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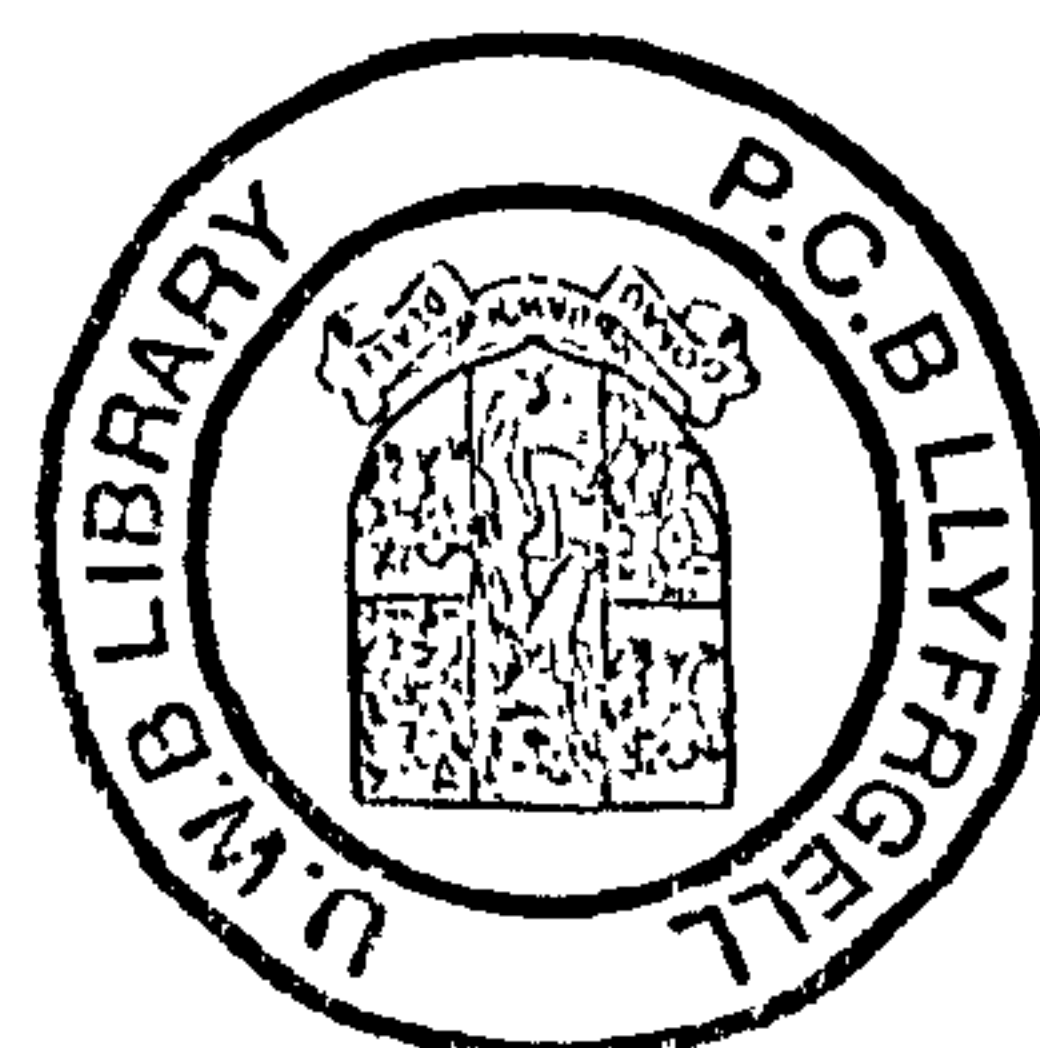
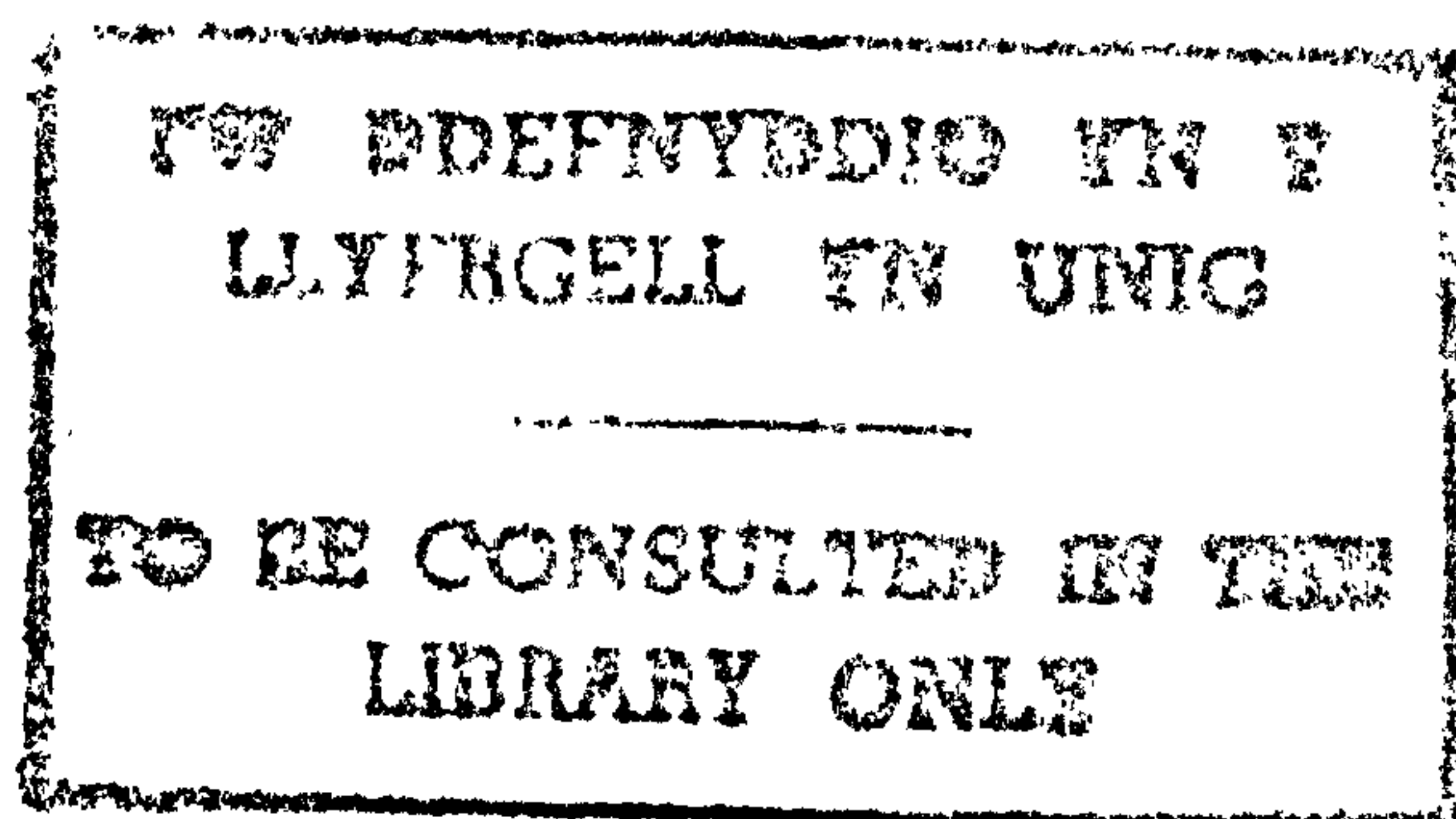
THE FORAGING BEHAVIOUR OF SHALLOW WATER CRABS.

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A thesis presented in the partial fulfilment of the requirements of the University of
Wales, Bangor.

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SUMMARY

This is a study of the foraging behaviour of *Carcinus maenas* on *Mytilus edulis* and of *Thalamita danae* on *Perna viridis*. Particular attention is given to differences arising in foraging behaviour as a result of intraspecific prey heterogeneity and experimental protocol.

Intersite and temporal differences in the population density, shell morphology, biomass and byssal attachment strength of *Mytilus edulis* were found. Byssal attachment strength and shell strength were highly variable amongst individuals of a similar size.

Carcinus maenas is strongly heterochelous. Intraspecific differences in the chelal mechanics, but not in the chelal geometry, were recorded; major chelae of large male crabs were significantly stronger than the major chelae of females and small males.

Stomach content analyses showed that *Carcinus maenas* has a broad diet in which *Mytilus edulis* forms an important component.

Intersite differences in *Mytilus edulis* shell morphology altered the foraging behaviour of *Carcinus maenas*, and intersite and temporal variations in mussel flesh weight altered the prey value curves. Both *C. maenas* and *Thalamita danae* were highly prey size-selective when foraging on groups of different sized mussels, the size of prey most vulnerable to predation altering with the size composition of the group.

The handling times of mussels for both species of crab were reduced when mussels were presented as part of a group as compared to when mussels were presented singly. For *Carcinus maenas* the reduced handling times resulted from the less extensive gleaning of mussel shells whilst for *Thalamita danae* reduced handling times appeared to result from the greater use of a more time efficient opening technique.

When *Carcinus maenas* were presented with mussels of differing attachment strengths, crabs selected more weakly attached mussels over those with a more firm and rigid attachment. This selection did not appear to be based on prey value or prey length but rather on the resulting slight movement of weakly attached mussels whenever these were touched by a foraging crab.

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CONTENTS

	Title	i
	Summary	ii
	Declaration	iii
	Acknowledgements	iv
	Table of Contents	v
	List of Plates	x
	List of Tables	xi
	List of Figures	xv
Chapter 1	General Introduction	1
Chapter 2	Characteristics of <i>Mytilus edulis</i> populations	9
2.1.	Introduction	9
2.2.	Materials and Methods	11
2.2.1.	Site descriptions of Aberffraw and Church Island	11
2.2.2.	Determination of population density and population structure of <i>Mytilus edulis</i>	13
2.2.3.	Relationship between shell surface area, biomass and size	16
2.2.4.	Shell strength and strength of byssal attachment	16
2.3.	Results	19
2.3.1.	Population densities	19
2.3.2.	Allometric relationships	28
2.3.3.	The shell strength of <i>Mytilus edulis</i>	36
2.3.4.	The strength of byssal attachment in Aberffraw and Church Island mussels	39
2.4.	Discussion	45
2.5.	Summary	52

Chapter 3	Chelal Morphology and Natural Diet of <i>Carcinus maenas</i>	55
3.1.	Introduction	55
3.2.	Materials and methods	58
3.2.1.	Description of the chelal morphometrics of <i>Carcinus maenas</i>	58
3.2.2.	Mechanical advantage	59
3.2.3.	The natural diet of <i>Carcinus maenas</i>	61
3.3.	Results	62
3.3.1.	Morphometrics	62
3.3.2.	Chelal strength	67
3.3.3.	The <i>Carcinus maenas</i> populations occurring at Church Island and Aberffraw	71
3.3.4.	The natural diet of <i>Carcinus maenas</i>	71
3.4.	Discussion	77
3.5.	Summary	84
Chapter 4	The Foraging Behaviour of <i>Carcinus maenas</i>	86
4.1.	Introduction	86
4.2.	Materials and Methods	88
4.2.1.	Collection and maintenance of <i>Carcinus maenas</i> and <i>Mytilus edulis</i>	88
4.2.2.	Foraging behaviour of <i>Carcinus maenas</i>	89
4.2.3.	Prey value	91
4.2.4.	Prey size selection	92
4.3.	Results	94
4.3.1	Foraging Behaviour	94
4.3.2.	The relationships between shell length and breaking, eating and handling time	97
4.3.3.	Prey value	110

4.3.4.	Prey size selection	117
4.4.	Discussion	122
4.5.	Summary	129
Chapter 5	Foraging Behaviour of <i>Carcinus maenas</i> on Groups of <i>Mytilus edulis</i>	132
5.1	Introduction	132
5.2	Materials and Methods	134
5.2.1	Collection and maintenance of <i>Carcinus maenas</i> and <i>Mytilus edulis</i>	134
5.2.2	Prey value experiments	134
5.2.2.1	Experiment 1. Prey value and foraging behaviour when mussels are presented singly and as part of a group	134
5.2.2.2	Experiment 2. The effect of learning on prey value	136
5.2.3	Prey vulnerability	138
5.2.3.1	Experiment 3. Differences in prey vulnerability	138
5.2.3.2	Experiment 4. Differences in prey vulnerability with shore level	138
5.3	Results	139
5.3.1	Prey handling	139
5.3.2	Prey value for when mussels presented singly and when mussels presented as part of a group	143
5.3.3	The effect of learning on the prey value	146
5.3.4	Prey vulnerability	155
5.4	Discussion	155
5.5	Summary	164
Chapter 6	Foraging Behaviour of <i>Thalamita danae</i> on the green-lipped mussel, <i>Perna viridis</i>.	166
6.1.	Introduction	166

6.2.	Materials and Methods	167
6.2.1.	The <i>Perna viridis</i> population	167
6.2.2.	Chelal morphometrics of <i>Thalamita danae</i>	169
6.2.3.	Foraging behaviour of <i>Thalamita danae</i> on the mussel <i>Perna viridis</i>	169
6.3.	Results	171
6.3.1.	The <i>Perna viridis</i> population	171
6.3.2.	The chelal morphometrics of <i>Thalamita danae</i>	173
6.3.3.	Foraging behaviour of <i>Thalamita danae</i>	177
6.3.3.1.	Prey handling procedures	177
6.3.3.2.	Foraging behaviour of <i>Thalamita danae</i> on individual mussels and on groups of mussels	179
6.3.3.3.	Prey size vulnerability	181
6.4.	Discussion	181
6.5.	Summary	190
Chapter 7	The effects of <i>Mytilus edulis</i> attachment strength of the foraging behaviour of <i>Carcinus maenas</i>	192
7.1.	Introduction	192
7.2.	Materials and Methods	193
7.2.1.	Collection and maintenance of <i>Carcinus maenas</i> and <i>Mytilus edulis</i>	194
7.2.2.	The effect of <i>Mytilus edulis</i> attachment strength on prey selection by <i>Carcinus maenas</i>	194
7.2.3.	Comparison of the attachment strengths of artificially attached and naturally occurring <i>Mytilus edulis</i>	197
7.3.	Results	197
7.3.1.	Foraging behaviour of <i>Carcinus maenas</i> on attached <i>Mytilus edulis</i>	197
7.3.1.1.	Handling techniques	197
7.3.1.2.	Selection for <i>Mytilus edulis</i> with different attachment strengths	198

7.3.2.	The attachment strength of <i>Mytilus edulis</i> in the laboratory and in the field	206
7.4.	Discussion	210
7.5.	Summary	216
Chapter 8	General Discussion	217
	References	223

List of Plates

- 2.1. *Mytilus edulis* shells from the low shore at Church Island (A) and the high shore at Aberffraw (B).
- 3.1. Photographs of food remains found in the stomachs of *Carcinus maenas*.
 - A. Fragments of *Mytilus edulis*.
 - B. White calcareous plates of barnacles.
 - C. Crescent shaped pieces of brown algae.

List of Tables

- 2.1 Coefficients of allometry between various size variables of *Mytilus edulis* valve variables, together with a test for departure from isometry.
- 2.2 Seasonal variation in flesh weight with shell length for monthly samples of *Mytilus edulis* from Church Island. Log transformed regression constants are derived from the equation $y=Ax^b$ where y is dry tissue weight and x is shell length.
- 2.3 Seasonal variation in flesh weight with shell length for monthly samples of *Mytilus edulis* from Aberffraw. Log transformed regression constants are derived from the equation $y=Ax^b$ where y is dry tissue weight and x is shell length.
- 2.4 Seasonal variation in flesh weight with shell length for monthly samples of *Mytilus edulis* from Church Island. Log transformed regression constants are derived from the equation $y=Ax^b$ where y is dry tissue weight and x is shell width.
- 2.5 Seasonal variation in flesh weight with shell length for monthly samples of *Mytilus edulis* from Aberffraw. Log transformed regression constants are derived from the equation $y=Ax^b$ where y is dry tissue weight and x is shell width.
- 2.6 The relationships between minimum and maximum valve strength and shell length in *Mytilus edulis* as determined by least squares regression. Minimum and maximum valve strengths were compared using analysis of covariance (general linear model, MINITAB).
- 2.7 Valve strengths are compared between months for *Mytilus edulis* from Aberffraw and Church Island using analysis of covariance (general linear model, MINITAB).
- 2.8 Comparison of the strengths of *Mytilus edulis* shell valves between two sites (Aberffraw and Church Island) using analysis of covariance (general linear model, MINITAB). Comparisons are made between the minimum valve strengths, the maximum valve strengths and between the strengths of the left valves.
- 2.9 Slopes estimated by geometric mean regression with their 95% confidence intervals for the strength of byssus attachment against shell length along with a test for the significance of the correlation between these two variables.
- 3.1 The occurrence of right-handedness in populations of *Carcinus maenas* from Traeth Melynog, Aberffraw, Church Island.

- 3.2 Coefficients of allometry between major chelal height and carapace width in male and female *Carcinus maenas* from Traeth Melynog together with a test for departure from isometry.
- 3.3 Coefficients of allometry between chelal height and carapace width for the major chelae of male and female *Carcinus maenas* from Traeth Melynog, Aberffraw and Church Island. Differences between crabs from the three sites are tested using analysis of covariance (general linear model, MINITAB).
- 3.4 Coefficients of allometry between apodeme areas of the major chela and carapace width in male and female *Carcinus maenas* from Traeth Melynog together with a test for departure from isometry. The area of the closer apodeme plate in the minor chela is presented as a percentage of the area of the closer apodeme plate in the major chela.
- 3.5 Mean mechanical advantages for major and minor chelae of *Carcinus maenas* caught from Traeth Melynog. The mechanical advantage of the major chela is compared to the minor chela using Mann-Whitney U test. The lengths L1 and L2 in the minor chelae are expressed as a percentage of the corresponding lengths in the major chelae.
- 3.6 Percentage frequency of occurrence of prey items in the guts of *Carcinus maenas* from Church Island and Aberffraw (males and females combined).
- 4.1 The relationship between shell length and breaking (Tb), eating (Te) and handling (Th) times for *Carcinus maenas* feeding on *Mytilus edulis* from Church Island as determined by least squares regression (MINITAB) from two crabs in each of the following size classes, 30-35, 40-45, 50-55 mm CW and one crab from 60-65 mm CW size class. The relationships are derived from data which includes breaking, eating and handling times obtained when mussels were opened using the edge-chipping and boring techniques.
- 4.2 The relationship between shell length and breaking (Tb), eating (Te) and handling (Th) times for *Carcinus maenas* feeding on *Mytilus edulis* from Aberffraw as determined by least squares regression (MINITAB) from two crabs in each of the following size classes, 30-35, 40-45, 50-55 mm CW and one crab from 60-65 mm CW size class. The relationships are derived from data which includes breaking, eating and handling times obtained when mussels were opened using the edge-chipping and boring techniques.
- 4.3 The relationship between shell length and breaking (Tb) and handling (Th) times for *Carcinus maenas* feeding on *Mytilus edulis* from Church Island and Aberffraw determined by least squares regression (MINITAB) for two crabs in each of the following size classes, 30-35, 40-45, 50-55 mm CW and one crab from 60-65 mm CW size class.
- 4.4 Comparison of the breaking (Tb) and handling (Th) times of *Carcinus*

maenas on *Mytilus edulis* from Church Island and Aberffraw. Data from two crabs in each of the following size classes 30-35, 40-45, 50-55 mm CW and one crab from 60-65 mm CW size class are presented. Data were compared using analysis of covariance (general linear model, MINITAB), data obtained when edge-chipping and boring techniques excluded.

- 4.5 Number and size range of mussels eaten when *Carcinus maenas* was fed on *Mytilus edulis* from Church Island and Aberffraw.
- 5.1 The effect of prey presentation on the minimum, maximum and median percentages of flesh remaining in discarded *Mytilus edulis* shells attacked by *Carcinus maenas* together with a significance test between trial medians. Data derived from Experiment 1.
- 5.2 The effect of prey presentation on the minimum, maximum and median percentages of flesh remaining in discarded *Mytilus edulis* shells attacked by *Carcinus maenas* together with a significance test between trial medians. Data derived from Experiment 2.
- 5.3 The effect of prey presentation on the relationships between breaking times, handling times and shell lengths for three *Carcinus maenas* feeding on *Mytilus edulis*. Relationships obtained from least squares regression. Data derived from Experiment 1.
- 5.4 The effect of presenting *Mytilus edulis* within groups of different proportions to three *Carcinus maenas*. The total number of mussels eaten, the number encountered and the percentage eaten:encountered in each size class is presented. Data derived from Experiment 1. The optimal size classes of mussels, determined from the predicted prey value curves (Fig. 5.1A) are highlighted.
- 5.5 The effect of prey presentation on the relationships between breaking times, handling times and shell lengths for three *Carcinus maenas* feeding on *Mytilus edulis*. Relationships obtained from least squares regression. Data derived from Experiment 2.
- 5.6 Breaking times (T_b) and handling times (T_h) are compared between three feeding trials. Differences between the slopes and the intercepts in the equation $\ln y = a + bx$ are tested using analysis of covariance (general linear model, MINITAB). Data derived from Experiment 2.
- 5.7 The effect of presenting *Mytilus edulis* in groups to three *Carcinus maenas*. The total number of mussels eaten, the number encountered and the percentage eaten:encountered in each size class is presented. Data derived from Experiment 2. The optimal size classes of mussels, determined from the predicted prey value curves (Fig. 5.3A) are highlighted.

- 6.1 Coefficients of allometry for various combinations of size parameters in *Perna viridis* together with a test for departure from isometry (n=37)
- 6.2 Coefficients of allometry for various combinations of size parameters in the chelae of *Thalamita danae* together with a test for departure from isometry.
- 6.3 Daily feeding rates of *Thalamita danae* with an unlimited diet of *Perna viridis* presented in two different relative proportions, together with the maximum size of mussel consumed.
- 7.1 Total number of weakly (W) and firmly (F) attached *Mytilus edulis* in optimal and suboptimal size classes eaten by five sizes of *Carcinus maenas*. The number of mussels of each attachment type which were detached prior to being open and eaten or which were broken, without being detached, are also presented together with the percentage of all encounters with each mussel type which resulted in a mussel being opened and eaten.
- 7.2 Mean and median breaking (Tb) and handling (Th) times for two size classes of *Carcinus maenas* feeding on weakly (W) and firmly (F) attached *Mytilus edulis* in an optimal prey size class. Values include the time required to detach a mussel whenever this occurred prior to the mussel being opened. Median values are compared using the Mann-Whitney U test.
- 7.3 Minimum, maximum, mean and median persistence times are presented for five *Carcinus maenas* foraging on weakly (W) and firmly (F) attached *Mytilus edulis* in an optimal size class. Persistence times of crabs on mussels which were not detached during the persistence period are presented, together with persistence times which include data from mussels which were detached and subsequently rejected uneaten (data in brackets).
- 7.4 Minimum, maximum, mean and median persistence times are presented for five *Carcinus maenas* foraging on weakly (W) and firmly (F) attached *Mytilus edulis* in a suboptimal size class. Persistence times of crabs on mussels which were not detached during the persistence period are presented, together with persistence times which include data from mussels which were detached and subsequently rejected uneaten (data in brackets).
- 7.5 Differences between the median persistence times (presented in Tables 7.3 & 7.4) for five *Carcinus maenas* foraging on weakly and firmly attached *Mytilus edulis* in optimal and suboptimal size classes using the Mann-Whitney U test. Median persistence times which exclude data for mussels which were detached during the persistence period and median persistence times which include these data are both tested.

List of Figures

- 2.1. Location of the study sites around the Island of Anglesey.
- 2.2. Schematic diagram of *Mytilus edulis* viewed laterally and dorsally to illustrate the shell dimensions measured in this study.
- 2.3. Schematic diagram illustrating measurement of *Mytilus edulis* valve strength (A) and byssal attachment strength (B).
- 2.4. *Mytilus edulis* population densities (A) and the predicted flesh weights of three standard size mussels, 7.5, 17.5 and 27.5mm shell length (B) for mussels from the low shore at Church Island (closed circles) and from the high shore at Aberffraw (open circles).
- 2.5. The length-frequency distributions of *Mytilus edulis* populations at the high shore Aberffraw.
- 2.6. The length-frequency distributions of *Mytilus edulis* from the low shore at Church Island.
- 2.7. The length-frequency distribution and the population density of *Mytilus edulis* from the high and mid shore levels at Aberffraw in February and June 1997.
- 2.8. The surface area frequency distributions of *Mytilus edulis* from the high shore Aberffraw.
- 2.9. The surface area frequency distributions of *Mytilus edulis* from the low shore Church Island.
- 2.10. The biomass frequency distributions of *Mytilus edulis* from the high shore Aberffraw.
- 2.11. The biomass frequency distributions of *Mytilus edulis* from the low shore Church Island.
- 2.12. The predicted flesh weights of *Mytilus edulis* of three standard lengths; 7.5, 17.5 and 27.5mm (A) and three standard widths; 3.1, 7.5 and 12.0 mm, from the low shore at Church Island (closed circles) and from the high shore at Aberffraw (open circles).
- 2.13. The valve breaking strengths of *Mytilus edulis* from the low shore Aberffraw collected in November 1996. The minimum (open circle) and maximum (closed circle) valve strengths for each mussel are presented. Valve strengths in excess of the 245 Newtons which could be measured by

the digital electronic gauge are represented by closed triangles.

- 2.14. The relationship between *Mytilus edulis* byssal attachment strength and shell length. Comparisons of byssal attachment strength are made between months (A & B), between sites (C & D) and between positions within a mussel patch (E & F). Lines fitted to the data using geometric mean regression.
- 2.15. The byssal attachment strength of *Mytilus edulis* from Aberffraw. Data from mussels located at the edge (pluses) and in the centre (open circles) of a patch are presented together with data from mussels that were hummocked (closed triangles). Lines fitted by geometric mean regression.
- 3.1. Diagram of a chela showing the various morphometric features measured. The lengths L1 and L2 are used to calculate the mechanical advantage, p is the pivotal point. Arrows denote the directions through which the forces F1 and F2 act.
- 3.2. Allometric relationships between chelal height and carapace width in the major and minor chelae of male and female *Carcinus maenas* from Traeth Melynog. Arrows denote a change in slope amongst males < 40 mm CW and > 40 mm CW.
- 3.3. The number of male (open bar) and female (closed bar) *Carcinus maenas* caught intertidally at Church Island in each sampling month during the period January 1996 to June 1997. In each month the total number of crabs caught in six traps over a 24 hour period is presented.
- 3.4. The number of male (open bar) and female (closed bar) *Carcinus maenas* caught intertidally at Aberffraw in each of the sampling months during the period January 1996 to September 1997. In each month, the total number of crabs caught in six traps over a 24 hour period is presented.
- 3.5. The percentage frequency occurrence of different food types in the stomachs of male (closed bar) and female (open bar) *Carcinus maenas* from Church Island (A) and Aberffraw (B).
- 3.6. The percentage frequency of occurrence of different food types in the stomachs of red (closed bar) and green (open bar) male *Carcinus maenas* from Church Island (A) and Aberffraw (B).
- 4.1. The relationship between opening technique and shell length when *Carcinus maenas* fed on *Mytilus edulis* from Church Island (A) and Aberffraw (B). The sizes of mussels opened by outright crushing (O), directed crushing (DC) and edge-chipping/boring (ECB) are presented for crabs in the following size classes; 30-35, 40-45, 50-55 and 60-65mm CW.

- 4.2. Breaking times are plotted against shell length of *Mytilus edulis* from Church Island for *Carcinus maenas* of different carapace widths. Data were combined for the two crabs in the smallest size class of 30-35mm CW; (1 + 2), but kept separate for the two crabs in the 40-45 and 50-55 mm CW size classes; (1), (2). Only one crab was used in the size class 60-65mm CW. The linear regression equations presented in Table 4.1 are used to fit lines to the raw data.
- 4.3. Eating times are plotted against shell length of *Mytilus edulis* from Church Island for *Carcinus maenas* of different carapace widths. Data were combined for the two crabs in the smallest size class of 30-35mm CW; (1 + 2), but kept separate for the two crabs in the 40-45 and 50-55 mm CW; (1), (2) size classes. Only one crab was used in the size class 60-65mm CW. The linear regression equations presented in Table 4.1 are used to fit lines to the raw data.
- 4.4. Handling times are plotted against shell length of *Mytilus edulis* from Church Island for *Carcinus maenas* of different carapace widths. Data were combined for the two crabs in the smallest size class of 30-35mm CW; (1 + 2), but kept separate for the two crabs in the 40-45 and 50-55 mm CW size classes; (1), (2). Only one crab was used in the size class 60-65mm CW. The linear regression equations presented in Table 4.1 are used to fit lines to the raw data.
- 4.5. Breaking times are plotted against shell length of *Mytilus edulis* from Aberffraw for *Carcinus maenas* of different carapace widths. Data were combined for the two crabs in the smallest size class of 30-35mm CW; (1 + 2), but kept separate for the two crabs in the 40-45 and 50-55 mm Cwsize classes; (1), (2). Only one crab was used in the size class 60-65mm CW. The linear regression equations presented in Table 4.2 are used to fit lines to the raw data.
- 4.6. Eating times are plotted against shell length of *Mytilus edulis* from Aberffraw for *Carcinus maenas* of different carapace widths. Data were combined for the two crabs in the smallest size class of 30-35mm CW; (1 + 2), but kept separate for the two crabs in the 40-45 and 50-55 mm CW size classes; (1), (2). Only one crab was used in the size class 60-65mm CW. The linear regression equations presented in Table 4.2 are used to fit lines to the raw data.
- 4.7. Handling times are plotted against shell length of *Mytilus edulis* from Aberffraw for *Carcinus maenas* of different carapace widths. Data were combined for the two crabs in the smallest size class of 30-35mm CW; (1 + 2), but kept separate for the two crabs in the 40-45 and 50-55 mm Cwsize classes; (1), (2). Only one crab was used in the size class 60-65mm CW. The linear regression equations presented in Table 4.2 are used to fit lines to the raw data.

- 4.8. A summary of the relationships between prey length and breaking, eating and handling times for *Carcinus maenas* of different sizes feeding on *Mytilus edulis* from Church Island. Data were combined for the two crabs in the smallest size class of 30-35mm CW; (1 + 2), but kept separate for the two crabs in the 40-45 and 50-55 mm CW size classes; (1), (2). Only one crab was used in the size class 60-65mm CW. Relationships are derived from the regression equations presented in Table 4.1.
- 4.9. A summary of the relationships between prey length and breaking, eating and handling times for *Carcinus maenas* of different sizes feeding on *Mytilus edulis* from Aberffraw. Data were combined for the two crabs in the smallest size class of 30-35mm CW; (1 + 2), but kept separate for the two crabs in the 40-45 and 50-55 mm CW size classes; (1), (2). Only one crab was used in the size class 60-65mm CW. Relationships are derived from the regression equations presented in Table 4.2.
- 4.10. The time required by four size groups of *Carcinus maenas* to eat 1 gram of dried flesh when feeding on Church Island mussels. Data were combined for the two crabs in the smallest size class of 30-35mm CW; (1 + 2), but kept separate for the two crabs in the 40-45 and 50-55 mm CW size classes; (1), (2). Only one crab was used in the size class 60-65mm CW. Eating times were obtained using the regression equations relating eating time to shell length presented in Table 4.1.
- 4.11. A The relationships between prey value and shell length of Church Island *Mytilus edulis* for four size classes of *Carcinus maenas*. Prey value was calculated using the handling time-shell length regression equations presented in Table 4.1, which included data from the lengthier opening techniques of edge chipping and boring (open circles) and using the handling time-shell length regression equations presented in Table 4.3. which excluded data from these lengthier techniques (closed circles). Arrows denote those sizes of prey predicted to be the most profitable.
- B The size of Church Island *Mytilus edulis* most vulnerable to four sizes of *Carcinus maenas* when prey presented to crabs in groups of five mussels in each of five size classes; 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length.
- 4.12. A The relationships between prey value and shell length of Aberffraw *Mytilus edulis* for four size classes of *Carcinus maenas*. Prey value was calculated using the handling time-shell length regression equations presented in Table 4.2, which included data from the lengthier opening techniques of edge chipping and boring (open circles) and using the handling time-shell length regression equations presented in Table 4.3. which excluded data from these lengthier techniques (closed circles). Arrows denote those sizes of prey predicted to be the most profitable.
- B The size of Aberffraw *Mytilus edulis* most vulnerable to four sizes of

Carcinus maenas when prey presented to crabs in groups of five mussels in each of five size classes; 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length.

- 4.13. Seasonal variations in the prey value of Church Island *Mytilus edulis*. Prey value was calculated using the flesh weight - shell length regression equation determined for mussels in September 1996 (closed circles) and February 1997 (open circles), presented in Table 2.2 and the handling time-shell length regression equations presented in Table 4.3. Arrows denote the size of mussel predicted to be most optimal.
- 4.14. Seasonal variations in the prey value of Aberffraw *Mytilus edulis*. Prey value was calculated using the flesh weight - shell length regression equations determined for mussels in June 1997 (closed circles) and November 1996 (open circles), presented in Table 2.2 and the handling time-shell length regression equations presented in Table 4.3. Arrows denote the size of mussel predicted to be most optimal.
- 4.15. The relationships between prey value and shell length of Church Island *Mytilus edulis* (closed circles) and Aberffraw *M. edulis* (open circles) for four size classes of *Carcinus maenas*. Prey values were calculated using the flesh weight-shell length regression equations determined in July 1996, presented in Tables 2.2 & 2.3 and the handling time - shell length regression equation presented in Tables 4.3. Arrows denote the size of mussel predicted to be the most profitable.
- 4.16. The relationships between prey value and shell length of Church Island *Mytilus edulis* (closed circles) and Aberffraw *M. edulis* (open circles) for four size classes of *Carcinus maenas*. Prey values were calculated using the flesh weight-shell length regression equations determined in March 1996, presented in Tables 2.2 & 2.3 and the handling time - shell length regression equation presented in Tables 4.3. Arrows denote the size of mussel predicted to be the most profitable.
- 4.17. The number of *Mytilus edulis* from Church Island (closed bar) and Aberffraw (hatched bar) eaten by four size classes of *Carcinus maenas* when mussels from the two sites are presented together.
- 5.1. A. Prey value curves for three *Carcinus maenas* (42.3, 44.5, 54.0 mm CW) when foraging on *Mytilus edulis* presented singly (closed circles, Trial 1), as part of group comprising five mussels in each of the following size classes; 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length (pluses, Trial 2) and as part of a group comprising 11, 7, 3, 3, 1, mussels in the following size classes 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length respectively (crosses, Trial 3). Arrows denote those sizes of mussel predicted to be the most profitable.

B. The number of mussels eaten by each crab (42.3, 44.5, 54.0 mm CW)

over a five day period when mussels were presented as part of group comprising five mussels in each of the following size classes; 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length (closed bar, Trial 2) and as part of a group comprising 11, 7, 3, 3, 1, mussels in the following size classes 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length respectively (hatched bar, Trial 3).

- 5.2. Comparison of (A) prey value curves (predicted flesh content of mussel/handling time) with (B) adjusted prey value curves (predicted flesh eaten/handling time) determined when three *Carcinus maenas* (42.3, 44.5, 54.0 mm CW) foraged on *Mytilus edulis* presented singly (closed circles), as part of group comprising five mussels in each of the following size classes; 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length (pluses) and as part of a group comprising 11, 7, 3, 3, 1, mussels in the following size classes 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length respectively (crosses).
- 5.3. A. Prey value curves for three *Carcinus maenas* (52.4, 52.8, 54.1 mm CW) when foraging on *Mytilus edulis* presented singly (closed circles, Trial 1), as part of group comprising five mussels in each of the following size classes; 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length (pluses, Trial 2) and singly (crosses, Trial 3). Arrows denote those sizes of mussel predicted to be the most profitable.

B. The number of mussels eaten by each crab (52.4, 52.8, 54.1 mm CW) over a five day period when mussels were presented as part of group comprising five mussels in each of the following size classes; 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length (closed bar, Trial 2).
- 5.4. Comparison of (A) prey value curves (predicted flesh content of mussel/handling time) with (B) adjusted prey value curves (predicted flesh eaten/handling time) determined when three *Carcinus maenas* (52.4, 52.8, 54.1 mm CW) foraged on *Mytilus edulis* presented singly (closed circles), as part of group comprising five mussels in each of the following size classes; 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length (pluses) and again singly (crosses).
- 5.5. The number of *Mytilus edulis* consumed each day by four different sizes of *Carcinus maenas* when mussels were presented as five mussels in each of the following size classes, 5-10, 10-15, 15-20, 20-25, 25-30mm shell length (closed bar) and when mussels were presented as 11, 7, 3, 3, 1, individuals in the following size classes 5-10, 10-15, 15-20, 20-25, 25-30mm shell length respectively (hatched bar).
- 5.6. The number of *Mytilus edulis* consumed each day by three size classes of *Carcinus maenas* when presented with 11, 7, 2, 2, 3 mussels respectively in the following size classes, 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length; representative of the population from the high shore Aberffraw

(closed bars), and with 10, 3, 3, 2, 5, 2, mussels respectively in the following size classes 5-10, 10-15, 15-20, 20-25, 25-30, 30-35 mm shell length; representative of the mid shore population at Aberffraw (open bars).

- 6.1. Location of study sites in Hong Kong.
- 6.2. Length-frequency distribution of *Perna viridis* from the high shore level at Wu Kai Sha.
- 6.3. The relationship between chelal height (A), apodeme area (B) and carapace width in *Thalamita danae*. Data are presented for both the major (closed circles) and the minor (open circles) chelae.
- 6.4. A. Breaking times plotted against shell length of *Perna viridis* when mussels presented singly (closed circles) and mussels presented as part of a group (open circles). Data from mussels opened by the insertion technique are marked with an 'i'. Lines fitted by eye.

B. Handling times plotted against shell length of *Perna viridis* when mussels presented singly (closed circles) and mussels presented as part of a group (open circles). Data from mussels opened by the insertion technique are marked with an 'i'. Handling times (Th) are related to shell length (SL) by the following regression equations which have been fitted to the raw data.
mussels presented singly: $\ln Th = 4.09 + 0.233 SL$
mussels presented as part of a group: $\ln Th = 4.55 + 0.128 SL$.

C. Prey value of *Perna viridis* to *Thalamita danae* when mussels presented singly (closed circles) and as part of a group (open circles) to the crab. Prey value was determined using the above handling time - shell length regression equation and the flesh weight - shell length regression equation presented in Table 6.1. Arrows denote the size of mussel predicted to be the most optimal.
- 6.5. The number of *Perna viridis* consumed each day by three sizes of *Thalamita danae* when mussels were presented in groups comprising five mussels in each of the following size classes, 10-15, 15-20, 20-25, 25-30, 30-35mm shell length (closed bars) and when mussels were presented in groups comprising 1, 2, 9, 10, 3 mussels respectively in the size classes 10-15, 15-20, 20-25, 25-30, 30-35mm shell length (open bars).
- 7.1. Schematic diagram illustrating the way in which 'weak' (A) and 'firm' (B) attachment were attained.
- 7.2. The number of weakly and firmly attached *Mytilus edulis* in an optimal size class (10-15 mm shell length) eaten by *Carcinus maenas* of 41.1 mm CW over a three day period.

- 7.3. The number of weakly and firmly attached *Mytilus edulis* in an optimal size class (10-15 mm shell length) eaten by *Carcinus maenas* of 43.8 mm CW over a three day period.
- 7.4. The number of weakly and firmly attached *Mytilus edulis* in an optimal size class (10-15mm shell length) eaten by *Carcinus maenas* of 44.3 mm CW over a three day period.
- 7.5. The number of weakly and firmly attached *Mytilus edulis* in an optimal size class (15-20mm shell length) eaten by *Carcinus maenas* of 54.3 mm CW over a three day period.
- 7.6. The number of weakly and firmly attached *Mytilus edulis* in an optimal size class (15-20mm shell length) eaten by *Carcinus maenas* of 54.8 CW mm over a two day period. Data were not obtained for a third day since the crab stopped eating.

CHAPTER 1.

GENERAL INTRODUCTION

Predation is a powerful biotic force and the behaviour of predators can profoundly influence the structure of the communities in which they occur. The effects of predation may be seen at several different levels; population, community and evolutionary. Predatory activity can have a beneficial effect on a community. Depressing the number of individuals of a prey species which is a superior competitor for example may enhance the biodiversity of the community (Paine, 1966; Menge, 1983). In areas of intense predatory pressure, the settlement and/or establishment of a prey population can be prevented (Blundon and Kennedy, 1982a; Jensen and Jensen, 1985; Sanchez-Salazar *et al.*, 1987a). The scarcity of the cockle, *Cerastoderma edule*, from the low shore at Traeth Melynog, North Wales, has been shown to result directly from the intense predatory behaviour of the shore crab, *Carcinus maenas* (Sanchez-Salazar *et al.*, 1987a). Thus, predation can influence the distribution of the prey species which may consequently be restricted largely to areas that are inaccessible to the predator, such areas provide an effective spatial refuge. Some prey species seek to minimise the risk of predation by altering their behaviour, the copepod *Acartia hudsonica* for instance, fed less in the hours of daylight when the visual predator, the three-spined stickleback, *Gasterosteus aculeatus* was present (Bollens and Stearns, 1992). Predation can also exert a powerful evolutionary pressure; the development of spines on tropical gastropods is generally considered to result from predation pressure from decapod crustaceans (Zipser and Vermeij, 1978). Evolutionary pressure can also work on the predator as well as the prey and the predominance of right-handedness amongst crabs feeding on hard-shelled molluscs is thought to arise as a way of dealing with the dextral spiralling of gastropod shells (Ng and Tan, 1985). This led Vermeij (1977) to conclude that the structure of a predator's feeding appendages and the external structure of its prey species result, at least in part, from a co-evolutionary arms race. The influence of predation is thus profound and an understanding of the mechanisms underlying it important to the study of the interactions between predator and prey species.

Ultimately the relationship between the morphology and strength of the predator's feeding appendages and the morphology and strength of the prey will determine the range of prey sizes and the type of prey that the predator can consume (Brown *et al.*, 1979; Kaiser *et al.*, 1992). Studies investigating these relationships provide the researcher with information concerning the fundamental foraging scope of the predator, i.e. the potential range of prey that the predator can consume. But simple determination of the fundamental foraging scope is not adequate to describe the foraging behaviour of predators and their potential impact on the community. Many predators are highly prey selective. Selection of a particular prey species or of a particular prey size has been observed in a diverse array of animal groups including decapod crustaceans (Juanes, 1992), birds (Sutherland, 1982), fish (Croy and Hughes, 1991; Juanes and Conover, 1994) and molluscs (Hughes and Burrows, 1991; McQuaid, 1994). The fundamental foraging scope will differ from the realised foraging scope, i.e. the size and type of prey that are actually consumed in the field, and it is this that needs to be determined if the vulnerability of prey is to be accurately assessed.

In recent years models have been developed to explain the mechanisms underlying prey selection and to predict which types of prey are most vulnerable: The prime model has been the Optimal Foraging Theorem under the energy maximisation premise (see Hughes, 1980 for review). The selection of a prey type or size is assumed to confer some sort of selective advantage on the predator. Under the energy maximisation premise, net energy intake is assumed to be proportional to the fitness of the predator and thus selection of prey which maximises the predator's net rate of an energy intake is an optimal strategy. The currency of optimal foraging theory under this premise is E/T , the assimilated energy per unit foraging time, or prey value. This can be calculated for a range of prey types and sizes and observed prey selection can be tested against predictions made from this model. A central premise to this theory is that the predator has the ability to assess the prey value of an individual prey item and is able to rank it in relation to others that it encounters. Although there is evidence that animals do feed optimally (e.g. Elner and Hughes, 1978; Hughes and Elner, 1979; Juanes and Conover, 1994), there is little evidence that predators have this ability to assess prey value. The ability of the common shore crab, *Carcinus maenas*, to actively

select amongst a highly variable prey species, *Mytilus edulis*, is explored in this thesis.

The Optimal Foraging Theorem provides a simple yet valuable theoretical framework in which to analyse foraging behaviour. Many studies have used the decapod/hard-shelled mollusc relationship to test predictions from the optimal foraging model (e.g. Elner and Hughes, 1978; Hughes and Seed, 1981; ap Rheinallt, 1986; Davidson, 1986). There are sound reasons for this since hard-shelled molluscs occur over discrete size ranges and it is relatively easy to measure both their size and energy content. Different components of the predator's foraging behaviour with such prey are easily observed and decapods often consume large quantities of the prey such that data can be quickly collected. Moreover, both decapods and hard-shelled molluscs are common, easy to collect and easy to maintain under laboratory conditions. Additionally many hard-shelled molluscs such as mussels, clams and oysters form commercially important food stocks which lends further importance to such studies (Ropes, 1968; Walne and Dean, 1972; Arnold, 1984; Huang *et al.*, 1985; Sponaugle and Lawton, 1990).

My study extends work that has previously been conducted on the European shore crab, *Carcinus maenas* foraging on hard-shelled molluscs (e.g. Elner and Hughes, 1978; Hughes and Elner, 1979; Elner and Raffaelli, 1980; Cunningham, 1983; Jubb *et al.*, 1983; Ameyaw-Akumfi and Hughes, 1987) and concentrates on the relationship between this predator and the mytilid prey species, *Mytilus edulis*. During the course of this studentship the opportunity arose to examine briefly another crab/mollusc predator/prey interaction, that between the tropical-subtropical portunid, *Thalamita danae* and the green-lipped mussel, *Perna viridis*, in Hong Kong. Despite evidence that *T.danae* is a significant predator of *P.viridis*, which forms an important commercial aquaculture stock throughout Asia (Huang *et al.*, 1985) little previous work has been conducted on this predator/prey relationship (Seed, 1990a).

Carcinus maenas is a brachyuran, or true crab. It belongs to the family Portunidae which contains crabs that are characterised by their flattened fifth pair of pereopods. *C.maenas* is native to Europe where it is found in abundance from the eulittoral zone down to depths of 60 metres (Ingle, 1980). Its distribution within this depth range depends on age, moult stage (as indicated by carapace colour), season and

sex (Crothers, 1968; Atkinson and Parsons, 1973; Hunter and Naylor, 1993; Warman *et al.*, 1993). Whilst part of the *C.maenas* population, the juveniles, tends to be resident in the intertidal or shallow sublittoral zones shore and part subtidally; larger red crabs, i.e. those in an extended intermoult period, an element of the population is tidally migratory, foraging up the shore on the flood tide and retreating on the ebb (Hunter and Naylor, 1993; Warman *et al.*, 1993). Although omnivorous *C.maenas* is a natural predator of hard-shelled molluscs, which often form a significant component of its diet (Ropes, 1968; Elner, 1978; Elner, 1980, Raffaelli *et al.*, 1989) and it has been found to be an ideal experimental animal, responding well to life in the laboratory aquaria (see for example Hughes and Elner, 1978). Furthermore *C.maenas* has been steadily extending its geographical range and is now found in North America and Australia (see Cohen *et al.*, 1995; Grosholz and Ruiz, 1995; Lafferty and Kuris, 1996, and references therein), where it often out competes indigenous crab species and destroys stocks of hard-shelled molluscs (Ropes, 1968). An understanding of the mechanisms underlying prey selection and the determination of prey most vulnerable to attack is therefore particularly important.

Mytilus edulis is a member of the family Mytilidae. It is a common bivalve mollusc which can be found from the high intertidal zone down to the sublittoral zone throughout much of the cooler waters of the northern and southern hemispheres (Seed and Suchanek, 1992). *M.edulis* can survive in a wide range of environmental conditions and thrives both on sheltered and wave-exposed shores. Features of this bivalve alter with the environmental conditions in which it is found, influencing the population density and structure, shell morphology, flesh weight and byssal attachment strength; populations living on shores receiving moderate to high wave action tend to have high population densities, a more elongate shell form (Seed, 1968) and stronger byssal attachment strength (Witman and Suchanek, 1984) than those living on shores with relatively little wave action. Variations may also occur between tidal elevations and typically mussels from the low shore are faster growing, more elongate in shape and prone to wide oscillations in population density resulting from high densities of settlement but also high predation rates (Seed, 1980a). In contrast, those populations from the high shore tend to consist of slower growing and smaller individuals which

posses a more tumid shell; these populations are also relatively stable in terms of their densities than those occurring on the low shore. High shore populations tend to have a greater shell-flesh weight ratio (Seed, 1980a) and this, together with their more rounded shell may result in these mussels being relatively stronger than those from a low shore population. A tidally foraging predator, such as *Carcinus maenas*, may therefore encounter such variations in *M.edulis* populations even over a single foraging excursion and factors such as shell shape, flesh weight, byssal attachment strength and population density may all significantly affect the foraging behaviour of this predator.

Previous studies have shown that *Carcinus maenas* feeds optimally on bivalves such as *Mytilus edulis* (Elner and Hughes, 1978; Jubb *et al.*, 1983) and *Cerastoderma edule* (Sanchez-Salazar *et al.*, 1987b) and on gastropods such as *Nucella lapillus* (Hughes and Elner, 1979), *Littorina saxatilis* (= *rudis*) and *Littorina compressa* (= *nigrolineata*) (Elner and Raffaelli, 1980), that is it selects those sizes of prey which maximise its net energy intake. Elner and Hughes (1978) concluded that *C.maenas* actively selected optimally sized mussels, rejecting small individuals on the basis of their size and large individuals on the basis of their shell strength, the 'Prey Evaluation Hypothesis'. Further investigations into the foraging behaviour of *C.maenas* with *M.edulis* led Jubb *et al.*, (1983) to propose an alternative 'Relative Stimulus Hypothesis', where the active selection of the optimally sized mussels was mediated by integrating stimuli received by the legs (size and number of mussels touched) and the chelae (shell strength of the mussel held in the claws). However, when foraging on gastropods, the selection of the optimal size of prey appeared to be an entirely passive response to encounter rate and shell strength, both of which increased with increased prey size. Since *C.maenas* could not open the largest gastropods this passive response led to medium sized gastropods (the optimal size) predominating in the diet (Hughes and Elner, 1979; Elner and Raffaelli, 1980). It seems somewhat strange that a predator should actively select for size in one species of prey yet passively select another. This thesis will address this apparent paradox.

Experiments investigating the foraging of *Carcinus maenas* on *Mytilus edulis* have often presented the prey in a somewhat artificial way for example as unattached

individuals scattered randomly over the floor of the aquarium (Elner and Hughes, 1978; Jubb *et al.*, 1983). Recently however, there has been a call for a more context-sensitive approach to foraging behaviour experiments, that considers the way in which the predator is likely to encounter the prey species in the field (Sponaugle and Lawton, 1990, Lawton and Zimmer-Faust, 1992). If the results of foraging behaviour observed in the laboratory are to be used to assess prey vulnerability in the field then elements of the natural environment need to be taken into consideration. Indeed, experiments which have been made more context-sensitive have not only illustrated that prey vulnerability can be altered (West and Williams, 1986; Lee and Kneib, 1994; Hughes and Seed, 1997) but have also provided additional information regarding the mechanisms underlying prey selection which were not observed in more simplistic experimental protocols (Hughes and Seed, 1997; Seed and Hughes, 1997). The experiments described in this thesis have taken the first steps towards a more context-sensitive approach to foraging studies, using the information gained from previous experiments as a departure point.

The effect of predation on a prey species has often been investigated solely in terms of the effect on the density and structure of the prey population (e.g. Pollock, 1979; Griffiths and Seiderer, 1980; Sanchez-Salazar *et al.*, 1987a; Seed 1990a). However, predation in the field will be modified through the influence of environmental structure and dynamics. Structural elements of the environment alter predatory behaviour for example the sea horse, *Hippocampus erectus* which is an ambush predator in areas of high seagrass but a pursuit predator where seagrass is absent (James and Heck, 1994). Environmental structure has also been shown to alter predation intensity (Arnold, 1984; Leber, 1985; Sponaugle and Lawton, 1990) and prey size selectivity (Lee and Kneib, 1994) in predatory decapods. Environmental dynamics such as wave action may regulate the relative importance of predation compared to competition as a structuring force within certain rocky shore communities (Menge, 1978; Griffiths and Hockey, 1987), and can also alter certain features of the prey population. In marine mussels, for example, shell shape, byssal attachment strength, flesh weight and population structure (Seed, 1968; Witman and Suchanek, 1984; Young, 1985) are all significantly altered by the environment. Although such

factors could affect the value of the prey to the predator by making it more difficult to open, detach or access, the effect of intraspecific differences in prey on foraging behaviour has been largely ignored. Such differences could be important amongst different populations of prey and this thesis investigates the effect of intraspecific variability on the foraging behaviour of both *C.maenas* and *Thalamita danae*. The ability of *C.maenas* to differentiate between individual prey items offering the same prey value is also investigated.

Chapter 2 documents the characteristic features of two populations of *Mytilus edulis*, one population from the high shore of a wave-exposed site, Aberffraw, the other from a low shore of a wave-sheltered site, Church Island. Both of these sites are located on the island of Anglesey off the coast of North Wales. These populations represent the extreme forms of *M.edulis* that a locally foraging crab is likely to encounter. Those variables such as population structure, shell morphology, flesh and shell weight, byssal attachment strength and shell strength, which are most likely to influence crab foraging behaviour and compared between individuals from the two prey populations. Chapter 3 documents the chelal morphology of *Carcinus maenas*. The abundance and size distribution of *C.maenas* at Aberffraw and Church Island are briefly investigated and the rationale for using these two mussel populations in subsequent laboratory experiments is verified by investigating the natural diets of crabs at these locations. Chapter 4 records the foraging behaviour of *C.maenas* when presented with mussels from Aberffraw and Church Island. Prey value curves are derived for mussels from both populations and the ability of crabs to select between contrasting prey items is investigated. The way in which mussels are presented to the crabs and the subsequent effect on foraging behaviour, predicted prey value and prey size vulnerability is documented in Chapters 5 and 6; Chapter 5 concentrates on the predator/prey relationship between *C. maenas* and *M. edulis* and Chapter 6 extends this approach to the predator/prey pairing of *Thalamita danae* and *Perna viridis*. Little work has previously been carried out on this species pair which can perhaps be considered the subtropical-tropical equivalent of the *C.maenas* and *M.edulis* interaction. Chapters 5 and 6 take the first steps towards a more context sensitive approach to foraging experiments. This approach is extended in Chapter 7 where the

foraging behaviour of *C.maenas* on attached *M. edulis* is investigated. In this chapter not only is the ability of *C.maenas* to select for prey of greater value investigated but the mechanisms underlying such selection are also explored.

CHAPTER 2

CHARACTERISTICS OF *MYTILUS EDULIS* POPULATIONS.

2.1. INTRODUCTION

The bivalve mollusc, *Mytilus edulis*, is a member of the family Mytilidae and is widely distributed throughout the temperate waters of both the Northern and Southern hemispheres (Seed and Suchanek, 1992). It is tolerant of a wide range of conditions and can be found in fully saline to estuarine waters and in sheltered to wave-exposed locations (Seed and Suchanek, 1992). Whilst *M.edulis* can be found from the subtidal to the splash zone, it attains dominance in the intertidal, where the upper and lower boundaries of its zonation are controlled by competition and predation rather than physiological factors (Seed and Suchanek, 1992). The broadly triangular shell shape of *M.edulis* arises from the reduction of the anterior end of the body and the expansion of the posterior region. This shape, whilst unusual amongst the bivalves as a whole, is characteristic of the mytilids and is associated with the retention of the byssus threads into adulthood (Morton, 1992). The byssus threads are proteinaceous structures secreted by the glands at the base of the muscular foot. They are used primarily for secure anchorage and *M.edulis* can be found typically on hard substratum where it attaches to the surface, or on semi-consolidated substratum where it attaches to individual particles of sand (Meadows and Shand, 1989). *M.edulis* is a filter feeder and its survival on intertidal rocky shores, where high water movement guarantees a continuous supply of suspended particulate food, is dependent on this ability to form this strong attachment to the substrata with its byssus threads and it is on these shores that *M.edulis* frequently becomes the space dominant organism (Witman and Suchanek, 1984; Lintas and Seed, 1994). In attaching to the substrata these mussels orient themselves so that the anterior, umbonal, end of the shell is close to the substrata whilst the expanded posterior region, through which the inhalent water stream enters

the shell, projects into the water flow. Their shape is therefore highly adaptive and is ideal for organisms which live in dense assemblages (Seed, 1980b, Morton, 1992).

Mytilus edulis is an important intertidal organism not only because mussel assemblages can be highly productive (Leigh *et al.*, 1987) but also because of their ability to form large stable beds which alter the local physical and chemical conditions. The formation of these beds results in the creation of microniches and mussel beds typically have a dense and rich assemblage of flora and fauna associated with them (Lintas and Seed, 1994; Seed, 1996). Both the mussels and their associated fauna and flora are important food for predators.

The environment has been shown to have a profound effect on the density and structure of mussel populations and on shell morphology, flesh and shell weights by controlling factors such as food supply, recruitment, growth rates and emersion times (Seed, 1968; Kopp, 1979; Griffiths, 1981; Cheung and Tse, 1993; Richardson *et al.*, 1995). General trends can be recognised; mussels from higher tidal levels tend to have a slower growth rate, smaller maximum shell length, a greater shell width and poorer condition relative to mussels from lower regions of a shore (Seed, 1968; Kopp, 1979, Seed, 1980; Griffiths, 1981; Cheung and Tse, 1993; Richardson *et al.*, 1995). Mussel populations from more wave-exposed shores tend to have a greater population density (Seed, 1968), poorer condition (Richardson *et al.*, 1995) and stronger attachment (Harger, 1970; Witman and Suchanek, 1984) than those occupying more sheltered shores.

Since *Mytilus edulis* can survive under a wide range of environmental conditions it is not surprising that a high degree of variability in its population structure and density (Lintas and Seed, 1994) shell morphology (Seed, 1968) flesh and shell weights (Seed, 1973) and byssal attachment strength (Harger, 1970; Witman and Suchanek, 1984; Young, 1985) have all been reported. Foraging crabs such as *Carcinus maenas* are thus likely to encounter variations amongst mussel populations between shores and between different tidal levels. The characteristics of the prey population could significantly influence crab foraging behaviour. Population structure of the prey species determines the size of prey items available to the predator whilst shell morphology will influence the way in which the predator handles the prey. Shell

strength, flesh weight and byssal attachment strength could all affect the value of the prey to the predator by influencing handling time. This chapter examines the characteristic features of mussel populations taken from two physically contrasting environments, one from the upper shore level of a wave-exposed shore at Aberffraw and one from the low tidal level of a sheltered shore in the Menai Strait. The sites chosen represent two extreme types of rocky shores that *M. edulis* can colonise and this is reflected in the characteristic features of these mussel populations. The study was carried out over an 18 month period so that any seasonal changes occurring within these populations were also recorded. During one month of the study an additional comparison was made between the populations at the high and mid shore levels at the wave-exposed site. This was carried out in order to assess the variations between mussel populations separated by only a few metres.

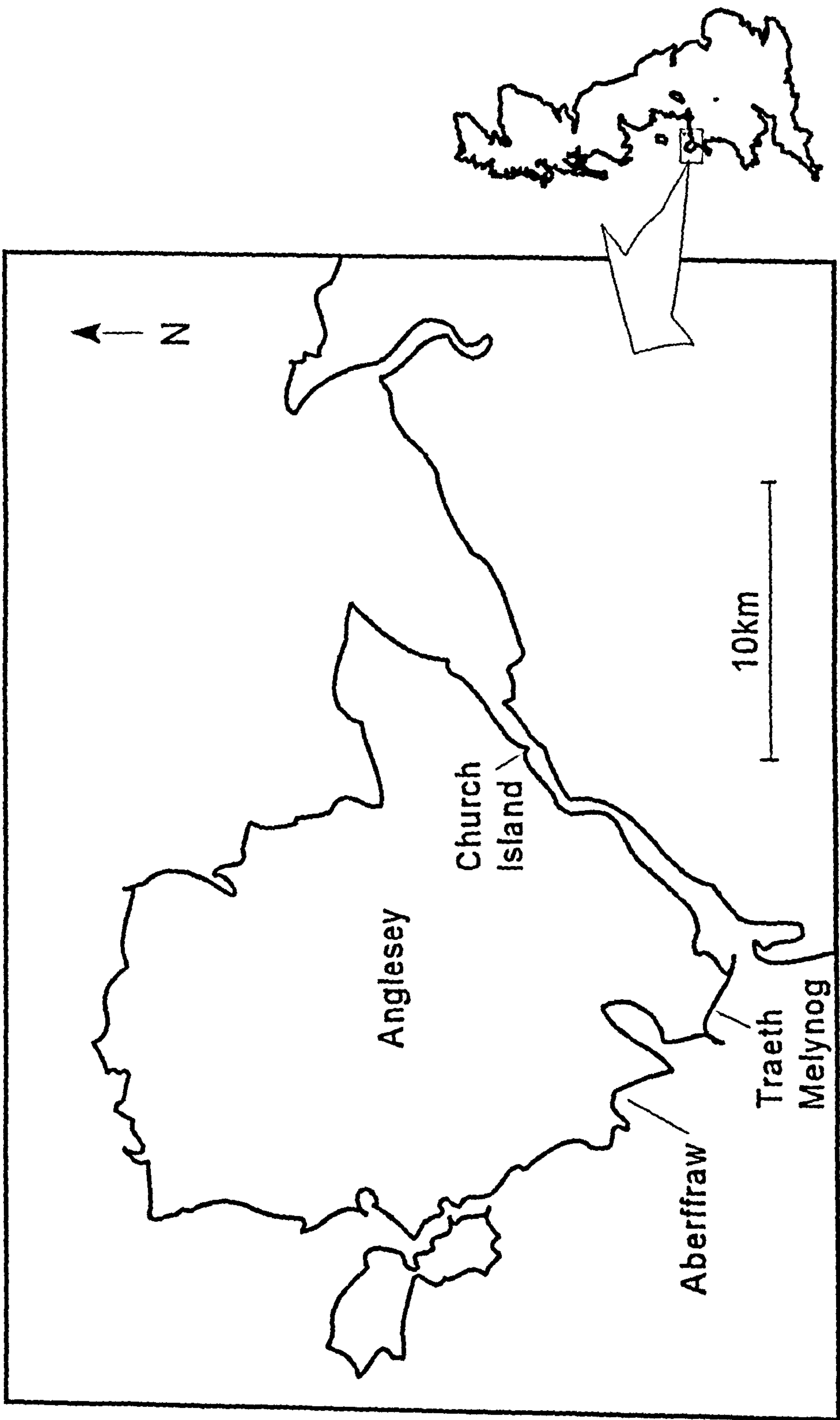
2.2. MATERIALS AND METHODS

2.2.1. Site descriptions of Aberffraw and Church Island.

The two study sites were located at Aberffraw and Church Island on Anglesey off the North Wales coast (Fig.2.1). Aberffraw is a sandy bay encircled by rocks located on the south-west side of Anglesey. It is a moderately wave-exposed shore facing the prevailing south westerly wind. A small river dissects the bay from north-east to south-west. The dominant sedentary fauna present on the rocky outcrops are *Mytilus edulis* and barnacles. These are present in abundance at high and mid shore levels but are absent at the lower shore levels. Large numbers of dogwhelks, *Nucella lapillus*, are also present. There is little flora present at this site; seaweed species tend to be restricted to encrusting forms such as *Hildenbrandia rubra* and *Corallina elongata* which occurs mainly in rock pools along with small anemones, *Actinia equina*.

Church Island is situated in the Menai Strait off the south-east coast of Anglesey (Fig.2.1) and is joined to Anglesey by a small causeway. The Menai Strait was formed by glacial action and is up to 21m deep (Young, 1987). Although sheltered

Figure 2.1. Location of the study sites around the Island of Anglesey.



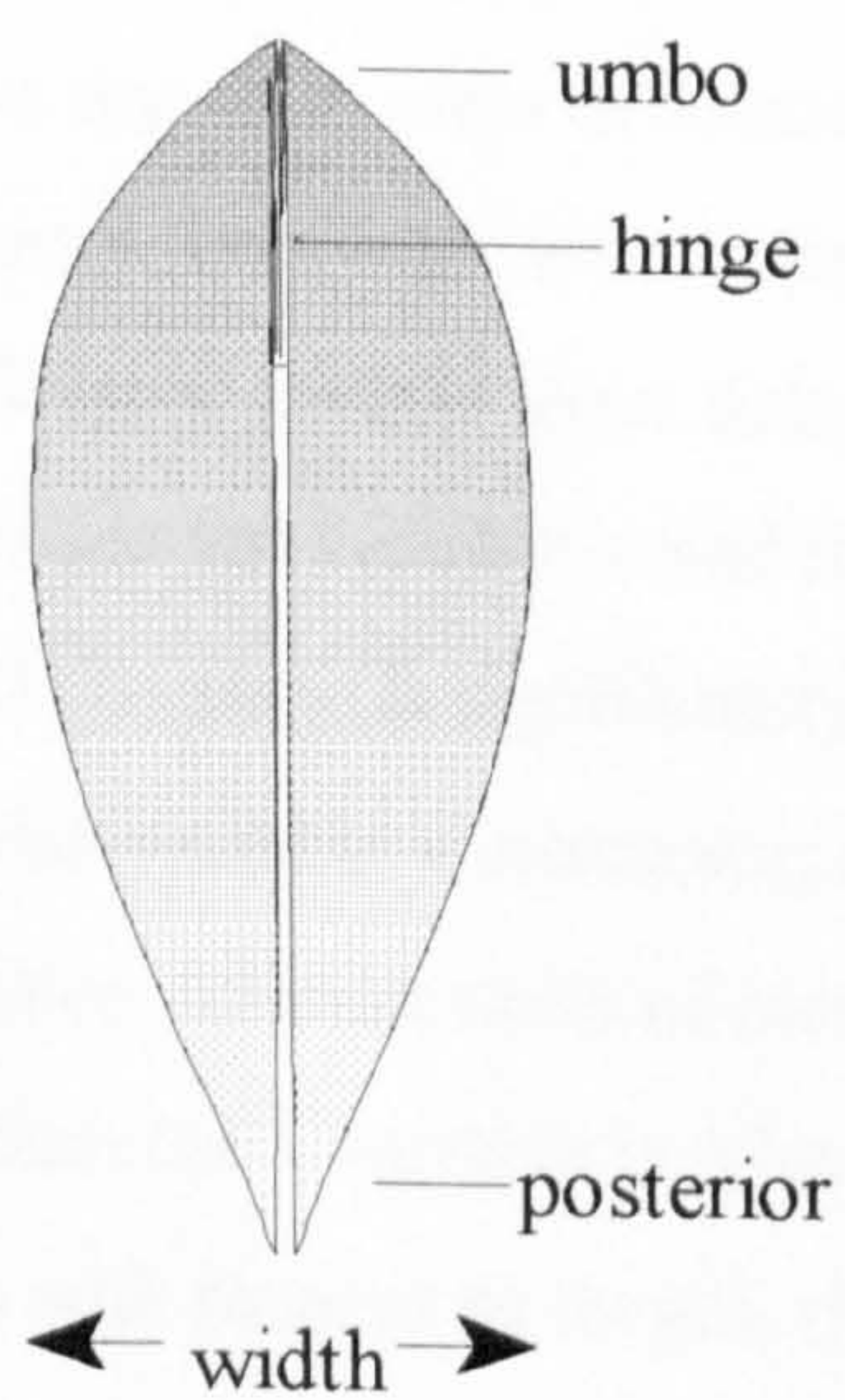
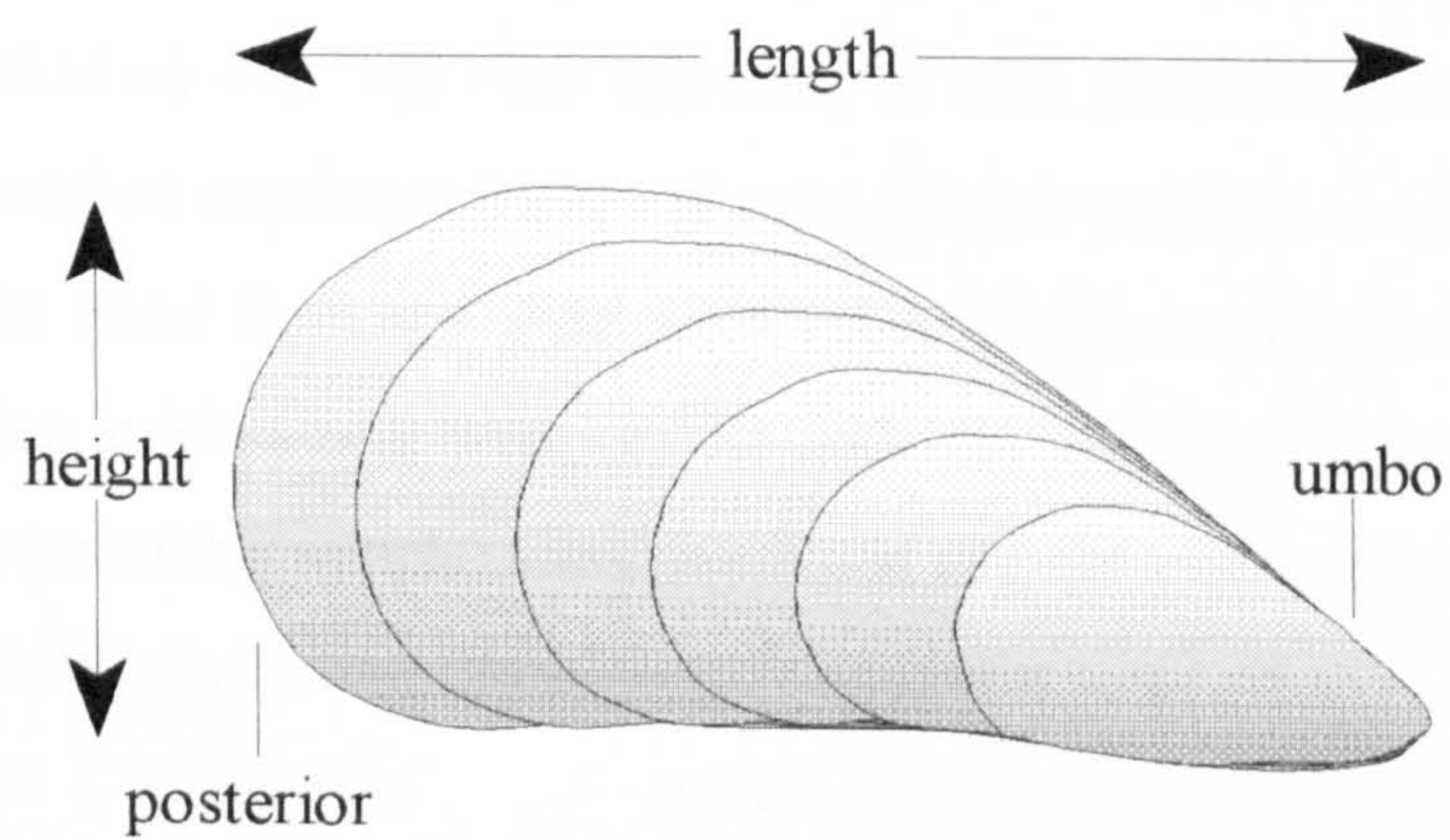
from direct wave impact, Church Island is located in a high tidal flow regime; tidal waters in the Strait can flow at up to 8 knots (Young, 1987). *Mytilus edulis* is found only in the low shore in a gully between two small islands where tidal flow is particularly strong. The fauna at this site is especially rich, owing mainly to the strong flushing effects of the tide. The mid to high shore levels are dominated by luxurious growths of fucoid algae.

These two populations of *Mytilus edulis* were selected not only to represent the markedly different physical conditions under which mussels can survive and grow but also because the size range of mussels at the two sites were broadly similar. This was considered to be important if comparisons of the physical characteristics (other than their size) of these mussels and the foraging behaviour of *Carcinus maenas*, on the two populations were to be made (see Chapter 4).

2.2.2. Determination of population density and population structure of *Mytilus edulis*.

The mussel populations were sampled bimonthly from January 1996 until June 1997 (Church Island) or September 1997 (Aberffraw). The Church Island population was also sampled in June and October 1995 whilst additional samples were taken from the mid-shore at Aberffraw in February and June 1997. Different sizes of mussel were not homogeneously distributed in the field, therefore a 10cm x 10cm quadrat was used to sample the mussel population to ensure that the full range of mussel sizes were included in a sample. At each site in each of the sampling months four random quadrats were thrown and the mussels within these collected and returned to the laboratory. Since each quadrat contained a large number of mussels, a subsample of 1/10 of each quadrat was taken. This was done by placing each sample in a tray marked into tenths, in which the sample was stirred until all mussel sizes were evenly distributed throughout the tray and a subsample was taken. The mussels within this subsample were counted and the length, the maximum anterior-posterior distance (Fig. 2.2) of each individual measured to the nearest 0.1mm using vernier calipers. From these data population densities and percentage length-frequency distributions of the populations

Figure 2.2. Schematic diagram of *Mytilus edulis* viewed laterally and dorsally to illustrate the shell dimensions measured in this study.



could be calculated.

From the remainder of the samples taken from each site 24-35 individuals were selected so as to include a broad size range of mussels present within these populations. Shell length, shell height (the maximum dorsal-ventral distance) and shell width (the maximum valve inflation) (Fig.2.2) were measured to the nearest 0.1mm using vernier calipers. The shell of each individual was then gently scraped to remove any encrusting organisms, the valves pulled slightly apart, and any sediment within the mantle cavity flushed out. The flesh and shell of each mussel were then separated, placed in pre-weighed aluminium boats and oven dried to constant weight at 60°C over three days. The dried flesh and shell were subsequently re-weighed to the nearest microgram using an electronic balance. At each site, shell length, height, width and weight data from monthly samples were combined and the relationships between pairs of variables investigated using the allometric equation:

$$y = Ax^b$$

which, when logarithmically transformed becomes:

$$\log y = a + b \cdot \log x$$

where x and y are pairs of variables and a and b are constants estimated by least squares regression using the statistical programme, MINITAB. The allometric equation can be used to investigate the rate of change of one variable with respect to another. When the two variables have the same units of measurement then a slope (b) that is equal to unity indicates isometry, that is the two variables change at the same relative rate. If the slope is significantly greater than unity then the variable y is increasing at a relatively greater rate than the variable x and the relationship is said be positively allometric. Alternatively, if the slope is significantly less than unity then the relationship is negatively allometric with variable x increasing at a relatively faster rate than variable y. When the variables have different units of measurement then different criteria for isometry apply. Thus, when the y variable is related to the x variable by a square relationship, e.g. surface area with respect to length, then isometry is achieved when $b = 2$ and when variable y is related to variable x by a cubic relationship, e.g. weight with respect to length, an isometric relationship occurs when $b = 3$. Departure from isometry was tested using the Student's t-test and the regression lines for pairs

of variables compared between sites using analysis of covariance (general linear model, MINITAB). Flesh weight-shell length and flesh weight-shell width relationships were determined separately for each month at each site using least squares regression (MINITAB).

2.2.3. Relationship between shell surface area, biomass and size.

Predictions of shell height, width, dry flesh and shell weights derived from the regressions of these variables upon shell length were subsequently used to convert the monthly shell length-frequency data to distributions of shell surface area and biomass within the two populations. The midpoint of each length class was taken and the surface area and biomass for this size class calculated using the following equations:

Surface area = $(\text{mean}(\text{length} + \text{height} + \text{width}))^2$ (From Ambaryianto and Seed, 1991)

Biomass = $(\text{dried flesh weight} \times \text{shell length}) + (\text{dried shell weight} \times \text{shell length})$

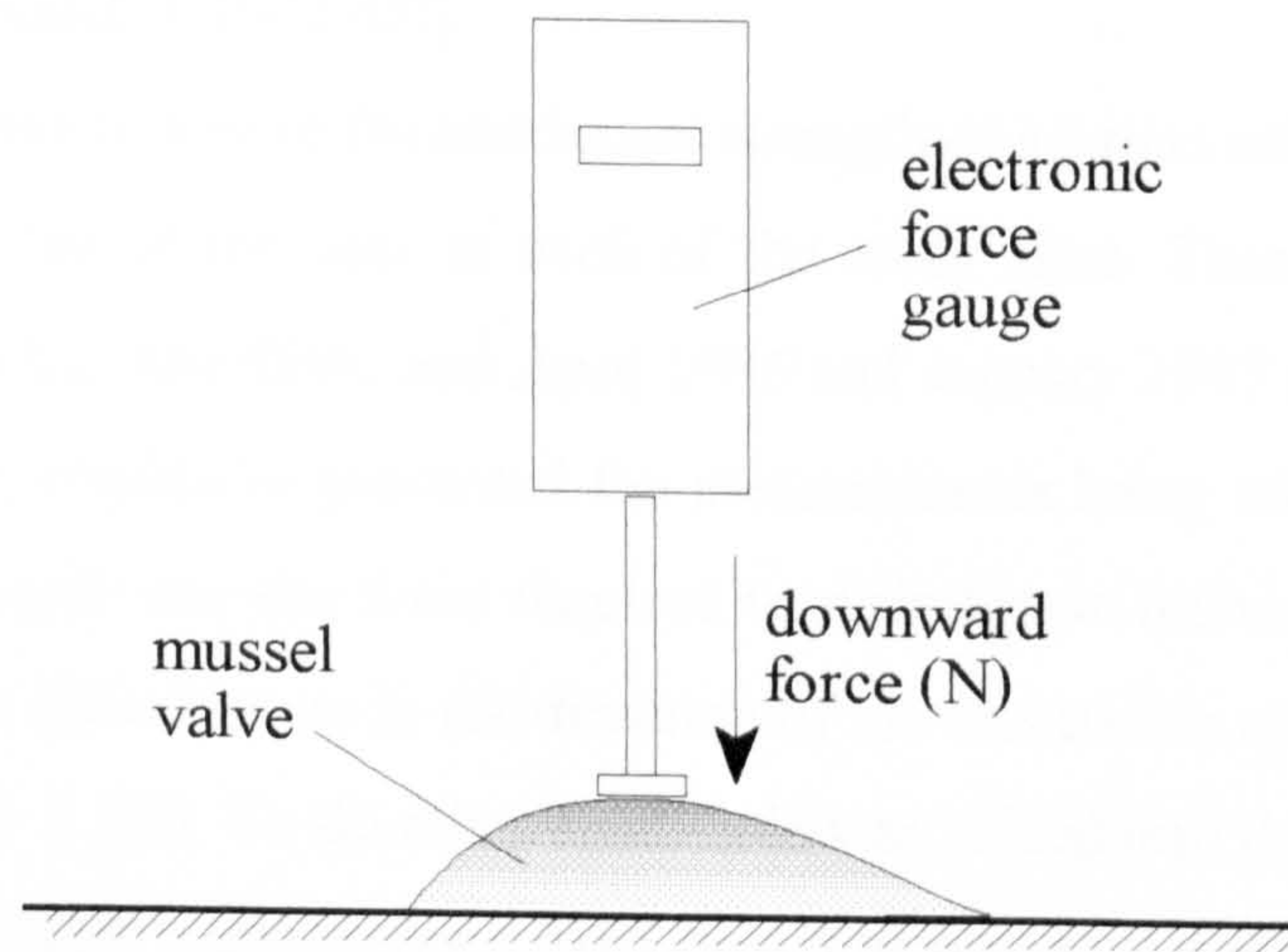
The surface area and biomass calculated for the midpoint of each size class were then multiplied by the total number of individuals in that size class and converted to a percentage frequency. Percentage frequency biomass was not calculated for the two samples from Church Island in 1995 because flesh and shell weights were not recorded nor were they calculated for the two samples taken from the mid shore at Aberffraw.

2.2.4. Shell strength and strength of byssal attachment.

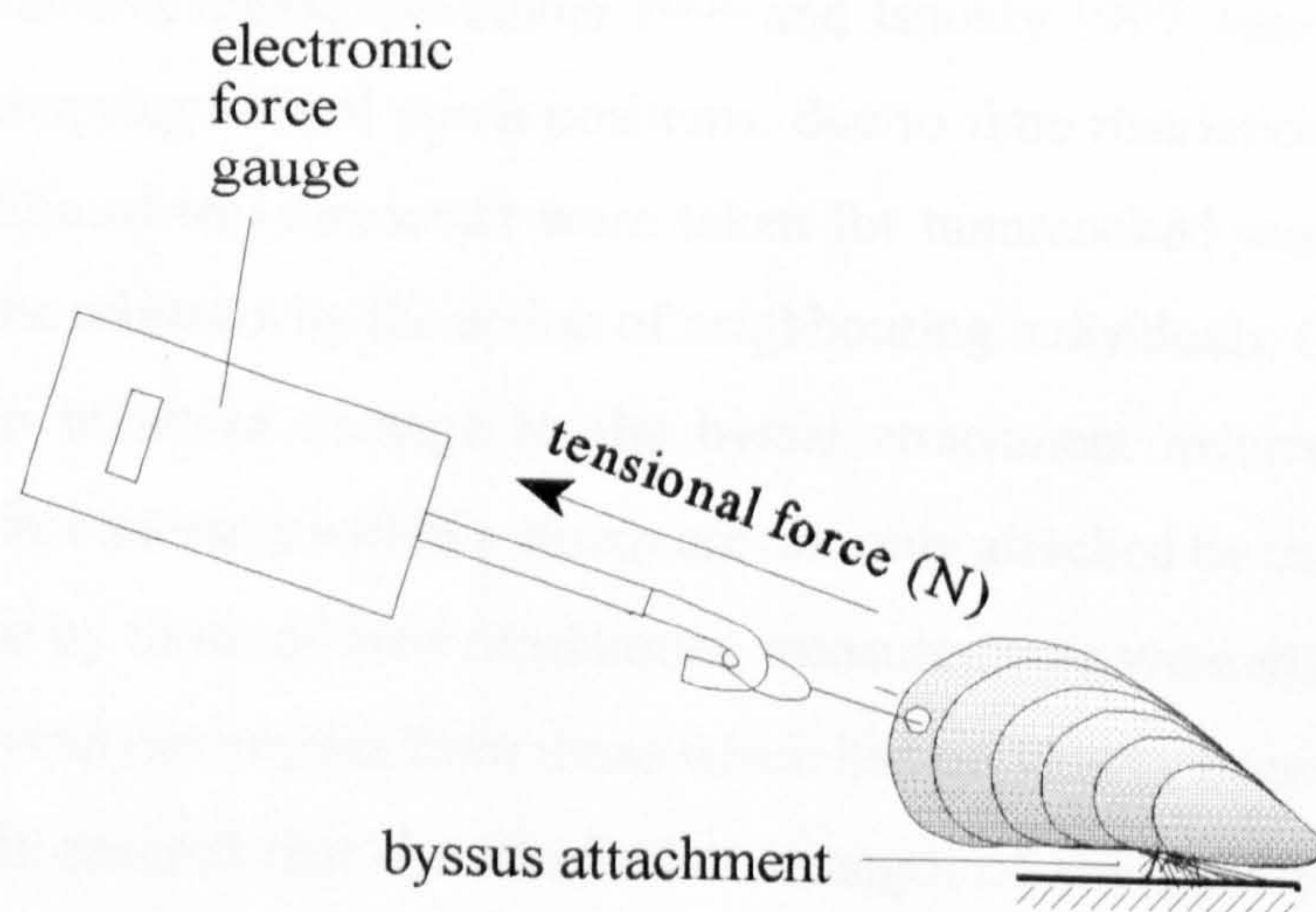
The shell strength of *Mytilus edulis* from Aberffraw and Church Island was measured in two of the sampling months, March and November 1996. An additional measurement of shell strength for mussels from the high and mid shore at Aberffraw was made in June 1997. For each sample between 20 and 37 individuals were taken over the size range 6 - 26mm and their shell length, height and width measured to the nearest 0.1mm using vernier calipers. The two valves of each individual mussel were separated and the shell strength of each valve measured using a digital electronic gauge (ANTANA AGF) with a flat surface attachment which was brought down on the most domed part of the shell valve (Fig. 2.3A). Shell strength was measured in Newtons as

Figure 2.3. Schematic diagram illustrating measurement of *Mytilus edulis* valve strength (A) and byssal attachment strength (B).

A.



B.



the force required to break the valve. For each individual mussel two breaking forces were therefore recorded, the minimum force, i.e. the strength of the weaker valve, and the maximum force, i.e. the strength of the stronger valve. Both the dependent variable (shell strength) and the independent variable (shell length) were log transformed. Minimum and maximum breaking strengths were compared by analysis of covariance (general linear model, MINITAB).

Field measurements of the attachment strength of *Mytilus edulis* were taken at two different times of the year at each of the study sites. These were April and November 1996 for Aberffraw and April 1996 and January 1997 for Church Island where poor tidal conditions prevented the measurements being taken in November. Attachment strength was the force required to dislodge an individual mussel when pulled away from the substrata in the direction of the orientation of the mussel to the substrata (see Fig. 2.3B). To do this a small hole was drilled into the posterior end of a mussel through both valves using a hand-held drill with a 1/16 inch drill bit. A wire loop, which was attached to a digital electronic force gauge (ANTANA AGF) was then threaded through this hole and the force required to detach the mussel measured in Newtons (Fig. 2.3B). The length of the mussel was measured to the nearest 0.1 mm using vernier calipers subsequent to its removal. During April 1996, measurements of attachment strength were recorded for mussels occupying the centre and the edge of a patch. Measurements during November 1996 and January 1997 were recorded only for mussels occupying central patch positions, due to time restrictions, although at Aberffraw additional measurements were taken for hummocked mussel, i.e. those raised clear of the substrata by the action of neighbouring individuals. Care was taken at all times to minimise damage to the byssal attachment incurred by drilling. Furthermore, since mussels within a clump are not only attached by their own byssus threads but also by those of their neighbours, measurements were made on mussels separated by several centimetres from those which had previously been removed from the clump. This ensured that the attachment strength of any mussel had not been affected (weakened) by the removal of a neighbouring mussel.

2.3. RESULTS

2.3.1. Population densities.

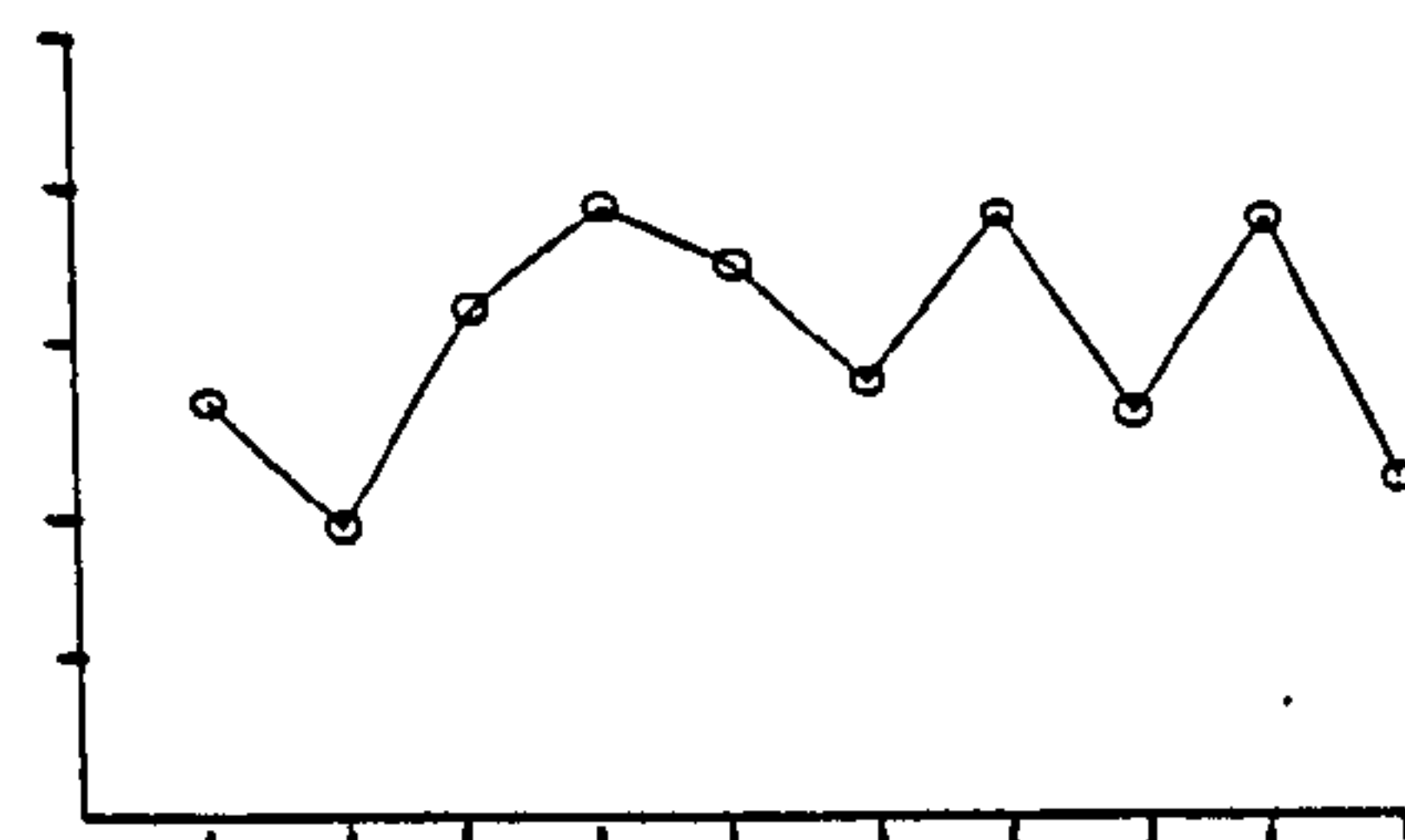
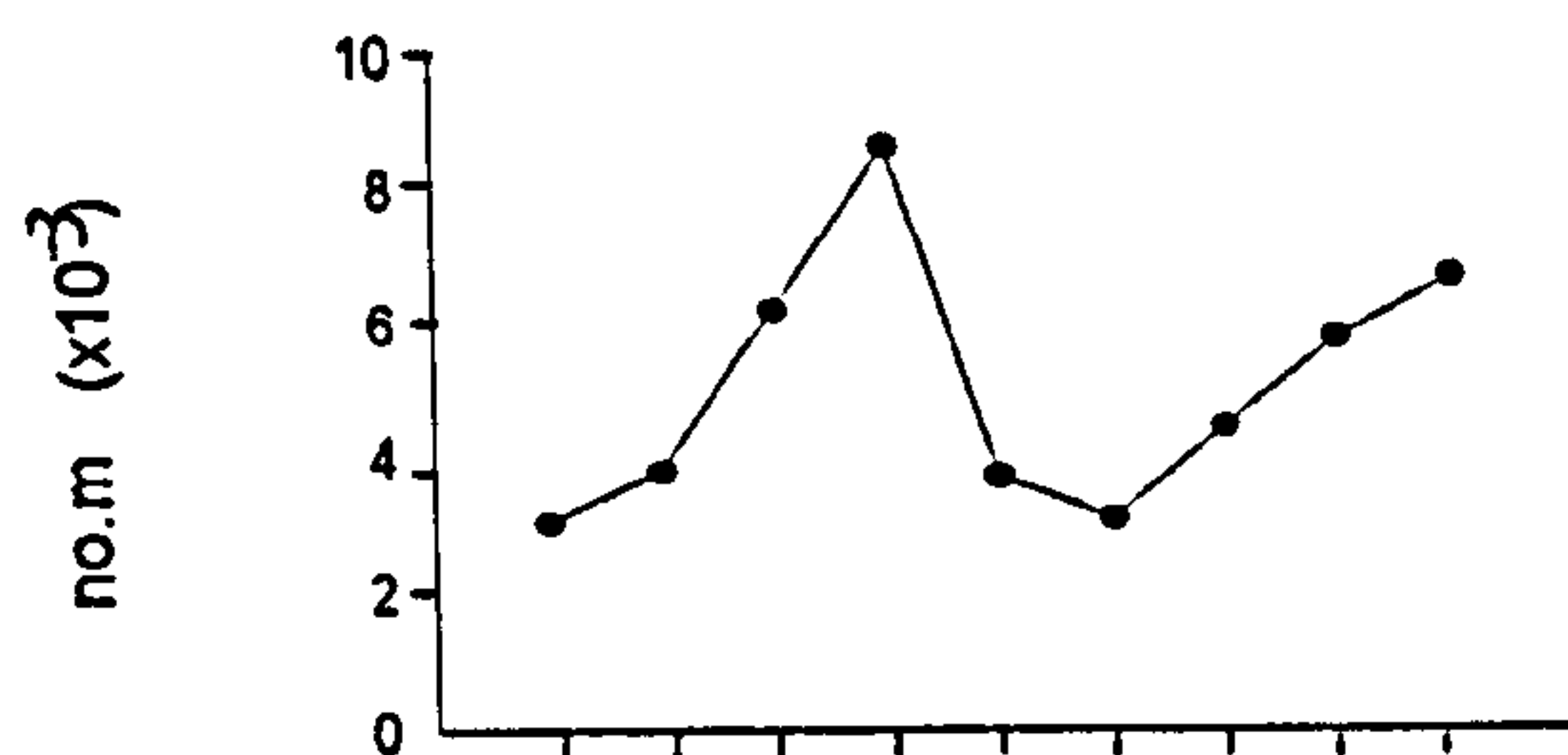
The population density of mussels from the low shore at Church Island appeared to demonstrate a seasonal pattern with densities oscillating widely from a low density in January 1996 and November 1996 to high densities in July 1996 and June 1997 (Fig. 2.4A). Whilst the population densities of high shore Aberffraw mussels did oscillate there was no obvious seasonal pattern. Throughout the 18 month sampling period the length-frequency distributions of Aberffraw mussels remained relatively constant with a distinctly skewed distribution towards the smaller sized classes (<5mm) (Fig. 2.5). There was no obvious period of recruitment to the population and the maximum size of mussels within this population always fell within the 25-35mm size range. The length-frequency distributions of mussels in the Church Island population varied throughout the two-year period with a noticeable shift in terms of relative importance towards the smallest size class (<5mm) (Fig. 2.6). This was coupled with a steady increase in the maximum size of mussel within the population, from 20-25mm in the initial sample (June 1995) to 55-60mm in the final sample (June 1997) (Fig. 2.6).

Figure 2.7 shows that the population density of mussels in the high shore at Aberffraw remained constant between February and June 1997 as did the relative proportions of the different size classes within the population. In contrast the population density of mussels in the mid shore population at Aberffraw changed during this period, increasing from February to June (Fig. 2.7). This increase corresponded to an increase in the percentage frequency of individuals occurring within the smallest size class (shell length < 5mm) (Fig. 2.7)

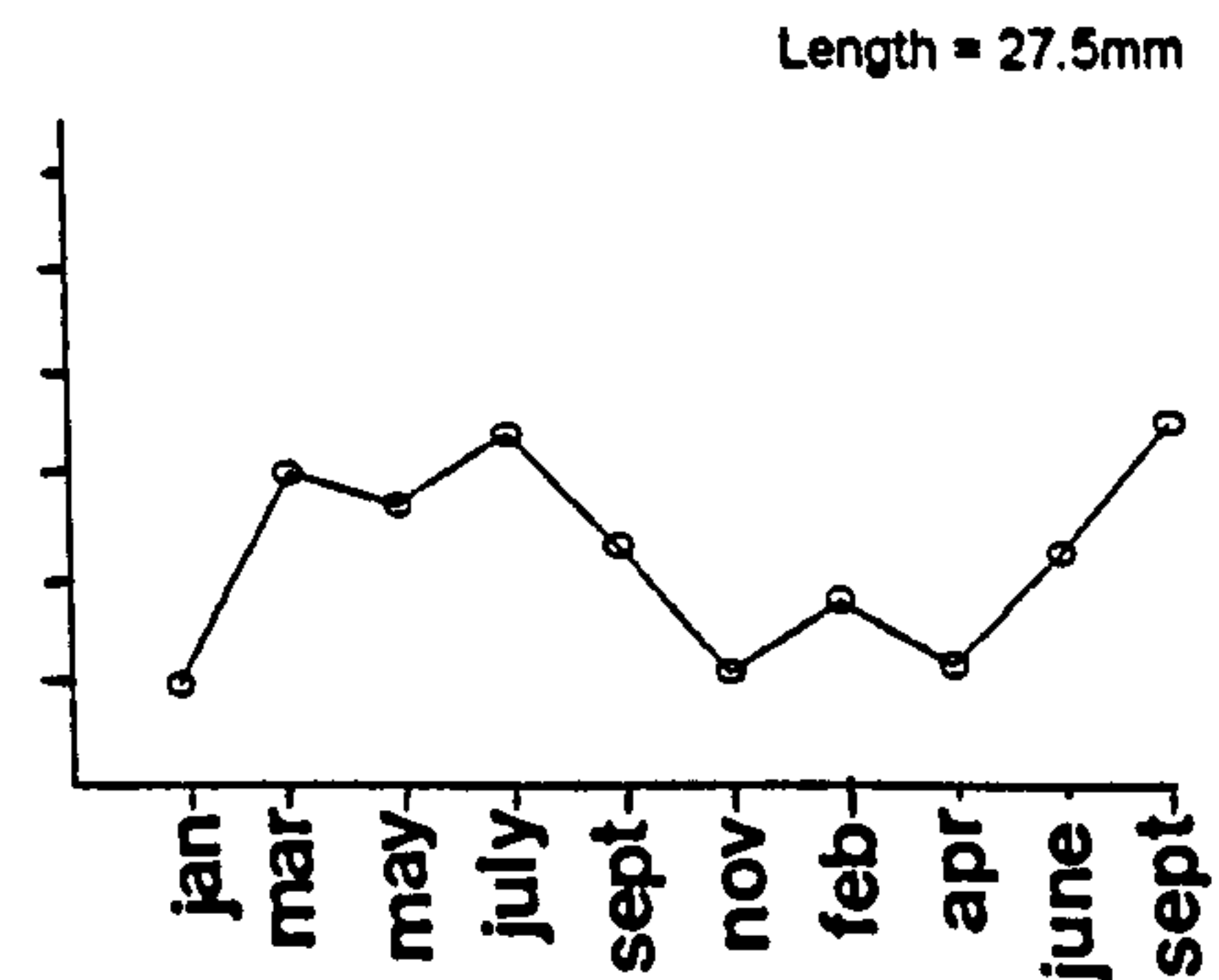
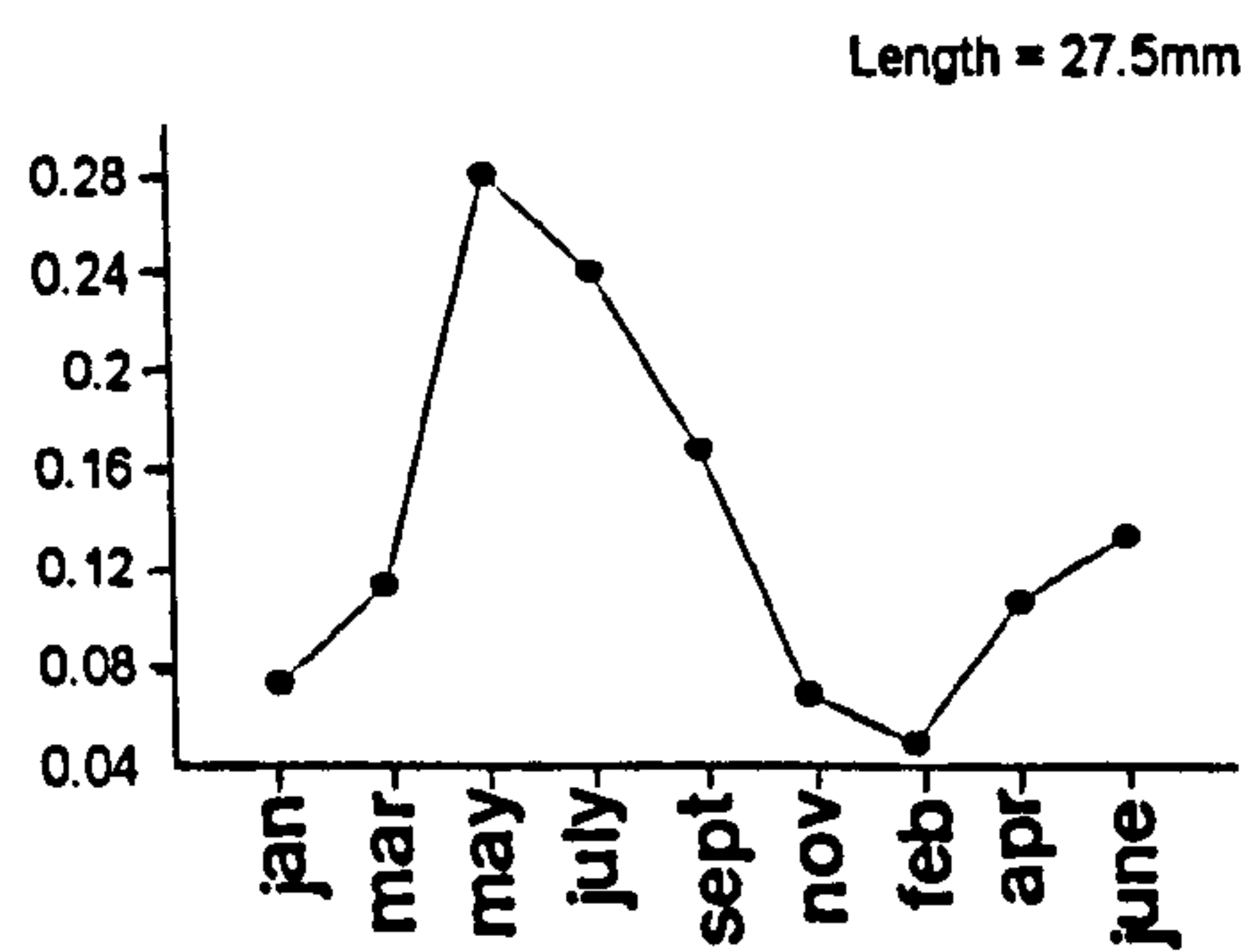
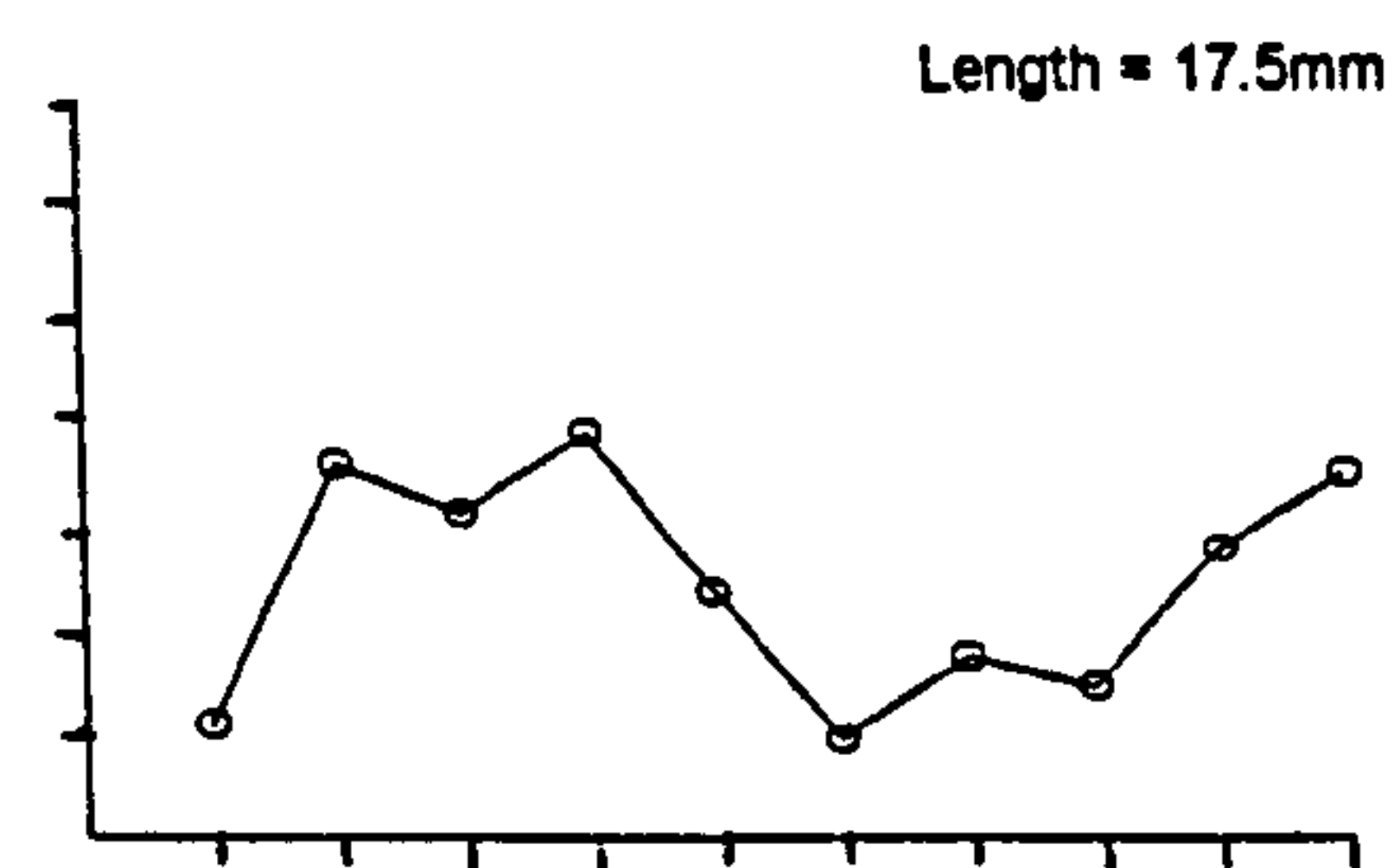
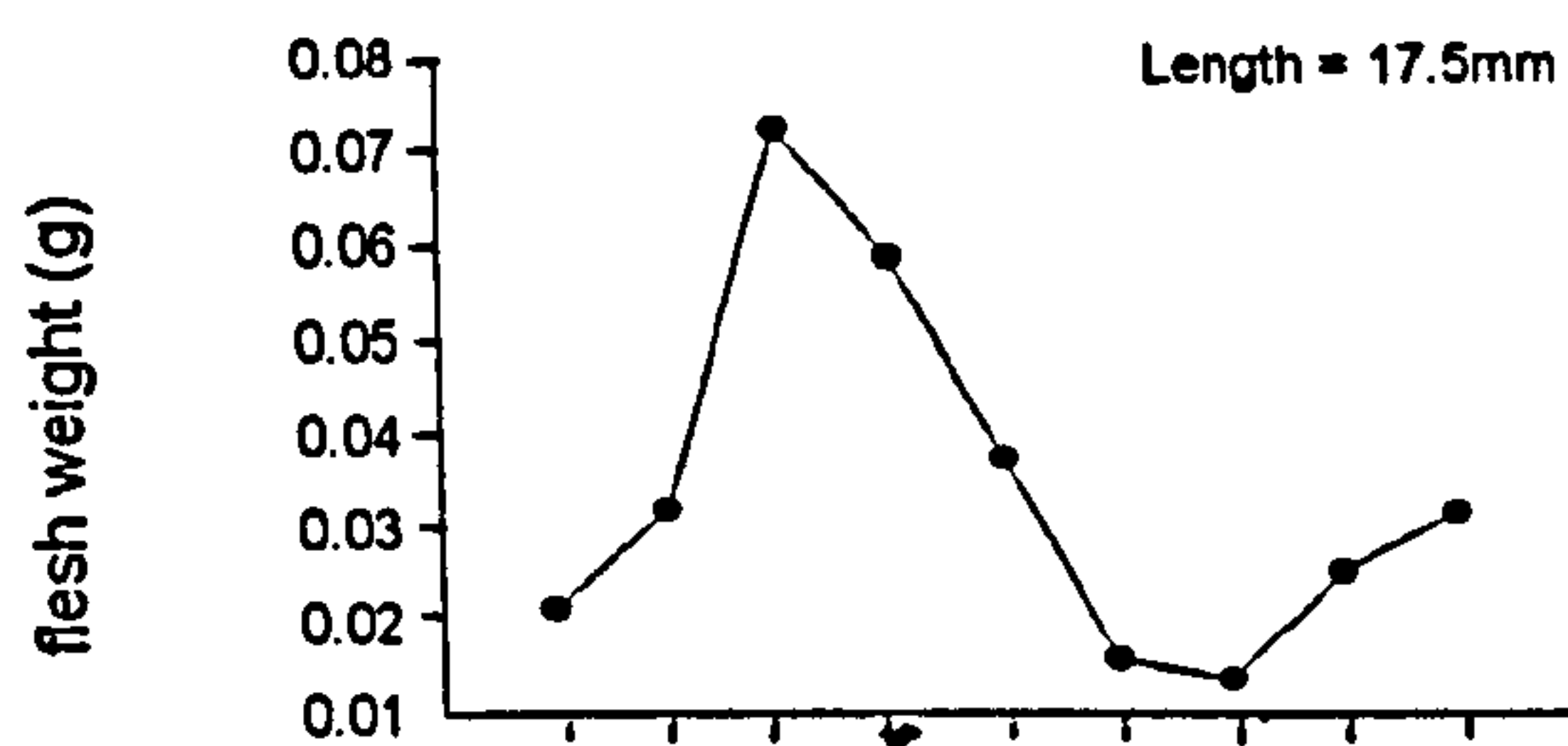
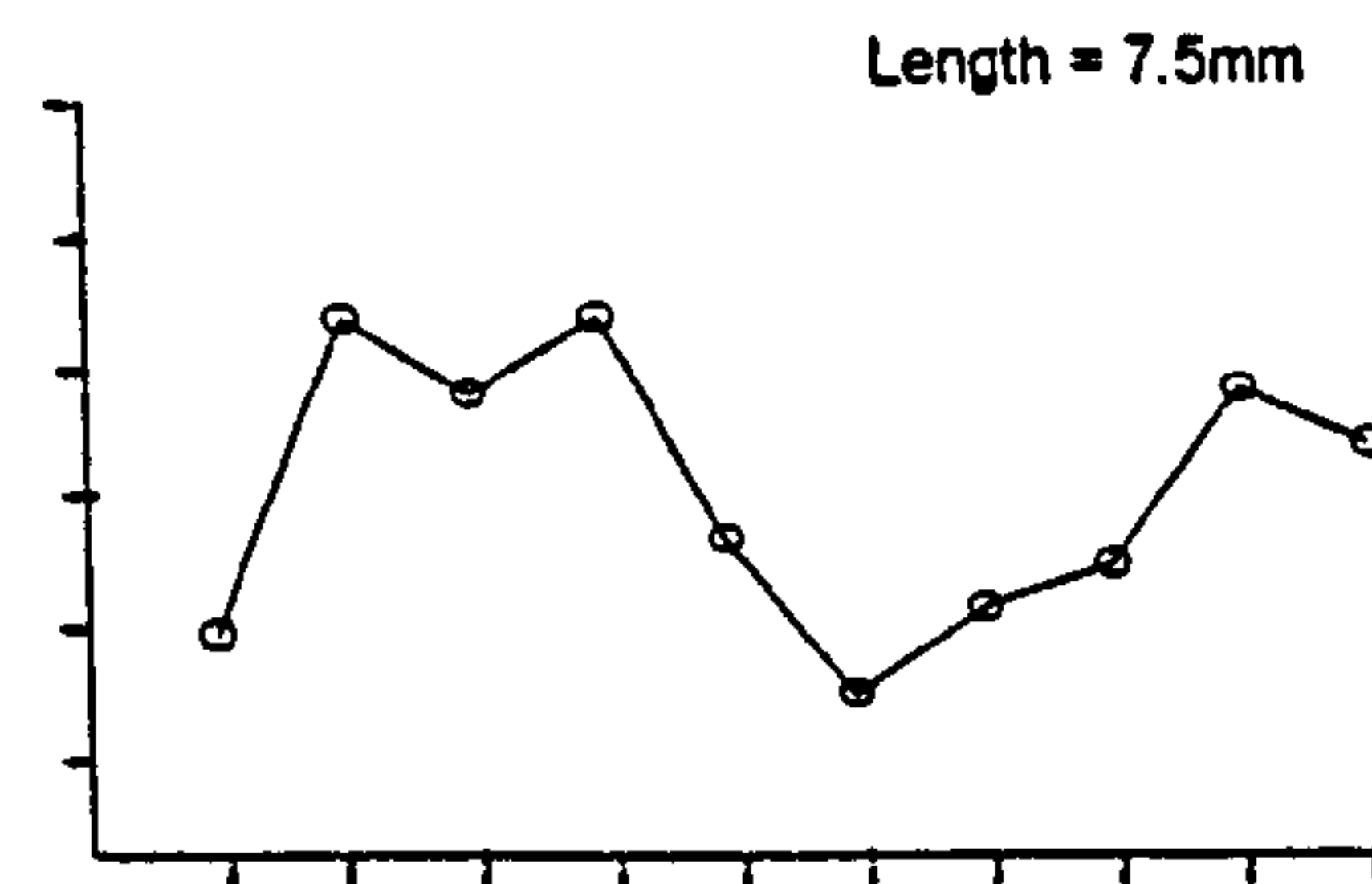
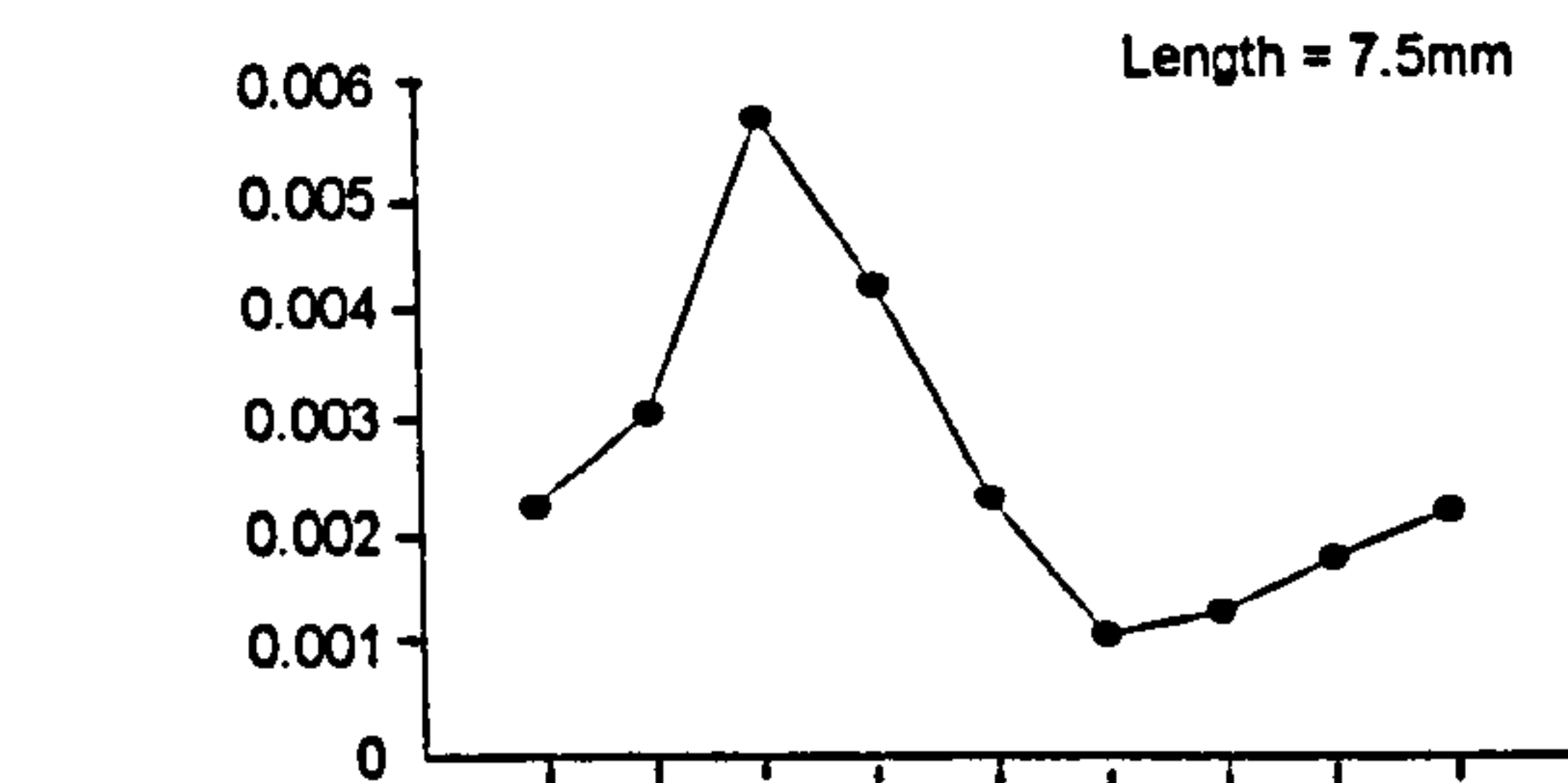
The surface area and biomass-frequency distributions did not reflect those of the length-frequency distributions of the two mussel populations (Figs. 2.8-2.11). The distribution of surface area within the size classes of mussels at Aberffraw (Fig. 2.8) showed no clear pattern except that the size class with the smallest surface area consistently occurred amongst the smallest size class of mussels (<5mm). This is the converse of the result found for the length-frequency distribution where the smallest

Figure 2.4. *Mytilus edulis* population densities (A) and the predicted flesh weights of three standard size mussels, 7.5, 17.5 and 27.5mm shell length (B) for mussels from the low shore at Church Island (closed circles) and from the high shore at Aberffraw (open circles).

A



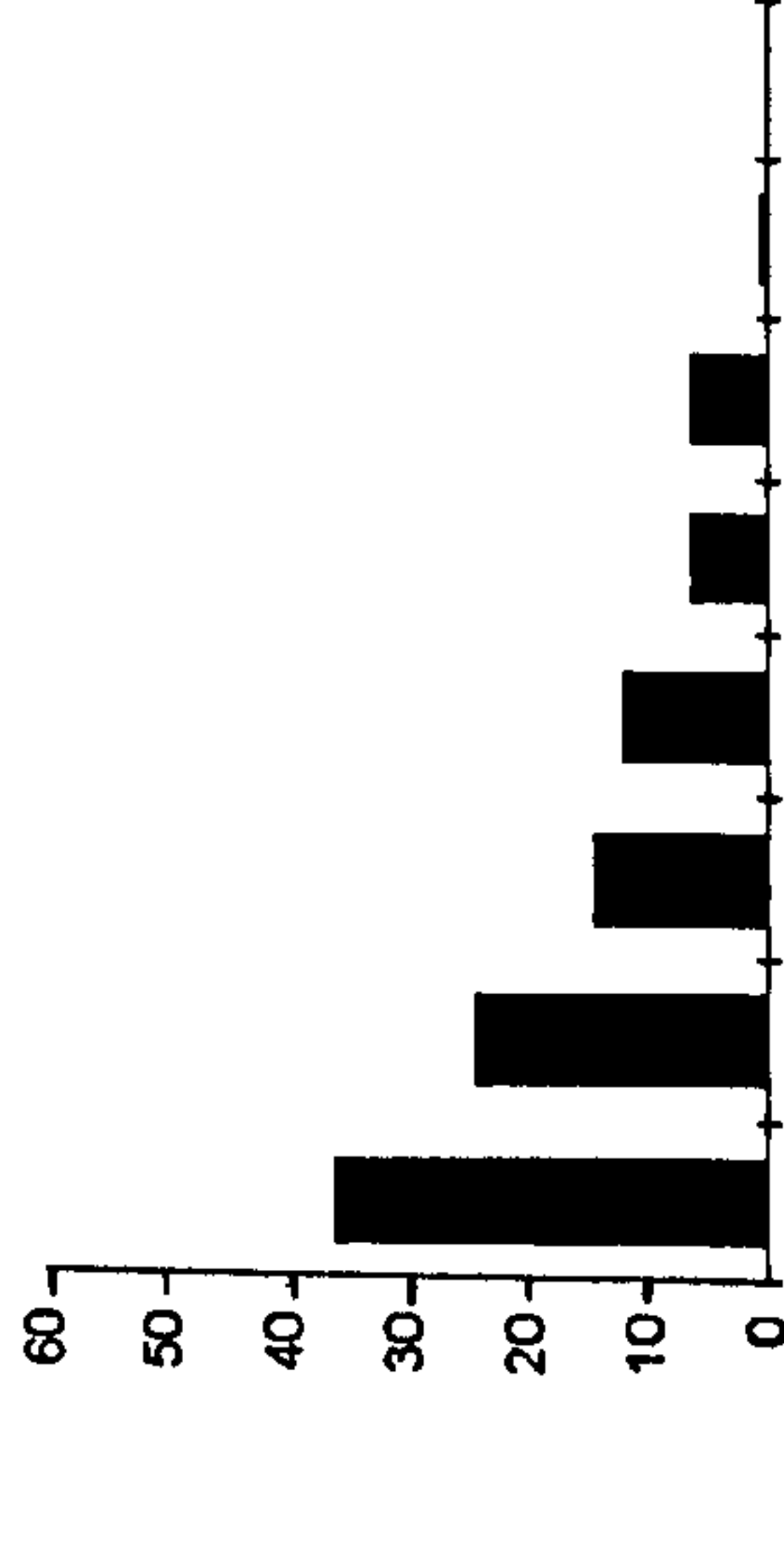
B



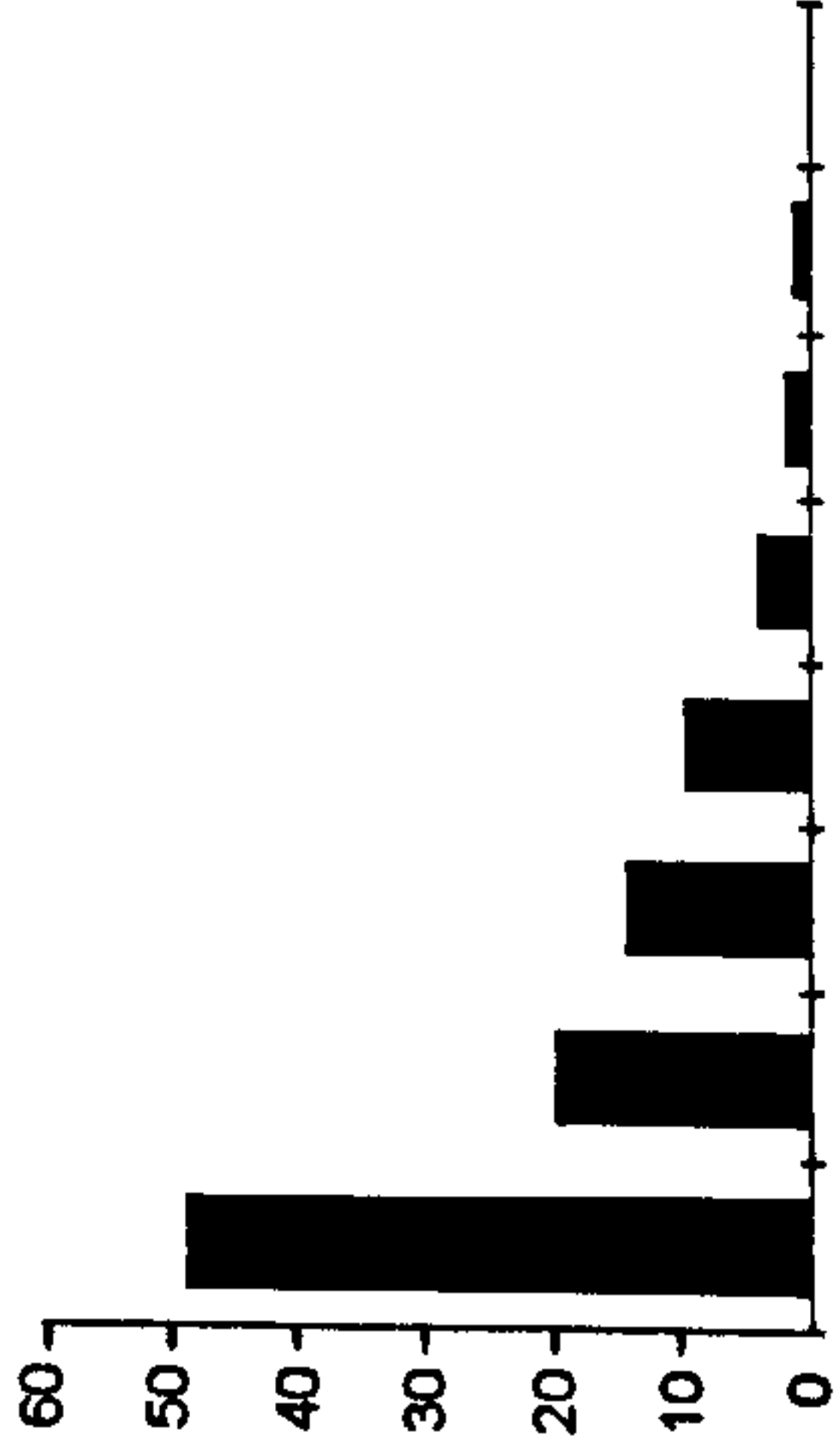
month

Figure 2.5. The length-frequency distributions of *Mytilus edulis* populations at the high shore Aberffraw.

January 1996



March 1996



May 1996



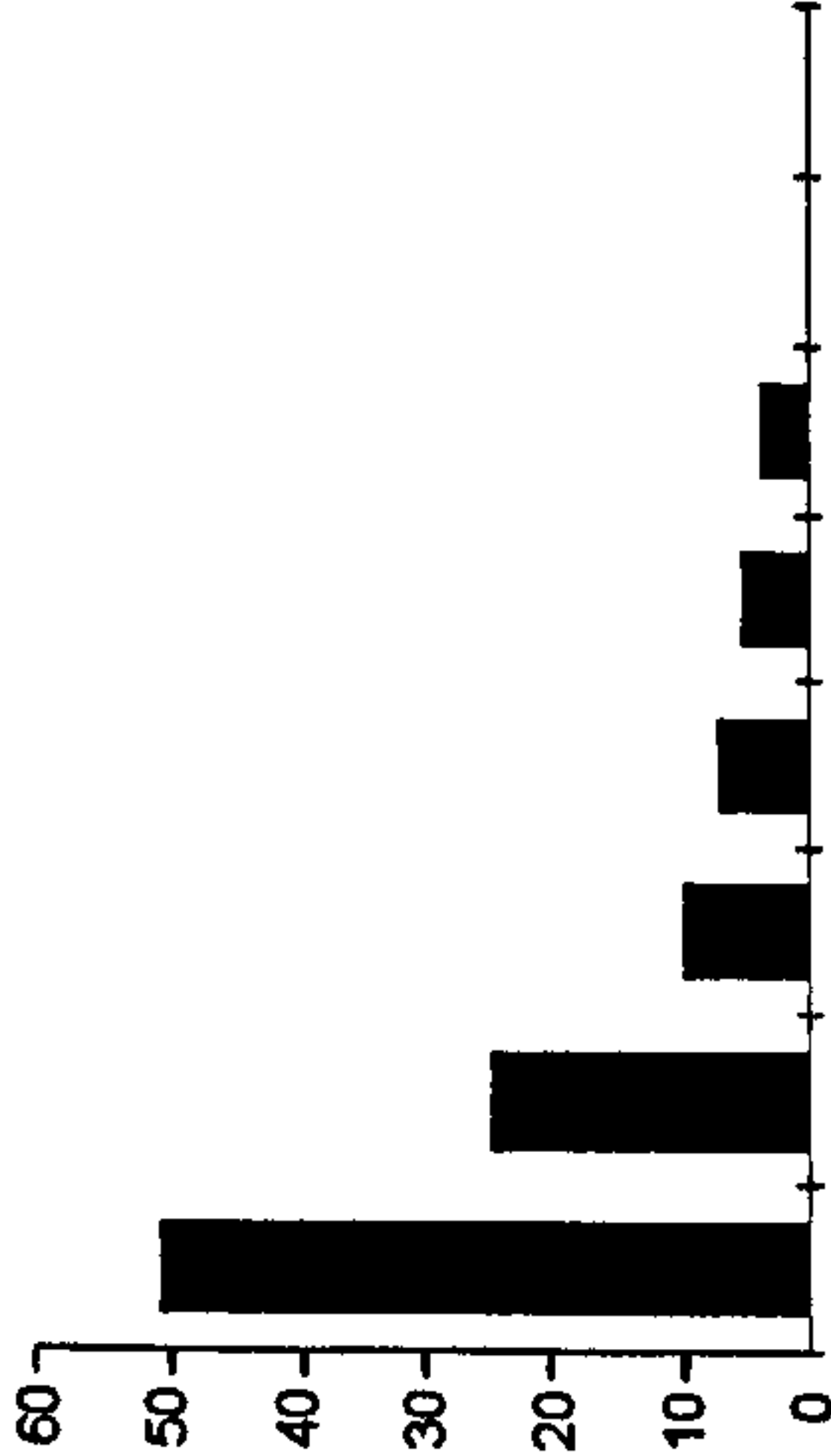
July 1996



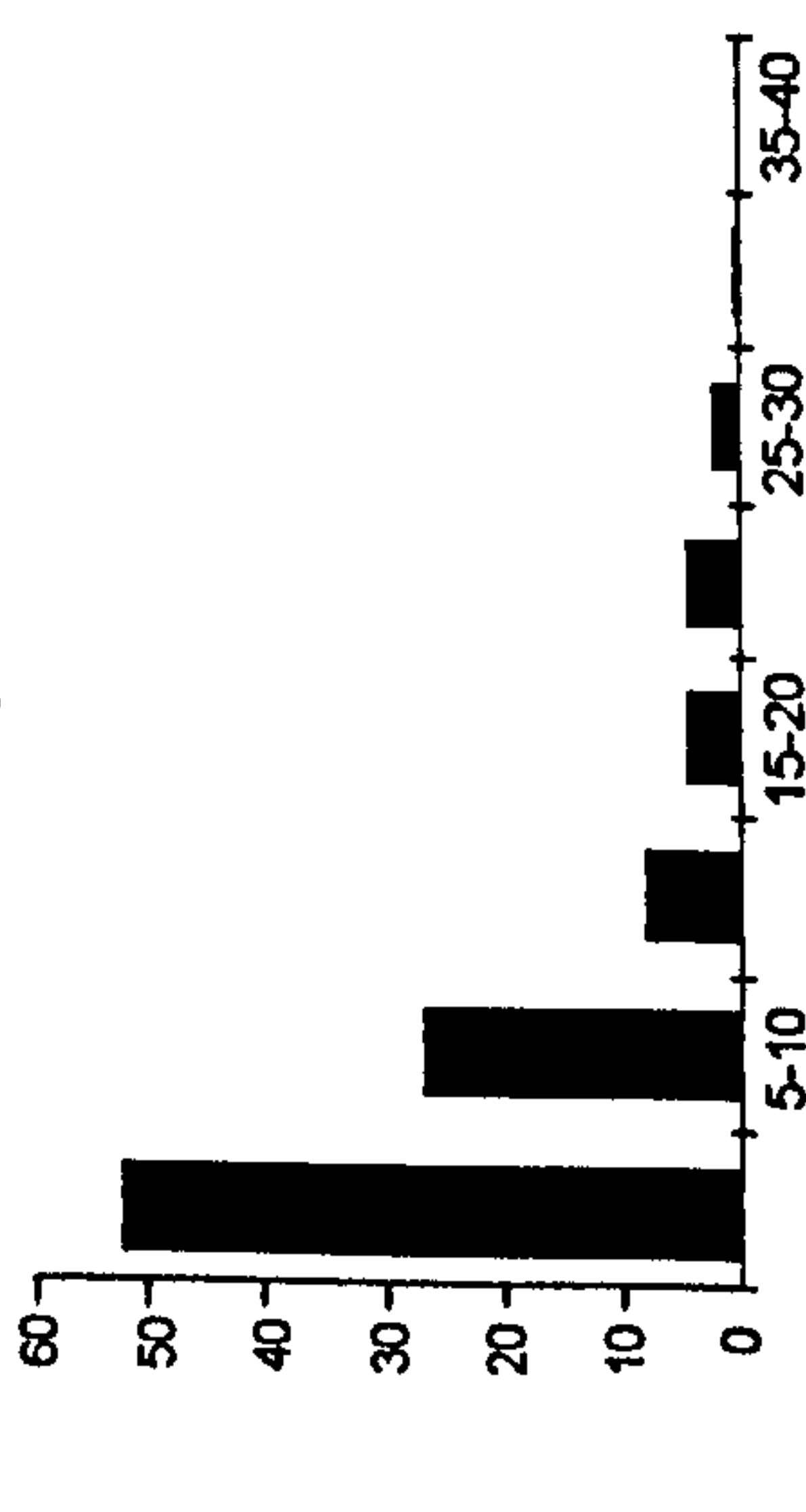
January 1996



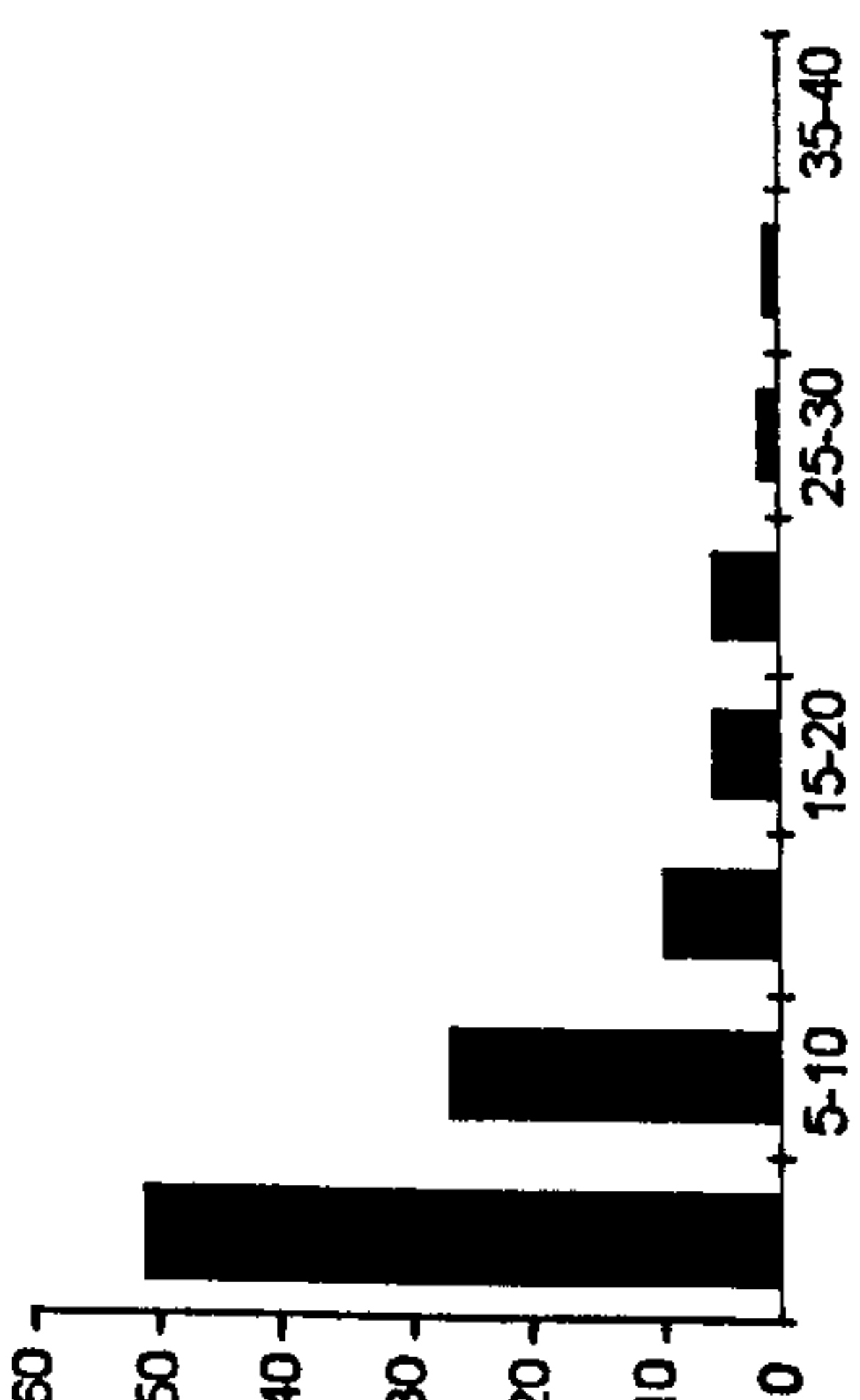
November 1996



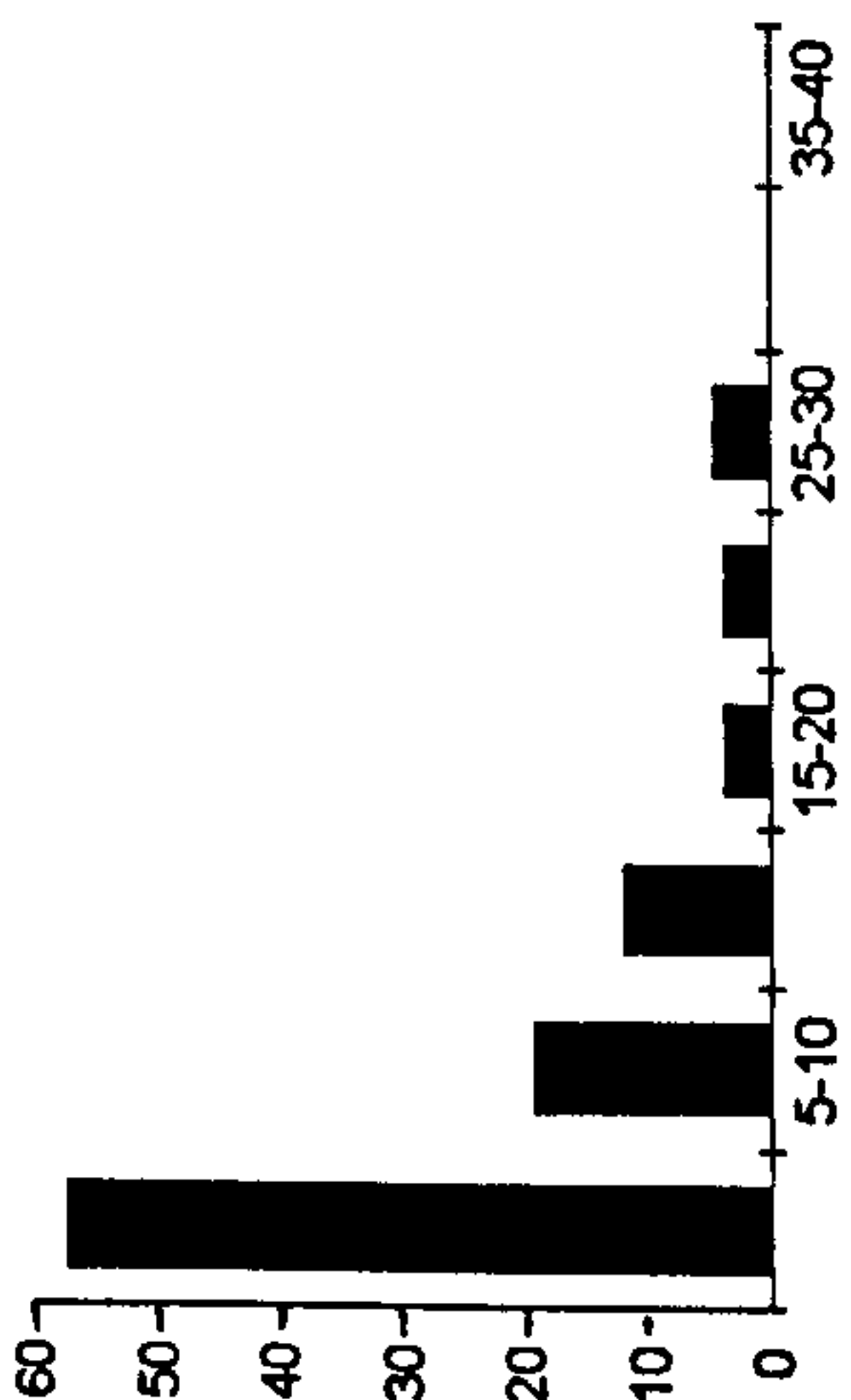
February 1997



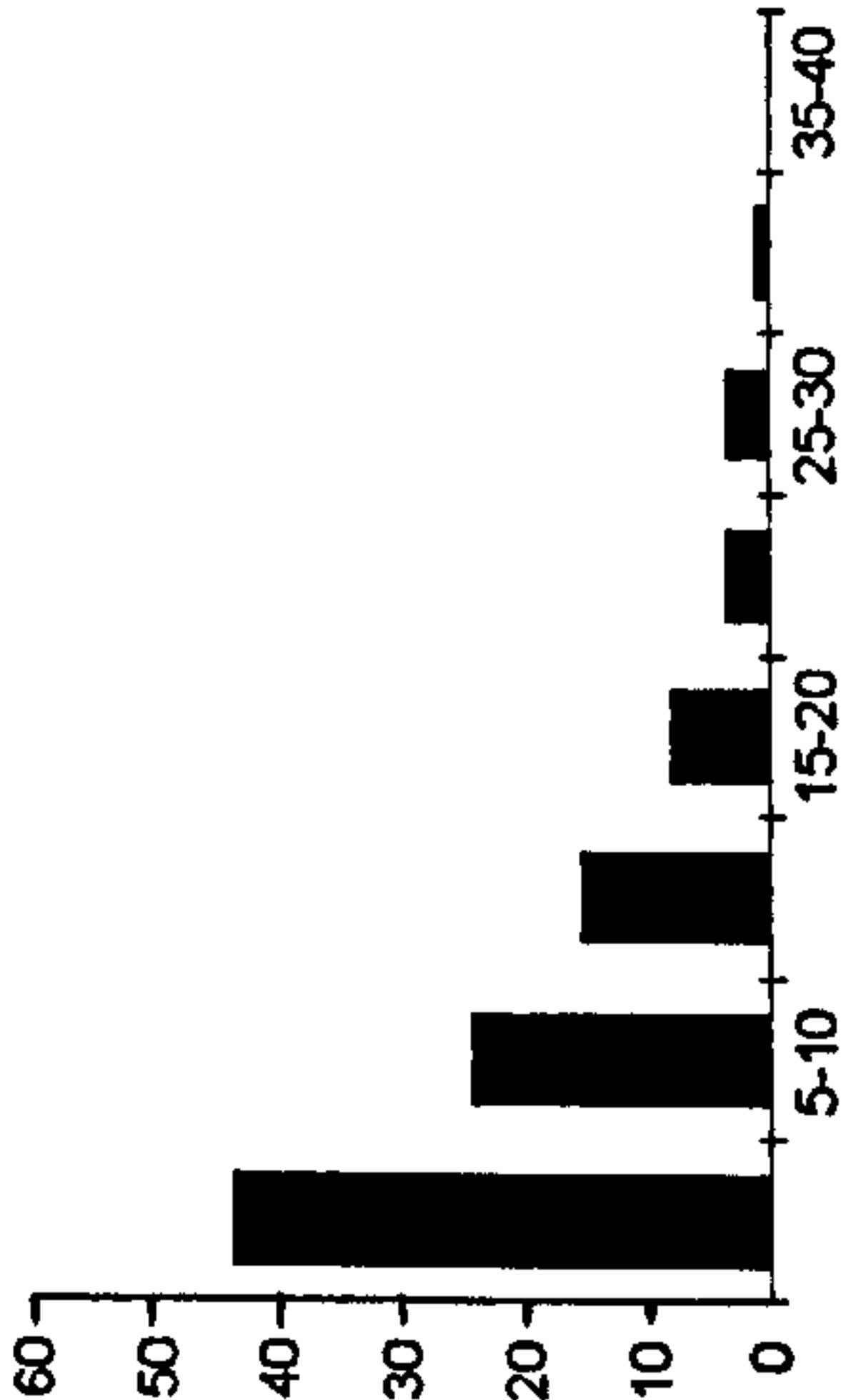
April 1997



June 1997

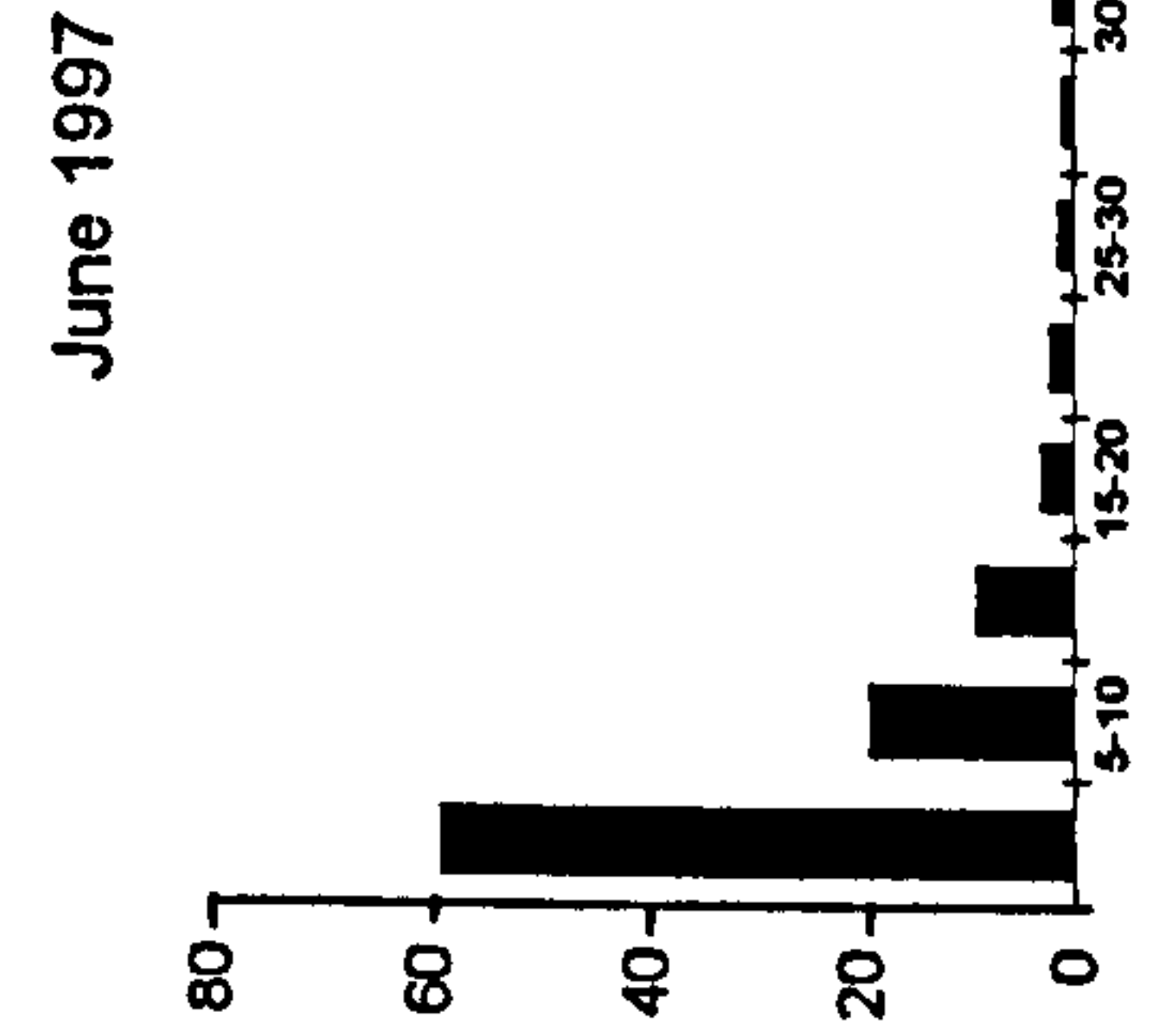
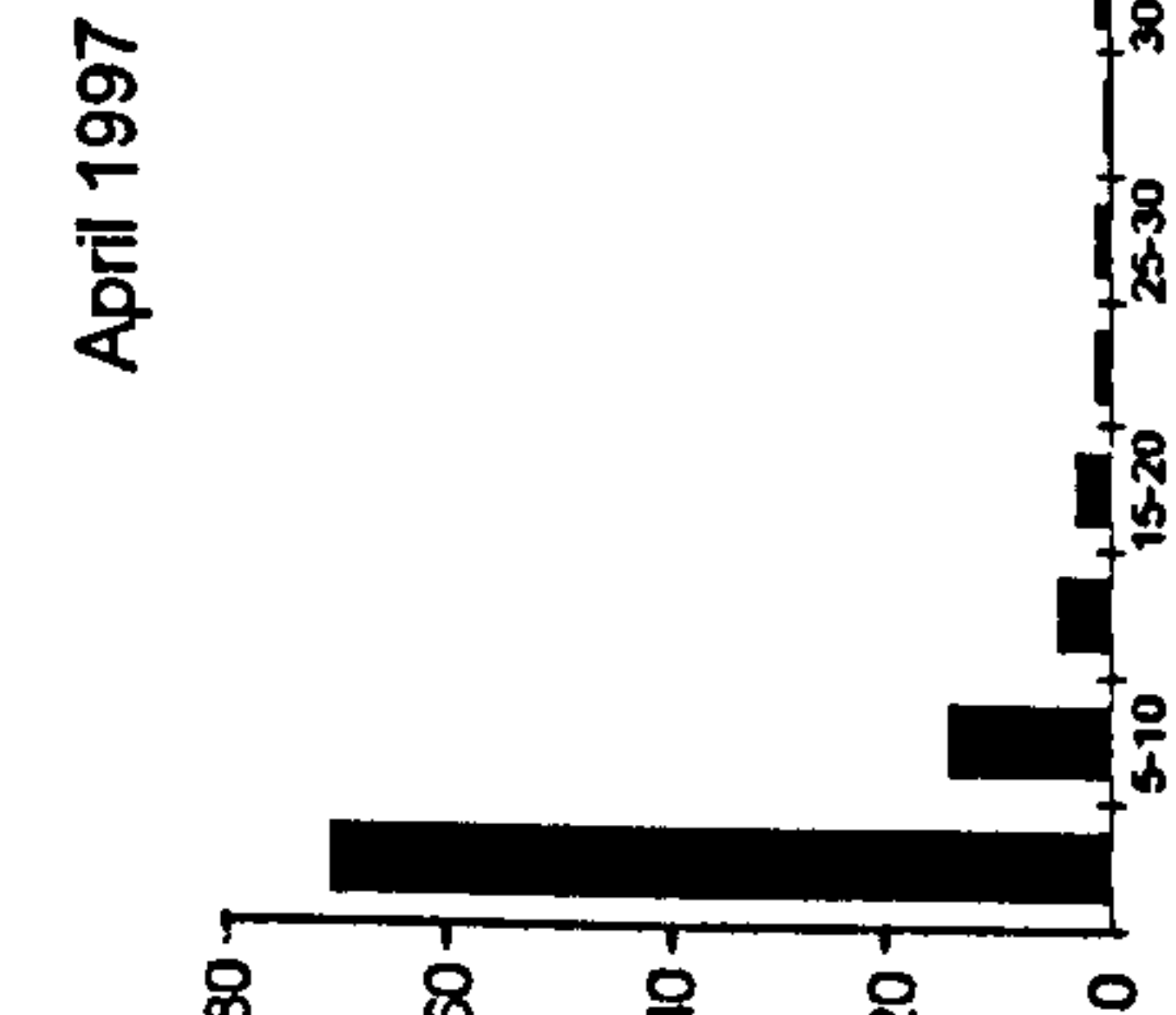
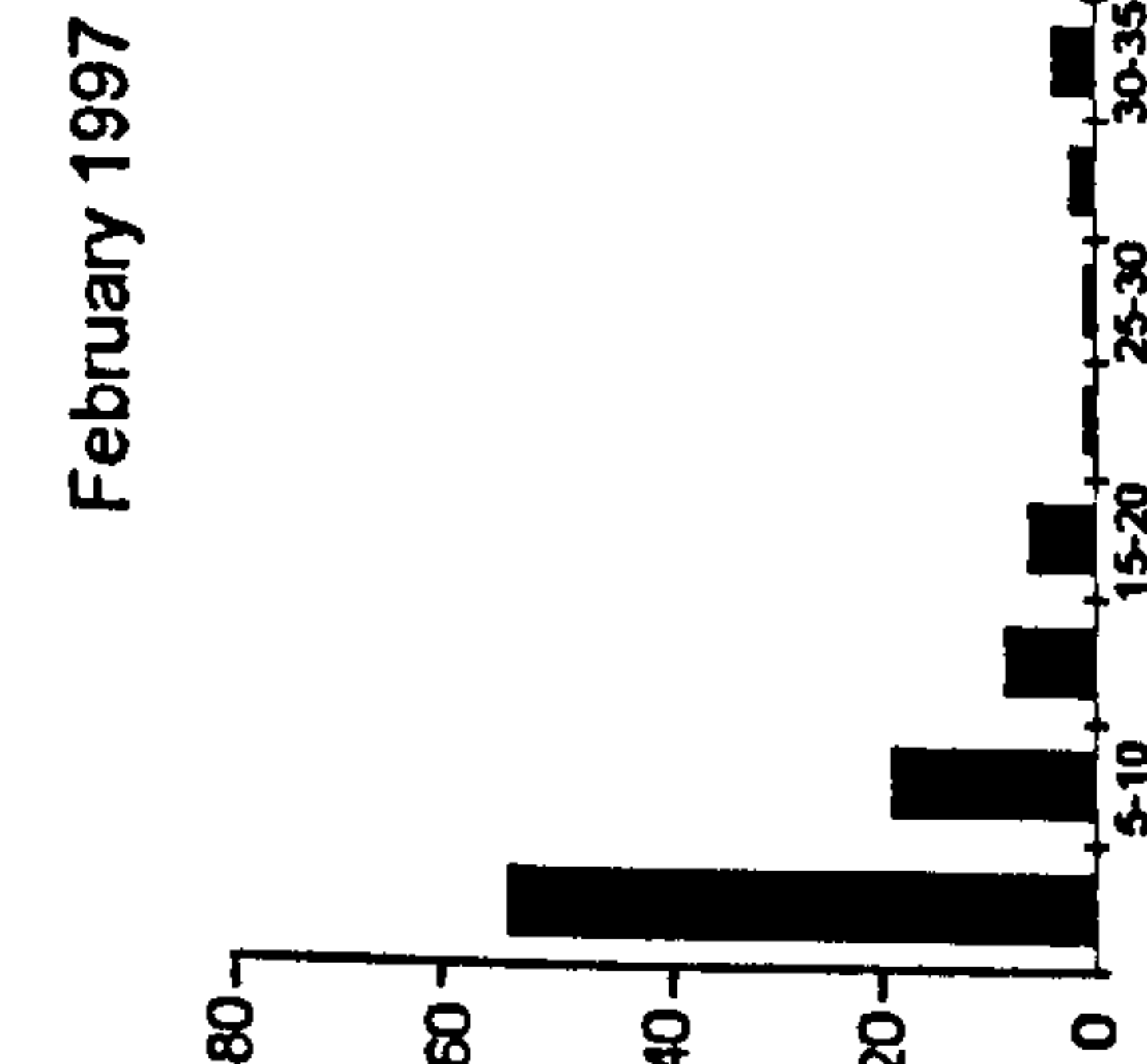
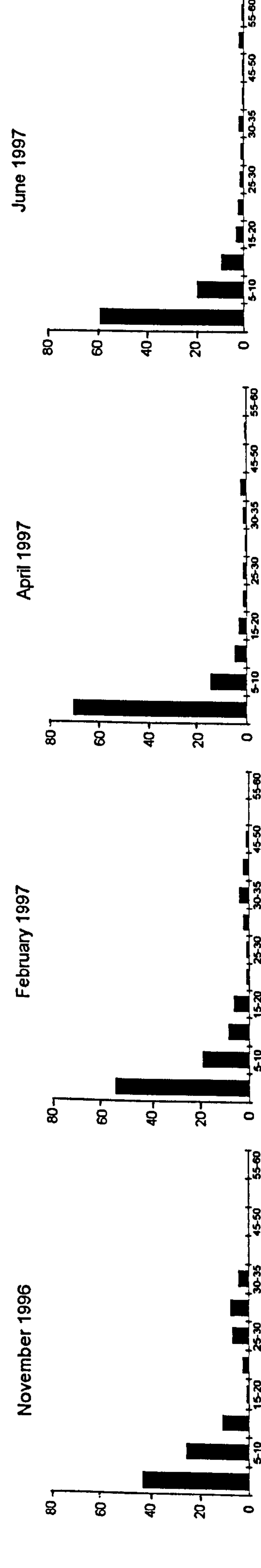
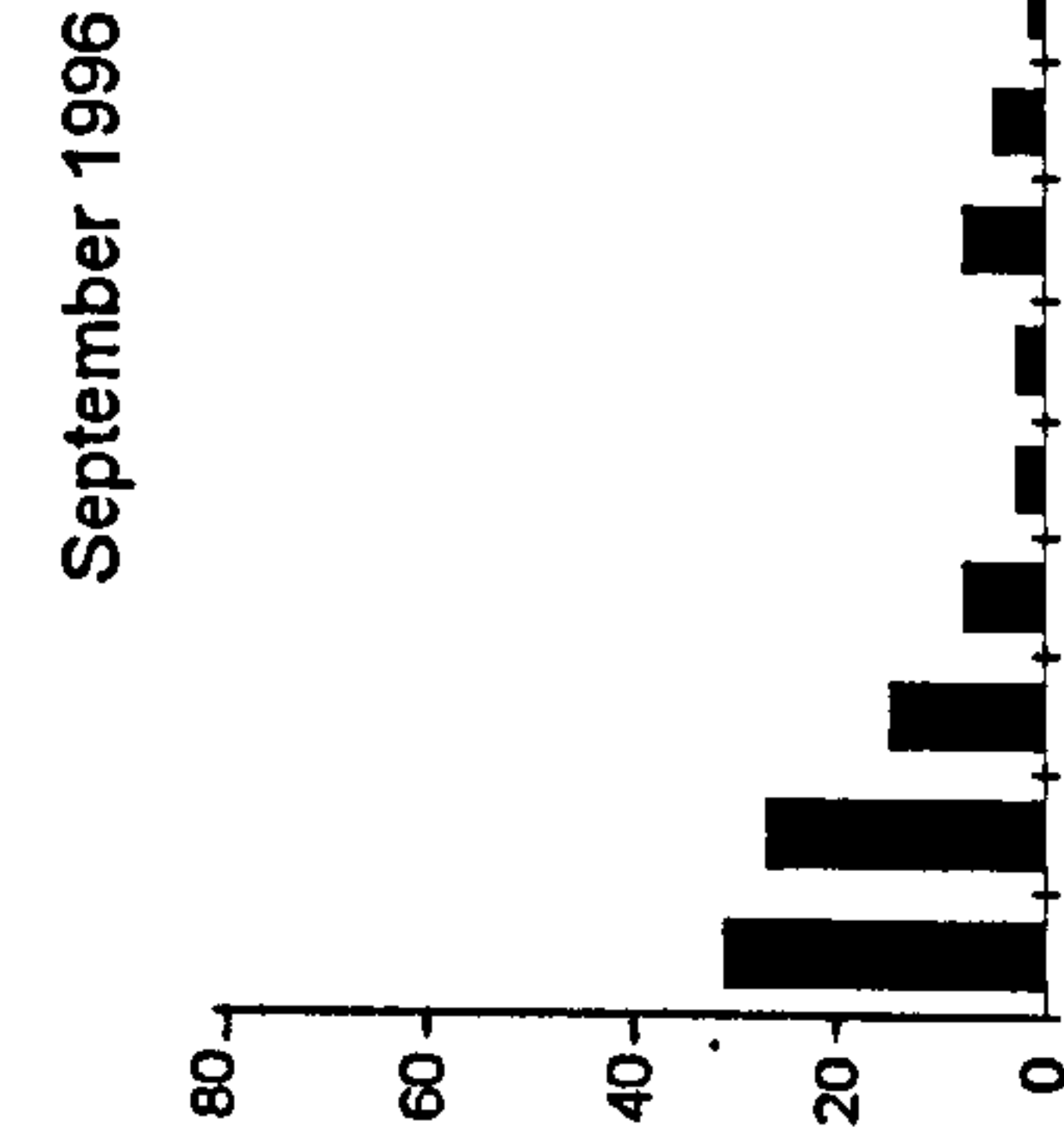
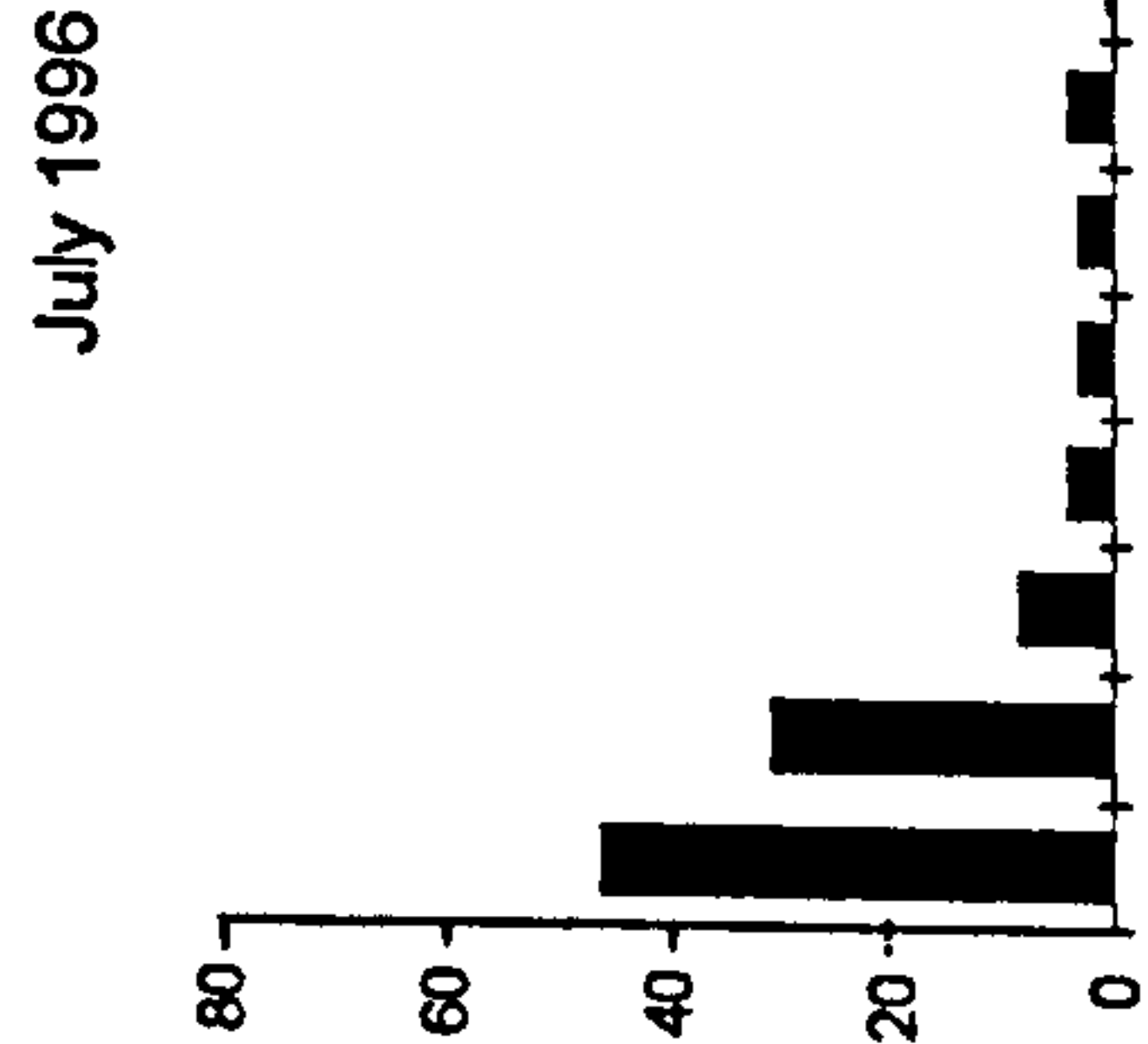
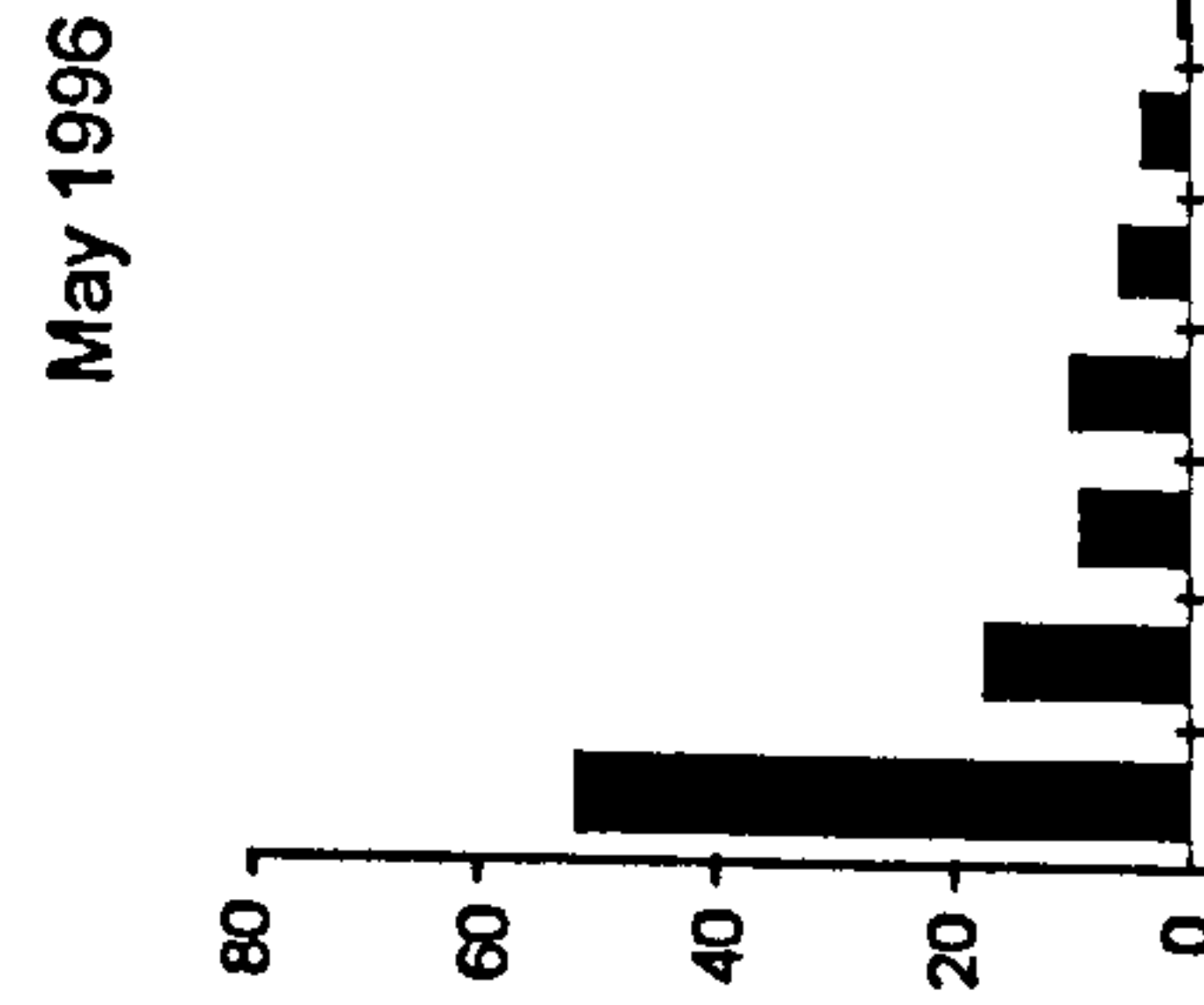
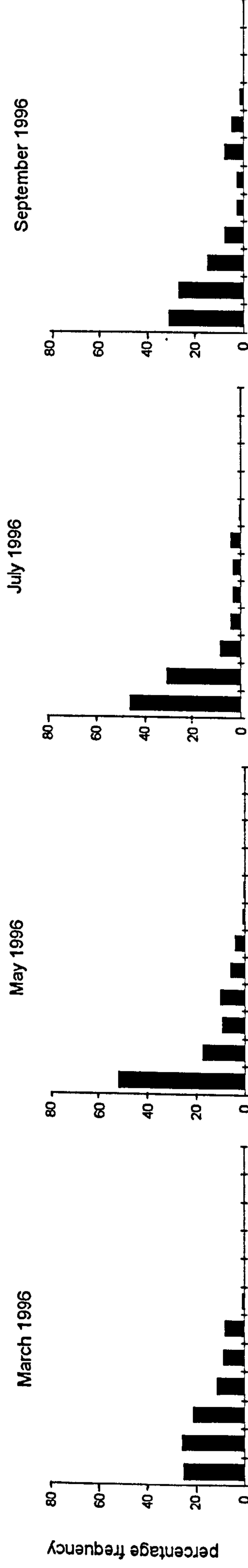
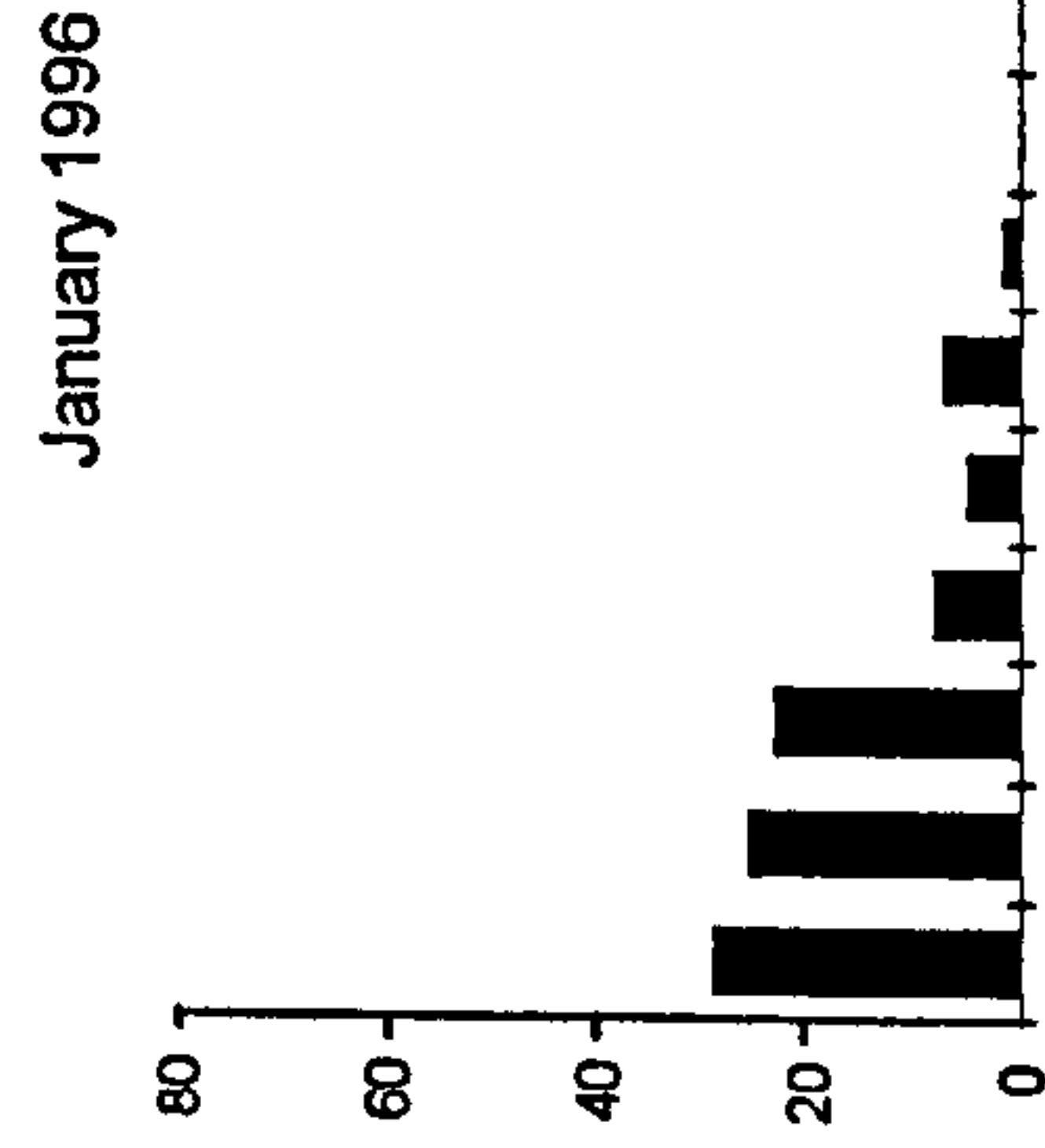
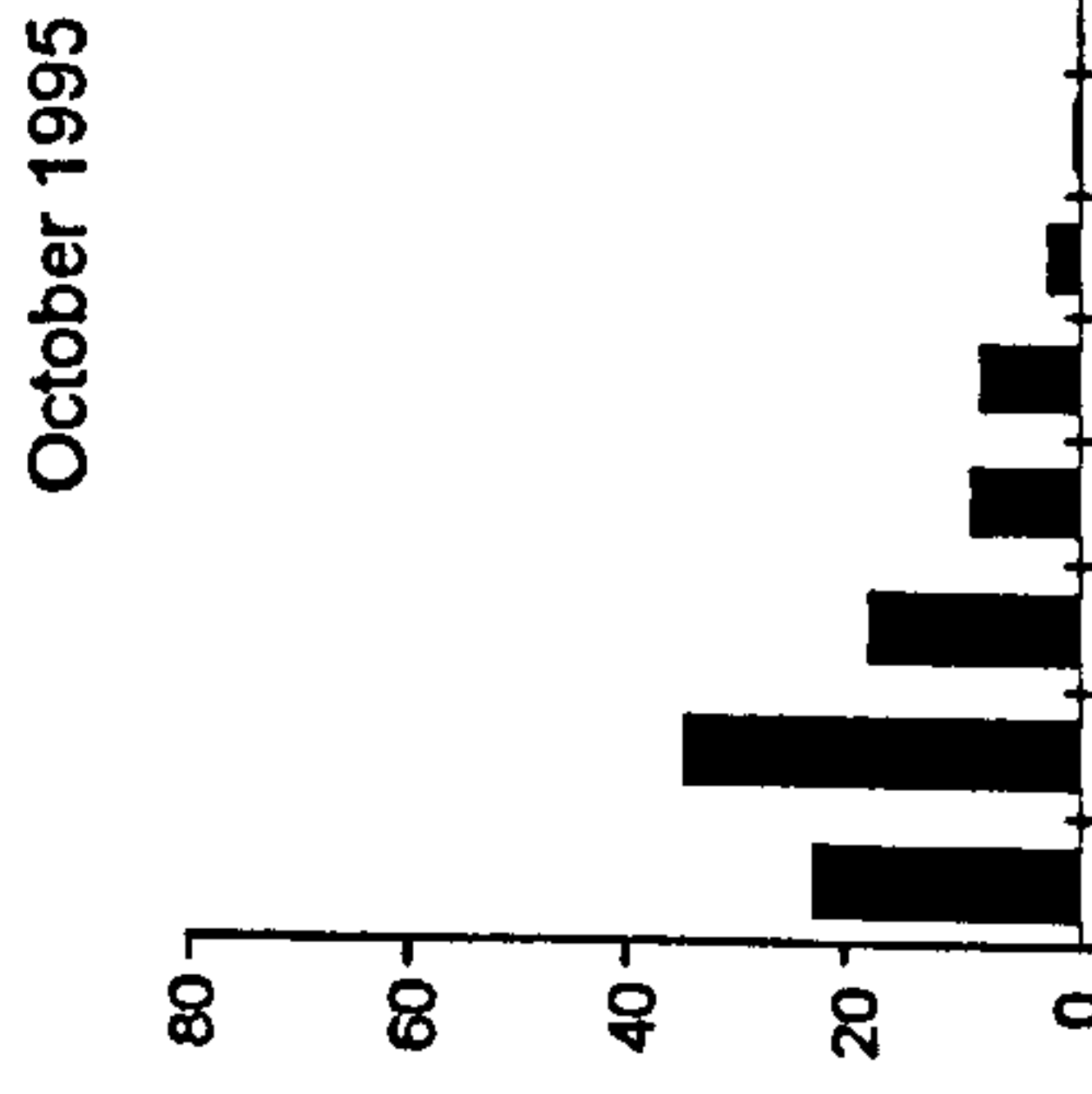
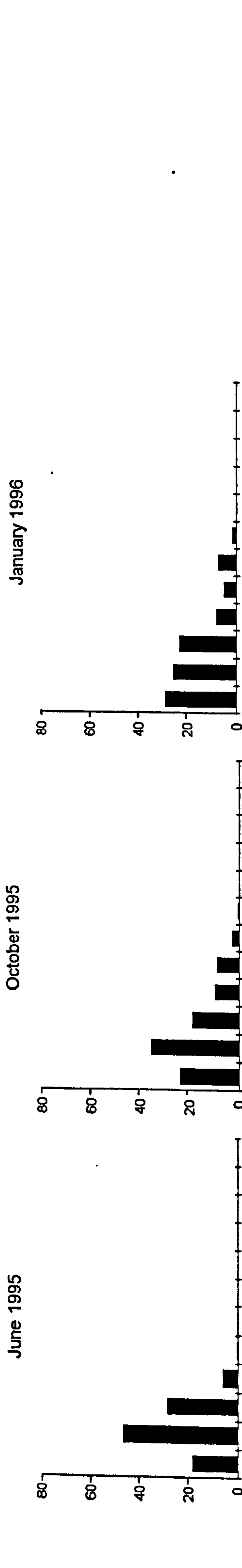


September 1997



shell length (mm)

Figure 2.6. The length frequency distributions of *Mytilus edulis* from the low shore at Church Island.

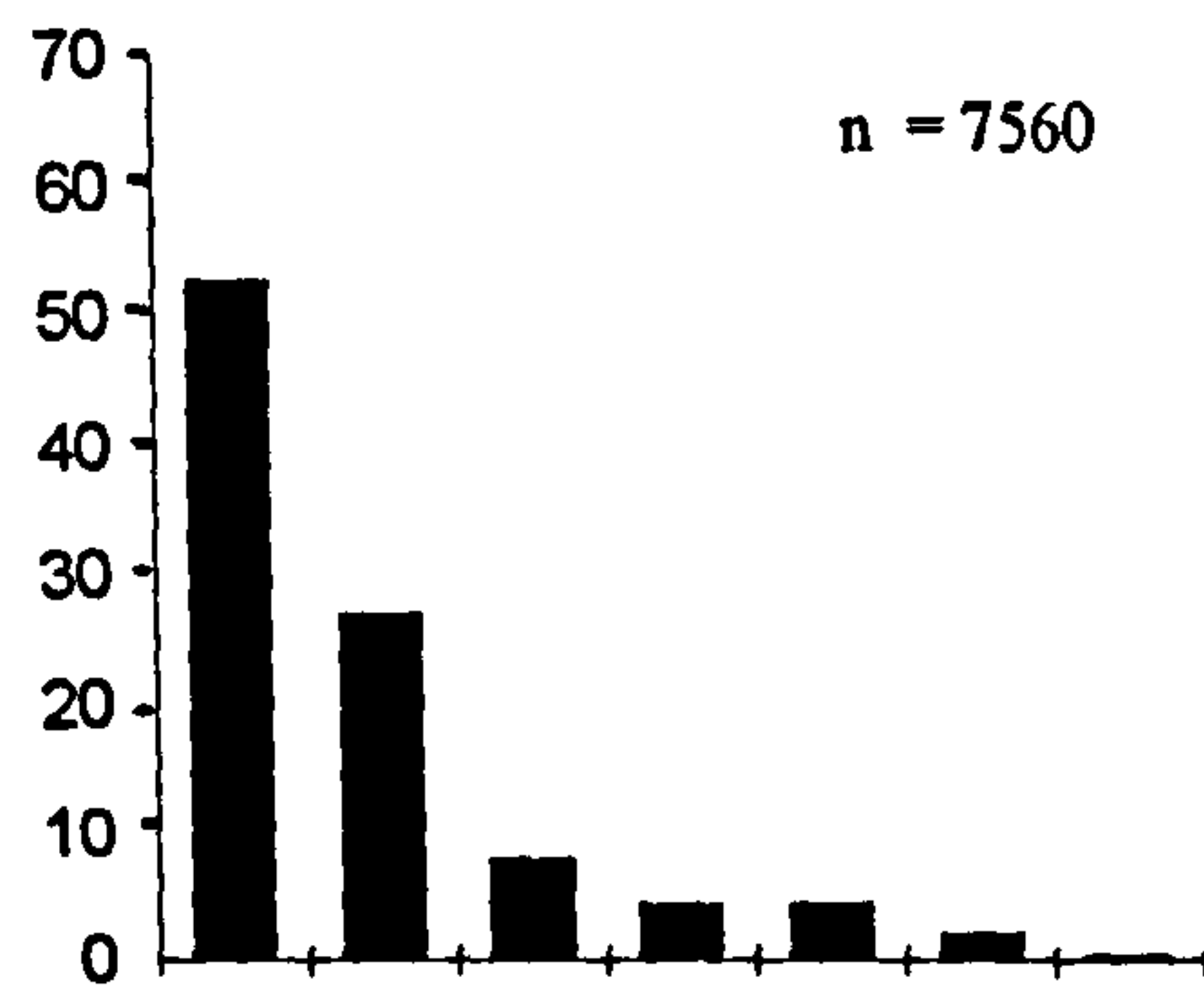


shell length (mm)

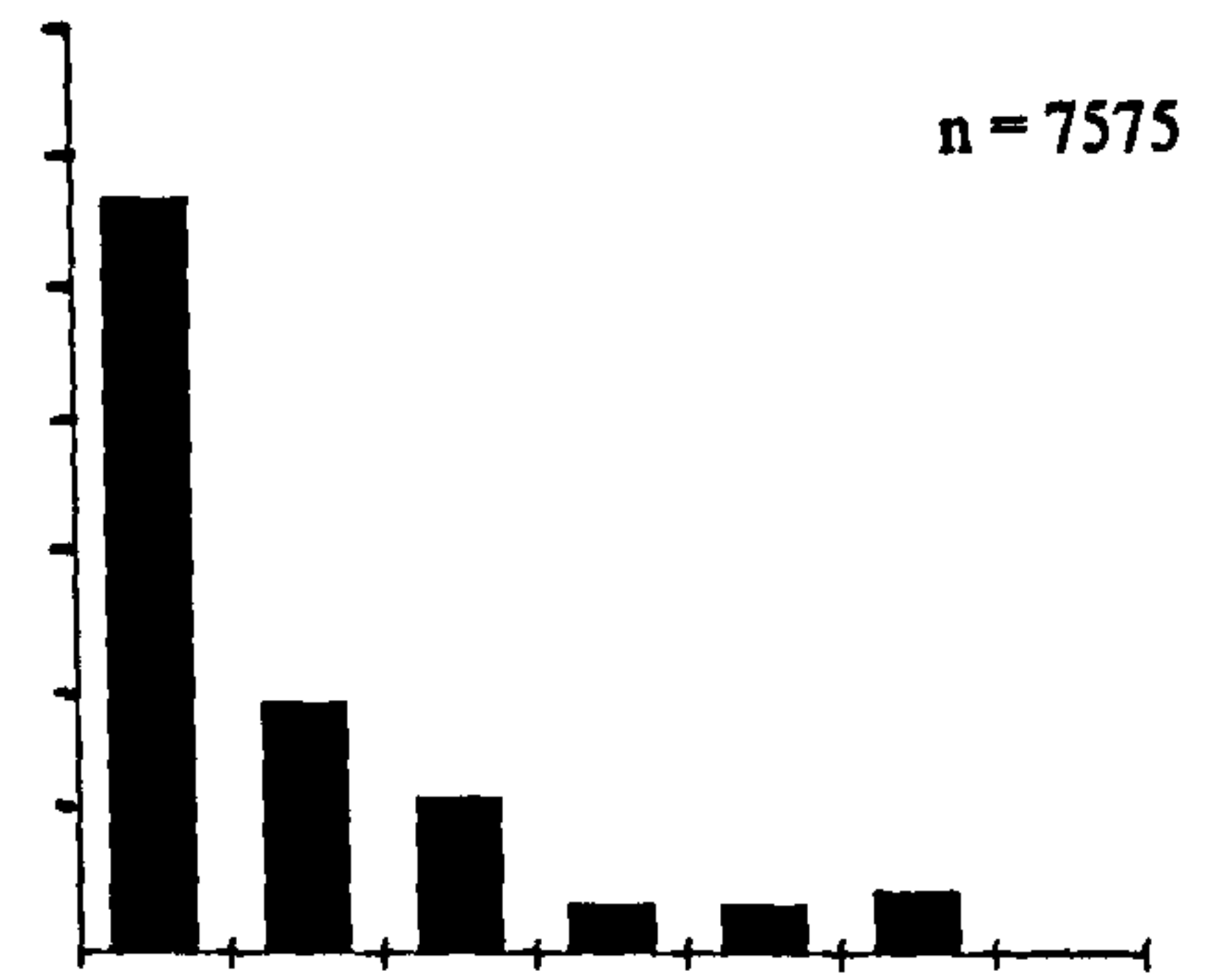
Figure 2.7. The length-frequency distribution and the population density of *Mytilus edulis* from the high and mid shore levels at Aberffraw in February and June 1997.

percentage frequency

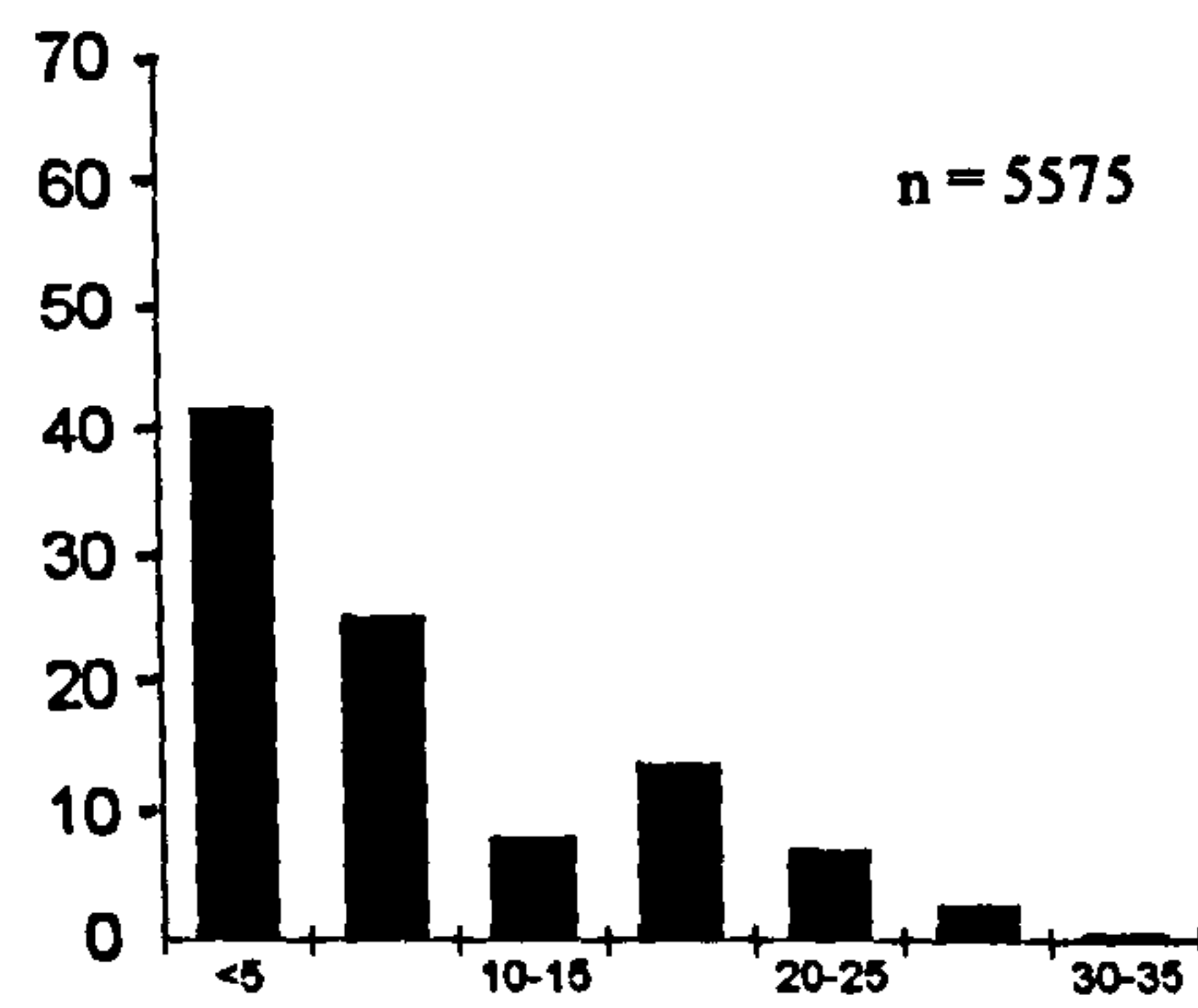
February high shore



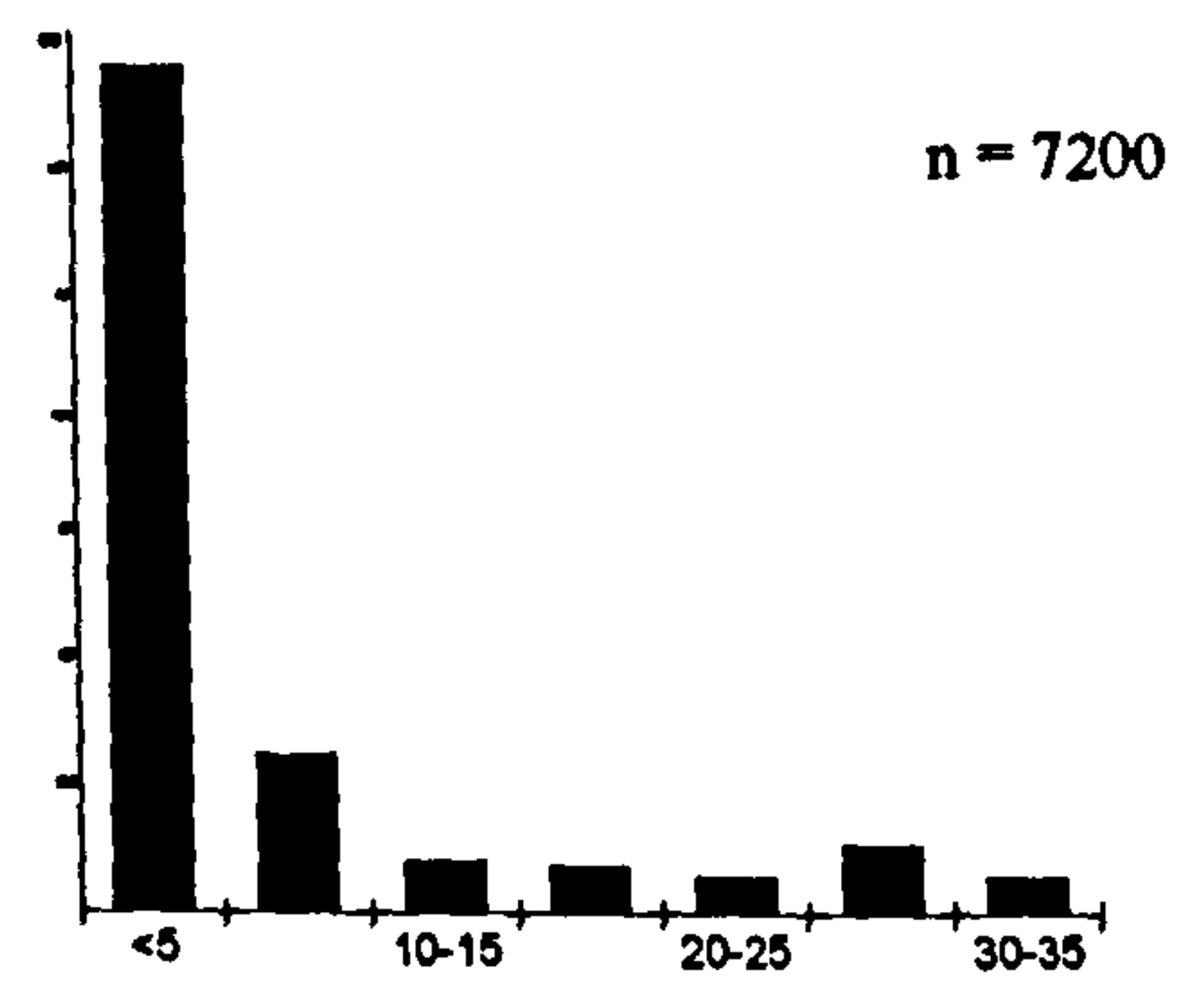
July high shore



February mid shore



July mid shore



shell length (mm)

Figure 2.8. The surface area frequency distributions of *Mytilus edulis* from the high shore Aberffraw.

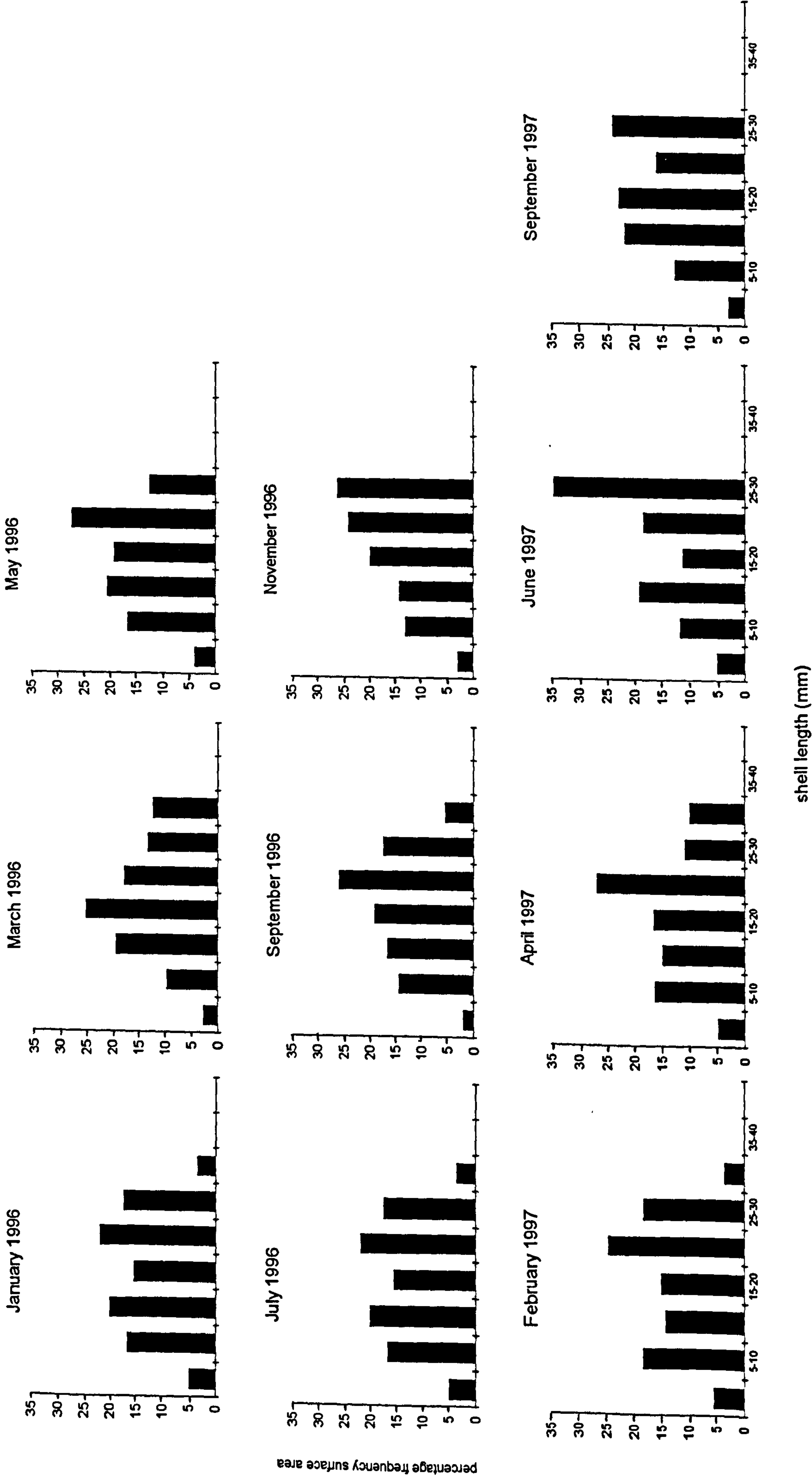
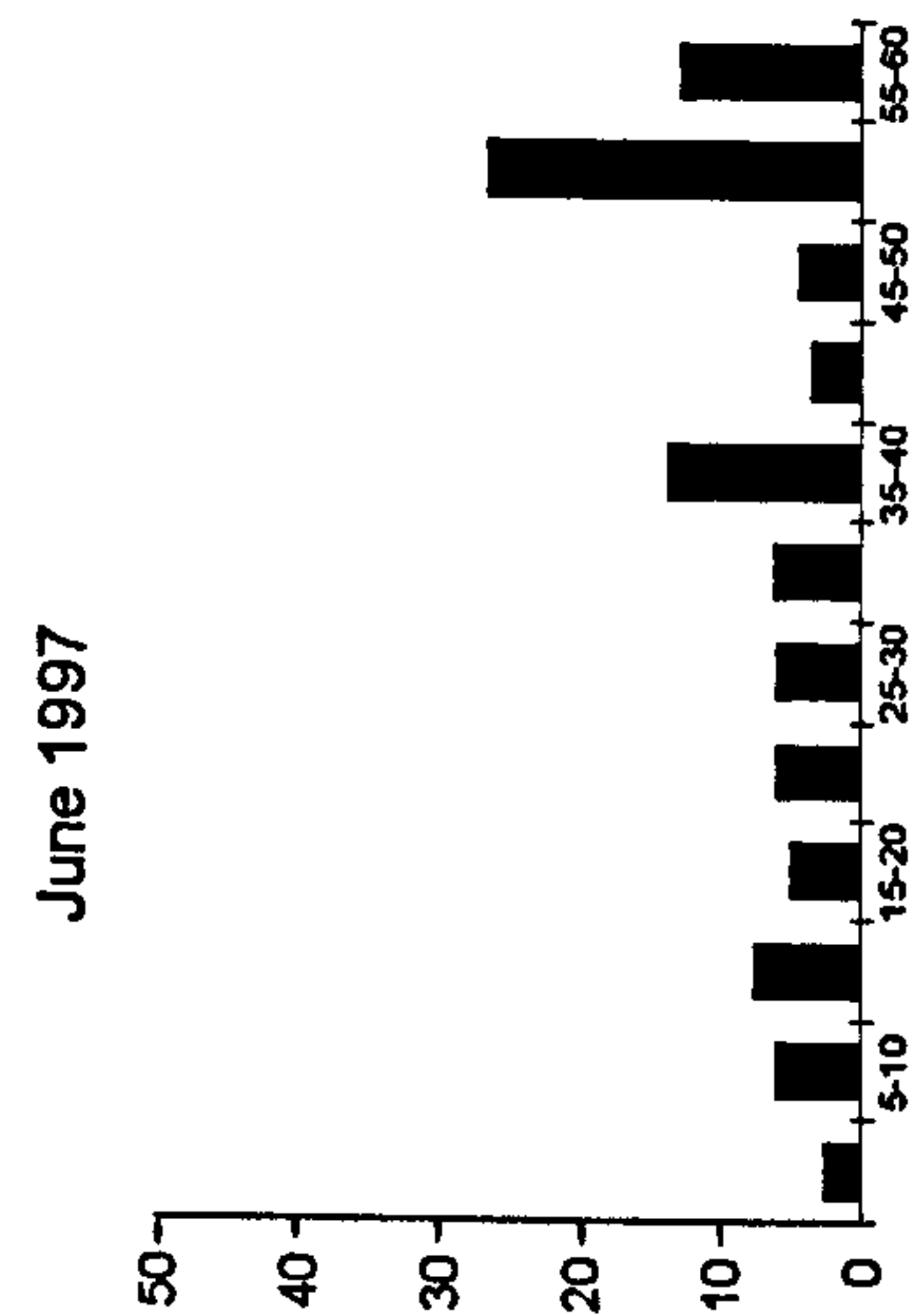
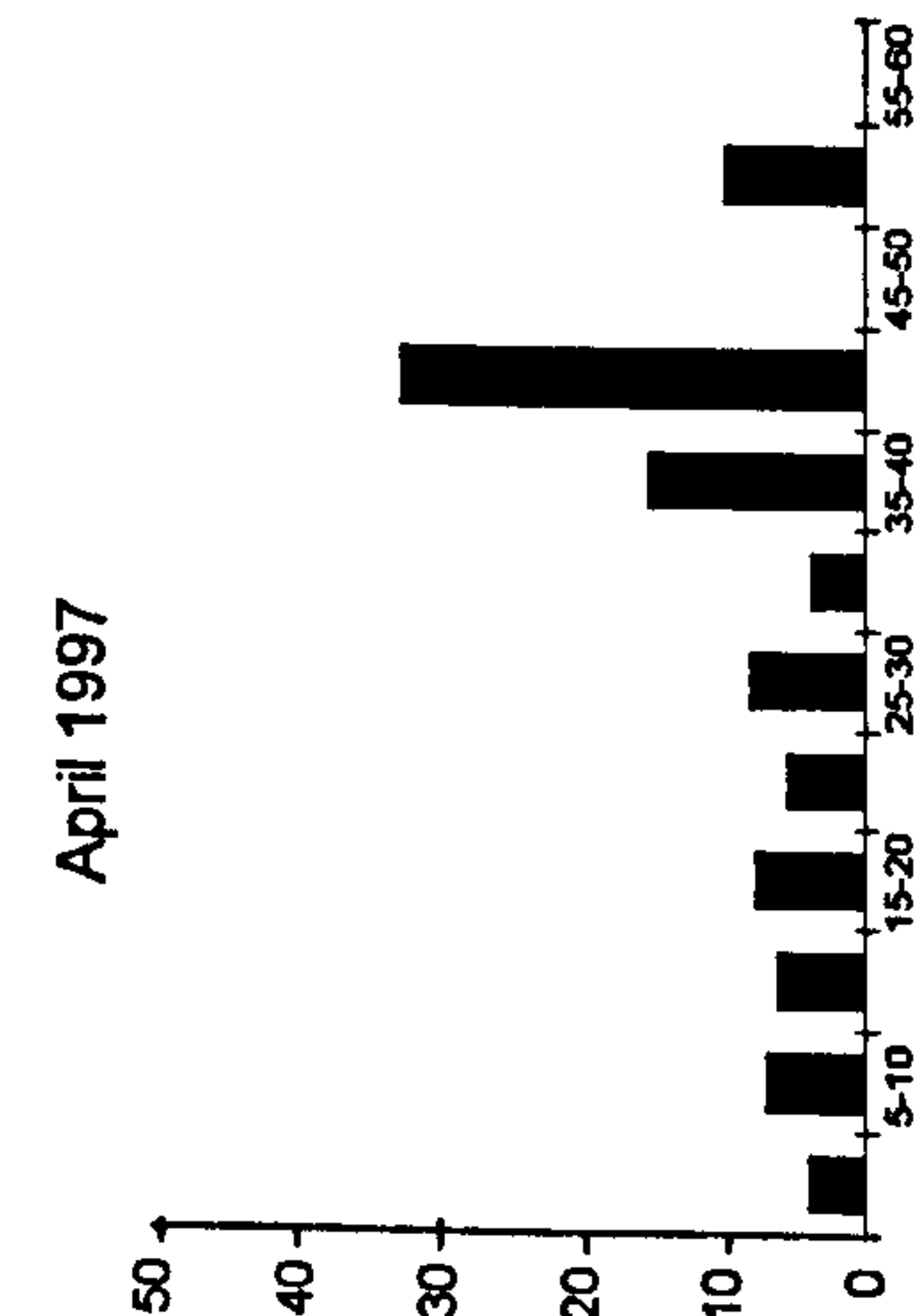
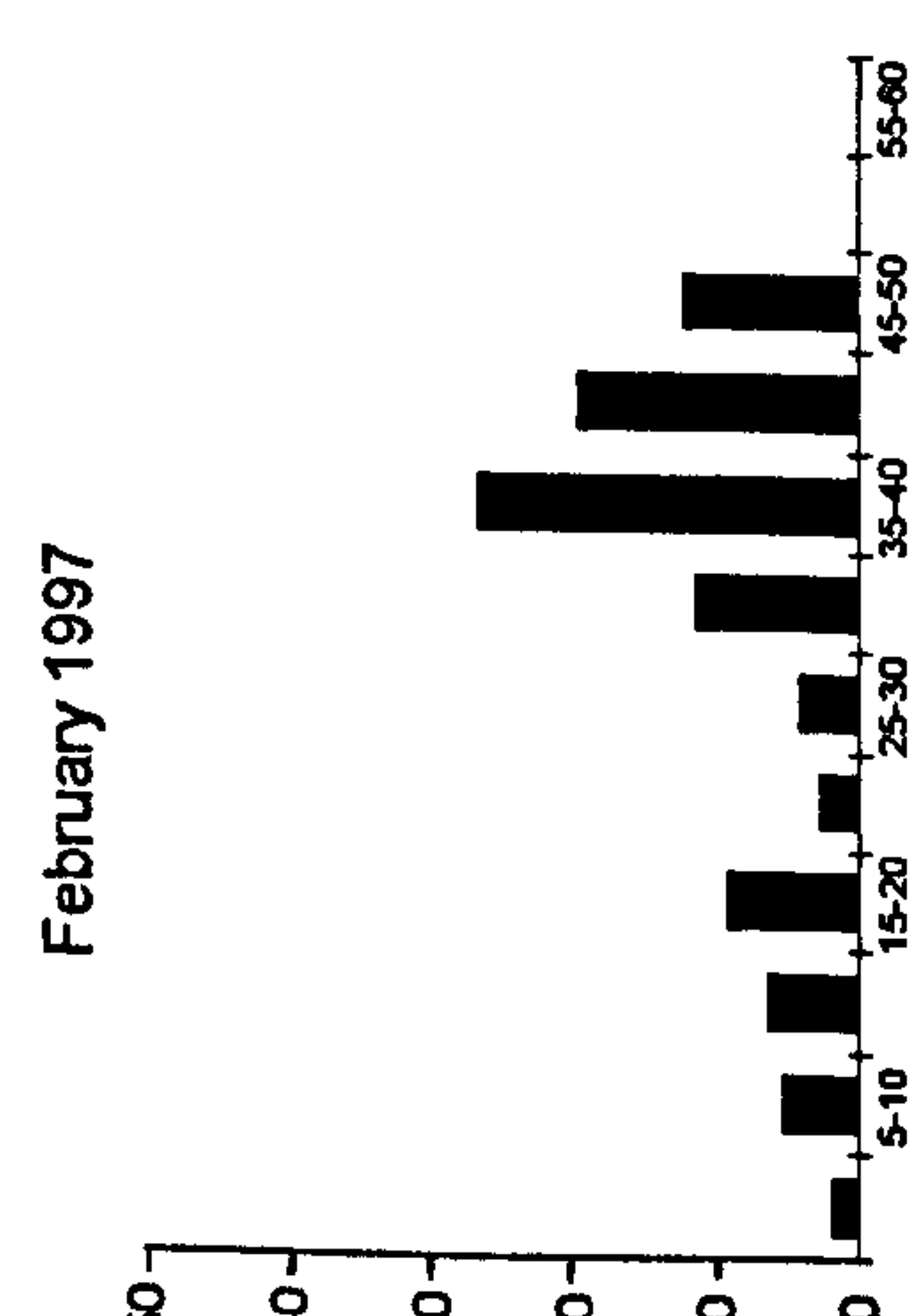
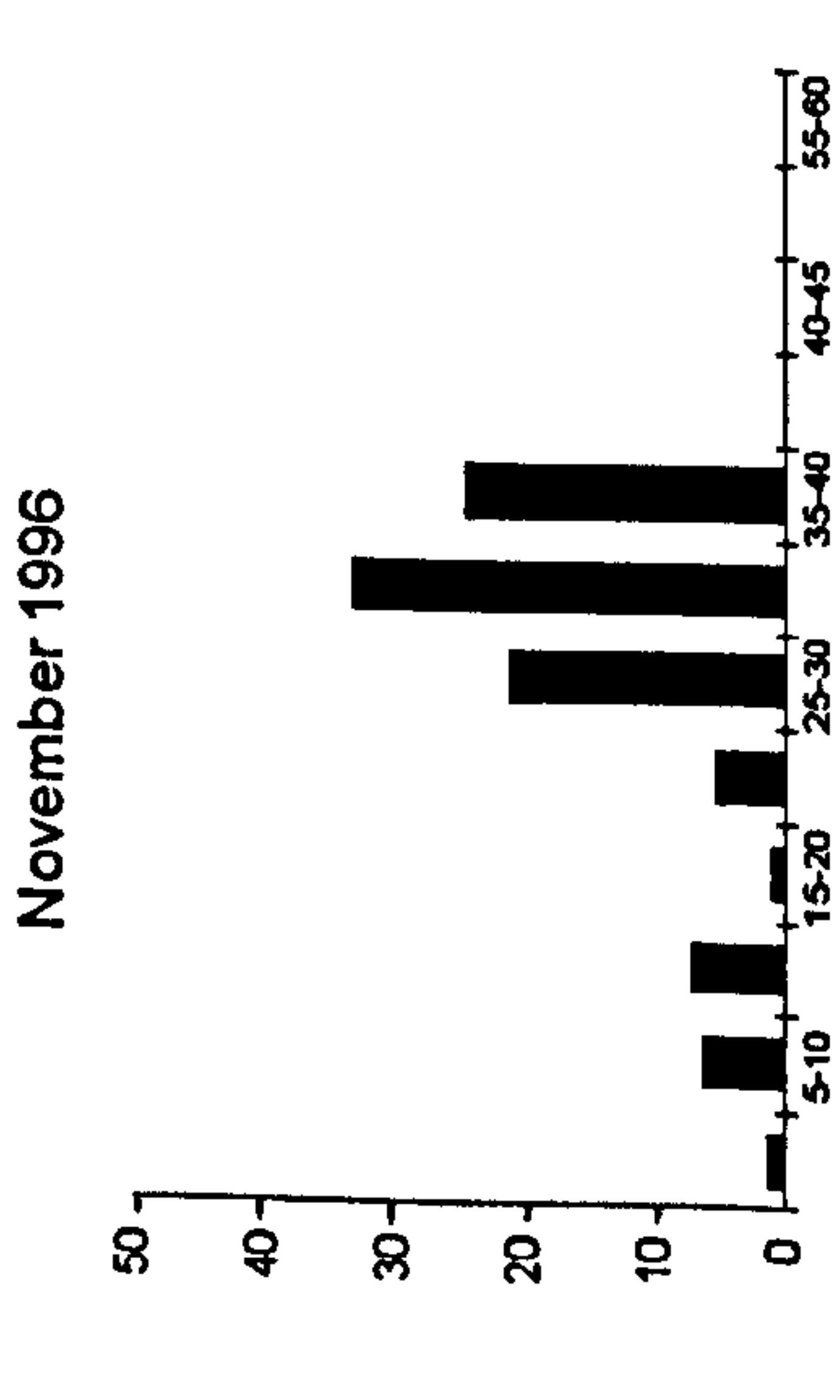
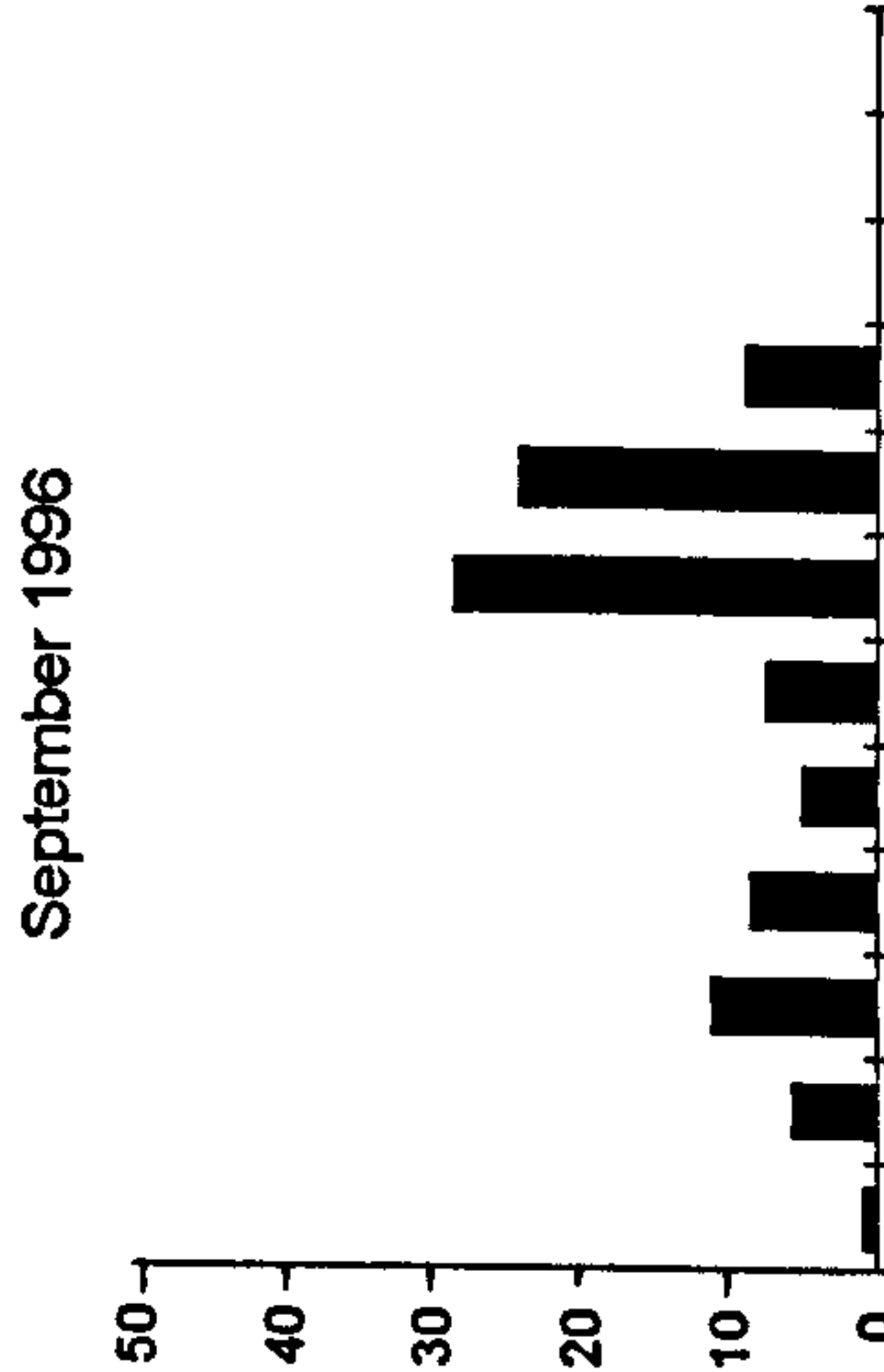
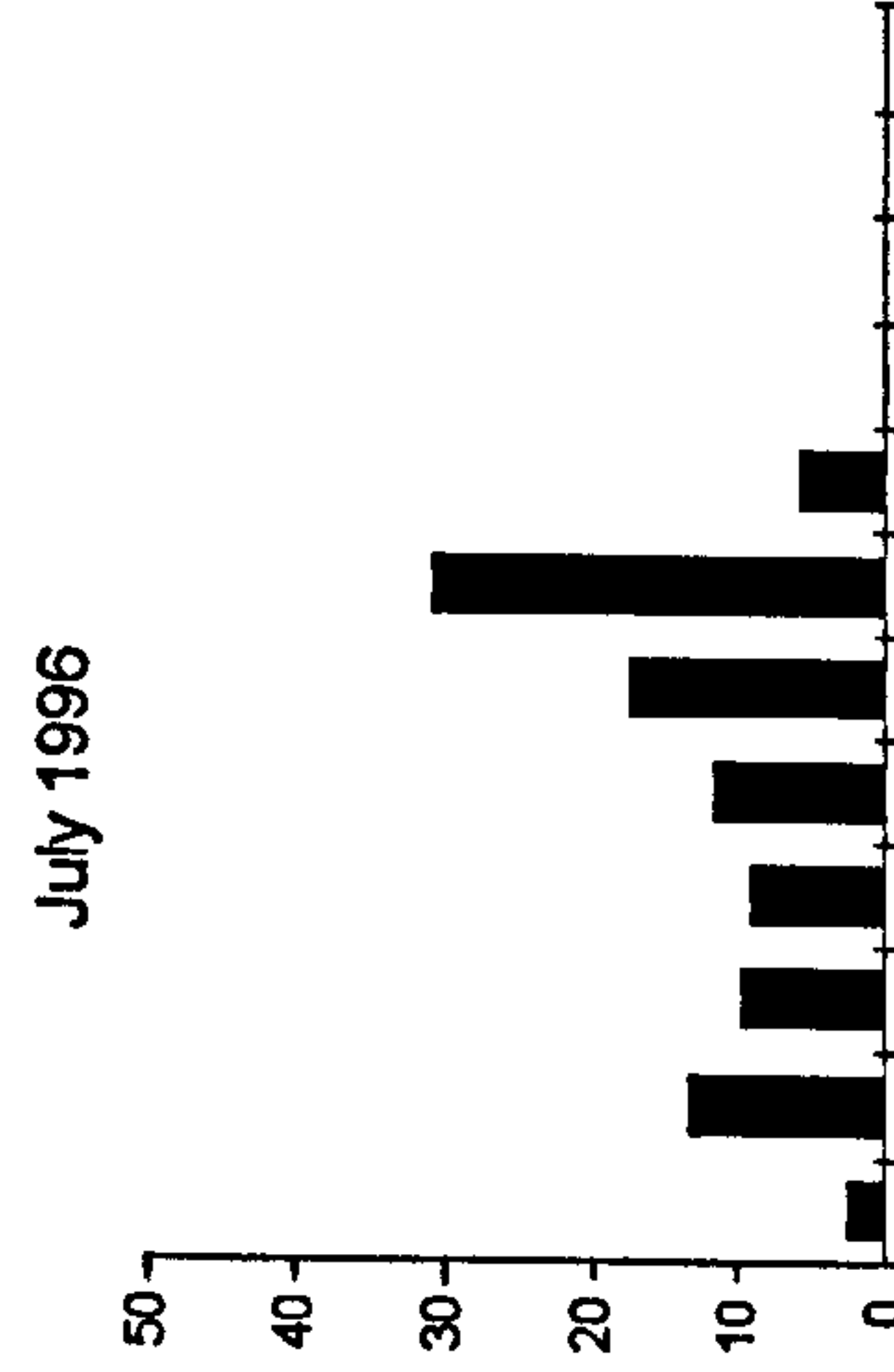
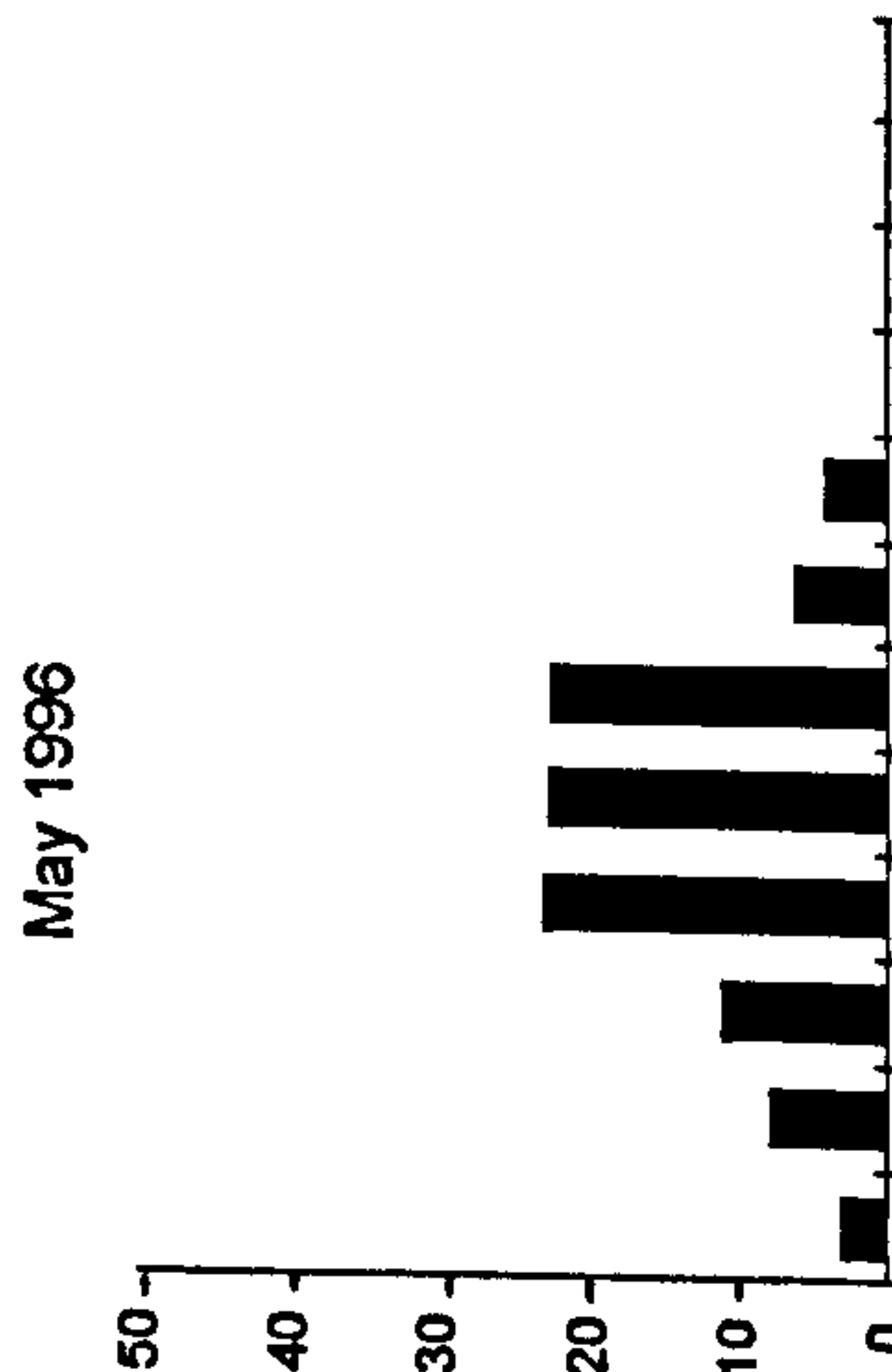
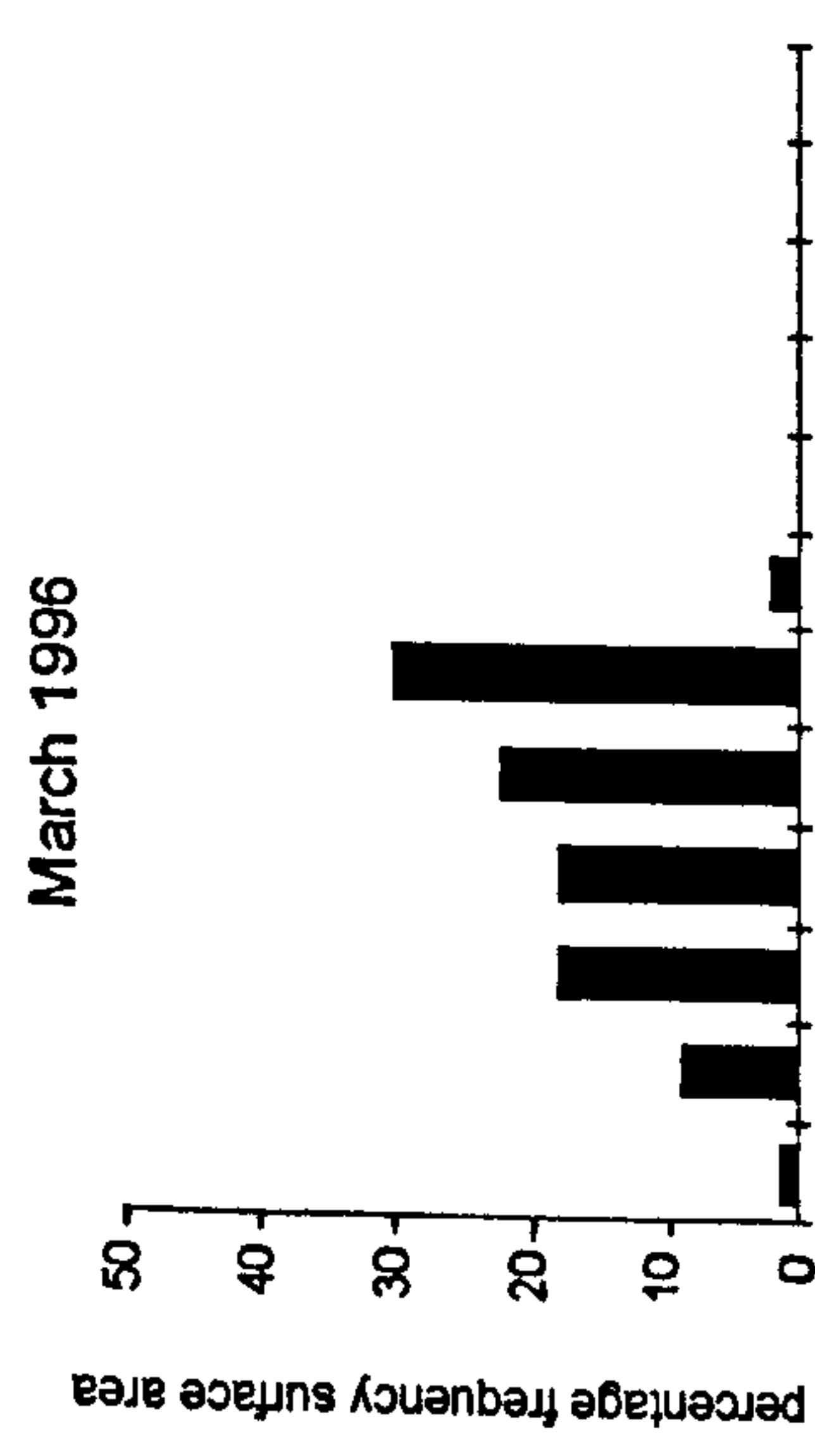
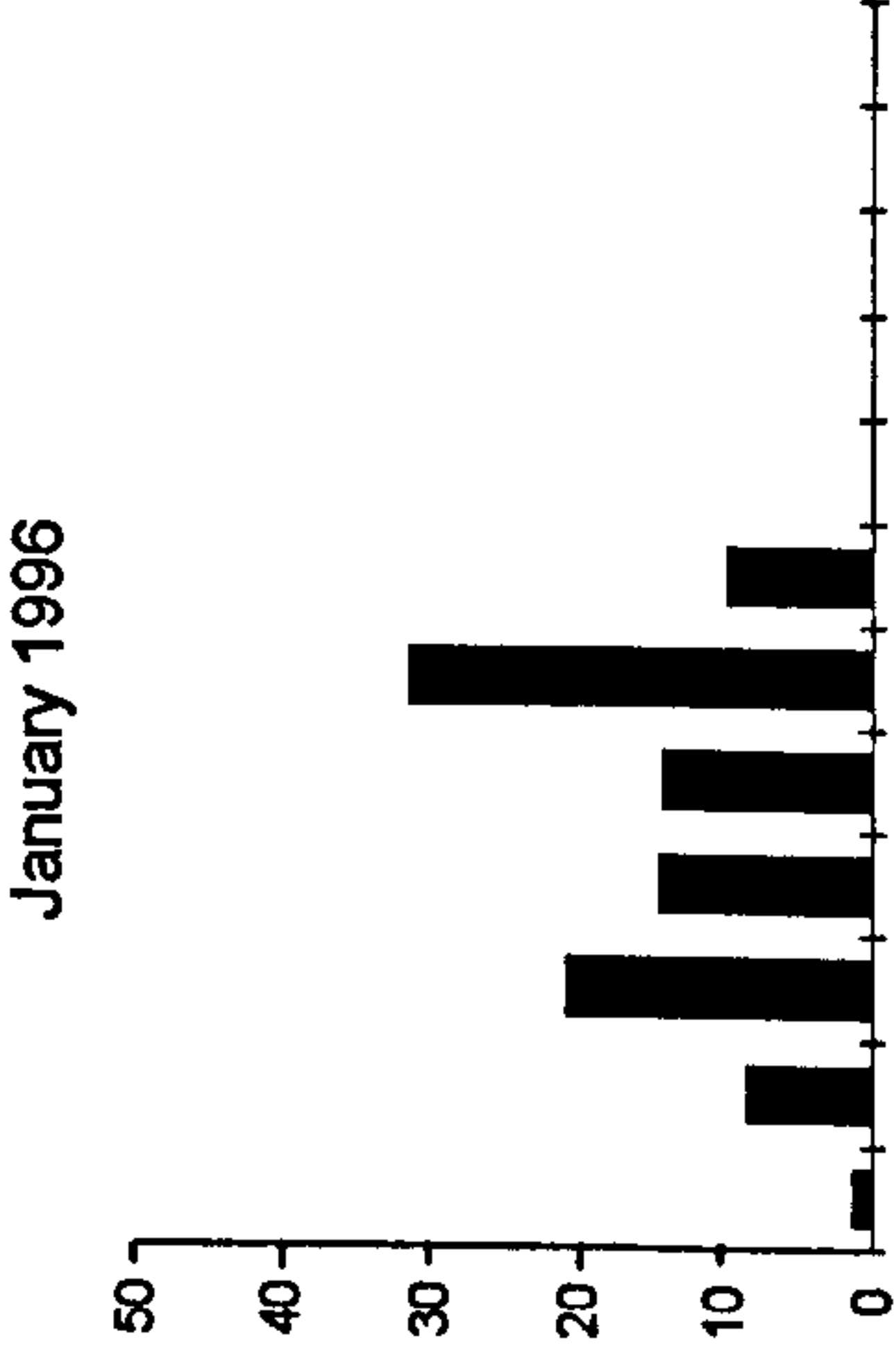
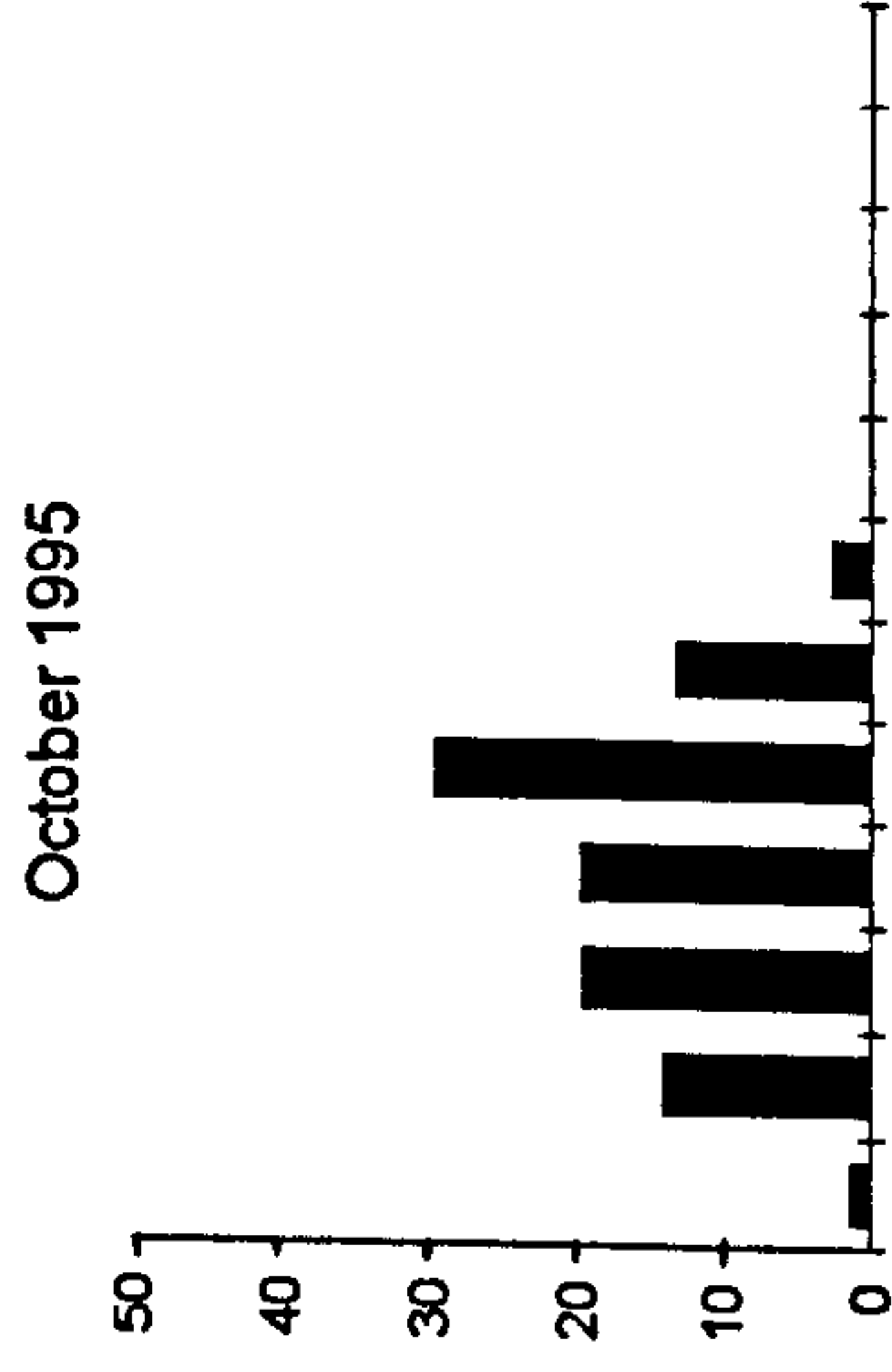
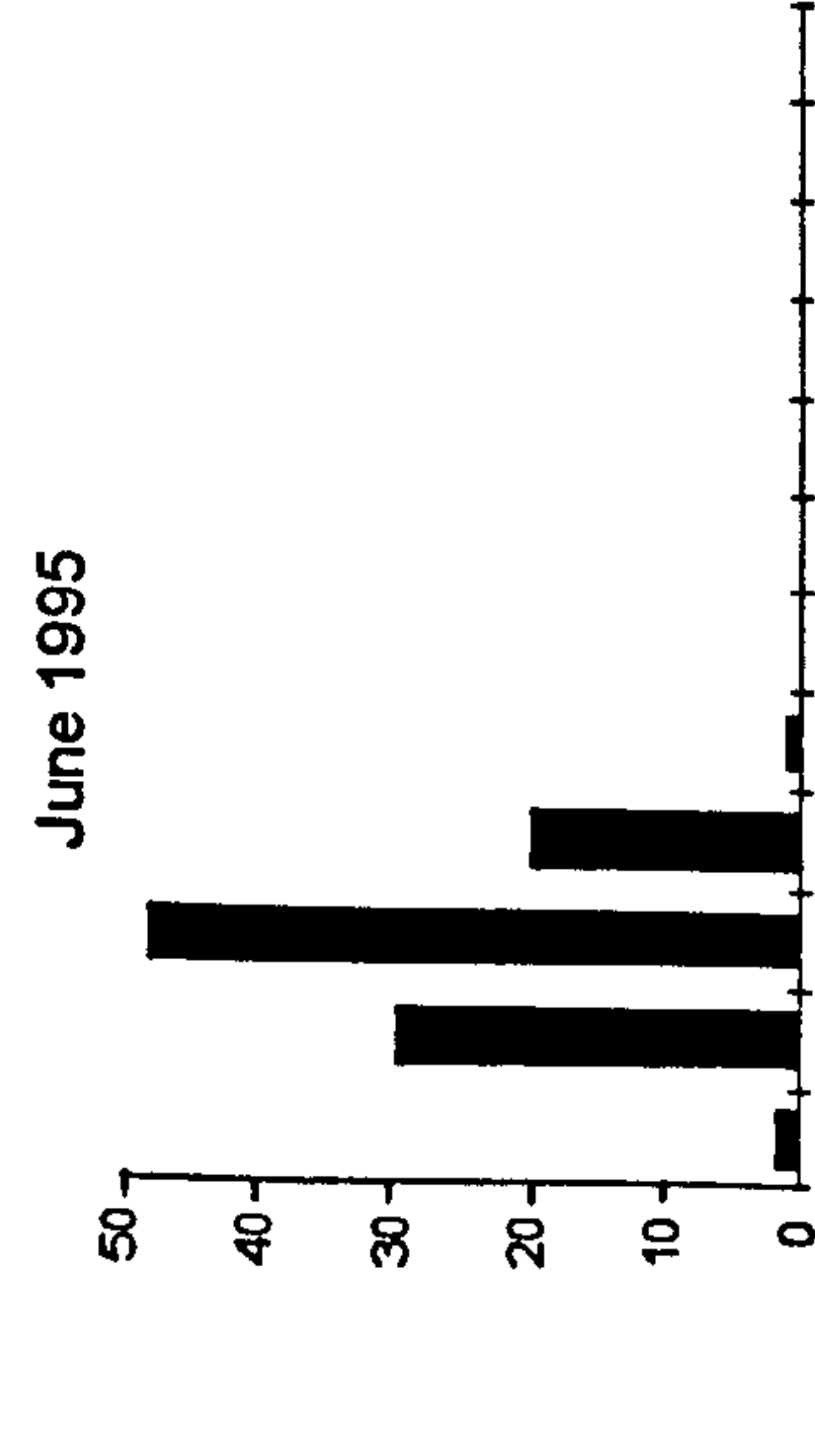


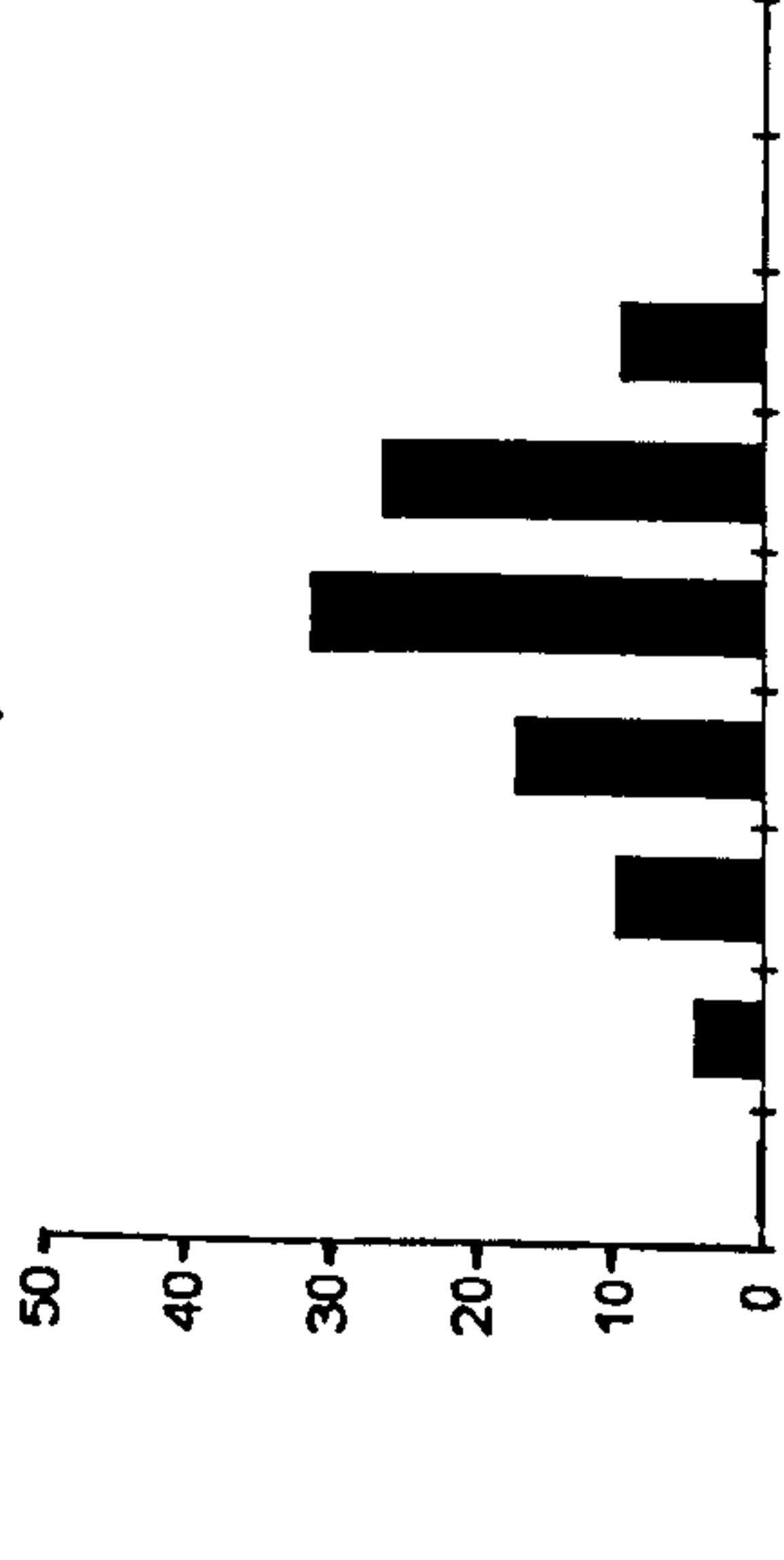
Figure 2.9. The surface area frequency distributions of *Mytilus edulis* from the low shore Church Island.



shell length (mm)

Figure 2.10. The biomass frequency distributions of *Mytilus edulis* from the high shore Aberffraw.

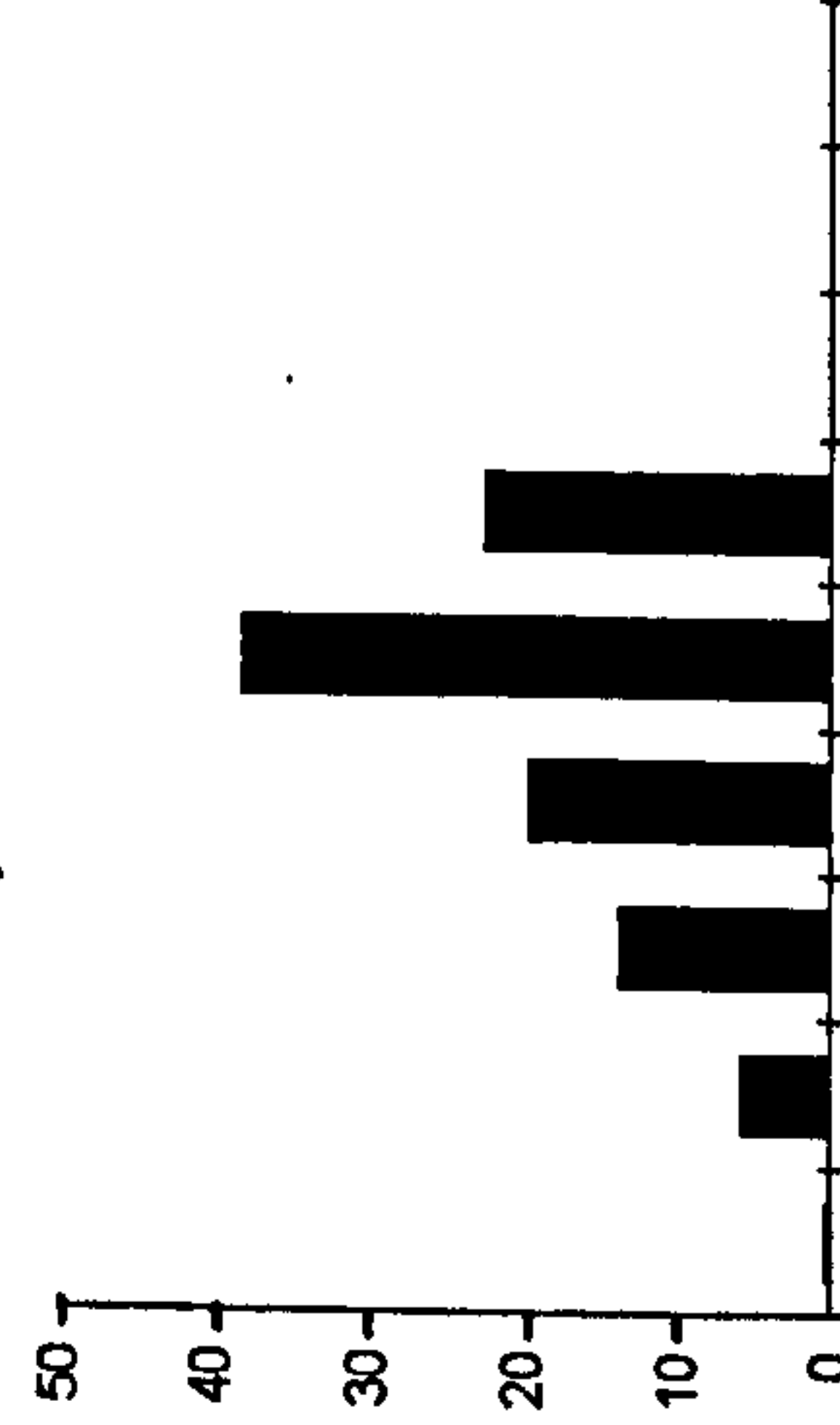
January 1996



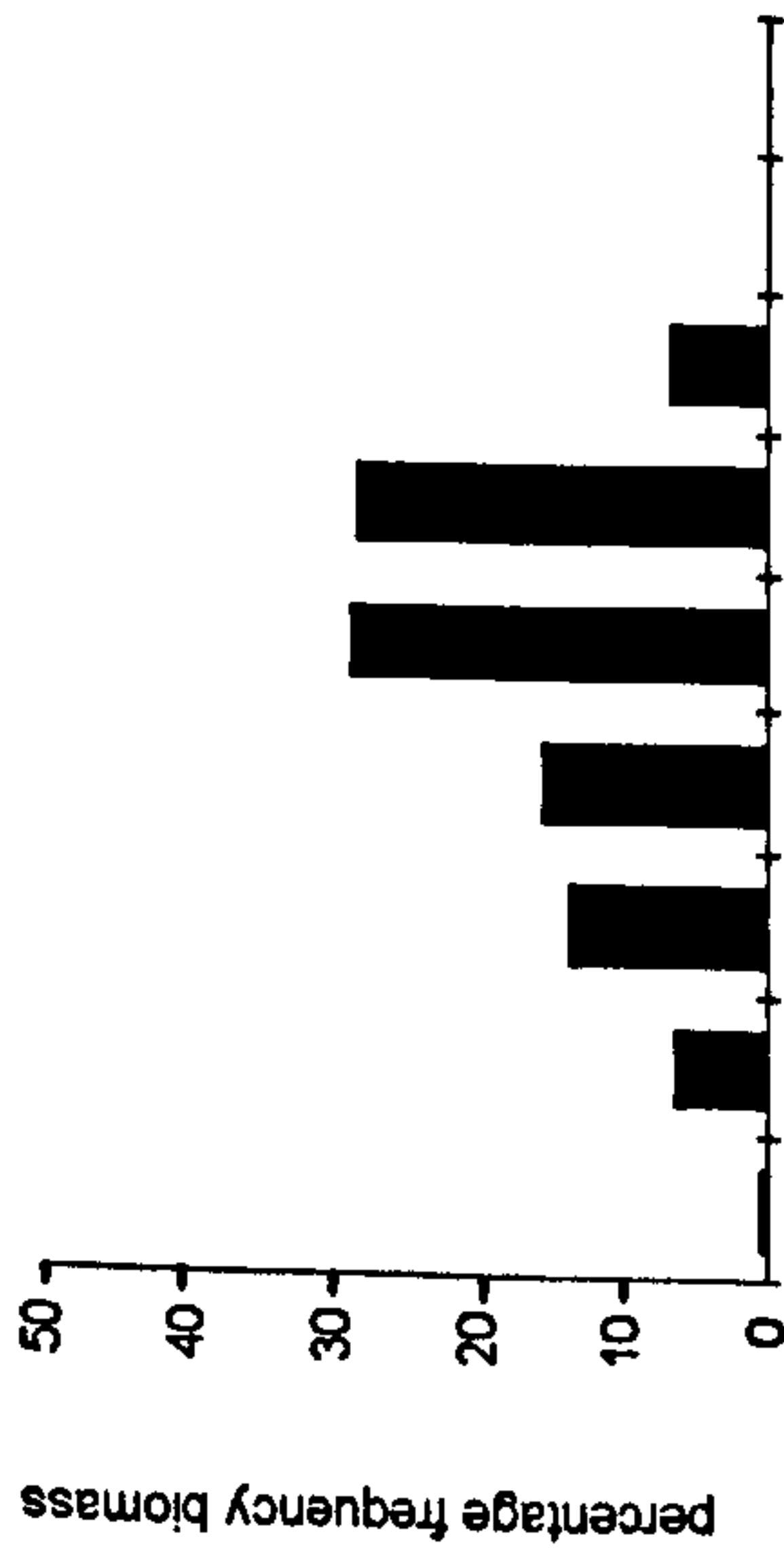
March 1996



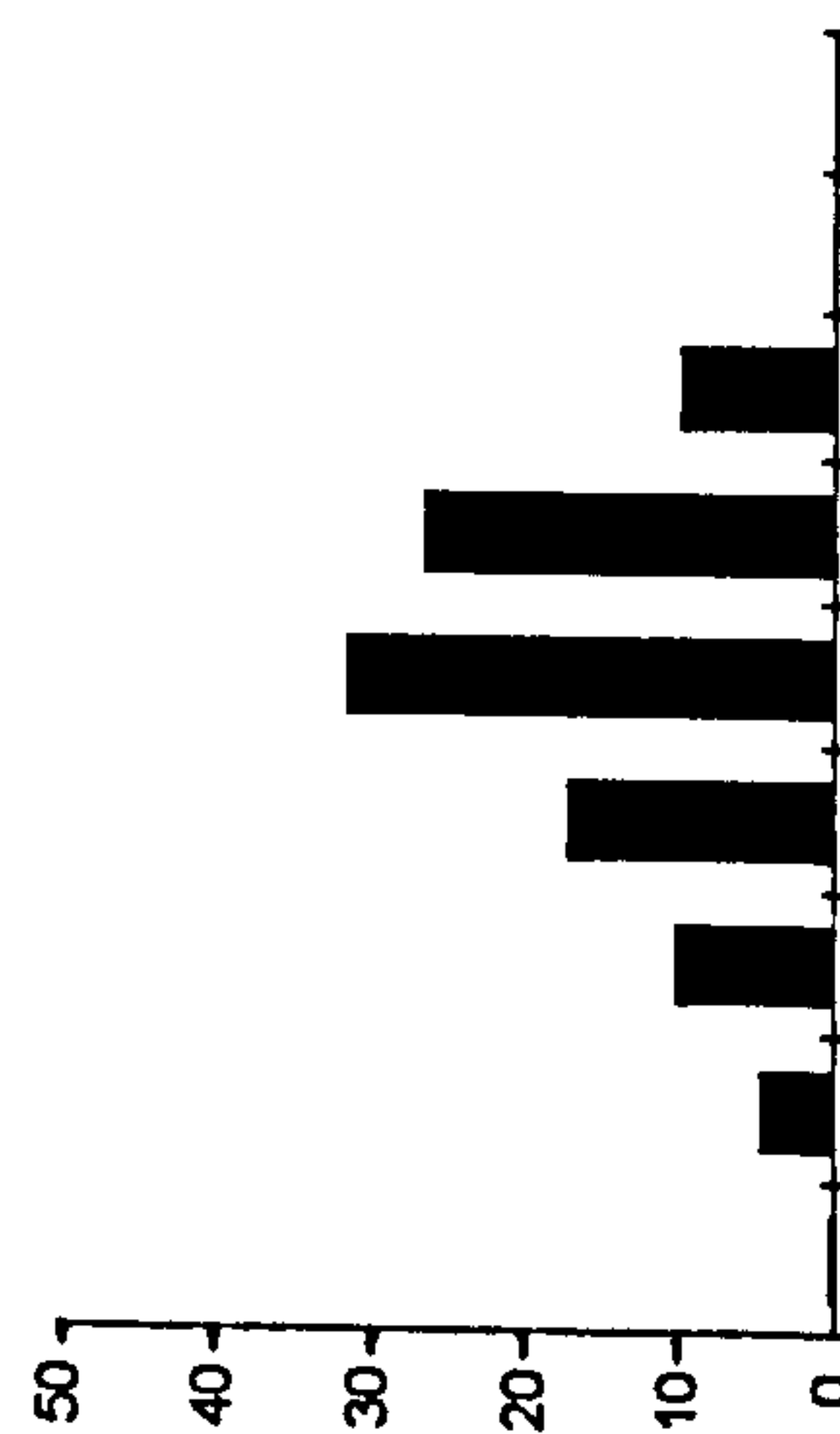
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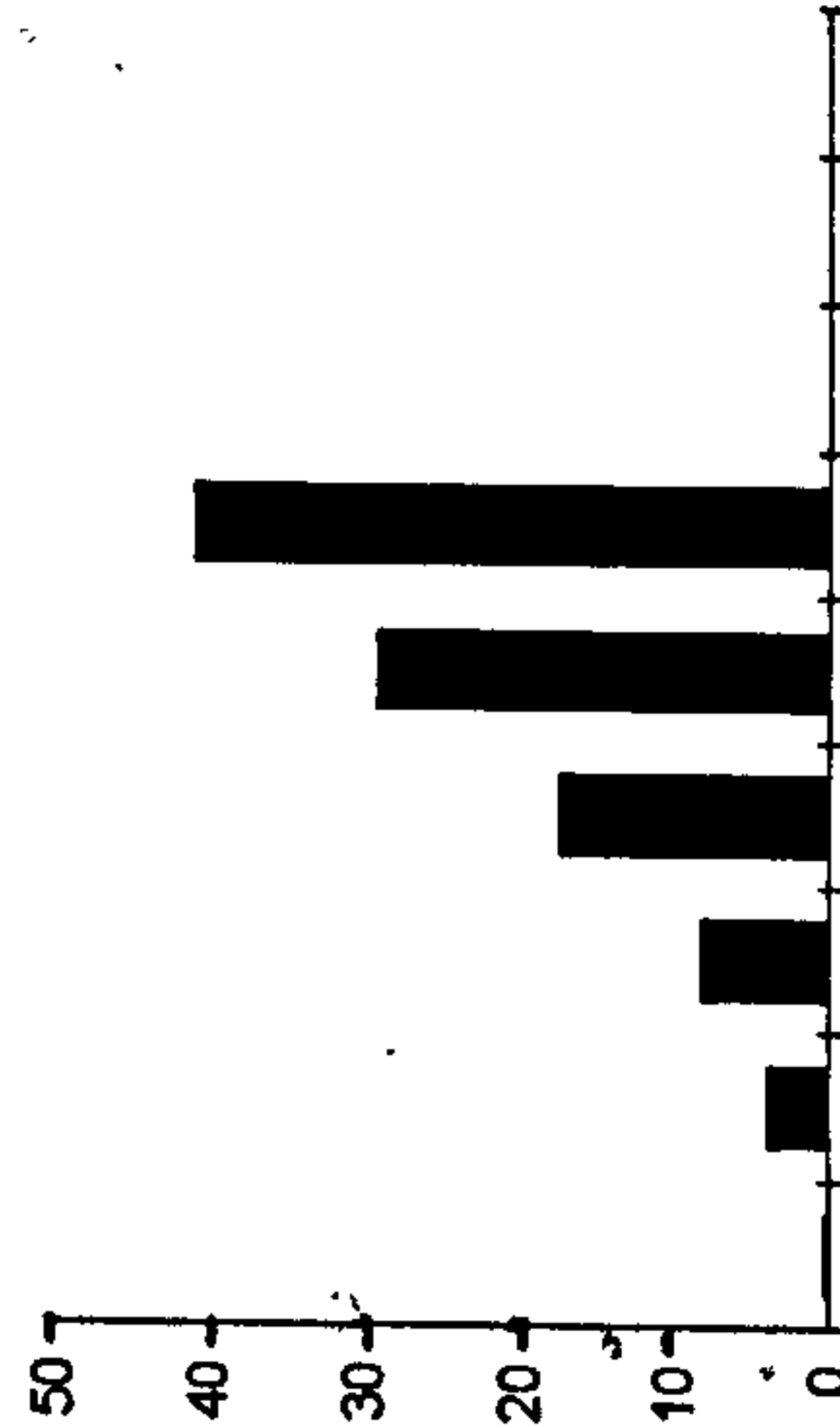
July 1996



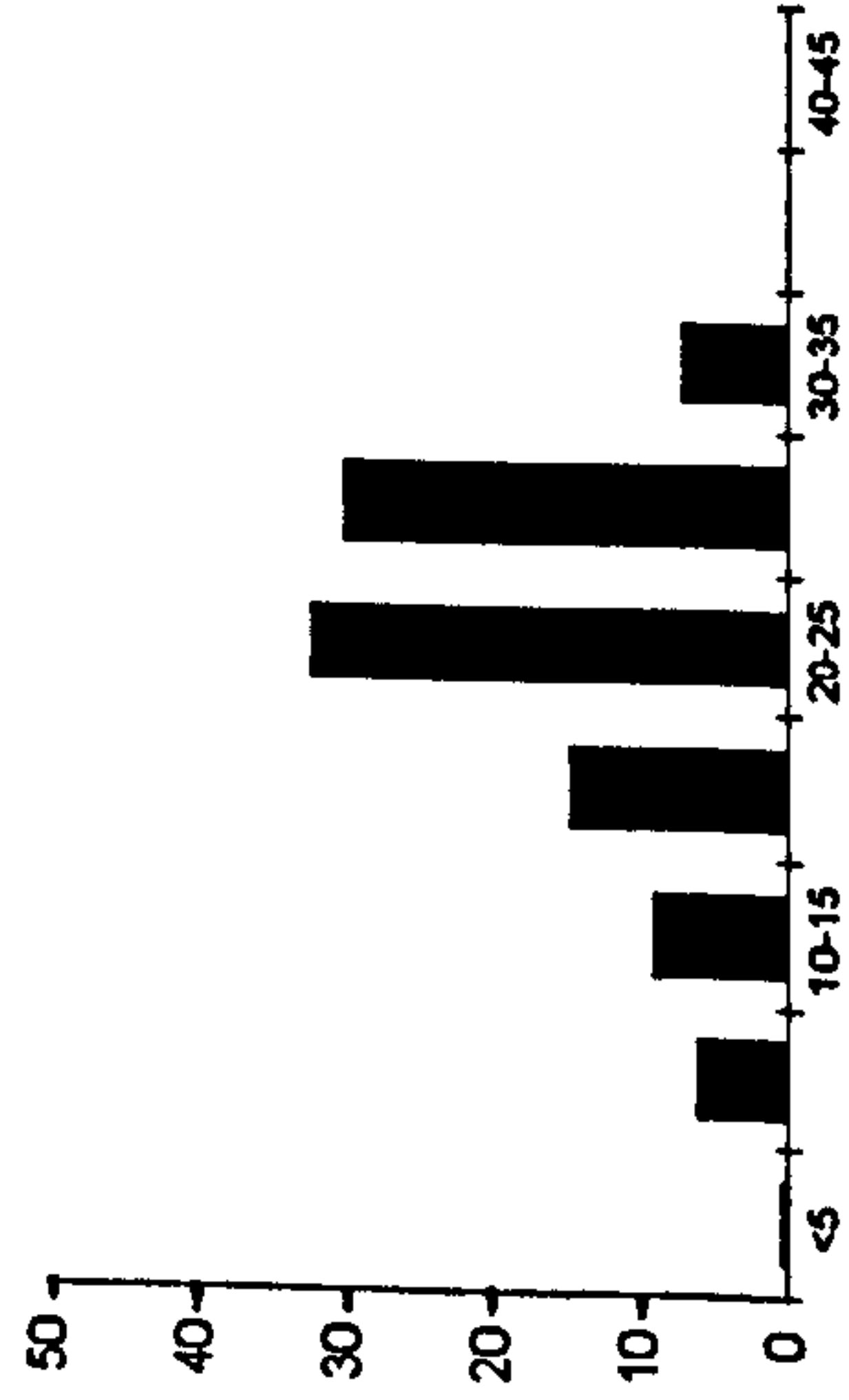
September 1996



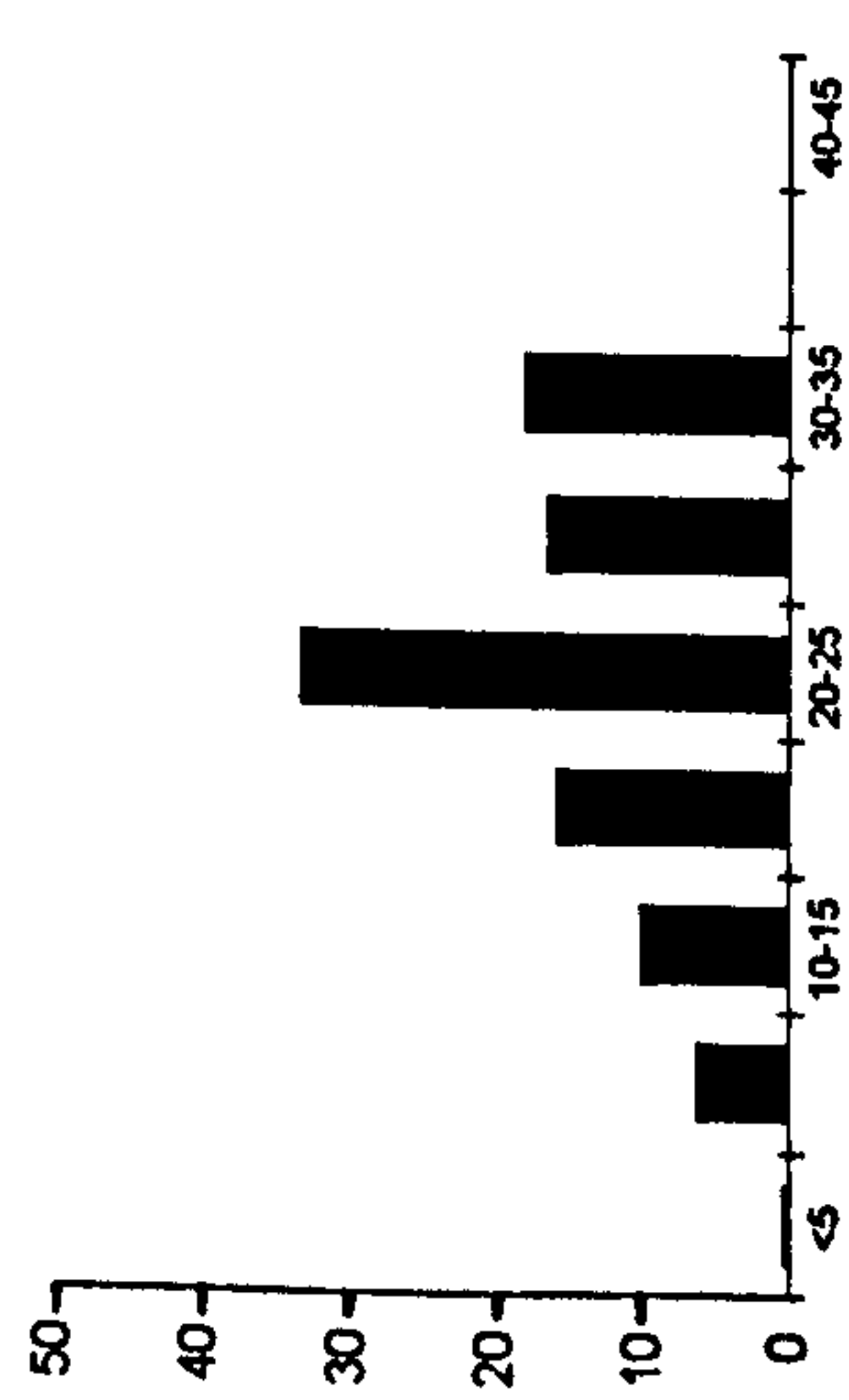
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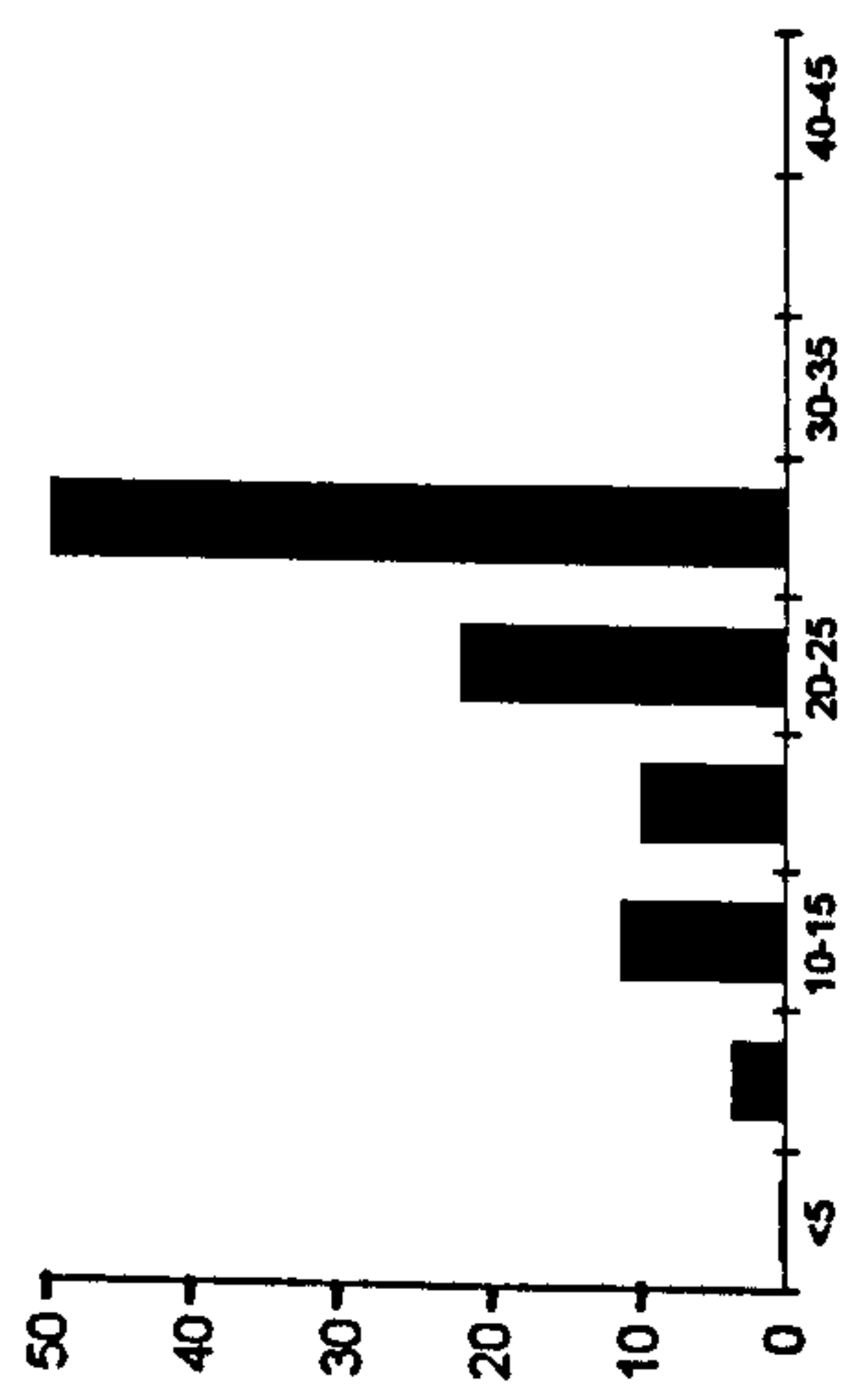
February 1997



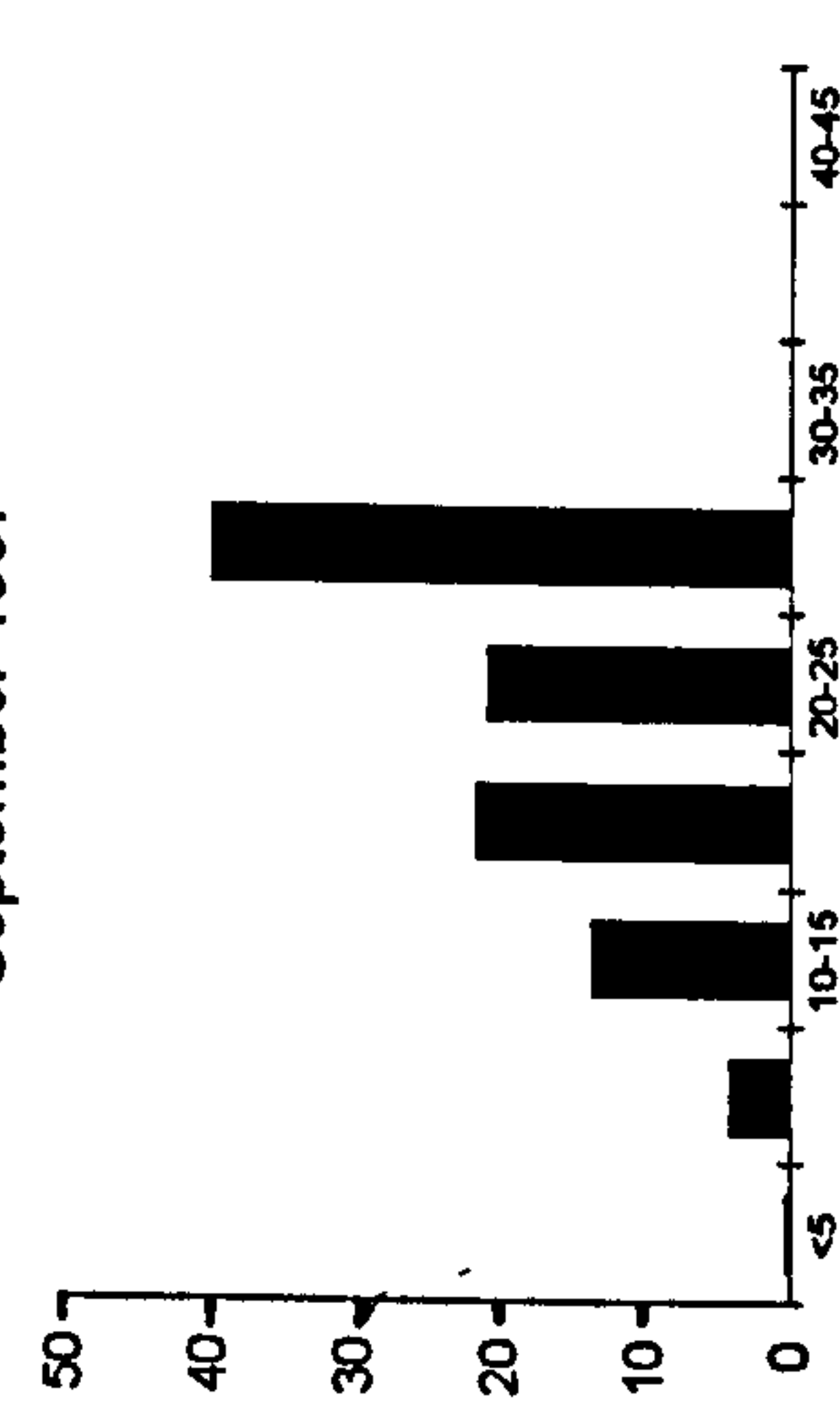
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June 1997

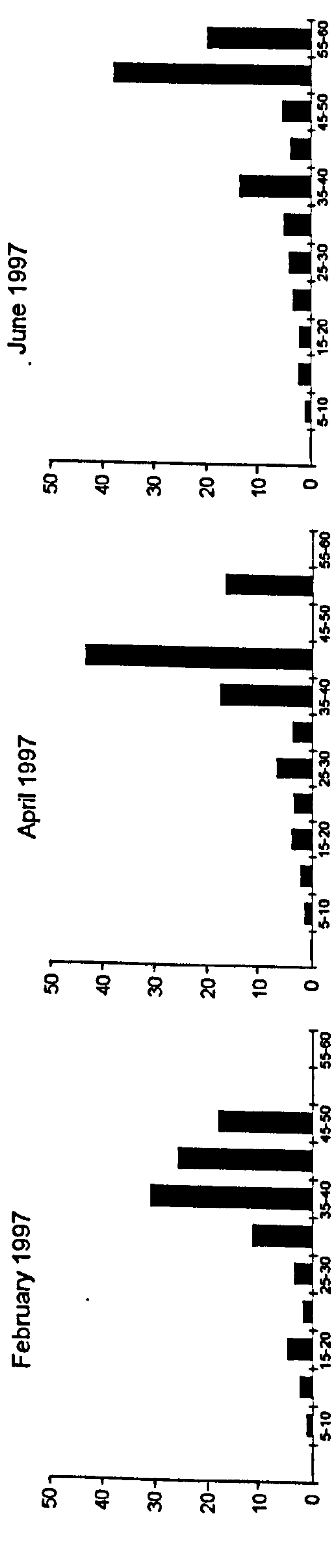
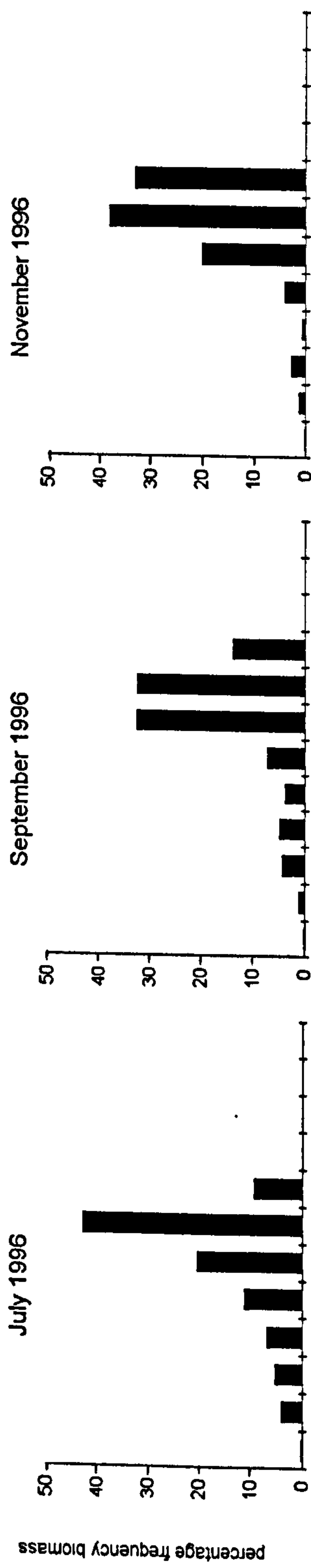
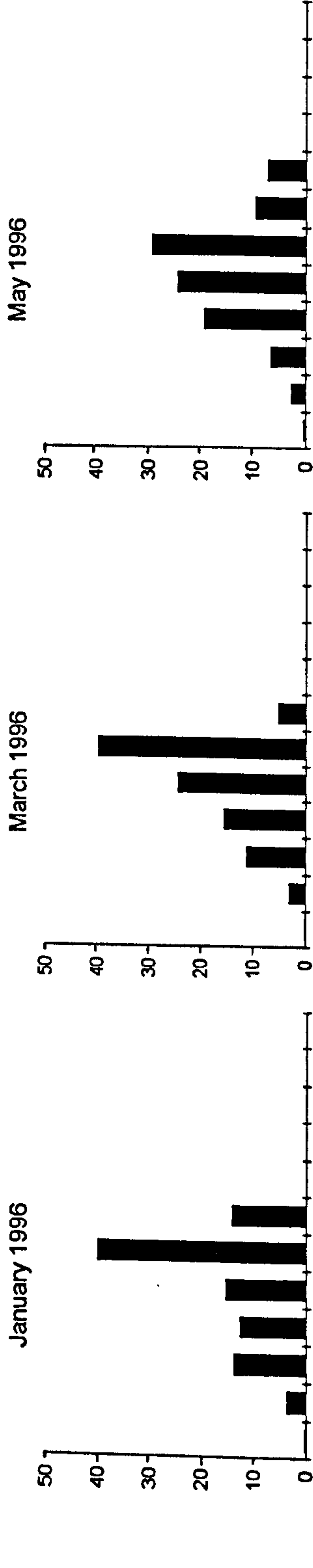


September 1997



shell length (mm)

Figure 2.11. The biomass frequency distributions of *Mytilus edulis* from the low shore Church Island.



shell length (mm)

size class consistently contained most individuals. At Church Island the smallest size classes were also the least important in terms of the distribution of surface area (Fig. 2.9). The pattern of distribution of surface area changed over the two-year sampling period, with the most important size class shifting from the middle to the largest sizes classes. This was the reverse of the pattern found at this site for the distribution of length-frequency over the same period. A clearer pattern emerged in the distribution of biomass at Aberffraw, with the middle to larger size classes forming the most important group (Fig. 2.10). Once again, however, there was no marked trend over the 18 month sampling period. The percentage frequency distribution of biomass at Church Island reflected that of surface area with the larger size classes becoming increasingly important over the sampling period (2.11).

2.3.2. Allometric relationships.

For both populations shell height, shell width, shell weight (Table 2.1) and flesh weight (Tables 2.2 & 2.3) were all highly correlated with shell length as indeed was flesh weight with shell width (Tables 2.4 & 2.5). Although none of the variables were independent, the high correlation between pairs of variables meant that it was viable to use simple linear regression to determine the relationships between them. Over the size range investigated, mussels from both sites differed from each other in several respects. In all three populations shell height was negatively allometric with respect to length (Table 2.1) indicating that mussels become proportionately more elongate with increased length. However, the regression slopes differed significantly between mussels from the high shore at Aberffraw and from the low shore at Church Island (general linear model, slopes: $F = 121.06$, d.f. = 590, $p < 0.001$) with mussels from Church Island having a significantly greater shell height than mussels of comparable length from the high shore at Aberffraw. No significant differences between the shell height-shell length relationships of mussels from the mid and high shore levels at Aberffraw were found (slopes: $F=0.11$, d.f. = 394, $p>0.05$; intercepts: $F=0.03$, d.f.=394, $p>0.05$). The shell width of mussels from the high shore at Aberffraw was positively allometric with respect to shell length, whilst this relationship

Table 2.1. Coefficients of allometry between various size variables of *Mytilus edulis* valve variables, together with a test for departure from isometry.

Dependent variable (y)	Independent variable (x)	Aberffraw high shore						Aberffraw mid shore						Church Island					
		a	b	r	t	p	n	a	b	r	t	p	n	a	b	r	t	p	n
Shell height	Shell length	-0.11	0.861	0.991	20.74	**	313	-0.11	0.857	0.995	15.12	**	82	-0.16	0.925	0.992	10.43	**	278
Shell width	Shell length	-0.43	1.050	0.989	5.67	**	313	-0.41	1.020	0.944	1.57	ns	82	-0.41	0.996	0.987	0.42	ns	278
Shell weight	Shell length	-4.38	3.150	0.989	5.58	**	312	-4.32	3.070	0.999	1.84	ns	82	-4.24	2.990	0.991	0.49	ns	278

a, b = coefficients of the log transformed allometric equation $\log y = a + b \cdot \log x$

r = product moment correlation coefficient

t = test statistic

** p < 0.01

ns = no significant difference

Table 2.2. Seasonal variation in flesh weight with shell length for monthly samples of *Mytilus edulis* from Church Island. The regression coefficients, a and b, are derived from the equation $\log y = a + b.\log x$ where y is dry tissue weight and x is shell length.

Month	Year	a	b	r	n
January	1996	-5.01	2.69	0.981	26
March		-4.95	2.78	0.997	30
May		-4.87	3.00	0.993	30
July		-5.11	3.12	0.990	29
September		-5.54	3.31	0.983	28
November	1997	-5.76	3.19	0.984	35
February		-5.34	2.80	0.984	35
April		-5.51	3.15	0.990	31
June		-5.44	3.17	0.991	34

Table 2.3. Seasonal variation in flesh weight with shell length for monthly samples of *Mytilus edulis* from the high shore, Aberffraw. The regression coefficients, a and b, are derived from the equation $\log y = a + b \cdot \log x$ where y is dry tissue weight and x is shell length. The relationships between dried flesh weight and shell length determined for *M.edulis* from the mid shore (MS) at Aberffraw in two months are also included.

Month	Year	a	b	r	n
January	1996	-5.32	2.93	0.985	26
March		-4.82	2.80	0.995	23
May		-4.94	2.86	0.998	27
July		-4.88	2.87	0.987	29
September		-5.29	3.07	0.992	30
November		-5.71	3.22	0.985	32
February	1997	-5.44	3.12	0.992	33
April		-5.09	2.80	0.993	36
June		-4.84	2.75	0.971	41
September		-5.20	3.10	0.996	35
February (MS)	1997	-5.22	2.93	0.988	40
July (MS)	1997	-5.03	2.89	0.992	42

Table 2.4. Seasonal variation in flesh weight with shell length for monthly samples of *Mytilus edulis* from Church Island. The regression coefficients, a and b, are derived from the equation $\log y = a + b.\log x$ where y is dry tissue weight and x is shell width.

Month	Year	a	b	r	n
January	1996	-3.89	2.74	0.989	26
March		-4.03	2.99	0.992	30
May		-3.71	3.07	0.995	30
July		-3.91	3.14	0.989	29
September		-4.11	3.17	0.990	28
November		-4.28	3.01	0.987	35
February	1997	-4.03	2.66	0.987	35
April		-4.09	3.07	0.987	31
June		-4.04	3.15	0.992	34

Table 2.5. Seasonal variation in flesh weight with shell length for monthly samples of *Mytilus edulis* from Aberffraw. The regression coefficients, a and b, are derived from the equation $\log y = a + b.\log x$ where y is dry tissue weight and x is shell width.

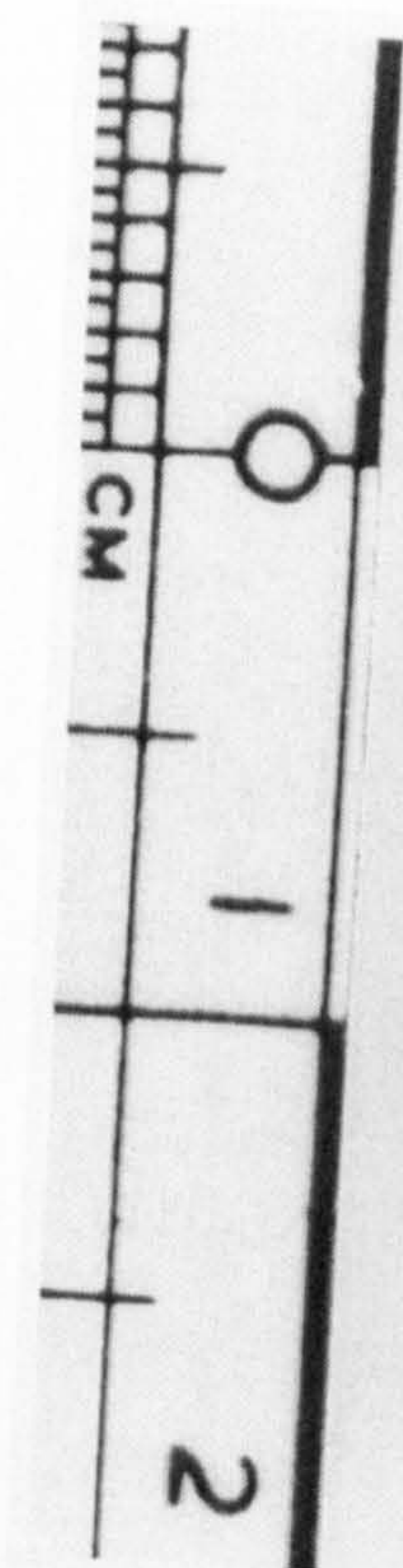
Month	Year	a	b	r	n
January	1996	-4.32	2.97	0.986	26
March		-3.72	2.64	0.992	23
May		-3.67	2.61	0.994	27
July		-3.79	2.87	0.988	29
September		-3.97	2.88	0.994	30
November		-4.26	2.87	0.990	32
February	1997	-4.08	2.87	0.982	33
April		-3.85	2.63	0.993	36
June		-3.64	2.52	0.992	41
September		-3.86	2.83	0.993	35

was one of isometry in mussels from both the mid shore Aberffraw and the low shore Church Island populations (Table 2.1). It was not surprising, therefore, to find that the regression slopes differed significantly between mussels from the high shore Aberffraw and the low shore Church Island ($F = 138.09$, d.f. = 590, $p < 0.001$) and approached significance between the tidal levels at Aberffraw (slopes: $F=2.98$, d.f. = 394, $p = 0.085$). Shell weight increased in a positively allometric fashion for mussels from the high shore at Aberffraw but was one of isometry for mid shore mussels from Aberffraw and low shore mussels from Church Island. Similarly Aberffraw mussels had significantly heavier shells than those of comparable length from Church Island (slopes: $F = 20.62$, d.f. = 589, $p < 0.001$) although no significant differences were found between the shell weight-shell length relationship in mussels from the two shore levels at Aberffraw (slopes: $F=1.88$, d.f.=390, $p>0.05$; intercepts: $F=0.65$, d.f. =390, $p>0.05$). Thus, as mussels from the high shore at Aberffraw increase in length they become relatively more elongate, wider and heavier than those from Church Island.

Differences were also observed in the external structure of the mussel; Church Island mussels tended to be smoother, less ridged and with a more acute angle at the posterior margins, as viewed dorsally, (Plate 1) than those from Aberffraw. Compared with Church Island mussels, those from Aberffraw were usually more heavily encrusted with barnacles and showed greater shell erosion, particularly around the umbo where the nacreous layer was often exposed (Plate 1).

Dried flesh weights varied significantly between the sampling months both at the high shore, Aberffraw site (slopes: $F= 5.38$, d.f. = 312, $p < 0.001$) and the low shore, Church Island site (slopes: $F = 6.57$, d.f. = 277, $p < 0.001$). The flesh weight-shell length regression equations are presented in Tables 2.2 & 2.3 and were used to predict the flesh weights of three standard size mussels, 7.5, 17.5 and 27.5mm shell length, in each of the sampling months. Figure 2.4B plots these predicted flesh weights against sampling months from which it can be seen that the differences were largely seasonal (Fig. 2.4B): flesh weight increased through the summer months and decreased through the winter. For the Church Island population the peak in flesh weight in May 1996 and the prior increase in flesh weight between February 1997 and April 1997 seems to correspond well with the large increase in the numbers within the smallest size

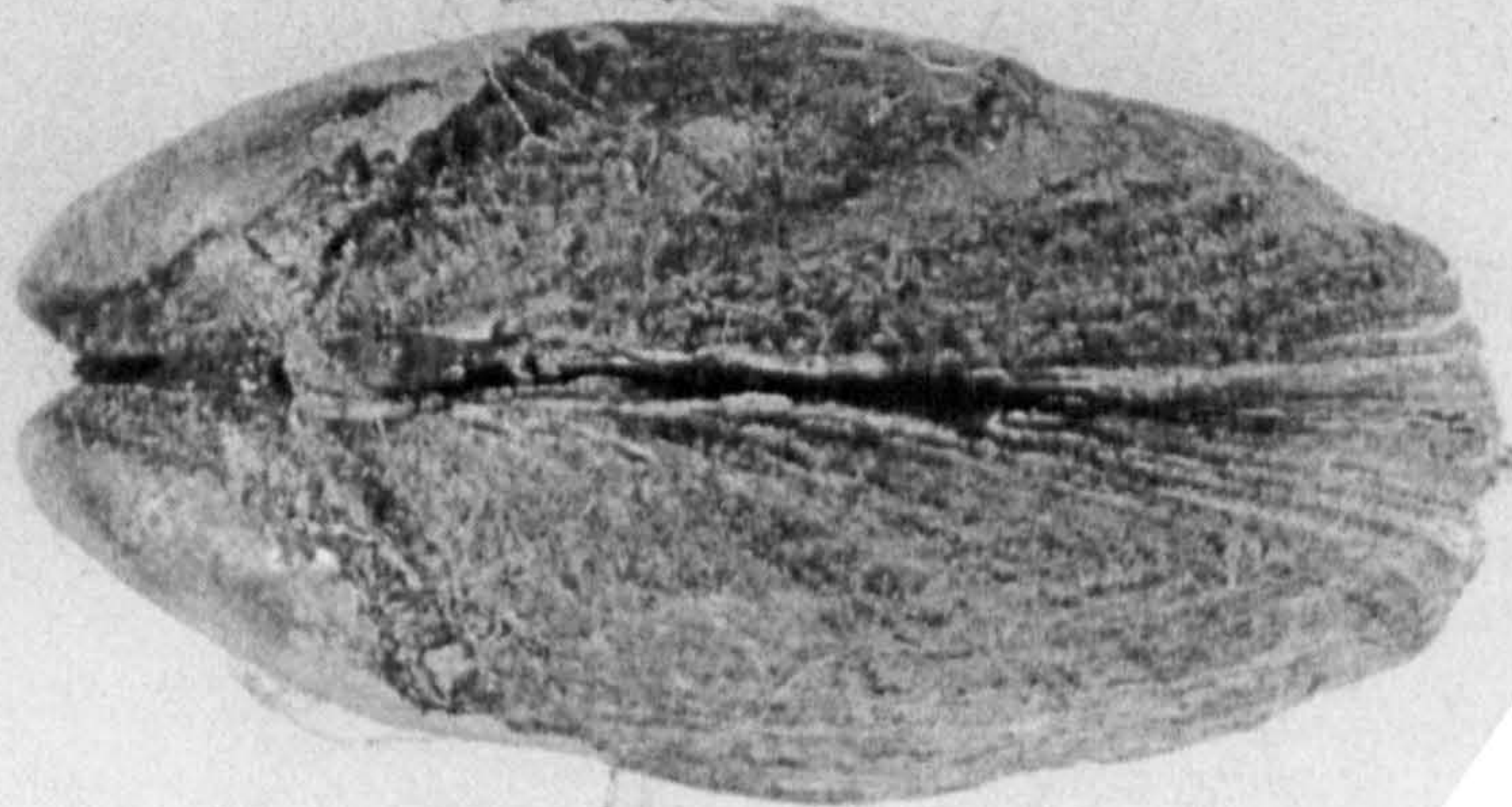
Plate 2.1. *Mytilus edulis* shells from the low shore at Church Island (A) and the high shore at Aberffraw (B).



A.



B.



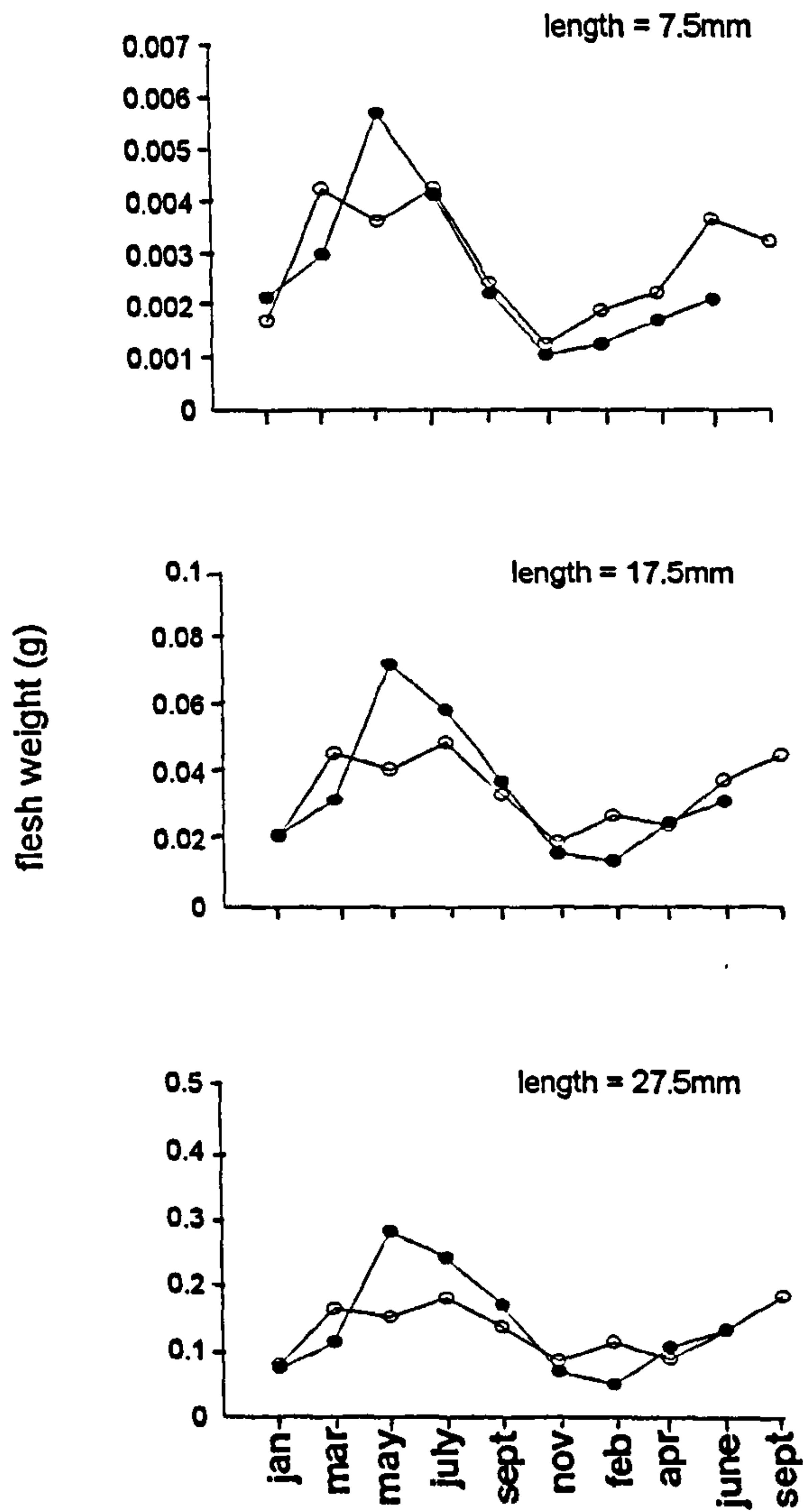
classes during those months (Fig. 2.6) and the observed change in population density (Fig. 2.4A). This was not observed in the Aberffraw population. When plotted against shell length, mussels from neither site contained consistently more flesh per unit length (2.12A). Using the shell width-shell length regression equation for mussels from the high shore, Aberffraw (Tables 2.4 & 2.5), the standard lengths were converted to standard widths; 3.1, 7.5 and 12.0mm. The flesh weight-shell width equations presented in Table 2.1 were subsequently used to predict the flesh weights for mussels of these widths from both Aberffraw and Church Island. It can be seen from Figure 2.12B that when flesh weight is plotted against shell width a more consistent relationship emerged with Church Island mussels tending to have a greater flesh weight than those of comparable size from Aberffraw. Since flesh weight varies seasonally, flesh weights were compared between mussels from the two tidal levels at Aberffraw for both February and June. Flesh weight did not differ significantly between shore levels in either February (slopes: $F=3.19$, d.f.=72, $p = 0.079$; intercepts: $F=2.15$, d.f.=72, $p>0.05$) or June (slopes: $F=3.57$, d.f.= 82, $p = 0.062$ intercepts: $F=3.64$, d.f. =82, $P>0.05$) although it can be seen that differences between the slopes did approach significance.

2.3.3. The shell strength of *Mytilus edulis*.

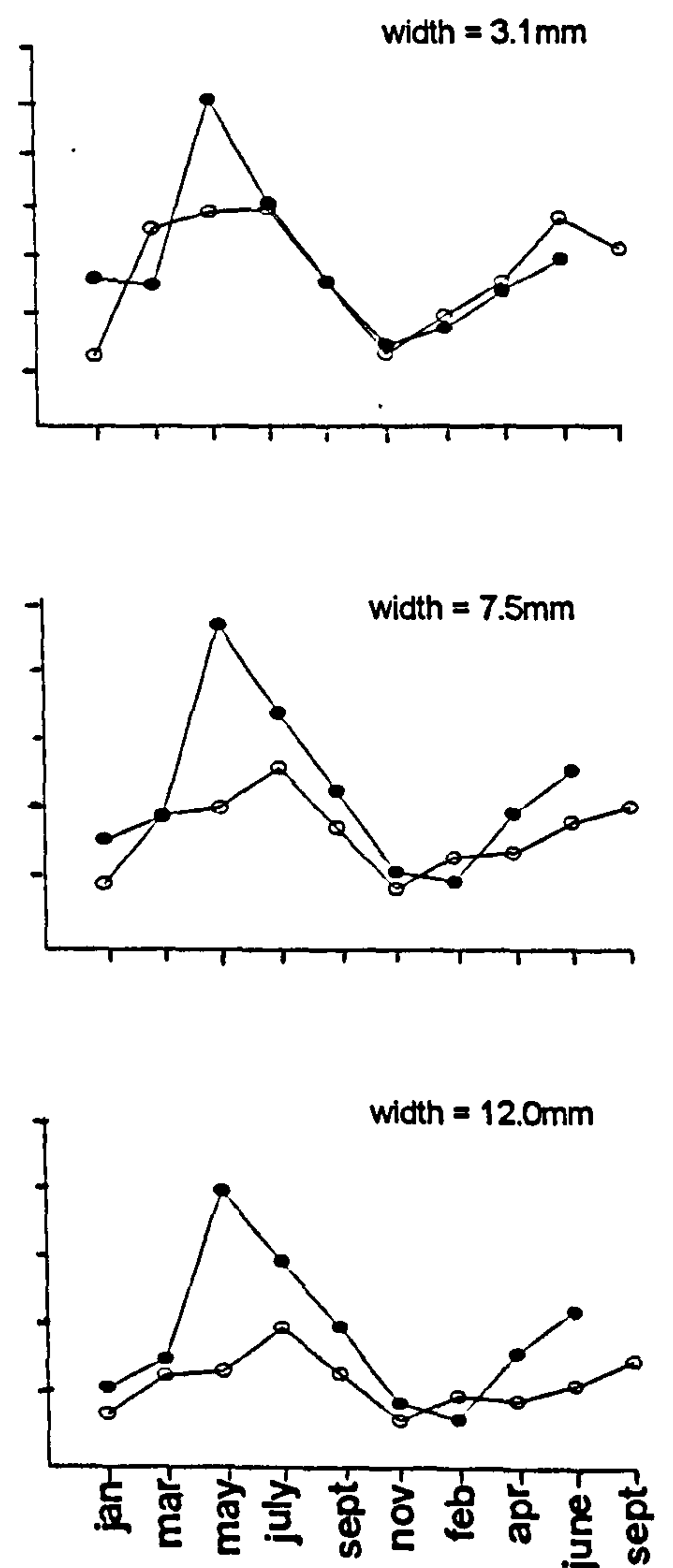
Shell strength increased exponentially with shell length quickly reaching the maximum 245 Newtons that could be recorded using this digital electronic force gauge, at around 25mm shell length. Data were linearised by log transformation of both the independent and dependent variables and shell strengths were highly correlated with shell lengths (Table 2.6). When minimum and maximum breaking strengths were compared there was generally no significant difference between the two over the size range investigated (Table 2.6). The exception to this was the sample taken from Church Island in November 1996 where the two slopes differed significantly (general linear model, $F = 5.67$, d.f. = 28, $p<0.05$). Both the breaking strength and the magnitude of the difference between the minimum and the maximum breaking strengths could be highly variable. The minimum breaking strength of one mussel shell could be

Figure 2.12. The predicted flesh weights of *Mytilus edulis* of three standard lengths; 7.5, 17.5 and 27.5mm (A) and three standard widths; 3.1, 7.5 and 12.0 mm (B), from the low shore at Church Island (closed circles) and from the high shore at Aberffraw (open circles).

A



B



month

Table 2.6. The relationships between minimum and maximum valve strength and shell length in *Mytilus edulis* as determined by least squares regression . Minimum and maximum valve strengths were compared using analysis of covariance (general linear model, MINITAB).

Site	Month	Minimum				Maximum				Slopes (b)		Intercepts (a)		
		a	b	r	n	a	b	r	n	F	p	F	p	
Aberffraw	HS	November	-1.82	2.82	0.907	35	-1.89	3.07	0.948	31	0.66	ns	0.04	ns
	HS	March	-1.08	3.09	0.888	27	-1.32	2.56	0.934	27	1.57	ns	3.08	ns
	HS	June	-1.84	2.80	0.864	35	-1.24	2.49	0.829	33	0.59	ns	1.33	ns
	MS	June	-1.10	2.22	0.791	40	-0.80	2.14	0.872	37	0.05	ns	0.44	ns
Church Island	LS	November	-0.62	2.75	0.915	30	-1.01	2.32	0.915	29	3.47	ns	5.67	*
	LS	March	-0.58	2.61	0.891	20	-0.79	2.09	0.931	20	1.76	ns	3.48	ns

HS = High Shore

MS = Mid Shore

LS = Low Shore

a, b = coefficients in the equation $\log y = a + b \cdot \log x$, where x= shell length and y = valve strength
* = $p < 0.05$

ns = no significant difference

similar to the maximum breaking strength of another of similar size, thus perhaps accounting for the non-significant results. Figure 2.13 uses data from mussels taken from Aberffraw in November to illustrate the variability in breaking strengths.

Comparisons between the months November and March at Church Island and November, March and July at Aberffraw revealed no significant differences between either the minimum or the maximum breaking strengths (Table 2.7). Data from November and March were therefore combined for each site and differences between the sites investigated. No significant difference was found between the minimum breaking strengths of mussels at either site, although a significant difference was found between the maximum breaking strength with mussels from Aberffraw having a relatively higher maximum breaking strength (Table 2.8). This difference was significant regardless of whether the maximum breaking strength was regressed on shell length or shell width, i.e. it was not simply a function of increased valve inflation in Aberffraw mussels conferring greater strength. Shell strength is usually measured using only one of the pair of valves of an individual mussel. Since it is equally likely that either valve would be the stronger of the pair the strength of the left valve was compared between the sites. No significant difference was found between the strength of the left valve for mussels from Aberffraw and Church Island nor were significant differences found between either the minimum or the maximum breaking strengths of mussels from the mid and high shore at Aberffraw (Table 2.8).

2.3.4. The strength of byssal attachment in Aberffraw and Church Island mussels.

Correlations between mussel length and attachment strength were significant for all samples except for hummocked mussels at Aberffraw (Table 2.9). Although all the correlations were positive, indicating an increase in attachment strength with shell length, measurements of attachment strength were highly variable over all mussel lengths (Fig. 2.14 A-F). These data did not meet the assumptions of the simple linear regression model in that both variables were dependent variables and the correlation between them was often low, consequently the raw data were analysed using the

Figure 2.13. The valve breaking strengths of *Mytilus edulis* from the low shore Aberffraw collected in November 1996. The minimum (open circle) and maximum (closed circle) valve strengths for each mussel are presented. Valve strengths in excess of the 245 Newtons which could be measured by the digital electronic gauge are represented by closed triangles.

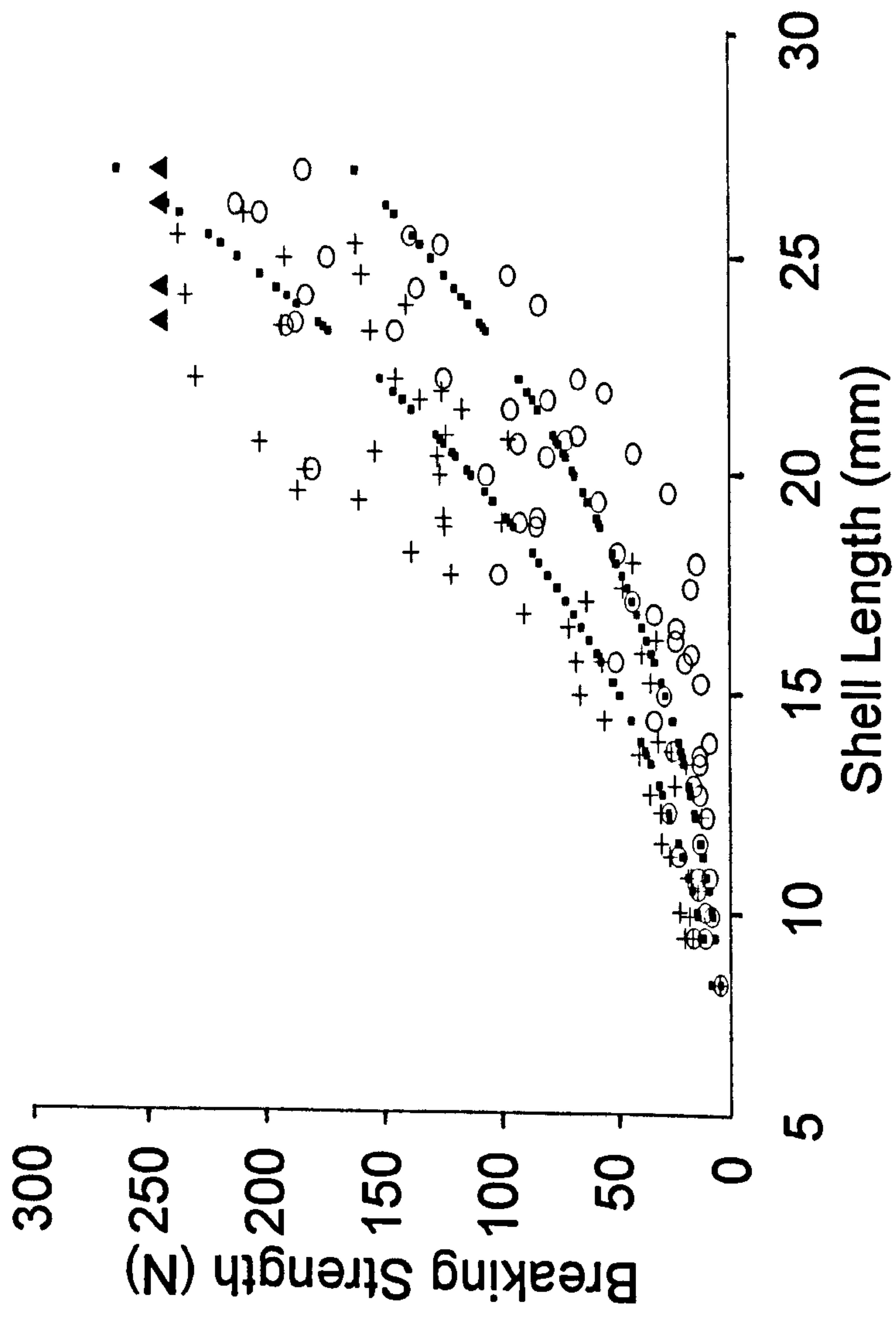


Table 2.7. Valve strengths are compared between months for *Mytilus edulis* from Aberffraw and Church Island using analysis of covariance (general linear model. MINITAB).

Site	Month	Dependent variable (y)	Independent variable (x)	Slopes (b)			Intercepts (a)		
				F	p	n	F	p	n
Aberffraw	November, March, June	Minimum	Shell length	0.20	ns	97	0.26	ns	97
	November, March, June	Maximum	Shell length	1.98	ns	91	1.66	ns	91
Church Island	November, March	Minimum	Shell length	1.10	ns	50	0.89	ns	50
	November, March	Maximum	Shell length	0.66	ns	49	0.41	ns	49

a, b = coefficients in the equation $\log y = a + b \cdot \log x$, where x = shell length and y = valve strength
ns = no significant difference
n = number of mussel valves used.

Table 2.8. Comparison of the strengths of *Mytilus edulis* shell valves between two sites (Aberffraw and Church Island) using analysis of covariance (general linear model, MINITAB). Comparisons are made between the minimum valve strengths, the maximum valve strengths and between the strengths of the left valves.

Sites		Dependent variable (y)	Independent variable (x)	Slopes (b)		Intercepts (a)	
				F	p	F	p
Aberffraw HS	Church Island LS	Minimum	Shell length	0.24	ns	0.21	ns
		Maximum	Shell length	9.63	**	-	-
Aberffraw HS	Church Island LS	Maximum	Shell width	10.75	**	-	-
Aberffraw HS	Church Island LS	Left Valve	Shell length	1.97	ns	1.72	ns
Aberffraw HS	Aberffraw MS	Minimum	Shell length	2.11	ns	2.09	ns
		Maximum	Shell length	0.93	ns	0.97	ns

HS = high shore

MS = mid shore

LS = low shore

a,b = coefficients in the equation $\log y = a + b.\log x$, where y is valve strength

** = $p < 0.01$

ns = no significant difference

n = number of mussel valves

Table 2.9. Slopes estimated by geometric mean regression with their 95% confidence intervals for the strength of byssus attachment against shell length along with a test for the significance of the correlation between these two variables.

Month	Site	Position in Patch	b	95% C.I.	n	r	p
April 1996	Church Island	Inside	0.9003	+/- 0.1792	50	0.731	**
		Edge	0.8826	+/- 0.2014	38	0.742	**
	Aberffraw	Inside	0.6582	+/- 0.1992	37	0.481	**
		Edge	0.7787	+/- 0.1793	43	0.684	**
November 1996	Aberffraw	Inside	0.5599	+/- 0.1741	40	0.345	*
		Hummock	0.0722	+/- 0.0505	10	0.512	ns
January 1997	Church Island	Inside	0.5350	+/- 0.1316	40	0.722	**

b = slope estimated by the geometric mean regression

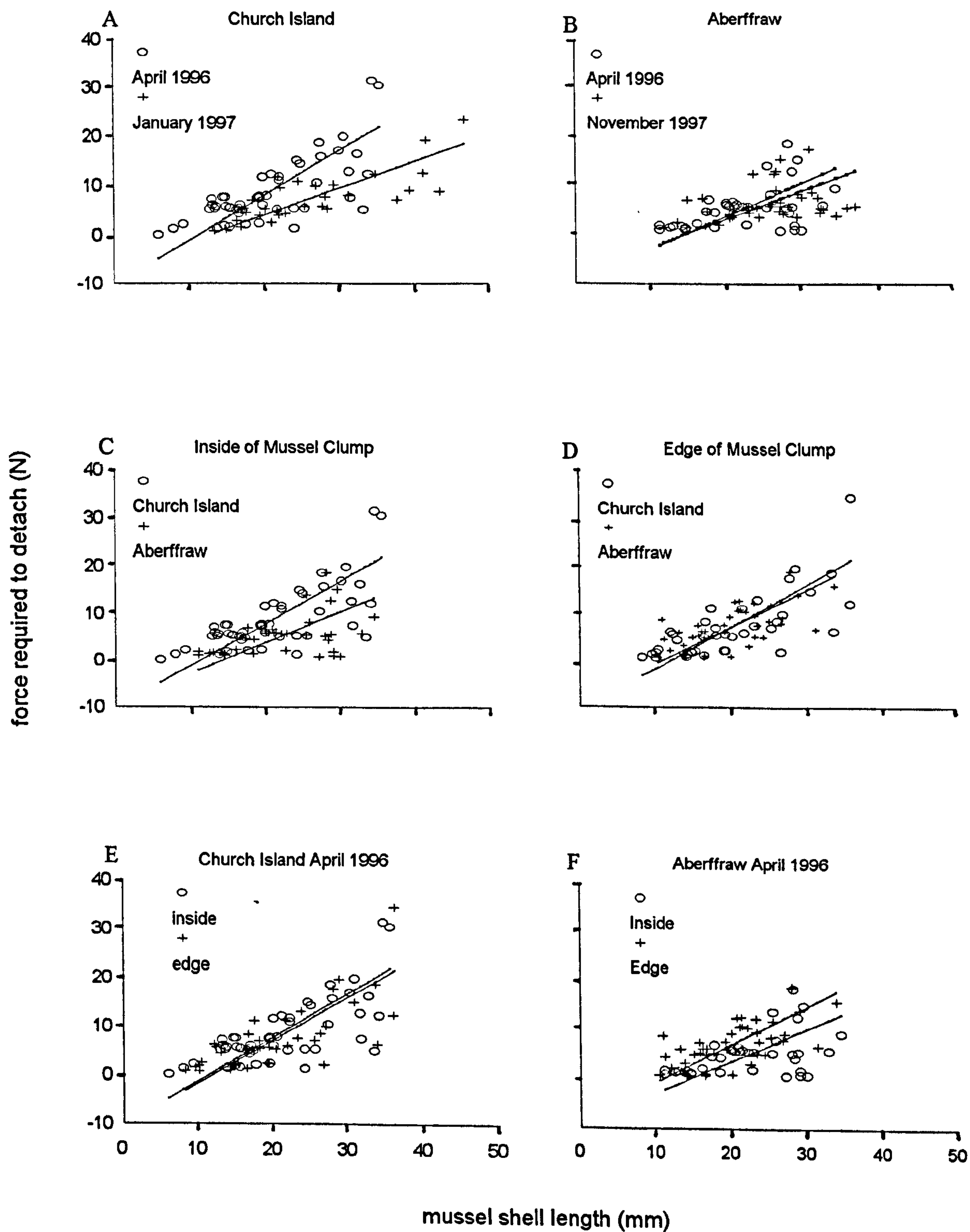
r = correlation coefficient

** = $p < 0.01$

* = $p < 0.05$

ns = not significant at $p > 0.05$

Figure 2.14. The relationship between *Mytilus edulis* byssal attachment strength and shell length. Comparisons of byssal attachment strength are made between months (A & B), between sites (C & D) and between positions within a mussel patch (E & F). Lines fitted to the data using geometric mean regression.



geometric mean regression model with 95% confidence intervals fitted to the slope.

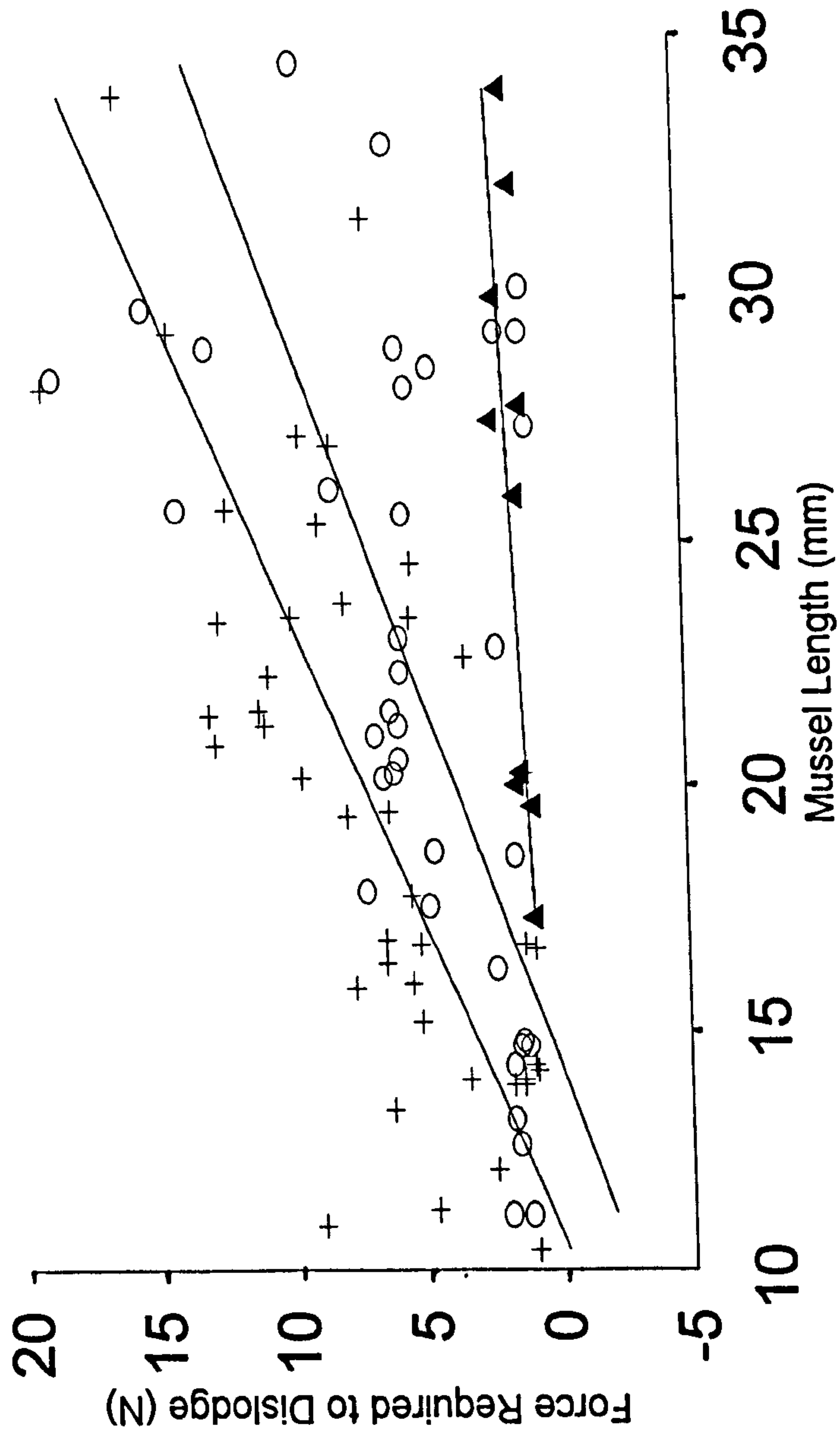
Seasonal differences in the attachment strength of mussels positioned in the inside of a patch were found at Church Island where mussels were more strongly attached in the spring (April 1996) than in winter (January 1997) (Fig. 2.14A, Table 2.9). No such seasonal difference was found for the mussel population at Aberffraw (2.14B, Table 2.9). No significant intersite differences in attachment strengths of mussels were detected in either April or in November and January for either mussels located centrally within a patch or mussels located on the edge of a patch (Figs. 2.14C & D, Table, 2.9).

No significant difference was found between the regression slopes of attachment strengths-shell length amongst mussels from the inside of a patch and those from the edge at Church Island during April (Fig. 2.14E, Table 2.9). Similarly no significant difference could be detected between the slopes of these two variables amongst Aberffraw mussels although mussels positioned at the edge appear to be consistently more strongly attached (Fig. 2.14 F): This was particularly noticeable amongst the larger sizes of mussel (2.15). The attachment strength of hummocked mussels at Aberffraw was consistently low with detachment never requiring in excess of 2.2 Newtons. In some cases this was an order of magnitude less than for non-hummocked mussels of a similar size occupying the inside or edge positions at this site. The attachment strength of hummocked mussels differed significantly from the attachment strength of non-hummocked mussels (Table 2.9). It appears therefore that mussels from Aberffraw are most strongly attached at the edge of a patch, less strongly attached in the centre of a patch and least strongly attached when they are hummocked (Fig. 2.15).

2.4. DISCUSSION

Differences in population density, population structure, shell morphology, biomass and attachment strength occurred between mussel populations at Church Island and Aberffraw as well as seasonally within each of these populations. The patterns that emerged from these populations generally reflect those reported in

Figure 2.15. The byssal attachment strength of *Mytilus edulis* from Aberffraw. Data from mussels located at the edge (pluses) and in the centre (open circles) of a patch are presented together with data from mussels that were hummocked (closed triangles). Lines fitted by geometric mean regression.



previous studies of *Mytilus edulis* (Seed, 1968; 1969; Witman and Suchanek, 1984) as well as in other mussel species such as *Mytilus californianus* (Fox and Coe, 1943; Kopp, 1979; Robles *et al.*, 1990), *Choromytilus meridionalis* (Griffiths, 1981), *Perna viridis* (Cheung and Tse, 1993) and *Septifer virgatus* (Richardson *et al.*, 1995).

Population densities oscillated at both Aberffraw and Church Island but whilst these variations seemed to follow a seasonal pattern at Church Island no such trend was observed at Aberffraw. This may be related to the tidal elevations from which these samples were taken. Mussels from Church Island were from the low shore and would therefore spend longer periods of time immersed than those mussels from the high shore at Aberffraw. Longer immersion times will facilitate recruitment, and settlement of *M. edulis* has previously been shown to be greater in the low shore levels than in the high shore levels (Seed, 1969). The clear seasonal increase in population density in July 1996 and June 1997 at Church Island probably reflects this, whilst the absence of any clear seasonal increases in density in the high shore population at Aberffraw probably reflects the more limited recruitment to this population. Interestingly a large increase in density was observed between February and June 1997 in the mid shore population at Aberffraw, which paralleled the increase in population density at Church Island at the same time but which contrasted with the lack of any marked change in the high shore Aberffraw population. Thus, the different emersion/immersion regimes that populations separated by only several metres live under, may affect their population dynamics. Furthermore, Seed (1969) found that periods of high settlement were often followed by periods of intense predation and this may explain the subsequent decrease in population density in September 1996, following the peak in July, within the Church Island population. In both the Church Island population and the mid shore population at Aberffraw increases in density coincided with increases in the relative importance of the smallest size class (<5mm shell length) supporting the proposal that mussels were indeed recruiting to these populations.

Together with the lack of seasonal trends in population density, the structure of the Aberffraw population remained relatively stable over the sampling period whereas at Church Island it changed quite dramatically. Most noticeably the largest

size of mussel occurring within the high shore Aberffraw population remained small (<35 mm shell length) whilst in the Church Island population there was a steady increase in the largest size of mussel occurring, from 20-25mm shell length in the initial sample to 55- 60 mm shell length two years later. Previous studies have shown that mussels from high tidal levels which spend relatively little time immersed suffer reduced growth rates (Seed and Suchanek, 1992) which in turn generally results in smaller maximum shell length than amongst mussels from low tidal populations (Seed, 1968; Kopp, 1979; Griffiths, 1981, Robles *et al.*, 1990). This may have important consequences for predators of mussels, many of which are size selective (see Elner and Hughes, 1978; Meire, 1992). Moreover in predatory crabs such as *Carcinus maenas* (Elner, 1978) and *Necora* (= *Liocarcinus*) *puber* (ap Rheinallt and Hughes, 1985) an upper limit to the size of mussel that can be consumed often exists, and this may be set by mechanical constraints such as crab strength and chelal gape. In both Church Island and Aberffraw populations the distribution of mussel biomass is concentrated in the larger size classes of mussels which, if too large to be opened by a predatory crab, could effectively reduce the value of such a population to the predator.

Seed (1968) showed that ontogenetic shifts occurred in the shell morphology of *Mytilus edulis*. Amongst larger mussels, the rate of increase in shell height compared to that in shell length decreased whilst shell width increased with respect to shell length such that older mussels are relatively more elongate and wider than younger mussels. Since allometry investigates the rate of increase in one variable relative to that of another variable and since within any one mussel population the length of a mussel can be assumed to be related to age, then the allometric equations relating shell variables to length can provide information about these ontogenetic shifts in mussel shape. The negative allometric relationship between shell height and shell length reported in all three populations in this study indicates that larger, older mussels are relatively more elongate than smaller, younger individuals. The positively allometric shell width-shell length relationship in mussels from the high shore at Aberffraw indicates that these mussels become relatively wider as they increase in size. Differences were reported in the relationships between pairs of shell variables depending on where the mussels had been collected. Mussels from the high shore at Aberffraw were significantly more

elongate and wider than those of a similar length from the low shore at Church Island and such differences have previously been recorded in *M. edulis* between tidal levels (Seed, 1968) as well as for other mussel species (Kopp, 1979; Cheung and Tse, 1993).

Although in any one population shell length may be related to age, mussels of the same length living under different environmental conditions may be quite different in their age. Many studies have found that the rate of growth of high shore mussels is slower than those from the low shore (Seed, 1968; Griffiths, 1981; Richardson *et al.*, 1995) and mussels of the same size from the low shore as mussels from the high shore are likely to be younger. It is likely therefore, that mussels from Church Island are younger and therefore do not exhibit the ontogenetic shifts in shell shape to the same extent as those from the high shore at Aberffraw. Indeed, the smooth shell structure of Church Island mussels and the ridged, abraded structure of Aberffraw mussels are respectively typical of fast and slow growing mussels (Seed, 1968). The relationship between shell weight and shell length mirrored that between shell width and shell length with mussels from the high shore at Aberffraw being significantly heavier than those of comparable length from the low shore at Church Island. Similar tidal differences have previously been recorded in *M. edulis* (Seed, 1968), *Mytilus californianus* (Kopp, 1979) *Choromytilus meridionalis* (Griffiths, 1981) and *Septifer virgatus* (Richardson *et al.*, 1995).

It had been expected that *Mytilus edulis* from the high shore at Aberffraw would contain proportionately less flesh than mussels of a similar size from Church Island, reflecting the findings of previous studies (Seed, 1973). However, whilst this was sometimes true, it was not consistently the case, especially for the smallest standard size of mussel looked at (7.5mm length). The relationships between flesh weights and widths, however, indicated that this was in part due to the greater shell width of Aberffraw mussels, which presumably increased the internal volume of the shell, thus accommodating a greater amount of flesh within the valves. Although flesh weights oscillated with month in mussels from both Aberffraw and from Church Island, oscillations in the mussels from Church Island were greater and appeared to mirror the increase in population densities. In previous studies on *Mytilus edulis chilensis* (Gray, 1997) and *P. viridis* (Cheung and Tse, 1993) such flesh weight increases have been

associated with increases in gonad size. The dramatic decrease in flesh weight in May 1996 and the subsequent increase in numbers in July 1996 may therefore be attributable to gamete release and recruitment to the population. Cheung and Tse (1993) found that in *Perna viridis* increases in gonad weight was greater in mussels from the lower shore and this may explain why such clear seasonal oscillations occurred in the low shore population at Church Island.

Shell thickness and the degree of valve inflation have both been shown to be important factors in determining shell strength in hard-shelled molluscs, with greater shell thickness and inflation conferring increased strength (Blundon and Kennedy, 1982b; Boulding, 1984). For this reason the wider and heavier mussel shells from Aberffraw were expected to be relatively stronger than the narrower shells of mussels from Church Island. However, although there was indeed a significant difference between the maximum breaking strengths, no such differences were found between the minimum valve strength, which is arguably more important in terms of the vulnerability of these prey. There may be several reasons for this disparity. Seed (1968) demonstrated that *Mytilus edulis* from the high shore had a slower growth rate than those from low tidal levels, therefore in the high shore, mussels will be relatively older than those of a comparable length in the low shore. These mussels will therefore have been exposed for a longer period of time to shell weakening factors such as failed predation attempts and environmental abrasion. This conclusion is supported by the observation that mussels from the high shore at Aberffraw exhibited areas of exposed nacre indicative of severe abrasion, whereas mussels from Church Island did not. In effect the strength enhancing features of the Aberffraw shells may be negated by their longer exposure to environmental abrasion. It is therefore proposed that the maximum valve strength is more representative of the potential strength of a valve whilst the minimum strength reflects the realised strength. More important than the intersite differences in shell strength is the high degree of variability in the shell strengths of similar sized mussels within a particular population. The minimum force required to break one mussel shell, for example, could be the same as the maximum force required to break a shell of similar size and whilst larger mussels generally have stronger shells this is not always the case. This implies that predators foraging on mussels probably

cannot rely on shell length alone as a measure of prey vulnerability.

Although there was a positive correlation between byssal attachment strength and shell length, this was, like shell strength, highly variable amongst mussels of similar size from the same population. This has also been a feature of previous studies of *Mytilus edulis* attachment strength (Harger, 1970; Witman and Suchanek, 1984). Given that byssal threads are produced in direct response to variations in a range of environmental conditions which include water temperature (Van Winkle, 1970; Allen *et al.*, 1976; Young, 1985), water flow (Van Winkle, 1970, Young, 1985, Dolmer and Svane, 1994) and salinity (Van Winkle, 1970; Allen *et al.*, 1976), such variability in attachment strength is perhaps not surprising. Furthermore, when the attachment strength of isolated mussels is measured there is a positive correlation between length and attachment strength (Harger, 1970); since clumped mussels are not only attached by their own byssal threads but also by those of their neighbours it can be assumed that the strength of attachment of a mussel located within a patch will also be influenced by the size of the surrounding mussels (Witman and Suchanek, 1984).

The seasonal variation in attachment strength of Church Island mussels is consistent with previous findings for *Mytilus edulis* at other sites. Both Price (1982) and Young (1985) found that attachment strength increased through the spring into the summer months following cycles of environmental factors such as wind speed and temperature. No comparable seasonal pattern was demonstrated amongst the Aberffraw mussels, probably reflecting either the greater variation in attachment strengths of these mussels, or the effects of other factors which might mask a seasonal trend. Aberffraw mussels, for example, experience longer emersion periods which would not only create greater metabolic stress but also restrict the time available for the secretion of byssus threads.

Whilst it might have been anticipated that attachment strength would be greater for mussels within a patch than for those at the patch periphery, since the more centrally placed mussels will be surrounded by many other mussels all of which could attach to the individual and thus enhance its attachment strength, this was not found either in this study or in a previous study on *Mytilus edulis* carried out by Witman and Suchanek (1984). Although surrounding mussels may indeed increase the degree of

attachment, the effect of close grouping and the growth of centrally placed mussels within a limited space will generally result in hummocking (Seed, 1969; Bertness and Grosholz, 1985) whereby the centrally placed mussels are forced upwards away from the substratum thus significantly weakening their attachment. Hummocked mussels at Aberffraw were significantly more weakly attached than mussels from the edge of a patch and those non-hummocked mussels from the inside of a patch. This conclusion is further supported by the absence of any difference between centrally and peripherally positioned mussels at Church Island where the mussel bed appeared to be monolayered.

The lack of significant differences in the strength of mussel attachment between the sites was somewhat surprising given that previous studies have shown attachment strength of mussels increases with wave-exposure presumably as a response to increased physical impact (Harger, 1970; Witman and Suchanek, 1984). However, whilst mussels at Aberffraw are exposed to strong wave action, the mussels at Church Island live in a strong tidal flow; these two different forms of water movement could have the same end effect on the strength of attachment since mussels from both populations would need to be strongly attached to retain their position.

This study has demonstrated the highly plastic nature of *Mytilus edulis*. All the variables investigated altered in some way either geographically or temporally. In addition a high degree of variability between individual mussels within a population emerged. These factors should be considered when studies are carried out into the nature of a mussel population especially with regard to laboratory experiments in which *M. edulis* is used as a prey species, since intraspecific differences could alter foraging behaviour and thus the conclusions drawn from foraging experiments.

2.5. SUMMARY

- The density of mussels in both the high shore population at Aberffraw and the low shore population at Church Island oscillated over the sampling period, but whilst there was a clear seasonal trend to these oscillations in the population densities at Church Island, no such trend was observed in the high shore Aberffraw population. There were

significant temporal variations in the dried flesh weights of mussels from both populations. Like population density, there were clear seasonal variations in the flesh weights of mussels from Church Island, but no clear pattern to the variations in flesh weight in mussels from the low shore Aberffraw.

- Flesh weights differed between the two populations but were not consistently greater in mussels of comparable size from either the high shore Aberffraw or from the low shore at Church Island.

- The allometric relationships between shell variables revealed ontogenetic shifts in shell morphology; larger (= older) mussels from both the high shore at Aberffraw and the low shore at Church Island were relatively more elongate than smaller mussels within these populations. Mussels from the high shore Aberffraw also became proportionately wider as they increased in shell length.

- The morphology of *Mytilus edulis* differed significantly between the two sites. Mussels from the high shore at Aberffraw were significantly wider and more elongate than mussels of comparable size from the low shore at Church Island. Mussels from the high shore at Aberffraw also had significantly heavier shells than similar sized individuals from Church Island.

- The significantly heavier and more inflated valves of Aberffraw mussels were expected to be stronger than the narrower, lighter valves of Church Island mussels. Although significant differences did exist between the maximum valve strengths no differences were found between the minimum valve strengths which reflect the “realised” strength, i.e. the weakest force required to break a valve. Although valve strength was positively correlated to shell length it was highly variable amongst mussels of similar sizes.

- No intersite differences were found in byssal attachment strength. Seasonal differences in attachment strength were found in the Church Island population whilst

significant differences corresponding with the position of a mussel in a clump were found in the Aberffraw mussel population; centrally placed, hummocked mussels were more weakly attached than non-hummocked mussels. Like shell strength, byssal attachment was positively correlated to shell length but was highly variable between mussels of similar sizes.

CHAPTER 3.

CHELAL MORPHOLOGY AND NATURAL DIET OF *CARCINUS MAENAS*.

3.1. INTRODUCTION

The decapod crustacean, *Carcinus meanas*, is a native European Atlantic brachyuran crab. It also occurs around the coast of North America, South Africa and Australia where its presence is thought to be the result of accidental introduction (Elner, 1981; Cohen *et al.*, 1995), probably through the discharge of ballast water (Cohen *et al.*, 1995). *C.maenas* is a member of the family Portunidae, the swimming crabs, and like other members of this family its fifth pair of pereopods (legs) have dorso-ventrally flattened dactyli, which act like paddles and form the “swimming legs”. These are not as well developed in *C.maenas* as in other portunid species but are still characteristic of the family. The first pair of pereopods are modified to form the chelae (claws).

Carcinus maenas has a hard calcified exoskeleton. This has a protective function and provides a site for internal muscle attachment but means that growth has to occur through a series of moults. This is the process by which a new exoskeleton is grown under the old which is subsequently shed through breakage along predetermined lines of weakness (Warner, 1982). The new exoskeleton is initially soft, although the hardening process begins immediately, and is inflated by water to increase body size. Prepubertal moults can be rapid but moulting slows down after the onset of reproductive maturity at around 30mm carapace width (Ingle, 1980). Males and females are essentially similar in appearance but can be distinguished by differences in the number and shape of the abdominal segments. Female *C.maenas* have six abdominal segments which are quite wide and rounded whilst males have five segments which are narrow and triangular in shape. Sexual dimorphism also occurs in the size, but not structure, of the chelae (Lee and Seed, 1992) and females tend to be less

aggressive (Crothers, 1967). *C.maenas* is capable of autotomising limbs and regenerating new ones (Crothers, 1967; Ingle, 1980), evasive autotomisation may occur as an escape mechanism from predators (Crothers, 1967) and occurs along predetermined lines. When this occurs, a limb bud is formed and regrowth begins immediately. Although regeneration has its advantages, it also means that energy is diverted away from normal growth which results in a smaller than predicted individual at the subsequent moult (Juanes and Hartwick, 1990 and references therein).

Carcinus maenas exhibits a variety of exoskeletal colours as an adult which range from green, through orange to red. A pattern in the progression of this coloration is apparent in males, but not in females (see Reid *et al.*, 1997). Immediately after moulting male crabs are green in colour, the red colour developing throughout the intermoult period, showing itself first at the arthrodial membranes, between the joints. The red coloration is thought to result from the breakdown of pigments in the exoskeleton (Reid *et al.*, 1997). Studies into the intraspecific differences between green and red crabs have shown that they differ from one another physiologically; red crabs are less oxy- and osmo-tolerant than green crabs (Reid *et al.*, 1989; Reid and Aldrich, 1989), they also have greater chelal strength and are more aggressive (Kaiser *et al.*, 1990).

Around the British Isles, *Carcinus maenas* is a common and ubiquitous species. It is found from the eulittoral zone down to depths of 60 metres (Ingle, 1980), can survive in salinities ranging from 4‰ to 34‰ (Crothers, 1967) and thus is found in estuaries as well as fully saline habitats. Its distribution is dependent on age, sex, moult stage and season (Crothers, 1968; Atkinson and Parsons, 1973; Hunter and Naylor, 1993; Warman *et al.*, 1993). A *C.maenas* population can be broadly divided into three groups. The first group comprises juveniles of less than 30 mm carapace width which tend to remain permanently on the shore at all states of the tide (Hunter and Naylor, 1993; Warman *et al.*, 1993). The second group of crabs are those which migrate with the tide, foraging on the flood tide and retreating on the ebb (Hunter and Naylor, 1993). Medium sized green male and female crabs migrate from the midshore to the top of the shore whilst larger male crabs of both red and green forms migrate onto the lower shore from the subtidal, these migrations start in spring and cease in the autumn

months (Atkinson and Parsons, 1973). Within this group there appears to be a strong sexual bias towards males (Hunter and Naylor, 1993; Warman *et al.*, 1993). The third group consists mainly of red crabs which remain permanently below the low water mark (Warman *et al.*, 1993).

Crabs have the potential to influence greatly the community structure (Ebling *et al.*, 1964; Jensen and Jensen, 1985; Sanchez-Salazar *et al.*, 1987a; Seed, 1990a), morphology (Vermeij, 1977) and life history tactics (Seed and Brown, 1978) of their prey species with consequences for population, community and evolutionary ecology. The chelae are the primary feeding appendages and their morphology and strength, coupled with the behaviour and distribution of the predator and prey populations, will determine inter- and intra- specific prey vulnerability. The determination of prey vulnerability and the mechanisms underlying this is an area of great importance and has been the subject of much research (e.g. Elner and Hughes, 1978; Hughes and Seed, 1981; Jubb *et al.*, 1983). Clear relationships have been demonstrated between claw and prey types, with aspects of the chelal morphology determining both upper and lower limits to prey size boundaries, dexterity, strength and speed (Brown *et al.*, 1979; ap Rheinallt and Hughes, 1985). Additionally, recent research has shown that prey type can also influence crab chelal morphology. Smith and Palmer (1994) working on the crab *Cancer productus*, for example, found that those individuals reared experimentally on hard-shelled prey developed larger and stronger claws than those raised on nutritionally identical but unshelled prey.

The active predatory lifestyle of the crab *Carcinus maenas* suggests that this crab may play an important role in structuring coastal and estuarine communities. Many experiments have been undertaken to determine the vulnerability of various prey species to this predator. These experiments have often been carried out using bivalve prey, in particular *Mytilus edulis* (e.g. Elner and Hughes, 1978; Jubb *et al.*, 1983; Cunningham and Hughes, 1984; Ameyaw-Akumfi and Hughes, 1987). There are good reasons for this since bivalve prey occur in discrete and easily measurable sizes, components of the predator's handling time are easy to discern and the amount of prey consumed can be quickly recorded (Micheli, 1995). Results from such experiments have provided valuable information as to how *C. maenas* chooses and handles its prey

but this decapod/bivalve, predator/prey system may not be representative of what actually occurs in the field. For example, Choy (1986) working on the portunid, *Necora puber* found that whilst in the laboratory this crab would readily eat *M. edulis* but would only eat algae after a prolonged period of starvation, results from gut content analyses of crabs taken from the field demonstrated that algae were, in fact, the predominant natural food type of this crab. Determination that the prey species used in laboratory feeding experiments is important to the predator's natural diet is therefore necessary if conclusions drawn from laboratory feeding experiments are to be extended to the field situation.

The aim of this chapter is to document the chelal morphology of *Carcinus maenas* and the relationship between this and the natural diet of the crab. Particular attention is paid to intraspecific differences arising from gender, size and colour. The *C. maenas* population was sampled at Church Island and Aberffraw to establish co-occurrence with the *Mytilus edulis* populations at these sites, and the contribution of *M. edulis* to the diet of *C. maenas* investigated. This was done to establish the validity of doing foraging experiments using this predator species and mussels from these two sites.

3.2. MATERIALS AND METHODS

3.2.1. Description of the chelal morphometrics of *Carcinus maenas*.

Naive *Carcinus maenas* were caught off Traeth Melynog in February 1995 by trawling with a 2-metre beam trawl for 15mins. Traeth Melynog is a south-facing sandy bay off the south west of Anglesey (see Chapter 2, Fig. 2.1) and it was from here that experimental crabs were collected (see Chapters 4, 5, & 7). All crabs were returned to the laboratory and frozen until required. The sex and the handedness, i.e. which chela was the major chela, of each crab was recorded. The geometry of the major and minor chela was recorded and the carapace width (maximum distance between the distal teeth) and the maximum chelal height (cross-sectional dimension) of the major and minor chelae were measured to the nearest 0.1mm using vernier calipers.

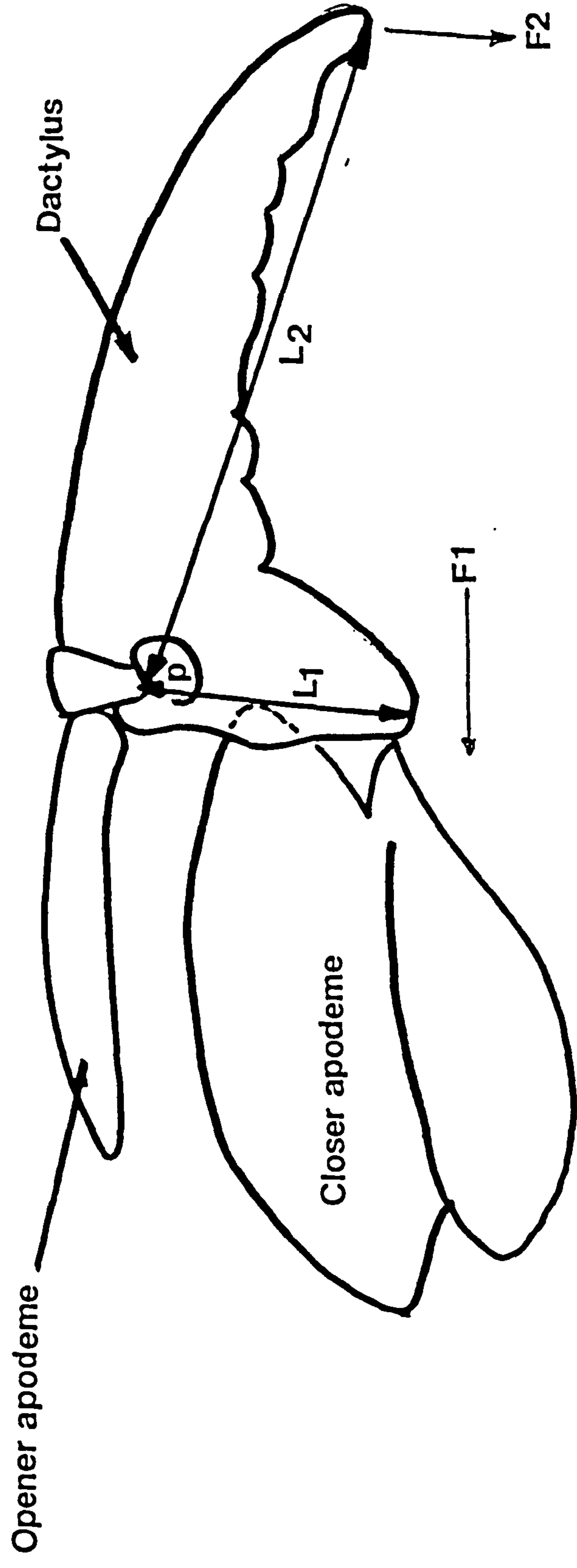
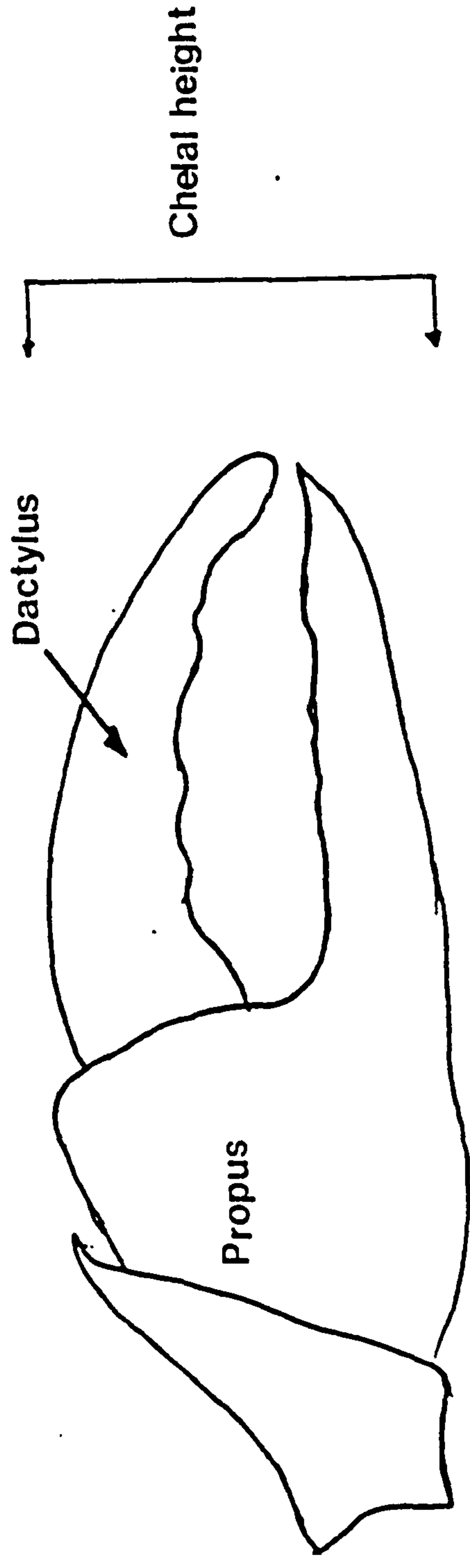
The crushing power of a crab's claw is in part dependent on the magnitude of force initially produced by the closer muscle located within the propus. This muscle is attached to the closer apodeme plate the area of which can be correlated to the force produced (Warner *et al.*, 1982) and can therefore be used to investigate intraspecific differences in chelal strength. The closer apodeme plates were dissected out from the propus (Fig. 3.1) of 31 larger males (CW > 40 mm), 9 small males (CW < 40 mm) and 19 female crabs. Major and minor apodeme plates were dried and attached to a blank 35 mm slide and projected onto a sheet of acetate on which their outline could be traced. A second slide on which there was a grid divided into 1 mm squares was then superimposed on top of the outline and the number of 1 mm squares contained within the outline were counted allowing the area of the apodeme plate to be computed. The large males were subdivided into red and green individuals, an individual was considered to be green if there was no discoloration of the arthrodial membranes, whilst an individual was considered to be red if both the arthrodial membranes and the exoskeleton had become red in colour.

The relationships between chelal height, closer apodeme plate area and carapace width (CW) were examined by fitting pairs of variables to the allometric equation, $y = Ax^b$, which upon log transformation becomes $\log y = a + b \cdot \log x$, using least squares regression as described for *Mytilus edulis* in Chapter 2, section 2.2.2. Departure from isometry was tested using the Student's t-test. Regression equations were compared to one another using analysis of covariance (general linear model, MINITAB) to investigate intraspecific differences in the relationship between pairs of variables.

3.2.2. Mechanical advantage.

The force that a chela can exert is not only dependent on the strength of the initial force produced within the chela but also on the way that this is modified by the crab's chelal lever system. The initial force (F1) is dependent on the type and mass of the closer muscle - related to the apodeme area (Warner and Jones, 1976; Vermeij, 1977; Warner *et al.*, 1982). Modification of the initial force occurs through the crab's

Figure 3.1. Diagram of a chela showing the various morphometric features measured. The lengths L_1 and L_2 are used to calculate the mechanical advantage, p is the pivotal point. Arrows denote the directions through which the forces F_1 and F_2 act.



chelal lever system such that force F_2 will be the actual force produced at the chelal tip (Fig. 3.1). The effect of this lever system is described by the ratio of the lengths L_1 to L_2 (Fig. 3.1) where L_1 equals the distance from the pivotal point to the point of insertion of the closer apodeme plate and L_2 is the distance from the pivotal point and the tip of the dactylus. This ratio is the mechanical advantage (MA) produced at the chelal tip which is correlated to F_2 and can therefore be used as a measure of the force exerted. Mechanical advantage will alter with changes in the proportions of dactylus length and chelal height. A high mechanical advantage denotes a strong but slow-acting claw whereas a low mechanical advantage indicates a fast but weaker chela.

The mechanical advantages of the major and minor chelae were calculated by measuring the lengths L_1 and L_2 to the nearest 0.1mm using vernier calipers. The mechanical advantages were determined in 31 large males (>40mm CW), 19 females and 9 small male (<40mm CW) crabs. The large males were further subdivided into red and green individuals. Mechanical advantages were compared between major and minor chelae as well as between gender, size and colour using the non parametric Mann-Whitney U test.

3.2.3. The natural diet of *Carcinus maenas*.

The *Carcinus maenas* populations at Church Island and Aberffraw were sampled bimonthly from January 1996 until July 1997. At each site two baited traps were put down at each of three tidal levels. The lowest pair of traps at Church Island and the highest pair at Aberffraw were placed adjacent to, but not on, the local mussel bed. The bait (Mackerel) was placed in small plastic drinks bottles which had six rows of holes pierced down the sides. In this way crabs would be attracted to the smell of the bait but they would not be able to eat it. Crabs caught in the traps were collected at low tide on two consecutive tidal cycles, returned to the laboratory and frozen until analysed. Maximum carapace width and the height of major and minor chela were measured to the nearest 0.1mm using vernier calipers and the relationship between these variables determined using regression analysis. The regression lines were subsequently compared with those from crabs caught at Traeth Melynog using analysis

of covariance (general linear model, MINITAB). This was done to determine whether or not any major differences between chelal morphology occurred between the crab population from which experimental crabs were drawn from and the crab populations at the sites where the mussels occurred. The sex, handedness and colour of the crabs were also recorded. Crabs were categorised as being green, orange or red in colour, orange crabs being defined as those with red arthrodial membranes but with some green exoskeleton coloration. The carapace was gently pulled away from the crab's body to reveal the foregut which could then be removed intact. The foregut was then cut open and the stomach contents washed out into a Petri dish with distilled water before being examined under a dissecting microscope. Organisms were identified mainly from recognisable hard parts which were left undigested in the gut. Diet was analysed using the percentage occurrence method previously described by Williams (1981). This method simply records the rate of inclusion of a particular prey item in the diet of a predator population and is calculated using the following equation.

$$\text{Percentage occurrence for the } i\text{th prey type} = (a_i / n) \times 100$$

where a_i is the number of crabs whose gastric mills contained prey type i and n is the number of crabs in the sample (excluding those with empty stomachs). Prey items were categorised into broad taxonomic groups, except where a particular prey item occurred in high abundance. The rate of inclusion animals, algae and plants and molluscs were also separately calculated. Differences between the diets of males and females, crabs caught at Church Island and Aberffraw and red and green males (from both sites) were investigated using Chi squared tests on the major prey categories.

3.3. RESULTS

3.3.1. Morphometrics

Carcinus maenas is strongly heterochelous with right-handedness significantly predominating in both males and females in all three crab populations (Table 3.1). Heterochely was also observed in the morphology of the claws. Whilst the chelal tips overlap on both the major and minor chelae, the dactylus remains in contact with the

Table 3.1. The occurrence of right-handedness in populations of *Carcinus maenas* from Traeth Melynog, Aberffraw, Church Island.

Sex	Site	Right-Handed ¹		χ^2	n	p
Male	Traeth Melynog	172	(85.1)	99.82	202	***
	Aberffraw	62	(77.5)	33.38	80	***
	Church Island	145	(78.0)	58.15	186	***
Female	Traeth Melynog	93	(88.6)	62.49	105	***
	Aberffraw	81	(78.6)	33.80	103	***
	Church Island	71	(74.0)	22.04	96	***

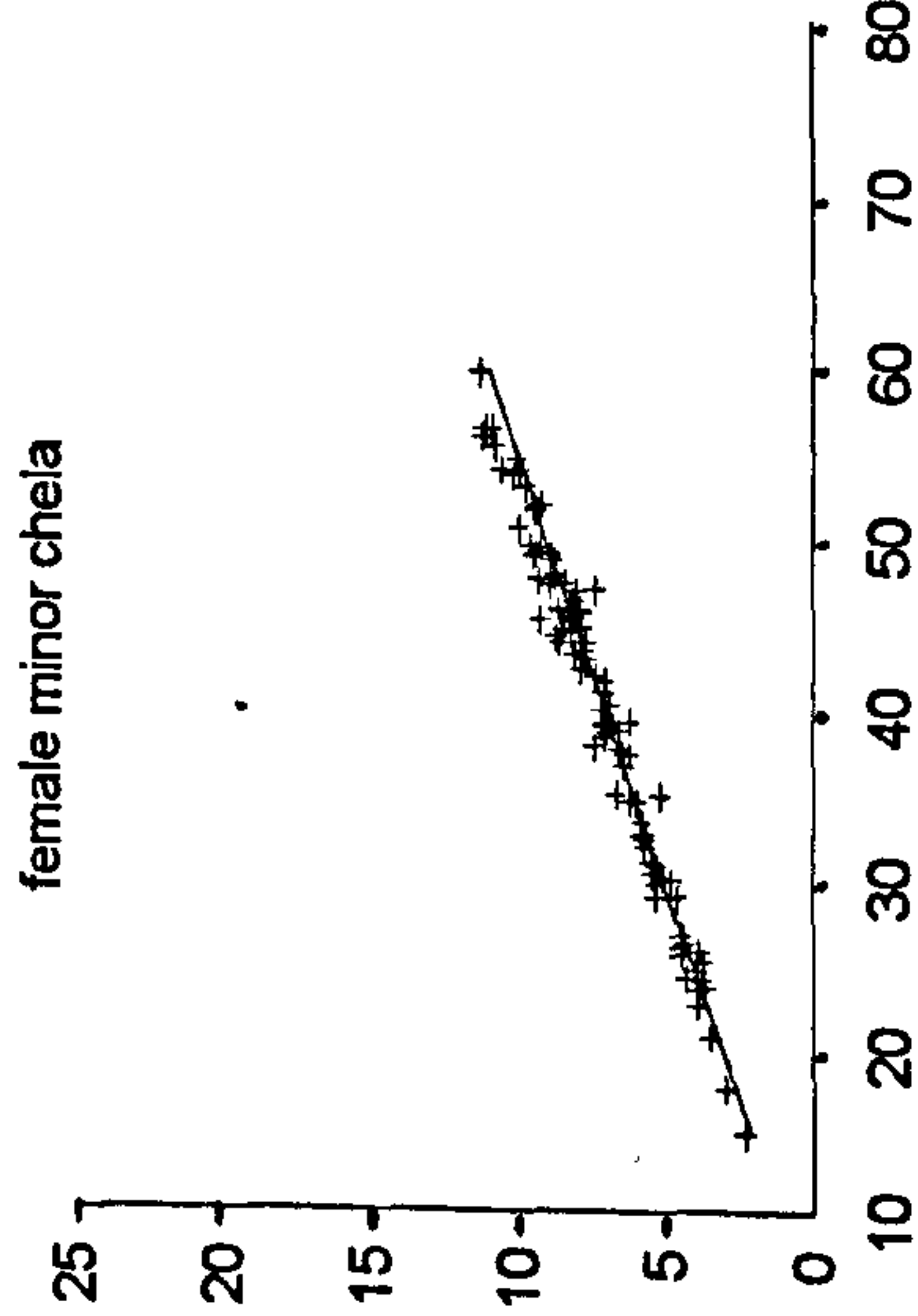
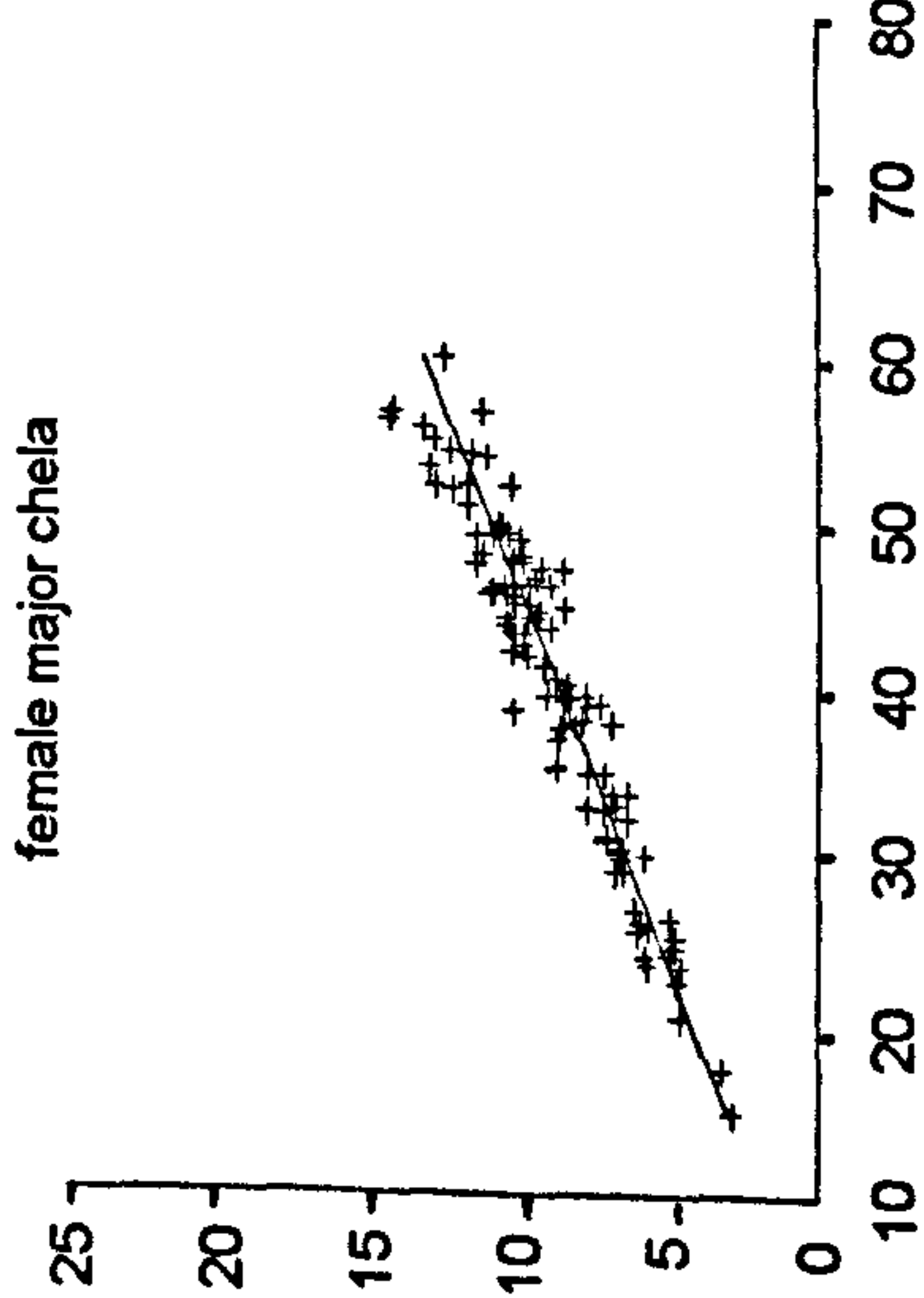
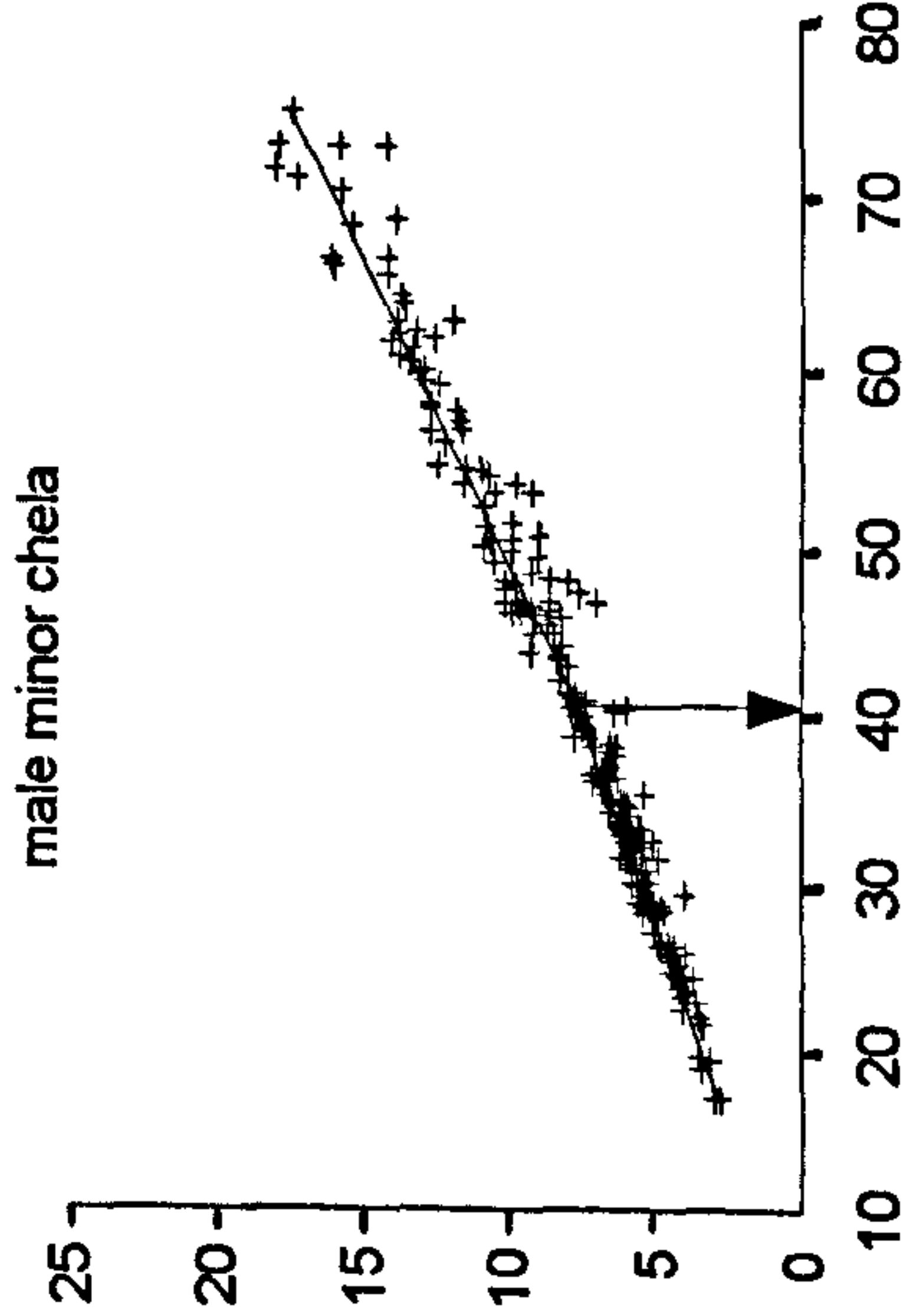
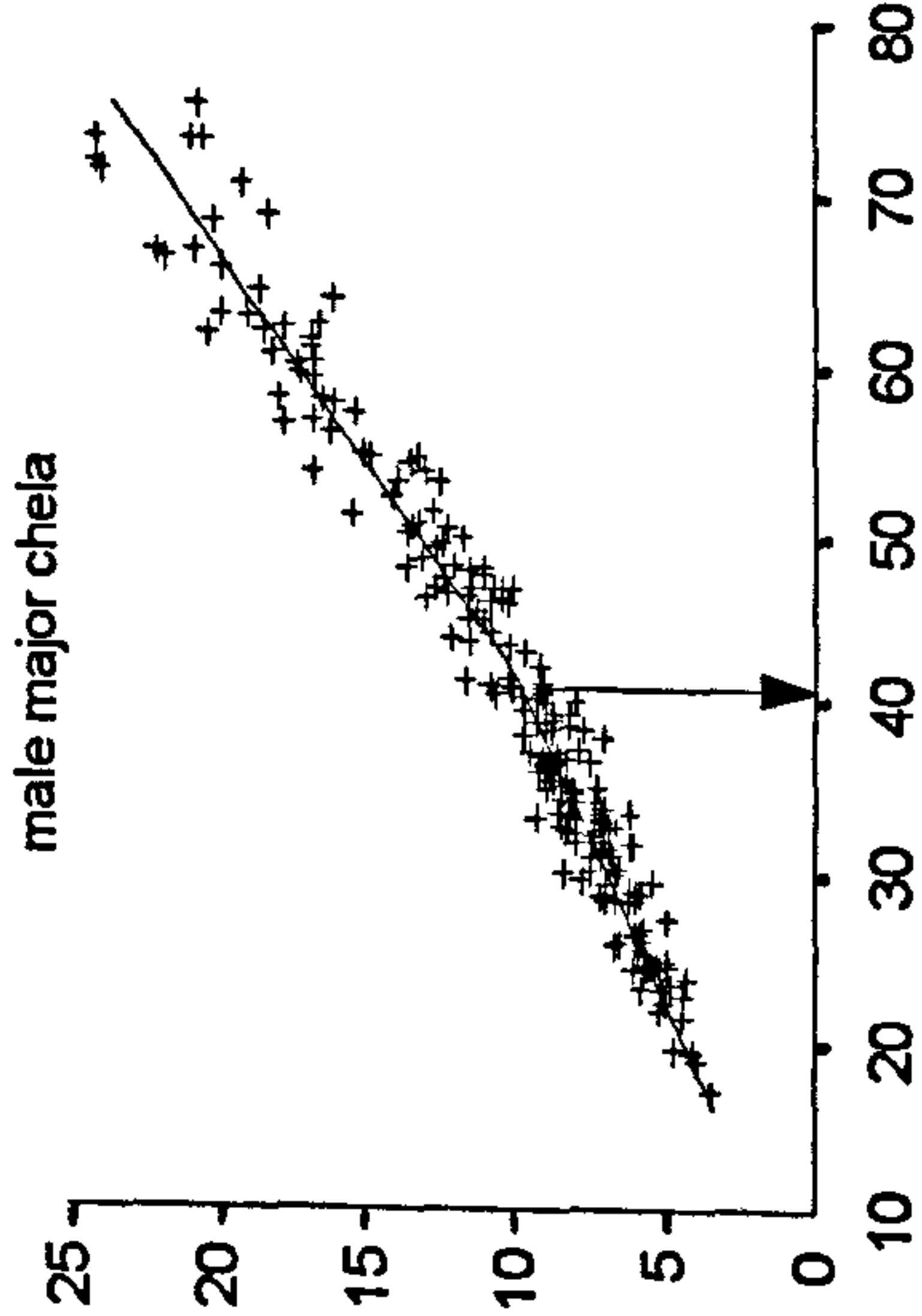
*** $p < 0.0001$; Critical value for $\chi^2 = 15.14$; d.f. = 1
¹ = number of crabs that are right-handed in the sample (%)
n = number of crabs in the sample

propus for one third to one half of the length of minor chela thus contrasting with the major chela where the dactylus and propus are more or less, fully disjoined, i.e. gape, along the claw length. The major chela therefore has an elliptical space into which the prey can be inserted. This gape also sets the lower limit of prey that can be successfully handled with this chela, since no pressure can be exerted on those prey items which in all linear dimensions are smaller than this gape. The major chela has molariform teeth on both the dactylus and the propus; which are broader proximally and rounder distally thus providing a large surface area over which force can be applied. The major chela of *C.maenas*, however, lacks the large proximal peg-like structure found in many other portunid crabs and which is thought to be an adaptation to feeding on hard-shelled prey (Vermeij, 1977). In contrast to the major chela, minor chelal teeth are sharp and triangular, interlocking for effective shearing or tearing when the claw closes. No marked sexual differences in the geometry of the claws were observed.

Figure 3.2 illustrates the relationship between chelal height and carapace width, for crabs caught at Traeth Melynog, whilst the regression equations for these relationships are presented in Table 3.2. Marked differences can be observed between male and female crabs. In male crabs this relationship clearly alters at around 40 mm CW (Fig. 3.2). Amongst smaller individuals, the relationship between major chelal height and carapace width is one of isometry (Table 3.2) and the regression slope is not significantly different to that for small female crabs (general linear model, slopes: $F = 0.59$, d.f. = 163, $p > 0.05$). For male crabs greater than 40 mm CW, major chelal height is positively allometric with respect to carapace width (Table 3.2) and the regression slope differs significantly from that of female crabs of this size ($F = 11.12$, d.f. = 143, $p < 0.01$) where the relationship remains isometric. A similar change is seen in the relationship between chelal height and carapace width in the minor chelae of males, but not in female crabs (Fig.3.2). Interestingly, minor chelal height for both male and female crabs was positively allometric with respect to carapace width (Table 3.2) over the whole range of sizes measured. No significant differences in the relationship of major chelal height to carapace width could be detected between red and green males (slopes: $F = 2.17$, d.f. = 30, $p > 0.05$). No significant differences were detected for either male or female crabs when the slopes for major chelal height against carapace

Figure 3.2. Allometric relationships between chelal height and carapace width in the major and minor chelae of male and female *Carcinus maenas* from Traeth Melynog. Arrows denote a change in slope amongst males < 40 mm CW and > 40 mm CW.

chela height (mm)



carapace width (mm)

Table 3.2. Coefficients of allometry between major chelal height and carapace width in male and female *Carcinus maenas* from Traeth Melynog together with a test for departure from isometry.

Sex	CW (mm)	Dependent variable (y)	Independent variable (x)	Major chela			Minor chela				
				b	t	p	n	b	t	p	n
Males	>40	Chelal height	CW	1.42	8.348	**	86	1.33	7.180	**	86
	<40	Chelal height	CW	1.11	2.603	ns	116	1.10	3.298	**	116
Females	<40 + >40	Chelal height	CW	1.06	2.128	ns	105	1.14	8.140	**	105
	>40	Chelal height	CW	1.01	0.093	ns	57	1.24	3.798	**	57
	<40	Chelal height	CW	1.06	1.067	ns	48	1.11	3.187	**	48

b = the coefficient of the slope in the equation $y=Ax^b$

t = test statistic

** = significant at $p<0.01$;

ns = no significant departure from isometry.

width derived from the crab populations from Church Island and Aberffraw were compared with those for crabs from Traeth Melynog (Table 3.3). Differences between minor chelal heights were not tested since they did not meet the assumptions of the test: these data were neither homogeneous nor normally distributed (see Fry, 1993).

3.3.2. Chelal strength

The regression equations relating major closer apodeme plate area to carapace width are presented in Table 3.4. Regressions of the major closer apodeme plate area on chelal height and minor closer apodeme plate area on carapace width and chelal height did not meet the assumptions of the general linear model, i.e. data were neither normal nor homogeneous. However Table 3.4 shows that for chelal pairs the areas of the minor closer apodeme plates were on average between 36.7% and 47.9% less than the areas of the major closer apodeme plates. Major closer apodeme plate area was highly correlated with carapace width. For large male crabs (red and green colour morphs combined) closer apodeme plate area was positively allometric with respect to carapace width (Table 3.4) suggesting that these crabs were proportionately stronger with increase in size. In contrast the major closer apodeme plate area of female and small male crabs was isometric with respect to carapace width (Table 3.4). When regression slopes were compared, the slope for large male crabs (red and green colour morphs combined) was significantly greater than that for females of comparable size (general linear model, $F = 19.6$, d.f. = 50, $p < 0.001$). There was no significant difference between slopes the major apodeme areas of large red and green males ($F = 0.85$, d.f. = 31, $p > 0.05$).

Mechanical advantage for both major and minor chelae of male and female crabs are presented in Table 3.5. Mechanical advantage was relatively constant and showed no marked variation with carapace width. Major chelae always operated at significantly greater mechanical advantage than the minor chelae (Table 3.5). This was largely due to differences in the length L1 between a pair of chelae rather than to differences in the length L2 (Table 3.5), i.e. to the major chela being taller rather than to the minor chela being longer. This is perhaps not surprising given that chelal height

Table 3.3. Coefficients of allometry between chelal height and carapace width for the major chelae of male and female *Carcinus maenas* from Traeth Melynog, Aberffraw and Church Island. Differences between crabs from the three sites are tested using analysis of covariance (general linear model, MINITAB).

Sex	Dependent variable (y)	Independent variable (x)	Traeth Melynog		Aberffraw		Church Island		Slopes (b)		Intercepts (a)	
			a	b	a	b	a	b	F	p	F	p
Male	Chelal height	CW	-1.29	1.42	-1.42	1.50	-1.29	1.43	0.50	ns	0.61	ns
Female	Chelal height	CW	-0.67	1.01	-1.07	1.25	-1.04	1.23	1.93	ns	1.93	ns
												n
												343
												235

a,b = coefficients in the regression equation $\log y = a + b.\log x$
 ns = no significant difference
 n = number of crabs used in analysis

Table 3.4. Coefficients of allometry between apodeme areas of the major chela and carapace width in male and female *Carcinus maenas* from Traeth Melynog together with a test for departure from isometry. The area of the closer apodeme plate in the minor chela is presented as a percentage of the area of the closer apodeme plate in the major chela.

Sex	Colour	CW (mm)	Dependent variable (y)	Independent variable (x)	b	r	t	p	n	MinAA:MajAA ¹
male	red+green	> 40	majAA	CW	2.82	0.958	5.223	**	31	55.2
	green	>40	majAA	CW	2.73	0.955	3.559	**	19	54.3
	red	>40	majAA	CW	3.10	0.943	3.180	**	12	57.8
	green	<40	majAA	CW	2.19	0.981	1.161	ns	9	54.4
Female	-	<40+>40	majAA	CW	1.95	0.971	0.431	ns	19	63.3

MinAA = minor chelal apodeme area
MajAA = major chelal apodeme area
b = coefficient from the allometric equation $y=Ax^b$
r = coefficient of correlation
t = test statistic
** p < 0.01
ns = no significant departure from isometry
¹ = mean values

Table 3.5. Mean mechanical advantages for major and minor chelae of *Carcinus maenas* caught from Traeth Melynog. The mechanical advantage of the major chela is compared to the minor chela using the Mann-Whitney U test. The lengths L1 and L2 in the minor chelae are expressed as a percentage of the corresponding lengths in the major chelae.

Crab variables			Mechanical advantage				Minor:Major (%)		
Sex	Colour	CW (mm)	Major chela ¹	n	Minor chela ¹	n	U	p	L1 L2
male	red + green	> 40	0.367 (0.036)	31	0.279 (0.021)	30	1404.0	***	70.5 92.4
	green	> 40	0.362 (0.043)	19	0.280 (0.025)	19	533.0	***	71.1 91.4
	red	> 40	0.376 (0.021)	12	0.276 (0.013)	11	210.0	***	69.4 94.4
	green	< 40	0.335 (0.033)	9	0.257 (0.007)	7	108.0	***	69.9 92.0
female	-	< 40 + > 40	0.329 (0.030)	19	0.264 (0.030)	19	530.0	***	77.7 96.6

¹ = all values are means (+/- 1 standard deviation)

n = number of crabs in the sample.

U = Mann-Whitney U test statistic

*** = significant at p <0.001

has already been shown to be greater for the major chela than for the minor chela. The chelae of larger crabs (>40 mm CW, red and green colour morphs combined) operate at a significantly greater mechanical advantage of those of small crabs (< 40mm CW) (major: $U = 711.0$, d.f. = 39, $p < 0.05$; minor chela $U = 642.0$, d.f. = 36, $p < 0.01$) and of female crabs (major chela: $U = 963.0$, d.f. = 49, $p < 0.001$; minor chela: $U = 858.0$, d.f. = 48, $p < 0.05$) reflecting the results obtained from the comparisons of chelal height. There was no significant difference between the mechanical advantages of large red and green male crabs for either claw type (major: $U = 280.0$, d.f. = 30, $p > 0.05$; minor: $U = 301.6$, d.f. = 29, $p > 0.05$).

3.3.3. The *Carcinus maenas* populations occurring at Church Island and Aberffraw.

The numbers of *Carcinus maenas* caught in the traps placed in the intertidal zone changed markedly over the sampling period at both Church Island and Aberffraw, with relatively high population densities reported during the summer and autumn and much lower densities during winter and spring (Figures 3.3 & 3.4). Crabs moved on shore during spring, the number caught onshore increased through the summer months until the autumn. From Figures 3.3 & 3.4 it can be seen that male crabs tended to be larger than females caught onshore. Both red and green crabs were found in these onshore traps.

3.3.4 The natural diet of *Carcinus maenas*.

A total 626 crab stomachs were dissected of which 351 contained food. No pattern in the percentage occurrence of crabs with empty stomachs emerged over the sampling period. Analysis of stomach contents revealed that *Carcinus maenas* has a broad diet consuming both plants and animals, sedentary and mobile species. More of the stomachs examined contained animal material than algal and plant material (Table 3.6). Identification of prey in the stomachs largely relied on the presence of hard parts, which could be used to characterise a particular prey type. *Mytilus edulis* could be

Figure 3.3. The number of male (open bar) and female (closed bar) *Carcinus maenas* caught intertidally at Church Island in each sampling month during the period January 1996 to June 1997. In each month the total number of crabs caught in six traps over a 24 hour period is presented.

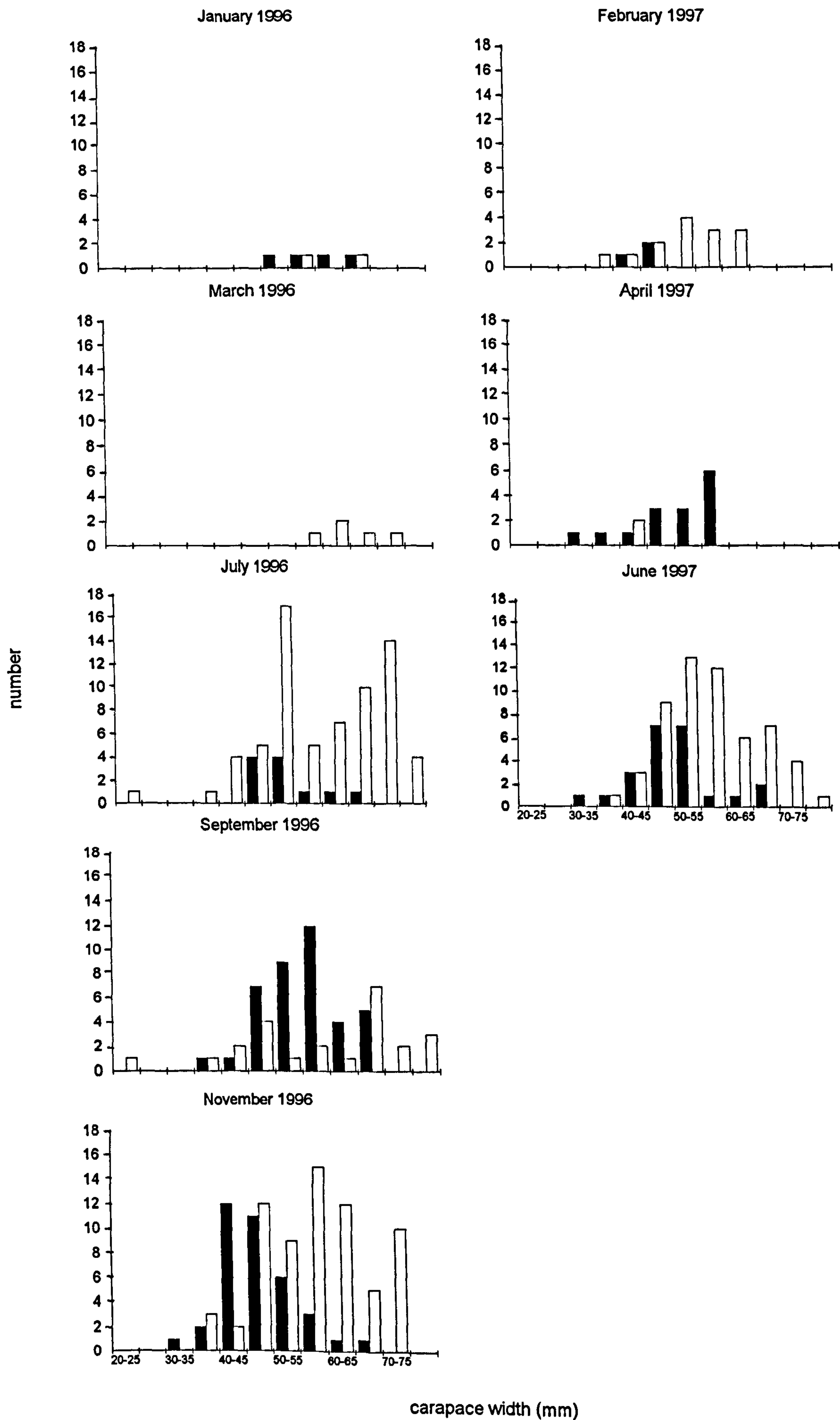
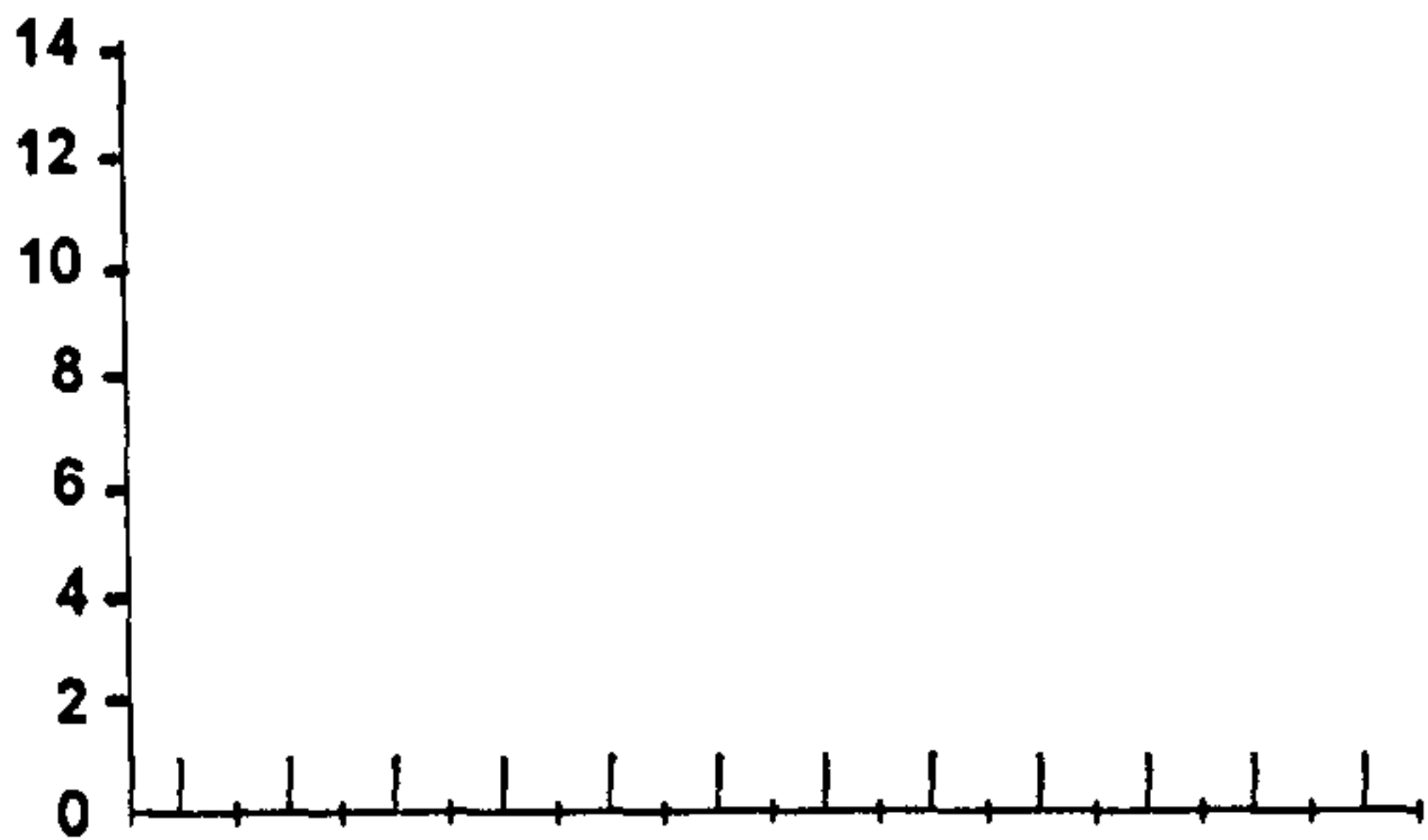
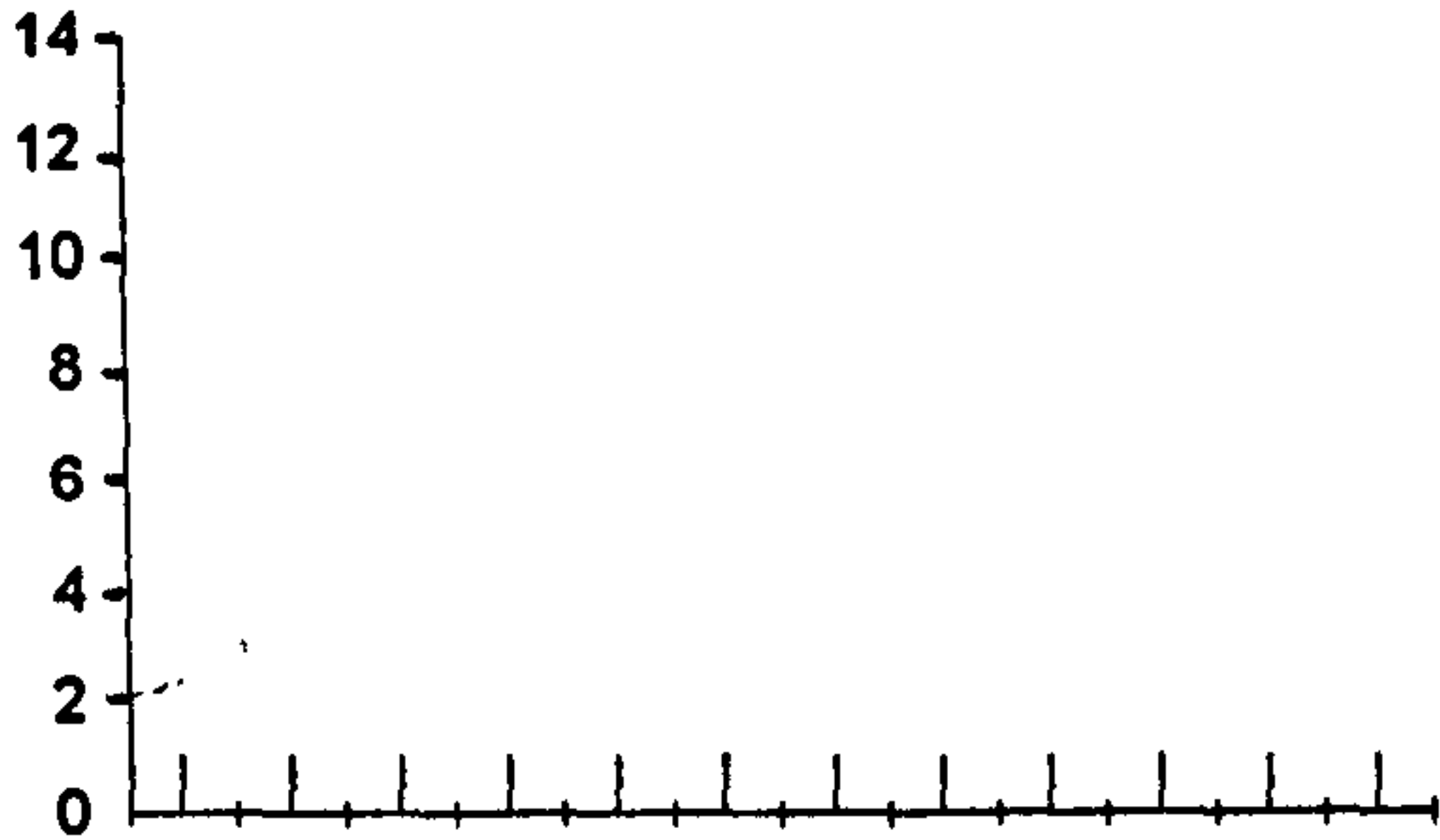


Figure 3.4. The number of male (open bar) and female (closed bar) *Carcinus maenas* caught intertidally at Aberffraw in each of the sampling months during the period January 1996 to September 1997. In each month, the total number of crabs caught in six traps over a 24 hour period is presented.

January 1996

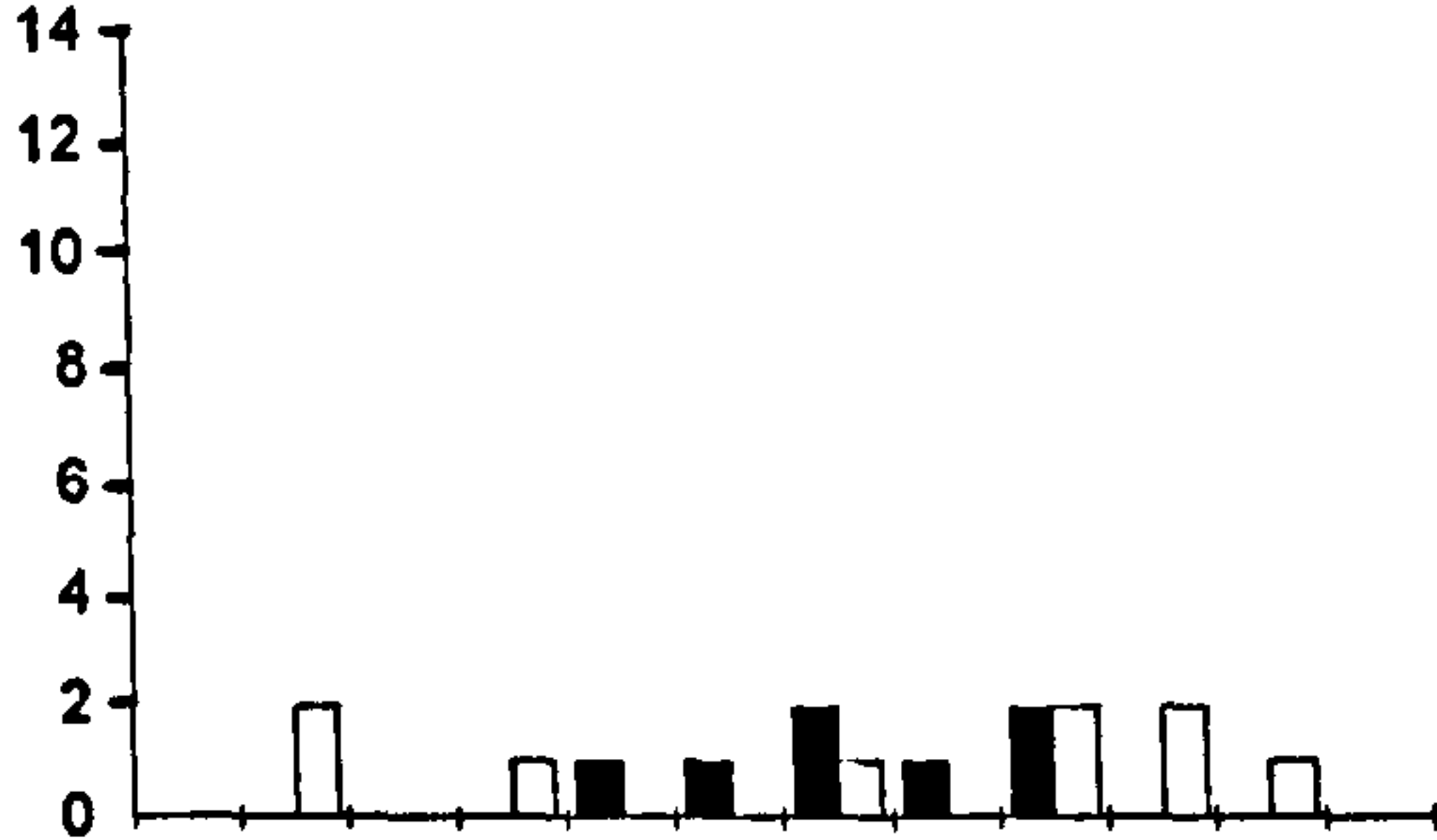
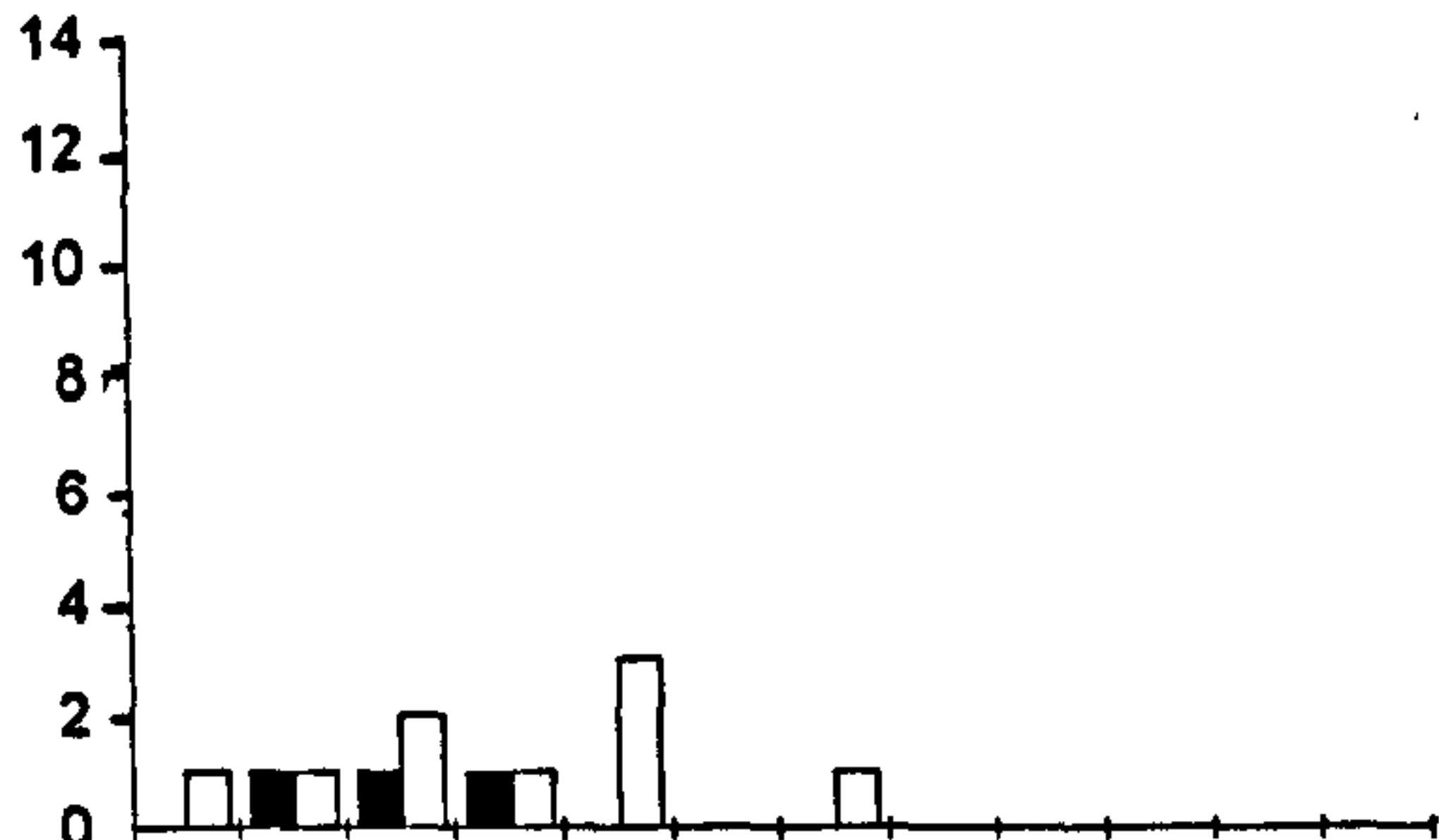


February 1997



March 1996

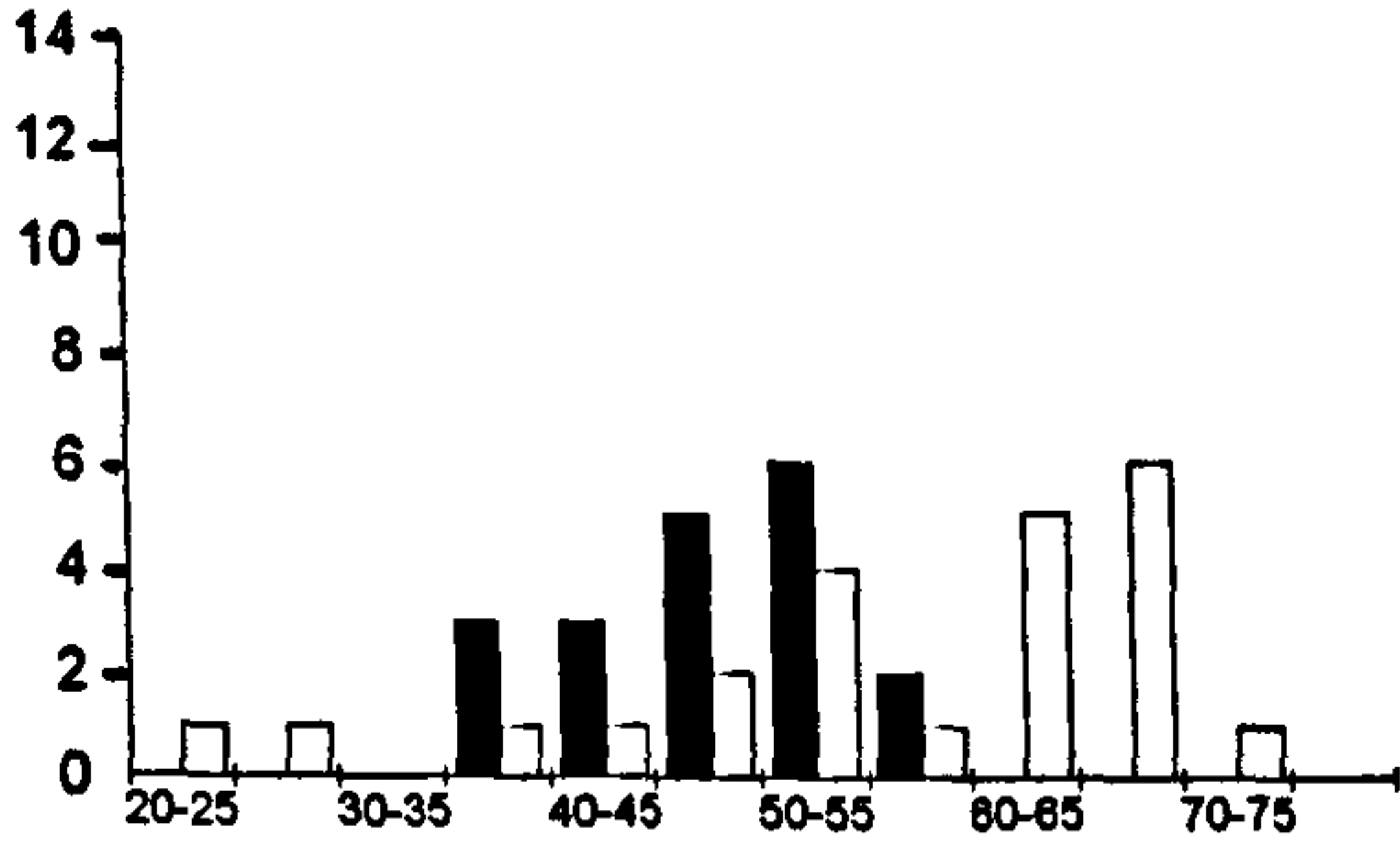
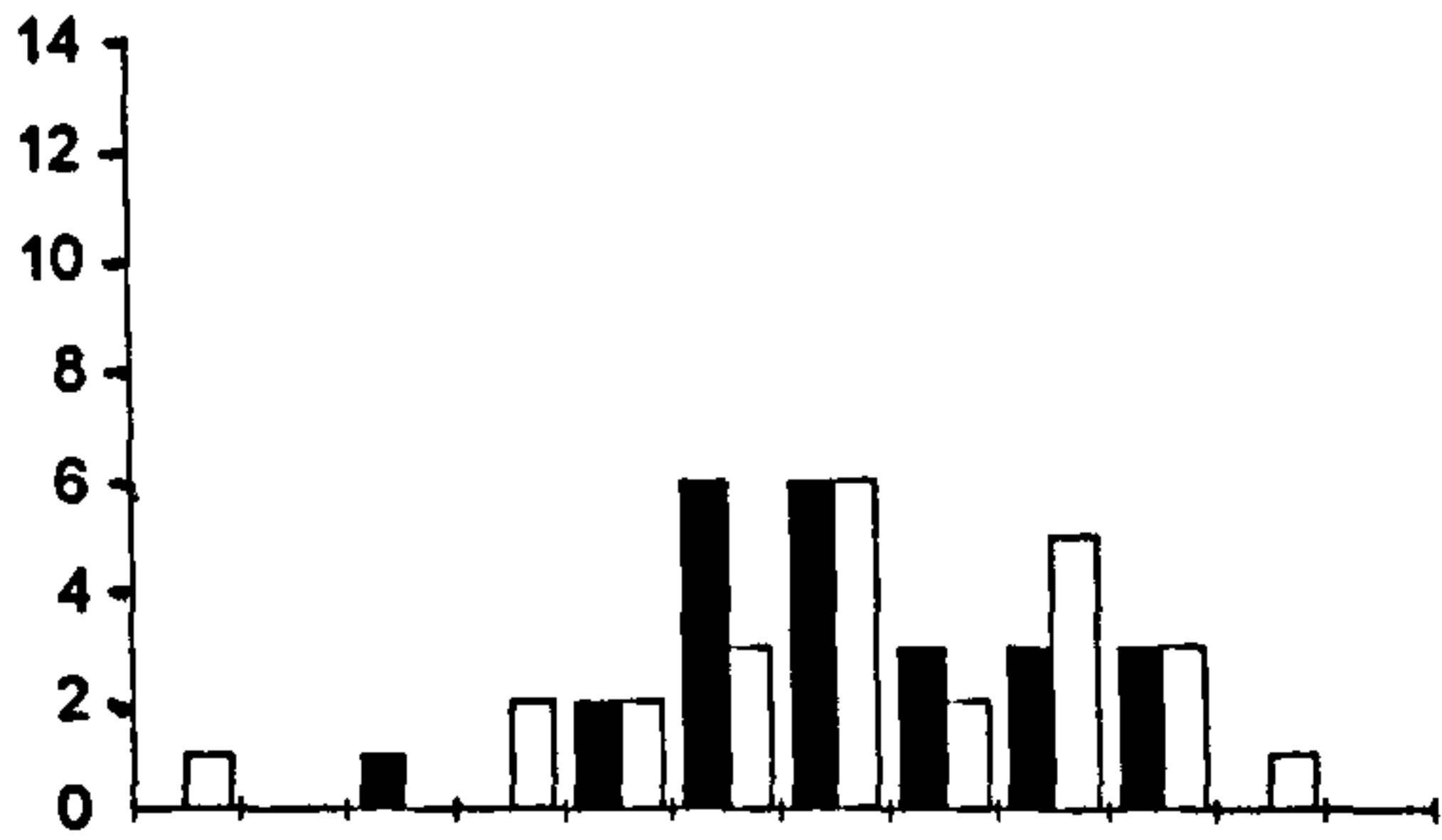
April 1997



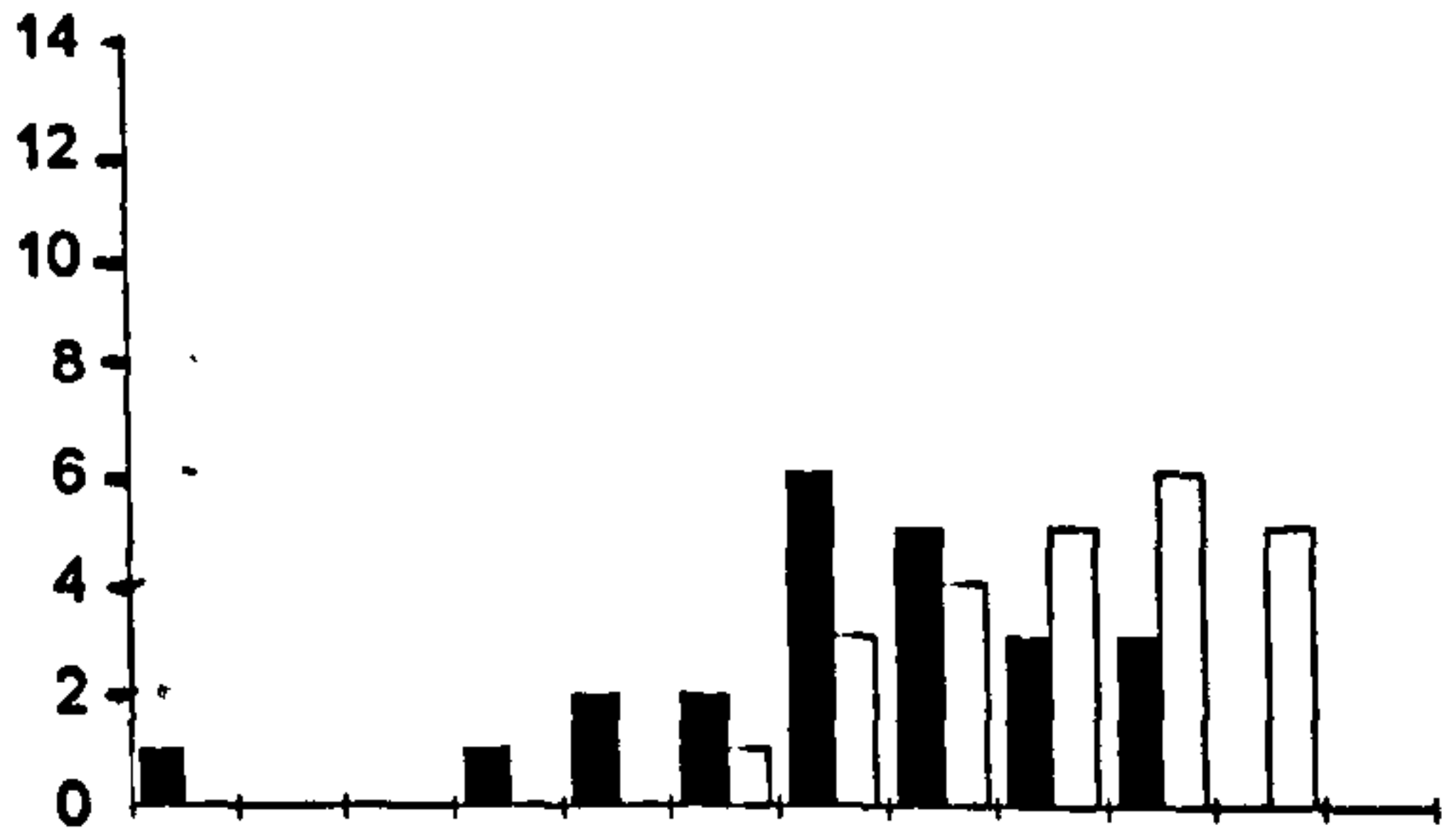
July 1996

June 1997

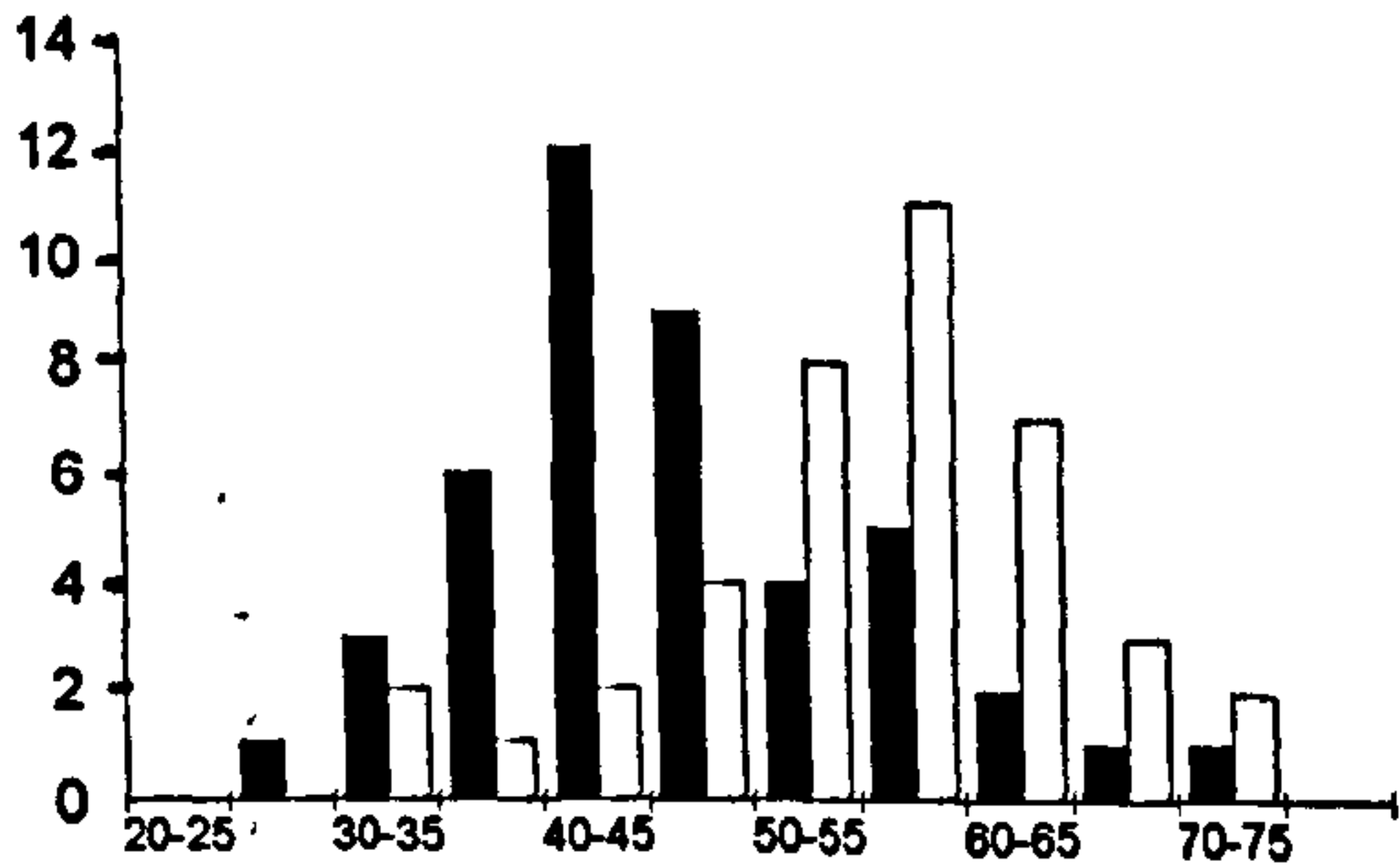
number



September 1996



November 1996



carapace width (mm)

Table 3.6. Percentage frequency of occurrence of food items in the guts of *Carcinus maenas* from Church Island and Aberffraw (males and females combined).

Taxonomic Group	Church Island	Aberffraw
	(n=209)	(n=142)
Animals	85.6	71.1
Molluscs	46.4	35.9
<i>Mytilus edulis</i>	40.2	29.6
Gastropods	11.0	3.52
Bivalves	5.7	7.0
Barnacle sp.	36.4	25.4
Crustaceans	35.9	34.5
Polychaetes	6.2	4.9
Fish	7.2	5.6
Other Animals	11.0	5.6
Hydroids	5.3	0
Algae and Plants	35.9	29.6
Brown Algae	24.4	18.3
Green Algae	6.2	9.7
Red Algae	4.8	2.1
Plants	5.3	2.8
Sediment	5.3	28.9
Unidentified	7.2	6.3

identified from characteristic shell markings, umbo shape and the occasional inclusion of byssus threads (Plate 3.1A). The size of mussel umbos and hinge structures, as well as the translucency of the shell indicated that these mussel fragments came mainly from smaller mussels (< 5mm shell length). Sometimes fragments from larger mussels, identifiable from the size of the fragment and the deeper, non-translucent coloration, were found. Barnacles were recognised from the presence of their characteristic hard white calcareous plates (Plate 3.1B). Both barnacles and *M. edulis* were found frequently and were easily identifiable; for these reasons these prey types were counted separately. Crustaceans, other than barnacles, included amphipods, shrimps, hermit crabs as well as small shorecrabs. These could be identified by their exoskeletal structure and coloration. Other small prey items included gastropods, identified from their columella or opercular plates, bivalves, polychaetes which could be recognised from their chitinous jaws and their chaetae, bryozoans, hydroids and sea urchins. The inclusion of fish in the diet was probably due to crabs accessing the bait. Some stomachs contained no recognisable parts but instead were filled with a brownish liquid; presumably representing the digested or semi-digested soft tissues; this could not be identified and was listed as unidentified. Brown algae occurred as distinctive bite-sized crescent pieces (Plate 3.1C). Red, green and filamentous algae were also present in some stomachs as was terrestrial material such as leaf and twig fragments.

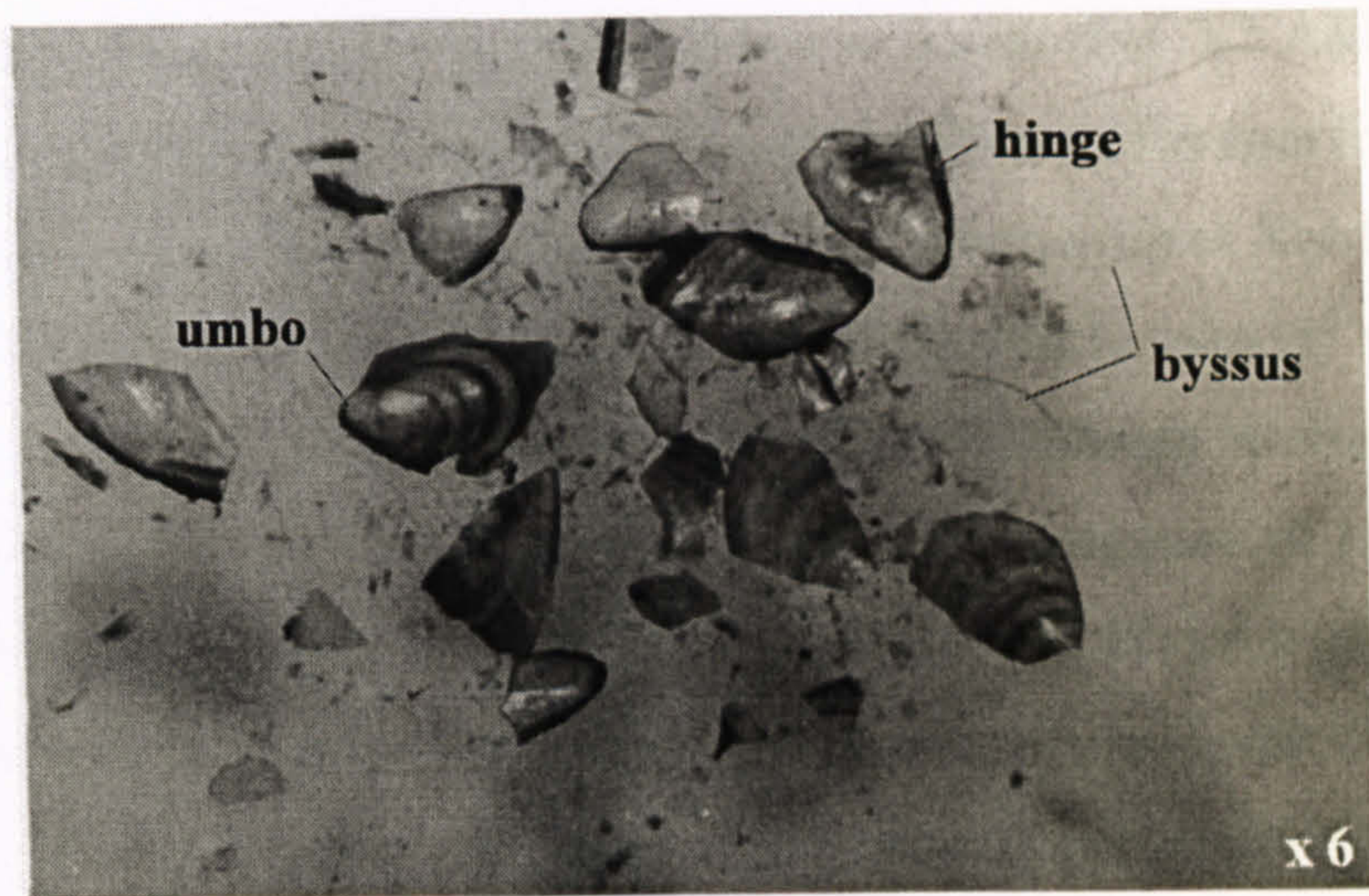
Molluscs appeared to be a particularly important component of the diet (Table 3.6), largely due to the high rate of inclusion of *Mytilus edulis* in the diet, which occurred in 29.6% and 40.2% of all stomachs at Aberffraw and Church Island respectively (male and female crabs combined). The three other major food groups were barnacles, crustaceans (excluding barnacles) and brown algae (Table 3.6). From Table 3.6 it can be seen that the diets of *Carcinus maenas* from Aberffraw and Church Island were broadly similar in content. Male crabs from Church Island had a significantly greater inclusion rate of barnacles ($\chi^2 = 5.11$, d.f. = 1, $p < 0.05$) and the inclusion of sediment in the stomachs was greater at Aberffraw than at Church Island both for male ($\chi^2 = 18.23$, d.f. = 1, $p < 0.0001$) and female crabs ($\chi^2 = 13.51$, d.f. = 1, $p < 0.001$). Hydroids were sometimes found in the stomachs of *C. maenas* from Church Island but were never reported in the stomachs of crabs from Aberffraw. The diets of

Plate 3.1. Photographs of food remains found in the stomachs of *Carcinus maenas*.

A. Fragments of *Mytilus edulis*.

B. White calcareous plates of barnacles.

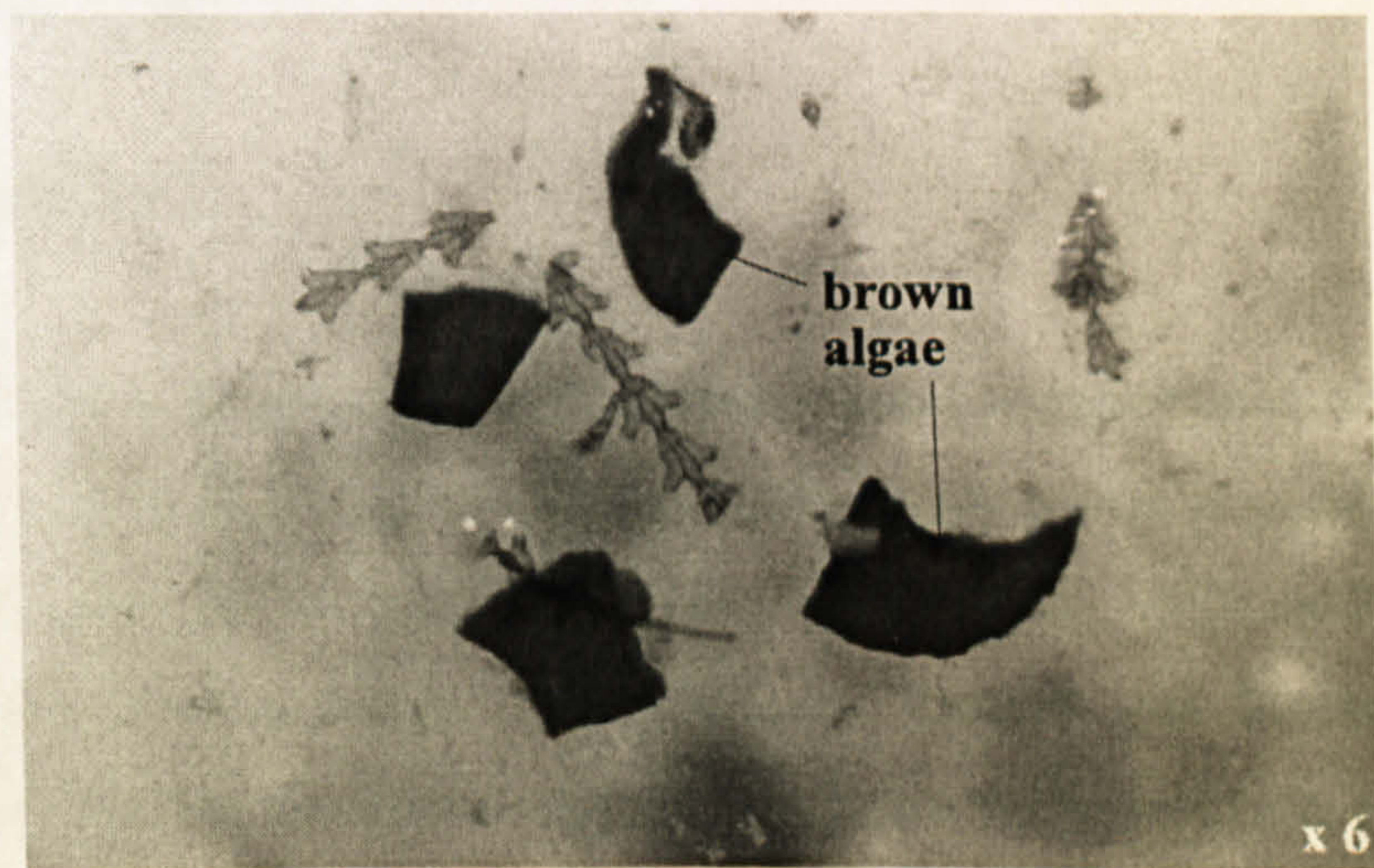
C. Crescent shaped pieces of brown algae.



A. *Mytilus edulis*



B. Barnacles



C. Brown algae

male and female *C.maenas* at both of the sites were similar (Fig. 3.5 A&B) despite sexual differences in chelal morphology and the only significant difference found in the diets of the sexes was in the percentage occurrence of barnacles at Aberffraw (Fig. 3.5B) where the rate of inclusion was less for males than for females ($\chi^2 = 7.54$, d.f. = 1, $p < 0.01$). Since there were generally no significant differences between the diets of male and female crabs, except for the percentage occurrence of barnacles at Aberffraw, stomach contents were combined and the diets of crabs caught in the summer (July 1996, September 1996, June 1997) were compared with those caught in the winter (all other months). At Church Island crabs consumed significantly more crustaceans in the summer months ($\chi^2 = 10.99$, d.f. = 1, $p < 0.001$), whilst amongst crabs from Aberffraw the inclusion of brown algae was significantly greater during the winter than in the summer ($\chi^2 = 5.82$, d.f. = 1, $p < 0.05$).

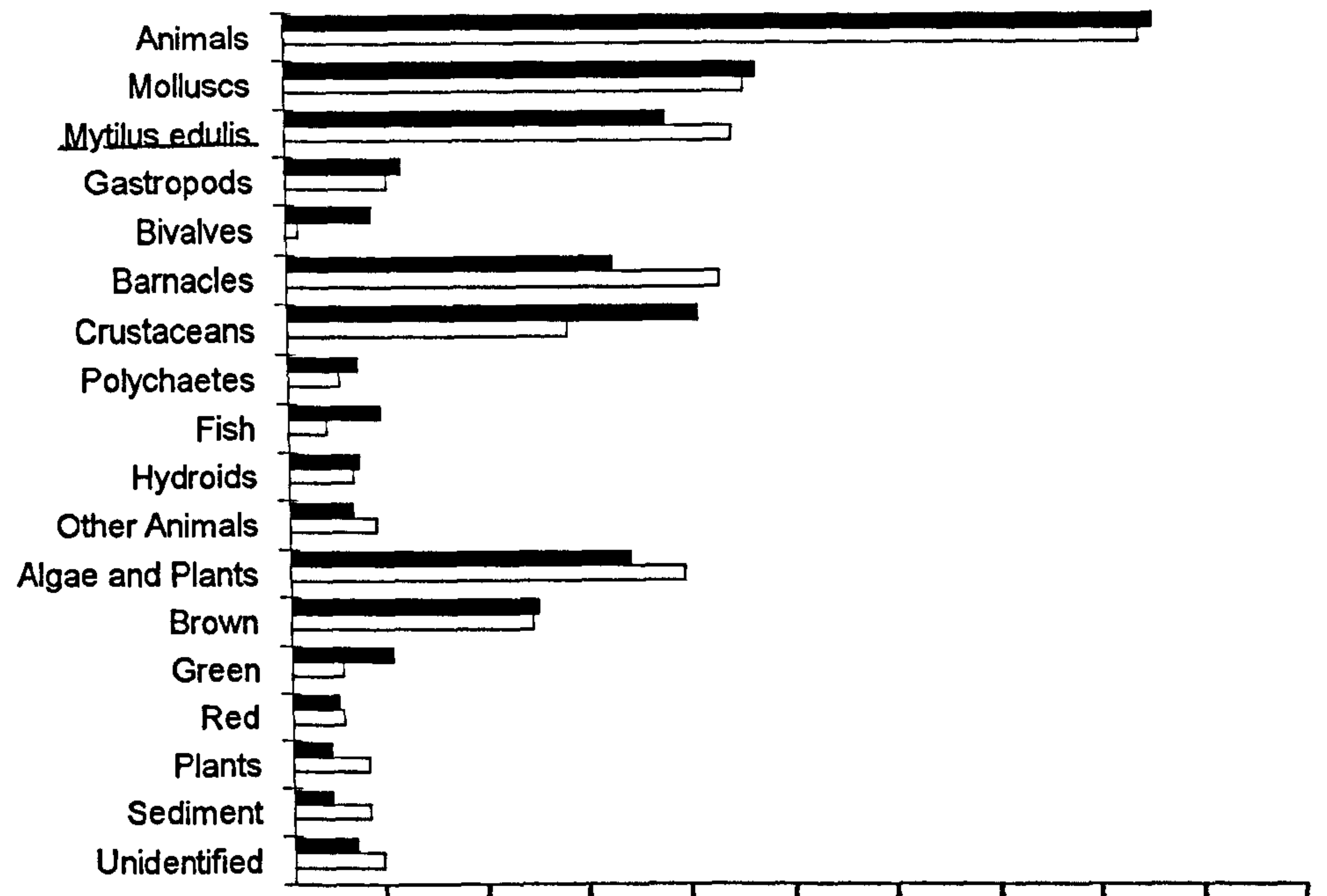
Whilst there were few differences between male and female crabs there were significant differences between the diets of red and green males at each site (Fig. 3.6 A&B). The rate of inclusion of *Mytilus edulis* in the diet of red crabs from Aberffraw was significantly greater than that for green crabs from the same site ($\chi^2 = 4.05$, d.f. = 1, $p < 0.05$), whilst barnacles were significantly more important in the diet of green crabs than in red crabs ($\chi^2 = 4.75$, d.f. = 1, $p < 0.05$). At Church Island the rate of inclusion of algae and plants (including brown algae) and brown algae in the diet of green crabs was significantly greater ($\chi^2 = 6.36$, d.f. = 1, $p < 0.05$; $\chi^2 = 5.16$, d.f. = 1, $p < 0.05$) than in red crabs. In general, green male crabs appeared to have a somewhat broader diet than red males and this was particularly noticeable for crabs from Aberffraw (Fig. 3.6B).

3.4. DISCUSSION

Elnor (1980) has argued that crab chelae form a template upon which feeding behaviour is determined and subsequent studies have shown a good correlation between crab chelal type and feeding behaviour (Brown *et al.*, 1979; ap Rheinallt and Hughes, 1985; Seed and Lee, 1995; Behrens Yamada and Boulding, 1998). Heterochely in both the size and structure of the chelae is often found in crabs feeding

Figure 3.5. The percentage frequency occurrence of different food types in the stomachs of male (closed bar) and female (open bar) *Carcinus maenas* from Church Island (A) and Aberffraw (B).

A.



B.

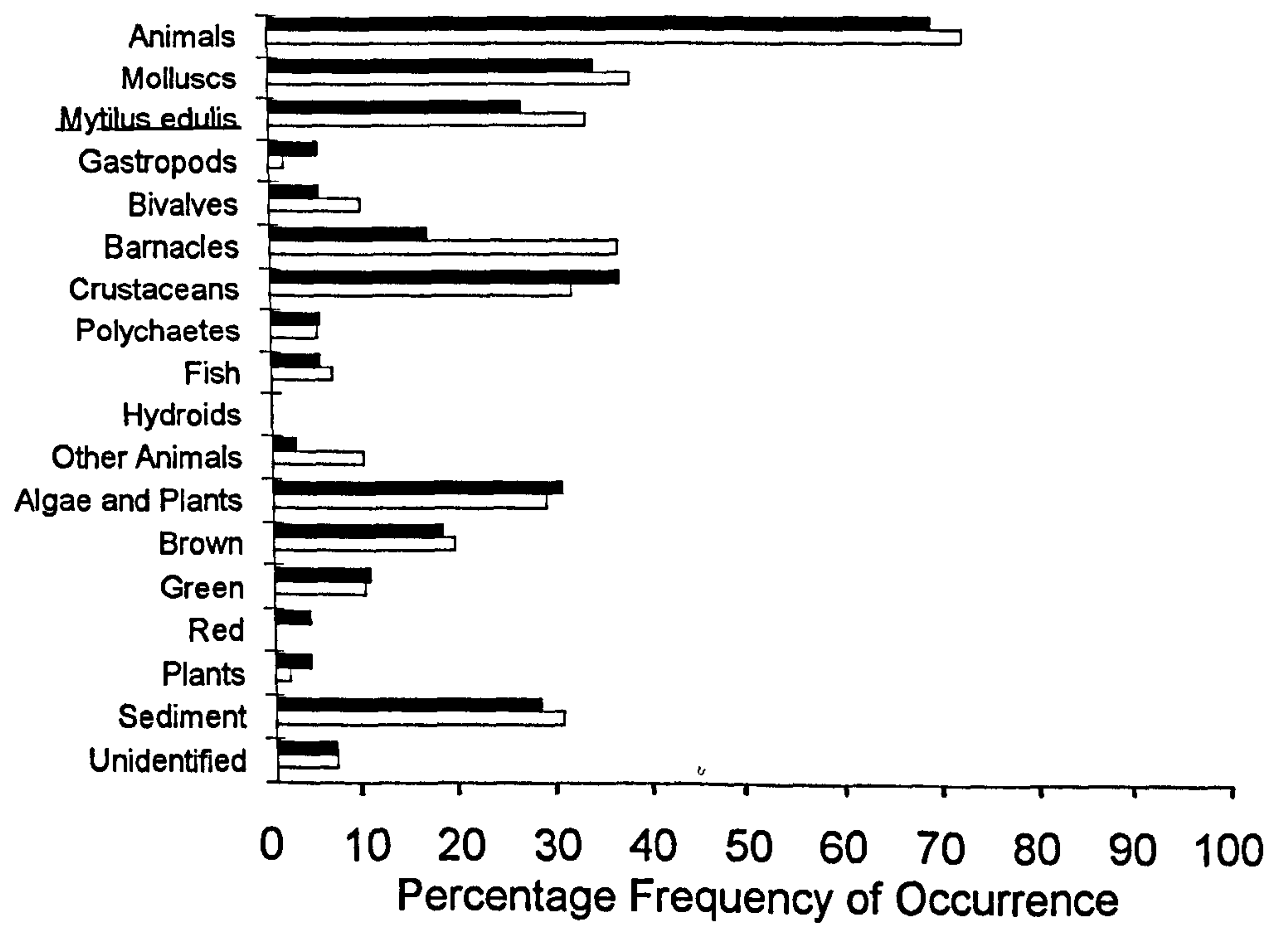
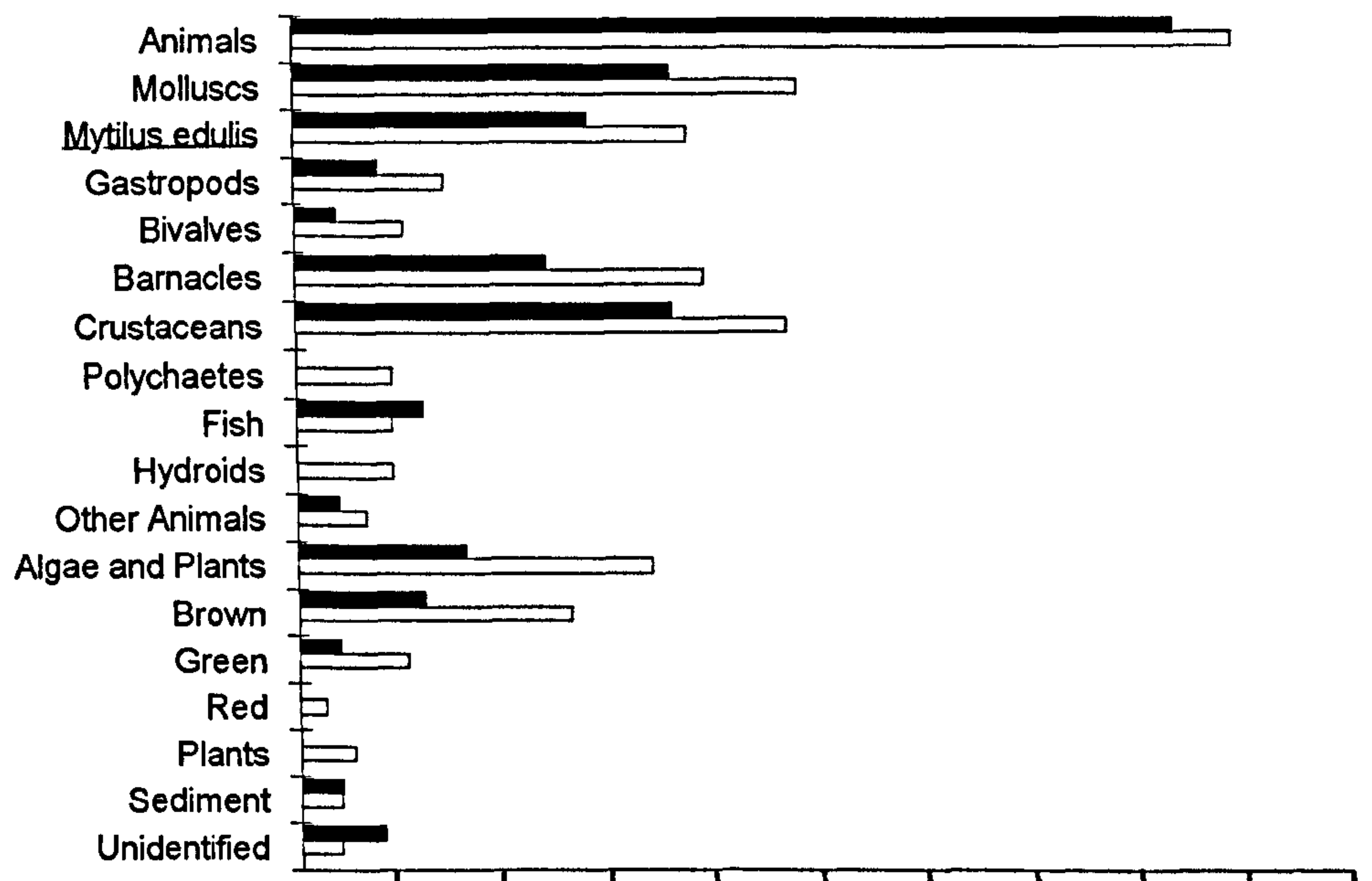
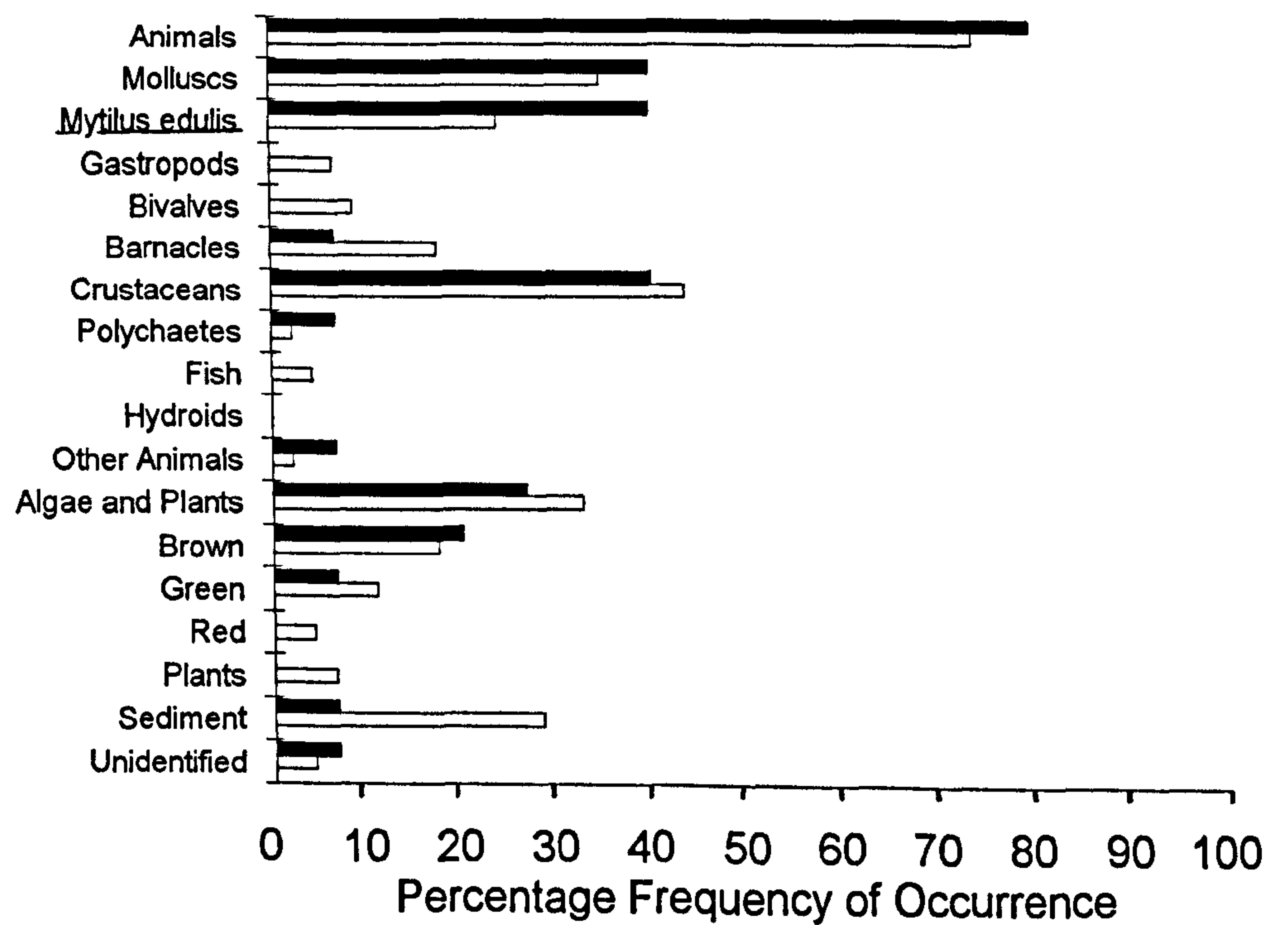


Figure 3.6. The percentage frequency of occurrence of different food types in the stomachs of red (closed bar) and green (open bar) male *Carcinus maenas* from Church Island (A) and Aberffraw (B).

A.



B.



on hard-shelled prey (Seed, 1993) and this condition was prominent in all three *Carcinus maenas* populations examined in this study, which also demonstrates that hard-shelled prey were major components of the crabs diet. In all three populations the right chela was predominantly the larger one. Previous studies also found that right-handedness predominated in *C. maenas* populations (Lee and Seed, 1992; Abello *et al.*, 1993) and this is thought to be a general characteristic of heterochelous crab species (Seed and Hughes, 1995). Left-handedness arises mainly through the loss of the major, right chela at a previous moult after which the minor, left claw subsequently becomes the major chela over the succeeding moults (see references in Abello *et al.*, 1993). To access the flesh of hard-shelled prey, crabs require sufficiently large chelae to be able to crush the shells whilst retaining sufficient dexterity to remove the flesh. The simplest solution to this problem is to have two different chelal types which perform two different functions and this is demonstrated in both sexes of *C. maenas*. The larger, major chela operates at a higher mechanical advantage and has a greater closer apodeme plate area indicating a greater chelal strength. This coupled with its blunt teeth and disjointed area indicates that it is adapted to crushing prey (Brown *et al.*, 1979). The smaller minor chela is faster but weaker as reflected in its lower mechanical advantage and smaller closer apodeme plate area. The sharp, interlocking triangular teeth indicates that it can apply effective tearing or shearing forces (Brown *et al.*, 1979), whilst the slender nature of the claw suggests that it is more dexterous thereby allowing it to handle prey more efficiently. Indeed the mechanical advantage of the minor chela of male *C. maenas* (0.28) is similar to that found for the major chela of the portunid, *Callinectes sapidus*, 0.23 (Blundon and Kennedy, 1982b), which has been shown to be very efficient at gleaning the flesh from mussel shells (Hughes and Seed, 1981). Experiments with *C. maenas* feeding on hard-shelled prey have shown that this is indeed the way in which the two chelae are used (Elner and Hughes, 1978; Chapter 4 this study) and this is consistent with behaviour observed for other heterochelous crabs feeding on hard-shelled prey, e.g. *Thalamita danae* (Seed, 1990a), *Eriphia laevimana* (Coombes and Seed, 1992), *Ovalipes catharus* (Davidson, 1986). The requirement for a strong chela to break hard-shelled prey does not in itself explain the predominance of right-handedness and Abello *et al.* (1993) actually found that left-

handed *C.maenas* were more successful in mate competition implying that the selective force for right-handedness must be strong. It has previously been proposed that right-handedness is an evolutionary adaptation to feeding on the dextrally coiled gastropods (Ng and Tan, 1985) and although this study did not find gastropods to be of great importance in the diet of *C.maenas*, previous studies have indeed demonstrated the importance of such prey (Ropes, 1968; Raffaelli *et al.*, 1989). Stomach content analysis showed that *C.maenas* is a generalist omnivore. This supports the conclusions of earlier works (e.g. Ropes, 1968; Elner, 1977, 1981; Raffaelli *et al.*, 1989). The mechanical advantage of the minor chela is similar to that found for the major chela of other portunids, *Callinectes sapidus*, 0.23 (Blundon and Kennedy, 1982b) and *Necora depurator*, 0.25 (Warner and Jones, 1976). These species are described as having fast claws that are adapted for feeding on fast moving prey: thus the dimorphism between the chelae may be seen not only as a solution to the problem of feeding on hard-shelled prey but also as a way of exploiting a range of prey types.

Major differences in chelal morphometrics, but not geometry, were found between male and female *Carcinus maenas* during this study. The greater chelal height, mechanical advantage and larger apodeme area (crabs > 40mm CW), all indicate that the major claw of male crabs is proportionally stronger than that of the female crabs of a similar size. Such sexual dimorphism has been documented in other species of portunid crabs (see Seed and Lee, 1995) and may allow males to exploit a wider range of hard-shelled prey. However, both *C.maenas* (Elner and Hughes, 1978) and other crab species, (see Juanes, 1992), tend to select sizes of hard-shelled prey items which are substantially smaller than the maximum size that can be opened. This suggests that the advantage to male crabs of possessing relatively larger major chela would only be conferred in extreme circumstances where only larger sizes of prey are available. The results of this study support this conclusion since there were no differences in the percentage occurrence of molluscs in the stomachs of males and females at either site. Furthermore the lack of a proximal peg, regarded as an adaption to feeding on hard-shelled prey (Vermeij, 1977) and the omnivoric diet of *C.maenas* suggests that it is not realistic, therefore, to consider form and function of the chelae as purely the result of predation on hard-shelled prey. The chelae also serve other functions and for males

these include fighting for mates (Lee and Seed, 1992). The change in relationship between male major chelal height and carapace width documented in this study has been reported in other studies to occur around 30mm (Lee and Seed, 1992) and 35mm (Raffaelli *et al.*, 1989). Furthermore, this study found that mechanical advantage, a measure of grip strength, was significantly greater in large male crabs than in small. This change appears to coincide with the onset of sexual maturity (Lee and Seed, 1992) indicating that greater chelal strength maybe associated with fighting for mates rather than with exploiting a food source.

No significant differences in mechanical advantage, apodeme area or chelal height were found between red and green crabs. Since these features are part of, or related to, the exoskeleton, their proportions are determined at moult, whereas crab colour is a function of the length of the intermoult period (Reid *et al.*, 1997). The absence of any differences in chelal morphometrics of red and green crabs agrees with the findings of Kaiser *et al.*, (1990), however, these are not the only factors determining chelal strength. Kaiser *et al.* (1990), for example, found that the mass of the closer muscle and of the dactylus was greater in red crabs than in green male crabs of a similar size, indicating that red crabs can both generate a greater force within their claws. Red crabs could out-compete green crabs and preferred larger mussels and Kaiser *et al.* (1990) postulated that this should lead to red crabs out-competing green crabs in areas where they co-occurred and some differences in feeding habits between the two colour morphs were observed in the present study. Red crabs tended to have a somewhat narrower diet than green crabs which may be due to red crabs dominating favoured prey types and forcing green individuals to feed on less favoured prey. Differences in diet may also be due to the inclusion of a proportion of newly moulted (green) crabs which have not yet fully hardened and therefore exhibit different feeding habits. Ropes (1968) found that in “very soft-shelled” *Carcinus maenas* the rate of inclusion of molluscs was less than for “hard-shelled” individuals whilst Choy (1986) found a higher frequency of occurrence of algae in the stomachs of *Necora puber* in the summer months and attributed this to a higher degree of moulting at this particular time of year.

At both study sites the number of *Carcinus maenas* caught in intertidal cages

were low compared with other studies which have recorded much higher catches both in the Menai Strait (Warman *et al.*, 1993) and at Aberffraw (Mascaro *pers. comm.*). Previous research has shown that the onset of tidal migrations generally coincides with an increase in water temperature in the Spring, with numbers reaching a maximum in the Autumn (Atkinson and Parsons, 1973). A similar seasonal trend was reported in this study, with few *C.maenas* present on the shore in the early months of the year and numbers increasing through the Summer reaching a maximum in Autumn. At both study sites it can be concluded that mussels and crabs co-occurred.

The range of prey found in the stomachs of *Carcinus maenas* was similar to that reported in previous studies on this species (Ropes, 1968; Elner 1977, 1981; Raffaelli *et al.*, 1989), although differences did arise in the relative importance attributed to the individual prey types reflecting the opportunistic nature of this predator. Seasonal differences in diet may be regarded as a response by the crab population to the altering availability of prey items throughout the year, i.e. the diet of *C.maenas* broadly reflects what is available in the natural environment further illustrating the opportunistic nature of this predator.

Mytilus edulis was of prime importance in the diet of *Carcinus maenas* at both study sites. It was the single most important prey item, in terms of occurrence in the stomachs of crabs at Church Island whilst at Aberffraw it was the second. This confirmed the validity of using mussels from these sites in laboratory experiments. Although the high frequency of inclusion of *M.edulis* found in this study was similar to that previously reported for *C.maenas* elsewhere (Ropes, 1968; Elner, 1981; Raffaelli *et al.*, 1989) it was much greater than the <10% inclusion rate reported by Elner (1977) in a study of this species carried out in the Menai Strait. In that study, however, crabs were sampled some distance from a mussel bed, whereas in this study crabs were collected next to naturally occurring mussel beds. These results strongly suggest that *C.maenas* preferentially consumes *M.edulis* whenever this species is encountered. The high frequency of *M.edulis* in the diet of *C.maenas* on mussel beds both at Aberffraw and at Church Island indicates that *C.maenas* has the potential to influence the structure of these local mussel populations as previously demonstrated for this predator with other bivalve species (Ropes, 1968; Walne and Dean, 1972;

Sanchez-Salazar *et al.*, 1987a;).

The nature of the mussel shell fragments found in the stomachs of *Carcinus maenas* indicates that the mussels consumed were mainly small individuals (< 5mm) suggesting that the effect of crab predation might be most severe during the early stages of mussel growth. However, the percentage occurrence method of diet analysis relies on the presence of recognisable hard parts; mussel shell and byssus threads, occurring in the stomach. This assumes that mussels over the whole size range that are available to predation are eaten in the same manner. Research shows that this is not the case and the handling techniques used by *C. maenas* when feeding on mussels are size specific (Elner, 1978; Chapter 4). Very small mussels are generally crushed outright and small fragments are often ingested. In contrast larger mussels are broken in specific places and are broken into larger pieces. This size-specific difference in opening techniques may explain the apparent preference for small mussels; their presence in the stomach resulting from different handling methods rather than differential predation rates and it should be noted that larger fragments were sometimes found indicating that larger mussels were also eaten.

3.5. SUMMARY

- *Carcinus maenas* is strongly heterochelous, its two chelae differ both in terms of their mechanics and their geometry and this can be related to different functions. The major chela is significantly larger than the minor chela. The larger apodeme plate of the major chela indicates that a larger initial force is produced within this chela than in the minor chela whilst the significantly larger mechanical advantage of the major chela further increases the force produced at the chelal tip. This larger force acts through blunt, molariform teeth which form an effective crushing area contrasting with the interlocking triangular teeth of the minor chela which are better suited to tearing flesh.
- The larger, major chela occurred predominantly on the right side of the crab. Right-handedness has previously been recorded in other populations of *Carcinus maenas* and consistent with that observed in other populations of *C. maenas*. Such right-handedness

is characteristic of heterochelous crabs.

- Intraspecific differences in chelal mechanics, but not in chelal geometry, were recorded. The relationship between major chelal height, apodeme plate area and carapace width altered at around 40 mm CW in male crabs. Chelal height and apodeme plate area are both positively allometric relative to chelal height in large male crabs. In female and small male crabs these variables are isometrically related. Major chelal height, apodeme plate area and mechanical advantage of large male crabs (> 40mm CW) were significantly larger than those of female crabs of a similar size and those of small male crabs (< 40mm CW). Thus large male crabs are able to exert a significantly greater crushing force with their major chela than either female crabs or small male crabs. There were no differences in the relationships between chelal variables amongst small male and small female crabs nor were any differences found in large red and green crabs

- Analyses of stomach contents confirmed that *Carcinus maenas* has a broad diet in which *Mytilus edulis* forms an important component; mussels were found in the stomachs of 40.2% of crabs caught at Church Island and in 29.6% of the stomachs of crabs caught at Aberffraw.

- Despite the different chelal morphology of male and female crabs, their diets were broadly similar. The only significant difference found was that at Church Island male crabs ate significantly fewer barnacles than female crabs.

- Significant differences existed between the diets of red and green crabs. Red crabs had a narrower dietary range which may arise from their ability to out-compete green crabs. At Aberffraw the rate of inclusion of *Mytilus edulis* in the diet of red crabs was significantly greater than in the diet of green crabs which appeared to predate more heavily on barnacles. Green crabs caught at Church Island had a significantly higher inclusion rate of algae than their red conspecifics.

CHAPTER 4.

THE FORAGING BEHAVIOUR OF

CARCINUS MAENAS.

4.1. INTRODUCTION

Carcinus maenas is a natural predator of hard-shelled molluscs (e.g. Ropes, 1968; Elner, 1978; Elner, 1980; Raffaelli *et al.*, 1989; Chapter 3). It can become a pest on commercial stocks (Walne and Dean, 1972) and has the potential to influence population structure of its major prey species (Ebling *et al.*, 1964; Seed and Brown, 1978; Sanchez-Salazar *et al.*, 1987a). Prey selection by *C. maenas* on hard-shelled molluscs, and mechanisms underlying this selection are therefore of considerable interest and have been intensively studied (e.g. Elner, 1977; Elner and Hughes, 1978; Hughes and Elner, 1979; Jubb *et al.*, 1983; Cunningham and Hughes, 1984; Elner and Raffaelli, 1980; Ameyaw-Akumfi and Hughes, 1987).

Optimal foraging theory provides a useful framework in which the foraging behaviour of predators, including *Carcinus maenas*, has been investigated (reviewed by Hughes, 1980). Under the energy maximisation premise of this theory it is assumed that net energy intake is proportional to predator fitness and that predators should therefore seek to maximise their net rate of energy intake. This approach assumes that other factors which can affect the fitness of an organism, such as the risk of predation, do not interfere with its foraging behaviour. Net energy yield has been defined as the energy content of the prey item divided by the time taken to handle the prey item (E/Th); this is the prey value, or profitability of the individual prey item to the predator. When prey value is measured against some measure of prey size, then the optimal size of prey for that particular predator, i.e. that which maximises energy intake, can be determined. If the predator is foraging optimally, it should select prey of the most profitable size when presented with an abundance of prey in each size category. Optimal foraging is tested by presenting the predator with a choice of prey sizes in order to determine whether it actively selects those items which have previously been predicted to optimise energy intake (Hughes, 1980).

Carcinus maenas has been shown to feed optimally on the mussel, *Mytilus edulis*, selecting prey of a size which maximises its energy intake (Elner and Hughes, 1978; Jubb *et al.*, 1983; Cunningham, 1983; Ameyaw-Akumfi and Hughes, 1987). Although there is no agreement on the precise mechanism underlying such size selection, evidence presented in the above studies suggests that *C.maenas* actively selects the optimal size of prey. In these previous studies the ability of *C.maenas* to distinguish between prey of different size and value has been tested using mussels taken from a single location. However, the ability of *C.maenas* to distinguish between prey features other than shell length, which may affect the value of individual prey items, has not previously been investigated. Differences in shell morphology and flesh content have been documented for *M.edulis* from different shore elevations (Seed, 1968; 1980a; Chapter 2). Moreover differences in shell morphology in *Mytilus californianus* from different tidal elevations are known to influence opening techniques used by the lobster, *Panulirus interruptus* (Robles *et al.*, 1990). Differences in shell morphology may result in different handling times even amongst prey of similar shell length; for example, the degree of shell inflation in clams affected their vulnerability to *Cancer productus* predation (Boulding, 1984). Since prey value is defined as E/Th , this will be influenced by differences in either handling time or flesh content. It is conceivable, therefore, that even prey items of the same species and the same size but from different tidal elevations may have quite different values. Thus, a tidally foraging predator, such as *C.maenas*, could encounter prey items different in their profitability even within a single foraging bout. If *C.maenas* does indeed forage optimally it should be able to distinguish one prey type from another and select prey with the highest net energy yield. The question is, on what basis is this choice likely to be made?

Hughes and Elner (1979) found that dogwhelks, *Nucella lapillus*, from wave-exposed and wave-sheltered shores had different shell morphologies and flesh contents. Laboratory observations of the behaviour of *Carcinus maenas* on the two morphs of *N.lapillus* of the same size showed that although *C.maenas* “selected” the more profitable type of prey this selection arose passively as a result of crabs attacking every prey item encountered, but subsequently rejecting those prey items that did not yield within a limited period of time. The more profitable prey type were those with weaker

shells (which reduced E/Th) and these, therefore, tended to break within the limited persistence time. Thus, it has yet to be demonstrated that *C.maenas* can actively select between individuals of the same prey species, which are of the same size but which have different prey values.

This chapter documents the foraging behaviour of *Carcinus maenas* on *Mytilus edulis* taken from two contrasting locations, the high shore at Aberffraw on the open southwest coast of Anglesey, and the low shore at Church Island in the Menai Strait. Aberffraw is a wave-exposed shore whilst Church Island is sheltered from wave action and in Chapter 2 it was shown that mussels of similar size from these two sites were markedly different with respect to their shell morphology and flesh content and therefore potentially in their value as prey items for foraging shorecrabs. This chapter examines the foraging behaviour of crabs when presented with mussels from these two sites. Prey value curves are derived and predictions from these are compared to prey size selection in prey choice experiments. Seasonal changes in prey value curves which result from the seasonal variations in mussel flesh weights (see Chapter 2, section 2.3.2.) are also investigated.

4.2. MATERIALS AND METHODS

4.2.1. Collection and maintenance of *Carcinus maenas* and *Mytilus edulis*.

Naive *Carcinus maenas* used in the following experiments were collected between July and October 1996 by trawling off Traeth Melynog. This was done using a small Dory with a 2-metre wide beam trawl (0.5cm mesh size) trawling for 15 mins. Traeth Melynog is a sheltered south-facing bay located on Anglesey at the southwestern end of the Menai Strait, North Wales (see Chapter 2, Fig. 2.1). It is a gently sloping sandflat with no rocky outcrops and whilst the cockle, *Cerastoderma edule*, is abundant at this site the mussel, *Mytilus edulis*, is virtually absent. These crabs are unlikely therefore to have encountered mussels in their recent past and consequently were assumed to be “naive” with respect to their ability to handle these prey. Since one of the aims of this chapter was to compare the foraging behaviour and

handling times of *C.maenas* on mussels of differing shell morphology, it was considered important to use crabs with limited recent experience of handling mussels in order to minimise the likelihood that any differences arising might simply result from crabs being more experienced with mussels of a particular shell morphology.

In the laboratory, crabs were kept individually in plastic aquaria (30cm x 30cm x 20cm) filled to a depth of 5cm with seawater, under conditions of ambient light levels and water temperatures. Water was changed daily and any sediment and faecal debris siphoned off. Opaque plastic aquaria were used in order to minimise any visual disturbance which may influence crab foraging behaviour. Prior to the start of the first experiment crabs were maintained in the aquaria for one week so as to acclimatise them to laboratory conditions. During this period they were fed on mussel flesh in order to maintain their “naive” condition. To minimise potential differences in foraging behaviour arising from differences in chelal morphology, only male, green and undamaged crabs were used in these experiments (Kaiser *et al.*, 1990). If a crab stopped eating, moulted or died during the course of an experiment it was not replaced; instead the experiment was restarted using a new crab. It was important that single crabs were followed through each experiment because differences in handling ability are known to occur even amongst crabs of similar size.

Mytilus edulis were collected from the low shore at Church Island and the high shore at Aberffraw. At each site mussels were gathered from a limited area so as to standardise shell characteristics and flesh weights which are known to exhibit marked variations with tidal elevation (see Chapter 2 and references therein). To ensure that mussels used in these experiments were in good condition they were freshly collected every two weeks and kept in the laboratory under running seawater and conditions of ambient water temperature and light levels. Only unattached mussels which were free from epibionts and which had no apparent shell damage were presented to crabs.

4.2.2. Foraging behaviour of *Carcinus maenas*

The foraging behaviour of *Carcinus maenas* when presented with mussels from Aberffraw and Church Island was determined using two crabs from each of the

following size classes; 30-35, 40-45, 50-55mm and one from the size class 60-65mm carapace width (CW). This experiment consisted of two trials; in the first trial mussels from Aberffraw were presented to crabs whilst in the second trial mussels from Church Island were presented. Given repeated exposure to this prey *C.maenas* can significantly improve the efficiency with which it handles *Mytilus edulis* (Cunningham and Hughes, 1984). To be certain that any differences arising between trials was not due to improved handling efficiency, a three day period was allowed to elapse between trials, during which time crabs were fed only on mussel flesh for the first two days and left unfed for the third. This procedure also ensured that the hunger levels of the crabs were the same in both trials. It has previously been shown that *C.maenas* possess an endogenous circadian rhythm in locomotory activity (Naylor, 1958), care was therefore taken that crabs were offered mussels during the same period of the day, i.e. late morning to afternoon, to avoid any potential differences in foraging behaviour arising because of this rhythm.

In each trial a series of unattached mussels over a range of sizes (from 5 to 35 mm shell length) were presented individually and in random sequence to each crab. The shell length of each mussel was measured to the nearest 0.1 mm using vernier calipers, before being lowered gently into the aquaria. The techniques used by crabs to detect, attack and open prey items were recorded and the following events timed to the nearest second using a stopwatch: Breaking time (T_b): the time from when the mussel was first picked up, through any periods of prey manipulation, until the mussel was broken and the first bite of the exposed flesh taken, Eating time (T_e): the time from the first bite of flesh until the mussel shell was finally discarded; T_e also included any further periods of prey manipulation and shell breakage, Handling time (T_h = T_b + T_e): the time from when the mussel was first picked up until the shell was finally discarded having been opened and the flesh removed and eaten. Once a crab had discarded a successfully attacked prey item a period of one hour was allowed to elapse before the next mussel was introduced; this minimised any variation in handling times arising from differences in hunger levels. Shell remains discarded by the crab were removed from the aquaria before the next mussel was introduced thereby preventing any chemical or tactile stimuli from the discarded mussel shell influencing any

subsequent feeding behaviour of the crab on the unopened mussel.

Breaking, eating and handling times for mussels from each site were plotted against prey shell length and the relationship between these variables determined using linear regression (least squares, MINITAB). These data had to be linearised prior to regression analysis and several transformations of the data were tried, the most suitable transformation being that which maximised the correlation coefficient, r . The handling time-shell length regression equations were subsequently used in section 4.4 in the determination of prey value. The regression equations relating T_e to shell length for crabs feeding on mussels from Church Island were combined with the flesh weight-shell length equation determined for mussels from Church Island in July 1996 (see Chapter 2, Table 2.2) in order to determine the relationship between mussel size and gleaning efficiency for different sizes of crab. The time required to glean one gram of flesh from mussels of 10, 15, 20, 25 and 30 mm shell length was determined. Regression lines for breaking and handling time on shell length were compared for mussels from the two sites using analysis of covariance (general linear model, MINITAB). Evidence from the prey selection experiments (see section 4.3.4.) together with the resistance of crabs to feeding on prey items which required the lengthier opening techniques suggests that edge-chipping and boring will rarely be used in the field, and therefore the relationship between breaking times, handling times and shell length were also calculated excluding these data. This was done using linear regression (least squares, MINITAB) and relationships between breaking times, handling times and shell length obtained when crabs fed on mussels from Church Island were again compared with those obtained when crabs fed on mussels from Aberffraw using analysis of covariance (general linear model, MINITAB).

4.2.3. Prey value.

Prey value was determined for mussels from Aberffraw and Church Island, defined as E/T_h , where E is the energy content or dry flesh weight of the prey item and T_h is the handling time. This definition, however, does not take into account differences in the metabolic costs arising through different stages of the handling

process (see Hughes, 1980). Since energy content and handling time can both be predicted from shell length, curves relating prey value to prey length were derived by dividing the predicted yield of flesh (using the equations determined for mussels from Church Island and Aberffraw in July 1996, Tables 2.2 & 2.3) by the predicted handling time for each size of mussel eaten (determined in section 4.2.2.). From these curves the optimal size of mussel, where net energy intake (E/Th) is maximised, could be predicted and compared to the size of preferred mussel as determined in the prey size selection experiments (section 4.2.4).

It was shown earlier (Chapter 2) that the relationship between dried flesh weight and shell length varied throughout the year. Consequently, the predicted prey value curves will also be expected to vary seasonally. This effect was investigated by using the flesh weight-shell length regression equations from two months in which the regression slopes varied most significantly (Tables 2.2 & 2.3). For Church Island mussels this was September 1996 and February 1997 whilst for Aberffraw mussels it was November 1996 and June 1997.

The relationship between flesh weight and prey length varies not only seasonally but also amongst mussels of comparable size from the two sites. Thus, in certain months, the flesh content of mussels from Aberffraw was greater than those for Church Island mussels whilst in other months the reverse was true (see Chapter 2. Fig. 2.12A). By using Figure 2.12A, two months were identified in which the difference in flesh weight was significant, one in which Aberffraw mussels contained a relatively greater amount of flesh (March 1996) and one in which Church Island mussels contained a relatively greater amount of flesh (July 1996). The flesh weight-shell length regression equations determined for mussels from both sites in these months (see Tables 2.2 & 2.3) were subsequently combined with the handling time-shell length regression equations to investigate intersite variations in prey value curves.

4.2.4. Prey size selection.

Prey size selection was investigated under conditions of unlimited prey availability. This experiment consisted of two trials. In the first trial crabs were

presented with mussels from Aberffraw and in the second trial they were presented with mussels from Church Island. A three day period was allowed to elapse between the two trials in which crabs were fed mussel flesh during the first two days and left unfed for the third, thus returning crabs to their “naive” state and standardising hunger levels between trials. Crabs were housed individually in aquaria and the same crabs were used in both trials to allow direct comparison. The protocol of each trial was the same; thus three crabs in each of the following size classes; 30-35, 40-45, 50-55, 60-65mm CW were presented with five unattached mussels in each of the following five size classes; 5-10, 10-15, 15-20, 20-25 and 25-30mm shell length which were placed haphazardly over the aquaria floor. Crabs were allowed to feed for six hours each day for seven consecutive days. The six hours feeding period represented a single tidal cycle and therefore the period of time that would perhaps normally be available to a tidally foraging predator. The number of mussels eaten in each size class was recorded every two hours and the shells of those that had been eaten were removed and replaced with mussels of a similar size. To maintain constant prey availability. Shell remains were removed to prevent chemical and tactile stimuli from the opened mussels influencing the behaviour of crabs on unopened prey. Shell remains were inspected to determine which opening technique had been used. The size class of the most frequently eaten mussels was considered to be the preferred size class and this was compared to the size class previously predicted to be the most profitable.

The above experiment was then repeated using a mixture of mussels from Church Island and Aberffraw. Each crab was presented with five Church Island and five Aberffraw mussels in each of the following size classes; 5-10, 10-15, 15-20, 20-25 and 25-30mm shell length so that a total of 50 mussels were presented to each crab. Mussels were colour coded with small dabs of coloured Tippex® so that they could easily be distinguished from each other during the experimental period. Each crab was allowed to feed on a group of mussels for eight hours during which time the number of mussels eaten was recorded after four hours and at the end of the eight hour period. After four hours any mussels that had been eaten were replaced with ones of similar size to maintain constant prey availability. This procedure was repeated every day for seven consecutive days.

4.3. RESULTS

4.3.1. Foraging behaviour

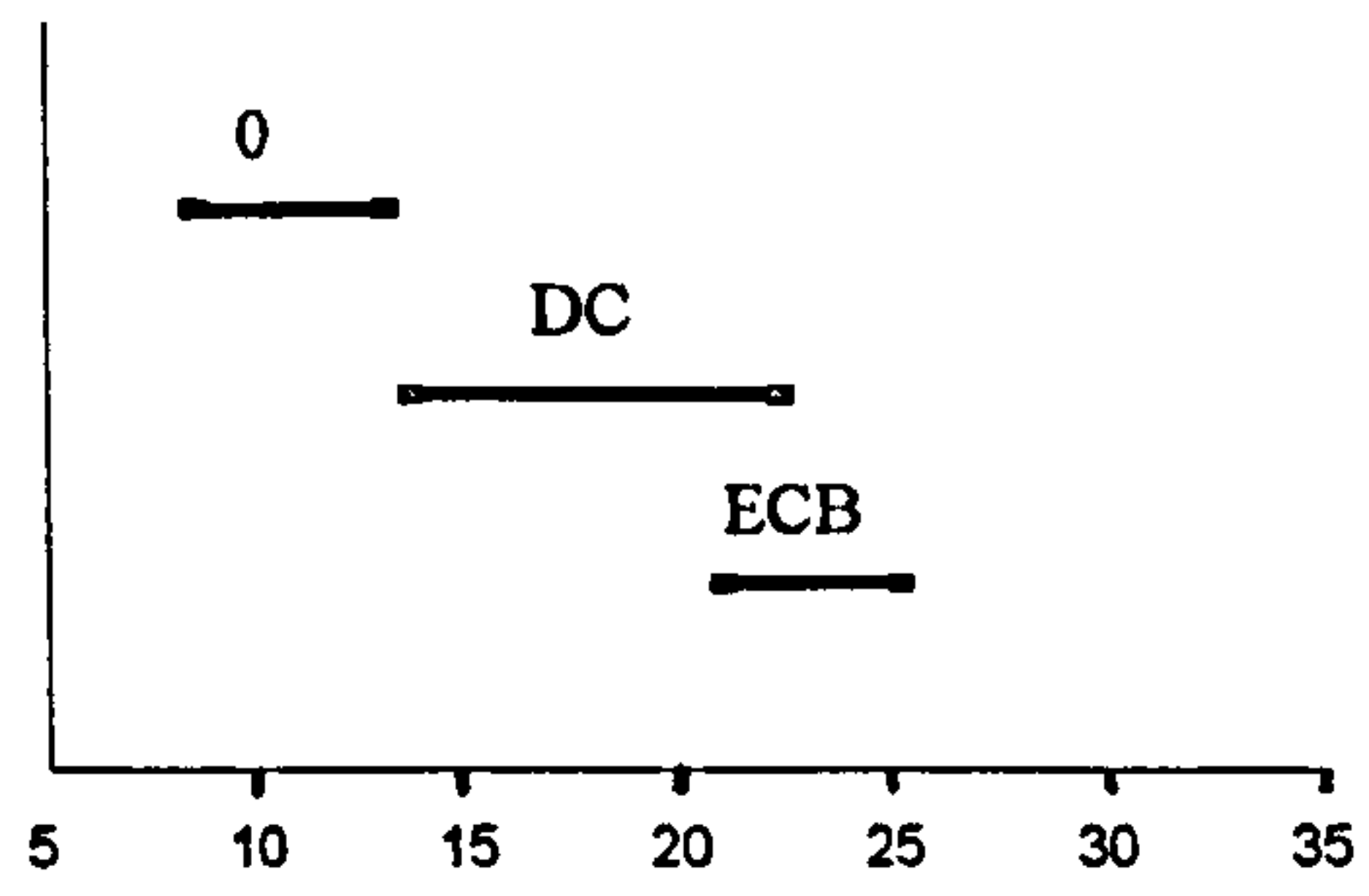
Foraging was generally prefaced by a period of vigorous movement of the maxillipeds (mouthparts) and by movement of the chelae in front of the mouth. When mussels were placed into the aquaria, crabs would orientate their antennules in the direction of the prey and these would start to flick at an increased rate. The crab would then move in the general direction of the prey sweeping the aquarium floor with its outstretched chelae and pereopods (walking legs). Mussels were picked up by the chelae or, if they were first touched by the pereopods, swept under the body and brought forwards to the chelae. This indicated that *Carcinus maenas* probably located its prey mainly by touch; vision seemed to be used in prey detection only when a prey item moved.

When feeding on mussels, *Carcinus maenas* uses its dimorphic chelae for different functions. The smaller (minor) chela holds the mussel whilst the larger (major) chela attempts to break the shell. If the mussel is successfully opened, the minor chela and the maxillipeds are then used to separate the flesh from the shell; because of its large size and general lack of dexterity, the major chela is rarely used for this purpose. Individual mussels were thoroughly gleaned and pieces of mussel shell were often passed through the mouthparts several times before being discarded; shell fragments which were accidentally dropped were swept up by the chelae and anterior walking legs to be further gleaned. After a piece of mussel shell had been thoroughly gleaned, it was discarded, often at chelal length from the crab before the crab moved away in search of other prey items.

A range of prey-size dependent opening techniques were observed. Outright crushing: the smaller mussels (Fig.4.1 A&B) were held by the minor chela and immediately crushed outright by the major chela. There was no manipulation of the prey prior to the application of force and the site of application of this force was indiscriminate. Only one crushing attempt was required to break the mussel. The minor chela and mouthparts of the crab often had difficulty separating the flesh from the shell

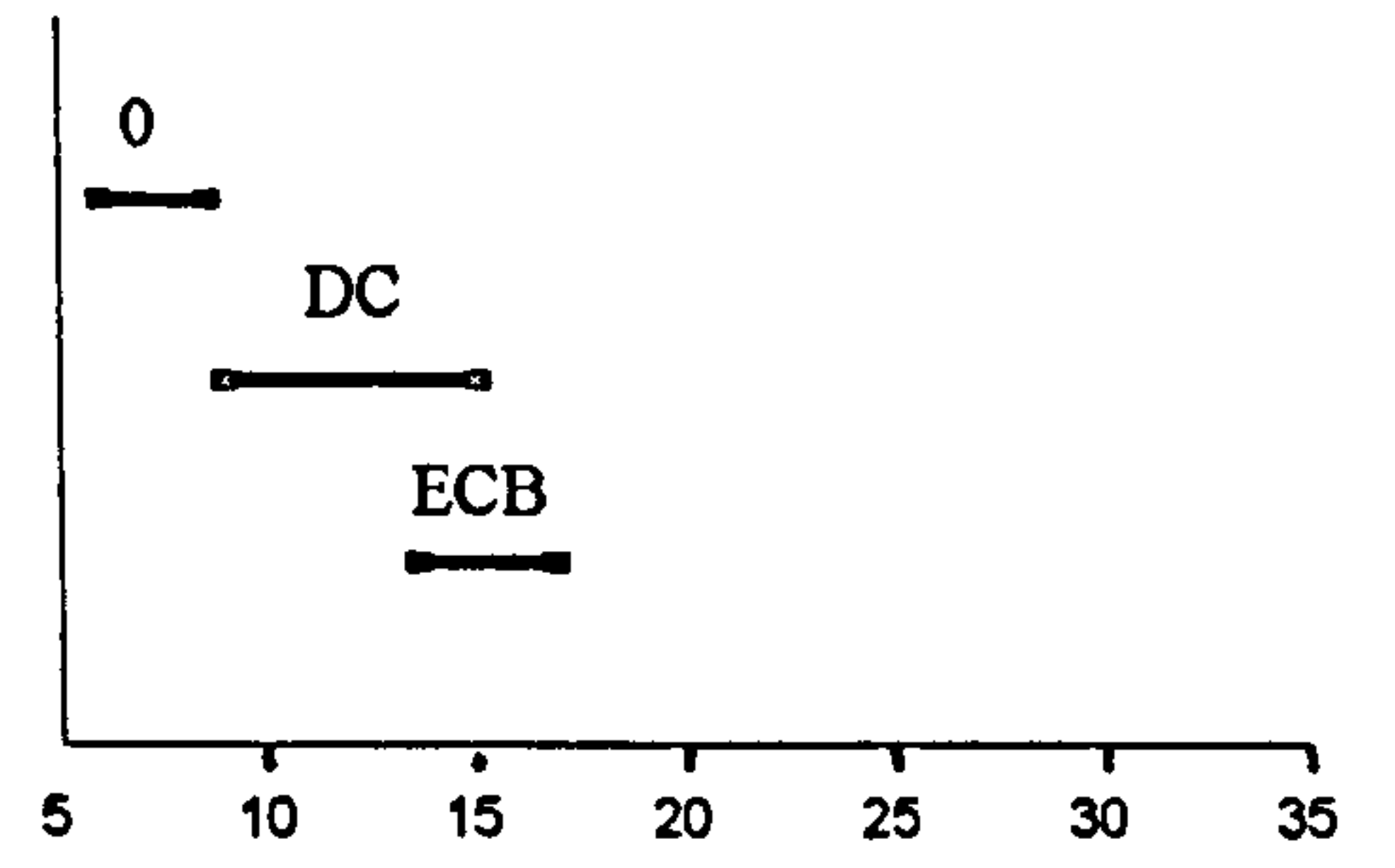
Figure 4.1. The relationship between opening technique and shell length when *Carcinus maenas* fed on *Mytilus edulis* from Church Island (A) and Aberffraw (B). The sizes of mussels opened by outright crushing (O), directed crushing (DC) and edge-chipping/boring (ECB) are presented for crabs in the following size classes; 30-35, 40-45, 50-55 and 60-65mm CW.

A

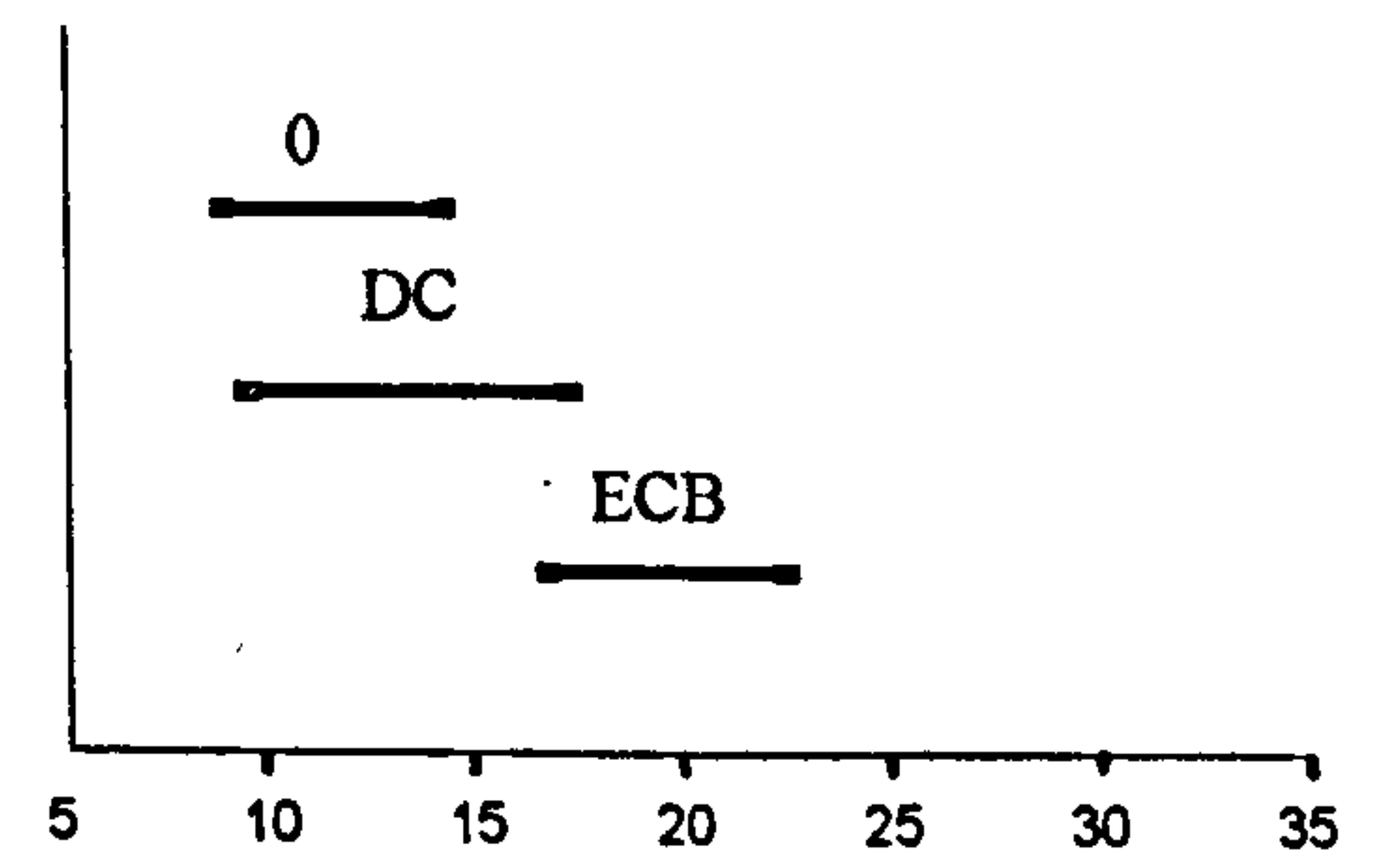
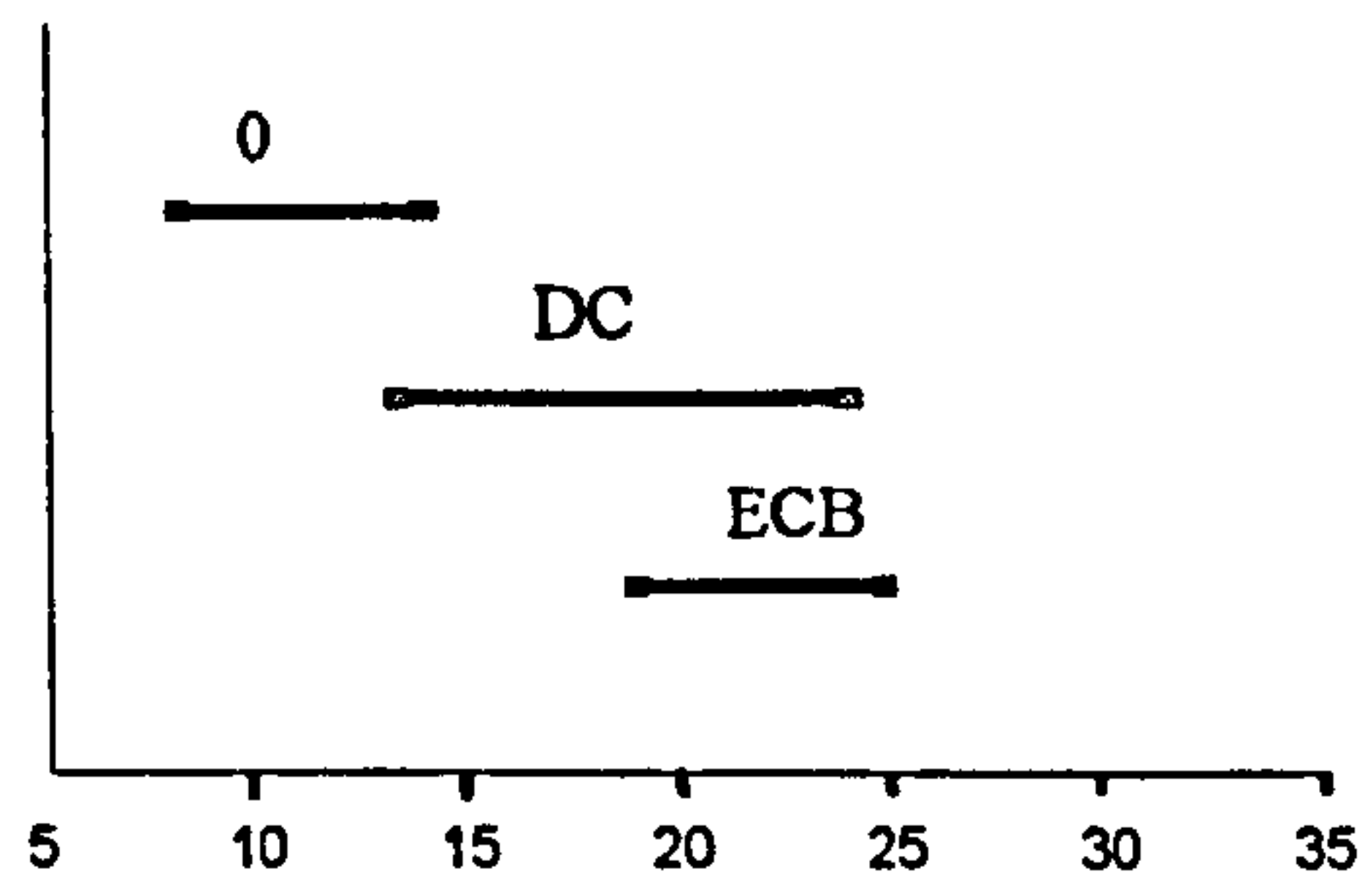


B

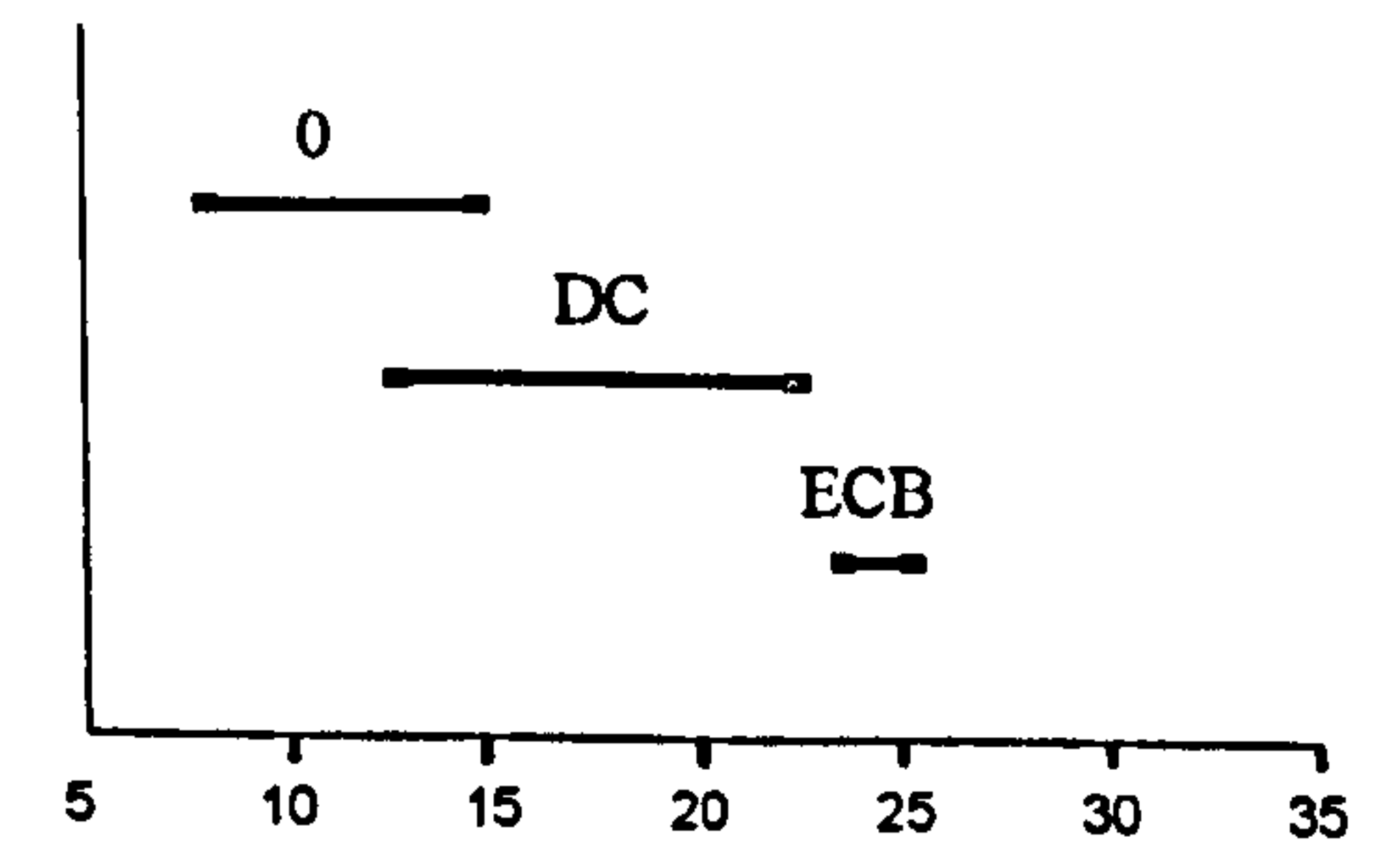
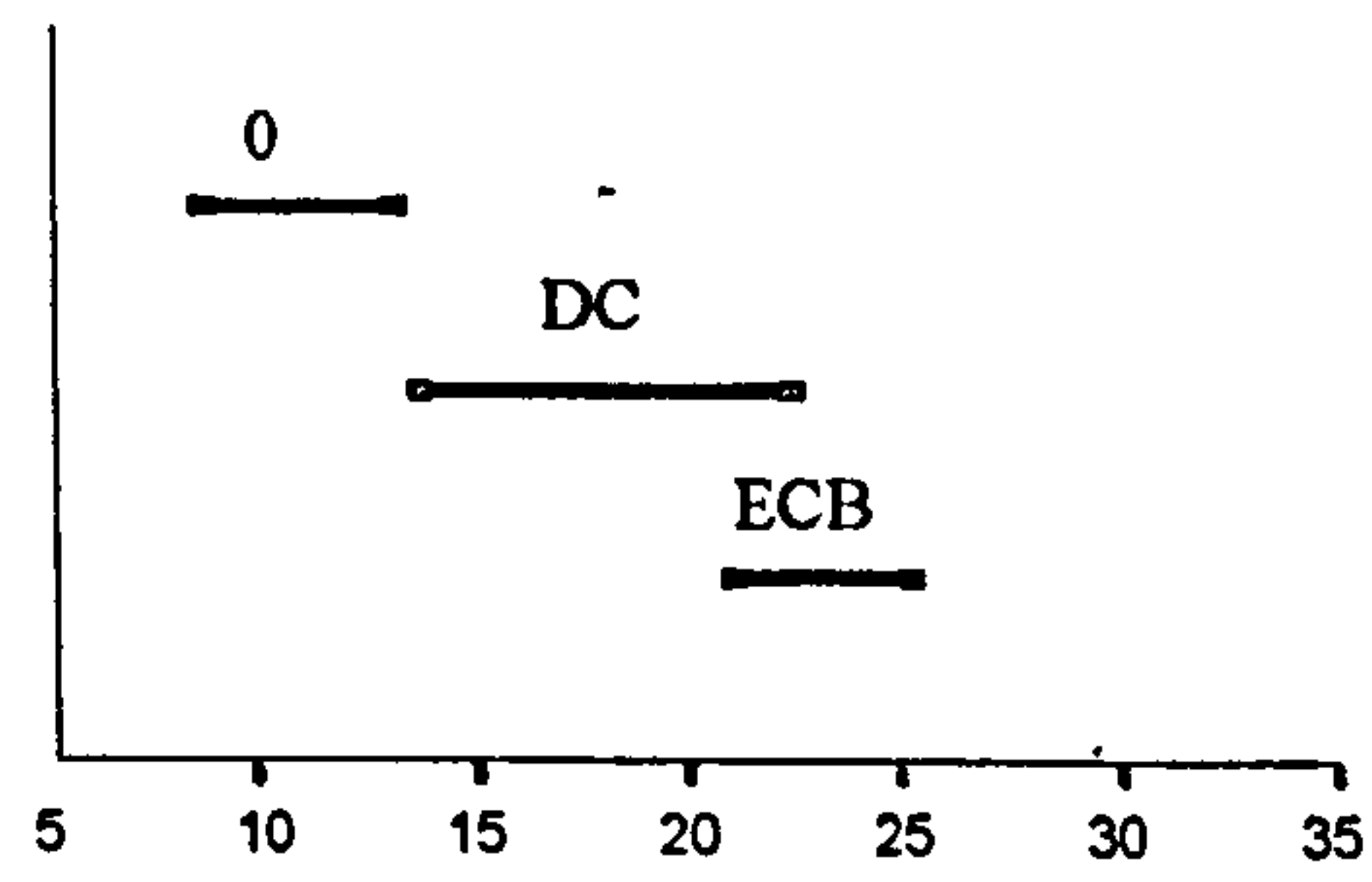
30-35 mmCW



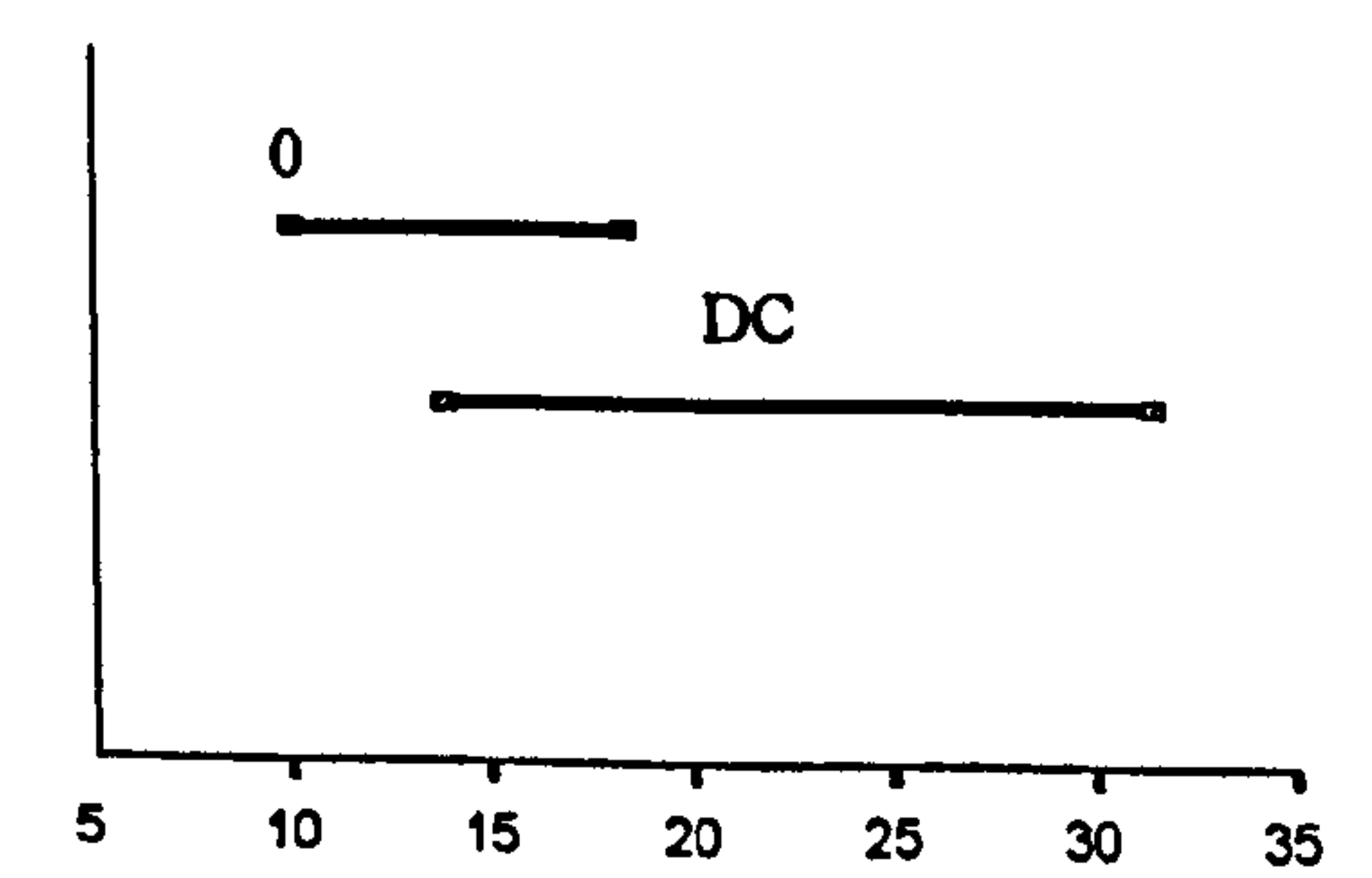
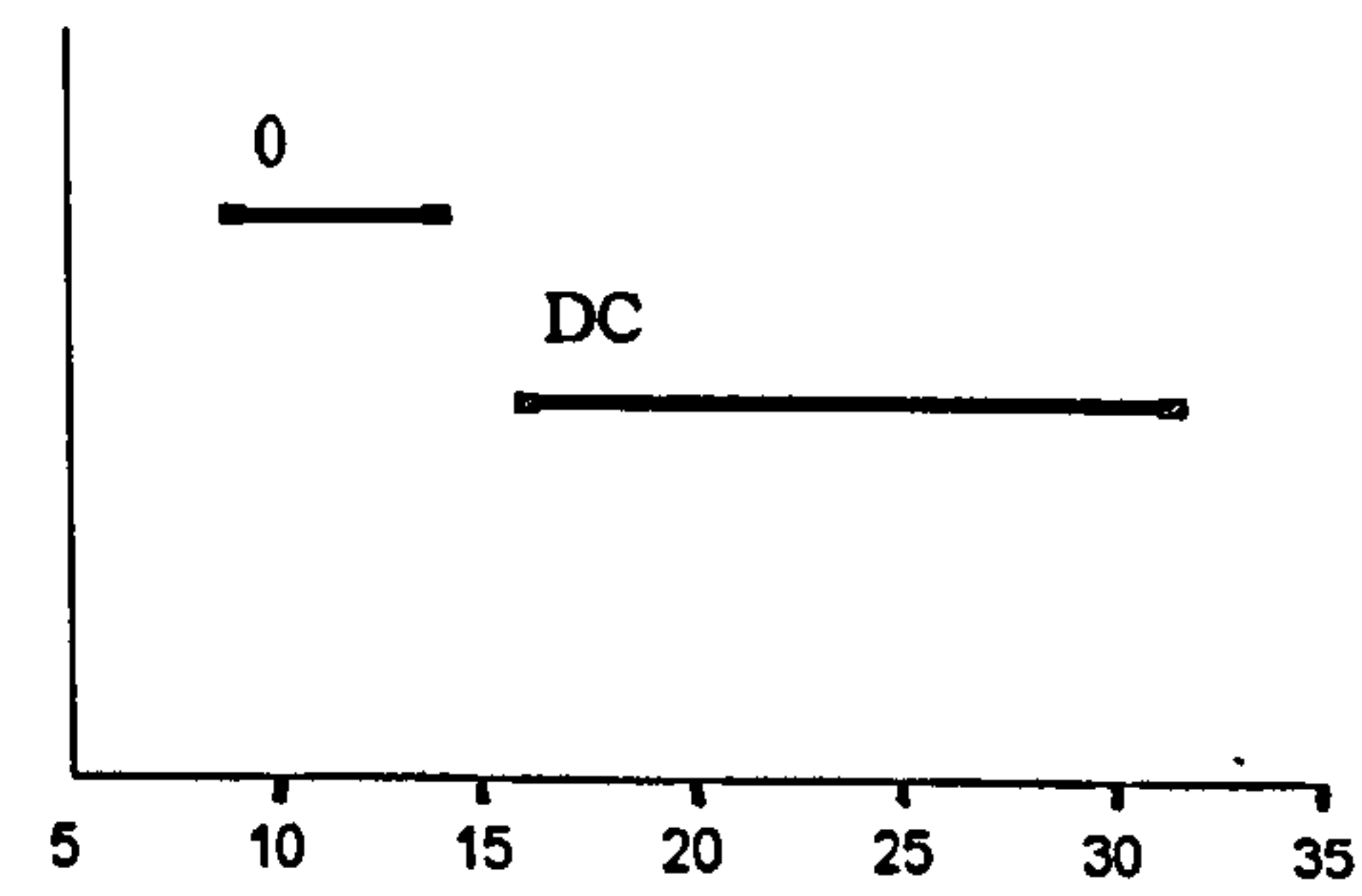
40-45mm CW



50-55 mm CW



60-65mm CW



Shell Length (mm)

and consequently fragments of the shell were usually ingested and there were few shell remains when this opening technique was employed. Directed crushing: larger mussels (Fig. 4.1 A & B) were rotated by the chelae, mouthparts and anterior walking legs prior to the first application of force from the major chela. Crushing attempts were directed on either the umbo or the posterior end of the mussel. These larger prey items could not be opened successfully with a single application of force and mussels were repeatedly reorientated and rotated in the major chela by the mouthparts, the minor chela and the anterior walking legs between successive crushing attempts. Crushing attempts could alternate between the umbo and the posterior of the shell but crabs opened significantly more prey by umbo crushing than by posterior crushing amongst mussels from both Church Island ($\chi^2 = 6.78$, d.f.=1, $p < 0.01$) and Aberffraw ($\chi^2 = 20.43$, d.f.=1, $p < 0.01$). The weaker umbonal end of the prey was also the area most frequently attacked first. The plane of force application was either lateral or dorso-ventral across the mussel valves. Using this technique mussel shells had to be broken several times to allow the crab full access to the mussel flesh. Boring: this rather time-consuming opening technique was used on larger mussels when attempts to open them by crushing had failed. The propus tip of the major chela was used to “bore” through the shell by applying force at a weak spot usually close to the hinge region, whilst the minor chela and anterior walking legs were used to steady the prey. Eventually a hole would be formed by the tip of the propus and this was subsequently enlarged by a sawing action of the propus. The two shell valves were then separated either by insertion of the more slender minor chela into the hole in order to sever the adductor muscles or by the insertion of both chelae into the hole to pull the two shell valves apart. Mussel shells attacked in this way were usually left relatively intact except for a characteristic hole where the attack had taken place. Edge-chipping: this time consuming method of attack, like boring, was also used on large mussels which did not succumb to repeated crushing attempts. Here the minor chela and anterior pereopods supported the mussel, usually by the umbo, whilst the major chela applied a dorsal-ventral shearing force over the posterior regions of the valves. Repeated application of force resulted in pieces of the posterior shell being gradually chipped off. The crab persisted with this method until sufficient shell had been chipped away to enable the slender minor chela to be

inserted between the valves and the posterior adductor muscle severed; alternatively the major chela could be inserted and twisted between the valves thus forcing them apart. Mussel shells opened in this way typically remained intact but had a very ragged edge to the posterior regions of the shell valves. Edge-chipping was never observed on large mussels from Aberffraw whereas a mixture of edge-chipping and boring was used to open large mussels from Church Island.

From Figure 4.1 A & B it can be seen that the use of different opening techniques was dependent on prey size. Moreover, the prey size at which there was a change between techniques varied with crab size. Thus, larger crabs could open larger mussels by outright crushing than could smaller crabs and consequently did not resort to the lengthier handling methods until they larger prey items were encountered. Indeed the largest crab never used the boring or edge-chipping techniques on the size range of mussels presented to it in this experiment. Crabs appeared to employ a characteristic attack sequence and the lengthier opening methods of boring and edge-chipping were only ever applied after crushing attempts had proved unsuccessful. However, it should be noted that it was quite difficult to get crabs to apply the boring and edge chipping techniques since larger mussels were generally rejected when crushing attempts failed and several large mussels had to be presented successively before these lengthier handling techniques were adopted. Furthermore there was no evidence that these handling methods were used during the prey size-selective feeding experiments (section 4.3.4) and they were never observed when crabs were foraging on groups of mussels (see Chapter 5). This suggests that these lengthier techniques are rarely used in the field. Moreover, chelal damage was sometimes observed in crabs which were forced to use the boring technique or which persisted with crushing attempts on large mussels, clearly demonstrating the real risk involved when feeding on particularly resistant prey items.

4.3.2. The relationships between shell length and breaking, eating and handling times.

The relationships between mussel shell length and breaking (T_b) and handling

(Th) times were best described by exponential functions which could be linearised by \log_e transformation of the dependent (y) variable (Tables 4.1 & 4.2). Eating time (Te) had been expected to vary as a cubic function of shell length since flesh weight and shell length were related in this way (see Chapter 2, Tables 2.2 & 2.3); however, like Tb and Th, a logarithmic relationship best described this relationship (Tables 4.1 & 4.2). Data for the two smallest crabs (30-35mm CW) were combined as there were rather few data points for separate analyses and when the data were plotted together there appeared to be no difference in the breaking or handling times between these two crabs. This did not apply to larger crabs (40-45mm and 50-55mm CW) and these data were consequently kept separate. The relationships between shell length and breaking, eating and handling times for crabs feeding on Church Island and Aberffraw mussels are shown in Figures 4.2 - 4.4 and Figures 4.5 - 4.7 respectively.

It can be seen from Figures 4.2 - 4.7 that Tb, Te, and Th are highly variable even between mussels of similar size. Variations in Tb probably arise from differences in the shell strength of individual mussels and may also be affected by the initial orientation of the mussel in the major chela when the force is first applied. Differences in Te may be due to variations in the amount of flesh between individual mussels or to differing crab hunger levels. Since Th is defined as the sum of Tb and Te variations in Th can arise from variability in either of these factors. Variations in Tb, Te and Th between crabs of similar size may result from differences in chelal morphology or previous experience of handling mussels (although the latter had hopefully been minimised by using “naive” crabs). It is also evident from Figures 4.8 & 4.9 that the predicted curves relating Tb, Te and Th to prey length also vary with crab size, probably due to the increased chelal strength of larger crabs. Figure 4.10 shows the time taken for crabs of different size to glean one gram of mussel flesh. Eating times for smaller crabs were greater than for larger crabs especially amongst the larger prey items. Generally the time required to glean one gram of flesh from mussels of different sizes declined to a minimum value with increasing prey length before increasing again amongst larger mussels (Fig. 4.10). The elevated eating times for the smaller prey items probably reflects the difficulty in gleaning these mussels whilst the elevated times for larger mussels may reflect a decreasing hunger level whilst feeding on these mussels.

Table 4.1. The relationship between shell length and breaking (Tb), eating (Te) and handling (Th) times for *Carcinus maenas* feeding on *Mytilus edulis* from Church Island as determined by least squares regression (MINITAB) for two crabs in each of the following size classes, 30-35, 40-45, 50-55mm CW and one crab from the 60-65mm CW size class. The relationships are derived from data which includes breaking, eating and handling times obtained when mussels were opened using the edge-chipping and boring techniques.

Crab Cw (mm)	Dependent variable (y)	Independent variable (x)	a	b	r	n
30-35 (1+2)	ln Tb	Shell length	-1.03	0.547	0.90	21
40-45 (1)	"	"	-0.55	0.423	0.83	17
(2)	"	"	0.43	0.67	0.92	20
50-55 (1)	"	"	-0.76	0.394	0.92	16
(2)	"	"	0.25	0.286	0.93	20
60-65	"	"	3.00	0.068	0.69	18
30-35 (1+2)	ln Te	Shell length	3.04	0.222	0.89	21
40-45 (1)	"	"	3.72	0.158	0.81	17
(2)	"	"	3.56	0.142	0.92	19
50-55 (1)	"	"	2.31	0.232	0.91	16
(2)	"	"	2.99	0.134	0.94	20
60-65	"	"	4.05	0.089	0.87	18
30-35 (1+2)	ln Th	Shell length	2.07	0.368	0.93	21
40-45 (1)	"	"	2.53	0.286	0.85	17
(2)	"	"	3.35	0.181	0.91	20
50-55 (1)	"	"	1.90	0.297	0.97	16
(2)	"	"	2.40	0.201	0.95	20
60-65	"	"	4.37	0.086	0.91	18

a,b = coefficients in the linear regression equation $\ln y = a + bx$.
r = product moment correlation coefficient
n = number of mussels eaten.
(1+2) = data combined for the two crabs.
(1) = data from the first crab in that size class
(2) = data from the second crab in that size class

Table 4.2. The relationship between shell length and breaking (Tb), eating (Te) and handling (Th) times for *Carcinus maenas* feeding on *Mytilus edulis* from Aberffraw as determined by least squares regression (MINITAB) for two crabs in each of the following size classes, 30-35, 40-45, 50-55mm CW and one crab from the 60-65mm CW size class. The relationships are derived from data which includes breaking, eating and handling times obtained when mussels were opened using edge-chipping and boring techniques.

Crab CW (mm)	Dependent variable	Independent variable	a	b	r	n
30-35 (1+2)	ln Tb	Shell length	-1.58	0.529	0.93	23
40-45 (1)	"	"	-1.42	0.481	0.90	15
(2)	"	"	-0.73	0.340	0.86	20
50-55 (1)	"	"	-0.90	0.352	0.83	15
(2)	"	"	0.17	0.281	0.88	14
60-65	"	"	1.85	0.155	0.88	20
30-35 (1+2)	ln Te	Shell length	3.19	0.218	0.75	24
40-45 (1)	"	"	3.10	0.224	0.80	15
(2)	"	"	3.58	0.163	0.77	20
50-55 (1)	"	"	2.80	0.181	0.90	15
(2)	"	"	3.51	0.136	0.87	14
60-65	"	"	3.65	0.122	0.86	19
30-35 (1+2)	ln Th	Shell length	2.08	0.342	0.91	24
40-45 (1)	"	"	2.29	0.308	0.93	14
(2)	"	"	3.14	0.208	0.81	20
50-55 (1)	"	"	2.39	0.230	0.91	14
(2)	"	"	2.81	0.206	0.93	14
60-65	"	"	3.98	0.117	0.90	21

a,b = coefficients in the linear regression equation $\ln y = a + bx$.
r = product moment correlation coefficient
n = number of mussels eaten.
(1+2) = data combined for the two crabs.
(1) = data from the first crab in that size class
(2) = data from the second crab in that size class

Figure 4.2. Breaking times are plotted against shell length of *Amytilus edulis* from Church Island for *Carcinus maenas* of different carapace widths. Data were combined for the two crabs in the smallest size class of 30-35mm CW; (1 + 2), but kept separate for the two crabs in the 40-45 and 50-55 mm CW size classes; (1), (2). Only one crab was used in the size class 60-65mm CW. The linear regression equations presented in Table 4.1 are used to fit lines to the raw data.

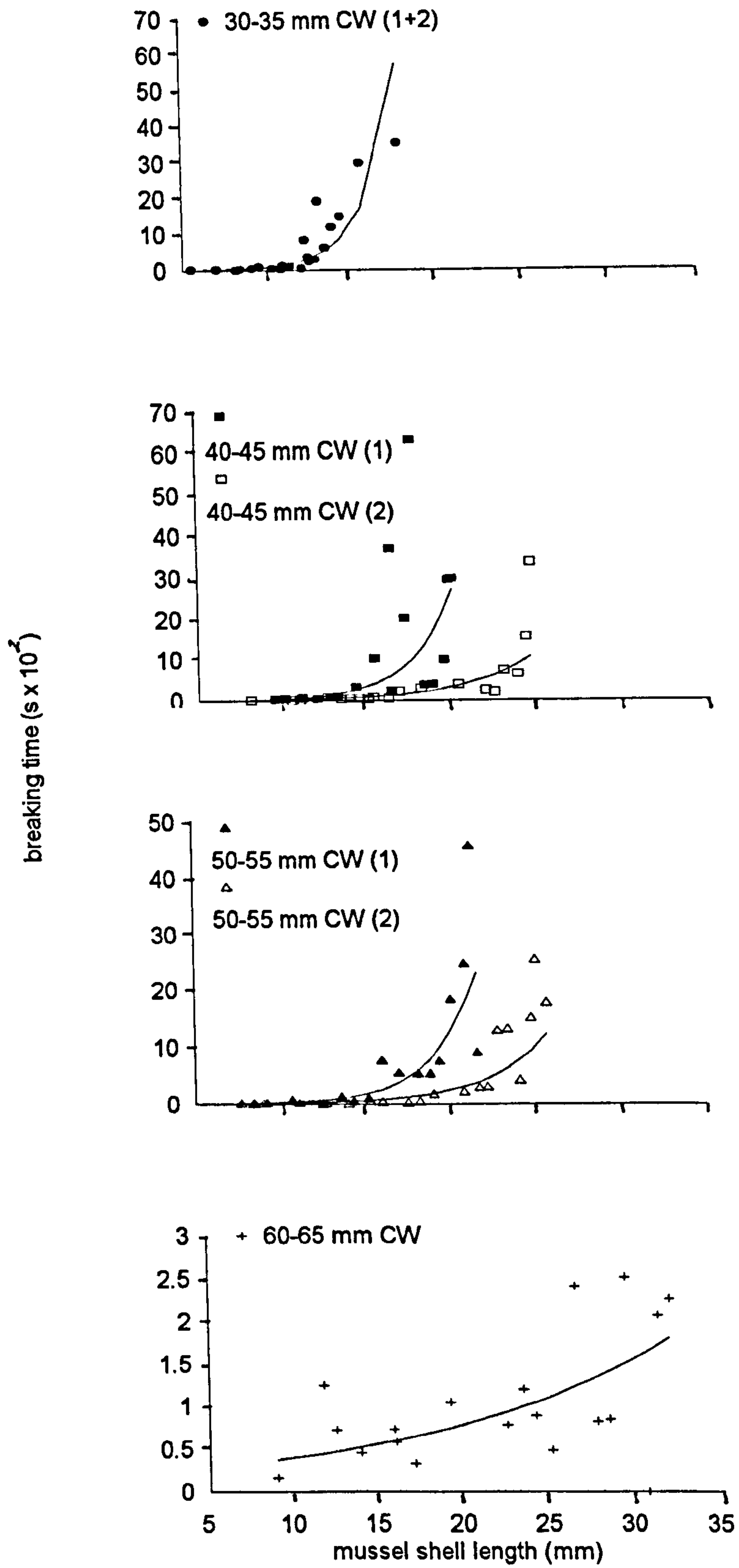


Figure 4.3. Eating times are plotted against shell length of *Mytilus edulis* from Church Island for *Carcinus maenas* of different carapace widths. Data were combined for the two crabs in the smallest size class of 30-35mm CW; (1 + 2), but kept separate for the two crabs in the 40-45 and 50-55 mm CW; (1), (2) size classes. Only one crab was used in the size class 60-65mm CW. The linear regression equations presented in Table 4.1 are used to fit lines to the raw data.

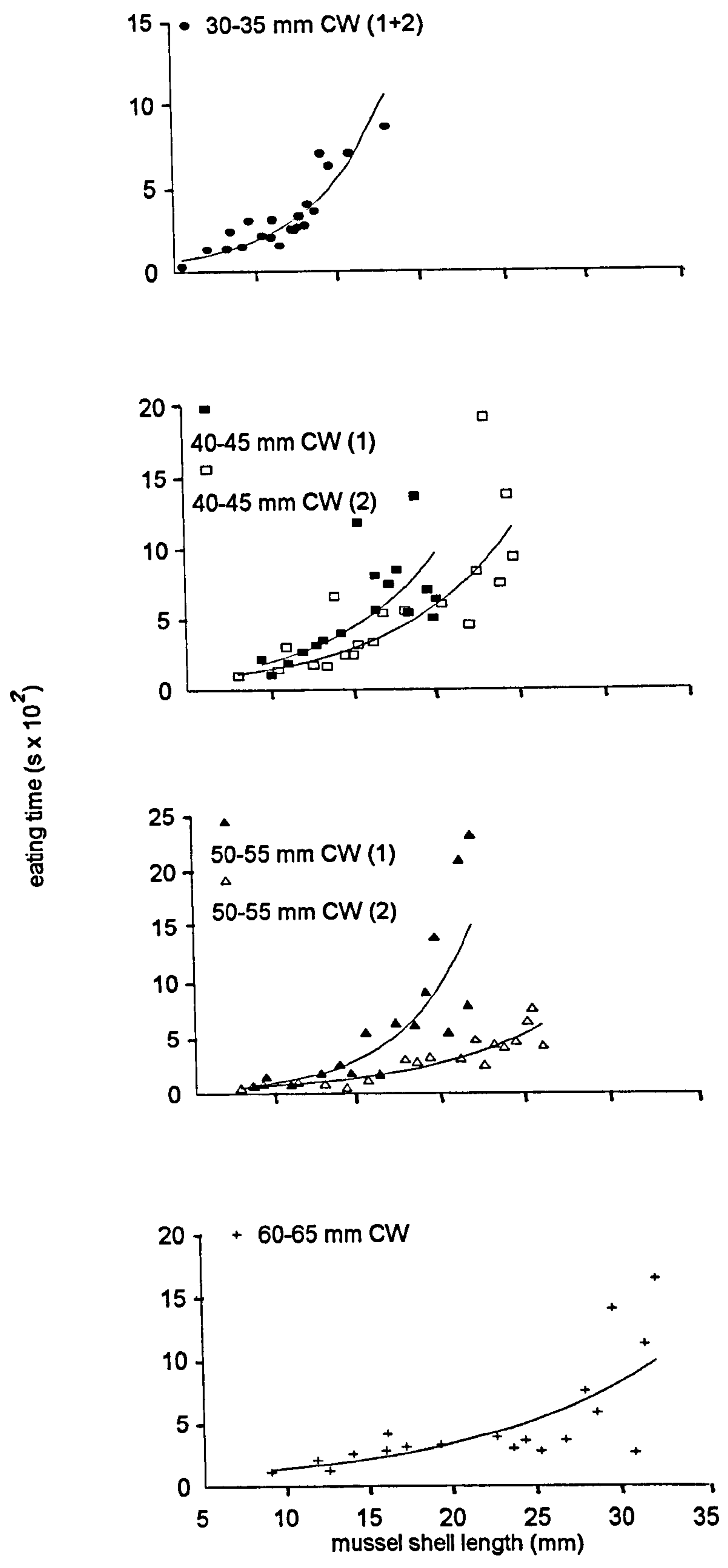


Figure 4.4. Handling times are plotted against shell length of *Mytilus edulis* from Church Island for *Carcinus maenas* of different carapace widths. Data were combined for the two crabs in the smallest size class of 30-35mm CW; (1 + 2), but kept separate for the two crabs in the 40-45 and 50-55 mm CW size classes; (1), (2). Only one crab was used in the size class 60-65mm CW. The linear regression equations presented in Table 4.1 are used to fit lines to the raw data.

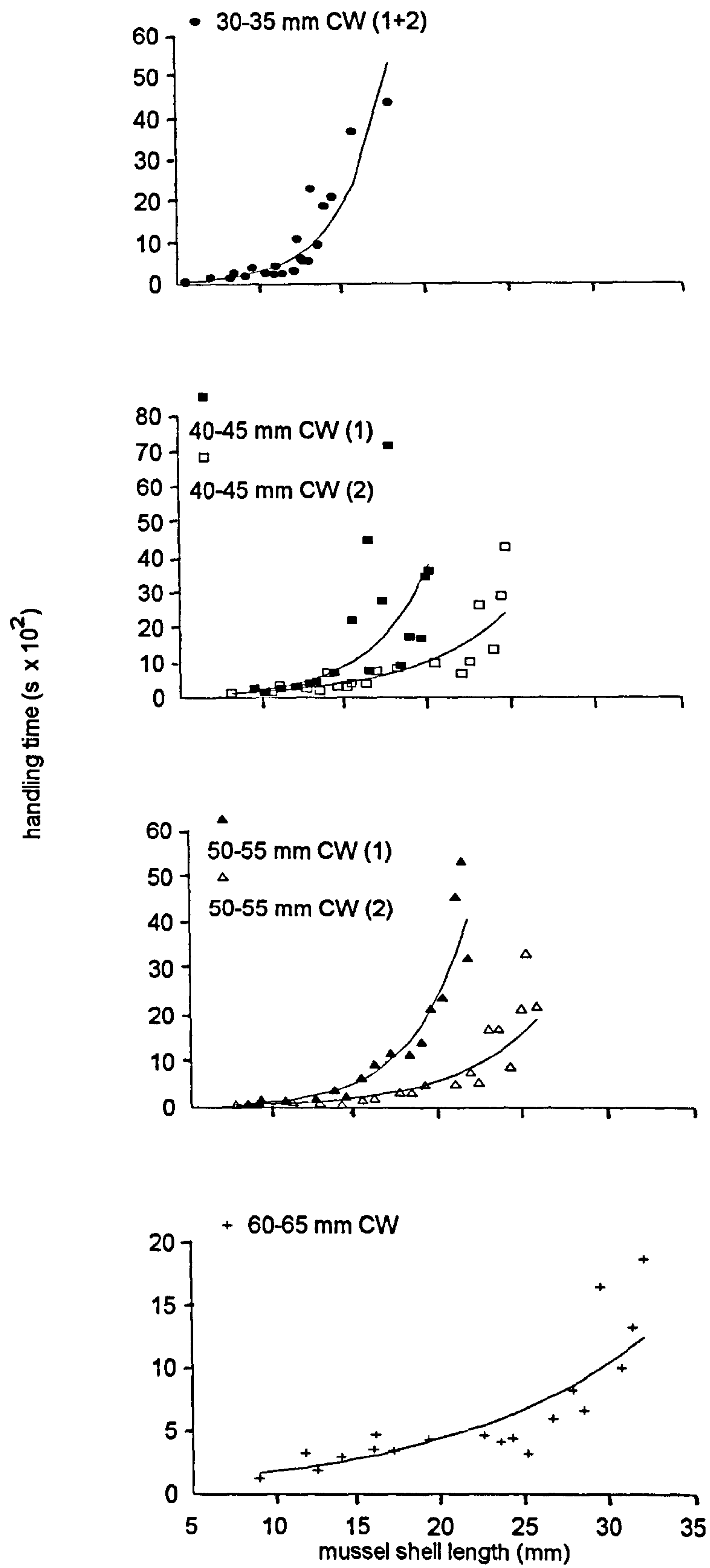


Figure 4.5. Breaking times are plotted against shell length of *Mytilus edulis* from Aberffraw for *Carcinus maenas* of different carapace widths. Data were combined for the two crabs in the smallest size class of 30-35mm CW; (1 + 2), but kept separate for the two crabs in the 40-45 and 50-55 mm Cwsize classes; (1), (2). Only one crab was used in the size class 60-65mm CW. The linear regression equations presented in Table 4.2 are used to fit lines to the raw data.

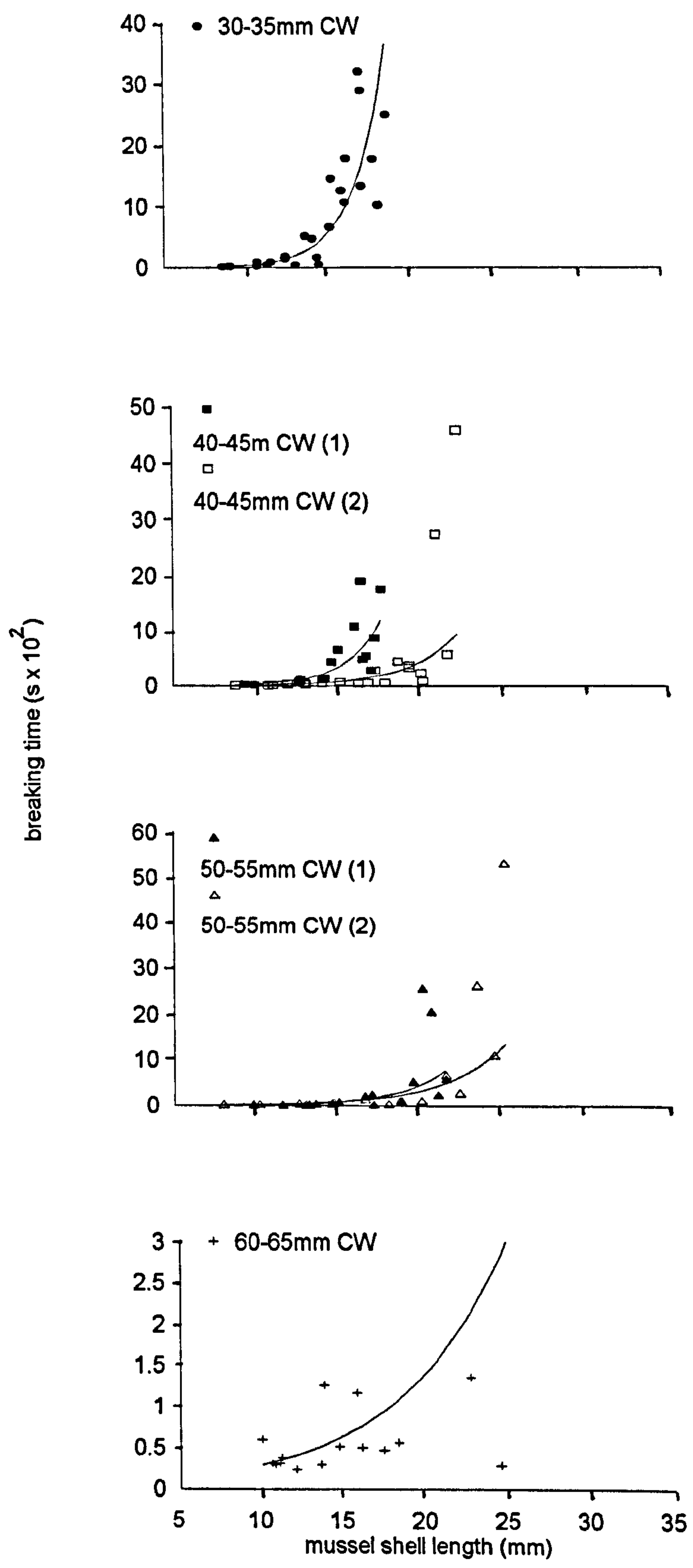


Figure 4.6. Eating times are plotted against shell length of *Mytilus edulis* from Aberffraw for *Carcinus maenas* of different carapace widths. Data were combined for the two crabs in the smallest size class of 30-35mm CW; (1 + 2), but kept separate for the two crabs in the 40-45 and 50-55 mm CW size classes; (1), (2). Only one crab was used in the size class 60-65mm CW. The linear regression equations presented in Table 4.2 are used to fit lines to the raw data.

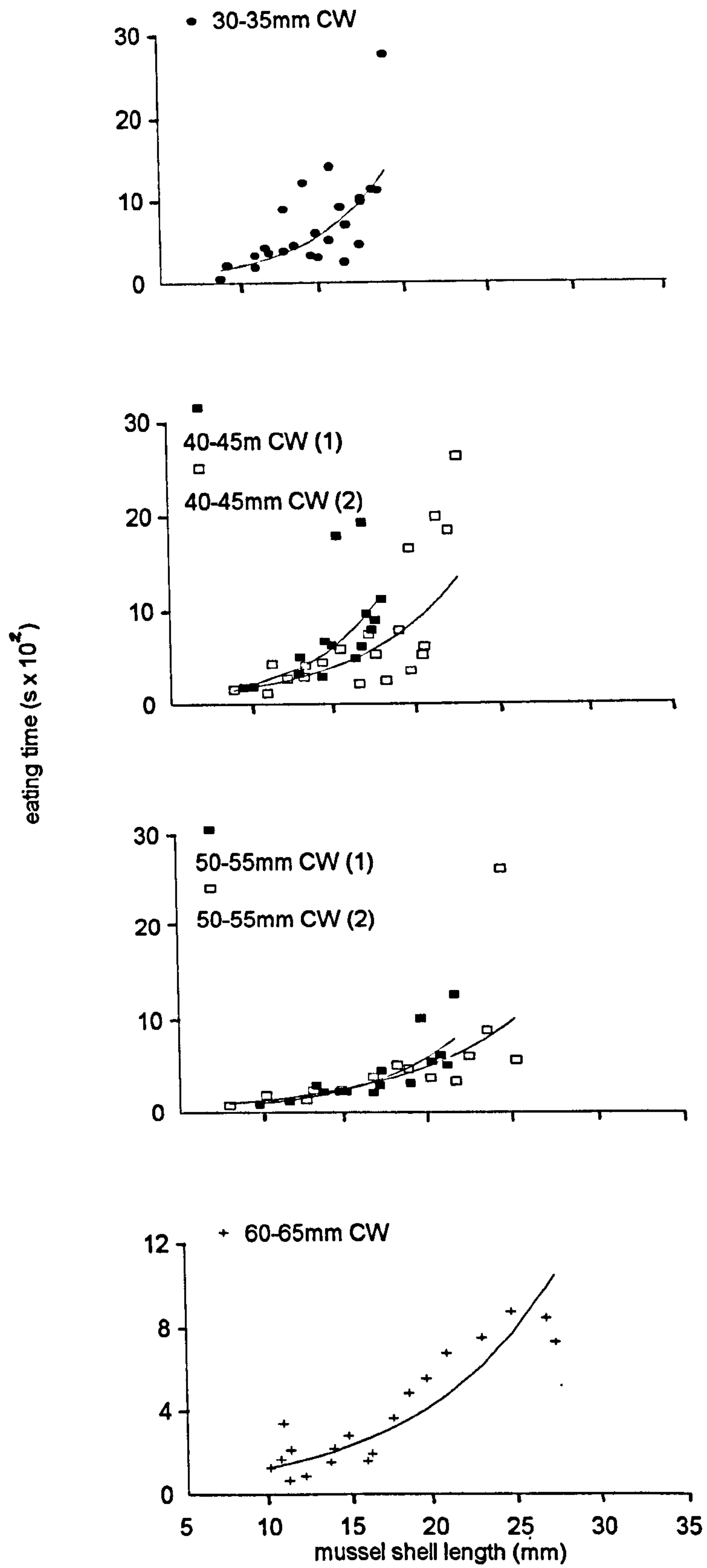


Figure 4.7. Handling times are plotted against shell length of *Mytilus edulis* from Aberffraw for *Carcinus maenas* of different carapace widths. Data were combined for the two crabs in the smallest size class of 30-35mm CW; (1 + 2), but kept separate for the two crabs in the 40-45 and 50-55 mm Cwsize classes; (1), (2). Only one crab was used in the size class 60-65mm CW. The linear regression equations presented in Table 4.2 are used to fit lines to the raw data.

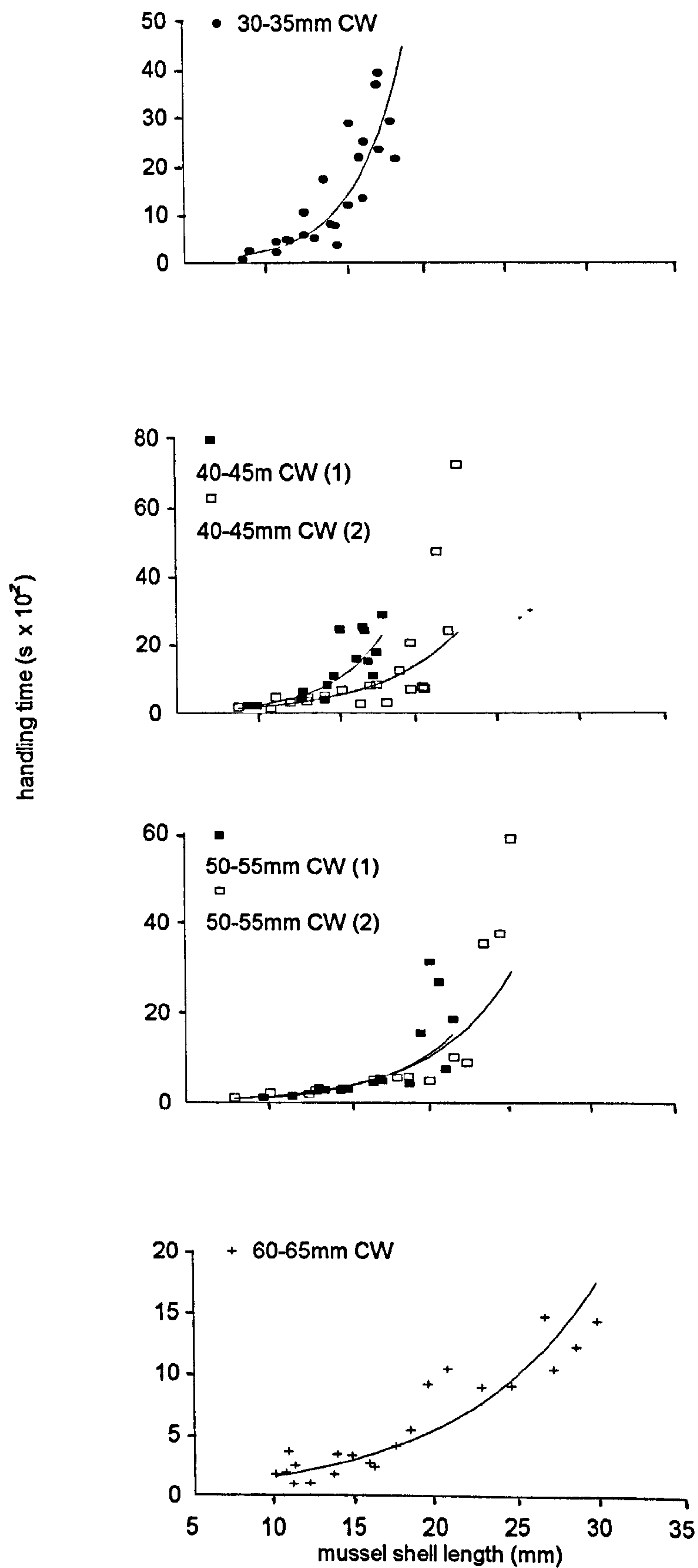


Figure 4.8. A summary of the relationships between prey length and breaking, eating and handling times for *Carcinus maenas* of different sizes feeding on *Mytilus edulis* from Church Island. Data were combined for the two crabs in the smallest size class of 30-35mm CW; (1 + 2), but kept separate for the two crabs in the 40-45 and 50-55 mm CW size classes; (1), (2). Only one crab was used in the size class 60-65mm CW. Relationships are derived from the regresion equations presented in Table 4.1.

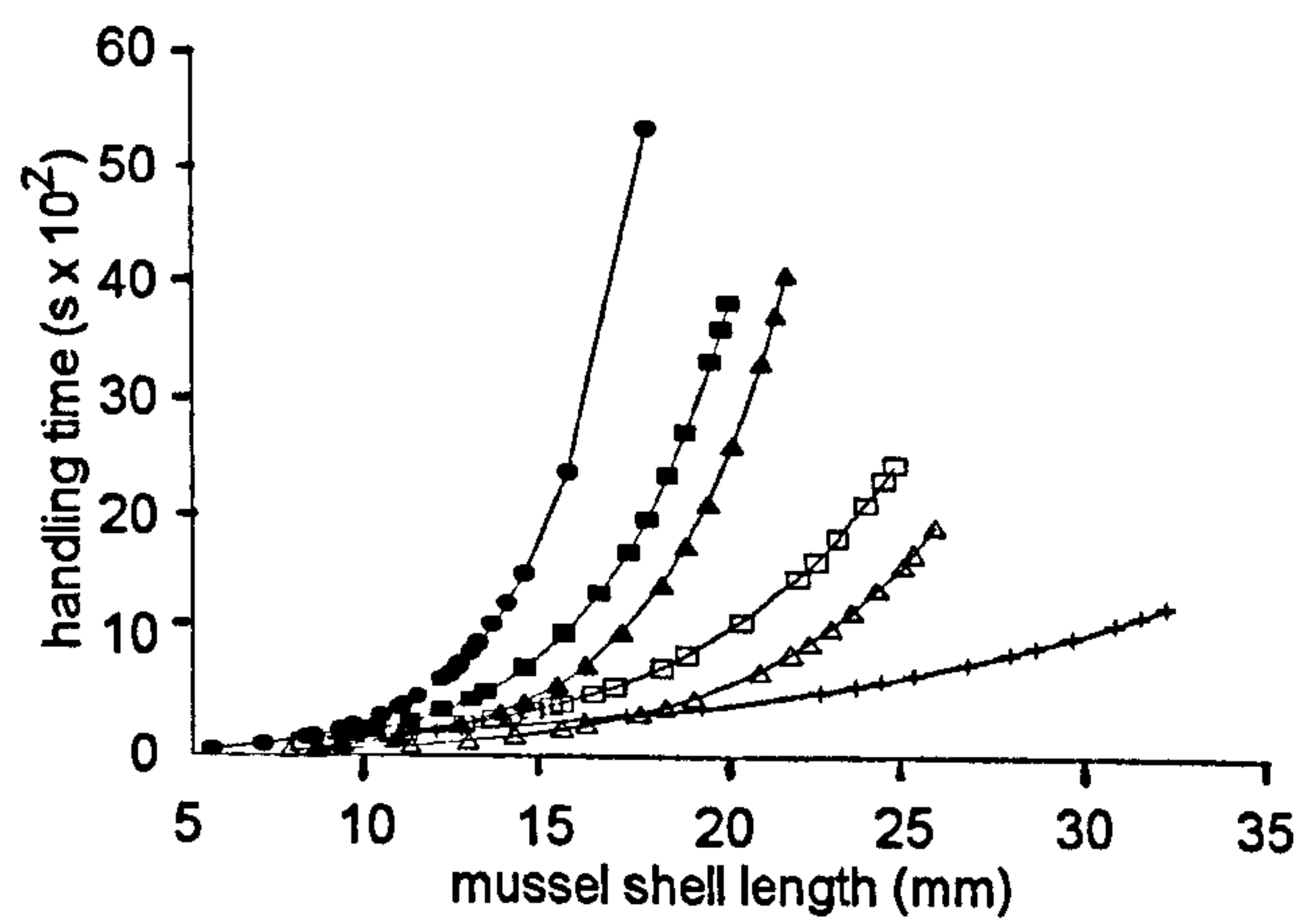
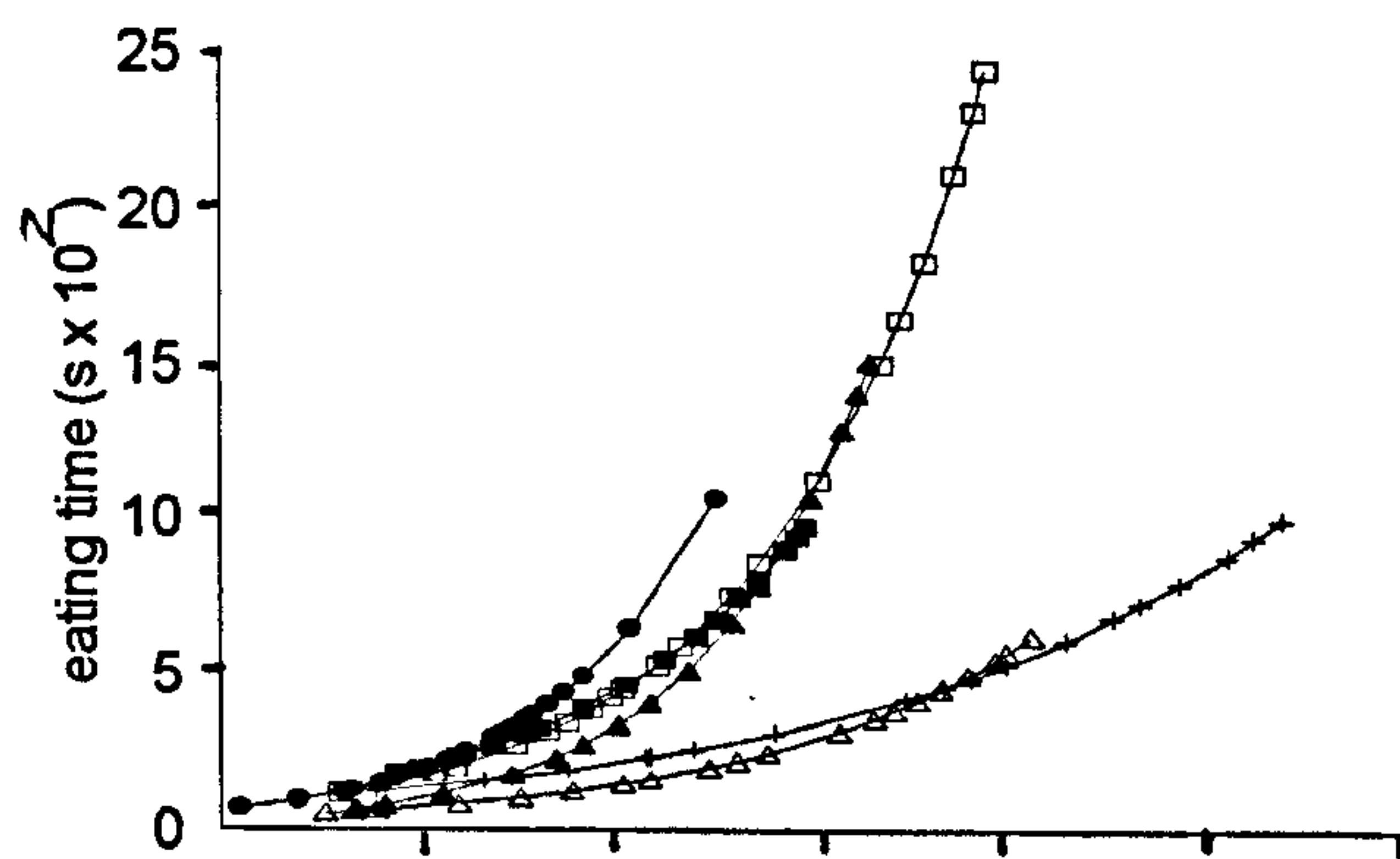
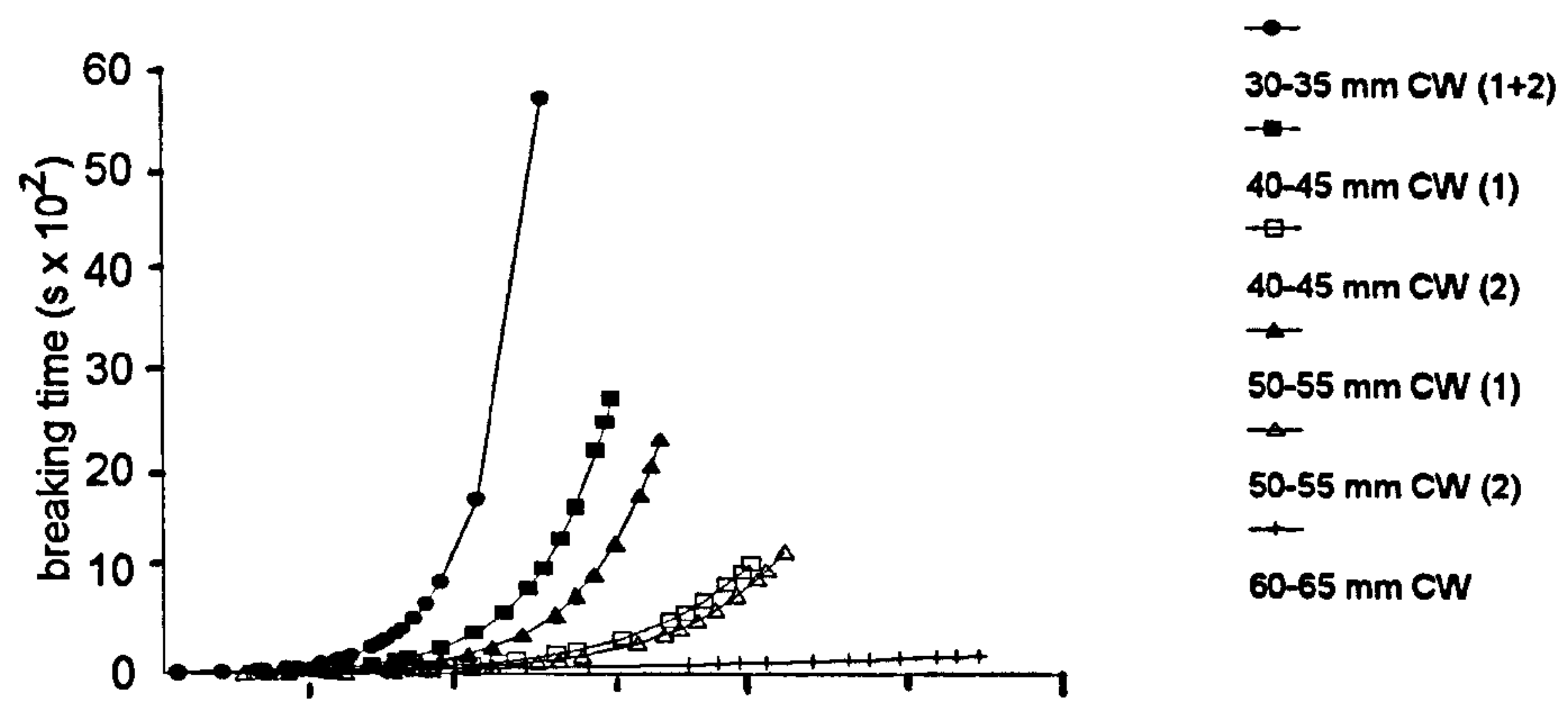


Figure 4.9. A summary of the relationships between prey length and breaking, eating and handling times for *Carcinus maenas* of different sizes feeding on *Mytilus edulis* from Aberffraw. Data were combined for the two crabs in the smallest size class of 30-35mm CW; (1 + 2), but kept separate for the two crabs in the 40-45 and 50-55 mm CW size classes; (1), (2). Only one crab was used in the size class 60-65mm CW. Relationships are derived from the regresion equations presented in Table 4.2.

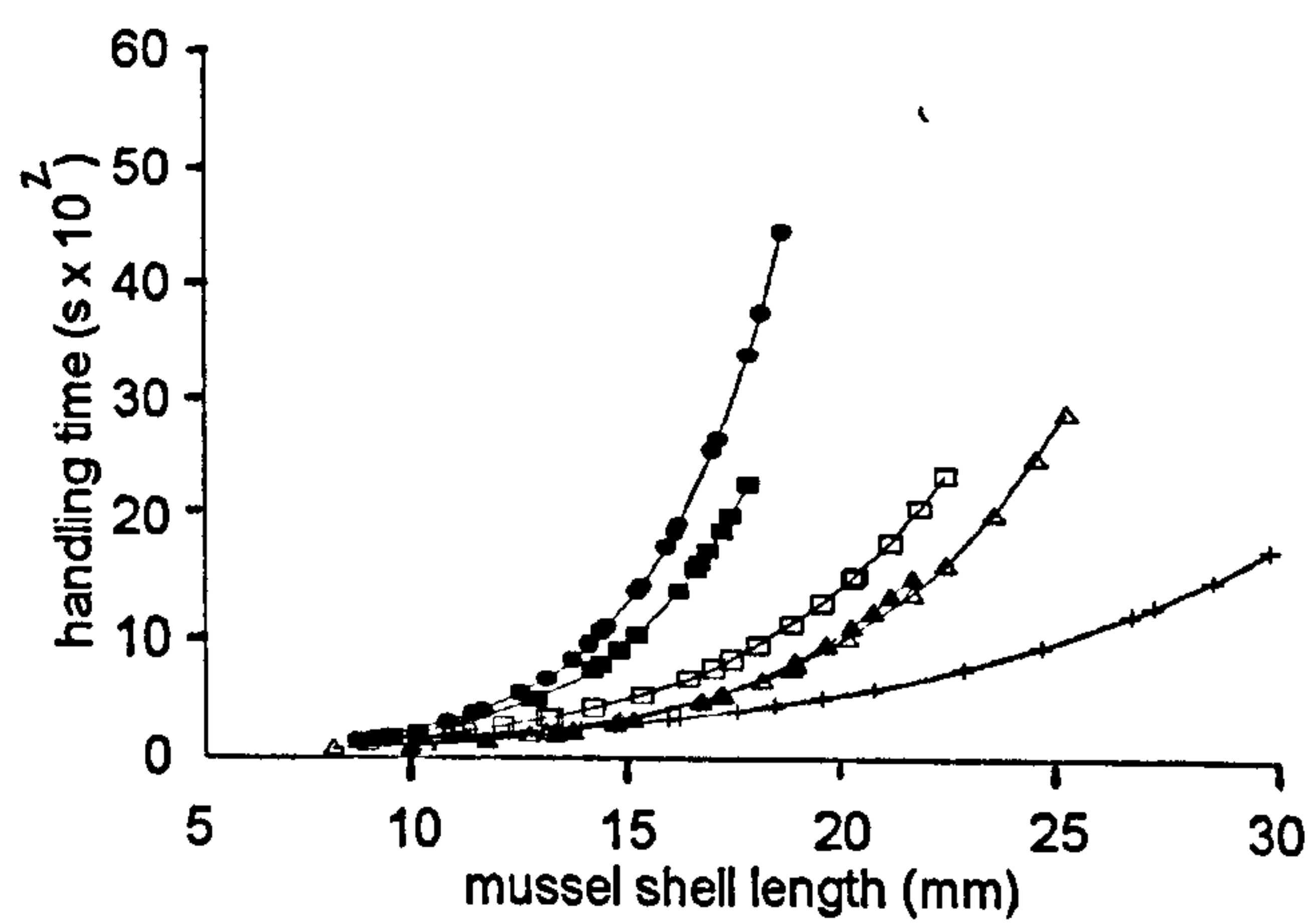
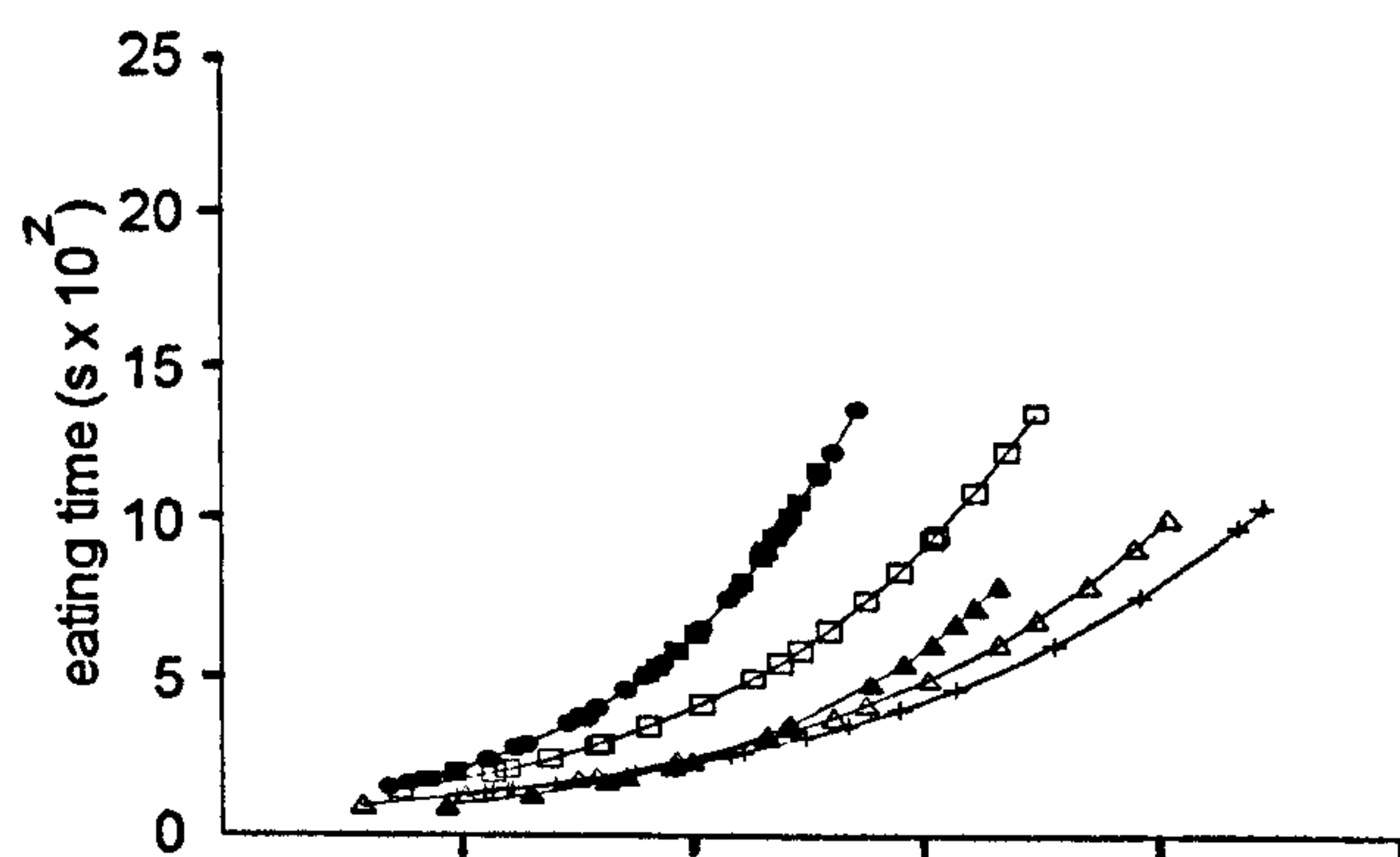
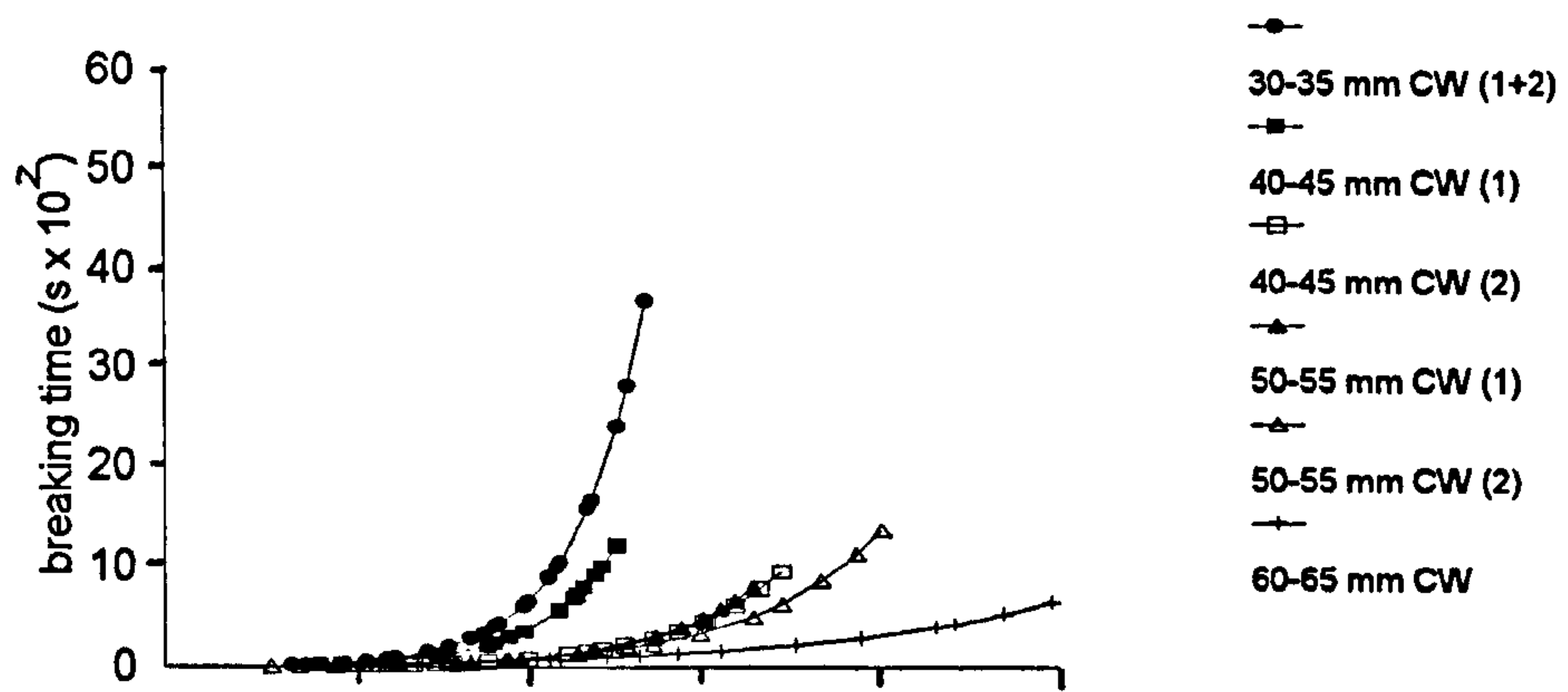
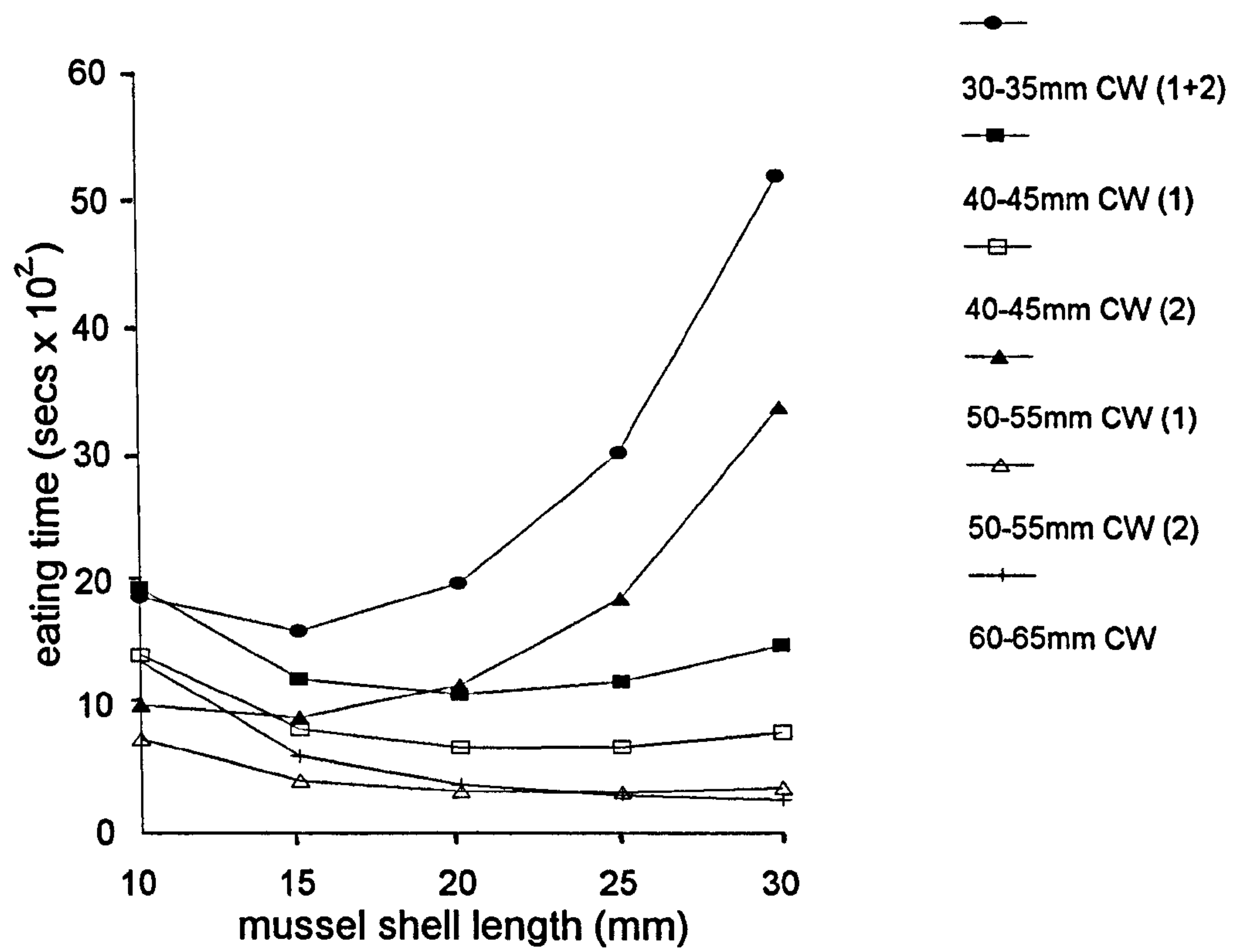


Figure 4.10. The time required by four size groups of *Carcinus maenas* to eat 1 gram of dried flesh when feeding on Church Island mussels. Data were combined for the two crabs in the smallest size class of 30-35mm CW; (1 + 2), but kept separate for the two crabs in the 40-45 and 50-55 mm CW size classes; (1), (2). Only one crab was used in the size class 60-65mm CW. Eating times were obtained using the regression equations relating eating time to shell length presented in Table 4.1.



Breaking and handling times derived when data from mussels opened by boring or edge-chipping is excluded is presented in Table 4.3. From Table 4.4. it can be seen that in general there was no difference between the breaking and handling times of mussels from Church Island and Aberffraw. The exceptions may be due to individual differences in mussel shape and the chelal morphology of the crab, both of which are quite variable. Differences between eating times of crabs feeding on Church Island and Aberffraw mussels were not tested because the eating time-shell length regression equations did not meet the assumptions of the general linear model in that the errors were non-normally distributed (see Fry, 1993, pg. 86).

4.3.3. Prey value.

Lawton and Hughes (1985) found that when the cancrid crab, *Cancer pagurus*, fed on the gastropod, *Nucella lapillus*, different prey value curves were obtained when a single regression equation of handling time-shell length was used and when several regression equations, each associated with a different opening technique, were used. Consequently in this study prey value curves were derived using both the regression equations obtained when data from the lengthier opening techniques were included (Tables 4.1 & 4.2) and those obtained when these data were excluded (Table 4.3). Prey value curves derived for Church Island and Aberffraw mussels are shown in Figures 4.11A & 4.12A. All prey value curves are domed in shape but the inclusion of data when boring and edge-chipping were used effectively elevates the predicted handling times over the whole size range (Figs. 4.11A & 4.12A) and thus depresses the predicted prey values. Furthermore, the predicted optimal prey size was larger when these data were excluded from the analysis.

Prey value curves also varied seasonally according to the flesh content of the mussels. When a flesh weight-shell length equation from a summer month (September at Church Island and June at Aberffraw) was used prey values at both sites were higher than when a similar regression equation was used from a winter month (February at Church Island and November at Aberffraw) (Figs. 4.13 & 4.14). The predicted optimal mussel size changed; thus, whilst larger mussels were predicted to be optimal during

Table 4.3. The relationship between shell length and breaking (Tb) and handling (Th) times for *Carcinus maenas* feeding on *Mytilus edulis* from Church Island and Aberffraw determined by least squares regression (MINITAB) for two crabs in each of the following size classes, 30-35, 40-45, 50-55mm CW and one crab in the size class 60-65mm CW. Relationships derived from data obtained when edge-chipping and boring techniques were used are excluded.

Crab	Dependent variable (y)	Independent variable (x)	Church Island				Aberffraw			
			a	b	r	n	a	b	r	n
CW (mm)	ln Tb	shell length	-0.39	0.467	0.87	16	-0.75	0.440	0.81	14
30-35 (1+2)										
40-45 (1)	"	"	0.34	0.336	0.87	11	-0.98	0.441	0.92	12
(2)	"	"	1.11	0.215	0.91	16	0.27	0.266	0.88	18
50-55 (1)	"	"	-0.38	0.364	0.90	14	-0.90	0.352	0.83	15
(2)	"	"	0.75	0.207	0.90	14	1.10	0.205	0.83	10
60-65	"	"	3.00	0.068	0.69	18	1.85	0.1550	0.88	20
30-35 (1+2)	ln Th	shell length	2.58	0.308	0.90	16	2.70	0.282	0.82	14
40-45 (1)	"	"	3.31	0.206	0.96	10	2.40	0.297	0.93	11
(2)	"	"	3.84	0.143	0.89	16	3.81	0.266	0.88	18
50-55 (1)	"	"	2.13	0.278	0.97	14	2.39	0.230	0.91	14
(2)	"	"	3.06	0.155	0.97	13	3.67	0.143	0.96	11
60-65	"	"	4.37	0.086	0.91	18	3.98	0.117	0.90	21

(1+2) = data combined for the two crabs
1 = data from the first crab in the size class
2 = data from the second crab in the size class
a,b = coefficients in the linear regression equation ln y = a + bx
r = product moment correlation coefficient
n = number of mussels eaten

Table 4.4. Comparison of the breaking(Tb) and handling (Th) times of *Carcinus maenas* on *Mytilus edulis* from Church Island and Aberffraw. Data from two crabs in each of the following size classes, 30-35, 40-45, 50-55 mm CW and from one crab in the 60-65 mm CW size class are presented. Data were compared using analysis of covariance (general linear model, MINITAB), data obtained when edge-chipping and boring are excluded.

Crab CW (mm)	Dependent variable		Independent variable (x)	Slopes ³		Intercepts ⁴		n
	(y)			F	p	F	p	
30-35 (1+2)	ln Tb		Shell length	0.05	ns	0.07	ns	30
	ln Th		Shell length	0.16	ns	0.02	ns	30
40-45 (1)	ln Tb		Shell length	1.43	ns	1.11	ns	23
	ln Th		Shell length	4.28	ns	2.08	ns	21
40-45 (2)	ln Tb		Shell length	1.29	ns	1.32	ns	34
	ln Th		Shell length	0.19	ns	0.00	ns	34
50-55 (1)	ln Tb		Shell length	0.02	ns	0.14	ns	29
	ln Th		Shell length	0.56	ns	0.00	ns	29
50-55 (2)	ln Tb		Shell length	0.00	ns	0.15	ns	24
	ln Th		Shell length	0.42	ns	4.52	*	24
60-65	ln Tb		Shell length	10.78	*	-	-	38
	ln Th		Shell length	3.76	ns	1.36	ns	39

(1+2) = data combined for the two crabs
(1) = data from first crab in size class
(2) = data from second crab in size class
n = number of mussels eaten

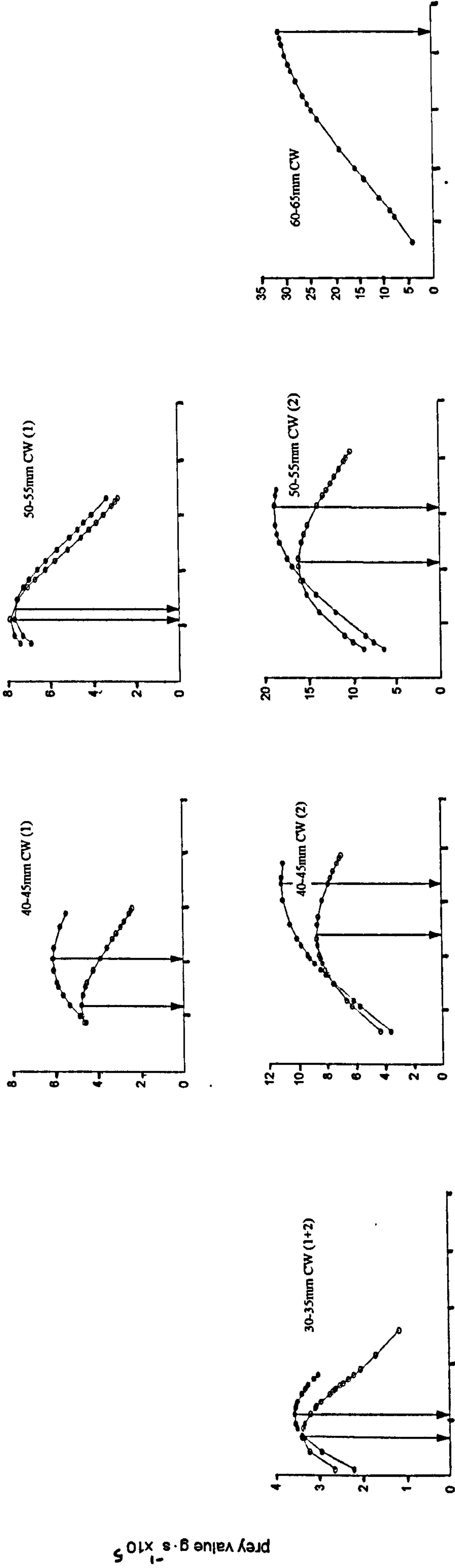
³ = comparison of the slopes from the regression equation $\ln y = a + bx$
⁴ = comparison of the intercepts from the regression equation $\ln y = a + bx$
ns = no significant difference
* = significant difference at $p < 0.05$

Figure 4.11.

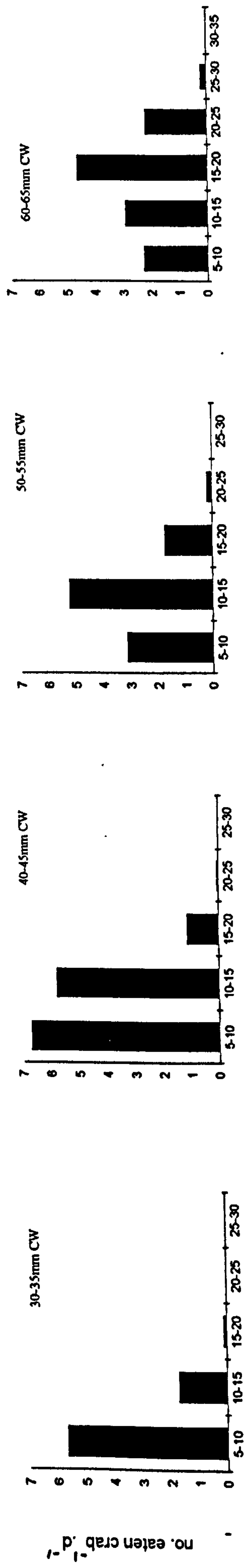
A The relationships between prey value and shell length of Church Island *Mytilus edulis* for four size classes of *Carcinus maenas*. Prey value was calculated using the handling time-shell length regression equations presented in Table 4.1, which included data from the lengthier opening techniques of edge chipping and boring (open circles) and using the handling time-shell length regression equations presented in Table 4.3, which excluded data from these lengthier techniques (closed circles). Arrows denote those sizes of prey predicted to be the most profitable.

B The size of Church Island *Mytilus edulis* most vulnerable to four sizes of *Carcinus maenas* when prey presented to crabs in groups of five mussels in each of five size classes; 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length.

A



B



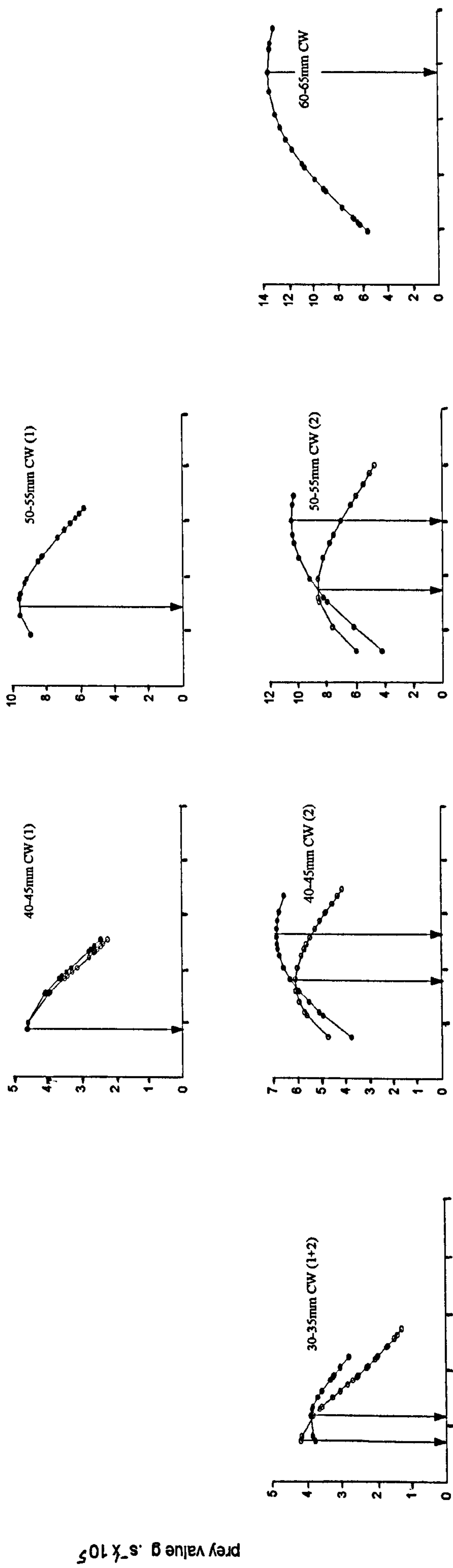
mussel shell length (mm)

Figure 4.12.

A The relationships between prey value and shell length of Aberffraw *Mytilus edulis* for four size classes of *Carcinus maenas*. Prey value was calculated using the handling time-shell length regression equations presented in Table 4.2, which included data from the lengthier opening techniques of edge chipping and boring (open circles) and using the handling time-shell length regression equations presented in Table 4.3. which excluded data from these lengthier techniques (closed circles). Arrows denote those sizes of prey predicted to be the most profitable.

B The size of Aberffraw *Mytilus edulis* most vulnerable to four sizes of *Carcinus maenas* when prey presented to crabs in groups of five mussels in each of five size classes; 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length.

A



B

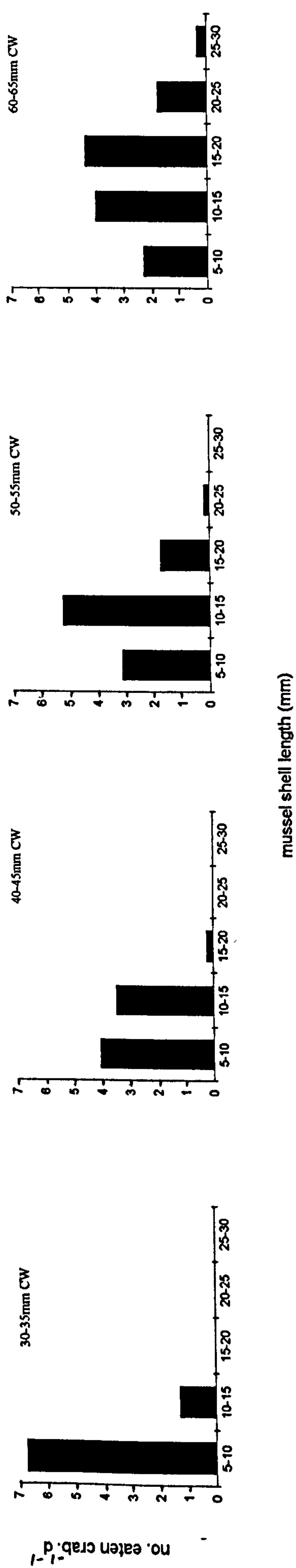


Figure 4.13. Seasonal variations in the prey value of Church Island *Mytilus edulis*. Prey value was calculated using the flesh weight - shell length regression equation determined for mussels in September 1996 (closed circles) and February 1997 (open circles), presented in Table 2.2 and the handling time-shell length regression equations presented in Table 4.3. Arrows denote the size of mussel predicted to be most optimal.

prey value g . s⁻¹ 10⁵

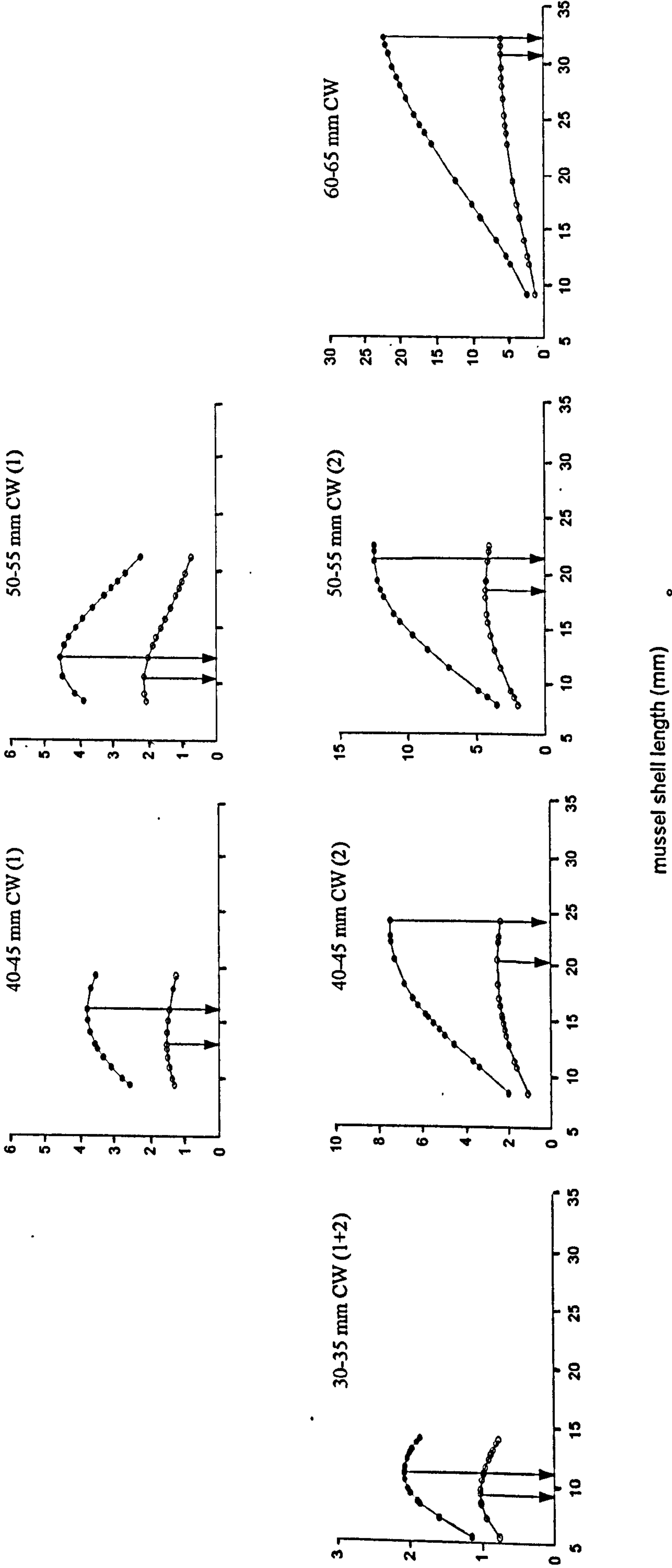
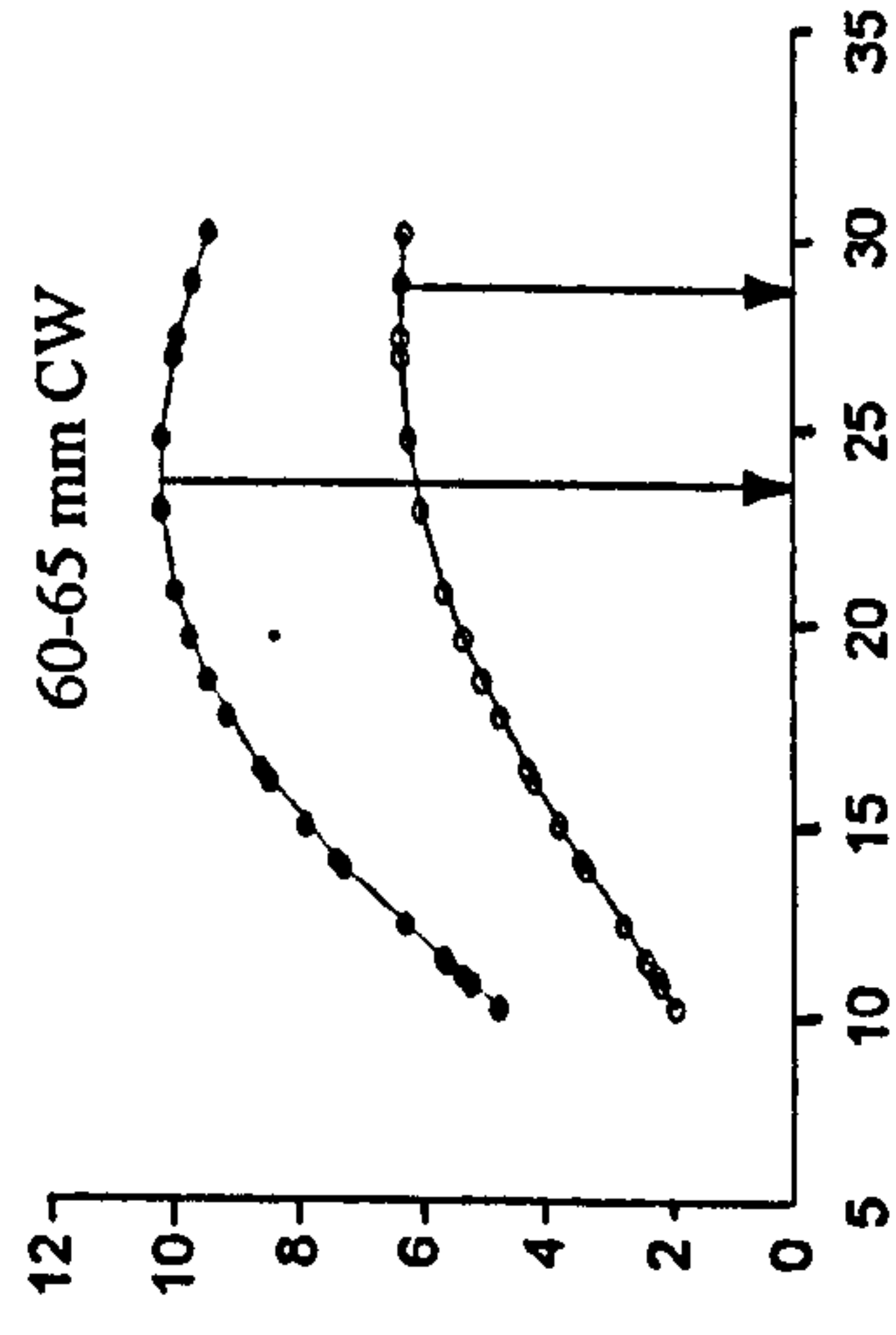
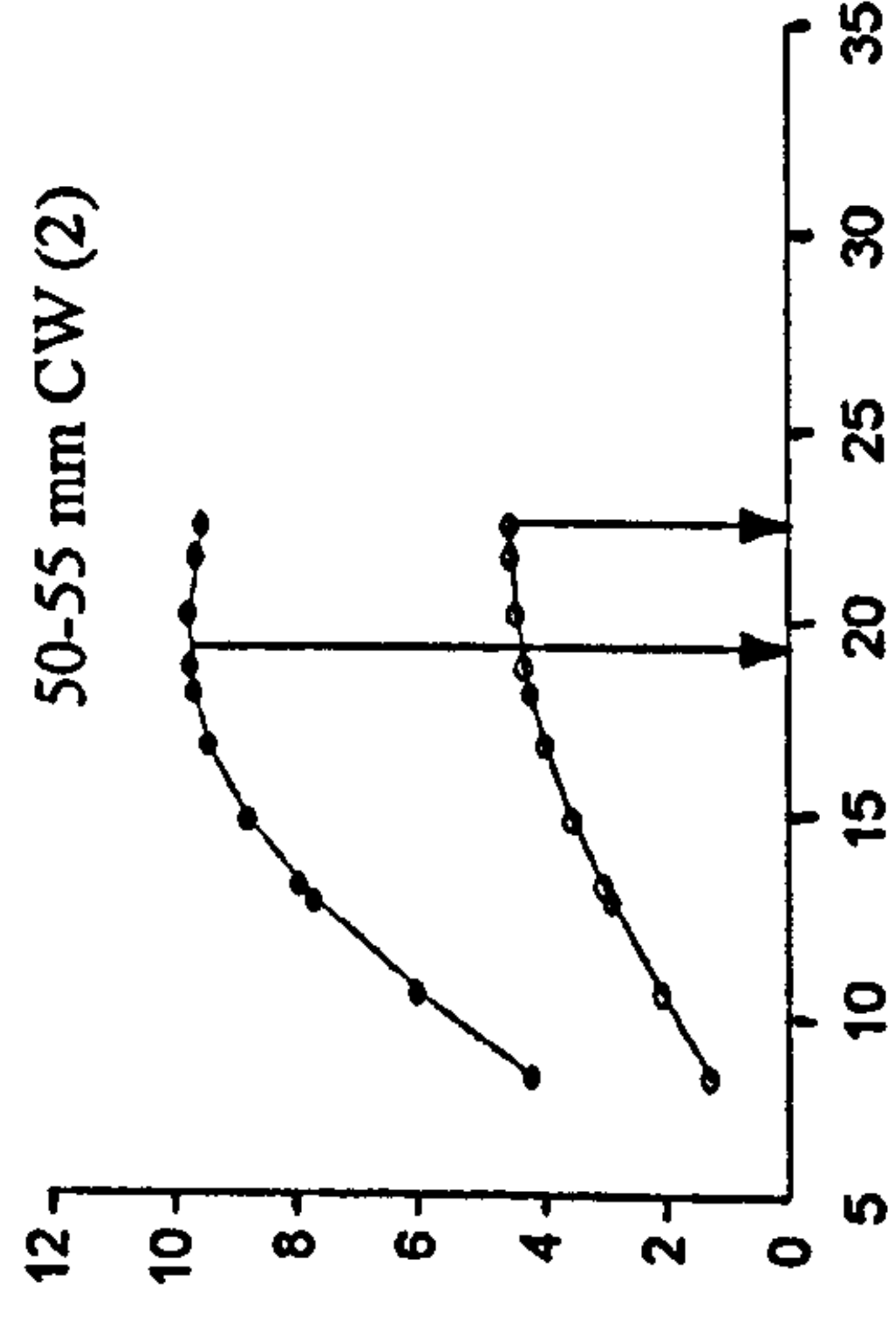
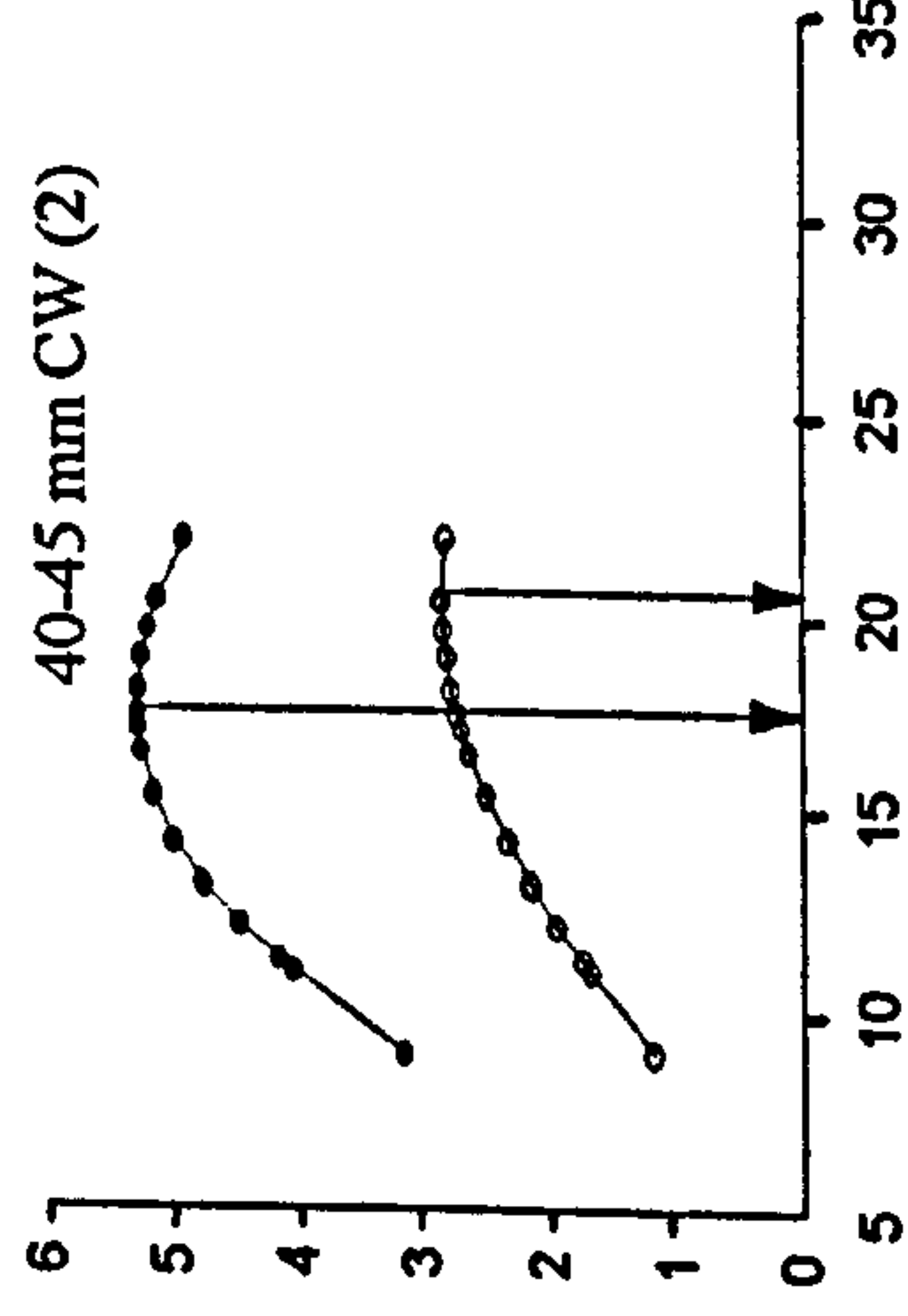
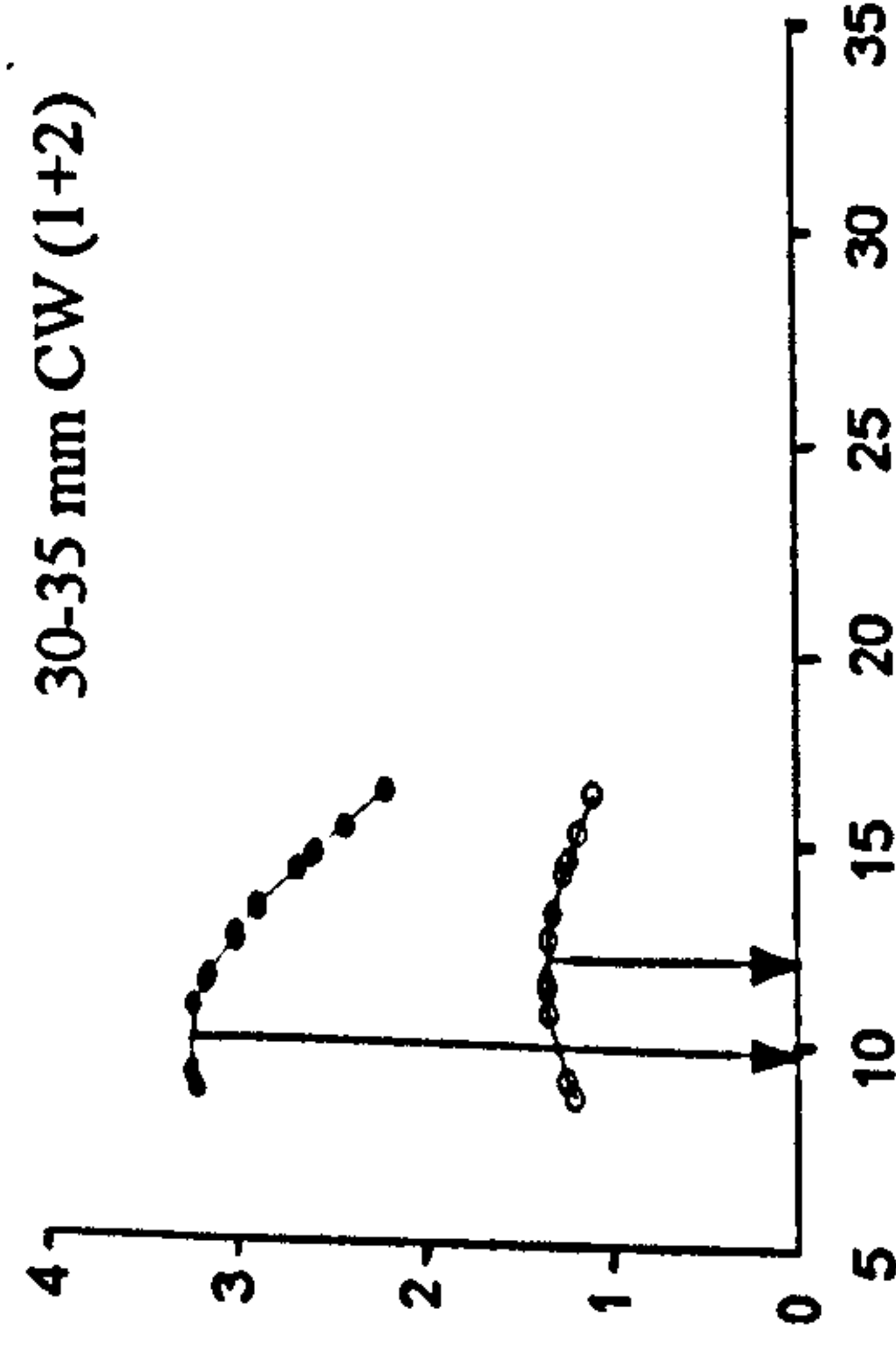
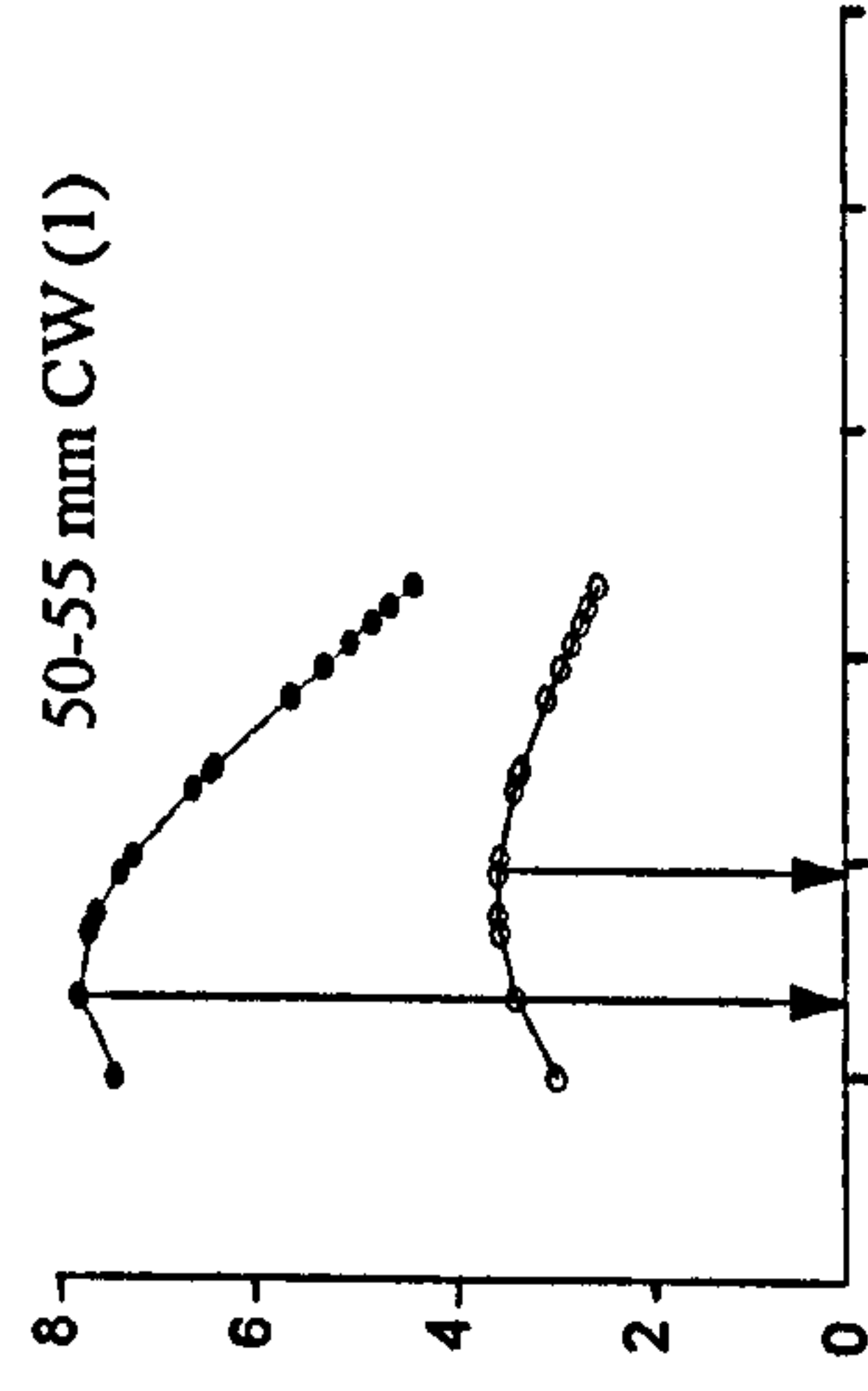
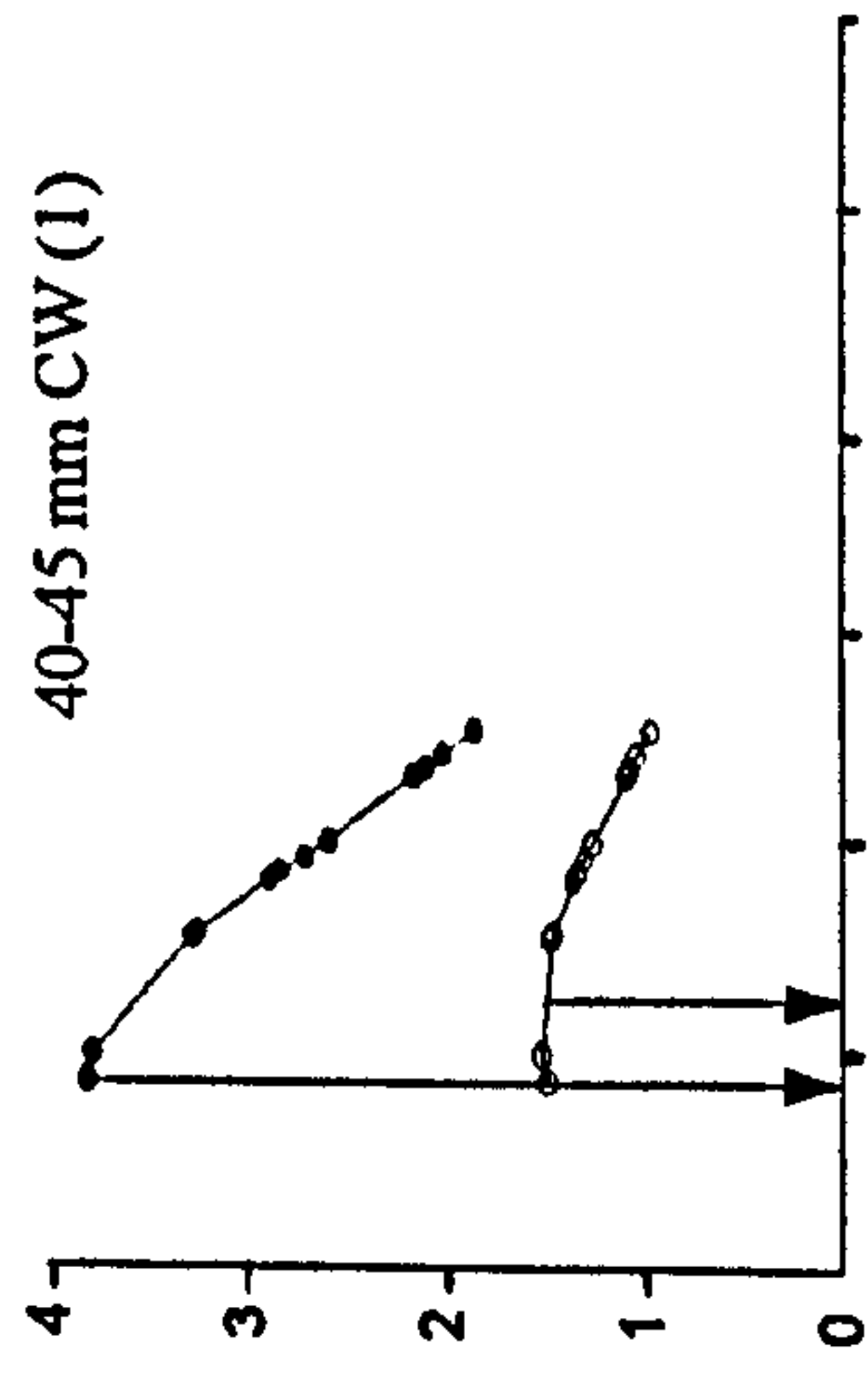


Figure 4.14. Seasonal variations in the prey value of Aberffraw *Mytilus edulis*. Prey value was calculated using the flesh weight - shell length regression equations determined for mussels in June 1997 (closed circles) and November 1996 (open circles), presented in Table 2.2 and the handling time-shell length regression equations presented in Table 4.3. Arrows denote the size of mussel predicted to be most optimal.



mussel shell length (mm)

the summer at Church Island, smaller mussels were predicted to be optimal at Aberffraw (Figs. 4.13 & 4.14 respectively). This reflects the complex interaction between the power curve relating dried flesh weight to shell length and the exponential curve relating handling times to shell length. When prey value curves for Church Island mussels were compared to those from Aberffraw no clear pattern emerged (Figs. 4.15 & 4.16). When the flesh weight-shell length equations derived from July 1996 were used, mussels from Church Island were generally, but not always, more profitable. When equations from March 1996 were used, mussels from neither site were consistently more profitable.

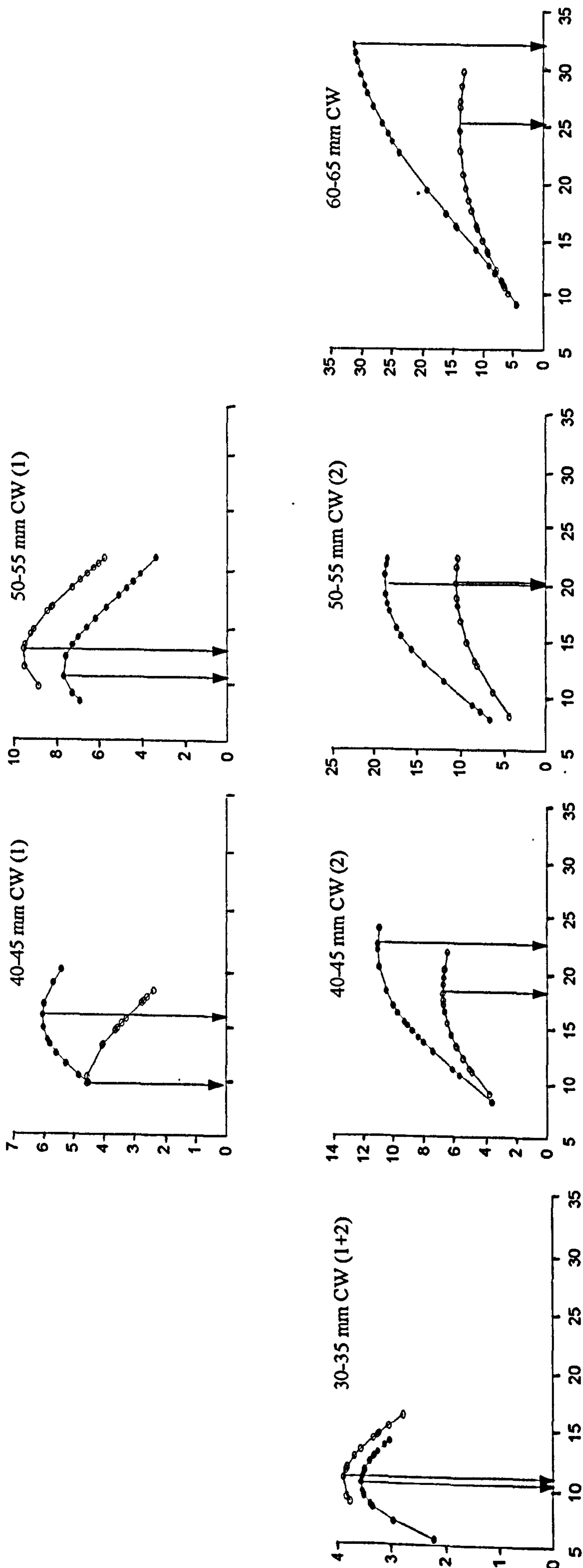
4.3.4. Prey size selection.

Carcinus maenas showed a clear preference for certain size ranges of mussel, the preferred size increasing with increase in size of crab. Although the preferred size of mussel was similar for Church Island and Aberffraw mussels (Fig. 4.17) the largest size class that *C. maenas* were able to consume were from Church Island (Table 4.5). Despite the clear preferences shown for certain size groups of mussels, crabs always included a wider range of mussel sizes in their diet. This was not due to any lack of availability of prey of the preferred size and to any consequent switching to other size classes, since prey of all size ranges were always available. When the discarded shell remains were examined there was no evidence that the lengthier opening techniques of edge-chipping and boring were used. When the optimal size of prey (see section 4.3.3.) is compared with the preferred size of prey (Figs. 4.11 & 4.12) it is clear that crabs tended to eat mussels that were smaller than the optimal size. A better coincidence between predicted prey value and preferred prey size occurred when prey value was calculated with data that included handling times from mussels opened by boring or edge-chipping (Figs. 4.11 & 4.12). However, since there was no evidence of these techniques being used in this experiment, nor in the experiments presented in Chapter 5, it is suggested that these techniques are rarely, if ever, used when mussels were presented in groups and thus this comparison is not valid.

When Church Island and Aberffraw mussels were presented simultaneously,

Figure 4.15 The relationships between prey value and shell length of Church Island *Mytilus edulis* (closed circles) and Aberffraw *M.edulis* (open circles) for four size classes of *Carcinus maenas*. Prey values were calculated using the flesh weight-shell length regression equations determined in July 1996, presented in Tables 2.2 & 2.3 and the handling time - shell length regression equation presented in Tables 4.3. Arrows denote the size of mussel predicted to be the most profitable.

Prey value g .s⁻¹x10⁵



mussel shell length (mm)

Figure 4.16. The relationships between prey value and shell length of Church Island *Mytilus edulis* (closed circles) and Aberffraw *M.edulis* (open circles) for four size classes of *Carcinus maenas*. Prey values were calculated using the flesh weight-shell length regression equations determined in March 1996, presented in Tables 2.2 & 2.3 and the handling time - shell length regression equation presented in Tables 4.3. Arrows denote the size of mussel predicted to be the most profitable.

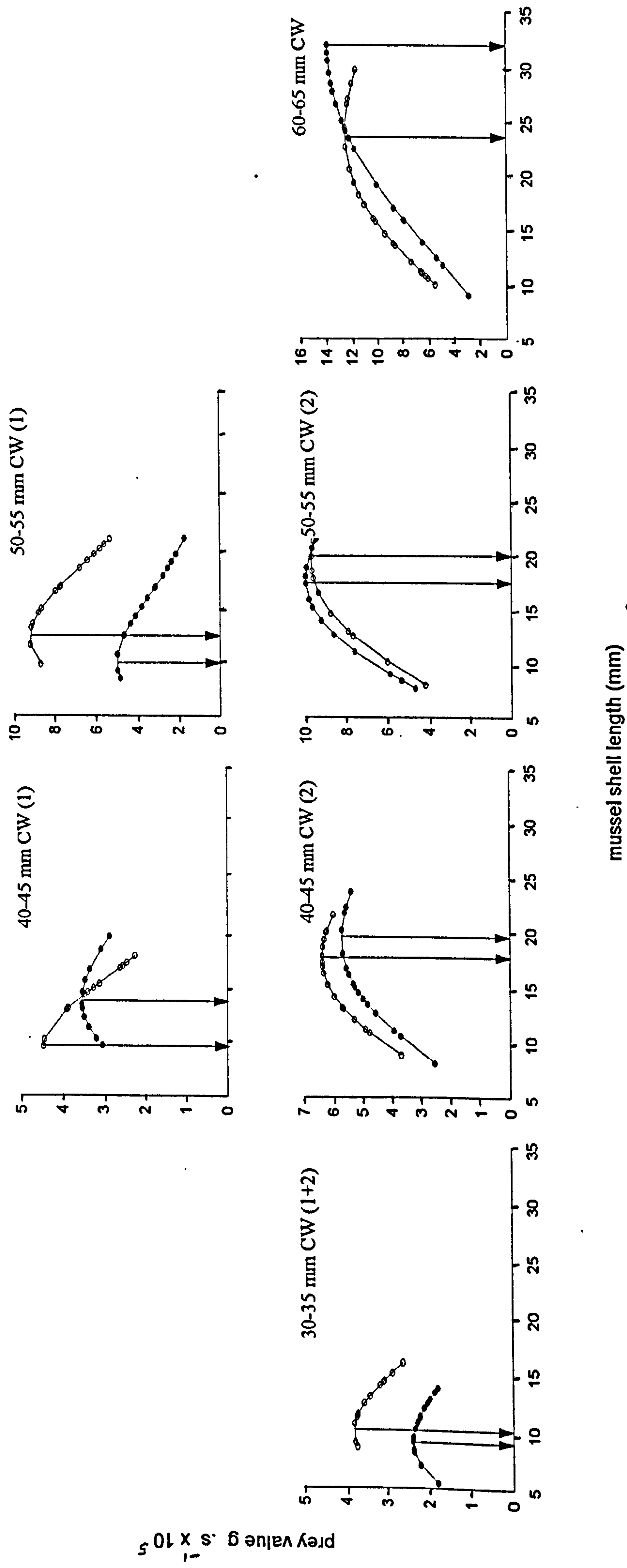


Figure 4.17. The number of *Mytilus edulis* from Church Island (closed bar) and Aberffraw (hatched bar) eaten by four size classes of *Carcinus maenas* when mussels from the two sites are presented together.

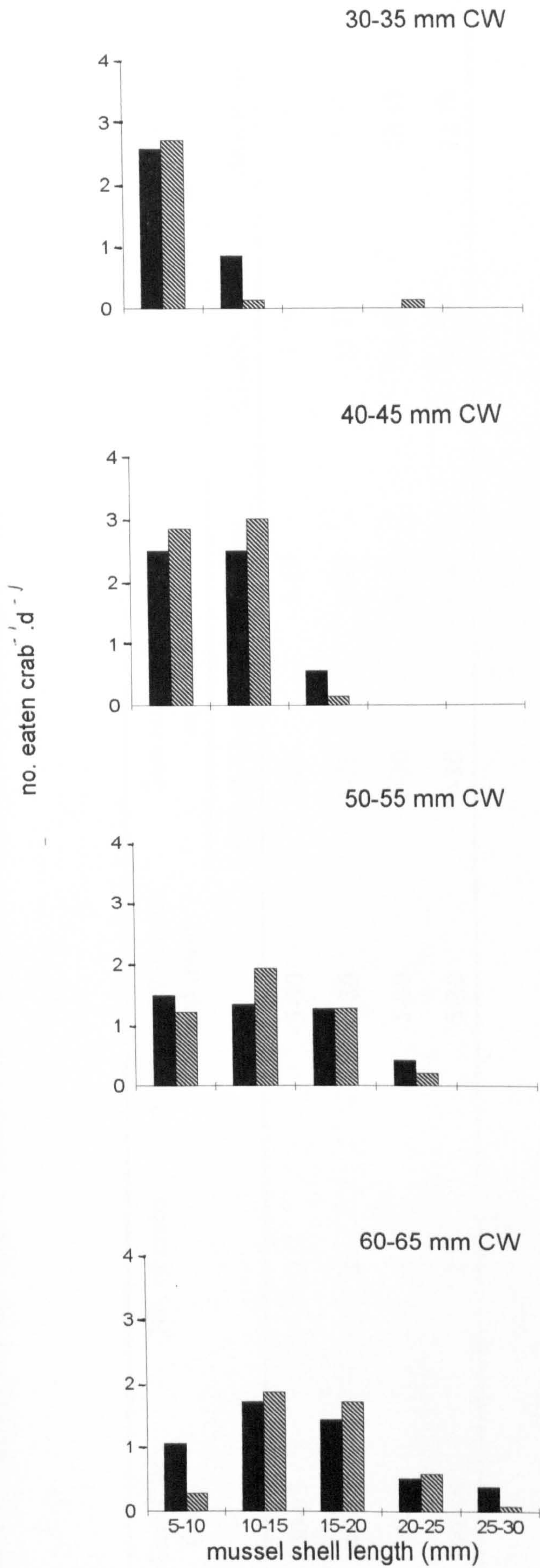


Table 4.5. Number and size range of mussels eaten when *Carcinus maenas* was fed on *Mytilus edulis* from Church Island and Aberffraw.

Crab CW (mm)	No. of crabs	Size range of mussels offered (mm)		Size range of mussels eaten (mm)		No. of mussels eaten 6hrs ⁻¹ crab ⁻¹	
		Church Island		Church Island	Aberffraw	Church Island	Aberffraw
30-35	3	5-30	5-20	5-15		7.48	8.00
40-45	3	5-30	5-25	5-20		13.71	7.76
50-55	3	5-30	5-30	5-25		12.48	10.33
60-65	3	5-30	5-30	5-30		12.29	12.79

crabs showed no clear preference for mussels from either site. Moreover, the pattern of prey-size selection remained the same as that obtained when Church Island and Aberffraw mussels were presented separately.

4.4. DISCUSSION

Carcinus maenas primarily uses chemical and tactile sense organs to detect its prey. Increased flicking of the antennules and their orientation towards a prey item when this is placed in the aquarium indicates that chemoreceptors present on the antennules (Crothers, 1967) are probably used to locate prey. Hair-like structures on the walking legs are sensitive to tactile stimuli (Crothers, 1967) and mussels touched by the legs were quickly gathered under the body and drawn towards the mouthparts. Vision appeared to be used only when the prey moved. Similar prey detection mechanisms have also been reported for *Callinectes sapidus* (Hughes and Seed, 1981), *Necora puber* (ap Rheinallt and Hughes, 1985) and *Ovalipes catharus* (Davidson, 1986) when these portunid species were observed foraging on mussels. Thus, whilst portunids are able to detect the presence of mussels from a distance, they are able only to 'assess' those which they are in immediate contact with.

The upper limit to the size of hard-shelled prey that can be opened by *Carcinus maenas* was set by mechanical constraints imposed by the chelae and by the prey. This upper limit seems to be set by increased shell strength, as suggested by the inability of *C. maenas* to crush larger prey items, and by increased shell width which prevented larger mussels from being fully accommodated in the chelal gape of the major chela. As crab size increased so too did the maximum size of mussel that could be opened, reflecting the greater strength associated with larger chelae.

Carcinus maenas employs a range of prey-size dependent opening techniques when feeding on *Mytilus edulis*. The methods used by *C. maenas* to manipulate and open mussels result from the interaction between the relative strengths and morphologies of the chelae and the shell valves of the prey. As mussels increase in length their shells become stronger and wider (see Chapter 2). The claws of *C. maenas* are not excessively strong and can generate sufficient crushing force to break only the

smaller size ranges of mussel outright (Elner, 1978). When larger mussels are encountered, a single strong crushing force is applied by the major chela and if the mussel shell does not yield to this, it is followed by a series of weaker pulses of force (Elner, 1978). Boulding and Labarbera (1986) described a similar pattern for *Cancer productus*, when this cancrid crab attacked the clam, *Protothaca stamina*. Both *Carcinus maenas* and *Cancer productus* exerted compressive forces weaker than the actual strength of the prey shell. It has been suggested that these weak forces create and extend microfractures present within the shell structure, which eventually cause the shell to fail (Currey and Kohn, 1976). Chemoreceptors are present on the chelae, mouthparts and legs of *Carcinus maenas* (Crothers, 1967) and the continuous rotation of mussels by these appendages between successive breaking attempts probably serves to detect weak spots in the shell from which mussel body fluids are leaking and where subsequent pulses of force can be directed.

By exploiting inherent weak spots within the shell structure of its molluscan prey, *Carcinus maenas* not only bypasses the need to develop larger and stronger chelae but also reduces the risk of chelal damage which can result from excessive application of force (Juanes and Hartwick, 1990) and which was observed in these experiments when crabs were forced to feed on very large mussels. The use of slower opening techniques such as edge-chipping and boring probably evolved either through the inability of crabs to crush larger prey items or because these large prey items could not be fully accommodated within the chelal gape. The sequential use of different opening techniques observed during these experiments is a common feature in the foraging behaviour of decapod crustaceans on hard-shelled molluscan prey (e.g. Hughes and Seed, 1981; ap Rheinallt and Hughes, 1985; Davidson, 1986; Robles *et al.*, 1990, Seed, 1990a; Hughes and Elner 1998).

The edge-chipping technique used by *Carcinus maenas* to open larger mussels has also been reported for other portunids (e.g. *Callinectes sapidus* Hughes and Seed, 1981, *Ovalipes catharus* Davidson, 1986 and *Thalamita danae* Seed, 1990a) which feed on mussels. Hughes and Seed (1981) proposed that posterior edge-chipping was a prey-specific opening technique, the narrow and elongate shape of mussels allowing crabs to achieve the necessary purchase on the shell margin. Edge-chipping, however,

is not the only method used to open larger mussels and, as observed in this investigation, *C.maenas* can also use a shell boring tactic. The extent to which boring and edge-chipping opening techniques were used differed when *C.maenas* fed on mussels from Church Island and Aberffraw. Such differences seemed to be related to the different shell morphologies of mussels from these two physically contrasting environments. When attempting to open cockles, *Cerastoderma edule*, *C.maenas* apparently never used the edge-chipping technique (Sanchez-Salazar *et al.*, 1987b) arguably because of the more globular morphology and interlocking shell valves of this particular prey species. When presented with cockles *C.maenas* endeavoured to insert its chelae between the margins of the valves in order to force them apart (Sanchez-Salazar *et al.*, 1987b). This “insertion” technique is somewhat similar to the “boring” technique that *C.maenas* uses on *Mytilus edulis*. Observations during the present study showed that when *C.maenas* fed on Aberffraw mussels, only shell boring was used to open larger mussels. However, when *C.maenas* fed on Church Island mussels both edge-chipping and shell boring were successfully employed to open large mussels. Shells of large Aberffraw mussels were much broader and globular than the narrower shells of Church Island mussels, and the edge-chipping method for these mussels, as for cockles, was much less effective. *C.maenas* therefore does not appear to have a fixed set of handling methods for each prey species but rather can alter its foraging behaviour according to the specific morphological features of its molluscan prey. This conclusion is broadly supported by the results of a previous study of the foraging behaviour of the spiny lobster, *Panulirus interruptus* on the mussel, *Mytilus californianus* by Robles *et al.* (1990) who found that the opening techniques used by *P.interruptus* varied according to the shore level from which the mussels had been collected. Mussels from the lower shore had a more acute angle between the posterior margins of their valves, similar in this respect to mussels from Church Island (see Chapter 2), and were opened using the edge-chipping technique; mussels from the high shore, which had a more obtuse angle between the posterior valve margins, similar to mussels from Aberffraw, were opened using an insertion technique. Since marked differences in shell morphology of *M.edulis* can occur between shores and shore levels (chapter 2 and references therein) the suite of handling methods and the flexibility in

their use allows *C.maenas* to exploit a much wider range of mussels than if it relied on fixed patterns of foraging behaviour.

When allowed to feed on groups of mussels, *Carcinus maenas* demonstrated a high degree of prey-size selectivity, foraging preferentially on mussels well below the maximum size that could be opened. This propensity for the smaller size ranges of hard-shelled molluscs is well documented in decapod crustaceans (see Juanes, 1990 for overview). The precise reason for such selection remains unclear but may be due to one or several of the following reasons. The large items of hard-shelled prey that can be opened by predatory decapods tend to have a low prey value because, although these prey items have a high flesh content, the amount of time required to open and eat them is relatively greater. This was true for *C.maenas* feeding on *Mytilus edulis* in this study. Under the energy maximisation premise of optimal foraging theory these items of lower profitability should not be included in the diet. Furthermore the longer handling times required to open the larger and more resistant prey items are disadvantageous to a tidally foraging predator such as *C.maenas* (Dare and Edwards, 1981; Hunter and Naylor, 1993) for which time will constrain the extent of foraging activity. In this study *C.maenas* appeared to be less responsive to visual stimuli when it was manipulating or consuming a prey item, a feature also noted for *Callinectes sapidus* when feeding on the mussel *Geukensia demissa* (Hughes and Seed, 1981). *C.maenas* is vulnerable to predation, e.g. from Herring gulls (Dumas and Witman, 1993) and such loss of visual sensitivity may leave it more vulnerable to attack. Moreover, larger shelled molluscan prey items also require greater chelal force to open them and this can result in claw damage which Juanes and Hartwick (1990) considered to be a limiting factor in prey selection. If constant loading by the chela weakens the shell of its prey then the crab must also be accumulating similar stress forces in its own chelae (Juanes and Hartwick, 1990). Just as persistent crushing attempts are thought to extend microfractures in the shell of the prey, they may also extend similar microfractures present within the chelae. Chelal damage was observed in this study when crabs were forced to feed on large resistant mussels. Such chelal damage would result not only in reduced foraging capability and a reduced ability to win mates in fights but would also divert energy away from overall growth during the intermoult

period (Juanes and Hartwick, 1990 and references therein).

In the laboratory *Carcinus maenas* fed extensively on both Church Island and Aberffraw mussels, consuming up to 13 mussels.crab⁻¹.6hr⁻¹ from the size range 5-30mm shell length. The majority of mussels at both of these sites fell within this size range (see Chapter 2, Figs. 2.5 & 2.6). However, mussels and shorecrabs generally coexisted over the 18-month study period at both Church Island and Aberffraw (see Chapters 2 & 3). For predator and prey species to coexist in this way the prey generally requires some kind of refuge from the predator (Connell, 1970). Similar patterns of prey-size selectivity arose when *C.maenas* fed on mussels from both Church Island and Aberffraw but the population dynamics of the two prey populations differed from one another. This means that the effect of size-selective predation is likely to differ between the two local mussel populations. In the Church Island population, there was an increase in the number of larger mussels occurring over the 18-month study period. The effect of such a shift ought to reduce the effect of crab predation as larger mussels will not only reach a size refuge where they are no longer attractive to foraging crabs but also provide an effective refuge for smaller mussels which have settled amongst them (Griffiths and Hockey, 1984). The size structure of the Aberffraw mussel population, by contrast, was relatively stable over the study period. Here the largest mussels were consistently around 30 mm in shell length which were within the size that could be eaten by the larger crabs. However, these mussels were located in the upper shore which probably constitutes an effective spatial refuge since the foraging time available to a tidally migrating predator will be limited.

The shape of predicted prey value curves can be used to provide information concerning the interaction between predator and prey. Prey value is defined as flesh weight ingested per unit of handling time. Thus, the prey curves will depend on the relative relationship between flesh weight and both breaking and eating times, which are themselves affected by prey shell strength and flesh weight as well as claw morphology and crab hunger levels. When *Carcinus maenas* fed on mussels, the resulting prey value curves were domed, indicating that medium sized prey should be the most profitable. Whilst smaller mussels are easily broken their flesh yield is low and the chelae are unable to glean efficiently, thus effectively reducing their profitability.

As mussels increase in size their flesh content increases as an approximate cubic function of shell length whereas handling time increases exponentially. Thus, amongst large mussels, energy yield is high but the handling times are also elevated which thus effectively reduces their profitability. These domed prey value curves contrast with the monotonically decreasing curves obtained when *Callinectes sapidus* (Hughes and Seed, 1981) and *Ovalipes catharus* (Davidson, 1986) fed on mussels. For these portunids the smallest size classes of prey were the most profitable since these were more easily crushed and the more slender, dextrous chelae of these fast-moving crabs are more efficient at gleaning the flesh from the shell fragments; breaking times, however, increased steeply with increasing prey size so that larger mussels became less profitable.

Prey value curves form an integral part of the framework within which the basis of a predator's foraging behaviour has been studied (Hughes, 1980). Optimal foraging theory under the energy maximisation premise assumes that net energy intake is directly proportional to the fitness of the predator, and predicts that a predator should feed in such a way as to maximise net energy intake by selecting those size ranges of prey which maximise profitability (Charnov, 1976; Hughes, 1980). Prey value curves obtained during this study suggest that *Carcinus maenas* ought to select medium sized prey. The coincidence between predicted and preferred prey size is seen as evidence of optimal foraging. Yet, whilst prey value is determined by allowing crabs to feed sequentially on single items of prey, prey-size selection is determined by presenting groups of prey items of mixed size ranges. This assumes that the behaviour of the predator remains constant when foraging on prey presented individually as when prey is presented in mixed size groups. However, evidence from the experiments presented in this chapter, and those presented in Chapter 5, suggests that this is probably not the case. Thus, although the slow opening techniques of boring and edge-chipping were used when mussels were presented individually, *C. maenas* did not appear to use these methods when prey were presented in a mixed group.

Lawton and Hughes (1985) investigated the foraging behaviour of the cancrid crab, *Cancer pagurus*, when presented with the gastropod, *Nucella lapillus*, and found that individual prey value curves could be fitted to handling time data obtained when

different handling techniques were used. By combining these separate curves a more accurate prediction of the preferred size class was obtained than when a single regression equation of handling time-shell length was used. In the present study, curves were fitted to data sets which included the handling times for the slower opening techniques and to data sets which excluded these data, the latter reflecting the situation that arises when prey are presented in groups. The correlation between predicted optimal prey size and preferred prey size was less clear when the slower handling times were excluded. This suggests that previous coincidences between preferred prey size and optimal prey size predicted from prey value curves may not have been due to selection by the crab but rather to some other factor. This view is further supported when the effect of seasonally variable flesh weight-shell length equations (see Chapter 2) on prey value curves is considered. When these different equations were used to predict prey value, not only were mussels found to be more profitable during the summer (July and September for Church Island and Aberffraw respectively) than in the winter (February and November, Church Island and Aberffraw respectively), but the size of mussel predicted to be the most profitable also altered. However, factors influencing handling time, such as shell breaking strength are expected to remain constant (see Chapter 2). Although *C.maenas* has the ability to learn from previous experience (Cunningham and Hughes, 1984) it is unlikely that crabs can keep track of seasonal changes in flesh weight and thus changes in prey value. It is perhaps unlikely therefore, that *C.maenas* selects its prey solely on the basis of energy return.

Generally no significant differences were detected in the breaking and handling times of crabs feeding on mussels from Aberffraw or Church Island. Those differences which did arise are probably attributable either to the highly variable nature of the prey or to individual differences between crabs. Whilst no significant differences were found between the shell strengths of mussels from Aberffraw and Church Island, differences might have been anticipated given their different shell morphologies. When prey value curves are compared, no consistent pattern emerged; mussels from Church Island were not always more profitable than those from Aberffraw either between individual crabs or over the whole range of mussel sizes. This can be attributed to the complex inter-relationship between flesh weight- shell length (an approximately cubic relationship)

and the handling time-shell length (an exponential relationship). Seasonal variations in these relationships also occurred with the result that Aberffraw mussels were more profitable than Church Island mussels of comparable size in certain months whilst the reverse was true at other times of the year. Such variations could clearly make prey selection based on energy return alone highly unlikely. Given that breaking times of Aberffraw and Church Island mussels were broadly similar, the lack of any apparent selection for mussels from one site over those from the other was not surprising.

4.5 SUMMARY

- *Carcinus maenas* appeared to use chemical and tactile sense organs to detect *Mytilus edulis*, whilst the use of vision appeared to be limited to detecting movement. This is consistent with the foraging behaviour observed in other portunids feeding on hard-shelled molluscan prey.
- The upper limit to the size of mussel that could be opened appeared to be set by mechanical constraints imposed by the chelae. The greater valve strength of larger mussels deterred crabs from persisting with them; chelal damage sometimes resulted when crabs were forced to feed on these larger mussels. In addition, the greater width of larger mussels prevented crabs from gaining an adequate purchase on the shell from which to apply a crushing force. Larger crabs were able to open larger mussels reflecting their increased chelal strength.
- Within the size range of prey that could be opened, *Carcinus maenas* used a suite of prey-size dependent opening techniques, with small mussels being crushed outright, medium-sized mussels succumbing after continuous crushing attempts directed at the umbo or the posterior of the valves and the largest mussels being opened by the labourious opening techniques of edge-chipping and boring. Opening techniques are employed sequentially, thus crabs initially attempted to open mussels using crushing techniques, only utilising the more time consuming methods if crushing attempts failed.

- Differences in the shell morphology of mussels from Aberffraw and Church Island induced differences in the foraging behaviour of *Carcinus maenas* on the largest prey items. *C. maenas* used a mixture of edge-chipping and boring to open the narrower mussels from Church Island whilst the more tumid shape of the Aberffraw mussels prevented crabs from gaining purchase on the posterior valve margins and thus, only the boring technique was used to open larger mussels from this site.
- *Carcinus maenas* were highly size-selective when feeding on groups of mussels, selecting prey sizes well below the maximum size that could be eaten. There was no evidence that the lengthier handling techniques of edge-chipping and boring were used when prey of a smaller size available were available.
- Prey value curves were domed such that medium sizes of mussel were predicted to be optimal. Whilst small mussels were quickly broken, the yield of flesh was low and crabs were inefficient at gleaning these sizes of prey. Although flesh weight increases as an approximate cubic function of shell length, handling times increase in an exponential manner, thus at large mussel sizes low prey value results from elevated handling times on these sizes of prey.
- Prey value curves derived from the regression of flesh weight and handling times on shell length were variable. The inclusion of data derived from the lengthier opening techniques elevated handling times, lowered the predicted prey value and altered the size of prey predicted to be the most profitable. Similarly the seasonal variations in the flesh weight-shell length regression equations resulted in different prey value curves. Given that prey value curves and the predictions made from them are variable, the coincidence between optimal size of mussel, predicted from prey value curves, and the preferred size of mussel, determined from the prey size selection experiments may result from mechanisms other than the active selection for the optimal size of prey.
- Few differences were found between the breaking and handling times of mussels from Aberffraw and from Church Island despite differences in their shell morphology

and flesh content. There was no apparent selection by *Carcinus maenas* for mussels from one site over those from the other.

CHAPTER 5

FORAGING BEHAVIOUR OF *CARCINUS MAENAS* ON GROUPS OF *MYTILUS EDULIS*.

5.1. INTRODUCTION

Prey-size selection is a common feature of the foraging behaviour of decapod crustaceans when presented with hard-shelled molluscs (see Juanes, 1992 for review). Much research has focused on the size of prey most vulnerable to the predator and the mechanisms underlying size-selective predation (e.g. Elner and Hughes, 1978; Hughes and Elner, 1979; Seed and Hughes, 1981; Davidson, 1986; Ameyaw-Akumfi and Hughes, 1987). These foraging studies have used the ratio of flesh weight to prey handling time as a measure of prey value or profitability, and when this is plotted against some measure of prey size, the shape of the resultant curve provides useful information concerning the interaction between features of both the predator and the prey. From such prey value curves the optimal prey size, i.e. that which maximises the intake of energy (\equiv flesh weight) per unit handling time, can be predicted and this can then be tested against the size of prey preferred when the predator is presented with a choice of prey size classes. If the predator selects the prey predicted to be most profitable then it is considered to be foraging optimally by maximising its net energy intake. However, if the size of prey selected differs from that predicted then explanations other than energy maximisation such as the need to reduce chela wear or damage or the minimising foraging time in order to reduce predation risk are sought to explain foraging patterns (see Juanes and Hartwick (1990) and Hughes and Seed (1981)). In these foraging studies, therefore, the shape of prey value or profitability curves and the determination of prey size most vulnerable to predation have formed the central framework in which predictions of foraging behaviour are tested.

Nevertheless, there are certain flaws in this framework for example, prey value is generally determined by presenting the predator sequentially with single items of prey of different size whilst prey preference is determined by presenting prey in mixed size groups, often as equal numbers in each of several size classes (e.g. Elner and

Hughes, 1978; Davidson, 1986; Seed, 1990a). This assumes that the foraging behaviour of the crabs is the same under both situations. However, in Chapter 4 it was shown that *Carcinus maenas* does not appear to use the more time consuming opening techniques of boring and edge-chipping when it is feeding on mixed size ranges of mussels within a group, and the inclusion or exclusion of data obtained when these techniques are used altered the prey value curves and resulted in different predictions (see Chapter 4). A similar result was obtained by Lawton and Hughes (1985) working on the crab, *Cancer pagurus*, when foraging on the gastropod, *Nucella lapillus*: The shape of the prey value curves altered when they were derived from a single regression of handling times on prey size and when these were derived by combining different handling time-shell length regression equations each associated with a different opening technique. Ideally, therefore, prey value curves and prey preference should be derived in the same way.

Since prey value is defined as flesh weight divided by handling time and since flesh weight is predicted from flesh weight-shell length equations, a further assumption when calculating prey value is that the predator consumes all the prey flesh. However, Jubb *et al.* (1983) reported that when foraging on *Mytilus edulis*, *Carcinus maenas* left 20-70% of the flesh uneaten in the discarded shells. If this is taken into account and prey value curves calculated using the predicted flesh eaten rather than the total predicted flesh of a prey item, potentially the shapes of the resulting curves may be different; this may provide additional information about the interaction between predator and prey.

By simply manipulating the relative number of prey in different size classes offered to crabs, prey size vulnerability has been shown to alter (Elner and Hughes, 1978; Jubb *et al.*, 1983; Davidson, 1986) the actual proportions of mussels included in the diet reflecting the relative proportions in which they were presented. Vulnerability of prey in the field may therefore depend upon the local structure of the prey population itself. Thus, if results of experiments conducted in the laboratory are to be extrapolated to the field situation then they ought to broadly reflect the situation prevailing in the field. Such a context-sensitive approach has already been advocated by Sponaugle and Lawton (1990) and Lawton and Zimmer-Faust (1992).

In this chapter the foraging behaviour of *Carcinus maenas* on groups of *Mytilus edulis* is described and compared to that when feeding on mussels presented individually. The vulnerability of *M.edulis* when presented in proportions which reflect those in which they occur in the field is also investigated.

5.2. MATERIALS AND METHODS

5.2.1. Collection and maintenance of *Carcinus maenas* and *Mytilus edulis*.

Crabs and mussels were collected and maintained as described in Chapter 4, section 4.2.1.

5.2.2. Prey value experiments

5.2.2.1. Experiment 1. Prey value and foraging behaviour when mussels are presented singly and as part of a group.

In this first experiment the effect of presenting mussels as part of a group on their value to *Carcinus maenas* was examined during August - November 1995. The experiment comprised three trials and in each of the three trials three crabs 42.3, 44.5, 54.0 mm CW were used. The same three crabs were used in each trial to ensure that any differences arising between trials did not result from differences between crabs. Individual crabs were fed on mussels, presented both singly and as part of a group, and the relationship between prey value and prey length determined. Prior to their presentation to crabs, the length of each mussel was measured to the nearest 0.1mm using vernier calipers and the shell marked by placing a small dot of a liquid whitener on the valves; when dry each mussel was then coded using a black permanent marker pen. As in Chapter 4, a three day period prior to each of the three trials was allowed to elapse during which time crabs were fed solely on mussel flesh for the first two days and left unfed for the third day. This procedure was designed to establish/restore crabs to a "naive" state and also to standardise hunger levels between trials to ensure that

any differences arising between trials could not be attributed to learning or to different hunger levels. Mussels used in this experiment were all collected from the low shore at Church Island

In the first trial each of the three crabs was presented with single mussels over a range of sizes from 5-30mm shell length. Mussels were presented to the crabs in random sequence, the methods used to manipulate and open mussels were observed and the breaking and handling times (see Chapter 4, section 4.2.2. for definitions) were recorded to the nearest second. Discarded shell remains were collected after each successful attack and any flesh remaining within these shells was removed, dried to constant weight at 60°C over three days, and weighed to the nearest microgram. In the second trial, following the three day period in which to return the crabs were returned to their "naive" state, the same three crabs were then each presented with five mussels in each of the following length classes; 5-10, 10-15, 15-20, 20-25 and 25-30 mm. Crabs were allowed to feed on these mixed groups of 25 unattached mussels for two consecutive hours during which time they were observed continually and breaking and handling times were recorded together with the methods used to open each prey item. Any mussel that was picked up, regardless of whether it was subsequently eaten or not, was regarded as having been "encountered" by a foraging crab. Thus, when crabs were allowed to feed on mussels presented as part of a group, the ratio of mussels eaten to mussels encountered could be calculated for each prey size class. Any mussels eaten were immediately removed and replaced with ones of similar size, thus maintaining constant prey density and preventing unopened mussels being obscured by the accumulation of shell debris. Following the two-hour feeding period, any flesh remaining in the discarded shells was removed, dried and weighed as before. This trial was repeated daily for five consecutive days. Trial 3 followed a further three day period in which crabs were returned to their "naive" state. Each crab was then presented with a group of 25 unattached mussels of the following length classes; 5-10, 10-25, 15-20, 20-25 and 25-30 mm mixed in the proportion of 11, 7, 3, 3, 1. This proportion was established from the relative abundance of these size classes within the natural mussel population at Church Island during October 1995 (see Chapter 2) and thus reflected the approximate proportions in which these mussels would be

encountered by a foraging crab. Each crab was allowed to feed for two consecutive hours each day for five consecutive days. Crabs were continually observed during the two hour period and breaking times and handling times together with the methods used to open mussels, were recorded. The number of mussels in each of the five size classes eaten was calculated as a percentage of those encountered. Mussels were replaced as eaten and any flesh remaining in discarded shells was removed at the end of the foraging bout, dried and weighed.

The percentage of flesh left in discarded shells was used as a measure of the extent to which crabs successfully harvested the flesh from these mussels and was calculated by dividing the amount of remaining flesh by the total flesh content predicted for that particular size of mussel from Church Island in July 1996 (Table 2.2). The percentage of flesh left in discarded shells was compared between the three trials using the non-parametric Kruskal Wallis test.

The relationships between breaking times, handling times and shell length were determined using least squares regression and compared between the three trials using analysis of covariance (general linear model, MINITAB). Regression equations relating handling times to prey length were used for predictive purposes in the calculation of prey value, where prey value was defined as E/Th and E was calculated from the regression equation relating dry flesh weight to prey length (July 1996, Church Island, Table 2.2). Prey value was then related to mussel shell length in order to predict the most valuable size of prey for any given crab. Adjusted prey values $(E-L)/Th$, where E is the predicted mussel flesh weight and L is the amount of flesh left in the discarded shell, were also determined and related to mussel shell length.

5.2.2.2. Experiment 2. The effect of learning on prey value.

This second experiment was broadly similar to the previous experiment and was designed to ascertain whether handling efficiency improved between trials. The experiment was conducted during April-June, 1997 using three crabs of 52.4, 52.8 and 54.1 mm CW. The experiment comprised three trials and the same crabs were used in each trial. As in the previous experiment, prior to the start of a trial, crabs were fed

mussel flesh for two days and left unfed for a third to return crabs to a “naive” state to ensure that differences arising were not due to differences in hunger levels. Mussels were collected from Aberffraw and marked as before (see section 5.2.2.1.) prior to presentation to a crab. In the first trial crabs were presented with single unattached mussels in random sequence from the size range 5-30 mm shell length. Breaking and handling times were recorded together with the method used to open the mussels. Flesh remains from discarded shells were retained and dried. In the second trial, following the three day period in which crabs were returned to their “naive” state, the same three crabs were each presented with a group of 25 unattached mussels comprising the following length size classes 5-10, 10-25, 15-20, 20-25 and 25-30mm in the proportions 11, 7, 3, 3, 1. Each crab was allowed to feed for two consecutive hours during which time the shells of any mussels which had been eaten were removed and replaced with mussels of similar size. This was done so as to maintain constant prey density and to prevent the accumulation of shell debris from obscuring the smaller mussels. Crabs were observed continuously during the two hour period and breaking and handling times were recorded together with the mussel opening techniques used. This procedure was repeated every day for five consecutive days and the percentage of encountered mussels that were eaten calculated for each mussel size class. A further three day period was then allowed to elapse before the third trial. This was the same as the first trial in that crabs were presented with single unattached mussels in random sequence from the size range 5-30 mm shell length; breaking and handling times were recorded together with the opening method.

The percentage of flesh remaining in discarded shells was calculated using the flesh weight-shell length equation determined for mussels from Aberffraw in March 1997 (Table 2.3) and compared between trials using the non-parametric Kruskal Wallis test. The relationships between breaking times, handling times and shell length were determined using least squares regression and compared between the three trials using analysis of covariance (general linear model, MINITAB). Prey value was calculated for each trial using the flesh weight-shell length equation for mussels from Aberffraw during March 1997 (Table 2.3) and the appropriate handling time-shell length regression equations. Adjusted prey value curves were then calculated as before.

5.2.3. Prey vulnerability

5.2.3.1 Experiment 3. Differences in prey vulnerability

This experiment investigated prey size vulnerability when mussels were presented as equal numbers in each of several size classes and when they were presented in a modified proportion comparable to that in a natural mussel population. This experiment was conducted during October 1995 and used ten crabs ranging from 35 to 65 mm CW. The experiment consisted of two trials and the same crabs were used in both trials. Mussels were obtained from the low shore at Church Island. In the first trial each crab was presented with five mussels in each of the following five size classes; 5-10, 10-15, 15-20, 20-25, 25-30mm shell length. Crabs fed on these 25 unattached mussels for six consecutive hours each day. During this time the number of mussels eaten in each size class was recorded and their shell remains removed to prevent unopened mussels from becoming obscured by the shell debris. Any mussels that had been eaten were replaced with ones of a similar size to maintain constant prey availability. This procedure was repeated every day for seven consecutive days. After the three day period in which crabs were returned to their "naive" state, the same crabs were then presented with 25 unattached mussels, 5-10, 10-15, 15-20, 20-25 and 25-30 mm shell length in the modified proportion of 11, 7, 3, 3, 1. This proportion was identical to that recorded in the Church Island mussel population in October 1995. As before, crabs were allowed to feed on groups of mussels for six hours each day, during which time the number of mussels eaten was recorded every two hours and any discarded shells removed and replaced with ones of similar size. The procedure was followed for seven consecutive days. No direct observations of crab foraging behaviour were made in either trial.

5.2.3.2. Experiment 4. Differences in prey vulnerability with shore elevation.

This experiment was conducted in June 1997 and it was designed to investigate

prey vulnerability when mussels are presented in two different proportions comparable to naturally occurring populations on the same shore but from different tidal elevations. The experiment therefore tests whether the foraging behaviour of *Carcinus maenas* might change during a foraging excursion. The crabs used were from 40 to 65 mm CW and the experiment consisted of two trials, prior to each trial, crabs were fed on mussel flesh for two days and left unfed for a third day. Mussels used in this experiment were taken from the high shore at Aberffraw. Crabs were presented with 11, 7, 2, 2, 3 mussels respectively in the following size classes, 5-10, 10-15, 15-20, 20-25 and 25-30 mm shell length. This proportion was derived from a sample taken from the high shore at Aberffraw in June 1997 (see Chapter 2, Fig. 2.7). The same procedure outlined in section 5.2.3.1. was followed, crabs were fed for six consecutive hours, the number of mussels eaten recorded every two hours and the discarded shells removed and replaced with ones of a similar size. This procedure was followed for five consecutive days. After the three day period elapsed, the same crabs were presented with 10, 3, 3, 2, 5, 2 mussels in the following size classes, 10-15, 15-20, 20-25, 25-30, 30-35 mm shell length respectively. This proportion had been derived from a sample taken from the mid-shore at Aberffraw in June 1997 (Fig. 2.7) The same procedure as outlined above was followed. No direct observations of crab foraging behaviour were made in either trials.

5.3. RESULTS

5.3.1. Prey handling.

When feeding on individual mussels, *Carcinus maenas* employed the same range of techniques to open *Mytilus edulis* as previously described in Chapter 4. These techniques were prey-size dependent; smaller mussels were crushed outright, medium-sized mussels were opened after several crushing attempts, whilst the more time consuming boring and edge-chipping methods were used only to open larger mussels. However, when fed on groups of mussels, crabs used only the shell crushing techniques and neither boring nor edge-chipping were observed. Since different handling curves

have been associated with different opening methods (see Chapter 4; Lawton and Hughes, 1985) the analysis of breaking and handling times when mussels were presented singly included only those data where mussels had been crushed. This enabled direct comparison of breaking and handling times to be made between trials in which foraging behaviour on individual and groups of mussels was being investigated.

When feeding on mussels presented singly, crabs generally spent a long time gleaning mussel flesh once the shell had been opened. The posterior adductor muscle was normally severed, either by cutting through it or by pulling the valves apart, and crabs were often observed picking at the posterior adductor muscle and mantle edge flesh with the tips of their chelae. Any shell fragments which were accidentally dropped were gathered by the pereopods and passed to the mouthparts for further gleaning. Only after the shell had been thoroughly gleaned and discarded did the crab initiate further search behaviour. Crabs would sometimes persist for several hours when trying to open the larger mussels and rejection of a prey item was rarely observed.

When grouped mussels were presented, *Carcinus maenas* generally gathered several mussels beneath their bodies simultaneously, using all the pereopods to contact the prey. Two mussels were often held, one in each chela, before one was eventually rejected. During the manipulation of a prey item by the chelae the pereopods remained outstretched, exploring the immediate vicinity for further prey items. This behaviour, which frequently resulted in a high rejection rate as the held mussel was often dropped in favour of another prey item that had been touched by the pereopods, usually stopped once the mussel held in the chela was opened, but generally resumed before the mussel had been thoroughly gleaned. Tables 5.1 & 5.2 show that more flesh was generally left in the discarded mussel shells at the end of a foraging bout on grouped prey than when prey had been presented singly. On the occasions when a large mussel was accepted from the group the crab would often move out of contact with other mussels until this mussel had been opened or rejected.

Table 5.1 The effect of prey presentation on the minimum, maximum and median percentages of flesh remaining in discarded *Mytilus edulis* shells attacked by *Carcinus maenas* together with a significance test between trial medians. Data derived from Experiment 1.

Crab CW (mm)	Trial 1 individuals ¹				Trial 2 group ²				Trial 3 modified group ³				H values		
	n	Min.	Max.	Median	n	Min.	Max.	Median	n	Min.	Max.	Median	H	d.f.	p
42.3	16	3.70	35.54	10.63	15	4.75	98.39	25.25	48	0.95	84.60	19.28	10.02	2	**
44.5	15	3.08	29.81	5.76	40	0.00	50.88	11.26	80	0.00	66.57	12.86	8.97	2	*
54.0 ⁴	13	5.35	27.17	14.70	38	0.00	98.40	25.24	-	-	-	-	-	-	-

¹ Trial 1, mussels presented singly

² Trial 2, mussels presented as five individuals in each of the following five size classes 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length

³ Trial 3, mussels presented as a group comprising the following size classes 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length in the modified proportion of 11, 7, 3, 3, 1.

⁴ Crab stopped eating during Trial 3, no data available.

n = number of discarded mussel shells from which flesh was removed

Min. = the minimum recorded percentage of flesh remaining in a mussel shell

Max. = the maximum recorded percentage of flesh remaining in a mussel shell

H = Kruskal-Wallis test statistic

d.f. = degrees of freedom

* = significant at p < 0.05

** = significant at p < 0.01

Table 5.2. The effect of prey presentation on the minimum, maximum and median percentages of flesh remaining in discarded *Mytilus edulis* shells attacked by *Carcinus maenas* together with a significance test between the trial medians. Data derived from Experiment 2.

Crab CW (mm)	Trial 1 individuals ¹ % flesh left				Trial 2 group ² % flesh left				Trial 3 individuals ³ % flesh left				H values		
	n	Min.	Max.	Median	n	Min.	Max.	Median	n	Min.	Max.	Median	H	d.f.	p
52.4	26	0.00	13.14	5.30	59	0.00	82.22	11.12	28	0.00	15.16	4.66	32.19	2	***
52.8	31	0.00	18.90	5.28	32	0.00	78.92	9.58	26	0.00	16.73	7.54	13.53	2	**
54.1	29	1.42	20.77	5.21	45	3.23	78.09	13.90	29	0.00	15.78	6.24	37.16	2	***

¹ Trial 1, mussels presented singly

² Trial 2, mussels presented as a group comprising the following size classes, 5-10, 10-15, 15- 20, 20-25, 25-30mm shell length in the modified proportion 11, 7, 3, 3, 1.

³ Trial 3, mussels presented singly

n = number of discarded mussel shells from which flesh was removed

Min. = the minimum recorded percentage of flesh remaining in a mussel shell in a trial.

Max. = the maximum recorded percentage of flesh remaining in a mussel shell in a trial.

H = Kruskal-Wallis test statistic

d.f. = degrees of freedom

** = medians significantly different at p < 0.01

*** = medians significantly different at p < 0.001

5.3.2. Prey value for when mussels presented singly and when mussels presented as part of a group.

The largest crab (CW = 54mm) stopped eating during the third trial and subsequently moulted one week later therefore only data from the first two trials were analysed for this particular crab. The regression equations relating breaking and handling times to shell length are presented in Table 5.3. Data were linearised by the \log_e transformation of the dependent (y) variable and breaking and handling times for each crab were compared between trials using analysis of covariance (general linear model, MINITAB). No significant differences could be detected between trials for either of the two smallest crabs although the slopes of both breaking and handling times were significantly different for the largest crab (Tb, $F=7.11$, d.f.=51, $p<0.05$; Th, $F=4.70$, d.f.=54, $p<0.05$). Differences in prey value resulting from the way in which prey was presented are evident (Fig. 5.1A) even though handling times did not always differ significantly. When mussels were presented as a group rather than individually, the size of prey predicted to be the most profitable changed. For the two smaller crabs the most profitable prey size shifted to a smaller size class whilst for the largest crab the most profitable size shifted to a larger size class. Moreover, when mussels were presented as a group the relative number of mussels in each size class also influenced prey value, the size predicted to be the most valuable shifting to the smaller size classes through the sequence individual, grouped and modified proportion. The vulnerability of mussels also altered with variations in the relative proportions that different sizes were presented in (Fig. 5.1B). When the number of mussels in the smallest size class was increased (the modified proportion, Trial 3) then the vulnerability of these sizes also increased.

The amount of flesh left in the discarded mussel shells differed significantly between trials for both the smaller crabs (Table 5.1) and for the largest crab (Mann-Whitney U, $W=204.0$, d.f. =49, $p<0.05$) with more flesh remaining in the shells when mussels were presented as a group. Furthermore, the range of values for the percentage of flesh left in discarded mussel shells was always greater in the trials where mussels were presented as part of a group (Table 5.1). When the prey value curves

Table 5.3. The effect of prey presentation on the relationships between breaking times, handling times and shell length for three *Carcinus maenas* feeding on *Mytilus edulis*. Relationships obtained from least squares regression. Data derived from Experiment 1.

Crab CW (mm)	Trial	Dependent variable (y)	Independent variable (x)	a	b	r	n
42.3	Individuals ¹	Ln Th	Shell length	3.80	0.143	0.880	16
	Group ²			3.11	0.162	0.660	16
	Modified ³			3.27	0.188	0.843	54
	Individuals ¹	Ln Tb	Shell length	1.11	0.215	0.910	16
	Group ²			1.41	0.194	0.755	16
	Modified ³			1.88	0.179	0.760	54
	Individuals ¹	Ln Th	Shell length	3.31	0.206	0.956	10
	Group ²			2.63	0.277	0.622	42
	Modified ³			2.34	0.300	0.826	87
44.5	Individuals ¹	Ln Tb	Shell length	0.51	0.313	0.936	10
	Group ²			-0.14	0.407	0.706	40
	Modified ³			0.71	0.349	0.802	87
	Individuals ¹	Ln Th	Shell length	2.13	0.278	0.973	14
	Group ²			2.80	0.203	0.843	42
	Individuals ¹	Ln Tb	Shell length	-0.38	0.364	0.903	14
	Group ²			1.23	0.216	0.744	40
	Individuals ¹	Ln Th	Shell length	2.13	0.278	0.973	14
	Group ²			2.80	0.203	0.843	42
54.0 ⁴	Individuals ¹	Ln Th	Shell length	2.13	0.278	0.973	14
	Group ²			2.80	0.203	0.843	42
	Individuals ¹	Ln Tb	Shell length	-0.38	0.364	0.903	14
	Group ²			1.23	0.216	0.744	40

¹ = Trial 1, mussels presented singly

² = Trial 2, mussels presented as five individuals in each of the following size classes, 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length

³ = Trial 3, mussels presented as a group comprising the following size classes, 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length in the modified proportion of 11, 7, 3, 3, 1.

⁴ Crab stopped eating during Trial 3, no data available

a, b = coefficients in the regression equation $\ln y = a + bx$

r = product moment correlation coefficient

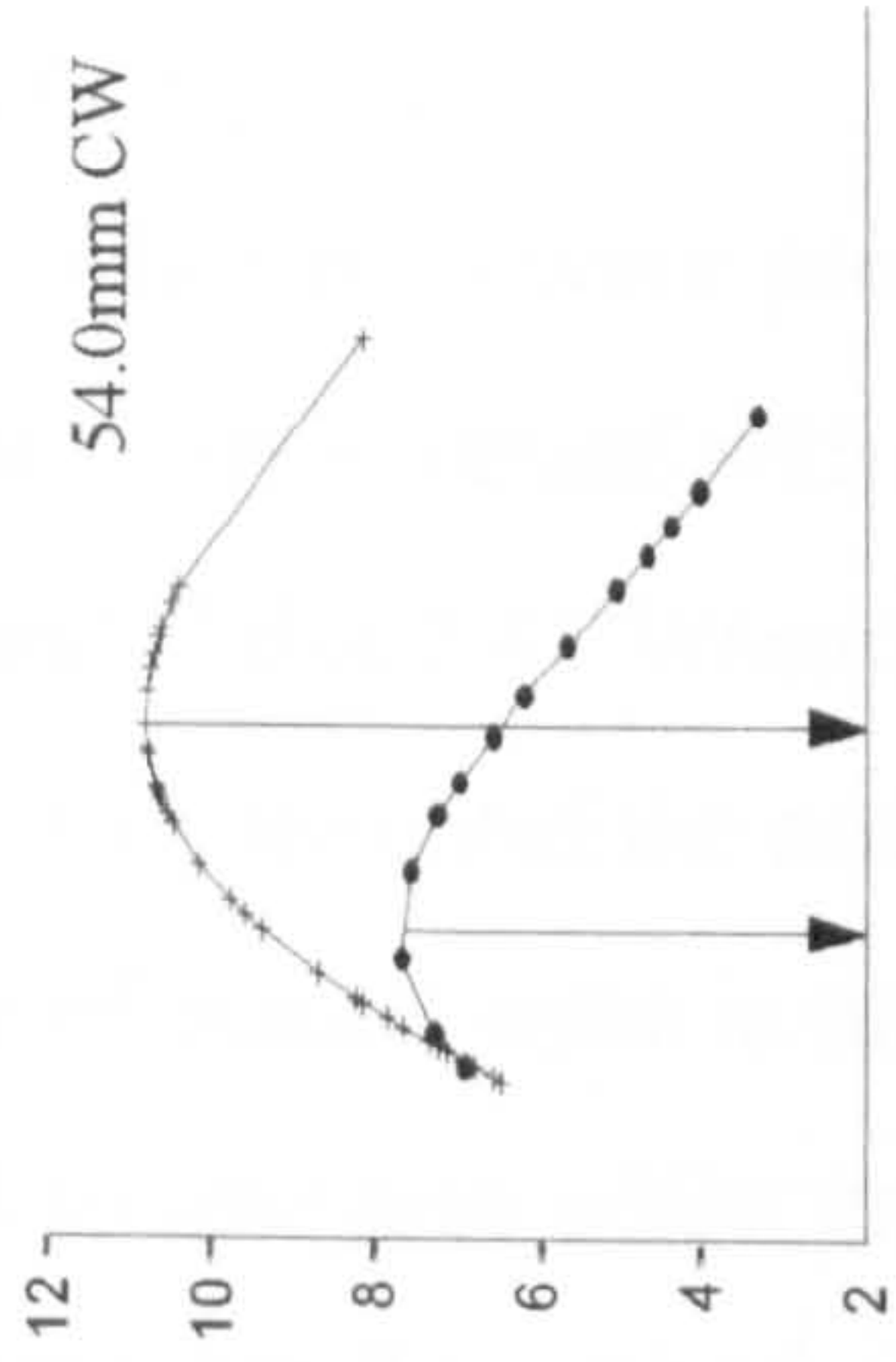
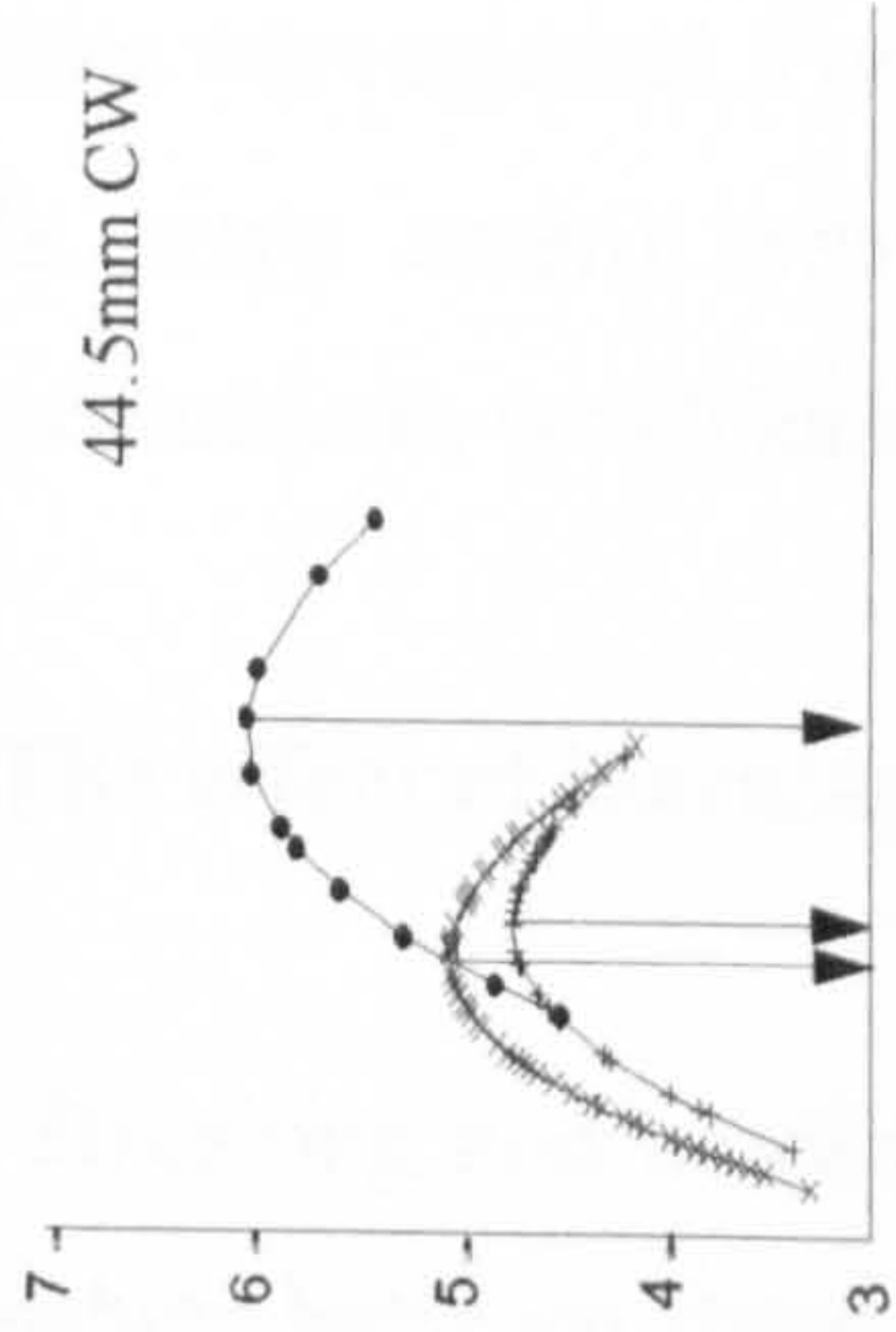
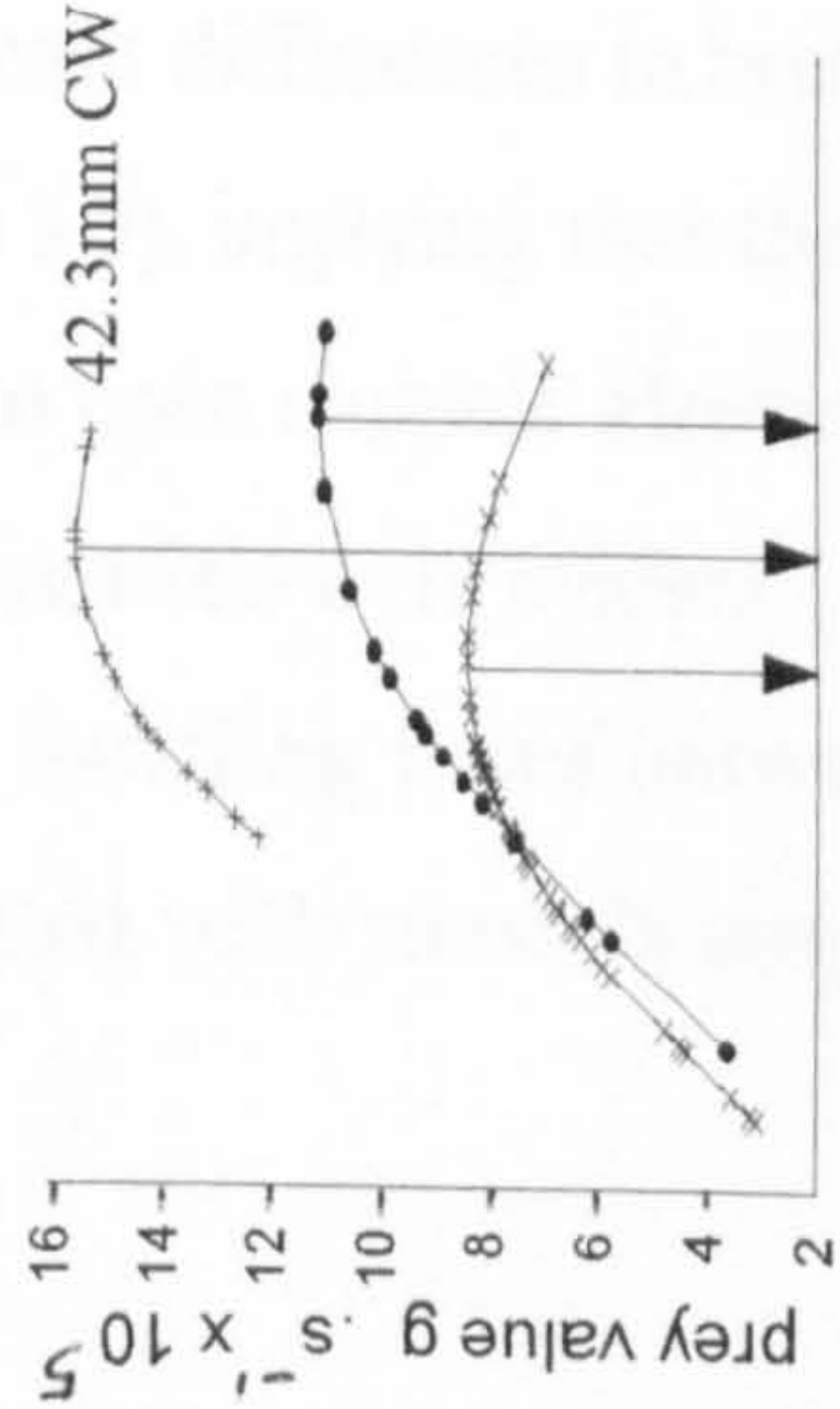
n = number of mussels used in the analysis

Figure 5.1.

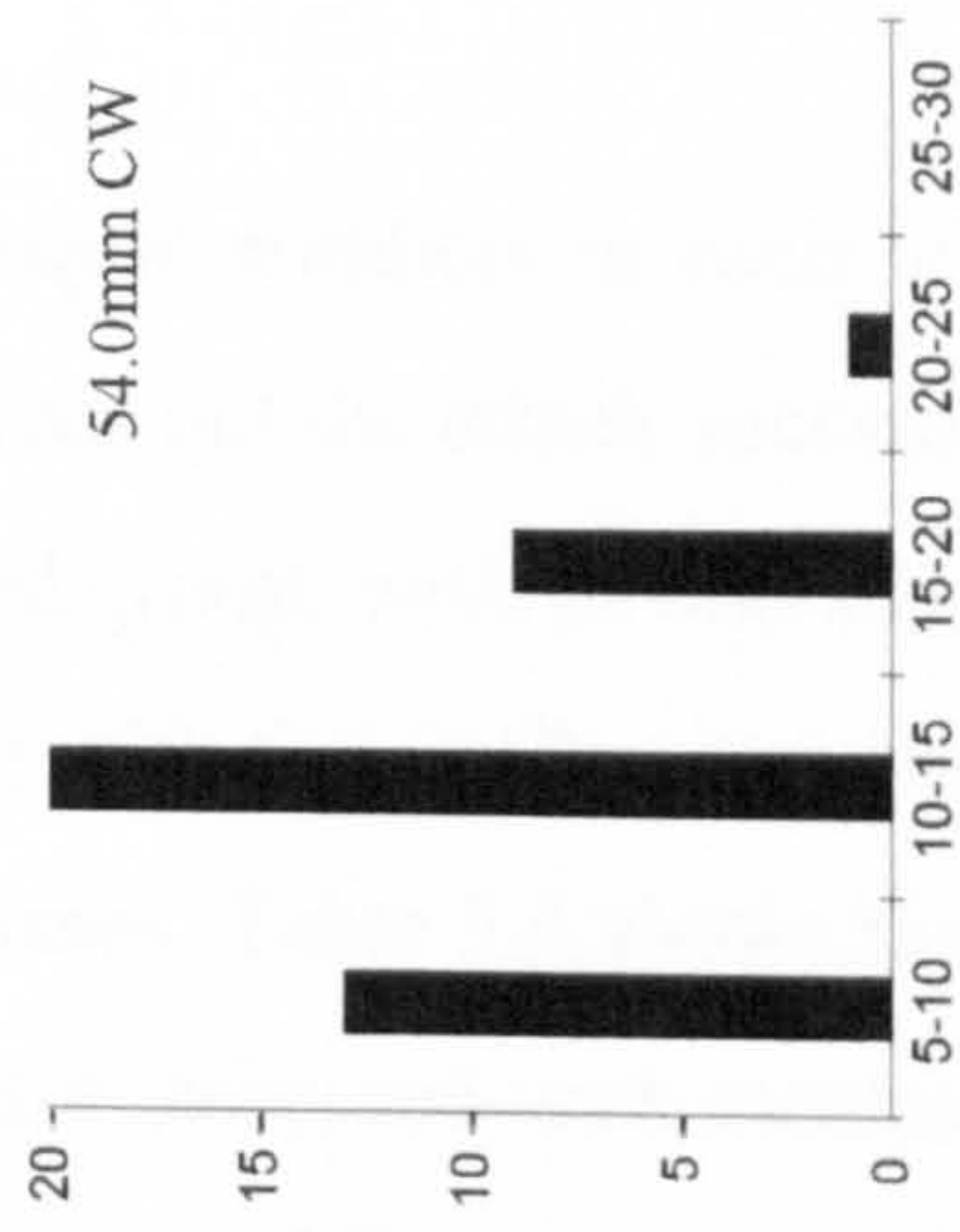
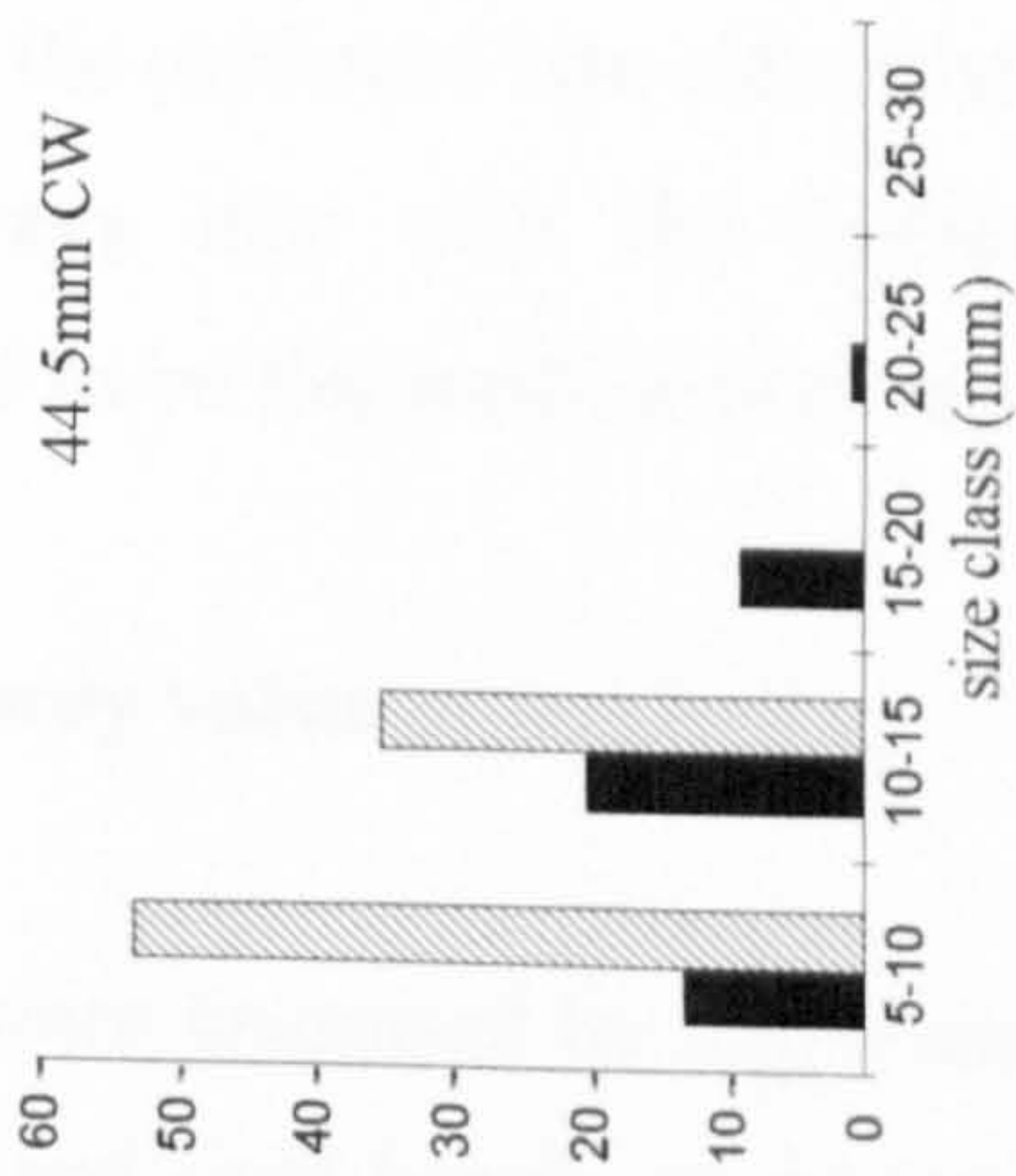
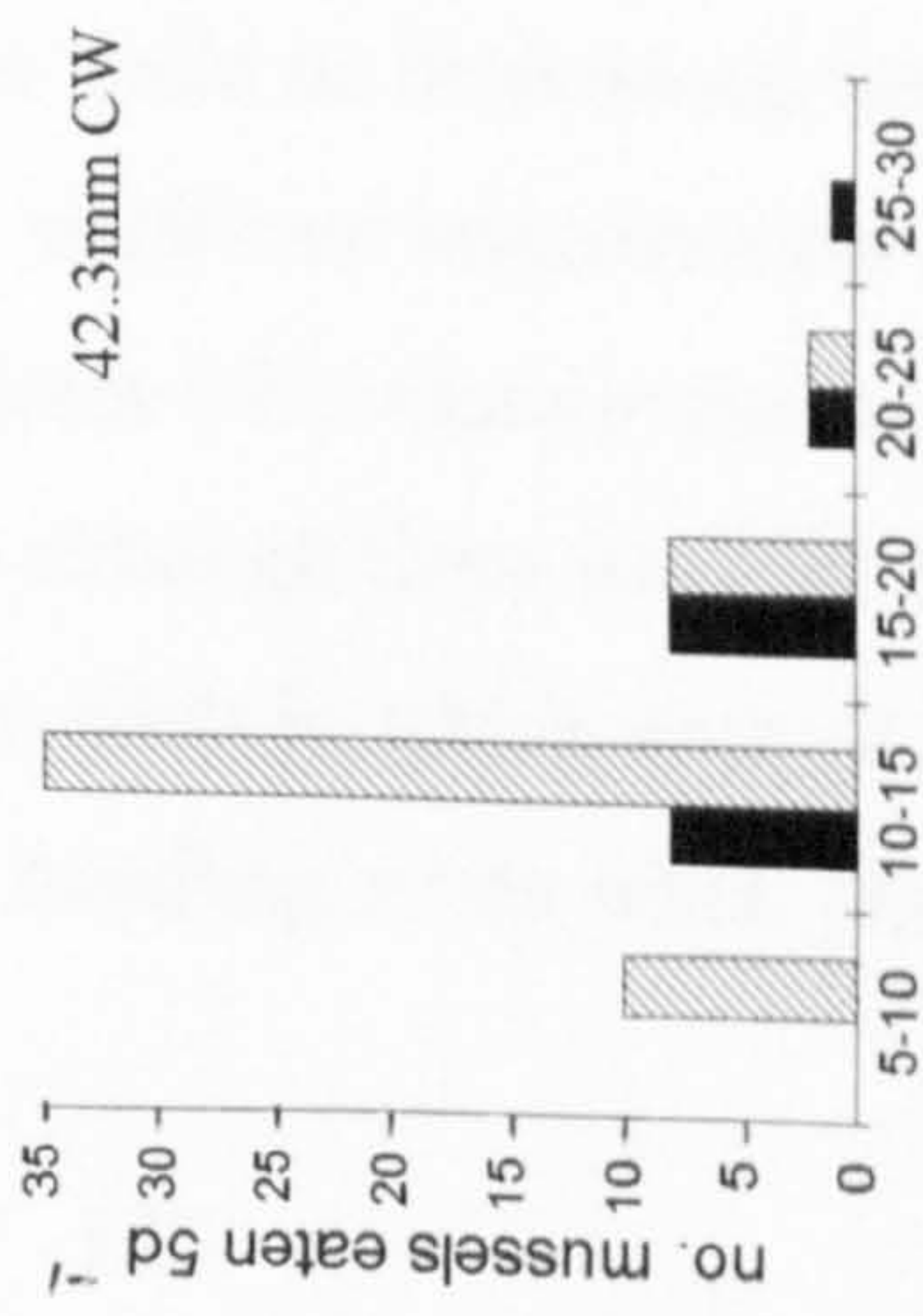
A. Prey value curves for three *Carcinus maenas* (42.3, 44.5, 54.0 mm CW) when foraging on *Mytilus edulis* presented singly (closed circles, Trial 1), as part of group comprising five mussels in each of the following size classes; 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length (pluses, Trial 2) and as part of a group comprising 11, 7, 3, 3, 1, mussels in the following size classes 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length respectively (crosses, Trial 3). Arrows denote those sizes of mussel predicted to be the most profitable.

B. The number of mussels eaten by each crab (42.3, 44.5, 54.0 mm CW) over a five day period when mussels were presented as part of group comprising five mussels in each of the following size classes; 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length (closed bar, Trial 2) and as part of a group comprising 11, 7, 3, 3, 1, mussels in the following size classes 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length respectively (hatched bar, Trial 3).

A



B



(predicted flesh content/predicted handling time, or E/Th) were compared with the adjusted prey value curves (predicted flesh eaten/predicted handling time, or $(E-L)/Th$) (Fig. 5.2) it is clear that increased consumption of flesh when mussels are presented singly does not influence the basic shape of the curve, nor does it affect its position relative to the other prey value curves derived from trials where mussels are presented as part of a group.

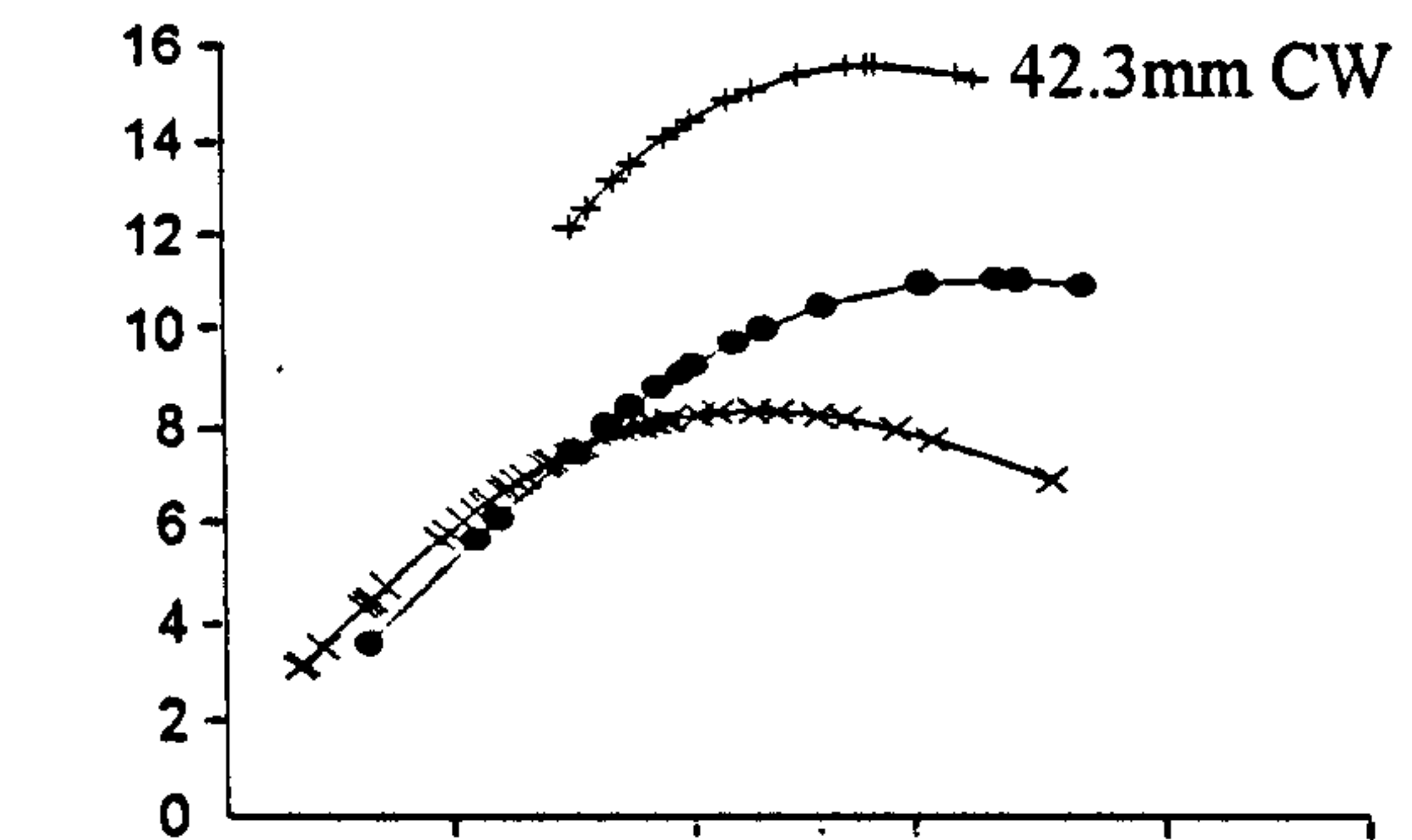
When prey were presented in equal numbers in each of the five size classes encounter rate increased with prey size class but the attack success rate (number eaten) decreased (Table 5.4). When the modified group, with its bias towards the smaller size classes, was presented the encounter rate with the smaller mussels increased as did the number of mussels eaten in these size classes. Table 5.4 shows that attack success rate tended to decrease whilst encounter rate increased with increasing mussel size. It is also clear that the optimal size class predicted from the prey value curves in Figure 5.1A was not always the size class with the highest ratios of prey eaten:prey encountered (highlighted in Table 5.4), indeed up to 80% of encountered prey in these size classes were rejected. Furthermore, the preferred size class (that from which most mussels were eaten) was not always that with the highest ratios of prey eaten:encountered, which instead tended to be the smallest prey size class (Table 5.4).

5.3.3. The effect of learning on the prey value.

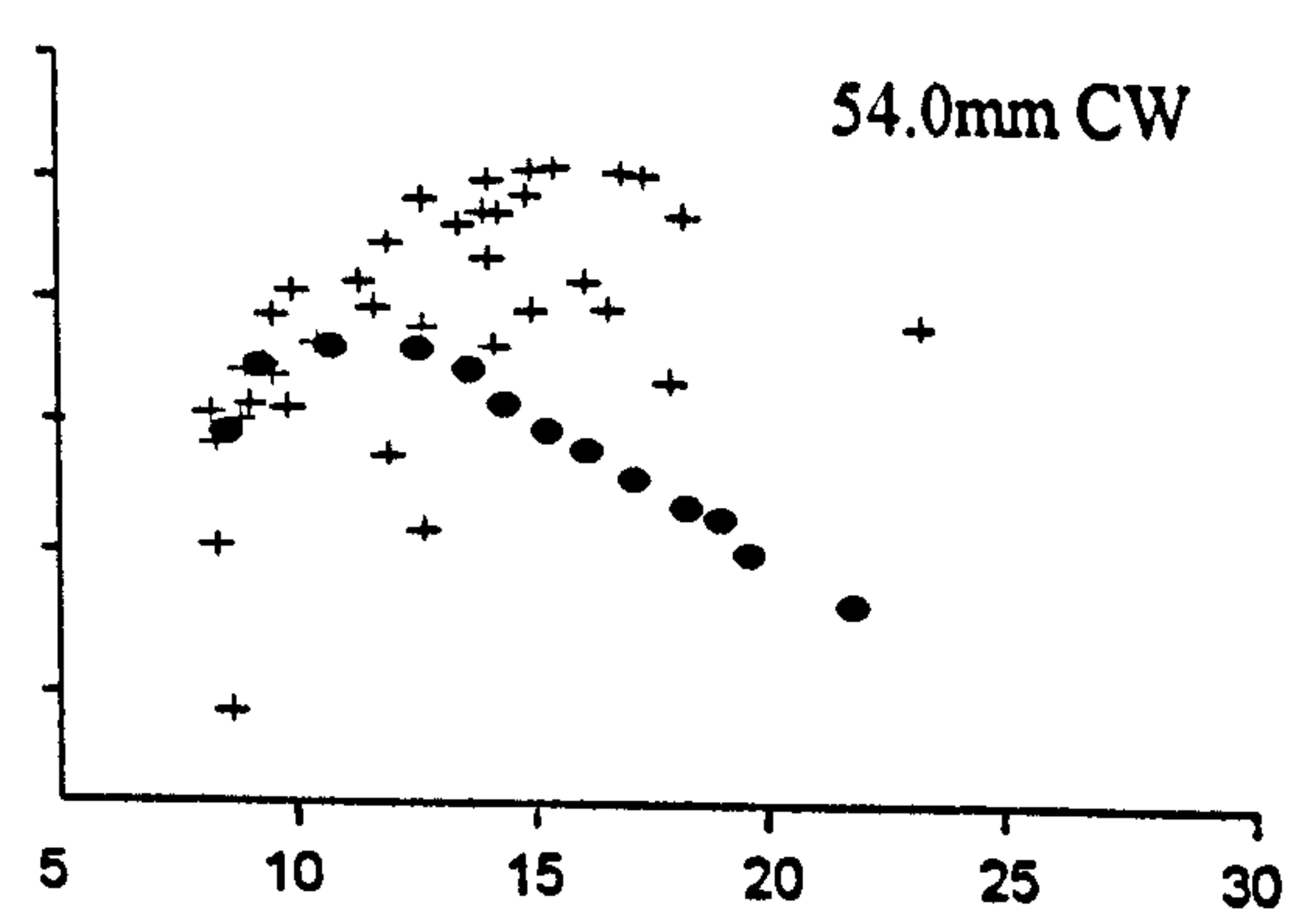
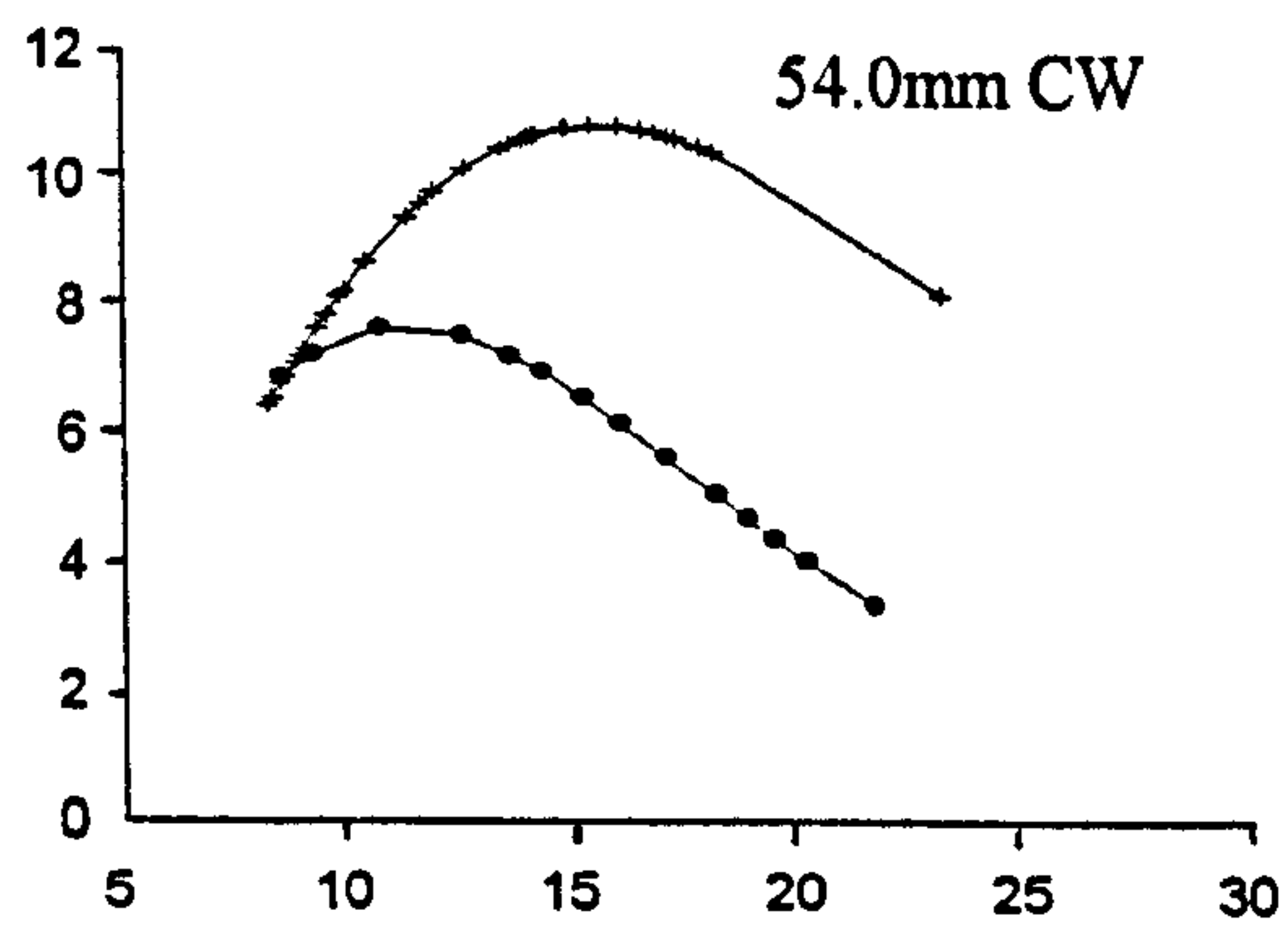
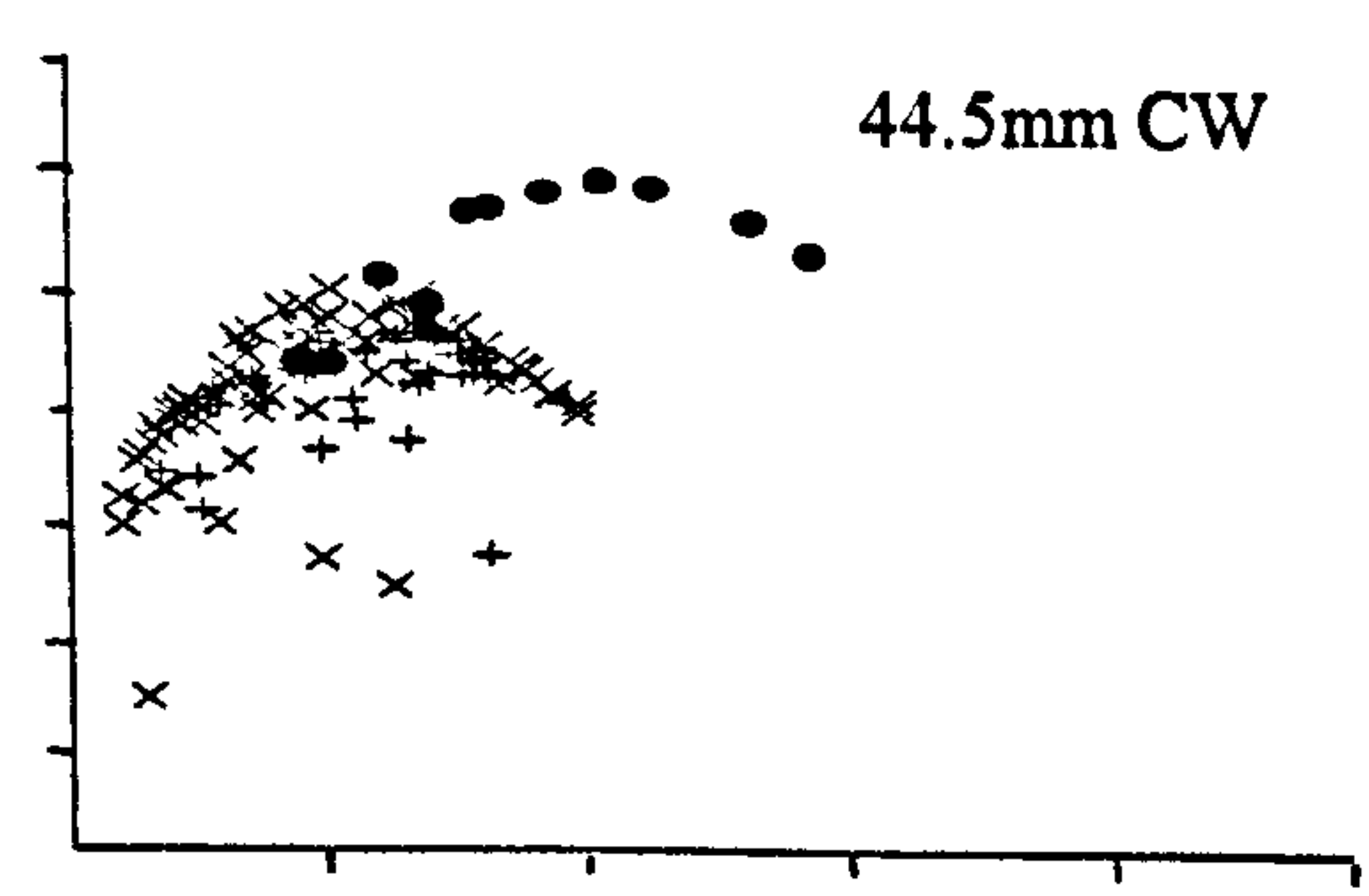
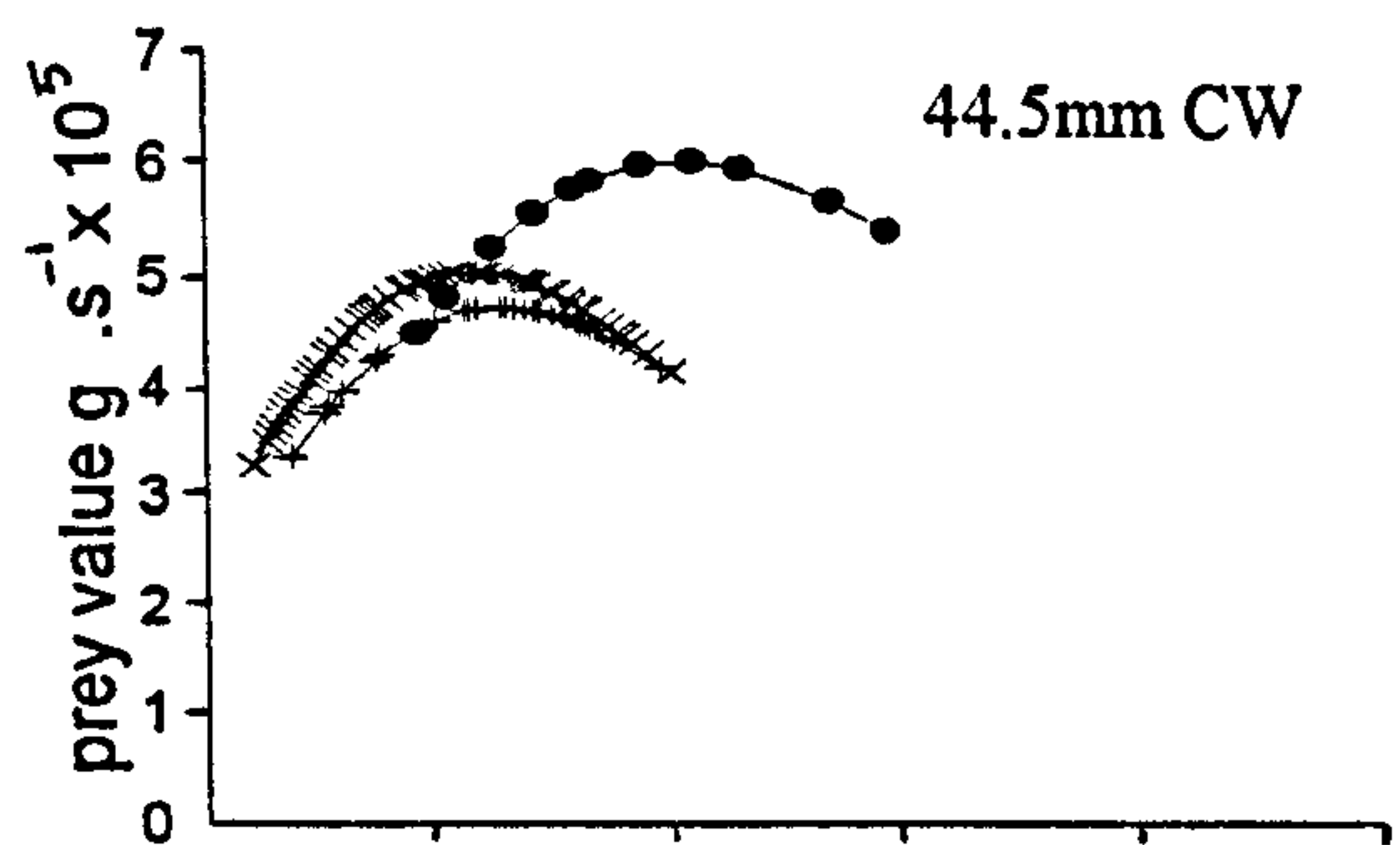
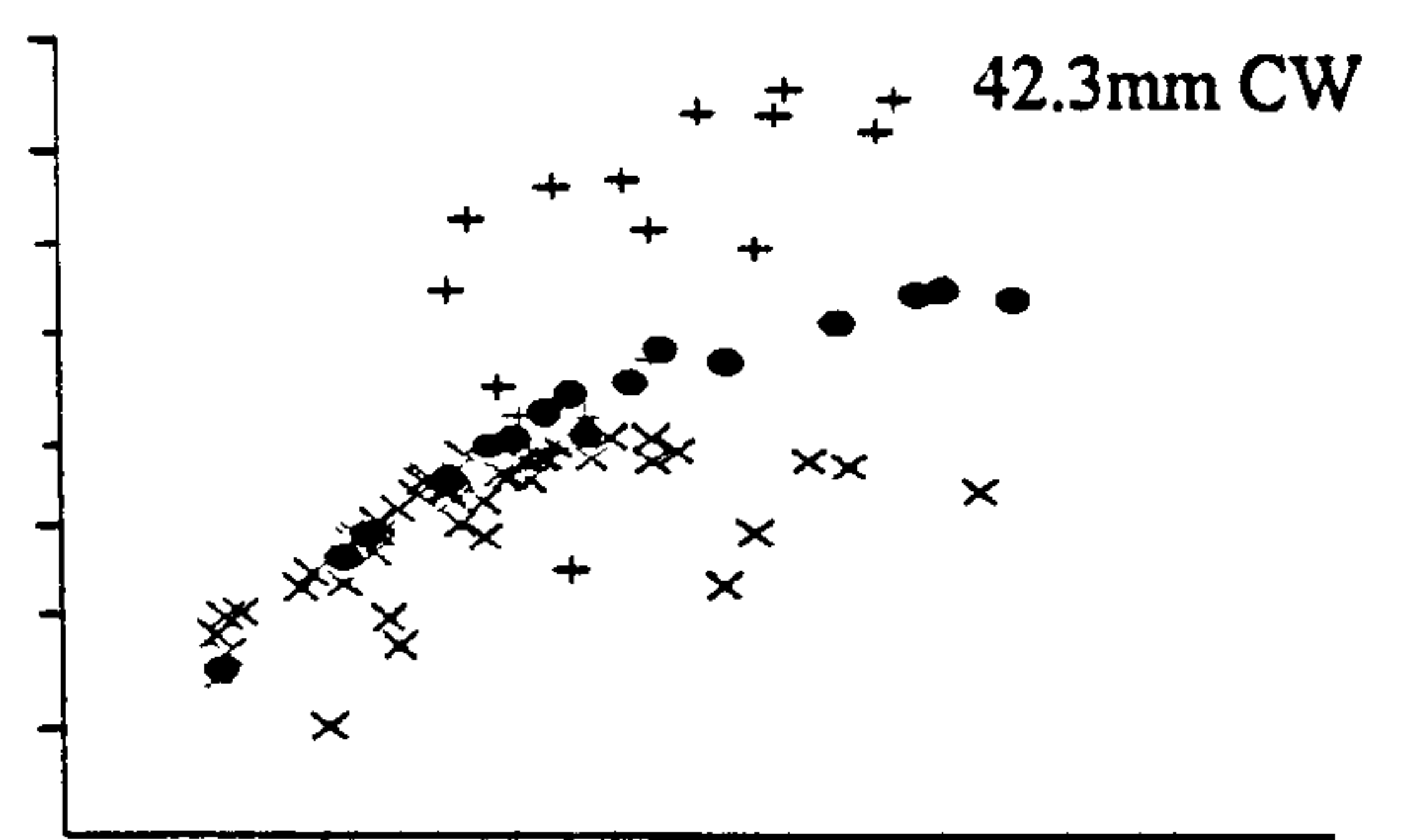
Breaking and handling times were linearised by \log_e transformation and the relationships between these variables and shell length, as determined by regression analysis, are presented in Table 5.5. Breaking and handling times were compared between trials using analysis of covariance (general linear model, MINITAB). No significant differences in breaking times could be determined between the three trials (Table 5.6), implying that there was no significant improvement in the ability of these crabs to open mussels. However, significant differences in the handling times between the three trials were evident (Table 5.6) although there were no significant differences in the handling times between the two trials in which each of the three crabs were presented with mussels singly. Thus, handling times when prey were presented in

Figure 5.2. Comparison of (A) prey value curves (predicted flesh content of mussel/handling time) with (B) adjusted prey value curves (predicted flesh eaten/handling time) determined when three *Carcinus maenas* (42.3, 44.5, 54.0 mm CW) foraged on *Mytilus edulis* presented singly (closed circles), as part of group comprising five mussels in each of the following size classes; 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length (pluses) and as part of a group comprising 11, 7, 3, 3, 1, mussels in the following size classes 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length respectively (crosses).

A



B



shell length (mm)

Table 5.4. The effect of presenting *Mytilus edulis* within groups of different proportions to three *Carcinus maenas*. The total number of mussels eaten, the number encountered and the percentage eaten:encountered in each size class is presented. Data derived from Experiment 1. The optimal size classes of mussels, determined from the predicted prey value curves (Fig. 5.1A) are highlighted.

		Group ¹				Modified group ²			
Crab CW (mm)	Mussel size (mm)	No. eaten	No. encountered	Eaten:encountered	%	No. eaten	No. encountered	Eaten:encountered	%
42.3	5-10	0	1	-	-	11	13		84.6
	10-15	8	8	100	100	13	44		75.1
	15-20	8	16	50.0	50.0	8	26		30.8
	20-25	1	49	20.4	20.4	2	38		5.3
	25-30	1	129	0.7	0.7	0	33		0.0
44.5	5-10	12	16	75.0	75.0	57	65		87.7
	10-15	30	36	83.3	83.3	37	81		45.7
	15-20	2	66	3.0	3.0	0	30		0.0
	20-25	0	58	0.0	0.0	0	25		0.0
	25-30	0	80	0.0	0.0	0	18		0.0

Table 5.4 (cont.). The effect of presenting *Mytilus edulis* within groups of different proportions to three *Carcinus maenas*. The total number of mussels eaten, the number encountered and the percentage eaten:encountered in each size class is presented. Data derived from Experiment 1. The optimal size classes of mussels, determined from the predicted prey value curves (Fig.s) are highlighted.

Crab CW (mm)	Mussel size (mm)	Group ¹				Modified group ²			
		No. eaten	No. encountered	Eaten:encountered	%	No. eaten	No. encountered	Eaten:encountered	%
54.0 ³	5-10	13	14		92.9	-	-		-
	10-15	21	29		72.4	-	-		-
	15-20	9	44		20.5	-	-		-
	20-25	1	42		2.3	-	-		-
	25-30	0	85		0.0	-	-		-

¹ = Trial 2, mussels presented as five individuals in each of the following size classes, 5-10, 15-20, 20-25, 25-30 mm shell length

² = Trial 3, mussels presented as a group comprising the follwoing size classes, 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length in the modified proportion of 11, 7, 3, 3, 1.

³ = Crab stopped eating during Trial 3, no data available.

Table 5.5. The effect of prey presentation on the relationships between breaking times, handling times and prey length for three *Carcinus maenas* feeding on *Mytilus edulis*. Relationships obtained from least squares regression. Data derived from Experiment 2.

Crab CW (mm)	Trial	Dependent variable (y)	Independent variable (x)	a	b	r	n
52.4	Individuals ¹	Ln Th	Shell length	3.42	0.186	0.889	29
	Group ²			2.46	0.197	0.850	60
	Individuals ³			3.33	0.174	0.892	28
	Individuals ¹	Ln Tb	Shell length	0.195	0.261	0.856	28
	Group ²			0.607	0.223	0.764	55
	Individuals ³			0.237	0.268	0.898	27
	Individuals ¹	Ln Th	Shell length	3.74	0.174	0.952	32
	Group ²			2.20	0.215	0.922	33
	Individuals ³			3.48	0.166	0.817	26
52.8	Individuals ¹	Ln Tb	Shell length	0.16	0.269	0.927	32
	Group ²			-0.11	0.263	0.891	33
	Individuals ³			-0.53	0.297	0.819	26
	Individuals ¹	Ln Th	Shell length	3.38	0.171	0.937	29
	Group ²			2.43	0.184	0.853	48
	Individuals ³			3.54	0.145	0.936	30
	Individuals ¹	Ln Tb	Shell length	0.75	0.216	0.818	29
	Group ²			0.12	0.233	0.843	48
	Individuals ³			0.82	0.182	0.858	30

¹ = Trial 1, mussels presented singly

² = Trial 2, mussels presented as a group comprising the following size classes, 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length in the modified proportion of 11, 7, 3, 3, 1

³ = Trial 3, mussels presented singly

a, b = coefficients in the regression equation $\ln y = a + bx$

r = product moment correlation coefficient

n = number of mussels used in the analysis

Table 5.6. Breaking times (Tb) and handling times (Th) are compared between three feeding trials¹. Differences between the slopes and the intercepts in the equation $\ln y = a + bx$ are tested using analysis of covariance (general linear model, MINITAB). Data derived from Experiment 2.

Crab CW (mm)	Dependent variable (y)	Independent variable (x)	Slopes (b)		Intercepts (a)		
			F	p	F	p	n
52.4	Ln Th	Shell length	0.54	ns	3.50	*	117
	Ln Tb	Shell length	0.86	ns	0.25	ns	110
52.8	Ln Th	Shell length	2.58	ns	8.72	***	91
	Ln Tb	Shell length	1.24	ns	0.59	ns	91
54.1	Ln Th	Shell length	1.81	ns	5.08	**	107
	Ln Tb	Shell length	1.05	ns	0.68	ns	100

¹ = Trial 1, mussels presented singly

Trial 2, mussels presented as a group comprising the following size classes, 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length in the proportion 11, 7, 3, 3, 1

Trial 3, mussels presented singly

ns = no significant differences

* = significant at $p < 0.05$

** = significant at $p < 0.01$

*** = significant at $p < 0.001$

groups differed from those obtained when prey were presented individually, and the differences could not be attributed to learning by the crab; handling times were lower when prey were presented as part of a group. The effect of this can be seen in Figure 5.3A where lower handling times elevated prey value curves such that all sizes of mussels eaten by the crabs were predicted to be more profitable than when mussels were presented singly. The size of prey predicted to be most profitable also changed (Fig. 5.3A); in groups the most profitable size of prey was smaller than when mussels were offered singly. When prey value curves from the three trials are compared to prey vulnerability, determined in Trial 2, in which mussels were presented in groups to the crabs, it can be seen that the predicted optimal sizes of mussel did not always coincide with the preferred size of mussel (Fig 5.3B).

The amount of flesh remaining in discarded mussel shells differed significantly between the three trials, and from Table 5.2 it can be seen that significantly more flesh remained when prey was presented as part of a group. In Figure 5.4 prey value, i.e. the predicted flesh weight divided by the predicted handling time (E/Th) is compared to adjusted prey value, i.e. the predicted amount of flesh eaten in each mussel, divided by the predicted handling time ($(E-L)/Th$). No difference in the relationship between the prey value curves was evident with prey value remaining higher when prey were presented as part of a group. It is concluded, therefore, that the extensive gleaning of mussel shells that occurs when prey are presented singly is inefficient and that the increased energy gain does not offset the increased handling times required.

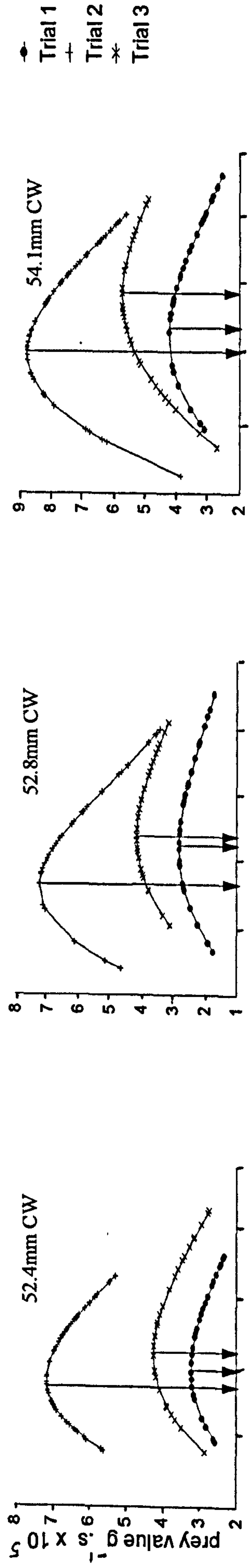
Table 5.7 shows the relationship between the number of mussels eaten in each size class together with their encounter rates. The number of encounters with the smallest size group was always low although the percentage of these mussels that were eaten relative to those encountered was high (60-83%). The preferred size class, i.e. that from which most mussels were eaten, was not necessarily that which had the highest eaten:encounter rate; indeed up to 70% of mussels encountered in those size classes were rejected. Furthermore, the predicted optimal prey size class, i.e. that which should be selected if crabs are foraging optimally under the energy maximisation premise, did not consistently have the highest eaten:encounter rates either.

Figure 5.3.

A. Prey value curves for three *Carcinus maenas* (52.4, 52.8, 54.1 mm CW) when foraging on *Mytilus edulis* presented singly (closed circles, Trial 1), as part of group comprising five mussels in each of the following size classes; 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length (pluses, Trial 2) and singly (crosses, Trial 3). Arrows denote those sizes of mussel predicted to be the most profitable.

B. The number of mussels eaten by each crab (52.4, 52.8, 54.1 mm CW) over a five day period when mussels were presented as part of group comprising five mussels in each of the following size classes; 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length (closed bar, Trial 2).

A



B

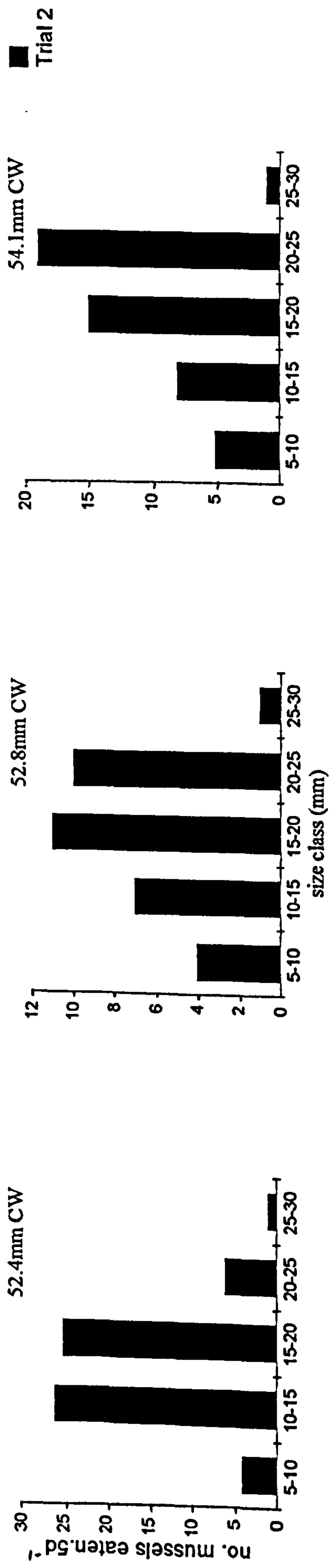
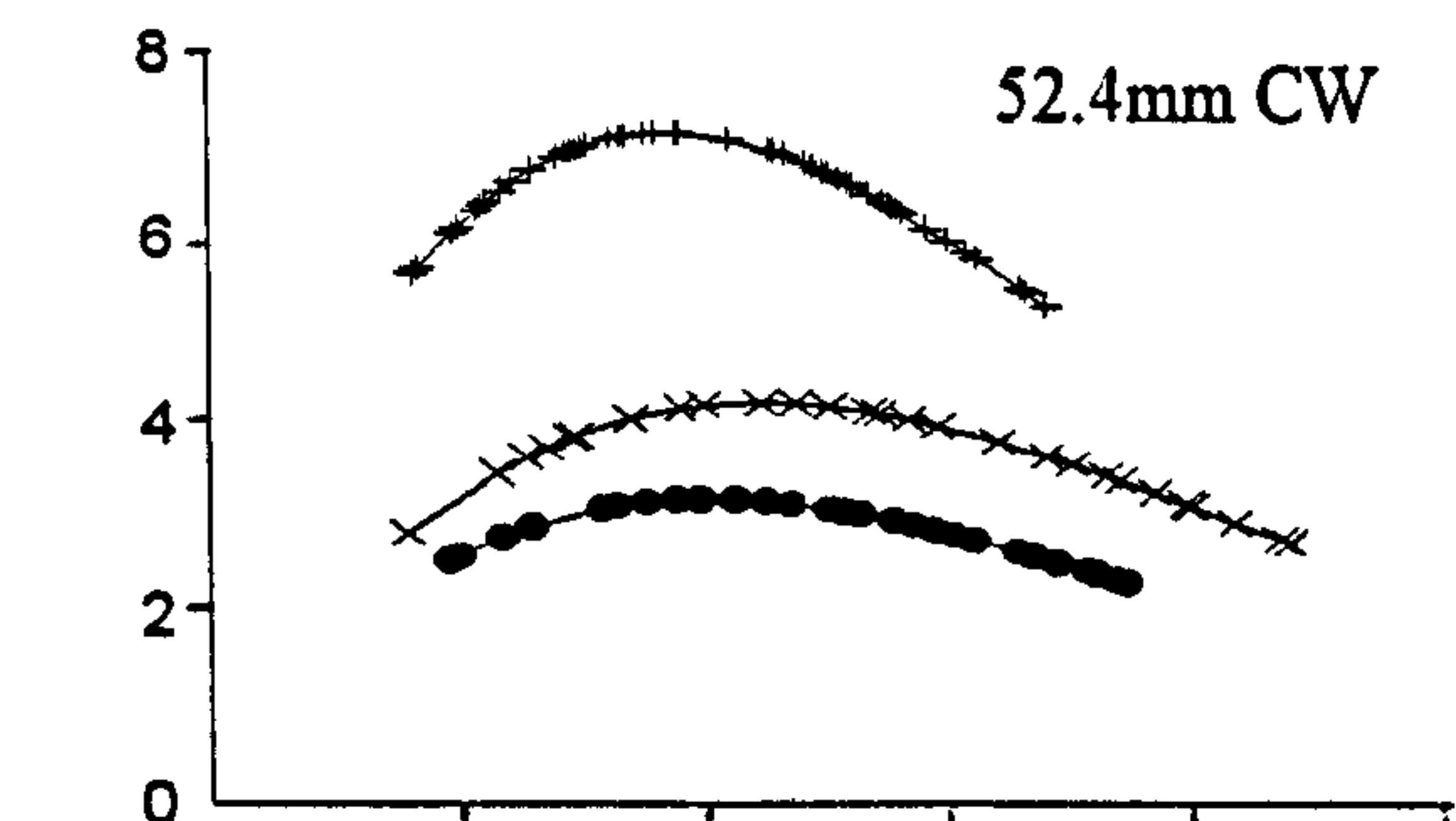
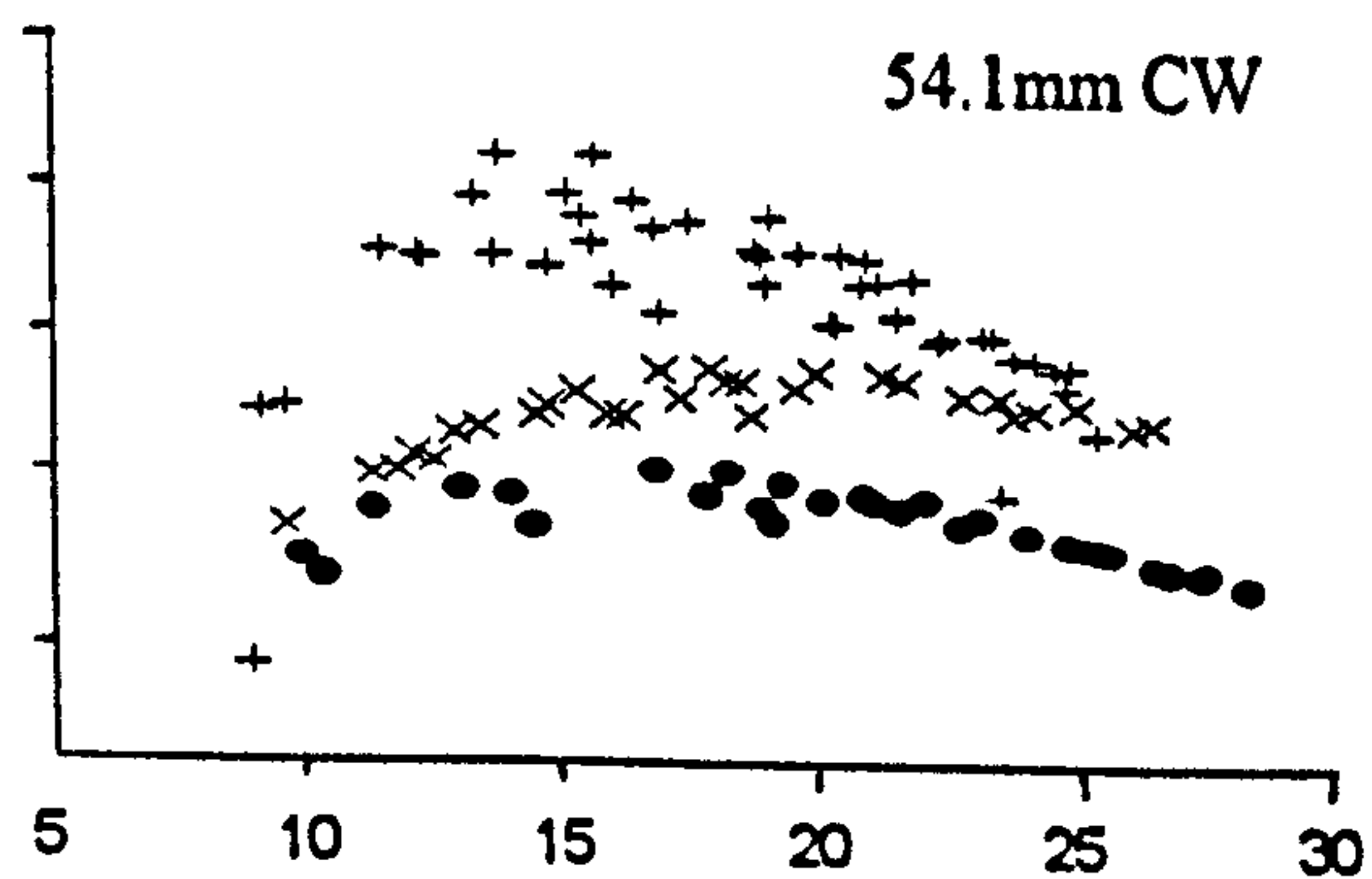
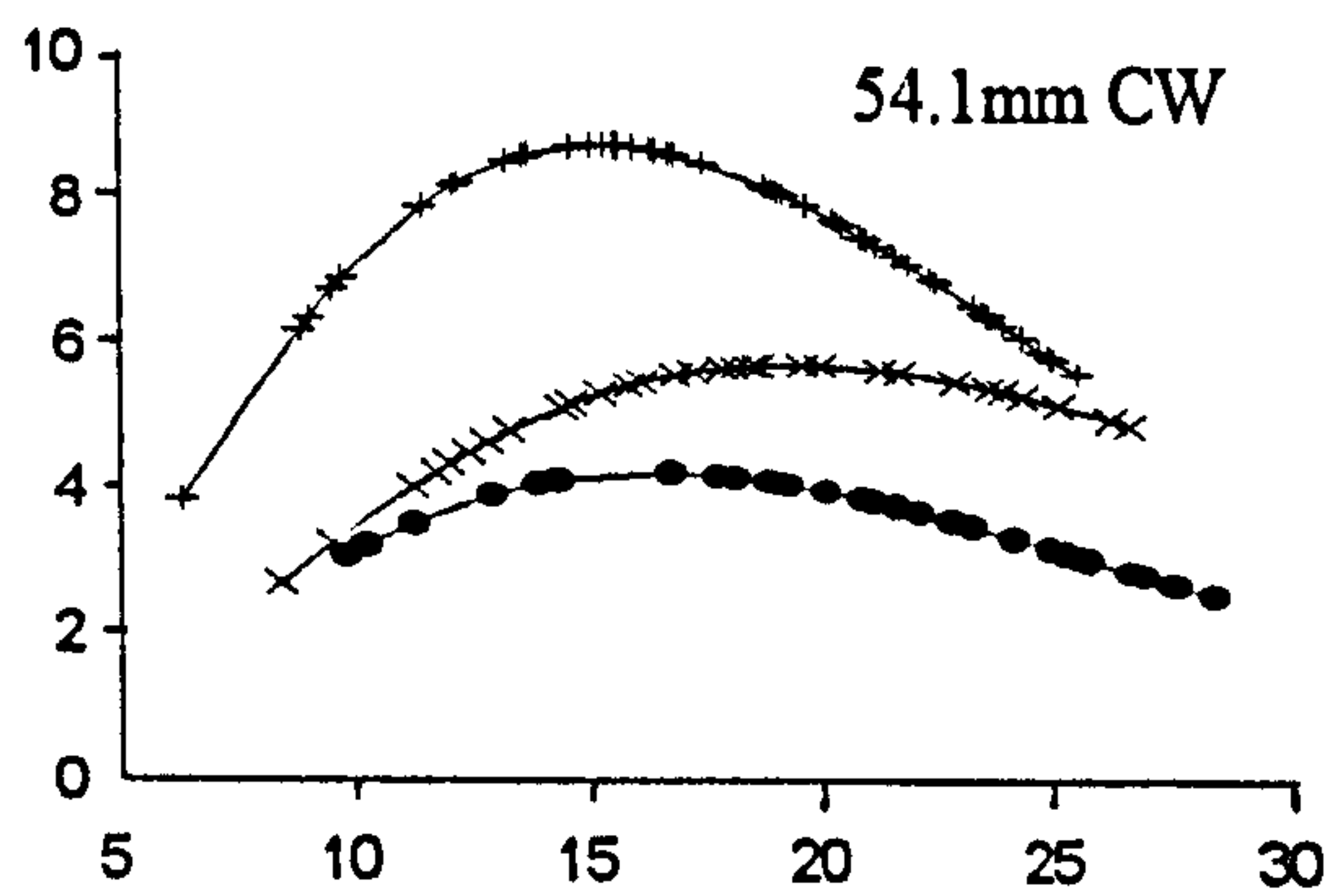
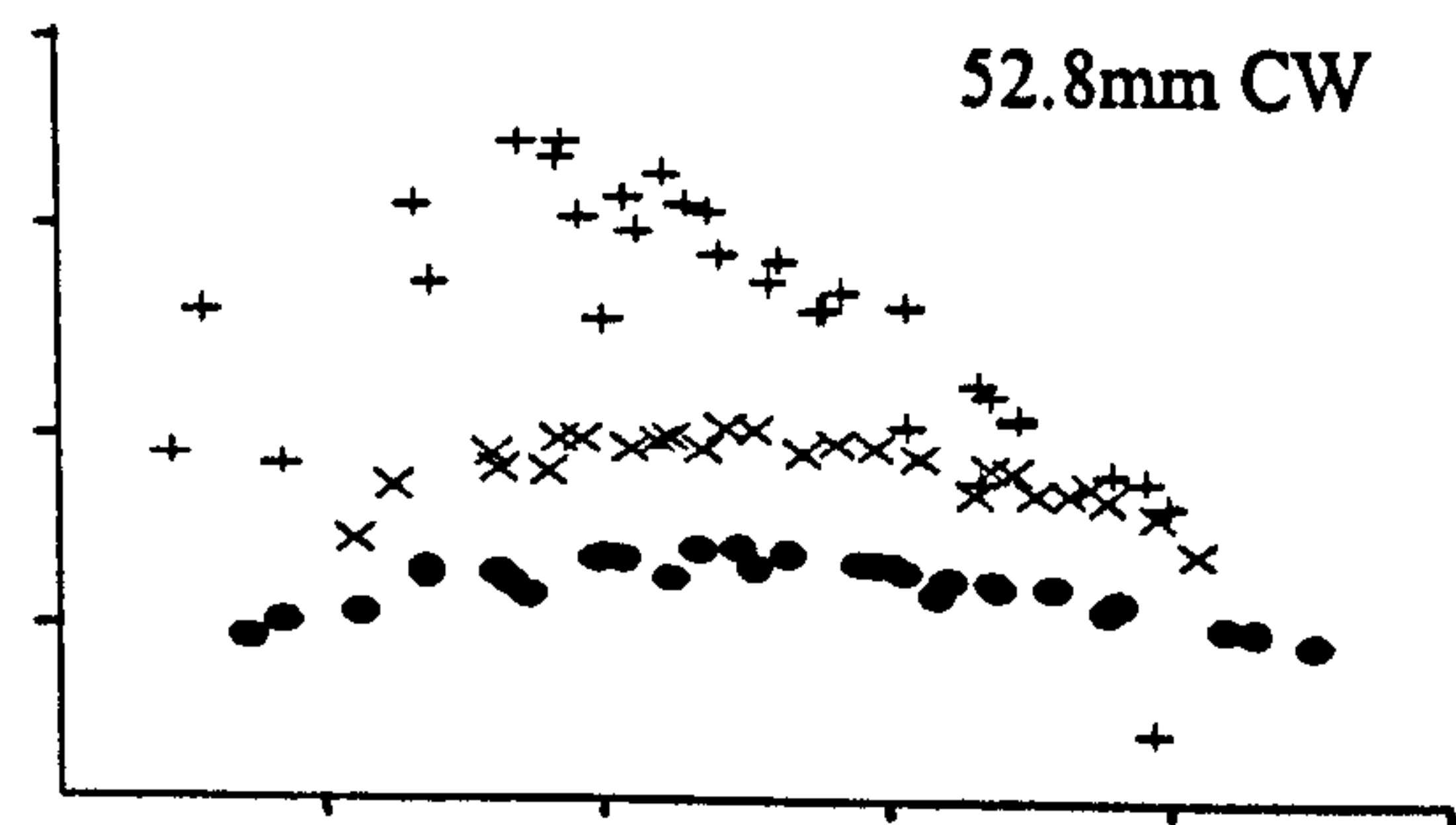
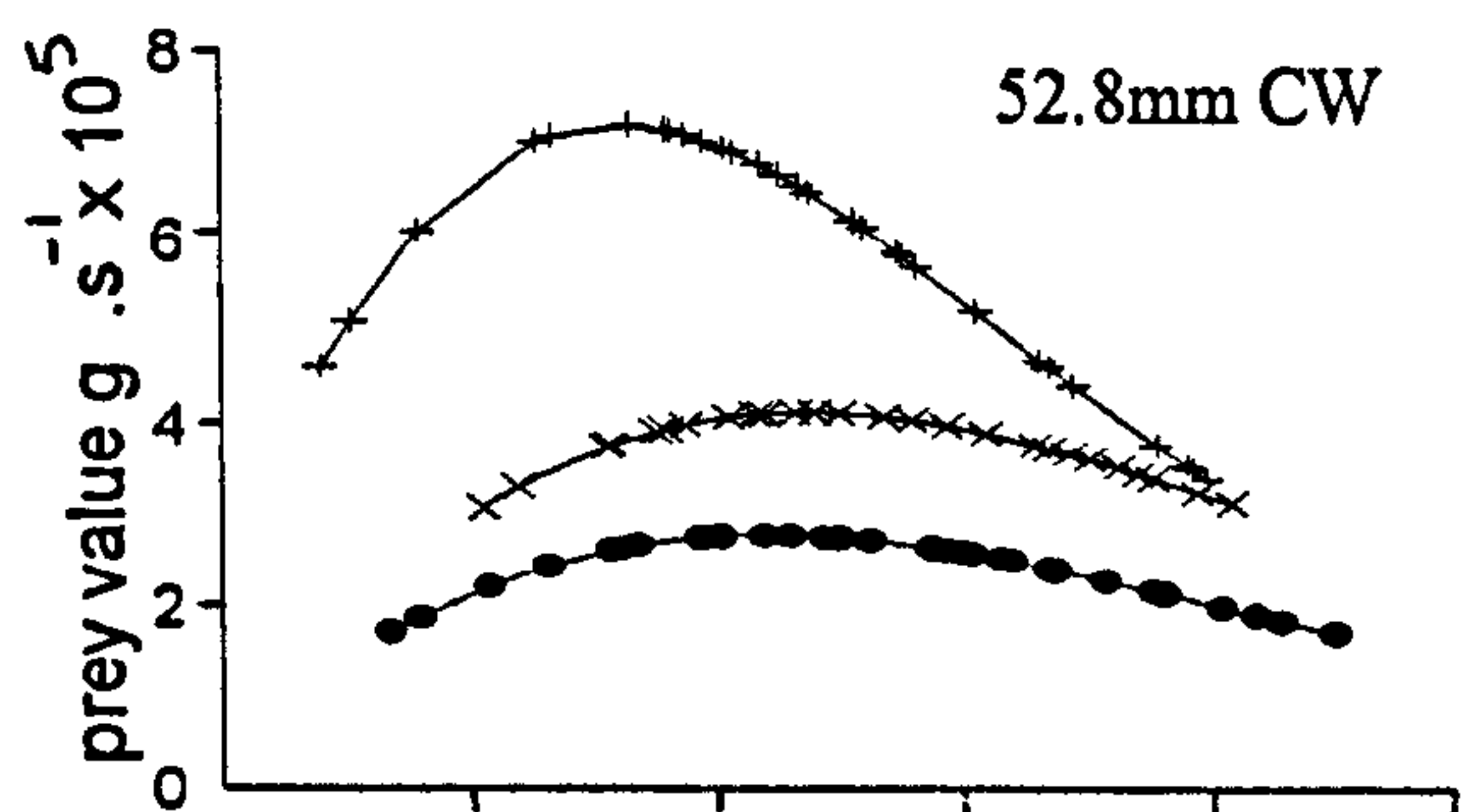
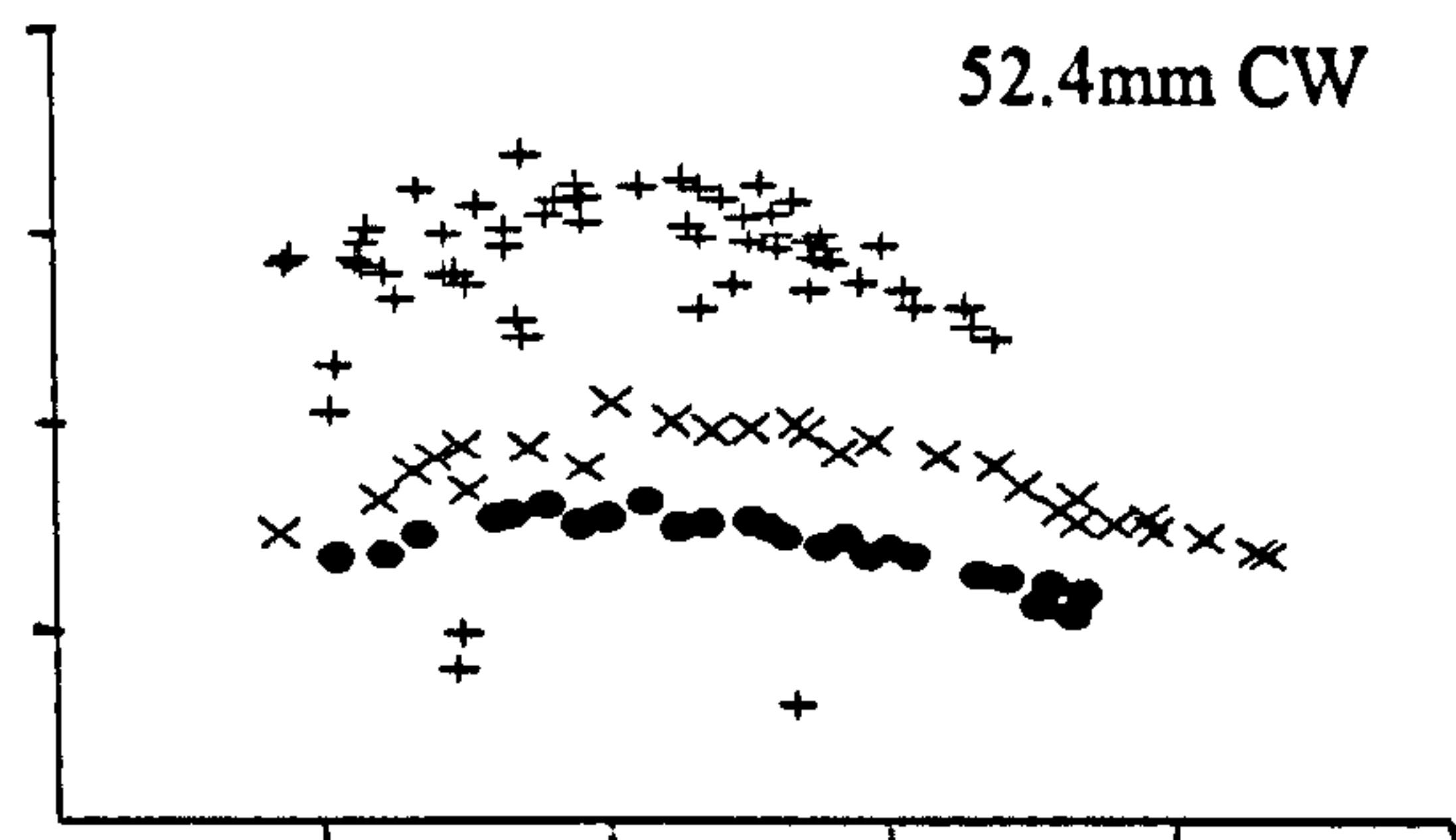


Figure 5.4. Comparison of (A) prey value curves (predicted flesh content of mussel/handling time) with (B) adjusted prey value curves (predicted flesh eaten/handling time) determined when three *Carcinus maenas* (52.4, 52.8, 54.1 mm CW) foraged on *Mytilus edulis* presented singly (closed circles), as part of group comprising five mussels in each of the following size classes; 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length (pluses) and again singly (crosses).

A



B



shell length (mm)

Table 5.7. The effect of presenting *Mytilus edulis* in groups¹ to three *Carcinus maenas*. The total number of mussels eaten, the number encountered and the percentage eaten:encountered in each size class is presented. Data derived from Experiment 2. The optimal size classes of mussels, determined from the predicted prey value curves (Fig. 5.3A) are highlighted.

Crab CW (mm)	Mussel size (mm)	No. eaten	No. encountered	% Eaten:encountered
52.4	5-10	4	6	66.7
	10-15	27	28	96.4
	15-20	24	38	63.2
	20-25	5	37	13.5
	25-30	1	22	4.6
52.8	5-10	3	5	60.0
	10-15	7	11	63.6
	15-20	9	14	64.3
	20-25	10	33	30.3
	25-30	1	11	9.1
54.1	5-10	5	6	83.3
	10-15	9	14	64.3
	15-20	14	22	63.6
	20-25	19	33	57.6
	25-30	1	11	9.1

¹= Trial 2, mussels were presented in groups comprising the following size classes, 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length in the proportion 11, 7, 3, 3, 1, respectively.

5.3.4. Prey vulnerability.

Clear prey size preferences were demonstrated by all crabs feeding on the two groups of mussels with unlimited prey availability in Experiment 3 (Fig.5.5). When mussels were presented in equal numbers in each of several size classes (Trial 1) the size of preferred prey clearly increased with crab size (Fig. 5.5). However, this trend was less obvious when mussels were presented in the modified proportions (Trial 2) where there was a greater bias towards the smaller size classes of prey. Comparison of the two trials (Fig. 5.5) showed that when mussels were presented in the modified proportion the preferred size of prey shifted to the smaller size classes, reflecting what had previously been observed in the prey value trials in Experiment 1.

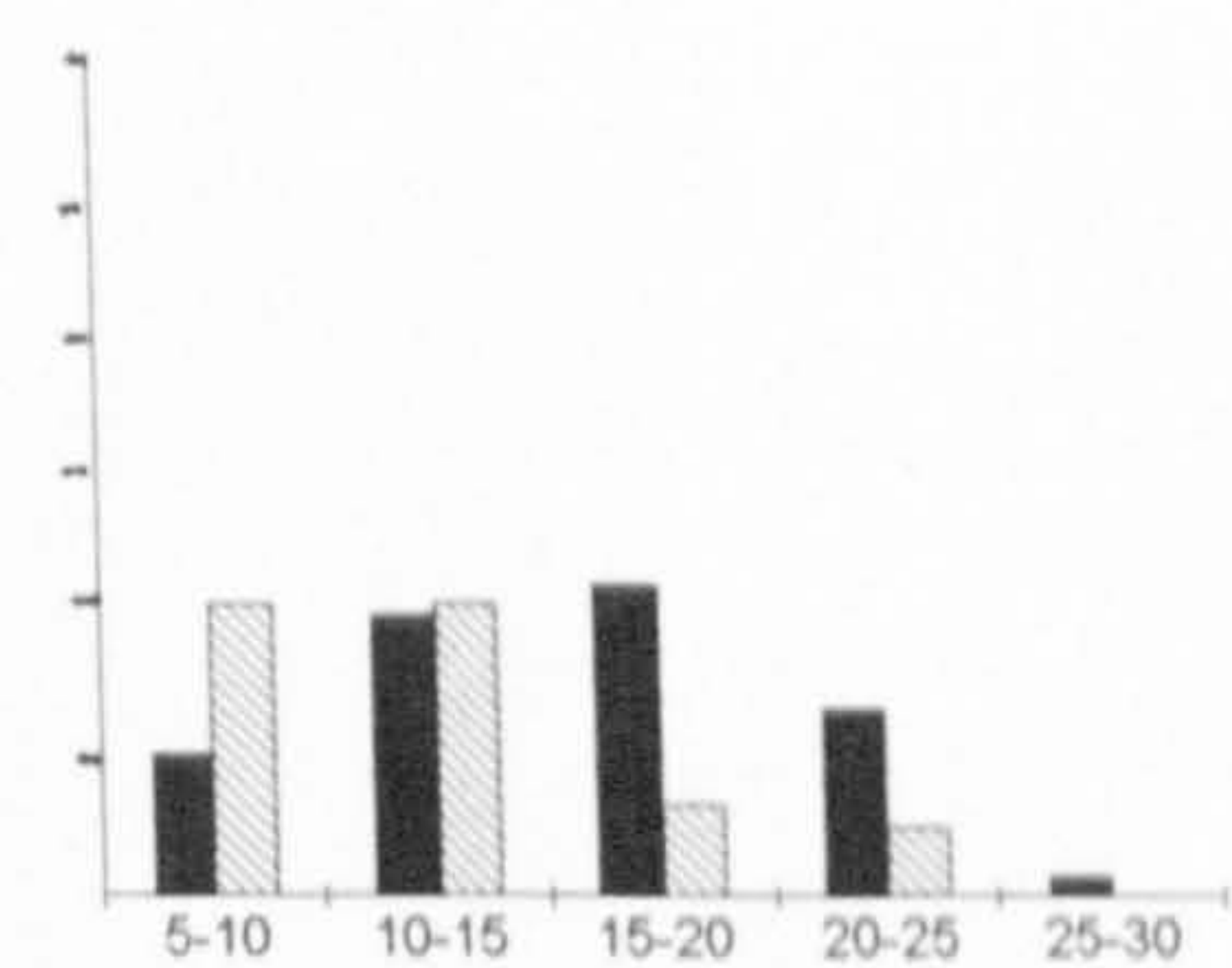
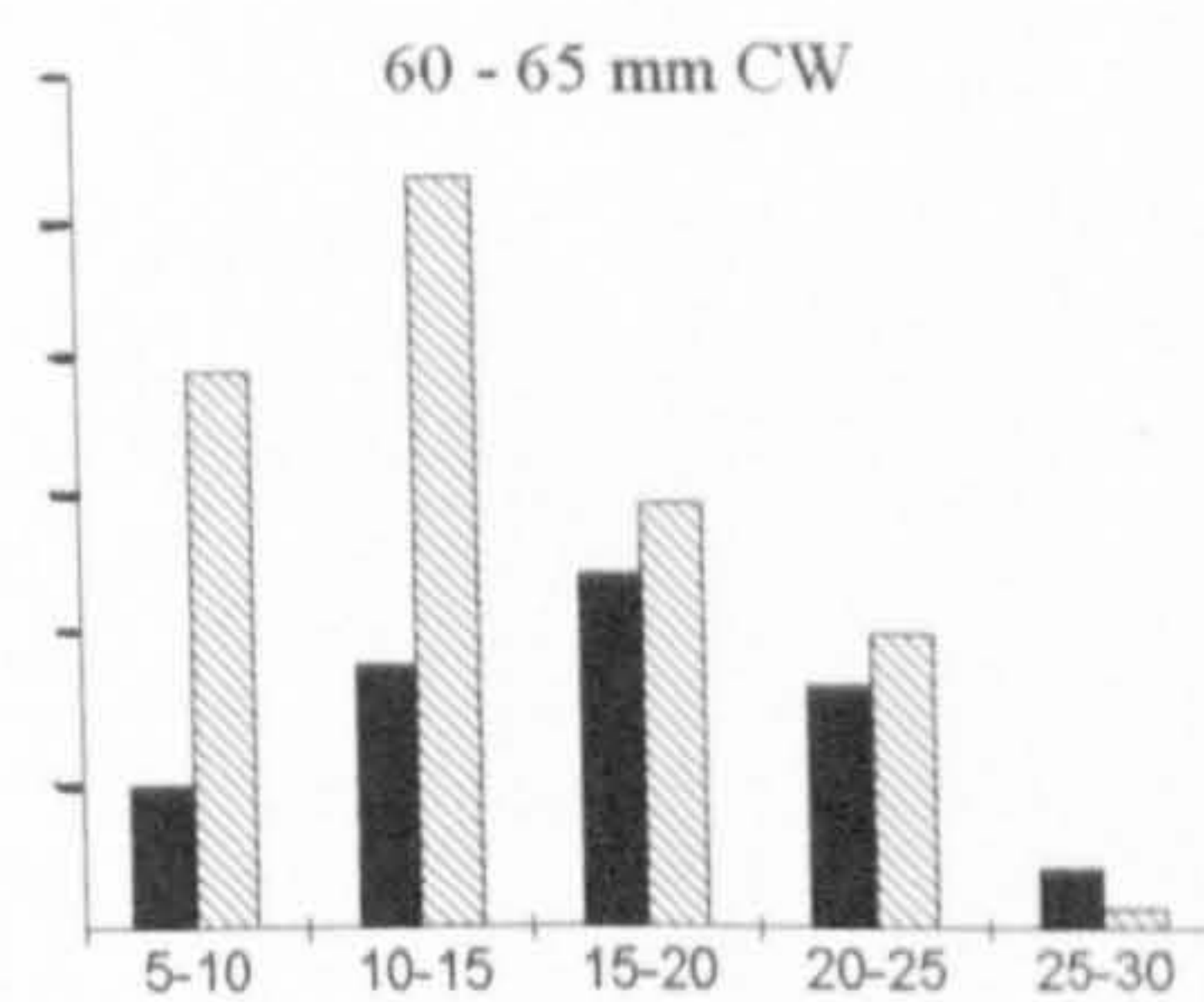
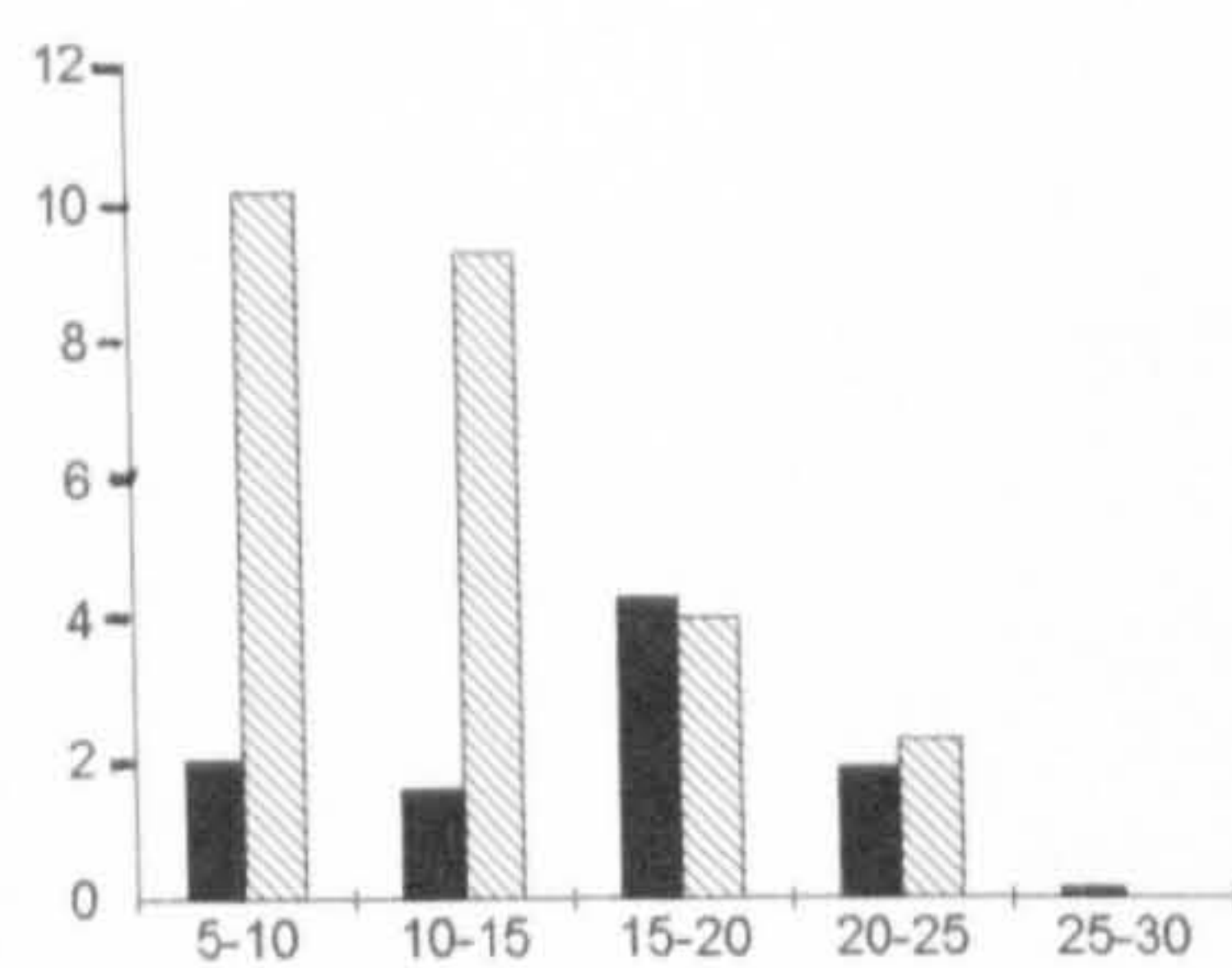
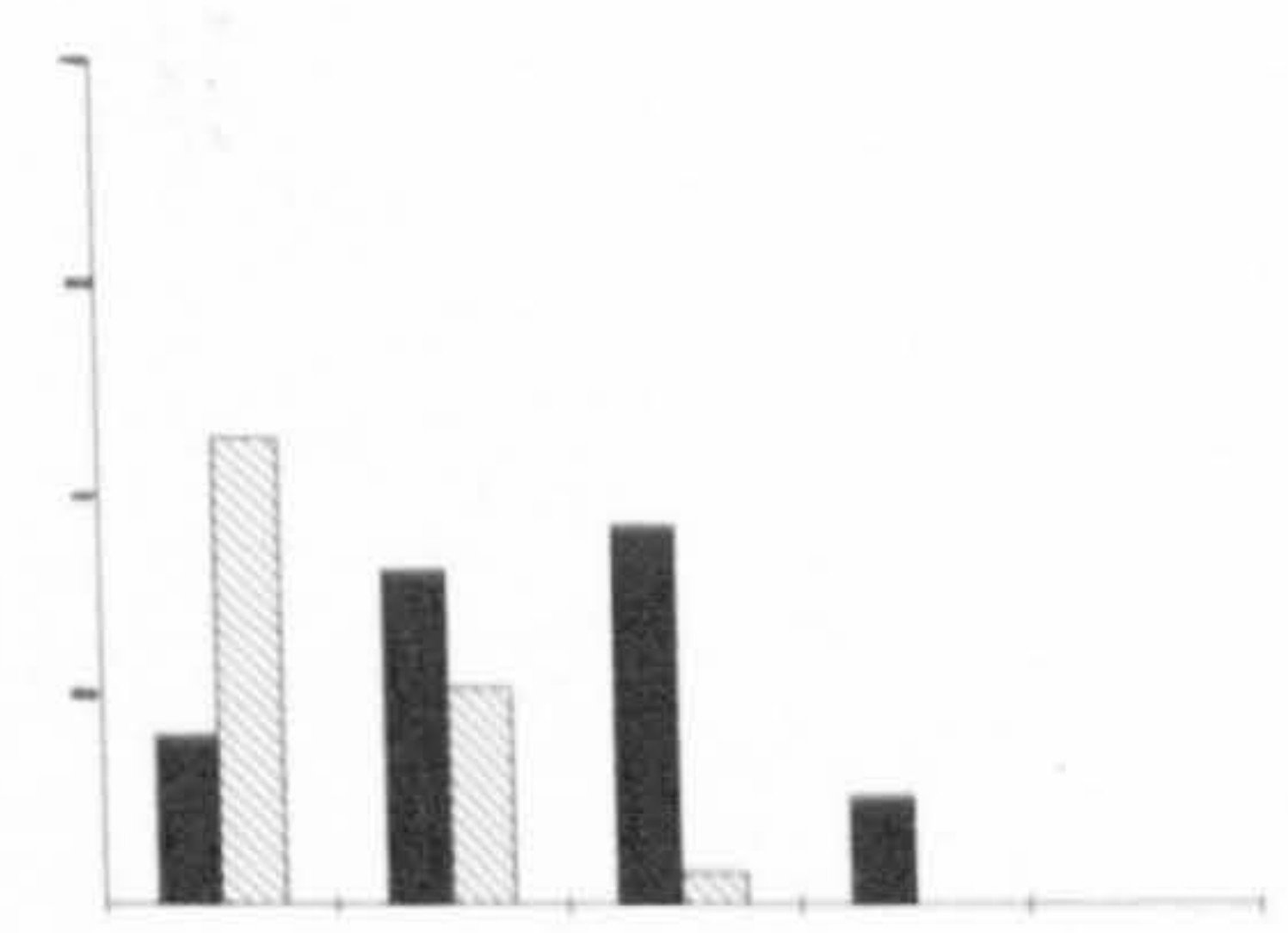
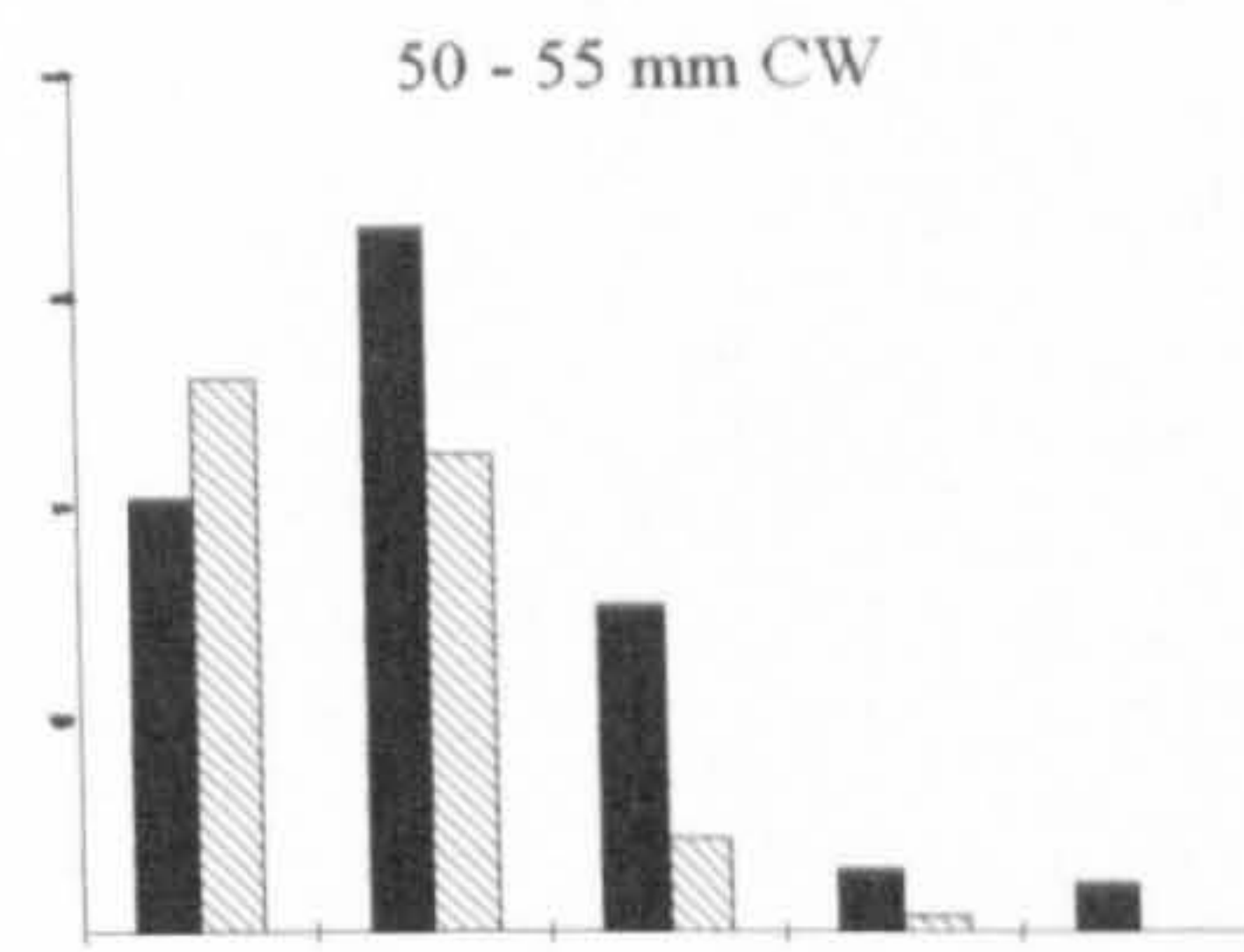
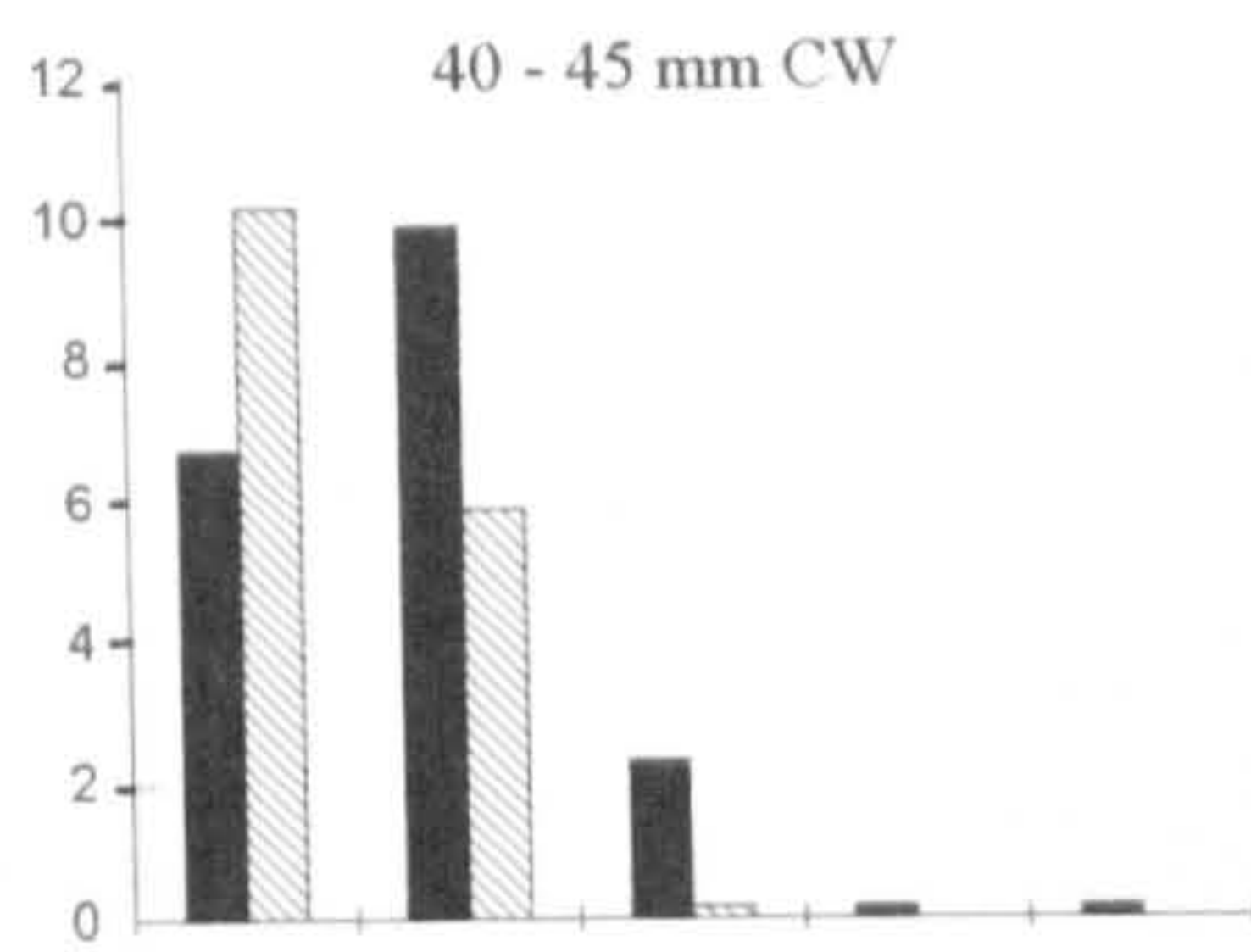
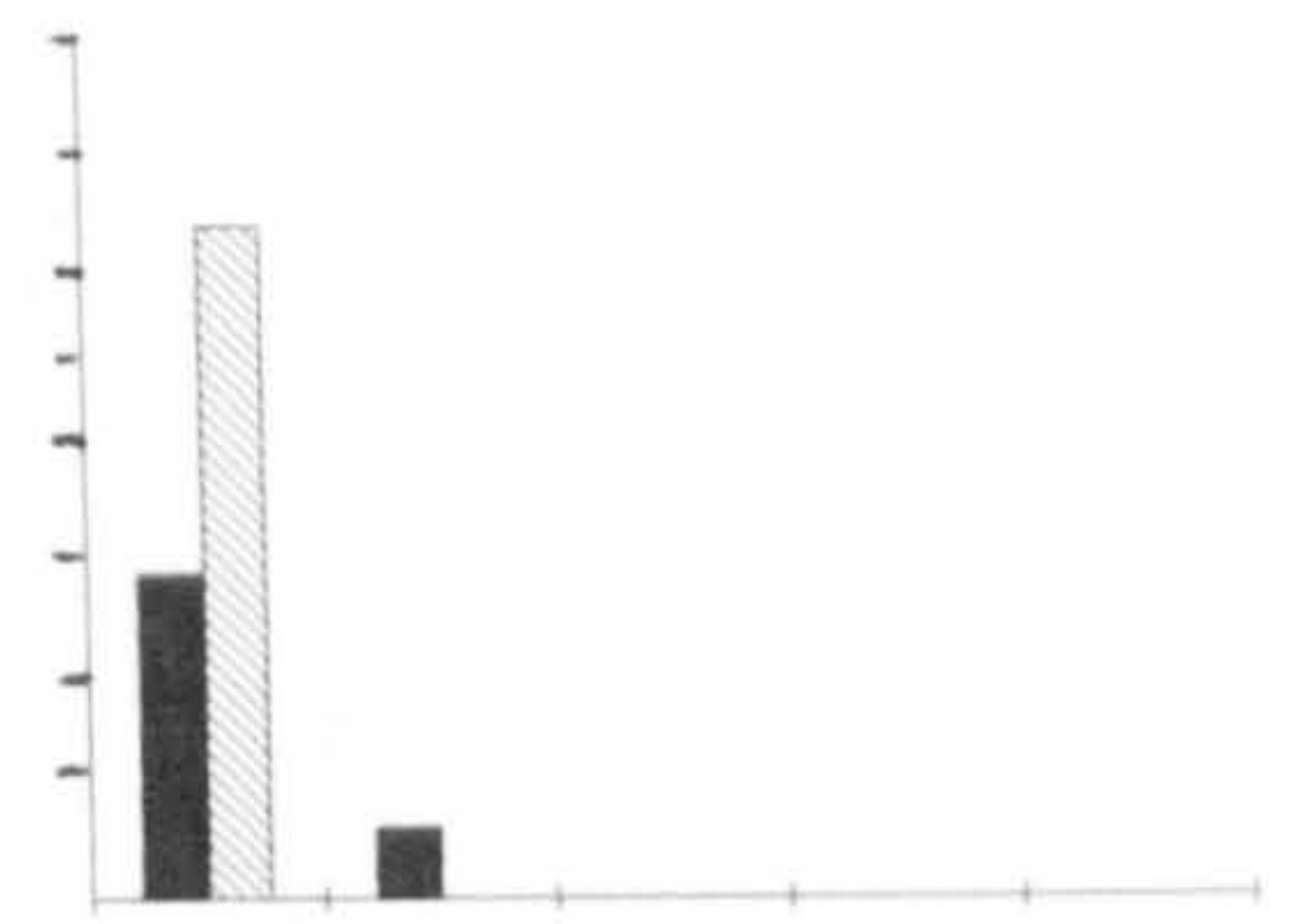
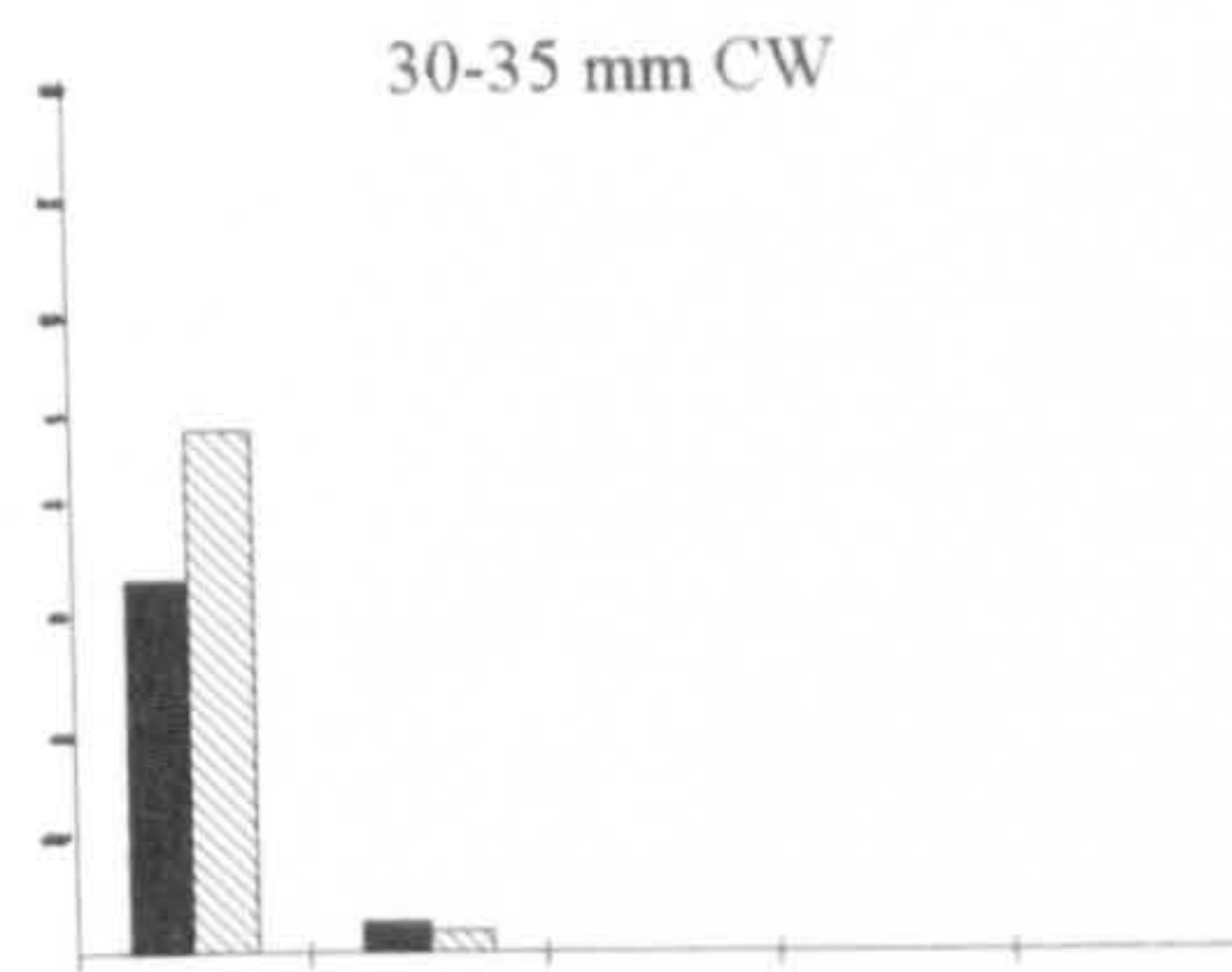
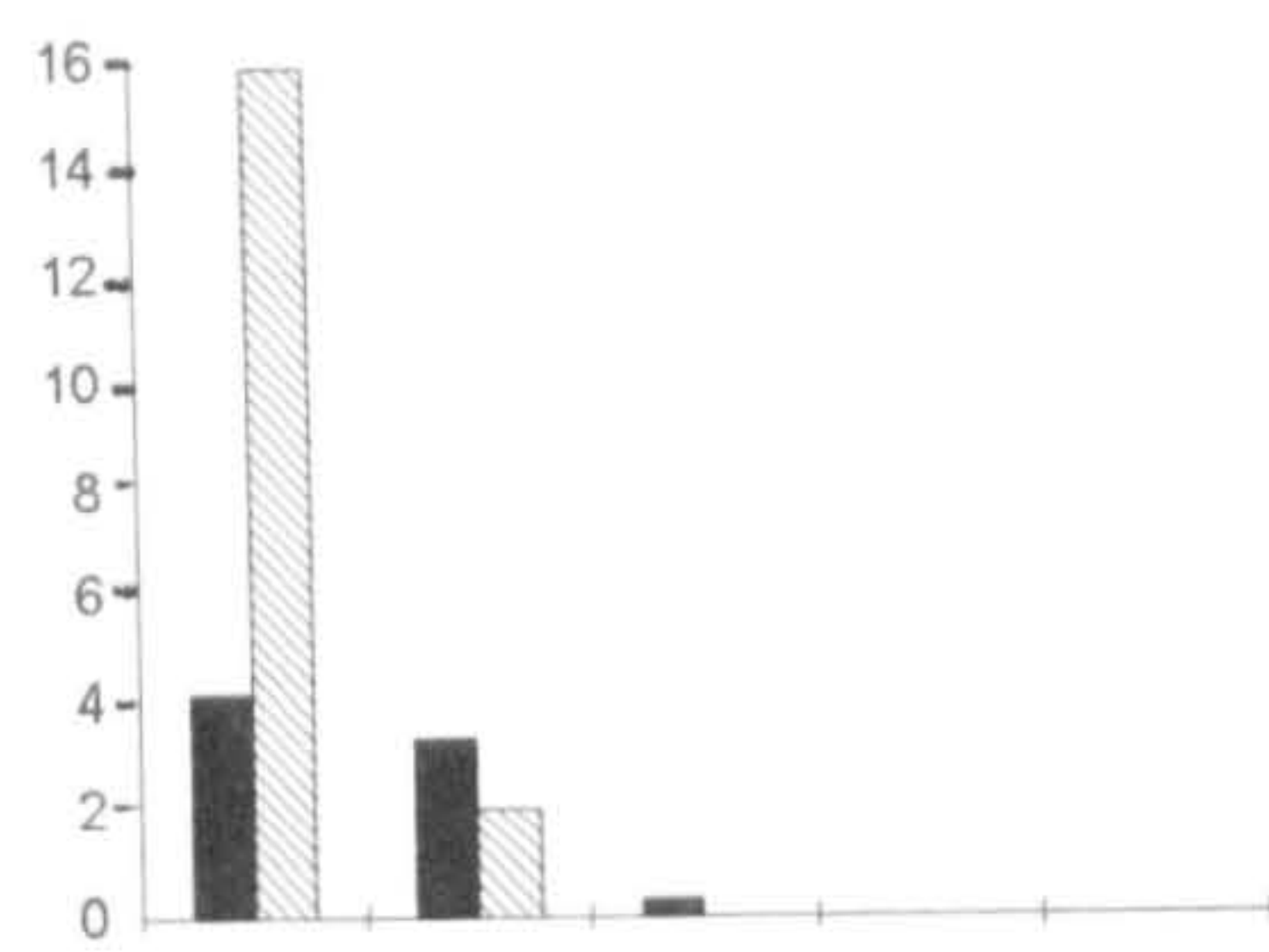
Differences arose in prey size selectivity when crabs were allowed to feed on mussels presented in the proportions typical of the high shore population and mid shore mussel populations at Aberffraw (Experiment 4) (Fig. 5.6). When crabs fed on the simulated high shore population, which contained proportionately more mussels in the smaller size classes, a greater number of these were included in the diet.

5.4. DISCUSSION

When mussels were presented in a group of mixed sizes, *Carcinus maenas* did not use the more time-consuming opening techniques of boring and edge-chipping thus confirming the findings presented in Chapter 4. This behaviour conforms to that predicted by the energy maximisation premise of the optimal foraging theory. Mussels opened by boring or edge-chipping techniques tend to be larger and have relatively greater handling times which thus reduces their profitability; consequently they should not be eaten if prey of greater value are also present. However, in Chapter 4 it was proposed that *C.maenas* probably does not select its prey solely on the basis of profitability. Further evidence to support this proposal is presented in this chapter and an alternative explanation for this reluctance to feed on larger mussels when smaller, more profitable prey are available, is presented. The selection of prey smaller than the maximum size that can be opened is a consistent pattern in the behaviour of decapod

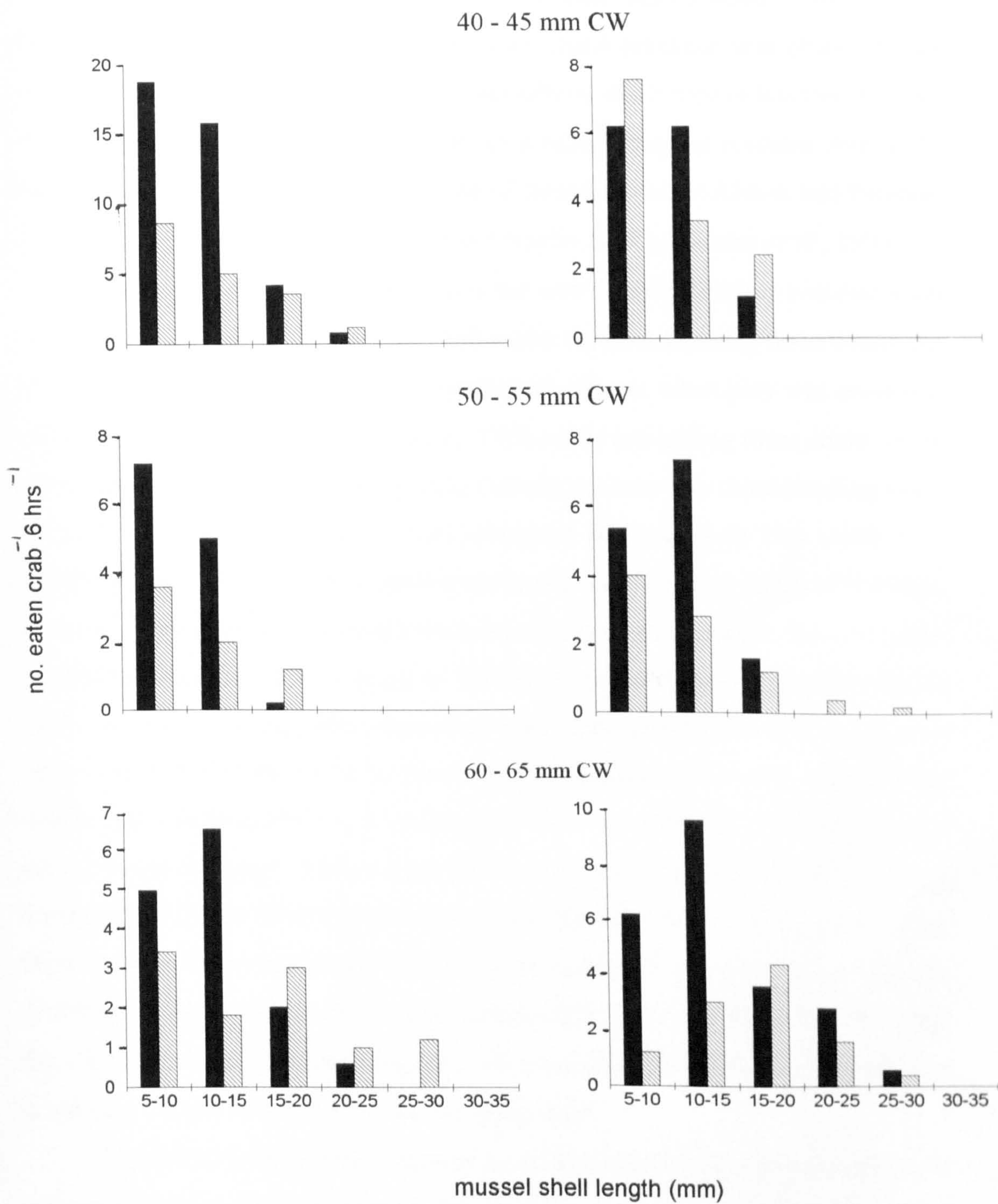
Figure 5.5. The number of *Mytilus edulis* consumed each day by four different sizes of *Carcinus maenas* when mussels were presented as five mussels in each of the following size classes, 5-10, 10-15, 15-20, 20-25, 25-30mm shell length (closed bar) and when mussels were presented as 11, 7, 3, 3, 1, individuals in the following size classes 5-10, 10-15, 15-20, 20-25, 25-30mm shell length respectively (hatched bar).

no. eaten crab .d



mussel shell length (mm)

Figure 5.6. The number of *Mytilus edulis* consumed each day by three size classes of *Carcinus maenas* when presented with 11, 7, 2, 2, 3 mussels respectively in the following size classes, 5-10, 10-15, 15-20, 20-25, 25-30 mm shell length; representative of the population from the high shore Aberffraw (closed bars), and with 10, 3, 3, 2, 5, 2, mussels respectively in the following size classes 5-10, 10-15, 15-20, 20-25, 25-30, 30-35 mm shell length; representative of the mid shore population at Aberffraw (open bars).



crustaceans when foraging on hard-shelled molluscs. Juanes (1992) proposed that this selection for smaller size ranges of resistant prey minimised chelal damage which might be induced by the repeated loading of the prey shell. Indeed when *C.maenas* was forced to feed on larger *Mytilus edulis* some chelal breakage was observed (see Chapter 4). The selection of smaller size classes of prey which require less time to open is also an entirely appropriate behaviour for a tidally foraging predator such as *C.maenas* where tides may limit the amount of foraging time (Atkinson and Parsons, 1973; Dare and Edwards, 1981; Hunter and Naylor, 1993; Warman *et al.*, 1993).

Prey value curves varied according to the way in which the prey was presented to crabs. Such variations resulted from differences between handling times which, for all but the two smallest crabs, were significantly shorter when prey was presented within a group than when presented singly. Differences in handling times could not be attributable to the use of different opening techniques since only those handling times for prey which had been crushed were compared in the analysis. Nor could these differences in prey value curves be entirely attributed to the learning ability of *Carcinus maenas*. Cunningham and Hughes (1984) found that when *C.maenas* fed on *Mytilus edulis*, breaking times were reduced to 30% of the original value after crabs had fed on 5-6 mussels and although this information was rapidly gained it was lost slowly over several days. Whilst the breaking times differed significantly between trials for the largest crab (54.0mm CW) in Experiment 1 where the effect of presenting prey in groups was investigated, there were no differences amongst the trials in Experiment 2 where the potential effect of learning was investigated. Furthermore, in this second experiment no differences could be detected in handling times between the first and third trials, in which prey items were presented singly. It is concluded, therefore, that the observed reduction in handling time when mussels were presented as part of a group must be due to some effect of the group itself.

Significantly more flesh remained in the discarded shells when mussels were presented in groups, indicating that reduced handling times were probably due to the shorter periods of time spent gleaning an opened mussel. When a crab fed on a group of mussels its pereiopods were generally in contact with several mussels simultaneously and a mussel held in the chelae would often be rejected for one touched by a

pereiopod. Jubb *et al.* (1983) proposed that such behaviour arose from the crab's response to the relative strengths of stimuli received simultaneously from the chelae and pereiopods. The strength of the stimulus received from the pereiopods is thought to increase with mussel size and the number of mussels touched, whilst the chelal stimulus increases with mussel size; usually the chelal stimulus overrides the pereiopod stimulus once the mussel has started to yield. The acceptance or rejection of a mussel held in the chelae is therefore a balance between conflicting stimuli. The rejection of mussels before their flesh has been fully harvested may have a similar explanation. Chemoreceptors are present on the mouthparts and chelae (Crothers, 1967) and the strength of the stimulus received from the mussel will presumably decrease as the mussel flesh is progressively harvested. If, at the same time, the crab is in contact with other mussels then a point will be reached when the chelal stimulus will be weaker than that received from the pereiopods. This point will presumably be reached before the mussel is fully gleaned. When crabs are feeding on mussels presented singly then there is little to interfere with the chelal stimulus and consequently the mussel is fully gleaned. This behaviour is probably energetically advantageous since initially flesh is easily extracted from the opened mussel, but this will become increasingly more difficult when only the more adherent adductor muscles and mantle tissue is left. The harvesting of mussel flesh will therefore become progressively less efficient and less energy (flesh weight) will be gained per unit of handling time. This is evident when prey value curves which use the amount of predicted flesh in each size of mussel, are compared with adjusted prey value curves which use the predicted amount of flesh eaten; increased flesh intake when mussels are presented singly does not compensate for the increased time required to handle these prey. Where a significant difference was detected in handling times amongst trials, both prey value and adjusted prey value were greater when mussels were presented as part of a group than when they were presented singly to crabs.

The size range of *Mytilus edulis* most vulnerable to predation by *Carcinus maenas* usually correlates with the size of mussel predicted to be the most profitable, suggesting that *C. maenas* "selects" prey which maximises its net energy intake (see Elner and Hughes, 1978; Cunningham, 1983; Ameyaw-Akumfi and Hughes, 1987).

However, in the present study, when the proportion of mussels eaten to those encountered was analysed, it was found that up to 80% of the mussels in the size classes predicted to be the most profitable were rejected. Under the energy maximisation premise of the optimal foraging theory, prey of the most profitable size should always be eaten when encountered (Hughes, 1980). The rejection of a high proportion of “optimal” prey makes it unlikely therefore *C.maenas* selects its prey solely on the basis of its energy return. The rejection of a high proportion of optimally sized mussels recorded in this study was also observed by Jubb *et al.*, (1983) who proposed the ‘Relative Stimulus Hypothesis’. Under this hypothesis the observed patterns of prey selection arise from the balance of stimuli received from the chelae and the pereopods. Small mussels held in the chelae should be rejected because this stimulus will be overridden by the stimulus received from those contacted by the pereopods; large mussels should be rejected because they cannot easily be opened. Such behaviour would result in the preferred predation of medium sized mussels. Whilst these different effects of stimuli were observed, and certain aspects of the data presented here conformed to the Relative Stimulus Hypothesis, this hypothesis predicts that a high proportion of small mussels should be rejected immediately; this, however, did not happen since the smallest mussels tended to be eaten as encountered.

Hughes (1980) suggested that the coincidence between the shape of the predicted prey value curve and the pattern of prey-size selection when *Carcinus maenas* forages on *Mytilus edulis*, may in fact be a passive function related to the chelal mechanics. Such passive selection appears to explain the foraging behaviour of the portunid *Necora puber* when feeding on *M.edulis* (ap Rheinallt, 1986). The mechanical efficiency of the chelae of *N.puber* when used on mussels of different sizes is reflected in the handling times used to calculate prey value. If a crab accidentally drops smaller mussels due to the lack of chelal dexterity and abandons larger mussels which do not yield after a certain time, then the observed pattern of “selection” will mirror that of the prey value curve. Results from the experiments presented in this chapter, however, do not support this mechanism of prey selection. If this was indeed the mechanism underlying the patterns of prey vulnerability, then similar patterns of size selection would be expected when mussels are presented in equal numbers in each

of several size classes and when these same size classes were presented in a modified proportion biased towards the smaller categories. Instead there were strong shifts in predation intensity towards the smaller size classes of prey for all sizes of crab. Furthermore, in the smallest size class of prey, the proportion of mussels eaten to those encountered was high (> 60%) which would not have been expected if these crabs lacked chelal dexterity.

An alternative hypothesis of prey size selection is therefore proposed in which the observed patterns of selection arise from the passive response of the crab to encounter rate, which increases with prey size, and attack success rate, which decreases with prey size. When prey is presented in equal numbers in each of several size classes medium sized prey should predominate in the diet. This appears to be the mechanism underlying prey selection in many fish (see Juanes and Conover, 1994 and references therein) and appeared to be the mechanism underlying size selection by *Carcinus maenas* in this study. When mussels were presented as five individuals in each of five size classes encounter rate increased, but attack success rate decreased, with increasing mussel size. If prey-size preference was the result of active selection by the predator then the preferred prey size-class and the prey size-class with the highest eaten to encounter ratio should always correspond. This, however, was not consistently true in this study, occurring only in 3 out of 7 occasions when crabs exhibited a clear preference for a particular size class. It is concluded, therefore, that the observed patterns of prey selection in *C.maenas* occur passively as a result of encounter and attack success rate, with larger mussels being excluded from the diet because they are difficult to break, and smaller mussels being excluded because they are less frequently encountered. This conclusion supports the findings of Davidson (1986) who showed that when *Mytilus edulis aeteonus* was presented in equal numbers in each of several size classes to the portunid, *Ovalipes catharus*, medium sized mussels predominated in the diet. However, small mussels were nearly always eaten when encountered and the proportion of small mussels in the diet could be increased simply by increasing their proportion in the sample.

In a review of the prey-size selection patterns exhibited by decapod crustaceans foraging on hard-shelled molluscs Juanes (1992) found that there was a clear

preference for smaller prey size classes. Exceptions did occur especially in experiments which used less resistant, thinner-shelled bivalves such as mussels for which medium size ranges predominated in the diet. The results of the experiments presented in this chapter suggest that small mussels are preferred by *Carcinus maenas* but they do not necessarily dominate the diet because of the low encounter rates with these prey. The relatively easily crushed shell of *Mytilus edulis* enables quite large individuals to be exploited; these large mussels are also more frequently encountered when equal numbers in each of several size classes are presented and medium size classes thus dominate the diet. This pattern does not occur when harder-shelled molluscs such as oysters, cockles and clams are used as prey (Juanes, 1992) because the maximum size that can be opened is more restricted so that size selection by the predator is naturally driven towards the smaller size classes. Again it is concluded that the pattern of predation of mussels by shorecrabs is mainly a result of encounter rates and prey strength.

The vulnerability of hard-shelled molluscs to crab predation has previously been shown to alter when structural elements of the environment are included in the experiments (e.g. Arnold, 1984; West and Williams, 1986; Sponaugle and Lawton, 1990; Lin, 1991; Lee and Kneib, 1994). Under these more natural conditions the intensity of predation effort may be reduced (Arnold, 1984; Sponaugle and Lawton, 1990; Lin, 1991) and the size of prey most vulnerable to predation altered as the environment provides an effective refuge for certain size classes within the population (West and Williams, 1986; Lee and Kneib, 1994). The results presented in this study indicate a further possibility, since prey vulnerability also varies according to the size structure of the mussel population. This is important because population structure of *Mytilus edulis* can vary not only between shores (see Chapter 2) but also with shore elevation (Lintas and Seed, 1994) and a wide-ranging, tidally foraging predator such as *Carcinus maenas* may encounter these variations even within a single foraging excursion. By increasing the relative abundance of mussels in the smaller size classes, the size range most vulnerable to crab predation also shifted to the smaller prey size classes (see Fig. 5.5). This shift, however, could not be attributed simply to the depletion of the prey size class previously determined to be most vulnerable to

predation when prey of each size class were presented in equal numbers. None of the experimental crabs ate all of the mussels in the previously preferred size class, strongly suggesting that the shift in vulnerability was a real response by crabs to changes in the proportion of the size classes of prey presented. Vulnerability also shifted when prey was presented in two different proportions, reflecting their relative availability in a high shore and in a mid shore mussel population (Fig. 5.6). Smaller size classes of prey were relatively more abundant in the high shore population and when crabs fed on this simulated population smaller mussels were more vulnerable to predation than when crabs fed on the mid shore proportion which comprised more mussels in the larger size classes; indeed in this simulated mid shore population larger mussels actually became more vulnerable. Clearly foraging behaviour and hence prey vulnerability, can vary even within a single shore.

Attention has often been focused on the effect of predators on their prey populations (e.g. Ebling *et al.*, 1964; Pollock, 1979; Griffiths and Seiderer, 1980; Seed, 1990a). This study, however, demonstrates that the structure of the prey population may also influence prey size selection by the predator. Flexibility in the foraging behaviour of *Carcinus maenas* should have a positive effect for both prey and predator populations. It was shown in Chapter 4 that when crabs were presented with mussels in equal numbers in each of several size classes, the patterns of prey-size selection were broadly similar for mussels from the wave-exposed site at Aberffraw and from the more sheltered site at Church Island. The flexibility of the foraging behaviour of *C. maenas* on *Mytilus edulis*, however, suggests that the actual vulnerability of mussels in the field at these two sites should be different. The seasonal changes in the size structure of the Church Island population should result in a reduction in predation pressure over time. Initially (June 1995) this population was dominated by small individuals which were particularly vulnerable to predation by virtually all size ranges of crabs. However, as the mussels within this population increase in size, predation intensity should shift towards the larger size classes. This would not only reduce predation effort on juvenile mussels thus allowing mussel stock replenishment, but would reduce intraspecific predation pressure as smaller crabs would not then have to compete with larger conspecifics for the same size classes of prey. The temporally

more stable size structure of the Aberffraw mussel population would suggest that predation pressure ought to be fairly constant over the different size classes. A large proportion of the *C.maenas* population in the Menai Strait is tidally foraging (Hunter and Naylor, 1993) and would thus be expected to encounter mussel populations that can differ over relatively small spatial scales. This study has demonstrated that *C.maenas* could modify its behaviour according to the relative abundance of prey items encountered during a single foraging bout.

5.5. SUMMARY

- The manner in which *Mytilus edulis* were offered to *Carcinus maenas* significantly influenced foraging behaviour, the resultant prey value curves, and prey size vulnerability.
- Foraging behaviour depended largely on whether mussels were presented singly or as part of a group. The time-consuming techniques typically used to open larger, more resistant mussels, were not observed when smaller mussels, which were more easily opened, were available. Moreover, crabs did not glean mussels to the full extent when they were presented as part of a group.
- Handling times were usually longer when crabs fed on mussels presented singly rather than as part of a group but this could not be attributed to increasing handling efficiency since breaking times generally were not significantly different. Instead this appeared to result from a decrease in the extent to which mussels were gleaned when presented as part of a group. This behaviour seems to be energetically advantageous because the prolonged gleaning of single mussels appeared to be less efficient.
- The mechanism underlying prey selection did not appear to be based solely on prey evaluation as previously proposed by Hughes and Elner (1978) since a high proportion of prey in the predicted optimal prey size classes was rejected. Equally, foraging behaviour did not appear to conform precisely to the behaviour predicted by the

Relative Stimulus Hypothesis proposed by Jubb *et al.* (1983) since smaller size classes were rarely rejected.

- Prey selection by *Carcinus maenas* appeared to be based on a passive response to increasing encounter rate and decreasing attack success rate with increasing prey size. Prey size vulnerability varied according to the relative proportions in which different size classes were offered.

- The flexible foraging strategy adopted by *Carcinus maenas* thus appears appropriate for a tidally foraging predator which may encounter prey that varies in its population structure both spatially and temporally.

CHAPTER 6.

FORAGING BEHAVIOUR OF *THALAMITA DANAЕ* ON THE GREEN-LIPPED MUSSEL, *PERNA VIRIDIS*.

6.1. INTRODUCTION

Perna viridis is a tropical-subtropical mytilid distributed throughout the waters of south and east Asia (Lee and Morton, 1985). Its distribution extends longitudinally from the Persian Gulf to the southwest Pacific and latitudinally from Papua New Guinea to Southern Japan where it is replaced by its temperate counterpart, *Mytilus edulis* (Huang and Cai, 1984, in Huang *et al.*, 1985). It is widely distributed throughout the waters surrounding Hong Kong but attains dominance in polluted environments such as Tolo Harbour, where densities of 35,000.m⁻² have been recorded (Huang *et al.*, 1985). The success of *P.viridis* in polluted environments is attributable both to its tolerance of high concentrations of pollution and low concentrations oxygen as well to the reduced levels of competition and predation in these conditions (Lee and Morton, 1985). It is found in the intertidal zone from +1.0m CD down to -10m CD and attaches to rocks and pier pilings by its byssus threads. The population structure of *P.viridis* varies from one locality to another and with tidal level and season (Huang *et al.*, 1985; Seed, 1990 ; Cheung, 1993; Cheung and Tse, 1993). It has a fast growth rate, which makes it an important commercial food stock throughout Asia (Huang *et al.*, 1985 and references therein).

Thalamita danae is a portunid crab found in the waters of Hong Kong and exhibits similar patterns of foraging behaviour to its temperate counterpart, *Carcinus maenas*. *T.danae* is a tidally foraging species with a broad diet of which *Perna viridis* form an important component (Seed, 1990c). Although *T.danae* is known to feed rapaciously on small mussels and despite evidence that it has the potential to affect the size distribution of *P.viridis*, little work has previously been conducted on the foraging behaviour of this species (Seed, 1990a).

Thalamita danae and *Perna viridis* may be regarded as the subtropical-tropical equivalent of the temperate water *Carcinus maenas* and *Mytilus edulis* relationship.

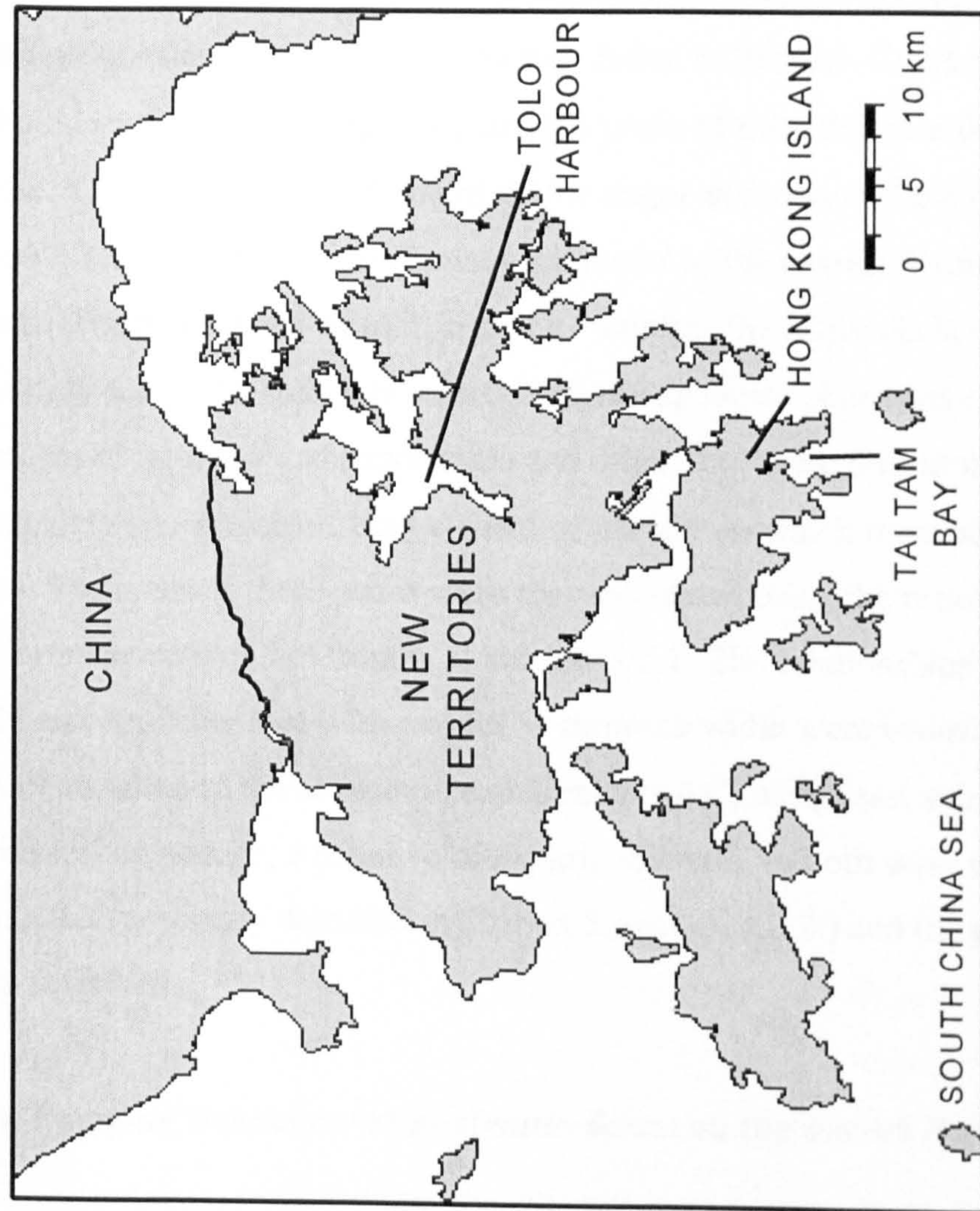
The foraging behaviour of *C.maenas* on *M. edulis* is extremely flexible and both prey value and prey vulnerability can vary according to the way in which prey is presented to foraging crabs (see Chapters 4 & 5). *T.danae* will encounter the differences that are known to exist in the structure of *P. viridis* populations both spatially and temporally (Huang *et al.*, 1985; Seed, 1990a; Cheung, 1993; Cheung and Tse, 1993) and a flexible foraging mechanism similar to that exhibited by *C.maenas* would clearly seem to be advantageous. This chapter documents the foraging behaviour of *T.danae* on *P.viridis* and investigates how prey value and prey vulnerability varies according to how prey is presented. The study was carried out in November and December 1996 during a short visit to the Swire Marine Laboratory in Hong Kong.

6.2. MATERIALS AND METHODS

6.2.1. The *Perna viridis* population.

Mussels were sampled at Tolo Harbour, a partially enclosed bay on the northeast side of the New Territories, Hong Kong (Fig. 6.1). Tolo Harbour has a poor flushing rate (Cheung, 1993) and is heavily polluted with both domestic and industrial waste (Lee and Morton, 1985). Despite these high concentrations of pollution *Perna viridis* occurs at high densities both intertidally and subtidally (Huang *et al.*, 1985). Samples of *P. viridis* were collected from pier pilings (+1.0 m CD) at Wu Kai Sha in Tolo Harbour (Fig. 6.1). All the mussels present within three 10 cm x 10 cm quadrats were removed and returned to the laboratory. The shell length of each mussel was measured to the nearest 0.1 mm, using vernier calipers, to determine the size distribution of the mussel population. Shell length, height and width (see Chapter 2, Fig. 2.2) of 37 mussels within the size range 5-35mm shell length were then measured to the nearest 0.1 mm and the flesh and shells of these mussels separated from one another. Flesh and shells were then placed separately in individual aluminium foil boats and dried to constant weight at 60°C over three days before being weighed to the nearest microgram. Pairs of data were then fitted to the allometric equation $y = Ax^b$ which, when log transformed, becomes $\log y = a + b \cdot \log x$, using least squares

Figure 6.1. Location of study sites in Hong Kong.



regression as described for *Mytilus edulis* in Chapter 2.

6.2.2. Chelal morphometrics of *Thalamita danae*.

Thalamita danae were collected from Tai Tam, a bay on the southeast side of Hong Kong Island (Fig. 6.1). Sampling was carried out at the innermost edge to the bay which was sheltered from the more wave-exposed conditions of the South China Sea. The site was mainly sandy with occasional boulders, but the upper reaches were dominated by mangroves. *Perna viridis* was absent at this site. Crabs occurred under the boulders and were caught by placing a piece of fresh fish in a dip net next to a boulder. Carapace width and height of the major and minor chela (see Chapter 3, section 3.2.1.) of nine male crabs were measured to the nearest 0.1mm using vernier calipers. The handedness of each crab, i.e. whether the major chela occurred on the left or right side of the crab, was recorded. Closer apodeme plates were removed from the propus of the major and minor chela and dried; they were then attached to a blank 35mm slide and projected onto a sheet of acetate on which their outlines could be traced. The areas of these plates were then calculated using the procedure described for *Carcinus maenas* in Chapter 3, section 3.2.1. The relationships between chelal height and apodeme area with respect to carapace width were investigated by fitting pairs of variables to the allometric equation, $y = Ax^b$, using least squares regression. Mechanical advantage, a measure of the grip strength, of both were measured as the ratio L1/L2 (previously described in Chapter 3, section 3.2.2.) and the geometry of the claws described.

6.2.3. Foraging Behaviour of *Thalamita danae* on the mussel *Perna viridis*.

Thalamita danae used in the following experiments were collected from Tai Tam Bay using a dip net as above. In the laboratory crabs were kept individually in plastic aquaria (43cm x 33cm x 23cm) filled to a depth of 10 cm with circulating seawater. All crabs were kept under conditions of ambient temperature and natural light conditions. The sides of the aquaria were covered with black plastic in order to

minimise visual disturbance to the crabs. *Perna viridis* were freshly collected every week to ensure that mussels presented to crabs were in good condition, and were kept in the laboratory under conditions of running seawater and natural light. Only undamaged crabs and mussels that appeared to be in good condition were used in the experiments.

The foraging behaviour of male *Thalamita danae* (71.0mm CW) on mussels presented either as individuals or as part of a group was investigated and the prey value of the mussels determined in both of these situations. In both of the trials individual mussels were measured to the nearest 0.1 mm shell length and then numbered using a permanent marker pen so that each mussel could be identified throughout. In each trial breaking and handling times (see Chapter 4, section 4.2.2. for definitions) were recorded to the nearest second using a stopwatch. The prey handling procedure and methods used to open the prey were also recorded. The discarded shells of opened mussels were removed immediately and any flesh remaining within these mussels was removed, dried at 60°C for three days and subsequently weighed to the nearest microgram. A three day period preceded the first and second trial, during which time the crab was fed solely on mussel flesh for the first 48 hours and left unfed for the subsequent 24 hours. In Chapter 5 it was found that the procedure was sufficient to ensure that any differences reported between the trials were not due to learning or to differing hunger levels of *Carcinus maenas*. In the first trial, the crab was offered mussels singly and unattached. These mussels ranged from 9.0-16.1 mm shell length and were presented in random sequence. If the crab rejected a mussel this was removed and replaced with a smaller individual. The trial lasted for four days. In the second trial, the same crab was presented with a group of 25 unattached mussels comprising five individuals in each of the following size classes; 10-15, 15-20, 20-25, 25-30 and 30-35 mm shell length. The crab was then allowed to feed on the group of mussels for two hours each day, during which time its feeding behaviour was continuously observed and breaking and handling times recorded together with the techniques used to open mussels. Discarded shells of those mussels that had been opened were immediately removed and replaced with ones of similar size, in order to maintain constant prey availability and to prevent unopened mussels from becoming obscured by shell debris.

The trial lasted for three days.

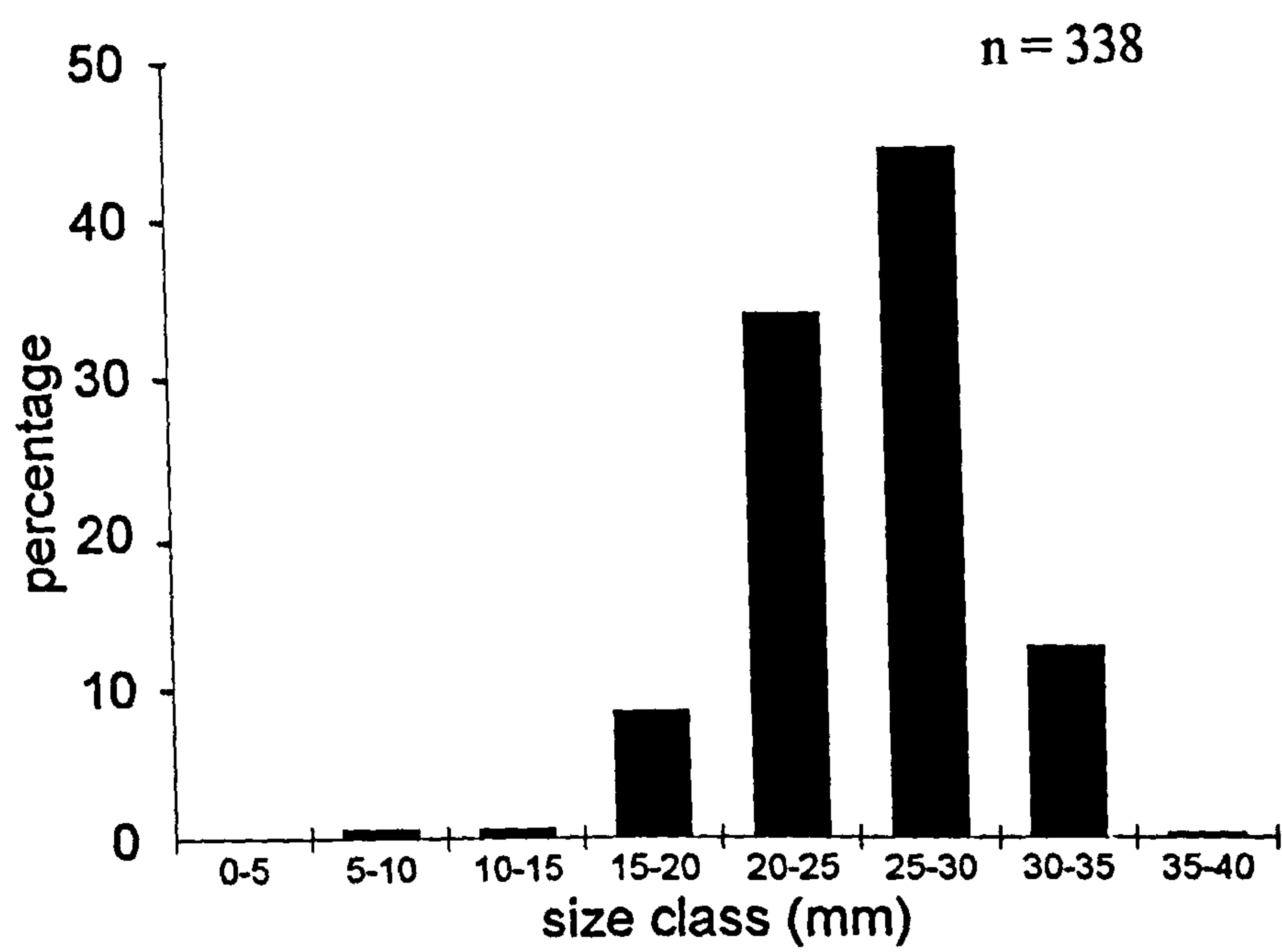
The effect of altering the relative abundance of different sizes of prey on the vulnerability of mussels to crab predation was investigated under conditions of unlimited prey availability. Three male *Thalamita danae* (26.8, 30.4, 38.7 mm CW) were used in two trials; the same three crabs were used in both trials to ensure that any differences which arose were not due to differences between individual crabs. Prior to the first and second trial, each crab was fed solely on mussel flesh for 48 hours and left unfed for a further 24 hrs to ensure that any differences arising in foraging behaviour were not due to learning or to different hunger levels. In the first trial crabs were each presented with five mussels in each of the following size classes; 10-15, 15-20, 20-25, 25-30, 30-35 mm shell length. The number of mussels eaten in each size class was recorded every 12 hrs during which time the shells of any mussels that had been eaten were removed and replaced with ones of comparable size to maintain a constant prey availability. Crabs were allowed to feed on these mussels for five consecutive days. In the second trial the same crabs were then presented with 25 mussels but in the modified proportion of 1, 2, 9, 10 and 3 mussels respectively in the following size classes; 10-15, 15-20, 20-25, 25-30 and 30-35 mm shell length. This proportion reflected the relative abundance of those mussels within the natural *Perna viridis* population in the high shore at Wu Kai Sha (see section 6.3.1.). The number of mussels eaten was recorded and the shells of eaten mussels removed and replaced by mussels of similar size every 12 hrs over a period of five consecutive days. No direct observations of crab foraging behaviour were made during these two trials.

6.3. RESULTS

6.3.1. The *Perna viridis* population

The population density of *Perna viridis* in the high shore at Wu Kai Sha averaged 112 ± 9 mussels/10cm². The population structure was unimodal with most mussels falling within the 20-30 mm size class (Fig. 6.2). There were surprisingly few mussels less than 15mm shell length present within this population. The allometric

Figure 6.2. Length-frequency distribution of *Perna viridis* from the high shore level at Wu Kai Sha.



relationships between several size variables of *P. viridis* are summarised in Table 6.1. All size variables were highly correlated and negatively allometric with respect to shell length over the size range investigated. Thus, as shell length in these mussels increases individuals become proportionally narrower, more elongate and lighter both in terms of their flesh and shell weight.

6.3.2. The chelal morphometrics of *Thalamita danae*.

Whilst *Thalamita danae* is heterochelous, possessing one larger, more robust claw and one smaller, more slender claw there is no tendency towards right-handedness ($\chi^2 = 0.11$, d.f. =1, $p > 0.05$) as described in *Carcinus maenas* (Chapter 3) and the larger chela could occur on either the right or the left-hand side of the crab. The geometry of the two chelae is dissimilar. The larger, or major, chela has a proximal peg-like structure on the dactylus which is not present on the smaller, or minor, chela. Major chelal teeth are broad in contrast with those of the minor chela which are sharp and triangular. For any individual crab the height of the major chela and the area of its closer apodeme plate is greater than in the minor chela. The relationships between chelal height, apodeme area and carapace width are illustrated in Figure 6.3 (A&B) and the linear regression equations describing these relationships are presented in Table 6.2 together with the coefficients of allometry. Chelal height in both the major and the minor chela is positively allometric with respect to carapace width, indicating that both chelae become proportionally larger with increase in body size. However, whilst the area of the apodeme plate in the minor chela is positively allometric with respect to carapace width, in the major chela the relationship is one of isometry even though the slope ($b = 2.57$) was positive. It should be noted, however, that these data are based on a relatively small number of crabs. Mechanical advantage is remarkably constant between crabs and is independent of crab size. The major chela operates at a significantly greater mechanical advantage (0.33 ± 0.03) than the minor chela (0.26 ± 0.02), (Mann-Whitney $U = 124.0$, d.f. =8, $p < 0.001$) due largely to differences in L1, which is on average 24% shorter in the minor chela, rather than to differences in L2 which, on average, is only 3% shorter in the minor chela.

Table 6.1. Coefficients of allometry for various combinations of size parameters in *Perna viridis* together with a test for departure from isometry (n=37).

Dependent variable (y)	Independent variable (x)	a	b	r	t	p
Shell height	Shell length	-0.056	0.843	0.991	8.473	**
Shell width	Shell length	-0.254	0.845	0.980	5.374	**
Flesh weight	Shell length	-4.574	2.471	0.979	6.173	**
Shell weight	Shell length	-3.712	2.475	0.990	8.812	**

a, b = coefficients in the log transformed allometric equation $\log y = a + b.\log x$

r = the product moment correlation coefficient

t = test statistic

** = significant departure from isometry at $p < 0.01$

Figure 6.3. The relationship between chelal height (A), apodeme area (B) and carapace width in *Thalamita danae*. Data are presented for both the major (closed circles) and the minor (open circles) chelae.

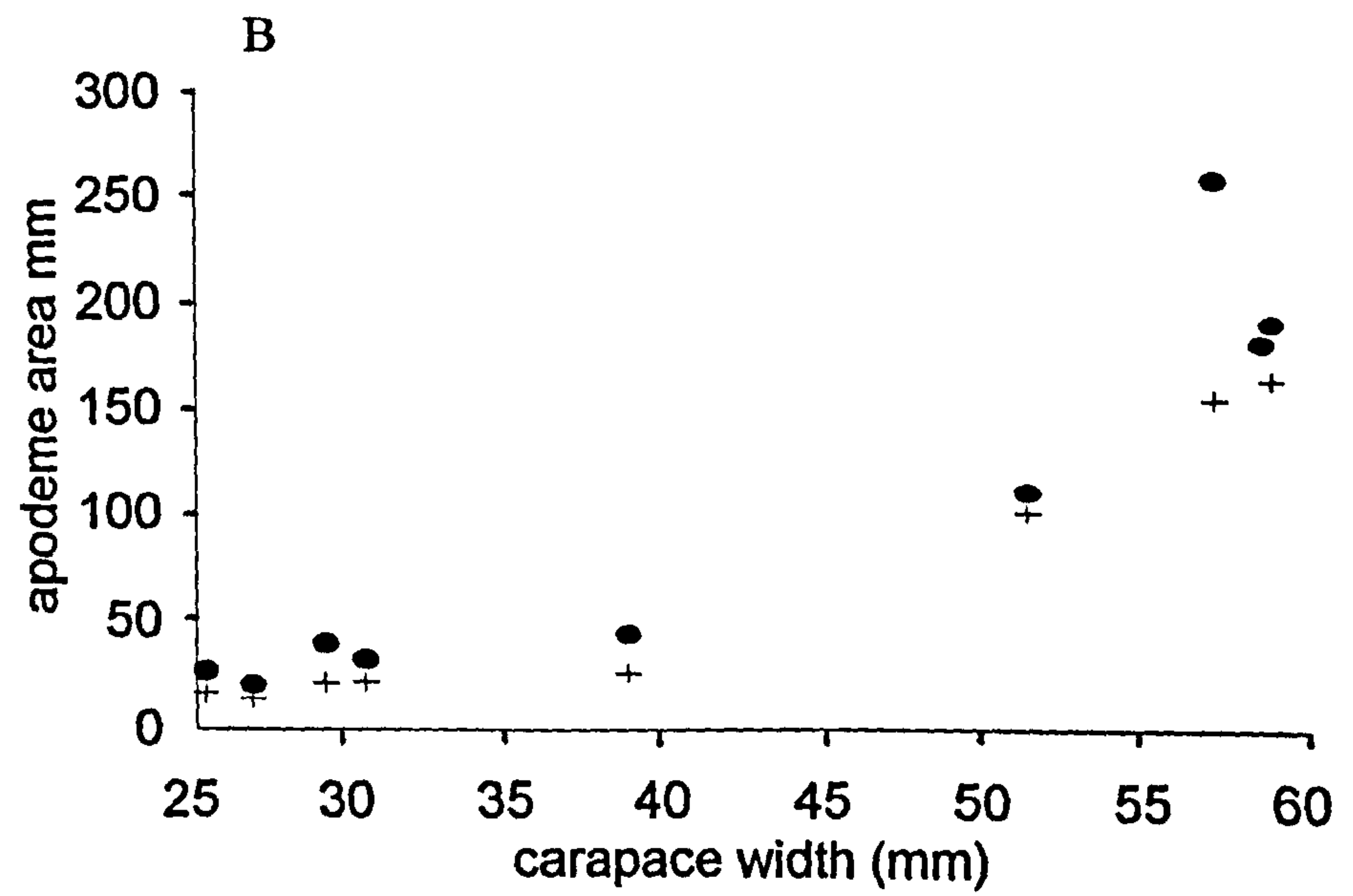
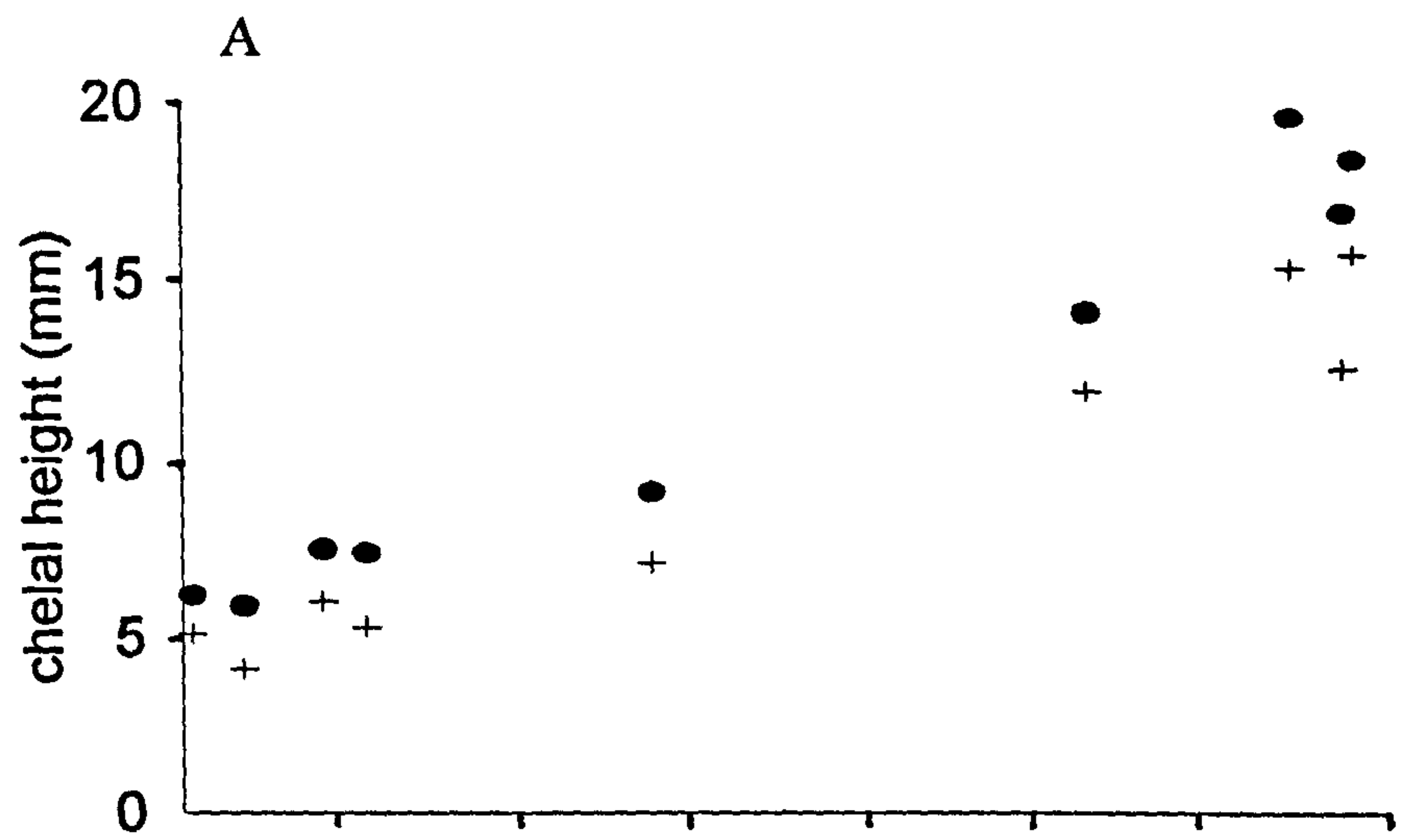


Table 6.2. Coefficients of allometry for various combinations of size parameters in the chelae of *Thalamita danae* together with a test for departure from isometry.

Dependent variable (y)	Independent variable (x)	Major chela					Minor chela						
		a	b	r	t test	p	n	a	b	r	t test	p	n
Chelal height	CW	-1.09	1.32	0.986	3.865	**	9	-1.31	1.39	0.973	3.312	*	9
Apodeme plate area	CW	-2.27	2.57	0.967	2.220	ns	9	-2.87	2.85	0.973	3.070	*	8

a, b, = coefficients in the log transformed allometric equation $\log y = a + b.\log x$

r = product moment correlation coefficient

ns = no significant departure from isometry

* = significant departure from isometry at $p<0.05$

** = significant departure from isometry at $p<0.01$

6.3.3 Foraging behaviour of *Thalamita danae*.

6.3.3.1 Prey Handling Procedures.

Thalamita danae responded to the introduction of mussels into the aquaria with rapid antennule flicking, suggesting a chemosensory element to prey detection. Additionally it responded to both the movement and the touch of a mussel indicating that visual and tactile components are also involved in prey search behaviour. Feeding bouts were generally prefaced by movements of the mouthparts and active searching of the aquarium floor using sweeping motions of the chelae to gather up any encountered prey items.

Prey handling techniques observed for *Thalamita danae* when feeding on *Perna viridis* were broadly similar to those previously described for *Carcinus maenas* when feeding on *Mytilus edulis* (Chapter 4). Mussels were usually gathered by the walking legs and drawn forward beneath the carapace to the chelae. The major chela was used to apply a crushing force to the prey whilst the minor chela, the pereopods and occasionally the mouthparts were used to hold and manipulate the prey. A range of prey size dependent opening techniques were observed. Outright crushing: small mussels (<12mm) were crushed outright with a single application of force from the major chela. There was little or no manipulation of the mussel prior to the application of the force and the site of application was indiscriminate. No attempt was made to separate the flesh from the shell, both of which were passed to the mouthparts, resulting in relatively few shell fragments being discarded. Directed crushing: larger mussels were crushed with forces applied to the posterior or anterior end of the mussel with posterior crushing attempts generally proving more successful. The plane of application of force was either lateral or dorso-ventral across the mussel. Prior to the application of the first force, mussels were rotated in the chelae for a period of up to 40 seconds and mussels were also frequently turned and reorientated in the chelae between successive crushing attempts. These periods of prey manipulation presumably serve to detect and subsequently exploit weak spots in the shell. Once the mussel was

opened, flesh was torn out by the minor chela and mouthparts. Shell fragments which had been dropped were gathered up by sweeping movements of the chelae and pereopods and then passed forwards to the mouthparts for further gleaning. Both outright crushing and directed crushing had previously been observed in *C.maenas* foraging on *M.edulis* (Chapter 4). Wedging technique: this was used when crushing attempts have proved unsuccessful. The propus tip of the major chela was used to force a way into the shell whilst the minor chela and anterior pair of legs held the mussel. This “wedging” technique was usually applied mid-ventrally at the point where the byssus threads emerge from the shell. This technique was never observed in *C.maenas* when feeding on *M.edulis* but can perhaps be regarded as analogous to the “boring” technique that *C.maenas* uses on larger mussels. Once the chela had been inserted, it was pulled along the length of the mussel until the posterior adductor muscle was severed or the shell became weakened and broke. Insertion: *T.danae* employed a further technique when preying on *P.viridis*, which was never observed for *C.maenas* feeding on *M.edulis*. This insertion technique was possible because gaping *P. viridis* did not appear to be sensitive when touched by *T.danae* which did not therefore automatically close its valves when handled by the crab. This apparent insensitivity enabled *T.danae* to insert either of its chelae into the gape between the two mussel valves and sever the posterior adductor or attempt to break one of the valves. In this way larger mussels were quickly and easily opened. When this technique was used the mussel valves remained virtually intact.

When feeding on a group of mussels *Thalamita danae*, like *Carcinus maenas* (Chapter 5) tended to gather and hold two mussels simultaneously, one in each chela. Whilst a mussel was being manipulated in the chelae, *T.danae* would use its pereopods to sense the surrounding mussels. This behaviour usually ceased when the mussel held in the chelae was finally opened. When *T.danae* selected a larger mussel then it often moved out of contact with other mussels and retreated to a corner of the aquarium where the prey item was manipulated; this behaviour mirrored that of *C.maenas* (Chapter 5).

6.3.3.2. Foraging behaviour of *Thalamita danae* on individual mussels and on groups of mussels.

Breaking and handling times increased with shell length when mussels were presented either individually or in a group (Fig. 6.4 A&B). The relationship between breaking time and shell length was not adequately described by either a power or a logarithmic function in either trial and the curves in Figure 6.4A were fitted by eye. However, it is evident that breaking times when mussels were presented in a group were less than those for similar sized mussels when these were presented singly. The relationship between handling times and prey shell length could be linearised by log_e transformation of the dependent variable and the regression equations describing the relationships between these two variables are presented in Figure 6.4B. Handling times, like breaking times, increased more rapidly when mussels were presented singly (Fig. 6.4B) and the difference in the relationships between handling time and prey length in the two trials approached statistical significance (general linear model, slopes: $F=3.31$, $d.f.=22$, $p=0.085$). When mussels were presented as a group, the relatively rapid insertion opening method was employed more often than when mussels were presented singly (Fig. 6.4B).

Prey value was defined as E/Th , where E is the flesh weight of an individual mussel, calculated using the flesh weight-shell length presented in Table and Th is the handling time, calculated using the appropriate handling time - shell length regression equation derived in section 6.2.3 and presented in Figure 6.4B. Since handling times in the two trials were different it is not surprising to find that prey value also varied although the basic dome shape of the prey value curve remained the same. As Figure 6.4C shows, presenting mussels as part of a group increased their value over the whole size range of prey investigated. The most valuable predicted prey size shifted between the two trials from just over 10 mm shell length, when mussels were presented singly, to just under 20 mm shell length when mussels were presented as a group. The maximum size of mussel that could be opened also differed between the two trials shifting from 16.1 mm shell length when mussels were presented singly to 22.6 mm when they were presented in a group.

Figure 6.4.

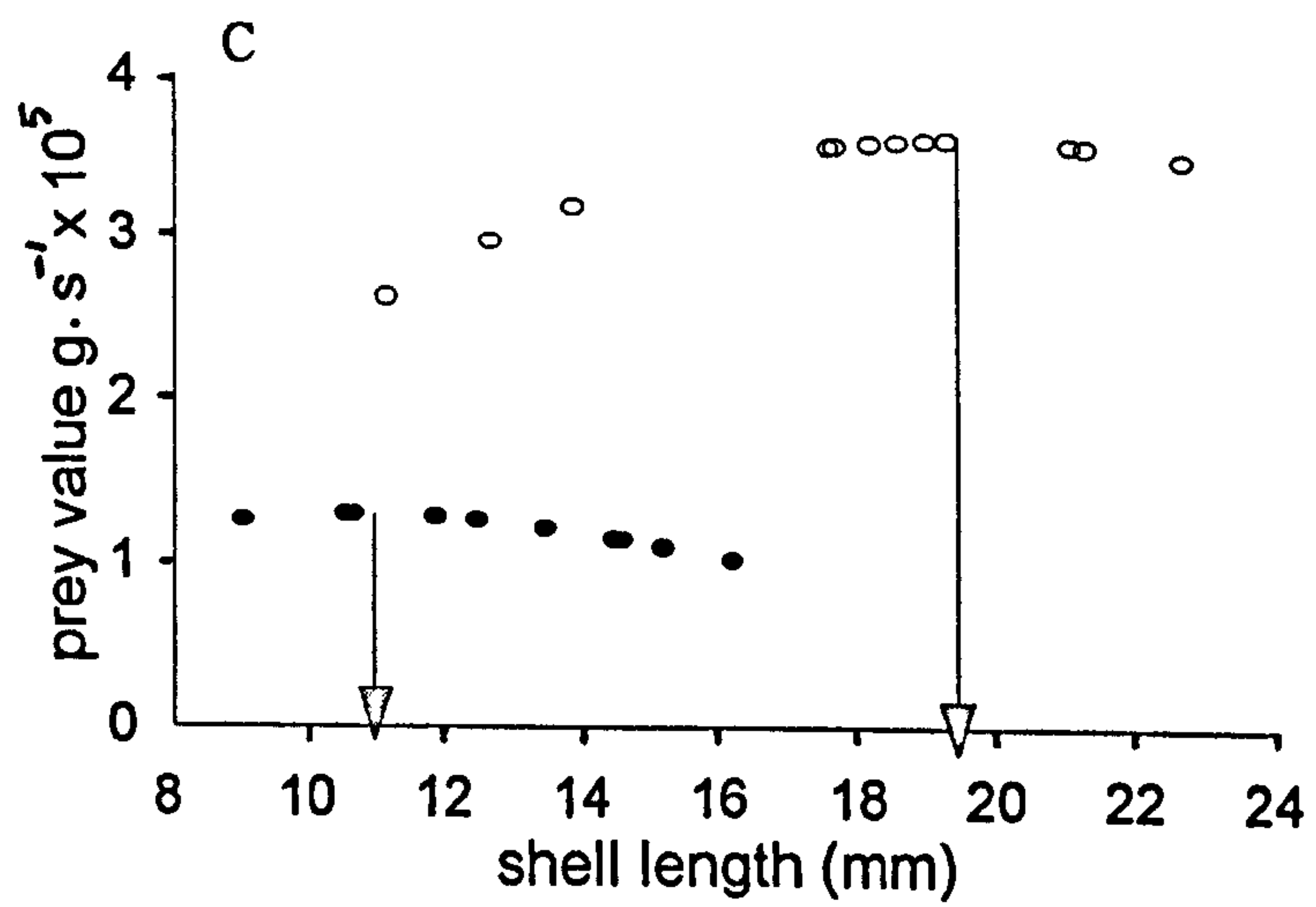
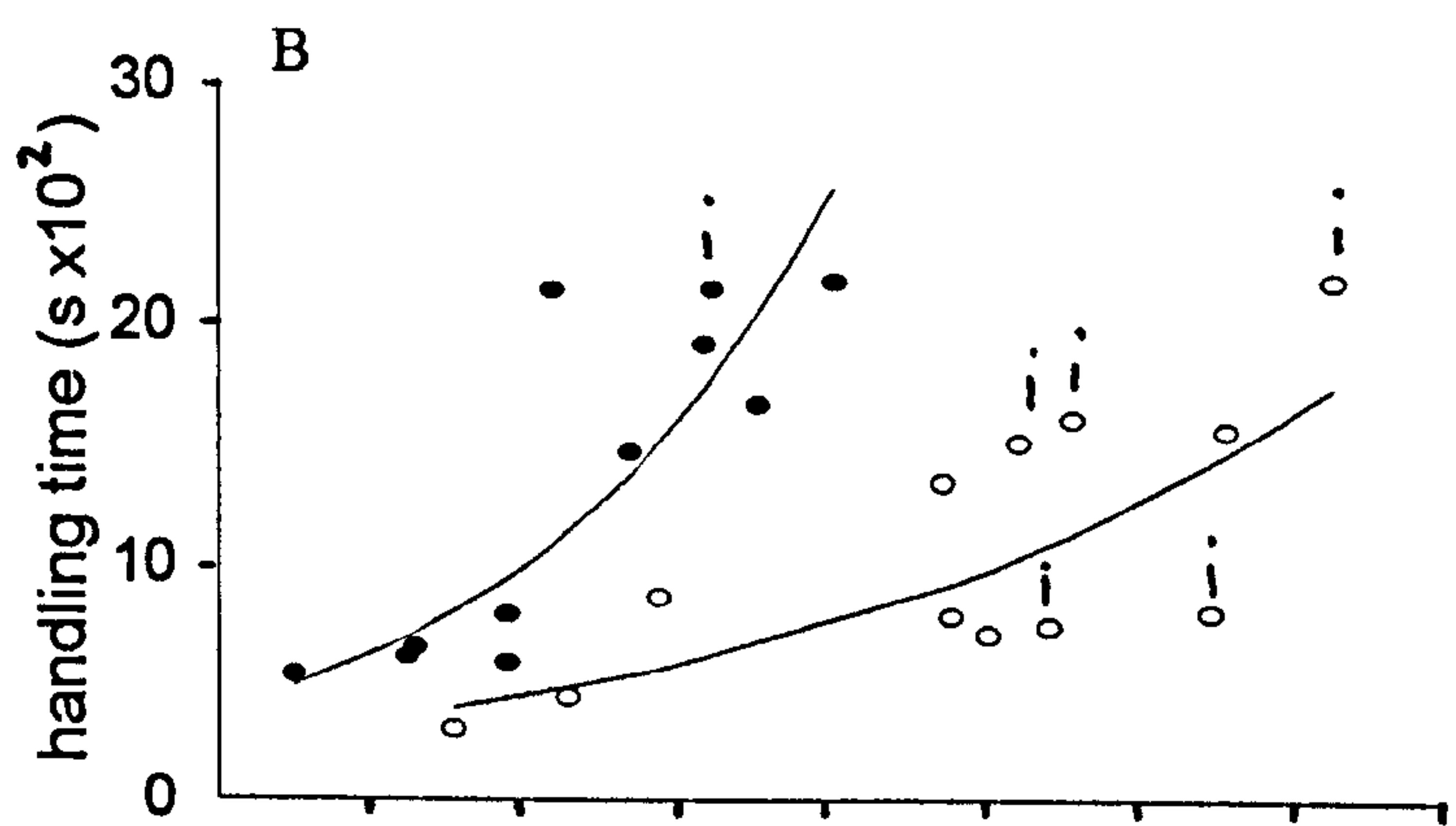
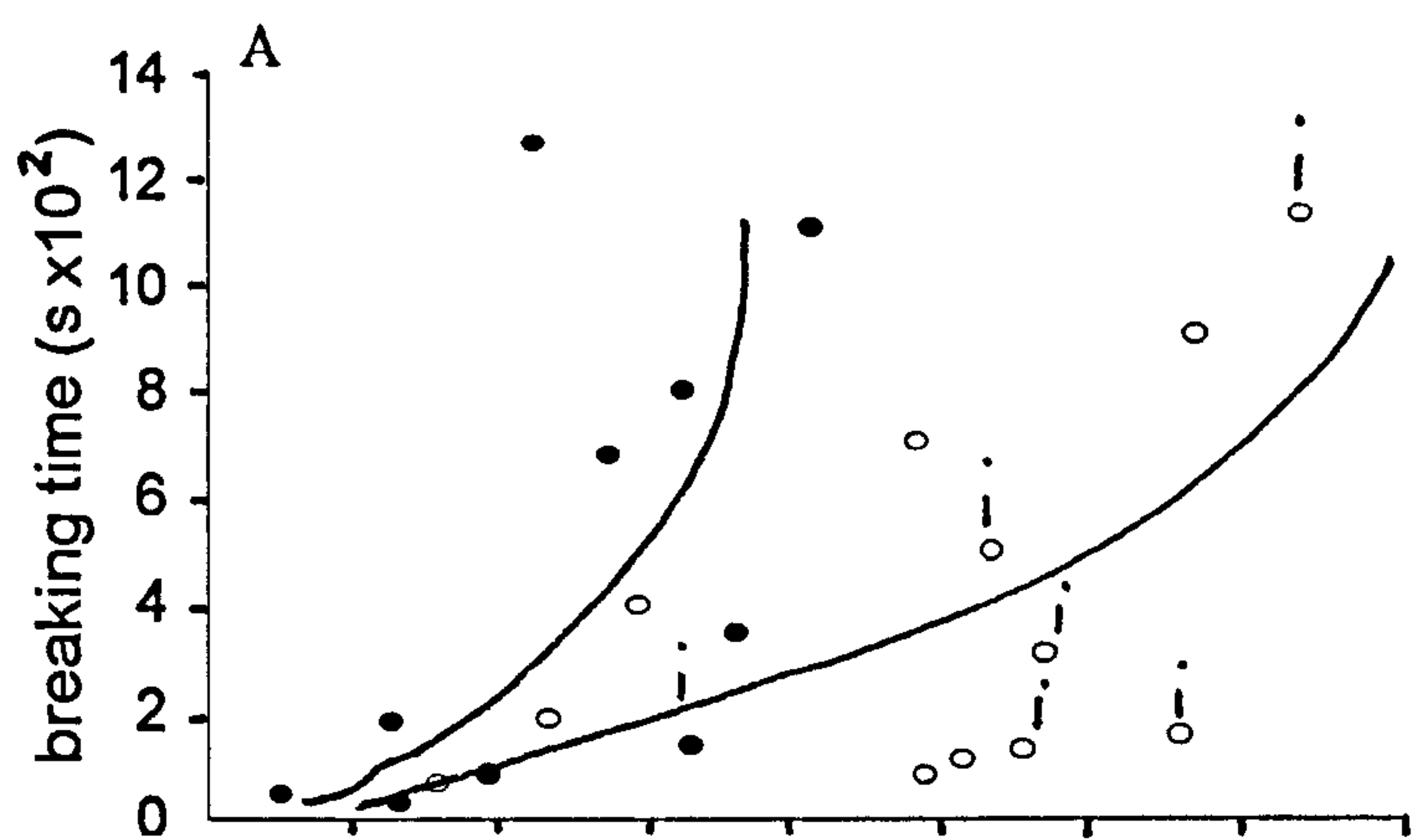
A. Breaking times plotted against shell length of *Perna viridis* when mussels presented singly (closed circles) and mussels presented as part of a group (open circles). Data from mussels opened by the insertion technique are marked with an 'i'. Lines fitted by eye.

B. Handling times plotted against shell length of *Perna viridis* when mussels presented singly (closed circles) and mussels presented as part of a group (open circles). Data from mussels opened by the insertion technique are marked with an 'i'. Handling times (Th) are related to shell length (SL) by the following regression equations which have been fitted to the raw data.

mussels presented singly: $\ln Th = 4.09 + 0.233 SL$

mussels presented as part of a group: $\ln Th = 4.55 + 0.128 SL$.

C. Prey value of *Perna viridis* to *Thalamita danae* when mussels presented singly (closed circles) and as part of a group (open circles) to the crab. Prey value was determined using the above handling time - shell length regression equation and the flesh weight - shell length regression equation presented in Table 6.1. Arrows denote the size of mussel predicted to be the most optimal.



The percentage flesh remaining in discarded mussel shells was calculated by dividing the amount of flesh left in shells by the amount of flesh predicted to be contained within a shell of that length, using the flesh weight-shell length equation in Table 6.1. The median percentage flesh remaining was 1.5% for mussels presented singly and 4.7% for mussels presented as part of a group. No significant differences were found between these median values using the non-parametric Mann-Whitney U test ($U = 170.0$, d.f. = 23, $p > 0.05$) indicating that the efficiency of gleaning in both trials was similar.

6.3.3.3. Prey size vulnerability.

The relative proportions in which mussels of different size classes were presented to *Thalamita danae* influenced foraging behaviour. In both trials the feeding rates of *T. danae* were low (Table 6.3) and decreased when mussels were presented in the modified proportion which reflected their relative abundance in a naturally occurring *Perna viridis* population. A clear size preference was evident in both sets of foraging experiments although this preference differed between the trials (Fig. 6.5). When mussels were presented in equal numbers in each of the five size classes (Trial 1) the smallest size class was preferred but when presented in the modified proportion (Trial 2) the preferred size shifted to larger size classes (Fig. 6.5). The number of mussels in the modified group was biased towards larger prey size classes and the shift in vulnerability reflected this.

6.4. DISCUSSION

The high population density of *Perna viridis* recorded at Tolo Harbour in this study was similar to that previously reported by Huang *et al.* (1985). This reflects both the ability of *P. viridis* to thrive in polluted environments and the low levels of interspecific competition associated with such areas (Lee and Morton, 1985). The size range of *P. viridis* recorded in this investigation however, was rather narrower and the maximum size was substantially lower than that reported for other *P. viridis*

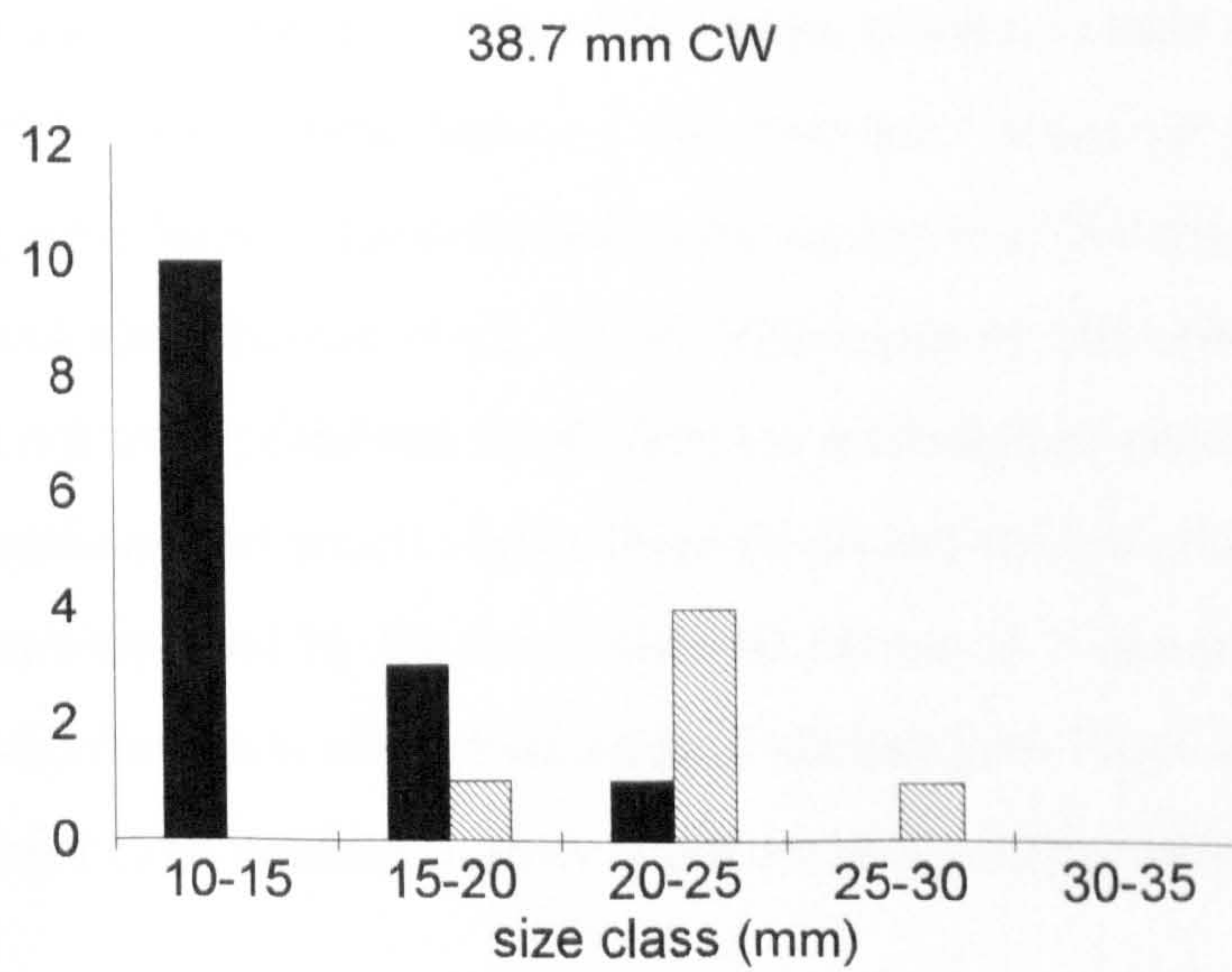
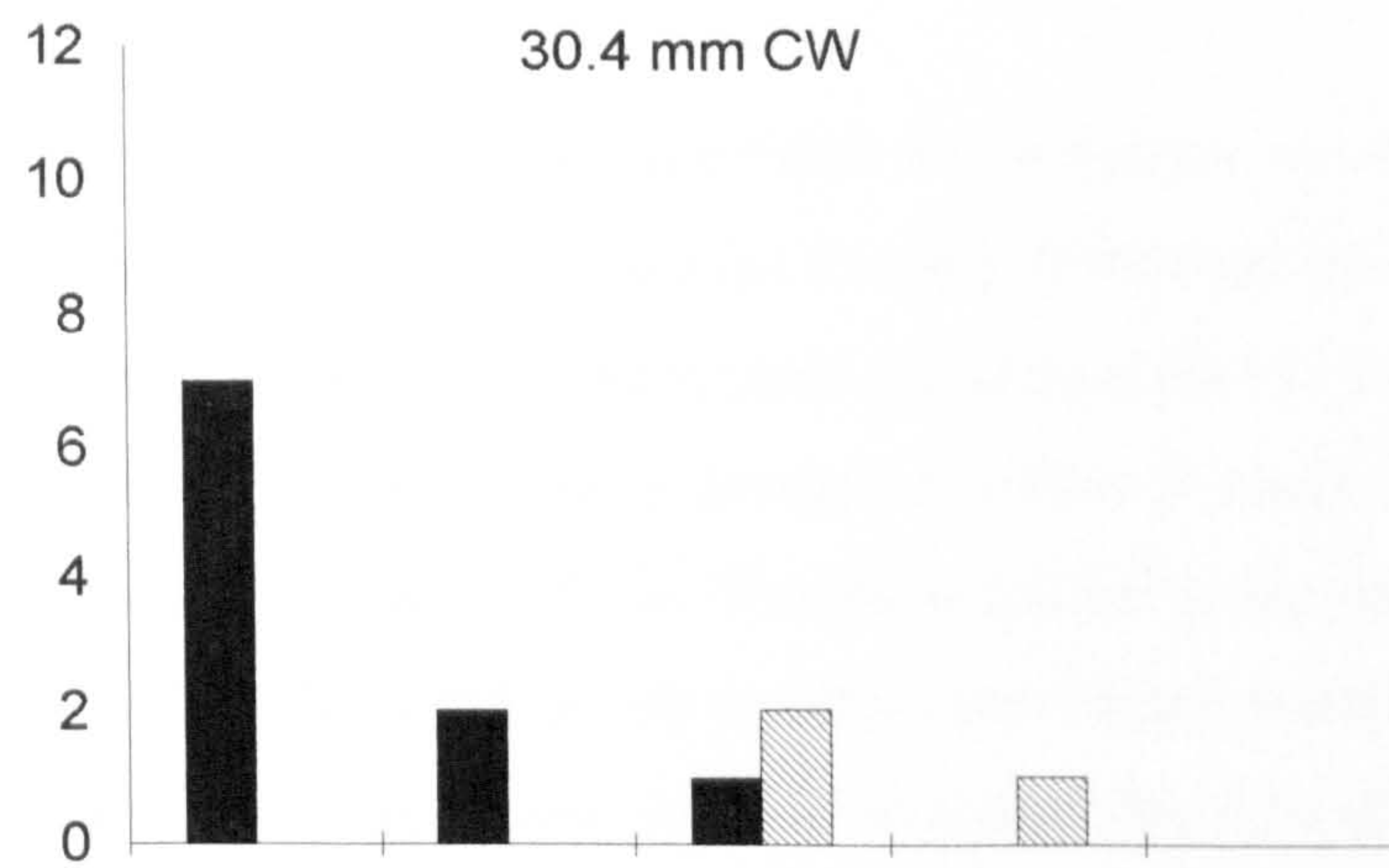
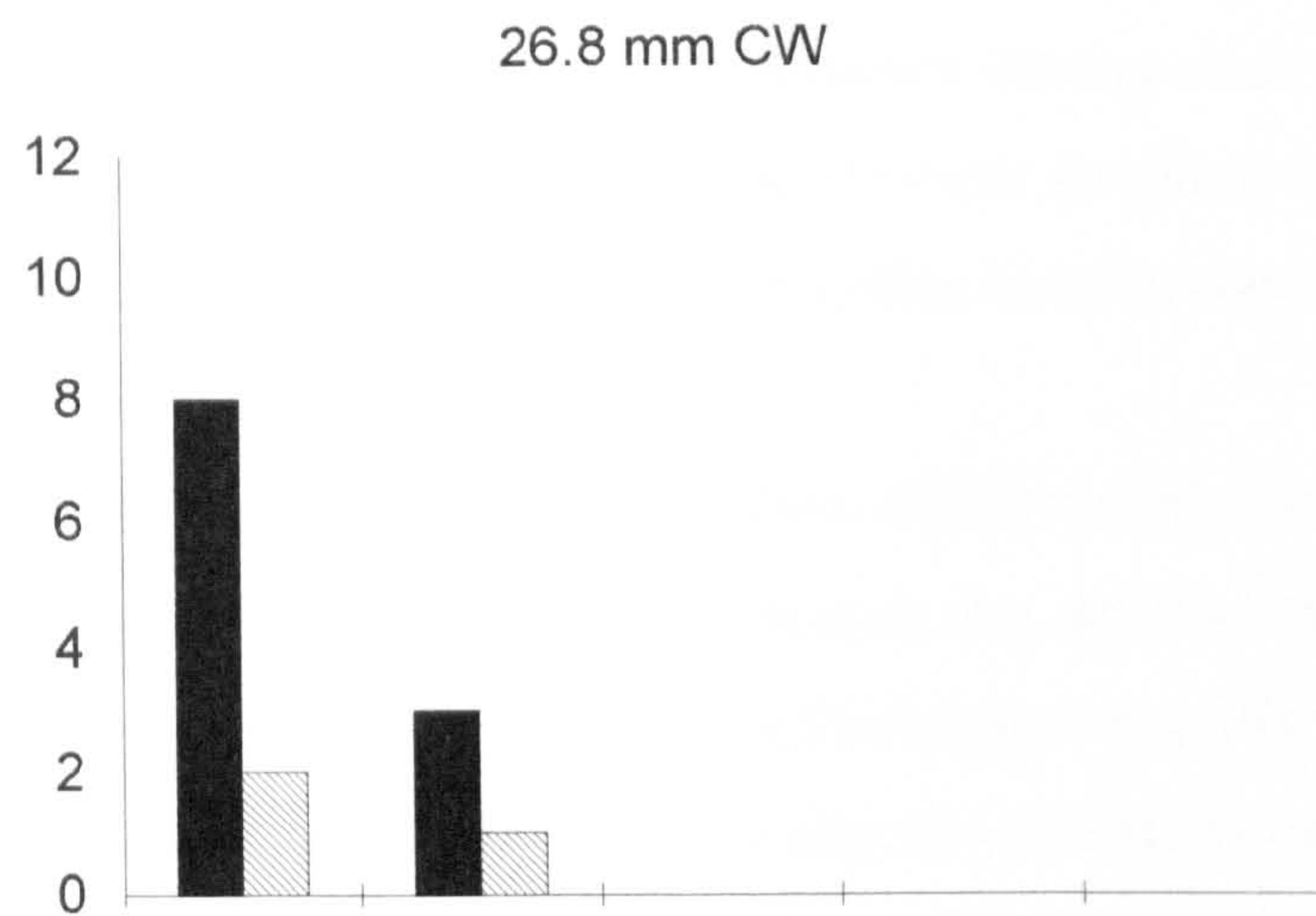
Table 6.3. Daily feeding rates of *Thalamita danae* with an unlimited diet of *Perna viridis* presented in two different relative proportions, together with the maximum size of mussel consumed.

Crab CW (mm)	Group ¹				Modified Group ²			
	No. consumed	Duration of expt. (Days)	Max. size consumed	No. mussels eaten. crab ⁻¹ .d ⁻¹	No. consumed	Duration of expt. (Days)	Max. size consumed	No. mussels eaten. crab ⁻¹ .d ⁻¹
26.8	11	5	18.6	2.2	3	5	17.3	0.6
30.4	10	5	20.6	2.0	3	5	25.4	0.6
38.7	14	5	22.0	2.8	6	5	26.1	1.2

¹ = Five mussels were presented in each of the following size classes; 10-15, 15-20, 20-25, 25-30, 30-35mm shell length
² = Mussels were presented as 1, 2, 9, 10, 3 individuals in the following size classes 10-15, 15-20, 20-25, 25-30, 30-35mm shell length respectively;
this proportion represented the relative abundance of these size classes in a field population.

Figure 6.5. The number of *Perna viridis* consumed each day by three sizes of *Thalamita danae* when mussels were presented in groups comprising five mussels in each of the following size classes, 10-15, 15-20, 20-25, 25-30, 30-35mm shell length (closed bars) and when mussels were presented in groups comprising 1, 2, 9, 10, 3 mussels respectively in the size classes 10-15, 15-20, 20-25, 25-30, 30-35mm shell length (open bars).

no. mussels consumed 5 days -1



populations (e.g. Huang *et al.*, 1985; Seed, 1990a). Whilst this may simply reflect the higher tidal levels from which these mussels were collected, larger mussels may have been selectively removed by local mussel gatherers; Huang *et al.* (1985) previously noted that the distribution patterns of some *P.viridis* populations are the result of human disturbance and that such populations are often characterised by larger numbers of small individuals.

Previous studies have revealed a positive allometric relationship between shell width and shell length in several species of mussels, e.g. *Mytilus edulis* (Seed, 1968); *Mytilus californianus* (Kopp, 1979) indicating that as these mussels grow they develop a proportionally wider more tumid shell. The negative allometric relationship between shell width and shell length reported for *Perna viridis* in this study was therefore somewhat surprising suggesting that as *P.viridis* increases in size it develops a proportionately narrower shell.

Decapod chelae have been described as templates upon which feeding behaviour is determined (Elner, 1980) and the foraging behaviour of *Thalamita danae* reflects its chelal morphology. The mechanical advantage (MA) of a chela describes the extent to which the initial force produced within a chela is altered by its morphology (Warner and Jones, 1976). The force applied at the chelal tip increases with increased MA but the speed of any resultant movement decreases (Warner and Jones, 1976) and to a certain extent this will determine the type of prey that can be effectively exploited. Brown *et al.* (1979) proposed that claws with a high MA were specialised for feeding on hard-shelled prey whilst those with a low MA belonged to generalist predators. The mean MA of the major chela recorded for *T.danae* in this study was 0.33 which falls between the extreme values of 0.50 for *Menippe mercenaria*, a predator of hard-shelled molluscs and 0.22 for the generalist forager, *Procambrus clarkii* (Brown *et al.*, 1979). This suggests that although the chelae of *T.danae* are not overspecialised for feeding on hard-shelled molluscs they do have a degree of specialisation which allows them to exploit this particular prey type. This conclusion is supported by the heterochelous nature of *T.danae*, a condition often associated with decapods which feed on hard-shelled prey (Seed and Hughes, 1995). The larger major chela contains a closer apodeme with a larger surface area for muscle

attachment. This indicates that a greater volume of closer muscle is contained within the propus of the major chela and that a greater initial force can be generated by this claw. Furthermore the higher mechanical advantage of the major chela indicates that a relatively greater force will be delivered, but this will be delivered more slowly, particularly suitable for a claw which delivers a strong compressive force (Brown *et al.*, 1979).

Mechanical advantage values presented in this study were calculated for the chelal tip but it should be noted that there exists a series of potential MAs along the length of the chela and these will be realised wherever the claw comes into contact with the prey. The magnitude of these MA's will progressively increase towards the pivotal point of the chela as the size of the lever length L2 decreases (see Chapter 3, section 3.2.2.) The interaction between the geometry of the chelae, particularly the way in which the prey can be accommodated in the claw, and the morphology of the prey, are therefore important in determining the predator's ability to crush hard-shelled prey. The relatively greater force generated in the major chela will act through its blunt molariform teeth thus creating an effective crushing surface (Brown *et al.*, 1979). The proximal peg located at the back of the major chela of *Thalamita danae* operates at maximum MA thus, a relatively greater force would be applied to prey by the peg than by the chelal tip, indeed Hughes and Elner (1998) found that the MA at the peg of the calappid crab, *Calappa ocellata* was double that at the chelal tip. The presence of such a peg is widely recognised as an adaptation to feeding on hard-shelled prey since large forces act through a small surface area thus creating a very high point load, without the need for a large structural investment in the claws itself (Vermeij, 1977; Brown *et al.*, 1978; Hughes and Seed, 1981; Seed and Hughes, 1995). Similar pegs are also present on the major chela in other portunids such as *Necora puber* (ap Rheinallt, 1986) and *Callinectes sapidus* (Hughes and Seed, 1981) and are probably instrumental in enabling these crabs to exploit larger size ranges of hard-shelled prey than might otherwise be predicted. The weaker forces produced by the minor chela operate through sharp triangular teeth which are better adapted for shearing or shredding softer material such as flesh (Brown *et al.*, 1979). Observations made during the feeding experiments presented in this chapter support this differential use of the two chelae by *T.danae*. The

mechanical advantage and occlusive geometry of the chelae of *T.danae* are similar to those described for *N. puber* and *Carcinus maenas*, both of which have an omnivorous diet in which hard-shelled prey forms a significant component (Choy, 1986; Elner, 1981). Analysis of stomach contents shows that *T.danae* too has a broad diet in which hard-shelled prey are well represented (Seed, 1990). Like *N.puber*, the flattened posterior walking legs of *T.danae* suggest that it is a highly mobile predator capable of feeding on fast-moving prey whilst the presence of a proximal peg and dimorphic chelae are adaptations for feeding on hard-shelled prey. The chelae of *T.danae* can thus provide an effective solution to the different demands placed on these structures as a result of feeding on different types of prey, some of which require strength and some of which require speed and dexterity.

Thalamita danae utilises a range of prey-size dependent opening techniques when feeding on mussels and this has been observed in other portunids including *Carcinus maenas*, *Callinectes sapidus*, *Necora puber* and *Ovalipes catharus*, (Elner and Hughes, 1978; Hughes and Seed, 1981; ap Rheinallt and Hughes, 1985; Davidson, 1986 respectively). The use of different techniques results from the interaction between the chelal strength and morphology with the strength and shape of the prey shell. Evidence from studies on *C.maenas* (Elner, 1978) and *Cancer productus* (Boulding and Labarbera, 1986) shows that the forces generated by the major chelae of these crabs are only sufficient to crush open relatively small bivalve prey. Larger prey items are broken by the repeated loading of the prey shell (Elner, 1978; Boulding and Labarbera, 1986) which gradually extends microfractures already present in the shell microstructure (Currey and Kohn, 1976).

The use of much slower opening techniques, such as wedging, by *Thalamita danae* occurs only when prey is too strong to be opened by the crushing techniques and/or too large to be accommodated within the chelal gape. Wedging thus enables *T.danae* to extend the size range of prey that can be eaten and simultaneously reduces the risk of chelal damage which could arise when attempting to crush particularly resistant prey. Crushing techniques appear to be used by most portunid species but the slower opening methods vary with both predator and prey species. The “insertion” technique described for *T.danae* has not previously been documented in other portunid

species and seems likely to be a prey-species specific technique since it exploits the apparent insensitivity of gaping *Perna viridis* when touched by *T.danae*.

When *Perna viridis* were presented to *Thalamita danae* breaking times increased rapidly with shell length. This reflects the change to the slower opening techniques required for larger more resistant prey. When mussels were presented in groups breaking times did not increase as steeply as when they were presented singly. This can be attributed to the greater use of the relatively quicker opening technique, insertion, when mussels are presented as part of a group. Handling times, like breaking times, were more protracted when mussels were offered singly. Since there was no significant difference in the amount of flesh left in discarded *P.viridis* shells when mussels were presented singly rather than as part of a group, it is concluded that *T.danae* harvests mussel flesh to the same extent regardless of how the mussels are presented. Differences in handling times were therefore presumably attributable to the different use of opening methods and not to the extent to which mussel flesh was harvested from the shell. Profitability curves when prey were presented singly or in groups were both domed, indicating that whilst small mussels were quickly crushed energy returns were low, whereas the higher energy yields from larger prey size classes were largely offset by longer handling times required to open them. The shorter handling times when mussels were presented in groups, suggests that these mussels have a higher predicted prey value. Furthermore, the size of prey predicted to be the most optimal was not fixed but varied according to the way in which prey was presented.

Similarities existed between the foraging behaviour of *Thalamita danae* on *Perna viridis* and that of *Carcinus maenas* on *Mytilus edulis* (see Chapter 5). The way in which mussels were presented to the crabs, for example, affected the handling times and therefore predicted prey values. Moreover, the size of prey predicted to be most profitable varied according to the way in which this was presented to the predator. However, the reasons for the slower handling times when crabs fed on groups of mussels differed between species. In Chapter 5 it was suggested that the presence of other mussels might interfere with the foraging behaviour of *C.maenas*, causing it to reject a prey item before the flesh had been fully harvested. *T.danae* however,

harvested the flesh from the mussels to the same extent regardless of how these were presented. Consequently the presence of other mussels must not have produced a sufficiently strong stimulus to induce the crab to reject a mussel that had not been fully gleaned in favour of another one. Instead, differences in handling times seemed to arise from the greater use of the less time consuming "insertion" opening method. This method relies on the crab encountering a gaping mussel and the chances of this occurring would increase when mussels were presented as part of a group. Similar findings have been reported for the oystercatcher, *Haemotopus ostralegus*, when feeding on infaunal bivalves (Hulscher, 1976; Wanink and Zwarts, 1985). When oystercatchers fed on bivalves at higher prey densities, their prey intake increased. This was because oystercatchers apparently avoided closed bivalves selecting instead those with gaping valves and at higher population densities of prey the chances of encountering such individuals was greatly enhanced. *T.danae* follows the incoming tide to feed on *P.viridis* (Seed, 1990a) which typically occurs in dense assemblages (Huang *et al.*, 1985; Lee, 1985). As these mussels become immersed by the flooding tide many of them will open their shell valves in order to feed. The use of the "insertion" method would allow *T.danae* to exploit large mussels relatively easily and quickly whilst reducing other costs such as handling time, an important consideration for a tidally foraging predator (Hughes and Seed, 1981) and chelal damage, which is a potentially limiting cost to predators feeding on hard-shelled prey (Juanes and Hartwick, 1990).

Prey-size selectivity has been shown to be a consistent feature in experiments investigating the foraging behaviour of portunids on hard-shelled prey (e.g. Elner and Hughes, 1978; Hughes and Seed, 1981; ap Rheinallt, 1985; Davidson, 1986; Sanchez-Salazar *et al.*, 1987b). Such size-selectivity has potentially important ramifications for the prey species at both the population and community levels and may also account for some of the observed prey distribution patterns (e.g. Ebling *et al.*, 1964; Sanchez-Salazar *et al.*, 1987a; Seed, 1990a). Portunids can be significant predators of commercial shellfish stocks (Walne and Dean, 1972; Sponaugle and Lawton, 1990) and their foraging behaviour is therefore important in economic terms. In South East Asia, *Perna viridis* is an important aquaculture species (Huang *et al.*, 1985) and since it has been estimated that a single foraging *Thalamita danae* can consume up to 325 small

mussels over a period of six months (Seed, 1990a) a thorough understanding of the vulnerability of *P.viridis* to predation by this crab is clearly important to the commercial fishery. Some studies which have investigated the vulnerability of prey to a particular predator have presented prey in equal numbers in several size classes (e.g. Seed, 1980c; 1990a). The size classes suffering the heaviest losses to predation are deemed the most vulnerable. However, research has shown that by manipulating the relative proportions of prey presented to the predator the vulnerability of prey in the different size classes may be altered (Elner and Hughes, 1978, Jubb *et al.*, 1983; Davidson, 1986). This was also demonstrated in the present study when the vulnerability of *P.viridis* to *T.danae* predation was investigated using two different proportions of prey, one comprising equal numbers in each of several size classes and the other when these size classes were presented in the same relative proportions to those in a field population of *P.viridis*. The observed shift in mussel vulnerability towards larger size classes when prey was presented in the modified proportion could not simply be attributed to the "eating out" of the previously "preferred" prey size class because the feeding rates of *T.danae* on *P.viridis* were very low and these mussels were always available. Instead, it may be inferred that *T.danae* has the ability to respond to changes in the relative abundance of the different size classes of prey and "adjust" its selection accordingly.

Such a shift in foraging behaviour may be an active or a passive response to the altered prey proportions. Studies by Elner and Hughes (1978) and Ameyaw-Akumfi and Hughes (1987) investigating the foraging behaviour of *Carcinus maenas* on *Mytilus edulis* found that suboptimal size classes of prey were initially rejected several times before they were eventually included in the diet if an optimal size of prey was not encountered - active selection. Alternatively, it has been concluded that the relative proportion of different prey sizes within the diet of planktivorous fish is the result of passive selection, resulting from the effect of prey encounter rates, which increase with prey surface area, and attack success rates, which decrease with increased prey size (Juanes and Conover, 1994 and references therein). Evidence presented in Chapter 5 supports this latter hypothesis as the likely mechanism underlying prey selection by *C.maenas* when feeding on *M.edulis*. Both active and

passive mechanisms would result in an observed shift in prey vulnerability with changes in prey proportions. No evidence was found in this study of the foraging behaviour of *Thalamita danae* on *Perna viridis* to support either hypothesis. However, regardless of the mechanism underlying such a shift in size preference, a flexible foraging strategy is essential to a predator such as *T.danae* which preys extensively on species like *P.viridis* whose size distribution can vary significantly both between tidal levels and between different shores (Huang *et al.*, 1985).

6.5. SUMMARY

- The chelae of *Thalamita danae* are characteristic of a predatory crab whose diet includes a high proportion of hard-shelled molluscs but which does not specialise on these types of prey. *T.danae* is heterochelous; the major chela possesses a proximal peg and has a mechanical advantage somewhat higher than that found amongst crabs that are generalist foragers. Such characteristics are generally associated with crabs that predate hard-shelled molluscs although the mechanical advantage of the major chela is lower than that generally found amongst crabs that specialise on these types of prey.
- The heterochelous nature of the chelae can be related to their different functions. The major chela operates at a significantly higher mechanical advantage and possesses a larger closer apodeme plate than the minor chela. Thus a larger force can be generated by the major chela which acts through blunt, molariform teeth which provide an effective crushing surface. The smaller forces exerted by the minor chela act through sharp triangular teeth making this claw better for tearing flesh and manipulating prey.
- *Thalamita danae* uses a range of prey-size dependent opening techniques, broadly similar to those previously recorded for other portunid crabs. However, a previously unrecorded technique, chelal insertion, was observed when *T.danae* fed on *Perna viridis*. This may be specific to this particular prey species and enables *T.danae* to exploit gaping *P.viridis* which seem to be relatively insensitive when handled by this crab.

- The foraging behaviour of *Thalamita danae* differed when prey items were presented singly and when they were presented as part of a group. Handling times were lower when mussels were presented in a group and this resulted in higher prey values.

- *Thalamita danae* exhibits a flexible foraging behaviour. Preferred prey size was not fixed but varied according to the relative proportions in which different sizes of prey were presented. Such behaviour is entirely appropriate for a predator foraging on a heterogeneously distributed prey species.

CHAPTER 7.

THE EFFECTS OF *MYTILUS EDULIS* ATTACHMENT STRENGTH ON THE FORAGING BEHAVIOUR OF *CARCINUS MAENAS*.

7.1. INTRODUCTION

Optimal foraging theory under the energy maximisation premise has often provided the framework within which foraging behaviour has been studied. This assumes that fitness is proportional to energy gained per unit of foraging time and predicts that predators should actively search for prey which will maximise their energy intake (Hughes, 1980). Thus, for every predator there should be an optimal size of prey which ought to be selected preferentially. Previous laboratory studies on the foraging behaviour of *Carcinus maenas* on the mussel, *Mytilus edulis* (e.g. Elner and Hughes, 1978) found that the predicted optimal prey size and the size of prey actually preferred in prey choice experiments coincided, strongly suggesting that the shorecrab foraged in an optimal fashion. Flesh weight (= energy content) and handling times were highly correlated with prey size, and the behaviour of *C.maenas* suggests that it has the ability to recognise and actively select for particular size classes of prey. Elner and Hughes, (1978) proposed that *C.maenas* rejected small mussels on the basis of their length and large mussels on the basis of their shell strength.

However, the way in which prey has normally been presented to crabs in these laboratory feeding experiments has been rather artificial for example mussels have generally been presented as non-attached individuals scattered over the floor of the aquarium. This does not therefore accurately reflect how the predator encounters these prey in the field. Recent work shows that by setting experiments in a more environmental context the foraging behaviour and prey selection of the predator can be significantly altered (see Chapter 5; West and Williams, 1986; Sponaugle and Lawton, 1990; Lee and Kneib, 1994; Hughes and Seed, 1995). In the field, *Mytilus*

edulis typically occur in dense aggregations with individuals attached both to each other and to the substratum by means of byssal threads (see Chapter 2 and references therein). Experiments indicate that *Carcinus maenas* detaches mussels before it manipulates and attempts to open them (Cunningham, 1983; Ameyaw-Akumfi and Hughes, 1987). The time taken to detach an individual mussel therefore represents a cost to the predator. When non-attached mussels are presented to crabs, prey value, or profitability, can be defined as E/Th , where E is the flesh weight and Th the time required to open and eat that mussel. However, when mussels are attached to a substratum then their profitability to the predator has to be redefined as $E/(Th+Tr)$ where Tr is the time taken to detach to the mussel. Consequently mussels that are more strongly attached will have a lower prey value than mussels of similar size but more weakly attached.

This chapter examines whether *Carcinus maenas* forages optimally under the energy maximisation premise when presented with mussels of similar size but different attachment strengths. Mussels were either weakly or firmly attached to tiles and the foraging behaviour of *C.maenas* on these mussels observed. If *C.maenas* can indeed assess prey value and relate this to some feature of the mussel then it ought to select individuals that are more weakly attached. However, if prey value is assessed solely on prey length and shell strength then crabs ought not to discriminate between weakly and strongly attached mussels.

7.2. MATERIALS AND METHODS

7.2.1. Collection and maintenance of *Carcinus maenas* and *Mytilus edulis*.

Experiments were conducted between June and October 1996. Experimental crabs were collected from Traeth Melynog by trawling (see Chapter 4) and were kept individually in plastic aquaria (30cm x 30cm x 20cm) filled to a depth of 5cm with seawater at ambient temperature. All experiments were conducted under ambient light levels. Water was changed daily and any faecal debris siphoned off. Two size classes of crabs were used, 40-45 mm and 50-55 mm CW. Only male, green crabs were used

in order to avoid potential differences in foraging behaviour arising from differing chelal morphologies (Elner, 1980; Kaiser *et al.*, 1990). If a crab stopped eating, moulted or died during the experimental period it was not replaced; instead the experiment was restarted using a new crab. This was done so as to allow direct comparisons of breaking and handling times within a trial. Crabs were kept in the laboratory for at least one week prior to the start of the experiment in order to allow them to acclimatise to the laboratory conditions. During this period they were fed solely on mussel flesh.

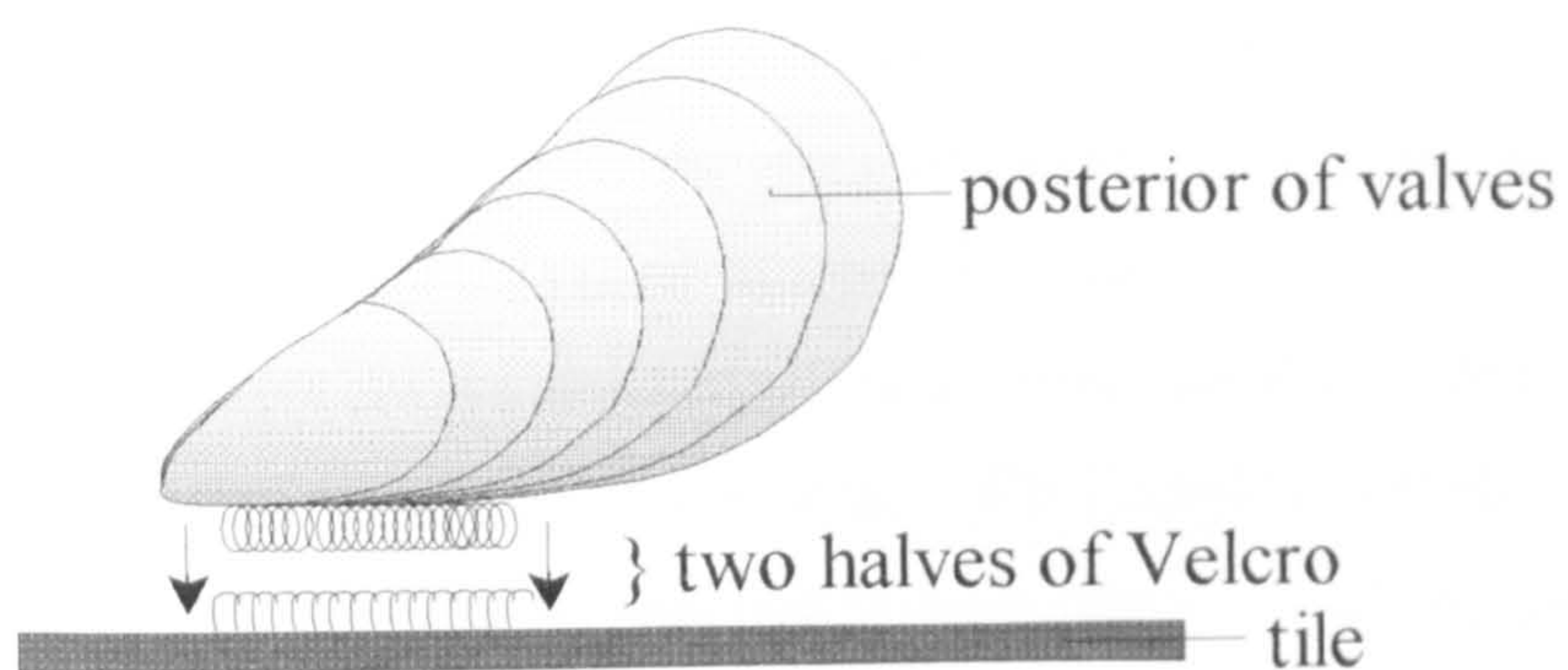
Mussels were collected from the high shore at Aberffraw every 1-2 weeks throughout the experimental period. This ensured that all mussels used in the experiments were in good condition. Care was taken to collect mussels from a restricted area of the shore in order to standardise flesh and shell characteristics, which in *Mytilus edulis* can be extremely variable (Seed, 1968). Mussels were kept in the laboratory in running sea water and under conditions of ambient light and temperature and only undamaged mussels which were free from epibionts were presented to crabs.

7.2.2. The effect of *Mytilus edulis* attachment strength on prey selection by *Carcinus maenas*.

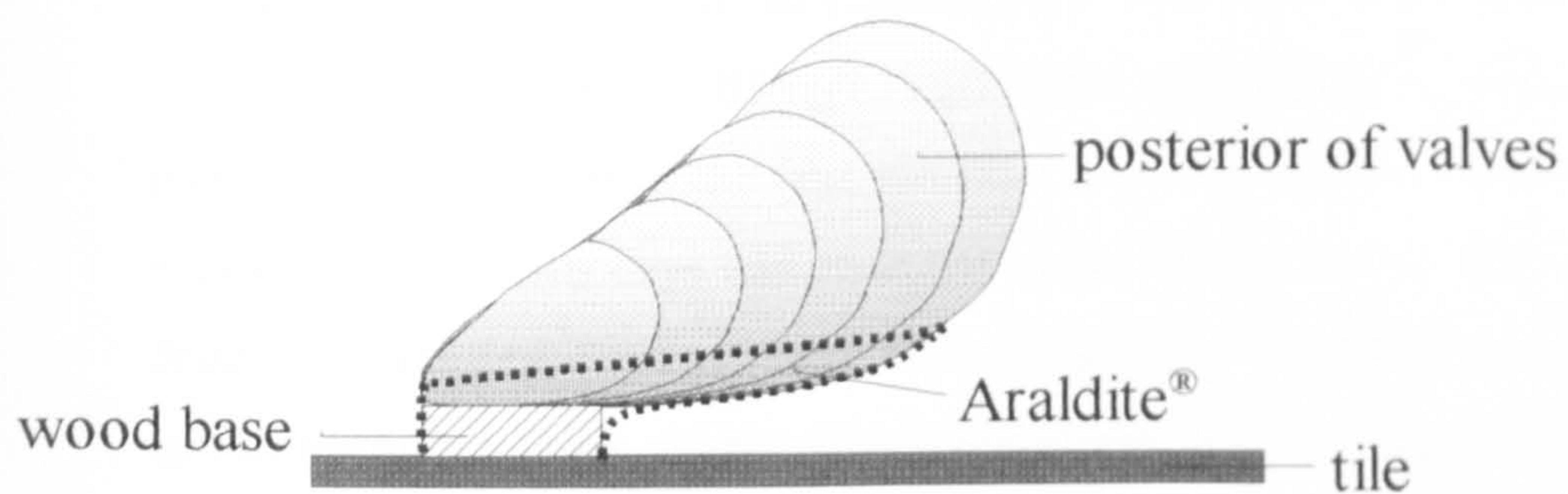
Ceramic tiles, 11cm x 11cm, were marked with a grid of 36 points (6 x 6) and a single mussel attached at each of the points so that 36 mussels could be presented simultaneously to an individual crab. Of these 36 mussels, 18 were 'weakly' attached and 18 'firmly attached'. Mussels were attached 1.5 cm apart and 'weak' and 'firm' mussels were alternated in order to ensure that the crab had equal access to both types of prey items. 'Weak' attachment was accomplished by cutting pieces of Velcro into squares 1 cm x 1 cm and securing the hooked half to the tile using quick setting epoxy resin ([®]Araldite Rapid) and the other half to the anterior dorsal part of the mussel shell (Fig. 7.1A) using a small amount of Super Glue (Loctite[®]). Velcro was used because it enabled the attached mussel to move slightly when touched, thereby simulating the movement of a mussel attached by byssal threads. 'Firm' attachment was achieved by first securing a piece of balsa wood 1cm x 1cm x 0.2cm to the tile using the quick

Figure 7.1. Schematic diagram illustrating the way in which ‘weak’ (A) and ‘firm’ (B) attachment were attained.

A. Weak Attachment



B. Firm Attachment



setting [®]Araldite adhesive and then attaching a mussel to this piece of wood using first a small drop of Super Glue and then [®]Araldite which was applied around the umbones (Fig. 7.1B). Mussels rigidly attached in this way did not visibly move when touched by a crab. Attaching the mussel to the piece of wood rather than directly to the tile ensured that the mussel was raised to a height similar to one attached by means of Velcro. Mussels were always attached by the anterior dorsal part of their shell so that the two valves were still able to gape ventrally. The [®]Araldite was allowed to cure for one hour before the tile, with the attached mussels, was lowered into the experimental aquarium.

Two trials were run with each crab, the first using an optimal size class of mussel and the second using a suboptimal size class. The optimal mussel length for crabs of 40–45 mm had previously been determined to be 10–15 mm whilst mussels 15–20 mm in length were used as suboptimal prey. For crabs 50–55 mm CW mussels of 15–20 mm and 20–25 mm shell length respectively were used as optimal and suboptimal prey. Prior to the start of the first trial, and between the two trials, crabs were fed mussel flesh for two days and then left unfed for 24 hours. This procedure was designed to restore the crabs to their “naive” state (see Chapter 4, section 4.2.) and to standardise hunger levels. Each trial was conducted over three days with crabs feeding on a set of mussels for two hours each day. During this two hour foraging period the following events were timed using a stopwatch: removal time (Tr), the time from when an attached mussel was first touched until it was removed from its base; breaking time (Tb), the time from when a mussel was first touched and manipulated until the crab took its first bite of the flesh, this included removal time; handling time (Th), the time from when a mussel was first touched and manipulated, though breakage and eating until the mussel shell was finally rejected, this included removal time; persistence time (Tp) - the time from when a crab first started to manipulate a mussel until the crab rejected the mussel having been unsuccessful in its attempts to open it. The way in which prey was handled, the methods used to detach and open the prey, and the number of mussels encountered, were also recorded. Encountered mussels included those which were eaten, those which were manipulated but subsequently rejected, and those which were touched but rejected.

7.2.3. Comparison of the attachment strengths of artificially attached and naturally occurring *Mytilus edulis*.

In order to determine how the attachment strengths of the artificially attached mussels compared with those occurring naturally in the field, the forces required to detach 10 'weak' mussels and 10 'firm' mussels from the 15-20mm length class were determined. This was carried out using the methodology described in Chapter 2, section 2.2.4. Thus, a small hole was drilled through both valves posteriorly using a hand held drill. Mussels were then attached either "weakly" or "firmly" and a wire loop was threaded through the hole and attached to a digital electronic force gauge. The mussel was pulled away from the tile in the direction of its orientation to the tile and the required force measured in Newtons. Forces required to remove these experimental mussels were then compared to forces previously reported for naturally occurring mussels of comparable size (see Chapter 2).

7.3. RESULTS

7.3.1. Foraging behaviour of *Carcinus maenas* on attached *Mytilus edulis*.

7.3.1.1. Handling techniques.

When a ceramic tile on which mussels were attached, was introduced into an aquarium, *Carcinus maenas* would move towards it until it made contact with the mussels. Initially the crab fed on mussels from the edge of the tile, moving across the tile during the course of the experiment. Crabs spread their pereopods and chelae when foraging so that several mussels were usually contacted simultaneously. In this way the crab was able to assess continuously its immediate environment and rejection of attached and detached prey items held by the chelae for one touched by the pereopods was frequently observed. Occasionally larger mussels were detached and taken into a corner of the aquarium to be further manipulated.

Mussels were detached in several ways. Crabs sometimes used their cutter

chela to sever both firmly and weakly attached mussels at their anterior dorsal point of attachment. Another method of detachment was that of levering where a foraging crab would grasp the posterior part of a mussel in its crusher claw and apply a twisting or levering force. Whilst this method led to the detachment of 'weakly' attached individuals, 'firmly' attached mussels were often broken posteriorly before they could be detached (Table 7.1). When this happened crabs did not continue in their attempt to detach the mussel but simply gleaned the flesh from both parts of the broken shell. Those mussels weakly attached by Velcro were sometimes detached accidentally by the pereopods whilst another mussel was simultaneously being manipulated by the chelae; the detached mussel was then usually gathered under the body by the pereopods.

7.3.1.2. Selection for *Mytilus edulis* with different attachment strengths.

Attachment strength appeared to play a key role in prey selection, with crabs tending to select more of the weakly attached mussels (Table 7.1) particularly when crabs were feeding on larger, suboptimal mussels. Crabs responded much more strongly to weakly attached mussels which tended to move slightly whenever they were touched. When a crab simultaneously touched mussels with different attachment strengths, the more rigidly attached mussel was generally rejected in favour of the more weakly attached and moveable individual. The result of this behaviour is illustrated in Figures 7.2-7.6 which clearly show an initial preference for weakly attached mussels. From these figures it is also evident that the number of firmly attached mussels eaten increases throughout the course of a trial. This may be attributable to the decreasing numbers of weakly attached mussels available to the foraging crab.

Despite this apparent preference for weakly attached mussels and the differences in handling methods used for these prey, no significant differences in breaking or handling times of weakly and firmly attached mussels were recorded (Table 7.2) suggesting that profitability does not differ significantly between attachment types and that consequently there is no energetic reason for preferring more weakly attached mussels. Comparisons were drawn between mussels in the optimal size class only because insufficient data were available to compare breaking and handling times

Table 7.1. Total number of weakly (W) and firmly (F) attached *Mytilus edulis* in optimal and suboptimal size classes eaten by five sizes of *Carcinus maenas*. The number of mussels of each attachment type which were detached prior to being opened and eaten¹ or which were broken, without being detached², are also presented together with the percentage of all encounters with each mussel type which resulted in a mussel being opened and eaten.

Crab CW (mm)	Mussel size (mm)	Attachment type	Eaten		Detached ¹		Broken, no detachment ²		Eaten:Encountered	
			No.	(%)	No.	(%)	No.	(%)		(%)
41.1 ³	10-15	W	47	(77.0)	46	(97.9)	1	(2.1)	77.1	
		F	14	(23.0)	3	(21.4)	11	(78.6)	23.0	
	15-20	W	11	(100)	11	(100)	0	(0)	15.5	
		F	0	(0)	0	(0)	0	(0)	tfd	
43.8 ³	10-15	W	45	(57.7)	42	(93.3)	3	(6.7)	69.2	
		F	33	(42.3)	9	(27.3)	24	(72.7)	42.3	
	15-20	W	10	(100)	10	(100)	0	(0)	9.3	
		F	0	(0)	0	(0)	0	(0)	tfd	
44.3 ³	10-15	W	35	(83.3)	32	(91.4)	3	(8.6)	41.2	
		F	7	(16.7)	3	(42.9)	4	(57.1)	10.9	
	15-20	W	11	(91.7)	11	(100)	0	(0)	17.2	
		F	1	(8.3)	1	(100)	0	(0)	1.9	

Table 7.1. (cont.) Total number of weakly (W) and firmly (F) attached *Mytilus edulis* in optimal and suboptimal size classes eaten by five sizes of *Carcinus maenas*. The number of mussels of each attachment type which were detached prior to being opened and eaten¹ or which were broken, without being detached², are also presented together with the percentage of all encounters with each mussel type which resulted in a mussel being opened and eaten.

Crab CW (mm)	Mussel size (mm)	Attachment type	<u>Eaten</u>		<u>Detached¹</u>		<u>Broken, no detachment²</u>		<u>Eaten:Encountered</u> (%)	
			No.	(%)	No.	(%)	No.	(%)		(%)
54.3 ⁴	15-20	W	23	67.6%	22	95.7%	1	4.3%		59.0
		F	11	32.4%	2	18.2%	9	81.8%		34.4
	20-25	W	11	91.7%	10	90.9%	1	9.1%		17.2
		F	1	8.3%	0	0.0%	1	100.0%		2.1
54.8 ⁴	15-20	W	11	50.0%	10	90.9%	1	9.1%		50.0
		F	11	50.0%	6	54.5%	5	45.5%		42.3
	20-25	W	7	63.6%	7	100.0%	0	0.0%		11.7
		F	4	36.4%	4	100.0%	0	0.0%		5.6

t.f.d. = too few data

³ optimal sizes, 10-15 mm shell length; suboptimal sizes, 15-20 mm shell length

⁴ optimal sizes, 15-20 mm shell length; suboptimal sizes, 20-25 mm shell length

Figure 7.2. The number of weakly and firmly attached *Mytilus edulis* in an optimal size class (10-15 mm shell length) eaten by *Carcinus maenas* of 41.1 mm CW over a three day period.

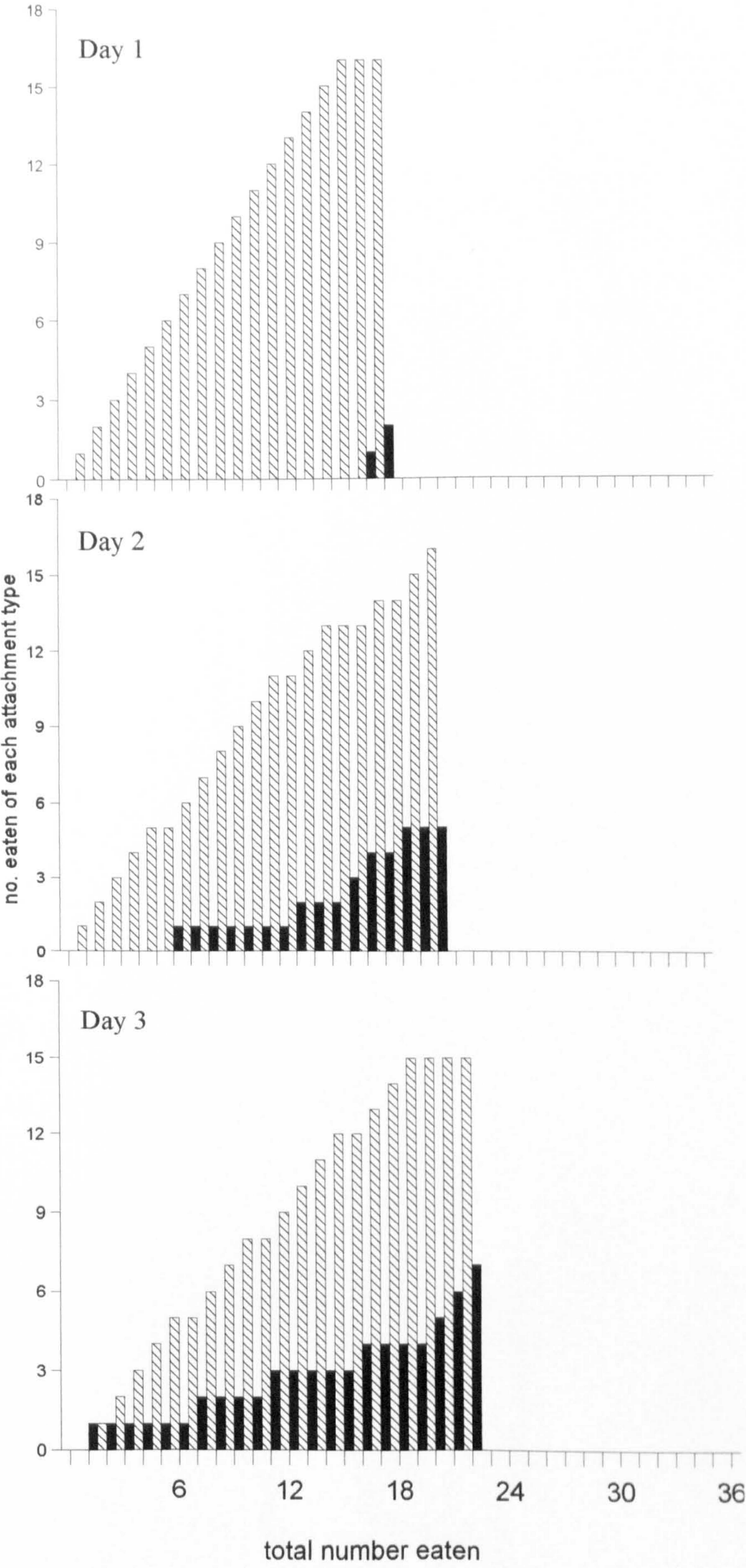


Figure 7.3. The number of weakly and firmly attached *Mytilus edulis* in an optimal size class (10-15 mm shell length) eaten by *Carcinus maenas* of 43.8 mm CW over a three day period.

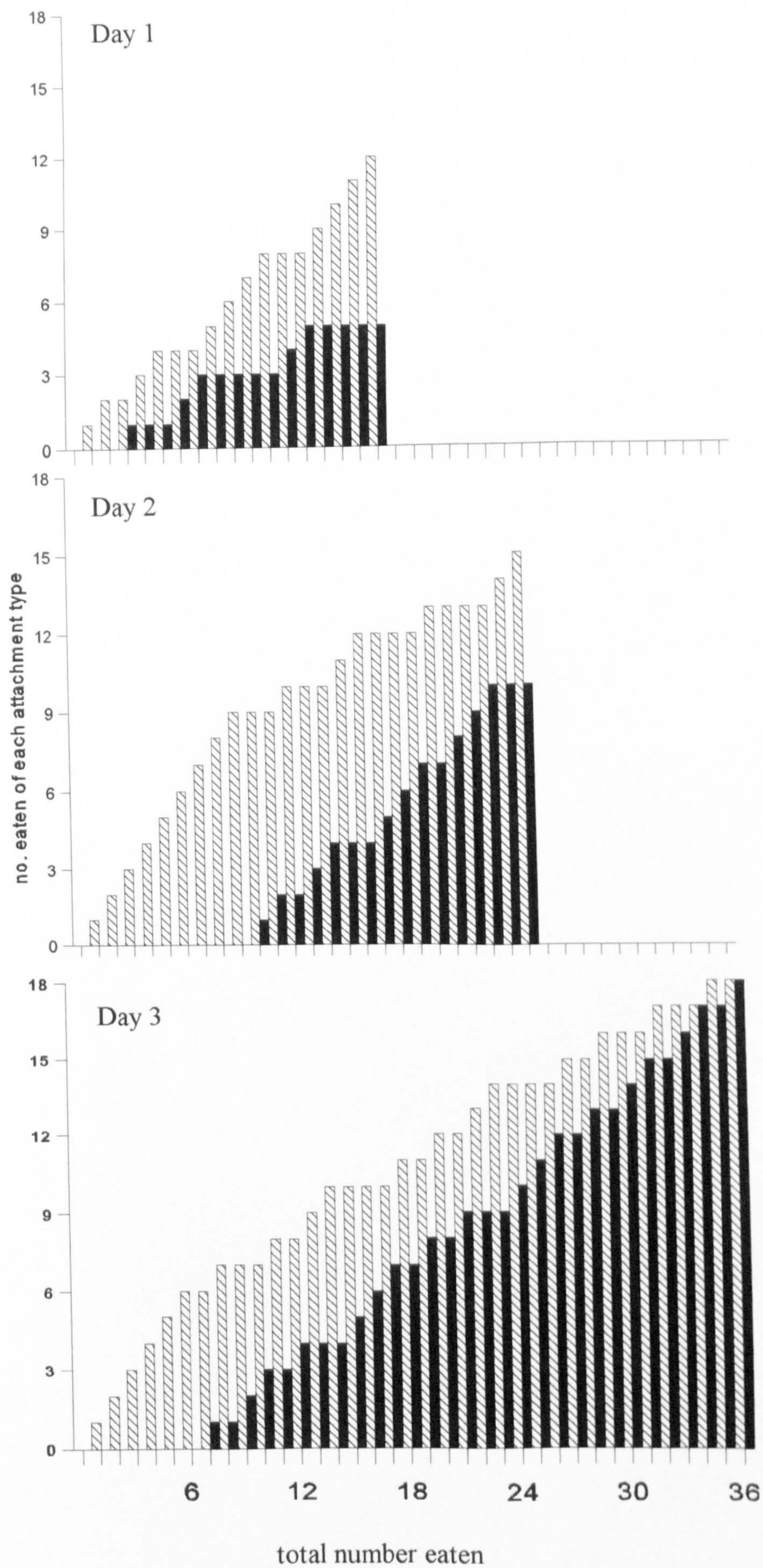


Figure 7.4. The number of weakly and firmly attached *Mytilus edulis* in an optimal size class (10-15mm shell length) eaten by *Carcinus maenas* of 44.3 mm CW over a three day period.

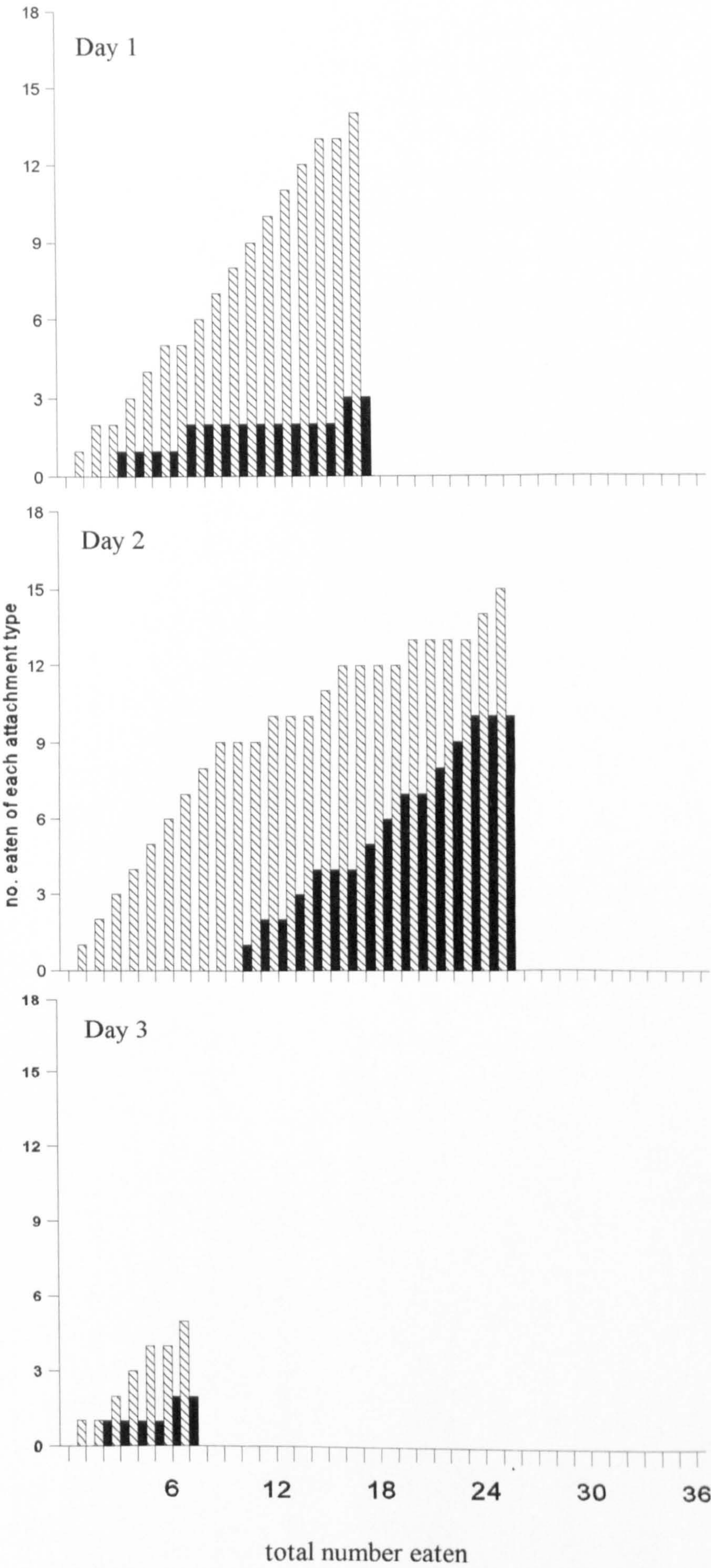


Figure 7.5. The number of weakly and firmly attached *Mytilus edulis* in an optimal size class (15-20mm shell length) eaten by *Carcinus maenas* of 54.3 CW mm over a three day period.

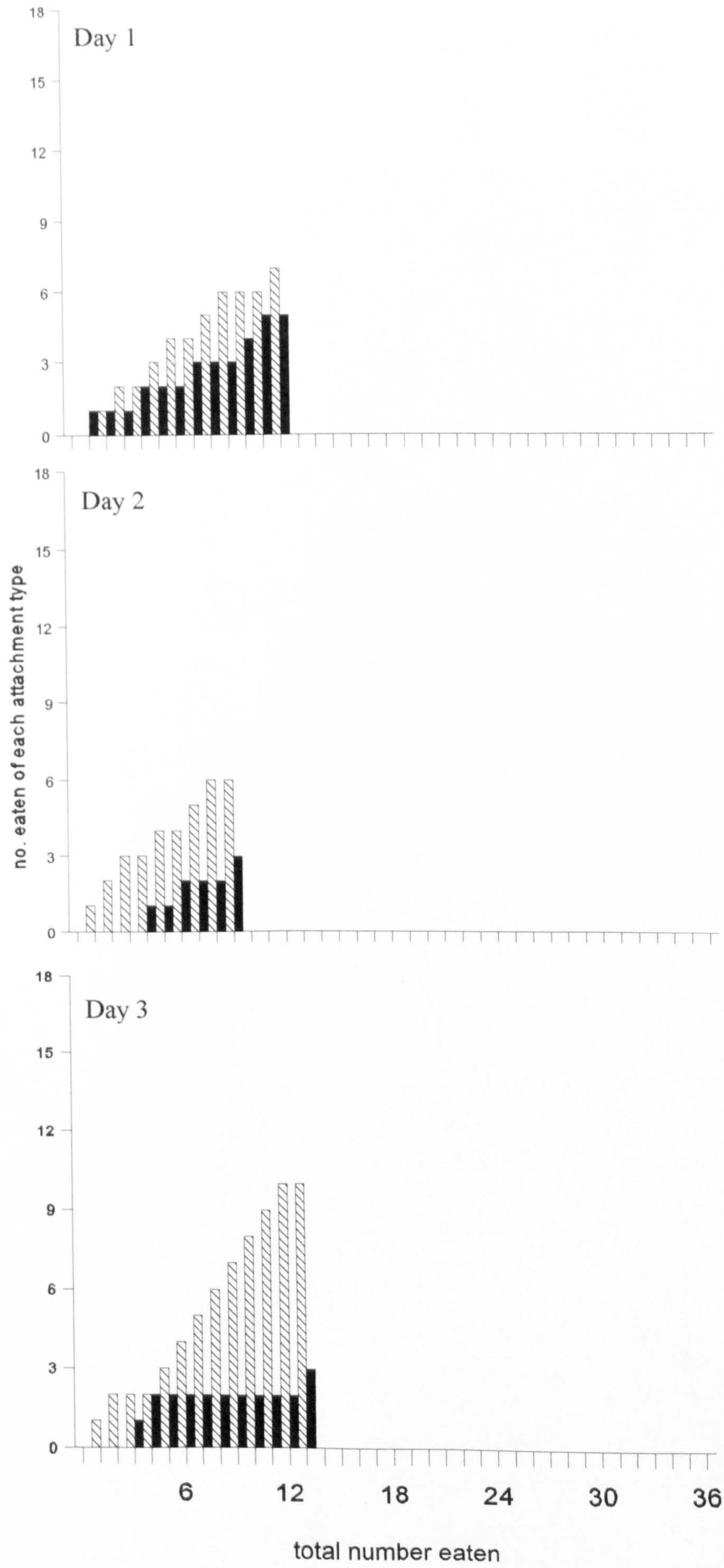


Figure 7.6. The number of weakly and firmly attached *Mytilus edulis* in an optimal size class (15-20mm shell length) eaten by *Carcinus maenas* of 54.8 CW mm over a two day period. Data were not obtained for a third day since the crab stopped eating.

54.8 mm CW

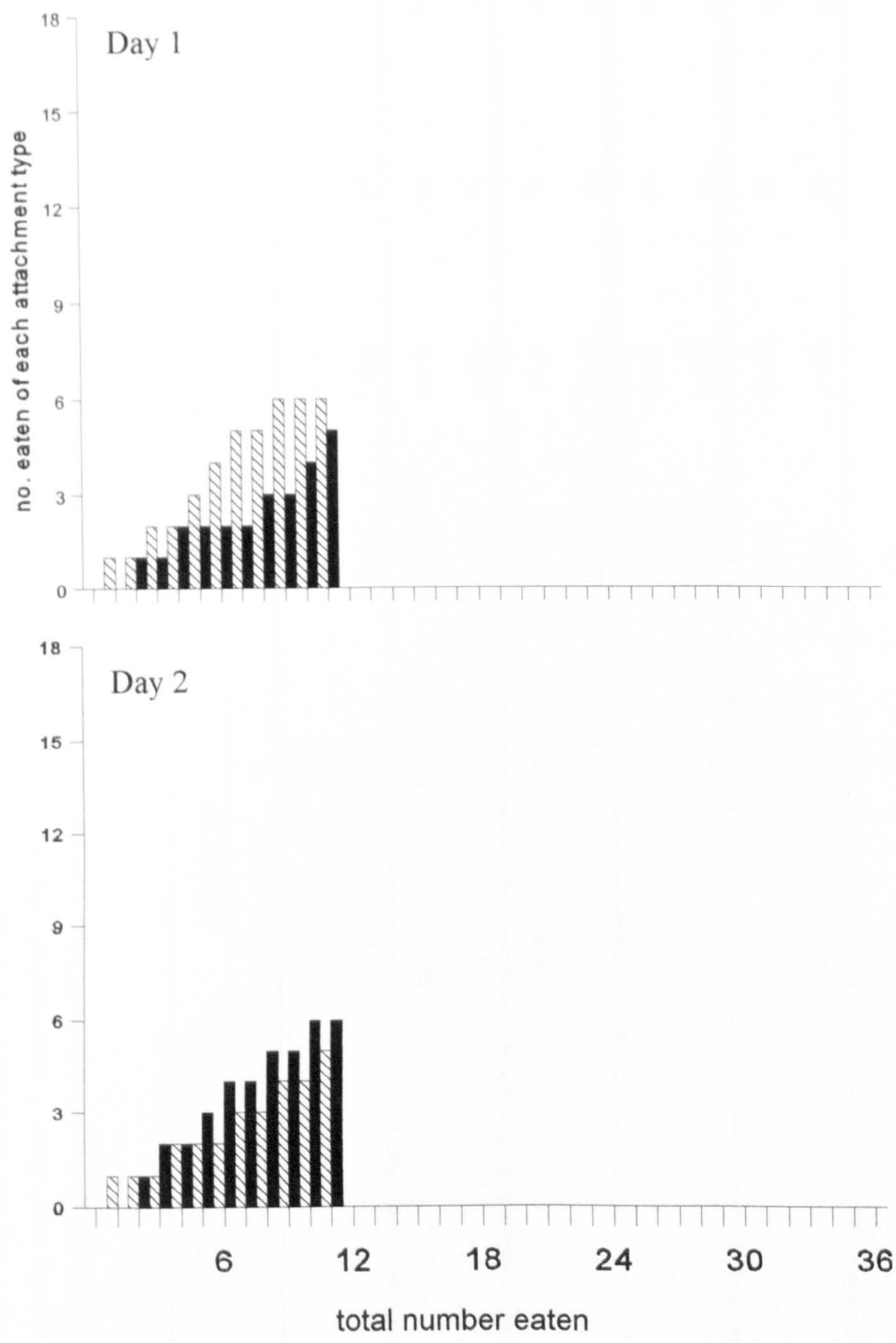


Table 7.2. Mean and median breaking (Tb) and handling (Th) times for two size classes of *Carcinus maenas* feeding on weakly (W) and firmly (F) attached *Mytilus edulis* in an optimal prey size class. Values include the time required to detach a mussel whenever this occurred prior to the mussel being opened. Median values are compared using the Mann-Whitney U test.

Crab CW (mm)	Mussel size (mm)	Handling procedure	Mean (secs)		Median (secs)		Significance
			W	F	W	F	
41.1	10-15	Tb	73.1	127.2	59.0	59.5	ns
		Th	253.6	343.0	230.0	318.0	ns
43.8	10-15	Tb	76.8	74.7	40.0	41.0	ns
		Th	204.8	212.9	130.0	164.0	ns
44.3	10-15	Tb	156.3	92.3	89.0	56.0	ns
		Th	396.1	296.6	320.0	264.0	ns
54.3	15-20	Tb	79.33	61.80	72.0	64.5	ns
		Th	399.6	348.4	397.0	296.5	ns
54.8	15-20	Tb	244.3	130.5	166.0	106.0	ns
		Th	488.8	294.1	393.0	329.5	ns

ns = not significant at p<0.05
n = number of mussels

between weakly and firmly attached mussels in the suboptimal size class as few of these mussels were detached (Table 7.1).

When weakly attached mussels were encountered crabs were more likely to persist in their attack until the prey item had been successfully opened (Table 7.1) than when more firmly attached mussels were encountered. A summary of persistence times of crabs on both optimally and suboptimally sized mussels are presented in Tables (7.3 & 7.4). Persistence times with mussels that were not detached during the persistence period were short, ranging from 2 secs-2 mins and averaging less than 0.5 min. When data were included for mussels which were detached during the persistence period but then subsequently rejected, persistence times increased to a maximum of 16 mins, but averaged less than 1.5 mins. Median persistence times (Table 7.3 & 7.4) are compared in Table 7.5 using the non-parametric Mann-Whitney U test. For mussels which were not detached during the persistence period no significant differences were found between the persistence times with weakly and firmly attached mussels. However, when data were included for mussels which were detached and subsequently manipulated during the persistence period, persistence times for weakly and firmly attached mussels were significantly different or approached significance for the smallest size group of crabs (Table 7.5) with longer persistence times for weakly attached mussels. However, since it was largely the more weakly attached mussels that were detached and subsequently manipulated before being rejected (see Tables 7.3 & 7.4) this comparison was essentially between the persistence times for mussels that were either detached or not detached during the persistence period.

7.3.2. The attachment strength of *Mytilus edulis* in the laboratory and in the field.

The forces required to detach 'weakly' attached mussels were quite low ($1.33 \pm 1.10\text{N}$) and broadly of the same order as those required to remove naturally occurring mussels of similar size from the Aberffraw population in November 1996 ($3.95 \pm 2.62\text{N}$). Although the forces required to remove the 'firmly' attached mussels were much greater ($31.37 \pm 11.75\text{N}$) similar detachment forces were reported for somewhat larger mussels ($>30\text{mm}$ shell length) in the Church Island

Table 7.3. Minimum, maximum, mean and median persistence times are presented for five *Carcinus maenas* foraging on weakly (W) and firmly (F) attached *Mytilus edulis* in an optimal size class. Persistence times of crabs on mussels which were not detached during the persistence period are presented, together with persistence times which include data from mussels which were detached and subsequently rejected uneaten (data in brackets).

Crab CW (mm)	Attachment type	Minimum (secs)	Maximum (secs)	Mean (secs)	Median (secs)	n
41.1 ¹	W	7	37 (216)	17.0 (41)	13.0 (24.0)	5 (11)
	F	2	63 (63)	17.0 (17)	13.0 (13.0)	45 (45)
43.8 ¹	W	6	13 (209)	8 (44)	7.0 (25.0)	3 (15)
	F	3	53 (65)	17 (19)	15.0 (15.5)	43 (44)
44.3 ¹	W	2	34 (214)	13 (36)	11.5 (16.0)	14 (27)
	F	2	79 (79)	11 (11)	8.0 (8.0)	53 (53)
54.3 ²	W	2	16 (64)	10 24	12.0 (15.5)	5 (8)
	F	5	51 (51)	21 21	18.0 (18.0)	7 (7)
54.8 ²	W	2	30 (106)	18 (34)	19.0 (22.0)	4 (12)
	F	13	51 (51)	26 (24)	21.0 (20.5)	10 (12)

¹ optimal sizes 10-15 mm shell length

²optimal sizes 15-20 mm shell length

n = total number of mussels each crab persisted with during the course of the trial.

Table 7.4. Minimum, maximum, mean and median persistence times are presented five *Carcinus maenas* foraging on weakly (W) and firmly (F) attached *Mytilus edulis* in a suboptimal size class. Persistence times of crabs on mussels which were not detached during the persistence period are presented, together with persistence times which include data from mussels which were detached and subsequently rejected uneaten (data in brackets).

Crab CW (mm)	Attachment type	Minimum (secs)	Maximum (secs)	Mean (secs)	Median (secs)	n
41.1 ¹	W	2	35 (941)	13 (92)	9.0 (35.0)	11 (41)
	F	2	56 (56)	15 (15)	12.5 (12.5)	22 (22)
43.8 ¹	W	2	78 (286)	17 (34)	7.0 (12.0)	57 (80)
	F	2	37 (43)	11 (11)	7.0 (7.0)	39 (40)
44.3 ¹	W	4	115 (583)	26 (73)	21.0 (30.0)	17 (36)
	F	4	44 (955)	15 (72)	12.0 (12.0)	18 (20)
54.3 ²	W	2	62 (120)	14 (21)	9.0 (10.0)	30 (35)
	F	2	52 (52)	12 (12)	9.5 (9.5)	26 (26)
54.8 ²	W	2	113 (223)	20 (35)	11.0 (11.0)	22 (22)
	F	2	197 (213)	23 (27)	14.0 (15.0)	59 (59)

¹ suboptimal sizes, 15-20 mm shell length

² suboptimal sizes, 20-2 5mm shell length

n = total number of mussels each crab persisted with during the course of the trial.

Table 7.5. Differences between the median persistence times (presented in Tables 7.3 & 7.4) for five *Carcinus maenas* foraging on weakly and firmly attached *Mytilus edulis* in optimal and suboptimal size classes using the Mann-Whitney U test. Median persistence times which exclude data for mussels which were detached¹ during the persistence period and median persistence times which include these data² are both tested.

Crab CW (mm)	Mussel Size (mm)	<u>Without detachment¹</u>		<u>With detachment²</u>	
		p	n	p	n
41.1 ³	10-15	>0.7	50	<0.06	56
	15-20	>0.7	33	<0.01	63
43.8 ³	10-15	t.f.d.	-	<0.06	59
	15-20	>0.4	96	<0.02	120
44.3 ³	10-15	>0.3	67	<0.001	80
	15-20	>0.1	35	<0.05	56
54.3 ⁴	15-20	>0.1	12	>0.9	15
	20-25	>0.6	56	>0.1	61
54.8 ⁴	15-20	>0.4	14	>0.9	24
	20-25	>0.2	81	>0.9	106

³ optimal mussels, 10-15 mm shell length; suboptimal mussels, 15-20 mm shell length

⁴ optimal mussels, 15-20 mm shell length; suboptimal mussels, 20-25 mm shell length
t.f.d. = too few data

population during April 1996 when a maximum force of 34.3N was recorded for a mussel of 36.2mm shell length (Chapter 2, Fig. 2.14D).

7.4. DISCUSSION

Previous laboratory studies have found that when foraging on mussels *Carcinus maenas* feeds optimally by selecting those size ranges of prey that maximise net energy intake (Elner and Hughes, 1978; Jubb *et al.*, 1983). However, in these studies crabs have generally been presented with non-attached mussels spread at random over the floor of the aquarium. The selection of optimally sized mussels appears to be an active process with the crab evaluating prey items in its chelae before either accepting or rejecting them (Elner and Hughes, 1978). *C.maenas* would thus appear to have the ability to assess prey value through some feature of the prey itself. Elner and Hughes (1978) proposed that shorecrabs rejected mussels smaller than the optimal size on the basis of their length and rejected mussels larger than the optimal size on the basis of their shell strength. This has become known as the Prey Evaluation Model of prey selection.

When non-attached mussels are presented to crabs, prey value can be defined as the flesh weight of the mussel divided by the handling time (E/Th). In the experiments presented in this chapter, however, crabs were presented with mussels that were attached to the substratum. Since previous experiments have shown that *Carcinus maenas* generally detaches a mussel before it is manipulated and eaten (e.g. Cunningham, 1983; Ameyaw-Akumfi and Hughes, 1987) prey value is suitably redefined as $E/(Th + Tr)$ where Tr is the time taken to remove the mussel from the substratum before handling commences. In experiments reported here all mussels presented to a crab within a single trial were from the same restricted size class and it is assumed, therefore, that they would all have similar flesh weights (E) and would require similar handling times (Th). It was predicted that the time required to detach a mussel (Tr) should be less for weakly attached mussels and that, consequently, the profitability of these mussels would be greater than for more firmly attached mussels. If *C.maenas* is indeed able to assess prey value accurately then it should preferentially

predate the more weakly attached mussels. Alternatively, if *C.maenas* assesses its prey solely on the basis of prey length or on shell strength, then equal numbers of mussels should be eaten irrespective of attachment type.

Throughout these experiments strong selection for weakly attached mussels was observed. This was evident from the greater number of prey items eaten, the greater proportion of eaten to encountered mussels, and the order in which weakly and strongly attached mussels were eaten. Such findings support previous work carried out on *Callinectes sapidus* (e.g. Lin, 1990; Hughes and Seed, 1995) which preferentially predated weakly attached marsh mussels. Contrary to the initial prediction, however, there was no significant difference between the total handling times of *Carcinus maenas* when predating weakly and firmly attached mussels and consequently no difference in prey value between these mussels. It is concluded, therefore, that the probability of a mussel being consumed is not influenced either by its energy return to the crab, or by its shell length or strength, but rather by its attachment strength. This need not imply that *C.maenas* does not maximise its net energy intake but rather that it may do so through an alternative mechanism.

Implicit to the Prey Evaluation Model is the ability of the predator to assess prey value through some external feature and to rank the prey accordingly. In experiments where non-attached *Mytilus edulis* are presented to *Carcinus maenas*, shell length is probably a reliable indicator of prey value since both mussel flesh weight (E) and handling times (Th) of these mussels vary in a fairly predictable way with shell length (Elner and Hughes, 1978, Chapter 4 & 5). However, in the field, where mussels are attached and prey value includes the additional cost of removal time, mussel shell length is a less reliable indicator of prey value. The underlying reason for this is that although a significant positive correlation between byssal attachment strength and mussel shell length exists, attachment strength is highly variable not only with wave-exposure and position of a mussel within a patch, but also between individual mussels of the same length from the same location (see Chapter 2 and references therein). In the field situation therefore, the time required by a crab to remove a mussel of a particular size will be highly variable and consequently shell length will less reliably indicate the value of that prey item. When the foraging behaviours of *C.maenas* on the

gastropods *Nucella lapillus* (Hughes and Elner, 1979) and *Littorina saxatilis* and *L. compressa* (Elner and Raffaelli, 1980) were studied, it was found that shore crabs did not actively select for optimal sizes of prey but instead attacked all prey items encountered, rejecting prey which did not yield within a limited period of time. Such behaviour was concluded to be appropriate for a prey species with an unpredictable value and one with which the predator had low rates of encounter thus denying the predator the opportunity to learn specific foraging skills (Hughes and Elner, 1979). Indeed, given that in the current study the persistence times with mussels which were not detached during the persistence period, were low (2secs-2mins) and broadly comparable to those reported for *C.maenas* when foraging on *N.lapillus* (0.25-2.75mins) (Hughes and Elner, 1979) it would seem that when confronted with attached mussels *C.maenas* adopts a similar foraging strategy.

When foraging on attached mussels, *Carcinus maenas* would often touch several mussels simultaneously thereby enabling the crab to assess the attachment strength of one prey item relative to that of another. This behaviour suggests that selection for weakly attached mussels is less dependent on the actual strength of attachment and more dependent on strength relative to other mussels in the same location. This conclusion is further supported from observations of *Callinectes sapidus* feeding on the marsh mussel, *Geukensia demissa* (Hughes and Seed, 1995) and on the clam, *Mercenaria mercenaria* (Micheli, 1995). Within a group of attached mussels those which are the most weakly attached relative to neighbouring mussels, may still be strongly attached in absolute terms. A tactile predator such as *C.maenas* can only evaluate those prey items with which it makes contact. Features of the prey will vary not only between individuals but also between patches; for example, mussels on the outside of a clump tend to be more strongly attached than mussels of the same size within the clump (see Chapter 2 and references therein). By limiting its persistence time a crab will be "encouraged" to move out of a poor patch and seek a more favourable patch in which to feed. Having a limited persistence time is thus an effective strategy for dealing with a heterogeneous environment.

Although prey value is normally calculated for a single prey item it can also be calculated for a single foraging bout, in which case the net energy intake of the crab

is $E/(T_h + T_p)$ where T_p is the time spent handling a prey item which is not subsequently eaten. For the predator to forage optimally T_p should be minimised. In the field mussels tend to occur in dense aggregations where only the posterior regions of their valves project beyond the clump thereby limiting the ability of a foraging crab to accurately assess shell length. If a mussel has to be removed from a clump prior to any breaking attempts (e.g. Cunningham, 1983; Ameyaw-Akumfi and Hughes, 1987) then a certain amount of time has already been invested before the crab can "decide" whether the mussel is of the "optimal size" or not. If the removed mussel is subsequently rejected then the time spent on its extraction from the clump must be regarded as a waste of energy which will effectively reduce the net energy intake over the whole foraging bout. This is perhaps analogous to the situation that arises when crabs forage on infaunal prey, where the size of individual prey items presumably cannot be determined until they have been fully excavated. Blundon and Kennedy (1982b) observed that *Callinectes sapidus* never rejected clams that they had uncovered although clams lying on the surface were occasionally ignored. Similarly West and Williams (1986) found that *C. sapidus* showed no evidence of size-selective predation when its prey, *Geukensia demissa*, was buried within the sediment. A positive correlation exists between byssal attachment strength and shell length in *Mytilus edulis* but the attachment strength of any given size of mussel is variable (see Chapter 2, Fig. 2.13). Thus, when a foraging shorecrab is presented with several mussels simultaneously, it should select those individuals which are more weakly attached as this will reduce the likelihood that these prey items will be too large for the crab to open. Both Cunningham (1983) and Ameyaw-Akumfi and Hughes (1987) found that the optimal (medium) size range of mussels predominated in the diet of *Carcinus maenas* when it was allowed to feed on natural clumps of *M. edulis*. Such selection, however, could presumably arise as a result of their response to mussel attachment strengths.

Persistence times with mussels increased when these were detached prior to being rejected compared with those where mussels had been rejected before detachment occurred. Moreover, when persistence times with mussels detached during the persistence period were compared, differences were found between the median

persistence times for weakly and firmly attached mussels, at least amongst the smaller crabs. Since it was mainly the more weakly attached mussels that were detached these differences were essentially between the persistence times for mussels detached during this period and mussels not so detached. This strongly suggests that foraging *Carcinus maenas* respond to a hierarchy of stimuli, in this case slight mussel movement and then shell strength, persisting only for a limited amount of time in response to each stimulus. This is supported by the observations of Abby-Kalio (1989) who found that inflicting damage on the mussel shell encouraged *C. maenas* to persist with opening attempts. Both byssal strength and shell strength are positively correlated with shell length in *Mytilus edulis* (see Chapter 2), but there is a high degree of variation in both of these relationships such that a weakly attached mussel does not necessarily have a weak shell. No single prey feature can provide the predator with accurate information about all the other features which may affect prey handling time and hence prey value. Adopting a limited persistence time with each prey variable is thus an effective way of dealing with several features of the prey which affect handling time but which are themselves subject to a high degree of variability. In this series of experiments it was sometimes observed that a mussel which had been successfully detached and was in the process of being manipulated by the chelae was subsequently dropped in response to the perceived movement of an alternative mussel touched by the sensitive pereopods. This suggests that *C. maenas* can integrate its response to several different stimuli relative to one another. This corresponds to the behaviour predicted by Jubb *et al.*, (1983) under the Relative Stimulus Hypothesis which states that the retention of a mussel held in the chela is dependent on the strength of stimuli received from the chela relative to the strength of stimuli received from the pereopods. Chelal stimulus relates to mussel shell strength whilst pereopod stimulus probably relates to mussel size (Jubb *et al.*, 1983) but could also presumably relate to attachment strength. By integrating its response to several different stimuli from simultaneously encountered prey, *C. maenas* can effectively assess more prey in a shorter period of time than if it adopted a strategy whereby it tested each prey and each feature of the prey individually. Consequently this would minimise T_p and therefore maximise net energy intake over a single foraging bout.

Carcinus maenas is not the only predatory decapod which has been shown to select its prey in response to stimuli received from the prey, *Callinectes sapidus*, for instance, was shown to be strongly size-selective when feeding on groups of the clam, *Mercenaria mercenaria*, but such size selectivity could be altered by the response of the crab to different shell strengths (Micheli, 1995). When *C.sapidus* was presented with mixtures of live clams and empty clam shells, crabs would select the more brittle, empty shells regardless of their size. Shell strength was considered to be the prime stimulus and the driving force behind prey selection. Similarly, Hughes and Seed (1981) found that whilst *C.sapidus* was strongly size-selective when feeding on groups of non-attached marsh mussels, *Geukensia demissa*, no evidence for such selection was found when these crabs were presented with firmly attached mussels (Hughes and Seed, 1997). Instead, crabs persisted with and ate those mussels which moved slightly when touched by a crab regardless of their size. *C.maenas* would appear to follow this same general pattern of prey selection.

The preference for mussels with weaker attachment strengths demonstrated in this chapter, together with the significant positive correlation between byssal attachment strength and shell length of *Mytilus edulis* (see Chapter 2 and references therein) suggests that *Carcinus maenas* should feed selectively on smaller size ranges of mussels in the field. However, naturally occurring mussel clumps have a complex structure with larger mussels providing a spatial refuge for smaller individuals which, as juveniles, settle extensively on the byssal threads of adult conspecifics (Bertness and Grosholz, 1985). Thus access to smaller mussels in natural clumps is often limited and predation effort may then be shifted to larger size classes of prey (Lin, 1990; Lee and Kneib, 1994). The observed selection for medium size ranges of *M.edulis* when *C.maenas* fed on natural mussel clumps (Cunningham, 1983; Ameyaw-Akumfi and Hughes, 1987) may therefore result from a passive response of crabs to slight movements of the more weakly attached mussels, which would have the effect of driving prey selection down to the smaller size classes, and to the more limited access to these smaller mussels which would thus drive selection towards larger size classes of prey.

7.5. SUMMARY

- *Carcinus maenas* selected weakly attached mussels over those that were more firmly attached. Such selection was based neither on prey value nor on prey length but rather on the resulting slight movement of weakly attached mussels whenever these were touched by a foraging crab.
- Amongst attached mussels, particularly those occurring in densely packed clumps, prey value is not easily determined on the basis of shell length, partly because this variable does not provide a reliable indicator of byssal attachment strength and hence of prey value, and partly because of the difficulty in assessing the size of any individual mussel within the clump.
- A more appropriate foraging strategy will therefore be one which maximises the likelihood that any mussel removed from a clump will be of a size which can be easily opened. Since a positive correlation exists between byssal attachment strength and shell length in *Mytilus edulis*, the apparent response of *Carcinus maenas* to relative attachment strength would appear to provide such a mechanism.
- When foraging on attached mussels *Carcinus maenas* persists with any given mussel for a limited period of time, after which the prey item is rejected. This strategy is similar to that previously reported for *C. maenas* when foraging on the dogwhelk, *Nucella lapillus* (Hughes and Elner, 1979).
- Limited persistence time coupled with its apparent response to relative byssal strengths will encourage *Carcinus maenas* to move out of low value mussel patches, where factors such as strong attachment and valve strength reduce the value of the mussels to the predator and into more favourable foraging patches, where the value of mussels is higher. Such foraging behaviour provides an effective mechanism for dealing with a particularly variable prey species.

CHAPTER 8

GENERAL DISCUSSION

Optimal foraging theory under the energy maximisation premise has provided the framework in which foraging studies of many different species of predator have been conducted (see Hughes, 1980 for review). This premise assumes that net energy intake is proportional to predator fitness and predicts, therefore, that a predator should forage in such a way as to maximise its energy intake per unit handling time (E/Th). Studies of the foraging behaviour of *Carcinus maenas* on hard-shelled molluscan prey has confirmed that this is indeed what this predator does when given a choice of a range of prey sizes; selecting those sizes of prey which maximise its net energy intake. Much research has subsequently concentrated on the mechanisms underlying such prey-size selection (Elner and Hughes, 1978; Hughes and Elner, 1979; Elner and Raffaelli, 1980; Jubb *et al.*, 1983; Ameyaw-Akumfi and Hughes, 1987). Three different mechanisms have been proposed to explain this behaviour. Elner and Hughes (1978) proposed that the selection of optimal sized *Mytilus edulis* by *C. maenas* arises through active selection, suboptimal prey being rejected after a brief period of manipulation in the chelae and mouthparts during which time their prey value is assessed. This is known as the Prey Evaluation Hypothesis. Theoretically optimally sized prey should be eaten whenever they are encountered (Charnov, 1976; Hughes, 1980) and this led Jubb *et al.* (1983) to propose the Relative Stimulus Hypothesis to explain the observation that a proportion of optimally sized mussels were always rejected by *C. maenas*. This hypothesis postulates that the retention or rejection of a grasped mussel depends on the relative strengths of conflicting stimuli received from mussels grasped in the chelae and mussels touched by the pereopods. A third behavioural mechanism seemed to explain the foraging behaviour of *C. maenas* on the gastropods, *Nucella lapillus*, *Littorina compressa* and *L. saxatilis* (Hughes and Elner, 1979; Elner and Raffaelli, 1980). The selection of optimal sizes of gastropods did not arise from active selection but was rather the passive outcome of attacking all prey items encountered and rejecting those which did not yield within a limited period of time.

It therefore appears that *Carcinus maenas* has developed distinct mechanisms

for different molluscan prey types. However, both this and previous studies have found that *C.maenas* has a broad diet and differences found between the relative contributions of different prey types between different studies suggests that this crab is a highly opportunistic predator (see Ropes, 1968; Elner, 1977; Elner, 1981; Raffaelli *et al.*, 1989). It therefore has to be questioned whether such an opportunistic predator would evolve distinct mechanisms for dealing with different prey types. The results of experiments presented in this thesis suggest that the foraging behaviour of *C.maenas* on *Mytilus edulis* incorporates elements of both the passive mechanism of prey selection, previously observed when this crab foraged on gastropods, as well as elements of the Relative Stimulus Hypothesis. The three different mechanisms outlined above may actually be facets of a more generalised foraging mechanism; these particular facets having been highlighted by the choice of experimental protocols.

Like previous studies of the foraging behaviour of *Carcinus maenas* on *Mytilus edulis*, clear selection for certain sizes of prey was observed and there was a broad coincidence between the size of preferred prey and that predicted to be most optimal (Elner and Hughes, 1978; Jubb *et al.*, 1983). However, in this thesis it is proposed that such selection does not occur solely through the active selection of prey since certain aspects of the data appear to be inconsistent with the Prey Evaluation Hypothesis. Primarily the active selection of optimal size classes of prey relies on the ability of the predator to accurately assess prey value. Elner and Hughes (1978) proposed that crabs rejected mussels larger than the optimal size on the basis of shell strength whilst smaller mussels were rejected on the basis of their shell length, with which flesh weight and handling time, and therefore prey value, were proposed to alter in a characteristic manner. However, it was shown in Chapter 2 that for *M.edulis* the relationships between shell length and variables affecting prey value were highly variable, for example, byssal attachment strength and shell strength varied between similar sized individuals, there were intersite variations in shell morphology and the flesh weight-shell length relationship altered both with site and season. When all of these factors are taken into account it can be concluded that the prey value of *M.edulis* is also highly variable and therefore shell length will not provide an accurate indicator of prey value. Indeed it was shown in Chapter 4 that intersite and seasonal differences in mussel flesh

weight altered the size of mussel predicted to be optimal. Consequently, it would be exceedingly difficult to evaluate such prey items solely on the basis of their shell length

More direct evidence that *Carcinus maenas* does not actively select its prey is provided in Chapter 5. If *C. maenas* were able to accurately assess the value of a prey item and if it were foraging optimally it should always accept prey of optimal size whenever these are encountered (Charnov, 1976; Hughes, 1980). However, in Chapter 5 it was found that *C. maenas* rejected up to 80% of mussels in the predicted optimal size class, contrary to the Prey Evaluation Hypothesis and whilst the rejection of a proportion of these mussels is predicted by the Relative Stimulus Hypothesis the acceptance of a high proportion of mussels from the smallest size class is contrary to predictions made under this hypothesis (see Jubb *et al.*, 1983). Furthermore, the preferred prey size class, i.e. that from which most mussels were eaten, did not consistently correspond to the size class with the highest eaten to encounter rates, suggesting that the 'preference' for a particular size of mussel was not the result of any sort of active selection. Instead the analyses of the proportion of mussels eaten to the numbers encountered by size class strongly suggests that preference for a particular size of prey is a passive result of increasing encounter rate and decreasing success rate with increased mussel size and this is comparable to the mechanism proposed by Hughes and Elner (1979) and Elner and Raffaelli (1980) for *C. maenas* preying on gastropods. It was concluded that it was inappropriate for *C. maenas* to use the prey evaluation mechanism when foraging on gastropods because the prey value of these hard-shelled molluscs is unpredictable (Hughes and Elner, 1979; Elner and Raffaelli, 1980). Given that it has already been concluded that the prey value of *M. edulis* in the field is also highly variable then it would be entirely appropriate for *C. maenas* to adopt a similar foraging strategy on mussels as it does on gastropods. Support for this view is provided by the limited persistence times of *C. maenas* with those attached mussels that were rejected before they were either detached or broken (Chapter 7). These persistence times were comparable to those reported for *C. maenas* with *Nucella lapillus* (Hughes and Elner, 1979).

It would appear that the opportunistic strategy of attacking all potential prey items encountered is modified when *Carcinus maenas* is in contact with more than one

item of prey. When several prey items are encountered simultaneously, *C.maenas* responds to the strongest stimuli. The result of such behaviour is the incomplete gleaning of a mussel that is presented as part of group (Chapter 5) and the rejection of a mussel held in the chelae for an alternative mussel touched by the sensitive pereopods (Chapters 5 & 7). This behaviour is entirely compatible with that predicted by the Relative Stimulus Hypothesis (Jubb *et al.*, 1983). When foraging on a group of mussels *C.maenas* may receive several different stimuli from different prey items, each of these stimuli, will provide information about that prey item. For example, although an encountered mussel may have weak byssal attachment it may prove to have a particularly strong and resistant shell. By integrating its response to several different stimuli *C.maenas* can quickly gain information about several prey at a time thus minimising persistence time and maximising energy intake over a foraging bout. Indeed it was shown in Chapter 5 that the incomplete gleaning of a mussel shell when mussels were presented as part of a group was energetically advantageous.

This investigation has emphasised the need to set crab foraging experiments in a more realistic context. The foraging behaviour of both *Thalamita danae* and *Carcinus maenas* changed when prey was presented either singly or as part of a group. *C.maenas* did not employ the more time consuming opening techniques of boring and edge-chipping when feeding on groups of mussels, nor did it fully glean the mussel shells when they were presented in this way. *T.danae* utilised the more efficient opening technique of chelal insertion more frequently than when presented with prey items individually. Consequently this led to the derivation of different prey value curves which predicted different optimal prey sizes under the different experimental protocols. Since prey value curves provide the framework against which predictions from foraging theories can be tested it is important that they are obtained under similar experimental conditions as apply when predictions from these are being tested. For example, in foraging experiments prey value curves are often derived by presenting individual prey items to the predator whilst the actual preference for a particular prey type is generally tested by presenting the predator with groups of prey items.

It has previously been demonstrated that structural elements of the environment can alter vulnerability (e.g. Leber, 1985; Sponaugle and Lawton, 1990;

Lee and Kneib, 1994). This study demonstrated that the actual structure of the prey population can also affect prey vulnerability. When *Carcinus maenas* and *Thalamita danae* were allowed to forage on groups of mussels, the most vulnerable size of prey varied according to the relative proportions that each prey size class were presented in. Since the principle prey species of both *C. maenas* and *T. danae* are themselves commercially important, such information could prove invaluable in the development of a more passive environmental control.

By presenting the prey in a more realistic context additional information concerning the underlying mechanisms of prey selection has been obtained. The selection of weakly attached mussels in preference to those that were more rigidly and firmly attached appeared to be due to the slight movement detected in these mussels when they were touched by a foraging crab rather than to their profitability or size as previously reported (Cunningham, 1983; Ameyaw-Akumfi and Hughes, 1987). Similar results have been obtained by Hughes and Seed (1997) for the portunid, *Callinectes sapidus*. In experiments where *C. sapidus* was presented with single mussels, *C. sapidus* appeared to respond to shell length, however when mussels were attached to a substratum weakly attached mussels were selected irrespective of shell length. If the main aim of foraging experiments is to elucidate the underlying mechanisms of prey selection then these experiments need to be set in a more realistic context. Furthermore results presented in this thesis highlighted the importance of using the same individual crab through a series of trials. This enabled direct comparisons to be made between the results obtained under different experimental protocols and differences arising between trials could therefore be directly attributed to changes in crab behaviour rather than to inherent differences between individual crabs.

Optimal foraging studies have often considered optimisation at the microlevel, e.g. choice between two individual prey items with different prey values. Zimmer-Faust (1987) suggests however, that optimisation may not occur at this level but may occur at macrolevels, for instance over a foraging bout or even over the lifetime of a predator. Findings presented in this thesis broadly agree with this argument. *Carcinus maenas*, for example, did not appear to be able to select between prey of different prey value, which would be optimisation at the microlevel, but optimisation at other scales

may have been observed. The most vulnerable size range of prey was not fixed but varied with the relative proportions in which different size classes of prey were presented to both *C.maenas* and *Thalamita danae* and the optimal prey size was not always the most vulnerable. In foraging experiments prey value is usually defined as energy yield to handling time, E/Th and the optimal size of prey is defined as that which maximises the net energy intake of the predator. However, unless the predator is feeding on prey which is uniformly of the optimal size, then there is another element of cost, in addition to handling time, that is the time taken to search for a prey item of the optimal size. If this applies then the search time (T_s) required to find the optimal size of prey when a crab is foraging on a group of mussels should also be considered, so that prey value then becomes defined as $E/(Th + T_s)$. If the predator has a fixed search image and preys only on the optimal size of prey then, when these prey items are scarce, their value to the predator will be effectively reduced by the longer search time required to locate them. However, if the predator has a flexible search image it will predate on the more frequently encountered prey items; T_s will therefore be reduced and energy gain should be maximised. Since tactile predators such as *C.maenas* and *T.danae* can only evaluate the prey items they are immediately in contact with and do not know what the size structure of a neighbouring patch is like, this mechanism is an effective way of maximising energy in a heterogeneous environment.

Furthermore this flexible foraging strategy will reduce intraspecific competition between the predators. It was shown that when a group of *Mytilus edulis* was composed of a large number of small mussels all sizes of *Carcinus maenas* preferentially fed on these, but when equal numbers in each of several size classes were presented to the crabs, prey size selectivity shifted to the larger size classes for the larger crabs. Therefore when small prey are scarce in the population larger predators will not out compete smaller predators for these and this will be advantageous to the species as a whole.

REFERENCES

- Abello, P., Warman, C.G., Reid, D.G. & Naylor, E., 1993. Differential mating success of right- and left-handed forms of the shore crab *Carcinus maenas* (L.) (Crustacea: Brachyura). *Quantified Phenotypic Responses in Morphology and Physiology. Proceedings of the Twenty Seventh European Marine Biology Symposium*. Ed. Aldrich, J.A.C.
- Abby-Kalio, N.J., 1989. Learning and the role of cue reinforcement in the shell cracking behaviour of the shore crab, *Carcinus maenas* (L.). *Behavioural Processes*, 18, 141-153.
- Allen, J.A., Cook, M., Jackson, D. J., Preston, S. & Worth, E.M., 1976. Observation on the rate of production and mechanical properties of the byssus threads of *Mytilus edulis* L. *Journal of Molluscan Studies*, 42, 279-289.
- Ambariyanto & Seed, R., 1991. The infestation of *Mytilus edulis* Linnaeus by *Polydora ciliata* (Johnston) in the Conwy estuary, North Wales. *Journal of Molluscan Studies*, 57, 413-424.
- Ameyaw-Akumfi, C. & Hughes, R.N., 1987. Behaviour of *Carcinus maenas* feeding on large *Mytilus edulis*. How do they assess their optimal diet? *Marine Ecology Progress Series*, 38, 213-216.
- ap Rheinallt, T., 1986. Size selection by the crab *Liocarcinus puber* feeding on mussels *Mytilus edulis* and on the shore crabs *Carcinus maenas*: the importance of mechanical factors. *Marine Ecology Progress Series*, 29, 45-53.
- ap Rheinallt, T. & Hughes, R.N., 1985. Handling methods used by the velvet swimming crab *Liocarcinus puber* when feeding on molluscs and shore crabs. *Marine Ecology Progress Series*, 25, 63-70.
- Arnold, W.A., 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* (Linne). *Journal of Experimental Marine Biology and Ecology*, 80, 207-219.
- Atkinson, R.J.A. & Parsons, A.J., 1973. Seasonal patterns of migration and locomotor rhythmicity in populations of *Carcinus maenas*. *Netherlands Journal of Sea Research*, 7, 81-93.
- Behrens Yamada, S. & Boulding, E.G., 1998. Claw morphology, prey size selection and foraging efficiency in generalist and specialist shell-breaking crabs. *Journal of Experimental Marine Biology and Ecology*, 220, 191-211.

- Bertness, M.D. & Grosholz, E., 1985. Population dynamics of the ribbed mussel, *Geukensia demissa*: The costs and benefits of an aggregated distribution. *Oecologia (Berlin)*, **67**, 192-204.
- Blundon, J.A. & Kennedy, V.S., 1982a. Refuges for infaunal bivalves from blue crab, *Callinectes sapidus* (Rathbun) predation in Chesapeake Bay. *Journal of Experimental Marine Biology and Ecology*, **65**, 67-81.
- Blundon, J.A. & Kennedy, V.S., 1982b. Mechanical and behavioural aspects of blue crab, *Callinectes sapidus* (Rathbun), predation on Chesapeake Bay bivalves. *Journal of Experimental Marine Biology and Ecology*, **65**, 47-65.
- Bollens, S.M. & Stearns, D.E., 1992. Predator-induced changes in the diel feeding cycle of a planktonic copepod. *Journal of Experimental Marine Biology and Ecology*, **156**, 179-186.
- Boulding, E.G., 1984. Crab-resistant features of shells of burrowing bivalves: Decreasing vulnerability by increasing handling time. *Journal of Experimental Marine Biology and Ecology*, **76**, 201-223.
- Boulding, E.G. & Labarbera, M., 1986. Fatigue damage: Repeated loading enables crabs to open larger bivalves. *Biological Bulletin*, **171**, 538-547.
- Brown, S.C., Cassuto, S.R. & Loos, R.W., 1979. Biomechanics of chelipeds in some decapod crustaceans. *Journal of Zoology (London)*, **188**, 143-159.
- Charnov, E.L., 1976. Optimal foraging: attack strategy of a mantid. *American Naturalist*, **110**, 141-151.
- Cheung, S.G., 1993. Population dynamics and energy budgets of green-lipped mussel *Perna viridis* (Linnaeus) in a polluted harbour. *Journal of Experimental Marine Biology and Ecology*, **168**, 1-24.
- Cheung, S.G. & Tse, S.F., 1993. Effect of tidal height on desiccation tolerance, body condition and population structure of the green-lipped mussel *Perna viridis* (L). In *Proceedings of the Second International Conference on the Marine Biology of the South China Sea*. Hong Kong University Press.
- Choy, S.C., 1986. Natural diet and feeding habits of the crabs *Liocarcinus puber* and *Liocarcinus holsatus* (Decapoda, Brachyura, Portunidae). *Marine Ecology Progress Series*, **31**, 87-99.
- Cohen, A.N., Carlton, J.T. & Fountain, M.C., 1995. Introduction, dispersal and potential impacts of the green crab *Carcinus maenas* in San Francisco Bay, California. *Marine Biology*, **122**, 225-237.
- Connell, J.H., 1970. A predator-prey system in the marine intertidal region. *Ecological*

Coombes, M.R.A. & Seed, R., 1992. Predation of the black mussel *Septifer virgatus* by the red-eyed crab *Eriphia laevimana smithii* (Xanthidae). *Asian Marine Biology*, 9, 245-258.

Crothers, J.H., 1967. The biology of the shore crab *Carcinus maenas* (L.). 1. The background - anatomy, growth and life history. *Field Studies*, 2, 407-434.

Crothers, J. H., 1968. The biology of the shore crab *Carcinus maenas* (L.). 2. The life of the adult crab. *Field Studies*, 2, 579-614.

Croy, M.I. & Hughes, R.N., 1991. Effects of food supply, hunger, danger and competition on choice of foraging location by the fifteen-spined stickleback, *Spinachia spinachia* L.. *Animal Behaviour*, 42, 131-139.

Cunningham, P.N., 1983. Predatory activities of shore crab populations. Ph.D. Thesis, University of North Wales, Bangor.

Cunningham, P.N. & Hughes, R.N., 1984. Learning and predatory skills by shorecrabs *Carcinus maenas* feeding on mussels and dogwhelks. *Marine Ecology Progress Series*, 16, 21-26.

Currey, J.D & Kohn, A.J., 1976. Fracture in the crossed-lamellar structure of *Conus* shells. *Journal of Material Science*, 11, 1616-1623.

Dare, P.J. & Edwards, D.B., 1981. Underwater television observations on the intertidal movements of shore crabs, *Carcinus maenas*, across a mudflat. *Journal of the Marine Biological Association (United Kingdom)*, 61, 107-116.

Davidson, R.J., 1986. Mussel selection by the paddle crab *Ovalipes catharus* (White): Evidence of flexible foraging behaviour. *Journal of Experimental Marine Biology and Ecology*, 102, 281-299.

Dolmer, P. & Svane, I., 1994. Attachment and orientation of *Mytilus edulis* L. in flowing water. *Ophelia*, 40, 63-74.

Dumas, J.V. & Witman, J. D., 1993. Predation by Herring Gulls (*Larus argentatus* Coues) on two rocky intertidal crab species (*Carcinus maenas* (L) and *Cancer irroratus* Say). *Journal Experimental Marine Biology and Ecology*, 169, 89-101.

Ebling, F.J., Kitching, J.A., Muntz, L. & Taylor, C.M., 1964. Experimental observations of the destruction of *Mytilus edulis* and *Nucella lapillus* by crabs. *Journal of Animal Ecology*, 33, 73-82.

Elnor, R.W., 1977. The predatory behaviour of *Carcinus maenas* (L.). Ph.D. Thesis. University College of North Wales, Bangor.

Elner, R.W., 1978. The mechanics of predation by the shore crab, *Carcinus maenas* (L.), on the edible mussel, *Mytilus edulis* L. *Oecologia (Berlin)*, **36**, 333-344.

Elner, R.W., 1980. The influence of temperature, sex and chela size in the foraging behaviour of the shore crabs, *Carcinus maenas* (L.). *Marine Behavioural Physiology*, **7**, 15-24.

Elner, R.W., 1981. Diet of green crab *Carcinus maenas* (L.) from Port Hebert, Southwestern Nova Scotia. *Journal of Shellfish Research*, **1**, 89-94.

Elner, R.W. & Hughes, R.N., 1978. Energy maximisation in the diet of the shore crab, *Carcinus maenas*. *Journal of Animal Ecology*, **47**, 103-116.

Elner, R.W. & Raffaelli, D.G., 1980. Interactions between two marine snails, *Littorina rudis* Maton and *Littorina nigrolineata* Gray, a predator, *Carcinus maenas* (L.) and a parasite, *Microphallus similis* Jagerskiold. *Journal of Experimental Marine Biology and Ecology*, **43**, 151-160.

Fox, D.L. & Coe, W.R., 1943. Biology of the Californian sea mussel *Mytilus californianus*. II. Nutrition, metabolism, growth and calcium deposition. *Journal of Experimental Zoology*, **93**, 205-249.

Fry, J.C., 1993. Biological data analysis. The Practical Approach Series. Oxford University Press.

Glaus, K.J., 1968. Factors influencing the production of byssus threads in *Mytilus edulis*. *Biological Bulletin of the Marine Biology Laboratory, Woods, Hole*, **135**, 420.

Gray, A.P., 1997. The ecology of the mussel *Mytilus edulis chilensis* from three sites in the Falkland Islands. Ph.D. Thesis. University of North Wales, Bangor.

Griffiths, R.J., 1981. Population dynamics and growth of the bivalve, *Choromytilus meridionalis* (Kr.) at different tidal levels. *Estuarine, Coastal and Shelf Science*, **12**, 101-118.

Griffiths, C.L. & Seiderer, J.L., 1980. Rock-lobsters and mussels - Limitations and preferences in a predator-prey interaction. *Journal of Experimental Marine Biology and Ecology*, **94**, 95-109.

Griffiths, C.L. & Hockey, P.A.R., 1987. A model describing the interactive roles of predation, competition and tidal elevation in structuring mussel populations. *South African Journal of Marine Science*, **5**, 547-556.

Grosholz, E.D. & Ruiz, G.M., 1995. Spread and potential impact of the recently introduced European green crab, *Carcinus maenas*, in central California. *Marine Biology*, **122**, 239-247.

- Harger, J.R.E., 1970. The effect of wave impact on some aspects of the biology of sea mussels. *Veliger*, **12**, 401-414.
- Huang, Z.G. & Cai, R.X., 1984. Marine Biofouling and its Prevention. China Ocean Press, Beijing. (In Chinese).
- Huang, Z.G., Lee, S.Y. & Mak, P.M.S., 1985. The distribution and population structure of *Perna viridis* (Bivalvia: Mytilacea) in Hong Kong waters. In *Proceedings of the Second International Workshop on the Malacofauna of Hong Kong and Southern China, Hong Kong, 1983*, Ed. Morton, B. & Dudgeon, D. Hong Kong University Press.
- Hughes, R.N., 1980. Optimal foraging theory in the marine context. *Oceanography and Marine Biology Annual Review*, **18**, 423-481.
- Hughes, R.N. & Elner, R.W., 1979. Tactics of a predator, *Carcinus maenas*, and morphological responses to the prey *Nucella lapillus*. *Journal of Animal Ecology*, **48**, 65-78.
- Hughes, R.N. & Burrows, M.T., 1991. Diet selection by dogwhelks in the field: an example of constrained optimization. *Animal Behaviour*, **42**, 47-55.
- Hughes, R.N. & Seed, R., 1995. Behavioural mechanisms of prey selection in crabs. *Journal of Experimental Marine Biology and Ecology*, **193**, 225-238.
- Hughes, R.N. & Seed, R., 1981. Size selection of mussels by the Blue Crab *Callinectes sapidus* energy maximizer or time minimizer. *Marine Ecology Progress Series*, **6**, 83-89.
- Hughes, R.N. & Seed, R., 1997. Behavioural mechanisms of prey selection in crabs. *Journal of Experimental Marine Biology and Ecology*, **193**, 225-238.
- Hughes, R.N. & Elner, R.W., 1998. Foraging behaviour of a tropical crab, *Calappa ocellata* Holthuis, feeding upon the mussel, *Brachidontes domingensis* (Lamarck). *Journal of Experimental Marine Biology and Ecology*, **133**, 93-101.
- Hulscher, J.B., 1976. Localisation of Cockles (*Cardium edule* L.) by the oystercatcher (*Haemotopus ostralegus* L.) in darkness and daylight. *Ardea*, **64**, 292-310.
- Hunter, E. & Naylor, E., 1993. Intertidal migration by the shore crab *Carcinus maenas*. *Marine Ecology Progress Series*, **101**, 131-138.
- Ingle, R.W., 1980. British Crabs. British Museum (Natural History). Oxford University Press.
- James, P.L. & Heck Jr., K.L., 1994. The effects of habitat complexity and light intensity on ambush predation within a simulated seagrass habitat. *Journal of*

Experimental Marine Biology and Ecology, 176, 187-200.

Jensen, K.T. & Jensen, J.N., 1985. The importance of some epibenthic predators on the density of juvenile benthic macrofauna in the Danish Wadden Sea. *Journal of Experimental Marine Biology and Ecology*, 89, 157, 174.

Juanes, F., 1992. Why do decapod crustaceans prefer small-sized molluscan prey? *Marine Ecology Progress Series*, 87, 239-249.

Juanes, F. & Hartwick, E.B., 1990. Prey selection in Dungeness crabs: The effect of claw damage. *Ecology*, 71, 744-758.

Juanes, F. & Conover, D.O., 1994. Piscivory and prey size selection in young-of-the-year blue fish: Predator preference or size-dependent capture success? *Marine Ecology Progress series*, 114, 59-69.

Jubb, C.A., Hughes, R.N. & ap Rheinallt, T., 1983. Behavioural mechanisms of size-selection by crabs, *Carcinus maenas* (L.) feeding on mussels, *Mytilus edulis* L.. *Journal of Experimental Marine Biology and Ecology*, 66, 81-87.

Kaiser, M.J., Hughes, R.N. & Reid, D.G., 1990. Chelal morphometry, prey size selection and aggressive competition in green and red forms of *Carcinus maenas* (L.). *Journal of Experimental Marine Biology and Ecology*, 140, 121-134.

Kaiser, M.J., Westhead, A.P., Hughes, R.N. & Gibson, R.N., 1992. Are digestive characteristics important contributors to the profitability of prey? *Oecologia*, 90, 61-69.

Kopp, J.C., 1979. Growth and the intertidal gradient in the sea mussel, *Mytilus californianus* Conrad, 1837. *The Veliger*, 22, 51-56.

Lafferty, K.D. & Kuris, A.M., 1996. Biological control of marine pests. *Ecology*, 77, 1989-2000.

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. *Marine Ecology Progress Series*, 27, 143-154.

Lawton, P. & Zimmer-Faust, R.K., 1992. Context-sensitivity in crab foraging studies. *American Zoologist*, 32, 396-404.

Leber, K.M., 1985. The influence of predatory decapods, refuge and microhabitat selection on seagrass communities. *Ecology*, 66, 1951-1964.

Lee, S.Y. & Seed, R., 1992. Ecological implications of cheliped size in crabs: Some data from *Carcinus maenas* and *Liocarcinus holsatus*. *Marine Ecology Progress Series*, 84, 151-160.

- Lee, S.Y., 1985. The population dynamics of the green mussel, *Perna viridis* (L.) in Victoria Harbour, Hong Kong - dominance in a polluted environment. *Asian Marine Biology*, 2, 107-118.
- Lee, S.Y., 1995. Cheliped size and structure: The evolution of a multi-functional decapod organ. *Journal of Experimental Marine Biology and Ecology*, 193, 161-176.
- Lee, S.Y. & Morton, B., 1985. The Hong Kong Mytilidae. In *Proceedings of the Second International Workshop of the Malacofauna of Hong Kong and Southern China, Hong Kong, 1983*. Ed. Morton, B. & Dudgeon, D. Hong Kong University Press.
- Lee, S.Y. & Kneib, R.T., 1994. Effects of biogenic structure on prey consumption by the xanthid crabs *Eurytium limosum* and *Panopeus herbstii* in a salt marsh. *Marine Ecology Progress Series*, 104, 39-47.
- Leigh, E.C., Paine, R.T., Quinn, J.F. & Suchanek, T.H., 1987. Wave energy and intertidal productivity. *Proceedings of the National Academy of Sciences of the United States of America*, 84, 1314-1318.
- Lin, J., 1991. Predator-prey interactions between blue crabs and ribbed mussels living in clumps. *Estuarine and Coastal Shelf Science*, 32, 61-69.
- Lintas, C. & Seed, R., 1994. Spatial variation in the fauna associated with *Mytilus edulis* on a wave exposed rocky shore. *Journal of Molluscan Studies*, 60, 165-174.
- McQuaid, C.D., 1994. Feeding behaviour and selection of bivalve prey by *Octopus vulgaris* Cuvier. *Journal of Experimental Marine Biology and Ecology*, 177, 187-202.
- Meadows, P.S. & Shand, P., 1989. Experimental analysis of byssus thread production by *Mytilus edulis* and *Modiolus modiolus* in sediments. *Marine Biology*, 101, 219-226.
- Meire, P.M., 1992. The impact of bird predation on marine and estuarine bivalve populations: A selective review of patterns and underlying causes. In *Bivalve Filter Feeders In Estuarine and Coastal Ecosystem Processes*. Ed. Dame, R.F. Ecological Sciences, 33.
- Menge, B.A., 1978. Predator activity in a rocky intertidal community. Relationship between predator foraging activity and environmental harshness. *Oecologia (Berlin)*, 34, 1-16.
- Menge, B.A., 1983. Components of predation intensity in the low zone of the New England rocky intertidal region. *Oecologia (Berlin)*, 58, 141-155.
- Micheli, F., Behavioural plasticity in prey-size selectivity of the blue crab *Callinectes sapidus* feeding on bivalve prey. *Journal of Animal Ecology*, 64, 63-75.

- Morton, B., 1992. The evolution and success of heteromyarian form in the Mytiloida. In *The Mussel Mytilus: Ecology, Physiology, Genetics and Culture*. Ed. Gosling, E.M., Elsevier Press.
- Ng, P.K.L. & Tan, L.W.H., 1985. "Right-handedness" in heterochelous calappid and xanthid crabs - suggestions for a functional advantage. *Crustaceana*, **49**, 98-100.
- Paine, R.T., 1966. Food web complexity and species diversity. *American Naturalist*, **100**, 65-75.
- Pollock, D.E., 1979. Predator-prey relationships between the rock lobster, *Jasus lalandii* and the mussel, *Aulocomya ater* at Robben Island on the Cape West Coast. *Marine Biology*, **52**, 347-356.
- Price, H.A., 1982. An analysis of factors determining seasonal variation in the byssal attachment strength of *Mytilus edulis*. *Journal of the Marine Biological Association (United Kingdom)*, **62**, 147-155.
- Raffaelli, D., Conacher, A., McLachlan, H. & Emes, C., 1989. The role of epibenthic crustacean predators in an estuarine food web. *Estuarine, Coastal and Shelf Science*, **28**, 149-160.
- Reid, D.G., Abello, P., McGaw, I.J. & Naylor, E., 1989. Phenotypic variation in sympatric crab populations. In *Phenotypic responses and individuality in aquatic ectotherms*. Ed. J.C. Aldrich, Japaga, Dublin.
- Reid, D.G. & Aldrich, J.C., 1989. Variations in response to environmental hypoxia of different colour forms of the shore crab, *Carcinus maenas*. *Comparative Biochemistry and Physiology*, **92**, 535-539.
- Reid, D.G., Abello, P., Kaiser, M.J. & Warman, C.G., 1997. Carapace colour, intermoult duration and the behavioural and physiological ecology of the shore crab, *Carcinus maenas*. *Estuarine, Coastal and Shelf Science*, **44**, 203-211.
- Richardson, C.A., Seed, R., Brotohadikusumo, N.A. & Owen, R., 1995. Age, growth and allometric relationships in *Septifer virgatus* (Bivalvia: Mytilidae). *Asian Marine Biology*, **12**, 39-52.
- Robles, C., Sweetnam, D. & Eminike, J., 1990. Lobster predation on mussels: Shore level differences in prey vulnerability and predator preferences. *Ecology*, **71**, 1564-1577.
- Ropes, J.W., 1968. The feeding habits of the green crab, *Carcinus maenas* (L.). *Fishery Bulletin U.S.A.*, **67**, 183-203.
- Sanchez-Salazar, M.E., Griffiths, C.L., Seed, R., 1987a. The interactive roles of predation and tidal elevation in structuring populations of the edible cockle,

Cerastoderma edule. *Estuarine, Coastal and Shelf Science*, **25**, 245-260.

Sanchez-Salazar, M.E., Griffiths, C.L. and Seed, R., 1987b. The effects of size and temperature on the predation of cockles *Cerastoderma edule* (L) by the shore crab *Carcinus maenas*. *Journal of Experimental Marine Biology and Ecology*, **111**, 181-193.

Seed, R., 1968. Factors influencing shell shape in the mussel *Mytilus edulis*. *Journal of the Marine Biological Association (United Kingdom)*, **48**, 561-584.

Seed, R., 1969. The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed rocky shores. II. Growth and Mortality. *Oecologia (Berlin)*, **3**, 317-350.

Seed, R., 1973. Absolute and allometric growth in the mussel *Mytilus edulis* L. (Mollusca: Bivalvia). *Proceedings of the Malacological Society London*, **40**, 343-357.

Seed, R., 1980a. Variations in the shell-flesh relationships of *Mytilus*: The value of sea mussels as items of prey. *Veliger*, **22**, 219-221

Seed, R., 1980b. Shell growth and form in the Bivalvia. In *Skeletal Growth and Aquatic organisms*. Eds Rhoads, D.C. & Lutz, R.A. Pgs 23-67. Plenum Press, New York.

Seed, R., 1980c. Predator-prey relationships between the mud crab *Panopeus herbstii*, the Blue Crab, *Callinectes sapidus* and the Atlantic ribbed mussel *Geukensia* (= *Modiolus*) *demissa*. *Estuarine and Coastal Shelf Science*, **11**, 445-458.

Seed, R., 1990a. Predator-prey relationships between the swimming crab *Thalamita danae* Stimpson (Decapoda: Portunidae) and the mussels *Perna viridis* (L.) and *Brachiodontes variabilis* (Krauss). In *Proceedings of the Second International Marine Biology Workshop: The Marine Flora and Fauna of Hong Kong and Southern China, Hong Kong, 1986*. Ed. Morton, B. Hong Kong University Press.

Seed, R., 1990b. Morphology, occlusive geometry and mechanical advantage in the chelae of *Thalamita danae* Stimpson and *Thalamita crenata* (Latreille) (Decapoda: Portunidae) from Hong Kong. In *Proceedings of the Second International Marine Biology Workshop: The Marine Flora and Fauna of Hong Kong and Southern China, Hong Kong, 1986* Ed. Morton, B. Hong Kong University Press.

Seed, R., 1990c. Behavioural and mechanical aspects of predation by the swimming crab *Thalamita danae* on the green-lipped mussel *Perna viridis*. *Trophic Relationships in the Marine Environment. Proceedings of the 24th European Marine Biology Symposium*. Ed. Barnes, M. & Gibson, R.N. Aberdeen University Press.

Seed, R., 1993. Crabs as predators of marine bivalve molluscs. *The Biology of the South China Sea. Proceedings of the First International Conference on the Marine Biology of Hong Kong and the South China Sea*. Hong Kong University Press.

Seed, R. & Brown, R.A., 1978. Growth as a strategy for survival in two marine bivalves, *Cerastoderma edule* and *Modiolus modiolus*. *Journal of Animal Ecology*, **47**, 283-292.

Seed, R. & Suchanek, T.H., 1992. Population and community ecology of *Mytilus*. In *Developments in Aquaculture and Fisheries Science*, 25, The mussel *Mytilus*: Ecology, Physiology, Genetics and Culture. Ed. Gosling, E.

Seed, R. & Hughes, R.N., 1995. Criteria for prey size-selection in molluscivorous crabs with contrasting claw morphologies. *Journal of Experimental Marine Biology and Ecology*, **193**, 177-195.

Seed, R. & Lee, S.Y., 1995. Mechanical and behavioural aspects of predation in two contrasting species of predatory crabs, *Eriphia laevimana smithii* (Xanthidae) and *Thalamita danae* (Portunidae). In *Proceedings of the second international conference on the marine biology of the South China Sea, Guangzhou, China, April 3-7, 1993*. Ed. Morton, B., Gonzhou, X., Renhin, Z., Sinpei, P. & Guoxing, C.

Seed, R. & Hughes, R.N., 1997. Chelal characteristics and foraging behaviour of the blue crab, *Callinectes sapidus* Rathbun. *Estuarine, Coastal and Shelf Science*, **44**, 221-229.

Smith, L.D. & Palmer, A.R., 1994. Effects of manipulated diet on size and performance of Brachyuran crab claws. *Science*, **246**, 629-744.

Sponougle, S. & Lawton, P., 1990. Portunid crab predation on juvenile hard clams: effects of substrate type and prey density. *Marine Ecology Progress Series*, **67**, 43-53.

Sutherland, W.J., 1982. Do oystercatchers select the most profitable cockles? *Animal Behaviour*, **30**, 857-861.

Van Winkle Jr. W., 1970. Effect of environmental factors on byssal thread formation. *Marine Biology*, **7**, 143-148.

Vermeij, G.J., 1977. Patterns in crab claw size: The geography of crushing. *Systematic Zoology*, **26**, 138-151.

Walne, P.R. & Dean, G.J., 1972. Experiments on predation by the shore crab, *Carcinus maenas* L., on *Mytilus* and *Mercenaria*. *International Council for the Exploration of the Sea*, **34**, 190-199.

Wanink, J. & Zwarts, L., 1985. Does optimally foraging oystercatcher obey the functional response? *Oecologia (Berlin)*, **67**, 98-106.

Warman, C.G., Reid, D.G. & Naylor, E., 1993. Variation in the tidal migratory behaviour and rhythmic light-responsiveness in the shore crab, *Carcinus maenas*.

Journal of the Marine Biological Association (United Kingdom), **73**, 355, 364.

Warner, G.F., 1977. *The Biology of Crabs*. Elek Science, London.

Warner, G.F. & Jones, A.R., 1976. Leverage and muscle type in crab chelae (Crustacea: Brachyura). *Journal of Zoology (London)*, **180**, 57-68.

Warner, G.F., Chapman, D., Hawkey, N. & Waring, D.G., 1982). Structure and function of the chelae and chela closer muscles of the shore crab *Carcinus maenas* (Crustacea: Brachyura). *Journal of Zoology (London)*, **196**, 431-438.

West, D.L. & Williams, A.H., 1986. Predation by *Callinectes sapidus* (Rathbun) within *Spartina alterniflora* (Loisel) marshes. *Journal of Experimental Marine Biology and Ecology*, **100**, 75-95.

Williams, M.J., 1981. Methods for analysis of natural diet in Portunid crabs (Crustacea: Decapoda: Portunidae). *Journal of Experimental Marine Biology and Ecology*, **52**, 103-113.

Witman, J.D. & Suchanek, T.H., 1984. Mussels in flow: Drag and dislodgement by epizoans. *Marine Ecology Progress Series*, **16**, 259-268.

Young, G.A., 1985. Byssus-thread formation by the mussel *Mytilus edulis*: effects of environmental factors. *Marine Ecology Progress Series*, **24**, 261-271.

Young, G.A., 1997 . *The Menai Strait: A Review and Bibliography of Literature From The Wolfson Library*.

Zimmer-Faust, R.K., 1987. Substrate selection and use by a deposit-feeding crab. *Ecology*, **68**, 955-971.

Zipser, E. & Vermeij, G.J., 1978. Crushing behaviour of tropical and temperate crabs. *Journal of Experimental Marine Biology and Ecology*, **31**, 155-172.