

# Fate and consumption of discarded by-catch in the Spencer Gulf prawn fishery, South Australia

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## Abstract

Discarded by-catch in prawn fisheries is likely to affect trophic balance including the population structure and function of both the exploited species and scavengers on discards. The Spencer Gulf prawn fishery consists of 39 trawlers operating about 60 days a year with a management system allowing large differences in spatial effort. Such a system provides opportunities to study spatial effects of fishing in relation to habitat and fishing effort. In this study, the occurrence and consumption of scavengers on the Spencer Gulf prawn fishing grounds were studied at five sites subjected to different historical fishing effort and further estimated through field and laboratory experiments. Baited video experiments showed that the most common scavengers on discarded by-catch were Degens leatherjacket (*Thamnaconus degeni*), blue crabs (*Portunus pelagicus*) and sealice (a group of several species of isopods and amphipods), notably *Natatolana woodjonesi*, with variable abundances between sites and day/night. Scavenger abundance and consumption was higher at night than during the day. Total abundance and consumption during the day showed a negative correlation to historical trawl hours, while during the night showed a positive correlation. In the laboratory, in contrast to groups, individual leatherjackets showed little interest in bait. Consumption rates for both leatherjackets and blue crabs showed a logarithmic trend depending on bait species. The results showed that during the day blue crabs and leatherjackets were the dominating scavengers while during the night it was Port Jackson sharks and in particular sealice. The effects of site, historical trawl hours and relative importance of the scavenging species are discussed.

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## 1. Introduction

In prawn and shrimp trawling, the proportion of non-target species (by-catch) can be high but with substantial variation between and within geographical regions (Andrew and Pepperell, 1992; Alverson et al., 1994). Little is known about the fate and consumption of discarded by-catch and to what extent it affects ecosystems (Andrew and Pepperell, 1992; Kennelly, 1995). The likely ecological effects of discarded by-catch are on trophic linkages and food web dynamics (see Hall, 1999; Kaiser et al., 2006). Discarded by-catch provides increased opportunities for benthic scavengers to feed opportunistically on carrion (Hall, 1999). Carrion, however, is spatially and temporally an infrequent food resource and a single meal may sustain individuals for long periods (Britton and Morton, 1994). Wassenberg

and Hill (1990) divided discarded by-catch into two categories: that which floats and that which sinks, and found that of the by-catch discarded from Moreton Bay prawn trawlers, only 3% floats while the rest sinks. The discarded by-catch species that sink do so rapidly, spending only 5–10 min in the water column where they are susceptible to surface and mid-water scavengers such as dolphins and sharks (Kennelly, 1995; Svane, 2005). However, most of the sinking material ends up on the seabed where it becomes available as food for benthic scavengers (Wassenberg and Hill, 1990; Britton and Morton, 1994; Kennelly, 1995; Moore and Wong, 1995; Ramsay et al., 1997; Hill and Wassenberg, 2000).

Discards that settle on the bottom attract a variety of scavenging benthic species depending on the type of environment, and may constitute as much as 6–13% of the annual secondary production (Groenewold and Fonds, 2000). Aggregations of scavengers around by-catch can reach densities of up to 200 times that of the background populations, and for some species may persist for up to 3 days (Veale et al., 2000). In the north-

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western Mediterranean, Bozzano and Sarda (2002) reported that 48–64% of all fishery discards were consumed after 12 h immersion and more than 90% after 24 h. The mean rate of consumption was estimated to be  $23.8 \pm 5.7$  g/h on the shelf and  $30.8 \pm 10.5$  g/h on the slope, indicating that depth influenced consumption rates. Many animals inhabiting the deep sea floor are specialised as scavengers, such as the isopod *Natatolana borealis*, and rely on fall-out from the surface due to the lack of *in situ* primary production (Collins and Bagley, 1999; Johansen, 2000; Castro et al., 2005).

In Spencer Gulf, the prawn fishing fleet operates through a spatial management system and catches about 2000 t of prawns (*Penaeus (Melicertus) latisulcatus*) (Flegel, 2007) per year. The discarded by-catch from prawn trawling is variable both in space and time and constitutes about 4000 t per year (Carrick, 1997; Dixon et al., 2005). The fished areas vary slightly in depth (20–40 m) and the benthic environments are variable and heterogeneous. The substrata of the Spencer Gulf trawl grounds are sandy, and in many places with strong tidal currents, the sediments are coarse sand and gravel in ripples or patches. In such areas, the coarser grains are covered with rhodoliths forming

so-called “popcorn bottoms”. Spencer Gulf is an inverse estuary with a mean annual salinity of  $\sim 45$  ppt at the head (El-Sabh et al., 1997; Nunes Vaz et al., 1990).

The occurrence and consumption of surface scavengers in Spencer Gulf prawn fishery have previously been reported (Svane, 2005). The purpose of this study was to identify the most common mid-water and benthic scavengers feeding on by-catch in the Spencer Gulf prawn fishery, quantify their occurrence at bait (discard species) and estimate consumption rates. This study was done by conducting a series of “cafeteria experiments”, using baited traps and underwater video, and through a series of laboratory feeding experiments to estimate feeding rates of the three most common scavenging species.

## 2. Materials and methods

### 2.1. Selection of study areas

Five sites were selected representing areas of different fishing intensity (trawl hours) along a north-south gradient in Spencer Gulf (Fig. 1). Site 1:  $33^{\circ}11.1'S$ ,  $137^{\circ}36.0'E$  (Western Shoal);

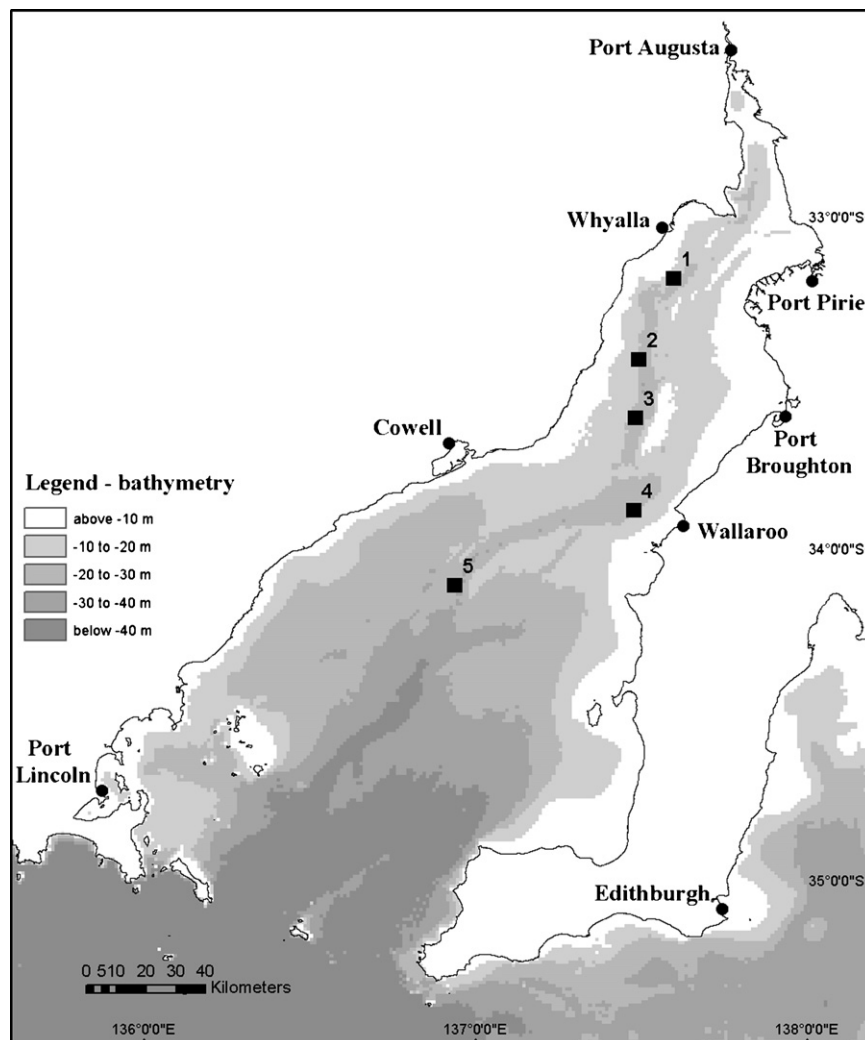


Fig. 1. Map showing Spencer Gulf and the positions of the five selected stations for this study.

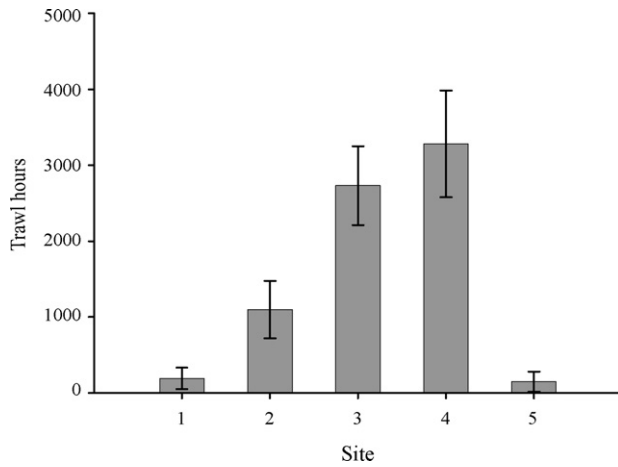


Fig. 2. The annual mean numbers of trawl hours reported at five selected stations in Spencer Gulf during the period of 1987–1998. Error bars are 95% CI.

Site 2: 33°25.8'S, 137°29.6'E (Plank Pt); Site 3: 33°36.3'S, 137°29.0'E (Middle Bank); Site 4: 33°53.0'S, 137°28.8'E (Walaroo); Site 5: 34°06.5'S, 136°56.3'E (the Gutter). The depth at the five sites was between 21 and 33 m. Data on effort were obtained using logbook recordings of trawl hours reported from administrative fishing blocks during 1987–1998 (see Dixon et al., 2005). Data from blocks that include a site, plus that from the neighbouring blocks were pooled and the 12-year annual mean with 95% confidence interval was calculated for each site (Fig. 2). The areas at the five sites represent about 70% of the total fishing effort (Dixon et al., 2005).

## 2.2. Fate and consumption of discards: field experiments

### 2.2.1. Cafeteria experiments

A digital video camera (Canon MV1) in an underwater housing was mounted vertically on a galvanised rig above a steel mesh grid measuring 1 m × 1 m. The distance from the focal plane to the grid base was 120 cm, allowing a full photographic view using a wide-angle lens. During the night, light was supplied by a 50-W underwater daylight photographic lamp controlled by an adjustable timer set to 5-min intervals of light and darkness.

Field experiments on scavenger occurrence and consumption were conducted during the day and night, four times at each of the five sites. At each site and time, four replicated “cafeteria experiments” were conducted with the rig suspended mid-water and four with it on the bottom. Four batches of four different by-catch species (red mullet (*Upeneichthy vlamingi*), squid (*Sepioteuthis australis*), leatherjacket (*Thamnaconus degeni*) and sand trevally (*Pseudocaranx wrighti*)) were used as bait and attached to the grid base with one species in each quarter section using 1 mm steel wire. The camera was activated and the rig lowered over the side of the research vessel, and placed on the bottom for 30 min before being retrieved.

Each 30 min of video footage of the grid was analysed by recording the species and numbers present in 2-min intervals (15 observations). Each night trial was analysed by recording species and numbers present two times during each 5-min period of light with 2-min intervals (12 observations).

On one cruise, batches of four species of by-catch, namely Degens leatherjacket, squid, bulls eye (*Parapriacanthus elongatus*) and red mullet, were pre-weighed in the laboratory, numbered and frozen. On board, the bait was thawed before being used for the “cafeteria experiments”. After 30 min exposure to scavengers, the rig was retrieved and the remaining bait packed and frozen in order to be re-weighed in the laboratory, and the consumed weight subsequently calculated.

### 2.2.2. Sealice occurrence and consumption (field experiments)

Sampling was carried out during both the day and night during two cruises. At each site four weighted baskets, each containing four baited traps with the same bait species (sand trevally) were used to determine the occurrence of sealice. The traps were made from a 1-l plastic container or similar size PVC tubing with a 10-mm hole drilled through the centre of the bottom and lid to allow sealice access. Additional 2 mm holes were drilled through the lid and bottom to ensure ventilation and release of odour. At each site, all four baskets were lowered to the bottom at the same time and then retrieved at 8-min intervals, with the final four traps retrieved after 30 min submersion. Sealice collected from each trap were placed in numbered sample bags, frozen and taken to the laboratory for recording. Identification was carried out according to Bruce (1986).

Feeding rates were calculated using the initial and final bait weight and by dividing the weight eaten with the number of sealice per minute bottom time to obtain a feeding rate in grams per minute per sealouse.

### 2.2.3. Statistical analyses of field experiments

Consumption data for cafeteria experiments were analysed using two-way ANOVAs with site and time as fixed effects. Occurrence data were analysed for each scavenger group (sharks and rays, leatherjackets, blue swimmer crabs and sealice) using two-way ANOVAs with site and time as the main effects. The total number of sealice caught in traps during 30 min bottom time and their consumption rate at each station were analysed using one-way ANOVA. All data sets were tested for normality and homogeneity of variances using Kolmogorov–Smirnov test and Levene’s test, respectively, as provided by the statistical software SPSS v.15.0 (SPSS Inc., Chicago, IL, USA). Post hoc comparisons were done using the Turkey HSD test or Dunnett C-test when appropriate. In SPSS, partial  $\eta^2$  values are provided as a substitute for effect size (Pallant, 2005). The Spearman rank order correlation ( $\rho$ ) was used to correlate abundance, consumption and historical trawl hours. These tests are only indicative of the strength of the relationship because the calculated significance levels are strongly influenced by sample size and the focus should be on the amount of shared variance (see Pallant, 2005).

## 2.3. Consumption (laboratory experiments)

### 2.3.1. Consumption by individual Degens leatherjackets

Degens leatherjackets were captured using cylindrical 20 mm mesh traps baited with sand trevally in Boston Bay, Port Lincoln.

After capture the leatherjackets were transported within 30 min to Lincoln Marine Science Centre and allowed to acclimatise in laboratory tanks with flow through seawater (54 l/h at 17 °C) before use.

Twelve glass aquaria (25H × 20W × 40D cm) wrapped in black plastic were set up with flow through seawater (54 l/h) at 17 °C. Individual leatherjacket's weight, sex and length were recorded before they were placed in each aquarium. They were allowed to acclimatise for 24 h without food. Weighted portions of sand trevally collected by trawling were hooked onto a small piece of wire and lowered into each aquarium. Baits were re-weighed from four randomly selected aquaria at 2.5, 6 and 9 h, respectively.

### 2.3.2. Consumption by groups of *Degens leatherjackets*

Leatherjackets were observed to eat more voraciously when kept in groups. Therefore, a series of consumption experiments were conducted using groups of leatherjackets. Four large (1.0H × 1.0L × 0.5D m) fibreglass tanks with flow through seawater (54 l/h) at 17 °C were set up, each containing 17 pre-weighed leatherjackets. The leatherjackets were allowed to acclimatise for 24 h without food before experiments were carried out. Bait consisting of about 110 g of squid, red mullet, sand trevally or leatherjacket was placed in each of the four tanks. The bait was re-weighed after 4, 8, 16 and 32 min, respectively, and placed back into the tanks after each weighing until the experiment was terminated at 32 min. The experiments were replicated four times. All weights in both experiments were corrected for weight change from immersion in water (estimated in separate experiments) and standardised by dividing by the weight of the leatherjacket(s) (g/g eaten).

### 2.3.3. Consumption by blue crabs

Undamaged, and apparently healthy, blue swimmer crabs were selected from the catch obtained during field experiments, had their claws bound and were placed in iced seawater to lower their metabolism for transportation to the laboratory. Crabs were subsequently maintained in large (9000 l) outdoor tanks with sterilised shell grit as substratum and flow through aerated seawater. Crabs were fed daily a combination of crushed fresh mussels (*Mytilus galloprovincialis*) and frozen surf clams (*Donax deltooides*). A total of 74 crabs were used in experiments with an exact 50:50 sex ratio in three size classes (60–84, 85–109 and 110–140 mm carapace width). Blue crabs were held at and experiments conducted at SARDI Aquatic Sciences Laboratory at West Beach in Adelaide.

Experiments with blue crabs included the measurement of foregut clearance and consumption as a function of time. Foregut clearance was measured for crabs of 85–109 mm by repeating the experiment described by Wassenberg and Hill (1987) using sand trevally as food. Wassenberg and Hill (1987) found that blue crabs (81–162 mm CL) from tropical Queensland (Australia) waters cleared 50% of the foregut by 1.5 h, and 95% by 6 h when fed either prawn heads or whiting after a 24-h starvation period. We repeated the laboratory experiment with blue crabs (85–109 mm CL) from temperate South Australian waters. Crabs were starved for 24 h before being fed at experimental

time 0 and again at either 1.5, 4 or 6 h, respectively, in seawater temperatures of  $23.3 \pm 0.9$  °C to measure proportion of food consumed relative to starvation time.

Consumption experiments involved the estimate of food uptake (g/g crab) by blue crabs over five time intervals (4-, 8-, 16-, 32- and 64-min) for four discard species: squid, red mullet, sand trevally, and *Degens leatherjacket*. Eleven clear plastic aquaria (44H × 66L × 38W cm each) covered with black plastic, to reduce disturbance and direct light, were set up outdoors with flow through seawater (54 l/h) at natural ambient temperature ( $23.3 \pm 0.9$  °C). A perforated (2 mm thick) plastic divider was inserted diagonally into each aquarium allowing for two crabs per tank. Each aquarium contained sterile shell grit of approximately 3–4 cm in depth as substratum.

Consumption was measured for the three size classes and both sexes in separate experiments. At least 48 h prior to experimentation, crabs were tagged for individual identification and randomly placed in experimental tanks for acclimatisation. Tags were small (10 mm × 4 mm) plastic coded strips, attached posteriorly on the carapace using a spatula and a small drop of Selleys™ 'Supa Glue'. Each consumption experiment consisted of 4 crabs per time interval (20 crabs in total). Crabs were starved for at least 6 h prior to and between experiments, allowing foregut clearance (Wassenberg and Hill, 1987).

All consumption experiments followed the same protocol. A whole bait item (fish/squid) was blotted dry and weighed (accurate to 0.1 g). The bait was then skewered onto a thin piece of galvanised wire. Bait items were randomly assigned a consumption time for which a crab was allowed to feed. Baits were then administered to the crabs randomly. After each of the five time intervals, the remaining baits were collected, blotted dry and re-weighed. All weights were corrected for autogenic change and standardised to g/g crab. Crabs that did not feed were disregarded for that experiment.

### 2.3.4. Statistical analysis of consumption (laboratory experiments)

*Leatherjackets*: a single factor ANOVA was used to test for effects of time in the consumption experiments, while a two-factor ANOVA was used to test for effects of time and species of by-catch during the consumption experiments. *Blue crabs*: a four-way ANOVA with size, sex, time, and species as fixed effects and consumption (g/g) as the dependent variable was used. The data were analysed using the statistical software package SPSS 15.0 as described above.

## 3. Results

### 3.1. Occurrence of scavengers

At all five sites, mid-water (15 m) and bottom (25–32 m) "cafeteria experiments" were conducted by day and night. The results showed that in mid-water, during 30 min of immersion ( $n = 15$ ), no scavengers appeared in the video footage and no bait was consumed. Accordingly, mid-water consumption of discarded by-catch was considered negligible.

Four species were observed as the dominating bottom scavengers in cafeteria experiments; Degens leatherjacket during the day, sealice (*Natantolana woodjonesi*, *N. viridis* and a group of unidentified amphipods) during the night, and blue crabs, Port Jackson sharks (*Heterodontus portusjacksoni*) and smooth stingray (*Dasyatis brevicaudata*) during both day and night. Other species were attracted to the cafeteria experiments, but these were few in numbers and were not observed to feed. These were sand trevally (*P. wrighti*), striped trumpeter (*Pelates octolineatus*) and wavy grubfish (*Parapercis haackei*).

The occurrence of blue crabs at bait at the five sites during the day and night is shown in Fig. 3A. A two-way ANOVA on  $\log_{10}(x+1)$  transformed data with homogeneous variances and occurrence (no/obs) as the dependent variable showed a significant effect of site ( $P < 0.001$ ,  $F_{[4,120]} = 11.178$ , partial  $\eta^2 = 0.289$ ) and time ( $P = 0.009$ ,  $F_{[1,120]} = 7.141$ , partial  $\eta^2 = 0.061$ ) with no interactions ( $P = 0.167$ ,  $F_{[4,120]} = 1.649$ , partial  $\eta^2 = 0.057$ ). The partial  $\eta^2$  values showed a low probability of type I error for site (large effect) but a higher probability for time (moderate effect). A Tukey HSD post hoc test only separated Site 5 from the other sites. The results showed that blue crabs occurred at bait abundantly at all sites with the exception of Site 5, and occurred more often during the day than at night. A decline in crab occurrence, particularly during the night, from

the north to the south of the gulf was evident. Medium to large sized crabs (85–140 mm CL) were the most frequent at baited sites.

The occurrence of Degens leatherjacket at bait at the five sites is shown in Fig. 3B. Degens leatherjackets were voracious scavengers occurring in relatively large numbers at Site 5, attacking bait during the day within a short time after the camera rig was established on the bottom. A two-way ANOVA on fourth root transformed data with heterogeneous variances with site and time as fixed factors and occurrence (no/obs) as the dependent variable showed a significant effect of site ( $P < 0.001$ ,  $F_{[4,120]} = 43.060$ , partial  $\eta^2 = 0.610$ ) and time ( $P < 0.001$ ,  $F_{[1,120]} = 53.537$ , partial  $\eta^2 = 0.327$ ) with no interactions ( $P = 0.203$ ,  $F_{[4,120]} = 1.513$ , partial  $\eta^2 = 0.052$ ). The partial  $\eta^2$  values showed a large effect for both factors with low probability for type I error. A Dunnett's *C*-test separated the sites ( $1 = 2 = 3 \neq 4 \neq 5$ ). The results showed that Degens leatherjackets were more abundant at Sites 4 and 5 than elsewhere and occurred more often during the day than at night.

Sealices were extremely voracious scavengers that occurred at baits during the night but were never observed during the day (Fig. 3C). A one-way ANOVA on  $\log_{10}(x+1)$  transformed data with homogeneous variances and occurrence (no/obs) as the dependent variable showed a significant effect of site

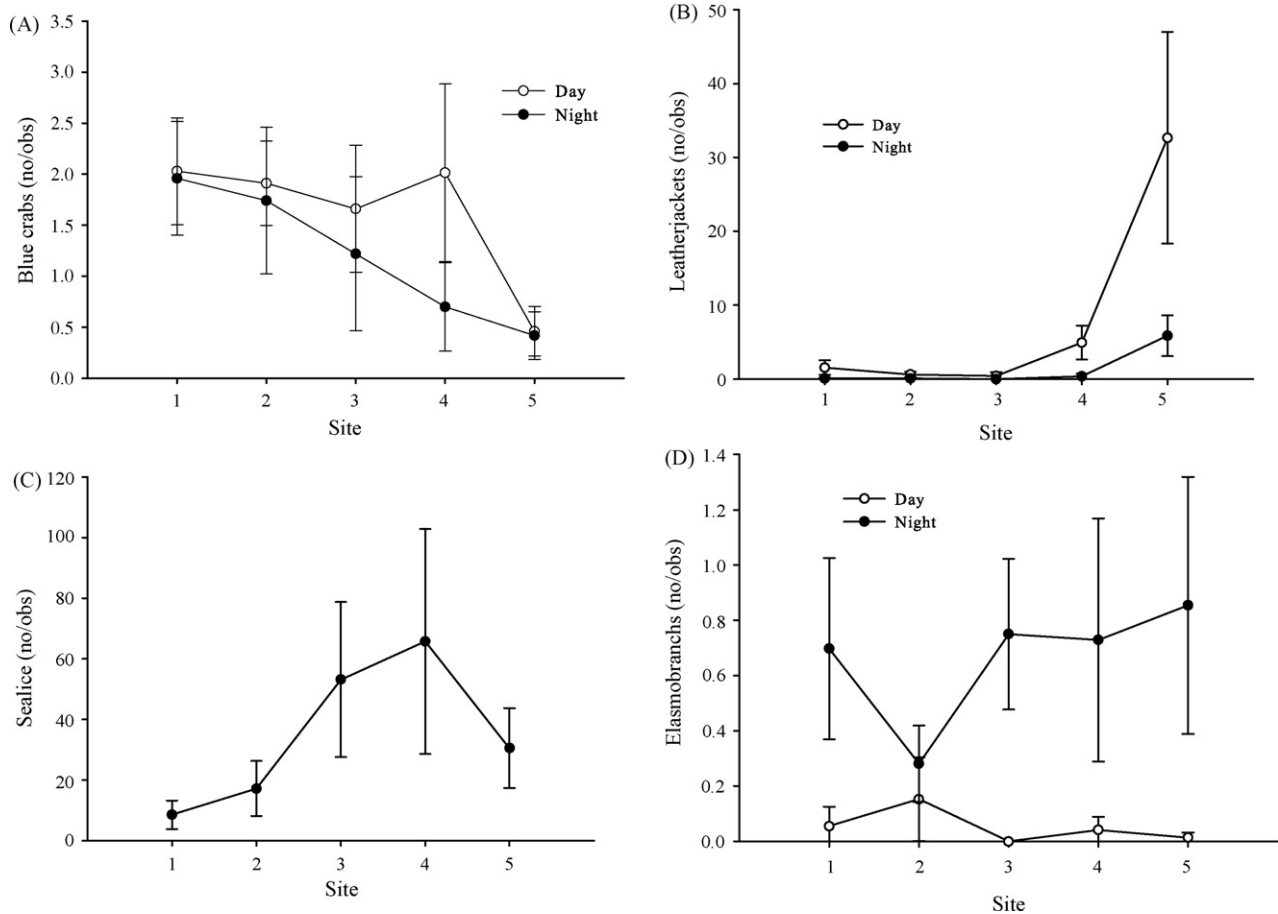


Fig. 3. The occurrence (no/obs) of scavengers at bait (cafeteria experiments) at five sites in Spencer Gulf. (A) Blue swimmer crab (*Portunus pelagicus*), (B) Degens leatherjacket (*Thamnaconus degeni*), (C) sealice, and (D) elasmobranchs (Port Jackson shark: *Heterodontus portusjacksoni*, smooth stingray: *Dasyatis brevicaudata*, and southern fiddler ray: *Trygonorrhina fasciata*). Error bars are 95% CI.

( $P < 0.001$ ,  $F_{[4,60]} = 10.384$ , partial  $\eta^2 = 0.430$ ). The partial  $\eta^2$  values showed a large effect and thus a low probability of type I error. A Tukey HSD test separated the sites  $1 \neq (3 = 4 = 5)$ ,  $2 \neq (3 = 4)$  and  $1 = 2$ . The result showed that sealice abundance at bait was higher at Sites 3–5 than elsewhere (Fig. 3C).

The occurrence of elasmobranchs, which primarily constituted Port Jackson sharks and smooth stingrays, at bait is shown in Fig. 3D. A two-way ANOVA on fourth root transformed data with heterogeneous variances with site and time as fixed factors and occurrence (no/obs) as the dependent variable showed no significant effect of site ( $P = 0.904$ ,  $F_{[4,120]} = 0.258$ , partial  $\eta^2 = 0.009$ ) but a significant effect of time ( $P < 0.001$ ,  $F_{[1,120]} = 92.123$ , partial  $\eta^2 = 0.456$ ) with no interaction ( $P < 0.05$ ,  $F_{[4,120]} = 2.431$ , partial  $\eta^2 = 0.081$ ). The partial  $\eta^2$  values showed a large effect for the significant factor time with subsequent low probability of type I error. The result showed that elasmobranch occurrence at baits was highly variable among sites but more frequent at night than during the day. Smooth stingrays (>1 m width) occurred during the day but had difficulties accessing the grid due to their size, but when successful they forcefully removed all the bait. The number of stingrays recorded was 9 individuals at Site 2 and 2 individuals at Site 4. Port Jackson sharks were commonly feeding on the bait offered but in low numbers with large variations (Fig. 3D). The occurrence of Port Jackson sharks at night varied with a mean of 0.3–0.9 individual per observation. However, when Port Jackson sharks occurred, they usually consumed all of the bait.

The combined occurrence of the dominating scavengers is shown in Fig. 4A. The result of a two-way ANOVA on double transformed data (square root of  $\log_{10}(x+1)$ ) with homogeneous variance, site and time as fixed factors, and occurrence (no/obs) as the dependent variable showed a significant effect of site ( $P < 0.001$ ,  $F_{[4,120]} = 11.303$ , partial  $\eta^2 = 0.292$ ) and time ( $P < 0.001$ ,  $F_{[1,120]} = 15.335$ , partial  $\eta^2 = 0.122$ ) with significant interactions ( $P < 0.001$ ,  $F_{[4,120]} = 7.069$ , partial  $\eta^2 = 0.204$ ). The significant interaction was caused by interference at Site 5 making the effect of time inconsistent at that site relative to the other sites (Fig. 4A). A Tukey HSD post hoc test separated the Sites 1 and 2 from 4 and 3 from 5. It is evident that the highest scavenger activity in terms of number of individuals occurred at bait at Sites 3 and 4 at night and at Site 5 at both day and night. This pattern is primarily affected by the dominating occurrence of sealice at Sites 3 and 4 at night, and Degens leatherjackets at Site 5 at day, mixed with irregular occurrence of elasmobranchs at all sites.

### 3.2. Consumption during cafeteria experiments

Consumption of bait (southern calamari, red mullet, Degens leatherjacket, and sand trevally) at the five sites during the day and night is shown in Fig. 4B. A two-way ANOVA on untransformed data with homogeneous variances with time and site as fixed factors and consumption (g/g) as the dependent variable showed a significant effect of time ( $P = 0.029$ ,  $F_{[1,31]} = 5.487$ , partial  $\eta^2 = 0.207$ ), no significant effect of site ( $P = 0.592$ ,  $F_{[4,120]} = 0.714$ , partial  $\eta^2 = 0.120$ ), and a signifi-

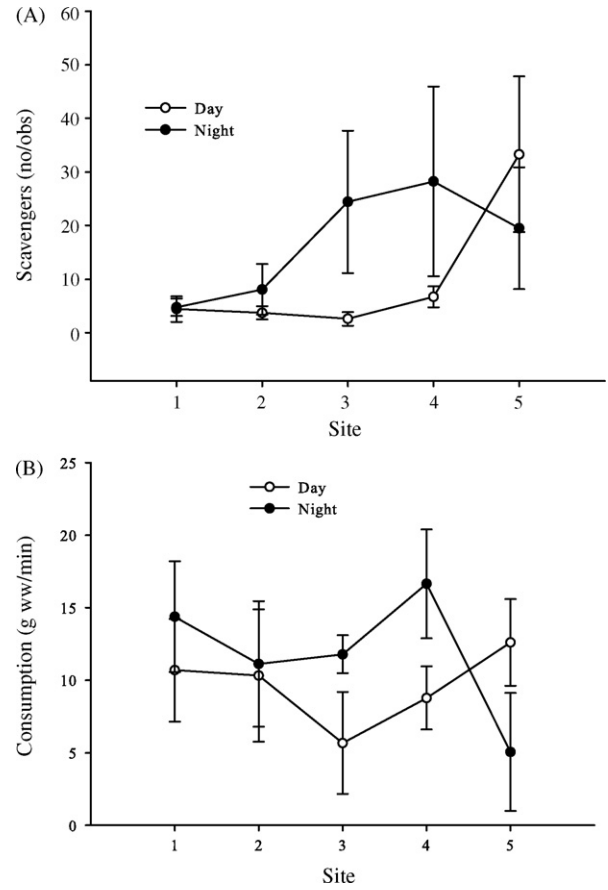


Fig. 4. The occurrence of all scavengers (A) and consumption (B) of by-catch in cafeteria experiments at five sites in Spencer Gulf during day and night. Error bars are 95% CI.

cant interaction ( $P = 0.004$ ,  $F_{[4,31]} = 5.350$ , partial  $\eta^2 = 0.505$ ) caused by interference at Site 5 where a change in scavenger composition and abundance occurred (Figs. 3 and 4A). Large variations were caused when large elasmobranchs consumed all of the bait before the end of the experiments. The results showed that consumption was higher during the night than at day at all sites with the exception of Site 5, which showed the reverse. However, a high level of correlation between scavenger occurrence and consumption during the day and night combined was evident (Spearman's  $\rho = 0.436$ ,  $P = 0.016$ ,  $n = 30$ ). The mean consumption for all sites was  $9.67 \text{ g ww/min} \pm 1.20\text{S.E.}$ , and for day and night was  $7.70 \text{ g ww/min} \pm 1.37\text{S.E.}$  and  $11.76 \text{ g ww/min} \pm 1.91\text{S.E.}$ , respectively. At the times when only elasmobranchs were present (mostly Port Jackson sharks) the mean consumption was  $24.9 \pm 6.5\text{S.E. g}$  per individual per 30 min observation.

### 3.3. Consumption rates: laboratory and field experiments

#### 3.3.1. Sealice

Fig. 5 shows the number of sealice caught and their consumption in baited traps during 30-min on the bottom at each station. A one-way ANOVA on  $\log_{10}(x+1)$  transformed abundance data (no/trap) with homogeneous variances showed a significant effect of site ( $P < 0.001$ ,  $F_{[4,96]} = 16.546$ , partial  $\eta^2 = 0.421$ )

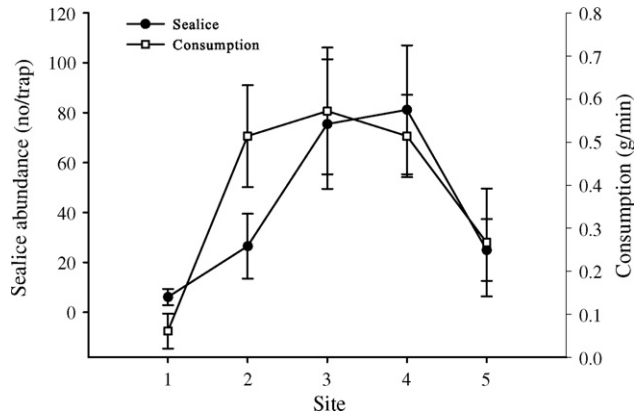


Fig. 5. Occurrence and consumption by sealice at five sites in Spencer Gulf. Error bars are 95% CI.

indicated by the large numbers trapped at Sites 3 and 4. A Tukey HSD test separated the sites  $1 \neq (2 = 5) \neq (3 = 4)$ . The traps accordingly confirmed the pattern of occurrence observed in the cafeteria experiments (Fig. 3C). A one-way ANOVA on square root transformed consumption data (g/min) with homogeneous variances also showed a significant effect of site ( $P < 0.001$ ,  $F_{[4,96]} = 15.843$ , partial  $\eta^2 = 0.411$ ). The partial  $\eta^2$  value showed a large effect with low probability of type I error. A Tukey HSD test separated sites  $1 \neq 5 \neq (2 = 3 = 4)$ . A significant correlation between sealice occurrence and consumption was evident (Spearman's  $\rho = 0.619$ ,  $P < 0.001$ ,  $n = 89$ ). The relationship between consumption ( $y$ : g/min) and number of sealice ( $x$ ) was found to be  $y = 0.0051x + 0.1654$ ,  $R^2 = 0.6293$ . The mean consumption rate for all five sites was estimated to be  $0.55 \pm 0.09$  S.E. g per individual per 30 min.

### 3.3.2. Individual leatherjackets

In separate aquaria experiments where bait (sand trevally) was supplied at time 0 and re-weighed after 12 min (0), 2.5, 6 and 9 h, respectively, individual Degens leatherjackets was found to take approximately 9 h before resuming feeding (Fig. 6). A two-way ANOVA with time and sex as fixed factors on consumption

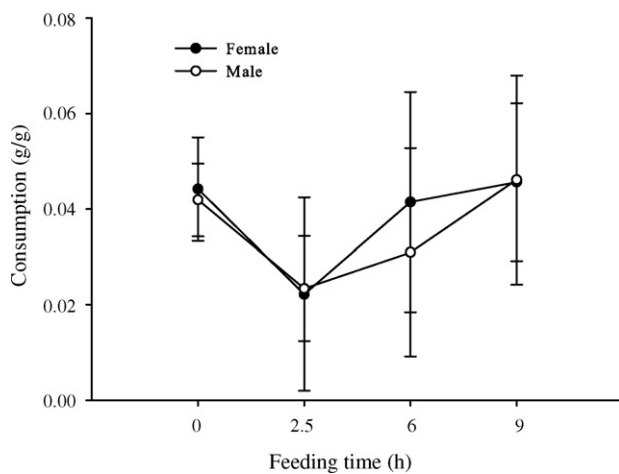


Fig. 6. Consumption (g/g) of single Degens leatherjackets (*T. degeni*) male and females in laboratory experiments. Bait provided at time 0 and the remains retrieved at time 0, 2.5, 6 and 9 h. Error bars are 95% CI.

data (g/g) with heterogeneous variances, revealed a significant effect of time ( $P = 0.025$ ,  $F_{[3,86]} = 3.278$ , partial  $\eta^2 = 0.112$ ), no significant effect of sex ( $P = 0.631$ ,  $F_{[1,86]} = 0.232$ , partial  $\eta^2 = 0.003$ ) and no interactions ( $P = 0.906$ ,  $F = 0.185_{0.05[3,86]}$ , partial  $\eta^2 = 0.007$ ). However, a large variation between individual leatherjackets was evident. The partial  $\eta^2$  value showed a moderate to large effect size for the significant factor time with a subsequent low probability of type I error. Nevertheless, the significant effect of time was entirely due to the low consumption after 2.5 h, which was significantly different from consumption at time 0 (Dunnett C post hoc test). The results suggest that individual leatherjackets showed little interest in bait, but our observations showed that feeding increased when several individuals were kept together. Consumption was found to be independent of sex despite an obvious dimorphism where males are much larger than females. Consequently, further experiments were performed on groups of leatherjackets without separating males and females.

### 3.3.3. Groups of leatherjackets

Consumption rate estimates of the four different species of by-catch all showed a strong logarithmic trend irrespective of bait type (Fig. 7). A two-way ANOVA on square root transformed consumption data (g/g) with homogeneous variances with bait species and time as fixed effects showed a significant difference between the amounts consumed of the different bait species ( $P < 0.001$ ,  $F = 97.741_{[3,96]}$ , partial  $\eta^2 = 0.786$ ) and the time bait were exposed to leatherjackets ( $P < 0.001$ ,  $F_{[3,96]} = 22.109$ , partial  $\eta^2 = 0.453$ ) with no significant interactions ( $P = 0.541$ ,  $F_{[9,96]} = 0.886$ , partial  $\eta^2 = 0.091$ ). The partial  $\eta^2$  values showed large effect sizes for both bait species and time, with low probability of type I errors. A Tukey HSD post hoc test showed that squid was consumed in significantly larger quantities than red mullet, followed by sand trevally and leatherjacket with no significant difference between consumption of the two latter species. In all bait species experiments, each successive time period had a significantly

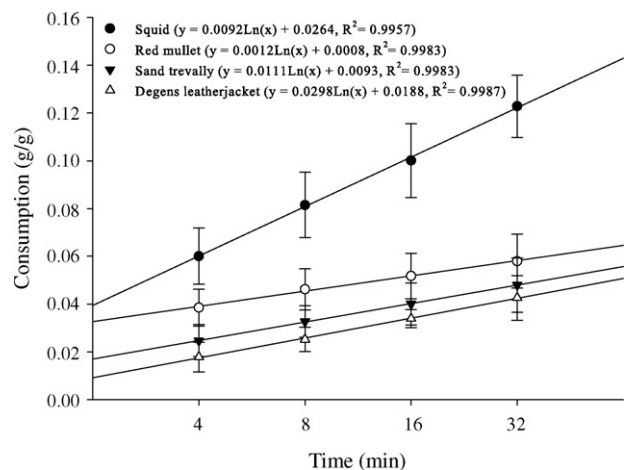


Fig. 7. Consumption (g/g) by groups of Degens leatherjacket (*T. degeni*) of four commonly occurring by-catch species. Bait provided at time 0 and the remains retrieved at time 0, 2.5, 6 and 9 h. Error bars are 95% CI. Equations,  $R^2$  values and the best logarithmic fits are shown.

greater amount of bait consumed. However, the rate of consumption was higher between 4 and 8 min in all experiments. The maximum consumption rate (0–4 min) was highest for squid (15.0 mg/(g/min)) followed by red mullet (9.9 mg/(g/min)) and trevally and leatherjackets (6.2 and 4.4 mg/(g/min)), respectively. The mean consumption rate for 30 min was estimated to be 1.48 g/individual using the median weight for Degens leatherjacket caught in trawls (24.5 g).

### 3.3.4. Blue crabs

The results showed a gut clearance of 100% by 6 h and approximately 50% after 1.5 and 4 h starvation, respectively, when fed sand trevally, consumed over a 16-min period ( $0.060 \pm 0.017$  g/g crab). We found that hunger level (consumption) did not significantly differ between a 24-h and a 6-h starvation period after initial feeding (Student's *t*-test;  $t = -0.536$ , d.f. = 12,  $P > 0.05$ ).

A four-way ANOVA on data with heterogeneous variances with size, sex, time, and species as fixed factors and consumption (g/g) as the dependent variable showed a significant effect of sex ( $F_{[1,231]} = 5.221$ ,  $P = 0.024$ , partial  $\eta^2 = 0.041$ ), time ( $F_{[4,231]} = 13.832$ ,  $P > 0.01$ , partial  $\eta^2 = 0.310$ ) and species ( $F_{[3,231]} = 5.942$ ,  $P = 0.001$ , partial  $\eta^2 = 0.127$ ) with no significant effect of size ( $F_{[2,231]} = 3.023$ ,  $P = 0.052$ , partial  $\eta^2 = 0.047$ ) and no significant interactions. The partial  $\eta^2$  values were small for size and sex indicating a high probability for type I error while for time and species they were large and medium-large, respectively, indicating a low probability of type I errors. These two latter factors had a power larger than 0.8. A Dunnett *C*-test separated consumption of squid from red mullet and sand trevally, but not from Degens leatherjacket. The results showed that females consume significantly more than males (0.0388 and 0.0308 g/g, respectively). However the statistical power to separate differences between sexes was low. Consumption increased as a function of time with relatively high consumption of squid and low consumption of red mullet (at 16 min; squid:  $0.0449 \pm 0.0106$  g/g; Degens leatherjacket:  $0.0340 \pm 0.0118$  g/g; sand trevally:  $0.0331 \pm 0.0114$  g/g; red mullet:  $0.0280 \pm 0.0121$  g/g) (Fig. 8). The differences between bait species reflected the variable difficulties for crabs when cutting through the tough skin of the bait, which contributed to the poor homogeneity of variances for this dataset. Consumption rates showed logarithmic trends (Fig. 8).

### 3.4. Scavenger occurrence and consumption

The relative consumption of discarded by-catch during the day and night at the five studied sites in the Spencer Gulf is shown in Fig. 9A and B, respectively. The graphs are based on the occurrence of the most important scavengers at cafeteria experiments and their mean consumption rates determined by field (sealice) and laboratory experiments (blue crabs, Degens leatherjacket). For elasmobranchs (mostly Port Jackson shark), consumption rates were estimated using observations from the cafeteria experiments where only they occurred. The results showed that during the day blue crabs and leatherjackets dominated as consumers (Fig. 9A). Blue crabs dominated Sites 1–3

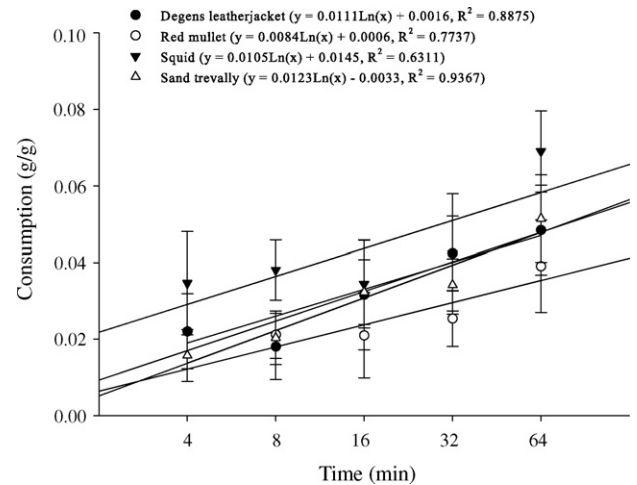


Fig. 8. Consumption (g/g) by blue crabs (*P. pelagicus*) of four commonly occurring by-catch species. Bait provided at time 0 and the remains retrieved at time 4, 8, 16, 32 and 64 min. Error bars are 95% CI. Equations,  $R^2$  values and the best linear fits are shown.

with increasing dominance of Degens leatherjacket at Sites 4 and 5. This pattern is largely in accordance with the occurrence of blue crabs and leatherjackets observed in cafeteria experiments (Fig. 3A and B). During the night (Fig. 9B), the pattern of consumption changed with the occurrence of sealice and more sharks as scavengers. The occurrence and consumption of scavengers during the day at the five sites were negatively correlated to the 12-year mean annual trawl hours at each

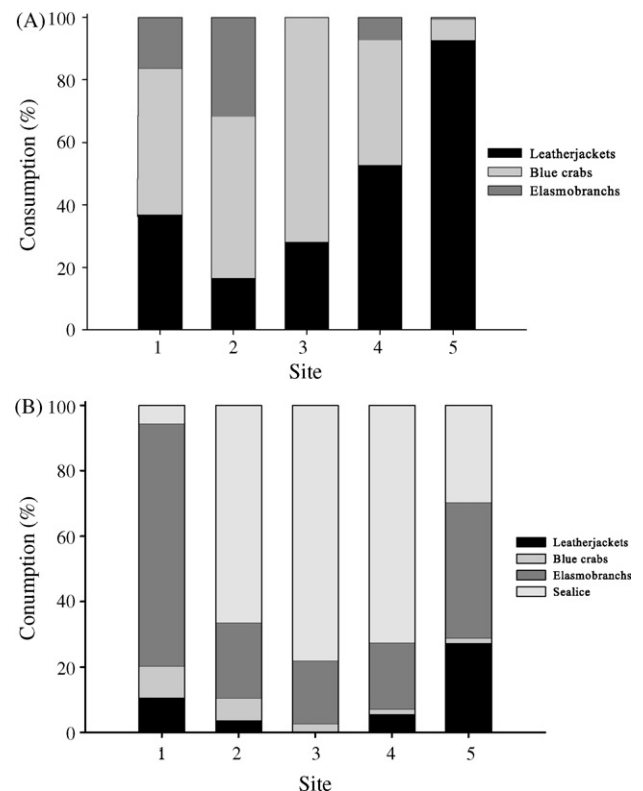


Fig. 9. The relative consumption at day (A) and night (B) by the most important scavenger species at five sites in Spencer Gulf.



site (Spearman's  $\rho$ : occurrence =  $-0.876$ ,  $P < 0.001$ ; consumption =  $-0.469$ ,  $P = 0.078$ ,  $n = 15$ ) (Figs. 2 and 4A and B). The large number of Degens leatherjackets at Site 5 contributed to the negative correlation. The occurrence and consumption of scavengers during the night was positively correlated to trawl hours (Spearman's  $\rho$ : occurrence =  $0.577$ ,  $P = 0.024$ ; consumption =  $0.589$ ,  $P = 0.021$ ,  $N = 15$ ) (Figs. 2 and 4A and B). This correlation was strongly influenced by the occurrence and consumption of sealice in particular, which was positively correlated to historical trawl hours reported at the five selected sites (Spearman's  $\rho$ : occurrence =  $0.535$ ,  $P < 0.001$ ; consumption =  $0.330$ ,  $P = 0.002$ ,  $N = 89$ ) (Figs. 2 and 3C). The occurrence of sealice was variable and possibly influenced by weather conditions and the moon phase. The relative consumption by blue crabs during the night is likely to be overestimated because observations showed that crabs did not feed with the same intensity as during the day (Fig. 3A) and when sealice were abundant, crabs were not observed to settle and feed. Similarly, leatherjackets occurred at baits during the night in lower numbers than during the day (Fig. 3B) but were not observed to feed during the night. Accordingly, sealice were observed to be the most dominating scavengers during the night with a rate of 0.55 g per individual per 30 min.

## 4. Discussion

### 4.1. Fate of discards: cafeteria experiments

The introduction of carrion through discards from trawl fisheries is likely to affect the energy flow and food webs by subsidising consumer populations (Ramsay et al., 1997). In the Spencer Gulf prawn fishery, discards are not distributed evenly, but are likely to be a function of trawl hours at any given place, although the proportion of recapture and survival of discarded by-catch has not been considered.

Carrion is a spatially and temporally infrequent food resource in the sea. In the absence of human interference, few marine animals die as a consequence of natural senescence, thereby becoming available as carrion for scavengers (Britton and Morton, 1994). In Spencer Gulf, the most common scavengers observed were leatherjackets, notably Degens leatherjacket, blue crabs and sealice, dominated by *N. woodjonesi*. In addition, Port Jackson shark and stingray play an important role.

While the blue swimmer crab is an important scavenger on discards in the Spencer Gulf ecosystem, it is also a dominant species in the prawn fishery by-catch (Carrick, 1997; Dixon et al., 2005). Many previous studies on the feeding ecology of *Portunus pelagicus* have indicated that it is an opportunistic carnivore, acting as either a predator or scavenger, depending on local availability of food items (Williams, 1982; Wassenberg and Hill, 1987; Edgar, 1990; Sukumaran and Neelakantan, 1997; Wu and Shin, 1998). The natural diet of *P. pelagicus* includes a wide variety of sessile and slow moving invertebrates, with small bivalves and ophiuroids (brittle stars) found to dominate (Williams, 1982; Sukumaran and Neelakantan, 1997; Wu and Shin, 1998). However, stomach content analyses have shown that *P. pelagicus* consumes a wide variety of decaying flesh

as well, indicating its scavenging tendencies (Sukumaran and Neelakantan, 1997). More crabs occurred at bait during the day than the night for three of the five sites, indicating that feeding on carrion occurred primarily during the day (Fig. 3A). At night, crabs did not appear to feed, but did tear up bait thus facilitating consumption by other scavengers. This night behaviour appeared to be influenced by sealice abundance.

Juvenile Degens leatherjackets are inhabitants of shallow seagrass beds of Spencer Gulf while the adults school deeper and relatively close to the bottom. Other species of leatherjackets join the schools, including bridled leatherjacket (*Acanthaluteres spilomelanurus*) and rough leatherjacket (*Scobinichthys granulatus*). The literature provides little information regarding the feeding ecology of leatherjackets in general and no studies seem to have been carried out on Degens leatherjacket. Leatherjackets are important consumers in seagrass assemblages and have been found to be generalists feeding on a variety of food items (Bell et al., 1978; Last, 1983; Buchmore et al., 1984; Edgar and Shaw, 1995). However, Degens leatherjacket dominated as scavengers only at Site 5 (Fig. 3B).

Sealice constitutes a group of marine scavengers composed of several isopod and amphipod crustaceans. Bird (1981) described the group as being eminently carnivorous, active swimmers and voracious scavengers active at night where they aggregate at carrion in swarms. In Spencer Gulf, the dominating species are isopods of the genus *Natanolona* (Cirolanidae), notably *N. woodjonesi* and *N. viridis*. Bruce (1986) lists 31 species of *Natanolona* that are known to inhabit Australian waters.

There is little information on the ecology of the Australian *Natanolona* species and most published work is on *N. borealis*, a deep sea species occurring in the northern hemisphere (Bird, 1981; Moore and Wong, 1995; Taylor and Moore, 1995; Wong and Moore, 1995; Johansen, 1996). It has been reported that these isopods burrow in the sediment during the day, emerging primarily at dusk to feed, and return to the sediment before dawn (Stepien and Brusca, 1985). Sealice are voracious scavengers that feed on carrion and may attack living animals by entering the body cavity through the gills or anus and consuming their prey from the inside (Hammer and Zimmerman, 1979; Hammer, 1981). Sealice are considered a pest in many fisheries because they rapidly consume bait and may attack animals that are caught, whether in nets, pots or hooked. The number of sealice observed in the video footage (Fig. 3C) was probably underestimated because many enter the carrion and are otherwise difficult to observe in videos due to high swimming speed. Johansen (2000) estimated that *N. borealis* was attracted to bait from a maximum distance of 190 m and swam at a speed of 4.5–18.7 cm/s. The cafeteria experiments showed that the accumulation rate of *N. woodjonesi* was constant during a 30-min period. Because sealice responded to bait within 2 min, the maximum distance travelled to bait, using the swimming speed reported for *N. borealis*, could be about 75–300 m within the 30-min period of bait deployment.

This study shows that benthic scavengers play an important role in the Spencer Gulf ecosystem with higher occurrence during the night than the day (Fig. 4A). Consumption at cafeteria experiments (Fig. 4B) reflects the abundance. By far the most

important scavengers were Degens leatherjacket during the day, sealice during the night, and blue crabs, which appeared to feed primarily during the day. Elasmobranchs, primarily Port Jackson sharks, were observed during the night, while few large stingrays appeared during the day (Fig. 3D). By-catch was not approached mid-water but only when it reached the bottom (see Erzini et al., 2003). Poiner et al. (1998) used a video camera to estimate scavenger abundance where prawn trawling occurs north of Cape Grenville off the Queensland coast (far northern section of the Great Barrier Reef Marine Park) and found that in more than fifty 30 min camera deployments only between one and nine scavengers (mean  $2.3S.D. = 2.49$ ), mostly fish, fed on the bait. In this study during 30 min deployment during the day, up to about 30 leatherjackets (Site 5) and 2 blue crabs per observation fed on bait. During the night, blue crab occurrence was observed to be lower, but in addition a large number of sealice were furiously competing for the bait.

#### 4.2. Consumption rates: laboratory experiments

Our observations showed that leatherjackets kept individually are less interested in feeding than when two or more are together (Fig. 6). Accordingly, in further experiments on feeding, leatherjackets were kept in experimental groups arbitrarily chosen to be 17 individuals per aquarium, mimicking the densities observed around bait in the field.

The differences in the amount of bait consumed between the four by-catch species can probably be explained by differences in flesh structure. Squid and red mullet have much softer flesh and so could be more easily consumed compared to sand trevally and leatherjackets. Leatherjacket group consumption rates were higher during the initial 4–8-min period in all experiments, and then gradually declined following broadly a logarithmic function, reaching a plateau, indicating gut fullness (Fig. 7).

Schooling Degens leatherjackets feeding on discarded by-catch are between 60 and 120 mm long (females 60–90 mm, males 80–120 mm) and weight between 7 and 40 g ww (females 7–19 g, males 12–40 g). This implies that a median size Degens leatherjacket of 90 mm length will consume between 90 and 308 mg/min of by-catch depending on bait species. On average, the consumption rate over 8 min (time when consumption rate was highest) averaged for all bait species for a single Degens leatherjacket was 9.0 mg/(g/min). Our observations in the field have shown that when schools of Degens leatherjackets feed on discarded by-catch most will be consumed within 8 min.

Variation in consumption between male and female portunid crabs is a contentious topic in the literature (Williams, 1982; Choy, 1986; Sumpton and Smith, 1990; Kawamura et al., 1995; Sukumaran and Neelakantan, 1997). Our studies showed that when consumption rates for both sexes were compared, a significant difference was found, although with low power reflecting high variability. The majority of studies reported in the literature suggest that no feeding differences occur between the sexes of portunid crabs (Choy, 1986; Sumpton and Smith, 1990; Williams, 1982).

Most studies on the feeding ecology of portunid crabs have focussed on variations in the diet composition between size

classes (Cerda and Wolff, 1993; Choy, 1986; Sukumaran and Neelakantan, 1997; Williams, 1982). This study showed that crabs feeding on four discard species exhibited positive logarithmic consumption rates with significant differences detected between bait species (Fig. 8). Under laboratory conditions, individual crab consumption increased over the 64-min experiment. This implies that in the absence of competitors, a crab will feed on bait for a far longer period than observed in the field, which supports the conclusion by Clark et al. (1999) that foraging decreases in the presence of other crabs. However, it should be noted that this study did not take into account moult stage of crabs, although crabs that did not appear to feed were excluded from experiments. Moulting may have been an extraneous variable that would have affected consumption estimates for the small size class in particular (Gannon, 1990).

Using logarithmic equations for consumption as well as length–weight equations, consumption on discard for an individual crab can be estimated. Medium to large sized crabs (85–140 mm CL) were found to occur most frequently at baited sites in the field. The mean consumption rate for a crab of 112.5 mm carapace length (mean weight of 219.8 g) can be calculated at 7.03 g during 16 min (0.032 g/g), after which the foregut is full. It would be expected that a crab reach foregut fullness during more than one feeding event because discarded by-catch is dumped from trawlers in large amounts at any one time. Taking into consideration the time it takes to clear the foregut (6 h), an estimate of hourly consumption for a medium to large sized crab (sexes and discard species pooled) is thus 0.0053 g/g body weight per h.

Consumption estimates were found to vary significantly between the discard species being consumed. Red mullet, sand trevally and Degens leatherjackets were eaten at a significantly lower rate than squid. The amount of food consumed was affected by the interaction between species and time allowed to feed. This may have been caused by the very different textures between bait items, food preference, moult stage or a combination of these and possibly other factors. However, consumption of all species increased logarithmically, with a high statistical fit of the data for each.

According to Carrick (1997) the relative abundances of the most important discard species caught in prawn trawls in Spencer Gulf are sand trevally (10.5%), Degens leatherjacket (5.7%), rough leatherjacket (1.2%), silverbelly (1.2%) and squid (Southern calamary) (0.9%). Squid has previously been observed to be a significant food item in the stomach content of *P. pelagicus* when feeding on by-catch (Choy, 1986; Williams, 1982). Similarly, laboratory results have indicated that the blue crab does show a preference for squid, more so than any other species tested (Rheinallt and Hughes, 1985). Crabs may select for food that maximises their net rate of energy intake (Hughes, 1979; Pyke, 1984). Micheli (1995) reported size selective conditioning for bivalve prey in the blue crab *Callinectes sapidus* and suggested that crabs learn to choose prey, which lower the associated cost of claw wear. Red mullet is a soft tissue fish, probably more so than silverbelly and squid, and the significance of any preference among by-catch species is unclear.

### 4.3. Relative consumption

Consumption rates of carrion reported in the Catalan Sea (northwestern Mediterranean) are 20–30 g/h (Bozzano and Sarda, 2002). In this study consumption was found to be 164.6 g/h, which is eight times higher. The mid-water experiments did not reveal any scavengers, which is in accordance with the results of Wassenberg and Hill (1990) who found in a study on discards in the Moreton Bay prawn fishery that only 2 of 185 baits from 23 vertical set lines were eaten. Spencer Gulf is an oligotroph environment with a large number of generalist predators and scavengers especially teleosts and elasmobranchs (finfish, sharks and rays). These species appear to contribute significantly to the total biomass. Ramsay et al. (1997) suggested that the impact of carrion on scavenger species might be affected by local natural food supply. In the field, competition between individuals and species food preference is likely to be an over-riding factor although most of the scavenger species in Spencer Gulf appear to be generalists.

This study showed that the relative consumption between the dominant scavenger species was different between sites and between day and night (Fig. 9A and B). By far the most voracious scavengers during the day were leatherjackets towards south and blue crabs towards north and during the night sealice, which occurred in large numbers particularly at Sites 2–4 where the highest historical number of trawl hours are also recorded. At these sites, sealice are likely to consume at least 60–80% of the discarded by-catch.

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