ISSN 0308 - 5589

MINISTRY OF AGRICULTURE, FISHERIES AND FOOD
DIRECTORATE OF FISHERIES RESEARCH

FISHERIES RESEARCH TECHNICAL REPORT

No. 73

Predation on juvenile Pacific oysters (*Crassostrea gigas* Thunberg) and mussels (*Mytilus edulis* L.) by shore crabs (*Carcinus maenas* (L.))

P.J.Dare, G.Davies and D.B.Edwards

LOWESTOFT,1983

MINISTRY OF AGRICULTURE, FISHERIES AND FOOD
DIRECTORATE OF FISHERIES RESEARCH

FISHERIES RESEARCH TECHNICAL REPORT
NUMBER 73

Predation on juvenile Pacific oysters (*Crassostrea gigas* Thunberg) and mussels (*Mytilus edulis* L.) by shore crabs (*Carcinus maenas* (L))

P J DARE, G DAVIES and D B EDWARDS

LOWESTOFT 1983

The authors:

P J Dare, B Sc Ph D, is a Principal Scientific Officer, who, at the time of the investigations was in the Fish and Shellfish Cultivation Group and was stationed at The Fisheries Experiment Station, Conwy. He is now in Fish Stock Management, Section 3, of the Directorate of Fisheries Research and is based at the Fisheries Laboratory, Lowestoft.

G Davies, B Sc, at the time of the investigations was a Higher Scientific Officer in The Fish and Shellfish Cultivation Group of the Directorate of Fisheries Research and was based at The Fisheries Experiment Station, Conwy. He has since retired from the Ministry.

D B Edwards is a Scientific Officer in the Fish and Shellfish Cultivation Group of the Directorate of Fisheries Research and is based at the Fisheries Experiment Station, Conwy.

Fish. Res. Tech. Rep., MAFF Direct. Fish. Res., Lowestoft, (73), 15 pp.

CONTENTS

1. Introduction

The shore crab or green crab, *Carcinus maenas* (L), is a very widespread and often abundant predator and scavenger along the coastline and estuaries of Europe; it occurs also on the north-east coast of the USA. This crab takes a great variety of prey (Crothers, 1968) and is recognised to be an important predator of juvenile (spat and seed) molluscs in many natural and cultivated fisheries. Serious damage is caused to stocks of soft-shell clams, *Mya arenaria* L, in New England, USA (Ropes, 1968); to American hard-shell clams, *Mercenaria mercenaria* L, in Britain (Walne and Dean, 1972); to palourdes, *Venerupis* (= *Tapes*) spp., in Portugal (Vilela, 1950); flat oysters, *Ostrea edulis* L, in France (Marin *et al.*, 1973); and to mussels, *Mytilus edulis* L, in Britain (Dare and Edwards, 1976) and the Netherlands (Korringa, 1976). To minimise losses, cultivators sometimes protect bivalve stocks behind meshed fences or barriers which are designed to exclude most shore crabs of predatory size, i.e., those larger then 20 mm carapace width. Such fences have been described by Smith *et al.* (1955), Marin *et al.* (1973) and Davies *et al.* (1980).

The feeding behaviour of shore crabs has been investigated in both the field and the laboratory, and attempts have been made to assess the potential impact of crab predation on cultivated and natural populations of bivalve molluscs. For instance, predation on mussels has been studied either in cages on the shore (Ebling *et al.*, 1964) or in aquarium tanks (Perkins *et al.*, 1964; Perkins, 1967; Seed, 1969; Walne and Dean, 1972). Several workers have concentrated mainly on the relationship between crab size and the maximum size of mussel which can be opened. Elner (1978, 1980) and Elner and Hughes (1978) examined the actual mechanics of predation on mussels and have indicated a foraging strategy for *C. maenas* which involves an optimal prey size for each size of crab. It is now thought (e.g., Reise, 1977) that shore crabs may be important in controlling the distribution and abundance of various bivalves, as well as of other invertebrates such as polychaete worms. The food consumption of captive juvenile or O-group crabs (< 20 mm width) fed on mussel flesh was reported by Klein Breteler (1975) while that of adult crabs fed on a diet of squid mantle was measured at different temperatures by Wallace (1973).

Predation of oysters by this crab has received much less attention. Preliminary studies with Pacific oysters, *Crassostrea gigas* Thunberg (Parsons, 1974), and with flat oysters (Marin *et al.*, 1973), have indicated the vulnerability of both species to crab attack. Walne and Davies (1977) ascribed heavy losses of unprotected *C. gigas* spat mainly to crab predation and also showed the value of protecting spat within meshed containers.

This report presents the results of laboratory and field experiments made in North Wales between 1974 and 1977 with the following aims: (1) to measure the relative vulnerability of successive sizes of juvenile Pacific oysters and mussels to crab attack; (2) to assess the degree of protection (mesh size) required to safeguard oyster seed of any given size; (3) to determine when each bivalve species reaches 'crab-proof' size and no longer requires protection from crabs.

2. Materials and methods

2.1 Laboratory experiments

Laboratory feeding studies were carried out in an indoor aquarium system and (for mussels only) in a large outside tank at the Ministry's laboratory at Conwy, North Wales.

2.1.1 *Aquarium experiments*

Shore crabs were collected from the Menai Strait, 30 km from the laboratory, using baited traps set on the shore at Tal-y-foel, Anglesey. At this site, crabs were known to prey heavily on young mussels (Dare and Edwards, 1976) and upon seed oysters unless protected within, respectively, fenced enclosures and meshed containers (Davies *et al.*, 1980; Walne and Davies, 1977). Captured crabs were acclimated to captivity by storage in communal tanks where they were fed a diet of small mussels (unopened) for about two weeks prior to an experiment. Six sizes of crabs were studied: 25, 35, 45, 55, 65 and 75 (each ± 1) mm carapace width; width being measured between the lateral carapace 'teeth'. In an experiment, each size group contained 11-16 individuals but not all sizes were tested simultaneously. About 80% of crabs used were males, this being the predominant sex in the shore population at Tal-y-foel for much of the year (Dare and Edwards, in press). Crabs larger than 65 mm width were exclusively males.

During an experiment, crabs were housed individually in clear polystyrene tanks (28 x 18 cm) containing 15 cm depth of running sea water. A 64-tank, indoor aquarium was supplied by a recirculation system incorporating a biological filter. Temperatures in the system could not be controlled and they changed slowly from 12-13°C in winter and spring to 20-22°C in summer. Only apparently healthy crabs were selected; individuals parasitised by *Sacculina carcini* or with damaged limbs were rejected. The crabs were starved for two days prior to use so as to standardise hunger levels. Wherever possible, each experiment was conducted with a new batch of crabs. Crabs which died or moulted during an experiment were replaced by other acclimated crabs of appropriate sizes kept in reserve. Of all crabs used in aquarium trials, 8.9% moulted and a further 4.8% died either during or within a few days after an experiment. Moulting was most prevalent in the 35, 45 and 55 mm crabs (17.5% 11.0%, 13.5% respectively) but infrequent (0-6%) in the other three groups. Death accounted for 7-10% of crabs in the 55, 65, 75 mm groups compared with only 1-1.5% of 25, 35 and 45 mm crabs.

Pacific oyster seed were obtained from the laboratory's hatchery-produced stocks grown intertidally in meshed containers at Tal-y-foel. The following size (liveweight) classes were used: 0.5 g (0.5-0.9 g), 1 g (1.0-1.9 g), 2 g (2.0-2.9 g), 3 g, ... 12 g. The smaller classes were first-year (0-group) stock; larger classes had overwintered and were second-year (I-group) stock. Because feeding experiments were spread over three years, wide variations in prey quality, i.e., shell morphology and food value, were unavoidable in each prey size class.

Mussel seed were collected from stocks situated between low water marks of neap and spring tides in Morecambe Bay, and were relaid onto plots at Tal-y-foel (Dare and Edwards, 1976). Seed were taken from the same stocks as those being transplanted to the Menai Strait for cultivation by a local firm. Six sizes of mussel were used: 15, 20, 25 . . . . . 40 mm (each ± 1 mm) shell length. The 15-30 mm seed were first-year (0-group) stock, 35 mm were second-year (I-group), and 40 mm were third-year (II-group) stock. Mean live weights and dry flesh content were also measured for each size, using the methods of Dare and Edwards (1976). All mussels used were free from barnacles (*Balanus* spp.) and other encrustations.

Oyster experiments: In the first experiment, spanning four months (July-November), all crabs were offered a particular size of oyster for 4-10 days in succession and were then switched to a new prey size for a similar period, and so on. The daily number of oysters offered to each crab ranged from two to ten, most frequently two to five, depending upon the relative sizes of crab and oyster. The number of oysters eaten was recorded daily and eaten prey were replaced by others of similar size. Consumption data were discarded for crabs which moulted or died during, or within 14 days of the completion of, an experiment.

Four other experiments were replicated trials in which four size groups of crabs, each of 16 individuals, were offered four sizes of oyster for five-day periods in rotation. Each trial thus lasted 20 days. From two to five oysters were offered daily to each crab, depending on the relative sizes, and daily consumption was monitored as before. A new batch of 64 crabs was used for each trial, the sizes of crabs and oysters being altered as required.

Mussel experiments: A brief study was possible during three months, August-October, but was restricted by limited availability of seed mussels. Feeding and monitoring procedures were usually the same as described above for oysters, except that only three crabs of each size were used, and feeding periods were reduced to 2-4 days for each size of mussel. Each crab was offered 2-40 mussels daily according to relative sizes of crab and mussel. Surplus prey on offer was achieved for 90% of the time. Three experiments were conducted, each using a fresh batch of crabs, and data were obtained for 505 crab-days.

2.1.2 *Outdoor tank experiments*

Crab predation on intertidal and sublittoral mussels was compared simultaneously with a large-scale factorial experiment set up in a 14 m^2 concrete tank in the laboratory grounds. The experiment lasted 32 days (1 October-2 November) during which sea water temperatures fell from *c.* 14°C to *c.* 11°C. The tank was filled to a depth of 75 cm with sea water which was changed three times during the period. Two contrasting stocks of mussels were obtained from the Menai Strait: (i) intertidal – from 1.8 m above extreme low water spring tides, i.e., about the level of low water of poor spring tides; (ii) sublittoral – from 3.5 m below extreme low water spring tides. Both populations were divided into 5 mm size groups, 10-14 mm, 15-19 mm . . . . . 45-49 mm, and each size group comprised 100-300 mussels sub-divided into five replicate batches. The mussel groups were contained in ten wooden trays, each of which was divided into seven 30 cm x 30 cm compartments. The trays were placed alongside one another and occupied 5.5 m^2 (40%) of the tank's floor area. Finally, a population of 100 freshly-caught crabs (one trawl catch) was introduced into the tank. Crab widths ranged from 23 to 74 mm but were mainly 45-65 mm. The numbers of mussel survivors were counted after 13 and 32 days; surviving crabs were assessed after 32 days.

2.2 Field experiments

The relative vulnerabilities of different stocks and sizes of juvenile Pacific oysters and mussels to crab attack under natural conditions were determined on the shores of the Menai Strait at Tal-y-foel and at Bangor respectively.

2.2.1 *Pacific oysters*

The survival of unprotected seed of 0.5-10 g liveweight was assessed by a series of factorial experiments at different tidal levels during the course of one year. The effect of partially protecting seed with meshed covers was also examined; the results of that experiment have already been reported (Walne and Davies, 1977) but will be re-examined and integrated into this report. Also direct observation of crabs attacking *C. gigas* seed was made by means of closed-circuit underwater television (Dare and Edwards, 1981): on 13 October 1975, two batches of 50 oysters – of mean liveweights 0.5 g (0.4-0.6 g range) and 1 g (0.8-1.2 g) – were placed on two small trays (0.1 m^2 area) on the mud at a level between low water marks of neap and spring tides, and the numbers and feeding activities of crabs were observed, on a monitor screen 150 m away on shore, for 4 h during a high tide period.

2.2.2 *Mussels*

The relative vulnerability of sublittoral and intertidal seed was measured by a replicated experiment of 23 days duration (28 August-20 September) sited on a low level mudflat 1.8 m above extreme low water of spring tides (ELWS). Sea temperatures averaged 15.5°C.

Five mussel stocks were compared: (i) sublittoral, from ELWS – 3.5 m; (ii) shallow sublittoral, ELWS – 0.5 m; (iii) low intertidal, ELWS + 1.5 m; (iv) ELWS + 1.8 m; (v) ELWS + 2.0 m. All were Menai Strait mussels except stock (v) which was from Conwy; populations (i) and (iv) were the same as those used one month later for the outdoor tank experiment (section 2.1.2). The format of the Bangor field experiment followed that of the latter experiment except that only two replicates were used per population size group and there were fewer mussels in each replicate (usually 50-100, but only 25-45 for scarcer sizes).

Direct observation of crabs attacking mussels was made using underwater television at Tal-y-foel. On 29 July 1975, 300 loosely embyssed seed, of 20 mm mean length (range 15-30 mm) and weighing 350 g, were placed in an open tray of 0.1 m^2 area. The tray was set on the beach at about mean low water of neap tides. Crab activity and mussel mortality were recorded during eight hours over a high tide cycle.

3. Results

3.1 Predation on Pacific oysters

Crabs were seen to use the larger claw (master chela) to crush and break into oysters. Shells were fractured in various regions – near the umbo, in the centre, or at the posterior end – usually by transverse or oblique fractures (Figure 1). Often both shell valves were damaged and separated; sometimes the margins were chipped and small holes pierced through one or both valves.

3.1.1 *Relative vulnerability of oyster sizes*

The average daily (24 h) numbers of oyster seed eaten per crab in the laboratory aquarium experiments are shown for

Figure 1 Examples of crab damage to shells of juvenile Pacific oysters during laboratory feeding experiments.

different combinations of crab and oyster sizes in Figure 2 A–C. These results refer only to crabs which were successful feeders during an experiment. Consumption data have been combined for all temperatures. Although there were indications that crabs tended to eat more oysters at higher temperatures (18-21°C) than at lower (12-16°C) the differences were not consistently significant, probably due to the considerable differences in individual crab behaviour as well as to the variability in oyster shell structure, especially between batches. Only broad trends and relationships can therefore be discerned.

Over the range of oyster sizes tested, consumption rates for all sizes of crab fell sharply with increasing size of oyster. Average levels of consumption were low, especially when compared with crabs feeding on mussel seed of similar size (see later), and did not exceed 3 oysters per day per crab even when the largest crabs were offered 0.5-0.9 g seed. Possibly feeding rate was at times depressed by the limited numbers of oysters offered which could have reduced the chances of crabs finding more vulnerable prey individuals each day. As expected, larger crabs ate more oysters of a given size than did smaller crabs, although differences were not always significant, due again to the wide variability in both prey and predator. In particular, 65 mm and 75 mm crabs did not differ in performance.

From the trends in consumption curves it is possible to calculate, for each crab size, the approximate maximum size of intertidal oyster which can be opened (section 3.1.3).

3.1.2. *Crab feeding success*

The frequency of crabs feeding successfully on different sizes of oyster are plotted separately in Figure 2 A–C. The proportion of crabs which succeeded in opening oysters declined rapidly with increasing size of prey. Only when 55-75 mm crabs were presented with the smallest seed was 100% successful feeding achieved. For each crab size linear regressions of percentage feeding success on size of oyster (Table 1) were obtained, by arcsin transformation. These regressions were then used to calculate the oyster size at which feeding success dropped to zero, i.e., the smallest size which could not be opened (Table 2). For practical purposes this can be regarded as being also the maximum vulnerable size for each crab size group; the difference between the two sizes would be < 1 g. With respect to the largest crabs, this oyster size will correspond to the fully 'crab-proof' size for that particular stock of oysters. Such a concept is of significance for cultivators.

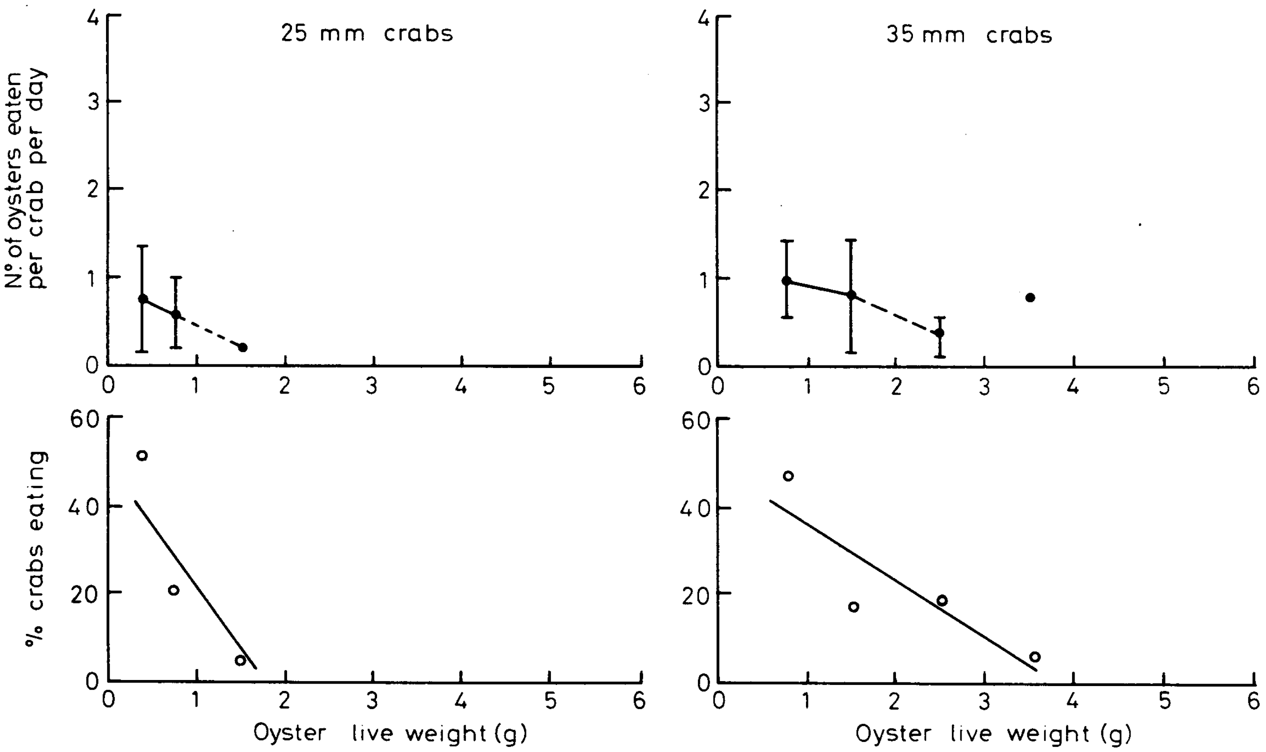

Figure 2 Daily consumption of Pacific oyster seed at 12-21°C by shore crabs in relation to size of oyster and size of crab, together with the proportions of crabs which fed successfully, during laboratory experiments. Vertical bars denote ± 95% confidence limits. Points in parentheses refer to small samples of crabs (< 5 animals for 25–55 mm groups, < 10 for 65–75 mm groups).

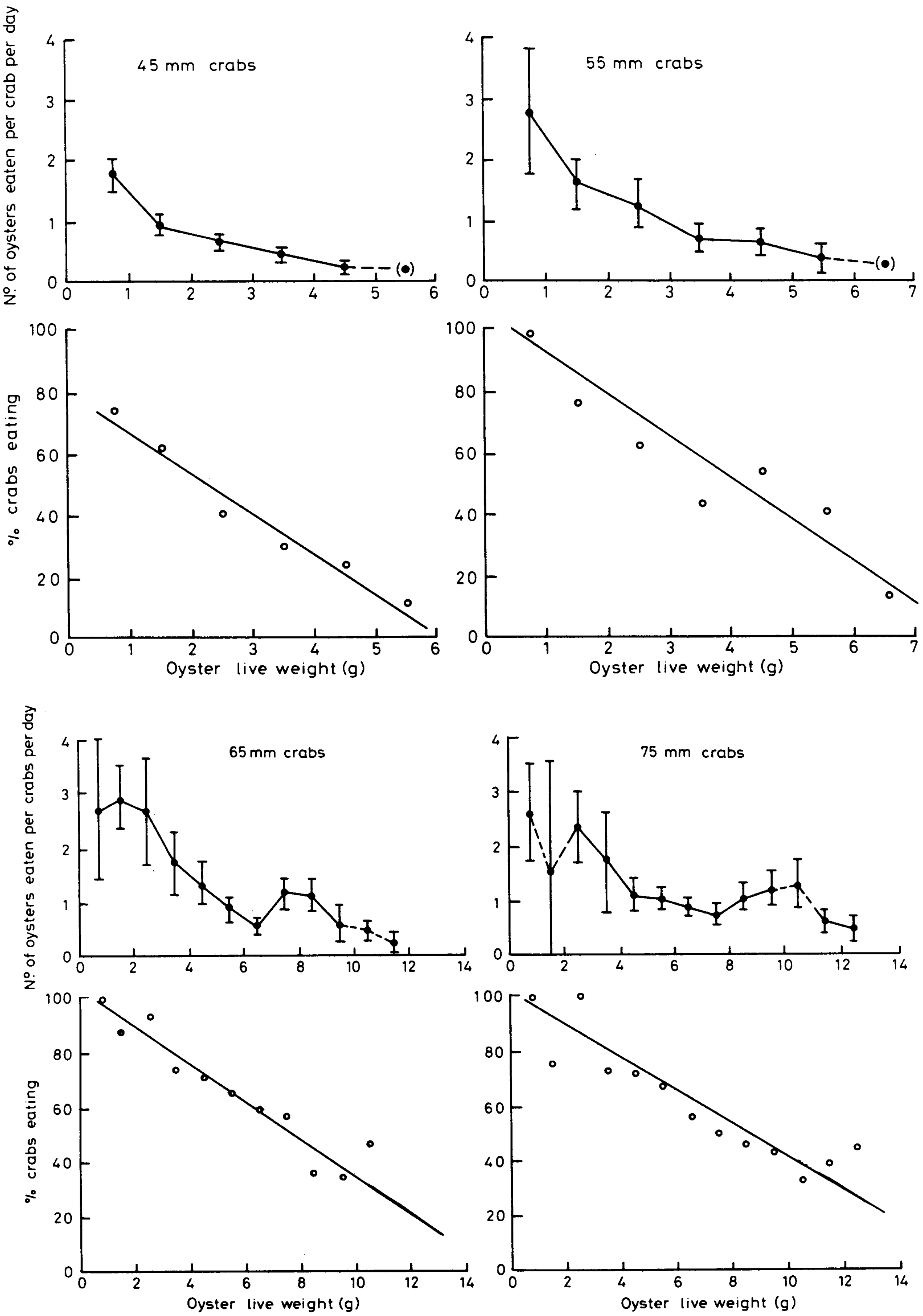

Figure 2 Continued

Table 1 **Regression data for percentage of crabs feeding successfully (y) on size (g) of Pacific oyster (x), See Figure 2; expressed as transformed (arcsin) values.**

75 mm crabs	$y = -3.92x + 79.73$	$r = -0.848$	$t = 5.30$
65 ” ”	$y = -4.67x + 82.99$	$r = -0.928$	$t = 6.72$
55 ” ”	$y = -9.08x + 82.66$	$r = -0.903$	$t = 4.71$
45 ” ”	$y = -7.91x + 63.23$	$r = -0.986$	$t = 11.98$
35 ” ”	$y = -9.30x + 45.34$	$r = -0.900$	$t = 2.93$
25 ” ”	$y = -19.94x + 46.09$	$r = -0.953$	$t = 4.43$

All 't' values for difference of slope from zero are significant at $P < 0.05$ except that for 35 mm crabs.

Table 2 **Estimation of the maximum size of *C. gigas* vulnerable to crabs of different sizes**

Crab size (carapace width mm)	Max. vulnerable oyster size (g) estimated from:		Maximum size (g) observed eaten
	A Daily feeding rate (Figure 2)	B % crabs feeding (Table 1)	
75	16.1	20.3	12.5$^+$
65	12.3	17.8	11.5$^+$
55	8.7	9.1	6.5
45	5.8	8.0	5.5
35	3.6	4.9	3.5
25	1.8	2.3	1.5

These data are fitted by the following regressions (Figure 3):

A $\ln y = 1.9937 \ln x + \ln 0.0030$ ($r = 1.000$; 4 df)
B $\ln y = 1.9708 \ln x + \ln 0.0042$ ($r = 0.989$; 4 df)

where x = crab size (mm), y = oyster size (g liveweight).

$^+$ These were the largest oyster sizes available

3.1.3 *Maximum size of oyster eaten*

Table 2 shows the differences between the estimates from both sets of data. The data conform to power curves and are therefore plotted as log : log regressions in Figure 3; equations are given in a footnote to Table 2.

The smallest adult crabs (25 mm) could open intertidal oysters up to about 2 g in weight, whereas the largest crabs (75 mm) could successfully tackle even 16-20 g oysters (55-60 mm shell length) on occasion. Such large crabs, however, are comparatively rare (Figure 4): 85% of the Tal-y-foel crabs caught in funnel traps on the shore in summer were in the range 25-55 mm carapace width. During June-August, crabs are most numerous and those 25 mm and larger actively forage up and down the shore during high tide (Naylor, 1962; Dare and Edwards, in press). Most crabs smaller than 20 mm tend, on the other hand, to be sedentary and do not undertake twice-daily intertidal migrations. The crab population structure at Tal-y-foel is probably typical of crabs in other, similar mollusc cultivation areas in Britain. Figure 4 suggests that predation will come largely from crabs smaller than 55 mm, and will thus (Figure 3) be concentrated on unprotected seed below 9 g liveweight (*c.* 40-45 mm shell length). For cultivation purposes, therefore, the effective 'crab-proof' size for intertidal oysters should be around 10 g (45 mm). Sublittoral oysters, however, may remain quite vulnerable at 10 g (Parsons, 1974) due to their thinner shells resulting from faster growth.

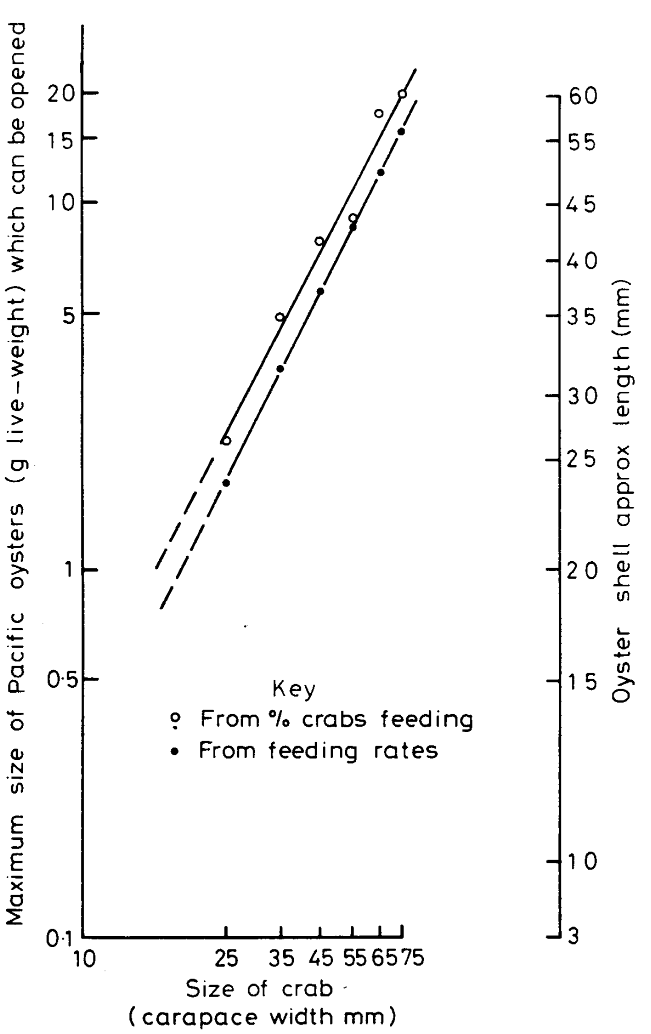

Figure 3 Relationship between size of crab and the largest size of intertidally grown Pacific oyster which could be opened in 24h during laboratory experiments. • = from daily consumption graphs (Figure 2); o = from feeding success regressions (Table 2).

There is reason to believe that laboratory results can overestimate the predation potential of crabs, and that smaller oyster sizes in nature could be less vulnerable than in the aquarium. In the aquarium crabs could feed without interference from others for 24 h, with no constraints imposed by tidal cycles and predators, and with no choice of alternative (perhaps easier) prey species. Hence the maximum size of oyster opened at leisure in undisturbed conditions could exaggerate the performance of many crabs on the shore. If one assumes that an individual crab optimises its foraging so as to enable it to eat at least one prey animal during a tide cycle, i.e., two prey per day, then from Figure 2 the following estimates of the largest sizes of oyster which could be eaten at a rate of two oysters per day can be obtained:

crab size (mm)	35	45	55	65	75
oyster size (g)	< 0.25	< 0.5	~ 1.25	~ 3	~ 3

On these assumptions, predation in nature could be confined mainly to oysters below 3-4 g liveweight, and be less than laboratory studies indicate for 5-9 g oysters.

3.1.4 *Field observations*

The two shore experiments tended to confirm that predation intensity on Pacific oysters available under tidal conditions may indeed be less than that suggested by aquarium experiments.

In the main experiment (Walne and Davies, 1977) the beneficial effects of protecting seed within mesh covers were clearly demonstrated. Table 3, recalculated from data in their Tables 4 and 7, shows that the first month's average mortality of 50 unprotected small (< 3 g) seed was very high whereas that of larger (> 5 g) unprotected seed was only 2-4%. Numerous broken shells indicated that crab predation was a major cause of loss in these experiments. The results of Walne and Davies tend, therefore, to support the view that laboratory data on maximum vulnerable size may overestimate predation unless expressed in more realistic terms, such as the maximum size which can be eaten at a rate of two oysters per day.

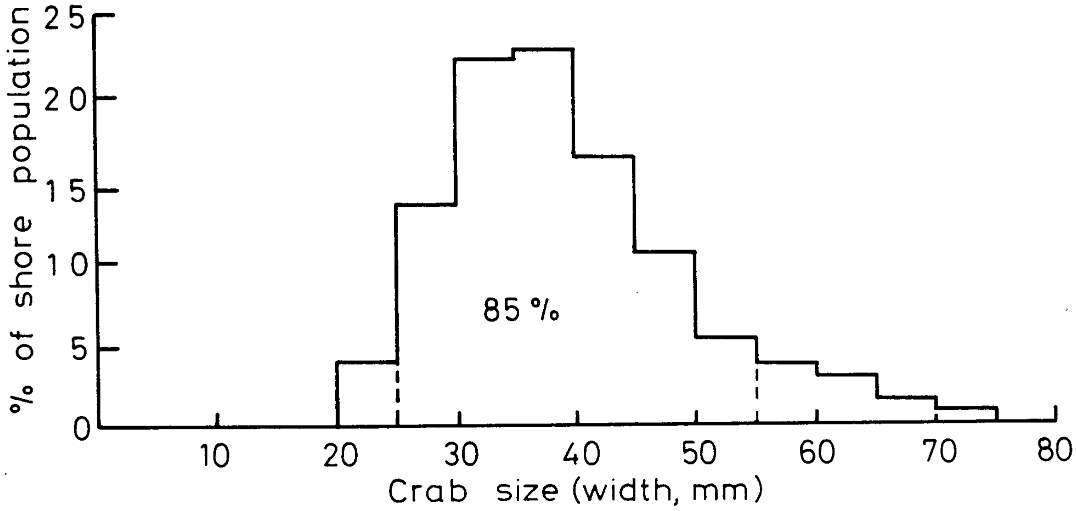

Figure 4 Average size structure in June-August of the mobile intertidal shore crab population at Tal-y-foel (from funnel trap catches).

Table 3 The mean survival of juvenile Pacific oysters, with and without protective mesh covers, on the shore at Tal-y-foel (MLWST, 4.5% exposure) from April 1974 to March 1975 (Recalculated from Walne and Davies (1977) Tables 4 and 7)

Initial live weight (g)	% survival after 30 days Mesh 12.5 mm	Mesh 36 mm	No Mesh
0.2 – 0.9	93.9	46.5	36.4
1.0 – 2.9	98.2	74.3	52.2
3.0 – 4.9	98.8	84.5	83.0
5.0 – 6.9	n.d.	n.d.	95.9
8.0 – 10.9	n.d.	n.d.	98.2

n.d. = No observations made.

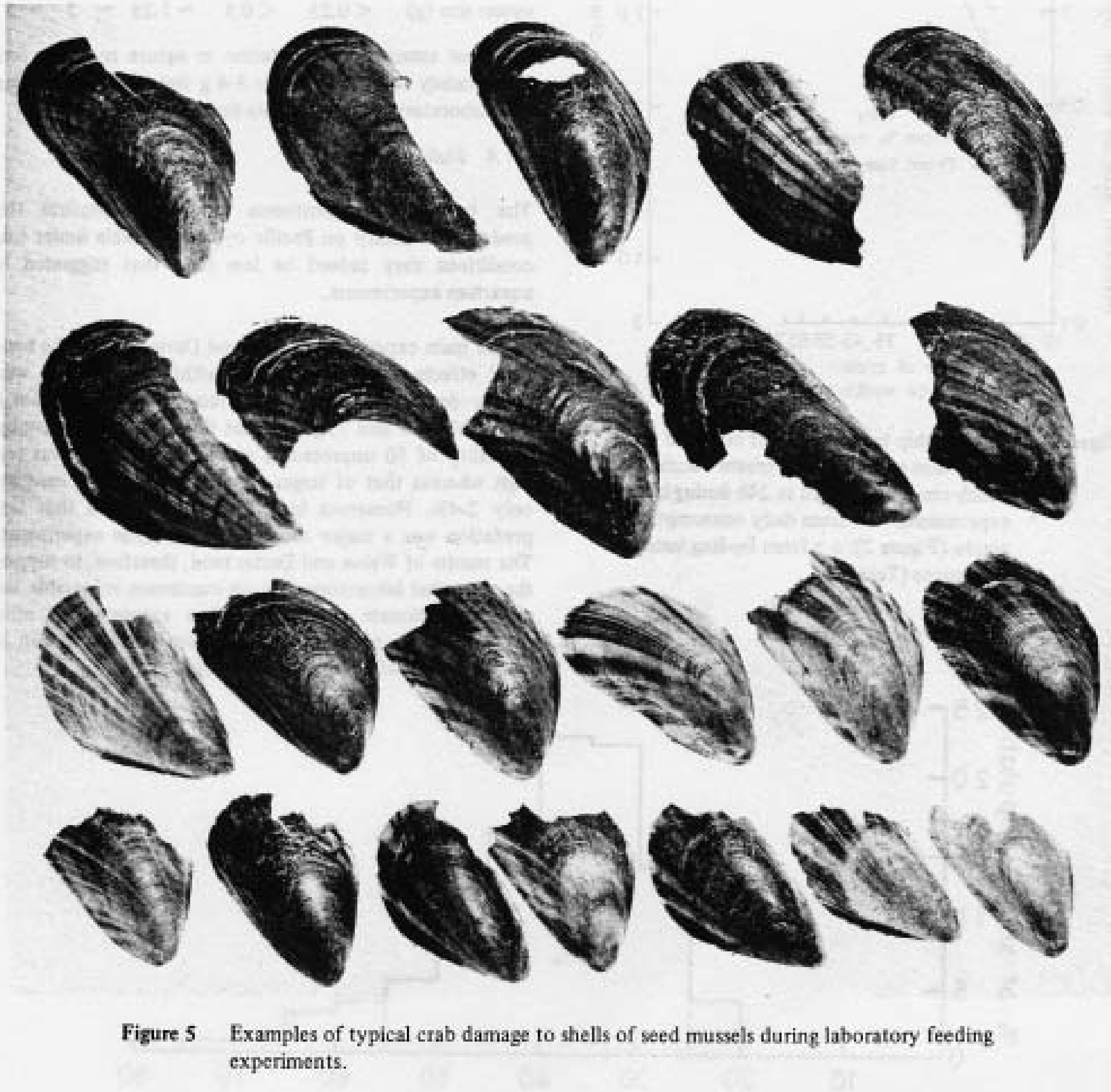

Figure 5 Examples of typical crab damage to shells of seed mussels during laboratory feeding experiments.

Television surveillance of 0.5 g and 1 g seed oysters exposed to crabs showed that during 4 h of immersion the oysters were visited by 40-50 crabs, mainly 30-45 mm in width. Up to five crabs occurred together on the tray but most showed little obvious interest in the seed, and only four attempted to take an oyster: three of them each ate a 0.5 g seed, while the other picked up but then rejected a 1 g oyster. Total oyster mortality over 4 h was 6% for 0.5 g and zero for 1 g seed. This loss rate was lower than expected from the maximum size relationship (Figure 3). Possibly crabs were more interested in seeking alternative prey on this beach, for example small mussels and polychaete worms. In a similar experiment with seed mussels (section 3.2.3) crab predation was intense.

3.2 Predation on mussels

The methods employed by shore crabs to open mussel shells have been studied in detail by Elner (1978) who described five distinct methods of attack which depend partly on the relative sizes of crab and mussel: (i) simple crushing, (ii) umbone crushing, (iii) posterior crushing, (iv) boring, (v) posterior edge chipping. Individual crabs often used a succession of methods. In our field and laboratory experiments evidence of all these forms of attack was found (Figure 5).

3.2.1 *Daily consumption rates*

The numbers of mussels eaten per day at 22°C are summarised (Table 4) according to size of mussel and crab, and plotted in Figure 6. Information for the smallest crabs (25 mm) is necessarily based on small samples because of their relative scarcity in traps. All crabs readily ate mussels and they consumed 15-25 mm seed often at very high average rates, exceeding 10 mussels per crab per day (Figure 6). Feeding rates declined sharply with increasing size of mussel and with decreasing size of crab. A regression is obtained by plotting the data on log : log scale (Table 5). Consumption rates are expressed as whole liveweight and as dry flesh weight in Figure 7.

These results were obtained at a temperature of 22°C, several degrees higher than peak summer temperatures in British waters. Lower consumption rates would be expected over the usual spring-summer temperature range of 10-17°C. Wallace (1973) found that crabs acclimated to 24°C consumed, on average, 2.4 times as much squid mantle per day as those crabs acclimated to 10°C. Although no tests could be made with mussels at more representative temperatures, the potential of shore crabs to rapidly devastate seed mussel lays in summer is clearly demonstrated. This view is supported by some observations of sustained high feeding

Table 4 The daily consumption by shore crabs in aquarium tanks at 22°C when offered mussels of various sizes (Nos. eaten per day per crab ± 95% conf. limits. Actual numbers of crabs are given in parentheses. Small samples are bracketed.)

Crab size (mm)	Size of mussel (mm) 15	20	25	30	35	40
75	–	[32.50 (2)]	13.33 ± 4.30 (9)	9.14 ± 2.16 (13)	2.39 ± 1.27 (13)	1.14 ± 0.44 (14)
65	–	[19.00 (3)]	12.44 ± 3.74 (18)	3.50 ± 1.76 (10)	1.14 ± 0.48 (22)	–
55	–	[21.33 (3)]	12.56 ± 2.96 (18)	1.52 ± 0.60 (21)	1.00 ± 0.41 (31)	–
45	–	9.61 ± 2.71 (18)	[3.00 (3)]	0.21 ± 0.19 (33)	–	–
35	15.50 ± 4.49 (8)	[7.67 (3)]	–	1.22 ± 0.64 (9)	–	–
25	[7.00 (1)]	[2.00 (1)]	0.67 ± 0.86 (6)	–	–	–

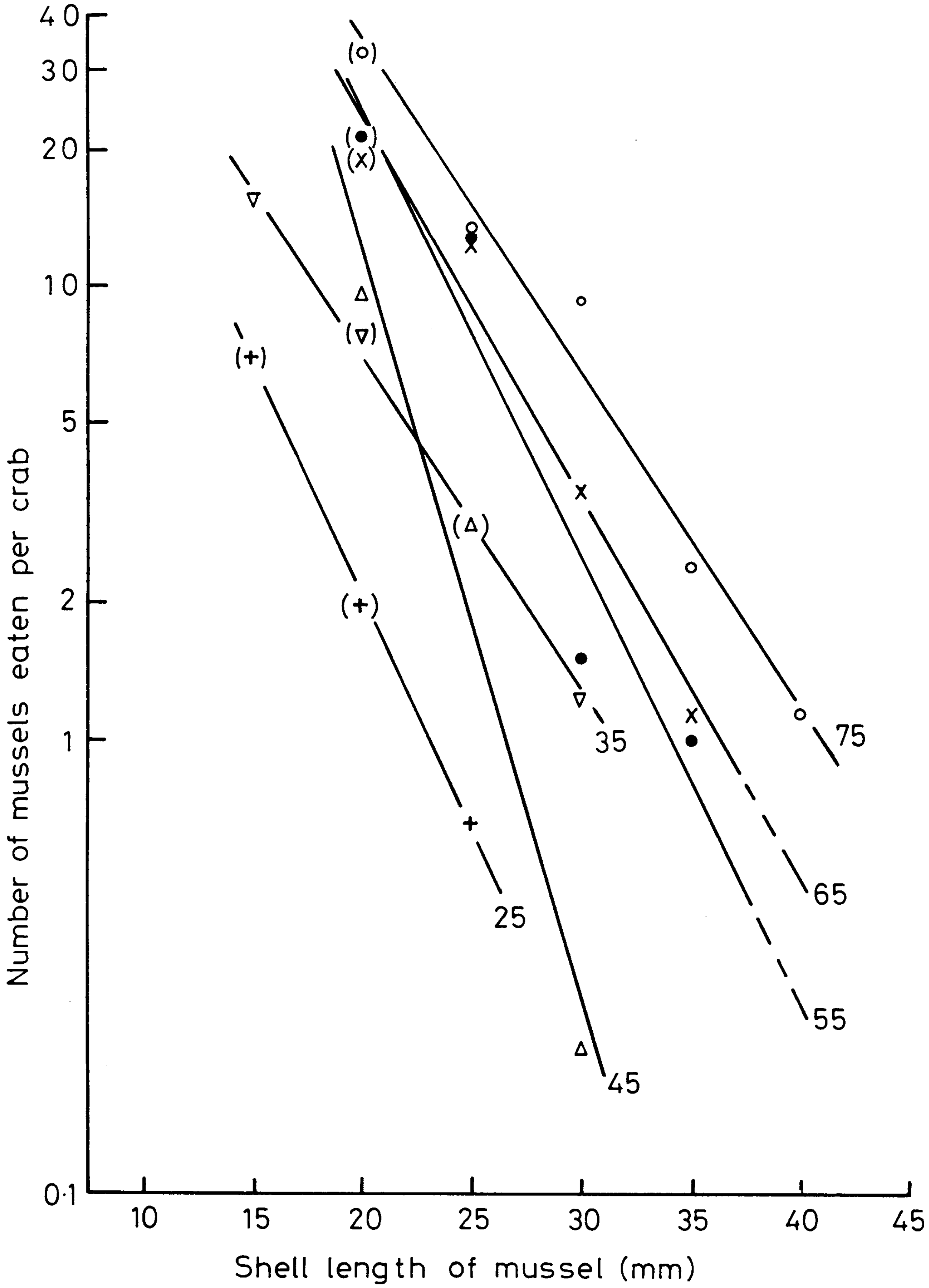

Figure 6 Daily consumption of seed mussels by shore crabs, at 22°C, in relation to size of mussel and size of crab, during laboratory experiments (see Table 5 for regression data). Crab size group symbols are: 25 mm + , 35 mm ▽, 45 mm △, 55 mm ● , 65 mm x , 75 mm o . Small samples are plotted in parentheses.

rates on 15-30 mm mussels at 9-20°C reported by Perkins (1967). The observed size structure of the *Carcinus* population on the shore in summer (Figure 4) suggests that most predation losses of mussels will be caused by the 25-55 mm crabs.

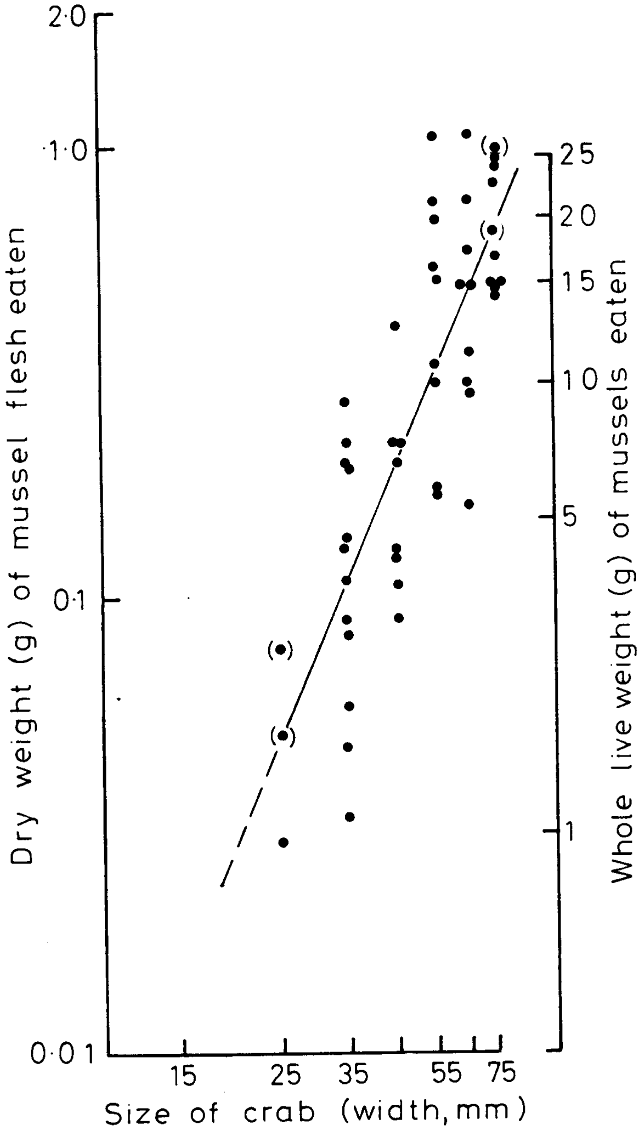

Figure 7 Daily consumption of seed mussels, at 22°C, expressed in terms of dry flesh weight and approximate liveweight in relation to crab size; from laboratory experiments. The regression is: $\ln y = 2.406 \ln x + \ln 0.000021$ ($r = 0.825$; 49df) where y is dry weight (g) consumed and x is crab carapace width (mm). Each point denotes average daily intake over 3-6 days for an individual crab, except points in parentheses which are for one day only.

Table 5 Regressions for Figure 6.

Crab size (mm)			
75	$\log y = \log 1000.98 - 0.17x$	$r^2 = 0.98$	$n = 5$
65	$\log y = \log 1155.05 - 0.19x$	$r^2 = 0.96$	$n = 4$
55	$\log y = \log 2237.3 - 0.23x$	$r^2 = 0.92$	$n = 4$
45	$\log y = \log 25819.5 - 0.38x$	$r^2 = 0.95$	$n = 3$
35	$\log y = \log 216.0 - 0.17x$	$r^2 = 1.00$	$n = 3$
25	$\log y = \log 230.2 - 0.23x$	$r^2 = 1.00$	$n = 3$

where x = mussel shell length (mm), y = number of mussels eaten per day, n = number of mussel length groups.

From the plotted regressions in Figure 6, the maximum sizes of mussels likely to be eaten in the field at a rate of two per day, i.e., one per tide, are estimated as:

Crab size (mm)	25	35	45	55	65	75
Mussel size maximum *(mm)	20	27	24	30	32	36

(* to nearest mm below)

Table 6 Comparison of the size compositions of shore crabs visiting and eating seed mussels offered on a tray at Tal-y-foel, from underwater television observations, 29 July 1975.

Crab size (mm)	A. No. of crabs visiting	B. No. of crabs eating	$\frac{B}{A}$ (%)
20 – 29	3	0	0
30 – 39	24	5	20.8
40 – 49	35	9	25.7
50 – 59	20	11	55.0
60 – 69	7	6	85.7
70 – 79	1	1	100
	90	32	

3.2.2 *Relative vulnerability of mussel sizes*

The largest sizes of mussel which crabs were capable of opening in 24 h are shown in Figure 8, based on actual performances. Crabs of 25 mm width could open mussels of 25 mm shell length (*c* 1.5 g) while the largest (75 mm)

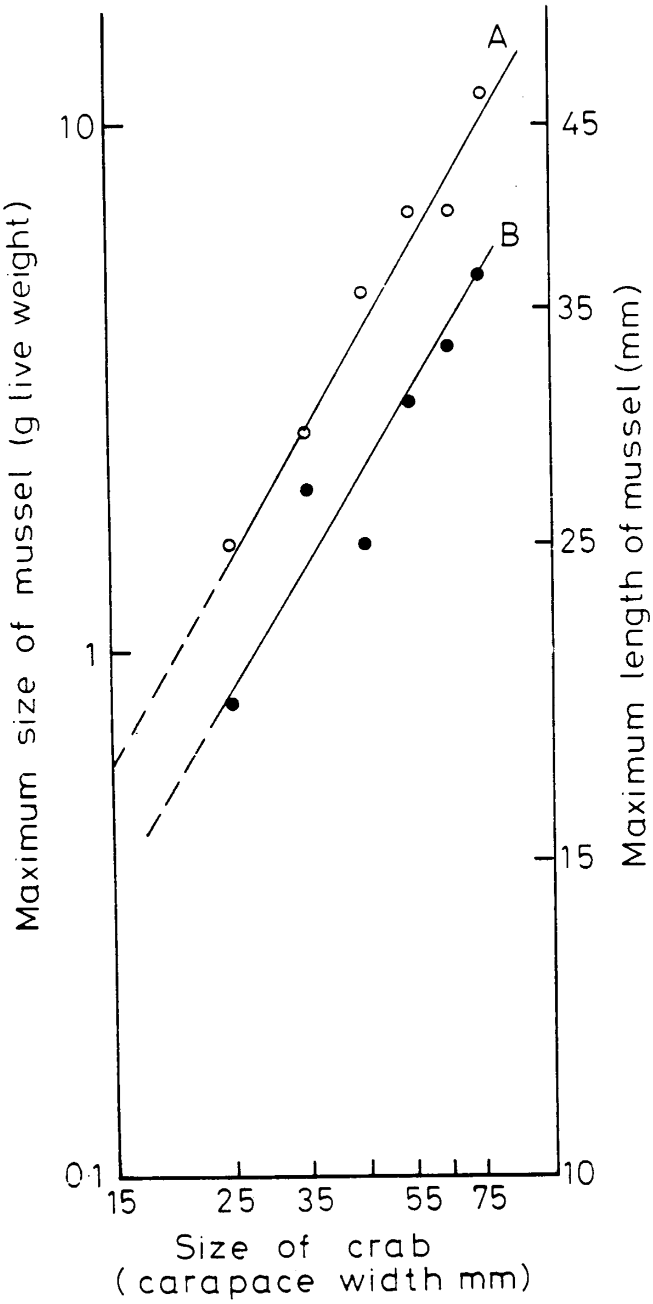

Figure 8 Relationship between size of crab and size (mm) of intertidal mussel eaten: (A) for largest mussel which could be opened in laboratory experiments ($\ln y = 0.5626 \ln x + \ln 4.081$; $r = 0.988$, 4df); (B) for largest sizes of mussel consumed at the rate of 2 per day (from Figure 6).

crabs opened *c* 45 mm (10 g) mussels. These low shore mussels would therefore be vulnerable to attack until they had grown to *c* 45 mm. However, because 75 mm (and 65 mm) crabs are usually scarce (Figure 4) predation in the field might be much reduced once mussels have reached 40 mm (*c* 7 g).

Comparing Figure 8 with the corresponding and rather similar regression for oyster vulnerability (Figure 3) shows that a given size of crab could open larger (by weight) oysters than it could mussels. Such a difference in performance is perhaps explicable by the presence of thin 'window' areas in the valves of many *C. gigas; Mytilus* shells lack such obviously weak features.

Crab performance and consumption of mussels, as of oysters, in the laboratory are unlikely to be typical of crabs foraging on mussel lays on the shore. A more realistic guide to mussel vulnerability is perhaps provided by considering the sizes of mussel which crabs were capable of eating at the rate of two per day. Such an index (Figure 8) shows that the maximum sizes for 75 mm and 65 mm crabs would then be mussels of 36 mm and 32 mm length respectively. On this basis, crab predation on the shore should be virtually ended once mussels have grown to around 35 mm.

The results from the 32-day experiment in an outdoors tank are given in Figure 9A. In both stocks of mussels, survival improved rapidly with increased shell length, from zero for <20 mm mussels to 70-75% for 40-45 mm mussels, and to 85-90% for 47-50 mm mussels. There was a suggestion that at intermediate shell lengths (25-40 mm) the intertidal mussels survived better than did sublittoral mussels. Thus, 50% survival occurred at 28 mm for intertidal mussels but not until 36 mm for sublittoral mussels. Survival of 35 mm intertidal stock was *c* 70%. Most of the dead mussels had clearly been broken open by crabs. Some of the larger dead mussels showed no damage, however, and may have died through causes other than predation.

The results from the 23-day experiment under natural conditions on Bangor mudflats are shown in Figure 9B. A litter of crushed shells in the trays afforded abundant evidence of crab predation. The survival curves are similar in form to those from the outdoors tank experiment (Figure 9A). The combined data have been examined by an analysis of variance for the five populations and for four size groups, covering the range 20-39 mm. Survival improved significantly with increasing shell length ($F = 15.18$, for 3 and 32 df). In three of the size groups survival was better than in the next smaller group; in the fourth group, 35-39 mm, the difference from the 30-34 mm group was not quite significant.

Mussels from different populations, i.e., tidal levels, also varied in vulnerability ($F = 7.48$, for 4 and 32 df). Thus, population mean survival tended to increase with greater height above extreme low water level of spring tides, with the deeper sublittoral mussels being most heavily predated. Unfortunately, the data do not permit more detailed evaluation of any relationship there may be between exposure

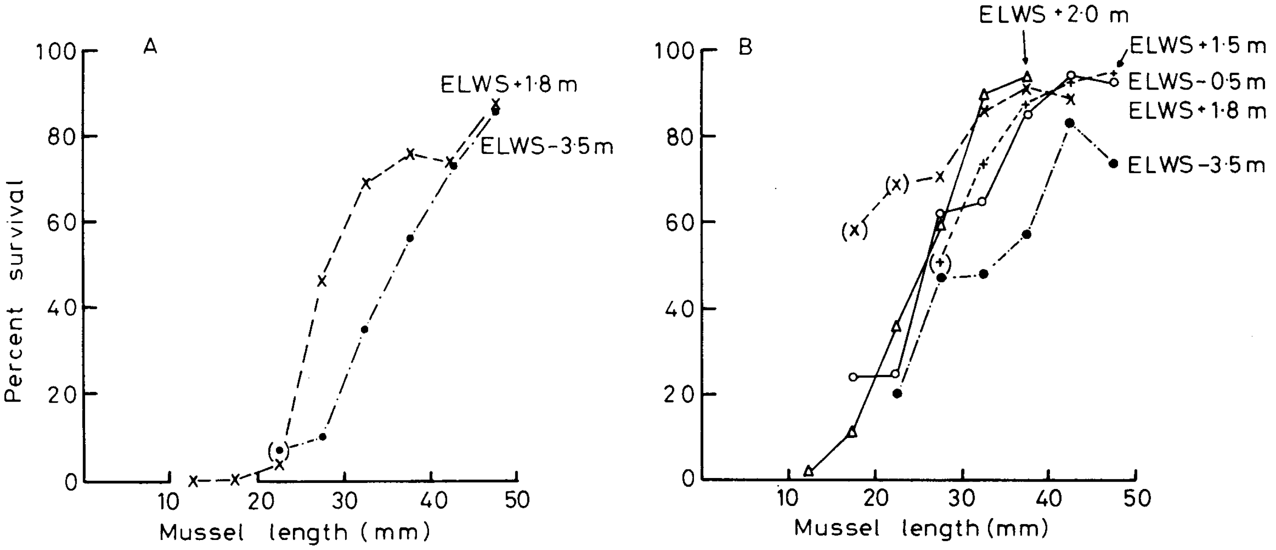

Figure 9 Survival of Menai Strait mussels of different sizes and origins against shore crab predation: (A) in an outdoors tank with 100 crabs for 32 days; (B) on a mudflat under natural conditions for 23 days. Mussel origins are given as tide levels relative to extreme low water mark spring tides; points for small samples (⩽ 30 mussels) are shown in parentheses.

level of a stock and its resistance to crab attack. It may be noted that, as in the outdoors tank, predation of intertidal mussels was concentrated on sizes below 35 mm, this group displaying 90% survival at Bangor.

3.2.3 *Underwater television observations*

During eight hours immersion, from 3.5 h before until 4.5 h after high water, the 15-30 mm mussels were visited by at least 100 crabs, of which 33 (perhaps more) were seen to take and eat mussels. Predation accounted for 73 mussels (24.3%) weighing 80 g (23%). Crab size was estimated using the known width of mesh on the tray floor. The estimated sizes of crabs preying on the mussels compared with those visiting (Table 6) shows that most of the predation was due disproportionately to the larger, >50 mm, crabs. Possibly an intraspecific size hierarchy excluded the smaller crabs from the confined space on the tray; on open lays such competition should be minimal.

3.3 Mesh penetration by crabs

Oyster growers employ a wide range of plastic mesh covers and containers to protect different sizes of young stock from predators and the elements, as well as for ease of separating and handling seed during the nursery stage. Oyster, clam and mussel seed can also be protected within net fence enclosures (Davies *et al.*, 1980). In this section, we consider the relationship between mesh size and the smallest crab which can be excluded. There are two relevant factors: (i) maximum dimension (diagonal, diameter) of mesh apertures; (ii) body length of crabs, i.e., the shorter antero-posterior carapace axis, because crabs move sideways through apertures and will tilt the body angle as required.

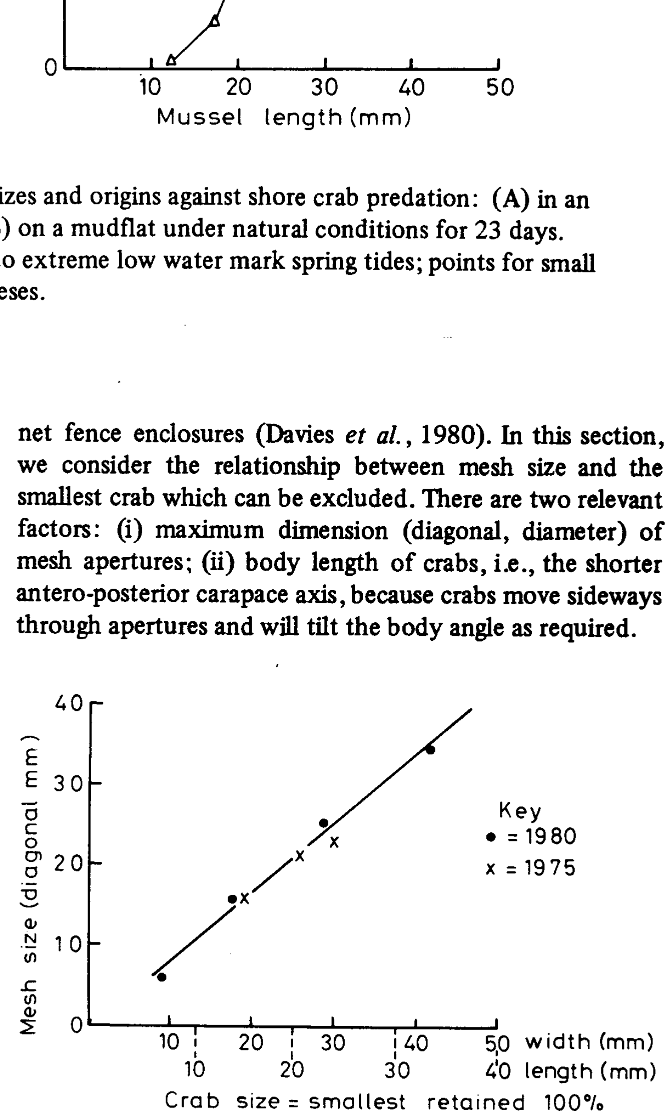

Figure 10 Relationship between mesh size and the smallest size of shore crab at which 100% were retained on the mesh.

Table 7 **Mesh size requirements for the protection of intertidal seed oysters* against shore crabs**

Size of oyster		Smallest size of crab against which protection needed		Maximum mesh size† required for total exclusion‡	
Live weight (g)	Shell length (mm)	Carapace width (mm)	Carapace length (mm)	Diagonal (mm)	Square (mm)
0.5	15	13	10	8	5
1	20	18	14	12	8
2	25	26	21	19	13
3	30	32	25	24	16
4	33	37	30	29	20
5	35	41	33	32	22
6	38	45	36	35	24
7	40	49	39	39	27
8	43	52	42	41	28
9	45	55	44	43	30
10	47	58	46	45	31

* Both Pacific and flat oysters

† To nearest 1 mm below

‡ Required mesh size for total crab exclusion may be too large to retain some individual Pacific oysters of the size to be protected; thus a smaller mesh may be needed to prevent loss of any seed.

Figure 10 shows the results of laboratory tests in which batches of freshly trapped crabs sorted themselves, in air, through a stack of four descending mesh sizes of polythene netting: the mesh sizes were 34, 25, 16 and 6 mm diagonal aperture. A strong correlation is evident between mesh size and the minimum body length of excluded crabs. As may be expected, a crab will readily pass through a mesh the diagonal of which equals or is larger than the crab's own body length. Carapace length (y) of Tal-y-foel crabs is related to carapace width (x) by the regressions:

♂♂ $y = 0.796\,x + 0.027$, $r = 0.996$ (n = 126 crabs),

♀♀ $y = 0.844\,x - 1.487$, $r = 0.989$ (n = 108 crabs).

The sizes of mesh needed to protect fully from crab attack various sizes of oyster seed up to 10 g liveweight are given in Table 7, derived from Figures 3 and 10. The table can be applied also to flat oysters, in which the shell length : liveweight relationship is sufficiently similar to that of the Pacific oyster.

4. Discussion

The results presented in this report and those from other studies, in particular Walne and Dean (1972), Elner (1978 and 1980), together indicate that the predator-prey relationship between shore crabs and bivalve molluscs is complex. Elner and Hughes (1978) found that with captive crabs there was a preferred size of mussel for a particular size of crab, which theoretically should enable the crab to forage optimally and thereby maximise its food intake. There are no reports confirming that such a strategy occurs on natural mussel beds. It is likewise evident that crab feeding activity and food consumption can vary widely, not only between individuals – especially influenced by moult and reproductive status – but also with temperature (Wallace, 1973) and perhaps between populations (Walne and Dean, 1972). Furthermore, the vulnerability of a particular bivalve population to *Carcinus* predation will itself depend on such highly variable characters as shell size, shape and thickness, perhaps also on the presence or absence of barnacle encrustations, and on the availability of alternative, easier or preferred prey species. Thus, our laboratory and field experiments suggested that Menai Strait crabs preyed much more readily on young mussels than they did on Pacific oyster seed which is a recently introduced species to this area.

A broad relationship between crab size and size of oyster or mussel which can be opened is apparent from all the experiments, from which has been derived the maximum vulnerable size for each prey species. These values should be regarded as approximations or guide-lines for cultivators, for they may vary with type of bivalve stock and environmental factors as noted above. Furthermore the performance, and especially food consumption rates, of crabs in the wild under tidal conditions probably differ markedly from that of captive crabs maintained under totally artificial feeding regimes. It is therefore not realistic to predict predation intensities on cultivated mussels or oysters from the results of laboratory studies. Much more detailed studies would need to be carried out under natural conditions before such predictions could be made.

From the cultivation aspect, the aim should be to fully protect juvenile oysters (of any species) until they reach at least 5 g, and preferably 8-10 g. The benefits of protecting mussel lays within fenced enclosures for the first year of cultivation have been clearly demonstrated, with up to eight-fold increases in final yield compared with that from open lays (Davies *et al.*, 1980); by contrast, seed mussels on unprotected lays can be expected to suffer high predation losses until they have grown to 35-40 mm mean length.

5. References

CROTHERS, J. H., 1968. The biology of the shore crab, *Carcinus maenas* (L). 2. The life of the adult crab. Fld. Stud., *2*: 579-614.

DARE, P. J. and EDWARDS, D.B., 1976. Experiments on the survival, growth and yield of relaid seed mussels (*Mytilus edulis* L.) in the Menai Strait, North Wales. J. Cons. int. Explor. Mer, *37*: 16-28.

DARE, P.J. and EDWARDS, D. B. 1981. Underwater television observations on the intertidal movements of shore crabs, *Carcinus maenas*, across a mudflat. J. mar. biol. Ass. U.K., *61*: 107-116.

DARE, P.J. and EDWARDS, D.B., in press. Abundance and population structure of shore crabs (*Carcinus maenas* (L.)) on a mollusc cultivation ground. Fish. Res. Tech. Rep., MAFF Direct. Fish. Res., Lowestoft.

DAVIES, G., DARE., P. J. and EDWARDS, D. B., 1980. Fenced enclosures for the protection of seed mussels (*Mytilus edulis* L.) from predation by shore crabs (*Carcinus maenas* (L)). Fish. Res. Tech. Rep., MAFF Direct. Fish. Res., Lowestoft, (56), 14 pp.

EBLING, F. J., KITCHING, J. A., MUNTZ, L. and TAYLOR, C. M., 1964. The ecology of Lough Ine. XIII; Experimental observations of the destruction of *Mytilus edulis* and *Nucella lapillus* by crabs. J. Anim. Ecol., *33*: 73-82.

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

ELNER, R. W., 1980. The influence of temperature, sex and chela size in the foraging strategy of the shore crab, *Carcinus maenas* (L). Mar. Behav. Physiol., *7*: 15-24.

ELNER, R. W. and HUGHES, R. N., 1978. Energy maximization in the diet of the shore crab, *Carcinus maenas*. J. Anim. Ecol., *47*: 103-116.

KLEIN BRETELER, W. C. M., 1975. Food consumption, growth and energy metabolism of juvenile shore crabs, *Carcinus maenas*. Neth. J. Sea Res., *9*: 255-272.

KORRINGA, P., 1976. Farming Marine Organisms Low in the Food Chain. Vol. 1. A Multidisciplinary Approach to Edible Seaweed, Mussel and Clam Production. Elsevier, Amsterdam, 264 pp.

MARIN, J., BELLAIL, R. and LATROUITE, D., 1973. Prédation de l'huître plate, *Ostrea edulis*, par le crab enragé, *Carcinus maenas*. ICES, C. M. 1973/K:11, 5 pp. (mimeo)

NAYLOR, E., 1962. Seasonal changes in a population of *Carcinus maenas* (L) in the littoral zone. J. Anim. Ecol., *31*: 601-609.

PARSONS, J., 1974. Advantages in tray cultivation of Pacific oysters (*Crassostrea gigas*) in Strangford Lough, N. Ireland. Aquaculture, *3*: 221-229.

PERKINS, E. J., WILLIAMS, B. R. H. and HINDE, A., 1964. The biology of the Solway Firth in relation to the movement and accumulation of radioactive materials. XII. Laboratory investigations. UKAEA, Health Physics and Safety Department, Chapelcross, P. G. Report (578) (cc), 11 pp.

PERKINS, E. J., 1967. Some aspects of the biology of *Carcinus maenas* (L). Trans. Dumfriesshire and Galloway Nat. Hist. Antiquar. Soc., 3rd ser., *44*: 47-56.

REISE, K., 1977. Predator exclusion experiments in an intertidal mud flat. Helgoländer wiss. Meeresunters., *30*: 263-271.

ROPES, J. W., 1968. The feeding habits of the green crab, *Carcinus maenas* (L). Fishery Bull. Fish. Wildl. Serv. U.S., *67*: 183-203.

SEED, R., 1969. The ecology of *Mytilus edulis* L. (Lamellibranchiata) on exposed rocky shores. II. Growth and mortality. Oecologia (Berl.), *3*: 317-350.

SMITH, O. R., BAPTIST, J. P. and CHIN, E., 1955. Experimental farming of the soft-shell clam *Mya arenaria*, in Massachusetts, 1949-1953. Comml Fish. Rev., *17* (6), 1-16.

VILELA, H., 1950. Vida bentónica de *Tapes decussatus* (L). Trav. Sta. Biol. Mar. Lisbonne, (53), 120 pp.

WALLACE, J. C., 1973. Feeding, starvation and metabolic rate in the shore crab *Carcinus maenas*. Mar. Biol., *20*: 277-281.

WALNE, P. R. and DEAN, G. J., 1972. Experiments on predation by the shore crab, *Carcinus maenas* L., on *Mytilus* and *Mercenaria*. J. Cons. int. Explor. Mer, *34*: 190-199.

WALNE, P. R. and DAVIES, G., 1977. The effect of mesh covers on the survival and growth of *Crassostrea gigas* Thunberg grown on the sea bed. Aquaculture, *11*: 313-321.

Bas 253828/B16200 15c 9/83 TP