each hermit crab species.

To determine their dry weight, stomach contents were filtered (using numbered pre-dried and weighed filter papers), placed in a drying oven at 60°C for 24 h and weighed to an accuracy of 0.01 mg. Differences in the relationship between crab size (thorax length) and dry weight of stomach contents were examined using analysis of covariance (ANCOVA) on \ln -transformed data, treating crab size as a covariate and fishing disturbance (unfished control or fished treatment) as a factor.

In October 1995 the sampling protocol was repeated at the same site. The beam trawl used for sampling was of a similar design to the one used in April but was not identical. On this occasion crabs were not preserved for stomach contents analysis and only 1 control wayline was sampled. The primary objective was to obtain a size-frequency distribution, based on the chelal height of the right cheliped, for crabs from the control and treatment wayline before and after fishing for both *Pagurus bernhardus* and *P. prideaux*. Cheliped height was used as it is quick to measure; removing crabs from their shells in order to measure thorax length would be costly in terms of time and often be fatal for the animal. Measurements made during the stomach content sampling showed strong correlation between cheliped height, crab weight and thorax length (regression equations generally had an adjusted R^2 value of around 0.90). When catch numbers became very large, random subsampling was carried out, such that when over 150 individuals had been measured subsequent catches were not sampled. Differences in size-frequency distributions between the control and treatment waylines for each day were tested using the Kolmogorov-Smirnov test.

RESULTS

Catch numbers of hermit crabs

April 1995. For *Pagurus bernhardus* catch numbers were significantly higher on the commercially trawled wayline 2 and 3 d after fishing (Table 2). On the fourth day after fishing, the difference between the fished wayline and the unfished control area was no longer significant, although numbers were still higher on the fished wayline (Table 2). The mean number of crabs on the control wayline was very similar throughout the

Table 2. *Pagurus bernhardus*, *P. prideaux*. April 1995. Densities of crabs on the control and treatment lines at time periods before and after fishing the treatment wayline with a 4 m beam trawl, including 95% confidence limits (assuming a Poisson distribution). Results of ANOVA between catch densities (log transformed) on the control and treatment waylines [ns: not significant ($p > 0.05$)]

Days before/ after fishing	Average number caught per 1000 m ²		ANOVA		
	Control	Treatment	F	df	p
<i>Pagurus bernhardus</i>					
Before	9.7 ± 1.8	4.5 ± 1.9	0.33	14	ns
1 d after	5.0 ± 1.3	12.8 ± 2.9	2.04	16	ns
2 d after	7.1 ± 1.5	81.8 ± 7.9	24.59	15	<0.001
3 d after	7.6 ± 1.4	60.5 ± 6.2	20.98	18	<0.001
4 d after	6.0 ± 2.1	40.6 ± 5.6	3.16	8	ns
<i>Pagurus prideaux</i>					
Before	7.3 ± 1.6	6.4 ± 2.2	0.00	14	ns
1 d after	4.9 ± 1.3	6.3 ± 2.0	1.29	16	ns
2 d after	9.2 ± 1.7	13.7 ± 3.2	2.66	15	ns
3 d after	8.5 ± 1.5	6.3 ± 2.0	0.03	18	ns
4 d after	8.6 ± 2.6	4.8 ± 1.9	3.24	8	ns

Table 3. *Pagurus bernhardus*, *P. prideaux*. October 1995. Densities of crabs on the control and treatment lines at time periods before and after fishing the treatment wayline with a 4 m beam trawl, including 95% confidence limits (assuming a Poisson distribution). Results of ANOVA between catch densities (log transformed) on the control and treatment waylines [ns: not significant ($p > 0.05$)]

Days before/ after fishing	Average number caught per 1000 m ²		ANOVA		
	Control	Treatment	F	df	p
<i>Pagurus bernhardus</i>					
Before	23.3 ± 3.0	36.1 ± 5.3	1.54	13	ns
1 d after	48.4 ± 5.6	73.6 ± 7.5	2.12	9	ns
2 d after	38.8 ± 5.0	151.0 ± 9.8	15.11	10	<0.01
3 d after	44.4 ± 5.3	72.6 ± 6.8	0.34	10	ns
<i>Pagurus prideaux</i>					
Before	20.0 ± 2.8	40.5 ± 5.6	2.32	13	ns
1 d after	47.9 ± 5.5	44.7 ± 5.9	0.13	9	ns
2 d after	56.4 ± 6.0	37.9 ± 4.9	0.83	10	ns
3 d after	54.0 ± 5.9	21.1 ± 3.7	10.99	10	<0.01

experiment (range 5.0 ± 1.3 to 9.7 ± 1.8) For *P. prideaux* there were no significant differences between numbers on the control and treatment waylines.

October 1995. For *Pagurus bernhardus* catch numbers were significantly higher on the commercially trawled wayline 2 d after fishing (Table 3). For *P. prideaux* numbers were significantly higher on the control wayline on the third day after fishing (Table 3). Catch numbers of both species were higher in October than in April; this was probably a seasonal effect.

Size-frequency distributions

Before fishing the size-frequency distribution of *Pagurus bernhardus* on the treatment wayline was not significantly different from that on the control wayline (Fig. 1). However, after trawling with the commercial gear the size distribution of *P. bernhardus* on the treatment wayline became skewed towards larger size classes of crabs. This difference was significant for each of the 3 days following fishing (Fig. 1). For *P. prideaux* significant differences were found between size distributions on the

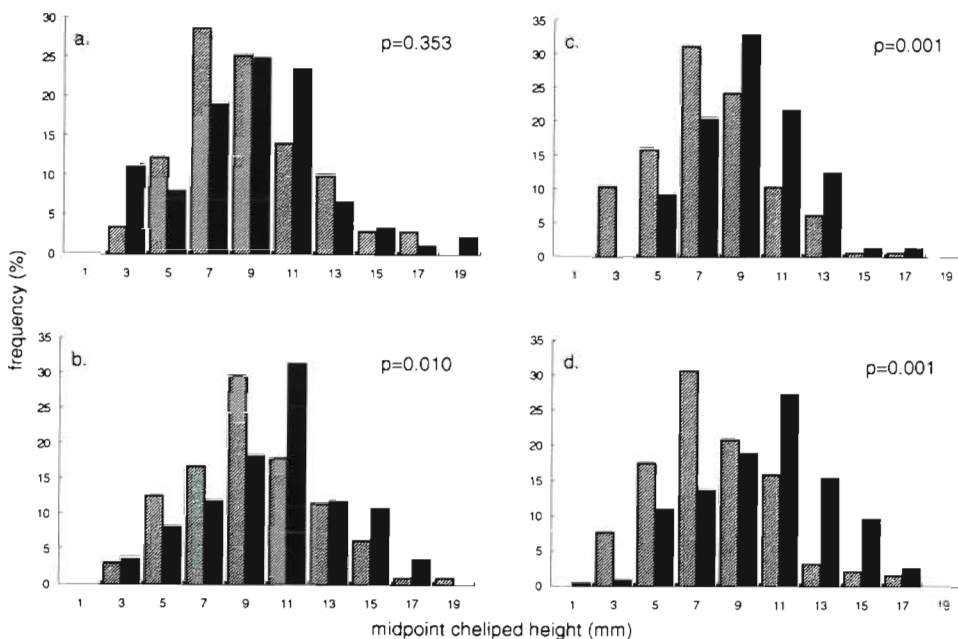


Fig. 1. *Pagurus bernhardus*. Size-frequency distributions of hermit crabs caught before and after fishing on the control (▨) or treatment (■) waylines. (a) Before fishing; (b) 1 d, (c) 2 d, (d) 3 d after fishing. Also showing results of the Kolmogorov-Smirnov test (p)

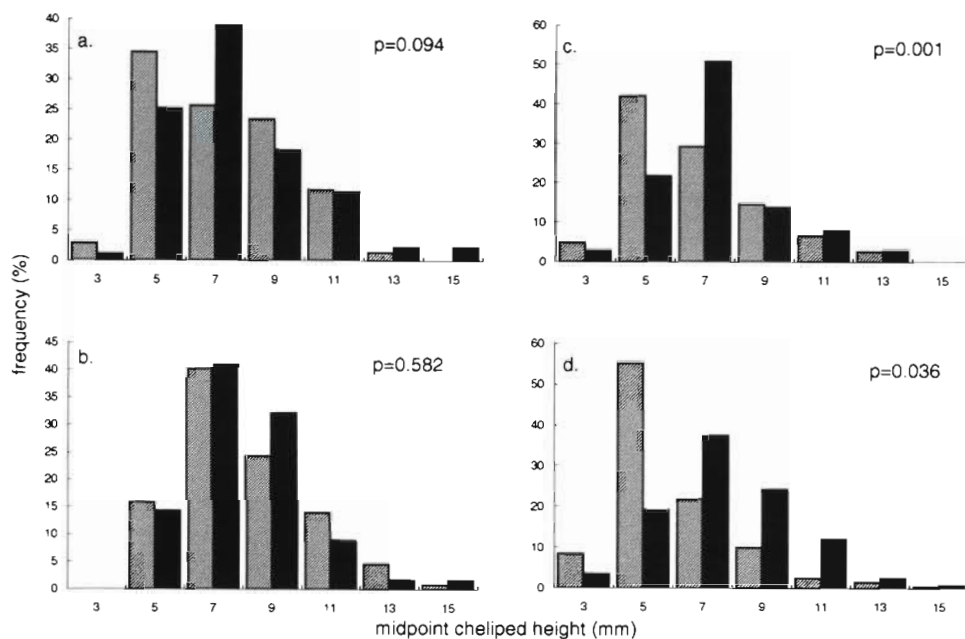


Fig. 2. *Pagurus prideaux*. Size-frequency distributions of hermit crabs caught before and after fishing on the control (▨) or treatment (■) waylines. (a) Before fishing; (b) 1 d, (c) 2 d, (d) 3 d after fishing. Also showing results of the Kolmogorov-Smirnov test (p)

control and treatment waylines on the second and third day after fishing (Fig. 2). However, these differences appear to be due to increased numbers of small crabs on the control wayline, rather than an increase in the numbers of large crabs on the treatment wayline.

Food intake

***Pagurus bernhardus*.** The relationship between $\ln(\text{thorax length})$ and $\ln(\text{dry weight of stomach con-}$

Table 4. *Pagurus bernhardus*, *P. prideaux*. Test for differences between waylines (control or treatment) in the relationship between weight of stomach contents and crab size. ANCOVA on model: $\ln[\text{dry weight of stomach contents (mg)}] = a + b \cdot \ln[\text{thorax length (mm)}]$ using wayline as a factor. For fitted models, see Figs. 3 & 4

Days before/ after fishing	Model	ANCOVA, $p > F$	
		Different intercepts	Different slopes
<i>Pagurus bernhardus</i>			
Before	0.0009	0.7593	0.8377
1 d after	0.0001	0.0488	0.6183
2 d after	0.0001	0.0156	0.1174
3 d after	0.0057	0.0020	0.0635
4 d after	0.0001	0.3069	0.3738
<i>Pagurus prideaux</i>			
Before	0.0001	0.7520	0.0940
1 d after	0.0022	0.2224	0.7237
2 d after	0.0001	0.8148	0.0909
3 d after	0.7757	0.0921	0.8601
4 d after	0.1522	0.6418	0.7056

tents) was linear (Fig. 3). Before fishing had taken place there were no significant differences between models for the control or treatment waylines (Table 4). However, for 3 d following beam trawling there were significant differences between intercepts of the control and treatment samples, with the intercept for the fished wayline being higher than that for the control wayline (Fig. 3). On the final (fourth) day there were no significant differences in the intercepts or slopes (Fig. 3).

***Pagurus prideaux*.** The relationship between $\ln(\text{thorax length})$ and $\ln(\text{dry weight of stomach contents})$ was found to be linear before fishing and for 2 d after fishing. The intercepts and slopes were not significantly different between lines (Table 4) and therefore a common line was fitted to the data (Fig. 4). On the third and fourth days after fishing the model was not significant (Table 4) and therefore no line was fitted (Fig. 4).

Hermit crab diets

The following phyla were observed in the stomach contents: Crustacea (amphipods, copepods, isopods, body parts of larger unidentified Crustacea), Annelida (polychaetes), Mollusca (bivalves, gastropods), Cnidaria (hydroids), Echinodermata (echinoids and holothurians), Bryozoa, Sarcomastigophora (foraminiferans). Also observed were eggs of unknown origin (in 3 stomachs) and a single fish scale. Identification to species level was rarely possible due to the macerated nature of the digesta. In both species the most common phyla were Crustacea, Annelida and Mollusca (Tables 5 & 6).

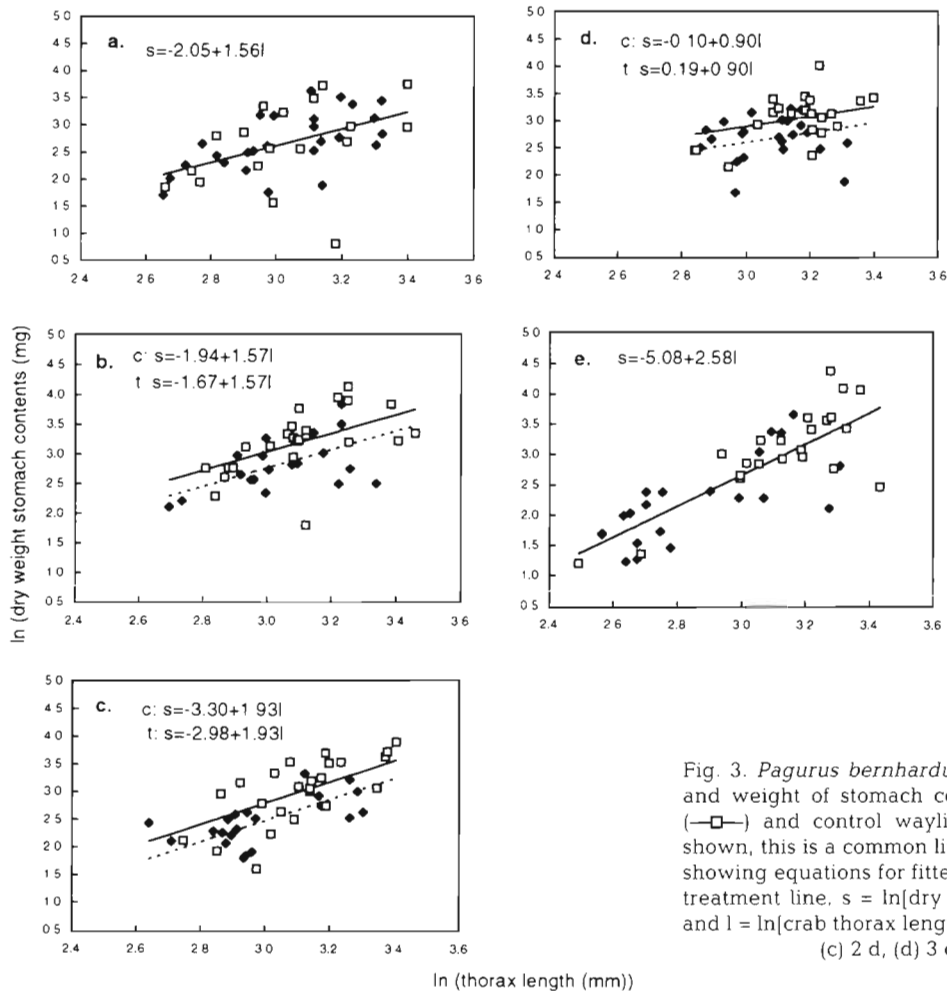


Fig. 3. *Pagurus bernhardus*. Relationship between crab size and weight of stomach contents for the treatment wayline (—□—) and control wayline (··◆··); where only 1 line is shown, this is a common line fitted to the whole dataset. Also showing equations for fitted line(s) where c = control line, t = treatment line, s = \ln [dry weight of stomach contents (mg)] and l = \ln [crab thorax length (mm)]. (a) Before fishing; (b) 1 d, (c) 2 d, (d) 3 d, (e) 4 d after fishing

Cluster analysis and subsequent multidimensional scaling (MDS) of the stomach contents data (percentage points) showed that the diets of *Pagurus bernhardus* and *P. prideaux* fell into 2 significantly different groups (Fig. 5, ANOSIM, $R = 0.729$, $p < 0.001$). All phyla observed were found in both species' stomachs,

with the exception of a fish scale which was found in a single *P. bernhardus*. Therefore the difference in dietary composition is probably attributable to differences in the proportions of phyla consumed. *P. prideaux* appeared to consume a larger proportion of molluscs and crustaceans and a smaller proportion of

Table 5. *Pagurus bernhardus*. Diet composition. Percentage points for each group in the stomach contents

Days before/ after fishing	Wayline	Crusta- ceans	Poly- chaetes	Molluscs	Echino- derms	Hydroids	Bryo- zoans	Forami- niferans	Eggs	Fish	Unidenti- fied
Before	Control	5.2	4.3	10.4	0.8	1.9	1.9	0.3	0.0	0.0	75.3
	Treatment	4.2	8.9	3.9	0.0	1.5	1.8	0.3	0.0	0.0	79.4
1 d after	Control	17.5	6.8	7.4	1.3	1.7	2.2	0.3	1.3	0.0	61.5
	Treatment	33.2	29.5	3.4	2.3	0.2	0.6	0.1	0.0	0.0	30.7
2 d after	Control	4.7	7.6	3.7	0.6	2.5	1.5	0.0	0.0	0.0	79.3
	Treatment	8.1	16.8	9.1	4.7	0.4	1.4	0.3	0.0	0.0	59.1
3 d after	Control	6.8	5.5	11.3	5.1	3.7	1.3	0.1	0.0	0.0	66.2
	Treatment	2.2	14.0	12.8	6.2	1.7	2.9	0.2	0.0	0.0	60.0
4 d after	Control	6.3	9.3	4.3	2.0	1.3	2.3	0.5	0.0	0.0	74.0
	Treatment	4.2	10.0	6.4	2.0	2.9	3.5	0.3	0.0	0.1	70.4

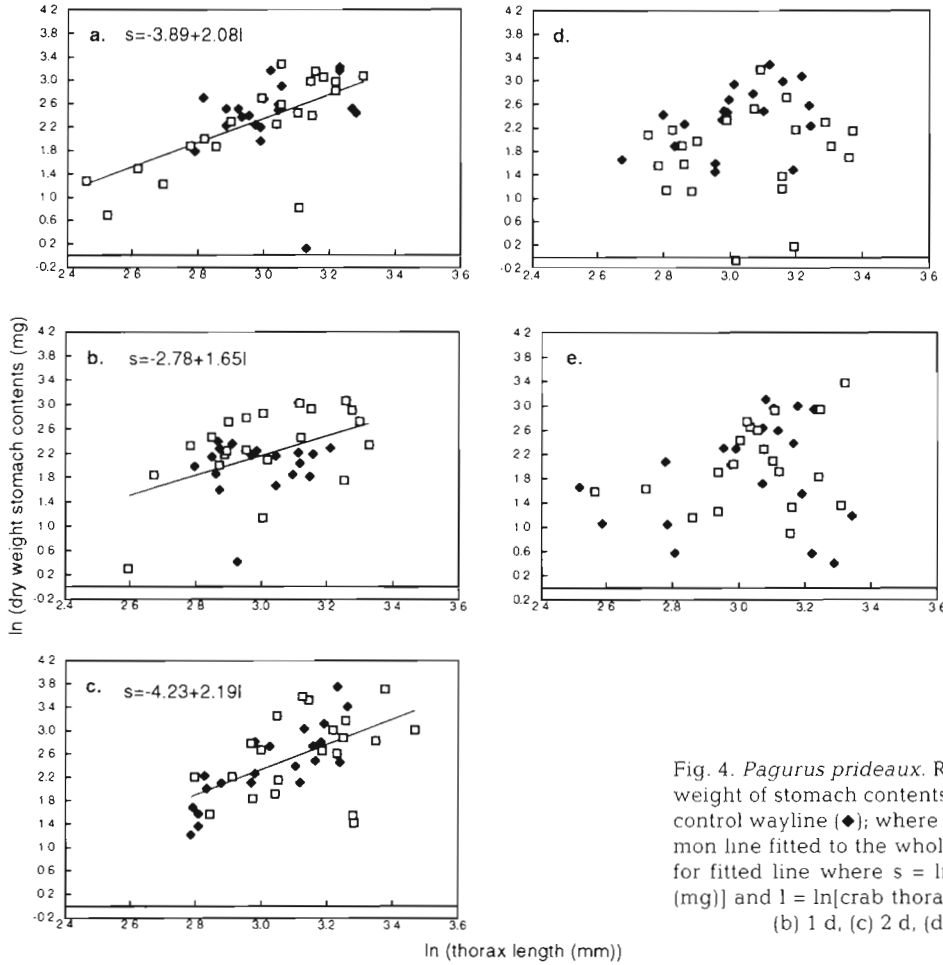


Fig. 4. *Pagurus prideaux*. Relationship between crab size and weight of stomach contents for the treatment wayline (□) and control wayline (◆); where a fitted line is shown, this is a common line fitted to the whole dataset. Also showing equations for fitted line where $s = \ln[\text{dry weight of stomach contents (mg)}]$ and $l = \ln[\text{crab thorax length (mm)}]$. (a) Before fishing; (b) 1 d, (c) 2 d, (d) 3 d, (e) 4 d after fishing

polychaetes than *P. bernhardus* (Tables 5 & 6). *P. bernhardus* also appeared to have a more diverse diet than *P. prideaux* (mean number of phyla identified per stomach: *P. bernhardus* 2.8 ± 0.16 , *P. prideaux* 2.3 ± 0.14 ; *t*-test $p < 0.001$; Shannon diversity index: *P. bernhardus* 0.85, *P. prideaux* 0.77).

The MDS ordination plot indicated that the diets of *Pagurus bernhardus* collected on the trawled wayline the first day after fishing had the least similarity to those collected on the control waylines (Fig. 5). This difference appears to be due to an increase in the proportions of crustaceans and polychaetes in the diet (Table 5).

Table 6. *Pagurus prideaux*. Diet composition. Percentage points for each group in the stomach contents

Days before/after fishing	Wayline	Crustaceans	Polychaetes	Molluscs	Echinoderms	Hydroids	Bryozoans	Foraminiferans	Eggs	Unidentified
Before	Control	7.9	3.2	17.3	0.7	0.0	0.4	1.0	0.0	69.4
	Treatment	8.0	7.4	10.1	0.1	0.0	0.4	1.9	0.0	72.0
1 d after	Control	10.3	3.0	10.0	0.0	0.0	0.3	1.0	0.3	75.2
	Treatment	23.8	8.2	10.7	0.8	0.1	0.7	1.1	0.0	54.6
2 d after	Control	4.5	4.9	13.1	0.0	0.0	0.7	1.3	0.0	75.7
	Treatment	18.3	7.7	11.2	0.9	0.0	0.2	1.2	0.0	60.5
3 d after	Control	6.1	3.0	21.2	0.9	0.0	0.0	0.5	0.0	68.4
	Treatment	8.8	5.8	14.4	4.0	0.1	0.1	0.3	0.7	65.7
4 d after	Control	11.1	11.1	7.4	1.1	0.3	0.3	2.0	0.0	66.7
	Treatment	7.3	8.5	11.2	3.0	0.3	0.1	1.0	0.0	68.4

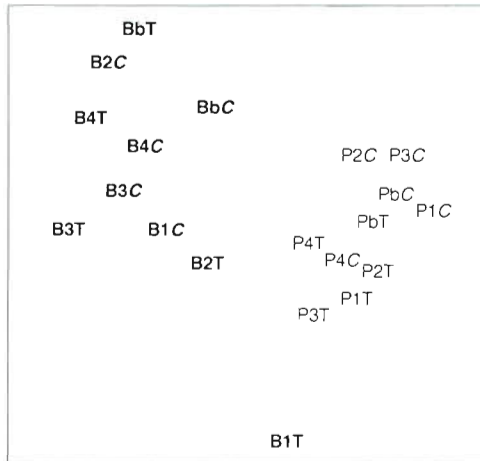


Fig. 5. *Pagurus bernhardus*, *P. prideaux*. MDS plot showing groupings based on stomach contents (stress = 0.14). Nomenclature (XYZ) as follows: X = species (B = *P. bernhardus*, P = *P. prideaux*), Y = days before/after fishing (b = before, 1 = 1 d, 2 = 2 d, 3 = 3 d, and 4 = 4 d after), Z = wayline (C = control, T = treatment)

DISCUSSION

Our results demonstrate that *Pagurus bernhardus* respond strongly to trawling disturbance, rapidly migrating onto a trawled wayline and increasing their food intake whilst in that area. However, no similar response was detected for *P. prideaux*.

The mean density of *Pagurus bernhardus* in the trawled area was significantly higher than in the control areas 2 and 3 d after fishing. The mean density of hermit crabs peaked after 2 d, decreasing on the third day, suggesting that *P. bernhardus* were migrating into the trawled area for 2 d following fishing.

The proportion of large *Pagurus bernhardus* was much greater in the trawled area than in the adjacent controls. This may be due to either size-specific differences in rates of migration, or to competitive exclusion of smaller crabs. Competitive exclusion of smaller *P. bernhardus* occurs when intraspecific competition for food becomes intense (Ramsay et al. 1997), however, in this study, we have no direct measure of the intensity of competition in the trawled area. It seems likely that larger *P. bernhardus* would move faster over longer distances, and may thus arrive more quickly in the trawled area.

Pagurus bernhardus caught in the trawled area consumed more food than those in the adjacent untrawled areas. This suggests that the migration onto the trawled wayline is a response to increased food availability as a result of trawling disturbance. Within the range studied, the amount of extra food gained by foraging in the trawled area increased with increasing crab size [indicated by the parallel lines fitted to the

relationship between ln(crab size) and ln(dry weight of stomach contents)]. The estimated amount of extra food consumed by a crab with a thorax length of 22 mm (the mean thorax length in this study) varied from 5.7 mg dry wt (1 d after fishing) to 4.9 mg dry wt (3 d after fishing)

Changes in dietary composition for *Pagurus bernhardus* collected on the fished wayline occurred on the first day after fishing. This change was expressed as an increase in the proportions of crustaceans and polychaetes in the diet. Although difficult to identify with certainty, the majority of crustaceans in the diet appeared to be amphipods, and the more identifiable polychaetes appeared to be *Lagis koreni*. Kaiser & Spencer (1994) found that gurnards and whiting feeding in areas disturbed by fishing increased their intake of the amphipod *Ampelisca spinipes*. *A. spinipes* is a tube dwelling species and Kaiser & Spencer (1994) postulated that trawling may disturb the amphipod from its tube, making it more vulnerable to predation. *L. koreni* is encased within a brittle tube constructed of sand grains and lives at the sediment/water interface. Consequently it is vulnerable to damage and displacement by trawling. It seems likely that the increase in stomach content weights after fishing is at least partly due to *P. bernhardus* feeding on infaunal animals which have been exposed or damaged by the action of the beam trawl, making them easier to find and capture than would normally be the case. It might be expected that *P. bernhardus* would feed on larger items which have been damaged by the beam trawl, such as soft tissues of *Spatangus purpureus*, *Ensis* spp. or *Laevicardium* sp. which have been found in fish stomachs on trawled areas (Kaiser & Spencer 1994). However, if this were so, one would expect the results to show an increase either in those taxa or in the proportion of unidentified digesta. No such result was obtained, which suggests that the crabs were mainly feeding on smaller infaunal animals that were damaged or exposed by the beam trawl.

It appears that *Pagurus prideaux* neither migrate into trawled areas nor obtain more food from within the trawled area. The increased numbers of *P. prideaux* on the control wayline 3 d after fishing was unexpected. The control wayline catches contained higher numbers of small crabs than the trawled wayline, suggesting aggregations of small individuals. However, the possible reasons for these aggregations are unclear.

The different responses of the 2 species to trawling disturbance could result from either competitive interactions or niche separation. It is possible that *Pagurus bernhardus* is competitively superior to *P. prideaux*, excluding the latter from the resource-rich areas of recently trawled ground. The alternative possibility is

that whilst *P. bernhardus* readily adopts the role of scavenger, *P. prideaux* is less likely to do so. Although the diets of both species include the same taxa, *P. prideaux* appears to consume a larger proportion of molluscs but fewer polychaetes compared with *P. bernhardus*. The diversity of the diets also appears to differ between species, with *P. bernhardus* frequently consuming other taxa in addition to crustaceans, molluscs and polychaetes, such as hydroids, echinoderms and bryozoans. This could indicate that *P. bernhardus* is a more generalist predator and scavenger than *P. prideaux*. A more detailed study of the diet of the 2 species, identifying prey to species level, would be necessary to draw any firm conclusions on this point. However, *P. bernhardus* does have a wider geographical and depth distribution than *P. prideaux* and may therefore occupy a broader niche-space. It is also possible that olfactory abilities differ between the 2 species, with *P. bernhardus* being better at sensing damaged prey in the trawled area.

The present study suggests that *Pagurus bernhardus* gain a significant amount of extra food by foraging in areas disturbed by beam trawling, and other studies have shown that *P. bernhardus* feed on fisheries discards (Kaiser & Spencer 1996a, Ramsay et al. in press). It has been suggested that where fisheries activity increases the food supply to a predator population, an expansion of that population might occur (Furness 1984, Furness et al. 1988, Berghahn 1990, Wassenburg & Hill 1990, Kaiser & Spencer 1995), especially for species where the mortality due to fishing is low, as is the case for *P. bernhardus* (Fonds 1994, Kaiser & Spencer 1995). Previous work has shown that increasing the food supply to 3 different crab species led to an increase in the fecundity in the population (Fusaro 1978, Wenner et al. 1987). However, neither of these studies linked this increase in fecundity to increased adult population size. Mortality in 1 or several of the planktonic developmental stages and dispersal of larvae may play an important part in the population dynamics of many marine invertebrates (Morgan 1995) and may be more important than the supply of food to adults. It is also possible that the availability of empty shells is an important controlling factor in hermit crab populations (Vance 1972), in which case increasing the food supply to the adult population would make little difference. However, if food availability in the adult stage is a controlling factor in populations of *P. bernhardus* it is possible that beam trawling could lead to increased population densities of this species. Further work is required to elucidate the relationship between feeding behaviour and population dynamics of other predatory species before conclusions can be drawn as to whether this is a mechanism by which fishing may cause long-term changes in benthic community structure.

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LITERATURE CITED

- Berghahn R (1990) On the potential impact of shrimping on trophic relationships in the Wadden Sea. In: Barnes M, Gibson RN (eds) Trophic relationships in the marine environment. Proc 24th Eur Mar Biol Symp. Aberdeen University Press, Aberdeen, p 130-140
- Bergman MJN, Hup M (1992) Direct effects of beam trawling on macrofauna in a sandy bottom sediment in the southern North Sea. ICES J Mar Sci 49:5-11
- Bergman MJN, Santbrink JW van (1994) Direct effects of beam trawling on macrofauna in sandy areas off the Dutch coast. In: de Groot SJ, Lindeboom HJ (eds) Environmental impact of bottom gears on benthic fauna in relation to natural resources management and protection of the North Sea. Netherlands Institute for Fisheries Research (NIOZ) Report 1994-11, Den Burg, Texel, p 179-208
- Blaber SJM, Wassenberg TJ (1989) Feeding ecology of the piscivorous birds *Phalacrocorax varius*, *P. melanoleucos* and *Sterna bergii* in Moreton Bay, Australia: diets and dependence on trawler discards. Mar Biol 101:1-10
- Clarke KR, Warwick RM (1994) Change in marine communities: an approach to statistical analysis and interpretation. Natural Environmental Research Council, Plymouth Marine Laboratory, Plymouth
- Craeymeersch JA (1994) Environmental impact of bottom gears on benthic fauna in relation to natural resources management and protection of the North Sea. In: de Groot SJ, Lindeboom HJ (eds) Environmental impact of bottom gears on benthic fauna in relation to natural resources management and protection of the North Sea. Netherlands Institute for Fisheries Research (NIOZ) Report 1994-11, Den Burg, Texel, p 209-236
- Erri Babu D (1988) 'Glandular pockets' of the integument and feeding mechanism in *Pagurus bernhardus* (Crustacea: Anomura). Mar Biol 99:315-323
- Fonds M (1994) Mortality of fish and invertebrates in beam trawl catches and the survival chances of discards. In: de Groot SJ, Lindeboom HJ (eds) Environmental impact of bottom gears on benthic fauna in relation to natural resources management and protection of the North Sea. Netherlands Institute for Fisheries Research (NIOZ) Report 1994-11, Den Burg, Texel, p 131-146
- Freire J, Fernández L, González-Gurriarán E (1991) Diel feeding pattern of *Liocarcinus depurator* (Brachyura: Portunidae) in the Ría de Arousa (Galicia, NW Spain). Ophelia 33:165-177
- Furness RW (1984) Seabird-fisheries relationships in the north-east Atlantic and North Sea. In: Nettleship DN, Sanger GA, Springer PF (eds) Marine birds: their feeding ecology and commercial fisheries relationships. Canadian Wildlife Service Special Publication. Dartmouth, Nova Scotia, p 162-169
- Furness RW, Hudson AV, Ensor K (1988) Interactions between scavenging seabirds and commercial fisheries around the British Isles. In: Burger J (ed) Seabirds and other marine vertebrates: competition, predation and other interactions. Columbia University Press, New York, p 240-268

- Fusaro C (1978) Food availability and egg production: a field experiment with *Hippa pacifica* Dana (Decapoda, Hippidae). *Pac Sci* 32:17–23
- Gerlach SA, Ekstrom DK, Eckardt PB (1976) Filter feeding in the hermit crab *Pagurus bernhardus*. *Oecologia* 24: 257–264
- Hudson AV, Furness RW (1988) Utilization of discarded fish by scavenging seabirds behind whitefish trawlers in Shetland. *J Zool (Lond)* 215:151–166
- Hynes HBN (1950) The food of freshwater sticklebacks (*Gasterosteus aculeatus* and *Pyosteus pungitius*) with a review of methods used in studies of the food of fishes. *J Anim Ecol* 19:36–58
- Jackson HG (1913) *Eupagurus*. LMBC Mem Typ Br Mar PL Anim 21:1–79
- Kaiser MJ, Rogers SI, McCandless DT (1994) Improving quantitative surveys of epibenthic communities using a modified 2 m beam trawl. *Mar Ecol Prog Ser* 106:131–138
- Kaiser MJ, Spencer BE (1994) Fish scavenging behaviour in recently trawled areas. *Mar Ecol Prog Ser* 112:41–49
- Kaiser MJ, Spencer BE (1995) Survival of by-catch from a beam trawl. *Mar Ecol Prog Ser* 126:31–38
- Kaiser MJ, Spencer BE (1996a) Behavioural responses of scavengers to beam trawl disturbance. In: Greenstreet SPR, Tasker ML (eds) Aquatic predators and their prey. Blackwell Scientific Publications, Oxford, p 116–123
- Kaiser MJ, Spencer BE (1996b) The effects of beam-trawl disturbance on infaunal communities in different habitats. *J Anim Ecol* 65:348–358
- Morgan SG (1995) Life and death in the plankton: larval mortality and adaptation. In: McEdward L (ed) Ecology of marine invertebrate larvae. CRC Press, Boca Raton, p 279–321
- Nickell TD, Moore PG (1992) The behavioural ecology of epibenthic scavenging invertebrates in the Clyde Sea area: laboratory experiments on attractions to bait in moving water, underwater TV observations in situ and general conclusions. *J Exp Mar Biol Ecol* 159:15–35
- Orton JH (1927) On the mode of feeding of the hermit-crab *Eupagurus bernhardus*, and some other Decapoda. *J Mar Biol Ass UK* 14:909–921
- Pike RB, Williamson DI (1959) Observations on the distribution and breeding of British hermit crabs and the stone crab (Crustacea: Diogenidae, Paguridea and Lithodae). *Proc Zool Soc Lond* 132:551–567
- Ramsay K, Kaiser MJ, Hughes RN (1997) A field study of intraspecific competition for food in hermit crabs (*Pagurus bernhardus*). *Estuar Coast Shelf Sci* 44: in press
- Santbrink JW van, Bergman MJN (1994) Direct effects of beam trawling on macrofauna in a soft bottom area in the southern North Sea. In: de Groot SJ, Lindeboom HJ (eds) Environmental impact of bottom gears on benthic fauna in relation to natural resources management and protection of the North Sea. Netherlands Institute for Fisheries Research (NIOZ) Report 1994-11, Den Burg, Texel, p 147–178
- van Beek FA, van Leeuwen PI, Rijnsdorp AD (1990) On the survival of plaice and sole discards in the otter-trawl and beam-trawl fisheries in the North Sea. *Neth J Sea Res* 26: 151–160
- Vance RR (1972) Competition and mechanism of coexistence in three sympatric species of intertidal hermit crabs. *Ecology* 53:1062–1074
- Wassenberg TJ, Hill BJ (1987) Feeding by the sand crab *Portunus pelagicus* on material discarded from prawn trawlers in Moreton Bay, Australia. *Mar Biol* 95:387–393
- Wassenberg TJ, Hill BJ (1990) Partitioning of material discarded from prawn trawlers in Moreton Bay. *Aust J Mar Freshwater Res* 41:27–36
- Wenner AM, Ricard Y, Dugan J (1987) Hippid crab population structure and food availability on Pacific shorelines. *Bull Mar Sci* 41:221–233
- Williams MJ (1981) Methods for analysis of natural diet in portunid crabs (Crustacea, Decapoda, Portunidae). *J Exp Mar Biol Ecol* 52:103–113

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