

**PREDATION BY CRABS ON ROCKY SHORES IN
NORTH-EAST ATLANTIC**

by

ANA CATARINA FERREIRA DA SILVA

A thesis submitted to the University of Plymouth
in partial fulfilment for the degree of

DOCTOR OF PHILOSOPHY

School of Biological Sciences
Faculty of Science

October 2008

*To the University of Plymouth!
A great source of knowledge!*

ana silva

University of Plymouth
Library

Item No. 9007938389

Shelfmark
THESIS 577.649 SIL

IN LOVING MEMORY OF MY GRANDPARENTS



Illustration by Sandra Antunes

"When one animal preys on others of almost every class, ... the profusion of any one of these last may cause such general feeders to subsist more exclusively upon the species thus in excess, and the balance may thus be restored"

Lyell, 1832

Predation by crabs on rocky shores in North-East Atlantic

Ana Catarina Ferreira da Silva

Abstract

Highly mobile predators are known to have an important influence on shallow-water habitats. There is, however, little information about the role of crabs on the ecology of rocky shores. Here I examine the extent and consequences of predation by crabs on shores in the North-East Atlantic. The specific aims of this thesis are to: investigate spatial variation in use of the intertidal by crabs along a horizontal gradient of exposure to wave action and a vertical gradient of tidal elevation; assess their use of the intertidal as a feeding area by examining stomach content composition; examine the extent of connectivity between the subtidal and intertidal habitats as a consequence of predation by crabs, investigate the ecological role of crabs as predators in the intertidal, and to assess the importance of behavioral and morphological factors in determining the outcomes of these predator-prey interactions.

Field sampling showed that on shores in southwest Britain, the abundance of *Carcinus maenas*, *Necora puber* and *Cancer pagurus* varied between high and low-tide, with the vertical gradient of tidal height and horizontal gradient of exposure to wave action. Crabs were typically more abundant on the lower shore than on the upper shore. *C. maenas* and *N. puber* were more abundant on sheltered shores than on exposed shores, while *C. pagurus* showed the opposite pattern. Individuals captured at high-tide were on average larger than those captured at low-tide. Stomach content analysis of individuals captured with traps at high-tide showed that all three crabs feed on intertidal prey including limpets, chitons and algae. In a mark-recapture field experiment, I demonstrate the migration of sublittoral crabs into the intertidal during high-tide. Subsequent manipulative field experiments showed that predation by crabs can have a considerable effect on abundance of limpets. Laboratory experiments showed that *Necora puber* has a preference for smaller limpets, indicating that the population structure of these grazers may also be modulated by predation. On shores of differing exposure in Portugal I examine cheliped morphological variation of *Eriphia verrucosa* in response to variation in prey abundance. Chelipeds were typically larger on exposed shores, where hard shelled prey such as mussels were more abundant than they were on sheltered shores, which were dominated by chitons and algae.

Predation by crabs therefore appears to have an important ecological role in shallow-water habitats by influencing intertidal prey populations and establishing an important trophic link between intertidal and subtidal habitats. The implication of predation by crabs on the ecology of rocky shores is discussed.

CONTENTS

List of Figures	8
List of Tables	11
CHAPTER 1	17
General introduction	18
1.1. Thesis overview	18
1.2 Physical and biological factors in the intertidal	20
1.2.1 Physical gradients on the shore	20
1.2.2 Biological factors	23
1.3 Role of predation	25
1.4 Role of mobile predators in establishing linkages between the intertidal and adjacent subtidal habitats	28
1.5 Effects of predation	30
1.6 The role of intraspecific morphological variability in predator-prey encounters	31
1.7 Summary of chapter aims and contribution to current knowledge	35
CHAPTER 2	39
Influence of tidal phase, height and exposure to wave action on the abundance of mobile decapod predators on rocky shores	40
2.1 Abstract	40
2.2 Introduction	41
2.3 Methods	44
2.4 Results	51
2.5 Discussion	64
CHAPTER 3	70
Population dynamics of crabs and their temporal and spatial movements on rocky shores	71
3.1 Abstract	71
3.2 Introduction	72
3.3 Methods	76
3.4 Results	81
3.5 Discussion	91
CHAPTER 4	96
Predation by small mobile aquatic predators regulates populations of the intertidal limpet <i>Patella vulgata</i>	97

4.1 Abstract.....	97
4.2 Introduction	98
4.3 Methods	100
4.4 Results	106
4.5 Discussion.....	115
CHAPTER 5.....	120
Preferential feeding by the crab <i>Necora puber</i> Linnaeus on differing sizes of <i>Patella vulgata</i> Linnaeus.....	121
5.1 Abstract.....	121
5.2 Introduction	122
5.3 Methods	124
5.4 Results	129
5.5 Discussion.....	134
CHAPTER 6.....	140
Morphological variation in the cheliped of <i>Eriphia verrucosa</i> across shores of differing exposure to wave action	141
6.1 Abstract.....	141
6.2 Introduction.....	142
6.3 Methods	145
6.4 Results	152
6.5 Discussion.....	162
CHAPTER 7.....	166
General discussion.....	167
7.1 Novel findings.....	167
7.2 Patterns of predator activity in the intertidal	169
7.3 Role of predation in shallow-water ecosystem processes.....	171
7.4 Future research	175
7.5 Methodological considerations	177
7.6 Concluding remarks	181
REFERENCES	182
APPENDICES.....	225
Appendix 1.....	225
Appendix 2.....	226

List of Figures

- Figure 2.1. Standard commercial trap fixed on the shore and used for sampling during high-tide. 45
- Figure 2.2. Main crab species sampled at low and high-tides in southwest Britain..... 52
- Figure 2.3. Mean abundance (\pm S.E.) of predators captured at high-tide “as collected” and “adjusted for duration of immersion” (total period of fishing) between the upper and lower shore and between sheltered and exposed shores. Histograms show SNK tests summary of significant effects (Table 2.1a). Treatments with identical lowercase letters were not significantly different..... 56
- Figure 2.4. Size frequency histograms of predators captured in the intertidal during high-tide. Open arrow = modal class for individuals captured during high-tide, filled arrows = modal class for individuals captured during low-tide (shown for comparison). Note different scales on horizontal axes between species..... 57
- Figure 2.5. Examples of prey items removed from the stomachs of *Carcinus maenas*, *Necora puber* and *Cancer pagurus*. A – Operculum of *Gibbula umbilicalis*, B – Shell remains and radula of *Patella* spp., C – plates and radula of *Lepidochitona cinereus*, D – Plates of barnacles (scale bar = 10 mm), (scale bar A-C = 50 mm). 62
- Figure 3.1. Example of elastomer (circled) and external marking (arrowed) on *Carcinus maenas*.....77
- Figure 3.2. Recapture of crabs moving between tidal phases (A-C) and between shore levels (D-F) pooled across the two shores and for one year sampling. Shaded bars represent individuals marked at low-tide and white bars represent individuals marked at high-tide.....83
- Figure 3.3. Size-class average survival estimates (ϕ) for *Carcinus maenas*, *Necora puber* and *Cancer pagurus* sampled at high and low-tides (pooled across shores) for one year sampling period. An average of 30% of high-tide individuals were recaptured at low-tide at a given time. Data were fit to the most parameterised model with survival and recapture probability variable over time $\{\phi(t), p(t)\}$87

Figure 3.4. Size-class average growth estimates for crabs sampled at high and low-tides (pooled across shores) for summer (June – August 2006) and winter (December 2006 – February 2007).....	89
Figure 4.1. Cage treatments.....	102
Figure 4.2. Average abundance (a) and average size (b) (\pm SE) of limpets in various predator exclusion treatments after two months (T2). Effects were consistent between sites and shores. Treatments sharing similar lower case letters did not differ significantly (SNK test, $p < 0.05$, $n = 3$).	109
Figure 4.3. Cumulative frequency distributions for sizes of limpets at the start of the experiment (T1) and after two months (T2). Results of Kolmogorov-Smirnov tests show differences in frequencies between T1 and T2. N.B at T2 (dotted line) some of the smaller sizes were no longer present.	110
Figure 4.4. Total attack time for each predator species (average \pm SE) (A) and time spent on each behaviour type (Table 4.3) by each predator species (average \pm SE) (B-E). Treatments sharing similar lower case letters did not differ significantly (SNK tests, $p < 0.05$; $n = 20$).	114
Figure 5.1. Relationship between the carapace width and cheliped size (propodus height – see Figure 6.1a, M1) of <i>Necora puber</i>	129
Figure 5.2. Size of the largest limpet (<i>Patella vulgata</i>) consumed in relation to cheliped size of <i>Necora puber</i>	129
Figure 5.3. Average frequency (\pm S.E.) of limpets consumed per crab size class when crabs were presented with a choice of prey sizes (CW-Carapace width).....	130
Figure 5.4. Average time (seconds \pm S.E.) taken by <i>Necora puber</i> to remove or crush <i>Patella vulgata</i> according to predator and prey size.....	133
Figure 6.1. <i>Eriphia verrucosa</i>	147
Figure 6.2. Linear distances used to evaluate size (a) and shape (b) of the crusher claw of <i>E. verrucosa</i> according to wave exposure. The approximate position of landmarks (o) and semilandmarks are shown.	148
Figure 6.3. Principal Components examining the relationship between claw linear measurements (see Figure 6.1a) and sex of <i>E. verrucosa</i> according to shore exposure. A vector overlap of cheliped measured distances is included to examine their contribution to explain the variance between exposures.....	155

Figure 6.4. Principal Components examining the relationship between claw geometric measurements (see Figure 6.1b) and sex of <i>E. verrucosa</i> according to shore exposure.	158
Figure 6.5. Regression effects of carapace width and shore exposure on cheliped height for males and females.....	159
Figure 6.6. Distance based redundancy analysis examining the relationship between claw linear measurements and diet composition of <i>E. verrucosa</i> according to shore exposure. The measure M2 was found to be positively correlated with M1 in Draftman plots analysis and thus removed to avoid redundancy.....	161
Figure 7.1. Role of crabs in rocky shore food webs according to exposure to wave action. Width of arrows indicates energy of flow. Cm – <i>Carcinus maenas</i> , Np – <i>Necora puber</i> , Cp – <i>Cancer pagurus</i> Colored arrows represent the new findings of my study; the remaining links were interpreted from several published literature.....	170
Figure 7.2. General interpretation of movements (shown by arrows) of sublittoral and intertidal crabs (no particular species represented) on the shore throughout the tidal cycle (MLWST and MHWST – Mean low and high water at spring tides). A representation of the sizes of predators undertaking these movements is given by the relative size of the crabs.	173

List of Tables

Table 2.1. ANOVA comparing the abundance of three common predators between tidal levels and shores of different exposure to wave action, individuals were captured during high-tide using traps. a) comparison of the total number of individuals captured during high-tide (raw data); b) comparison of the number of individuals adjusted for differences in the period of immersion (total period of fishing). Significant p-values are shown in bold. The directions of significant effects are shown in Figure 2.3.	54
Table 2.2. Summary of Chi-Square tests to examine the association between shore level and exposure to wave action on sex ratio of predators captured at night-time high-tide. Relative proportions shown bracketed. Significant p-values are in bold.....	58
Table 2.3. ANOVA comparing the abundance (a) and size (b) of intertidal crabs recorded during day-time low-tide between tidal levels and shores of different exposures. Significant p-values are in bold.	60
Table 2.4. Relative abundance (%) of prey items across shore height and exposure, and the percentage of the total number of prey items in the stomach of predators captured in traps at high-tide. Rank abundance shown in brackets.	63
Table 3.1. Recapture rates of the crabs collected in the intertidal from two shores in one year estimated by pooling data from high and low-tides.	81
Table 3.2. Relative proportions and summary of chi-square results examining the association of crabs only tagged and recaptured at high-tide and those only captured and recaptured at low-tide across all shores and dates.....	83
Table 3.3. Seasonal (summer and winter) average estimates of crab density (individuals.m ²) based on individuals marked and recaptured on the shore at high-tide.....	82
Table 3.4. Average size (\pm SE) of individuals marked and only recaptured at low and high-tides across all shores and dates.....	85
Table 3.5. Average monthly population size (\pm SE) across shores and for all species estimated from the Petersen model. Estimates of annual density per shore based on animals collected at both tidal phases are also given for each species.....	87
Table 4.1. ANOVA comparing the abundance (Sqrt (X+1) transformed data, Cochran's test: C = 0.26, not significant) and size (untransformed data, Cochran's test: C = 0.15, not significant) of limpets among treatments after 2 months of predator exclusion (T2). Significant effects are shown in bold. Outcomes of Student-Newman-Keuls are shown in Figure 4.1a,b.	107

Table 4.2. ANOVA comparing the detachment force (Ln (X+1) transformed data, Cochran's test: C = 0.22, not significant) required to remove limpets of differing sizes, from the substratum at each of two shores and two sites within shores (NB. The effect of time was not significant (p>0.45) and has been removed from analysis by pooling, see methods). Significant effects are shown in bold. Outcomes of Student-Newman-Keuls test on sizes (\pm SE): Small (4.91 ± 0.78 newtons) < Large (22.54 ± 0.19 newtons).	111
Table 4.3. Description of behaviour types adopted by crabs in encounters with limpets. The critical factor corresponds to the feature which observations suggested contributed the most to the success of the predation event.	112
Table 5.1. Summary of Chi-Square tests based on the height of <i>Necora puber</i> master chela and prey size. Degrees of freedom are ($k-1$) with k being the number of size choices (na = not applicable because limpets of those sizes had been previously shown not to be vulnerable to tested crab sizes). Chi-square statistic indicates whether the proportions of sizes consumed when choice was available differed to those when choice was absent (ns = not significant).	132
Table 6.1. ANOVA comparing the abundance and mean size (carapace width) of <i>E. verrucosa</i> between shores of differing exposure to wave action. Significant effects are shown in bold.	153
Table 6.2. Summary of results of PERMANOVA permutation tests on stomach content composition of <i>Eriphia verrucosa</i> for factors shore exposure, sex and shores and, results of SIMPER analysis of species contribution for differences between shores of differing exposure. Number of permutations used = 9999.	154
Table 6.3. Summary of results of PERMANOVA permutation tests on claw linear (a) and shape (b) measurements for factors shore exposure, sex and shores and, results of SIMPER analysis of distances contribution for differences according to shore exposure and sex. Number of permutation used = 9999. The last interaction was removed in shape analysis as it did not contribute to variance patterns (p>0.35).	156

Acknowledgements

This study has been funded by a studentship awarded by the Portuguese Government (FCT- SFRH/BD/19077/2004). It was developed in the U.K. at the University of Plymouth and the Marine Biological Association of the United Kingdom and at the Guia Marine Laboratory in Portugal.

I would like to thank and express my gratitude to Professor Steve Hawkins and Dr. Diana Boaventura for their guidance and support throughout this study. To Diana, thank you for support in making this PhD possible. I especially thank Dr. Richard Thompson whose ever present support, patience and advice have made this journey an invaluable experience. I am very grateful for his help in solving more than academic matters and challenge to improve my personal skills.

I am also very grateful to Ann Torr and Richard Ticehurst of the MBERG - University of Plymouth, who endured the challenges of extensive and hard-labouring fieldwork and allowed me to collect valuable data with an enthusiasm that only they can transmit. Many thanks to Emily Brewster, Sónia Brazão, Patricia Masterson, Mark Browne and Louise Firth for help in field sampling. I extend this gratitude to all the volunteer students whom I am in debt with: Penelope, Adam, Leonie, Daniel, Victoria, Mark, Oliver, Josef, and a number of others too many to be listed. Many thanks to Peter Rendle at the MBAUK whose expertise in sampling crabs was most useful, and to Roger Haslam at the University of Plymouth whose technical assistance solved many experimental challenges.

My stay in the U.K. was one of the most special experiences of my life because of my dear friends Awantha Dissanayake and Mark Browne. Ao Waz estou eternamente grata pela alegria de viver e partilha da sua fantástica pessoa, contigo cresci para além do que sonhei ser possível para mim. To Mark I am grateful for the ever present friendship, constant laughter and support to expand my personal limits. To both, I thank the special meaning you gave to my "Anisms", the endurance of my endless moaning about the weather and the amazing experiences in Ride and Cuba!

Many friends looked after me in the UK and I wish to thank Stewart Niven, Patricia Masterson, Sara Carless and Laure Noel for their support in

making me feel at home. I also thank Catarina, who was always there with a cake when I faltered.

Because this great adventure would not have started without the encouragement of my secondary school biology teacher, I also wish to acknowledge the value of having someone believing in you.

This work would not have been possible without the encouragement and unconditional support from my family. Vocês suportaram a minha ausência "egoísta" durante estes longos anos com a certeza orgulhosa de que perseguia mais um sonho da minha vida. É com vocês que eu partilho agora a sua concretização. To my parents I wish to thank the most for their sacrifices in getting me this far. To Sofia, Lena, Marta, Paula, Cátia, and Nikki and Sónia in particular, thank you for always being there for me; you have made a world of difference! Finally, to Pedro, the most positive person I know, thank you so much for having fulfilled another of my dreams. A ti estou eternamente grata 55 vezes pelo apoio incondicional e magia que trouxeste ao desafio mais difícil da minha vida.

Author's Declaration

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award.

This study was financed with the aid of a studentship from the Fundação para a Ciência e Tecnologia (FCT-Portugal) and carried out at the University of Plymouth in collaboration with the Marine Biological Association of the United Kingdom and the Guia Marine Laboratory in Portugal.

Publications:

Silva, A.C.F.; Hawkins, S.J.; Boaventura, D.M. & Thompson, R.C. (2008). Predation by small aquatic predators regulates populations of the intertidal limpet *Patella vulgata* (L.). *Journal of Experimental Marine Biology and Ecology in press.*

Relevant scientific conferences were regularly attended at which work was presented:

7th International Temperate Reef Symposium

26/06/06 – 01/07/06

University of California at Santa Barbara, USA

Oral presentation: *Activity of predators on rocky shores during high-tide.*

Silva, A.C.F; Boaventura, D.M.; Hawkins, S.J. & Thompson, R.C.

42nd European Marine Biology Symposium

27/08/07 – 31/08/07

Christian Albrechts University, Kiel, Germany

Oral presentation: *Effects of aquatic predators on intertidal limpets.*

Silva, A.C.F; Boaventura, D.M.; Hawkins, S.J. & Thompson, R.C.

43nd European Marine Biology Symposium

08/09/08 – 12/09/08

Azores University, Azores, Portugal

Oral presentation: *You are what you eat. Phenotypic plasticity in Eriphia verrucosa*

Silva, A.C.F; Boaventura, D.M.; Hawkins, S.J. & Thompson, R.C.

XV Iberian Symposium of Marine Biology Studies (SIEBM)

09/09/08 – 13/09/08

Madeira, Portugal

Poster presentation: *Foraging patterns of intertidal crustacean predators: riding the waves?*

Silva, A.C.F; Boaventura, D.M.; Hawkins, S.J. & Thompson, R.C.

Word count of main body of thesis: 46,540

Signed *A.C.F. Silva*

Date *14/10/08*

CHAPTER 1

General introduction

General introduction

1.1. Thesis overview

Rocky shores form an interface between the land and the sea and represent an extensive coastal habitat worldwide (e.g. Hawkins & Jones 1992, Raffaelli & Hawkins 1996). The ecology of animals and plants in intertidal rocky shores has been extensively studied across the world, and this research has strongly contributed to the development of ecological concepts which have been applied to other areas of ecology (e.g. Dayton 1971, Connell 1972, Paine 1974, Menge 1976, Bertness & Leonard 1997). The suitability of rocky shores for ecological studies is associated with their ease of access during low-tide, their sharp and defined environmental gradients, their hard substratum which allows experiments to be easily secured and, in addition, many of the organisms are either sessile or slow moving. Hence, rocky shore habitats are ideal for experimental manipulation (Hawkins & Jones 1992, Raffaelli & Hawkins 1996).

Most notably, the ecology of these habitats is strongly driven by environmental gradients. These are vertical with tidal elevation determined by the duration of immersion, and horizontal across shores according to exposure to wave action (see Raffaelli & Hawkins 1996). In addition to the differential physiological tolerance of organisms to these overarching physical gradients, the proximate distribution of organisms within the intertidal is determined by biological factors including competition, behaviour and predation (Menge 1976). Despite the extensive use of shores for experimental study of both physical and biological factors influencing the dynamics of the sessile and sedentary assemblages present (see reviews in Hawkins et al. 1992, Underwood 2000),

relatively little work has been done on the ecology of mobile predators that access the rocky shore during high-tide such as fish and crabs (but see Robles et al. 1990, Burrows et al. 1999, Rilov & Schiel 2006b, Jones & Shulman 2008). The influence of these organisms on the ecology of rocky shores will be the focus of this thesis.

In this general introduction I will start by briefly reviewing the physical and biological factors that influence the ecology of rocky shores. As well as directly influencing the abundance of organisms, physical factors modulate biological interactions such as competition and predation (Underwood 1985, Jonsson et al. 2006). Thus, the effects of predation by mobile aquatic organisms must be placed in the context of vertical and horizontal gradients on the shore (e.g. Menge 1978a, Robles et al. 1990, Yamada & Boulding 1996). I will then specifically examine predator-prey interactions, by reviewing what is already known on slow moving predators such as whelks and starfish, together with a summary of our limited knowledge on highly mobile aquatic species.

Subtidal and intertidal habitats have traditionally been considered as separate systems (but see Rilov & Schiel 2006a, Jones & Shulman 2008). The high motility of predators such as crabs and fish may, however, potentially lead to the establishment of extensive ecological linkages between these habitats, which in turn will be influenced by predator abundance and population structure (Edwards et al. 1982, Rilov & Schiel 2006b, Jones & Shulman 2008). The role of these mobile predators in establishing subtidal-intertidal linkages will be discussed. The impact of predation on key structuring species such as grazers will then be reviewed, before focussing on the role of intraspecific variability in predator-prey interactions as a consequence of mechanical constraints and size

refuges. This introductory chapter concludes by outlining the overall rationale of the thesis and the specific aims of each of the chapters.

1.2 Physical and biological factors in the intertidal

1.2.1 Physical gradients on the shore

There are two major physical gradients influencing the distribution of intertidal organisms: the vertical gradient from the sea to the land along which the intensity of physical factors such as aerial exposure, temperature and desiccation vary, and the horizontal gradient of exposure to wave action along which organisms have to cope with or exploit differing levels of hydrodynamic forces (Raffaelli & Hawkins 1996).

Sea-land vertical gradient

This is the most apparent gradient on rocky shores. Intertidal marine organisms tolerate aerial exposure to varying degrees and species are distributed along the marine-terrestrial gradient according to their physiological limitations (Raffaelli & Hawkins 1996). Thus, for most intertidal organisms and sessile species in particular, there is a general correlation between degree of tolerance to physical factors and vertical elevation. One of the most influential accounts on intertidal ecology named *zonation between tidemarks* describes these patterns of species vertical distribution on broad geographical scales (Stephenson & Stephenson 1949, 1972). Similar vertical patterns of distribution also occur in terrestrial systems, for example, vegetation along an altitude gradient on mountain slopes (Russell 1991); such distribution patterns are, however, far less condensed than those in the intertidal zone. In other aquatic

systems subject to tidal influence such as estuaries, vertical patterns can be less apparent as water flow, sedimentation and salinity become more important environmental forces than tidal influence (e.g. Kimmerer 2002, Giberto et al. 2004).

Most of our knowledge on the vertical organisation of intertidal species has been gathered from experiments and observations of sessile or slow-moving organisms since these are easier to experimentally manipulate (e.g. Connell 1961, Menge 1978a). For mobile predators and crabs in particular which are the focus of this thesis, most observations have been made at low-tide and indicate that these predators can be found at all shore levels (e.g. Lohrer et al. 2000, Flores & Paula 2001, Cannicci et al. 2002).

Horizontal gradient of exposure to wave action

Many aquatic ecosystems are influenced to some extent by water flow and these include freshwater (Hynes 1979), estuarine (Kimmerer 2002) and marine habitats (Nybakken 1997). For example, the macroinvertebrate community colonising rock substrata in streams varies substantially with spate events (Rosser & Pearson 1995). Also, the resilience and health of estuarine mussel populations is negatively affected by high flow rainfall events (Oliver et al. 2008). Unlike the vertical gradient, the horizontal gradient from sheltered bays to exposed headlands is not a unidirectional stress gradient (Hawkins & Jones 1992, Raffaelli & Hawkins 1996). Many organisms such as suspension feeders (e.g. barnacles) prosper in exposed conditions due to greater supply of seston and reduced siltation (e.g. Jenkins 2005). On exposed locations, high shore organisms also benefit from wave splash reducing desiccation stress. Similarly,

some algae such as kelps do better in moderate wave action due to increased supply of nutrients (Raffaelli & Hawkins 1996).

Wave action is, however, a major physical factor influencing the distribution and structure of intertidal assemblages (Ballantine 1961, Lewis 1964, Menge & Sutherland 1976, Menge 1978b, Sousa 1979, Burrows et al. 2008). Intertidal organisms on exposed shores have morphological, physiological and behavioural adaptations to regimes of high dislodgement and pulling hydrodynamic forces (Denny 1985). For example, limpets are often smaller but more abundant at exposed locations (Denny et al. 1985, Hobday 1995, Jenkins & Hartnoll 2001), whelks on exposed shores have reduced growth rates compared to those at sheltered locations (Etter 1996), and algae adapt their morphology according to exposure conditions (D'Amours & Scheibling 2007, Wolcott 2007).

With populations of highly mobile predators, which are the focus of this thesis, a large part of our knowledge on the influence of wave exposure comes indirectly from studies of gastropods, where large size, thick shells and a small aperture are typically found on sheltered shores, thought to be adaptations to a higher abundance of highly motile predators such as crabs in those shores (e.g. Kitching et al. 1966, Hughes & Elner 1979, Crothers 1983, Hughes & Seed 1995, Hughes 2000). Edwards et al. (1982) have emphasized the need to experimentally assess the variation in the distribution of mobile predators and its underlying causes.

1.2.2 Biological factors

Competition, biologically generated habitats, behaviour, grazing and predation are key biological factors setting distribution patterns and structuring intertidal assemblages (Underwood 1985, Raffaelli & Hawkins 1996).

Competition for resources either food or space, is important in the intertidal but is also regarded as a major biological force regulating both terrestrial and other marine systems (Menge & Sutherland 1976, Schoener 1983, Morin 1999, Chase 2002). In the intertidal, competition is known to be particularly important between sessile species such as barnacles and mussels (Connell 1961, Menge & Sutherland 1976), but also for more mobile species such as limpets (Boaventura et al. 2002b, Boaventura et al. 2003). Competition also interacts with other biological forces such as predation and with physical factors such as wave action, which often lessen the strength of competition by reducing densities of competing organisms (e.g. Connell 1961, Gurevitch et al. 2000).

Habitat structural complexity is a key biological factor influencing diversity of assemblages and abundance of organisms in both terrestrial and aquatic environments (Heck & Wetstone 1977, Hicks 1980, August 1983, Stoner & Lewis III 1985). In the intertidal, increased structural complexity can ameliorate environmental stresses during low-tide and provide additional habitat (Leonard 2000). For example, higher diversity and abundance of organisms have been reported to be associated with barnacles than on open rock (Thompson et al. 1996); mussel beds (Seed 1996) and fucoid algae can provide surface for attachment and refuge from desiccation and wave action for invertebrates such as limpets (Hawkins 1981, Williams & Seed 1992, Seed 1996, Moore et al.

2007); and barnacles can also provide refuge from grazing (Hawkins 1981, Lubchenco 1983).

The behaviour of animals can be decisive in structuring intertidal assemblages (Hughes 1980a, Chapman 2000, Rochette & Dili 2000). Larval behaviour in the water column (Paula et al. 2001, Eaton 2003, Queiroga et al. 2006) and whilst settling (Connell 1985, Thompson et al. 1998, Jenkins 2005) can strongly influence distribution patterns, and hence community structure. Many slow moving animals (e.g. limpets, Wolcott 1973) and mobile organisms (e.g. crabs, Mosknes 2002, Lee 2004) have behaviour patterns which keep them within their physiological tolerance limits and directly set distribution patterns. Also, preference behaviours of predators for particular prey types can fundamentally alter the distribution of prey populations. In Australia, preferential predation by the crab *Ozius truncatus* on smaller sizes of gastropods on the lower shore results in a size gradient of these snails with younger individuals obtaining refuge higher on the shore (Chilton & Bull 1984).

Predation is a key biological factor structuring terrestrial and aquatic communities (Hughes 1980b, Price et al. 1980, Schowalter et al. 1986, Hunter & Price 1992), thereby influencing ecosystem functioning. Its effects have been suggested to be stronger in the intertidal than in other marine and terrestrial systems (Sih et al. 1985). The influence of predation is well documented for rocky shores around the world and is considered to be a key factor determining the structure of intertidal assemblages (see reviews in Menge & Sutherland 1976, Hughes 1980b, Sih et al. 1985, Connolly & Roughgarden 1999, Chase 2002, Robles & Desharnais 2002). Because predation is the main topic of this thesis, it will be discussed in more detail in the following sections.

Spatial variation of intertidal species along vertical and horizontal gradients of the shore can typically be explained only by considering both physical and biological forces (reviews in Underwood 1985, Wootton 1993, Raffaelli & Hawkins 1996), and recruitment is a typical result of such interaction.

Recruitment regimes are primarily determined by the oceanographic context and coastal geomorphology (Roughgarden & Baxter 1985). Recruitment is also an important structuring factor on rocky shores as most marine species have a pelagic stage in their life cycle (Thorson 1966). Variation in recruitment, i.e., the input of new individuals to the population, can limit adult population size (e.g. Hawkins & Hartnoll 1982, Connell 1985, Sutherland 1990) and alter the importance of biological interactions as these can be intensified in high recruitment events and less important when low recruitment events occur (Menge et al. 1985, Gaines & Bertness 1992, Menge 1992).

Recruitment can strongly interact with competition: if recruitment of a dominant competitor is low, then a weaker competitor can be prevented from being completely excluded (Menge 1991, Southward 1991). Recruitment and post-settlement biological forces such as predation have been suggested to be responsible for the spatial and temporal variation of crab distribution (McDonald et al. 2001, Paula et al. 2001, Flores et al. 2002, Mosknes 2002, Silva et al. 2006, Pardo et al. 2007).

1.3 Role of predation

Predation is the consumption of one organism (prey) by another organism (predator) in which the prey is alive when the predator first attacks it (Begon et al. 1996). Predation has been considered to involve either carnivorous or herbivore predators, the first often consuming the entire prey while herbivores

often only remove part of a prey individual (Begon et al. 1996). Although the distribution patterns of sessile prey are in the first instance determined by settlement and post-settlement events in the marine environment, predators can subsequently alter prey distributions and control their abundance with cascading effects on the population dynamics of other species that feed or shelter amongst these prey. This can be illustrated by the presence of predation haloes around crevices occupied by predators: with increasing distance from crevices where dogwhelks take refuge, the probability of encountering smaller barnacle prey decreases (Fairweather 1988, Johnson et al. 1998).

Predation intensity varies spatially along the horizontal gradient of wave exposure and vertical gradient of tidal elevation (Menge 1978b, 1983, Sih et al. 1985). This is directly linked to changes in predator identity, abundance, population structure and distribution along those gradients. In the intertidal, predation is generally considered to be stronger on sheltered shores due to the higher abundance of consumers (Connell 1972, Menge 1978a). This generalisation, however, has been questioned by Underwood and Denley (1984) who advocate more experimental evidence. Studies on this topic have generally focused on sedentary grazers such as limpets and slow moving predators such as whelks, starfish and hermit crabs (Connell 1972, Paine 1976, Menge 1978b, Bertness 1981). For example, field studies have shown that the predatory activity of whelks and the movement of snails are reduced in conditions of strong wave action (Menge 1978b, Burrows & Hughes 1989, Pardo & Johnson 2004, Rilov et al. 2005), while limpets exert a stronger grazing activity at exposed than at sheltered locations (Jenkins 1999, Jenkins et al. 1999). Many predators such as dogwhelks (*Nucella lapillus*) take refuge from

wave action but forage when conditions are favourable (Hughes et al. 1992, Hughes & Burrows 1994).

Wave exposure directly influences prey abundance, in general with greater abundance of algae and molluscs (not including limpets) on sheltered shores, while filter feeders such as barnacles and mussels are more commonly associated with high flow conditions (Ballantine 1961, Lewis 1964, 1968). However, wave action can also indirectly influence predation pressure by introducing variation in prey availability (here interpreted as abundance) to which predators are responsive (Robles et al. 1990). It has also been suggested that crabs (e.g. *Carcinus maenas*, *Necora puber*, *Cancer pagurus* and *Pachygrapsus crassipes*) can be less abundant and less effective predators on high energy shores due to scarcity in refuge and disturbance by wave action during foraging excursions (Muntz 1965, Robles et al. 1989, Lau & Martinez 2003), however no study has specifically tested this.

Intertidal predation is also thought to be greater on the lower shore where there are larger densities of aquatic predators and where the foraging time during periods of submersion is maximised (Sih et al. 1985, Robles & Desharnais 2002). It has been argued, however, that this generalisation also requires further experimentation (Underwood & Denley 1984). Predators that have limited mobility such as whelks, are typically restricted to shore levels where their prey are more abundant (e.g. Burrows & Hughes 1989, Hughes & Burrows 1994). A similar scenario is apparent for the few studies of highly mobile predator species, where some crabs and fish have been found to be common at specific shore levels (e.g. Burrows et al. 1999, Faria & Almada 2006). Differences in the vertical distribution of crabs may be related to

variations in habitat complexity and refuge availability (Lohrer et al. 2000), prey abundance and distribution (Dare & Edwards 1981), and environmental (e.g. temperature) and biological (e.g. predation) factors (Pellegrino 1984, Warman et al. 1993, Cannicci et al. 1999a). Most studies on the crab movements on the rocky shore have categorised vertical distribution during low-tide, when most species of crabs are not active (but see Dare & Edwards 1981, Burrows et al. 1999), and little is known about vertical distribution at high-tide, when some prey become more accessible and environmental stresses such as desiccation are reduced (but see Robles et al. 1990, Rilov & Schiel 2006b, Jones & Shulman 2008).

1.4 Role of mobile predators in establishing linkages between the intertidal and adjacent subtidal habitats

Rocky shores are a transition system between the terrestrial and aquatic environments and are an important feeding ground for mobile terrestrial and aquatic predators such as birds, crabs and fish (Raffaelli & Hawkins 1996). Through these movements associated with foraging, refuge or other needs, and in particular when they take place across system boundaries, these organisms can be involved in linking ecological processes that would otherwise be separated.

It has long been suggested that crabs and fish migrate into the intertidal during high-tide (Naylor 1958, 1962, Edwards et al. 1982, Kaiser et al. 1993, Warman et al. 1993). The extent of this subtidal-intertidal linkage has not, however, been described for many species. Little is known about the influence that mobile aquatic predators (crabs and fish) exert when feeding on intertidal

prey, reflecting the difficulty involved in developing appropriate experiments and in making direct observations. The paucity of studies on this type of predator is also a reflection of their high motility. This mobility also has, however, an important influence on predation due to the potential for rapid redistribution of predation intensity (Underwood & Fairweather 1992).

Most of our knowledge about the usage by crabs of the intertidal as foraging grounds is based on the common shore crab *Carcinus maenas* (e.g. Edwards 1958, Naylor 1962, Crothers 1967, 1968, Dare & Edwards 1981, McGaw & Naylor 1992, Hunter & Naylor 1993, Warman et al. 1993, Warman & Naylor 1995, Burrows et al. 1999, Mascaró & Seed 2001). Nevertheless, there is further evidence suggesting that mobile aquatic predators affect a variety of prey species and have a considerable influence on intertidal assemblages. For example, low-shore and subtidal crabs control the abundance of intertidal littorinids on some Pacific shores (Yamada & Boulding 1996), and lobsters control the abundance of midshore mussel populations in southern California (Robles et al. 1990). These predators are also an important cause of mortality in the early life stages of prey including on juvenile gastropods and bivalves (e.g. Ojeda & Dearborn 1991, O'Connor et al. 2008).

Additionally, much uncertainty remains about whether crabs take permanent residence in the intertidal or commute between subtidal and intertidal habitats. A transient behaviour of crab species could increase the magnitude of subtidal-intertidal trophic linkages. Such linkages have been shown between subtidal crabs and fish which control the abundance of low shore mussel assemblages on Pacific rocky shores (see Rilov & Schiel 2006b), but have not been investigated on European rocky shores. In the case of crabs, smaller animals, which are also vulnerable to predation themselves, may

choose to remain in refuges during high-tide while larger ones, which are often found on subtidal areas, may commute between habitats in order to maximise their feeding time. Information about predator size and sex is of considerable importance to this topic as they have been shown to be key factors influencing predator choice for type and/or size of prey (Seed & Hughes 1995, Freire et al. 1996, Mascaró & Seed 2001, Spooner et al. 2007). In general, large predators consume more frequently larger and more diverse prey than their smaller conspecifics and males may have differing diets from females.

1.5 Effects of predation

Predation is known to influence prey assemblages in two ways: i) direct effects by reducing prey density with consequences for prey assemblage structure and, ii) indirect effects by causing changes in behavioural and morphological characteristics of prey. The most evident consequence of a predatory force is its lethal effects, controlling prey populations by removing individuals or biomass. In extreme situations, consumers can even be responsible for localised prey extinctions (Schoener et al. 2001). Indirect effects include alterations of prey morphology, growth and behaviour (e.g. Palmer 1985, Palmer 1990, Vadas et al. 1994, Connell 1998, Trussell et al. 2003, Coleman et al. 2004, Brookes & Rochette 2007), increased biodiversity by reducing the abundance of a dominant competitor (e.g. Paine 1966, Menge & Sutherland 1976, see discussion in Underwood & Denley 1984, Navarrete & Menge 1996) and maintaining patchiness in prey distributions (e.g. Petraitis 1995).

Studies on intertidal predation have greatly focused on the effects of non-carnivore predators and particularly the role of grazers in controlling algal assemblages. The most studied grazers are limpets which have been identified as key herbivorous predators on rocky shores where they are known to control the distribution limits and abundance of algae (Hawkins & Hartnoll 1983, Hawkins & Hartnoll 1985, Hawkins et al. 1992, Boaventura et al. 2002a, Coleman et al. 2006). As for carnivorous predators, many studies have established the importance of slow moving predators such as starfish and whelks, which can be responsible for controlling the distribution and abundance of mussels, limpets and barnacles on Pacific and Atlantic shores (e.g. Connell 1970, Dayton 1971, Paine 1974, Menge 1976, Lubchenco 1978, Hughes & Dunkin 1984a, Fairweather 1985, Hughes & Drewett 1985, Burrows & Hughes 1989).

The importance of predation is most evident when it involves control over keystone prey species. In a pioneering study, Paine (1966, 1974) showed that predation by the starfish *Pisaster ochraceus* was responsible for the control over populations of the mussel *Mytilus californianus*, a dominant competitor for space, thus providing evidence that predation may promote diversity.

1.6 The role of intraspecific morphological variability in predator-prey encounters

Influence on prey vulnerability

Prey availability can be defined as a combination of prey abundance in the immediate foraging arena of the predator and their vulnerability to the predator (Gawlik 2002). The balance between prey defences and the ability of the predator to overcome those prey features defines prey vulnerability. Intertidal

prey have developed several characteristics which may deter predators, including adaptations in morphology, chemical defences, physiology and behaviour (reviewed by Sih 1987, Vadas et al. 1994, Yamada et al. 1998, Morissette & Himmelman 2000, Trussell et al. 2003, Cotton et al. 2004, Brookes & Rochette 2007, Markowska & Kidawa 2007, Nicastrò et al. 2007). One of the most investigated aspects of prey and predator characteristics is the role played by size in the outcome of their interactions.

Prey size can represent a mechanical constraint for predators and decrease prey vulnerability. Arguably the most developed theory on predation - *Optimal Foraging Theory* (Pyke et al. 1977, Hughes 1980a, Sih & Christensen 2001) - interprets prey size as a key element in the feeding behaviour of predators. This theory predicts that optimally sized prey are always chosen and that progressively more suboptimal sizes are then accepted as the availability of the more advantageous prey declines (Hughes 1980a).

In the intertidal, prey often have size gradients along the shore profile, thus introducing variability in prey availability and quality. For example, many gastropod species such as the limpets *Lottia digitalis* in California (e.g. Hobday 1995) exhibit a shore-level size gradient, with larger individuals occupying higher tidal heights. The foraging behaviour of predators is hence presumably linked to the hierarchy of a particular prey on the predator food preference list and predator-prey encounter rate (e.g. Jackson & Underwood 2007, Markowska & Kidawa 2007). While mobile predators can actively maximise encounter rates, slow moving predators are more limited in their access to the most profitable prey (Chesson 1983).

Prey size selection is an important component in the process by which communities are structured by predation (Sih et al. 1985, Hines et al. 1990). Predator preferences and the relative availability of preferred types can determine prey population structure (e.g. Chilton & Bull 1986). Preference for food sizes has extensively been studied for crabs. This research has primarily focused on optimal prey size with typical model prey being species of barnacles, snails and bivalves (e.g. Elner & Hughes 1978, Hughes & Seed 1981, ap Rheinault 1986, Yamada & Boulding 1996, Johnson et al. 1998). In general, there is a pattern of crab preference for smaller molluscan prey which may be explained by the mechanical cost of shell breaking or prey extraction, including claw damage and energy depletion (Juanes 1992). Very little is known about the impact that these mobile predators may have on the population structure of other intertidal structuring gastropods such as limpets, and on possible cascading effects on community structure.

Influences of the surrounding environment on predator success

Studies of phenotype are considered to provide useful information on the relationship between an organism and its environment (Wainwright 1991). Most of the evidence on the phenotypic response of prey is from studies on gastropods: snail populations subject to high crab predation pressure often develop thicker, more elaborated and larger shells compared to their congeners in locations where predation pressure is reduced (e.g. Vermeij 1974, Trussell 1996, Yamada et al. 1998, Trussell & Nicklin 2002, Brookes & Rochette 2007). This is often described as predator-prey "arms race": where predators exert intensive pressure, gastropods display greater shell thickness which in turn requires the development of predator-offense mechanisms, i.e., a

co-evolution of anti-predator defence and predator-offense mechanisms can occur.

Studies on predator-prey interactions which aim, however, to understand the importance of phenotype in the predator success have mainly focused on the characteristics of the prey species. Consumption of different prey may have consequences for the dynamics of prey populations but also for life history of predators, including their phenotype which is often overlooked. Nevertheless, the available evidence shows that predators may also respond morphologically to diet. For example, it has been reported that there is a direct relationship between the lantern size of sea urchins and their choice for a durophagous diet, i.e., larger lanterns allowed the intake of hard shelled prey (Hagen 2008). Our understanding of the influence of intraspecific variability on predator success (reflected on its diet) remains incomplete, in the way that the relationship between the morphology of predator feeding structure (e.g. jaw in fish or claw in crabs) and the proportional consumption of prey types has not been investigated for many predators.

Phenotypic plasticity is defined as the ability of a particular genotype to produce different phenotypes in response to environmental variation (Pigliucci 2005). Hence, to understand to what extent predator morphology responds to prey intake, studies have to work at scales where variation in prey availability (here interpreted as abundance and quality such as shell thickness) occur. For crabs, the main focus of my thesis, chelipeds have a major role in the feeding behaviour (Hughes 2000). Evidence suggests that at large spatial scales, claw characteristics can vary considerably, with temperate species considered to be morphologically more specialised for attacking hard-shelled prey than tropical

species, arguably as a result of the intensive coevolution between predators and prey (Vermeij 1976, Vermeij 1977, Hughes & Elner 1989).

In the intertidal, ecological processes often occur at small spatial scales along environmental gradients with predator and prey assemblages varying in composition and abundance. Studies on claw phenotype variation as a result of diet have often not taken into consideration prey availability on the shore, and are often based on laboratory tests where predator and prey type and size are manipulated (e.g. Smith & Palmer 1994, Freire et al. 1996, Yamada & Boulding 1998). However, if prey vary in their abundance along intertidal gradients, then so does their availability to predators.

1.7 Summary of chapter aims and contribution to current knowledge

In general, the present work aims to: i) analyse the foraging patterns of *Carcinus maenas*, *Necora puber* and *Cancer pagurus* at large (between shores) and small (sites within shores) spatial scales under the constraints of environmental factors such as wave action and desiccation with tidal height, ii) evaluate the strength of the subtidal-intertidal link established by these crabs, iii) evaluate the role of their predation pressure in structuring intertidal limpet populations, iv) examine limpet size refuge and establish whether there is a crab preference for prey sizes and, v) assess phenotypic variability in crab claw morphology as a reflection of changes of prey availability between shores of differing exposure to wave action. A more detailed description of the rationale underlying these objectives is presented below.

In order to better understand the effects of predation on intertidal assemblages, it is necessary to know where, when and how many predators forage in the intertidal (Hughes 1980b). Chapter two aims to reduce the current gaps in our knowledge by assessing crab identity, population structure and abundance across the vertical and horizontal shore gradients during immersion, when intertidal prey are most accessible to mobile aquatic predators. To compare crab activity and distribution on the shore, low-tide transects were also made for the vertical and horizontal shore gradients. Crabs were diverse and abundant predators at the locations examined. The diet of these predators in relation to prey abundance was also quantified in order to provide a clearer understanding of their role in structuring intertidal assemblages. This thesis also aimed to clarify the importance of the intertidal as a feeding ground for crabs and describe variations in their abundance and population structure at small (meters) and large spatial scales (kilometres).

Mark-recapture studies have proved to be reliable approaches to the study of activity patterns of mobile organisms in terrestrial and marine habitats including birds (e.g. Garamszegi et al. 2004), snakes (e.g. Bonnet et al. 2002), fish (e.g. Burrows et al. 2004) and lobsters (e.g. Behringer et al. 2008). In Chapter 3, I used a relatively long-term (one year) and large scale (two shores) mark-recapture study for the three most abundant crab species, *Carcinus maenas*, *Necora puber* and *Cancer pagurus*. This work aimed to better understand their patterns of movement between subtidal and intertidal habitats and investigate population size, and parameters such as survival and growth rates. This work also provided information on the strength of the link established between subtidal and intertidal habitats by these mobile predators.

Our current knowledge on the role played by mobile predators in structuring prey populations is limited because it is based on relatively few prey species, mainly barnacles and mussels. The effect of predators on other key intertidal species has been largely overlooked. Hence, the objective of Chapter 4 was to quantify the importance of mobile aquatic predators on intertidal prey populations, by experimentally measuring the effects of predation by crabs and small fish on the abundance and population structure of limpets at small (sites) and large spatial scales (shores). The role of these highly mobile predators in shaping intertidal prey has not been extensively investigated in Britain, despite there being indirect (e.g. diet descriptions) and direct evidence (e.g. video observations) that the intertidal is a common foraging ground for crabs and fish (e.g. Norman & Jones 1992, Hunter & Naylor 1993, Warman et al. 1993, Burrows et al. 1999). Limpets were chosen as model prey species because they are known to be key grazers on shores in the North-East Atlantic (Hawkins & Hartnoll 1983, Hawkins et al. 1992), hence, if any predatory control is exerted on limpets, their grazing pressure could be reduced with cascading effects on community structure. In addition, the assessment of diet composition in Chapter 2 showed that limpets were an important (up to 40%) dietary item for crabs on these shores.

Subsequently, prey choice and mechanical constraints in prey handling were compared using crabs and limpet prey in Chapter 5. In Chapter 4, results showed that smaller size limpet classes suffered the most predation, suggesting that there may be active selection by crabs according to limpet size. Hence, the aim of Chapter 5 was to use *Necora puber* and *Patella vulgata*, common intertidal species, as a predator-prey model to examine the size refuge of limpets, identify the mechanical constraints involved and test for limpet size

preference. By examining the limits of the prey size range and selectivity for specific prey size classes, it is possible to hypothesize about impacts of predators on prey population structure and hence, indicate the potential for cascading effects on associated assemblages.

The abundance of intertidal prey species varies greatly along the horizontal shore gradient of wave exposure (Ballantine 1961). The extent of phenotypic responses of crabs to variation in prey availability along wave exposure gradients is currently unknown and will be the focus of Chapter 6. In this chapter, the research aimed to investigate phenotypic (size and shape) variability in the claw morphology of *Eriphia verrucosa* (a common intertidal crab in southwest Europe - Portugal) along a gradient of wave exposure associated with differences in prey availability, and establish the relationship with its diet by examining stomach content composition. The question posed was whether differential predation along a wave exposure gradient could explain potential spatial patterns in claw size and shape, i.e., was prey availability a possible mechanism explaining the morphological variation of the cheliped these crabs.

Cheliped morphology is related to the choice of prey and handling efficiency (Hughes 2000). Different frequencies of claw morphology patterns are therefore likely to have consequences for the abundance and population structure of prey (particularly size structure), and potentially influence the evolutionary trends in prey morphology. The novelty of this work is that the majority of studies have approached the subject from a prey perspective often examining changes in the body morphology of shelled prey and overlooking responses of predator morphology.

The thesis concludes by integrating the major results and conclusions from the various chapters in the General Discussion, Chapter 7.

CHAPTER 2

**Influence of tidal phase, height and exposure to wave
action on the abundance of mobile predatory decapod
(Crustacea) on rocky shores**

Influence of tidal phase, height and exposure to wave action on the abundance of mobile decapod predators on rocky shores

2.1 Abstract

Little is known about the factors regulating the distribution of crabs in the intertidal during high-tide. Here, the effects of exposure to wave action and tidal elevation on the abundance, population structure and stomach contents of predatory decapods were examined on rocky shores in southwest Britain. Crabs were recorded using traps deployed at high-tide and by direct observation in refuge habitats during low-tide. *Carcinus maenas* (L.), *Necora puber* (L.) and *Cancer pagurus* (L.) were the most abundant species during both high and low-tides. Animals captured during high-tide were considerably larger than those present at low-tide. This indicates that studies of predator-prey interactions in the intertidal are likely to underestimate the potential role of crabs as predators if sampling is made at low-tide alone.

During periods of immersion the distribution of predators varied between species and was influenced by exposure to wave action and tidal elevation. This has important implications on the impact of predation by crabs in the intertidal zone. *Carcinus maenas* was the only species active during nocturnal low-tides when it was observed feeding on limpets in substantial numbers. Analyses of stomach contents from individuals captured at high-tide revealed that chitons and limpets were the most common hard-shelled prey species in the diet of these crabs. However, the relative abundance of prey consumed was not correlated with patterns of prey abundance along gradients of shore exposure or shore height.

2.2 Introduction

Predation has a key role in structuring intertidal assemblages and in the functioning of ecosystems (review in Menge 2000). Much remains unknown, however, about the abundance and distributions of highly mobile aquatic predators such as crabs foraging in the intertidal during high-tide (but see Menge 1983, Hunter & Naylor 1993, Rilov & Schiel 2006b, Jones & Shulman 2008), the period when species such as *Carcinus maenas* are most active (see Hunter & Naylor 1993, Warman & Naylor 1995, Burrows et al. 1999).

Previous observations on spatial patterns of decapod foraging during high-tide suggest that biological factors such as prey distribution are important (Robles et al. 1990). Much of our current knowledge of intertidal predator-prey interactions is, however, based on laboratory observations (e.g. ap Rheinault & Hughes 1985, Brousseau et al. 2001, Cotton et al. 2004) and informative but spatially limited observations at high-tide (e.g. Dare & Edwards 1981, Burrows et al. 1999). Highly mobile aquatic predators such as fish and crabs can forage throughout the intertidal during high-tide (Edwards et al. 1982, Faria & Almada 2006). Because handling times for their prey may be relatively short, it has been suggested that these predators could have a key influence on intertidal assemblages (Robles 1987, Yamada & Boulding 1996, Rochette & Dili 2000).

Intertidal prey abundance varies along major environmental gradients such as tidal elevation and exposure to wave action. Such gradients will also determine the duration and suitability of foraging windows for predators (e.g. Boulding et al. 1999, Faria & Almada 2006, Hollingsworth & Connolly 2006) thereby influencing their behaviour (e.g. Menge 1978b, Menge & Sutherland 1987). Hence, it can be predicted that predator abundance will vary between

tidal heights and shores of differing wave exposure. Abundance and behaviour of predators can be directly (e.g. by impeding prey handling) or indirectly (e.g. prey abundance) influenced by wave action and the time available for foraging will also be influenced by tidal height. Variability in predation pressure along environmental gradients has been described for slow moving predators like whelks, starfish and hermit crabs (Connell 1972, Paine 1976, Menge 1978b, Bertness 1981). Limited information exists, however, on the effect of these environmental gradients on the activity of crabs which can cover relatively large distances during the tidal cycle and may well have a greater impact on prey assemblages (but see Robles et al. 2001).

This study focuses on temporal and spatial patterns of crab distribution in Southwest Britain in relation to tidal phase, tidal elevation and shore exposure. The overall aim of this work was to increase our understanding of predator-prey dynamics on rocky shores. Predator identity, abundance and population structure was described for high and low-tides allowing a preliminary examination of the extent of connectivity between subtidal and intertidal habitats. Two well established methods, traps at high-tide and time search transects at low-tide were employed. These differing methodologies preclude formal quantitative comparisons between data collected at low and high-tides but, were useful to indicate differences in relative and population structure.

Ontogenetic stage and gender have been reported to influence predator distribution, behaviour and diet (e.g. Brousseau et al. 2001, Mascaró & Seed 2001, Buck et al. 2003, Bishop & Wear 2005, Spooner et al. 2007) and so, data analysis included testing for differences between juveniles and adults and between sexes for each species. *In situ* observations of crab feeding behaviour are difficult to obtain (but see Burrows et al. 1999) and so, stomach contents

have been widely used for analysis of crab diet (e.g. Williams 1981, Wear & Haddon 1987, Freire 1996, Bernardez et al. 2000, Cannicci et al. 2002). Stomach contents were used here to establish the importance of hard-shelled intertidal prey in diet of crabs foraging in the intertidal during high-tide.

Some crab species such as *Carcinus maenas*, *Pachygrapsus marmoratus* (Fabricius) and *Eriphia verrucosa* (Forsskål) are capable of withstanding long periods of exposure to air, particularly at night when desiccation stress is ameliorated (Newell et al. 1972, Cannicci et al. 1999b), by aerating the water around the gills or by using the branchial chambers to function like lungs (Warner 1977). Since crabs could be foraging at this time on shores in southwest Britain, observations were also made at low-tide to establish the extent of nocturnal foraging activity.

The specific null hypotheses of this study were that: (1) there are no differences in the abundance and population structure of crabs between the upper and lower shore or; (2) between sheltered and moderately exposed rocky shores during high and low-tides; (3) there is no foraging activity by crabs in the intertidal during nocturnal low-tides; (4) there are no differences in stomach contents composition among sexes and ontogenetic stages (juvenile and adult) or; (5) between shores of differing exposure and between tidal heights; (6) there is no relationship between the relative abundance of hard-shelled prey on the shore and that within the stomach contents of crabs; (7) crabs present in the intertidal at high-tide are intertidal in origin. By using a nested design (two shores within exposures and two sites per shore), the consistency of any patterns could be ascertained. Since several crab species inhabit shallow-water habitats in southwest Britain (Ingle 1983) and because these potentially have different settlement requirements, foraging patterns and range distributions

(Elner 1981, Norman & Jones 1992), I made *no a priori* species specific predictions about the effects of the tested environmental gradients or tidal phases on their distribution.

2.3 Methods

Study sites

This study was made during summer (June-September 2005), when predator activity is believed to be greatest (e.g. Naylor 1962, Choy 1986, Norman & Jones 1992, Nickell & Sayer 1998). Two moderately exposed (Thurlestone - 50°15'N, 35°1'W and Portwrinkle - 50°21'N, 4°18'W) and two moderately sheltered rocky shores (Mount Batten - 50°21'N, 4°07'W and Jennycliff - 50°21'N, 4°07'W), were examined and all are in southwest Britain. These shores were randomly chosen and representative of similar shores in the region.

Levels of shore exposure were confirmed using measures of mean flow conditions following Jonsson et al. (2006), via the dissolution of gypsum (CaSO_4) discs. Sets of twelve discs were attached to the rock surface ~ 3 m above CD for a single high-tide on each of two occasions at each location. Discs on moderately exposed shores dissolved significantly more quickly (~6gr/hour) than on more sheltered shores (~2gr/hour) ($p < 0.04$), giving a clear separation of wave action and water movement between locations. There were no significant differences ($p > 0.1$) between shores within exposures (Mount Batten = ~1.8gr/hour, Jennycliff = ~2.1gr/hour; Thurlestone = ~5.8gr/hour, Portwrinkle = ~6.2gr/hour). Two sites were examined on each shore (separated by approximately 60 m), hence it was possible to test for variation in abundance

of predators at large (1-50 km) and small (50 m) spatial scales. The tidal range during spring tides at these locations is approximately 6 m (0.8 - 5.5 m relative to chart datum, CD). Comparisons were made between the upper shore, approximately 4 m above CD, and the lower shore, approximately 1 m above CD.

Abundance, distribution and stomach contents of predators captured at high-tide

Standard commercial crab traps (55 cm long x 40 cm wide x 30 cm high, 1 cm mesh size) (Figure 2.1), made of moulded heavy duty plastic with two entrances of 8 cm diameter and a bait tube were used (Coastal Fishing Supplies U.K.). Such traps are a very efficient method to catch crabs (Miller 1990) and have been used in similar studies (e.g. Bell et al. 2003, Dunnington et al. 2005).



Figure 2.1. Standard commercial trap fixed on the shore and used for sampling during high-tide.

Preliminary trials showed that the main species of crabs present in southwest Britain, i.e., *Carcinus maenas*, *Necora puber* and *Cancer pagurus*

were captured by these traps and that a range of sizes were captured for each species. Trap design and mesh size (1cm) prevented subsequent escapes. The entrance diameter (8 cm) used allowed a good representation of sizes sampled as the limiting factor was crab carapace height and not length.

Three replicate traps were deployed on two separate occasions at each tidal level, shore, site permutation. These were fixed to the rock platform via anchoring points (Figure 2.1) and were separated by at least 40 m within a 30 m x 50 m area of shore. This was considered sufficient to ensure independence of the area fished by each trap (Miller 1990). Traps were baited with ~ 300gr fresh cut mackerel, *Trachurus trachurus* L. (this bait proved successfully in attracting crabs in preliminary trials) and left for a single nocturnal high-tide. Although crabs are thought to be mainly active during the night (Crothers 1967, Cannicci et al. 1999b), on two separate occasions, traps were deployed on both shores during a single diurnal high-tide to examine day-night differences in crab activity.

Since traps were likely to capture several species simultaneously, comparisons were made to assess potential non-independence as a consequence of inter-specific and intra-specific interactions. Thus, whether aggressive species affected the identity and abundance of subsequent individuals entering a trap and; the effects of larger individuals on smaller individuals (e.g. ap Rheinault & Hughes 1985, ap Rheinault 1986, Choy 1986, Freire & González-Gurriarán 1995) were examined.

The duration of deployments was consistent within shore levels (approximately 4 hours of immersion on the lower shore and 3 hours on the upper shore) but, to examine whether duration of immersion had an effect on

the abundance patterns found between tidal heights (differing duration of foraging window as a consequence of differing periods of immersion), a comparison of raw data and data adjusted for fishing time per tidal height was made.

All captured animals were frozen at -70°C . Since the presence of parasites or the moulting of crabs can hinder their feeding behaviour, only intermoult stage of parasite free predators were considered (Williams 1982). For each species, juveniles were defined as ≤ 35 mm in carapace width for *Carcinus maenas* (Crothers 1967), ≤ 40 mm for *Necora puber* (Norman & Jones 1993) and ≤ 40 mm for *Cancer pagurus* (Hall et al. 1993). The juvenile size differed between species because some such as *C. pagurus* attain larger adult sizes than the adults of other species such as *C. maenas* (see Crothers 1967, Hall 1979).

Analysis of the stomach content composition was made for all captured crabs to assess dietary composition. Hard body parts of animals such as limpets, barnacles and mussels were quantified in the guts of the crabs captured. The points method (Williams 1981) was used to examine the abundance of prey in the diet, since it is suitable for prey that are ingested in large recognizable pieces or in their entirety. This approach has been widely used to quantify stomach contents in crustaceans and fish (Jones 1968, Hill 1976, Williams 1981, Wear & Haddon 1987).

The following were counted: for limpets the number of radulae and pieces of shell (apex); for topshells the number of opercula or shell parts (apex); for chitons the number of radulae and anterior and posterior plates; for mussels the

number of valves or umbos; for barnacles the number of pairs of opercular plates.

Abundance and distribution predators and prey during low-tide

In addition to using traps to capture predators during immersion, low-tide observations during both day and night were made to establish the diversity, abundance and population structure of crabs. These data also provided an indication of whether predators caught at high-tide originated from intertidal refuges or migrated from the subtidal. For day low-tide sampling, one hour transect searches were made amongst boulders and crevices on two sampling occasions on the upper and lower at each site on all shores.

To establish the importance of nocturnal low-tide foraging on these shores, observations of tide-out predator activity were conducted at night on all shores on three occasions during summer 2005 (June-September). Preliminary observations indicated that the majority of predators that were active at this time were on the lower shore. Thus, 500 m² areas of the lower shore (1 m above CD) were visually surveyed by two observers for one hour. Carapace width and sex were recorded for all active crabs. Any predator-prey encounters were also recorded.

To establish the relationship between stomach contents and prey availability (here interpreted as abundance), the relative abundance of prey species was recorded using ten randomly located 50 cm x 50 cm quadrats on both the upper and lower shore at each site for all shores. For each quadrat, the number of individuals of mobile animals and percentage cover of barnacles and mussels were recorded.

Data analysis

For data collected during high-tide, predator abundance was compared for each species between shores of differing exposure and between tidal heights using ANOVA: sampling date (random with 2 levels: date 1 and date 2), shore level (orthogonal, fixed with 2 levels: upper and lower), shore exposure (orthogonal, fixed with 2 levels: moderately sheltered and moderately exposed), shore (random, nested within exposure with 2 levels) and site (random, nested within shores and exposures with 2 levels). The same design was used for low-tide abundance and size data. Nocturnal low-tide abundance data was analysed using the above mentioned design but excluding the factor "shore level" as only the lower shore was surveyed.

Cochran's test was used to check homogeneity of variance and appropriate transformations were made when this assumption was violated. Tests of homogeneity, ANOVA and SNK (Student-Newman-Keuls) *a posteriori* comparison tests were made using GMAV V5 for Windows (Underwood & Chapman 1998). No significant differences in predator abundance were found between sampling dates ($p > 0.3$) so data were subsequently pooled (Underwood 1997).

Possible biases in trap data as a result of predator interactions (e.g. aggression) were examined by testing for correlations between the numbers of *Necora puber*, a typically aggressive species, versus the number of other species and between relatively large and small individuals of each species based on maturation sizes (see high-tide predators section in methods).

Because traps were deployed for a full high-tide, those on the lower shore were immersed for longer than those on the upper shore. To establish the effect

of duration of immersion on capture rate, comparisons were made on raw data and data adjusted for total period of fishing (immersion period) at each shore level.

The size frequency distribution of predators at high-tide was compared across the factors tidal elevation and exposure to wave action using a Kolmogorov-Smirnov test with a Scheirer-Ray-Hare extension in order to test for interactions between factors (Sokal & Rohlf 1995). Chi-square tests were used to compare abundance of each sex between tidal heights and between shores of differing exposure. Spearman rank correlations were used to compare the relative abundance of prey in the stomach contents of predators with the relative abundance of prey on the shore.

Multivariate analyses were used to examine the effect of shore exposure and tidal elevation on prey abundance and on predator diet (PRIMER 6 & PERMANOVA, Plymouth Marine Laboratory, Plymouth, U.K). ANOSIM and PERMANOVA permutation tests were used to determine significant differences among factors. Bray-Curtis similarity coefficients were used to compare similarities between each pair of samples. To test the hypothesis that crab stomach content composition varied with shore exposure and tidal height, the following design with four factors was used for PERMANOVA tests on the crabs collected at high-tide: tidal height (orthogonal, fixed, two levels: upper and lower), shore exposure (orthogonal, fixed, two levels: moderately sheltered and moderately exposed), shore (random, 2 levels, nested in shore exposure) and site (random, 2 levels, nested in shore and exposure).

2.4 Results

Abundance and distribution patterns of predators during high-tide

The main species captured in traps during nocturnal high-tides were *Carcinus maenas* (418 individuals), *Necora puber* (216 individuals) and *Cancer pagurus* (131 individuals) (Figure 2.2). The spider crab *Maja squinado* Herbst (19 individuals) and some fish including the shore rockling *Gaidropsaurus mediterraneus* L. (3 individuals) and the shanny *Lipophrys pholis* L. (9 individuals) were captured occasionally but not in sufficient numbers to be included in subsequent analyses. This low fish catch was expected since traps are commercially designed to capture crabs. Large numbers of crabs of all three species were captured and this included a wide range of sizes, hence providing evidence that traps were an efficient method to study these crab populations. The maximum sizes of crabs captured were 73 mm for *C. maenas*, 102 mm for *N. puber* and 193 mm for *C. pagurus*. Very few individuals were captured during daytime high-tides (total of: *C. maenas* = 15, *N. puber* = 8, *C. pagurus* = 9), suggesting that the majority of crabs were active during nocturnal high-tides. Hence, analyses of high-tide data were made only for nocturnal high-tide deployments.

There were no correlations between the number of *N. puber* and the abundance of any other species (*C. maenas*: $R < 0.3$, $p > 0.1$; *C. pagurus*: $R < 0.5$, $p > 0.2$), or between large and small sizes within species in replicates (*C. maenas*: $R < 0.3$, $p > 0.1$; *N. puber*: $R < 0.2$, $p > 0.3$; *C. pagurus*: $R < 0.3$, $p > 0.1$). Hence, it would appear that traps were a reliable method of sampling crustaceans during high-tide and were not compromised by problems of non-independence. Similar results were observed by Miller (1978) who found no effect of crab agonistic interactions on catch levels.



Figure 2.2. Main crab species sampled at low and high-tides in southwest Britain.

Direct comparisons of traps between the upper and lower shore (not corrected for period of immersion) are probably representative of the foraging intensity exerted by predators on prey at a particular shore level (see Table 2.1a,b). Using this approach, the abundance of crabs differed significantly between shore levels and with exposure to wave action (Table 2.1a). There were no differences in abundance at smaller spatial scales between shores or sites in any analyses (Table 2.1a).

For *Carcinus maenas* and *Necora puber* there were significant shore level and exposure interactions (Table 2.1a): *C. maenas* was significantly more abundant on the upper tidal level on sheltered shores (Figure 2.3). In contrast, *N. puber* was more abundant at the lower tidal level on sheltered shores (Figure 2.3). For *C. pagurus* there were significant main effects of shore level and

exposure, with greater abundance on the lower shore than on the upper shore and on exposed rather than sheltered shores (Table 2.1a, Figure 2.3).

When data were adjusted for duration of immersion, similar patterns of predator distribution were apparent for *C. maenas*, but not for *Necora puber* and *Cancer pagurus* (Table 2.1b). For both *N. puber* and *C. pagurus*, there were no longer any significant effects of exposure to wave action, but a main effect of tidal level with greater abundance on the lower shore was evident.

Table 2.1. ANOVA comparing the abundance of three common predators between tidal levels and shores of different exposure to wave action, individuals were captured during high-tide using traps. a) comparison of the total number of individuals captured during high-tide (raw data); b) comparison of the number of individuals adjusted for differences in the period of immersion (total period of fishing). Significant p-values are shown in bold. The directions of significant effects are shown in Figure 2.3.

a)	Source of variation	<i>C. maenas</i>				<i>N. puber</i>			<i>C. pagurus</i>		
		df	MS	F	p	MS	F	p	MS	F	p
	Tidal Level = TL	1	4524.08	598.74	0.00	93.52	897.80	0.00	147.00	60.83	0.01
	Exposure = Exp	1	208.33	8.65	0.09	188.02	9.18	0.09	16.33	39.20	0.02
	Shore (Exp) = Sh (Exp)	2	24.33	0.28	0.07	20.52	1.23	0.38	0.41	0.18	0.84
	Site (Sh x Exp) = Si (Sh (Exp))	4	86.04	1.05	0.39	16.65	3.67	0.06	2.29	1.10	0.37
	TL x Exp	1	70.08	24.74	0.03	2.52	24.20	0.03	1.33	0.55	0.53
	TL x Sh (Exp)	2	2.83	0.03	0.96	0.10	0.03	0.97	2.41	0.72	0.54
	TL x Si (Sh (Exp))	4	84.87	1.03	0.40	3.81	0.84	0.51	3.37	1.62	0.19
	RES	32	82.20			4.54			2.08		
Cochran's test			C=0.32 (not significant)			C=0.26 (not significant)			C=0.28 (not significant)		

b)	Source of variation	<i>C. maenas</i>				<i>N. puber</i>			<i>C. pagurus</i>		
		df	MS	F	p	MS	F	p	MS	F	p
	Tidal Level = TL	1	508.73	172.25	0.00	12.26	48.25	0.02	6.50	29.54	0.03
	Exposure = Exp	1	16.17	15.50	0.06	5.97	10.78	0.08	1.06	15.12	0.08
	Shore (Exp) = Sh (Exp)	2	1.04	0.13	0.88	0.55	3.13	0.15	0.07	1.12	0.41
	Site (Sh x Exp) = Si (Sh (Exp))	4	8.28	0.84	0.51	0.17	0.34	0.84	0.06	0.53	0.71
	TL x Exp	1	7.89	49.23	0.01	0.06	0.25	0.66	0.00	0.02	0.89
	TL x Sh (Exp)	2	0.16	0.02	0.98	0.25	2.10	0.23	0.22	2.05	0.24
	TL x Si (Sh (Exp))	4	8.12	0.82	0.52	0.12	0.23	0.91	0.10	0.91	0.47
	RES	32	9.86			0.51			0.11		
Cochran's test			C=0.30 (not significant)			C=0.20 (not significant)			C=0.19 (not significant)		

The population structure of *Carcinus maenas* and *Cancer pagurus* varied significantly with tidal level (respectively $H = 11.9$, $df = 1$, $p < 0.001$ and $H = 53.9$, $df = 1$, $p < 0.001$) and exposure (respectively $H = 12.6$, $df = 1$, $p < 0.001$ and $H = 34.4$, $df = 1$, $p < 0.001$). For both species median size was significantly larger on the lower shore than on the upper shore (Figure 2.4). *C. maenas* was significantly larger on sheltered shores while *C. pagurus* was larger on exposed shores (Figure 2.4). The size distribution of *Necora puber* did not vary significantly between tidal levels or shore exposures (respectively $H = 5.7$, $df = 1$, ns and $H = 0.8$, $df = 1$, ns).

There were consistent patterns of more males than females in data collected during high-tide. Of the 48 traps deployed, 64% had more males than females. Of the crabs captured the proportion of males was 65% for *C. maenas*, 71% for *N. puber* and 73% for *C. pagurus*.

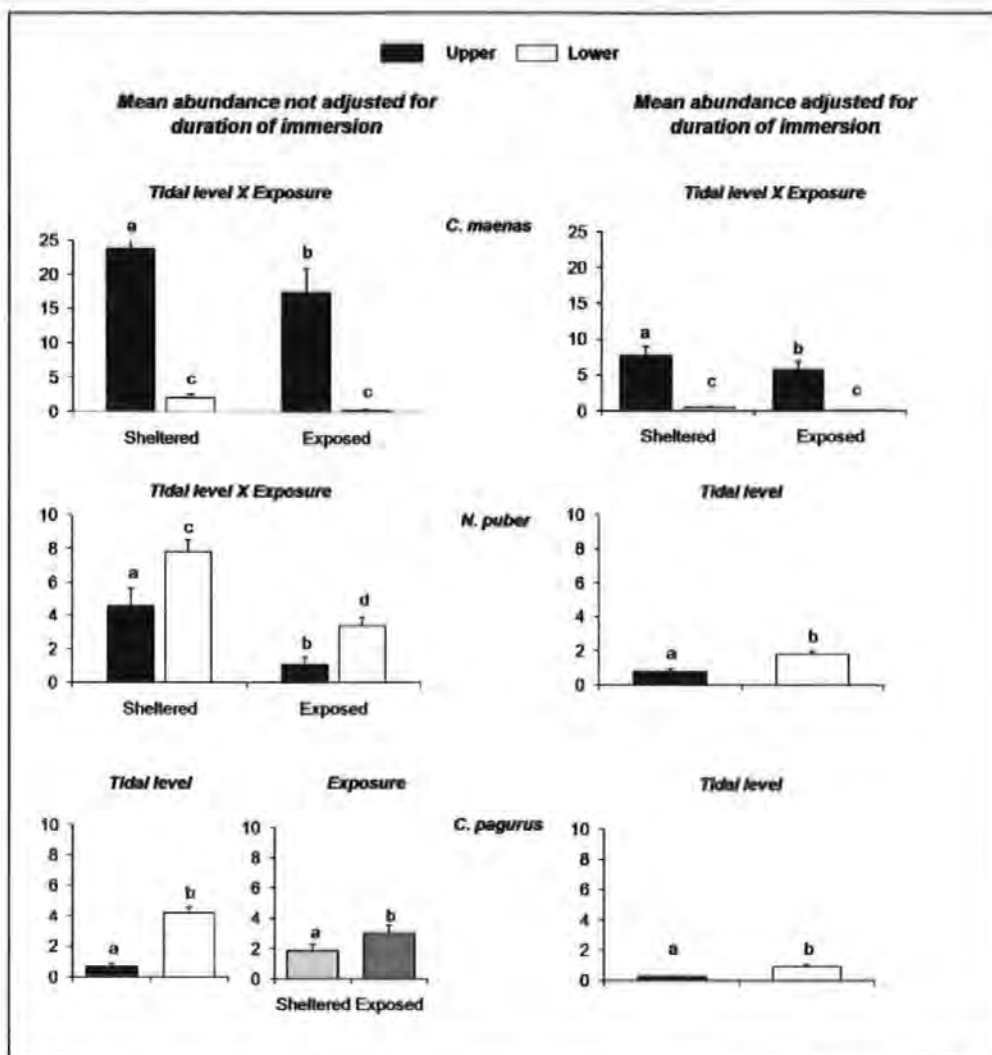


Figure 2.3. Mean abundance (\pm S.E.) of predators captured at high-tide “as collected” and “adjusted for duration of immersion” (total period of fishing) between the upper and lower shore and between sheltered and exposed shores. Histograms show SNK tests summary of significant effects (Table 2.1a). Treatments with identical lowercase letters were not significantly different.

Female *C. maenas* were more abundant on the upper shore while males were more abundant on the lower shore (Table 2.2). There were no apparent differences in the relative abundance of females and males for either *C. pagurus* or *N. puber* between shore levels.

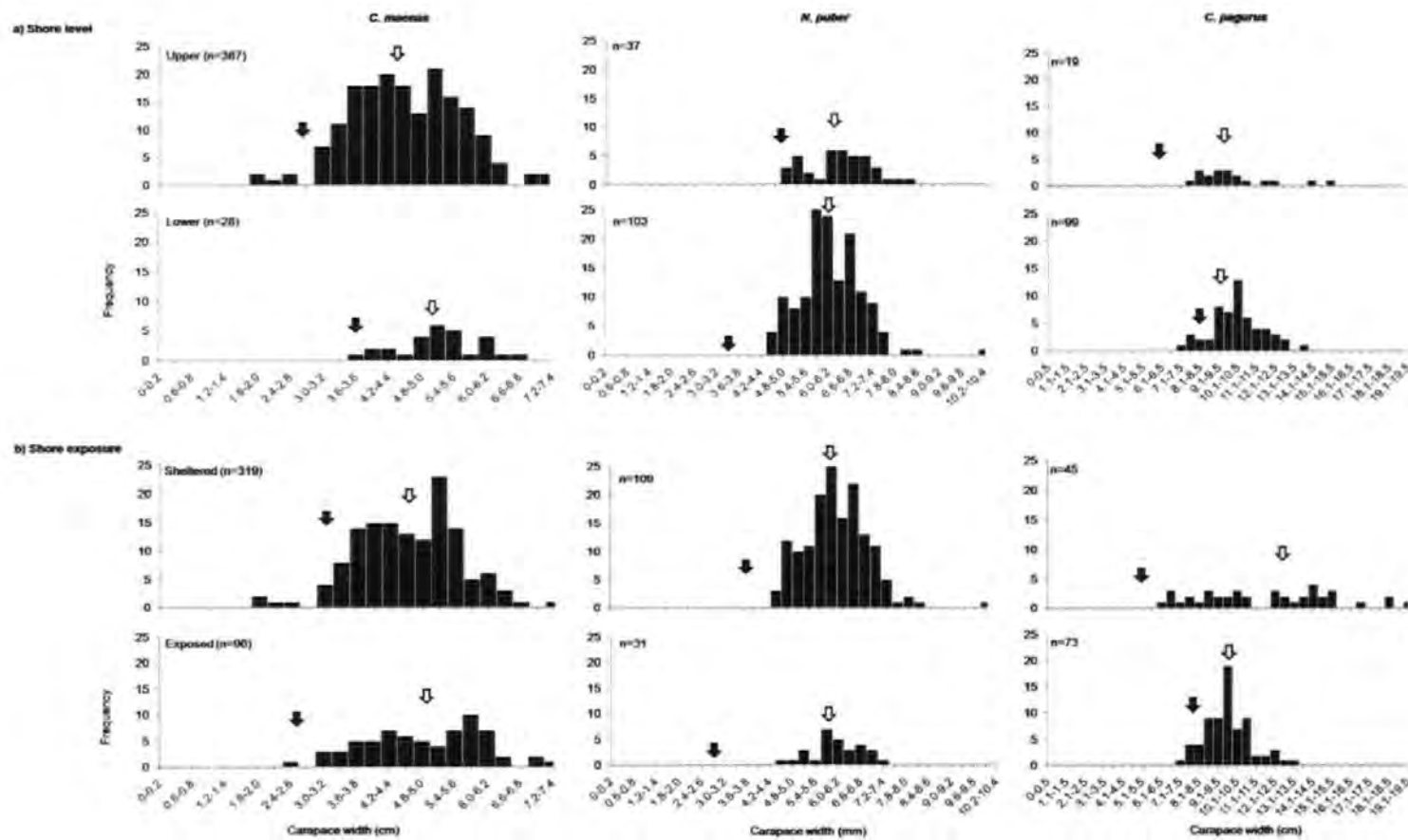


Figure 2.4. Size frequency histograms of predators captured in the intertidal during high-tide. Open arrow = modal class for individuals captured during high-tide, filled arrows = modal class for individuals captured during low-tide (shown for comparison). Note different scales on horizontal axes between species.

C. pagurus and *C. maenas* males were more abundant than females on shores of both exposures (Table 2.2), but no differences were found for *N. puber*.

Table 2.2. Summary of Chi-Square tests to examine the association between shore level and exposure to wave action on sex ratio of predators captured at night-time high-tide. Relative proportions shown bracketed. Significant p-values are in bold.

	<i>C.maenas</i>	<i>N. puber</i>	<i>C. pagurus</i>
Tidal level	$\chi^2(1,N=48)=6.791, p<0.01$		
	Upper: ♂ (0.4) < ♀ (0.6) Lower: ♂ (0.7) > ♀ (0.3)	$\chi^2(1,N=48)=0.075, ns$	$\chi^2(1,N=48)=0.244, ns$
Exposure	$\chi^2(1,N=48)=17.477, p<0.001$		$\chi^2(1,N=48)=16.037, p<0.001$
	Exposed: ♂ (0.6) > ♀ (0.4) Sheltered: ♂ (0.6) > ♀ (0.4)	$\chi^2(1,N=48)=2.204, ns$	Exposed: ♂ (0.6) > ♀ (0.4) Sheltered: ♂ (0.9) > ♀ (0.1)

Abundance and distribution of crabs at low-tide

In general, *Carcinus maenas* were significantly more abundant on the upper level of moderately sheltered shores, while *Necora puber* and *Cancer pagurus* were most abundant on the lower shore on both moderately exposed and sheltered shores (Table 2.3a, Figure 2.5). There were no differences in abundance at smaller spatial scales between shores or sites. *C. maenas* were larger (mean average difference in size ~12%) on the upper shore than on lower shore at moderately exposed locations (Table 2.3b, Figure 2.5). In contrast, the opposite effect was apparent on moderately sheltered shores with larger individuals (mean difference in size ~10%) on the lower shore than the upper shore. *N. puber* and *C. pagurus* were significantly larger on the upper shore than the lower shore on both moderately sheltered and exposed shores (Table 2.3b, Figure 2.5). There were no apparent differences in the relative abundance of females and males for crabs

collected during daylight at low-tide for all species at any of the sampling locations or tidal levels.

The only species that was observed to be active during nocturnal low-tides was *Carcinus maenas* with an average of 132.21 ± 5.43 (\pm SE) individuals foraging per hour. During these periods active individuals were significantly more abundant on sheltered shores than on exposed shores ($df_{1,16}$, $F = 91.81$, $p = 0.01$). This pattern of abundance mirrored that for data collected on the number of inactive individuals captured during daylight low-tides. There were no differences in abundance of *C. maenas* at smaller spatial scales between shores or sites. On average, fifteen predator-prey encounters were counted per hour of observations. The majority of these crabs were feeding on the limpets *Patella* spp. (average limpet size 15 mm).

The median size of predators captured at low-tide was clearly smaller than that of predators captured at high-tide (Figure 2.4), suggesting that larger individuals must move into the intertidal at high-tide from the subtidal, presumably to forage.

Table 2.3. ANOVA comparing the abundance (a) and size (b) of intertidal crabs recorded during day-time low-tide between tidal levels and shores of different exposures. Significant p-values are in bold.

(a)		Abundance									
Source of variation		<i>C. maenas</i>			<i>N. puber</i>			<i>C. pagurus</i>			
	df	MS	F	p	MS	F	p	MS	F	p	
Tidal level (TL)	1	140.62	62.15	0.01	160.62	321.11	0.00	16.25	21.50	0.04	
Exposure (Exp)	1	67.60	8.49	0.10	0.40	0.29	0.64	0.15	0.21	0.68	
Shore (Exp) = Sh (Exp)	2	7.96	1.57	0.31	1.36	1.25	0.37	0.73	0.98	0.44	
Site (Sh x Exp) = S4(Sh x Exp)	4	5.08	2.77	0.06	1.06	0.97	0.42	0.74	1.98	0.10	
TL x Exp	1	96.10	42.48	0.02	0.90	1.60	0.33	1.40	1.66	0.30	
TL x Sh (Exp)	2	2.28	0.79	0.51	0.56	1.00	0.44	0.75	1.53	0.32	
TL x S4 (Sh x Exp)	4	2.86	1.56	0.18	0.56	0.50	0.73	0.49	1.31	0.26	
RES	144	1.83			1.12			0.37			
Cochran's test		C = 0.13 (not significant)			C = 0.15 (not significant)			C = 0.15 (not significant)			
Transformation		(none)			(none)			(none)			
SNK tests		TL x Exp, SE=0.34 Exposed, Upper=Lower Sheltered, Upper=Lower** Upper, Exposed<Sheltered* Lower, Exposed=Sheltered			Tidal level, SE=0.08 Lower>Upper**			Tidal level, SE=0.09 Lower>Upper**			

(b)		Size									
Source of variation		<i>C. maenas</i>			<i>N. puber</i>			<i>C. pagurus</i>			
	df	MS	F	p	MS	F	p	MS	F	p	
Tidal level (TL)	1	0.37	22.04	0.04	0.94	482.13	0.00	78.59	85.24	0.00	
Exposure (Exp)	1	5.73	842.28	0.00	5.03	461.75	0.00	3.39	90.33	0.01	
Shore (Exp) = Sh (Exp)	2	0.00	0.34	0.73	0.00	3.28	0.14	0.03	1.42	0.34	
Site (Sb x Exp) = S4(Sb x Exp)	4	0.02	0.90	0.46	0.00	1.22	0.30	0.02	2.66	0.03	
TL x Exp	1	55.57	305.78	0.00	1.38	702.43	0.00	4.06	825.00	0.00	
TL x Sh (Exp)	2	0.01	1.81	0.27	0.00	5.03	0.08	0.00	0.06	0.94	
TL x S4 (Sh x Exp)	4	0.00	0.41	0.79	0.00	0.45	0.76	0.01	1.78	0.13	
RES	144	0.02			0.00			0.00			
Cochran's test		C = 0.11 (not significant)			C = 0.16 (not significant)			C = 0.11 (not significant)			
Transformation		none			Sqrt (X+1)			none			
SNK tests		TL x Exp, SE=0.02 Exposed, Upper>Lower** Sheltered, Upper>Lower** Upper, Exposed>Sheltered** Lower, Exposed<Sheltered**			TL x Exp, SE=0.00 Exposed, Upper=Lower Sheltered, Upper>Lower** Upper, Exposed<Sheltered** Lower, Exposed<Sheltered**			TL x Exp, SE=0.00 Exposed, Upper>Lower** Sheltered, Upper>Lower** Upper, Exposed=Sheltered** Lower, Exposed=Sheltered**			

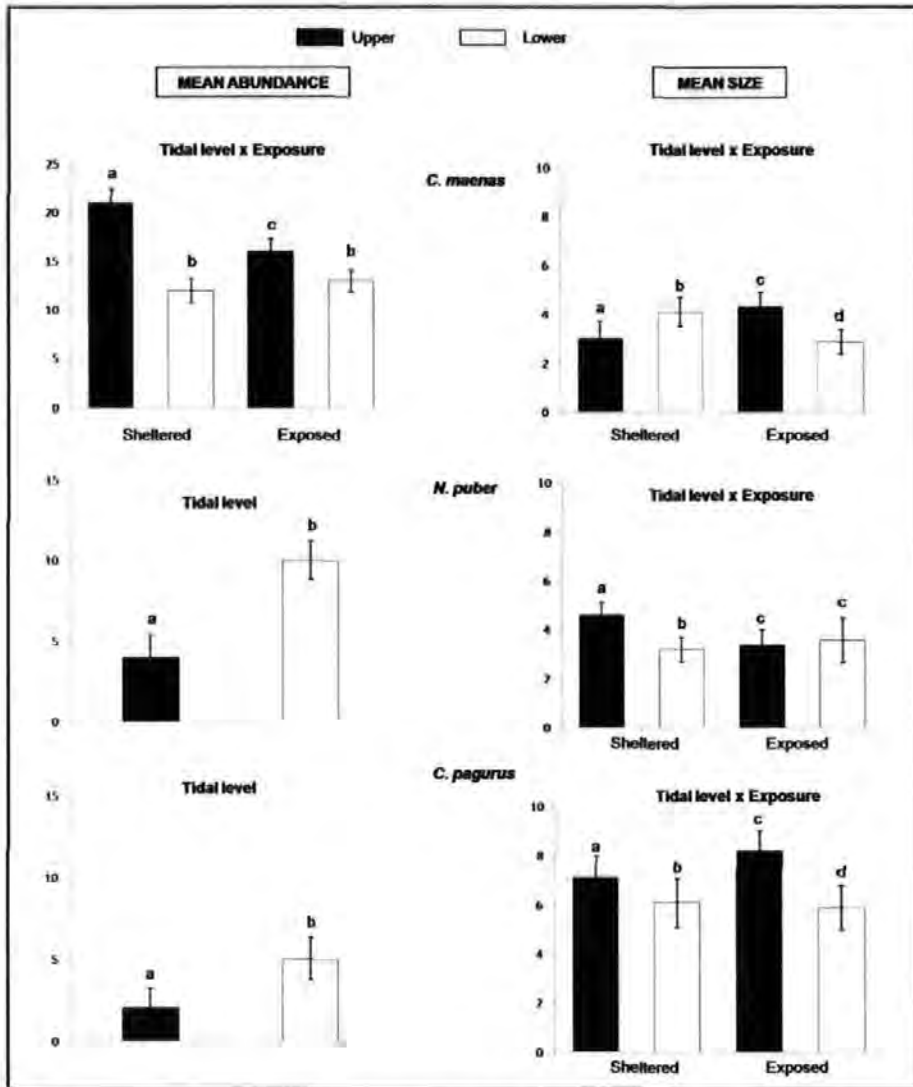


Figure 2.5. Mean abundance and size (\pm S.E.) of predators captured at low-tide between the upper and lower shore and between sheltered and exposed shores. Histograms show SNK tests summary of significant effects (Table 2.3a,b). Treatments with identical lowercase letters were not significantly different.

Predator stomach contents

The stomachs of 750 crabs were analysed. Irrespective of tidal height or shore exposure, the stomachs of the majority of these crabs were $\geq 30\%$ full. Only stomachs that were at least 50% full were used in analyses to minimise any possible bias associated with time of residence of food in the crab stomachs (Williams 1981). This is because some foods are slow to digest and others are fast. The chiton *Lepidochitona cinereus* (Linnaeus), the limpets *Patella* spp., the barnacle *Elminius modestus* Darwin, the mussel *Mytilus edulis* Linnaeus and brown algae *Laminaria* spp. were the most common prey items (see Figure 2.6) and accounted for more than 50% of the predator diet (Table 2.4).

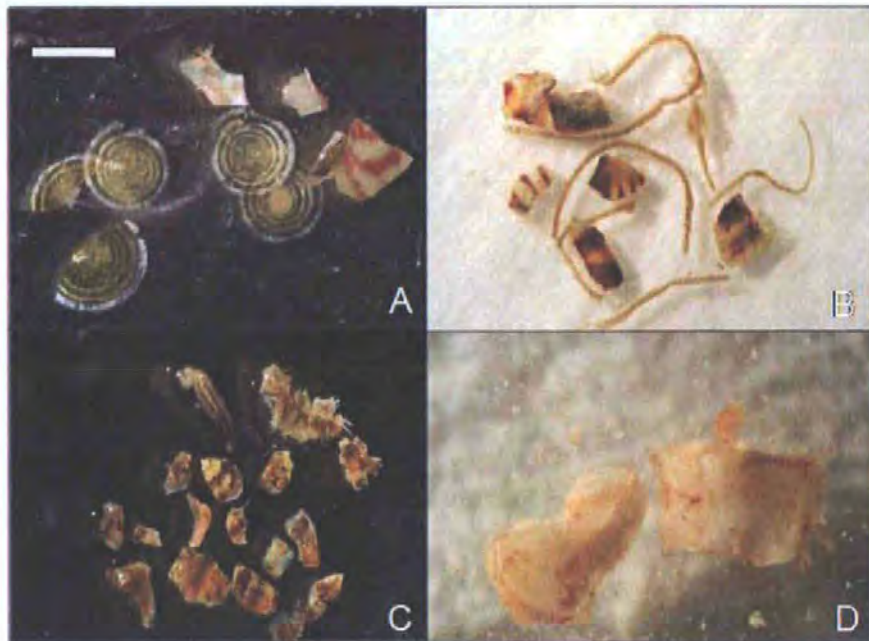


Figure 2.5. Examples of prey items removed from the stomachs of *Carcinus maenas*, *Necora puber* and *Cancer pagurus*. A – Operculum of *Gibbula umbilicalis*, B – Shell remains and radula of *Patella* spp., C – plates and radula of *Lepidochitona cinereus*, D – Plates of barnacles (scale bar = 10 mm), (scale bar A-C = 50 mm).

Of all prey items with hard body parts, limpets (*Patella* spp.) were the most common diet component, particularly for *Carcinus maenas* and *Cancer pagurus* (Table 2.4). Stomach contents of predators did not vary significantly with gender or age (juvenile and adult).

Table 2.4. Relative abundance (%) of prey items across shore height and exposure, and the percentage of the total number of prey items in the stomach of predators captured in traps at high-tide. Rank abundance shown in brackets.

Prey species		Percentage of prey species naturally available on the shore	Percentage of prey found in predator stomachs		
			<i>C. maenas</i>	<i>N. puber</i>	<i>C. pagurus</i>
Barnacles	<i>Chthamalus montagui</i>	Not quantified	0	6.5 (8)	7.1 (3)
	<i>Chthamalus stellatus</i>	39.9 (2)	1.1 (6)	0	3.6 (4)
	<i>Elminius modestus</i>	Not quantified	4 (5)	7.1 (7)	28.6 (2)
Gastropods	<i>Patella</i> spp	46.4 (1)	33.9 (2)	8.2 (6)	39.3 (1)
	<i>Littorina littorea</i>	1.4 (6)	0	10.6 (3)	3.6 (5)
	<i>Gibbula umbilicalis</i>	5.4 (3)	10.2 (4)	8.8 (5)	0
	<i>Osilinus lineata</i>	2.3 (4)	0	0	0
	<i>Nucella lapillus</i>	0.3 (8)	0	0	0
Polyplocophors	<i>Lepidochitona cinereus</i>	1.7 (5)	40.1 (1)	12.9 (2)	7.1 (3)
Bivalves	<i>Mytilus edulis</i>	0.6 (7)	10.7 (3)	29.4 (1)	0
Algae	<i>Laminaria</i> spp.	Not quantified	0	10 (4)	0

For all three crab species there were no differences in the diet composition between shores of differing exposure or tidal level (see Appendix 1). If number of permutations is < 30 (unique permutations column) then the P-value with the Monte Carlo correction [P(MC)] should be considered for interpretation of results (Anderson & Gorley 2007). This is because the Monte Carlo minimises any possible loss of power due to a reduced number of possible permutations in any term of the analyses (Anderson 2001a, c).

Distribution of prey species

Multivariate analysis of prey abundance showed significant differences in assemblages between shore levels ($R = 0.63$, $p < 0.001$) and much weaker differences between sheltered and exposed shores ($R = 0.11$, $p < 0.001$), shores within levels of exposure ($R = 0.11$, $p < 0.001$) and sites within shores ($R = 0.06$, $p < 0.001$).

The species contributing up to 90% of separation between shore levels (SIMPER) were: *Patella aspera*, *Gibbula umbilicalis* and *Balanus* spp. which dominated on the lower shore and, *Chthamalus* spp, *Patella vulgata*, *Osillinus lineata*, *Acanthochitona crinitus*, *P. depressa* and *Nucella lapillus* were more abundant on the upper shore. Ranks of prey abundance on the shore did not match ranks of prey abundance in the stomach contents of the crabs examined both for shore levels or shore exposures (Spearman correlation tests).

2.5 Discussion

Traps proved to be an efficient method to study crab populations on rocky shores at high-tide: three species were caught with this method. In 48 deployments a total of 765 crabs were captured including a wide range of sizes. Tests of data independency in traps showed there was no evidence of intra or inter-specific agonistic interactions occurred and so, the traps were considered to provide reliable data.

Spatial patterns in abundance of crabs

Crabs were clearly common predators in the intertidal during high-tide and their abundance was significantly influenced by exposure to wave action: *Necora puber* and *Carcinus maenas* were more abundant at moderately sheltered locations while *Cancer pagurus* was more abundant on moderately exposed shores. This pattern of distribution has not previously been described. Because these patterns of abundance were consistent across sampling dates and sites, it is likely that this is a general effect of exposure to wave action that can be extrapolated to similar shores in the region.

The major implication of these findings is that the impact of crabs on prey populations may be indirectly influenced by large spatial scale influences such as exposure to wave action, and stronger predation pressure may be exerted in sheltered locations. Crabs can exert significant control on the abundance and population structure of limpets in southwest Britain (Chapter 4), and so if predation by crabs is greater on sheltered shores where limpets are already less abundant (Hawkins & Hartnoll 1983, Jenkins et al. 1999), then there may be synergistic effects indirectly increasing algal abundance at these locations. In addition to the direct effects of wave action on algae imposing a mechanical size constraint whereby algae fronds are smaller at exposed locations (Wolcott 2007), it is possible that the abundance of algae is indirectly influenced by differences in predation on limpets and further increasing the potential for algae growth on sheltered shores.

Similar patterns of predator distribution were obtained independently of correcting data for hours of fishing according to shore levels. The overall pattern

being that the abundance of crabs differed between shore levels with greater abundance on the lower shore (except for *C. maenas*). This could result in a vertical predation gradient with higher pressure on the lower shore. The causes of this pattern in predator distribution across shore levels are not clear. However, habitat and prey availability (Robles et al. 1990, Holsman et al. 2006), competition and predation (Almany 2004) have all been suggested as important factors influencing the behaviour of these animals.

For all three crab species, males were more abundant than females and this pattern was consistent between shores. Similar findings were reported by Hunter & Naylor (1993) in the Menai Straits (U.K.) for *C. maenas*. According to these authors and Warman et al. (1993), males are the most active feeding individuals and are often larger than females, thus being able to cover larger distances on the shore.

Predators had a generalist diet which included a number of dominant prey species. Patterns in diet composition were not, however, related to the distribution of prey on the shore. Previous studies have reported that the diet of crabs can be driven by prey availability (abundance) (Paul 1981, Wear & Haddon 1987, Edgar 1990, Hsueh et al. 1992), while other studies indicate that accessibility of prey (capacity for predator to find, capture and ingest the prey), habitat (refuges) or preference for prey types or sizes are the main drivers (e.g. Cannicci et al. 2002, León & Stotz 2004, Pallas et al. 2006).

It was unexpected to find that chitons composed between 7% and 40% of the diet of these crabs suggesting that chitons are important intertidal prey, and this

has not been reported before. The chiton species eaten, *Lepidochitona cinereus*, is a cryptic grazer that lives on the underside of stones and in crevices and is mainly active at high-tide night when it feeds on the rock surfaces (Evans 1951). This coincides with the period of greatest crab activity. These chitons are relatively common (Silva, personal observation) and hence, it seems possible that crabs frequently encounter them during their foraging excursions.

Substantial numbers of *Carcinus maenas* were active during nocturnal low-tides. Foraging at low-tide has previously been reported for other species such as *Pachygrapsus marmoratus* (Flores & Paula 2001, Silva et al. 2004) but had not been quantified for *C. maenas*. Foraging during night-time rather than during daylight low-tide is likely to reduce desiccation pressure and reduce the risk of predation by birds or from fish during periods of immersion (e.g. Ahsanullah & Newell 1977, Ellis et al. 2005). The *C. maenas* that were active at night were feeding extensively on limpets with an average of 15 limpets being attacked per hour of observations, and constituting ~ 40% of the diet of *C. maenas* captured at high-tide. Hence, these ecologically important grazers (Hawkins & Hartnoll 1983, Jenkins et al. 2005, Coleman et al. 2006) would appear to be subject to considerable predation by crabs during both nocturnal low and high-water periods.

Trophic linkages between intertidal and subtidal habitats

Results supported the hypothesis that there is a strong trophic link between subtidal predators and intertidal prey. This was apparent because subtidal predators that differed in size from low-tide populations were captured during high-tide and their stomach contained intertidal prey species. This pattern has been

reported for *Carcinus maenas* in Menai Strait (UK) using similar methods to the ones used in the present study (e.g. Hunter & Naylor 1993, Warman et al. 1993), but had not been reported for *Necora puber* and *Cancer pagurus*, two highly abundant and commercially important species in Europe.

The results of the present work have important contextual implications for studies investigating the ecology of mobile predators and predator-prey interactions in shallow-water habitats, since low-tide observations of predator populations and their behaviour are likely to be unrepresentative. Large crustaceans such as the ones studied here can cover substantial areas of the shore at high water and hence can, forage upon a variety of species that would not be so readily accessible at low-tide. The difference in population structure between tidal phases may be related to refuge and prey availability (Holsman et al. 2006), intra-specific interactions between adults and juveniles (e.g. Fernandez et al. 1993, Mosknes 2004), predator avoidance (e.g. Kneib 1987), ontogenetic habitat shifts (e.g. Gibson 2003) or competition for refuges (e.g. Navarrete & Castilla 1990). Further work such as laboratory tests of inter-specific interactions and field experiments examining distribution of juveniles and adults would be required to clarify the importance of some of these factors.

Traditionally, subtidal and intertidal habitats have been considered separately due to logistical constraints in their study. The present work, however, suggests that there is an important trophic linkage created by foraging crabs between subtidal and intertidal habitats. This is evident from my data on commercially important species such as *Cancer pagurus* and *Necora puber* and the non-commercial species *Carcinus maenas*. Hence, these data suggest that in order to

fully understand the role of predators in shaping intertidal prey assemblages, it is necessary to take account of differences in foraging activities between tidal phases as well differing tidal levels and exposure. Based on predator density and stomach contents, it is evident from the present study that the importance of subtidal predators on rocky shore assemblages may previously have been underestimated (but see Rilov & Schiel 2006b, a, Jones & Shulman 2008). More research is therefore required to verify the importance and significance of top-down control by crabs in the intertidal; the most appropriate approach should be replicated manipulative experiments to establish the importance of these predator-prey interactions at a range of spatial scales.

CHAPTER 3

Population dynamics of crabs and their temporal and spatial movements on rocky shores

Population dynamics of crabs and their temporal and spatial movements on rocky shores

3.1 Abstract

Highly mobile subtidal predators such as fish and crabs are known to forage in the intertidal at high-tide, but the density of predators and their movements have not been described for many species. The occupation by individual crabs on the intertidal during high and low-tides was quantified for *Carcinus maenas*, *Necora puber* and *Cancer pagurus* by a one year mark-recapture study on two rocky shores in southwest Britain. The abundance of crabs at different shore levels, their population size and the survival and growth rates were analysed. This mark-recapture study was very successful with relatively high recaptures rates averaged across shores of 21% for *C. maenas*, 15% for *N. puber* and 10% for *C. pagurus*.

A comparison between the abundance of individuals present on the shore at high-tide with those present at low-tide showed considerable intertidal migration by *C. maenas*, *N. puber* and *C. pagurus*, thus indicating a clear link between the subtidal and intertidal habitats at these locations. There was a high fidelity of individuals and species to particular shore heights, and underlying mechanisms for these spatial patterns such as prey availability and agonistic interactions are discussed. Estimates of population size based on recapture of marked individuals at both high and low-tides indicated an annual density of 2.4 individuals.m² for *C. maenas*, 2.1 individuals.m² for *N. puber* and, 0.9 individuals.m² for *C. pagurus*. Average densities were higher in the summer (June-August) than in the winter (December-February) for all species on both shores.

Survival rates were estimated using the Cormack-Jolly-Seber model from multi-recapture analysis, and these were consistently high in this study with a minimum of 30% for all species. Survival was higher for larger individuals and, between species, was higher for *C. maenas* and subsequently for *N. puber* and *C. pagurus*. Growth rates were smaller for larger crabs and higher in the summer than in the winter. *C. pagurus* had the higher growth rate followed by *N. puber* and *C. maenas*. Intertidal crab migration probably exerts considerable impact on intertidal assemblages. This work informs management of *Cancer pagurus* and *Necora puber* which form an important fishery in Europe, as well as *Carcinus maenas* which is heavily exploited for bait in some areas.

3.2 Introduction

Large-scale movements (kilometres) are known to be an integral part of the life history of many crabs and these can be related to ontogenic shifts in resource use (e.g. Mosknes 2002), reproduction events (e.g. Aguilar et al. 2005) and seasonal migrations to avoid harsh environmental conditions (e.g. Allen 1966). However, frequent small-scale (meters) migrations associated with circadian and circatidal rhythms are also typical of many crab species (Edwards 1958, Naylor 1958, Dare & Edwards 1981, Reid & Naylor 1989, Chatterton & Williams 1994, Warman & Naylor 1995, Gibson 2003, Skov et al. 2005, Forward et al. 2007). For example, intertidal migration to forage by crabs has been extensively studied for the common shore crab *Carcinus maenas* (e.g. Edwards 1958, Naylor 1958, 1962, Crothers 1968, Dare & Edwards 1981, Reid & Naylor 1989, McGaw & Naylor 1992,

Hunter & Naylor 1993, Warman et al. 1993, Warman & Naylor 1995, Burrows et al. 1999, Mascaró & Seed 2001).

Necora puber, *Cancer pagurus* and *Carcinus maenas* are very abundant and these sublittoral and intertidal crabs have been shown to regularly forage at high-tide on shores in southwest Britain (see Chapter 2). The first two are commercially important but are considered to be primarily subtidal species and little is known about their intertidal migration patterns. Hence, it is important for our understanding of the functioning of rocky shores as a habitat and the management of these species, to study their population dynamics in a context of subtidal-intertidal linkage. The characterisation of the spatio-temporal patterns of movement, dispersal and habitat use of an organism is an important aspect of population and community ecology (Turchin 1991), and in the case of important predators can help predict their impact on prey populations.

To investigate the population dynamics of crabs it is vital to understand growth and survival patterns that determine structure of the populations. These estimates are important for understanding ecological processes which are size (i.e. diet) and density-dependent (i.e. predation, Sponaugle & Lawton 1990, competition, Miller & Smith 2003). Small individuals are subject to higher predation mortality and the faster they grow the more rapidly this mortality decreases (Jennings et al. 2001). In crabs, growth rate is strongly influenced by temperature with larger increments occurring in warmer months (Hartnoll 1982), thus knowledge of seasonal patterns is also important.

In subtidal habitats, the mark-recapture technique has been applied to large scale (kilometres) migration patterns of lobsters and crayfish (e.g. Bell et al. 2003, Dunnington et al. 2005), but has seldom been used to analyse small scale migration between the subtidal and intertidal habitats (but see Edwards 1958, Holsman et al. 2006). A key assumption of mark-recapture studies is that tag retention and visibility are reliable throughout the duration of the study.

A particular difficulty in crustacean tagging is the ability to identify individuals for long periods because of loss of external tags through ecdysis (Fitz & Wiegert 1991, Davis et al. 2004). Recently new technological improvements have allowed internal marking of crabs which are not lost during moulting. The Visible Implant Elastomer (VIE - Northwest Marine Technology TM) consists of a non-toxic biocompatible fluorescent liquid injected into the tissue of the crab with a hypodermic needle where it cures into a pliable solid (Jerry et al. 2001, Frisch & Hobbs 2006). It has been shown to be highly efficient for crustaceans such as prawns, crabs and lobsters and to have an extremely high moult-retention rate (consistently above 90%) for periods of up to 18 months (Godin 1996, Linnane & Mercer 1998, Spilseth & Morgan 2005, Clark & Kershner 2006, Frisch & Hobbs 2006). This is considerably more effective than clipping of appendages or use of streamer tags (e.g. Godin 1996, Linnane & Mercer 1998, Jerry et al. 2001, Davis et al. 2004, Spilseth & Morgan 2005, Frisch & Hobbs 2006).

Other advantages are that it is non-toxic for the studied species or if ingested by humans (Northwest Marine Technology TM, USA); the flexible nature of the compound minimises physical hindrance; it is cost-effective and externally visible therefore no specialised detection equipment is required; internal implementation

(ventral side) removes any possibility of entanglement or tag-induced predation (see Bergman et al. 1992, Frisch & Hobbs 2006). Additionally, the elastomer does not seem to alter behaviour, survival or potential for recapture and, there is a minimal mortality resulting from tagging procedure (Frisch & Hobbs 2006).

In my study, an individual field-based mark-recapture experiment was used on rocky shores in southwest Britain. The temporal and spatial movement patterns on the shore plus, growth and survival rates of individual *C. maenas*, *N. puber* and *C. pagurus* were examined over an annual cycle. Here, I describe the extent of movements by these crab species from the subtidal and from intertidal refuges into the intertidal zone to forage. A novel aspect of this work was that several species were studied simultaneously, together with information on tidal state allowing a comparison of distribution. This study also investigated population parameters of crab populations including survival and growth rates and estimates of population size which remain largely unknown for mobile intertidal foragers (but see Lee et al. 2006)

For each species, the following questions were asked: (1) are individuals present at the low-tide different from those present at high-tide; (2) are individuals associated with particular shore heights; (3) what are the annual survival and seasonal (winter and summer) growth rates and; (4) what are the population sizes? The consequences for intertidal community structure and ecosystem functioning are discussed, particularly the extent of connectivity between subtidal and intertidal habitats created by foraging of mobile predators.

3.3 Methods

Sampling sites and techniques

The study was made on two rocky shores (Mount Batten - 50°21'N, 4°07'W; Jennycliff - 50°21'N, 4°07'W) in southwest Britain. Two shore levels were defined: upper shore approximately 4 m above Chart Datum (CD), and the lower shore approximately 1 m above CD. Populations occupying the shore on nocturnal high-tides were sampled using standard commercial crab traps (55 cm long x 40 cm wide x 30 cm high, 1 cm mesh size), moulded in heavy duty plastic with two entrances of 8 cm diameter and a bait tube (Coastal Fishing Supplies U.K.). Traps are an efficient method to catch crabs and have previously been shown to be efficient in capturing the species considered in this study (Miller 1990, Chapter 2).

Traps were fixed to the rock platform via anchoring points (see Figure 2.1). On each sampling date, three traps were positioned at least 40 m apart within a 1000 m² area at each shore level on each shore and left for a single nocturnal high-tide when crab activity is greatest (Dare & Edwards 1981, Hunter & Naylor 1993). This separation was considered sufficient to ensure independence of the fished areas (see Miller 1990). Traps were baited with ~ 300gr fresh cut *Trachurus trachurus* L. (mackerel) as this bait had been proven successfully in preliminary trials.

In addition to using traps during high-tide, low-tide observations were made during the day to establish the extent to which predators captured at high-tide originated from intertidal refuges or were from subtidal populations. Surveys were made by performing one hour searches amongst boulders/crevices at each shore

level on both shores. The study was conducted over a one year period (September 2006-2007), and both high and low-tide sampling was undertaken for two days each spring tide approximately every 2-4 weeks, totalizing 24 recapture visits in one year.

Tagging

Only individuals larger than 10 mm carapace width were tagged since tag retention and survival rates are considered to be lower in smaller individuals (Linnane & Mercer 1998). Tagging was made *in situ* and tags were implanted ventrally by inserting the Visible Implant Elastomer (Northwest Marine Technology, Washington, USA), with a hypodermic syringe intramuscularly from the edge of the sternite to the basis segment of the pereopods. Care was taken to end the flow of elastomer before the needle was drawn back to prevent the elastomer from trailing out of the injection hole and curing externally. The volume of injected material was approximately 5 mm per individual.

Tags were clearly readable with the naked eye (see Figure 3.1), but visibility was enhanced by illumination with ultraviolet light. A combination of 5 colours and tag locations (i.e., left or right side in any of the pereopods) allowed individual markings for hundreds of individuals per shore. Initially, crabs were also tagged with exterior ventral markings to detect the 1st moult (see Figure 3.1).

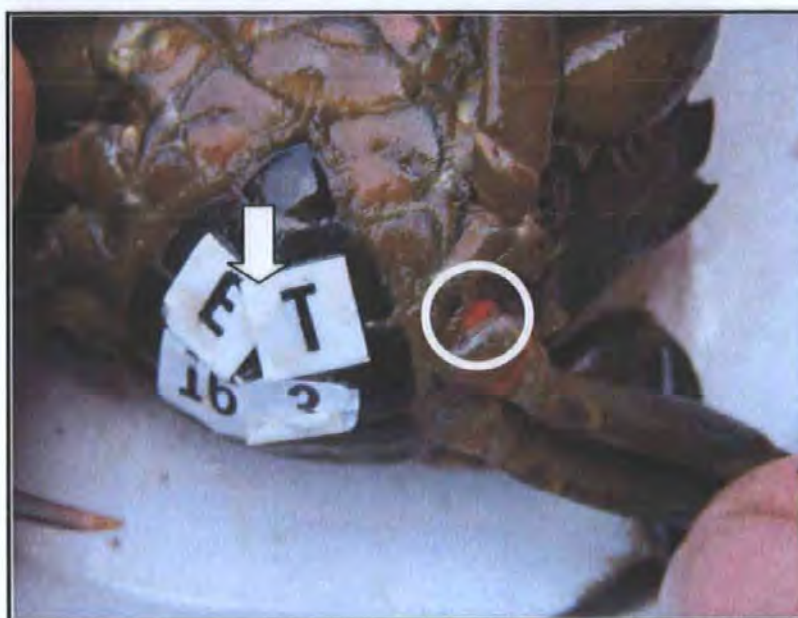


Figure 3.1. Example of elastomer (circled) and external marking (arrowed) on *Carcinus maenas*.

The external tagging procedure was, however, time consuming and was discontinued. High-tide individuals were distinguished from those at low-tide individuals with an individual code. After marking crabs were released as close as possible to the collection area. The following information was recorded upon capture and/or recapture: species, size (carapace width), sex, tidal phase (high or low-tide), state of hardening of carapace (as an indication of early post moult stage and recent ecdysis), tidal height (upper or lower shore) at the time of capture, and elastomer code and date.

Analysis of movement patterns

The extent of the migration from the subtidal into the intertidal was assessed by comparing the abundance of individuals present on the shore at high-tide with those present at low-tide. A winter (December 2006 – February 2007) - summer

(June-August 2007) comparison was made to examine seasonal differences in the average density of crabs marked and recaptured only during high-tide. This may inform about seasonal patterns of predation pressure. The individual fidelity to tidal levels was assessed for each species by quantifying the number of individuals that were successively recaptured at their tagging location for both tidal phases. A t-test was used to compare the average size (across shores and dates) of individuals marked and recaptured only during high-tide with those only marked and recaptured during low-tide. A chi-square test was made between the proportions of animals captured and recaptured at high-tide with those caught and recaptured at low-tide to establish whether there were two sub-populations, i.e., residents and migrants.

Analysis of population parameters

The time interval between mark and recapture visit was short (1 month); therefore, an assumption for constant population size between paired sampling dates was considered valid. Hence, the Peterson model for closed populations was used to estimate monthly population abundance using an unbiased estimator and then averaged across monthly estimates for a year (details in Seber 1982):

$$N = \frac{(M + 1)(C + 1)}{(R + 1)} - 1$$

where M = number of individuals marked in the first day; C = total number captured in the second day of sampling and, R = number of captures from the second day that bear marks from the first day.

The program MARK (White & Burnham 1999) was used to analyse mark-recapture data. The Cormack-Jolly-Seber model (see appendix 2) was chosen to estimate survival as this model is more flexible in the requirements regarding recaptures of marked animals (White 2007). It can be used for open populations where emigration as well as mortality can occur. It estimates survival from a multiple recapture field approach and includes procedures to test goodness-of-fit for models accounting for variable survival and capture rates over time (White 2007).

Seasonal growth was obtained for all species by averaging individual size increments per size class of individuals tagged at high and low-tides of both shores, in order to obtain a reasonable data representation ($n > 30$ for each season per species). For summer growth analysis were considered the individuals marked in June and then recaptured in August 2007, and for winter were considered the individuals marked in December 2006 and recaptured in February 2007. The density of crabs marked and recaptured only at high-tide was also estimated for the same seasons. One-way ANOVA was used to test for differences between annual survival rates of individuals captured and recaptured only during high-tide and those captured and recaptured only during low-tide.

3.4 Results

Efficiency of tags

The efficiency of the mark-recapture method was relatively high compared to other similar studies (see Lee et al. 2006) with an average recapture rate of 21% for *Carcinus maenas*, 15% for *Necora puber* and 10% for *Cancer pagurus*. The longest period between tagging (24/09/06) and recapture (11/08/07) was approximately 11 months, and the shortest 2 weeks (marking at 27/11/06, recapture at 10/12/06). Recapture levels were consistent for both shores.

Movement patterns

a) *Tidal phase*

In total, 594 individuals were marked at Mount Batten following high-tide capture and 481 were marked at low-tide. At Jennycliff 416 individuals were marked from high-tide capture and 471 were marked at low-tide. Recapture rates were high on both shores (Table 3.1).

Table 3.1. Recapture rates of the crabs collected in the intertidal from two shores in one year estimated by pooling data from high and low-tides.

	Recapture rate (%)	
	Mount Batten	Jennycliff
<i>Carcinus maenas</i>	22	19
<i>Necora puber</i>	14	16
<i>Cancer pagurus</i>	9	11

Of the individuals marked at low-tide across all shores, 14.7 % of *N. puber*, 18.8 % of *C. maenas*, and 15.3 % of *C. pagurus* were subsequently recaptured at high-tide (Figure 3.2 A-C). Of all individuals marked at high-tide across all shores,

7.0 % of *N. puber*, 22.7 % of *C. maenas*, and 13.6 % of *C. pagurus* were subsequently recaptured on the same shore at low-tide (Figure 3.2 A-C). Of the individuals marked at high-tide, on average 70.3 % of *N. puber*, 75.8 % of *C. pagurus* and 55.2 % of *C. maenas* were exclusively recaptured at high-tide. These patterns were consistent across shores and sampling occasions for all species.

Results from the chi-square test show that there is evidence supporting the hypothesis that, for all crabs species, there are two sub-populations of crabs on the shore (Table 3.2). There is a sub-population of crabs that migrate in and out with the tidal cycle (i.e. only captured and recaptured at high-tide) while other crabs are only present on the shore at low-tide and reside in the intertidal (i.e. only captured and recaptured at low-tide). This data provides evidence of a subtidal-intertidal linkage established by all three species.

Seasonal densities were also estimated taking into consideration the animals marked and recaptured only at high-tide for each shore in order to inform about seasonal variation in occupancy and hence predation pressure (Table 3.3). For all species and both shores, there was a trend for higher densities of crabs on the shore during the summer than in the winter (Table 3.3).

Table 3.3. Seasonal (summer and winter) average estimates of crab density (individuals.m²) based on individuals marked and recaptured on the shore at high-tide.

	Mount Batten (sampled area = ~ 1500 m ²)		Jennycliff (sampled area = ~ 1000 m ²)	
	Summer	Winter	Summer	Winter
<i>C. maenas</i>	3.6	3.3	3.0	2.4
<i>N. puber</i>	4.8	2.6	4.3	2.9
<i>C. pagurus</i>	2.4	1.9	2.2	1.1

Table 3.2. Relative proportions and summary of chi-square results examining the association of crabs only tagged and recaptured at high-tide and those only captured and recaptured at low-tide across all shores and dates.

Tagged	Relative Proportion of recaptures		Chi-square result
	Low-tide	High-tide	
Low-tide			
<i>Carcinus maenas</i>	0.8	0.2	Chi-square (N=120)=5.45, $p < 0.01$
<i>Necora puber</i>	0.6	0.4	Chi-square (N=35)=3.82, $p < 0.05$
<i>Cancer pagurus</i>	0.8	0.2	Chi-square (N=15)=5.21, $p < 0.01$
High-tide			
<i>Carcinus maenas</i>	0.3	0.7	Chi-square (N=70)=4.78, $p < 0.01$
<i>Necora puber</i>	0.2	0.8	Chi-square (N=80)=5.74, $p < 0.01$
<i>Cancer pagurus</i>	0.3	0.7	Chi-square (N=25)=4.32, $p < 0.01$

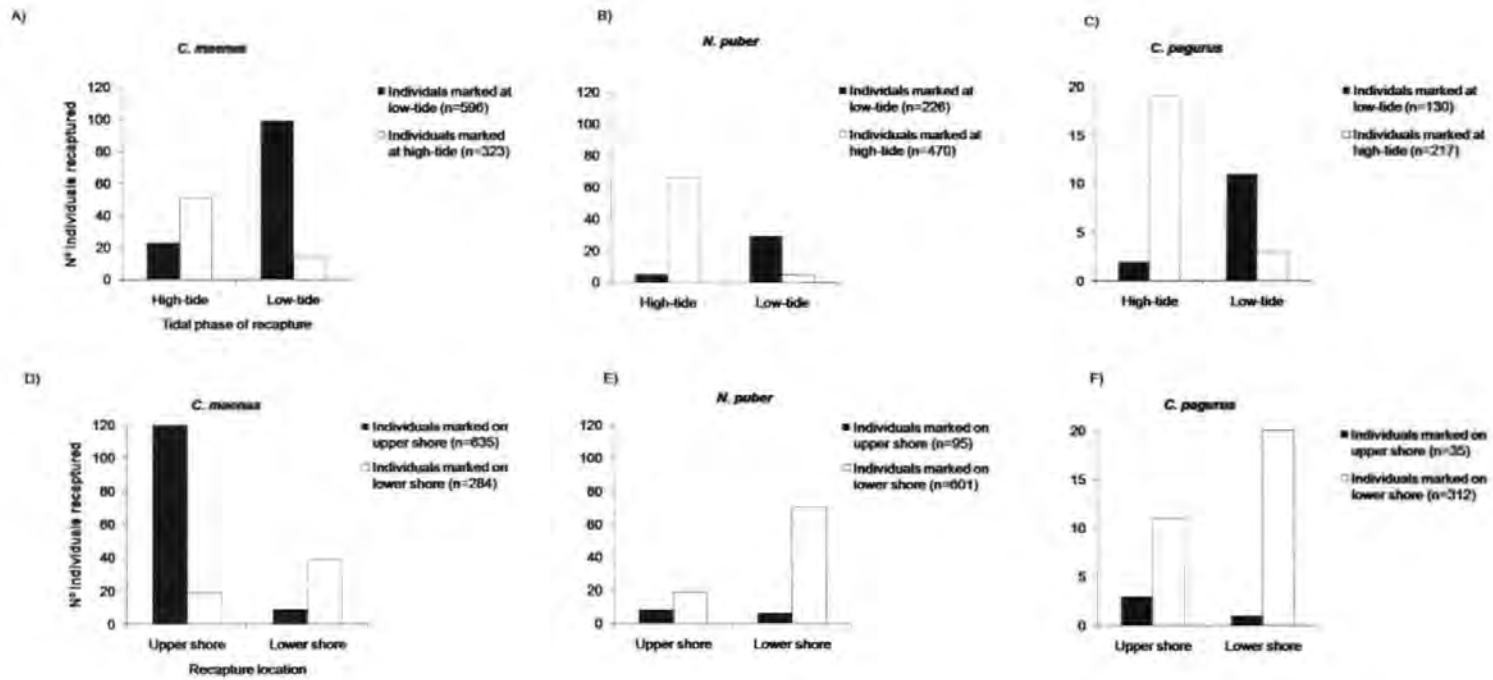


Figure 3.2. Recapture of crabs moving between tidal phases (A-C) and between shore levels (D-F) pooled across the two shores and for one year sampling. Shaded bars represent individuals marked at low-tide and white bars represent individuals marked at high-tide.

Table 3.4 shows that, for all three species, significantly larger individuals were captured with traps during high-tide than those captured in transects during low-tide.

Table 3.4. Average size (\pm SE) of individuals marked and only recaptured at low and high-tides across all shores and dates.

	Average size (cm \pm SE)		
	Low-tide	High-tide	t-test result
<i>Carcinus maenas</i>	3.1 \pm 0.09	4.6 \pm 0.31	t = 2.1, p = 0.03
<i>Necora puber</i>	4.2 \pm 0.15	6.1 \pm 0.24	t = 6.2, p = 0.04
<i>Cancer pagurus</i>	6.6 \pm 0.42	10.4 \pm 1.30	t = 4.3, p = 0.02

In summary, there were strong migration patterns of larger sublittoral individuals into the intertidal during high-tide for all crab species. Taking into consideration the long-term nature of this study and relatively high recapture rates (see above), it was considered that these patterns were representative.

b) Spatial movements

There was a high correspondence between the tidal level where individuals were first tagged and subsequent location of recapture for all species (Figure 3.2 D-F). Of the individuals marked on the upper shore across shores and subsequently recaptured on the lower shore, 42.1 % were *N. puber*, 6.9 % were *C. maenas* and 25.0 % were *C. pagurus* (Figure 3.2 D-F). Of all individuals marked on the lower shore across shores and subsequently recaptured on the upper shore, 21.1 % were *N. puber*, 32.7 % were *C. maenas* and 35.4 % were *C. pagurus*

(Figure 3.2 D-F). These patterns were consistent across shores and sampling occasions for all species.

Population parameters

Monthly estimates of population size were made for each shore using the Petersen model for closed populations by pooling tidal phase data, and densities were estimated for each shore (Table 3.5).

In general, annual survival rates (ϕ) were high, but this was size and species dependent. Larger individuals had higher rates regardless of the tidal phase of capture (Figure 3.3). For animals captured at low-tide, the average (\pm SE) survival rate across size classes was for *C. maenas* $44\% \pm 0.6$, $30\% \pm 1.7$ for *C. pagurus* and, $28\% \pm 0.8$ for *N. puber* (Figure 3.3).

Table 3.5. Average monthly population size (\pm SE) across shores and for all species estimated from the Petersen model. Estimates of annual density per shore based on animals collected at both tidal phases are also given for each species.

	Mount Batten (sampled area = ~ 1500 m ²)	Density (individuals.m ²)	Jennycliff (sampled area = ~ 1000 m ²)	Density (individuals.m ²)
<i>C. maenas</i>	3476 individuals (\pm 170)	2.31	2389 individuals (\pm 278)	2.38
<i>N. puber</i>	2883 individuals (\pm 239)	1.92	2243 individuals (\pm 219)	2.24
<i>C. pagurus</i>	1721 individuals (\pm 345)	1.14	641 individuals (\pm 419)	0.64

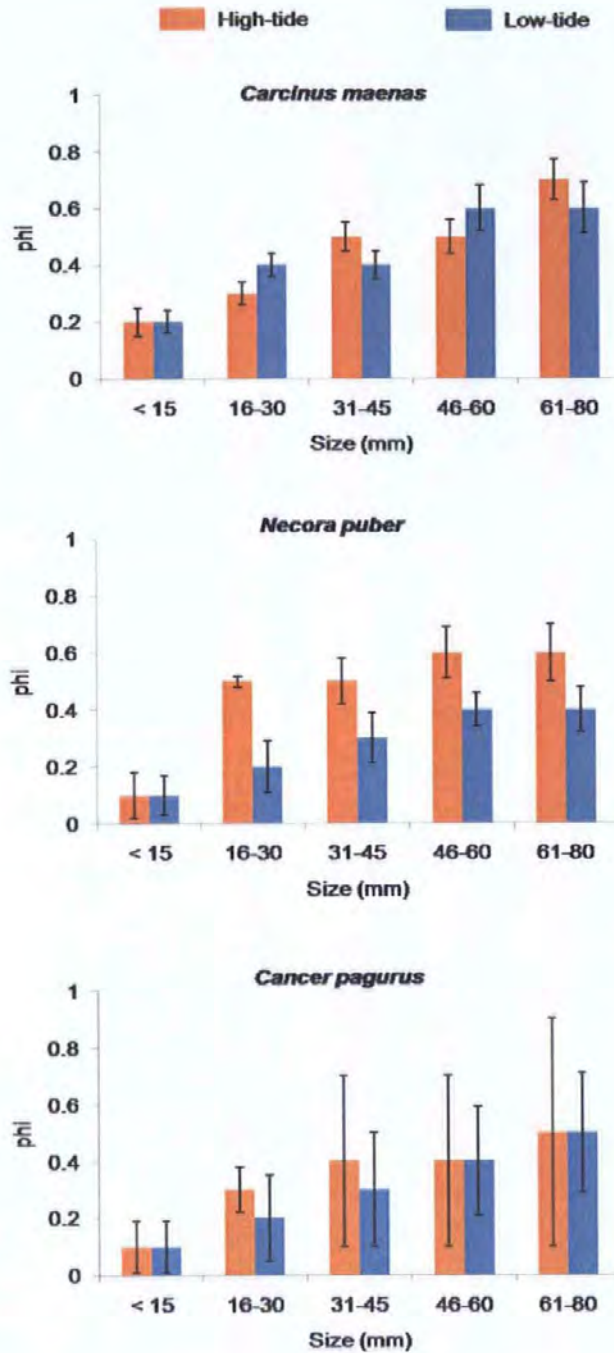


Figure 3.3. Size-class average survival estimates ($\phi \pm SE$) for *Carcinus maenas*, *Necora puber* and *Cancer pagurus* sampled at high and low-tides (pooled across shores) for one year sampling period. An average of 30% of high-tide individuals were recaptured at low-tide at a given time. Data were fit to the most parameterised model with survival and recapture probability variable over time $\{\phi(t), p(t)\}$.

For those individuals captured at high-tide and allowing for an average of 30% overlap with low-tide data for the individuals marked at high-tide but recaptured at low-tide at any given time, average survival was $46\% \pm 0.7$ for *N. puber*, $44\% \pm 0.5$ for *C. maenas* and, $34\% \pm 2.3$ for *C. pagurus* (Figure 3.3). There were no significant differences between the annual survival rate of individuals captured and recaptured only during high-tide and those captured and recaptured only during low-tide for *C. maenas* ($F_{1,148}$, $p > 0.05$), *N. puber* ($F_{1,68}$, $p > 0.05$) and *C. pagurus* ($F_{1,56}$, $p > 0.05$).

For all species, average growth rates were faster in the summer months than in the winter when interestingly growth still occurred. Larger individuals grew slower than smaller individuals (Figure 3.4). Irrespective of season and across initial sizes, the smallest size class of *Cancer pagurus* had the highest annual growth (8 mm – 16 mm), followed by *Necora puber* (6 mm – 13 mm) and *Carcinus maenas* (4 mm – 10 mm).

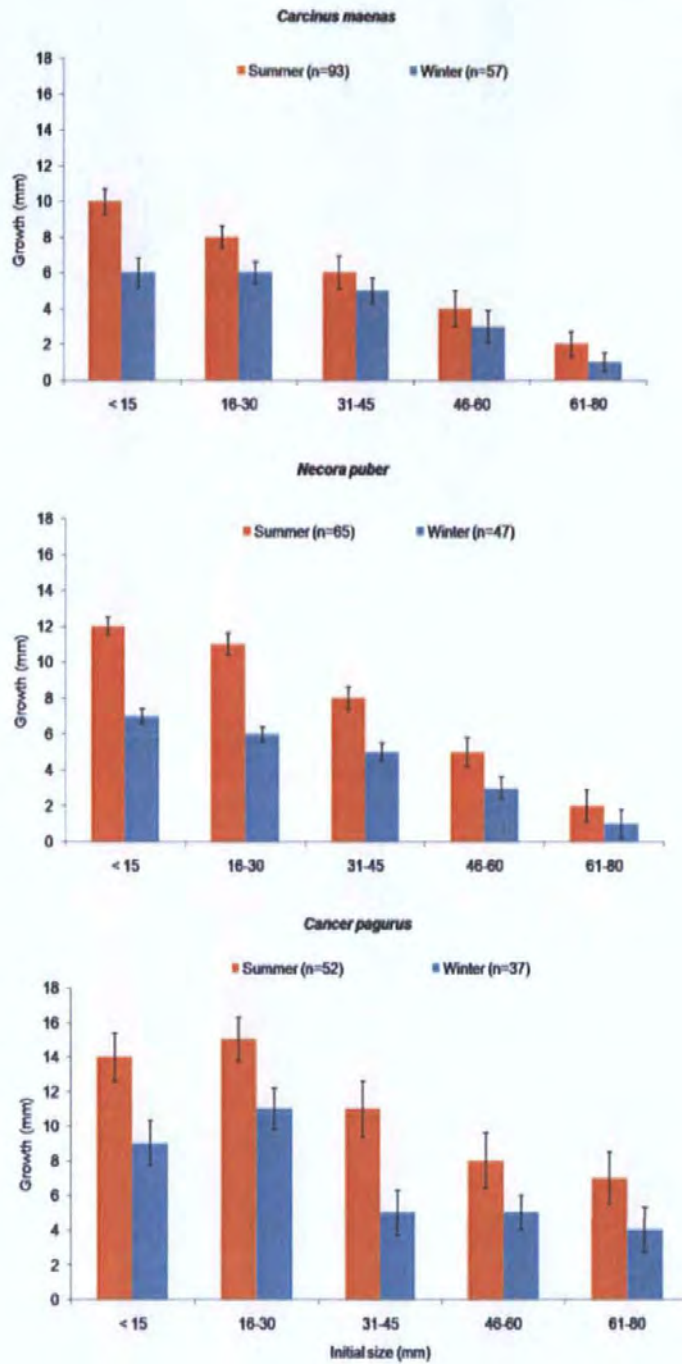


Figure 3.4. Size-class average growth estimates for crabs sampled at high and low-tides (pooled across shores) for summer (June – August 2006) and winter (December 2006 – February 2007).

3.5 Discussion

Methodological consideration

The long-term marking was very efficient for all crab species since recapture rates were high and recaptures occurred frequently (41% on average across species) after > 250 days from tagging date. Crabs were frequently recaptured more than once and the minimum number of crabs recaptured in a given day of sampling was 10. Hence, survival estimates were considered to be reliable since, accordingly to Seber (1982) bias in estimation occurs when the probability of recapture is low and recaptures are less than 3. Furthermore, because across shores a considerable number of individuals of the three crab species (for *N. puber* = 98 individuals, *C. maenas* = 131 individuals and for *C. pagurus* = 74 individuals) were successfully tracked for up to one year, this study offers reasonable certainty for migration levels between the subtidal and the intertidal and patterns across the shore vertical gradient.

Occupancy and population processes

The combined population sizes estimated for the three species on one tidal cycle indicates that ~ 4000 crabs in an approximately 1500m² area can be present on a single shore. By considering the large populations sizes and also the considerably high survival rates found for all species, it is likely that populations of intertidal prey groups are influenced to some extent by migrating crab predation since predation pressure may be considerable due to the large abundance of predators. Sublittoral predators including fish and crabs have been shown to control the intertidal abundance of mussels in New Zealand (Rilov & Schiel 2006b).

My data also showed that there are higher densities of all three crab species in the summer than in the winter during high-tide and also that considerable densities of all crabs are still present on the shore during high-tide in the winter. Previous studies have suggested that *C. maenas* undertakes offshore migrations in winter months with consequent strong decrease in littoral densities (Edwards 1958). My study contradicts this but supports the study of Naylor (1962) who indicated that *C. maenas* remains in the sublittoral during winter undertaking intertidal migrations at high-tide, and that increased densities of this crab can be found on the shore during warmer months. Since high-tide is the time when intertidal prey are most accessible, this suggests that higher predation pressure may occur in summer than in winter on these shores. This requires, however, further testing possibly with exclusion experiments deployed in summer and winter. Seasonal variation in predation pressure has been shown for other marine systems. For example, on soft intertidal substrata in Maine (USA), predation pressure by *C. maenas* on the clam *Mya arenaria* L. has been shown to be higher in the summer than in winter (Beal et al. 2001); while on intertidal sandflat the impact of tidal migrations by fiddler crabs on benthic assemblages is larger in summer months (Reinsel 2004).

Many ecological patterns are size dependent such as crab efficiency in handling different prey types and/or sizes (see Freire et al. 1996, Hughes 2000) and mortality where faster growth enhance survival (Jennings et al. 2001). Thus, size and growth rates may be relevant in the foraging behaviour of these predators. Growth rates were shown to vary between species. The edible crab *C. pagurus* appeared to be the fastest grower followed in decreasing order by *N. puber* and *C.*

maenas. Larger crabs had higher survival but lower growth rates, which is expected since their moulting frequency decreases with age (Hartnoll 1982). Growth rates were also higher in the summer than in the winter for all species, but some winter growth was also apparent. Crabs grow by moulting where the old exoskeleton is shed and a new one develops. Temperature is the environmental factor that most limits growth, with the general effect of shortening intermoult duration with a rise in temperature (Hartnoll 2001). Crabs suspend their feeding when moulting (Crothers 1967, Conan 1985) hence, shorter intermoult periods in the summer may suggest that some seasonal variation in predation pressure may occur.

Connectivity and site fidelity

A key finding in this study was the extent of a subtidal-intertidal linkage by all three species. On average (across species), 70% of the individuals that were present in the intertidal during high-tide were not present at low-tide. Similar patterns of extensive intertidal migration have been reported for *C. maenas* (Hunter & Naylor 1993) in the Menai Strait (U.K.), and subtidal *Cancer magister* has also been found to extensively explore intertidal resources in the U.S.A. (Holsman et al. 2006). Also, my data showed that individuals only present on the shore at high-tide are larger than those present at low-tide, thus indicating that high-tide individuals are subtidal migrants. Most studies on the subject suggest that sublittoral predator use intertidal areas mainly as feeding grounds (e.g. Robles et al. 1990, Burrows et al. 1999). In southwest Britain, results described in Chapter 2 showed that several intertidal prey groups such as limpets, chitons and barnacles are important dietary

items for *C. maenas*, *N. puber* and *C. pagurus*. Large population sizes were found in the present study for these crab species on both shores.

A second main finding in this study was that the migrant crabs had strong associations with differing tidal height: the majority of *C. pagurus* and *N. puber* were often recaptured on the lower shore where they had been marked, conversely the majority of *C. maenas* were captured on the upper shore. Regular migrations to preferred littoral habitats have been reported for other crab species such as *Cancer magister* in a NE Pacific Estuary (Holsman et al. 2006). Habitat complexity and prey availability have been discussed as possible causes for crab association with particular intertidal habitats (Kneib 1995, Eggleston et al. 1998, Lohrer et al. 2000). In addition, it has been suggested that during high-tide agonistic intra and interspecific interactions can result in segregation of species or size classes and affect the probability of survival (Kaiser et al. 1990, Navarrete & Castilla 1990). The results presented in Chapter two suggest that the high-tide distribution patterns of these crab species in southwest Britain is not directly related to prey availability.

Hence, further studies should aim to explore the alternative hypotheses where agonistic activities or differences in habitat structure between shore levels such as algae cover may be involved in explaining those patterns. During high-tide there were relatively high recapture rates of individuals of different species for the same shore level suggesting that interspecific agonistic interactions may not be a main force driving patterns of distribution in this study. Due to insufficient recaptures in the size range sampled at high-tide, it was not possible to detect a pattern of intraspecific variation in size with shore level, and thus hypothesize about the importance of agonistic size related interactions within species.

Concluding comments and further work

This work clearly establishes the existence of an extensive subtidal-intertidal link particularly for *N. puber* and *C. pagurus* and to a lesser extent *C. maenas*. The next step should establish predation pressure by sublittoral crabs on intertidal prey populations. Based on the evidence provided here, such studies should be sensitive to patterns in predator identity and abundance across different shore heights at high-tide when prey are accessible. Also, my results suggest that season-dependent predation pressure may be occurring on these shores but this has seldom been investigated (but see Reinsel 2004, Cannicci et al. 2007) and, since the abundance of many intertidal prey also varies seasonally (e.g. Underwood 1981, Menconi et al. 1999), it would provide an opportunity to better understand predator-prey dynamics. The information provided in my study on growth rates and survival allows a better understanding of the importance environmental conditions for their ecology and biology, a crucial tool for the management of these species.

CHAPTER 4

Predation by small mobile aquatic predators regulates populations of the intertidal limpet *Patella vulgata* (L.)

A modified version of this chapter has been accepted for publication to the *Journal of Experimental Marine Biology and Ecology*.

Predation by small mobile aquatic predators regulates populations of the intertidal limpet *Patella vulgata*

4.1 Abstract

Highly mobile predators such as fish and crabs are known to forage in the intertidal during periods of immersion. However, there is limited quantitative information on the extent to which these predators influence the abundance of grazing molluscs such as limpets, which are known to have a key role in structuring intertidal assemblages. Manipulative experiments were used in the present study to quantify the effect of these predators on the abundance of limpets (*Patella vulgata* L.). On the lower shore at two moderately sheltered rocky shores three treatments were prepared: complete cage, partial cage (cage control) and uncaged (natural condition). The complete cages excluded all predators, while the partial cage and uncaged treatments allowed full access to crabs and small fish. After two months, limpet abundance in uncaged and partial cage treatments had declined by around 50% compared to the complete cage treatment.

Population structure also changed between treatments with survival of larger individuals being greater than for smaller individuals on open and partial cage treatments compared to the complete cage treatment. The effects of excluding predators were consistent at small (meters) and large spatial scales (kilometres) and hence, it would appear that the outcomes of this research are generally applicable to similar shores in the region.

To explore the causes of these differential effects of predators according to limpet size, the detachment force required to remove limpets of differing sizes from

the shore was compared. This was around four times greater for larger individuals than for smaller ones indicating that smaller limpets were more vulnerable to predation. These effects were also consistent between locations. Subsequent laboratory observations showed that *Carcinus maenas* (L.), *Necora puber* (L.) and *Cancer pagurus* (L.) had differing handling behaviour, but were all highly efficient at removing limpets from substratum. Limpet shell width and attachment force appeared to be critical factors influencing their vulnerability to predation. Limpets are known to control the abundance of macroalgae on shores in the North-east Atlantic and hence the conclusions of this study are important to our broader understanding of intertidal ecology.

4.2 Introduction

Mobile predators are known to have a key role in structuring intertidal assemblages. For instance, Robles et al. (1990) and Rilov and Schiel (2006b) have shown that highly mobile aquatic predators (crabs, lobsters and fish) can regulate both the abundance and population structure of intertidal mussels, which are known to have a key role in structuring intertidal assemblages by providing habitat for a range of other species (Menge et al. 2008). There is limited information, however, on the strength of top-down control by highly mobile predators on populations of grazers such as limpets.

Patellid limpets are recognised as “keystone” grazers (sensu Power et al. 1996), regulating micro and macro algal abundance on rocky shores in the North-East Atlantic (Hawkins & Hartnoll 1983, Thompson et al. 2004, Jenkins et al. 2005,

Coleman et al. 2006, Jonsson et al. 2006). Limpets are consumed by a wide variety of predators including fish (Milton 1983), octopi (Ambrose 1986), crabs (Silva et al. 2004), other gastropods (Black 1978), starfish (Markowska & Kidawa 2007), birds (Bosman & Hockey 1989) and humans (Weber & Hawkins 2002).

Most quantitative studies on the effects of predation on limpet populations have, however, focused on birds (e.g. Hartwick 1981, Frank 1982, Bosman & Hockey 1989, Iwasaki 1993) or on relatively slow moving predators such as whelks (Black 1978). With the exception of work on phenotypic responses of limpets to predation by crabs (e.g. Lowell 1986), little is known about the importance of top-down regulation of limpets by highly mobile aquatic predators such as crabs and fish (but see Thompson et al. 2000, Silva et al. 2004).

Larger fish such as wrasse were not observed, neither were starfish. Although terrestrial predators such as birds and rodents can be important on some shores during periods of emersion (e.g. Feare 1971, Carlton & Hodder 2003), direct observation on the shores used in this study did not reveal any encounters between limpets and these predators. Human predation, although intensive further south in Europe (e.g. Macaronesia, Hawkins et al. 2000, Weber & Hawkins 2002) does not occur frequently on British shores. In addition, data recently collected using traps on nearby shores has indicated that substantial numbers of crabs (*Carcinus maenas*, *Necora puber* and *Cancer pagurus*) and occasionally small fish (blennies) forage in the intertidal during high-tide (Chapter 2). The individuals captured were typically larger than those found in the intertidal at low-tide indicating that some of these predators had moved up from the subtidal presumably to feed (Chapters 2 and 3). Stomach content analyses indicated that

limpets were a major part of the diet of the crabs captured (Chapter 2). Here a manipulative field experiment was used to test the following hypotheses: 1) that predation by crabs and small fish substantially reduces the abundance of limpets; 2) that predation is greater on smaller limpets and; 3) that the effects of predation are consistent at large (shores - km) and small (sites - m) spatial scales.

Attachment to the substratum is one of the principal defensive mechanisms available for limpets to reduce the success of attacks by their predators (Iwasaki 1993). Hence, field measurements were made to compare the detachment force required to dislodge small (10-20 mm) and large (20-30 mm) limpets. It was hypothesised that smaller limpets would have a smaller detachment force than larger individuals and hence would be more vulnerable to attack (Hypothesis 4). There is limited information on the techniques used by crabs to remove limpets from the substratum (but see Lowell 1986, Thompson et al. 2000) and so, laboratory observations were made to test the hypothesis that behaviour, handling time and success differed between *Carcinus maenas*, *Necora puber* and *Cancer pagurus* (Hypothesis 5).

4.3 Methods

Effects of predators on limpet populations

Cages were used to exclude predators from areas on two moderately sheltered shores in southwest Britain. These shores were similar in terms of their orientation and exposure to wave action and other environmental variables. They were separated by approximately 20 kilometres (Mount Batten 50°21'N, 4°07'W

and Looe 50°20'N, 4°27'W) and had similar assemblages including substantial numbers of limpets. Experimental treatments were established on the lower shore, below the barnacle dominated zone because previous work had shown the size and abundance of crabs was greater at this tidal level (Chapter 2). This shore level is also immersed for substantial periods of time (~14 hours per day), and would be expected to show greater effects of predation by aquatic predators than areas higher on the shore.

The dogwhelk *Nucella lapillus* (L.), a slow-moving predator that feeds on limpets and barnacles is found at this level, but it is much less abundant than higher on the shore (Hughes & Drewett 1985, Hughes & Burrows 1994). Hence, placing the experiment on the lower shore minimised the extent of predation by whelks. It was anticipated that dogwhelks might move into the experimental plots and it was planned to control this by manual removal. However, dogwhelks were never observed within or around the plots during the course of the experiment. Low-tide observations (each of one hour) were made on four occasions to establish whether predation by birds was important at these sites (cf. Coleman et al. 1999).

Two sites were selected on each shore. At each site, relatively flat areas of the shore were chosen. Limpets (mainly *Patella vulgata* with a few *P. depressa*) were patchily distributed within these areas (average 36 individuals \pm 11 per 0.25 m²; equivalent to around 140 individuals per m²). Treatments were applied to 30 cm x 30 cm areas with an average of 21 \pm 5 individuals per treatment (average size = 16 mm, range = 5 - 55 mm). Three treatments were applied: (1) Complete cages that totally excluded all predators (Figure 4.1); (2) Partial cages that

consisted of a square mesh cage, top cover and open sides; these provided procedural controls for the complete cages and also allowed us to isolate the effects of any larger predators (see below) and; (3) Uncaged natural 30 cm x 30 cm plots were marked by small screws. Five replicates of each treatment were randomly assigned to areas of the shore at each site. Care was taken to ensure there were no gaps between complete cages and the rock surface. Cages were 30 cm x 30 cm x 10 cm and made of a square mesh (5 mm x 5 mm) steel galvanised wire, layered with a coarser plastic coated steel wire mesh (30 mm x 30 mm) to maintain rigidity. Algal growth was occasionally observed and was removed as soon as detected.

Partial cages were identical to the complete cages but had side openings to allow entry of crabs and small fish. The height of the cages (10 cm) was chosen so that partial cages would permit access by crabs of the size commonly found on the shore at high-tide (see Chapters 2 and 3), and by small fish such as blennies, but would substantially restrict access by larger predators such as birds and wrasse (Labridae).

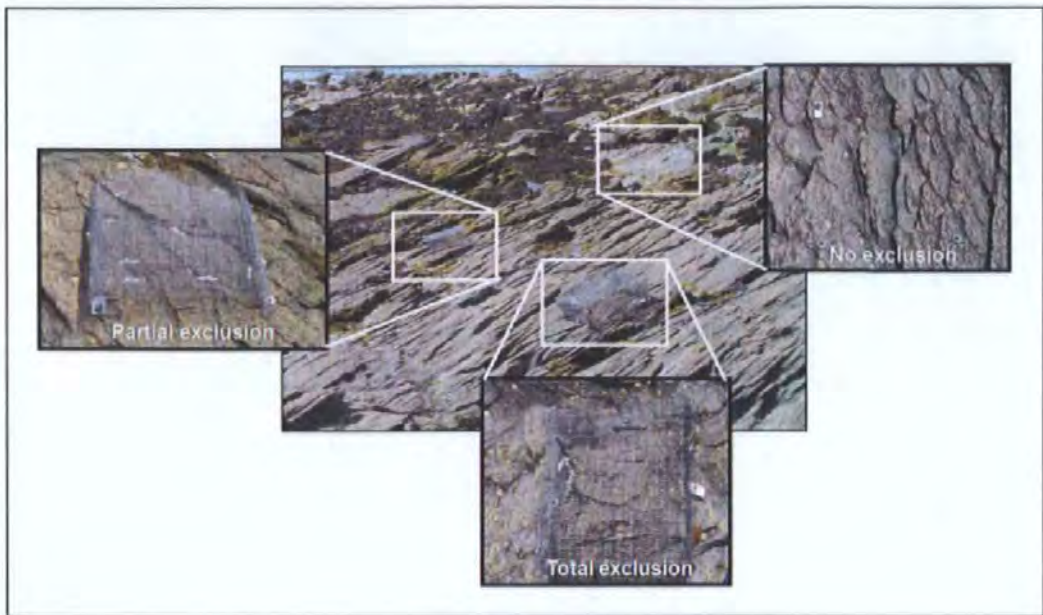


Figure 4.1. Cage treatments.

Logistically it would be exceedingly difficult to selectively allow access to only a particular type of mobile predator while excluding all other predators. Thus, the design of the procedural controls effectively enabled me to isolate the potential role of small predators from that of larger ones. If larger predators such as birds and larger fish were important, reduced limpet abundance would be evident in uncaged (natural) plots, which could be accessed by all available predators, compared to the partial cages which would considerably reduce the access of large predators.

Limpets inside each plot were individually tagged so that their movements could be followed and their length measured at the start (T1) and end of the experiment (T2). Tag loss was monitored every two weeks and tags replaced as necessary. The manipulation was maintained for 2 months from June to August

2007; during this period each experimental structure was regularly checked to ensure its integrity.

Limpet abundance and size data at the start (T1) and end of the experiment (T2) were compared using three factor ANOVA with "treatment" (fixed, orthogonal, three levels: total predator exclusion, cage control, uncaged treatment), "shore" (random, orthogonal, 2 levels: Mount Batten, Looe) and "site" (random, nested within shore, 2 levels) as factors. This design allowed a comparison of both the abundance and mean size of limpets among treatments at the start of the experiment and again after two months. Kolmogorov-Sminorv tests were used to compare size frequency of limpets within treatments between the beginning (T1) and end (T2) of the experiment.

Limpet detachment force

The force required to detach *Patella vulgata* of two differing sizes was measured *in situ* on the lower shore using the method described by Coleman et al (2004). This consisted of gluing an empty limpet shell (with a wire loop on top) to a live limpet and then by use of a hand held spring balance, measure the vertical force (Kg) required to detach the limpet from the substratum. The smaller size (10-20 mm) was chosen because it represented the modal size class present at these sites, and the larger size (20-30 mm) was used to represent older limpets for comparison.

Detachment force could only be measured at low-tide. Measurements during periods of immersion would have been more representative of conditions during predation events by aquatic predators, but the main objective of this experiment

was simply to give a relative comparison of the differences in detachment force between size classes. Detachment force was compared using a four-factor ANOVA with each of the following factors: "limpet size" (orthogonal, fixed, two levels: 10-20 mm and 20-30 mm), "date" (orthogonal, random, two levels), "shore" (orthogonal, random, two levels), "sites" (random, two levels, nested within shore). There were ten replicates of each size class at each site and sampling date.

Predator foraging behaviour

Laboratory observations were used to examine the behaviour of the common shore crab *Carcinus maenas* (size range: 4-5 cm carapace width), the velvet swimming crab *Necora puber* (size range: 5-6 cm carapace width) and the edible crab *Cancer pagurus* (size range: 6-7 cm carapace width) during encounters with limpets. These sizes were selected to represent the average size of individuals captured in the intertidal on nearby shores during high-tide (Chapter 2). Individuals were collected using baited traps deployed during high-tide, and then starved for seven days prior to behavioural trials. Crabs were excluded from observations if damaged, recently moulted or parasitized. Limpets were collected on the substratum to which they were attached by removing samples of the rock from the shore with a hammer and chisel. Individuals of 10-20 mm were chosen since they represented the size class that suffered greatest losses in the field experiment and were also the most common size on the shore. Limpets were kept in aquaria in the laboratory for 24 h before trials. Each individual predator and prey was used only once to maintain independence of data.

Twenty replicate trials were made for each predator-prey combination. Trials were conducted in 10l glass aquaria maintained in a 16:8 hr photoperiod at 15°C,

using one predator and five prey per trial. Prey were offered to predators 1 hour before darkness and infra-red video used to make observations during darkness as this is the time when crabs are most active (Naylor 1958). Predator handling behaviour was categorised according to the tactics used (described in Table 4.3); time taken to remove prey and the success rate were also recorded. For each type of behaviour, comparisons of time taken between species were made using 1-way ANOVA.

For all statistical analyses, Cochran's test was used to check homogeneity of variances prior to ANOVA and appropriate transformations were made when necessary. Tests of homogeneity, ANOVA and SNK (Student-Newman-Keuls) *a posteriori* comparisons were done using the statistical package GMAV5 (Underwood & Chapman 1998).

4.4 Results

The experimental treatments and tagging of individual limpets provided an effective way to quantify predation and to monitor the movement of limpets. The rate of tag loss was low (<1%) and so, tracking the loyalty of individuals to their home scars was very effective. In partial cage and uncaged treatments, less than 1% of the limpets ($n = 15$) moved outside the experimental plots during the course of the experiment, and the majority of these ($n = 8$) returned to the plots during subsequent monitoring. Hence, the emigration rate from these treatments was very low (<0.01%). Birds such as oystercatchers were not observed in the experimental

areas during low-tide day and visits to the shores at night did not reveal any other low-tide predators such as rodents.

There were no differences in the abundance of limpets between experimental treatments ($F_{2,48} = 0.56$, $p = 0.64$), shores ($F_{1,48} = 0.29$, $p = 0.64$) or sites ($F_{2,48} = 2.16$, $p = 0.12$) at the start of the experiment (T1). After two months (T2), however, there was a main effect of predator exclusion with the number of limpets surviving being significantly greater in complete cage treatments than in uncaged or partial cage treatments (Table 4.1). This effect was consistent across shores and sites within shores (Table 4.1).

Table 4.1. ANOVA comparing the abundance (Sqrt (X+1) transformed data, Cochran's test: $C = 0.26$, not significant) and size (untransformed data, Cochran's test: $C = 0.15$, not significant) of limpets among treatments after 2 months of predator exclusion (T2). Significant effects are shown in bold. Outcomes of Student-Newman-Keuls are shown in Figure 4.1a,b.

Source of variation	Limpet abundance				Limpet size		
	df	MS	F	p	MS	F	p
Treatment = Tr	2	13.73	39.73	0.02	0.30	32.02	0.03
Shore = Sh	1	0.91	1.03	0.41	0.03	0.41	0.58
Site = Si (Sh)	2	0.89	1.38	0.26	0.09	1.32	0.27
Tr x Sh	2	0.34	0.47	0.65	0.01	0.42	0.68
Tr x Si (Sh)	4	0.73	1.13	0.35	0.02	0.33	0.85
Residual	48	0.64			0.06		

The abundance of limpets in the complete cage treatment declined on average by 19% during the course of the experiment (empty shells were found in the cages), while in the partial cage and uncaged treatments much larger mortality

occurred (Figure 4.2a). The high degree of similarity in mortality values (approximately 69% and 71%) between the partial cage and uncaged treatment indicates that neither birds and large fish nor physical disturbances such as dislodgment by stones or other debris were not important sources of mortality at these sites during this study.

At the start of the experiment the average size of limpets across all treatments was 15 mm (range: 5 mm - 50 mm). There were no differences in the size of limpets between treatments ($F_{2,48} = 0.46$, $p = 0.57$), shores ($F_{1,48} = 0.34$, $p = 0.61$) or sites ($F_{2,48} = 1.45$, $p = 0.22$). After two months, however, the average size (\pm SE) within complete cages (16 ± 0.05 mm; range: 5 mm – 50 mm) was 33% smaller than in the uncaged treatments (24 ± 0.05 mm; range: 32 mm – 50 mm) and partial cage treatments (23 ± 0.09 mm; range: 30 mm - 51 mm), indicating that in plots exposed to predators survival was greater for larger limpets than for smaller individuals (Figure 4.2b).

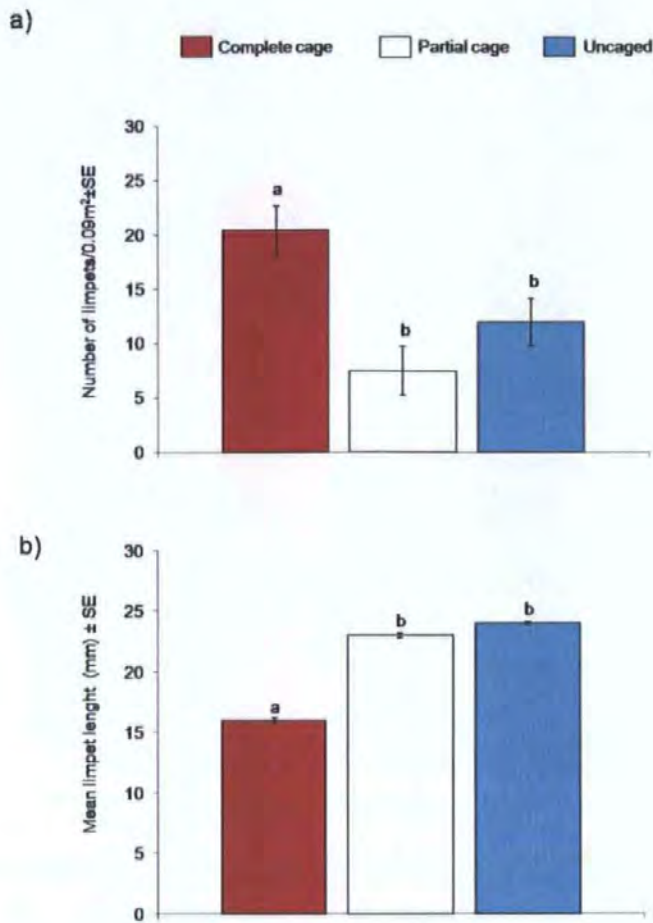


Figure 4.2. Average abundance (a) and average size (b) (\pm SE) of limpets in various predator exclusion treatments after two months (T2). Effects were consistent between sites and shores. Treatments sharing similar lower case letters did not differ significantly (SNK test, $p < 0.05$, $n = 3$).

This pattern was consistent across shores and sites within shores (Table 4.1). Kolmogorov-Sminorv tests showed a significant difference in population structure between T1 and T2 for the uncaged ($D = 0.60$, $p = 0.03$) and partially caged ($D = 0.60$, $p = 0.03$) treatments, but not in the complete cage ($D = 0.20$, $p = 0.975$) treatment (Figure 4.3).

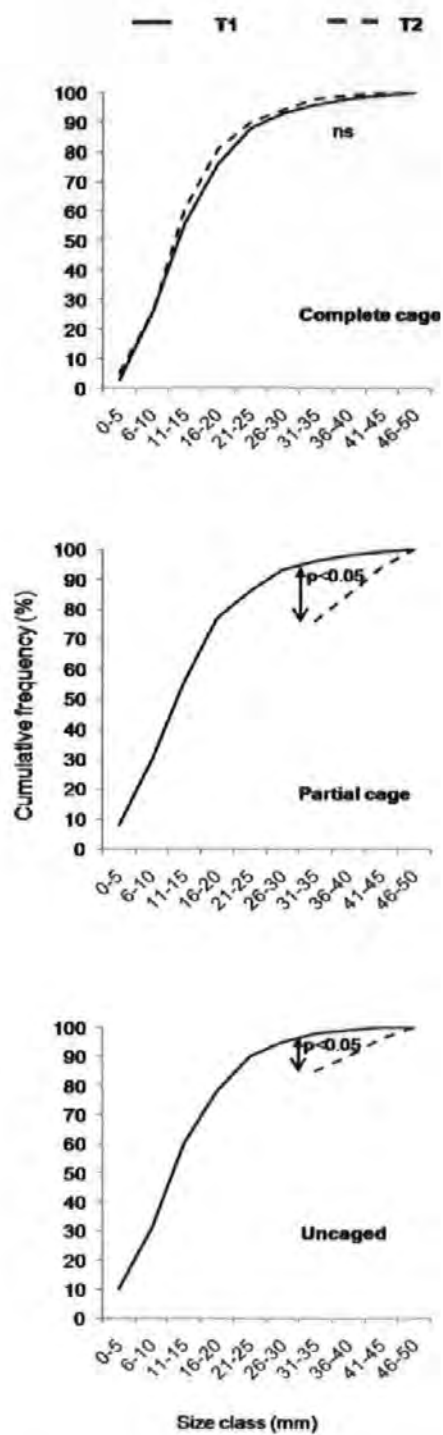


Figure 4.3. Cumulative frequency distributions for sizes of limpets at the start of the experiment (T1) and after two months (T2). Results of Kolmogorov-Smirnov tests show differences in frequencies between T1 and T2. N.B at T2 (dotted line) some of the smaller sizes were no longer present.

This size effect was caused by a shift in population structure towards larger limpets in the treatments that were exposed to predators.

Limpet detachment force

There were no significant differences in detachment force between sampling dates ($p > 0.45$); and so data were pooled for subsequent analysis (see Underwood 1997). The detachment force for larger limpets (24.00 ± 1.96 newtons, average \pm SE) was significantly greater than for smaller limpets (4.91 ± 0.98 newtons, average \pm SE; Table 4.2). This difference showed that smaller limpets were more vulnerable to predation by crabs than larger individuals. There were no differences in the detachment force between shores or sites within shores, indicating generality for similar shores in the region (Table 4.2).

Table 4.2. ANOVA comparing the detachment force (Ln (X+1) transformed data, Cochran's test: C = 0.22, not significant) required to remove limpets of differing sizes, from the substratum at each of two shores and two sites within shores (NB. The effect of time was not significant ($p > 0.45$) and has been removed from analysis by pooling, see methods). Significant effects are shown in bold. Outcomes of Student-Newman-Keuls test on sizes (\pm SE): Small (4.91 ± 0.78 newtons) < Large (22.54 ± 0.19 newtons).

Source of variation	df	MS	F	p
Size	1	66.89	223.13	0.04
Shore = Sh	1	0.13	2.65	0.24
Site = Si (Sh)	2	0.04	1.73	0.18
Size x Sh	1	0.29	6.62	0.12
Size x Si (Sh)	2	0.04	0.04	0.21
Residual	72	0.02		

Predator foraging behaviour

All three species of crab were successful in removing limpets from the substratum in laboratory observations, with success rates of 95% for *Necora puber*, 90% for *Cancer pagurus* and 92% for *Carcinus maenas*. Video observations showed that behaviour (as defined in Table 4.3) varied among species: for *C. maenas* the behavioural sequence was *Detection – Levering – Pulling*; for *N. puber* it was *Detection – Grasping/apex crushing – Pulling*; and for *C. pagurus* it was *Detection – Grasping/apex crushing*.

Table 4.3. Description of behaviour types adopted by crabs in encounters with limpets. The critical factor corresponds to the feature which observations suggested contributed the most to the success of the predation event.

Behaviour	Description	Critical factor
Physical detection	The 5 th pair of legs and/or chela placed in contact with prey	None detected
Grasping/Apex crushing	Major cheliped used to grip limpet shell longitudinally or crush apex	Limpet shell width
Levering	Tip of chela inserted at limpet shell margin and used as lever	Chela insertion and limpet detachment force
Pulling	Shell gripped and limpet pulled away from substratum	Limpet detachment force

The total attack time for each species was considered to be the time for a complete behavioural sequence, excluding the time taken to consume the limpet. In this respect, *Carcinus maenas* (52 seconds) and *Cancer pagurus* (54 seconds) were significantly ($F_{2, 59} = 518.5$, $p < 0.01$) faster than *Necora puber* (74 seconds;

Figure 4.4A). There were also significant differences among species in the time used for the behaviours “grasp/crush” and “pull” ($F_{1,39} = 82.7$, $p < 0.01$), but not for the average “detection” times ($F_{2, 59} = 0.63$, $p = 0.53$; Figure 4.4B, D-E). *C. maenas* spent less time “pulling” at any particular limpet than did *N. puber* (Figure 4.4E). *C. maenas* and *C. pagurus* had similar mean grasping times, but *N. puber* spent less time grasping ($F_{2, 59} = 1615.0$, $p < 0.01$; Figure 4.4C). Only *C. maenas* displayed the “lever” behaviour (Figure 4.4D).

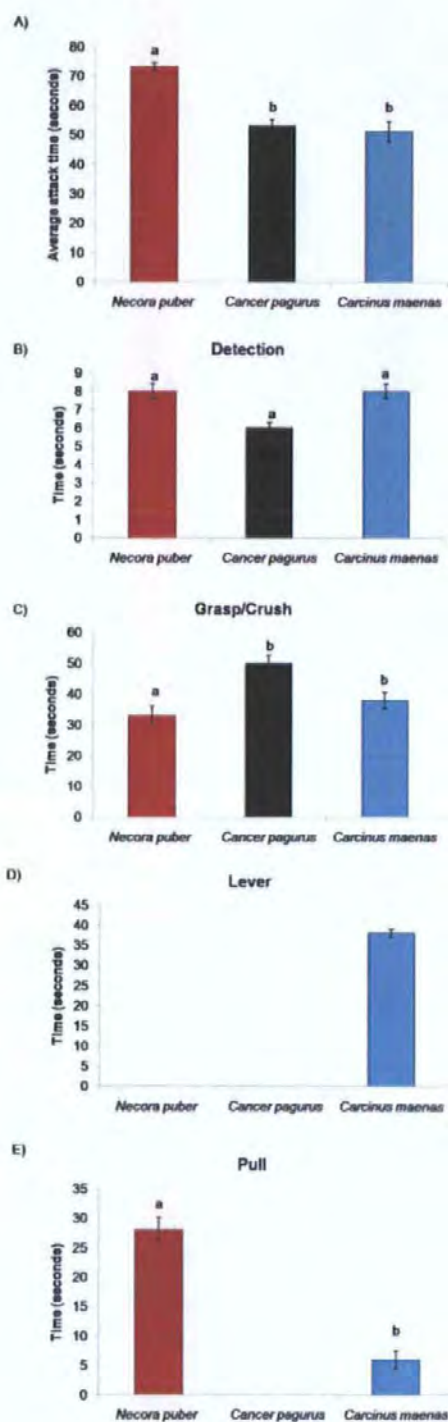


Figure 4.4. Total attack time for each predator species (average \pm SE) (A) and time spent on each behaviour type (Table 4.3) by each predator species (average \pm SE) (B-E). Treatments sharing similar lower case letters did not differ significantly (SNK tests, $p < 0.05$; $n = 20$).

4.5 Discussion

In the field study, there was a decline in limpet abundance in all treatments. However, this was considerably greater in treatments which allowed access to predators, compared to predator exclusion treatments. Emigration from treatments was low and there were no differences between the partial cage and the uncaged treatment, hence it would appear that differences among treatments were caused by differing levels of predation. There was some mortality in abundance in the complete cage treatment. There are various possible explanations for this, but we consider it most probably to have resulted from a shortage of food in those treatments (Underwood 1984). Similar effects have been observed in experiments examining competition using differing density treatments (e.g. Branch 1975, Thompson et al. 2001, Boaventura et al. 2002b, Boaventura et al. 2003).

Data from the open and partial cage treatments clearly showed that predators have a significant impact on limpet abundance. Allowing for the decline in abundance of 19% in the complete cage treatment, which cannot be assigned to predation, it would appear that predation must have accounted for at least 50% of the reduction in limpet numbers in both the open and partial cage treatments. Furthermore, because these effects were general among the spatial scales examined (shores and sites), they are likely to be consistent for similar shores in southwest Britain. The main predators of limpets on these shores are likely to be crabs and small fish. Other predators were not observed during either day or night. Further evidence for the lack of importance of larger predators is provided by the similarity in limpet abundance at T2 between the procedural control and the natural uncaged treatment.

These findings have broad implications for our understanding of rocky shore ecology. This study, conducted over 2 months, indicated that there was at least 50% greater reduction in limpet abundance due to predation in the uncaged and partial cage treatments than in the complete cage. Taking into consideration that limpets have annual recruitment, the yearly effects of predation on such cohorts could be quite substantial. Similar top-down control by mobile predators has been shown to regulate the abundance of juvenile mussels on rocky shores in New Zealand (Rilov & Schiel 2006b), and mesocosm studies in the U.K. have shown that predation by crabs can influence the diversity of intertidal prey assemblages (Griffin et al. 2008).

Results from the field experiment also indicated that predation was size-specific with small limpets being most vulnerable. Similar results have been observed for limpet predation by oystercatchers in Canada and South Africa (Hartwick 1981, Hockey & Branch 1983). Differential impacts of predation on limpets according to size class will influence the extent of grazing on these shores. Mortality of small limpets is known to be greater on the upper shore than on the lower shore because of physical factors and this is considered to be associated with emersion stress during low-tide (Branch 1985). The present data show that predation is an important factor controlling limpet abundance on the lower shore.

Studies of optimal foraging indicate that despite the lower energetic gains per individual consumed, it may be less costly for predators to consume smaller individuals because they are easier to handle than larger prey (e.g. Lawton & Hughes 1985, Enderlein et al. 2003). This principle is supported by the detachment measurements which showed there were differences in the forces required to

detach limpets from the substratum according to size. Hence, greater predation on smaller limpets observed in my experiment was most probably caused by differences in the ease of removal between small and large individuals.

Laboratory observations showed that crushing was an important means of attack by crabs. Small limpets would be also more vulnerable to this because crabs were only successful in attacking a limpet by crushing if their claw gape was wide enough to span the limpet across its shell width. This tactic was replaced by a pulling or leverage on larger shells. Similar observations by Lowell (1986) showed that the probability of an unsuccessful attack increases with the ratio of limpet size to crab size. Further research is required, however, to establish whether there are size refuges from predation by different species and other crab size to those examined here.

Attack times were rapid, ranging from 55 to 75 seconds for all crab species. Hence, a substantial number of limpets could be consumed during a relatively short high-tide period. The field experiments made in this study supported this observation and revealed substantial predation on limpets within two months during the summer. Sea temperatures are at their greatest at this time of the year and the metabolic requirements and hence, crab feeding rates are likely to be at their greatest. Further experiments could therefore be used to establish seasonal patterns in predation intensity and to determine the consequences of predation over longer time scales.

The results of the present study clearly show that the effects of predation are consistent over large spatial scales. Therefore, foraging by subtidal and intertidal

crabs is likely to be an important factor on the lower shore of similar shores elsewhere in southwest Britain. Other studies have also highlighted the importance of top-down control by predators on the dynamics of the subtidal-intertidal boundary (see Paine 1974, Rilov & Schiel 2006a, b, Jones & Shulman 2008). Removal of limpets is known to result in important changes in community structure altering species composition and biomass of canopy-forming macroalgae and associated assemblages (Hawkins 1981, Hawkins et al. 1992, Jenkins et al. 2005, Coleman et al. 2006, Jonsson et al. 2006). Hence, if limpets are regulated by mobile aquatic predators, then the balance between grazing and algal growth will also be indirectly influenced by top-down control.

Limpets are known to influence the upper vertical limit of macroalgal distribution on the shore (Boaventura et al. 2002a). The data presented here indicates that small aquatic predators remove significant numbers of limpets from the lower shore. Further experiments would be required to establish predation rates higher on the shore, however, data collected using traps at nearby sites showed greater abundance of crabs on the lower shore than the upper shore, presumably with associated consequences for limpet predation (Chapter 2). Hence, it is likely that while the vertical distribution of macroalgae is directly modulated by grazing it may also be indirectly regulated by predation on grazing molluscs. Aquatic predators such as crabs and fish will also have indirect effects on limpets restricting the timing and duration of their grazing activity (Branch 1985), and thus may have further indirect effects on intertidal assemblages.

On a larger scale, differences in the abundance of canopy-forming macroalgae between sheltered and exposed shores have been attributed to

variations in both wave action and limpet density (e.g. Jonsson et al. 2006). Little is known about the proximate factors controlling limpet density along wave exposure gradients (but see Jenkins et al. 1999, Thompson et al. 2005, Jonsson et al. 2006). Research on nearby shores demonstrated that crabs were significantly more abundant on sheltered than on exposed shores (Chapter 2). Hence, the direct and indirect effects of predation may also be greater on sheltered shores. Data from the present study illustrate the potential importance of the top-down regulation by mobile predators on moderately sheltered shores. Further work is now required to establish the extent to which lateral modifying factors such as tidal elevation and exposure to wave action influence the relative importance of such top-down regulation by crabs and grazers on intertidal assemblages, across broader spatial scales and environmental gradients.

CHAPTER 5

Preferential feeding by the crab *Necora puber* on differing sizes of *Patella vulgata*

Preferential feeding by the crab *Necora puber* Linnaeus on differing sizes of *Patella vulgata* Linnaeus

5.1 Abstract

The crab *Necora puber* Linnaeus is a common predator of limpets on rocky shores in the southwest Britain. There is, however, little information on the factors influencing predator-prey interactions between crabs and limpets. In this study, limpet size preference by crabs was examined for *N. puber* and the limpet *Patella vulgata* Linnaeus. Limpet size refuge, *N. puber* limpet size preference, and predator behaviour with differing prey size was examined in laboratory experiments.

N. puber was able to consume the majority of limpet sizes that were present on local shores (94%), with a size refuge for limpets larger than 41 mm shell length. Larger crabs were able to consume larger limpets. Feeding on larger limpets resulted in longer handling times and, larger individuals were not vulnerable to shell crushing by the crab. There were clear preferences by *N. puber* for smaller limpets. The maximum prey-size that a crab of a given size could consume and the general preference for smaller sizes are likely to be related to mechanical constraints, due to the greater tenacity of larger limpets and difficulties in crushing larger shells. This is important because selective size related predation will influence the population structure, and potentially reproductive success of limpets. These findings suggest that *N. puber* may have a previously unknown influence in the reproductive success of *P. vulgata* since these limpets change sex with size and smaller limpets (< 25 mm) are predominantly males.

5.2 Introduction

Most predators have some form of selective feeding behaviour and, as a consequence, prey may be taken according to their profitability in terms of energy gain for a particular predator rather than their density (Hughes & Seed 1981, Hughes & Dunkin 1984b, Hughes & Seed 1995, Singer 2000, Underwood et al. 2004). This profitability depends on the balance between handling costs and energy gain which varies with characteristics such as prey size. Many brachyurans exhibit selective foraging behaviour according to prey type and/or size. This behaviour has been extensively investigated for intertidal crabs feeding on various species of mollusc prey (e.g. Vermeij 1976, Vermeij 1977, Palmer 1985, Hughes 2000, Cannicci et al. 2002). These prey include snails and dogwhelks (e.g. Hughes & Elner 1979, Chilton & Bull 1986, Yamada & Boulding 1998, Jackson & Underwood 2007), mussels (Hughes & Seed 1981, ap Rheinault 1986) and clams (Micheli 1995).

Despite the evidence that limpets are an important component of the diet of crabs (Chapter 2, Lowell 1986, Iwasaki 1993, Silva et al. 2004), factors influencing interactions between crabs and limpets have not been extensively examined (but see Lowell 1986, Iwasaki 1993). It has, however, been shown that predation by crabs can influence the population structure of gastropod prey such as the snails *Nerita atramentosa* (Reeve) and *Bembicium nanum* (Lamarck) (Chilton & Bull 1984). Recent work using exclusion cages has shown that predation by intertidal and subtidal crabs (possibly together with small fish such as blennies) has a significant impact on the abundance of limpets on shores in southwest Britain, and that predation is greater on smaller individuals (Chapter 4). Patellid limpets are

important grazers in the intertidal of North-East Europe and can control the abundance of macro-algae (Southward 1964, Hawkins 1981, Hawkins & Hartnoll 1983, Hawkins et al. 1992, Boaventura et al. 2002a, Jenkins et al. 2005, Coleman et al. 2006, Jonsson et al. 2006). Thus, understanding the impact of predation on these grazers is important for our knowledge of intertidal ecology; and, in order to make predictions about the effects of predators according to prey abundance and size, we require a broader understanding of predator preferences (Sih et al. 1985).

Here, the importance of size selective foraging by crabs on limpet prey was assessed. The crab *Necora puber* L. and the patellid *Patella vulgata* L. were used to examine whether patterns of prey consumption observed in the intertidal are associated with predator preference for particular size classes. *Necora puber* is a commercially important species in Europe (ICES catch data, <http://www.ices.dk/>), and is known to forage on intertidal limpets during high-tide (Norman & Jones 1992, Chapter 2). Currently, the range of limpet size that this predator can handle is not known. If *N. puber* displays a size selective feeding behaviour it may influence limpet population structure and influence the reproductive output of limpet populations. Selective predation may also indirectly influence competitive interactions by reducing the density of some size classes. For example, patellid limpets have been shown to compete intraspecifically between sizes (Boaventura et al. 2003) and species (Boaventura et al. 2002b).

Crabs exert a pulling force when attacking limpets (Lowell 1986, Iwasaki 1993, Chapter 4) and so, it was predicted that the vulnerability of limpets to crab predation would vary with size since larger *P. vulgata* have stronger attachment (Grenon & Walker 1981). Hence, larger limpets are likely to require greater

handling times and this cost may influence prey choice. A series of laboratory experiments were used to examine: 1) the range of limpet sizes that *N. puber* can consume; 2) preference for particular prey sizes; 3) differences in predator handling behaviour according to prey size.

5.3 Methods

Study species and sites

Necora puber is abundant on rocky shores and is most abundant on the lower shore and shallow subtidal throughout the North-East Atlantic (Clark 1986). Like other portunids, it has an omnivorous diet including barnacles, mussels, limpets and algae (Chapter 2, Choy 1986, Norman & Jones 1990). In the intertidal, it forages mainly during nocturnal high-tides when it undertakes foraging excursions up the shore (Chapter 2). Male crabs, with a size range of 5 - 27 mm in major chela height, were collected from Mount Batten, a sheltered shore in southwest Britain (50°21'N, 4°07'W) where they had been previously found to feed on limpets (Chapter 2).

The cheliped height was used as a surrogate of size rather than carapace width (CW) because it directly determines the size of prey that can be consumed by means of grasping or crushing (Lee & Seed 1992, Yamada & Boulding 1998). Collected crabs were examined for any damage such as missing limbs and divided into four size-classes based on the natural variation of the height of their cheliped: ≤ 10 mm (~ 15-35 mm CW), 11-15 mm (~ 36-50 mm CW), 16-20 mm (~ 51-66 mm CW) and 21-25 mm (~ 67-80 mm CW).

The limpet *Patella vulgata* was used as prey because it was the most abundant species of limpet at the local shores and it is extensively distributed throughout the North-East Atlantic. *P. vulgata* was present in a range of sizes (3 – 66 mm, average size \pm S.E. = 18 ± 1 mm) making it ideal for size-selective feeding trials such as this.

Experimental set-up

Crabs were maintained in large aquaria (length x breadth x depth: 60 x 50 x 45 cm) at small densities (10 individuals) to minimise competitive interactions. Crabs were fed with cockle flesh for two weeks and then starved for three days to standardise their recent experience in prey handling and hunger. A constant flow of filtered seawater at 15°C was maintained in all tanks.

Limpets of shell length 5-60 mm were collected on the substratum to which they were attached by removing samples of the rock from the shore with a hammer and chisel. Limpets (together with the underlying rock) were separated into 5 mm classes and kept in large shallow tanks (length x breadth x depth: 150 x 60 x 10 cm) under similar environmental conditions to the crabs.

Trials were conducted in 10 l glass aquaria (30 cm x 40 cm x 20 cm). Natural rock slabs similar in surface texture (smooth limestone) were collected from the shore and cut to fit the tank bottom providing a natural attachment substratum for limpets. Limpets were transferred to these substrata approximately 24 hr prior to trials by detaching shells with a slight rotation movement of the shell while they were active. This method minimises the risk of damage to the mantle by avoiding pulling of the shell. Prey condition was checked before trials by tapping on the shell

to test for the expected clamping response. Predators were then introduced 1 hour before darkness (in a 16:8 photoperiod), and observations made during darkness when crabs are known to be active (Naylor 1958, Dare & Edwards 1981, Hunter & Naylor 1993, Cannicci et al. 1999a). Each predator and prey was only used once to maintain independence of data.

Prey were individually tagged with small numbered tags (Brady company-reference TMXM-0-49) to clearly identify size classes when counting and replacing the number of limpets consumed during the trials that involved choice of differing limpet sizes. A preliminary test was made using limpet of the 15-20 mm size class (vulnerable to all predator sizes) to confirm that the presence of tags did not influence consumption (tagged versus non tagged: $F_{1,39} = 1.47$, $p = 0.23$).

A separate size refuge experiment was made to examine the range of limpet sizes that crabs of different sizes could consume by presenting crabs of progressively increasing size with limpets of each size class. The experimental conditions were the same as for the preference trials. Trials ran for 48 h.

Experimental design

In order to examine the preference of *N. puber* for limpets of differing size classes, the two-stage experimental procedure described by Underwood and Clarke (2005) was followed. In the first stage the number of limpets consumed per size class is quantified when no choice of size is available to the predator and, in the second stage the proportion of different sized limpets consumed is determined when choice is available. Predators and prey were only used once to maintain data independence. Based on the limpet population structure in the field and on the

results of the limpet size refuge experiment, the prey size categories used were: 5-10 mm, 15-20 mm, 25-30 mm, 35-40 mm, 45-50 mm and 55-60 mm. These represented the size range available on the shore. A 5 mm class gap was chosen between categories to increase the contrast between size classes.

For stage 1 of the preference trials (limpet consumption when there is no choice), two replicate tests were made for each predator size class with independent animals being used in each test. Crabs were initially presented with three limpets from the smallest size-class and allowed to feed for 48hr during which any consumed prey were replaced. This procedure was repeated for each subsequent size-class. Crabs were only presented with limpet sizes which they had been shown to be able to handle in the limpet size refuge experiment (see above).

For stage 2 (limpet consumption when size selection is available), crabs were presented with limpets of each of the size-classes and allowed to feed for 48 h, and consumed limpets were replaced as before. Data from stage 1 and stage 2 were then used to test the null hypothesis that selection of prey size is random. In this design, since all prey items were replaced once eaten, there was no meaningful concept of number of prey items not eaten. This differs from the experimental protocol described in Underwood and Clarke (2005), however the same statistical procedure suggested by these authors was used with the exception that the number of prey not eaten is removed from calculations (See appendix A3-A4 in Underwood & Clarke 2005 for details on equations used). The assumptions are that each of the first stage tests lasts the same time and all prey items are replaced once eaten. A standard 2 x k test of association was used in a

contingency table, conditional on the observed total number of prey items eaten at each stage. In the present study there were M prey eaten in each first stage trial and N prey eaten in each second stage trial (all of the same length). It was tested whether the numbers eaten in each of the first stage trials $m_1, m_2, m_3, \dots, m_k$ differed from those eaten $n_1, n_2, n_3, \dots, n_k$ (adding to N) in the second stage trial. If the proportions eaten were significantly different, this is interpreted as evidence of preference.

The numbers of limpets of each size of prey consumed were then compared with the numbers expected under the null hypothesis using chi-square tests of association in a $2 \times k$ contingency table (degrees of freedom were based on the number of prey classes made available to crabs). Because in the experiment where the maximum limpet size a crab from a given size could consume was 41 mm for the largest tested crab, limpet-size classes 45-50 mm and 55-60 mm were not included in the preference tests.

To establish whether *Necora puber* had different handling behaviour with increasing prey size, video observations were made during the stage 1 experiment. Quantitative and qualitative video analyses of the method used by predators and prey handling time were made for five replicate predator-prey size pairs for each size combination.

5.4 Results

The cheliped size (major chela height) of *N. puber* was found to be in direct proportion to the width of the animal carapace (Figure 5.1), which is the most commonly taken size measure, suggesting that both measures can be used to indicate predation efficiency for this species.

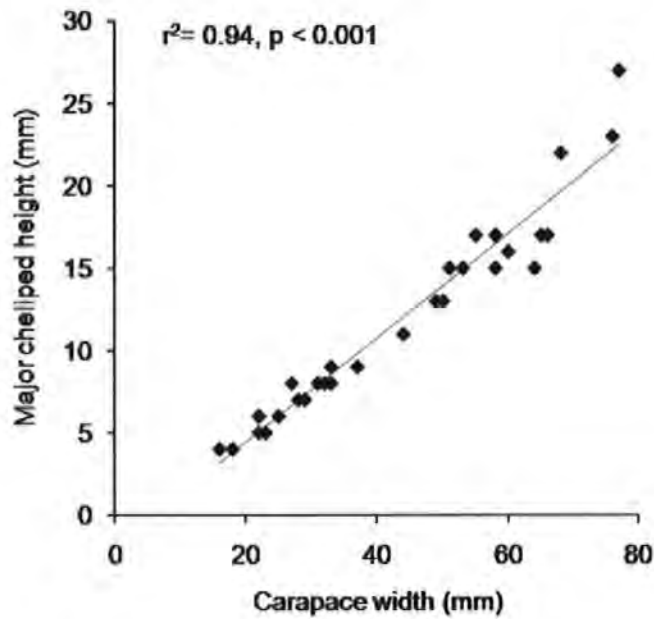


Figure 5.1. Relationship between the carapace width and cheliped size (propodus height – see Figure 6.1a, M1) of *Necora puber*.

The size of *Patella vulgata* consumed was positively related to the height of the major claw of *Necora puber*, showing that larger predators were able to consume larger prey (Figure 5.2). The largest limpet consumed was 41 mm by a crab of 25 mm major cheliped height (~ 75 mm carapace width) and the smallest limpet consumed was 9 mm. Because this crab size is close to the maximum *N. puber* size found on the shore (85 mm carapace width, A. Silva unpub. data), this

data suggests that limpets larger than 41 mm may not be vulnerable to predation by *N. puber*.

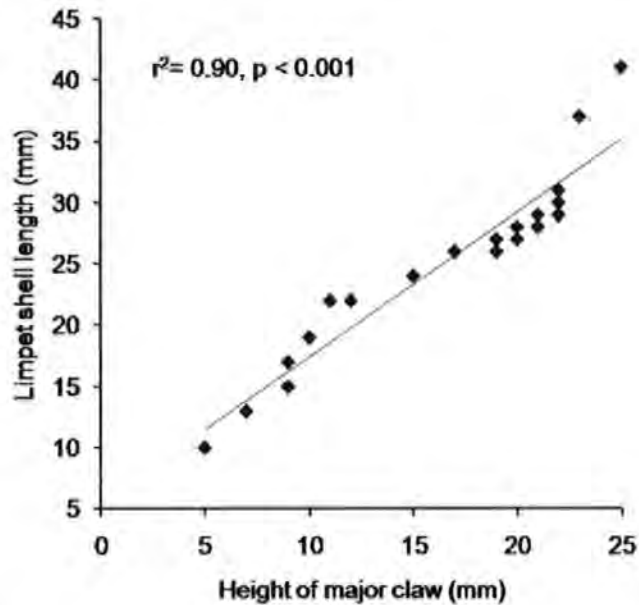


Figure 5.2. Size of the largest limpet (*Patella vulgata*) consumed in relation to cheliped size of *Necora puber*.

In the stage one of the experiment to establish size preference of limpet prey (no size choice available), smaller limpets were consistently consumed to a greater extent than larger limpets. This effect was consistent across all crab-size classes (Table 5.1). In the second stage of the experiment (when size choice was available), there was a clear correspondence between crab size and the frequencies of consumed prey sizes (Figure 5.3). The most consumed limpet size classes were consistently at the lower end of the range of sizes that a crab of a given size could consume. The largest crabs (21-25 mm major cheliped height) fed

more frequently on the 15-20 and 25-30 mm limpet classes. Intermediate size crabs fed predominantly on 15-20 mm limpets. The smallest crabs (5-10 mm major cheliped height) mostly consumed limpets of the smallest size class (5-10 mm).

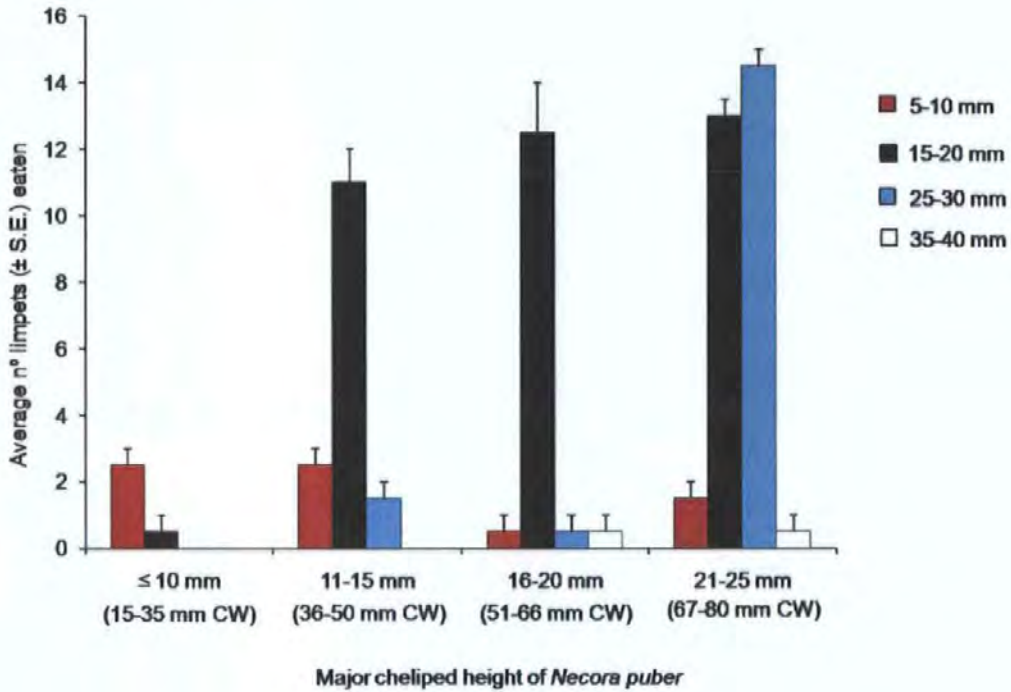


Figure 5.3. Average frequency (\pm S.E.) of limpets consumed per crab size class when crabs were presented with a choice of prey sizes (CW-Carapace width).

The proportions of sizes consumed when choice was present *versus* the proportions eaten when choice was absent are shown in Table 5.1. The null hypothesis of random feeding behaviour was rejected (chi-square tests, Table 5.1).

Table 5.1. Summary of Chi-Square tests based on the height of *Necora puber* master chela and prey size. Degrees of freedom are $(k-1)$ with k being the number of size choices (na = not applicable because limpets of those sizes had been previously shown not to be vulnerable to tested crab sizes). Chi-square statistic indicates whether the proportions of sizes consumed when choice was available differed to those when choice was absent (ns = not significant).

Crab size	Test 1		Test 2		Test 3		Test 4		Test 5		Test 6		Test 7		Test 8	
	10 mm		10 mm		11-15 mm		11-15 mm		16-20 mm		16-20 mm		21-25 mm		21-25 mm	
Stage	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2
N° of consumed prey																
Observed																
5-10 mm	5	3	7	2	13	3	11	2	10	1	9	0	1	1	2	2
15-20 mm	1	0	1	1	2	12	2	10	3	14	2	11	14	6	12	7
25-30 mm	na	na	na	na	1	2	0	1	3	0	2	1	2	14	1	15
35-40 mm	na	na	na	na	na	na	na	na	1	0	1	1	1	1	1	0
Expected																
5-10 mm	5.33	2.66	6.54	2.45	7.75	8.24	6.50	6.50	5.84	5.15	4.66	4.33	0.90	1.10	1.60	2.40
15-20 mm	0.66	0.33	1.45	0.54	6.78	7.21	6.00	6.00	9.03	7.98	6.74	6.25	9.00	11.00	7.60	11.40
25-30 mm	na	na	na	na	1.45	1.54	0.50	0.50	1.59	1.40	1.55	1.44	7.20	8.80	6.40	8.60
35-40 mm	na	na	na	na	na	na	na	na	0.53	0.48	1.03	0.96	0.80	1.10	0.40	0.60
Chi-square result	0.56		0.63		13.7		12.54		18.38		15.5		11.97		13.44	
Significance	ns		ns		p<0.05		p<0.05		p<0.05		p<0.05		p<0.05		p<0.05	

All crab size classes, except for the smallest crabs (≤ 10 mm) showed a preference for particular prey sizes, i.e. there were significant differences in the observed prey consumption and the expected values under the null hypothesis of no preference. This confirmed that *Necora puber* actively selected prey according to their sizes. Video observations indicated that there were qualitative differences in *Necora puber* attack behaviour according to *Patella vulgata* size, with the smallest limpets invariably being crushed across their width by all predator sizes. Larger limpets were handled by crabs initially inserting the tip of the chela under the shell edge, followed by grasping and then leverage/pulling force to detach the shell from the substratum. This last technique was more frequently used by smaller crabs while larger individuals were readily able to crush limpet shells.

There was a direct relationship between crab size and handling time with increasing limpet size, crabs with larger master claws had shorter handling times for a given prey size (Figure 5.4, n° of observations = 3 per size class combination).

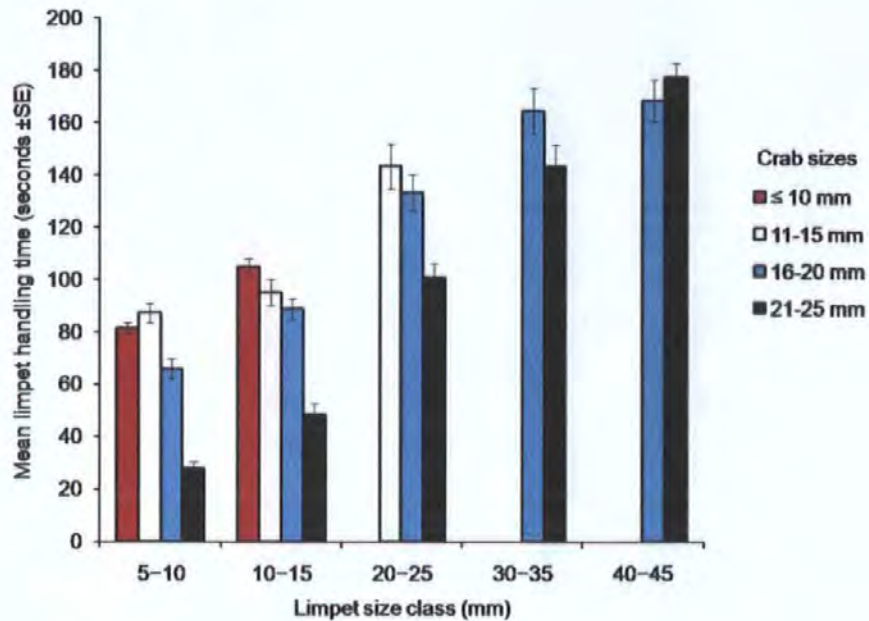


Figure 5.4. Average time (seconds \pm S.E.) taken by *Necora puber* to remove or crush *Patella vulgata* according to predator and prey size.

5.5 Discussion

The limpet *Patella vulgata* and the crab *Necora puber* provided a useful model to examine predator-prey size association between crabs and limpets. This study demonstrated that *N. puber* was able to consume a wide size spectrum of *P. vulgata*. There was, however, a size refuge for *P. vulgata* greater than 41 mm above which even the largest crabs (25 mm chela height) could not successfully remove limpets. Assessment of the limpet population structure in the field indicates that individuals larger than 40 mm represent ~ 6% of the population, implying that *N. puber* is able to handle the vast majority (94%) of the available prey.

The existence of a maximum prey size that a crab can eat has been reported for several other gastropod prey such as the snail *Littorina sitkana* Philippi (Yamada & Boulding 1998). *Necora puber* has been shown to have upper and lower size limits for consumption of the mussel *Mytilus edulis* L., with smaller individuals (up to 9 mm shell length) being difficult to grasp and larger individuals (16 mm shell length) being impossible to crush (ap Rheinault 1986). In the present study, no lower limit in limpet size was found and all sizes smaller than 41 mm were consumed by the largest crab.

This could be a consequence of small limpets being readily crushed without the need for grasping. According to Yamada and Boulding (1998), the upper limit in prey size consumed by crabs is related to mechanical constraints on crab chela size (height or gape), musculature and dentition. It was apparent from the video observations in this study that even the largest crab was unable to prise limpets > 41 mm from the rock. This suggests that the increase in tenacity (force of attachment per unit of foot area) with limpet size may be a decisive factor in determining prey vulnerability. Tenacity is positively related to limpet size (Grenon & Walker 1981) further supporting this hypothesis.

Comparisons between the numbers of prey consumed when no choice was available and the number when size choice was available showed that *Necora puber* was selective in the size of *Patella vulgata* consumed. For all crab sizes, the preferred limpet size was consistently for sizes toward the smaller end of those that were able to handle. Other studies on feeding behaviour with the dogwhelk *Nucella lapillus* L. and the bivalve *M. edulis* have shown the same trend for crabs to prefer smaller sizes within a size range (see review in Juanes 1992).

It is possible that other predatory portunids that forage in the intertidal may also have this size-selective behaviour. This may be particularly important for the cosmopolitan portunid *Carcinus maenas* L., which is one of the most abundant crabs in the southwest Britain (Chapters 2 and 3), and has already been shown to more readily consume smaller mussel prey (Elner 1978, Hughes & Elner 1979). In the present work, the crab *Necora puber* was chosen as the predator because little work has been done on predator-prey interactions with this species when compared to *C. maenas* (e.g. Walne & Dean 1972, Elner 1978, Elner & Hughes 1978, Hughes & Elner 1979, Cunningham & Hughes 1984, Kaiser et al. 1990, Lee & Seed 1992, Ekendahl 1998, Rovero et al. 2000, Trussell & Nicklin 2002, Smith 2004, Brookes & Rochette 2007).

Preference behaviour is frequently attributed to mechanical constraints imposed on predators due to the prey features such as overall size, thickness and strength (Juanes 1992). From this point of view, crabs are prevented from maximising their energy intake by consuming larger prey due to the probability of incurring damage or energy depletion as prey size increases (Juanes 1992). In the case of limpets, tenacity and shell-aspect ratio may represent important constraints for the predator. The only defensive behaviour that was observed for limpets in the present study was shell clamping. By maximising tenacity resulting in the shell tightly fitting to the substratum, crabs are prevented from inserting the tip of their chela under the shell edge, which was observed to be a key step for successful removal. A very tall or wide shell shape may also prevent a crab from using the crushing technique.

Under optimal diet predictions (Hughes 1980a), preference for smaller prey than the size that a predator can handle may be a compromise between the energy expenditure involved in prey handling, encounter rates and energy gain from prey consumption. In the present work, larger limpets required longer handling times and presumably more energy expenditure, suggesting that intermediate sized limpets could be more advantageous. Predator size also seems to be important in this relationship because larger crabs can crush larger prey and required less time than smaller crabs to handle prey of a given size. Hence, larger crabs are potentially more effective predators, and larger prey require the more energetically costly pulling/levering behaviour.

The average *P. vulgata* size on the shore was 18 mm \pm 3 and the most frequent size class was 15-20 mm which also corresponded to the most preferred size by *N. puber*. This indicates that the encounter rate of this crab with its preferred prey size is frequent. Potentially, intermediated sized limpets would not be an expected preferential prey based on their energy content since for instance, the gonadal tissue (high in lipid content) is smaller for 15-25 mm *P. vulgata* than for individuals larger than 30 mm (Blackmore 1969). Hence, *N. puber* of most sizes foraging on the shore are likely to choose the limpet size 15-20 mm because this is well within their handling mechanical ability, is common in its foraging area and would give the greatest net energy intake. This is apparent also on other studies; the crabs *Callinectes sapidus* Rathbun and *Cancer pagurus* L. were shown to prefer smaller mussels, *Modiolus demissa* Dillwyn and smaller *Nucella lapillus* L. when given a choice (Hughes & Seed 1981). Presumably this was because smaller individuals decreased handling time (which increased with prey size) and

increased profitability via the yield of flesh per unit time. Optimal foraging theory based on size-specific profitability requires that the chosen prey size maximises energy gain (Hughes & Seed 1995). Crabs in general prefer small-sized molluscan prey when a choice is available (Juanes 1992) and, in agreement with the results of the present study, predator mechanical constraints involved in handling of differing sizes such as claw height have been suggested to play a major role in crab preference for prey size (Blackmore 1969).

P. vulgata has been reported to be a protandric species changing sex at first maturity with males becoming females at approximately 30-40 mm (Orton 1928). Size selective predation pressure by *N. puber* on *P. vulgata* populations may influence the prey population structure and reproductive success with these effects being predator density-mediated. Hence, predation may affect the limpet population structure if particular size classes are removed from the population by intensive predation and, it may influence the reproductive success because *P. vulgata* up to 25 mm are only just maturing and are mostly male (Blackmore 1969). Hence, the reproductive balance of populations may be affected. Such predatory effects could be particularly important because the reproductive success and recruitment of patellid limpets is notoriously variable (Bowman 1977, Bowman 1985), and in years when recruitment levels are low, predation may be considerable. Further to this, selective foraging by *Necora puber* and other crabs could also modulate other biological processes that are important for the limpet population dynamics. Density-dependent intraspecific competition is high in *Patella vulgata* (Boaventura et al. 2002b) and so, if the frequency of various size classes is

altered by predation competitive balances could be affected. However, further work would be needed to confirm this.

A limitation of the present study is the extent of its applicability to the field (e.g. Crowe & Underwood 1998). As far as possible, natural conditions were mimicked, for example by using natural rock for trial arenas. Field experiments would be required, however, to establish the importance of crab behaviour and assess the extent of the size-specific predatory impact of *Necora puber* and other decapod intertidal foragers on natural patellid populations.

CHAPTER 6

**Morphological variation in the cheliped of *Eriphia*
verrucosa (Forsskål) across shores of differing exposure
to wave action**

Morphological variation in the cheliped of *Eriphia verrucosa* across shores of differing exposure to wave action

6.1 Abstract

Understanding the effects of predator-prey interactions at a community level requires information on the factors that determine interactions at an individual level. Here, the intertidal crab *Eriphia verrucosa* (Forsskål) was used as a model species to examine the link between functional morphology (cheliped size and form) and patterns of resource use on shores of differing exposure to wave action. Crab claw size and form are known to be related to feeding performance and thus could modulate predation effects on intertidal assemblages.

Multivariate ecomorphological analyses were used to identify patterns of association between claw morphology and prey consumption. The data indicated that claw size and shape varied between shores of differing exposure to wave action, revealing morphological variation in this species. Individuals from exposed locations had larger claws than those with similar carapace width from sheltered locations. This shift in claw size was accompanied by differences in stomach content composition between locations. Crabs were more abundant on sheltered shores but those from exposed locations were larger in carapace width and had ~ 55 % more hard shell prey (mussels and limpets) in their stomachs than those from sheltered shores. These data indicates a wave exposure gradient in durophagy (consumption of hard shell prey items) with greater consumption on exposed locations. Patterns of claw functional morphology provide a mechanistic explanation for these resource-use patterns along the wave exposure gradient.

The interaction between prey abundance and feeding morphology is likely to shape the diet of this species and this may influence the relative impact of predators in these differing habitats.

6.2 Introduction

Predation is known to be an important biological factor with direct (e.g. prey mortality) and indirect effects (e.g. effects on organisms associated with prey species) on population dynamics and community structure of marine ecosystems (e.g. Paine 1966, Paine 1974, Hughes 1980b, Menge et al. 1986). The rocky intertidal is recognised as a particularly tractable system to examine predator-prey interactions since predation effects are thought to be particularly strong (Sih et al. 1985). Predation is also known to interact with physical and other biological processes influencing its effects on prey populations (Menge & Sutherland 1987, Menge 1991, 2000). Hence, predator foraging and therefore predation pressure, are modulated by biological constraints and environmental factors, which subsequently determine realized patterns of prey consumption (Lawton & Zimmerfaust 1992).

Crabs are highly mobile predators and are known to have an important role in structuring assemblages on rocky shores worldwide (e.g. Ebling et al. 1964, Robles 1987, Burrows et al. 1999, Rilov & Schiel 2006b). It is therefore important to understand crab predation at the individual level in order to evaluate effects on prey populations. Traditionally, studies on predator-prey interactions have focused either on direct effects such as prey mortality, or indirect effects such as

morphology, physiology chemistry, life history or behaviour (e.g. Moller & Beress 1975, Phillips 1976, Vermeij 1978, Sih 1987, Trussell 1996, Dalziel & Boulding 2005). Studies on the predator-prey arms race between crabs and their gastropod prey are abundant, but these have mainly focused on consequences of predator-prey interactions in terms of defences developed by prey (but see Takeda & Murai 2003) and predator responses often are overlooked (e.g. Bertness & Cunningham 1981, Boulding 1984, Lowell 1986, Cotton et al. 2004, Brookes & Rochette 2007).

Phenotypic plasticity is the ability of a particular genotype to produce different phenotypes in response to environmental variation (DeWitt & Scheiner 2004). In marine systems, the ecological performance of differing predatory fish phenotypes has been extensively studied, showing that labrid fish develop stronger jaw crushing ability in environments where hard shell prey (gastropods) are common and more frequently consumed (e.g. Wainwright 1987, 1988, Wainwright & Richard 1995, Grubich 2003). Plasticity in crab foraging has, however, mainly been investigated in terms of behaviour (e.g. Hazlett 1995, Briffa et al. 1998), and there is little information on phenotypic morphological variation and associated functional responses according to differing environmental conditions.

The cheliped of crabs are of major importance as tools and weapons for feeding and defence (e.g. Hughes & Elner 1979, Smith & Palmer 1994, Freire et al. 1996) and for reproductive behaviour (Lee & Seed 1992, Hughes 2000). The cheliped is typically used to crush or detach prey (e.g. limpets, Lowell 1986, Iwasaki 1993, Silva et al. 2004, see also Chapter 4) and it is known to vary in musculature according to diet (Elner 1978, Brown et al. 1979, Smith & Palmer 1994, Freire et al. 1996, Hughes 2000) and mating interactions (Lee & Seed 1992).

Little has been done, however, to describe relationships between external physical and biological gradients and crab phenotypic variation (but see Takeda & Murai 2003), and hence the mechanisms underlying morphological responses are not well understood (DeWitt & Scheiner 2004).

Environmental factors have a strong influence on predation in shallow-water systems because these habitats are subject to frequent fluctuations in physical conditions due to the tidal influence (e.g. Menge 1978a, b). Differences in predator morphological traits in relation to wave action have not previously been examined. This study focuses on the role of exposure to wave action, an important environmental gradient in intertidal habitats, on the foraging pattern of the intertidal xanthid crab *Eriphia verrucosa* (Forsskål) and investigates the variation of predator claw morphology to those differing environmental conditions. Such information is important because patterns of claw morphology can have direct consequences for prey populations and potentially also have evolutionary consequences for their morphology (Vermeij et al. 1981, Vermeij 1982).

In this study, natural variations in stomach content composition of *E. verrucosa* were examined together with cheliped morphology at the individual level, in order to help describe phenotypic responses along the wave exposure gradient including indirect effects of changes in assemblage composition. It was hypothesized that crabs from sheltered locations would differ in cheliped form and size from those at exposed locations and that this would be related to differences in prey abundance and consumption. It was expected that this effect would be more pronounced for prey with hard exoskeletons since they are likely to require larger chelipeds in order to be crushed prior to consumption. Hence, patterns of

prey abundance were also compared between shores of differing exposure and related to the stomach content composition of *E. verrucosa*.

An additional aim of this study was to describe the abundance and population structure of *E. verrucosa* on shores of differing exposure, to provide context for any phenotypic morphological differences (see Flores & Paula 2001). The sex of predators was included in analysis since this can influence predator distribution (Mascaró & Seed 2001), behaviour (Buck et al. 2003, Bishop & Wear 2005, Spooner et al. 2007) and diet (Brousseau et al. 2001, Spooner et al. 2007).

For shores of differing exposure the following specific hypothesis were examined: (1) there are no differences in prey abundance; (2) there are no differences in the abundance and population structure of *E. verrucosa*; (3) there are no differences in stomach content composition of *E. verrucosa*; (4) there are no differences in claw size or shape between sexes; (5) claw shape and/or size do not explain possible differences in stomach content composition; (6) there is no relationship between crab size (carapace width and claw size) and the percentage of hard shelled prey found in their stomachs.

6.3 Methods

Study sites and collection methods

Two moderately exposed (Peralta - 39°17'26.56"N, 9°20'36.20"W & Porto Dinheiro - 39°13'54.99"N, 9°20'13.61"W) and two relatively sheltered rocky shores (Paimogo - 39°17'11.65"N, 9°20'25.88"W & Vale Pombas - 39°17'27.42"N, 9°20'27.27"W), hereafter named exposed and sheltered shores, were examined on

the central coast of Portugal. Levels of shore exposure were confirmed using measures of mean flow conditions via the dissolution of gypsum (CaSO_4) disks following Jonsson et al. (2006). Sets of twelve disks were attached to the rock surface ~ 3 m above CD for a single high-tide on two occasions at each location. No significant differences were found between dates ($p>0.05$) and so data were pooled. Disks on exposed shores dissolved significantly more quickly than those on sheltered shores ($p<0.05$), giving a clear separation of exposure between locations.

To quantify prey abundance, ten random 50 cm x 50 cm quadrats were sampled at two sites on the midshore at all four shores. The abundance of all species was recorded. *Eriphia verrucosa* is active during nocturnal low-tides (Flores & Paula 2001) and so, in order to assess crab population structure and collect specimens for stomach content analysis and cheliped morphology, three nocturnal collections were made on each shore during August-September 2007. An area of the midshore, approximately 100 m x 50 m, was searched by two observers for approximately one hour. *E. verrucosa* were collected by hand from the shore and frozen upon return to the laboratory (Figure 6.1).



Figure 6.6. *Eriphia verrucosa*.

Since the presence of parasites or the moulting of crabs can hinder their feeding behaviour (Williams 1982), the present study only considered the intermoult stage of parasite free crabs. The stomachs of thirty individuals per sex collected on each shore were analysed. The presence of hard body prey parts was then used to quantify the composition of predator diet following the percentage points method of Wear and Haddon (1987).

Morphometric analyses of cheliped size and shape

Linear measures of claw morphology were taken from approximately thirty *E. verrucosa* of each sex at each shore (Figure 6.2a). Only individuals with both chelipeds intact were used. Morphometric measures were taken from the crusher chela and its handedness was recorded for each individual. Carapace width was measured using digital callipers (± 1 mm).

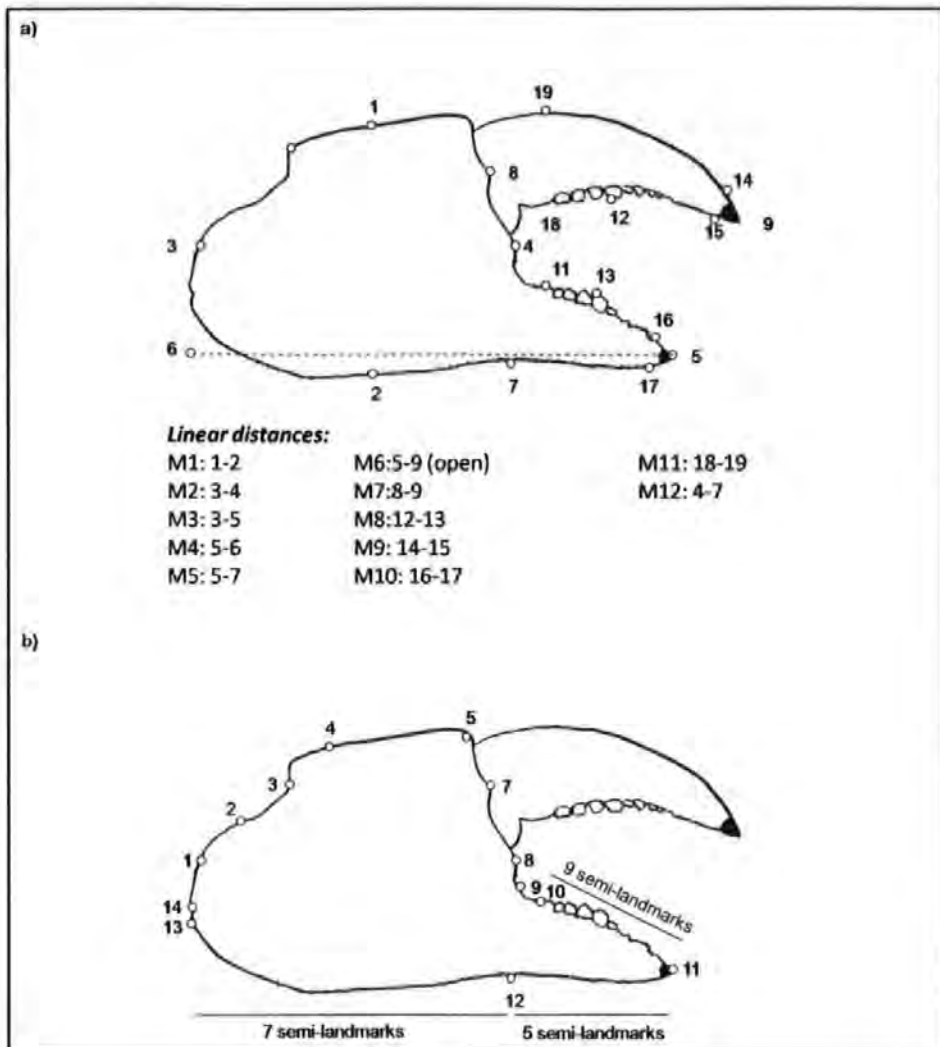


Figure 6.27. Linear distances used to evaluate size (a) and shape (b) of the crusher claw of *E. verrucosa* according to wave exposure. The approximate position of landmarks (○) and semilandmarks are shown.

Claw shape was then analysed using the landmark-based Geometrics method (Rohlf & Marcus 1993), which facilitated subsequent multivariate analysis (Adams et al. 2004). Photographic images of specimens were collected with individuals in the same orientation with the dorsal side of the cheliped facing upwards, using a scale and at the same focal distance thus avoiding any distortion.

Claw shape variables were obtained using the 13 landmarks depicted in Figure 6.2b. As suggested by Rosenberg (2002), landmarks were chosen for ease of identification and homology. To capture shape differences in zones of the chela where it was not possible to define homologous landmarks, a series of 21 sliding semi-landmarks were digitized in the upper margin of the pollex and in the ventral margin of the chela (Figure 6.2b). Landmarks x and y coordinates of each photograph were digits obtained using the program TpsDig2.

Landmarks were aligned using the Generalised Procrustes Analysis procedure (GPA) to remove non-shape variation in their coordinates, by scaling all specimens to unit size, translating them to a common location, and rotating them so that corresponding landmarks lined up as closely as possible (Rohlf & Slice 1990). As a result, a mean landmark configuration was obtained (consensus). From the aligned specimens, partial warp scores (non-uniform component) and uniform components were estimated. A relative warp analysis (similar to a principal component analysis) was made to the non-uniform component, thus generating a new set of shape variables. In order to give all landmarks equal weighting, the scaling option $\alpha=0$ was used (see Rohlf & Slice 1990).

Experimental design and data analysis

Differences in prey abundance according to wave exposure were compared using the Analysis of Similarities procedure (ANOSIM) based on standardised and square root data, using Bray-Curtis similarity matrix (Clarke & Warwick 2007) in the PRIMER package (Clarke & Gorley 2007). The following design was used: shore exposure (orthogonal, fixed, two levels: sheltered and exposed) and shore (random, 2 levels, nested in shore exposure) with ten replicates. The Similarity

Percentages (SIMPER) routine was then used to identify the species contributions for any differences detected according to exposure.

Univariate data on *E. verrucosa* abundance and mean size data was compared in GMAV5 (Underwood & Chapman 1998). The same experimental design was used to compare predator abundance, proportions of sexes and mean size for captured individuals. This had three factors: sampling date (random with 3 levels: date 1, 2 and 3), shore exposure (orthogonal, fixed with 2 levels: sheltered and exposed) and shore (random, nested within shore exposure with 2 levels). Cochran's test was used to check homogeneity of variances and appropriate transformations were made when this assumption was violated.

Multidimensional analyses based on permutation tests were used to examine predator stomach composition and cheliped morphology using PERMANOVA+ (Anderson & Gorley 2007). The PERMANOVA tests was chosen because it allows the analysis of complex experimental designs using multivariate data and examines interaction terms while maintaining robustness (Anderson 2001a, b, Anderson & Ter Braak 2003). For stomach content analysis, a similarity matrix was constructed using the Bray-Curtis similarity coefficient on fourth-root transformed data (Clarke 1993). The Similarity Percentages (SIMPER) routine was used to identify the contribution of prey species for the differences detected. Prior to analysis, all morphometric data for crabs were \log_{10} transformed. This transformation originates multivariate normal distributions in morphometric data (Ricklefs & Miles 1994).

To test the hypothesis that claw shape (geometric measures), size (linear measures) and stomach content composition varied according to exposures and sex, the following design with three factors was used for PERMANOVA tests: sex (orthogonal, fixed, two levels), shore exposure (orthogonal, fixed, two levels) and shore (random, 2 levels, nested in shore exposure). Euclidean distance was used as dissimilarity measure for morphometric analysis. Principal Coordinate Analysis (PCO) was used as an ordination method to visualize patterns in data and to establish the percentage of the variation explained by each factor.

The DistLM (Distance based linear models) and dbRDA (Distance based redundancy analysis) routines (based on the AIC model selection criterion and on BEST as a selection procedure) were used as a multiple regression procedure to test the hypothesis that variability in stomach composition could be explained by claw morphology. Specifically, the hypothesis that individuals with larger claws would have higher percentage of hard shell prey in their stomach was tested (For more information on PERMANOVA+ routines see Anderson 2001a, b, McArdle & Anderson 2001, Anderson 2005, Anderson & Gorley 2007).

An ANCOVA was made for each sex to test the effects of carapace width (covariate) and exposure on chelae height. The relationship between claw height/length ratio (CH/CL ratio) and carapace width was examined for all crabs collected on sheltered and exposed shores in order to assess whether claw dimensions could be used as a surrogate for crab size. To test whether carapace width and claw size reflected a functional response to prey consumption, regression was used to examine the relationship between CW and claw size and percentage of mussels present in the individual crab stomachs. Mussels were

chosen because these prey have a hard exoskeleton and are common in stomach contents and on the shore. Heterochely (i.e. having a differing crusher chela and pincer chela) was assessed using a MANOVA test on the above mentioned landmarks for 10 individuals randomly selected from each location (N=40). In all analyses, terms that did not contribute to variance ($p > 0.35$) were removed (see Underwood 1997) and this was stated where applicable.

6.4 Results

There were clear differences in prey abundance between shores of differing exposure ($R = 1$, $p = 0.03$). SIMPER analysis indicated that these differences resulted from a greater abundance of the mussel *Mytilus galloprovincialis* L. (22% more) and the alga *Corallina officinalis* Linnaeus (15% more) on exposed shores, while *Lepidochitona cinereus* L. (56% more) and *Gibbula umbilicalis* da Costa (36% more) were more abundant on sheltered shores.

E. verrucosa was significantly more abundant on sheltered shores (average \pm SE, 27 ± 5 individuals) than on exposed shores (average \pm SE, 11 ± 3 individuals) (Table 6.1). *E. verrucosa* was significantly larger in carapace width on exposed shores (average \pm SE, 43 ± 0.5 mm) than on sheltered shores (average \pm SE, 38 ± 0.7 mm) (Table 6.1). These patterns were consistent between shores within each exposure (Table 6.1). There were no significant differences in sex ratios between shores of differing exposure ($F_{1,16} = 0.99$, $p = 0.42$) or shores within exposures ($F_{1,16} = 1.42$, $p = 0.11$).

Table 6.1. ANOVA comparing the abundance and mean size (carapace width) of *E. verrucosa* between shores of differing exposure to wave action. Significant effects are shown in bold.

Source of variation	<i>E. verrucosa</i> abundance				<i>E. verrucosa</i> size		
	df	MS	F	p	MS	F	p
Shore exposure	1	833.3	38.46	0.02	0.30	21.24	0.04
Shore (Shore exposure)	2	21.6	0.27	0.77	0.01	0.57	0.58
Residual	8	80.6			0.02		
Cochran's test		C = 0.70 (not significant)			C = 0.43 (not significant)		

Multidimensional permutation analysis on the stomach contents of *E. verrucosa* showed that prey intake varied significantly between shores of different exposure but not between shores within exposure or with sex (Table 6.2). If number of permutations is < 30 (unique permutations column) then the P-value with the Monte Carlo correction [P(MC)] should be considered for interpretation of results (Anderson & Gorley 2007). This is because the Monte Carlo minimises any possible loss of power due to a reduced number of possible permutations in any term of the analyses (Anderson 2001a, c).

Differences across exposures resulted from greater consumption of the mussel *M. galloprovincialis* (~26% more), the gastropod *G. umbilicalis* (~ 45 % more) and the alga *C. officinalis* (~ 55 % more) on exposed shores, while the chiton *L. cinereus* (~ 19 % more) was more frequently found in the stomachs of animals collected on sheltered shores (Table 6.2 - SIMPER).

Table 6.2. Summary of results of PERMANOVA permutation tests on stomach content composition of *Eriphia verrucosa* for factors shore exposure, sex and shores and, results of SIMPER analysis of species contribution for differences between shores of differing exposure. Number of permutations used = 9999.

Variation in stomach content composition with shore exposure and sex							
Source of variation	df	SS	MS	Pseudo-F	P (perm)	Unique perms	P (MC)
Shore exposure = Exp	1	15513	15513	124.85	0.33	3	0.00
Sex	1	275.99	275.9	0.12	0.82	828	0.87
Shore (Exp) = Sh (Exp)	2	248.5	12.25	0.99	0.97	99.8	0.97
Exp x Sex	1	267.9	267.92	0.12	0.82	832	0.87
Sex x Sh (Exp)	2	4416.4	2208.2	1.77	0.11	9946	0.11
Residual	232	2.88	1245.1				
Total	239	3.09					
SIMPER (Shore exposure), average dissimilarity = 83.93							
Species	Exposed		Sheltered		% Contribution	Cumulative %	
	Average abundance		Average abundance	Average dissimilarity			
<i>Mytilus galloprovincialis</i>	1.00		0.59	30.69	36.57	36.57	
<i>Corallina officinalis</i>	0.84		0.25	21.18	25.24	61.81	
<i>Lepidochitona cinereus</i>	0.27		0.40	16.62	19.80	81.61	
<i>Gibbula umbilicalis</i>	0.21		0.08	7.11	8.47	90.08	

Larger crabs in carapace width had larger claws (height and length) for both sexes and exposures. Claw size varied significantly with sex and shore exposure (Table 6.3a). These differences were predominantly explained by exposure (72%) and then by sex (11%) (Figure 6.3). This pattern was associated with claw height (M1), length (M2) and propodus length (M3 & M4). This is evident by the length of the vectors for each measure, i.e., the longer the vector along a particular axis the better it explain the variance of each component. Males had larger claws (height & length) than females and, regardless of sex, crabs on exposed shores had larger claws (height, length) than those on sheltered shores (Table 6.3a - SIMPER).

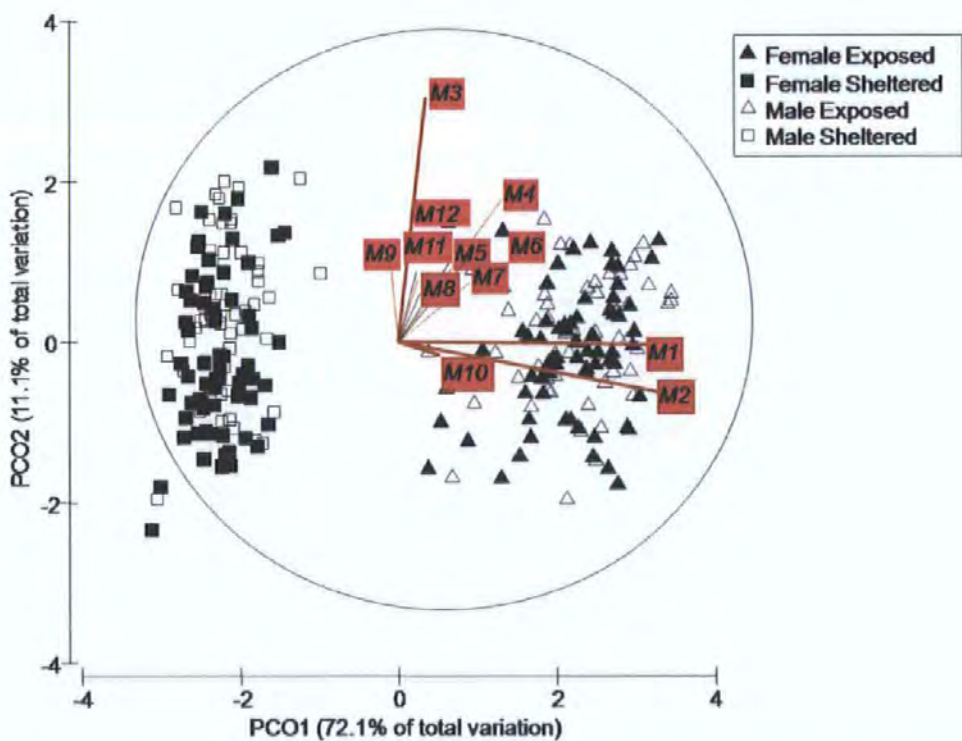


Figure 6.3. Principal Components examining the relationship between claw linear measurements (see Figure 6.1a) and sex of *E. verrucosa* according to shore exposure. A vector overlap of cheliped measured distances is included to examine their contribution to explain the variance between exposures.

Table 6.3. Summary of results of PERMANOVA permutation tests on claw linear (a) and shape (b) measurements for factors shore exposure, sex and shores and, results of SIMPER analysis of distances contribution for differences according to shore exposure and sex. Number of permutation used = 9999. The last interaction was removed in shape analysis as it did not contribute to variance patterns ($p > 0.35$).

a)

Source of variation	df	SS	MS	Pseudo-F	P (perm)	Unique perms
Shore exposure = Exp	1	13.5	13.5	7.6	0.003	999
Sex	1	1223.2	1223.5	378.1	0.001	998
Shore (Exp) = Sh (Exp)	2	6.5	3.2	1.4	0.14	997
Exp x Sex	1	3.3	1.8	1.8	0.18	999
Sex x Sh (Exp)	2	3.6	2.2	0.8	0.63	999
Residual	247	554.8				
SIMPER (Sex, Shore exposure)						
	Average size			Average size		
Measures	Exposed	Sheltered	Cumulative %	Males	Females	Cumulative %
Claw length (M2)	5.01	1.18	64.18	3.16	3.09	55.85
Claw height (M1)	2.73	0.65	83.17	1.78	1.65	72.49
Propodus (M3)	3.36	3.25	89.06	3.51	3.13	82.8
Propodus (M4)	3.4	2.92	93.64	3.18	3.15	89.97

Table 6.3. continued.

b)

Source of variation	df	SS	MS	Pseudo-F	P (perm)	Unique perms
Sex	1	8.8E-6	8.8E-6	2.7E-3	1	9923
Shore exposure = Exp	1	4.4 E-3	4.4 E-3	7.7E-1	0.62	9953
Shore (Exp) = Sh (Exp)	2	1.14 E-2	5.7 E-3	17.5E-1	0.06	9894
Exp x Sex	1	1.13 E-2	1.3 E-2	39.5E-1	0.00	9932
Residual	246	7.9 E-1	3.2 E-3			
SIMPER (Sex x Shore exposure)						
Av. measures						
Measures	Males-Exposed	Female-Exposed	Males-Sheltered	Females-Sheltered	% cumul. contribution	
Rw1	-2.5E-3	6.8E-3	2.7E-3	-6.7E-3	} > 80%	
Rw2	-1.1E-3	-7.1E-4	1.3E-3	6.4E-4		
Rw3	-9.6E-4	3.6E-4	1.0E-3	-3.1E-4		
Rw4	3.9E-3	-2.7E-3	2.5E-3	-2.2E-3		
Rw5	-2.3E-3	2.0E-3	-4.2E-3	2.5E-3		
Rw6	2.6 E-3	1.9E-3	-2.8E-4	-1.6E-3		
Rw7	5.9 E-3	4.4E-3	1.5E-3	-4.5E-3		
Rw8	-1.4 E-3	-1.0E-3	9.9E-4	9.7E-4		
Rw9	-9.2 E-3	6.3E-4	-6.3E-4	-7.3E-4		

Multivariate analysis of claw shape measurements (relative warps) indicated there was a significant interaction between sex and exposure to wave action (Table 6.3b), which explained ~12% and ~36% of the variation in claw shape respectively (Figure 6.4). Males had different claw shapes to females and females from sheltered locations had different claw shapes to males from exposed locations. In males, the coordinates related to length of the fixed finger (Rw1) plus the claw gape distance (Rw2) were the main drivers of the differences between exposures; while in females the same coordinates were related to claw length plus shape of the teeth on the fixed finger (Rw1) and length and thickness of the fixed finger (Rw2, Figure 6.2b).

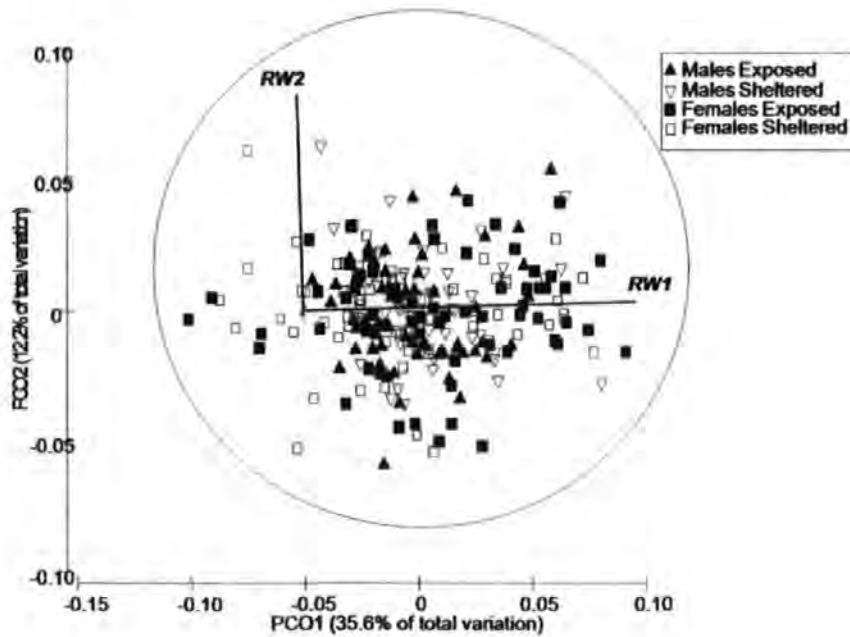


Figure 6.4. Principal Components examining the relationship between claw geometric measurements (see Figure 6.1b) and sex of *E. verrucosa* according to shore exposure.

This is evident by the length of the vectors for each measure, i.e., the longer the vector along a particular axis the better it explain the variance of each component. There were significant regression effects in the relationship between claw height and carapace width (covariate) between shores of differing exposure for both males ($F_{1,120} = 463.21$, $p < 0.001$) and females ($F_{1,120} = 647.96$, $p < 0.001$) (Figure 6.5).

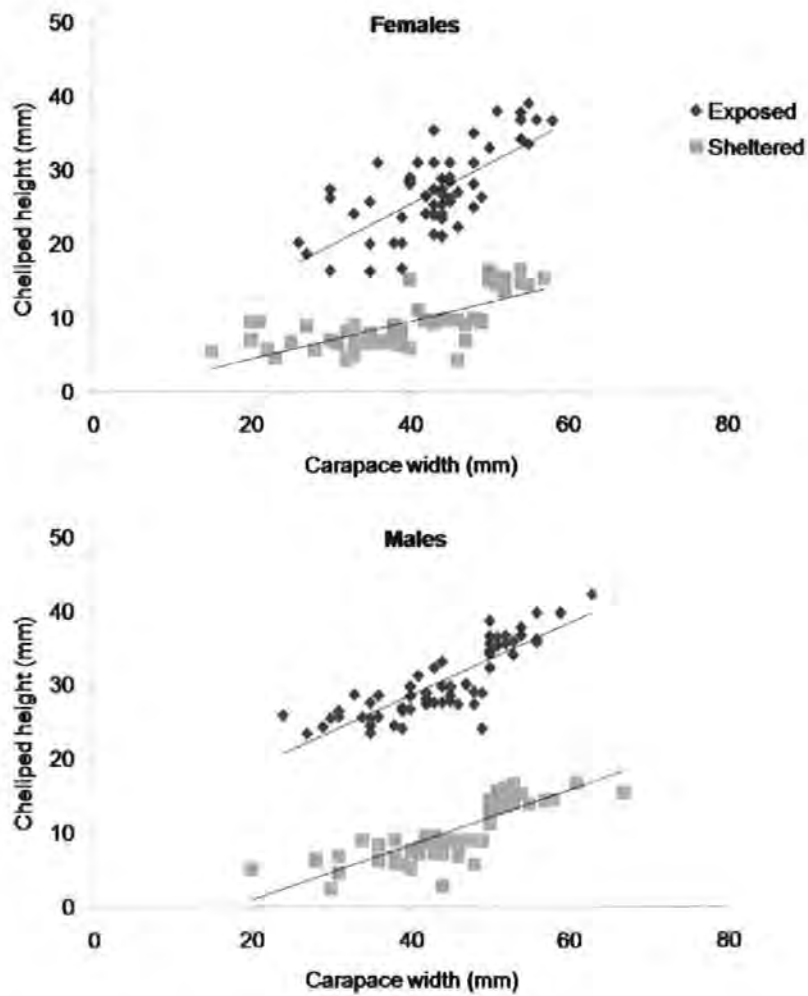


Figure 6.5. Regression effects of carapace width and shore exposure on cheliped height for males and females.

The DistLM procedure allows an overlap between two multivariate data sets in order to examine whether the over imposed variable explains a large percentage of the base data variation (Anderson & Gorley 2007). When testing the hypothesis that claw size and claw shape could explain patterns in stomach content composition between shores of different exposures, the DistLM procedure indicated that claw size was a significant factor (for the significant variables M1 and M2: Pseudo-F = 13.2, $p = 0.00$, proportion = 0.05) but not claw shape ($p > 0.21$ for all variables). It also showed that claw size explained most of the data variation between shores of differing exposure (Total % fitted variation = ~95%). The component 1 (RDA1) explained 75.6 % of the variance while the component 2 (RDA2) explained 19.6% of the variance. Specifically, claw height (M1) and length (M2, not shown because it gave a redundant contribution for data-Draftsman plots) were significantly associated with the variation in stomach contents according to wave exposure. This is visible through the length of the vectors of each measure, i. e, the longer the vector, the more it contributes for the explanation of the data variation. The BEST procedure selected claw height and length as the measures which explained most of the stomach content variation (AIC = 1710, $R^2 = 5.27E-2$, n° variables = 2) (Figure 6.6).

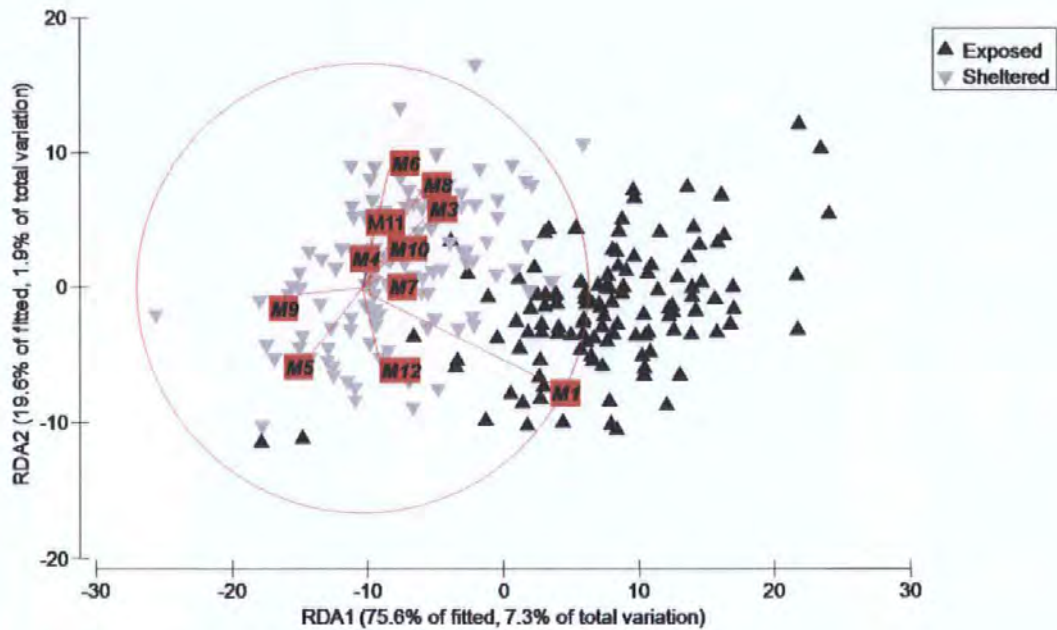


Figure 6.6. Distance based redundancy analysis examining the relationship between claw linear measurements and diet composition of *E. verrucosa* according to shore exposure. The measure M2 was found to be positively correlated with M1 in Draftman plots analysis and thus removed to avoid redundancy.

Thus, despite the fact that both size and shape of the claw varied significantly with exposure to wave action (see Tables 6.3 a, b), these results indicate that only claw size (not shape) was strongly related to differences in stomach content across the wave exposure gradient.

The relationship between claw height/length ratio (CH/CL ratio) and carapace width was examined in order to assess whether claw dimensions could be used as a surrogate for crab size. This showed that the CH/CL ratio was positively correlated with CW on exposed ($R^2 = 0.39$, $p = 0.02$) but not on sheltered shores ($R^2 = 0.03$, $p = 0.55$), indicating that larger claws were associated with larger animals on exposed shores.

There was a significant positive relationship between the propodus height (M1) and the percentage of mussels in stomachs of crabs from exposed locations ($R^2 = 0.04$, $p = 0.03$) but not for propodus length (M2; $R^2 = 0.46$, $p = 0.09$). This suggests that propodus height (and not length) is important to predict patterns of hard shell prey intake. Only M1 and M2 were analysed since these were the measures that contributed most to differences in claw size between shores of differing exposure (see Table 6.2). *E. verrucosa* showed typical heterochely for decapods crustaceans (λ Wilks = 0.122, $F = 4.13$, $p < 0.001$) with a larger crusher chela located on the right side.

6.5 Discussion

The multivariate analyses used in this study gave substantial advantages since it was possible to examine variation in crab morphology according to several *a priori* factors and examine relationships between sets of multivariate data, by using a combination of statistical tests (PERMANOVA, DistLM, dbRDA, ANOSIM, SIMPER, PCO).

The field based framework allowed direct tests of the influence of environmental variation (prey abundance) on claw phenotype and showed that crab cheliped was phenotypically sensitive to large scale variations (kilometres) in environmental factors. Such morphological variation of chela morphology can be significant at ecological (e.g. effects on prey abundance) and evolutionary (e.g. development of thicker shells in molluscan prey) time scales. Phenotypic variation was shown to be indirectly related to environmental conditions through variability in

prey abundance and prey intake (stomach contents). Nevertheless, other studies have shown that molluscs generally have thicker shells on sheltered shores where crabs are more abundant (e.g. Bertness & Cunningham 1981, Boulding et al. 1999). Much of the published literature on this efficiency-phenotype relationship is somewhat incomplete because predator diet and prey abundance are frequently not evaluated simultaneously (e.g. Freire et al. 1996, but see Smith 2004).

This study also showed that crabs predominantly consumed mussels and snails (*Gibbula umbilicalis*) in exposed locations, while chitons (*Lepidochitona cinereus*) were more heavily consumed in sheltered locations. These chitons are vulnerable to predation for two main reasons: they attain a maximum size of 2 cm on the shores studied and, when compared to gastropods such as limpets and snails, chitons have thinner shell plates and weaker attachment to the substratum (Silva, personal observation). It would be expected that larger claws would be advantageous on exposed shores for shell breaking, while such investment in claw reinforcement would not be required on sheltered shores where prey are more easily handled. The results in the present work fully support this prediction as smaller chelae were found on sheltered shores for crabs of similar size in carapace width. Hence, a shift in prey intake between shores of differing wave exposure was directly matched by a particular phenotypic expression.

There was a direct relationship between claw size and a proportion of hard shelled prey in *E. verrucosa* stomach contents, where larger chelae corresponded to a larger intake of prey with more resistant shells such as mussels and snails. This particular expression of claw genotype may influence mussel and topshells populations in two ways: in that the abundance and distribution of mussels and

snails maybe be limited by predation (ecological effect) and secondly, some evolutionary selection for stronger shells may be occurring due to the increased consumption on these species on exposed shores when compared to sheltered shores. In an extreme case, adaptive variation in predator feeding structures may contribute to a co-evolutionary arms race between durophagous (consumption of hard shell prey items) predators and shelled prey (sensu Sih 1987).

In terms of efficiency, crabs with larger claws have superior functional responses, i.e., a larger chela allows access to larger and/or different prey (Brown et al. 1979, Smith & Palmer 1994, Lee 1995, Seed & Hughes 1995, Freire et al. 1996). In the present study, crabs with larger claw height had more mussels in their diet than crabs with smaller claws. Claw height was found to be a major determinant of the percentage of mussels eaten on exposed shores. This phenotypic response in chela height has been reported previously for *Carcinus maenas* (L.) in response to mussel consumption (Elner 1980), but has not previously been described for *Eriphia* spp. Similar ecomorphological limitations in trophic performance have been reported for other organisms such as fish and echinoderms (Wainwright 1987, 1988, Hagen 2008). For instance, labrids have been shown to successfully exploit a relatively empty niche by developing stronger pharyngeal jaws when feeding on hard shell prey such as molluscs and urchins (Wainwright 1991).

The patterns of association between predator morphology, prey identity and intake rate shown in this study have important consequences for our understanding of the predatory efficiency of these crabs. If prey can be categorised into vulnerability groups based on the claw morphology of their predators (reflecting

performance features), then it may be possible to make predictions about morphology-diet relationships across ecological and evolutionary scales and so detect patterns of prey use between differing habitats. An example of such prey categorisation would be: i) prey that require strong claws for their shell to be broken (e.g. snails and mussels), ii) prey that require a moderate use of the claw (e.g. limpets and barnacles), iii) and prey where minimal claw use is required (e.g. some algae). In habitats where crabs have developed larger claws it may be predicted that prey of category i) are more consumed.

Due to trait-mediated effects, the vulnerability of some prey species may be considerably greater at exposed locations as was shown here for mussels on wave exposed shores. Geographical variation in crab performance has been shown for *Carcinus maenas* in southern areas of the Gulf of Maine, where crabs had larger chela and where molluscan prey were better defended than in Northern areas where prey were less robust (Smith 2004).

The ecological effects of *E. verrucosa* on the assemblage composition on shores of different exposure may thus be a direct consequence of morphological variation in chela size as well as predator abundance. Hence, the present study indicates that the natural variation in the claw morphology of these crabs between sheltered and exposed shores is most probably a response to environmental conditions influencing assemblage structure. Further research is now required to experimentally test the performance of varying morphological expressions of *E. verrucosa* claw genotype in order to inform quantitative predictions about the impact of these predators on prey assemblages.

CHAPTER 7

General discussion

General discussion

The main research questions posed in this thesis focus on natural variation in spatial and temporal patterns of abundance of mobile predators, particularly crabs. I examine how these predators exploit intertidal prey, and their role in intertidal food webs, community structure and ecosystem functioning. I demonstrate that these highly mobile predators have a key role in the ecology of shallow-water habitats. In this concluding chapter I first briefly summarise the major findings of the work (section 7.1), before discussing the underlying causes of the patterns described (section 7.2), and the role of predation by mobile predators in shallow-water systems (section 7.3). I outline priorities for further research based on existing knowledge gaps, and questions raised by the present study (section 7.4). I also make some considerations about the methods used in my study (section 7.5). I then make some concluding comments on the importance of crabs in shallow-water ecology (section 7.6).

7.1 Novel findings

Despite the limitations and logistic constraints outlined, my work has demonstrated that decapod crabs play a more important role in structuring intertidal communities and in shallow-water ecology than previously assumed. I show that there were substantial populations of *Carcinus maenas*, *Necora puber* and *Cancer pagurus* in the intertidal during both high and low-tides (~4000 individuals per tidal cycle in a ~ 1500m² area) on shores of southwest Britain, and that their occupancy patterns are dependent on environmental gradients of

exposure to wave action and tidal height (Chapters 2 and 3). Furthermore, I provided evidence of a strong intertidal migration by sublittoral crabs (Chapter 3). This is important in clarifying the importance of mobile predators in the intertidal. I also show that these crabs feed on various intertidal species particularly algae, chitons and limpets (Chapter 2), and that they can control the abundance of juvenile limpets (Chapter 4). Of particular interest was the proportion of chitons (*Lepidochitona cinereus*) in the diet of crabs suggesting that these organisms may be important as a key prey species for crabs on shores of North-West Europe. Chitons are key grazers elsewhere in the world (e.g. Moreno & Jaramillo 1983, Aguilera & Navarrete 2007) and in the absence of predation by crabs could have a more important role on shores in southwest Britain.

Following from the results of Chapter 4, I examined whether crabs had preferences for differing limpet sizes and showed that smaller limpets are the preferred prey of *Necora puber* (Chapter 5). Hence, these crabs may influence limpet population structure. Unlike many predator-prey arms race studies which have focused on prey alone, Chapter 6 established that predators can also respond morphologically (e.g. Vermeij 1977, Yamada & Boulding 1998), under the influence of environmental gradients on prey availability.

7.2 Patterns of predator activity in the intertidal

On rocky shores, sessile or slow moving species are often prey for crabs and these prey species vary in abundance along environmental gradients of wave action and desiccation stress (Stephenson & Stephenson 1949, Ballantine 1961, Lewis 1964). Until the present study, however, little was known about variation in abundance of predators along these gradients. In this thesis, I show that the crabs *Carcinus maenas*, *Necora puber* and *Cancer pagurus* vary in abundance and hence, their predatory intensity will also vary along environmental gradients (Chapters 2 and 3).

It has been argued that the role of predators is minimal in physically harsh portions of their prey's range and in general it has been suggested that predation pressure is stronger in sheltered locations (Connell 1975, Menge 1978a). My results for crabs contradict this generalisation. *Carcinus maenas* and *Necora puber* were more abundant in sheltered locations while *Cancer pagurus* was typically more abundant at exposed locations. Hence, it is likely that *C. maenas* and *N. puber* exert somewhat larger predation pressure on sheltered than on exposed shores (Figure 7.1).

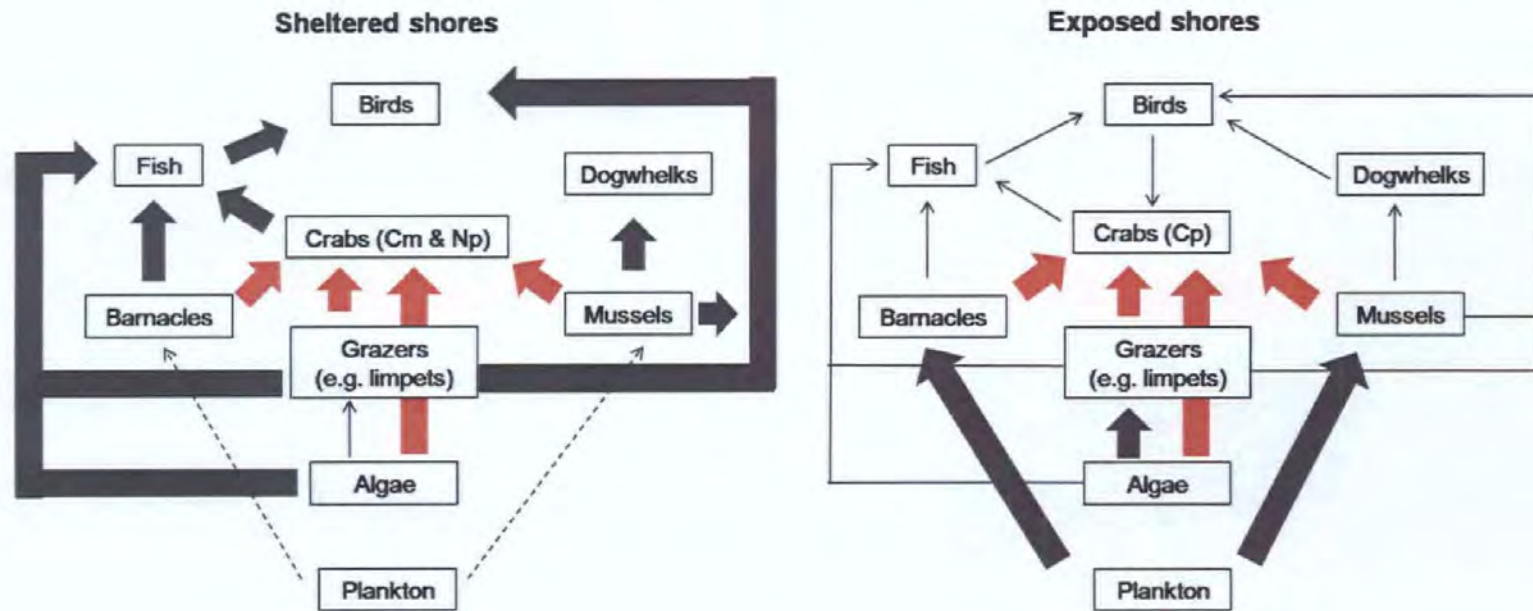


Figure 7.1. Role of crabs in rocky shore food webs according to exposure to wave action. Width of arrows indicates energy of flow. Cm – *Carcinus maenas*, Np – *Necora puber*, Cp – *Cancer pagurus*. Colored arrows represent the new findings of my study; the remaining links were interpreted from several published literature.

Predation pressure by crabs is therefore likely to vary across the wave exposure gradient (Chapter 2). This has important implications for intertidal dynamics. For example, limpets which have a key role in controlling algal assemblages (Hawkins 1981, Hawkins & Hartnoll 1983, Boaventura et al. 2002a, Jonsson et al. 2006) are less abundant on sheltered than on exposed shores (Jenkins et al. 1999). Results of this thesis suggest that predation by *C. maenas* and *N. puber* is likely to be higher on sheltered shores (Chapter 2, Figure 7.1), with significant effects on limpet abundance. Therefore, these predators may have an important indirect effect on algal assemblages by reducing limpet abundance on sheltered shores.

Various factors have been suggested to explain the reduced abundance of limpets on sheltered shores. For example, limited settlement success due to the physical dislodgement effect of algal fronds on sheltered shores (Hawkins & Hartnoll 1983, Hawkins et al. 1992). Algae are also responsible for trapping silt, which is detrimental for limpet grazing, (Hawkins & Hartnoll 1983, Hawkins et al. 1992, Jenkins et al. 1999, Jenkins & Hartnoll 2001). The relative abundance of mobile predators must also be incorporated into explanatory models of processes structuring communities along wave exposure gradients.

7.3 Role of predation in shallow-water ecosystem processes

Connectivity between sublittoral and intertidal habitats

A major gap in our knowledge of rocky shore ecology is the extent to which subtidal predators use intertidal resources (Edwards et al. 1982). This is because

the majority of the studies have focused on these habitats in isolation (e.g. Kennelly 1991, Norman & Jones 1992). The few studies that have examined both habitats simultaneously have seldom attempted to quantify migration by sublittoral predators, but have rather described their impacts (e.g. Rilov & Schiel 2006b). Field experiments reported in this thesis successfully quantified the abundance of intertidal and subtidal crabs, and showed that subtidal crabs *Carcinus maenas*, *Necora puber* and *Cancer pagurus* exhibit a strong subtidal-intertidal link that is consistent over space and time (Chapter 3). This had not been shown before for European shores although evidence of similar linkage has been described for shores in New Zealand (Rilov & Schiel 2006a).

An important implication of the present work is that studies on the role of predation in structuring intertidal prey assemblages may be biased if based only on data collected at low-tide. Based on evidence in Chapter 3 and from analysis of stomach contents (Chapter 2), my work clearly shows that the shore is an important foraging ground for sublittoral crabs. In the sublittoral, competition for resources and predation are thought to be important constraints on foraging (Robles et al. 1989, Robles et al. 1990) and hence, at high-water the intertidal provides an additional and possibly less exploited area of resources for subtidal organisms. I present here a schematic diagram summarising connectivity between the subtidal and intertidal habitats as a consequence of foraging by crabs (Chapters 2 and 3, Figure 7.2).

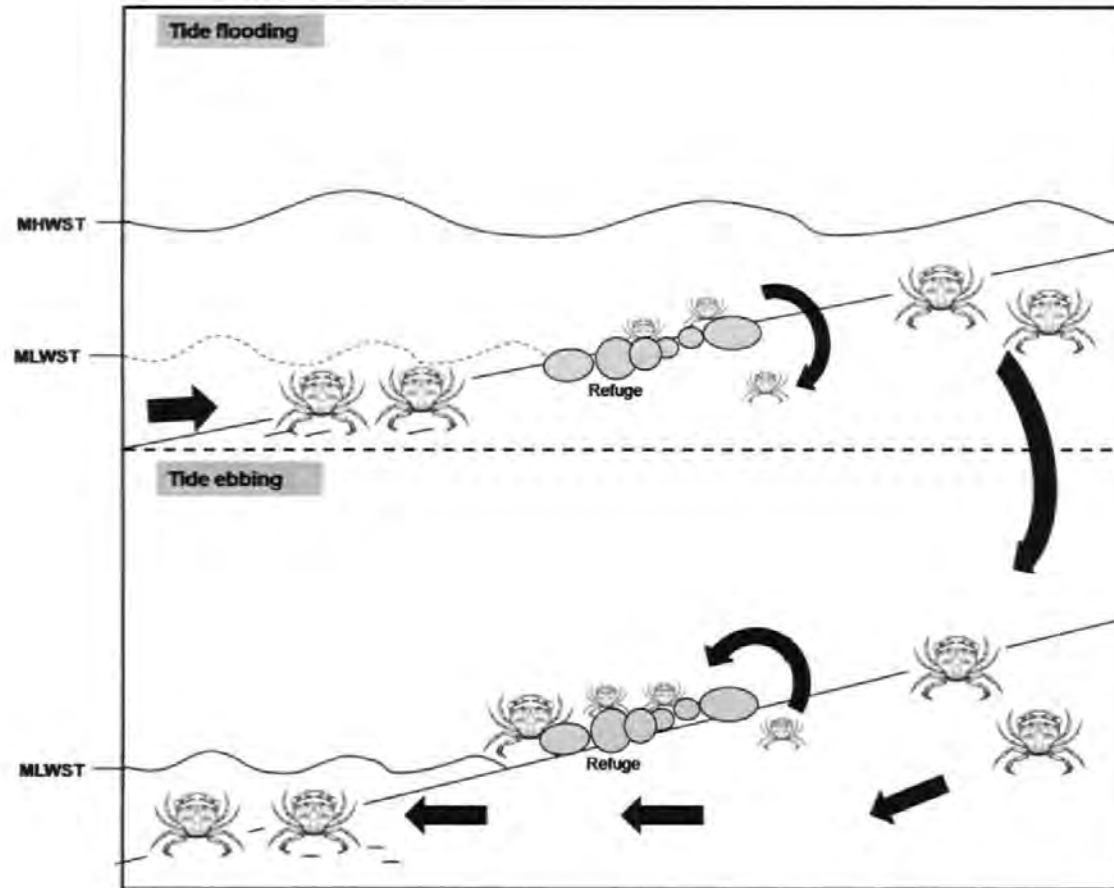


Figure 7.28. General interpretation of movements (shown by arrows) of sublittoral and intertidal crabs (no particular species represented) on the shore throughout the tidal cycle (MLWST and MHWST – Mean low and high water at spring tides). A representation of the sizes of predators undertaking these movements is given by the relative size of the crabs.

Crabs that are larger than those typically found on the shore during low-tide including *C. maenas*, *N. puber* and *C. pagurus*, undertake migrations into the intertidal during the tide flooding, thus establishing trophic subtidal-intertidal links (Figure 7.2). Smaller crabs that are intertidal residents remain on the shore throughout the tidal cycle and temporarily leave their refuges at high-tide to forage in surrounding areas (Figure 7.2). When these intertidal individuals attain adult sizes they most likely leave intertidal refuges and join the tidal migrating populations. Some of the large migrating individuals can be trapped by the tide on the shore and remain in refuges until the next high-tide (Figure 7.2). The majority of *C. maenas* had a distribution range up to the midshore, below the mean high water level at spring tides. In contrast, *N. puber* and *C. pagurus* remained mostly on the lower shore and to a lesser extent the midshore (Chapter 2).

All crab species were present on the shore throughout the tidal cycle (Chapter 2). The majority of individuals present on the shore during low-tide were smaller than those present during high-tide (Chapter 3), suggesting that the intertidal is an important nursery ground for these crabs. This has been described for *Carcinus maenas* (Mosknes 2002, Mosknes 2004) and for *N. puber* (Lee et al. 2006), as well as for other crab species in the North-West Atlantic (see Viscido et al. 1997). In this context, the rocky intertidal is comparable to other shallow-water systems such as sandy beaches (e.g. Burrows et al. 2004), estuaries (e.g. Ruiz et al. 1993, Giberto et al. 2004), mangroves Cannicci et al (1999a) and saltmarshes (e.g. Hollingsworth & Connolly 2006) which also function as nursery grounds for crabs and fish. Overall, my results emphasize that the subtidal and intertidal should

be considered as a continuous habitat, and this particularly so when considering the ecology of highly mobile species.

7.4 Future research

The findings of this thesis have prompted new questions for our understanding of shallow-water ecology. Little is known about the factors influencing crab abundance and distribution on rocky shores, for example, the role of recruitment variability at large spatial and temporal scales. In laboratory experiments, settlement of *N. puber* juveniles has been shown to vary according to hydrodynamic conditions which lead to differential settlement and abundance on natural substrata (Lee 2004). Here I show that the abundance of adult crabs varies along wave exposure gradients (Chapter 2). Additional work in other habitats such as sedimentary shores is now required to further examine the influence of the wave exposure on the distribution of predators. In addition to the connectivity between subtidal and intertidal habitats shown, there may also be connectivity via foraging migrations between hard and soft substrata.

Crabs are generally most active at night (Reid & Naylor 1989, Robles et al. 1989, Hunter & Naylor 1993, Warman et al. 1993, Cannicci et al. 1999b, Rilov & Schiel 2006b), which was the time when most of my sampling occurred. My study was, however, limited to the extent that it did not include a formal day-night comparison of crab activity on the shore at high-tide. It is possible that day-night variations in crab presence on the shore may occur, particularly with reduced densities during daytime high-tides, due to the presence of their predators such as

fish at high-tide (Warman et al. 1993). Further studies on the activity of crabs on the shore should aim to include day-night comparisons in order to assess whether their predation pressure is mainly restricted to nocturnal high-tides or if it occurs throughout the day. This is particularly important since some prey species may have differing activity periods between day and night (such as for chitons) and thus, their vulnerability to predation may vary.

Differential distribution of prey with tidal height has been shown to be important to explain the distribution of predatory lobsters (Robles et al. 1990), however, prey distribution did not explain patterns of abundance for the three crab species studied here. It remains to be tested whether habitat availability (Holsman et al. 2006), antagonistic factors such as competition and predation (Almany 2004) and preference for prey species or types (Chapter 5) influence the distribution of crabs during immersion. For most crab species, little is known about seasonal patterns of abundance and population structure. Many intertidal prey species such as barnacles, algae and mussels have seasonal patterns of recruitment (e.g. Underwood 1981, Watson et al. 2005, Nagarajan et al. 2006) hence, a combination of information on the abundance and distribution of predators and their prey at various temporal and spatial scales would provide the most useful basis for predictions about the impact of predators in the intertidal.

There is still considerable need for research on the impact of crabs and other sublittoral predators on prey species other than limpets (Chapter 3). Our knowledge about their impact on other intertidal prey such as snails, barnacles and chitons remains largely unknown but stomach content analysis of all three crabs indicated that these species were common prey items (Chapter 2). This information

is important to our understanding of rocky shore ecology since barnacles are key space occupiers (Jernakoff 1983) and provide a habitat for other species (Thompson et al. 1996). Additionally, as shown in Chapters 4 and 5, field studies on the impact of predators on prey populations can be complemented by laboratory experiments to answer specific questions about predator-prey interactions.

7.5 Methodological considerations

In this thesis, the use of a combination of methodological approaches including low-tide searches, trapping and underwater video observations at high-tide, and mark-recapture proved successful in studying crab populations. Three species *C. maenas*, *N. puber* and *C. pagurus* were captured in considerable abundance and across a wide range of sizes (Chapters 2 and 3). Each approach has specific limitations. Here I examine possible artefacts of sampling with traps at high-tide; limitations in the application of formal comparisons between data collected at high and low-tide data; and how to better estimate migration between habitats using marking-recapture.

The use of baited traps to assess the activity of crabs in the intertidal at high-tide proved very useful allowing replicated sampling at large (kilometres) and small (meters) spatial scales. Crab fishery studies also indicate that baited traps are the most effective method to capture crabs underwater (Miller 1990). However, sampling with traps may lead to experimental artefacts. Previous work has shown that when foraging in the subtidal, crabs such as *Cancer magister* and *Carcinus maenas* show aggressive behaviour and larger animals can displace smaller ones

from the traps (Kaiser et al. 1990, Holsman et al. 2006). Such agonistic interactions could introduce bias in the ability of traps to sample crab populations with some individuals influencing the entry of others. Kaiser (1990) and Holsman (2006) suggest that these agonistic encounters are likely to be reduced if crabs disperse from the subtidal into littoral habitats at high-tide because their foraging area will increase. Examination of trap data in the present study did not reveal any evidence of intra or interspecific agonistic interactions (see Chapter 2). Nevertheless, such interactions should be considered in future investigations using this sampling methodology. This could be further tested by conducting experimental manipulations with traps in laboratory trials or by videoing the entry of individuals into traps at high-tide.

The area sampled by traps is likely to vary with the amount of bait used and water movements on the shore (Miller 1990), and this could also influence abundance estimates. These effects could also be examined by deploying traps together with video surveillance. In my study, traps were set at similar distances and a standardised amount and type of bait was used to minimise differences in the area sampled by each trap. It would also be useful to future work to establish the effect of the size of trap entrance on capture (Miller 1990).

Crabs are typically active in the intertidal at high-tide and inactive at low-tide. This poses a methodological challenge to compare their abundance between tidal phases and researchers have often focused on just one tidal phase (e.g. Edwards 1958, Hunter & Naylor 1993, Warman et al. 1993). The same problem applies to studies of fish such as blennies that are confined to rockpools during low-tide. During high-tide, migration of organisms between the subtidal and intertidal

habitats can also alter the composition of predator assemblages (e.g. Burrows et al. 1999, Faria & Almada 2006). Low-tide sampling is limited to search effort whereby very large boulders and other inaccessible habitats such as deep crevices are not sampled. This topic deserves more attention and the use of timed searches of equal duration at low and high-tides in predefined areas of the shore could provide a more reliable data. Multiple depletion methods may also prove useful where set areas are repeatedly searched and abundance estimated, as have widely been used in freshwater systems such as rivers for estimating fish populations (Seber 1982).

Information on connectivity between adjacent habitats in freshwater habitats such as river beds and river banks (e.g. spiders and insects), and terrestrial habitats such as forests and adjacent open areas (e.g. birds), has been obtained by direct observation together with indirect methods such as isotope analyses of diet (e.g. Kollmann & Buschor 2003, Paetzold et al. 2005). Qualitative data on movements of marine mobile species such as fish and crabs between subtidal and intertidal habitats have been made using telemetry (e.g. Freire & González-Gurriarán 1998), underwater video (e.g. Dare & Edwards 1981, Burrows et al. 1999) and direct observation (e.g. Faria & Almada 2006). Quantifying the numbers of individuals migrating between these habitats could also provide a useful approach in understanding the impact and potential role of these predators in shaping intertidal prey populations. However, to be able to quantify the extent of intertidal migration by subtidal crabs (or fish) it is paramount to be able to differentiate between individuals that migrate from the subtidal and those that are resident in the intertidal.

In this thesis I tagged individuals at both low and high-tide and conducted recapture sampling during both tidal phases (Chapter 3). This allowed differences between resident and migrant individuals to be determined. Using this approach, it was possible to show that substantial numbers of sublittoral *C. maenas*, *N. puber* and *C. pagurus* undertake intertidal migrations. However, this approach was very time consuming and costly in terms of amount of tags (elastomer) required in order to obtain a suitable sample size (~ 200 individuals per species). There is also a need for data collected by tagging in the subtidal followed by subsequent recapture searches on nearby shores, in order to obtain accurate estimates of abundance of these populations and measure the extent to which they use the intertidal as a feeding area. This data would allow a better understanding of the ecological linkage established by migrant predators between shallow-water habitats, which my study (Chapters 2 and 3) suggests to form a continuous system for highly mobile species.

In summary, field ecologists need to use modern approaches such as telemetry and video surveillance to overcome methodological problems that constrain the study of mobile predators. Such methods will then allow hypotheses to be addressed concerning the role of predators in influencing intertidal assemblages the effects of which, despite recent advances (Rilov & Schiel 2006b, Jones & Shulman 2008) including this thesis, remain largely unknown for most species, habitats and locations.

7.6 Concluding remarks

My work has demonstrated that crabs play an important predatory role on rocky shores and that their distribution changes with the major environmental shore gradients. Strong linkages have been demonstrated between the intertidal and subtidal habitats, leading to considerable impact on prey populations and hence community structure and ecosystem functioning. This thesis sets predation by crabs into their environmental context, allowing a better understanding of their ecological role on rocky shores and shallow-water habitats. Underlying behavioural mechanisms were also explored and found to provide constraints on predatory activities and impact. I further showed that the intertidal and subtidal habitats form an ecological continuum and future research on shallow-water ecology should take this linkage into consideration.

REFERENCES

- Adams DC, Rohlf FJ, Slice DE (2004) Geometric morphometrics: ten years of progress following the 'revolution'. *Italian Journal of Zoology* 71:5-16
- Aguilar R, Hines AH, Wolcott TG, Wolcott DL, Kramer MA, Lipcius RN (2005) The timing and route of movement and migration of post-copulatory female blue crabs, *Callinectes sapidus* Rathbun, from the upper Chesapeake Bay. *Journal of Experimental Marine Biology and Ecology* 319:117-128
- Aguilera MA, Navarrete SA (2007) Effects of *Chiton granosus* (Frembly, 1827) and other molluscan grazers on algal succession in wave exposed mid-intertidal rocky shores of central Chile. *Journal of Experimental Marine Biology and Ecology* 349:84-98
- Ahsanullah RM, Newell RC (1977) The effects of humidity and temperature on water loss in *Carcinus maenas* (L.) and *Portunus marmoreus* (Leach). *Comparative Biochemistry and Physiology* 56A:593-601
- Allen JA (1966) The rhythms and population dynamics of decapod crustacea. *Oceanographic and Marine Biological Association* 4:247-265
- Almany GR (2004) Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. *Oecologia* 141:105-113
- Ambrose RF (1986) Effects of octopus predation on motile invertebrates in a rocky subtidal community. *Marine Ecology Progress Series* 30:261-273
- Anderson MJ (2001a) A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26:32-46

- Anderson MJ (2001b) Permutation tests for univariate or multivariate analysis of variance and regression. *Canadian Journal of Fisheries and Aquatic Sciences* 58:626-639
- Anderson MJ (2001c) Permutation tests for univariate or multivariate analysis of variance and regression. *Canadian Journal of Fisheries and Aquatic Sciences* 58:626-639
- Anderson MJ (2005) Permanova-Permutational multivariate analysis of variance, Auckland
- Anderson MJ, Gorley RN (2007) PERMANOVA+ for PRIMER: guide to statistical methods PRIMER-E, Plymouth
- Anderson MJ, Ter Braak CJF (2003) Permutation tests for multi-factorial analysis of variance. *Journal of Statistical Computation and Simulation* 73:85-113
- ap Rheinault T (1986) Size selection by the crab *Liocarcinus puber* feeding on mussels *Mytilus edulis* and on shore crabs *Carcinus maenas*: the importance of mechanical factors. *Marine Ecology Progress Series* 29:45-53
- ap Rheinault T, Hughes R (1985) Handling methods used by the velvet swimming crab *Liocarcinus puber* when feeding on molluscs and shore crabs. *Marine Ecology Progress Series* 25:63-70
- August PV (1983) The role of habitat complexity in structuring tropical mammal communities. *Ecology* 64:1495-1507
- Ballantine WJ (1961) A biologically-defined exposure scale for the comparative description of rocky shores. *Field Studies* 1:1-17
- Beal BF, Parker MR, Vencile KW (2001) Seasonal effects of intraspecific density and predator exclusion along a shore-level gradient on survival and growth

- of juveniles of the soft-shell clam, *Mya arenaria* L., in Maine, USA. *Journal of Experimental Marine Biology and Ecology* 264:133-169
- Begon M, Harper JL, Townsend CR (1996) *Ecology*, Vol. Blackwell Science, Oxford
- Behringer DC, Butler MJ, Shields JD (2008) Ecological and physiological effects of PaV1 infection on the Caribbean spiny lobster (*Panulirus argus* Latreille). *Journal of Experimental Marine Biology and Ecology* 359:26-33
- Bell MC, Eaton DR, Bannister RCA, Addison JT (2003) A mark-recapture approach to estimating population density from continuous trapping data: application to edible crabs, *Cancer pagurus*, on the east coast of England. *Fisheries Research* 65:361-378
- Bergman PK, Haw F, Blankenship HL, Buckley RM (1992) Perspectives on design, use, and misuse of fish tags. *Fisheries* 17:20-25
- Bernardez C, Freire J, Gonzalez-Gurriaran E (2000) Feeding of the spider crab *Maja squinado* in rocky subtidal areas of the Ria de Arousa (north-west Spain). *Journal of the Marine Biological Association of the United Kingdom* 80:95-102
- Bertness M, Cunningham C (1981) Crab shell-crushing predation and gastropod architectural defense. *Journal of Experimental Marine Biology and Ecology* 50:213-230
- Bertness MD (1981) Predation, physical stress, and the organization of a tropical rocky intertidal hermit crab community. *Ecology* 62:411-425
- Bertness MD, Leonard GH (1997) The role of positive interactions in communities: lessons from intertidal habitats. *Ecology* 78:1976-1989

- Bishop MJ, Wear SL (2005) Ecological consequences of ontogenetic shifts in predator diet: Seasonal constraint of a behaviourally mediated indirect interaction. *Journal of Experimental Marine Biology and Ecology* 326:199-206
- Black R (1978) Tactics of whelks preying on limpets. *Mar Biol* 46:157-162
- Blackmore DT (1969) Studies of *Patella vulgata* L. I. Growth, reproduction and zonal distribution. *Journal of Experimental Marine Biology and Ecology* 3:200-213
- Boaventura D, Alexander M, Della Santina P, Smith ND, Ré P, Cancela da Fonseca L, Hawkins SJ (2002a) The effects of grazing on the distribution and composition of low-shore algal communities on the central coast of Portugal and on the southern coast of Britain. *J Exp Mar Biol Ecol* 267:185-206
- Boaventura D, Cancela da Fonseca L, Hawkins S (2002b) Analysis of competitive interactions between the limpets *Patella depressa* Pennant and *Patella vulgata* L. on the northern coast of Portugal. *Journal of Experimental Marine Biology and Ecology* 271:171-188
- Boaventura D, Cancela da Fonseca L, Hawkins S (2003) Size matters: competition within populations of the limpet *Patella depressa*. *Journal of Animal Ecology* 72:435-446
- Bonnet X, Pearson D, Ladyman M, Lourdais O, Bradshaw D (2002) 'Heaven' for serpents? A mark-recapture study of tiger snakes (*Notechis scutatus*) on Carnac Island, Western Australia. *Austral Ecology* 27:442-450

- Bosman A, Hockey PAR (1989) Oystercatcher predation and limpet mortality: the importance of refuges in enhancing the reproductive output of prey populations. *Veliger* 32:120-129
- Boulding EG (1984) Crab-resistant features of shells of burrowing bivalves: decreasing vulnerability by increasing handling time. *Journal of Experimental Marine Biology and Ecology* 76:201-223
- Boulding EG, Holst M, Pilon V (1999) Changes in selection on gastropod shell size and thickness with wave-exposure on Northeastern Pacific shores. *Journal of Experimental Marine Biology and Ecology* 232:217-239
- Bowman RS (1985) The biology of the limpet *Patella vulgata* L. in the British Isles: spawning time as a factor determining recruitment success. In: Moore PG, Seed R (eds) *Ecology of the rocky coasts*. Hodder and Stoughton, London, p 178-815
- Bowman RSaL, J. R. (1977) Annual fluctuations in the recruitment of *Patella vulgata* L. *Journal of Marine Biological Association of the United Kingdom* 57:793-815
- Branch GM (1975) Mechanisms reducing intraspecific competition in *Patella* spp.: migration, differentiation and territorial behaviour. *Journal of Animal Ecology* 44:575-600
- Branch GM (1985) Limpets: their role in littoral and sublittoral community dynamics. In: Moore PG, Seed R (eds) *Ecology of the rocky coasts*. Hodder and Stoughton, London, p 97-116
- Briffa M, Elwood RW, Dick JTA (1998) Analysis of repeated signals during shell fights in the hermit crab *Pagurus bernhardus*. *Proceedings of the Royal Society of London Series B-Biological Sciences* 265:1467-1474

- Brookes JI, Rochette R (2007) Mechanism of a plastic phenotypic response: predator-induced shell thickening in the intertidal gastropod *Littorina obtusata*. *Journal of Evolutionary Biology* 20:1015-1027
- Brousseau DJ, Fillipowicz A, Baglivo JA (2001) Laboratory investigations of the effects of predator sex and size on prey selection by the Asian crab, *Hemigrapsus sanguineus*. *Journal of Experimental Marine Biology and Ecology* 262:199-210
- Brown SC, Cassuto SR, Loos RW (1979) Biomechanics of chelipeds in some decapod crustaceans. *Journal of Zoology* 188:143-159
- Buck TL, Breed GA, Pennings SC, Chase ME, Zimmer M, Carefoot TH (2003) Diet choice in an omnivorous salt-marsh crab: different food types, body size and habitat complexity. *Journal of Experimental Marine Biology and Ecology* 292:103-116
- Burrows MT, Gibson RN, Robb L, Maclean A (2004) Alongshore dispersal and site fidelity of juvenile plaice from tagging and transplants. *Journal of Fish Biology* 65:620-634
- Burrows MT, Harvey R, Robb L (2008) Wave exposure indices from digital coastlines and the prediction of rocky shore community structure. *Marine Ecology-Progress Series* 353:1-12
- Burrows MT, Hughes RH (1989) Natural foraging of the dogwhelk, *Nucella lapillus* (Linnaeus); the weather and whether to feed. *Journal of Molluscan Studies* 55:285-295
- Burrows MT, Kawai K, Hughes RN (1999) Foraging by mobile predators on a rocky shore: underwater TV observations of movements of blennies *Lipophrys*

- pholis* and crabs *Carcinus maenas*. Marine Ecology Progress Series 187:237-250
- Cannicci S, Fratini S, Vannini M (1999a) Use of time, space and food resources in the mangrove climbing crab *Selatium elongatum* (Grapsidae : Sesarminae). Marine Biology 135:335-339
- Cannicci S, Gomei M, Boddi B, Vannini M (2002) Feeding habits and natural diet of the intertidal crab *Pachygrapsus marmoratus*: opportunistic browser or selective feeder? Estuarine, Coastal and Shelf Science 54:983-1001
- Cannicci S, Gomei M, Dahdouh-Guebas F, Rorandelli R, Terlizzi A (2007) Influence of seasonal food abundance and quality on the feeding habits of an opportunistic feeder, the intertidal crab *Pachygrapsus marmoratus*. Marine Biology 151:1331-1342
- Cannicci S, Paula J, Vannini M (1999b) Activity pattern and spatial strategy in *Pachygrapsus marmoratus* (Decapoda:Grapsidade) from Mediterranean and Atlantic shores. Marine Biology 133:429-435
- Carlton JT, Hodder J (2003) Maritime mammals: terrestrial mammals as consumers in marine intertidal communities. Marine Ecology Progress Series 256:271-286
- Chapman MG (2000) Poor design of behavioural experiments gets poor results: examples from intertidal habitats. Journal of Experimental Marine Biology and Ecology 250:77-95
- Chase JN, P. A. Abrams, J. P. Grover, S. Diehl, P. Chesson, R.D. Holt, S.A. Richards, R.M. Nisbet & T. D. Case (2002) The interaction between predation and competition: a review and synthesis. Ecology Letters 5:302-315

- Chatterton TD, Williams BG (1994) Activity patterns of the New Zealand cancrid crab *Cancer novaezelandiae* (Jacquinot) in the field and laboratory. *Journal of Experimental Marine Biology and Ecology* 178:261-274
- Chesson J (1983) The estimation and analysis of preference and its relationship to foraging models. *Ecology* 64:1297-1304
- Chilton NB, Bull CM (1984) Influence of predation by a crab on the distribution of the size-groups of three intertidal gastropods in South Australia. *Marine Biology* 83:163-169
- Chilton NB, Bull CM (1986) Size-related selection of two intertidal gastropods by the reef crab *Ozius truncatus*. *Marine Biology* 93:475-480
- Choy SC (1986) Natural diet and feeding habits of the crabs *Liocarcinus puber* and *L. holsatus* (Decapoda, Brachyura, Portunidae). *Marine Ecology Progress Series* 31:87-99
- Clark JM, Kershner MW (2006) Size-dependent effects of visible implant elastomer marking on crayfish (*Orconectes obscurus*) growth, mortality, and tag retention. *Crustaceana* 79:275-284
- Clark PF (1986) North-east Atlantic crabs; an atlas of distribution, Vol. Marine Conservation Society, Ross-on-Rye
- Clarke B, Gorley R (2007) PRIMER6. Plymouth Marine Laboratory, Plymouth
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18:117-143
- Clarke KR, Warwick RM (2007) PRIMER-E, Plymouth Marine Laboratory, U.K.
- Coleman R, Goss-Custard J, Durell S (1999) Limpet *Patella* spp. consumption by oystercatchers *Haematopus ostralegus*: a preference for solitary prey items. *Marine Ecology Progress Series* 183:253-261

- Coleman RA, Browne M, Theobalds T (2004) Aggregation as a defense: Limpet tenacity changes in response to simulated predator attack. *Ecology* 85:1153-1159
- Coleman RA, Underwood AJ, Benedetti-Cecchi L, Aberg P, Arenas F, Arrontes J, Castro J, Hartnoll RG, Jenkins SR, Paula J, Della Santina P, Hawkins SJ (2006) A continental scale evaluation of the role of limpet grazing on rocky shores. *Oecologia* 147:556-564
- Conan GY (1985) Periodicity and phasing of moulting. In: Wenner AM (ed) *Factors in adult growth - Crustacean Issues, Vol 3*. A.A. Balkema, Rotterdam, p 73-101
- Connell JH (1961) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42:710-723
- Connell JH (1970) A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. *Ecological Monographs* 40:49-78
- Connell JH (1972) Community interactions on marine rocky intertidal shores. *Annual Review of Ecology and Systematics* 3:169-192
- Connell JH (1975) Some mechanisms producing natural structure in natural communities: a model and evidence from field experiments. In: Cody ML, Diamond JM (eds) *Ecology and evolution of communities*. The Belknap Press of Harvard University Press, Cambridge, p 461-490
- Connell JH (1985) The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *Journal of Experimental Marine Biology and Ecology* 93:11-45

- Connell SD (1998) Effects of predators on growth, mortality and abundance of a juvenile reef-fish: evidence from manipulations of predator and prey abundance. *Marine Ecology Progress Series* 169:251-261
- Connolly SR, Roughgarden J (1999) Theory of marine communities: competition, predation, and recruitment-dependent interaction strength. *Ecological Monographs* 69:277-296
- Cotton PA, Rundle SD, Smith KE (2004) Trait compensation in marine gastropods: Shell shape, avoidance behaviour, and susceptibility to predation. *Ecology* 85:1581-1584
- Crothers JH (1967) The biology of the shore crab *Carcinus maenas* (L.). I. The background - Anatomy, growth and life history. *Field Studies* 2:407-434
- Crothers JH (1968) The biology of the shore crab *Carcinus maenas* (L.). II. The life of the adult crab. *Field Studies* 2:579-614
- Crothers JH (1983) Variation in dogwhelk shells in relation to wave action and crab predation. *Biological Journal of the Linnean Society* 20:85-102
- Crowe TP, Underwood AJ (1998) Testing behavioural "preference" for suitable microhabitat. *Journal of Experimental Marine Biology and Ecology* 225:1-11
- Cunningham PN, Hughes RN (1984) Learning of predatory skills by shore crabs *Carcinus maenas* feeding on mussels and dogwhelks. *Marine Ecology Progress Series* 16:21-26
- D'Amours O, Scheibling RE (2007) Effect of wave exposure on morphology, attachment strength and survival of the invasive green alga *Codium fragile* ssp *tomentosoides*. *Journal Experimental Marine Biology Ecology* 351:129-142

- Dalziel B, Boulding EG (2005) Water-borne cues from a shell-crushing predator induce a more massive shell in experimental populations of an intertidal snail. *Journal of Experimental Marine Biology and Ecology* 317:25-35
- Dare PJ, Edwards DB (1981) Underwater television observations on the intertidal movements of shore crabs, *Carcinus maenas*, across a mudflat. *Journal of Marine Biological Association of the United Kingdom* 61:107-116
- Davis JLD, Young-Williams AC, Hines AH, Zmora O (2004) Comparing two types of internal tags in juvenile blue crabs. *Fisheries Research* 67:265-274
- Dayton PK (1971) Competition, disturbance and community organisation: provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* 41:351-&
- Denny MW (1985) Wave forces on intertidal organisms: a case study. *Limnology and Oceanography* 30:1171-1187
- Denny MW, Daniel TL, Koehl MAR (1985) Mechanical limits to size in wave-swept organisms. *Ecological Monographs* 55:69-102
- DeWitt TJ, Scheiner SM (2004) Phenotypic plasticity: functional and conceptual approaches, Vol. Oxford University Press, Oxford
- Dunnington MJ, Wahle RA, Bell MC, Geraldini NR (2005) Evaluating local population dynamics of the American lobster, *Homarus americanus*, with trap-based mark-recapture methods and seabed mapping. *New Zealand Journal of Marine and Freshwater Research* 39:1253-1276
- Eaton DR, J. Brown, J.T. Addison, S.P. Miligan & L.J. Fernand (2003) Edible crab (*Cancer pagurus*) larvae surveys off the east coast of England: implications for stock structure. *Fisheries Research* 65:191-199

- Ebling FJ, Kitching JA, Muntz L, Taylor CM (1964) The ecology of Lough Ine. XIII. Experimental observations of the destruction of *Mytilus edulis* and *Nucella lapillus* by crabs. *Journal of Animal Ecology* 33:73-82
- Edgar GJ (1990) Predator-prey interactions in seagrass beds. II. Distribution and diet of the blue manna crab *Portunus pelagicus* Linnaeus at Cliff Head, Western Australia. *Journal of Experimental Marine Biology and Ecology* 139:23-32
- Edwards DC, Conover DO, Sutter III F (1982) Mobile predators and the structure of marine intertidal communities. *Ecology* 63:1175-1180
- Edwards RL (1958) Movements of individual members in a population of the shore crab, *Carcinus maenas* L., in the littoral zone. *Journal of Animal Ecology* 27:37-45
- Eggleston DB, Etherington LL, Elis WE (1998) Organism response to habitat patchiness: species and habitat-dependent recruitment of decapod crustaceans. *Journal of Experimental Marine Biology and Ecology* 223:111-132
- Ekendahl A (1998) Colour polymorphic prey (*Littorina saxatilis* Olivi.) and predatory effects of a crab population (*Carcinus maenas* L.). *Journal of Experimental Marine Biology and Ecology* 222:239-246
- Ellis JC, Chen W, O'Keefe B, Shulman MJ, Witman JD (2005) Predation by gulls on crabs in rocky intertidal and shallow subtidal zones of the Gulf of Maine. *Journal of Experimental Marine Biology and Ecology* 324:31-43
- Elner RW (1978) The mechanisms of predation by the shore crab, *Carcinus maenas* (L.), on the edible mussel, *Mytilus edulis* L. *Oecologia* 36:333-344

- Elnor RW (1980) The influence of temperature, sex and chela size in the foraging strategy of the shore crab, *Carcinus maenas* (L.). *Marine Behaviour and Physiology* 7:15-24
- Elnor RW (1981) Diet of green crab *Carcinus maenas* (L.) from Port Herbert, southwestern Nova Scotia. *Journal of Shellfish Research* 1:89-94
- Elnor RW, Hughes RN (1978) Energy maximization in the diet of the shore crab, *Carcinus maenas*. *Journal of Animal Ecology* 47:103-116
- Enderlein P, S. Moorthi, Röhrscheidt H, Wahl M (2003) Optimal foraging versus shared doom effects: interactive influence of mussel size and epibiosis in predator preference. *J Exp Mar Biol Ecol* 292:231-242
- Etter RJ (1996) The effect of wave action, prey type, and foraging time on growth of the predatory snail *Nucella lapillus* (L.). *Journal of Experimental Marine Biology and Ecology* 196:341-356
- Evans F (1951) An analysis of the behaviour of *Lepidochitona cinereus* in response to certain physical features of the environment. *Journal of Animal Ecology* 20:1-10
- Fairweather PG (1985) Differential predation on alternative prey, and the survival of rocky intertidal organisms in New South Wales. *Journal of Experimental Marine Biology and Ecology* 89:135-156
- Fairweather PG (1988) Movements of intertidal whelks (*Morula marginalba* and *Thais orbita*) in relation to availability of prey and shelter. *Marine Biology* 100:63-68
- Faria C, Almada VC (2006) Patterns of spatial distribution and behaviour of fish on a rocky intertidal platform at high tide. *Marine Ecology Progress Series* 316:155-164

- Feare CJ (1971) Predation of limpets and dogwhelks by oystercatchers. *Bird Study* 3:121-129
- Fernandez M, Iribarne O, Armstrong D (1993) Habitat selection by young-of-the-year dungeness crab *Cancer magister* and predation risk in intertidal habitats. *Marine Ecology Progress Series* 92:171-177
- Fitz HC, Wiegert RG (1991) Tagging Juvenile Blue Crabs, *Callinectes-Sapidus*, with Microwire Tags - Retention, Survival, and Growth through Multiple Molts. *Journal of Crustacean Biology* 11:229-235
- Flores A, Paula J (2001) Intertidal distribution and species composition of brachyuran crabs at two rocky shores in Central Portugal. *Hydrobiologia* 449:171-177
- Flores AAV, Cruz J, Paula J (2002) Temporal and spatial patterns of settlement of brachyuran crab megalopae at a rocky coast in Central Portugal. *Marine Ecology Progress Series* 229:207-220
- Forward JRB, Thaler AD, Singer R (2007) Entrainment of the activity rhythm of the mole crab *Emerita talpoida*. *Journal of Experimental Marine Biology and Ecology* 341:10-15
- Frank PW (1982) Effects of winter feeding on limpets by black oystercatchers, *Haematopus bachmani*. *Ecology* 63:1352-1362
- Freire J (1996) Feeding ecology of *Liocarcinus depurator* (Decapoda:Portunidae) in the Ría de Arousa (Galicia, north-west Spain): effects of habitat, season and life history. *Marine Ecology* 126:297-311
- Freire J, González-Gurriarán E (1995) Feeding ecology of the velvet swimming crab *Necora puber* in mussel raft areas of the Ría de Arousa (Galicia, NW Spain). *Marine Ecology Progress Series* 119:139-154

- Freire J, González-Gurriarán E (1998) New approaches to the behavioural ecology of decapod crustaceans using telemetry and electronic tags. *Hydrobiologia* 371/372:123-132
- Freire J, Sampedro MP, González-Gurriarán E (1996) Influence of morphometry and biomechanics on diet selection in three portunid crabs. *Marine Ecology Progress Series* 137:111-121
- Frisch AJ, Hobbs J-PA (2006) Long-term retention of internal elastomer tags in a wild population of painted crayfish (*Panulirus versicolor* [Latreille]) on the Great Barrier Reef. *Journal of Experimental Marine Biology and Ecology* 339:104-110
- Gaines SD, Bertness MD (1992) Dispersal of juveniles and variable recruitment in sessile marine species. *Nature* 360:579-580
- Garamszegi LZ, Torok J, Michl G, Moller AP (2004) Female survival, lifetime reproductive success and mating status in a passerine bird. *Oecologia* 138:48-56
- Gawlik DE (2002) The effects of prey availability on the numerical response of wading birds. *Ecol Monogr* 72:329-346
- Giberto DA, Bremec CS, Acha EM, Mianzan H (2004) Large-scale spatial patterns of benthic assemblages in the SW Atlantic: the Rio de la Plata estuary and adjacent shelf waters. *Estuarine Coastal and Shelf Science* 61:1-13
- Gibson RN (2003) Go with the flow: tidal migration in marine animals. *Hydrobiologia* 503:153-161
- Godin DM, W.H. Carr, G. Hagino F. Segura, J. N. Sweney & L. Balkenship (1996) Evaluation of a fluorescent elastomer internal tag in juvenile and adult shrimp *Penaeus vannamei*. *Aquaculture* 139:243-248

- Grenon J, Walker G (1981) The tenacity of the limpet, *Patella vulgata* L.: an experimental approach. *Journal of Experimental Marine Biology and Ecology* 54:277-308
- Griffin JN, De la Haye KL, Hawkins SJ, Thompson RC, Jenkins SR (2008) Predator diversity and ecosystem functioning: Density modifies the effect of resource partitioning. *Ecology* 89:298-305
- Grubich J (2003) Morphological convergence of pharyngeal jaw structure in durophagous perciform fish. *Biological Journal of the Linnean Society* 80:147-165
- Gurevitch J, Morrison JA, Hedges LV (2000) The interaction between competition and predation: A meta-analysis of field experiments. *American Naturalist* 155:435-453
- Hagen NT (2008) Enlarged lantern size in similar-sized, sympatric, sibling species of Strongylocentrotid sea urchins: from phenotypic accommodation to functional adaptation for durophagy. *Marine Biology* 153:907-924
- Hall DJ, E.E. Werner, J. F. Gilliam, G.G. Mittelbach, D. Howard, C. G. Doner, J. Dickerman & A.J. Stewart (1979) Diel foraging behaviour and prey selection in the golden shiner (*Notemigonus crysoleucas*). *Journal of Fisheries Research Board Canada* 36:1029-1039
- Hall S, Robertson M, Basford D, Fryer R (1993) Pit-digging by the crab *Cancer pagurus*: a test for long-term, large-scale effects on infaunal community structure. *Journal of Animal Ecology* 62:59-66
- Hartnoll RG (1982) Growth. In: Abele LG (ed) *Embriology, Morphology and Genetics - The Biology of Crustacea*, Vol 2. Academic Press, p 111-196

- Hartnoll RG (2001) Growth in Crustacea - twenty years on. *Hydrobiologia* 449:111-122
- Hartwick B (1981) Size gradients and shell polymorphism in limpets with consideration of the role of predation. *Veliger* 23:254-264
- Hawkins S, Hartnoll R (1983) Grazing of intertidal algae by marine invertebrates. *Oceanogr Mar Biol Annu Rev* 21:195-282
- Hawkins SJ (1981) The influence of *Patella* grazing on the fucoid: barnacle mosaic on moderately exposed rocky shores. *Kieler Meeresforschungen* 5
- Hawkins SJ, Corte-Real H, Pannacciulli FG, Weber LC, Bishop JDD (2000) Thoughts on the ecology and evolution of the intertidal biota of the Azores and other Atlantic islands. *Hydrobiologia* 440:3-17
- Hawkins SJ, Hartnoll RG (1982) Settlement patterns of *Semibalanus balanoides* (L.) in the Isle of Man. *Journal of Experimental Marine Biology and Ecology* 62:271-283
- Hawkins SJ, Hartnoll RG (1985) Factors Determining the Upper Limits of Intertidal Canopy-Forming Algae. *Marine Ecology-Progress Series* 20:265-271
- Hawkins SJ, Hartnoll RG, Kain JM, Norton TA (1992) Plant-Animal interactions in the marine benthos. In: *Plant-animal interactions on hard substrata in the north-east Atlantic*, Vol 46. Clarendon Press, Oxford, p 1-32
- Hawkins SJ, Jones HD (1992) *Rocky shores. Marine field course guide*, Vol. Immel Publishing, London
- Hazlett BA (1995) Behavioural plasticity in crustacea: why not more? *Journal of Experimental Marine Biology and Ecology* 193:57-66
- Heck KL, Wetstone GS (1977) Habitat complexity and invertebrate species richness in tropical seagrass meadows. *Journal of Biogeography* 4:135-142

- Hicks GR (1980) Structure of phytoplankton harpacticoid copepod assemblages and the influence of habitat complexity and turbidity. *Journal of Experimental Marine Biology and Ecology* 44:157-192
- Hill BJ (1976) Natural food, foregut clearance rate and activity of the crab *Scylla serrata*. *Marine Biology* 34:109-116
- Hines AH, Haddon AM, Wiechert LA (1990) Guild structure and foraging structure and foraging impact of blue crabs and epibenthic fish in a subestuary of Chesapeake Bay. *Marine Ecology Progress Series* 67:105-126
- Hobday A (1995) Body-size variation exhibited by an intertidal limpet: influence of wave exposure, tidal height and migratory behaviour. *Journal of Experimental Marine Biology and Ecology* 189:29-45
- Hockey PAR, Branch GM (1983) Do oystercatchers influence limpet shell shape? *Veliger* 26:139-141
- Hollingsworth A, Connolly RM (2006) Feeding by fish visiting inundated subtropical saltmarsh. *Journal of Experimental Marine Biology and Ecology* 336:88-98
- Holsman KK, McDonald PS, Armstrong DA (2006) Intertidal migration and habitat use by subadult Dungeness crab *Cancer magister* in a NE Pacific estuary. *Marine Ecology-Progress Series* 308:183-195
- Hsueh P-W, McClintock JB, Hopkins TS (1992) Comparative study of the diets of the blue crabs *Callinectes similis* and *C. sapidus* from a mud-bottom habitat in mobile prey, Alabama. *Journal of Crustacean Biology* 12:615-619
- Hughes RN (1980a) Optimal foraging theory in the marine context. *Oceanography and Marine Biology An Annual Review* 18:423-481

- Hughes RN (1980b) Predation and community structure. In: Price JH, Irvine DEG, Farnham WF (eds) *The shore environment, Vol 2: Ecosystems*. Academic Press, London, p 699-728
- Hughes RN (2000) Crab claws as tools and weapons. In: Domenici P, Blake RW (eds) *Biomechanics in animal behaviour*. BIOS Scientific, Oxford, p 195-205
- Hughes RN, Burrows MT (1994) An interdisciplinary approach to the study of foraging behaviour in the predatory gastropod, *Nucella lapillus* (L.). *Ethology Ecology & Evolution* 6:75-85
- Hughes RN, Burrows MT, Rogers SEB (1992) Ontogenic changes in foraging behaviour of the dogwhelk *Nucella lapillus* (L.). *Journal of Experimental Marine Biology and Ecology* 155:199-212
- Hughes RN, Drewett D (1985) A comparison of the foraging behaviour of dogwhelks, *Nucella lapillus* (L.), feeding on barnacles or mussels on the shore. *Journal of Molluscan Studies* 51:73-77
- Hughes RN, Dunkin SB (1984a) Effect of dietary history on selection of prey, and foraging behaviour among patches of prey, by the dogwhelk, *Nucella lapillus* (L.). *J Exp Mar Biol Ecol* 79:159-172
- Hughes RN, Dunkin SDB (1984b) Behavioural components of prey selection by dogwhelks, *Nucella lapillus* (L.), feeding on mussels, *Mytilus edulis* L., in the laboratory. *Journal of Experimental Marine Biology and Ecology* 77:45-68
- Hughes RN, Elner RW (1979) Tactics of a predator, *Carcinus maenas*, and morphological responses of the prey *Nucella lapillus*. *Journal of Animal Ecology* 48:6-78

- Hughes RN, Elner RW (1989) Foraging behaviour of a tropical crab: *Calappa ocellata* Holthuis feeding upon the mussel *Brachidontes domingensis* (Lamarck). *Journal of Experimental Marine Biology and Ecology* 133:93-101
- Hughes RN, Seed R (1981) Size selection of mussels by the blue crab *Callinectes sapidus*: energy maximizer or time minimizer? *Marine Ecology Progress Series* 6:83-89
- Hughes RN, Seed R (1995) Behavioural mechanisms of prey selection in crabs. *Journal of Experimental Marine Biology and Ecology* 193:225-238
- Hunter E, Naylor E (1993) Intertidal migration by the shore crab *Carcinus maenas*. *Marine Ecology Progress Series* 101:131-138
- Hunter MD, Price PW (1992) Playing chutes and ladders - Heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73:724-732
- Hynes HBN (1979) *The Ecology of Running Waters*, Vol. Liverpool University Press, Liverpool
- Ingle RW (1983) Shallow-water crabs. In: *Synopses of the British Fauna*, Vol 27. Cambridge University Press, New York, USA, p 222
- Iwasaki K (1993) Analyses of limpet defense and predator offense in the field. *Mar Biol* 116:277-289
- Jackson AC, Underwood AJ (2007) Application of new techniques for the accurate analysis of choice of prey. *Journal of Experimental Marine Biology and Ecology* 341:1-9
- Jenkins SR (1999) Direct and indirect effects of a macroalgal canopy and limpet grazing in structuring a sheltered inter-tidal community. 188:81-92

- Jenkins SR (2005) Larval habitat selection, not larval supply, determines settlement patterns and adult distribution in two chthamalid barnacles. *Marine Ecology Progress Series* 74:893-904
- Jenkins SR, Coleman RA, Della Santina P, Hawkins SJ, Burrows MT, Hartnoll RG (2005) Regional scale differences in the determinism of grazing effects in the rocky intertidal. *Marine Ecology Progress Series* 287:77-86
- Jenkins SR, Hartnoll RG (2001) Food supply, grazing activity and growth rate in the limpet *Patella vulgata* L.: a comparison between exposed and sheltered shores. *Journal of Experimental Marine Biology and Ecology* 258:123-139
- Jenkins SR, Hawkins SJ, Norton TA (1999) Direct and indirect effects of a macroalgal canopy and limpet grazing in structuring a sheltered inter-tidal community. *Marine Ecology Progress Series* 188:81-92
- Jennings S, Kaiser MJ, Reynolds JD (2001) *Marine Fisheries Ecology*, Vol. Blackwell Science, Oxford
- Jernakoff P (1983) Factors affecting the recruitment of algae in a mishore region dominated by barnacles. *Journal of Experimental Marine Biology and Ecology* 67:17-31
- Jerry DR, Stewart T, Purvis IW, Piper LR (2001) Evaluation of visual implant elastomer and alphanumeric internal tags as a method to identify juveniles of the freshwater crayfish, *Cherax destructor*. *Aquaculture* 193:149-154
- Johnson MP, Hughes RN, Burrows MT, Hawkins SJ (1998) Beyond the predation halo: small scale gradients in barnacle populations affected by the relative refuge value of crevices. *Journal of Experimental Marine Biology and Ecology* 231:163-170

- Jones PL, Shulman MJ (2008) Subtidal-intertidal trophic links: American lobsters [*Homarus americanus* (Milne-Edwards)] forage in the intertidal zone on nocturnal high tides. *Journal of Experimental Marine Biology and Ecology* 361:98-103
- Jones RS (1968) A suggested method for quantifying gut contents in herbivorous fish. *Micronesica* 4:369-371.
- Jonsson PR, Granhag L, Moschella PS, Aberg P, Hawkins SJ, Thompson RC (2006) Interactions between wave action and grazing control the distribution of intertidal macroalgae. *Ecology* 87:1169-1178
- Juanes F (1992) Why do decapod crustaceans prefer small-sized molluscan prey. *Marine Ecology Progress Series* 87:239-249
- Kaiser MJ, Hughes RN, Gibson RN (1993) Factors affecting diet selection in the shore crab, *Carcinus maenas* (L.). *Animal Behaviour* 45:83-92
- Kaiser MJ, Hughes RN, Reid DG (1990) Chelal Morphometry, Prey-Size Selection and Aggressive Competition in Green and Red Forms of *Carcinus maenas* (L.). *Journal of Experimental Marine Biology and Ecology* 140:121-134
- Kennelly SJ (1991) Caging experiments to examine the effects of fishes on understory species in a sublittoral kelp community. *Journal of Experimental Marine Biology and Ecology* 147:207-230
- Kimmerer WJ (2002) Effects of freshwater flow on abundance of estuarine organisms: physical effects or trophic linkages? *Marine Ecology Progress Series* 243:39-55
- Kitching JA, Muntz L, Ebling FJ (1966) The ecology of Lough Ine. XV. The ecological significance of shell and body forms in *Nucella*. *Journal of Animal Ecology* 35:113-126

- Kneib RT (1987) Predation risk and use of intertidal habitats by young fishes and shrimp. *Ecology* 68:379-386
- Kneib RT (1995) Behaviour separates potential and realized effects of decapod crustaceans in salt marsh communities. *Journal of Experimental Marine Biology and Ecology* 193:239-256
- Kollmann J, Buschor M (2003) Edges effects on seed predation by rodents in deciduous forests of northern Switzerland. *Plant Ecology* 164:249-261
- Lau WY, Martinez MM (2003) Getting a grip on the intertidal: flow microhabitat and substratum type determine the dislodgement of the crab *Pachygrapsus crassipes* (Randall) on rocky shores and in estuaries. *Journal of Experimental Marine Biology and Ecology* 295:1-21
- Lawton P, Hughes RN (1985) Foraging behaviour of the crab *Cancer pagurus* feeding on the gastropods *Nucella lapillus* and *Littorina littorea*: comparisons with optimal foraging theory. *Marine Ecology Progress Series* 27:143-154
- Lawton P, Zimmerfaust RK (1992) Context-Sensitivity in Crab Foraging Studies. *American Zoologist* 32:396-404
- Lebreton JD, Burnham KP, Clobert J, Anderson DR (1992) Modeling Survival and Testing Biological Hypotheses Using Marked Animals - a Unified Approach with Case-Studies. *Ecological Monographs* 62:67-118
- Lee JT, J. Widdows, M. B. Jones & R.A. Coleman (2004) Settlement of megalopae and early juveniles of the velvet swimming crab *Necora puber* (Decapoda: Portunidae) in flow conditions. *Marine Ecology Progress Series* 272:191-202
- Lee JT, Ross C, Malcolm J (2006) Population dynamics and growth of juveniles of the velvet swimming crab *Necora puber* (Decapoda: Portunidae). *Marine Biology* 148:609-619

- Lee S, Seed R (1992) Ecological implications of cheliped size in crabs: some data from *Carcinus maenas* and *Liocarcinus holsatus*. *Marine Ecology Progress Series* 84:151-160
- Lee SY (1995) Cheliped size and structure: the evolution of a multi-functional decapod organ. *Journal of Experimental Marine Biology and Ecology* 193:161-176
- León RI, Stotz WB (2004) Diet and prey selection dynamics of *Cancer polyodon* in three different habitat types in Tongoy Bay, Chile. *Journal of Marine Biological Association of the United Kingdom* 84:751-756
- Leonard GH (2000) Latitudinal variation in species interactions: a test in the New England rocky intertidal zone. *Ecology* 81:1015–1030
- Lewis JR (1964) *The ecology of rocky shores*, Vol. English University Press, London
- Lewis JR (1968) Water movements and their role in rocky shore ecology. *Sarsia* 34:13-36
- Linnane A, Mercer JP (1998) A comparison of methods for tagging juvenile lobsters (*Homarus gammarus* L.) reared for stock enhancement. *Aquaculture* 163:195-202
- Lohrer AM, Fukui Y, Wada K, Whitlatch RB (2000) Structural complexity and vertical zonation of intertidal crabs, with focus on habitat requirements of the invasive Asian shore crab, *Hemigrapsus sanguineus* (de Haan). *Journal of Experimental Marine Biology and Ecology* 244:203-217
- Lowell RB (1986) Crab predation on limpets: predator behaviour and defensive features of the shell morphology of the prey. *Biol Bull* 171:577-596

- Lubchenco J (1978) Community development and persistence in a low rocky intertidal zone. *Ecological Monographs* 59:67-94
- Lubchenco J (1983) *Littorina* and *Fucus* - Effects of herbivores, substratum heterogeneity, and plant escapes during succession. *Ecology* 64:176-184
- Markowska M, Kidawa A (2007) Encounters between Antarctic limpets, *Nacella concinna*, and predatory sea stars, *Lysasterias* sp., in laboratory and field experiments. *Mar Biol* 151:1959-1966
- Mascaró M, Seed R (2001) Foraging behaviour of juvenile *Carcinus maenas* (L.) and *Cancer pagurus* L. *Marine Biology* 139:1135-1145
- McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: A comment on distance-based redundancy analysis. *Ecology* 82:290-297
- McDonald PS, Jensen GC, Armstrong DA (2001) The competitive and predatory impacts of the nonindigenous crab *Carcinus maenas* (L.) on early benthic phase Dungeness crab *Cancer magister* Dana. *Journal of Experimental Marine Biology and Ecology* 258:39-54
- McGaw IJ, Naylor E (1992) Distribution and Rhythmic Locomotor Patterns of Estuarine and Open-Shore Populations of *Carcinus maenas*. *Journal of the Marine Biological Association of the United Kingdom* 72:599-609
- Menconi M, Benedetti-Cecchi L, Cinelli F (1999) Spatial and temporal variability in the distribution of algae and invertebrates on rocky shores in the northwest Mediterranean. *Journal of Experimental Marine Biology and Ecology* 233:1-23
- Menge B, Sutherland J (1976) Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *The American Naturalist* 110:351-369

- Menge BA (1976) Organization of New England rocky intertidal community - role of predation, competition and environmental heterogeneity *Ecological Monographs* 46:355-393
- Menge BA (1978a) Predation intensity in a rocky intertidal community-Effect of an algal canopy, wave action and desiccation on predator feeding rates. *Oecologia* 34:17-35
- Menge BA (1978b) Predation intensity in a rocky intertidal community-Relation between predator foraging activity and environmental harshness. *Oecologia* 34:1-16
- Menge BA (1983) Components of predation intensity in the low zone of the New England rocky intertidal region. *Oecologia* 58:141-155
- Menge BA (1991) Relative importance of recruitment and other causes of variation in rocky intertidal community structure. *Journal of Experimental Marine Biology and Ecology* 146:69-100
- Menge BA (1992) Community regulation: under what conditions are bottom-up factors important on rocky shores? *Ecology* 73:755-765
- Menge BA (2000) Top-down and bottom-up community regulation in marine rocky intertidal habitats. *Journal of Experimental Marine Biology and Ecology* 250:257-289
- Menge BA, Chan F, Lubchenco J (2008) Response of a rocky intertidal ecosystem engineer and community dominant to climate change. *Ecology Letters* 11:151-162
- Menge BA, Lubchenco J, Ashkenas LR (1985) Diversity, heterogeneity and consumer pressure in a tropical rocky intertidal community. *Oecologia* 65:394-405

- Menge BA, Lubchenco J, Ashkenas LRaR, F. (1986) Experimental separation of effects of consumers on sessile prey in the low zone of a rocky shore in the Bay of Panama: direct and indirect consequences of food web complexity. *Journal of Experimental Marine Biology and Ecology* 100:225-269
- Menge BA, Sutherland JP (1987) Community regulation - variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *American Naturalist* 130:730-757
- Micheli F (1995) Behavioural plasticity in prey-size selectivity of the blue crab *Callinectes sapidus* feeding on bivalve prey. *Journal of Animal Ecology* 64:63-74
- Miller RJ (1978) Entry of *Cancer productus* to baited traps. *Journal Du Conseil* 38:220-225
- Miller RJ (1990) Effectiveness of crabs and lobster traps. *Canadian Journal of Fisheries and Aquatic Sciences* 47:1228-1251
- Miller TJ, Smith SG (2003) Modelling crab growth and population dynamics: insights from the blue crab conference. *Bulletin of Marine Science* 72:537-541
- Milton P (1983) Biology of littoral blennid fishes on the coast of south-west England. *J Mar Biol Assoc UK* 63:223-237
- Moller H, Beress L (1975) Effect on fishes of 2 toxic polypeptides isolated from *Anemonia sulcata*. *Marine Biology* 32:189-192
- Moore P, Hawkins SJ, Thompson RC (2007) Role of biological habitat amelioration in altering the relative responses of congeneric species to climate change. *Marine Ecology Progress Series* 334:11-19

- Moreno CA, Jaramillo E (1983) The role of grazers in the zonation of intertidal macroalgae of the Chilean coast. *Oikos* 41:73-76
- Morin PJ (1999) *Community Ecology*, Vol. Cambridge University Press, Cambridge
- Morissette S, Himmelman JH (2000) Decision of the asteroid *Leptasterias polaris* to abandon its prey when confronted with its predator, the asteroid *Asterias vulgaris*. *Journal of Experimental Marine Biology and Ecology* 252:151-157
- Mosknes P-O (2002) The relative importance of habitat-specific settlement, predation and juvenile dispersal for distribution and abundance of young juvenile shore crabs *Carcinus maenas* L. *Journal of Experimental Marine Biology and Ecology* 271:41-73
- Mosknes PO (2004) Interference competition for space in nursery habitats: density-dependent effects on growth and dispersal in juvenile shore crabs *Carcinus maenas*. *Marine Ecology Progress Series* 281:181-191
- Muntz L, F.J. Ebling & J.A. Kitching (1965) The ecology of Lough Ine. XIV. Predatory activity of large crabs. *Journal of Animal Ecology* 34:315-329
- Nagarajan R, Lea SEG, Goss-Custard JD (2006) Seasonal variations in mussel, *Mytilus edulis* L. shell thickness and strength and their ecological implications. *Journal of Experimental Marine Biology and Ecology* 339:241-250
- Navarrete S, Menge B (1996) Keystone predation and interaction strength: interactive effects of predators on their main prey. *Ecological Monographs* 66:409-429
- Navarrete SA, Castilla JC (1990) Resource partitioning between intertidal predatory crabs: interference and refuge utilization. *Journal of Experimental Marine Biology and Ecology* 143:101-129

- Naylor E (1958) Tidal and diurnal rhythms of locomotory activity in *Carcinus maenas* (L.). *Journal of Experimental Biology* 35:602-610
- Naylor E (1962) Seasonal changes in a population of *Carcinus maenas* (L.) in the littoral zone. *Journal of Animal Ecology* 31:601-609
- Newell RC, Ahsanull.M, Pye VI (1972) Aerial and aquatic respiration in shore crab *Carcinus maenas* (L.). *Comparative Biochemistry and Physiology* 43:239-&
- Nicastro KR, Zardi GI, McQuaid CD (2007) Behavioural response of invasive *Mytilus galloprovincialis* and indigenous *Perna perna* mussels exposed to risk of predation. *Marine Ecology Progress Series* 336:169-175
- Nickell LA, Sayer MDJ (1998) Occurrence and activity of mobile macrofauna on a sublittoral reef: diel and seasonal variation. *Journal of Marine Biological Association of the United Kingdom* 78:1061-1082
- Norman CP, Jones MB (1990) Utilisation of brown algae in the diet of the velvet swimming crab *Liocarcinus puber* (Brachyura: Portunidae). *Trophic Relationships in the Marine Environment Proc.24th European Marine Symposium*:491-502
- Norman CP, Jones MB (1992) Influence of depth, season and moult stage on the diet of the velvet swimming crab *Necora puber* (Brachyura, Portunidae). *Estuarine Coastal and Shelf Science* 34:71-83
- Norman CP, Jones MB (1993) Reproductive ecology of the velvet swimming crab, *Necora puber* (Brachyura:Portunidae), at Plymouth. *Journal of Marine Biological Association of the United Kingdom* 73:379-389
- Nybakken JW (1997) *Marine Biology - an ecological approach*. In. Addison-Wesley Educational Publishers Inc., USA, p 481

- O'Connor NE, Grabowski JH, Ladwig LM, Bruno JF (2008) Simulated predator extinctions: Predator identity affects survival and recruitment of oysters. *Ecology* 89:428-438
- Ojeda FP, Dearborn JH (1991) Feeding ecology of benthic mobile predators: experimental analyses of their influence in rocky subtidal communities of the Gulf of Maine. *Journal of Experimental Marine Biology and Ecology* 149:13-44
- Oliver LR, Seed R, Reynolds B (2008) The effect of high flow events on mussels (*Mytilus edulis*) in the Conwy estuary, North Wales, UK. *Hydrobiologia* 606:117-127
- Orton JH (1928) Observations on *Patella vulgata*. Part I. Sex-phenomena, breeding and shell growth. *Journal of Marine Biological Association of the United Kingdom* 15:851-862
- Paetzold A, Schubert CJ, Tockner K (2005) Aquatic terrestrial linkages along a braided-river: Riparian arthropods feeding on aquatic insects. *Ecosystems* 8:748-759
- Paine RT (1966) Food web complexity and species diversity. *American Naturalist* 100:65-75
- Paine RT (1974) Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* 15:93-120
- Paine RT (1976) Size-limited predation: an observational and experimental approach with *Mytilus-Pisaster* interaction. *Ecology* 57:858-873

- Pallas A, Garcia-Calvo B, Corgos A, Bernardez C, Freire J (2006) Distribution and habitat use patterns of benthic decapod crustaceans in shallow waters: a comparative approach. *Marine Ecology Progress Series* 324:173-184
- Palmer AR (1985) Adaptive value of shell variation in *Thais lamellosa*: effect of thick shells on vulnerability to and preference by crabs. *The Veliger* 27:349-356
- Palmer AR (1990) Predator size, prey size, and the scaling of vulnerability: hatchling gastropods vs. barnacles. *Ecology* 71:759-775
- Pardo LM, Johnson LE (2004) Activity and shelter use of an intertidal snail: effects of sex, reproductive condition and tidal cycle. *Journal of Experimental Marine Biology and Ecology* 301:175-191
- Pardo LM, Palma AT, Prieto C, Sepulveda P, Valdivia I, Ojeda FP (2007) Processes regulating early post-settlement habitat use in a subtidal assemblage of brachyuran decapods. *Journal of Experimental Marine Biology and Ecology* 344:10-22
- Paul RKG (1981) Natural diet, feeding and predatory activity of the crabs *Callinectes arcuatus* and *Callinectes toxotes* (Decapoda, Brachyura, Portunidae). *Marine Ecology Progress Series* 6:91-99
- Paula J, Dray T, Queiroga H (2001) Interaction of offshore and inshore processes controlling settlement of brachyuran megalopae in Saco mangrove creek, Inhaca Island (South Mozambique). *Marine Ecology Progress Series* 215:251-260
- Pellegrino CR (1984) The role of desiccation pressures and surface area/volume relationships on seasonal zonation and size distribution of four intertidal

- decapod crustacea from New Zeland: implications for adaptation to land.
Crustaceana 47:251-268
- Petraitis PS (1995) The role of growth in maintaining spatial dominance by mussels (*Mytilus edulis*). *Ecology* 76:1337-1346
- Phillips DW (1976) The effect of a species-specific avoidance response to predatory starfish on the intertidal distribution of two gastropods. *Oecologia* 23:83-94
- Pigliucci M (2005) Evolution of phenotypic plasticity: where are we going now? *Trends Ecol Evol* 20:481-486
- Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla JC, Lubchenco J, Paine RT (1996) Challenges in the quest for keystones. *Bioscience* 46:609-620
- Price PW, Bouton CE, Gross P, Mcpherson BA, Thompson JN, Weis AE (1980) Interactions among 3 levels - influence of plants on interactions between insect herbivores and natural enemies. *Annu Rev Ecol Syst* 11:41-65
- Pyke GH, Pulliam HR, Charnov EL (1977) Optimal foraging - Selective review of theory and tests. *Quarterly Review of Biology* 52:137-154
- Queiroga H, Almeida MJ, Alpuim T, Flores AAV, Francisco S, Gonzalez-Gordillo I, Miranda AI, Silva I, Paula J (2006) Tide and wind control of megalopal supply to estuarine crab populations on the Portuguese west coast. *Marine Ecology Progress Series* 307:21-36
- Raffaelli D, Hawkins S (1996) *Intertidal Ecology*, Vol. Chapman & Hall, London
- Reid DG, Naylor E (1989) Are There Separate Circatidal and Circadian Clocks in the Shore Crab *Carcinus maenas*? *Marine Ecology Progress Series* 52:1-6

- Reinsel KA (2004) Impact of fiddler crab foraging and tidal inundation on an intertidal sandflat: season-dependent effects in one tidal cycle. *Journal of Experimental Marine Biology and Ecology* 313:1-17
- Ricklefs RE, Miles DB (1994) Ecological and evolutionary inferences from morphology. In: Wainwright PC, Reilly SM (eds) *Ecological Morphology - Integrative organismal biology*. The University Chicago Press, Chicago and London, p 13-41
- Rilov G, Avital G, Yehuda B (2005) Effect of disturbance on foraging: whelk activity on wave-exposed rocky shores with minimal tidal range. *Marine Biology* 147:421-428
- Rilov G, Schiel DR (2006a) Seascape-dependent subtidal-intertidal trophic linkages. *Ecology* 87:731-744
- Rilov G, Schiel DR (2006b) Trophic linkages across seascapes: subtidal predators limit effective mussel recruitment in rocky intertidal communities. *Marine Ecology Progress Series* 327:83-93
- Robles C (1987) Predator foraging characteristics and prey population structure on a sheltered shore. *Ecology* 68:1502-1514
- Robles C, Desharnais R (2002) History and current development of a paradigm of predation in rocky intertidal communities. *Ecology* 83:1521-1536
- Robles C, Sweetnam D, Eminike J (1990) Lobster predation on mussels - shore level differences in prey vulnerability and predator preference. *Ecology* 71:1564-1577
- Robles C, Sweetnam DA, Dittman D (1989) Diel variation of intertidal foraging by *Cancer productus* L. in British Columbia. *Journal of Natural History* 23:1041-1049

- Robles CD, Alvarado MA, Deshamais RA (2001) The shifting balance of littoral predator-prey interaction in regimes of hydrodynamic stress. *Oecologia* 128:142-152
- Rochette R, Dili LM (2000) Mortality, behaviour and the effects of predators on the intertidal distribution of littorinid gastropods. *Journal of Experimental Marine Biology and Ecology* 253:165-191
- Rohlf FJ, Marcus LF (1993) A revolution in morphometrics. *Trends in Ecology & Evolution* 8:129-132
- Rohlf FJ, Slice D (1990) Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Zoology* 39:40-59
- Rosenberg MS (2002) Fiddler crab claw shape variation: a geometric morphometric analysis across the genus *Uca* (Crustacea : Brachyura : Ocypodidae). *Biological Journal of the Linnean Society* 75:147-162
- Rosser ZC, Pearson RG (1995) Responses of rock fauna to physical disturbance in 2 Australian tropical rain-forest streams. *Journal of the North American Benthological Society* 14:183-196
- Roughgarden J, Baxter YIaC (1985) Demographic theory for an open marine population with space-limited recruitment. *Ecology* 66:54-67
- Rovero F, Hughes RN, Chelazzi G (2000) When time is of the essence: choosing a currency for prey-handling costs. *Journal of Animal Ecology* 69:683-689
- Ruiz GM, Hines AH, Posey MH (1993) Shallow water as a refuge habitat for fish and crustaceans in nonvegetated estuaries - an example from Chesapeake Bay. *Marine Ecology Progress Series* 99:1-16
- Russell G (1991) Vertical distribution. In: *Intertidal and littoral ecosystems*, p 43-65

- Schoener TW (1983) Field experiments on interspecific competition. *Am Nat* 122:240-285
- Schoener TW, Spiller DA, Losos JB (2001) Predators increase the risk of catastrophic extinction of prey populations. *Nature* 412:183-186
- Schowalter TD, Hargrove WW, Crossley DA (1986) Herbivory in forested ecosystems. *Annu Rev Entomol* 31:177-196
- Seber GAF (1982) Estimation of animal abundance and related parameters, Vol. Charles Griffin & Company, London
- Seed R (1996) Patterns of biodiversity in the macro-invertebrate fauna associated with mussel patches on rocky shores. *Journal of the Marine Biological Association of the United Kingdom* 76:203-210
- Seed R, Hughes RN (1995) Criteria for prey size-selection in molluscivorous crabs with contrasting claw morphologies. *Journal of Experimental Marine Biology and Ecology* 193:177-195
- Sih A (1987) Predators and prey lifestyles: an evolutionary and ecological overview. . In: Kerfoot WC, Sih A (eds) *Predation direct and indirect impacts on aquatic communities*. University Press of New England, London, p 203-224
- Sih A, Christensen B (2001) Optimal diet theory: when does it work, and when and why does it fail? *Animal Behaviour* 61:379-390
- Sih A, Crowley P, McPeck M, Petranka J, Strohmeier K (1985) Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics* 16:269-331

- Silva ACF, Boaventura DM, Flores A, Ré P, Hawkins SJ (2004) Rare predation by the intertidal crab *Pachygrapsus marmoratus* on the limpet *Patella depressa*. *J Mar Biol Assoc UK* 84:367-370
- Silva IC, Dinis AM, Francisco SM, Flores AAV, Paula J (2006) Longitudinal distribution and lateral pattern of megalopal settlement and juvenile recruitment of *Carcinus maenas* (L.) (Brachyura, Portunidae) in the Mira River Estuary, Portugal. *Estuarine Coastal and Shelf Science* 69:179-188
- Singer (2000) Reducing ambiguity in describing plant-insect interactions: "preference", "acceptability" and "electivity". *Ecology Letters* 3:159-162
- Skov MW, Hartnoll RG, Ruwa RK, Shunula JP, Vannini M, Cannicci S (2005) Marching to a different drummer: Crabs synchronize reproduction to a 14-month lunar-tidal cycle. *Ecology* 86:1164-1171
- Smith LD (2004) Biogeographic differences in claw size and performance in an introduced crab predator *Carcinus maenas*. *Marine Ecology Progress Series* 276:209-222
- Smith LD, Palmer AR (1994) Effects of manipulated diet on size and performance of brachyuran crab claws. *Science* 264:710-712
- Sokal RR, Rohlf FJ (1995) *Biometry: the principles and practice of statistics in biological research*, Vol. W. H. Freeman and Company, New York
- Sousa WP (1979) Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecological Monographs* 49:227-254
- Southward AJ (1964) Limpet grazing and the control of vegetation on rocky shores. In: Crisp DJ (ed) *Grazing in Terrestrial and Marine Environments*. Blackwell Scientific, Oxford, p 265-273

- Southward AJ (1991) 40 years of changes in species composition and population-density of barnacles on a rocky shore near Plymouth. *Journal of the Marine Biological Association of the United Kingdom* 71:495-513
- Spilseth SA, Morgan SG (2005) Evaluation of internal elastomer tags for small, mature crabs. *Crustaceana* 78:1383-1388
- Sponaugle S, Lawton P (1990) Portunid Crab Predation on Juvenile Hard Clams - Effects of Substrate Type and Prey Density. *Marine Ecology Progress Series* 67:43-53
- Spooner EH, Coleman RA, Attrill MJ (2007) Sex differences in body morphology and multitrophic interactions involving the foraging behaviour of the crab *Carcinus maenas*. *Marine Ecology-an Evolutionary Perspective* 28:394-403
- Stephenson TA, Stephenson A (1949) The universal features of zonation between tide-marks on rocky coasts. *Journal of Ecology* 37:289-305
- Stephenson TA, Stephenson A (1972) *Life between tidemarks on rocky shores*, Vol. W.H. Freeman & Co, San Francisco
- Stoner AW, Lewis III FG (1985) The influence of quantitative and qualitative aspects of habitat complexity in tropical seagrass meadows. *Journal of Experimental Marine Biology and Ecology* 94:19-40
- Sutherland JP (1990) Recruitment regulates demographic variation in a tropical intertidal barnacle. *Ecology* 71:955-972
- Takeda S, Murai M (2003) Morphological and behavioural adaptations to the rocky substrate by the fiddler crab *Uca panamensis* (Stimpson, 1859): preference for feeding substratum and feeding mechanism. *Journal of Experimental Marine Biology and Ecology* 287:179-191

- Thompson RC, Jenkins SR, Bussel JA (2000) A method for recording predator-prey encounters between crabs and limpets using wax replicas. *J Mar Biol Assoc UK* 80:633-638
- Thompson RC, Moschella PS, Jenkins SR, Norton TA, Hawkins SJ (2005) Differences in photosynthetic marine biofilms between sheltered and moderately exposed rocky shores. *Marine Ecology Progress Series* 296:53-63
- Thompson RC, Norton TA, Hawkins SJ (1998) The influence of epilithic microbial films on the settlement of *Semibalanus balanoides* cyprids - a comparison between laboratory and field experiments. *Hydrobiologia* 376:203-216
- Thompson RC, Norton TA, Hawkins SJ (2004) Physical stress and biological control regulate the producer-consumer balance in intertidal biofilms. *Ecology* 85:1372-1382
- Thompson RC, Roberts MF, Norton TA, Hawkins SJ (2001) Feast or famine for intertidal grazing molluscs: a mis-match between seasonal variations in grazing intensity and the abundance of microbial resources. *Hydrobiologia* 445:229-229
- Thompson RC, Wilson BJ, Tobin ML, Hill AS, Hawkins SJ (1996) Biologically generated habitat provision and diversity of rocky shore organisms at a hierarchy of spatial scales. *Journal of Experimental Marine Biology and Ecology* 202:73-84
- Thorson G (1966) Some factors influencing the recruitment and establishment of marine communities. *Netherlands Journal of Sea Research* 3:267-293
- Trussell GC (1996) Phenotypic plasticity in an intertidal snail: The role of a common crab predator. *Evolution* 50:448-454

- Trussell GC, Ewanchuk PJ, Bertness MD (2003) Trait-mediated effects in rocky intertidal food chains: Predator risk cues alter prey feeding rates. *Ecology* 84:629-640
- Trussell GC, Nicklin MO (2002) Cue sensitivity, inducible defense, and trade-offs in a marine snail. *Ecology* 83:1635-1647
- Turchin P (1991) Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. *Ecology* 72:1253-1266
- Underwood AJ (1981) Structure of a rocky intertidal community in New South Wales: patterns of vertical distribution and seasonal changes. *Journal of Experimental Marine Biology and Ecology* 51:57-85
- Underwood AJ (1984) Vertical and seasonal patterns in competition for microalgae between intertidal gastropods. *Oecologia* 64:211-222
- Underwood AJ (1985) Physical factors and biological interactions: the necessity of ecological experiments. In: Moore PG, Seed R (eds) *The ecology of rocky coasts*. Hodder and Stoughton, London, p 372-390
- Underwood AJ (1997) *Experiments in Ecology. Their logical design and interpretation using analysis of variance*, Vol. Cambridge University Press
- Underwood AJ (2000) Experimental ecology of rocky intertidal habitats: what are we learning? *Journal of Experimental Marine Biology and Ecology* 250:51-76
- Underwood AJ, Chapman MG (1998) *GMAV5 for Windows*. Institute of Marine Ecology, University of Sydney
- Underwood AJ, Chapman MG, Crowe TP (2004) Identifying and understanding ecological preferences for habitat or prey. *Journal of Experimental Marine Biology and Ecology* 300:161-187

- Underwood AJ, Clarke KR (2005) Solving some statistical problems in analyses of experiments on choices of food and on associations with habitat. *Journal of Experimental Marine Biology and Ecology* 318:227-237
- Underwood AJ, Denley EJ (1984) Paradigms, explanations, and generalizations in models for the structure of intertidal communities on rocky shores. In: Strong Jr. DR, Simberloff D, Abele LG, Thistle AB (eds) *Ecological communities: conceptual issues and the evidence*. Princeton University Press, New Jersey, p 151-180
- Underwood AJ, Fairweather PG (1992) Marine Invertebrates. In: Crawley MJ (ed) *Natural Enemies The population biology of predators, parasites and diseases*. Blackwell Scientific publications, Oxford, p 206-224
- Vadas RL, Burrows MT, Hughes RN (1994) Foraging strategies of the dogwhelk, *Nucella lapillus* (L.): interacting effects of age, diet and chemical cues to the threat of predation. *Oecologia* 100:439-450
- Vermeij GJ (1974) Regional variation in tropical high intertidal gastropod assemblages. *Journal of Marine Research* 32:343-357
- Vermeij GJ (1976) Interoceanic differences in vulnerability of shelled prey to crab predation. *Nature* 260:135-136
- Vermeij GJ (1977) Patterns in crab claw size - Geography of crushing. *Systematic Zoology* 26:138-151
- Vermeij GJ (1978) *Biogeography and adaptation: patterns of marine life* Vol. Harvard University Press, Cambridge
- Vermeij GJ (1982) Unsuccessful predation and evolution. *The American Naturalist* 120:701-720

- Vermeij GJ, Schindel DE, Zipser E (1981) Predation through geological time - Evidence from gastropod shell repair. *Science* 214:1024-1026
- Viscido SV, Stearns DE, Able KW (1997) Seasonal and Spatial Patterns of an Epibenthic Decapod Crustacean Assemblage in North-west Atlantic Continental Shelf Waters. *Estuarine, Coastal and Shelf Science* 45:377-392
- Wainwright PC (1987) Biomechanical limits to ecological performance: mollusc-crushing by the Caribbean hogfish, *Lachnolaimus maximus* (Labridae). *Journal of Zoology* 213:283-297
- Wainwright PC (1988) Morphology and ecology - functional basis of feeding constraints in caribbean labrid fishes. *Ecology* 69:635-645
- Wainwright PC (1991) Ecomorphology: Experimental functional anatomy for ecological problems. *American Naturalist* 31:680-693
- Wainwright PC, Richard BA (1995) Predicting patterns of prey use from morphology of fishes. *Environmental Biology of Fishes* 44:97-113
- Walne PR, Dean GJ (1972) Experiments on predation by the shore crab, *Carcinus maenas* L., on *Mytilus* and *Mercenaria*. *Journal du Conseil International Exploration du Mer* 34:190-199
- Warman CG, Naylor E (1995) Evidence for multiple, cue-specific circatidal clocks in the shore crab *Carcinus maenas*. *Journal of Experimental Marine Biology and Ecology* 189:93-101
- Warman CG, Reid DG, Naylor E (1993) Variation in the tidal migration behaviour and rhythmic light-responsiveness in the shore crab, *Carcinus maenas*. *Journal of Marine Biological Association of the United Kingdom* 73:355-364
- Warner GF (1977) *The Biology of Crabs*, Vol. Elek Science, London

- Watson DI, O'Riordan RM, Barnes DKA, Cross T (2005) Temporal and spatial variability in the recruitment of barnacles and the local dominance of *Elminius modestus* Darwin in SW Ireland. *Estuarine Coastal and Shelf Science* 63:119-131
- Wear RG, Haddon M (1987) Natural diet of the crab *Ovalipes catharus* (Crustacea, Portunidae) around central and northern New Zealand. *Marine Ecology Progress Series* 35:39-49
- Weber L, Hawkins S (2002) Evolution of the limpet *Patella candei* d'Orbigny (Mollusca, Patellidae) in Atlantic archipelagos: human intervention and natural processes. *Biological Journal of the Linnean Society* 77:341-353
- White GC (2007) Mark and recapture parameter estimation. Colorado State University, Fort Collins
- White GC, Burnham KP (1999) Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46 Supplement:120-138
- Williams GA, Seed R (1992) Interactions between macrofaunal epiphytes and their host algae. In: John D, Hawkins SJ, Price J (eds) *Plant-Animal Interactions in the Marine Benthos*. Clarendon Press, Oxford, p 189-212
- Williams MJ (1981) Methods for analysis of natural diet in portunid crabs (Crustacea: Decapoda: Portunidae). *Journal of Experimental Marine Biology and Ecology* 52:103-113
- Williams MJ (1982) Natural food and feeding in the commercial sand crab *Portunus pelagicus* Linnaeus, 1766 (Crustacea : Decapoda : Portunidae) in Moreton Bay, Queensland. *Journal of Experimental Marine Biology and Ecology* 59:165-176

- Wolcott BD (2007) Mechanical size limitation and life-history strategy of an intertidal seaweed. *Marine Ecology Progress Series* 338:1-10
- Wolcott TG (1973) Physiological ecology and intertidal zonation in limpets (*Acmaea*): a critical look at limiting factors. *Biological Bulletin* 145:389-422
- Wootton JT (1993) Indirect effects and habitat use in an intertidal community: interactions chains and interaction modifications. *The American Naturalist* 141:71-89
- Yamada S, Boulding E (1996) The role of highly mobile crab predators in the intertidal zonation of their gastropod prey. *Journal of Experimental Marine Biology and Ecology* 204:59-83
- Yamada SB, Boulding EG (1998) Claw morphology, prey size selection and foraging efficiency in generalist and specialist shell-breaking crabs. *Journal of Experimental Marine Biology and Ecology* 220:191-211
- Yamada SB, Navarrete SA, Needham C (1998) Predation induced changes in behaviour and growth rate in three populations of the intertidal snail, *Littorina sitkana* (Philippi). *Journal of Experimental Marine Biology and Ecology* 220:213-226

APPENDICES

Appendix 1

Summary of results of PERMANOVA permutation tests on stomach content composition of *Carcinus maenas* (a), *Necora puber* (b) and *Cancer pagurus* (c) for factors shore level, shore exposure, shore and site. Number of permutations used = 9999 (see page 52).

a)

<i>Carcinus maenas</i>							
Source of variation	df	SS	MS	Pseudo-F	P (perm)	Unique perms	P (MC)
Shore level = SI	1	13669	13669	12.281	0.0908	829	0.012
Shore exposure = Exp	1	11738	11738	3.8191	0.3332	3	0.094
Shore (Exp) = Sh (Exp)	2	8147	3073.5	6.89	0.0675	315	0.087
Site (Sh (Exp)= Si (Sh(Exp)))	4	1784.3	446.08	0.527	0.8919	9934	0.880
SI x Exp	1	5614.5	5614.5	5.044	0.1074	835	0.063
SI x Sh (Exp)	2	2226.1	1113.1	1.0823	0.425	9948	0.418
SI x Si (Sh(Exp))	4	4076	1019	1.2081	0.2881	9932	0.284
Residual	32	27037	844.9				
Total	47	72282					

b)

<i>Necora puber</i>							
Source of variation	df	SS	MS	Pseudo-F	P (perm)	Unique perms	P (MC)
Shore level = SI	1	9650.8	9650.8	6.1902	0.1427	822	0.038
Shore exposure = Exp	1	5594.9	5594.9	1.5509	0.8727	3	0.282
Shore (Exp) = Sh (Exp)	2	7215.1	3607.6	4.8541	0.0684	315	0.101
Site (Sh (Exp)= Si (Sh(Exp)))	4	2972.8	743.19	0.7094	0.7549	9931	0.735
SI x Exp	1	1215.1	1215.1	0.7794	0.5545	832	0.549
SI x Sh (Exp)	2	3118.1	1559	2.8768	0.144	9960	0.082
SI x Si (Sh(Exp))	4	2187.8	541.94	0.51738	0.8083	9911	0.897
Residual	32	33520	1047.5				
Total	47	65455					

c)

<i>Cancer pagurus</i>							
Source of variation	df	SS	MS	Pseudo-F	P (perm)	Unique perms	P (MC)
Shore level = SI	1	2039.1	2039.1	1.112	0.408	830	0.425
Shore exposure = Exp	1	3401.6	3401.6	1.731	0.337	3	0.271
Shore (Exp) = Sh (Exp)	2	3930	1965	1.121	0.360	315	0.415
Site (Sh (Exp)= Si (Sh(Exp)))	4	7007.5	1751.9	2.498	0.079	9928	0.011
SI x Exp	1	1248	1248	0.680	0.551	833	0.578
SI x Sh (Exp)	2	3867.4	1833.7	7.480	0.062	9958	0.037
SI x Si (Sh(Exp))	4	980.55	245.14	0.349	0.863	9938	0.860
Residual	32	22438	701.12				
Total	47	44710					

Appendix 2

Cormack-Jolly-Seber model: live animal recaptures that are released alive

The use of models is useful because these link, in a formal manner, the data, assumptions, unknown parameters (e.g. survival and probability of recapture) and allows rigor in making inductive inferences via likelihood and information theory.

The Cormack-Jolly-Seber model (CJS) is a model which allows estimates of survival and capture probability from a multiple recapture experiment; (see Lebreton et al. 1992). The software used in my thesis (MARK, White & Burnham 1999) includes procedures to test goodness-of-fit for models accounting for variable survival and capture rates over time.

Live recaptures are the basis of the standard Cormack-Jolly-Seber model (White 2007). Marked animals are released into the population, often by trapping them from the populations. Then, marked animals are encountered by catching them alive and re-releasing them. If marked animals are released into the population on occasion 1, then each succeeding capture occasion is one encounter occasion.

Consider the following scenario (White 2007):

Release---S(1)---->Encounter 2-----S(2)---->Encounter3

Animals survive from initial release to the second encounter occasion with probability $S(1)$, and from second encounter occasion to the third encounter occasion with probability $S(2)$. The recapture probability at encounter occasion 2 is $p(2)$, and $p(3)$ is the recapture probability at encounter occasion 3. At least 2 re-encounter occasions are required to estimate the survival rate between the first release occasion and the first re-encounter occasion, i.e., $S(1)$. The survival rate between the last two encounter occasions is not estimable because only the product of survival and recapture probability for this occasion is identifiable.

The survival rates of the CJS model are labelled as $\Phi(1)$, $\Phi(2)$, etc., because the quantity estimated is the probability of remaining available for recapture. Thus, animals that emigrate from the study area are not available for recapture, so

appear to have died in this model. Thus, $\Phi(i) = S(i)(1 - E(i))$, where $E(i)$ is the probability of emigrating from the study area.

In my thesis I used the most parameterized model calculated by MARK software, with survival (ϕ) and probability of recapture (p) variable over time:

$$\{\phi_t, p_t\}$$

the subscript t denotes time-specific survival and recapture probabilities.

This model is the most flexible and is always the first to be tested.