

Vanderklift, M.A., Kendrick, G.A., Smit, A.J. (2006). Differences in trophic position among sympatric sea urchin species. *Estuarine, Coastal and Shelf Science* 66: 291-297.

Vanderklift, M.A., Ponsard, S. (2003). Sources of variation in consumer-diet delta N-15 enrichment: a meta-analysis. *Oecologia*: 136(2), 169-182.

Conference attendance, presentations, publications and/or outcomes to date

At this early stage in the Trophodynamics project, work has concentrated on the successful execution of the two major field studies of trophic relationships within Jurien Bay Marine Park, and on the laboratory processing and analysis of samples from this field work. We are now in a position to start examining and presenting preliminary results, and this will be the focus of our future dissemination efforts.

Plans for 2006 include:

- Presentation of the Trophodynamics project outline and preliminary results at the University of Nice, France and the Dauphin Island Sea Lab, USA.
- Assisting in the organisation of, and participating in, a Jurien Bay Marine Science symposium day, to be held in Jurien Bay in conjunction with CALM. This will assist in informing the local park managers, fellow Jurien-based researchers and general public of the Trophodynamics project and its significance for the region.
- Presentation of preliminary results at the SRFME Core and Collaborative Projects Symposium, held at CSIRO.
- Presentation of the Trophodynamics project outline and preliminary results at the Centre for Ecosystem Management (CEM) Seminar Series, held at ECU.
- Creation of a large poster detailing the Trophodynamics project, including preliminary results and future plans, to be displayed at ECU and other venues where appropriate.
- Project outline and preliminary results to be posted on a Trophodynamics project webpage within the Coastal Marine Ecosystem Research (CMER) website, based at ECU.

3.3.5 Ecological Interactions in Coastal Marine Ecosystems: Rock Lobster

Principal Investigators / Institutions

Dr Glenn Hyndes Senior Lecturer, School of Natural Sciences, Edith Cowan University, 100 Joondalup Drive, Joondalup WA 6027
Phone: 6304 5798 Fax: 6304 5509 Email: g.hyndes@ecu.edu.au

Lachlan MacArthur PhD Candidate, School of Natural Sciences, Edith Cowan University, 100 Joondalup Drive, Joondalup WA 6027
Phone: 6304 5010 Fax: 6304 5509 Email: l.macarthur@ecu.edu.au

Co Investigators / Institutions

Dr Russ Babcock Senior Research Scientist, CSIRO Marine and Atmospheric Research, Underwood Ave, Floreat WA 6014
Phone: 9333 6535 Fax: 9333 6555 Email: russ.babcock@csiro.au

Dr Mat Vanderklift Research Scientist, CSIRO Marine and Atmospheric Research, Underwood Ave, Floreat WA 6014 Phone: 9333 6536
Fax: 9333 6555 Email: mat.vanderklift@csiro.au

Executive Summary

The density and size structure of western rock lobster (*Panulirus cygnus*) populations within the Jurien Bay Marine Park have been determined from up to 15 sites stratified by depth, cross-shelf location and benthic habitat. Surveys have been conducted over four sampling periods, with a further two remaining. The results indicate that there are larger numbers of smaller lobster less than 60 mm carapace length (CL) on shallow inshore reefs with high seagrass coverage. All sites have lobster within the 60 to 80 mm (CL) size class, although densities are lower on the more offshore sites characterised by macroalgae. However, a number of exposed sites have not been consistently sampled due to high swell conditions, and some seasons have not yet been repeated so any conclusions at this stage must be considered preliminary. In addition, gut samples and stable isotope samples have been collected from 193 lobster specimens obtained over two seasons from sites differing in surrounding benthic habitat. Early results indicate that articulated coralline algae, in particular, contributes the highest to overall diet in terms of volume consumed, and this holds true over all habitats. However, stable isotope analysis indicates that other food sources may contribute more to lobster production. Research into the movements of rock lobster is currently underway using acoustic transmitters and receivers. Results will emerge early next year and will help us understand home-range, foraging and migration patterns within coastal waters.

Studies of major predator groups - rock lobster

The Western Australian rock Lobster *Panulirus cygnus* is the dominant invertebrate predator in coastal and shelf ecosystems between Northwest Cape and Cape Leeuwin. As such it is likely to have an important role in the dynamics of these ecosystems. Because of ontogenetic changes in the spatial distribution of western rock lobster these dynamics are likely to be complex, and interactions with a large commercial fishery have the potential to add further layers of complexity. Puerulus settle on shallow coastal reefs, where they spend the first months of their lives solitary and sheltering in small crevices in limestone reefs during the day and foraging at night in algal turf and seagrass habitats (Fitzpatrick *et al.* 1989, Jernakoff 1990). As they grow the young lobsters become less solitary and move into larger caves and crevices on deeper reefs where they shelter during the day (Jernakoff 1990). Less is known about the foraging and feeding of lobsters and the range of habitats that they use at this stage, which lasts until about the age of 4 years when many of the lobsters undertake long distance migration into deeper waters (>30m), well off the coastal reef systems (Phillips 1983). It is at around this time that the lobsters reach legal size and enter the fishery.

Gaps in our knowledge of rock lobster ecology in shallow waters relate primarily to two areas: habitat use and feeding; and population structure. Our understanding of how lobsters use deeper reefs, sandy areas, and seagrass habitats such as *Posidonia* meadows with respect to shelter and foraging, and the principal prey of lobsters in these habitats, is not complete. We know that lobsters of different sizes tend to be found in different habitats but it is unclear how the population structure of lobsters in shallow water may have changed as a result of fishing. Anecdotal historical reports describe large rock lobster as being present or common in shallow reef systems in the past, yet such individuals are now very rare in shallow coastal reef systems. Consequently, the historical role of rock lobsters in shallow coastal ecosystems (and the indirect effects of fishing on ecosystem structure and function) is difficult to assess.

In order to effectively study or to demonstrate the potential role of predation by rock lobster on coastal benthic communities, we require populations of lobsters with differing population structures and that vary over a range of population densities. The reason for this is simple. For example, we may design caging experiments to exclude lobsters but if they are not present, the exclusion will make little difference to the experimental results. This may be especially relevant to determining the influence of larger rock lobsters. One way of gaining access to such populations of lobsters is to use fished and unfished areas. Such areas are currently being established at Jurien and are potentially extremely useful experimental tools. However, it is not clear whether strong contrasts in lobster density or population structure will develop.

Studies of rock lobster populations in other parts of the world have shown, using no-take marine protected areas (MPAs), that there are significant changes to population structure and also to total biomass inside these areas relative to fished areas (Kelly et al 1999, Edgar and Barrett 1999, Lafferty and Kushner 2000), but such changes are not observed universally, possibly because either they lack suitable habitat (Mayfield et al 2000) or, where species are highly mobile, MPA boundaries fragment suitable habitat (Acosta 2001). Since most *P. cygnus* reach legal size and move into deeper water at the age of around 4 years, and most of the Sanctuaries within the Jurien Marine Park are located in relatively shallow waters, it may be that there is little if any detectable effect of fishing on shallow water populations.

Developing an understanding of the variation in density and population structure of rock lobsters, and its resulting consequences, is intimately related to ontogenetic shifts in habitat utilization. Broadly speaking lobsters settle on inshore reefs as puerulus and live in inshore areas until approximately the age of 4 yrs at which time they move into deeper shelf waters. Whether there are finer scale habitat preferences of lobsters within this framework is not clear. For example, is there an incremental shift of lobsters from coastal and lagoon reefs to offshore reefs as they grow older, and do lobsters prefer particular reef habitats? Also, vital to understanding the interactions of rock lobsters with benthic assemblages is the collection of data on how diet may vary with lobster size. Finally we need to know how lobsters use their habitat and the extent to which they move from one to another.

Need

Part of the rationale for basing SRFME collaborative projects in the Midwest relates to opportunities presented by the Jurien Bay Marine Park, however it will take some time for differences in predator abundance to develop and for the park to reach its potential as a useful tool for ecological research. Nevertheless it is important for studies to commence as soon as possible, for two reasons. Firstly, the convincing demonstration of any direct or indirect effects of fishing revealed by changes of fishing pressure in the park will rely on a BACI design. Therefore, we must act now to begin collecting all the necessary baseline data. Secondly, important information relating to trophic structure of coastal communities and how it varies among habitats as well as seasonally and interannually, can be collected now and will be a vital part of interpreting and potentially predicting any changes in ecological interactions that emerge as a result of park zoning. Given the high economic value of Western rock lobster and the greater emphasis on ecological effects of fishing through the EPB act, it is imperative that we gain a greater understanding of the impact of removal of rock lobster on the broader ecosystem. This study will mesh with other proposed and ongoing studies to provide a much better understanding of the movement of lobster and the flow of energy and nutrients at a range of spatial scales, from the small scale between habitats to larger cross-shelf scales. A conceptual diagram of the processes and patterns to be investigated is provided in Figure 3.29.

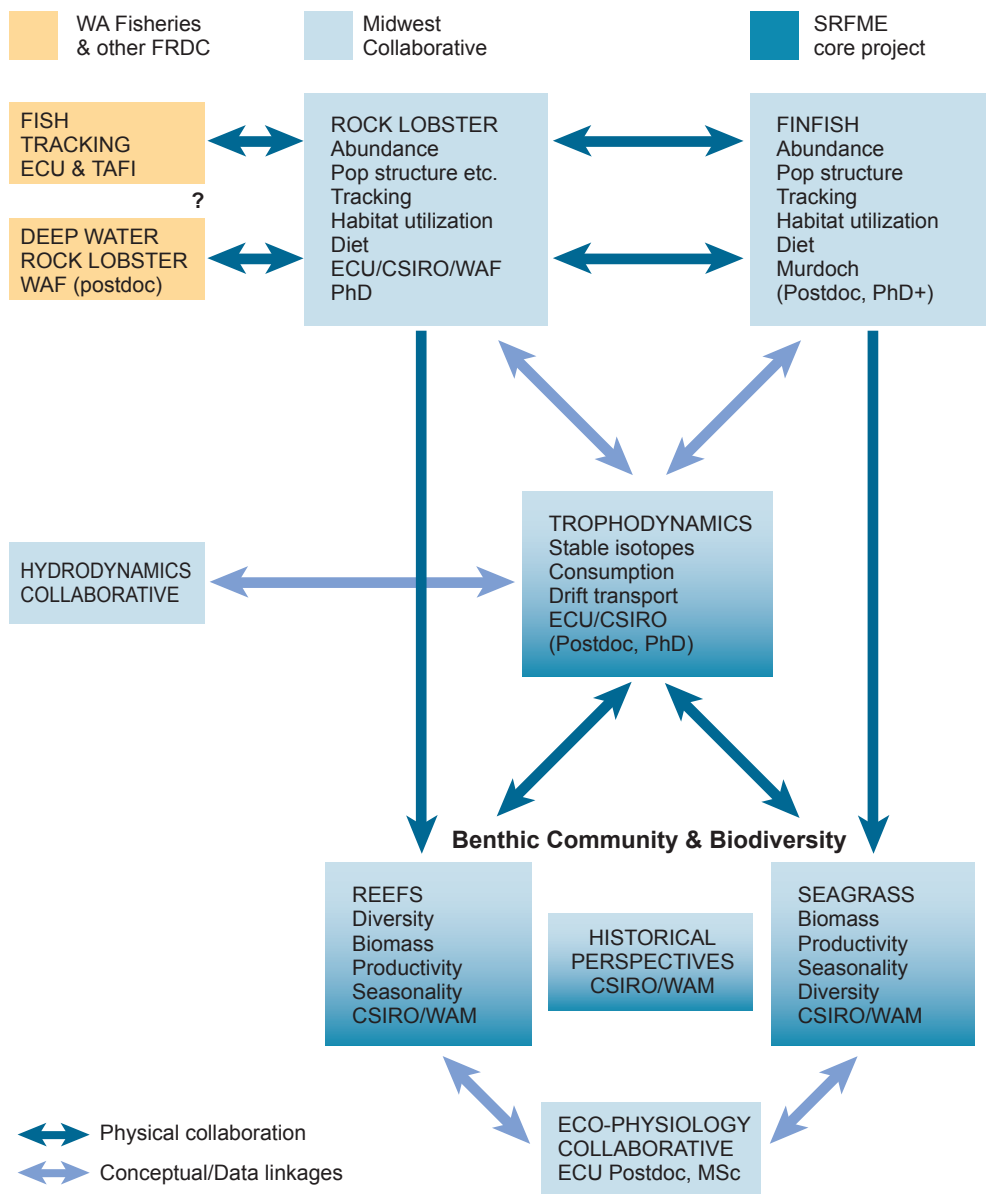


Figure 3.29: Midwest Collaborative Study Ecological interactions. The diagram indicates the main thematic components of the study, key institutional involvements, and their potential inter-relationships.

Objectives

The broad aim of this study is to determine the habitat use and trophic links of Western rock lobster in the mid-west region. This broad aim will be achieved through investigating the following specific objectives.

1. Determine the densities and size structure of western rock lobster in a range of different benthic habitats;
2. Determine the movement patterns of western rock lobster between reefs and foraging habitats;
3. Investigate dietary changes of western rock lobster with changes in size, habitat use and season; and
4. Provide baseline data that will allow the success of sanctuary zones in terms of increasing lobster abundance to be assessed in the future.

Methods

Lobster densities and population structures are being measured three times a year in October/ November, February/ March and July/ August on reefs less than 20 m depth. These sampling times allow comparisons of lobster abundance immediately before and after the 'whites' migration to deep water reefs as well as between open and closed seasons. Study sites are stratified according to habitat type, reef depth and cross-shelf location to account for physical habitat variability. In addition, sites are stratified with respect to levels of protection from fishing pressure, and include sanctuary zones, zones open only to commercial rock lobster fishing, and zones open to all kinds of fishing. Reef size, size of sanctuary and distance from sanctuary will be factored into analyses as co-variables. Sampling is being concentrated in two regions (e.g. Jurien and Green Head). The sampling philosophy is to study these areas within the Jurien Bay Marine Park intensively, rather than study all the zones in the park extensively. Portions of the core survey will be conducted in collaboration with CSIRO Marine Research as required to complete or extend the design as required.

Adult and sub-adult lobsters are being censused by divers using 30 x 5 m transects deployed parallel to the reef slope over reef habitat. Within each strata there are three sites, and four transects per site. The Carapace Length (CL) of all lobsters seen within transects is being estimated visually by trained and pre-calibrated divers. Data, including general habitat type, will be recorded in 5m blocks to enable subsequent spatial analysis.

Lobster diet is being determined from the gut contents of lobsters collected by divers within 1 hour of sunrise. Collections have been made in April and October 2006 from eight sites within four habitats (*Amphibolis* meadow, *Posidonia* meadow, shallow macroalgae/ *Amphibolis* pavement and deep sand/ pavement). Guts were taken from as wide a size range as possible and dissected immediately before being preserved in 70% ethanol. Contents are being identified to the lowest possible taxonomic level, classified according to trophic level, and quantified using image analysis of relative abundance.

In addition to gut content analysis, stable isotope analysis, to determine the levels of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in lobster flesh, is being conducted on the lobster collected from the habitats outlined above. Samples of primary producers, e.g. algae and seagrass, and potential lobster prey, e.g. gastropods and crustaceans, have also been collected concurrently from the same sites or sites adjacent to lobster collection sites. This will allow for the identification of primary producers and prey that are likely to contribute most to lobster production.

Lobster movements are being assessed across a range of spatial scales using several techniques. Standard Capture-Mark-Recapture using "spaghetti" tags inserted ventrally between the tail and carapace have been used to attempt to capture some information from the commercial and recreational fisheries. A subset of these animals have been tagged using colour coded tags placed around the base of the antennae and will allow for medium term re-sighting and identification of lobsters by divers. This method allows animals to be individually identified without handling and has proven useful in assessing levels of site fidelity over periods of 6-12 months.

Twenty four lobsters have been tagged using acoustic tags attached dorsally to the carapace using cable ties. This is allowing larger scale movements of animals to be tracked with an accuracy of approximately ± 100 m using an array of receivers covering an area of approximately 19 km². In particular, 4+ and 5+ year class animals have been targeted post-moulting in November and December 2006 as "whites". Most will be expected to take part in offshore migrations and may be picked up by offshore acoustic arrays, however some may remain in near-shore waters and establish long-term residence there (in the absence of fishing mortality). Therefore, in order to establish whether some animals remain resident on coastal reefs, the tracking is being conducted in the Boullanger sanctuary zone.

In addition, 18 lobster have been tracked over three sites differing in surrounding benthic habitat in order to assess important foraging habitat and lobster foraging range over typical coastal benthic habitats. These lobster have been tagged with acoustic tags in the manner outlined above and tracked using a boat operated acoustic receiver and directional hydrophone. Lobster were tracked during February 2006.

Results and Discussion

Lobster density and size-structure

Lobster density and population structure have been measured on coastal reefs during four sampling periods to date: November 2004, February /March 2005, August 2005 and November 2005. A further two trips remain (February /March 2006 and August 2006). The reefs surveyed are stratified by depth, distance from shore and major benthic habitat in order to determine how these factors may influence lobster density and population size-structure. In addition, some of these reefs are located within sanctuary zones and results will provide baseline data for examining the impact of these no-take zones on lobster populations. Reefs are sampled by SCUBA with the number of lobster and size estimates recorded over 4 replicate 30 x 5 m transects.

Results indicate that there is high inter-site variability in lobster densities as well as variability between sampling times (Fig. 3.30). There does not appear to be any clear relationship between habitat type and lobster densities nor between distance from shore and lobster density. For the midshore sites which were sampled on all occasions there does appear to be higher densities during November 2004 and 2005 than at other sampling times. The highest lobster densities were found at two inshore, seagrass dominated sites in November 2005 although further sampling is required to assess if this trend will repeat during subsequent years. A number of offshore sites have not been able to be sampled consistently due to high swell conditions (Fig. 3.30).

Length frequency histograms reveal that the carapace length (CL) of the majority of lobsters sampled fall between 45 and 80 mm (Fig. 3.31). Lobsters between 60 and 90 mm CL are found at nearshore, midshore and offshore sites, however smaller juveniles between 45 and 60 mm CL are more abundant in midshore and particularly nearshore sites and have not been recorded from offshore sites. For those sites located midshore there does not appear to be any relationship between lobster size and habitat type in that all sizes of lobster are found at both seagrass and macroalgae dominated habitat (Fig. 3.31).

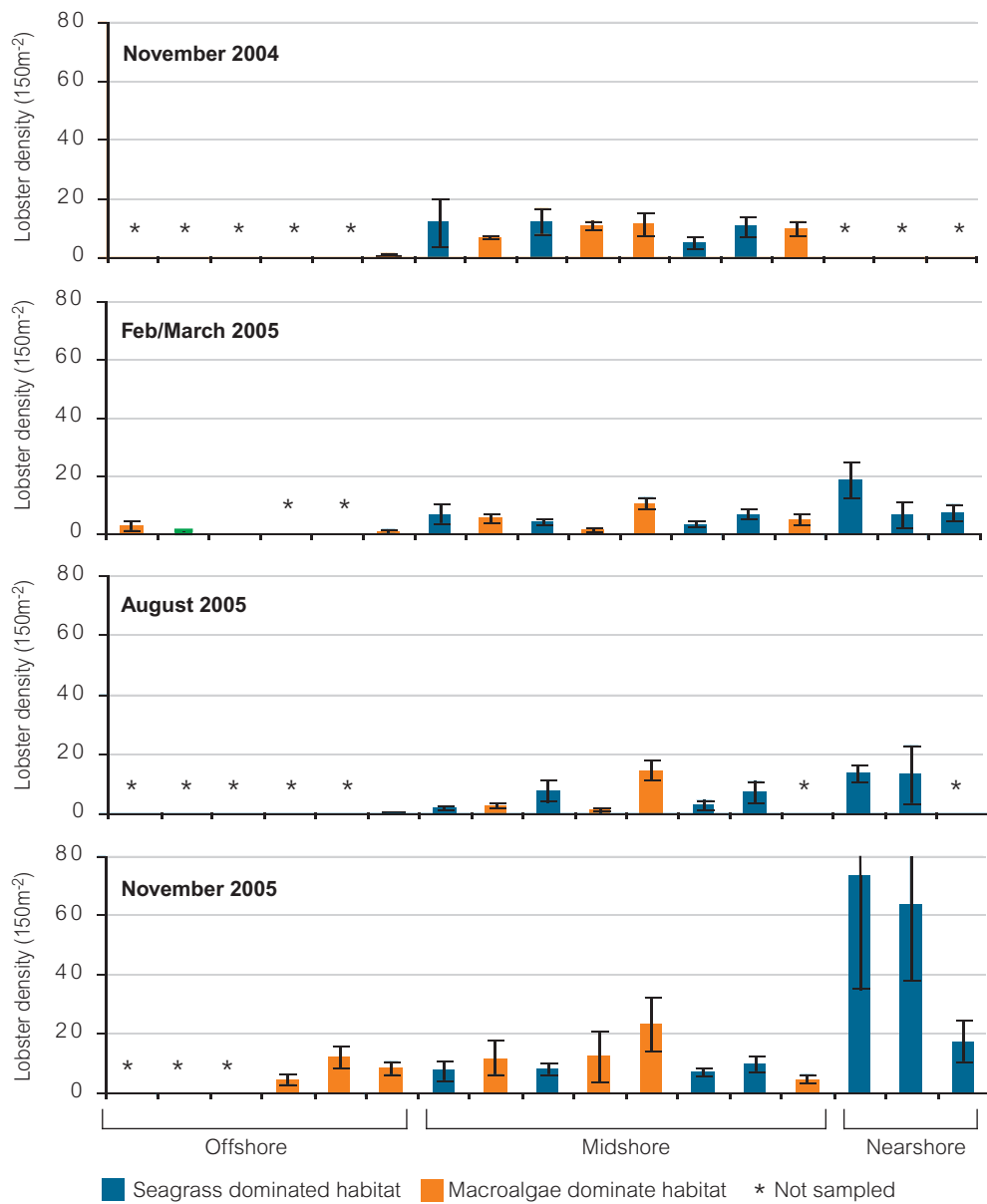


Figure 3.30: Density of lobster (± 1 se) surveyed between November 2004 and November 2005. “*” indicates site not sampled.

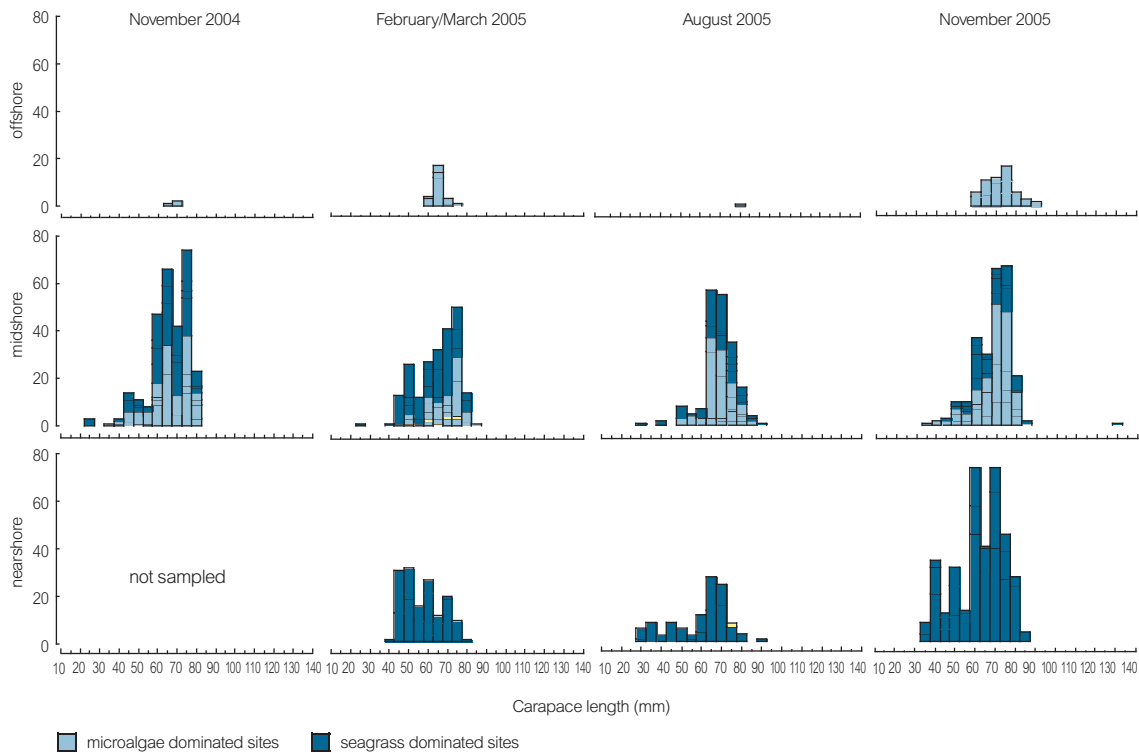


Figure 3.31: Carapace length frequency histograms of lobster collected between November 2004 and November 2005.

Lobster diet and trophic linkages

To investigate the diet and trophic interactions of western rock lobster 193 gut and stable isotope samples have been collected. Lobster were collected from four benthic habitat categories and from as wide a size range as possible (Table 3.4)

Table 3.4. Lobster numbers collected in April and October/ November 2005

Carapace length size class (mm)	Habitat							
	Deep low seagrass		Shallow pavement/ <i>Amphibolis</i>		<i>Posidonia sinuosa</i> meadow		<i>Amphibolis griffithii</i> meadow	
	Site							
	DC	DW	FN	FW	FS	OR	FE	BK
April 2005								
26-50	1	0	1	0	0	1	1	1
51-75	16	8	12	5	13	6	12	9
76-100	0	1	0	1	3	2	2	5
All sizes	17	9	13	6	16	9	15	15
October/ November 2005								
26-50	0	1	0	1	0	0	2	0
51-75	5	7	14	14	8	2	7	10
76-100	2	2	0	3	3	3	4	5
All sizes	7	10	14	18	11	5	13	15

Lobsters were collected within two hours of sunrise to minimise digestion of gut contents. Gut samples were then stored in 70% ethanol whilst flesh samples were frozen as soon as possible. To determine lobster diet, guts have been dissected and the volume of prey items contributing to each gut determined. This has been conducted for 50 of the guts collected to date.

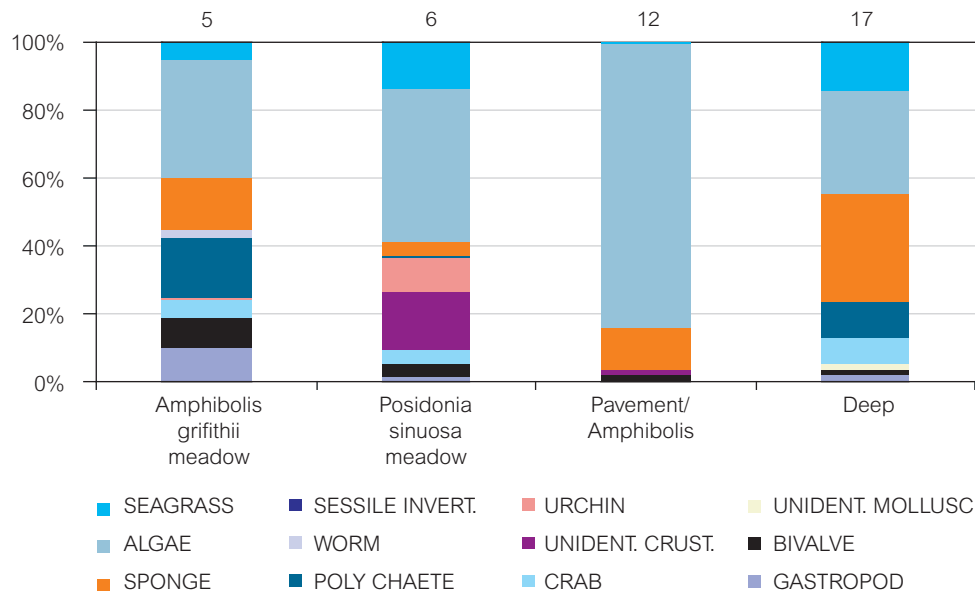


Figure 3.32: Major taxa contribution to total gut volume for lobster collected from four habitats during April 2005.

Preliminary results indicate that algae contribute greatly to overall gut volume for lobster from all habitat categories (Fig. 3.32). These algae comprise mainly articulated coralline algae such as *Haliptilon* and *Metagoniolithon* sp. Seagrass, sponge and polychaetes also comprise a relatively large proportion of gut volume in general. These results, although preliminary, indicate that lobster collected from shallow pavement/ *Amphibolis* habitat have a greater contribution of algae to their diets when compared to lobsters from other habitats, and consume only relatively small quantities of other food sources.

Stable isotope analysis, to determine the levels of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in lobster flesh, has been completed for a subset (87) of samples from the April 2005 collection period. Samples collected from the October/ November period are yet to be analysed. In addition, samples of primary producers, e.g. algae and seagrass, and potential lobster prey, e.g. gastropods and crustaceans, have been collected concurrently from the same sites or sites adjacent to lobster collection sites. This will allow for the identification of primary producers and prey that are likely to contribute most to lobster production.

Results from April 2005 indicate that whilst coralline algae such as *Haliptilon* and *Metagoniolithon* contribute a large amount to gut volume, the average $\delta^{13}\text{C}$ for these prey items are quite separate from that of lobster tissue (Fig. 3.33). This may indicate that other food sources may contribute more to lobster production.

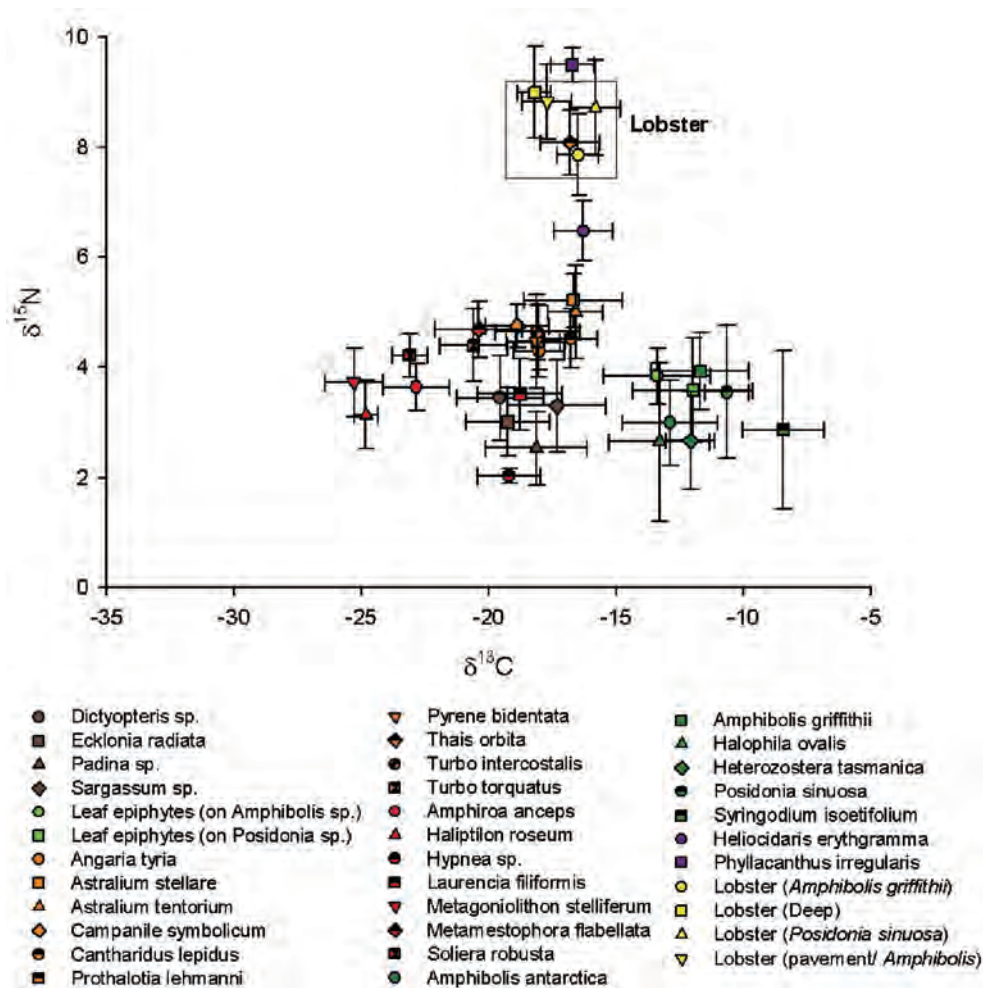


Figure 3.33: $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of lobster, primary producers and potential prey items collected from Jurien Bay during April 2005.

Lobster Movements

Lobsters movements are being assessed by the use of acoustic tags to study large-scale movements such as migration and nightly foraging movements. Twenty four lobsters have been tagged in the Boullanger sanctuary area within an array of fixed receivers. These receivers record lobster identification and time of reception when lobsters move within range. Lobsters were tagged in early December 2005 and we anticipate that migration movements may be recorded when data is uploaded and analysed.

Additionally, 18 lobsters have been tagged in three distinct benthic habitats (*Posidonia sinuosa*, *Amphibolis griffithii* and deep macroalgae habitat) and tracked using a manual receiver to determine foraging position during the night. On analysis, this data should reveal which habitats are used by foraging lobster and indicate how far lobster move during nightly foraging activities.

Acknowledgements

We wish to thank all the staff, students and volunteers who have assisted with the fieldwork to date. We also acknowledge funding support and in-kind support from the Strategic Research Fund for the Marine Environment, The Centre for Ecosystem Management and the School of Natural Sciences, Edith Cowan University.

References

- Acosta, C. A. (2001) Assessment of the functional effects of a harvest refuge on spiny lobster and queen conch populations at Glover's Reef, Belize. *Proceedings of the 52nd Gulf of Caribbean Fisheries Institute* 2: 212-221.
- Edgar, G. J. and Barrett, N. S. (1999) Effect of the declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants. *Journal of Experimental Marine Biology and Ecology*. 242: 107-144.
- Fitzpatrick J, Jernakoff P and Phillips B. F. (1989) An investigation of the habitat requirements of the post-juvenile stocks of the Western Rock Lobster. Final Report to the Fishing Industry Research and Development Council. Report No. 86/83.
- Jernakoff, P. (1990) Distribution of newly settled Western Rock Lobsters *Panulirus cygnus*. *Marine Ecology Progress Series* 66: 63-74.
- Kelly, S., MacDiarmid, A. B. and Babcock, R. C. (1999) Characteristics of spiny lobster, *Jasus edwardsii*, aggregations in exposed reef and sandy areas. *Marine and Freshwater Research* 50: 409-416.
- Lafferty, K. D. and Kushner, D. J. (2000) Population regulation of the purple sea urchin, *Strongylocentrotus purpuratus*, at the California Channel Islands. Pages 379-401. In: Brown, D. R., Mitchell, K. L. and Chang, H. W., Editors. *Proceedings of the Fifth California Islands Symposium*. Publication No. 99-0038. Minerals Management service, Camarillo, California.
- Mayfield, S., Branch, G. M. and Cockcroft, A. C. (2000) Relationships among diet growth rate, and food availability for the South African rock lobster (*Jasus lalandii*) (Decapoda, Palinuridae) *Crustaceana* 73: 815-834.
- Phillips BF (1983) Migration of pre-adult Western Rock Lobsters, *Panulirus cygnus*, in Western Australia. *Marine Biology* 76: 311-318.

Conference attendance and presentations

The main objective of the outputs and extension plan is to provide regular updates on the progress of the study to the funding body and stakeholders, and finally provide coastal managers with information pertaining to the linkages between different habitats within a marine mid-west coastal marine environment.

Information arising from the study will be disseminated through scientific publications, reports and presentations. Progress reports will regularly be provided to SRFME and a final report will summarise the overall findings. Scientific Publications will be submitted to appropriate peer-reviewed journals. Seminars will be presented at SRFME Symposia, relevant national and international conferences, and where deemed necessary, interest groups. A web site will be constructed and continually updated to inform stakeholders of new results.

Methods and preliminary results from the Rock Lobster Project have been disseminated through a PhD research proposal seminar within the School of Natural Sciences entitled "Habitat use, movements and trophic linkages of the western rock lobster within the Jurien Bay Marine Park".

A seminar of the same name was also given at the Australian Marine Sciences Association postgraduate student workshop held at Rottneest Island, 30 June - 1 July 2005.

Publications and/or outcomes to date

The study will provide descriptions of abundance, population structure, diet, home range and seasonal movement patterns of rock lobster in Jurien Bay Marine Park, thereby providing information on the temporal and spatial habitat utilization and population structure of western

rock lobster and any ontogenetic, temporal and spatial shifts in its diets. The study will provide a sound basis for understanding trophic relations at higher levels and will lay the groundwork for understanding what, if any, are the direct and indirect effects of fishing on coastal ecosystems. Furthermore, in combination with the compilation of data from the other related projects within the program, this study will help establish baseline data on the biodiversity and ecology of Jurien Bay Marine Park. Such base-line data is essential for assessing whether the size of current management zones within the marine park are adequate, and for future assessment of the effectiveness of management zones in the newly established Jurien Bay Marine Park.

3.3.6 Ecophysiology of Benthic Primary Producers

Investigators / Institutions

Professor Paul Lavery	Centre for Ecosystem Management, Edith Cowan University
Dr Russ Babcock	Marine and Atmospheric Research, CSIRO
Dr Ray Masini	Department of Environment (WA)
Dr Kathryn McMahon	Centre for Ecosystem Management, Edith Cowan University

Executive Summary

Reduction in the availability of light, due to a range of anthropogenic activities, has been identified as a major cause of benthic habitat loss. Understanding the role of light as a driver of ecosystem integrity is fundamental to managing the State's benthic marine ecosystems. Such knowledge can underpin the development of environmental quality criteria and identify indicators of sub-lethal stress in marine ecosystems, permitting early management intervention. To help fill current knowledge gaps, this project aims to determine the effect of different intensities, durations and timing of light reductions on *Amphibolis* ecosystems and to determine the subsequent patterns of recovery. The project is in its second year, and is due to be completed in late 2007.

In a two-phase project the response of the meadow-forming seagrass *Amphibolis griffithii* (Black) den Hartog to light reduction was examined. The first phase examined severe (>90%) light reductions over a 3-month period and a subsequent one month recovery period. The second phase examined the effects of varying the intensity and duration of light reductions. Morphological and physiological variables were measured in meadows subjected to reduction in light and in control plots. In the first phase experiment, leaf biomass, leaf cluster density and the number of leaves per cluster all declined in shaded plots and after 3 months were about 30%, 50% and 60% of the controls, respectively. Leaf extension was one third that of the control plots. Epiphyte biomass in shaded plots was 44% of the controls after 6 weeks shading and 18% after 3 months shading. Leaf chlorophyll concentration was affected by shading, but only in the upper canopy: shaded leaves had 55% more chlorophyll than control leaves. Shading reduced the carbohydrate stored in the rhizomes of shaded plants: sugars declined rapidly and continuously and after 3 months were less than 20% of controls; a decline in starch concentrations lagged that of sugars. All variables showed a significant shift towards the values in control plots 42 days after removal of shading, indicating capacity for recovery, though in many cases these remained significantly lower than the controls.

In the subsequent, phase 2 experiment significant reductions in seagrass and algal biomass were observed following three, six and nine months of moderate and heavy light reduction in plots shaded at the end of summer, where the maximum carbohydrate reserves were expected. After nine months shading no leaves remained. The abundance of