Western rock lobsters (*Panulirus cygnus* George.) in Western Australian deep-coastal ecosystems (35-60 m) are more carnivorous than those in shallow-coastal ecosystems.

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Abstract

The western rock lobster (*Panurilus cygnus*) is a conspicuous consumer in the coastal ecosystems of temperate Western Australia. We used stable isotope analysis and gut content analysis to determine the diet and trophic position of western rock lobsters from mid-shelf coastal ecosystems (35-60 m depth) at three locations. Lobsters were primarily carnivorous, and no consistent differences in diet were detected with varying lobster size, sex or among locations. The main components of the diet were bait (from the fishery) and small crustaceans — crabs and amphipods/isopods. Foliose red algae, bivalves/gastropods and sponges were minor contributors to diet. The diet of lobsters in deep-coastal ecosystems differed to results of previous studies of diets of lobsters from shallow coastal ecosystems. In particular, coralline algae and molluscs — important prey in studies of lobsters from shallow coastal ecosystems — were minor components of the diet. These differences are likely to reflect differences in food availability between these systems and potentially, differences in choice of prey by lobsters that inhabit deeper water. Given the high contribution of bait to lobster diet, bait is likely to be subsidizing lobster production in deep coastal ecosystems during the fishing season.

Keywords

Trophic relationships; bait; carnivores; diet; *Panulirus cygnus*; deep-coastal ecosystems.

1. Introduction

Knowledge of species' diets and trophic position is fundamental to understanding food webs which is key to understanding the dynamics of ecosystems. The composition of a consumer's diet can provide numerous insights including how energy is transferred through food webs, and the ultimate sources of production supporting food webs (Polis and Strong, 1996). Trophic position provides a general framework for understanding the direct and indirect interactions between predators and prey (Polis and Strong, 1996).

Understanding the diet and trophic position of spiny lobsters is important as their feeding ecology can strongly influence ecosystem structure (Tarr et al., 1996; Tegner and Dayton, 2000; Shears and Babcock, 2002; Langlois et al., 2005). Predation by spiny lobsters has caused differences in the abundances and sizes of their prey in New Zealand (Shears and Babcock, 2002; Langlois et al., 2005; Langlois et al., 2006b), Tasmania (Pederson and Johnson, 2006), South Africa (Tarr et al., 1996; Mayfield and Branch, 2000) and California (Tegner and Levin, 1983). These changes in prey abundance can lead to indirect effects on other elements of the ecosystem (e.g. Babcock et al., 1999).

The diet of spiny lobsters can change with lobster size (Goni et al., 2001; Mayfield et al., 2001; Langlois et al., 2006b). Differences in choice of prey have been demonstrated for *Jasus edwardsii*, with larger lobsters tending to choose large prey and smaller lobsters tending to choose small prey (Langlois et al., 2006b). Such patterns may relate to an increased ability of larger lobsters to consume larger, hard-shelled prey (Robles et al.,

1990), although prey choice may also be influenced by a relationship between energetic value of prey and energetic costs of prey capture and consumption (Hughes, 1980). Changes in choice of prey with increases in lobster size have been shown to affect prey community composition inside marine reserves where large lobsters are more abundant (Langlois et al., 2006a).

The western rock lobster (*Panulirus cygnus*) is conspicuous along the west coast of Australia (Phillips, 1990). Previous studies have found that juvenile *P. cygnus* consume a wide range of benthic biota including molluscs, polychaetes, small crustaceans and coralline algae (Joll and Phillips, 1984; Edgar, 1990; Jernakoff et al., 1993). However, these investigations have focused on shallow coastal ecosystems (<5 m depth). The diet of lobsters in deeper coastal ecosystems (>35 m depth) has been poorly studied. The size structure of lobsters in these deep-coastal ecosystems differs significantly from those in shallow water. Deeper coastal ecosystems are occupied by a greater proportion of adult lobsters; approximately 25% of *P. cygnus* in deeper water (>35 m) are >80 mm carapace length (unpublished catch and effort statistics, Department of Fisheries Western Australia 2007), while the proportion of >80 mm *P. cygnus* in shallow coastal ecosystems (<5 m) is approximately 4% (LD MacArthur, unpublished data). In addition, approximately 40% of the commercial catch of *P. cygnus* is taken from depths >35 m (unpublished catch and effort statistics, Department of Fisheries Western Australia 2007). The differences in lobster size structure between deep and shallow coastal ecosystems may therefore result in differences in diet, and so differences in trophic interactions by lobsters. Because of

this, the potential indirect effects of fishing between shallow and deep-coastal ecosystems may differ in important ways.

In this study, we used stable isotope and gut content analyses to determine the diet and trophic position of *Panulirus cygnus* in deep-coastal (35-60 m depth) ecosystems. Stable isotopes of carbon and nitrogen provide a low resolution estimate of diet integrated over long periods of time (months) that can help unravel complex food webs and identify important trophic relationships within ecosystems (Fry, 1988; Jennings et al., 1997; Davenport and Bax, 2002; Post, 2002). Analyses of gut contents provides higher resolution dietary information for a shorter time period — between ingestion and assimilation of food (Overman and Parrish, 2001) — and are also useful in verifying results from stable isotope analyses (Whitledge and Rabeni, 1997). The aim of this study was to determine diet and trophic position of *P. cygnus*, focusing on whether these varied spatially, or according to lobster size or sex.

2. Methods

2.1 Study area

This study was conducted at three locations on the west coast of Australia: Lancelin (30° 58.2 S, 114° 57.1 E), Jurien Bay (30° 12.5 S, 114° 39.1 E) and Dongara (29° 18.9 S, 114° 38.5 E). These locations span 200 km of coast near the center of the distribution of *P. cygnus*. Four sites were selected at Lancelin and Jurien Bay and five sites were selected at

Dongara, with sites separated by at least 2 km. Sites contained higher relief than the surrounding reef habitat, and were selected to maximize probability of encountering lobsters. The sites were located 20-40 km from the shore in 35-60 m depth. The sea floor is comprised of limestone reefs, which are remnants of Pleistocene/Holocene coastal sand dunes (Seddon, 1972; Searle and Semeniuk, 1985). Offshore reefs are typically low relief (<1 m relief) and are dominated by kelp, *Ecklonia radiata*, and sponges (Kris Waddington, unpublished data).

2.2. Collection

Divers breathing mixed gas (Enriched Air Nitrox, Trimix) from SCUBA apparatus collected biota at each site between 28th March and 10th April 2006. For reef biota, the entire contents of a 0.25m² quadrat were removed using a paint scraper and placed in a calico bag, ensuring no material was lost (n=2 per site for Dongara and Jurien Bay and n=3 per site for Lancelin). For sediment biota, cores (100 mm diameter × 200 mm deep) were collected from sediment adjacent to the reef (n=2 for each site). Small sample sizes reflect the difficulty of sampling at these depths. At the completion of each dive, samples were frozen for later sorting in the laboratory.

Lobsters were collected by the divers from three of the sites at each location. Lobsters were collected within 2 hours of sunrise using a noose and were between 53.7 and 144.6 mm carapace length (CL). Collection occurred soon after sunrise to minimise error associated with variable evacuation rates of gut contents (Waddington, In press).

Following collection, lobsters were immersed in an ice-slurry to induce a chill coma.

Lobster size, sex and moult stage were recorded. Lobster foreguts were then removed and frozen for later gut content analysis. A sample of muscle tissue for stable isotope analysis was dissected from the tail and frozen. Additional lobsters were collected from Jurien Bay using unbaited pots. Pots were set overnight and retrieved within one hour of sunrise and foreguts and tail muscle removed as described above. Baited pots were unsuitable for collecting lobsters for gut content analysis as the lobsters fed on bait in the pots, and so gut contents would be biased. Exclusion of the bait using 'bait savers' attracted isopods (*Natatolana* sp.), which the lobsters fed on, also causing bias (Kris Waddington personal observation, 2005). However, baited pots were suitable for collecting lobsters for stable isotope analysis, and were used to collect additional lobsters from Lancelin and Dongara between 20th and 30th April 2006.

2.3 Stable isotope analyses

In the laboratory, biota collected from quadrats and cores were defrosted, sorted, and identified to at least family level. Sediment cores were sieved and potential lobster prey removed. Bulk tissue of macroalgae, muscle tissue from tails of lobsters, and whole (or multiple whole) polychaetes, crabs, amphipods and isopods were used for stable isotope analysis. The flesh of imported mackerel (*Scomber* spp.) and Australian pilchards (*Sardinops sagax* Jenyns) – two baits commonly used in the fishery – were also analysed as they were possible lobster dietary items. All samples were rinsed in de-ionised water, dried in an oven at 60 °C until completely dry, then ground to a fine powder using a ball

mill grinder. Samples containing non-dietary carbonates (crabs, amphipods, isopods, coralline algae) were treated with 1M HCl to dissolve these non-dietary carbonates (Bunn et al. 1995).

Continuous-flow isotope ratio mass spectrometry using Europa Scientific (Roboprep-CN/Tracermass and ANCA-NT/20-20 units) and Isogas Sira 9 Instruments were used to measure $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. Most samples were analysed in dual isotope mode, allowing $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ to be measured simultaneously. Samples containing non-dietary carbonates were analysed for $\delta^{15}\text{N}$ prior to acid treatment, and analysed for $\delta^{13}\text{C}$ after acid treatment. Analytical precision of the instruments was 0.081 ‰ and 0.046 ‰ ($\pm$ se) for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ respectively. Cornflour, lobster muscle tissue and turnip calibrated against IAEA reference materials (IAEA-CH-6, IAEA-N-1, IAEA-N-2, USGS40, USGS41, USGS24) were used as internal standards for stable isotope analysis

2.4 Defining lobster dietary sources

The mixing model software IsoSource (Phillips and Gregg, 2003) was used to determine the range (1-99%) and mean contribution of each potential prey to lobster diet for each location (Lancelin n=25 lobsters, Jurien Bay n=19 lobsters, Dongara n=35 lobsters) (source increment 1%, tolerance 0.1). To reduce variability in mixing model outputs, we sought to combine similar diets prior to analysis. Only taxonomically related groups with similar life histories and feeding strategies were considered for combination (Phillips et al., 2005). The K nearest-neighbour randomization test was used to test for differences in

$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotope signatures of those groups considered for combination (Rosing et al., 1998), and taxa were combined if $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were not significantly different ($p < 0.05$).

The IsoSource method is appropriate when the number of dietary sources = $i+2$, where i is the number of elements (Phillips and Gregg, 2003). While no unique solution for the contribution of dietary sources exists, calculations yield the range of possible dietary source contributions to lobster diet (Phillips and Gregg, 2003). Values for consumer-diet discrimination (2.57‰ for $\delta^{15}\text{N}$ and 3.20‰ for $\delta^{13}\text{C}$), determined from a separate experiment (Waddington and MacArthur, In press) were used to ‘adjust’ stable isotope values before input to IsoSource. Sites within locations were pooled for these analyses.

2.5 Trophic position of lobsters

A continuous measure of trophic position of *P. cygnus* was calculated. A continuous measure of trophic position is useful in ecological studies as assigning organisms to discrete levels ignores processes such as omnivory and diet shifts (Polis and Strong, 1996; Vanderklift et al., 2006). The following formula modified from (Vander Zanden et al., 1997) was used to determine trophic position of lobsters:

$$\text{Trophic Position} = \frac{\text{lobster } \delta^{15}\text{N} - \text{macroalgae } \delta^{15}\text{N}}{2.57} + 1,$$

where 2.57 is the average consumer-diet discrimination between lobster tail muscle tissue and diet (Waddington and MacArthur, In press). The trophic position of lobsters was

calculated relative to the $\delta^{15}\text{N}$ value for macroalgae. The $\delta^{15}\text{N}$ values of red, green and brown algae were consistent.

2.6 Gut content analyses

Lobster foreguts were defrosted, blotted dry and weighed. After removing the gut contents, the foregut membrane was blotted dry and re-weighed. A quantitative index of gut fullness (GFI) was calculated for all lobsters collected by divers and using unbaited pots following Mayfield et al., (2000) as

$$\text{GFI} = \frac{\text{total foregut weight (g)} - \text{foregut membrane weight (g)}}{\text{total foregut weight (g)}} \times 100$$

The contents of lobster foreguts were rinsed into a 9.5 cm diameter petri dish and placed over a sheet with 60 randomly marked dots. The item over each dot was then identified to lowest possible taxonomic level using a dissecting microscope ($6.4\times - 40\times$ magnification), yielding a score out of a possible 60 for each prey (note that according to binomial probability, 60 points gives a 95% chance of recording a prey that makes up 5% or more of the gut contents (Vanderklift et al., 2006). The score for each prey was then multiplied by 100/60 to give percentage of each prey in the gut. Prey observed in the gut but not recorded using this method were assigned a value of 1%. Due to breakdown of dietary items in lobster guts, it was not always possible to identify prey to species level, and prey were more frequently identified to family level. Amphipods and isopod fragments could not be separated during identification so were combined.

All lobsters used in gut content analyses were in intermoult, and were caught by divers or using unbaited pots. Analyses were further restricted to lobster foreguts with GFI >10 to avoid biases introduced by individuals with guts containing few dietary items. Distance-based multivariate multiple regression, DISTLM (Legendre and Anderson, 1999; McArdle and Anderson, 2001) was used to test for relationships between gut content composition and lobster size, sex, location of capture (Lancelin, Jurien Bay, Dongara), method of capture (unbaited pot, diver) and gut fullness (GFI). The analysis was based on Bray-Curtis dissimilarities and significance was determined by 4 999 permutations of the raw data.

2.7 Prey electivity

Ivlev's index of prey electivity (Ivlev, 1961) was used to calculate electivity by *P. cygnus*. Ivlev's index of electivity (E) relates the proportional abundance of a prey on the benthos (determined from quadrats and sediment cores collected by divers) relative to the proportional abundance of that prey within a lobster gut as:

$$\text{Ivlev's index (E)} = \frac{r_i - p_i}{r_i + p_i},$$

where r_i represents the proportion of prey i on the benthos, and p_i represents the proportion of prey i in the gut of the lobster. Electivity of -1 indicates the prey is inaccessible, or there is total selection against the prey, while electivity of +1 indicates there is complete selection for the prey. A value near 0 indicates the item is consumed in proportion to its abundance on the benthos. Electivity was calculated for prey making up >1 % of gut contents. Due to insufficient sample size, lobsters at Lancelin and Dongara

were not considered. Ivlev's index can be biased by different availability of food to predators, and by differences in prey digestion rates (Kohler and Ney, 1982).

3. Results

3.1 Determination of diet using stable isotopes

The stable isotope values of the potential diets of western rock lobster were generally consistent between locations (Figure 1a-c). The range of values was similar for all three locations (between -28 ‰ and -12 ‰ for $\delta^{13}\text{C}$ and between 4 ‰ and 11 ‰ for $\delta^{15}\text{N}$). However at Dongara (Figure 1c), $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of amphipods/isopods were higher than the other two locations. Foliose red algae from Lancelin had lower $\delta^{13}\text{C}$, and higher $\delta^{15}\text{N}$, than foliose red algae from the other locations.

At all locations gut content analysis indicated that lobsters were omnivorous, preying on amphipods/isopods, crabs, bait, foliose red algae and sponges. However, the proportional contribution of each diet, as estimated by IsoSource, differed among the three locations (Figure 2a-c). One consistent pattern was that bait, crabs, and amphipods/isopods were likely to be important components of the diet at all locations. Bait was estimated to have contributed between 30 and 57% of the diet of lobsters at Lancelin, between 62 and 79% at Jurien Bay, and between 4 and 70% of diet of lobsters at Dongara. Crabs (Lancelin 0-50%; Jurien Bay 0-26%; Dongara 0-76%), and amphipods/isopods (Lancelin 0-54%; Jurien Bay 0-23%; Dongara 0-52%) were also likely to be important diets at all three

locations. Foliose red algae (Lancelin 6-25%; Jurien Bay 2-13%; Dongara 0-13%) and sponges (Lancelin 0-16%; Jurien Bay 0-11%; Dongara 0-15%) were likely to be of lesser importance. IsoSource also estimated that lobsters at Dongara might also prey on molluscs (bivalves and/or gastropods: 0-24%). These taxa were not observed in benthic samples collected from Lancelin or Jurien Bay and so were not included in the IsoSource analyses.

3.2 Trophic position

The trophic position of lobsters was calculated relative to the $\delta^{15}\text{N}$ value for macroalgae. The $\delta^{15}\text{N}$ values of red, green, and brown algae were consistent. Lobsters occupied the trophic positions expected by a first-order predator (i.e. ~ 2), with trophic position at each location between 1.90 and 2.18. Trophic positions varied significantly among locations (ANOVA: $F_{75,2} = 7.724$, $p < 0.001$), although the magnitude of differences was small. Post hoc Tukey tests indicated that lobsters from Lancelin occupied a significantly higher trophic level (2.18 ± 0.06 , $n=25$) than lobsters from Dongara (1.90 ± 0.05 , $n=35$) ($p < 0.001$) while lobsters from Jurien Bay were intermediate (2.01 ± 0.04 , $n=18$) and were not significantly different to lobsters from either Lancelin or Dongara.

3.3. Gut content analysis

Neither size, sex, location of capture, method of capture, nor gut fullness index were found to be significantly related to the composition of gut contents ($n=30$) (Tables 1 and

2). Thus all locations were combined for further analysis. The composition of food items in lobster foreguts were dominated by crabs (61.8%): bait (13.9%) and amphipods/isopods (9.1%) were also important (Figure 3). Bivalves/gastropods, foliose red algae, sponges, and polychaetes each comprised less than 2% of gut contents (Figure 3).

3.4 Electivity

Lobsters at Jurien Bay exhibited clear electivity for some prey (Figure 4). Such differences may result from selection for or against prey, differences in accessibility of prey, or differences in evacuation rates of prey from lobster foreguts. Amphipods/isopods and crabs were selected for by lobsters and/or were highly available to lobsters when foraging. Conversely, lobsters selected against polychaetes and/or polychaetes were less accessible to the lobsters during foraging. Bivalves/gastropods were selected for, although not as strongly as amphipods/isopods and crabs.

4. Discussion

At the locations sampled, western rock lobsters in deep coastal (35-60 m) ecosystems were primarily carnivorous, with a diet consisting mainly of crabs, amphipods/isopods and bait, and small quantities of bivalves/gastropods, sponges and red algae. The diet of lobsters did not vary with sex, size or among locations. While conclusions drawn in the current study are based on data from a small number of quadrats and lobsters for gut

content analyses, results of this study provide important quantitative information regarding the diet of western rock lobsters in previously inaccessible ecosystems.

Stable isotope analysis and gut content analysis each indicated that bait is an important component of lobster diet, contributing 30-80% of diet. Bait is available to the lobsters while the lobsters are in the pots as well as in the form of discards from the fishing fleet. The high relief sites we targeted will presumably also be targeted by fishermen, perhaps increasing the bait input on a localized scale. In addition, our surveys occurred during the months of April and May. While the commercial fishing season operates between 15th November and 30th June, maximum fishing effort in deep-coastal ecosystems occurs between January and May. Our survey occurred during peak fishing times in deep-coastal ecosystems, suggesting the average contribution of bait to lobster diet over the entire year might be lower. Considering the tissue turnover rate for decapod crustaceans is less than three months (Fantle et al., 1999; Waddington and MacArthur, In press), the high contribution of bait determined from stable isotope analysis might reflect higher consumption of bait during the fishing season. Nevertheless, given the likelihood of high bait contribution to lobster diet, and the known positive relationship between growth rate and food availability for *Panulirus cygnus* (Chittleborough, 1976), bait input is likely to provide a significant subsidy to lobster growth in these ecosystems during the ~5 months that the fishing fleet is present. Bait has also been shown to subsidise production of American Lobsters (*Homarus americanus*) in the Gulf of Maine (Saila et al., 2002). In the Gulf of Maine, bait was estimated to meet between one-quarter and one-third of lobster food requirements (Saila et al., 2002), which is comparable to the results from the

current study. When present, bait appears to be highly selected for by the lobsters. High selection of bait by lobsters may be because lobster pots provide a ready source of food and shelter, two important resources for spiny lobsters (Chittleborough, 1975; Eggleston and Lipcius, 1992). However, due to spatial and temporal variability in bait addition, formal comparison of electivity is not possible using Ivlev's electivity index (Ivlev, 1961).

Bait is imported from outside the study area, meaning it represents a direct subsidy to lobster production in these ecosystems (Saila et al., 2002). Addition of organic matter by fishing fleets to marine ecosystems has been shown to have consequences for the functioning of marine ecosystems worldwide, primarily through the enhancement of secondary production from trawl discards (Groenewold and Fonds 2000; Ramsay et al. 1997). It is highly likely that addition of organic matter in the form of bait may be having similar effects in Western Australian ecosystems, particularly given the oligotrophic nature of these systems (Lenanton et al. 1991). Further studies should be undertaken to investigate the potential effects of bait input in these systems.

The natural diet of western rock lobsters was dominated by crabs and amphipods/isopods, with sponges, algae, gastropods/bivalves and polychaetes less important. Crabs and amphipods/isopods were strongly selected for – or alternatively highly available to lobsters – relative to gastropods/bivalves, polychaetes, sponges and foliose red algae. Given the high biomass of sponges and red algae on the reef where lobsters were collected, the low importance of red algae and sponges to lobster diet is likely due to low

selection for these taxa. Polychaetes and gastropods have previously been shown to be important lobster prey in shallow coastal ecosystems (Joll and Phillips, 1984; Edgar, 1990; Jernakoff et al., 1993), suggesting the low proportion of these items observed in diet of lobsters in this study might be the result of low availability. Bivalves and gastropods were not frequently observed in benthic samples collected by divers in this study. While polychaetes were observed in samples collected by divers, they were most frequently observed within sponges collected from the benthos. A hypothesis for the low importance of polychaetes in lobster diet may relate to the burrowing habit of polychaetes (Netto et al., 1999; Abdo, 2007), providing a refuge from predation by lobsters.

The two techniques of dietary analysis employed in the current study gave differing outcomes for the proportional contribution of prey to lobster diet. Analysis using stable isotope data indicated bait was the most important component of lobster diet whereas gut content analysis indicated crabs were more important. Observed differences likely reflect the different time scales relevant for the two techniques (Overman and Parrish, 2001) and the variability in evacuation rates of prey from lobster guts (Waddington, In press). Gut content analysis provides an indication of lobster diet between ingestion and assimilation of prey (hours) whereas stable isotope analysis provides a time integrated description of lobster diet over the time scale equivalent to the tissue turnover rate (weeks to months) of the tissue analysed (Kling et al., 1992; Overman and Parrish, 2001). At the time lobsters were collected for gut content analysis crabs were the most important lobster prey. When the diet of lobsters was integrated over a longer period, bait was more important to lobster diet, likely reflecting the spatial and temporal variability of bait input to these

ecosystems. The relative contribution of crabs to lobster diet determined from gut content analysis could also be overestimated due to variability in evacuation rates of prey from lobster foreguts (Waddington, In press). A recent study indicated that prey with hard components were more slowly evacuated from lobster foreguts relative to diet items without these hard components (Waddington, In press). This suggests the relative contribution of crabs and bait may be overestimated in the current study relative to prey such as foliose red algae that are rapidly evacuated from lobster guts.

Diet of western rock lobsters in the current study differs to diet of western rock lobsters from shallow coastal ecosystems, which consume large quantities of algae (<10 m) (Joll and Phillips, 1984; Edgar, 1990; Jernakoff et al., 1993). Observed differences in lobster diet occur despite overlap in the lobster size: between 53.7 and 144.6 mm CL in the current study and 25 – 90 mm CL in the study by Edgar, (1990). It is therefore unlikely that lobster size/ontogenetic stage is driving observed differences in lobster diet. Lobsters in deep-coastal ecosystems predominantly consume animal prey (crabs, amphipods/isopods, and bait) and at Jurien Bay had a trophic position of 2.01. In contrast, lobsters from shallow coastal ecosystems at Jurien Bay had a trophic position between 1.50 and 1.60 (Lachlan MacArthur, Edith Cowan University, unpublished data) reflecting the importance of algae (primarily coralline algae) to lobsters in shallow coastal ecosystems (Joll and Phillips, 1984; Edgar, 1990; Jernakoff et al., 1993).

Differences in lobster diet between shallow and deep-coastal ecosystems may reflect differences in prey availability or prey choice between these ecosystems. Molluscs

comprise a high proportion of gut contents of lobsters from shallow coastal ecosystems (Joll and Phillips, 1984; Edgar, 1990; Jernakoff et al., 1993), but were poorly represented in gut contents in the current study. This low consumption of molluscs likely reflects low abundances of molluscs in the benthos, evidenced by the benthic samples collected from Lancelin and Jurien Bay. Two species of coralline algae commonly consumed by lobsters in shallow coastal ecosystems (*Jania affinis* and *Amphiroa anceps*) (Joll and Phillips, 1984) were not observed to be consumed in the current study, despite being present in deep-coastal ecosystems (average biomass $\sim 80 \text{ g. m}^{-2}$). This indicates differences in diet may also reflect differences in prey choice between shallow and deep-coastal ecosystems.

Differences in lobster diet between shallow coastal and deep-coastal ecosystems have implications when assessing the effect of lobster removal on these ecosystems. Removal of spiny lobsters (through fishing) reduces predation pressure on lower trophic levels (Tegner and Dayton, 2000). Differences in spiny lobster abundance due to differences in exploitation rates have been shown to have detectable effects on abundance of spiny lobster prey in California (Tegner and Levin, 1983), South Africa (Mayfield and Branch, 2000), New Zealand (Shears and Babcock, 2002; Langlois et al., 2005), and Tasmania (Pederson and Johnson, 2006). As lobsters inhabiting deep-coastal ecosystems are mostly carnivorous, the interaction between lobsters and macroinvertebrates is likely stronger than the interaction between lobsters and macroinvertebrate communities in shallow coastal ecosystems where lobsters are omnivorous. Thus, when assessing impacts of fishing on these ecosystems the effect of lobster removal on macroinvertebrate community composition is likely to be greater in deep-coastal ecosystems where lobsters

principally consume macroinvertebrates. In shallow coastal ecosystems, lobster removal may have weaker effects on macroinvertebrate community composition as lobsters also prey upon coralline algae.

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Tables

Table 1: Distance-based multivariate multiple regression (DISTLM) testing for the significance of variation in the composition of lobster guts contents explained by lobster size, lobster sex, location of capture, and method of capture. p-value determined by 4,999 permutations of the raw data.

Source of Variation	df	SS	MS	pseudo F	p value
All variables	5	12 268	2 453	1.30	0.216
Residual	19	35 749	1 881		
Total	24				

Table 2: Percentage composition of food in lobster foreguts at each location. All lobsters were caught by divers or in unbaited pots.

	Lancelin n=5 53.7-114.5 mm CL	Jurien Bay n=19 54.1-81.9 mm CL	Dongara n=6 64.1-144.6 mm CL
Prey Item	mean ($\pm$ se)	mean ($\pm$ se)	mean ($\pm$ se)
Crab	79.19 $\pm$ 10.61	54.90 $\pm$ 8.61	79.88 $\pm$ 7.16
Amphipods / Isopods	6.11 $\pm$ 4.73	10.01 $\pm$ 5.56	3.33 $\pm$ 3.12
Bait	8.02 $\pm$ 3.22	18.27 $\pm$ 7.42	8.9 $\pm$ 3.05
Sediment	0	9.37 $\pm$ 4.48	0
Bivalves/Gastropods	0.56 $\pm$ 0.43	1.61 $\pm$ 0.62	7.78 $\pm$ 4.84
Algae	2.22 $\pm$ 1.72	0.70 $\pm$ 0.34	0
<i>Sponge</i>	2.22 $\pm$ 1.72	0.94 $\pm$ 0.43	0

Figure captions

Figure 1: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of western rock lobsters and potential prey in deep coastal ecosystems off (a) Lancelin, (b) Jurien Bay, and (c) Dongara, Western Australia. Prey comprising <1% of diet (determined by gut content analysis) are not shown.

Figure 2: Distribution of feasible proportions of contribution of potential prey to diet of lobsters collected from (a) Lancelin (b) Jurien Bay and (c) Dongara. Outside tick marks represent range of feasible proportions (1-99%). Midline represents mean of feasible proportions. RA = Red Algae, A/I = Amphipods/Isopods, Sp. = Sponge, B/G = Bivalves/Gastropods.

Figure 3: Percentage (mean $\pm$ se, n=30) of diet categories in lobster foreguts at all locations. All lobsters were caught by divers or in unbaited pots. Diet categories comprising <1% of diet are not shown on graph. A/I = Amphipods/Isopods, Sed. = Sediment, B/G. = Bivalves/Gastropods.

Figure 4: Ivlev's index of prey electivity for taxa observed in the guts of lobsters collected from Jurien Bay (n=19). A/I = Amphipods/Isopods, Cr. = Crabs, RA = Red Algae, Poly = Polychaetes, B/G = Bivalves/Gastropods.

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