THE EVOLUTION OF SIZE-DEPENDENT HABITAT USE IN *CANCER* CRABS: EVIDENCE FROM PHYLOGENETICS, NATURAL SELECTION ANALYSIS, AND BEHAVIOURAL ECOLOGY

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ABSTRACT

Phylogenetic systematics can generate and test hypotheses about the evolutionary forces that shape the patterns of diversity seen in nature. I used data from adult morphology and the cytochrome oxidase I gene to reconstruct a phylogeny of crabs of the genus *Cancer*, and, in combination with information from laboratory and field experiments, I used this phylogeny to test the hypothesis that size-dependent habitat use is one of the primary selective pressures underlying the diversification of *Cancer* crabs.

Phylogenies inferred from the two separate data sets supported significantly different relationships among the *Cancer* taxa. Because the morphological data set likely reflected a high amount of character convergence, and because the phylogeny inferred from the COI data was generally consistent with the fossil record and the biogeography of the genus, the tree based on molecular characters was taken as a more accurate reflection of the genealogical relationships among *Cancer* taxa. This phylogenetic hypothesis suggests that, in general, *Cancer* crab body size is inversely correlated with the relative degree of habitat complexity, and that multiple origins of the use of more homogeneous habitats are associated with increased morphological change towards larger body sizes.

To test the functional significance of the results of the phylogenetic analyses, I examined the habitat preferences and behaviour of four morphologically diverse species of *Cancer* crabs in the laboratory with and without the presence of a predator. Regardless of the presence of the predator, all crabs preferred the most structurally complex habitat, the rock substrate. After the introduction of the predator, the preference for the rock habitat became significantly more pronounced only in the smallest species, but the activity levels of all crabs, except the largest species, significantly decreased. These results indicate that *Cancer* crabs may select their habitat or modify their behaviour in response to inversely size-dependent predation risk.

Finally, to test the hypothesis that *Cancer* crab body size and habitat use has evolved, in part, as adaptations to minimize the risk of predation, I used mark-recapture techniques to estimate the strength and form of selection on the size of adult red rock crabs, (*C. productus*) at a field site that lacked structural refuges. Analysis of capture histories indicated that there was weak directional selection for larger crabs, and suggested that claw damage reduced fitness.

Taken together, the results of my study provide the first comparative evidence that size-dependent predation may be one of the most significant selective pressures driving the evolution of morphological and ecological diversity in *Cancer* crabs.

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CHAPTER 1: GENERAL INTRODUCTION

Phylogenetic studies of adaptation are invaluable for testing hypotheses about the evolutionary forces that shape the patterns of morphological and ecological diversity seen in nature. This approach reflects the idea that the present covariation between an organisms' phenotype and its environment is the result of both current adaptation and past selection (Klingenberg and Ekau, 1996). Thus, combined with experimental studies, comparisons of interspecific differences can be used to evaluate hypotheses about the selective forces involved in the origin, maintenance and alteration of ecological and morphological features (Harvey and Purvis, 1991) that complement the results of experimental studies. Furthermore, this approach can be extended and used to study the processes and temporal patterns of character change, coadaptation, convergent and divergent adaptation, and phylogenetic constraints on ecological diversification (Brooks and McLennan, 1991).

Crabs of the genus *Cancer* (Crustacea: Decapoda: Brachyura) are a large (23 extant species), morphologically and ecologically diverse group of brachyuran crabs (Nations, 1975). As such, these animals are excellent subjects for a comparative study of the patterns and causes of covariation in morphological and environmental characters. Orensanz and Galluci (1988) suggested that the diversity of *Cancer* crabs primarily reflects adaptations in body size and habitat use that minimize the risk of predation. Habitat type or complexity often mediates predation risk (Gilliam and Fraser, 1987; Schlosser, 1987, 1988), moreover, vulnerability to predation is strongly dependent on body size in many marine crustaceans (Wahle and Steneck, 1992; Fernandez et al., 1993). Consequently, differences in habitat use among morphologically diverse *Cancer* species may primarily reflect size-dependent differences in vulnerability to predation (Orensanz and Galluci, 1988). Small, presumably more vulnerable *Cancer* crabs are likely to inhabit more structurally complex environments because these habitats contain structural refuges that provide protection from

predators. In habitats that lack structural refuges, the risk of predation may be higher. As a result, natural selection will likely favour increased body size because larger crabs may not have to depend on the protection of structural refuges to the same degree as smaller individuals.

The purpose of my thesis was to examine this hypothesis using a multifaceted approach. First, I reconstructed a phylogeny of the genus *Cancer* using data from molecular characters. I mapped body size and habitat use onto this phylogenetic tree to statistically evaluate the hypothesis that more morphological change occurred on the branches of the phylogenetic tree where a habitat shift took place than on those branches where no habitat shift was hypothesized to have occurred. Large, directed changes in morphological characters are expected in lineages in which habitat shifts are hypothesized to have occurred because a shift to a new habitat often involves substantial changes in selection pressures and, subsequently, the rapid evolution of new adaptations (McPeek, 1995). Thus, I expected increased morphological change towards larger body sizes in *Cancer* crabs to be associated with lineages that shifted to the use of more homogeneous habitat types.

Second, I tested the microevolutionary predictions about the functional significance of the covariation between habitat use and crab size generated by this phylogeny in the laboratory by examining habitat use with and without the presence of a predator for four morphologically variable *Cancer* species. I predicted that these four *Cancer* species would actively select their habitat to minimize the risk of predation, that differences in habitat use among these morphologically diverse crabs would primarily reflect species-specific, size-dependent differences in vulnerability to predation, and that differences in habitat use among the species would become more pronounced under an increased risk of predation.

Third, mark-recapture techniques were used to evaluate the strength and form of natural selection on size in a natural population of a *Cancer* species at a structurally homogeneous field site. Estimates of survival for crabs of varying sizes were employed to

construct a fitness function that related the probability of survival of individual crabs to body size. If vulnerability to predation varied inversely with *Cancer* crab body size, and if predation was a significant selective pressure on body size in this homogeneous habitat, I expected larger crabs to have higher probabilities of survival than their smaller conspecifics.

Each of these approaches by itself evaluates one component of the original hypothesis. By addressing the same question from three different perspectives, I was able to construct a more complete picture of the role of predation as a selective pressure on *Cancer* crab ecology and morphology. Therefore, by integrating morphological and ecological information with the phylogeny of the genus, my study has addressed one of the central questions of evolutionary biology: to what extent do current selection and shared ancestry affect the patterns of diversity we see in nature?

CHAPTER 2: PHYLOGENETICS OF CANCER CRABS AND THE EVOLUTION OF SIZE-DEPENDENT HABITAT USE

ABSTRACT

Phylogenetic systematics provides information that can be used to evaluate adaptive hypotheses within a comparative framework. I used data from adult morphology and the cytochrome oxidase I gene to reconstruct a phylogeny of crabs of the genus *Cancer*, and I used this phylogeny to examine the evolutionary history of ecological and morphological traits in *Cancer* crabs. Phylogenies inferred from the two data sets separately, although robust, supported substantially different relationships among *Cancer* taxa. Congruence analyses also indicated that the morphological and molecular characters provided significantly incongruent information. Because the morphological data set likely reflected a high amount of character convergence, and because the molecular phylogeny was generally consistent with the fossil record with respect to the date of origin, the pattern of diversification, and the biogeography of the genus *Cancer*, the tree inferred from the COI data set was interpreted as a more accurate representation of the genealogical relationships among *Cancer* crabs.

I used the tree inferred from the molecular data set to test the hypothesis that size-dependent habitat use is one of the primary adaptive processes underlying the diversification of *Cancer* crabs. Tracing habitat use onto the tree suggested that habitat shifts from structurally complex substrates (e.g. the rocky intertidal zone) to more homogeneous substrates (e.g. sand or mud) have evolved independently in three lineages. A test using phylogenetically independent contrasts indicated that these habitat shifts were accompanied by increased morphological change towards larger body sizes. Thus, closely related *Cancer* species have diverged considerably in their morphology, likely as an

adaptive response to the different selective pressures associated with different habitats. These macroevolutionary patterns support the hypothesis that the diversification of *Cancer* crabs is strongly related to size-dependent habitat use, and suggest that predation risk is one of the principal selective pressures underlying the patterns of covariation in crab body size and habitat use.

INTRODUCTION

The diversity of present-day organisms is the result of both historical (genealogical) and adaptive (ecological) causes. Thus, the comparative method, which combines statistical analyses with phylogenetic information, is an ideal technique with which to study the patterns and processes underlying the diversity that we see in nature. For example, phylogenies are frequently used to identify and statistically test hypotheses about the co-evolution of morphological and ecological characteristics. The relationship between an animal's environment and its phenotype is a central issue in evolutionary ecology because ecological traits, such as habitat use or foraging activity, are often strongly influenced by an organism's morphology (Creswell and Marsden, 1990; Losos, 1990), and phenotypic characteristics, such as body size, feeding habits, and mating systems, are commonly selected for by ecological features (Chown, 1994; Orensanz et al., 1995). In addition, both ecological and morphological features can influence the probability of speciation or extinction, significantly modifying the evolutionary history of a given group of animals (Klingenberg and Ekau, 1996).

Recent research has used the phylogenetic approach to examine the relationships between habitat use and morphological diversity in a variety of taxa (e.g. MacLeod, 1993; Chown, 1994; Klingenberg and Ekau, 1996; Soltis et al., 1996). Taken together, these studies have highlighted general patterns of association among habitat shifts, morphological change, and major cladogenic events. Marine crustaceans provide an excellent opportunity

to test hypotheses about the specific causes underlying the evolution of morphological diversity and habitat use because they occupy many different habitats with strongly dissimilar selective pressures. Past research on marine crustaceans has focused primarily on the functional relationship between these different habitat types and highly atomized phenotypic traits, such as claw shape (Lawton and Elner, 1985). However, marine crustaceans can also be utilized to study the relationship between habitat use and more ecologically significant phenotypic characters, such as body size (Chown, 1994), and the evolutionary consequences of ecological diversification.

Crabs of the genus *Cancer* (Crustacea: Decapoda: Brachyura) are ideal subjects with which to evaluate phylogenetic hypotheses of habitat adaptation in marine crustaceans. The genus is comprised of 23 extant species and at least 14 species described only from the fossil record (Nations, 1975). Commercial interests have encouraged much research into the ecology and life history of a few *Cancer* species (in particular, *C. magister* and *C. pagurus*), but little is known about the origin and diversification of the genus as a whole. Similarly, although *Cancer* species are highly morphologically variable and are distributed in a variety of habitats worldwide (Table 1; Nations, 1975; Lawton and Elner, 1985; Creswell and Marsden, 1990; Jensen, 1995), no study to date has evaluated the hypothesis that the diversity of *Cancer* crabs is the direct result of adaptation to specific habitats, and that this habitat specialization, in turn, arose as a strategy to minimize size-dependent vulnerability to predation (Orensanz and Galluci, 1988).

The main objective of this study was to infer a phylogeny of *Cancer* crabs using data from adult morphological characters and mitochondrial DNA sequence. I used this phylogeny to examine the evolutionary history of body size and habitat use in *Cancer* crabs, and tested the hypothesis that larger body sizes in *Cancer* crabs have evolved as a single directional trend from smaller body types. Based on paleontological and morphological evidence, Nations (1975) suggested that the relatively small, highly ornate

Table 1. Selected life-history characteristics for the species used in the molecular analysis. Sources of information: †= Nations, 1975; ¥= Lawton and Elner, 1985; ¶= Creswell and Marsden, 1990; *= Jensen, 1995.

Species (common name)	*Cancer* Subgenus†	Distribution*†	Reported Depth Range*¥¶	Primary Habitat Type		Relative Degree of Structural Complexity in Habitat	Maximum Male Carapace Width *¥¶ (mm)	Maximum Female Carapace Width *¥¶ (mm)
				Juvenile¥	Adult*¥			
Petrolithes cinctipes (Flat porcelain crab)	•	Porcher Island, British Columbia to Santa Barbara, California	Upper and middle intertidal	Not given separately	Under rocks on or near the outer coast; abundant in mussel beds	High	24	Not given separately
Hemigrapsus nudus (Purple shore crab)	•	Yakobi Island, Alaska to Bahia de Tortuga, Mexico	Upper and middle intertidal	Not given separately	Under rocks on exposed beaches; estuaries	High	56	34
Cancer oregonensis (Pygmy rock crab)	*Glebocarcinus*	Pribilof Islands to Palos Verdes, California	Low intertidal to 436 m	Intertidal rocky areas and kelp holdfasts	Under rocks in low intertidal; subtidally in broken shell	High	53	42
Cancer branneri (Furrowed rock crab)	*Romaleon*	Granite Cove, Alaska to Isla de Cedros, Baja California	Subtidal; to 179 m	Not given separately	Coarse gravel and sand; most abundant on broken shell	High	58	62
Cancer gracilis (Graceful crab)	*Metacarcinus*	Prince William Sound, Alaska to Bahia Playa Maria, Mexico	Low intertidal to 143 m	Not given separately	Mud, and muddy sand	Low	115	87
Cancer novaezealandiae (New Zealand rock crab)	*Metacarcinus*	New Zealand; North, South, Auckland and Chatham Islands; introduced to Tasmania and Victoria, Australia	Intertidal to 60 m	Not given separately	Fine sediment, under rocks, stones, and among seaweed	Intermediate	160	Not given separately
Cancer antennarius (Pacific rock crab)	*Romaleon*	Queen Charlotte Sound, British Columbia to Cabo San Lucas, Mexico	Low intertidal to 91 m	Under rocks at low shore	Mud, sand, gravel, and rock	Intermediate	178	148
Cancer borealis (Jonah crab)	*Metacarcinus*	Grand Banks to south of Tortugas, Florida	Intertidal to 870 m; most abundant at intermediate depths	Shallow sublittoral rock	Mud, sand and near shore rocky areas	Intermediate	180	130
Cancer productus (Red rock crab)	*Cancer* sensu stricto	Kodiak, Alaska to Isla San Martin, Baja California	Mid intertidal to 79 m	Intertidal rocky areas	Mud, sand, gravel, and boulder beaches	Intermediate	200	158
Cancer magister (Dungeness crab)	*Metacarcinus*	Pribilof Islands to Santa Barbara, California	From low intertidal to 230 m	Abundant intertidally	Common subtidally on sand and mud	Low	230	170
Cancer pagurus (Edible crab)	*Cancer* sensu stricto	From northwest coast of Norway, south to Portugal: Mediterranean Sea	Intertidal to 100 m	Intertidal rocky areas, kelp, mussel beds, and shallow sub-littoral	Primarily mud and sand, some rock	Low	267	242

crabs of the subgenus *Romaleon* are ancestral to the other *Cancer* species because *Romaleon* species appear earliest in the fossil record. According to Nations' hypothesis, crabs of the subgenus *Cancer* sensu stricto, which are characterized by large size, smooth carapace margins, pronounced lateral carapace expansions and unornamented chelipeds, are likely the most recently derived group in the genus. *Metacarcinus* species appear to represent an intermediate stage between *Romaleon* and *Cancer*. The evolutionary position of crabs of the subgenus *Glebocarcinus* remains unclear, as *Glebocarcinus* species have relatively large, wide carapaces yet retain a high degree of cheliped and carapace ornamentation.

I also tested the prediction that rapid and directed changes in body size have occurred along branches of the phylogenetic tree of *Cancer* crabs where habitat shifts are hypothesized to have occurred. Large, directed changes in morphological characters are expected in lineages in which habitat shifts are hypothesized to have occurred because a shift to a new habitat often involves substantial changes in selection pressures and, subsequently, the rapid evolution of new adaptations (McPeek, 1995). Therefore, I expected the evolution of larger crab body sizes, as proposed by Nations (1975, 1979), to be more rapid in lineages that shifted to more homogeneous habitat types. Relatively small, more vulnerable *Cancer* species tend to inhabit more structurally complex environments (i.e. the rocky intertidal zone; Table 1), possibly because such habitats contain a greater number of structural refuges that can provide protection from predators (Orensanz and Galluci, 1988). An evolutionary shift to more homogenous habitats (such as sand and mud) that lack such structural refuges may therefore be associated with strong selection for larger, less vulnerable phenotypes. These patterns of character association and rates of change would indicate that habitat use is one of the primary causes of interspecific variation in the body size of *Cancer* crabs, and that size-dependent habitat use may be one of the primary adaptive processes underlying the diversification of the genus.

MATERIALS AND METHODS

Taxa

All extant *Cancer* taxa were used in the morphological analyses, despite large amounts of missing data for the Asian and South American species. Due to the difficulty in obtaining specimens of the Asian and South American species, the molecular analyses were restricted to nine of the twenty-three extant *Cancer* species, including at least one species representative from each of the four subgenera proposed by Nations (1975). Two other crabs, *Hemigrapsus nudus* (Decapoda: Brachyura: Grapsidae), and *Petrolithes cinctipes* (Decapoda: Anomura: Porcellanidae), representing a different brachyuran family and decapod order, respectively, were used as the outgroups in all analyses. The outgroup taxa were chosen because of the relative ease of collection (Table 1).

Molecular Data Collection

DNA from all crab species was isolated from frozen or preserved (in 99% ethanol or guanidine isothiocyanate) specimens by crushing cheliped muscle tissue in Lifton buffer (0.2M sucrose, 0.05M EDTA, 0.1M Tris, 0.5% SDS). Total DNA was extracted from this homogenate using phenol-chloroform-isoamyl alcohol, precipitated in 70% ethanol with 0.7M sodium acetate and suspended in sterile distilled water. The primers S1718a or S1718b were used with A2238, A2316, A3500, or A3662 (Table 2) to amplify sequence from the mitochondrial cytochrome oxidase I (COI) gene using polymerase chain reaction (PCR). After processing with exonuclease I and shrimp alkaline phosphatase, double stranded PCR products were sequenced using 35^{S} and Sequenase™ kits (United States Biochemical), or 33^{P} Thermo Sequenase™ radiolabeled terminator cycle sequencing kits (Amersham Life Science) (30 cycles; 30 seconds at 95°C, 30 seconds at 60°C, and 60 seconds at 72°C). Sequences were aligned by eye using SEQAPP (Appendix 1). All COI products were sequenced in one direction (annealing with various 'S' primers; Table 2),

Table 2. Primer sequences used in the amplification and sequencing of the COI region. Primer numbers correspond to 3' positions in the *D. yakuba* genome (Clary and Wolstenholme, 1985).
Non-standard and mixed bases as follows: I=deoxyinosine, R=A+G, Y=C+T, M=A+C, W=A+T, D=A+T+G, H=A+T+C.

Primer Name	Primer Sequence 5'	3'
S1718a	GGA GGA TTT GGA AAT TGA TTA GTT C	
S1718b	GGA GGA TTT GGA AAT TGA TT	
S1834	AAG AGG WWT AGT AGA AAG WGG	
S1841	ATA GTA GAA AGA GGW GTT GG	
S1976	GTA AAY TTT ATA ACA AC	
S1991	ACM GTW ATT AAT ATA CG	
S2045	GTT TGA GCT GTA TTT AT	
S2118	TWY TAA CTG ACC GAA A	
S2219	ATT CTT ATT TTA CCY GCT T	
S2249	ATG ATT TCT CAY ATT GTT AG	
S2329	ACT GTA AAT ATA TGA TGA GCT CA	
S2417	ACW ATA ATT ATT GCY RTH CC	
A1887	ARR GGD GGR TAR ACR GTY CA	
A2051	CTR GTT TAT GGW GAR AAR CA	
A2064	GTA ATA AAW ACA GCT CAA	
A2238	GGY AAA ATW ARA ATA TAD AC	
A2316	TAA ATT ATY CCW ARG GTC CC	
A3389	TCA TAA GTT CAR TAT CAT TG	
A3500	TAA GAR TCA AAT TTC TAC TTG	
A3662	CCA CAA ATT TCT GAA CAT TGI CC	

and the opposite strand was also partially sequenced (annealing with various 'A' primers; Table 2) for all taxa to confirm that there were no inconsistencies in the sequence.

Morphological Data Collection

An extensive morphological character matrix was constructed from the literature (Appendix 2). Data were restricted to adult features because of the high degree of intraspecific variability in larval morphology (Orensanz and Galluci, 1988), although little morphological information was available for many of the Asian and South American Pacific *Cancer* crabs. The problem of missing data in phylogenetic reconstruction has been the subject of much debate in systematic literature (Patterson, 1981; Donoghue et al., 1989; Platnick et al., 1991; Bryant and Russel, 1992; Norell and Novacek, 1992; Novacek, 1992; Wilkinson, 1995). Large numbers of missing entries, common in fossil taxa, prevent satisfactory resolution of cladograms because the missing data produce large numbers of equally most parsimonious trees, clouding the relationships among taxa (Novacek, 1992).

Most studies cautiously include taxa with large amounts of missing data in phylogenetic analyses by implementing strategies to reduce the problem of missing data (Donoghue et al., 1989). For example, Bryant and Russel (1992) use maximum parsimony analyses to infer the unpreserved attributes of fossil taxa from the cladistic distribution of known characters in related taxa. Others exclude those taxa that have no effect upon the relationships inferred for other taxa but increase the numbers of equally most-parsimonious trees (Wilkinson, 1995). All of these approaches aid in constructing consensus trees with fewer ambiguous relationships. The strategy adopted in this paper was to evaluate and contrast the robustness of trees constructed with and without taxa with many missing characters. The results of this analysis determined whether such taxa could aid in the resolution of *Cancer* crab genealogy.

Phylogenetic Analyses

All phylogenetic analyses were conducted using PAUP (beta test version *d59; Swofford, 1997) with some tree length calculations and character mapping performed in MacClade 3.0 (Maddison and Maddison, 1992) and the validity of the molecular clock tested in PHYLIP 3.5c (Felsenstein, 1993). In both the morphological and molecular data sets, all characters were weighted equally and ACCTRAN was used for character optimizations to minimize parallelisms. Multiple state morphological characters were ordered because I believe that character transitions in *Cancer* crabs have occurred in a stepwise manner. Because of the large number of taxa and characters, both data sets were analyzed using maximum parsimony and the replicated heuristic algorithm with random stepwise addition (10 replicates). The robustness of trees inferred from these analyses was evaluated using bootstrap analyses with heuristic searching (1000 replicates; Felsenstein, 1985), decay indices (Bremer support; Bremer, 1994) and skewness analysis of tree length frequency distributions (distributions that are strongly skewed to the left indicate that parsimony has a high probability of inferring the true phylogeny; Hillis, 1991; Huelsenbeck, 1991; Hillis and Huelsenbeck, 1992). The molecular data set was also analyzed using neighbor-joining with the default settings under the Kimura two-parameter model to account for multiple substitutions, using maximum likelihood with a transition/transversion ratio of 2.0 under the Hasegawa-Kishino-Yano model to provide the highest likelihood, and I used the molecular data to generate a UPGMA tree, applying a molecular clock using a COI calibration developed for beetles by Juan et al. (1995, 1996).

Considerable debate in the systematic literature has centered on the analysis and ability of different types of data to accurately reflect phylogenetic history (Eernisse and Kluge, 1993; Larson, 1994; reviewed in deQueiroz et al., 1995). Most of this controversy focuses on the relative merits of morphological versus molecular characters (Lewin, 1985; Hillis, 1987) and the methods of combining such diverse information. The two main approaches are taxonomic congruence and total evidence: taxonomic congruence involves

inferring a consensus tree from separately-analyzed data sets, while total evidence uses character congruence to find the best-fitting topology for all of the available data (Eernisse and Kluge, 1993). The strategy followed in this paper was to analyze the congruence of the data sets first to determine whether the separate data sets should be combined.

Four methods were used to assess the extent of congruence between the two data sets. First, I evaluated the magnitude of the bootstrap values and decay indices on the trees inferred from each data set separately. Second, Templeton's Wilcoxon test (1983) was used to compare the topologies of the trees produced by maximum parsimony analyses of each data set. Templeton's test compares two topologies by summing the number of characters that undergo a different number of changes on the two trees. The sign and magnitude of these character by character differences are then analyzed using a Wilcoxon rank sum test. Third, to determine if the tree inferred from the combined data was only slightly suboptimal with respect to the trees inferred from each data set separately, the number of steps each data set required on the combined tree was compared to the number of steps required on the shortest trees inferred from the separate data sets (Swofford, 1991). Fourth, the Mickevich-Farris incongruence index (I_{MF}) (Swofford, 1991) and its associated statistical test (the partition homogeneity, or incongruence length difference test; Farris, 1994) were used to assess the extent of character incongruence between the data sets. I_{MF} values partition total character incongruence (homoplasies) into between and within data set components; smaller I_{MF} values indicate that the disagreement between two data sets is low relative to the amount of incongruence among characters within the separate data sets.

Character evolution

To examine the evolutionary history of habitat use and body size in *Cancer* crabs, maximum male carapace width and habitat type were mapped onto the most robust tree

inferred from the analyses above, and the probable evolutionary trends among these traits were inferred. Using descriptions in the literature, habitat type was described qualitatively by the relative degree of structural complexity in the preferred habitat type as low (primarily mud, sand, eelgrass, or kelp), high (primarily rock, gravel, and shell), or intermediate (the use of both habitat types) (Table 1). I pooled habitats of intermediate and high structural complexity in my phylogenetic analyses because statistical correlation tests of habitat type and body size require one variable to be dichotomous, and habitats of intermediate complexity were more similar to habitats of high heterogeneity than they were to habitats of low heterogeneity (see Table 1).

Species may be similar either because they have adapted to similar environments (convergence), or because the species are closely related and have inherited traits from a common ancestor (homology) (Clutton-Brock and Harvey, 1984; Felsenstein, 1985). If similarity is due to shared ancestry, values for related species can not be regarded as statistically independent data points (Clutton-Brock and Harvey, 1984; Felsenstein, 1985). Thus, to test hypotheses about the causes of macroevolutionary change in *Cancer* crab body size, I used evolutionary contrasts, a phylogenetic technique that accounts for the statistical non-independence among species due to their common ancestry. Specifically, I used the computer program CONTRAST and the method developed by McPeek (1995), which estimates character change along a single set of branches on a phylogeny, to statistically evaluate the hypothesis that more morphological change occurred on the branches of the phylogenetic tree where a habitat shift took place than on those branches where no habitat shift was hypothesized to have occurred. In my analyses, all branch lengths were set to one (standardized) because I assumed that character change occurred in relation to speciation events, rather than in relation to time.

RESULTS

Data

The COI data set consisted of 1072 characters, 307 of which were cladistically informative and 240 of which were informative within the ingroup (Appendix 1). Using all three nucleotide positions yielded pairwise distances ranging from 7.2% to 17.2% within the ingroup, 19.9% to 23.6% between ingroup taxa and outgroup species, and 23.0% between the two outgroups (Table 3).

The morphological data set included 44 characters, which comprise 13 carapace traits and 31 claw characters. Forty-one of these characters were cladistically informative in both the ingroup and the entire data set (Appendix 3). Restricting the data to those species for which molecular data was also available reduced the number of cladistically informative characters within the ingroup to 38, 37 of which were informative within the ingroup.

Phylogenetic Analyses

Ten thousand random trees were generated from each data set (two morphological sets, one molecular set) to analyze the skewness of tree length frequency distributions. G1 values indicated a strongly significant phylogenetic signal in all data sets (Table 4).

A) Molecular Analysis

Parsimony analysis of the molecular data yielded one tree of length 1043 (consistency index, CI = 0.587, retention index, RI = 0.383) (Figure 1). Bootstrap values and decay indices for this tree both gave strong support (99% and 21 steps, respectively) for the branch differentiating the *Cancer* genus from the outgroups and for four of the ingroup nodes (>70% and >3 steps, respectively). In particular, the monophyly of the two Atlantic species, *C. borealis* and *C. pagurus*, was supported by a high bootstrap value (81%) and decay index (5 steps). The only weak nodes on this tree were the clade

Table 3. Pairwise distance matrix for the COI data set.

	Pairwise differences between taxa										
	P. cinctipes	*H. nudus*	*C. branneri*	*C. antennarius*	*C. oregonensis*	*C. pagurus*	*C. productus*	*C. gracilis*	*C. novaezealandiae*	*C. borealis*	*C. magister*
P. cinctipes	•										
H. nudus	0.230	•									
C. branneri	0.226	0.220	•								
C. antennarius	0.227	0.232	0.137	•							
C. oregonensis	0.218	0.230	0.118	0.162	•						
C. pagurus	0.208	0.215	0.165	0.151	0.160	•					
C. productus	0.211	0.214	0.150	0.148	0.172	0.134	•				
C. gracilis	0.217	0.199	0.107	0.148	0.138	0.172	0.157	•			
C. novaezealandiae	0.213	0.236	0.163	0.072	0.165	0.146	0.146	0.169	•		
C. borealis	0.213	0.228	0.149	0.162	0.165	0.109	0.141	0.161	0.154	•	
C. magister	0.232	0.224	0.159	0.147	0.166	0.148	0.149	0.172	0.138	0.165	•

Table 4. Skewness analysis of random tree length frequency distributions.

Data set	Number of taxa	Number of characters	g1	gcrit	p
Morphological					
All extant species	24	44	-0.467	-0.12	<0.05
Species also analyzed using molecular data	11	44	-0.913	-0.28	<0.05
Molecular	11	1072	-0.834	-0.16	<0.05

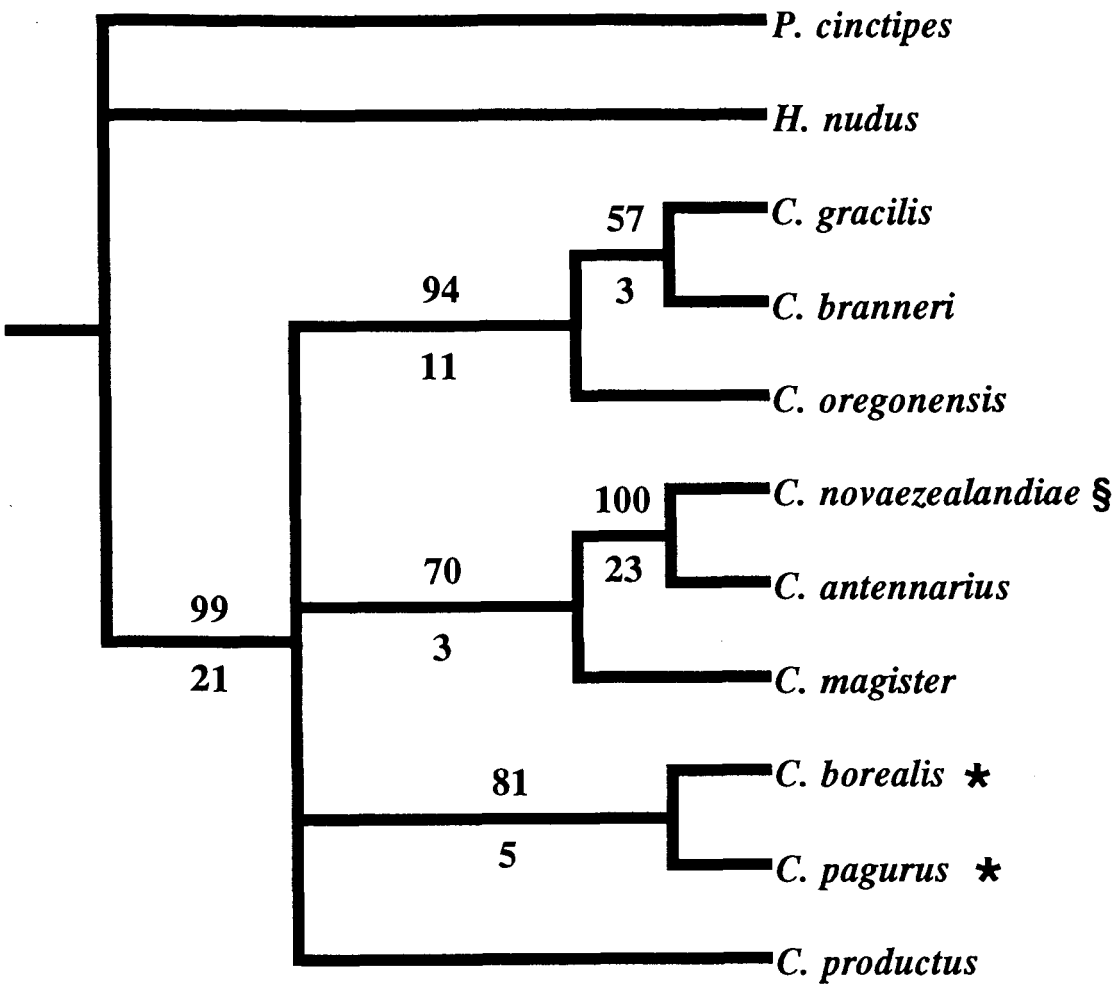

Figure 1. Results of maximum parsimony analysis of the molecular data set (one tree; length=1043, CI=0.587, RI=0.383; bootstrap values (1000 replicates) indicated above branches and decay indices shown below branches). * and § denote Atlantic and South Pacific species, respectively. Clades with less than 50% bootstrap support are collapsed.

containing *C. gracilis* and *C. branneri* (57%, 3 steps), the branch supporting *C. productus* (48%), and the clade encompassing the species from *C. gracilis* to *C. magister* (48%).

The topologies of the trees inferred from the neighbor joining (Figure 2) and the maximum likelihood analyses (Figure 3) were not significantly different from the tree inferred using maximum parsimony (Templeton's Wilcoxon rank-sum test; $p>0.50$; Table 5), nor were they significantly different from each other (Templeton's Wilcoxon rank-sum test; $p=0.50$; Table 5). All three topologies agreed with respect to the node connecting the two Atlantic species, the branch supporting *C. novaezealandiae*, *C. antennarius, and C. magister* and the clade containing *C. gracilis*, *C. branneri* and *C. oregonensis*. The only disagreement between the methods arose for nodes that were weakly supported in the parsimony tree.

I could not reject the validity of the molecular clock (Kishino and Hasegawa test; Ln L with clock = -6112.6811, Ln L without clock = -6109.2049, SD=2.6196; not significantly different); thus, I used the UPGMA tree generated by the molecular data to infer the dates of origin for each node. The UPGMA tree suggested that *Cancer* crabs arose during the Miocene, approximately 15 million years ago (Figure 4), and that the majority of the diversification within this clade occurred by the end of the Miocene, 5 million years before present. On this tree, Pacific species were the most basal taxa, and the clade containing *C. novaezealandiae*, the South Pacific species, and *C. antennarius*, a North Pacific crab, was the most recently derived group, diverging approximately 3-4 million years ago. The two Atlantic species (*C. pagurus and C. borealis*) were paired as sister-species, branching off from their Pacific ancestors approximately 9-10 million years before present.

B) Morphological Analyses

Maximum parsimony analysis of the morphological data set including all extant *Cancer* taxa yielded 13 most parsimonious trees (CI=0.350, RI=0.516) of length 286. The

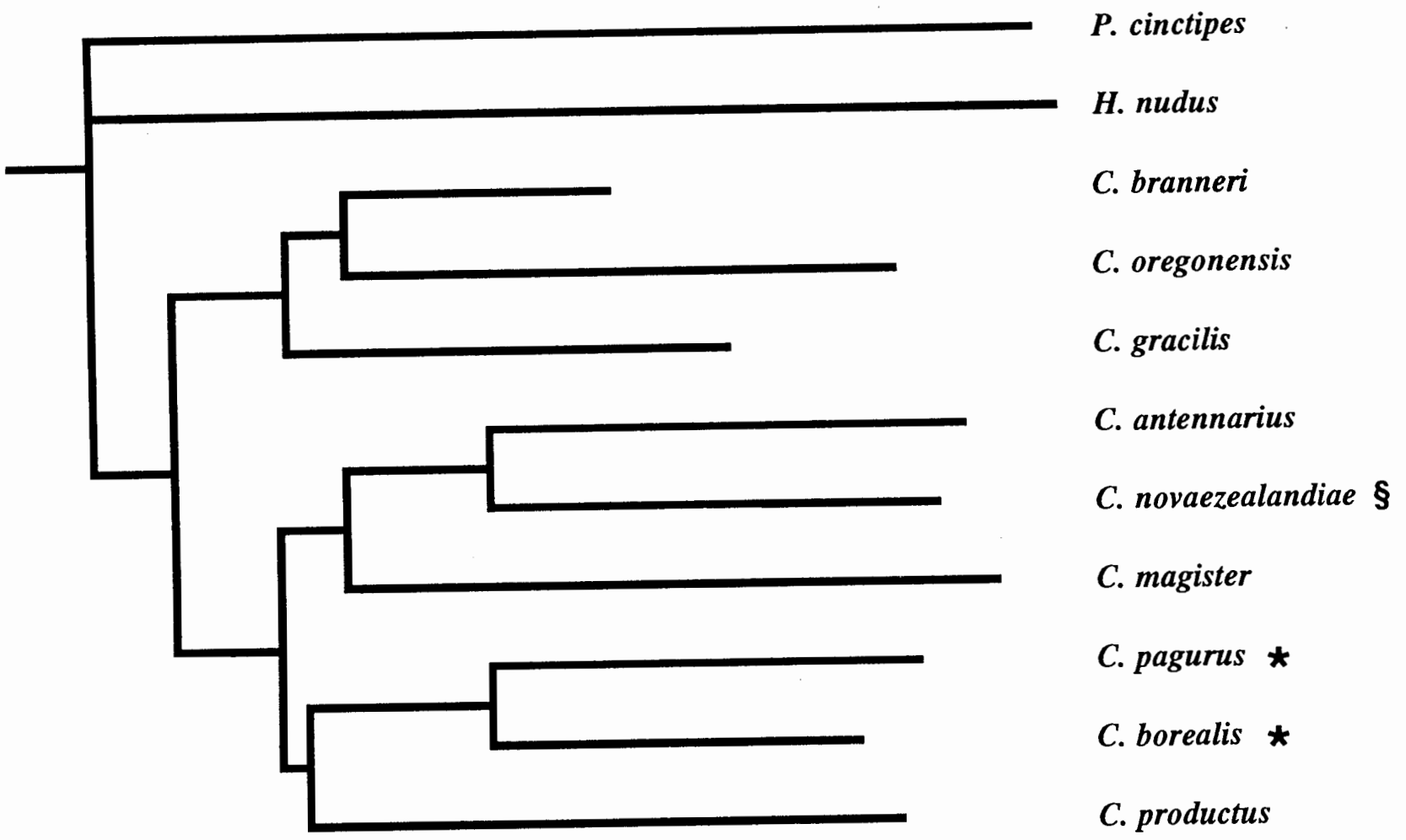

Figure 2. Results of neighbor-joining analysis of the molecular data set. * and § denote Atlantic and South Pacific species, respectively. Branch lengths represent estimated number of nucleotide substitutions.

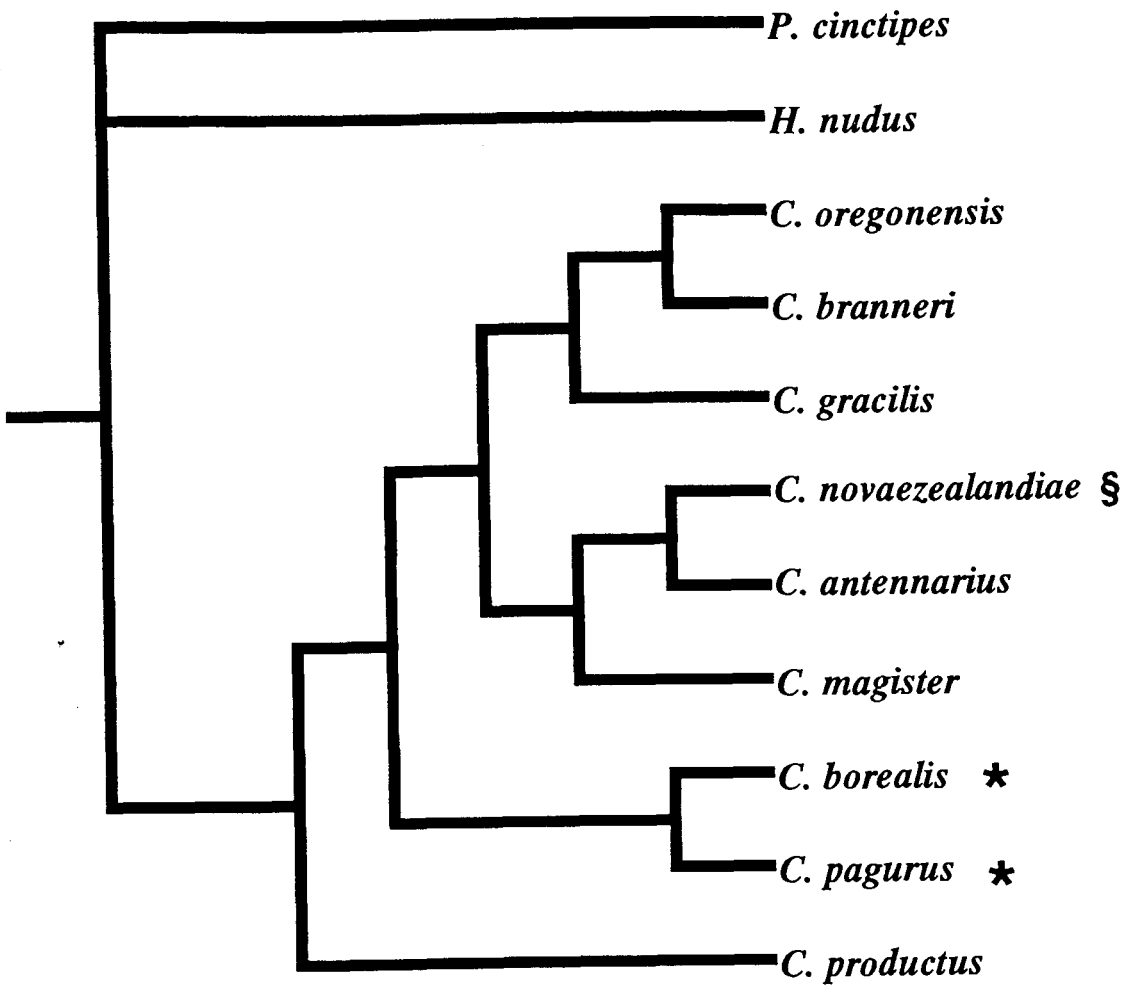

Figure 3. Results of maximum likelihood analysis of the molecular data set (ln likelihood= -5615.88). * and § denote Atlantic and South Pacific species, respectiveley.

Table 5. Templeton's (1983) Wilcoxon rank sum test of alternative trees. The normal approximation was used for values of n that exceeded 100 (Zar, 1984).

Topologies compared	Number of characters with different minimum number of changes (n)	Lowest sum rank (Ts)	Critical value (Tcrit)	p
Maximum parsimony vs Neighbor joining	53	621	494	>0.20
Maximum parsimony vs Maximum likelihood	26	143	98	$0.20 > p < 0.50$
Neighbor joining vs Maximum likelihood	35	272	195	0.50
Molecular (Max. Pars.) on Morphological	27	24	107	<0.001
Morphological on Molecular (Max. Pars.)	140	1583 (Z=6.97)	Zcrit=1955	<0.0001

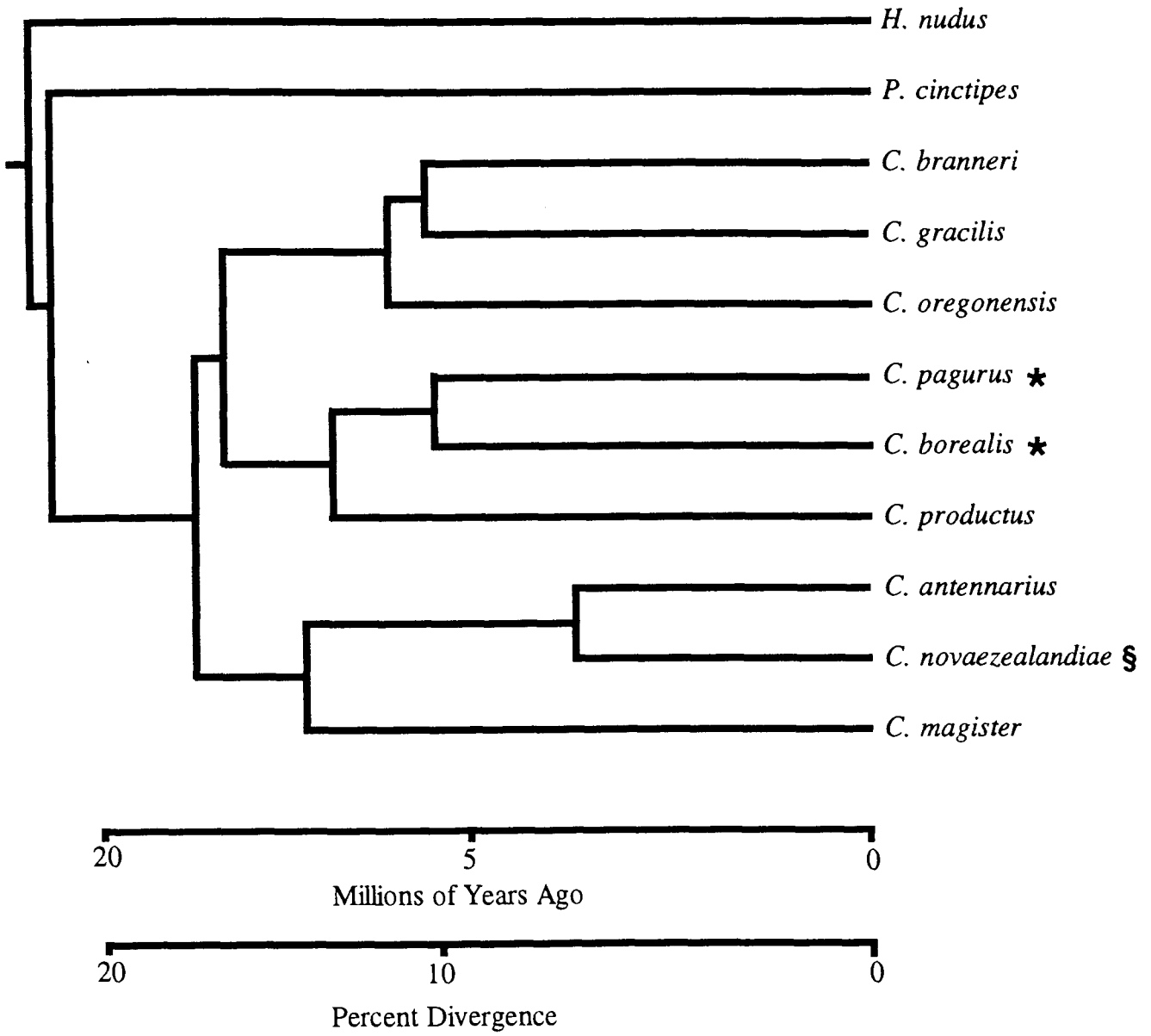

Figure 4. Results of the UPGMA analysis of the molecular data set. * and § denote Atlantic and South Pacific species, respectively. Clock calibrated using a COI calibration developed for beetles by Juan *et al.*, 1995, 1996.

strict consensus tree had little support within the ingroup (all nodes but one <60%), but the decay index (9 steps) and bootstrapping (96%) gave strong support for the monophyly of the genus *Cancer*.

I then restricted the morphological data set to include only those species for which molecular data was also available. Parsimony analysis of this reduced data set produced four trees with 167 steps (CI=0.557, RI=0.529). One thousand bootstrap replicates and the decay index again gave strong support for the branch differentiating the genus *Cancer* from the outgroups (98% and 8 steps, respectively) on the strict consensus tree (Figure 5). Similarly, three of the four resolved internal nodes were also supported by relatively strong bootstrap values (>75%) and decay indices (2 or 3 steps). However, the topology of this tree (Figure 5) differed significantly from the topology of the tree produced by maximum parsimony analysis of the molecular data (Figure 1) (Templeton's Wilcoxon rank-sum test; $p<0.001$; Table 5). None of the nodes agreed, particularly with respect to the two Atlantic *Cancer* species, which, instead of constituting a monophyletic group, formed two separate clades with the two Atlantic species paired with two Pacific taxa (Figure 5).

C) Congruence Analyses

The high but discordant bootstrap values and decay indices on the separate trees inferred from the molecular and morphological data, combined with the results of the Templeton's test (Table 5), supported substantially different relationships among the *Cancer* taxa.

To determine if a single tree existed that was only slightly suboptimal with respect to the trees inferred from each data set, the number of steps each data set required on the combined tree was compared to the number of steps required on the shortest trees inferred from the separate data sets (Swofford, 1991). The molecular and morphological data sets required 16 and 20 more steps, respectively, on the tree inferred from the combined data set than they did on the tree inferred from each data set separately. Likewise, the

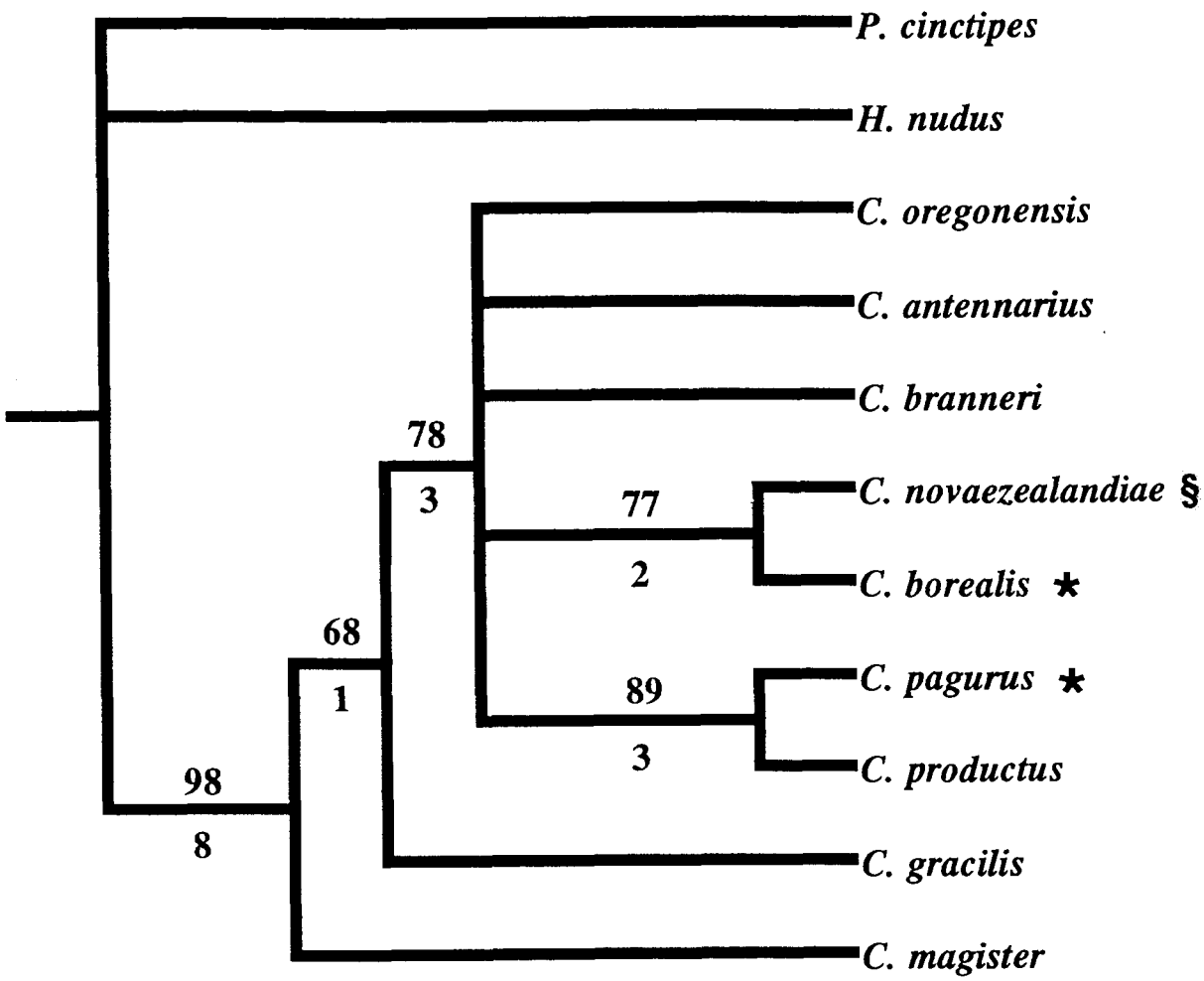

Figure 5. Results of maximum parsimony analysis of the morphological data set, showing the strict consensus tree (four trees; length=167, CI=0.557, RI=0.529); bootstrap values (1000 replicates) indicated above branches and decay indices shown below branches. * and § denote Atlantic and South Pacific species, respectively.

morphological data required 43 additional steps on the tree based on molecular data, and the molecular data set required 111 additional steps on the tree produced by the morphological data. These results suggest that neither data set fit a tree from the combined data well and that the topologies constructed from the separate data sets were substantially different.

The trees inferred from the separate morphological, molecular, and combined data sets each contained 74, 431 and 545 homoplasies, or extra steps, respectively. These extra steps are the difference between the amount of character change required (tree length) on the tree being evaluated and the minimum amount of change the characters could show on any tree. Analysis of character congruence yielded a congruence index (I_{MF}) of 0.0734, indicating that 7.34% of the total character incongruence was due to disparity between the data sets. Thus, the relative degree of between-data set incongruence was low relative to the extent of character incongruence within the two separate data sets. However, the incongruence length difference test indicated that this degree of incongruence between data sets was statistically highly significant ($p=0.001$).

All four congruence analyses suggested that the morphological traits and the molecular characters provided strongly incongruent information. To determine whether certain characters in each data set were obscuring the true phylogeny of *Cancer* crabs, I re-analyzed both data sets by excluding specific character types. First, I partitioned the molecular data set into hydrophobic and hydrophilic regions. Second, I excluded third position nucleotides, which often have a high substitution rate (Simon et al., 1994). Neither method yielded substantially different results. Third, I excluded the claw characters from a re-analysis of the morphological data, using the justification that claws may be under stronger selective pressures because of their role in a variety of functions, such as feeding, defense and mate acquisition (Orensanz and Galluci, 1988), and therefore may tend to be more convergent. However, the tree produced by this analysis was also weakly supported, and the two Atlantic species remained non-monophyletic.

My interpretation of the results of these analyses was that the morphological data set reflected a large amount of character convergence. Thirteen of the forty-four morphological characters (30%) supported a convergent relationship between *C. novaezealandiae* and *C. borealis*, and *C. pagurus* and *C. productus*; eight of these convergent characters (9, 14, 16, 17, 24, 41, 42, 44) were claw traits and five (6, 29, 30, 32, 35) were carapace features (Appendix 2), and most of these convergent traits are more functionally important in foraging, defense, and locomotory activities than the non-convergent characters. Given this high amount of convergence in the morphological data set, the tree inferred from the molecular data was likely a more accurate reflection of *Cancer* genealogy. Thus, only the tree reconstructed from the molecular characters was used in subsequent analyses to examine the phylogenetic relationship between body size and habitat use in *Cancer* crabs.

Evolution of habitat use and body size

Phylogenetic reconstruction of *Cancer* crab body size indicated that larger body sizes have not evolved as a single directional trend from smaller body types, as suggested by Nations (1975) (Figure 6). Instead, maximum male carapace width varied substantially across all branches, with no obvious phylogenetic pattern.

Mapping habitat use onto the phylogenetic tree suggested three independent transitions (in the lineages of *C. gracilis*, *C. pagurus*, and *C. productus*) from structurally complex environments to more homogeneous substrates. McPeek's (1995) method of phylogenetically independent contrasts revealed that the relative amount of change in the body size of these three lineages was significantly greater than the amount of change in branches where no shift in habitat use was hypothesized to have occurred (t-test, $p=0.047$). Average standardized contrasts with a habitat change (66.41; N=3, SD=18.57) was more than twice the average of contrasts without habitat shifts (29.19; N=5, SD=21.35).

Finally, as predicted, the character changes associated with the transition to more homogeneous substrates all reflected a substantial increase in relative body size. *C.*

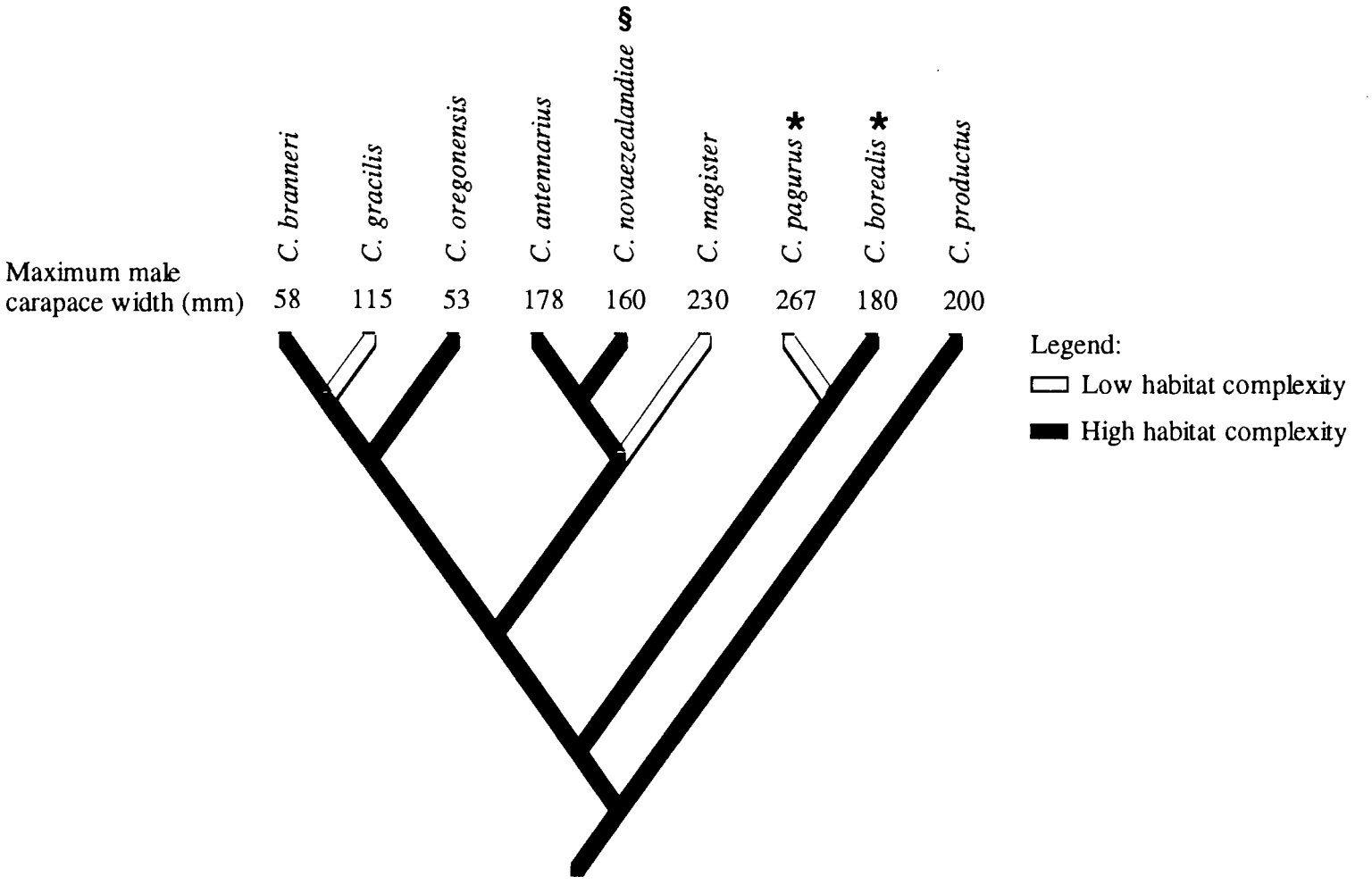

Figure 6. Phylogenetic reconstruction of habitat use and body size in *Cancer* crabs. * and § indicate Atlantic and South Pacific species, respectively.

magister and *C. productus*, the largest *Cancer* species (maximum male carapace width 230 mm and 267 mm, respectively), both evolved from intermediate-sized (approximately 180 mm carapace width) ancestors, while the body size of *C. gracilis* (maximum male carapace width 115 mm) is almost double that of their closest relatives (approximately 55 mm carapace width). Thus, the new selective pressures associated with structurally homogeneous environments appear to entail rapid adaptation towards a larger body size in *Cancer* crabs.

DISCUSSION

Phylogenetics of Cancer crabs

The phylogenetic trees inferred from morphological and molecular characters supported significantly different relationships among crabs of the genus *Cancer*. One possible explanation for this result may be that the morphological data set reflects a high amount of character convergence. This hypothesis is based on the fact that on the tree inferred from the morphological data, the two Atlantic species are paired with Pacific species that have equivalent ecological specializations. All four species (*C. pagurus*, *C. productus*, *C. borealis* and *C. novaezealandiae*) occur most frequently in intertidal and subtidal habitats of low to intermediate structural complexity, and prey primarily on hard-shelled species (Lawton and Elner, 1985; Creswell and Marsden, 1990; Jensen, 1995). As a result, all four species appear to have converged morphologically, particularly with respect to their stout, robust claws, and the shape of the carapace, which is thought to minimize lateral resistance to water flow in benthic habitats (Blake, 1985).

Because many of the morphological characters used in this study were claw characters, and, thus, likely highly selected traits, morphological tree resolution may be further improved by the inclusion of characters less subject to selective pressures that may lead to convergence, such as setae number, antennae form, and gonopod structure

(Jamieson, 1990; Abele, 1991). Unfortunately, such detailed information is lacking for many *Cancer* species, and as mentioned above, the use of taxa with many missing characters often yields poorly resolved trees. Previous phylogenetic studies of brachyuran crabs have also encountered large amounts of homoplasy in adult morphology (Spears et al., 1992), and researchers have analyzed spermatozoan ultrastructure (Jamieson, 1990), zoel morphology (Rice, 1980), fossil taxa (Schram, 1982), and molecular data (Vaughn and Taeger, 1976; Abele, 1991; Spears et al., 1992) in an attempt to minimize the problems of convergence.

Given the high amounts of morphological homoplasy in *Cancer* crabs, I believe that the molecular data set provides a more accurate guide to the genealogical relationships among *Cancer* taxa than the tree inferred from the morphological characters. Additional evidence for this hypothesis is provided by two other sources. First, the biogeographic implications of the molecular tree agree with the suggested dispersal pattern of *Cancer* crabs. Based on paleontological evidence, the genus is thought to have originated in the North Pacific, dispersing south along the coast of North and South America, west towards Japan, and north, across the Bering Strait to the Atlantic Ocean, speciating in each new area (Nations, 1975, 1979) (Figure 7). Thus, Atlantic species should be more closely related to one another than to any of the Pacific species, and indeed, in the tree inferred from the molecular phylogeny, the two Atlantic taxa form a monophyletic clade. Second, the molecular data is consistent with the fossil record of *Cancer* crabs (Figure 8). The stratigraphic distribution of *Cancer* crabs indicates that the genus arose in the Pacific in the early Miocene and diversified relatively rapidly. Such evidence agrees broadly with the UPGMA tree (Figure 4) generated by the molecular data. Based on this time scale, the *Cancer* genus did indeed arise in the early Miocene, most of the basal taxa are Pacific species, and the majority of the diversification within the genus did occur by approximately 5 million years ago, the end of the Miocene. The fossil record and the UPGMA tree also suggest that the date of divergence of the two Atlantic species occurred approximately six

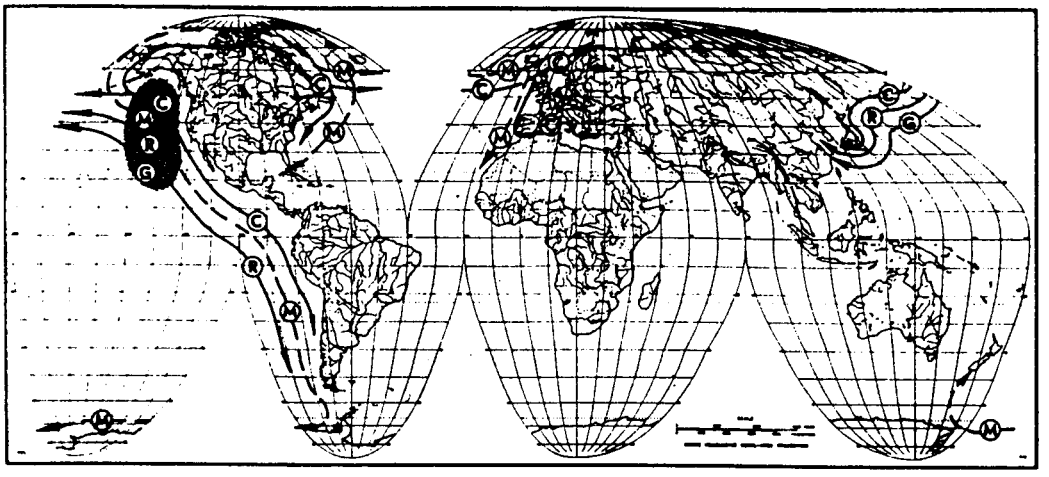

Figure 7. Suggested area of origin and hypothesized dispersal pattern of *Cancer* crabs. Probable area of origin indicated by hatching. Subgenera represented by letters: C=*Cancer*, G=*Glebocarcinus*, M=*Metacarcinus*, R=*Romaleon*. After Nations, 1975.

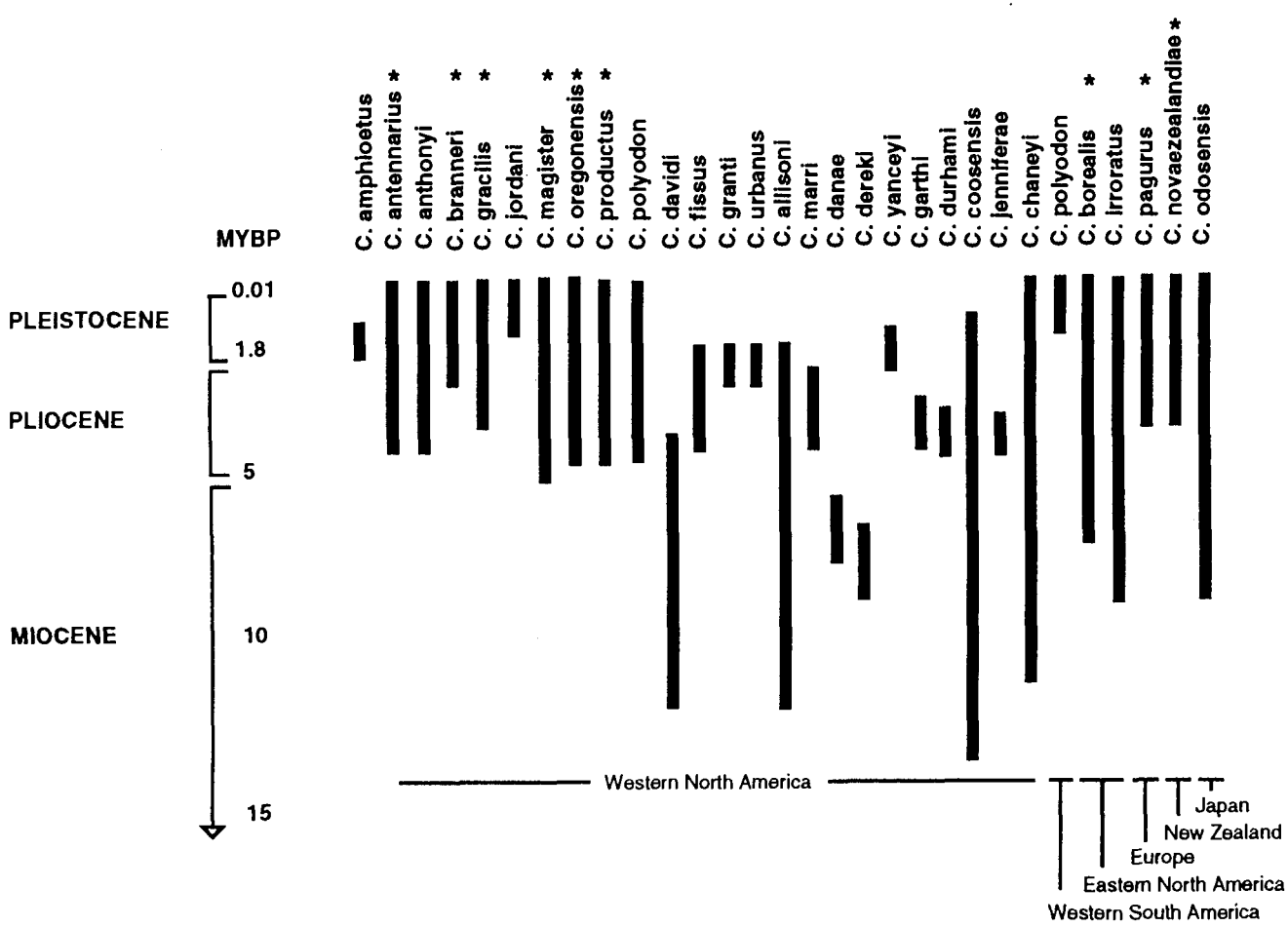

Figure 8. Stratigraphic distribution of *Cancer* crabs (after Nations, 1975). Starred taxa are those species for which molecular data was collected.

million years ago, well before the proposed date of submergence of the Bering Strait during the Early Pliocene (3.5 mya). This geological event enabled many species, such as gastropods, echinoderms, barnacles and marine vertebrates, to migrate between the north Pacific and Atlantic oceans (Vermeij, 1991). However, previous paleontological research and the molecular data collected in this study indicate that *Cancer* crabs were well diversified before the opening of the Bering Strait, furthermore, Atlantic *Cancer* fossils dating from approximately 8 to 10 million years ago have been found in the Atlantic (Nations, 1975). Thus, dispersal from the North Pacific and colonization of the Arctic-Atlantic basins likely occurred much earlier than 3.5 million years ago.

I conclude that the tree inferred from the molecular data has much greater predictive power than the tree based on morphological characters. Testing hypotheses of morphological and ecological adaptation using the molecular phylogeny has the additional advantage of reducing bias in the reconstruction of trait origin; using the characters under study to build trees can bias phylogenetic analyses against inferring multiple origins of a trait if parsimony is used to reconstruct the evolution of the trait in question (deQuerioz, 1996). Stronger resolution at the basal nodes of the molecular phylogeny may be obtained by using more closely related outgroups in future analyses. Rice (1980) used crab zoeal morphology to infer that the Cancridae and Portunidae (swimming crabs) are sister taxa. Thus, the use of portunid species such as *Carcinus maenas* (green crab) or *Callinectes sapidus* (blue crab), may provide more cladistically informative information than the outgroups used in this study.

Evolution of Cancer crab habitat use and body size

The tree inferred from the molecular data represents the first genealogical framework for analyzing the evolution of diversity among *Cancer* crabs. This phylogeny contradicts Nations' (1975, 1979) hypothesis that the evolution of *Cancer* crabs has followed a single directional trend from relatively small-bodied, highly ornate ancestors to

larger, unornamented forms. Instead, bursts of increased morphological change towards a larger body size have occurred in three independent *Cancer* lineages, and each of these evolutionary events was strongly associated with a habitat shift to a more structurally homogeneous substrate (Figure 6).

Selective pressures can change considerably with a change in habitat, driving the evolution of morphological adaptations. Thus, adaptations should evolve more rapidly in lineages where habitat shifts are hypothesized to have occurred than in lineages where species have remained in the same environment (McPeek, 1995). Previous researchers have noted that body size and habitat complexity are inversely correlated in *Cancer* crabs, and have suggested a causal relationship between these two characters and an adaptive role of both traits in the diversification of the genus *Cancer* (Lawton and Elner, 1985; Orensanz and Galluci, 1988). My results support this hypothesis, as the most pronounced changes in *Cancer* crab morphology occurred in lineages involving habitat shifts. Thus, size-dependent habitat use may be one of the primary adaptive processes driving the diversification of *Cancer* crabs.

My results are consistent with predation risk being a strong selective pressure underlying the patterns of covariation in *Cancer* crab morphology and ecology, and consequently, the diversification of the genus *Cancer*. In most crabs, predation risk decreases with increasing size (i.e., decreasing vulnerability) (Orensanz and Galluci, 1988; Wahle and Steneck, 1992); thus, if predation is an important selective pressure, relatively larger crabs should be selected for. Similarly, predation risk can be mediated by habitat use and complexity (Gilliam and Fraser, 1987; Schlosser 1987, 1988), as more complex environments often provide more potential refuges. My phylogenetic analysis revealed that *Cancer* crabs have adapted to habitats with few structural refuges (i.e. increased predation risk) by increasing in body size, suggesting that predation is an important selective pressures underlying the morphological and ecology diversity of *Cancer* crabs.

Finally, this study has three larger implications for future comparative analyses of the diversity of marine crustaceans. First, assuming that the tree inferred from the molecular data is a more accurate reflection of the genealogical relationships among *Cancer* species, there appears to be a substantial amount of evolutionary flexibility in the morphometric characters of *Cancer* crabs; closely related species are not always morphologically similar. Thus, morphological characters likely increase the amount of 'noise', obscuring the phylogenetic signal, and as a result, are of limited use in the reconstruction of brachyuran genealogy and the identification of patterns of ecological and morphological correlation.

Second, my phylogeny has provided an initial genealogical framework that future research can use to formulate and experimentally test hypotheses about the evolution of *Cancer* crabs. For example, my phylogenetic tree has identified a pattern of association between crab morphology and ecology that can be investigated experimentally in the laboratory and in the field (see Chapters 3 and 4). Such studies can determine the functional significance of the relationship between crab size, habitat type and diversification. Similarly, previous researchers have suggested that the variation in the habitat use and body size of *Cancer* crabs is also related to differences in diet, mating system and claw size and shape (Lawton and Elner, 1985; Orensanz and Galluci, 1988). The reconstruction of these characters on my phylogenetic tree will help to identify their historical role in the diversification of the genus *Cancer*.

Third, my results expand upon previous research on habitat use, adaptation, and diversification in crustaceans. Abele (1974) noted a strong correlation between the number of decapod species and the structural complexity of their habitat, and suggested that increasing substrate complexity allowed more species to coexist through the differential use of various microhabitats. Thus, body size adaptation to habitat type may be one of the mechanisms that has driven the ecological and morphological specialization and diversification of most crustacean species.

CHAPTER 3: PREDATION RISK AND HABITAT USE IN FOUR SPECIES OF *CANCER* CRABS

ABSTRACT

Predation is often implicated as one of the primary selective pressures influencing habitat selection. Consequently, variation in habitat use among different species can reflect species-specific adaptations to size-related differences in vulnerability. To test this hypothesis, I examined the habitat preferences and behaviour of four morphologically and ecologically diverse species of *Cancer* crabs (*C. oregonensis*, *C. gracilis*, *C. productus*, *C. magister*) in the laboratory with and without the presence of predatory rockfish (a cabezon; *Scorpaenichthyes marmoratus*). Regardless of the presence of the predator, all crabs preferred the most structurally complex habitat, the rock substrate. After the introduction of the cabezon, the preference for the rock habitat became significantly more pronounced only in the smallest crabs, *C. oregonensis*. *Cancer oregonensis* was the only species that buried significantly deeper with the addition of the predator, but the activity levels of all crabs, except *C. magister*, the largest species, significantly decreased in the presence of the predator. These results indicate that *Cancer* crabs actively select their habitat and modify their behaviour in response to perceived predation risk, and suggest that the perception of predation risk is inversely proportional to crab size. This study provides the first comparative evidence that predators can be an important selective pressure driving habitat selection and specialization in the crabs of the genus *Cancer*.

INTRODUCTION

Identifying the selective pressures underlying patterns of habitat use is a central issue in evolutionary ecology. Recent research has compared the relative significance of competition, food availability, and predation risk as selective agents involved in the use of particular habitats (Mittelbach, 1984; McNamara and Houston, 1986; Shirley et al., 1990; Williams et al., 1990; Sweitzer and Berger, 1992; Hughes et al., 1994). Given the immediate and severe fitness consequences of predation and the fact that virtually all animals are potential prey for others (Lima and Dill, 1990), predation is likely one of the most important selective pressures underlying habitat use for many animals.

Many studies of habitat use have examined how predators limit the distribution and abundance of animals in aquatic environments (Crowder and Cooper, 1982; Coull and Wells, 1983; Shulman, 1985; Eggleston et al., 1990). Most of this research has focused on mortality rates and habitat selection by benthic invertebrates in open sediment substrates (Virnstein, 1977; Nelson, 1979; 1981; Heck and Thoman, 1981; Choat, 1982; Quammen, 1984; Summerson and Peterson, 1984; Matilla and Bonsdorff, 1989; Aronson, 1989). However, the risks of predation in more structurally diverse marine ecosystems are not as well understood (Williams et al., 1994). Similarly, although age- or size-related differences in habitat use have been often been linked to predation risk in fishes and mammals (Schlosser, 1987; Werner and Hall, 1988; Sweitzer and Berger, 1992), much less is known about such responses in marine crustaceans (Eggleston and Lipcius, 1992).

Crabs of the genus *Cancer* (Crustacea: Decapoda: Brachyura) are ideal subjects for analyzing the role of size-dependent predation risk in the distribution and diversity of marine invertebrates. First, *Cancer* crabs are a large (23 extant species), morphologically and behaviourally diverse group of crabs (Nations, 1979), and as such, are excellent organisms for a comparative, size-related behavioural study. Second, *Cancer* crabs are distributed worldwide in a variety of marine habitats (Nations, 1979; Jensen, 1995),

enabling us to test hypotheses about ecological adaptation. Third, many *Cancer* crabs are economically important, and, as a result, fisheries researchers have already collected a considerable amount of information on their life histories. Fourth, *Cancer* crabs are an important prey item in the diet of many other marine species, such as rockfish, otters, octopi, sharks, sand stars and other crustaceans (Turner et al., 1969; Talent, 1982; Van Blaricom, 1982; Ambrose, 1984; Benech, 1986; Love et al., 1987), providing a good opportunity to study the effect of predation on the behaviour of marine invertebrates. Finally, previous research has suggested, but not tested, the hypothesis that the diversity of *Cancer* crabs is the direct result of adaptation to specific habitats, and that this habitat specialization, in turn, arose as a strategy to minimize vulnerability to predation (Orensanz and Galluci, 1988).

The main objective of this study was to investigate habitat selection in relation to predation risk in the laboratory using four species of *Cancer* crabs (*C. oregonensis, C. gracilis*, *C. productus*, *C. magister*) that differ considerably in maximum adult body size (Table 6). All four species are common off the west coast of Vancouver Island, British Columbia, and differ substantially in their morphology and ecology. *C. oregonensis*, the pygmy rock crab, is the smallest *Cancer* species (Figure 9a; Hart, 1982). This species is principally found subtidally or under rocks and in small crevices in the low intertidal zone, where it blocks the entrance to these cavities during daylight hours using its strong rounded carapace, emerging at night to feed on barnacles (Hart, 1982; Lawton and Elner, 1985; Jensen, 1995). *C. gracilis*, the graceful crab, a slightly larger species (Figure 9b), is most common subtidally in muddy substrates, where it forages on small bivalves and barnacles (Hart, 1982; Lawton and Elner, 1985). The large red rock crab, *C. productus* (Figure 9c), is a voracious predator and uses its massive, powerful chelipeds to consume a wide variety of gastropods and crustaceans in sandy, gravely areas and on well-protected boulder beaches (Nations, 1975; Hart, 1982; Lawton and Elner, 1985; Jensen, 1995). *C.*

Table 6. Life history characteristics of the four species used in the habitat selection experiment (sources: †=Rathbun, 1930; ¥=Hart, 1982; §=Jensen, 1995).

Species and Common Name	Distribution†¥§	Adult Habitat†¥§	Maximum Adult Carapace Width†¥§		Diet§
			Male	Female	
C. oregonensis Pygmy Rock Crab	Pribilof Islands to Palos Verdes, California	Under rocks in low intertidal, subtidally in shells	53mm	42mm	Small barnacles
C. gracilis Graceful Crab	Prince William Sound, Alaska, to Bahia Playa Maria, Mexico	Primarily subtidal on mud and sand	115mm	87mm	Small bivalves and barnacles
C. productus Red Rock Crab	Kodiak, Alaska, to Isla San Martin, Baja California	Common in gravel, sand, and rock from the middle intertidal to 79m	200mm	158mm	Clams, snails, mussels, barnacles and smaller crabs
C. magister Dungeness Crab	Pribilof Islands to Santa Barbara, California	Subtidal sandy bottoms and eelgrass, also found in the low intertidal to 230m	230mm	170mm	Clams, small crustaceans, fish

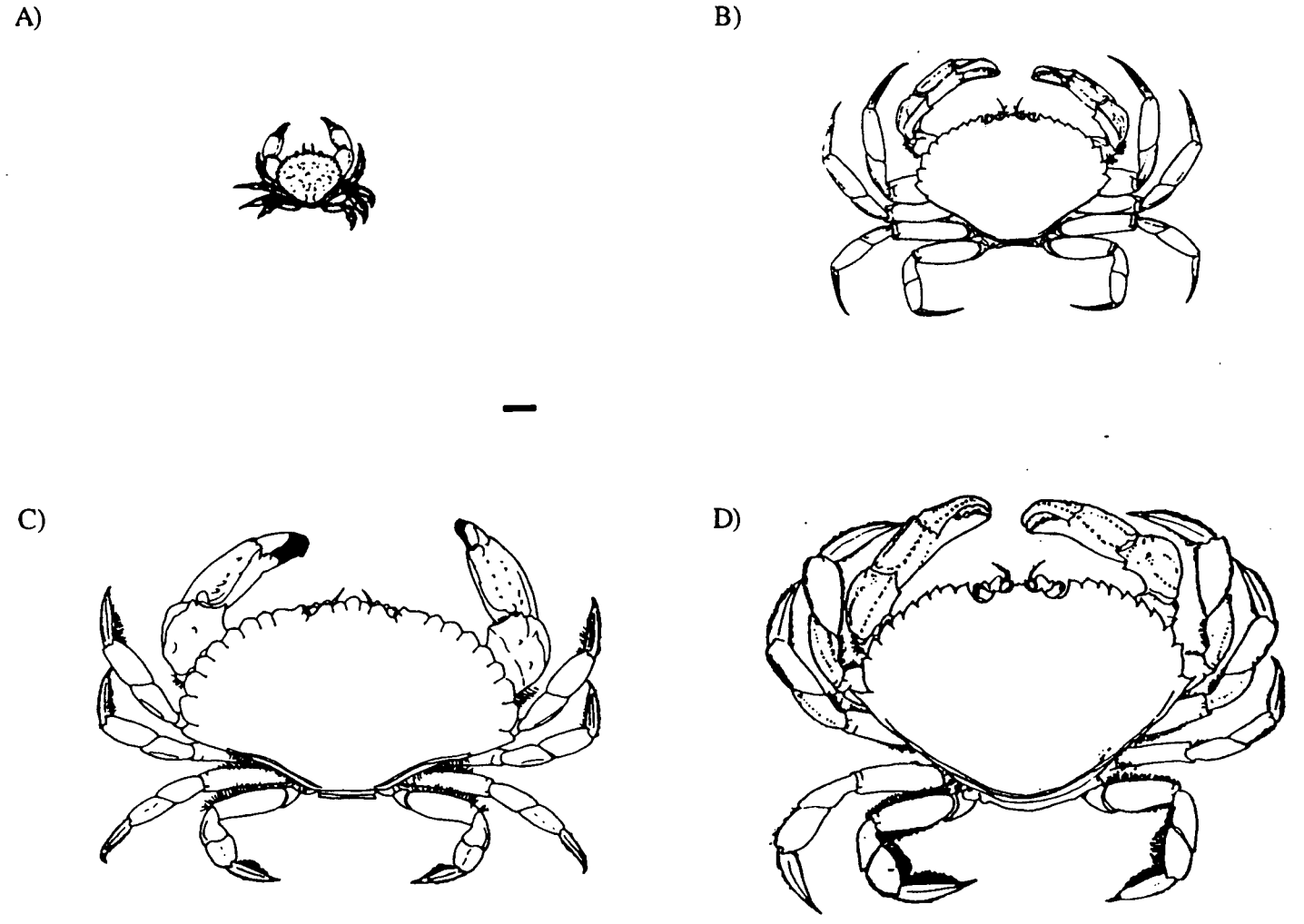

Figure 9. General morphology of a typical male crab of each of the four *Cancer* species used in the habitat selection experiment: a) *C. oregonensis*, b) *C. gracilis*, c) *C. productus*, d) *C. magister*. After Hart, 1982. Scale bar represents 25mm.

magister, the Dungeness crab, is the largest of these four species (Figure 9d; Hart, 1982). Primarily active at night, Dungeness crabs are often buried in sandy substrates and eelgrass beds with only the eyes and antennae exposed during daylight hours (Nations, 1975; Hart, 1982; Jensen, 1995). *C. magister* prey on a diversity of smaller or softer-bodied animals, including small clams, fish and other crustaceans (Lawton and Elner, 1985).

I hypothesized that these four *Cancer* species actively select their habitat to minimize the risk of predation. Predation risk is often mediated by habitat type and complexity in aquatic environments (Gilliam and Fraser, 1987; Schlosser, 1987, 1988); moreover, vulnerability to predation decreases with increasing body size in many crustaceans (Wahle and Steneck, 1992; Fernandez et al., 1993). Consequently, differences in habitat use among these morphologically diverse *Cancer* species may primarily reflect species-specific, size-dependent differences in vulnerability, and differences in crab habitat use are likely to become more pronounced under an increased risk of predation. Specifically, I expected the relatively small, presumably more vulnerable species (e.g., *C. oregonensis* and *C. gracilis*) to prefer more structurally complex environments (i.e., rocky substrates) because such habitats contain a greater number of structural refuges that provide protection from predators. Larger, less vulnerable species (such as *C. productus* and *C. magister*), may not have to depend on the protection of structural refuges to the same degree, and therefore, based on the consideration of predation alone, they were not expected to prefer any particular habitat.

MATERIALS AND METHODS

One hundred adult crabs of each of four *Cancer* species (*C. oregonensis, C. gracilis, C. productus, C. magister*), each representative of a different mean adult size (Table 2), were collected using crab traps and by hand from the intertidal and upper subtidal zones of Barkley Sound (48°53'N, 125°20'W), British Columbia, during May and June, 1996. Maturity was ascertained using Orensanz and Galluci's (1988) size-at-maturity life history schedules.

After capture, all crabs were weighed, sexed, and their carapace width (the widest distance between the tips of the anterolateral carapace teeth) was measured to the nearest tenth of a millimeter using Vernier calipers. The molt stage of each individual was identified using setal staging of the mouthparts (Moriyasu and Mallet, 1986; O'Halloran and O'Dor, 1988), and recently molted, pre-ecdysial, and ovigerous crabs were excluded from the experiment, as were those with missing or damaged chelae. The remaining 46 crabs of each species were labeled with small cryptic numbers affixed using Krazy Glue ™, separated by species and sex and allowed to acclimate to the lab for two weeks in 1.5m x 1m 2.36-l rectangular tanks filled to a depth of 15 cm with sand and supplied with free flowing unfiltered sea water at 11-12°C. All animals were fed *ad libitum* on the mussels *Mytilus trossulus* up until 48 hours prior to the experiment, then deprived of food until the trials began.

Six male cabezon (*Scorpaenichthyes marmoratus*; 70.5 - 89.5 cm in length), were obtained from local fishermen in late June, 1996, immediately prior to the trials. Cabezon are bottom dwelling rockfish and voracious predators of many crustaceans (Carrol and Winn, 1989). At capture I found remains of *Cancer* crab exoskeletons in the stomachs of four cabezon, verifying that they were indeed predators of *Cancer* crabs. During the experiment, cabezon were held in pairs in two 1.5m x 1.5m x 1.5m tanks supplied with running seawater.

The experiment was conducted in four 1.5m x 1.5m circular tanks, filled to a depth of 1.25 m with free flowing unfiltered sea water at ambient temperature (11.0-12.5°C) and salinity. Natural light provided all illumination, and air stones suspended just below the surface of the water aerated the tanks; these stones were removed during the trials to minimize water disturbance. The bottom of each tank was divided radially into three equal-sized 'habitats', each filled to a depth of 0.15 m with one of three substrates, representative of the most common crab habitat types found in Barkley Sound: 1) mud - silty organic matter, 2) sand - grain size less than 1mm, and 3) rock - sand with 10 rocks (10-20cm diameter) scattered throughout the habitat. All substrates were dried by air and filtered twice using 6.25 mm2 wire screens before the trials began to remove potential food items.

In each trial, one crab from each species was randomly chosen, placed in one of the test tanks, and every five minutes for the next hour, the location (substrate type and depth of burial) and the behaviour (standing, walking, burial or aggression) of all four crabs were noted. Depth of burial was described on a scale of 1 to 4 (Richards, 1992):

B1) Crab completely above substratum, only tips of walking legs submerged,

B2) Walking legs buried up to the level of the coxae in the substratum,

B3) Walking legs and less than half the carapace submerged,

B4) Crab completely buried (not visible) or more than half the carapace submerged.

After one hour, one of the six cabezon was randomly chosen to be introduced into each of the four tanks with as little disturbance as possible, and every five minutes for the following hour, position and behaviour were recorded for all crabs. Habitat-specific predation risk was estimated using the change in behaviour of the crabs after the addition of the predator. Behavioural changes were interpreted as a response to an increased perceived risk of predation, and were not simply attributed to the disturbance caused by introducing the fish into the tanks, because of the intensity and duration of the change in crab behaviour. Crabs did not bury themselves as often or as deeply after non-predatory disturbances of a similar magnitude (such as the introduction of a rock to the tank), and

following such disturbances, crabs resumed 'normal' behaviour in a short time, usually within thirty minutes of the initial event. In contrast, changes in crab behaviour following the addition of the predator were consistent across the entire hour (Mantel-Haenszel test; p=0.348), suggesting that crabs were responding to the predator *per se*, and not just the disturbance. Differences in the behaviour of crabs in tanks with and without a predator during the second hour (as a second control) was not examined because of the limited availability of tanks.

Forty-six trials were conducted per species, during which each crab was used only once, and approximately equal numbers of males and females were observed. The location, activity, and depth of burial of the crabs with and without the risk of predation were analyzed using one and two-way analyses of variance with Fisher's Least-Significant Difference Test. Contingency $\chi 2$ tests were used to analyze the relationship between time and depth of burial and habitat type.

RESULTS

The variation in overall size (carapace width) within each species was significantly less than the variation among all species (ANOVA; p=0.0001; Table 7). There were no significant behavioural differences among crabs of similar size but different species (p=0.152; analyses restricted to the crabs of the three species that overlapped in carapace width: *C. gracilis*, *C. productus*, and *C. magister*), and the size variation within each *Cancer* species had no significant effect on crab habitat use, activity level or burial depth (p=0.10 for all taxa). Thus, individual size was not used as a covariate in the analyses below.

Table 7. Mean (standard deviation) and range of carapace width of the four *Cancer* species used in the habitat selection experiment.

Species and Common Name	Sex	N	Mean (SD) (mm)	Range (mm)
C. oregonensis	Male	19	27.17 (6.26)	15.45 - 35.80
Pygmy Rock Crab	Female	27	28.70 (6.39)	16.05 - 39.67
C. gracilis	Male	23	90.86 (14.3)	58.40 - 116.76
Graceful Crab	Female	23	80.43 (10.42)	52.60 - 95.00
C. productus	Male	23	108.32 (32.82)	64.48 -164.30
Red Rock Crab	Female	23	100.69 (17.18)	70.40 - 131.35
C. magister	Male	23	143.71 (26.76)	94.25 - 184.80
Dungeness Crab	Female	23	139.18 (18.83)	94.10 - 171.60

To increase the clarity of the text and figures, significance values are summarized in Appendix 4.

Habitat Selection

All four *Cancer* species showed a significant preference for rock habitat when there was no predator present (Figure 10). While in the rock habitat, crabs tended to bury into the sand under the rocks, rather than utilizing crevices between rocks or spaces between stones and the sand. The preference for the rock habitat was greatest for *C. oregonensis* and *C. productus* (mean percent of total time spent in rock habitat 80.4% and 63.2%, respectively) and much weaker for *C. gracilis* (40.4%) and *C. magister* (40.8%). The proportion of time spent in the sand and rock substrates also differed significantly among the four species (Figure 2). *C. oregonensis* was found in sand less often (11.1%) than either *C. gracilis* or *C. magister* (28.8% and 37.7%, respectively), whereas *C. productus* and *C. oregonensis* occupied the rock habitat for a much greater proportion of time (see above) than the other two species. Two way analyses of variance also revealed an interaction between sex and habitat use in *C. gracilis* and *C. magister*. Female *C. gracilis* spent significantly more time in the rock habitat (55.4%) and less in sand (18.1%) than males (rock 25.4%, sand 39.5%). *C. magister* crab females were more frequently found in sand (54.0%) than rock (23.2%), and *C. magister* crab males preferred the rock habitat (rock 58.3%; sand 21.4%). Small crabs (<145mm carapace width in *C. magister*, < 90mm carapace width in *C. gracilis*) of both species did not differ significantly in the proportion of time each sex spent in the three habitat types (*C. magister*: $p=0.11$, *C. gracilis*: $p=0.09$).

The addition of the cabezon did not significantly change the proportion of time the crabs spent in each habitat, with the exception of the smallest species, *C. oregonensis* (Figure 1b). The presence of the predator greatly decreased the amount of time these animals spent in the sand substrate (from 11.1% to 2.7%) and significantly increased the proportion of time they spent in the rocks (from 80.4% to 90.0%).

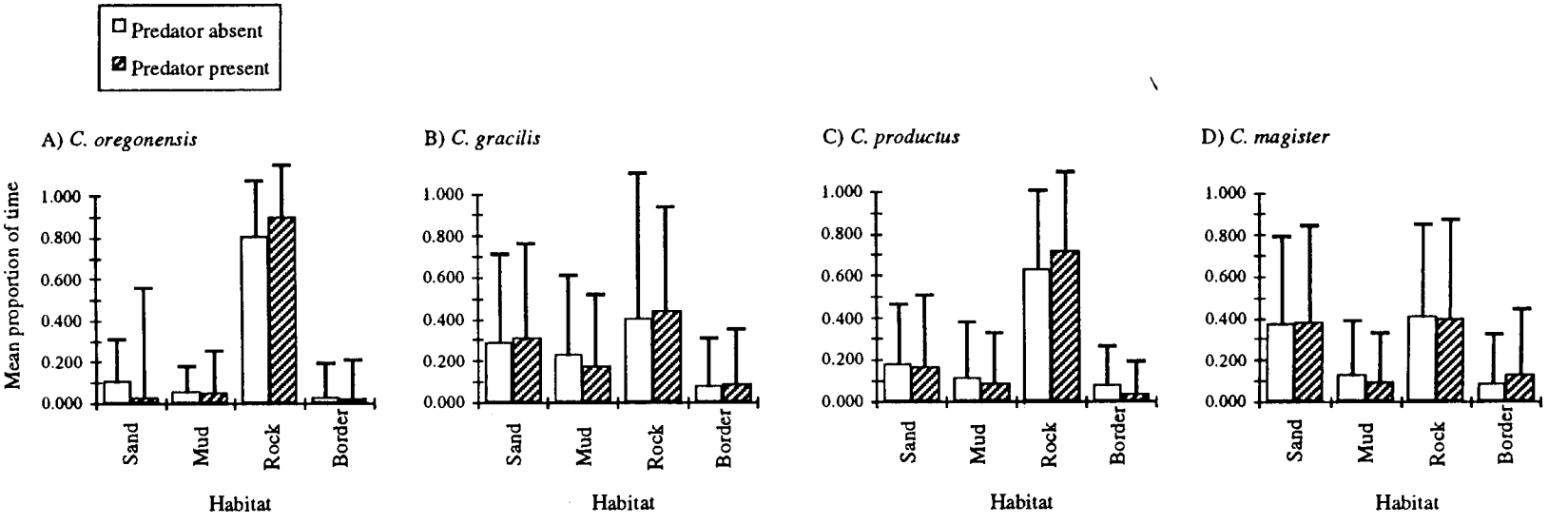

Figure 10. Mean proportion of total time spent in each habitat with and without the presence of a predator in four species of *Cancer* crabs. Bars represent one standard deviation.

Crab Activity

When no predator was present, three of the four *Cancer* species spent most of their time inactive and buried in the substrate (mean percent of total time spent inactive: *C. oregonensis* 85.2%, *C. gracilis* 90.0%, *C. magister* 88.1%; Figure 3). Individual *C. productus* were the most active crabs (35.0%), but they still were buried more often (49.6%) than they moved about. *C. magister*, the largest species, spent the greatest amount of time buried (79.9%), and *C. oregonensis*, the smallest crab, spent the greatest amount of time standing (56.9%).

After the introduction of the cabezon, the behaviour of most crab species changed markedly (Figure 11). Most crabs buried into the substrate within 5 minutes, and remained buried for the remainder of the trial. *C. magister* was the exception; the addition of a cabezon had no significant effect on its activities ($p>0.0874$; n=46; power=0.65). In the other three species, visible activity decreased significantly with a predator present: the mean proportion of time spent standing decreased from 28.3% to 9.1% in *C. oregonensis*, from 15.4% to 4.9% in *C. productus*, and from 19.0% to 5.8% in *C. gracilis*, while the mean proportion of time spent walking was shortened to 3.6% from 14.9% in C. oregonensis, to 13.0% from 35.0% in *C. productus*, and to 3.3% from 10.0% in C. gracilis. Similarly, the proportion of time these three species spent buried rose substantially (*C. oregonensis*; from 56.9% to 87.3%; *C. gracilis*; from 71.0% to 90.9%; *C. productus*; from 49.6% to 81.0%). The red rock crab, *C. productus*, was the only species that displayed aggression towards the predator (four crabs, mean proportion of time = 1.1%); individuals elevated themselves on their walking legs and raised and waved their chelipeds laterally. Regardless of predation risk, the proportion of time the crabs spent in each activity did not depend on substrate type ($\chi 2$ test, $p=0.120$).

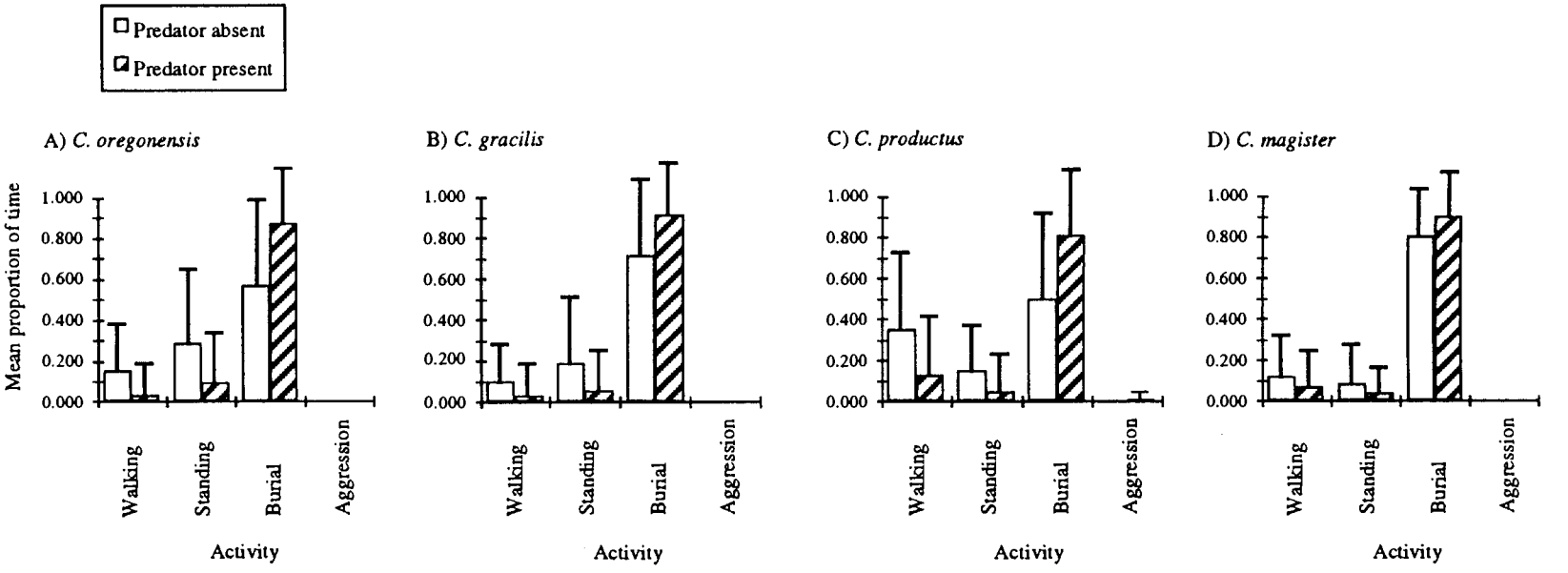

Figure 11. Mean proportion of total time spent in each activity with and without the presence of a predator in four species of *Cancer* crabs (all substrates combined). Bars represent one standard deviation.

Depth of Burial

With or without a predator, all crabs buried to the same depth independent of substratum type ($\chi 2$ test, p=0.230). With no predator present, the two smallest species (*C. oregonensis* and *C. gracilis*) buried shallower (depths B1 and B2 combined) significantly more often (33.7% and 39.3% of the total time, respectively) than they buried deeper (depths B3 and B4 combined) (21.4% and 28.8%, respectively). *C. productus* and *C. magister*, the larger species, did not vary significantly in their burial depth (Figure 12). There were no differences in depth of burial among the species, except that *C. magister* buried deeper (depth B3) significantly more often (31.0%) than *C. oregonensis* (9.6%).

The addition of a predator did not significantly alter the proportion of time the two largest species spent at each depth, but it was followed by a significant increase in burial depth (depths B3 and B4 combined) in both of the smaller species, *C. oregonensis* and *C. gracilis* (from 21.4% to 54.7% and from 28.8% to 58.7%, respectively; Figure 12).

DISCUSSION

Habitat use, activity level and the response to increased predation risk differed considerably among the four *Cancer* species in this study. When no predator was present, all four species preferred the most structurally complex substrate, the rock habitat, but the proportion of time spent in this substrate was significantly higher for the smallest species, *C. oregonensis*. Inactivity was also greatest in the relatively small species (*C. oregonensis* and *C. gracilis*) and, unexpectedly, the largest species, *C. magister*. There were no significant interspecific differences in burial depth. The addition of a predator intensified

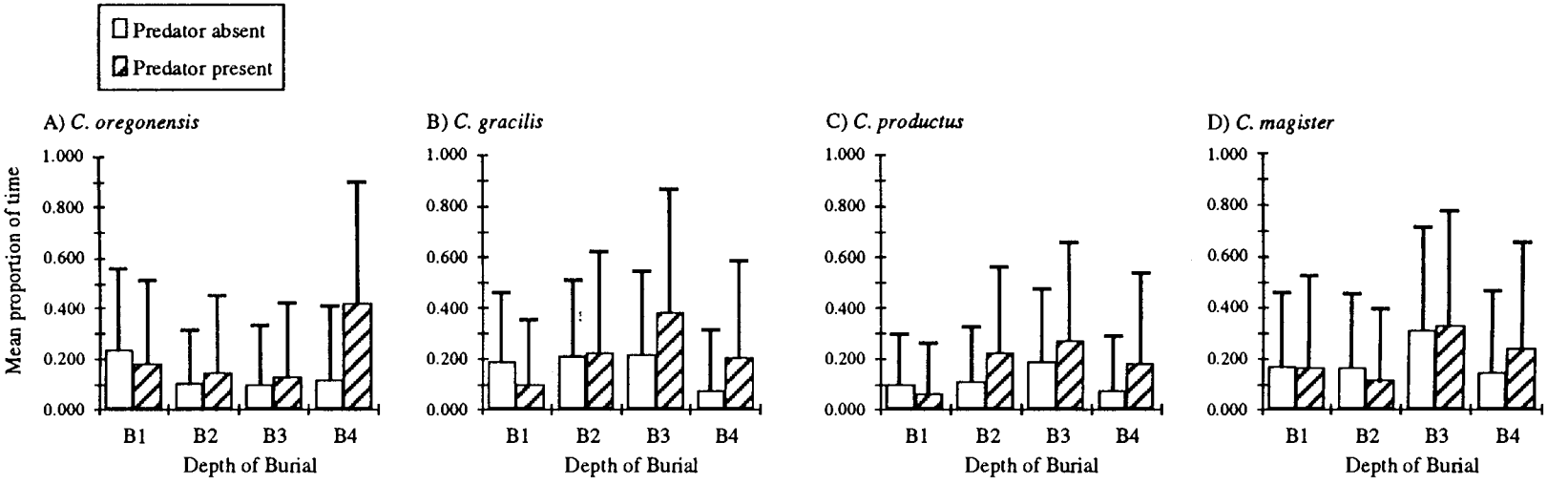

Figure 12. Mean proportion of total time spent at each burial depth with and without the presence of a predator in four species of *Cancer* crabs (all substrates combined). Depth of burial described qualitatively: B1) Crab completely above substratum, only tips of walking legs submerged, B2) Walking legs buried up to the level of the coxae in the substratum, B3) Walking legs and less than half the carapace submerged, B4) Crab completely buried (not visible) or more than half the carapace submerged (after Richards, 1992). Bars represent one standard deviation.

the observed differences; after the introduction of the cabezon, *C. oregonensis* (the smallest crabs) spent more time in the rock habitat, activity levels decreased in all species except C. magister (the largest crabs), and the two smallest species (*C. oregonensis* and *C. gracilis*) buried to a deeper depth. These results indicate that the avoidance of predators influences the habitat use and activity of *Cancer* crabs in a species-specific manner, and suggest that interspecific differences in mean adult size are a major component of this behavioural variation.

In many crabs, predation risk decreases with increasing size, except when the shell is soft, immediately following a molt (Orensanz and Galluci, 1988; Carroll and Winn, 1989; Wahle and Steneck, 1992). Consequently, if predation is an important selective pressure, smaller crab species should prefer more complex environments over open homogeneous substrates because complex habitats contain a greater number of potential refuges. Similarly, for smaller, more vulnerable species, burial and inactivity may be the most successful methods of avoiding detection by predators. Larger species, which have a refuge in their large body size during the intermolt period (Orensanz and Galluci, 1988; Carroll and Winn, 1989), were expected to have no obvious preference for any habitat type, but contrary to this prediction, *C. productus* and *C. magister* spent the greatest proportion of their time in the rocky habitat. However, because this habitat preference did not change with risk level, I conclude that predation risk does not significantly influence the habitat choice of these large crabs, although the presence of the cabezon did decrease the activity levels of the larger species, suggesting that large crabs did perceive the increased risk.

Although many other factors, such as food limitation, competition, moult stage, and reproductive condition also significantly affect crab habitat preferences (Day and Lawton, 1988; Shirley et al., 1990), and although crabs may be able to escape predatory attacks by fleeing, the results of this experiment, which controlled for most of these variables, correspond well with the observed distribution and behaviour of crabs in the field (Table

6). Most juvenile *Cancer* crabs are restricted to substrates that contain structural refuges, such as rocks, discarded shells and kelp, but adults of larger *Cancer* species are found in a much wider range of habitats (Table 6). Thus, predation pressure is likely one of the most important ecological pressures shaping the patterns of *Cancer* crab habitat use. In addition, *Cancer* crabs are slow-moving organisms relative to the locomotory abilities of their predators (personal observation); avoiding detection through the use of particular habitat types is likely a more successful anti-predator strategy than flight.

Of the two larger species, *C. productus* was significantly more active than all the other crabs, even under the risk of predation, but the largest species, *C. magister*, spent the greatest proportion of time buried, and buried to a deeper depth, regardless of predation risk. This unexpected observation may be the result of morphological differences between the two species. *Cancer productus* is a large, slow crab with a thick exoskeleton and strong chelae (Lawton and Elner, 1985; Orensanz and Galluci, 1988; Taylor and Palmer, personal communication). Such size and strength likely reduces predation risk; potential predators could be deterred by direct displays or attacks by the large powerful chelipeds. If so, this species may be able to afford to be more active, bury less often and bury to a shallower depth. *C. magister* is an even larger crab, but this species has the weakest chelae and thinnest carapace of any of the four *Cancer* species studied (Lawton and Elner, 1985; Orensanz and Galluci, 1988; Taylor and Palmer, personal communication). Therefore, in spite of its size, *C. magister* may experience an intermediate risk of predation, and buries more often and to a greater depth than *C. productus* to reduce its vulnerability.

In *C. gracilis* and *C. magister*, habitat preference depended on the sex of the crabs; *C. gracilis* females spent significantly more time in the rock habitat and less time in sand than males, and in *C. magister* females spent more time in sand than rock than did males. Although females of both species are significantly smaller than males (mean female size 73% and 75%, respectively, that of males; $p=0.0001$), the observed sex-related differences in habitat use can not be attributed simply to the size variation between the sexes because

the behaviour of small males differs significantly ($p=0.038$) from that of similar-sized females. Research on other decapods, such as blue crabs, *Callinectes sapidus*, has suggested that sex-related differences in habitat use reflect adaptations to mate availability and differences in physiological tolerances to temperature and salinity (Orth and Van Montfrans, 1987; Shirley et al., 1990; Williams et al., 1990). Further study is needed to determine the relative importance of these factors in the genus *Cancer*.

The data presented here provide the first comparative evidence that perceived predation risk differs among *Cancer* crabs. Given that vulnerability to predation is size-dependent in many other crustaceans, the differential response of the four *Cancer* species in this study likely reflects differences in mean adult body size. Consequently, predation may be one of the major factors driving habitat choice among species of the genus *Cancer*. Few interspecific studies of mobile, morphologically diverse, marine invertebrates have tested the hypothesis that distributional patterns are at least partly the result of active habitat selection under predation risk, although habitat structure and prey size are well known to strongly influence prey habitat preferences in aquatic environments. For example, small *C. magister* emigrate between structurally complex, sheltered habitats less frequently than larger adults because they are at greater risk of predation (Fernandez et al., 1993). Similarly, lobsters strongly associate with shelter-providing habitats for the first few years of life, but this association is less frequent as they grow to larger, less vulnerable sizes (Wahle, 1992; Wahle and Steneck, 1992), and the habitat separation of sunfish species changes significantly over their lifetime due to changes in feeding ability and vulnerability to predators associated with body size (Mittelbach, 1984).

Size-related predation risk also plays an important role in the habitat use of many terrestrial taxa. For example, juvenile porcupines primarily occupy low-risk areas, but the larger adults utilize higher risk habitats (Sweitzer and Berger, 1992), widow spiders move to larger, more profitable shrubs after one or two molts, when the risk of mortality is reduced by their increased size (Lubin et al., 1993), and small migratory birds have low

densities near the nests of predatory kestrels, while the densities of migratory and large-sized bird species are independent of the presence of kestrel nests (Suhonen et al., 1994). Taken together, evidence from aquatic and terrestrial species indicates that size-related predation risk can be a significant factor determining habitat use within many animal species.

Few studies have taken a comparative approach to investigate size-dependent predation risk and habitat selection. Interspecific differences in habitat use can test ideas about the selective forces involved in the evolution of ecological diversity (Harvey and Purvis, 1991), specifically, whether disparate habitat-related life history characteristics are adaptations to differences in size-specific predation. Instead, most multispecies studies have examined the roles that predation risk plays within single species, or the role that interspecific interactions, such as competition and territoriality, play in limiting the abundance of animals and determining community structure (Holt, 1984; Kotler, 1984; Hughes et al., 1994; Robertson, 1996). Although the distribution of animals often reflects tradeoffs between habitat-related risks of predation and other ecological factors, such as foraging profitability (Todd and Cowie, 1990) or competition (Robertson, 1996), the relative importance of size-specific predation as a selective force should be included in comparative explanations of the patterns of habitat use we see in nature.

Ultimately, habitat preferences may indirectly and directly affect other crab life-history traits, such as foraging activity, moulting decisions, and mating strategies, promoting further ecological, morphological, and behavioural specialization among closely-related animals. For example, because prey items are often found only in specific environments, habitat preferences can partly determine the diet of a predator (Orensanz and Galluci, 1988). Similarly, habitat complexity can influence the evolution of mating systems; in structurally heterogeneous habitats, males may be able to indirectly control access to females by monopolizing structural refuges, generating a resource-based polygynous mating system. The role of additional selective pressures, such as competition

and food availability, in the diversification of *Cancer* crabs requires further investigation. However, the results of this experiment indicate clearly that predation risk can modify the behaviour of *Cancer* crabs, and as such, it is likely an important ecological pressure in the evolution of these species.

CHAPTER 4: NATURAL SELECTION ON BODY SIZE IN THE RED ROCK CRAB, *CANCER PRODUCTUS*

ABSTRACT

Measurements of the impact of natural selection on intrapopulational phenotypic variation can be used to investigate the evolution of morphological and ecological diversity. I used mark-recapture techniques to estimate the strength and form of selection on the size of adult red rock crabs (*Cancer productus*) in a bay in Barkley Sound, British Columbia to test the hypothesis that larger body size is selected for in habitats of relatively low structural complexity. Over a two month period in 1996, 105 of 565 (~20%) marked crabs were recaptured. Analyses of capture histories for both sexes indicated weak directional selection for larger crabs with undamaged claws. These findings suggest that increased body size in *C. productus* may have evolved as an adaptation to minimize the risk of predation in homogeneous habitats, which have relatively few structural refuges.

INTRODUCTION

Data on natural selection can be used to study adaptation by quantifying the changes that selection causes in phenotypic characters (Arnold, 1983; Crespi and Bookstein, 1989; Crespi, 1990), identifying the ecological cause of selective processes (Wade and Kalisz, 1986); separating the indirect and direct effects of selection (Lande and Arnold, 1983; Manly, 1985), predicting evolutionary trajectories (Lande, 1979), and estimating the fitness function relating survival and reproductive success of individuals to the phenotypic characters under selection (Schluter, 1988). Measurements of selection are thus important

tools with which to test hypotheses about selective forces involved in the evolution of ecologically important life history traits, such as body size (Janzen, 1993).

Intraspecific differences in body size are of particular interest in life history theory because, in many organisms, individual survivorship is size-dependent. For example, larger juvenile turtles exhibit significantly higher survivorship than smaller individuals during the critical migration from nest site to water (Janzen, 1993), extreme phenotypes suffer increased mortality in lizards (Fox, 1975), and juvenile crabs move between structurally complex, sheltered habitats less frequently than larger adults because they are more vulnerable to predators (Fernandez et al., 1993). Such estimates of the relationship between survival and size enable us to predict and compare the probability of survival of individuals differing in size, to assess whether an optimum body size exists within the range of phenotypes expressed in a given population, and to test hypotheses about the fitness of individuals of different body sizes in different environments (Schluter, 1988).

Crabs of the genus *Cancer* (Crustacea: Decapoda: Brachyura) are ideal organisms with which to study the strength and form of natural selection on body size. First, crustaceans are highly morphologically variable and easy to catch, mark and recapture in large numbers (Gotshall, 1978). Thus, one can easily follow the survival of a large number of phenotypically variable individuals in the wild over time. Second, previous research has suggested that vulnerability to predation tends to decrease with increasing size in crustaceans (Orensanz and Galluci, 1988; Wahle and Steneck, 1992); moreover, many *Cancer* crab species actively select their habitat and modify their behaviour in response to inversely size-dependent predation risk (Richards, 1992; Chapter 2). Mortality rates and related life history variables are determined by size through size-dependent predation in many other indeterminately growing organisms (e.g., Brooks and Dodson, 1965). Consequently, *Cancer* crab survivorship and fitness may also be strongly influenced by size (e.g., Kirkpatrick, 1988). These lines of evidence suggest that *Cancer* crabs are likely subject to strong selection for body size. As such, they represent an excellent opportunity

to conduct a longitudinal (i.e. mark-recapture) study investigating the presence and form of natural selection on size. Mark-recapture is an effective method for studying selection pressures on morphological traits because it records individual phenotypic variation over a span of time during which selection may be taking place (Lande and Arnold, 1983; Arnold and Wade, 1984; Endler, 1986).

The purpose of this study was to assess the degree and type of selection on the adult body size of one of the most abundant Pacific *Cancer* species (red rock crab, *Cancer productus*) using mark-recapture techniques. *C. productus* ranges from Kodiak Island, Alaska to central California, and it is often encountered in gravely areas and on well-protected boulder beaches (Hart, 1982). Juveniles and smaller adults tend to prefer more structurally complex substrates, such as the rocky intertidal, while larger crabs are found from the middle intertidal to depths of 79 meters, primarily on more homogeneous habitats, such as sand and gravel. Voracious predators, they use their massive, powerful chelipeds to prey on the wide variety of gastropods and crustaceans found in these substrates (Lawton and Elner, 1985). *Cancer* crabs are themselves prey items in the diet of many predators, including rockfish, otters, octopi, sharks, sand stars and other crustaceans (Turner et al., 1969; Talent, 1982; Van Blaricom, 1982; Ambrose, 1984; Benech, 1986; Love et al., 1987). Red rock crabs frequently have damaged or missing appendages as the result of predatory attacks (Orensanz and Galluci, 1988), feeding on hard-shelled prey (Juanes, 1987), and intraspecific competition for mates (Juanes, 1987).

Orensanz and Galluci (1988) suggested that the adult body size of crabs of the genus *Cancer* is ultimately the result of adaptation to habitat-specific predation pressures. Small, presumably more vulnerable *Cancer* crabs are thought to inhabit more structurally complex substrates because such habitats contain a greater number of structural refuges that provide protection from predators. More structurally homogeneous habitats, in which refuges are relatively rare, may select for individuals that are larger in size, because larger crabs will not have to depend on the protection of structural refuges to the same degree.

Thus, I hypothesized that in an environment with a limited number of structural refuges (e.g., sandy bottom), larger *C. productus* individuals would survive better than smaller conspecifics because their increased size would decrease their relative risk of mortality due to predation.

MATERIALS AND METHODS

Capture and marking methods

To assess the degree of selective pressure on the size of *C. productus*, I caught and marked 565 adult (>80mm carapace width; adult size ascertained using Orensanz and Galluci's (1988) life-history schedules) red rock crabs at five mark-recapture locations within a bay on the east side of Dixon Island (48 51', 125 07'W) near Bamfield Marine Station, British Columbia, Canada. During a two month period (July and August of 1996), crabs were captured using five rectangular side-entry crab traps ($0.5m^3$) spaced at 100m intervals throughout the bay at depths varying from 15m to 30m and baited with frozen greenling (Hexagrammidae *sp*). I sampled in a bay with relatively narrow entrances rather than an inlet or open beach to reduce the amount of temporary emigration (temporary movement out of the study area during the experiment) in the population. All traps were positioned on the same type of substrate (sand), perpendicular to prevailing currents to attract crabs (Carroll and Winn, 1989), and sampled four times a day (at 0800, 1100, 1400, and 1700) for the first three weeks, and then twice a day (at 1100 and 1700) during the remaining four weeks. Due to the computational difficulty of analyzing such a large number of sampling occasions, capture histories were condensed into 7 weekly sampling periods for statistical analyses.

At first capture, all individuals were sexed, their degree of cheliped damage was noted (as presence or absence), and their carapace width and length were measured to the nearest tenth of a millimeter using Vernier calipers. Each crab was then individually

marked using a numbered T-bar tag (Floy Tag and Manufacturing) injected through the epimeral line, 2 to 6 mm from either the right of left coxopodite of the last walking leg, into the dorsal muscle above the interabdominal skeleton (Hurley et al., 1990). These tags are retainable through molts, and as such, the marks are not lost with the shedding of the exoskeleton. Crabs were then immediately returned to the area in which they were caught.

To estimate tag loss, forty randomly chosen crabs were marked with two tags, and if recaptured, the presence of both tags or the loss of one of the tags was noted. Only four of these crabs were recaptured, and all four individuals still had both tags intact. To assess the effect of tagging on molting, forty crabs were caught at a different location (Grappler Inlet) and observed in the lab for four months. Twenty of these crabs were tagged with the T-bar tag, and the frequency and success of molting were compared with the untagged individuals. All crabs that molted during the study were successful, regardless of the presence or absence of the tag, and no significant differences in molt frequency ($\chi 2=0.452$, df=1, p=0.798) were observed.

Differences in the location of capture between the sexes and between crabs with and without claw damage were analyzed statistically with Chi-Square tests.

Model theory and notation

Capture histories were analyzed using the program MARK (White and Burnham, 1997), which statistically tests and compares the fit of alternative models that compute conditional survivorship and recapture estimates independently. Under the Cormack-Jolly-Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965), which I used as a starting model, animals that emigrate from the study area are not available for recapture, and will appear to have died. Thus, the 'apparent' survival estimates calculated by MARK are the product of the probability of survival and (1-the probability of emigrating from the study area); in other words, 'apparent' survival is the probability that the animal remains alive and is available for recapture.

The notation for all models followed Lebreton et al. (1992), and survival and recapture probabilities were defined as:

ϕ_i = apparent survival; the probability that a crab alive and present in the study area during period i survives and is present in the area during period i + 1,

p_i = recapture rate; the probability that a crab present in the study area during period i is recaptured.

The Cormack-Jolly-Seber (CJS) model (Cormack, 1964; Jolly, 1965; Seber, 1965) was used as a starting model to test the significance of the independent variables of interest (sex, claw damage, and body size) in sequential model fitting (Table 1). Survival (ϕ) and recapture (p) probabilities are time (t) specific in the CJS model, thus the model is denoted by ($\phi_t p_t$). Group effects in survival or recapture probabilities (where the grouping variable was sex or degree of claw damage) are identified by the subscript notation (g), whereas (.) indicates that the probability of survival or recapture does not depend on any variable. For example, ($\phi.p_g$) indicates that survival does not vary over time or by group, and that the probability of recapture varies with group, but not time. Asteriks denote an interaction term, plus signs (+) indicate an additive effect, and $\phi(x)$ indicates a covariate (x).

Model selection and application

The CJS model assumes that:

1. Every individual has the same probability of being caught whether it is marked or unmarked,
2. Every marked individual has the same probability of surviving from time *t* to (*t*+1),
3. Individuals do not lose their marks, and
4. Sampling time is negligible in relation to the intervals between samples.

The laboratory and double-tag field experiments described above were used to test the third assumption, and the time spent handling and marking the animals was insignificant relative to the time between sampling periods, satisfying assumption 4. The remaining

assumptions of the full time-dependent CJS model ($\phi_t p_t$) were tested using the goodness-of-fit (GOF) tests in the program RELEASE (Burnham et al., 1987). The results of these analyses can detect both handling effects on survival (Brownie and Robson, 1983) and unequal catchability (Loery et al., 1987).

The results of the GOF tests and the laboratory and field tagging experiments indicated that all assumptions of the CJS model were met. Therefore, I proceeded to test the significance of the factors in the model and compare alternative models by sequential model fitting using the program MARK (White and Burnham, 1997). MARK determines the number of parameters in a model and calculates estimates of these parameters via numerical maximum likelihood techniques. The number of estimable parameters is then used to calculate the quasi-likelihood Akaike Information Criterion (QAIC). QAIC is

$$\left(\frac{-2\log(\text{Likelihood})}{c}\right) + 2K\left(\frac{2K(K+1)}{n_{ess} - K - 1}\right)$$

where c is the quasi-likelihood scaling parameter (corrects for extra binomial variation in the data), K is the number of parameters estimated, and n_{ess} is the effective sample size (White and Burnham, 1997). Models that differ in QAIC by more than a value of 2 are considered significantly different, and the most parsimonious model (lowest QAIC value) is taken as the better fit.

The estimates of apparent survival from the best-fitting model were used to compare the overall probability of survival among red rock crabs that differed in body size and claw condition. To assess whether an optimum body size existed within the range of phenotypes expressed in the study population, and to infer the strength and form of selection, if any, on body size in red rock crabs, estimates of apparent survival were plotted versus body size.

RESULTS

Nearly 20% (105 of 565) of the crabs that were marked and released were recaptured at least once by the end of this study. Eighteen crabs were recaptured twice, and one crab was recaptured a third time. At first capture, most crabs were caught at the traps nearest to the entrances to the bay ($\chi 2=73.75$, df=4, $p<0.001$). More males (408) were caught than females (157), and capture location differed significantly between the sexes ($\chi 2=11.17$, df=4, p=0.025), with more males than females caught at all traps.

One hundred and fifteen crabs (20.4%) displayed some degree of claw damage. The extent of the damage varied considerably among the crabs (from a broken dactyl tip to the loss of both chelipeds), but because I was interested only in the broad scale fitness effects of claw damage, all crabs with any cheliped injuries were pooled. Significantly more males (22.8%) than females (16.3%) exhibited some degree of cheliped damage ($\chi 2=5.39$, df=1, p=0.02), and large crabs (>140 mm carapace width) had injured chelipeds more often (32.9%) than their intermediate- ($\geq$110 mm and $\leq$ 140 mm carapace width) (20.3%) or small-sized (<110 mm carapace width) (14.0%) conspecifics ($\chi 2=12.36$, df=2, p=0.002).

The goodness-of-fit tests of the capture histories met the assumptions of the CJS model (TEST2 + TEST3; $\chi 2=13.59$, p=0.630); there was no significant heterogeneity in the capture, recapture or survival rates of marked and unmarked crabs. Thus, I was confident that the handling techniques did not affect mortality rates, that the behaviour of individuals near traps did not change, that previously caught crabs did not learn to seek out ('trap-happy') or avoid ('trap-shy') traps, and that trap position did not affect capture rates (Eberhardt, 1969; Carroll and Winn, 1989).

The CJS model was then used as a starting point for the analyses in MARK (White and Burnham, 1997). Initially, models of survival and recapture were constrained to be linear. The probability of survival and recapture did not significantly differ between the

sexes (Models 1-4, Table 8; $\chi 2=0.018$, $p>0.90$), so data for males and females were pooled in the following analyses. The extremely small $\chi 2$ value in my analyses of the effects of sex on survival and recapture suggest that there may be some dependence between male and female crabs (i.e. the presence of one sex affects the presence of the other). Red rock crabs are sexually dimorphic in morphology (maximum male carapace width: 200 mm; females: 158 mm; Jensen, 1995), and smaller *Cancer* crabs may be competitively inferior to larger conspecifics (Fernandez et al., 1993). Thus, the presence of a larger, more aggressive male in a baited trap may deter females from entering the same trap.

The inclusion of claw damage as a grouping variable in the basic linear model significantly increased model fit (Model 5, Table 8), as did the addition of carapace measures (length or width) as a covariate, although carapace length modeled survival and recapture significantly better (Model 10, Table 8) than did carapace width (Model 12, Table 8). Using carapace length as a covariate and claw damage as a grouping variable, I then fit a quadratic, rather than linear, model to the data (Model 13, Table 8). The quadratic model did not describe the variation in crab survival or recapture significantly better than any of the alternative models, nor did the inclusion of claw damage as a grouping variable in this quadratic model (Model 14, Table 8) significantly alter model fit. The linear model (Model 10, Table 8) was used to compare apparent survival among groups in subsequent analyses because it was a more conservative mathematical representation of crab survival and recapture than the quadratic model (Model 13, Table 8).

Crabs with damaged claws had a lower overall probability of survival ($\phi=0.908$) than crabs with no damage to their claws ($\phi=0.954$), but the probability of survival of both groups did not significantly vary over time (Model 10, Table 8). The probability of survival increased slightly with increasing body size for crabs with no claw damage (Figure 1; back logit transform of $y=0.78+1.47x$), but decreased with increasing size for damaged crabs (Figure 1; back logit transform of $y=1.88-2.38x$). Claw damage had no effect on the

Table 8. Summary of model selection for the capture-recapture data of individually marked red rock crabs, *Cancer productus,* in Dixon Island Bay, Barkely Sound, B.C. For model notation and explanation of calculations, see Materials and Methods (Deviance is the difference in the -2log(Likelihood) for the current model and the saturated model (model with a parameter for every encounter history); QAIC = quasi likelihood Akaike's information criterion).

Model	Number of parameters (np)	Deviance *	QAIC
I. Constrained linearly			
A. Using sex as the grouping variable			
1) ϕg*tpg	14	63.64	874.69
2) ϕg+tpg	14	67.24	875.51
3) ϕtpg+t	14	67.80	875.53
4) ϕ.pg	3	67.64	890.21
B. Using claw damage as the grouping variable			
5) ϕgpt	7	55.27	891.27
6) ϕtpt	7	57.62	893.62
(CJS model)			
7) ϕ.pt	7	58.10	894.10
8) ϕgp.	3	69.31	897.18
9) ϕ.p.	2	71.24	897.09
C. Using claw damage as the grouping variable and carapace width or length as a covariate			
10) ϕg,f(length)pt	10	849.43	869.76
11) ϕ.,f(length)pt	8	860.23	876.45
12) ϕg,f(width)pt	10	858.73	879.06
II. Quadratic; using carapace length as a covariate and claw damage as a grouping variable			
13) ϕg,f(length, length^2)pt	12	843.69	868.17
14) ϕ.,f(length,length^2)pt	9	849.91	868.18

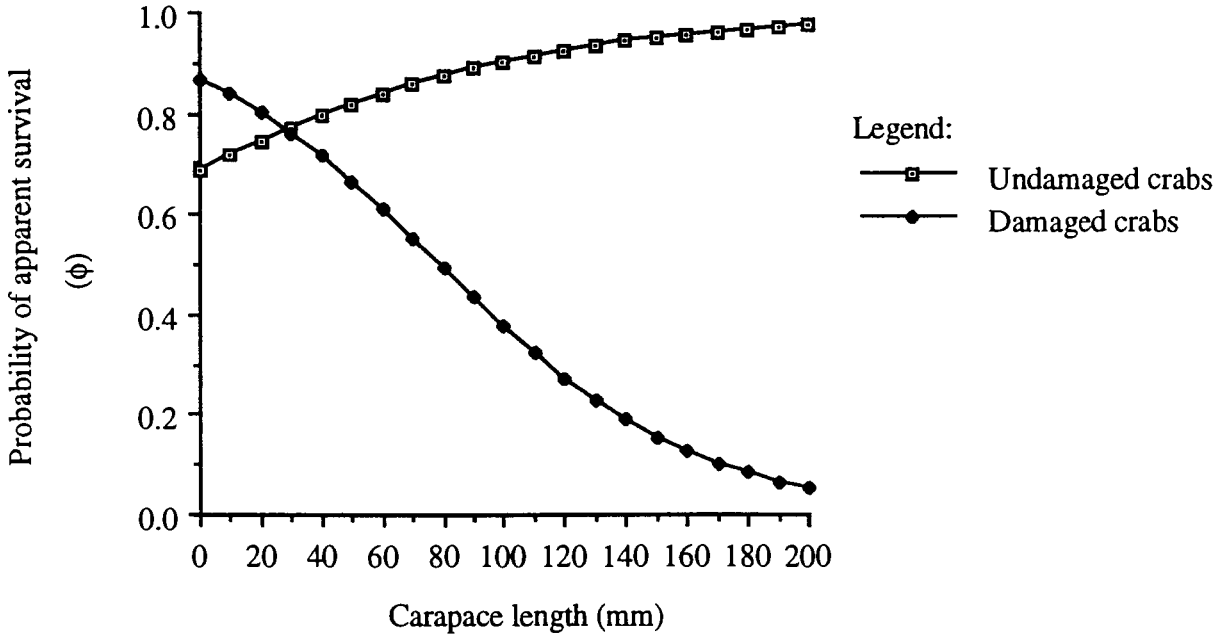

Figure 13. Probability of apparent survival for red rock crabs, *Cancer productus,* of varying size with and without claw damage.

probability of recapture, although recapture probabilities did decrease over the course of the study, from p=0.124 to p=0.031. This effect is likely the result of the decrease in sampling effort (from four times a day to twice a day) during the latter four weeks of the study, rather than a consequence of crabs learning to avoid the traps.

DISCUSSION

The results of this study indicate that there is weak directional selection for larger body size in both sexes of undamaged *C. productus*, and that individuals with damaged claws suffer a reduction in survivorship. These findings agree with the fitness implications of body size (Clutton-Brock et al., 1982; Hines, 1982; Drews, 1996) and physical injury (Smith, 1995) in many other organisms and provide the first evidence from the field that there is selection for body size in a species of *Cancer* crab.

In this study, larger crabs may have increased survivorship over smaller crabs because they are less susceptible to predation than smaller conspecifics (Carroll and Winn, 1989; Fernandez et al., 1993). However, the body size with the highest probability of survival is likely strongly dependent on habitat type. For example, in structurally complex environments, such as the rocky intertidal zone, individuals may be able to utilize structural refuges such as broken shells, rock crevices, and the underside of rocks, to avoid predators (Orensanz and Galluci, 1988). If predation is an important selective pressure, natural selection will likely favour body sizes that most effectively utilize these refuges. Caddy (1986) suggested that large refuges for crabs are rare. As a result, smaller individuals are likely selected for in structurally complex habitats. Conversely, because vulnerability to predation decreases with increasing size in many crustaceans (Orensanz and Galluci, 1988; Wahle and Steneck, 1992), larger phenotypes are likely selected for in structurally homogeneous substrates, such as sand and mud, which have fewer structural refuges

(Orensanz and Galluci, 1988). My study supports the second component of this argument: I found weak selection for increased body size in a population of adult *C. productus* inhabiting a sandy substrate.

Crabs with claw damage appeared to be selected against, particularly at larger body sizes. Claws are used in a wide variety of functions, including foraging, mate acquisition and defense, and protection from predators (Nations, 1975). Consequently, injury to or loss of a claw due to predation should greatly reduce fitness, as suggested by this analyses. Limb damage hinders the ability to escape from or defend against an attack by a predator in many animals (Dial and Fitzpatrick, 1984; Bildstein et al., 1989) and such damage can substantially lower individual fitness by reducing social status (Fox and Rotsker, 1982), foraging ability (Smith and Hines, 1991), growth rate (Smith, 1990), and fecundity (Dial and Fitzpatrick, 1981; Smith, 1992).

The decrease in the probability of apparent survival with increasing body size in crabs with damaged claws was unexpected. Larger *Cancer* crabs are less vulnerable to predators than smaller individuals, except when the exoskeleton is soft, during molting (Carroll and Winn, 1989). However, severe limb damage triggers precocial molts in many crustacean species, particularly in larger, older individuals, in which the intermolt period may be shortened by up to 40% (Skinner, 1985). Thus, claw damage may lower the probability of apparent survival in larger crabs by stimulating molting and increasing the risk of mortality due to predation.

These results are consistent with the hypothesis that predation is one of the major selective pressures on crab body size. Transplanting individual crabs to different environments and enclosing or tethering these animals in these habitats would greatly aid in more conclusively resolving the importance of predation and habitat type to red rock crab survival. Furthermore, because size is the dominant ecological attribute of individuals in many species (Werner and Gilliam, 1984; Sauer and Slade, 1987; Sebens, 1987), it is likely subject to many different selective forces. For example, the ability to acquire mates

(Salmon, 1983) and locate and defend resources (Dingle, 1983) is size-dependent in many marine crustacean species. Thus, future research on the size adaptations of *Cancer* crabs should include analyses of other potential selective pressures involved in the evolution of body size. As a final caveat, this study was limited to adult red rock crabs, and therefore was not able to determine the extent to which selection acted on size versus growth rate. A mark-recapture experiment that followed an entire population, including juveniles, over a longer period of time, would be better able to resolve this difference.

However, the results of this study are an initial attempt to resolve the survivorship implications of body size in one species of *Cancer* crab. Many important life history traits, such as foraging ability or habitat use, are often strongly influenced by an organism's morphology (Creswell and Marsden, 1990; Losos, 1990). Thus, this research has provided a basis with which future studies can test hypotheses about the role of size in the ecological diversification of *Cancer* crabs.

CHAPTER 5: CONCLUSIONS

Taken together, the results of this study provide strong support for the hypothesis that predation is one of the primary selective pressures underlying the variation in body size and habitat use of *Cancer* crabs (Orensanz and Galluci, 1988). Using phylogenetic reconstruction of *Cancer* crab habitat use and body size, I inferred that lineages in which habitat shifts to more homogeneous substrates were hypothesized to have occurred were accompanied by increased morphological change towards larger body sizes. This association suggests that *Cancer* crabs have adapted to habitats that lack structural refuges by increasing in size. In laboratory experiments, *Cancer* crabs modified their behaviour in response to perceived predation risk. The smallest *Cancer* species exhibited the greatest changes in habitat use, activity levels, and depth of burial in the presence of a predator, indicating that the perception of predation risk was inversely proportional to crab size. Finally, mark-recapture analyses found weak directional selection for larger individuals in a wild population of *Cancer* crabs on a structurally homogeneous substrate; in other words, larger crabs had a slightly higher probability of apparent survival in a habitat lacking structural refuges. Synthesis of these findings suggests that predation is indeed a significant selective pressure on the patterns of covariation between habitat use and body size in the genus *Cancer*.

These results do not preclude the possibility that the selective pressures of food availability and competition are also operating on *Cancer* crab morphology and ecology. However, my thesis has questioned the priority of these selective agents and demonstrated that they are certainly not the only processes underlying the patterns of ecomorphological variation seen in marine crustaceans.

Future research can test and expand upon these conclusions by:

1. Conducting a longer-term mark-recapture experiment on both juvenile and adult crabs to determine the strength and form of selection on growth rate versus size. This experiment could examine the ontogenetic changes in the probability of survival, accounting for age effects in size-related survival differences.

2. Studying the relationship of other selective pressures on body size. For example, optimal body size may involve a trade-off between foraging requirements and defensive capabilities. By examining the strength of such alternative selective pressures, we may be able to better model the adaptive function of a given phenotype.

3. Investigating habitat-specific rates of predation in the laboratory or in the field by following the survival of tethered or enclosed animals on substrates of varying structural complexity. Such studies provide the opportunity to directly test the assumption that mortality due to predation varies with habitat complexity.

4. Collecting cytochrome oxidase I sequence from additional *Cancer* species, particularly the South American and Japanese crabs, to add to the phylogenetic analyses. These taxa will enable us to test the generality of the association between the rate and direction of morphological change and habitat use in *Cancer* crabs.

In summary, my thesis centered on understanding the role of one selective pressure in the evolution of morphological and ecological diversity among the crabs of the genus *Cancer*. By focusing on the differences within one diverse group of animals, one can gain a more complete comprehension of the selective forces that shape the general patterns of diversity we see in nature.

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Appendix 1. Mitochondrial cytochrome oxidase I (COI) sequence used in the molecular analyses. PC=*Petrolithes cinctipes*, HN=*Hemigrapsus nudus*, CB=*Cancer branneri*, CA=*C. antennarius*, CO=*C. oregonenesis*, CPa=*C. pagurus*, CP=*C. productus*, CG=*C. gracilis*, CN=*C. novaezealandiae*, CBo=*C. borealis*, CM=*C. magister*.

Taxon Position

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          1                                                                                                   100
PC,   -ggaggatttggaaattgat tagttcccttaatattagga gcccccgatatggctttccc tcgtataaacaacataagat tttgattacttcccccatct
HN,   -ggaggatttggaaattgat tagttccactaatactaggg gcgccagacatagcattccc tcgtataaacaatataagat tttggcttttaccgccctct
CB,   -------------------- -------------------- -------------------- -------------------- --------------------
CA,   -ggaggatttggaaattgat tagttcctcttatattagga gctcctgatatagctttccc tcgtataaacaatatgagtt tttgactcttacctccttct
CO,   -ggaggatttggaaattgat tagttcccttaatactaggg gcacctgatatggctttccc ccgaataaataatataagat tttgacttttaccccccttca
CPa,  aggaggatttggaaattgat tagttcctcttatgctggga gcgcctgacatagcctttcc tcgaataaataacataagtt tctgattattacccccttca
CP,   -ggaggatttggaaattgat tagttcctcttatattagga gcccctgatatagctttccc gcgtataaacaacataaggt tttgattattacccccttct
CG,   -ggaggatttggaaattgat tagttcccttaatattagga gcccctgatatagctttccc tcgaataaatataataagat tttgacttcttcctccctcc
CN,   -------------------- -agttcctcttatattagga gctcctgatatagctttccc tcgtataaacaatatgagtt tttgactcttacctccttct
CBo,  -------------------- -agtcccttaatattagga gcacctgatatagcctttcc tcgaataaataatataagtt tctggttactacccccttca
CM,   -ggaggatttggaaattgat tagttcccctaatgctagga gcacccgatatagctttccc tcgtataaataatataagtt tctgactattacctccttct

        101                                                                                                   200
PC,   ctaacactccttctaataag aggaatagttgaaagaggtg ttggaacaggatgaactgtt tatccacctctttctgccag gattgcacacgcaggagctt
HN,   ttatcccttctttttaacaag aagaatagtagagagtggag ttggcacagggtgaactgtt taccctcccctctccgctgc tattgcccacgctggcgcct
CB,   -------------------- -------------------- -------------------- ---cctcctttagcaggagc tattgctcat--cggggcct
CA,   ctaacattactcctttataag aggtatagtagaaagaggag ttggaacaggctgaactgtt taccctcctttagcaggagc tattgctcatcgtggcgcct
CO,   ttaacactgcttcttataag aggtatggtagaaagagggg ttgggacaggatgaaccgtc taccctcctttagcgggggc tattgctcacgcaggggcct
CPa,  ctaacactacttcttataag aggaatagtagaaagaggag ttggaacagggtggactgtt tatcccccttagcaggtgc tattgcccacgctggagcct
CP,   ctaacccttcttcttataag aggattagtagaaagaggtg ttggaactggctgaactgtc taccctcctttagcaggtgc tattgcccatgcaggtgcct
CG,   ttaacattgctccttataag aggtatagtagaaagtggag ttgggacaggatgaactgtt tnccctcctttggcaggtgc tattgctcacgctggagcct
CN,   ctaactttacttcttataag aggaatagtagagagagggg ttggaacaggttggactatc taccctcccctagcgggcgc tattgctcatgctggagcct
CBo,  ttaaccctactcctttataag aggaatagtagaaagagggg ttggaacaggttggactgtt taccctcctttagcaggtgc tattgcccacgctggagctt
CM,   ttaaccttacttcttataag aggaatagtagaaagaggag taggaacaggatggaccgtc taccctcccttagcgggggc tatcgctcatgccggagcct

        201                                                                                                   300
PC,   ctgttgacatggggattttc tctctccatcttgcaggtat ttcttcgattctaggtgcag taaatttttataacaacagta attaatatacgaccgaaagg
HN,   ctgtcgatctcgggatttttc tcactacatcttgcaggggt ctcttcaatttttaggagcag taaatttttataactaccgtt attaatatacgatcttacgg
CB,   cagttgacataggaatttttc tccttacatttagcaggggt ttcttctatcttaggagctg taaatttttataacaactgta attaatatgcgatcctttgg
CA,   cagttgatataggaatttttc tccttacacttagcaggagt ttcttctatcttaggagctg taaacttttataacaaccgta attaatatacgatcttttgg
CO,   cagtagacataggaatttttt tccttgcatttagcaggggt gtcctctattttaggggctg taaacttttataacaactgtg attaacatgcgatctttttgg
CPa,  cagtagatatagggatttttt tctctccatttagcaggagt ttcttctatttttaggagctg taaatttttataacaactgta atcaacatacgatcatttgg
CP,   cagtagatatagggatcttt tcgcttcacttggcaggagt ttcctcaatcttaggagctg taaatttttataacaaccgta attaatatacgatcatttgg
CG,   cagttgatataggaatttttc tccttacacttagcaggagt ttcttctatcttaggggctg taaacttttataacaactgtg attaatatacggtcctttgg
CN,   cagtagatatgggaatctttt tctcttcatttagcaggagt ttcttctattctaggagctg taaatttttataacaactgta attaatatgcgctcatttgg
CBo,  cagtggacatggggatttttt tctcttcatttagctggggt ttcttcaatcctaggagctg tgaatttttataacaactgta atcaacatacggtcatttgg
CM,   cagtcgatataggaatcttt tcccttcatttacgtggggt ttcctctattttaggagcag taaatttttataacaaccgta attaacatacgttcttttgg

        301                                                                                                   400
PC,   agttacaatagaccgtatgc cacttttcgtttgagctgtt tttattactgctattctttt acttctttctttacctgtct tagccggagcaattaccatg
HN,   gaggacaatggaccaaatac ctctttttgtgtgagctgta ttcattactgctattctctt acttttatctcttccagttc tagcaggtgctatcactatg
CB,   gataaccttagatcaaatac ctctcttcgtttgagctgta tttattactgctatcctatt actcctctctctccctgttc tagcaggtgcaattactata
CA,   aataaccttagatcaaatac ctctctttgtttgagctgta tttattactgccatcctatt acttttatctctccctgtct tagcaggtgcaattactata
CO,   tataaccctagatcaaatac ctctttttcgtttgggctgta tttattacagctatcttact actactctctctgcctgttt tagcaggggcaattactata
CPa,  aataactctagaccaaatgc cacttttttgtctgagctgtc tttattactgctatccttttt acttctatcactccctgtct tagctggagccatcactatt
CP,   aataactctagaccaaatac cacttttttgtttgagccgta tttattactgccatcctttt acttttatctctcccagtat tagcaggagctattactata
CG,   aataaccttagaccaaatac ctctctttgtttgagctgta tttattaccgctatcctgtt acttttatctctccctgttt tagcaggtgcaattactatg
CN,   gataactttagaccaaatac cacttttttgtttgagctgta tttattactgctattctttt acttttatctctccctgttt tagcaggagcaattactata
CBo,  gataagcttagaccaaatac cacttttttgtttgggctgtg tttattactgccatcctttt gctgctatccctccctgttt tagccggagctattaccata
CM,   gataactttagatcaaatac cactcttcgtttgagctgta tttatcaccgctattctttt actactatcccttcctgtac tagcaggtgccatcactata

        401                                                                                                   500
PC,   cttctaacagaccgaaatct taatacctcgtttttttgacc ccgcggagg-tggagatcca gtactttaccaacatttatt ttgattcttcggtcaccctg
HN,   ttgcttactgatcgaaattt aaatacatctttctttgacc ctgctggcg-gggggggacca gttttataccaacatttatt ttggttctttggtcatcctg
CB,   ttattaactgatcgaaatct taatacttctttctttgacc ccgcaggag-gggtgaccct gttctttatcaacaccttttt ttgatttttgggcacccag
CA,   ttattgactgaccgaaatct taatacctcattctttgacc ccgcagagg-aggagaccct gttctttaccaacaccttttt ctgatttttgg-cacccag
CO,   ttattaactgaccgaaacct taatacttctttttcgacc cagcggagg-gggtgatcct gttctctatcaacaccttttt ttgattcttcgggcaccctg
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        501                                                                                                   600
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HN,   aagtttatattttgatctta cctgccttcggaatgatttc tcatattgttagtcaagaat ctggtaaaaaagaatctttt ggtactttgggtatgatttta
CB,   aagtatatattcttatttttg cctgcttttggaataatttc ccatattgtaagacaagaat ctgggaaaaaagagtcctttt gggaccctttggataatttta
CA,   aggttatatattcttatttta cctgcttttggataatttc tcatattgtgagacaagaat ctggtaaaaaagagtctttt gggaccctaggaataattta
CO,   aagtttatattctcattttt cctgcttttgggataatctc tcatattgatagacaagaat ctggtaaaaaagagtctttt gggacccttgg-atgattta
CPa,  aagtttatattcttatttta cccgcttttggtataatctc tcatattgtaagtcaagaat ctggaaaaaaagaatctttt ggtaccttaggaataattta
CP,   aagtatatattcttatttta ccggctttggaataatttc tcatattgtaagccaagaat ctgggaaaaaagaatctttt gggaccctaggataatcta
CG,   aagtctatattcttatctta cctgctttcggaataatctc ccatattgtaagacaagaat ctggtaaaaaagaatccttt gggaccccttggaataattta
CN,   aggtctatattctaatttta cctgcttttggtataatctc tcatattgtaagtcaagagt cggggaaaaaagaatccttt gggaccctaggaataattta
CBo,  aagtctatattcttatttta ccggctttggaataatttc tcatattgtaagccaagaat ctgggaaaaaagaatctttt gggacccgaggaataattta
CM,   aagtgtacattcttattcta cctgctttcggcataatctc tcatattgtaagccaagagt ctggaaaaaaagaatctttt ggaactttaggaataatcta
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   601                                                                                                  700
PC,  tgcaatattagctattggaa tcttaggatttattgtctga gctcatcacatgttttactgt tggaatagacgttgacacgc gagcttacttcacctcagca
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CB,  cgctatattggccattggta ttttaggctttgtggtctga gctcatcacatgtttacagt tggaatggacgttgatactc gagcttacttttacctcagct
CA,  cgccatattagctattggaa tcctagggtttgttgtttga gcacaccatatatttacagt gggtatagacgtagacaccc gagcctatttttacctcagcc
CO,  tgctatattagctattggta tcttaggttttgttgtttga gcccaccacatatttacagt tggaatggatgttgatactc gcgcttattttacttccgcc
CPa, tgctatactagccattggta ttctaggatttgttgtttga gctcatcatatatttacagt tggaatagatgtagatactc gcgcttactttacctccgcc
CP,  tgctatattagccatcggta ttttaggctttgttgtctga gcccaccatatatttacagt tggaatagatgttgataccc gagcttacttcacctcagcc
CG,  tgctatactagccattggta tcttaggttttgtagtctga gcccaccatatattcacagt cggaatagacgttgatactc gagcttacttttacctcagct
CN,  cgccatattagctattggaa tcctagggtttgttgtttga gcacaccatatatttacagt gggtatagacgtacacaccc gagcctattttacctcagcc
CBo, tgctatactagccattggta ttctaggatttgttgtctga gctcaccatatatttacagt cggaatagatgtagatactc gggcttactttacctcagcc
CM,  tgctatgttagccattggta ttttaggatttgttgtttga gctcatcatatatttacagt tggtatagacgtcgatacgc gagcttatttttacttcagcc

   701                                                                                                  800
PC,  acaataattattgctattcc cacaggaattaaaatttttа gttgactaggaactcttcag ggtaatcaaatagtctacag accctctataatttgagctc
HN,  acaataattattgctattcc cactggaattaaaatttttca gatgattaaggactctacat ggtacgcagatgaattactc cccgtccctattatgagccc
CB,  actataattattgccgttcc cactgggattaaaatcttta gttgactaaggactctccac ggaactcaaattaatttttag accttcaatgctttgagctc
CA,  actataattattgctgttcc caccggcatcaaaatttttа gttgattgagcacactccat ggaactcaaattaacttcag tccatctatactttgggccc
CO,  actataattattgctgttcc aactggaattaaaatcttta gttgactaagaactctccac ggaactcaaatcaattttag cccttcaatactttgagccc
CPa, actataattattgctgtacc taccggtattaaaatttttа gttggttaagaactctacat ggaacacaaattaactttag gccttctatactttgagccc
CP,  actataattattgctatccc cactggtattaaaatttttca gttgactaagaactcttcat ggaacacaaattaactttag gccttcgatactttgagccc
CG,  actataattattgccgtccc tactggaattaagatcttca gttgactaagaaccttcac ggaactcaaattaactttag accctcaatactttgggcct
CN,  actataattattgctgttcc caccggcatcaaaatttttа gttgattgagcacactccat ggaactcaaattaacttcag tccatctatactttgggccc
CBo, actataattattgctgtccc taccggaattaaaatttttа gttgattaaggacacttcat ggaactcaaattaattttag gccttctatgctctgagccc
CM,  actataattattgctgttcc tactggaatcaaaatttttа gttggctaagcactcttcac ggcacacaaatcaacttcag tccttctatactttgggctt

     801                                                                                                  900
PC,  taggttttatttttcttttt actgttggaggtcttacagg agtaattttagcaaactctt caattgacaccgtccttcat gacacatactatgtggtagc
HN,  tagggtttatcttcttattt actatcggaggattaactgg ggtagtactagctaattcat cgattgatattattctccat gatacatactatgtagttgc
CB,  taggttttatttttcttttc actgtaggaggattaactgg agtagttctagctaactctt ctcttgatattattcttcat gatacttactacgttgttgc
CA,  taggttttatttttctattc acagtggggggcctaactgg tgtagttttagccaattctt ctattgatatcatcctccat gatacttattatgttgttgc
CO,  taggtttcatttttcttttt actgtaggtgggttaacagg agtagttctagctaattctt ctattgatattatccttcat gacacttattatgttgttgc
CPa, taggttttatcttcttattt acagtaggtggattaactgg tgtagttttagctaattctt ccattgatattatcctccac gatacatattatgttgtagc
CP,  taggtttcatcttcctattt acagtaggaggactaactgg tgttgtattggccaactcct ctcttgacattattctccac gatacttattatgttgtagc
CG,  tagggtttatttttcctttt actgtaggaggattaactgg agtagttctagctaactctt ctatcgacattattcttcat gatacttactatgttgtagc
CN,  taggttttatttttctattc acagtgggggcctaactgg tgtagttttagccaattctt ctattgatatcatcctccat gatacttattatgttgtttgc
CBo, taggttttatttttttattt acagtaggaggattaacggg agttgttttagctaactctt caattgatattatcct---- --------------------
CM,  taggttttatcttcctattt acagtaggaggactaactgg agtagttttagccaattctt ctcttgatattattctccac gatacttattatgttgtttgc

     901                                                                                                 1000
PC,  tcattttcactatgtattat caatgggcgcagtattcgga attttcgccggtattaccca ctgattcccctattcacag gtctttccgttaatcccaaa
HN,  tcactttcattatgttcttt caataggagctgtattcgga attttcgctggggtagcaca ctgattctccttaataaccg gcctatccatgaaccctaaa
CB,  ccattttcactatgttctat ccataggagctgtgttcggt attttcgccggtatcgctca ttgattcccttttattcaccg gagtatctttaaaccctaag
CA,  tcatttccattacgtattat ctataggagctgtttttggt atttttgccggaatcgccca ttgatttcctcttttttactg gagtgtctttaaaccccaaa
CO,  tcatttccattatgttctat ctataggggctgtctttggg atcttcgccggtattgctca ctgattcccctttattcaccg gggtctctttaaaccctaaa
CPa, tcatttccattatgtattat cgataggagctgtatttggt atttttgctgggatctccca ttgattcccctttatttactg gggtttccttaaaatcctaaa
CP,  ccactttcattatgttttat ctataggagctgtttttggt atttttgccggaatctctca ttgatttcccctgttcaccg gtgtatccttaaacccaaaa
CG,  acactttcactatgtcctat ccataggtgctgtcttcggg attttcgccggaattgctca ttgattcccttttatttactg gagtt---------------
CN,  tcatttccattacgtattat ctataggagctgtttttggt atttttgccggaatcgccca ttgatttcctcttttttactg gagtgtctttaaaccccaaa
CBo, ------------gttttat ctataggtgctgtatttggt atttttgccggtatctccca ctgattcccctttattcaccg gggtttccttaaaccctaaa
CM,  ccatttccattacgttctat ctataggagctgtcttcgga atttttgctggaatcgccca ttgattcccttttttacag gtatatccttaaaccccaaa

  1001                                                                1072
PC,  tgattaaaaattcacttttc aactatattcctaggagtaa atttaacttttttttcctcaa cacttttttagg
HN,  tgattgaaagttcatttctt agttactttcatcggagtaa atctcacattcttccccaaa catttcctagg
CB,  tgacttaaaattcactttct tgtta---------------- -------------------- -----------
CA,  tgacttaaaatccactttct tgtaatgtttatcggagtta atactactttttcccgcaa catttttagg
CO,  tgacttaaaatccactttct tgttatgtttattggggtaa atactacttttcttttcctcaa catttctttagg
CPa, tgacttaaaatccactttct tgttatatttattggagtaa acataacttttttcctcaa catttcttagg
CP,  tgacttaaaatccatttttt tgttatatttacaggagtta acctcacttttttccctcaa catttttttagg
CG,  -------------------- -------------------- -------------------- -----------
CN,  tgacttaaaatccactttct tgtaatgtttatcggagtta atactacttttt-------- -----------
CBo, tgacttaaaatccactttct tgtgatatttatcggagtta atataacttttttccctcaa catttttttagg
CM,  tgacttaaaatccatttttct tgtaatatttattggggtta atacaacttttt--------- -----------
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Appendix 2. Characters and states used in the morphological analyses. All multistate characters (except 39) are ordered. Sources of information: Nations, 1975; Lawton and Elner, 1985 (characters 40-44), Jensen, 1995, and references therein.

1. Number of anterolateral teeth
   0: twelve
   1: ten
   2: nine
   3: three
   4: none
2. Number of posterolateral teeth
   0: none
   1: rudimentary
   2: one
   3: two
   4: three
3. Separation of anterolateral teeth
   0: no
   1: at base
   2: with fissures at base
   3: only by fissures
   4: not applicable
4. Curvature of anterolateral teeth
   0: absent
   1: present
   2: not applicable
5. Anterolateral teeth tip shape
   0: round
   1: single spine
   2: jagged
   3: not applicable
6. First anterolateral tooth shape
   0: acute
   1: triangular
   2: round
   3: not applicable
7. Carapace granule
   0: absent
   1: present
8. Number of dactyl teeth
   0: four
   1: five
   2: six
   3: seven
   4: eleven
   5: twelve
   6: many small
9. Outer dactyl carinae
   0: absent
   1: present
10. Outer dactyl ridges
   0: absent
   1: present
11. Outer dactyl setiferous pits
   0: absent
   1: present
12. Outer dactyl setiferous grooves
   0: absent
   1: present
13. Inner dactyl setiferous pits
   0: absent
   1: present
14. Number of dactyl spines
   0: none
   1: many small
   2: many large
15. Number of finger teeth
   0: four
   1: five
   2: six
   3: seven
   4: ten
   5: eleven
   6: many small
16. Outer finger carinae
   0: absent
   1: present
17. Outer finger ridges
   0: absent
   1: present
18. Inner finger setiferous pits
   0: absent
   1: present
19. Number of outer manus carinae
   0: none
   1: four
   2: five
   3: six
   4: seven
20. Number of outer manus setiferous pits
   0: absent
   1: present
21. Inner manus carinae
   0: absent
   1: present
22. Inner manus ridges
   0: absent
   1: present
23. Inner manus setiferous pits
   0: absent
   1: present
24. Manus spines
   0: absent
   1: present
25. Outer carpus carinae
   0: absent
   1: present
26. Outer carpus ridges
   0: absent
   1: present
27. Carpus spines
   0: absent
   1: present
28. Merus spines
   0: absent
   1: present
29. Frontal teeth shape
   0: rounded
   1: blunt
   2: triangular
   3: acute
   4: none
30. Degree of production of front of carapace
   0: none
   1: little
   2: moderate
   3: high
31. Degree of carapace aerolation
   0: none
   1: little
   2: moderate
   3: high
32. Carapace shape
   0: oval
   1: wide, sides concave
   2: round
33. Carapace hair
   0: absent
   1: present
34. Cheliped hair
   0: none
   1: little
   2: moderate
   3: high
35. Leg hair
   0: none
   1: little
   2: high
36. Dense finger material
   0: none
   1: <25% of finger
   2: <50% of finger
   3: >50 % of finger
   4: to proximal tooth
   5: to base of finger
37. Dense dactyl material
   0: none
   1: <25% of dactyl
   2: <50% of dactyl
   3: >50 % of dactyl
   4: to proximal tooth
   5: to base of finger
38. Finger tip colour
   0: absent
   1: present
39. Male carapace size
   0: small (<75 mm width)
   1: medium (≥75 x ≤180 mm width)
   2: large (>180 mm width)
40. Relative leg length
   0: small (<1.10)
   1: medium (≥ 1.10 x ≤ 1.20)
   2: large (> 1.20)
41. Relative claw size
   0: small (< 0.230)
   1: medium (≥ 0.230 x ≤ 0.280)
   2: large (> 0.280)
42. Mechanical advantage
   0: small (<0.340)
   1: medium (≥ 0.340 x ≤ 0.365)
   2: large (> 0.365)
43. Relative dactyl length
   0: small (< 0.500)
   1: medium (≥0.500 x ≤ 0.550)
   2: large (> 0.550)
44. Relative propodus height
   0: small (< 0.460)
   1: medium (≥ 0.460 x ≤ 0.500)
   2: large (> 0.500)

Appendix 3. Morphological data matrix. † denotes outgroup taxa, and * indicates those species for which molecular data was also available. Refer to Appendix 2 for character and state names.

P. cinctipes †	4042331601000060000000000101231201100000?????
H. nudus †	3011101400110050000000000010401201000000?????
C. antennarius *	2111101100111000114110000011122102244110221 2
C. branneri *	2111101301111221113011011011222113244102101 0
C. borealis *	2310211110111111014000010012130000441202212
C. gracilis *	2310011110111020103000010010011000000012000 0
C. magister *	1010211300110230113000111011311000??0210000
C. novaezealandiae *	1120211210111111014000010011211000044 11?????
C. oregonensis *	0011201100101000114000000010113010155102212 2
C. pagurus *	1130021000110010102000000011031100144120111 1
C. productus *	1120121000101000113010101010031100133120121 1
C. anthonyi	2121011000101000114110000011212000124121220 2
C. davidi	2220111201010110104000 01?1000110????????????
C. amphioetus	2410000101011101114000011011113100244 1??????
C. granti	2011201200010000003000011110222 1????????????
C. jordani	2311101201511010114100 01?0102221122331??????
C. fissus	2220021??????????000000001003 11????????????
C. polyodon	2111101311311010104000011011222113233 1??????
C. plebejus	2110211300?0?1100?00???110110110000111??????
C. porteri	2120221100 11?0100?11????011103100055 1??????
C. japonicus	0020021000 11?0010?10???1001?033100021 1??????
C. tumifrons	0120001001 21?0001?10???1011?133100044 1??????
C. nadaensis	2311101101 61?0110?11???110102221000??0??????
C. irroratus	2310121000 10?0001?30???0111?0111000111110000
C. bellianus	1120221101 11?1100?21???111112330022551??????
C. urbanus	2111201??????????????????????232????????????
C. danai	2010211??????????????????????31100??????????
C. gibbosulus	2111101010 11?0010?20???1101?122113?????????
C. dereki	2311101??????????????????????3311??????????
C. jenniferae	2120111??????????????????????210????????????
C. edwardsi	2420211110 11?0001?40???0011?211100033 1??????
C. marri	???0???3000000 1?00300011010?????0?????????
C. allisoni	???????0001110001 1?00000??????3????551??????
C. garthi	???????5000102????????????????1?0????????????
C. yanceyi	????????????????????400000?????22????????????
C. durhami	???????3000002401?3000111010?????????0??????
C. coosensis	???????3001002500030100110 1??1?0???301??????
C. chaneyi	???????0001011001140 0??0000????????221??????

Appendix 4. Summary of significance values for the differences in the mean proportion of time spent in each habitat, activity, and burial depth among the four crab species, with and without the predator present.

I. Among species comparisons				II. Within species comparisons				III. Before and after introduction of predator			
Independent variable	Degrees of freedom	F	p	Independent variable	Degrees of freedom	F	p	Independent variable	Degrees of freedom	F	p
A. Habitat (without predator)				A. *C. oregonensis*	(without predator)			A. *C. oregonensis*			
Sand	3	4.589	0.004	Habitat	3	134.242	<0.001	Sand	1	7.650	0.007
Mud	3	2.629	0.052	Activity	3	29.676	<0.001	Mud	1	0.528	0.470
Rock	3	10.284	<0.001	Depth of burial	3	3.336	0.021	Rock	1	4.755	0.032
Border	3	1.178	0.320	B. *C. gracilis*	(without predator)			Border	1	0.190	0.664
B. Activity (without predator)				Habitat	3	5.835	0.001	Standing	1	8.844	0.004
Walking	3	9.084	<0.001	Activity	3	61.948	<0.001	Walking	1	13.983	<0.001
Standing	3	3.320	0.021	Depth of burial	3	3.202	0.025	Burial	1	20.020	<0.001
Burial	3	6.496	<0.001	C. *C. productus*	(without predator)			B1	1	0.602	0.440
C. Depth of burial (without predator)				Habitat	3	32.868	<0.001	B2	1	0.276	0.601
B1	3	2.096	0.103	Activity	3	28.278	<0.001	B3	1	0.529	0.469
B2	3	2.145	0.096	Depth of burial	3	2.102	0.102	B4	1	15.376	0.000
B3	3	3.486	0.017	D. *C. magister*	(without predator)			B. *C. gracilis*			
B4	3	0.947	0.419	Habitat	3	10.106	<0.001	Sand	1	0.045	0.833
D. Habitat (with predator)				Activity	3	139.658	<0.001	Mud	1	0.591	0.444
Sand	3	8.063	<0.001	Depth of burial	3	2.426	0.067	Rock	1	0.121	0.728
Mud	3	1.619	0.187	E. *C. oregonensis*	(with predator)			Border	1	0.025	0.874
Rock	3	15.036	<0.001	Habitat	3	189.384	<0.001	Standing	1	7.848	0.006
Border	3	2.060	0.107	Activity	3	2.951	0.034	Walking	1	5.182	0.025
E. Activity (with predator)				Depth of burial	3	0.753	0.522	Burial	1	12.296	0.001
Walking	3	2.063	0.107	F. *C. gracilis*	(with predator)			B1	1	3.250	0.075
Standing	3	0.636	0.593	Habitat	3	6.903	<0.001	B2	1	0.005	0.942
Burial	3	1.145	0.332	Activity	3	274.086	<0.001	B3	1	3.017	0.086
Aggression	3	5.397	0.001	Depth of burial	3	3.445	0.018	B4	1	4.048	0.047
F. Depth of burial (with predator)				G. *C. productus*	(with predator)			C. *C. productus*			
B1	3	1.586	0.194	Habitat	3	45.741	<0.001	Sand	1	0.223	0.638
B2	3	1.522	0.211	Activity	3	132.839	<0.001	Mud	1	0.891	0.348
B3	3	2.631	0.052	Depth of burial	3	3.348	0.020	Rock	1	1.363	0.246
B4	3	2.711	0.047	H. *C. magister*	(with predator)			Border	1	2.836	0.096
				Habitat	3	8.609	<0.001	Standing	1	11.660	0.001
				Activity	3	277.306	<0.001	Walking	1	14.056	<0.001
				Depth of burial	3	2.972	0.033	Burial	1	18.762	<0.001
								B1	1	0.890	0.348
								B2	1	3.512	0.064
								B3	1	1.750	0.189
								B4	1	3.530	0.064

Appendix 4. continued

III. Before and after introduction of predator

Independent variable	Degrees of freedom	F	p
C. *C. magister*			
Sand	1	0.007	0.934
Mud	1	0.725	0.397
Rock	1	0.036	0.849
Border	1	0.269	0.606
Standing	1	1.955	0.165
Walking	1	2.332	0.130
Burial	1	2.984	0.088
B1	1	0.028	0.868
B2	1	1.000	0.320
B3	1	0.092	0.763
B4	1	1.300	0.257