

Why do decapod crustaceans prefer small-sized molluscan prey?

Francis Juanes *

Marine Sciences Research Center, State University of New York, Stony Brook, New York 11794-5000, USA

ABSTRACT: A survey of studies examining crab and lobster predation on hard-shelled molluscs indicated that most predators prefer small-sized prey when offered a range of sizes. I suggest that this pattern of preference for small-sized prey can be explained by considering the mechanical cost of predation. If predation costs are assumed to be non-renewable, then the probability of exhausting them can be included as an additional parameter in the classical diet breadth model. The importance of predation costs in determining prey size selection can be extended to other predators that use mechanical means to attack their prey.

INTRODUCTION

Prey size selection is an important component in the process by which communities are structured by predation (Paine 1974, 1976, Virnstein 1977, Summerson & Peterson 1984, Sih et al. 1985, Hines et al. 1990). Foraging theory (Stephens & Krebs 1986) has provided relatively simple models that can predict prey size (and type) preferences for generalized predator-prey combinations. The currency used to predict prey value (and thus relative prey rankings) in the classical version of the diet breadth model is the net rate of energy intake. A basic assumption of the diet breadth model is that energetic costs of predation do not vary with prey type or size (Krebs & McCleery 1984). This assumption is probably true when energetic expenditures due to predation, which are usually very small when compared to energetic intake, are compensated by energy gained through foraging. However, for those animals where energy expenditure is allocated from a fixed total budget, energy maximization may not be the appropriate currency with which to calculate prey rankings (Kacelnik & Houston 1984, Cheverton et al. 1985, Stephens & Krebs 1986). In these cases, predation costs represent mechanical or physiological con-

straints such that energy spent is essentially a non-renewable loss of foraging capacity. The first example of a non-replenishable mechanical constraint was the breakdown of the flight apparatus in honey bees (Schmid-Hempel et al. 1985, Kacelnik et al. 1986, Schmid-Hempel 1987). Schmid-Hempel and his colleagues used energetic efficiency (the ratio of energy gained to energy lost) as the currency that could accurately predict crop-filling behavior in honey bees. Juanes & Hartwick (1990) showed that energetic efficiency was a better currency (as compared to energy maximization rate) with which to predict prey size selection by a decapod crustacean feeding on a hard-shelled molluscan prey. Claw damage, defined as chela breakage and claw tooth wear, as a consequence of fatigue failure, was proposed as the limiting mechanical cost.

Field and laboratory experiments examining decapod crustacean predation on molluscs have produced many empirical observations of prey size preferences and the resulting impact on the community structure of commercially (usually) exploited populations (Ebling et al. 1964, MacKenzie 1977, Seed 1980, 1982, Jamieson et al. 1982, Peterson 1982, 1983; but see Hall et al. 1990 for an example where crab predation had trivial effects on benthic assemblages). Several of these studies have compared their observations with theoretical predictions of diet breadths based on energy maximization.

* Present address: Fisheries Centre, 2204 Main Mall, University of British Columbia, Vancouver, British Columbia, Canada V6T 1Z4

In this study, I determine how patterns in prey size preference may be a consequence of predator mechanical constraints when feeding on hard-shelled prey by reviewing those papers from the crustacean-mollusc predation literature in which quantitative measures of prey size rankings were collected. I then compare predictions of optimal prey sizes based on energy maximization to the observed preferred prey sizes, and suggest a way in which the risk of mechanical damage can be incorporated into the classic diet breadth model to produce more accurate predictions.

METHODS

Table 1 presents a summary of the 41 studies from the crustacean-mollusc predation literature which contained quantitative measures of prey size preference, defined as the rank order of choices. From each of these studies I extracted the range of predator sizes used, the range of prey sizes offered, the range of prey sizes selected when given a choice, and if available, the range

of optimal prey sizes (as predicted using energy maximization models). In 21 of the studies, authors determined prey size preferences from the observed number of individuals eaten in each size category without testing the results statistically. In the other 20 studies, size preferences were tested statistically by either testing whether the observed numbers consumed per size category differed from random expectation (e.g. Chi-squared test) or whether the mean number of prey consumed differed among prey size categories (e.g. *t*-test). In 36 of these studies bivalves were used as prey (Fig. 1), and in 8 snails were used (Fig. 2). Three (Studies 19, 29, 36) used both bivalve and gastropod prey. One of the snail studies, Study 38 (Lawton & Hughes 1985), used 2 prey species which are considered separately (as Studies 38 and 38.1). In 15 studies (with 17 prey species) there were predictions of optimal sizes based on the maximization of energy intake rate (Fig. 3). Eight studies were conducted in the field whereas the remainder were laboratory based.

Potential trends in the location of preferred prey size ranges relative to offered prey size ranges and pre-

Table 1. A summary of prey size selection studies using crabs and lobsters as predators, and bivalves and snails as prey. Optimal prey sizes were predicted using energy maximization models. *Field studies. NP: no prediction; ND: no data; SL: shell length; CW: carapace width; SH: shell height; CL: carapace length; SA: shell aperture. Statistical tests – NT: no statistical test was performed; TT: *t*-test; AN: ANOVA; GT: *G*-test; CS: Chi-squared; FT: Friedman test; UT: unknown test (a statistical test was performed but no other details are given by the authors). All measurements are in mm

Study no.	Predator	Predator size	Prey	Prey sizes offered	Prey sizes pref.	Opt. prey size	Test	Source
1*	<i>Neopanope sayi</i> <i>Cancer irroratus</i> <i>Callinectes sapidus</i>	6.2–17.2 CW 11.2–37.8 CW 8.1–20.2 CW	<i>Mercenaria mercenaria</i>	4.5–55 SL	4.5–15	NP	NT	MacKenzie (1977)
2	<i>Callinectes sapidus</i>	<75 CW 75–124 >125	<i>Mercenaria mercenaria</i>	5–50 SL	5–10 10 10–25	NP	TT	Arnold (1984)
3	<i>Carcinus maenas</i>	32.9 CW 32.5 37.1 38.0 46.2 45.5	<i>Mercenaria mercenaria</i>	4–7 SL 5–9 5–9 7–11 7–13 7–20	4 5 5 7 7 7	NP	NT	Walne & Dean (1972)
4*	<i>Panopeus herbstii</i>	15–25 CW	<i>Mercenaria mercenaria</i>	12–40 SL	12–20	NP	NT	Whetstone & Eversole (1978)
5*	<i>Neopanope sayi</i> <i>Ovalipes ocellatus</i> <i>Pagurus longicarpus</i>	19.6–21.3 CW 40.2–47.8 CW 9–11 CL	<i>Mercenaria mercenaria</i>	3–7 SL 3–7 1–3	3 3 1	NP	NT	Gibbons (1984)
6	<i>Callinectes sapidus</i>	<75 CW 75–125 >125	<i>Mercenaria mercenaria</i>	5–35 SL	5–10 5–15 5–25	NP	NT	Peterson (1990)
7	<i>Carcinus maenas</i>	35–40 CW 50–55 65–70	<i>Cerastoderma eduli</i>	5–35 SH 5–35 5–35	5 5–7 7	8–10 11–12 16–18	NT	Sanchez-Salazar et al. (1987)

Table 1 (continued)

Study no.	Predator	Predator size	Prey	Prey sizes offered	Prey sizes pref.	Opt. prey size	Test	Source
8	<i>Cancer productus</i>	35-41 CW 69-70 138-144	<i>Protothaca staminea</i>	5-40 SL 5-40 25-60	5-10 5-20 25-30	NP	GT	Boulding (1984)
9*	<i>Cancer anthonyii</i>	ND	<i>Protothaca staminea</i>	8-56 SL	<20	NP	NT	Peterson (1982)
10*	<i>Cancer magister</i>	141-155 CW	<i>Protothaca staminea</i>	26-65 SL	26-45	NP	CS	Pearson et al. (1981)
11	<i>Cancer magister</i>	165-182 CW	<i>Protothaca staminea</i>	15-45 SL	15-20	40-45	CS	Juanes & Hartwick (1990)
12	<i>Cancer magister</i>	>100 CW	<i>Clinocardium nuttalli</i> <i>Tapes japonicus</i> <i>Saxidomus giganteus</i> <i>Protothaca staminea</i>	10-70 SL 10-50 30-90 10-60	10-30 10-30 30-60 10-30	NP	NT	Jamieson (unpubl.)
13	<i>Callinectes sapidus</i> <i>Panopeus herbstii</i>	70-74 CW 26.0 42-43	<i>Geukensia demissa</i>	5-50 SL	5-30 5-20 10-30	NP	NT	Seed (1980)
14	<i>Callinectes sapidus</i>	74-117 CW	<i>Geukensia demissa</i>	10-50 SL	10-20	10-20	NT	Seed (1982)
15	<i>Callinectes sapidus</i>	85-117 CW 85-117	<i>Geukensia demissa</i>	20-40 SL 10-25	20-25 10-15	20-25 10-15	CS	Hughes & Seed (1981)
16	<i>Callinectes sapidus</i>	ND	<i>Geukensia demissa</i>	15-47 SL	15-38	NP	TT	Bertness & Grosholz (1985)
17	<i>Cancer pagurus</i> <i>Carcinus maenas</i> <i>Portunus</i> sp. <i>Eupagurus</i> sp.	78-150 CW 50-65 52-72 47-90	<i>Modiolus modiolus</i>	7-99 SL	15-50 7-50 7-34 7-34	NP	NT	Seed & Brown (1975)
18	<i>Jasus lalandii</i>	53 CL 61 96 107	<i>Aulacomya ater</i>	5-60 SL 5-60 5-60 5-60	5-10 10-15 10-25 25-35	50-60	NT	Griffiths & Seiderer (1980)
19*	<i>Carcinus maenas</i>	27-57 CW 34-41 45-57	<i>Mytilus edulis</i> <i>Nucella lapillus</i>	15-53 SL 10-25 SH	15-21 10-17 10-20	NP	NT	Ebling et al. (1964)
20	<i>Carcinus maenas</i>	70-75 CW	<i>Mytilus edulis</i>	12.5-22.5 SL 22.5-27.5	22.5 22.5	22.5 22.5	CS	Jubb et al. (1983)
21	<i>Carcinus maenas</i>	50-55 CW 60-65 70-75	<i>Mytilus edulis</i>	10-35 SL 10-35 10-35	12.5 17.5 22.5	17.5-20 22.5-25 27.5-30	NT	Elner & Hughes (1978)
22	<i>Liocarcinus puber</i>	70-80 CW	<i>Mytilus edulis</i>	10-17.5 SL 15-25 22.5-25	15-17.5 15-25 22.5-25	15-17.5 22.5-25 22.5-25	GT	ap Rheinallt (1986)
23	<i>Carcinus maenas</i>	60 CW 65-75	<i>Mytilus edulis</i>	35-45 SL 45-55	35 45	NP	UT	Ameyaw-Akumfi & Hughes (1987)
24	<i>Ovalipes catharus</i>	50-55 CW 80-85	<i>Mytilus edulis</i>	5-35 SL 5-35	10-15 15-20	5-10 5-10	NT	Davidson (1986)
25	<i>Panulirus interruptus</i>	59-129 CL	<i>Mytilus californianus</i>	10-100 SL	10-60	NP	CS	Robles et al. (1990)
26	<i>Calappa ocellata</i>	61.6-70.2 CW	<i>Brachidontes domingensis</i>	10-25 SL	10-25	10-25	GT	Hughes & Elner (1989)
27	<i>Acanthocyclus gayi</i> <i>A. hassleri</i>	11-15 CW 15-19 19-23 11-15 CW 15-19 19-23	<i>Perumytilus purpuratus</i>	3-21 SL 3-21 3-21 3-21 3-21 3-21	3-6 3-6 3-12 3-6 3-12 3-12	NP	GT	Navarrete & Castilla (1988)

(Table continued on next page)

Table 1 (continued)

Study no.	Predator	Predator size	Prey	Prey sizes offered	Prey sizes pref.	Opt. prey size	Test	Source
28	<i>Callinectes sapidus</i>	30-60 CW 121-180	<i>Mya arenaria</i>	15-35 SL 15-35	15-35 15-35	NP	AN	Blundon & Kennedy (1982)
29	<i>Ovalipes punctatus</i>	40-45 CW 45-50 50-65 40-45 45-65	<i>Donax serra</i> <i>Bullia rhodostoma</i>	25-60 SL 25-60 25-60 10-45 SL 10-45	25-30 25-35 35-40 15-20 25-30	NP	NT	Du Preez (1984)
30*	<i>Cancer irroratus</i> <i>Homarus americanus</i>	100-120 CW 65-105 CL	<i>Placopecten magellanicus</i>	30-110 SH 30-110	30-50 30-50	NP	NT	Jamieson et al. (1982)
31	<i>Cancer irroratus</i> <i>Homarus americanus</i>	90-100 CW 120-130 70-80 CL 130-140	<i>Placopecten magellanicus</i>	20-70 SH 20-70 20-70 20-70	20-30 20-30 20-30 30-40	NP	NT	Elner & Jamieson (1979)
32	<i>Cancer pagurus</i> <i>Liocarcinus puber</i> <i>Carcinus maenas</i>	61-141 CW 71-85 CW 45-75 CW	<i>Pecten maximus</i>	30-90 SH 40-60 40-60	30-40 40-50 40-50	NP	TT	Lake et al. (1987)
33	<i>Carcinus maenas</i> <i>Libinia emarginata</i> <i>Neopanope sayi</i> <i>Pagurus longicarpus</i>	41-65 CW 50 CW 21 CW 62 CL	<i>Argopecten irradians</i>	17-32 SH 17-32 17-32 17-32	17-23 17-23 17-23 17-23	NP	GT	Tettelbach (1986)
34	<i>Homarus americanus</i> <i>Cancer irroratus</i>	55-63 CL 85-98 32-46 CW 73-79 94-107	<i>Crassostrea virginica</i>	10-35 SL 10-35 10-35 10-35 10-35	10-25 10-20 10-15 10-20 20-25	NP	NT	Elner & Lavoie (1983)
35	<i>Callinectes sapidus</i> <i>Panopeus herbstii</i>	7-45 CW 70-100 6-20 CW 22-40	<i>Crassostrea virginica</i>	1-30 SH 1-30 1-30 1-30	1-5 1-10 1-5 1-10	NP	AN	Bisker & Castagna (1987)
36	<i>Menippe adina</i>	68.8-100.8 CW 49.6-110.9	<i>Crassostrea virginica</i> <i>Stramonita haemstoma</i>	10-100 SL 20-80 SL	10-40 20-35	10-100 35-50	GT	Brown & Haight (in press)
37	<i>Carcinus maenas</i>	60-70 CW	<i>Nucella lapillus</i>	6-16 SH 11-23 15-30	6-16 11-15.5 15-20	13-16 11-15.5 15-20	FT	Hughes & Elner (1979)
38	<i>Cancer pagurus</i>	82-86 CW 76-86 64-79	<i>Nucella lapillus</i> <i>Littorina saxatilis</i>	10-25 SH 10-25 10-25 SH	10-15 10-15 10-25	10-12 10-12 17-19	FT	Lawton & Hughes (1985)
39	<i>Carcinus maenas</i>	22-35 CW	<i>Littorina saxatilis</i>	2-8 SH	2-4	2-8	FT	Johannesson (1986)
40	<i>Ozius truncatus</i>	22-27.9 CL 28-33.9 34-39.9 40-45.9 22-27.9 CL 28-33.9 34-39.9 40-45.9	<i>Nerita atramentosa</i> <i>Bembicium nanum</i>	4-11.9 SH 4-11.9 SH	4-5.9 4-5.9 4-6.9 4-7.9 4-6.9 4-7.9 5-8.9 5-8.9	NP	NT	Chilton & Bull (1984)
41	<i>Ozius verreauxii</i>	47-51 CW	<i>Nerita scabricosta</i>	3-14 SA	3-12	10-12	NT	Hughes (1989)

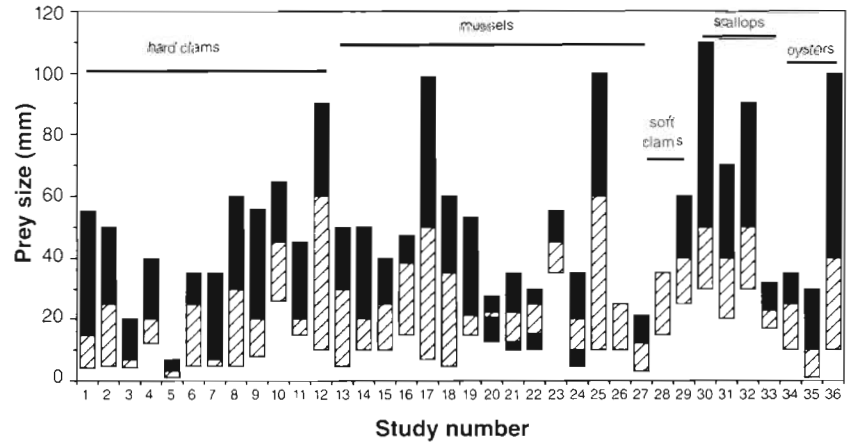


Fig. 1. Prey sizes offered and selected for those studies using bivalve molluscs as prey. Each histogram represents the range of prey sizes offered (i.e. solid plus hatched). The hatched region represents the range of prey sizes that were preferentially ingested by the predator (thus the solid region represents the 'less-preferred' prey sizes)

dicted optimal size ranges (as listed in Table 1) were tested by comparing their midpoints. Thus, the midpoint of the preferred size range could be either 'smaller', 'equal' or 'larger' than the midpoint of the offered or the optimal size range. The optimal vs preferred ranges were further analyzed by subdividing the data by prey type (e.g snails or bivalves). Bivalves were further subdivided into mussels (*Geukensia demissa*, *Mytilus edulis*, *Aulacomya ater* and *Brachidontes domingensis*), clams (*Cerastoderma eduli* and *Protothaca staminea*), and oysters (*Crassostrea virginica*). The overall counts were analyzed using a chi-squared test to detect differences from a random choice.

RESULTS

The data depicting those studies using bivalve molluscs as prey are shown in Fig. 1. It is clear that the trend of prey size preference is towards the lower part of the range offered. In all these studies the complete set of prey sizes was available to the predator. That is, they were capable of ingesting individuals over the whole range and frequently took prey from the upper part of the range offered. Nevertheless, it was the lower part of the range that was ingested preferentially (Table 2).

The exceptions to this pattern show either no size selection or preferences for intermediately-sized prey. Blundon & Kennedy (1982) (Study 28) using *Mya arenaria* as prey and Hughes & Elner (1989) (Study 26) using *Brachidontes domingensis* (a mussel) as prey, concluded that *Callinectes sapidus* and *Calappa ocellata* respectively showed no evidence of size selectivity. Studies 20, 21, 22 and 24 (Jubb et al 1983, Elner & Hughes 1978, ap Rheinallt 1986 and Davidson 1986, respectively) all used the common mussel *Mytilus edulis* as the prey item to examine prey size selection by

various predators. These studies all found that the intermediate sizes of prey were preferred, although all sizes of prey could be ingested.

Those studies using snails as prey also show a pattern of preference for small-sized prey (Fig. 2, Table 2). The 2 exceptions to this pattern showed a preference for intermediate sizes of *Bullia rhodostoma* by *Ovalipes punctatus* (Study 29; Du Preez 1984), and no size selectivity by *Cancer pagurus* feeding on *Littorina littorea* (Study 38.1; Lawton & Hughes 1985).

Fig. 3 compares the range of sizes preferred to the range of sizes predicted in those studies using optimal diet models. The more accurate predictions tended to occur in those studies using mussels as prey (e.g. Studies 14, 15, 20, 22, 26). Nine studies (7, 11, 18, 21, 36, 36.1, 37, 39, 41) showed preferences for prey sizes smaller than those predicted to be optimal. The other 3 studies either showed preferences for prey larger than the predicted size (Studies 24, 38) or for sizes both

Table 2. A comparison of the preferred vs offered or optimal prey size ranges. The midpoints of the preferred size ranges were either smaller, larger, or equal to the offered or optimal size ranges. Data from Table 1. *Significant χ^2 values ($p < 0.05$)

	Comparison			χ^2
	Smaller	Larger	Equal	
Offered vs preferred				
All data	100	7	6	158.76*
Bivalves	83	6	5	127.94*
Snails	19	1	1	30.86*
Optimal vs preferred				
All data	18	4	10	10.00*
Snails	5	2	2	2.00
Bivalves	13	2	8	8.32*
Mussels	8	2	8	4.00
Clams + oysters	5	0	0	9.98*
Clams + oysters + snails	10	2	2	9.14*

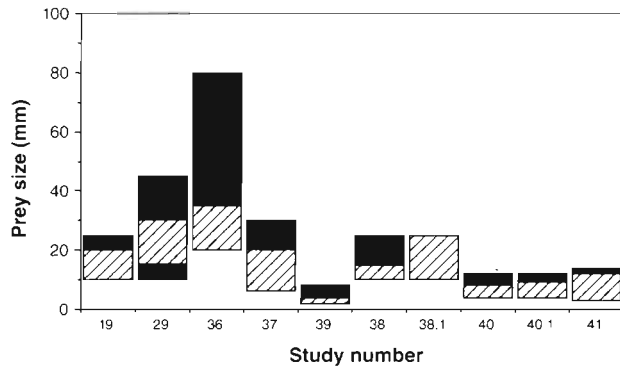


Fig. 2. Prey sizes offered and selected for those studies using snails as prey. Each histogram represents the range of prey sizes offered (i.e. solid plus hatched). The hatched region represents the range of prey sizes that were preferentially ingested by the predator

larger and smaller than the predicted optimal size range (Study 38.1). The statistical analyses suggest that predators generally select smaller prey than those predicted to be optimal (Table 2). This pattern appears to be consistent for all prey types except mussels (although the test is non-significant for snails, the few data available suggest a trend of preference for smaller than predicted snail sizes).

DISCUSSION

The results of the studies surveyed here show that there is an overall preference for smaller-sized prey by a wide variety of different-sized predators even though the predators are able to consume prey over the whole size range offered (Tables 1 & 2, Figs. 1 & 2). The exceptions to this pattern tend to include relatively soft-shelled bivalves such as *Mya* (where no size-preference was observed) and *Mytilus* (where intermediate prey sizes were often preferentially ingested).

A similar trend is apparent in the accuracy of the optimal prey size predictions using energy maximization rates. Thus for example, when relatively soft-shelled bivalves such as mussels (see Blundon & Kennedy 1982, Du Preez 1984, Currey 1988) are used as prey (Fig. 3; Studies 14, 15, 20, 21, 22, 37) fairly accurate predictions can be made from the classical optimal diet model, but when more robust molluscan prey such as snails, clams or oysters (see Boulding 1984, Pennington & Currey 1984, Currey 1988) are used, predicted prey sizes tend to be larger than those preferred by each predator (Fig. 3; Studies 7, 11, 18, 37, 38, 39; Table 2). Although smaller prey will have relatively smaller handling times they do not always have the highest ratios of prey caloric content to handling time (or profitability; Fig. 3), implying that there are features of the prey which constrain predators from maximizing energy intake rates and restrict their diet breadth. Such 'adaptive' features of the mollusc shell have been described as: length (overall size), thickness, strength, and shape among others (Vermeij 1978, Boulding 1984, Palmer 1985, Lowell 1986, Currey 1988, Stanley 1988). Some of these features have been observed to change due to the presence of decapod crustacean predators over short time periods (10 to 11 wk; Appleton & Palmer 1988), ecological time (decades; Vermeij 1982b, Seeley 1986), and over evolutionary time (Vermeij 1978, West et al. 1991). Various authors have thus suggested that predation type and intensity can be a driving force in the selection of molluscan prey morphology (Vermeij 1978, 1987, Palmer 1979, 1985, Bertness & Cunningham 1981, Signor 1985, West et al. 1991). The observed latitudinal increase in predator claw massiveness with increases in molluscan prey armature has been proposed as further evidence of predator-prey coevolution (Vermeij 1977, 1978, 1983, Zipser & Vermeij 1978, Vermeij & Currey 1980; but see Abele et al. 1981 for an alternative view). Although it is clear that strong selection pressures exist on molluscan prey such that they might evolve more

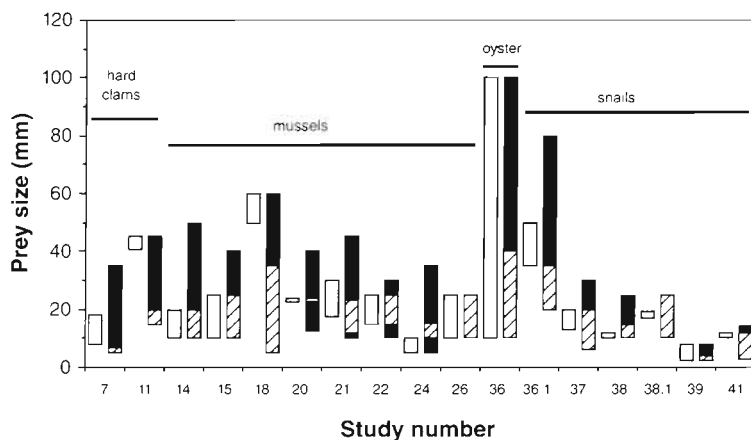


Fig. 3. A comparison of prey sizes selected and optimal prey sizes predicted from energy maximization models. Each study is represented by 2 bars. The open bar on the left represents the range of optimal prey sizes predicted. The bar on the right represents the range of prey sizes offered (solid plus hatched) and the portion of those selected (hatched region)

robust shells in response to predatory pressure (so as to increase relative survival probabilities), it is less clear how these prey adaptations can in turn affect predator morphologies. I suggest that predator morphology may be constrained by the risk of incurring damage when attempting to capture and ingest a prey item. Thus increases in anti-predator adaptations increase the probability of predator injury, leading to selection for more massive claws.

Non-lethal injury is generally assumed to be a consequence of predation by others and/or intra-specific aggression (Vermeij 1982a, Harris 1989). Juanes & Hartwick (1990) first noted the risk of claw damage (defined as chela breakage and claw-tooth wear) by Dungeness crabs when feeding on hard-shelled molluscan prey and suggested that this risk led to the preference for small-sized prey even though the largest prey had the highest profitabilities. Claw damage has been shown to have significant effects on feeding behaviour, growth, molting ability, regeneration load, mortality rates and reproductive success (Davis et al. 1978, Savage & Sullivan 1978, Sekkelsten 1988, Juanes & Hartwick 1990, Norman & Jones 1991, Smith & Hines 1991). There are various other reports of claw damage prevalence in natural populations of decapod crustaceans (Butler 1956, Durkin et al. 1984, Carvacho 1988, Shirley & Shirley 1988, Spivak & Politis 1989, Smith 1990), although for the most part, the effects of claw damage on foraging efficiency have remained largely undocumented because 'healthy-looking' predators are most often selected for experiments and damaged individuals are discarded without note.

The pattern of preference for small prey sizes observed here can be seen as reflecting the effect of molluscan morphological features constraining predator diet breadths. Shell strength, measured as the force required to achieve fracture, could be such a feature. Thus large shells, although breakable, require more energetic expense and increase the probability of claw damage by the predator. Molluscan shell strength has been shown to be exponentially related to shell thickness (Boulding 1984), mass (Currey 1988), length (Griffiths & Seiderer 1980, Kent 1981, Blundon & Kennedy 1982) and shape (Pennington & Currey 1984). Hence smaller-sized prey are relatively weaker and 'easier' to open, and require exponentially less strain and force to achieve breakage. Similarly, shell volume, which increases to the cube power of length, acts as a deterrent against crab predation by reducing the mechanical leverage of crab claws (Boulding 1984, Lin 1990). The number of pulses required to achieve breakage of a clam shell also seems to be an accelerating function of clam size (Boulding & LaBarbera 1986). Interestingly, crusher chela force in the American lobster increases linearly with body size (Elner &

Campbell 1981) suggesting that as body size increases, prey strength may increase more rapidly than predator strength. This inability to 'keep up' with shell shape and strength is demonstrated by the many studies that show a change in predator tactics as prey size increases beyond a critical size. Generally, crabs and lobsters are able to directly crush small molluscan prey. As prey size increases however, predators adopt a chipping technique in which the chela slips ventrally on the shell until the edge is chipped (Elner & Jamieson 1979, Seed 1980, 1982, Hughes & Seed 1981, Elner & Lavoie 1983, Boulding 1984, Davidson 1986, Juanes & Hartwick 1990). Shell breakage occurs as the crab inserts a dactyl or cheliped in the prey. This chipping technique increases shear stress on the shell surface (Boulding & LaBarbera 1986) suggesting that the probability of fatigue damage on the chelae teeth and the claw tips also increases.

Recent studies testing predictions of efficiency vs net energy maximization models have shown that observed foraging behaviors fell between the predictions of both models, although efficiency maximization tended to give more accurate predictions (Schmid-Hempel et al. 1985, Schmid-Hempel 1987, Welham & Ydenberg 1988, Tamm 1989, Juanes & Hartwick 1990). This result suggests that if these 2 currencies were incorporated into a composite currency more precise matches of predictions and observations could result. The main difference between the 2 currencies is whether or not energetic expenditures are allocated from a fixed budget and thus represent non-renewable losses which cannot be compensated for by future energy gains. The effects of energy costs on the optimal diet have been explored theoretically (Charnov 1973, Kacelnik & Houston 1984) and empirically (Fewell 1988, Lifjeld & Slagsvold 1988, Tamm 1989) although in most cases, these costs have been considered locomotory and renewable. Because energetic costs are generally small (and difficult to measure realistically) when compared to caloric benefits, net and gross intake rate models predict similar prey rankings (Kacelnik & Houston 1984, Juanes & Hartwick 1990).

If predation costs are considered a limited resource allocated from a fixed budget, the probability of incurring physiological or mechanical failure could be incorporated as an additional cost parameter into the classic diet breadth model in the form of a probability function (see Stephens & Krebs 1986). A resulting change in prey rankings would indicate a strong influence of the probability function (and thus predation costs) in determining diet breadth. The shape of this function and its relative importance would vary with prey characteristics (e.g. 'hard' vs 'soft' prey) and the physiological state of the predator (e.g. age, proximity to molting; see Abby-Kalio & Warner 1984, Kaiser et al. 1990).

Since the probability of incurring damage is also likely to be handling time-dependent, the proximal effects of energy costs on diet breadth will be confounded by time constraints (i.e. 'easier' prey will always incur lower handling times, although small prey will not always be the most profitable; see Fig. 3).

Cost limitation may be a significant determinant of diet breadth for a variety of predators that use mechanical means to attack their prey. For example, oystercatchers *Haematopus ostralegus* feeding on the common mussel either hammer a hole through the shell or stab between the intact valves to gain access to the soft tissues. The mean ventral thickness of mussels opened by oystercatchers is less than that of mussels present in a bed (Cayford & Goss-Custard 1990). Moreover, as mussel size increases, the difference in shell thickness between the mussels selected and those present increases (Meire & Eryvynck 1986). Beak damage is known to occur in oystercatchers, and birds with such damage seem to be most at risk of dying in severe winter weather (Swennen & Duiven 1983, J. D. Goss-Custard pers. comm.). Perhaps it is the risk of damage that explains why oystercatchers do not exclude small clams *Donax serra* from their diet, while kelp gulls *Larus dominicanus*, which open their prey by dropping them from a height of 6 to 10 m, take only large clams (Ward 1991). Many other studies have considered the role of predation costs and/or potential damage to the predator in determining its diet: energetic and time costs of foraging in harvester ants (Fewell 1988); tooth wear in wild reindeer (Skogland 1988); wear and tear of mouthparts in stream animals feeding on epilithic algae (Arens 1990); tooth breakage among large predatory mammals (Van Valkenburgh 1988); prey selection by molluscivorous fishes (Stein et al. 1984, Sloomweg 1987); risk of injury ('the dangerous prey hypothesis') in birds feeding on spiny catfish (Forbes 1989); and prey selection in 2 neotropical hover-gleaning birds (Sherry & McDade 1982).

In conclusion, when examining prey size preferences for different predator-prey combinations a pattern showing selection of smaller prey sizes emerges. This pattern suggests that decapod crustacean predators may be constrained from maximizing net energy intake rates when feeding on hard-shelled prey due to the probability of incurring damage as prey strength (and size) increases. This may be a general mechanism for foraging animals that are constrained by the allocation of a mechanical or a physiological cost from a fixed total budget. Future studies of prey size selection should thus consider the dynamic effects of predator and prey morphologies by incorporating empirical observations of predation costs and their ecological effects in more long-term analyses (Houston et al. 1988, Mangel & Clark 1988).

Acknowledgements. I thank J. Belmonte, S. Blake, F. Borrero, I. Cheng, D. Conover, S. Craig, J. Hare, R. N. Hughes, R. Marks, D. Martinez, M. McCartney, C. H. Peterson, E. Schultz, G. J. Vermeij, H. Vigil, H. Wilbur, and 3 anonymous reviewers for constructive criticism on previous versions of the manuscript. I am grateful to L. Clough for graphical inspiration. E. Charnov and P. Lawton provided helpful discussion in the early stages. This work was supported by an Electric Power Research Institute fellowship in population biology. This is contribution number 864 of the Marine Sciences Research Center.

LITERATURE CITED

- Abby-Kalio, N. J., Warner, G. F. (1984). Effects of two different feeding regimes on the chela closer muscles of the shore crab *Carcinus maenas* (L.). *Mar. Behav. Physiol.* 11: 209–218
- Abele, L. G., Heck, K. L. Jr, Simberloff, D. S., Vermeij, G. J. (1981). Biogeography of crab claw size: assumptions and a null hypothesis. *Syst. Zool.* 30: 406–424
- Ameyaw-Akumfi, C., Hughes, R. N. (1987). Behaviour of *Carcinus maenas* feeding on large *Mytilus edulis*. How do they assess the optimal diet? *Mar. Ecol. Prog. Ser.* 38: 213–216
- Appleton, R. D., Palmer, A. R. (1988). Water-borne stimuli released by predatory crabs and damaged prey induce more predator-resistant shells in a marine gastropod. *Proc. natl. Acad. Sci. U.S.A.* 85: 4387–4391
- ap Rheinallt, T. (1986). Size selection by the crab *Liocarcinus puber* feeding on mussels *Mytilus edulis* and on shore crabs *Carcinus maenas*: the importance of mechanical factors. *Mar. Ecol. Prog. Ser.* 29: 45–53
- Arens, W. (1990). Wear and tear of mouthparts: a critical problem in stream animals feeding on epilithic algae. *Can. J. Zool.* 68: 1896–1914
- Arnold, W. S. (1984). The effects of prey size, predator size, and sediment composition on the rate of predation of the blue crab, *Callinectes sapidus* Rathbun, on the hard clam, *Mercenaria mercenaria*. *J. exp. mar. Biol. Ecol.* 80: 207–219
- Bertness, M. D., Cunningham, C. (1981). Crab shell-crushing predation and gastropod architectural defense. *J. exp. mar. Biol. Ecol.* 50: 213–230
- Bertness, M. D., Grosholz, E. (1985). Population dynamics of the ribbed mussel, *Geukensia demissa*: the costs and benefits of an aggregated distribution. *Oecologia* 67: 192–204
- Bisker, R., Castagna, M. (1987). Predation on single spat oysters *Crassostrea virginica* (Gmelin) by blue crabs *Callinectes sapidus* Rathbun and mud crabs *Panopeus herbstii* Milne-Edwards. *J. Shellfish Res.* 6: 37–40
- Blundon, J. A., Kennedy, V. S. (1982). Mechanical and behavioral aspects of blue crab, *Callinectes sapidus* (Rathbun), predation on Chesapeake Bay bivalves. *J. exp. mar. Biol. Ecol.* 65: 47–65
- Boulding, E. G. (1984). Crab-resistant features of shells of burrowing bivalves: decreasing vulnerability by increasing handling time. *J. exp. mar. Biol. Ecol.* 76: 201–223
- Boulding, E. G., LaBarbera, M. L. (1986). Fatigue damage: repeated loading enables crabs to open larger bivalves. *Biol. Bull.* 171: 538–547
- Brown, K. M., Haight, E. S. (in press). The foraging ecology of the Gulf of Mexico stone crab, *Menippe adina* (Williams and Felder). *J. exp. mar. Biol. Ecol.*
- Butler, T. H. (1956). Abnormal appendages of the Pacific edible crab, *Cancer magister* Dana. Province of British

- Columbia: Provincial Museum Report for the year 1956. Victoria, p. 67–69
- Cayford, J. T., Goss-Custard, J. D. (1990). Seasonal changes in the size selection of mussels, *Mytilus edulis*, by oystercatchers, *Haematopus ostralegus*: an optimality approach. *Anim. Behav.* 40: 609–624
- Carvacho, A. (1988). On some abnormalities in the chelae of commercial crabs (Genus *Cancer*) from Baja California, Mexico. *Calif. Fish & Game* 74: 172–174
- Charnov, E. L. (1973). Optimal foraging: some theoretical explorations. Ph.D. dissertation, Univ. of Washington, Seattle
- Cheverton, J., Kacelnik, A., Krebs, J. R. (1985). Optimal foraging: constraints and currencies. In: Holldobler, G., Lindauer, M. (eds.) *Experimental behavioural ecology and sociobiology*. Fisher Verlag, Stuttgart, p. 109–126
- Chilton, N. B., Bull, C. M. (1984). Influence of predation by a crab on the distribution of the size-groups of three intertidal gastropods in Australia. *Mar. Biol.* 83: 163–169
- Currey, J. D. (1988). Shell form and strength. In: Trueman, E. R., Clarke, M. R. (eds.) *The Mollusca*, Vol. 11. Form and function. Academic Press, New York, p. 183–210
- Davidson, R. J. (1986). Mussel selection by the paddle crab *Ovalipes catharus* (White): evidence of flexible foraging behaviour. *J. exp. mar. Biol. Ecol.* 102: 281–299
- Davis, G. E., Baughman, D. S., Chapman, J. D., MacArthur, D., Pierce, A. C. (1978). Mortality associated with declawing stone crabs, *Menippe mercenaria*. Rep. T-522, South Florida Res. Ctr., Homestead
- Du Preez, H. H. (1984). Molluscan predation by *Ovalipes punctatus* (De Haan) (Crustacea: Brachyura: Portunidae). *J. exp. mar. Biol. Ecol.* 84: 55–71
- Durkin, J. T., Buchanan, K. D., Blahm, T. H. (1984). Dungeness crab leg loss in the Columbia River estuary. *Mar. Fish. Rev.* 46: 22–24
- Ebling, F. G., Kitching, J. A., Muntz, L., Taylor, C. M. (1964). The ecology of Lough Ine. XIII. Experimental observations of the destruction of *Mytilus edulis* and *Nucella lapillus* by crabs. *J. Anim. Ecol.* 33: 73–82
- Elnor, R. W., Campbell, A. (1981). Force, function and mechanical advantage in the chelae of the American lobster *Homarus americanus* (Decapoda: Crustacea). *J. Zool.* 193: 269–286
- Elnor, R. W., Hughes, R. N. (1978). Energy maximization in the diet of the shore crab, *Carcinus maenas*. *J. Anim. Ecol.* 47: 103–116
- Elnor, R. W., Jamieson, G. S. (1979). Predation of sea scallops, *Placopecten magellanicus*, by the rock crab, *Cancer irroratus*, and the American lobster, *Homarus americanus*. *J. Fish. Res. Bd Can.* 36: 537–543
- Elnor, R. W., Lavoie, R. E. (1983). Predation on American oysters (*Crassostrea virginica* [Gmelin]) by American lobsters (*Homarus americanus* Milne-Edwards), rock crabs (*Cancer irroratus* Say), and mud crabs (*Neopanope sayi*). *J. Shellfish Res.* 3: 129–134
- Fewell, J. H. (1988). Energetic and time costs of foraging in harvester ants, *Pogonomyrmex occidentalis*. *Behav. Ecol. Sociobiol.* 22: 401–408
- Forbes, L. S. (1989). Prey defences and predator handling behaviour: the dangerous prey hypothesis. *Oikos* 55: 155–158
- Gibbons, M. C. (1984). Aspects of predation by the crabs *Neopanope sayi*, *Ovalipes ocellatus*, and *Pagurus longicarpus* on juvenile hard clams *Mercenaria mercenaria*. Ph.D. dissertation, State Univ. of New York, Stony Brook
- Griffiths, C. L., Seiderer, J. L. (1980). Rock-lobsters and mussels – limitations and preferences in a predator-prey interaction. *J. exp. mar. Biol. Ecol.* 44: 95–109
- Hall, S. J., Raffaelli, D., Robertson, M. R., Basford, D. J. (1990). The role of the predatory crab, *Liocarcinus depurator*, in a marine food web. *J. Anim. Ecol.* 59: 421–438
- Harris, R. N. (1989). Nonlethal injury to organisms as a mechanism of population regulation. *Am. Nat.* 134: 835–847
- Hines, A. H., Haddon, A. M., Wiechert, L. A. (1990). Guild structure and foraging impact of blue crabs and epibenthic fish in a subestuary of Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 67: 105–126
- Houston, A., Clark, C., McNamara, J., Mangel, M. (1988). Dynamic models in behavioural and evolutionary ecology. *Nature* 332: 29–34
- Hughes, R. N. (1989). Foraging behaviour of a tropical crab: *Ozius verreauxii*. *Proc. R. Soc. Lond. (Ser. B.)* 237: 201–212
- Hughes, R. N., Elnor, R. W. (1979). Tactics of a predator, *Carcinus maenas*, and morphological responses of the prey, *Nucella lapillus*. *J. Anim. Ecol.* 48: 65–78
- Hughes, R. N., Elnor, R. W. (1989). Foraging behaviour of a tropical crab: *Calappa ocellata* Holthuis feeding upon the mussel *Brachidontes domingensis* (Lamarck). *J. exp. mar. Biol. Ecol.* 133: 93–101
- Hughes, R. N., Seed, R. (1981). Size selection of mussels by the blue crab *Callinectes sapidus*: energy maximizer or time minimizer? *Mar. Ecol. Prog. Ser.* 6: 83–89
- Jamieson, G. S., Stone, H., Etter, M. (1982). Predation on sea scallops (*Placopecten magellanicus*) by lobsters (*Homarus americanus*) and rock crabs (*Cancer irroratus*) in underwater cage enclosures. *Can. J. Fish. Aquat. Sci.* 39: 499–505
- Johannesson, B. (1986). Shell morphology of *Littorina saxatilis* Olivi: the relative importance of physical factors and predation. *J. exp. mar. Biol. Ecol.* 102: 183–195
- Juanes, F., Hartwick, E. B. (1990). Prey size selection in Dungeness crabs: the effect of claw damage. *Ecology* 71: 744–758
- Jubb, C. A., Hughes, R. N., ap Rheinallt, T. (1983). Behavioral mechanisms of size-selection by crabs, *Carcinus maenas* (L.) feeding on mussels, *Mytilus edulis* L. *J. exp. mar. Biol. Ecol.* 66: 81–87
- Kacelnik, A., Houston, A. I. (1984). Some effects of energy costs on foraging strategies. *Anim. Behav.* 32: 609–614
- Kacelnik, A., Houston, A. I., Schmid-Hempel, P. (1986). Central-place foraging in honey bees: the effect of travel time and nectar flow on crop filling. *Behav. Ecol. Sociobiol.* 19: 19–24
- Kaiser, M. J., Hughes, R. N., Reid, D. G. (1990). Chelal morphology, prey-size selection and aggressive competition in green and red forms of *Carcinus maenas* (L.). *J. exp. mar. Biol. Ecol.* 140: 121–134
- Kent, R. M. L. (1981). The effect of *Polydora ciliata* on the shell strength of *Mytilus edulis*. *J. Cons. int. Explor. Mer* 39: 252–255
- Krebs, J. R., McCleery, R. H. (1984). Optimization in behavioural ecology. In: Krebs, J. R., Davies, N. B. (eds.) *Behavioural ecology: an evolutionary approach*, 2nd edn. Sinauer Associates, Sunderland, p. 91–121
- Lake, N. C. H., Jones, M. B., Paul, J. D. (1987). Crab predation on scallop (*Pecten maximus*) and its implication for scallop cultivation. *J. mar. biol. Ass. U.K.* 67: 55–64
- Lawton, P., Hughes, R. N. (1985). Foraging behaviour of the crab *Cancer pagurus* feeding on the gastropods *Nucella lapillus* and *Littorina littorea*: comparisons with optimal foraging theory. *Mar. Ecol. Prog. Ser.* 27: 143–154
- Lifjeld, J. T., Slagsvold, T. (1988). Effects of energy costs on the optimal diet: an experiment with pied flycatchers *Ficedula hypoleuca* feeding nestlings. *Ornis Scand.* 19: 111–118

- Lin, J. (1990). Mud crab predation on ribbed mussels in salt marshes. *Mar. Biol.* 107: 103–109
- Lowell, R. B. (1986). Crab predation on limpets: behavior and defensive features of the shell morphology of the prey. *Biol. Bull.* 171: 577–596
- MacKenzie, C. L. (1977). Predation on hard clam (*Mercenaria mercenaria*) populations. *Trans. Am. Fish. Soc.* 106: 530–537
- Mangel, M., Clark, C. W. (1988). *Dynamic modeling in behavioral ecology*. Princeton Univ. Press, Princeton
- Meire, P. M., Ervynck, A. (1986). Are oystercatchers (*Haematopus ostralegus*) selecting the most profitable mussels (*Mytilus edulis*)? *Anim. Behav.* 34: 1427–1435
- Navarrete, S. A., Castilla, J. C. (1988). Foraging activities of Chilean intertidal crabs *Acanthocyclus gayi* Milne-Edwards et Lucas and *A. hassleri* Rathbun. *J. exp. mar. Biol. Ecol.* 118: 115–136
- Norman, C. P., Jones, M. B. (1991). Limb loss and its effect on handedness and growth in the velvet swimming crab *Necore puber* (Brachyura: Portunidae). *J. nat. Hist.* 25: 639–645
- Paine, R. T. (1974). Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* 15: 93–120
- Paine, R. T. (1976). Size-limited predation: an observational and experimental approach with the *Mytilus–Pisaster* interaction. *Ecology* 57: 858–873
- Palmer, A. R. (1979). Fish predation and the evolution of gastropod shell sculpture: experimental and geographic evidence. *Evolution* 33: 697–713
- Palmer, A. R. (1985). Adaptive value of shell variation in *Thais lamellosa*: effect of thick shells on vulnerability to and preference by crabs. *Veliger* 27: 349–356
- Pearson, W. H., Woodruff, D. L., Sugarman, P. C., Olla, B. L. (1981). Effects of oiled sediments on predation on the littleneck clam, *Protothaca staminea*, by the Dungeness crab, *Cancer magister*. *Estuar. coast. Shelf Sci.* 13: 445–454
- Pennington, B. J., Currey, J. D. (1984). A mathematical model for the mechanical properties of scallop shells. *J. Zool.* 202: 239–263
- Peterson, C. H. (1982). The importance of predation and intra- and interspecific competition in the population biology of two infaunal suspension-feeding bivalves, *Protothaca staminea* and *Chione undatella*. *Ecol. Monog.* 52: 437–475
- Peterson, C. H. (1983). Interactions between two infaunal bivalves, *Chione undatella* (Sowerby) and *Protothaca staminea* (Conrad), and two potential enemies, *Crepidula onyx* Sowerby and *Cancer anthonyi* (Rathbun). *J. exp. mar. Biol. Ecol.* 68: 145–158
- Peterson, C. H. (1990). On the role of ecological experimentation in resource management: managing fisheries through mechanistic understanding of predator feeding behaviour. In: Hughes, R. N. (ed.) *Behavioural mechanisms of food selection*. NATO ASI Series, Vol. G20. Springer-Verlag, Berlin, p. 821–846
- Robles, C., Sweetnam, D., Eminke, J. (1990). Lobster predation on mussels: shore-level differences in prey vulnerability and predator preference. *Ecology* 71: 1564–1577
- Sanchez-Salazar, M. E., Griffiths, C. L., Seed, R. (1987). The effect of size and temperature on the predation of cockles *Cerastoderma edule* (L.) by the shore crab *Carcinus maenas* (L.). *J. exp. mar. Biol. Ecol.* 111: 181–193
- Savage, T., Sullivan, J. R. (1978). Growth and claw regeneration of the stone crab, *Menippe mercenaria*. Florida Mar. Res. Publ. no. 32, Florida Dept Nat. Res., St Petersburg
- Schmid-Hempel, P. (1987). Efficient nectar-collecting by honeybees. I. Economic models. *J. Anim. Ecol.* 56: 209–218
- Schmid-Hempel, P., Kacelnik, A., Houston, A. I. (1985). Honeybees maximize efficiency by not filling their crop. *Behav. Ecol. Sociobiol.* 17: 61–66
- Seed, R. (1980). Predator-prey relationships between the mud crab *Panopeus herbstii*, the blue crab, *Callinectes sapidus* and the Atlantic ribbed mussel *Geukensia (=Modiolus) demissa*. *Estuar. coast. mar. Sci.* 11: 445–458
- Seed, R. (1982). Predation of the ribbed mussel *Geukensia demissa* by the blue crab *Callinectes sapidus*. *Neth. J. Sea Res.* 16: 163–172
- Seed, R., Brown, R. A. (1975). The influence of reproductive cycle, growth and mortality on the population structure in *Modiolus modiolus*, *Cerastoderma edule* and *Mytilus edulis*. In: Barnes, H. (ed.) *Ninth European Marine Biology Symposium*. Aberdeen University Press, Aberdeen, p. 257–274
- Seeley, R. H. (1986). Intense natural selection caused a rapid morphological transition in a living marine snail. *Proc. natl. Acad. Sci. U.S.A.* 83: 6897–6901
- Sekkelsten, G. I. (1988). Effect of handicap on mating success in male shore crabs *Carcinus maenas*. *Oikos* 51: 131–134
- Sherry, T. W., McDade, L. A. (1982). Prey selection and handling in two neotropical hover-gleaning birds. *Ecology* 63: 1016–1028
- Shirley, S. M., Shirley, T. C. (1988). Appendage injury in Dungeness crabs, *Cancer magister*, in Southeastern Alaska. *Fish. Bull. U.S.* 86: 156–160
- Signor, P. W. (1985). The role of shell geometry as a deterrent to predation in terebrid gastropods. *Veliger* 28: 179–185
- Sih, A., Crowley, P., McPeck, M., Petranka, J., Strohmeier, K. (1985). Predation, competition, and prey communities: a review of field experiments. *A. Rev. Ecol. Syst.* 16: 269–311
- Skogland, T. (1988). Tooth wear by food limitation and its life history consequences in wild reindeer. *Oikos* 51: 238–242
- Slootweg, R. (1987). Prey selection by molluscivorous cichlids foraging on a schistosomiasis vector snail, *Biomphalaria glabrata*. *Oecologia* 74: 193–202
- Smith, L. D. (1990). Patterns of limb loss in the blue crab, *Callinectes sapidus* Rathbun, and the effects of autotomy on growth. *Bull. mar. Sci.* 46: 23–36
- Smith, L. D., Hines, M. A. (1991). The effect of cheliped loss on blue crab *Callinectes sapidus* Rathbun foraging rate on soft-shell clams *Mya arenaria* L. *J. exp. mar. Biol. Ecol.* 151: 245–256
- Spivak, E. D., Politis, M. A. (1989). High incidence of limb autotomy in a crab population from a coastal lagoon in the province of Buenos Aires, Argentina. *Can. J. Zool.* 67: 1976–1985
- Stanley, S. M. (1988). Adaptive morphology of the shell in bivalves and gastropods. In: Trueman, E. R., Clarke, M. R. (eds.) *The Mollusca*, Vol. 11. Form and function. Academic Press, New York, p. 105–140
- Stein, R. A., Goodman, C. G., Marschall, E. A. (1984). Using time and energetic measures of cost in estimating prey value for fish predators. *Ecology* 65: 702–715
- Stephens, D. W., Krebs, J. R. (1986). *Foraging theory*. Princeton University Press, Princeton
- Summerson, H. C., Peterson, C. H. (1984). Role of predation in organizing benthic communities of a temperate-zone sea-grass bed. *Mar. Ecol. Prog. Ser.* 15: 63–77
- Swennen, C., Duiven, P. (1983). Characteristics of oystercatchers killed by cold stress in the Dutch Wadden Sea area. *Ardea* 71: 155–159

- Tamm, S. (1989). Importance of energy costs in central place foraging by hummingbirds. *Ecology* 70: 195–205
- Tettelbach, S. T. (1986). Dynamics of crustacean predation on the Northern bay scallop, *Argopecten irradians irradians*. Ph.D. dissertation, Univ. of Connecticut, Storrs
- Van Valkenburgh, B. (1988). Incidence of tooth breakage among large, predatory mammals. *Am. Nat.* 131: 291–302
- Vermeij, G. J. (1977). Patterns in crab claw size: the geography of crushing. *Syst. Zool.* 26: 138–152
- Vermeij, G. J. (1978). Biogeography and adaptation: patterns of marine life. Harvard Univ. Press, Cambridge
- Vermeij, G. J. (1982a). Unsuccessful predation and evolution. *Am. Nat.* 120: 701–720
- Vermeij, G. J. (1982b). Phenotypic evolution in a poorly dispersing snail after arrival of a predator. *Nature* 299: 349–350
- Vermeij, G. J. (1983). Intimate associations and coevolution in the sea. In: Futuyma, D. J., Slatkin, M. (eds.) *Coevolution*. Sinauer Assoc., Sunderland, MA, p. 311–327
- Vermeij, G. J. (1987). *Evolution and escalation*. Princeton University Press, Princeton
- Vermeij, G. J., Currey, J. D. (1980). Geographical variation in the strength of Thaidid snail shells. *Biol. Bull.* 158: 383–389
- Virnstein, R. W. (1977). The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. *Ecology* 58: 1199–1217
- Walne, P. R., Dean, G. J. (1972). Experiments on predation by the shore crab, *Carcinus maenas* L., on *Mytilus* and *Mercenaria*. *J. Cons. int. Explor. Mer* 34: 190–199
- Ward, D. (1991). The size selection of clams by African Black Oystercatchers and Kelp Gulls. *Ecology* 72: 513–522
- Welham, C. V. J., Ydenberg, R. C. (1988). Net energy versus efficiency maximizing by foraging ring-billed gulls. *Behav. Ecol. Sociobiol.* 23: 75–82
- West, K., Cohen, A., Baron, M. (1991). Morphology and behavior of crabs and gastropods from Lake Tanganyika, Africa: implications for lacustrine predator-prey coevolution. *Evolution* 45: 589–607
- Whetstone, J. M., Eversole, A. G. (1978). Predation on hard clams, *Mercenaria mercenaria*, by mud crabs, *Panopeus herbstii*. *Proc. natl. Shellfish. Ass.* 68: 42–48
- Zipser, E., Vermeij, G. J. (1978). Crushing behavior of tropical and temperate crabs. *J. exp. mar. Biol. Ecol.* 31: 155–172

This article was presented by C. H. Peterson, Morehead City, N. Carolina, USA

Manuscript first received: February 24, 1992

Revised version accepted: September 8, 1992