

THE PEA CRAB, *PINNOTHERES PISUM* (LINNAEUS, 1767), AND ITS ASSOCIATION WITH THE COMMON MUSSEL, *MYTILUS EDULIS* (LINNAEUS, 1758), IN THE SOLENT (UK)

CATHARINE M. C. HAINES,¹ MALCOLM EDMUNDS¹ AND
ARTHUR R. PEWSEY²

¹Department of Applied Biology
University of Central Lancashire
Preston, Lancashire PR1 2HE, England

²Department of Mathematics and Statistics
University of Central Lancashire
Preston, Lancashire PR1 2HE, England

ABSTRACT Pea crabs (*Pinnotheres pisum* (Linnaeus)) from 5366 mussels (*Mytilus edulis* (Linnaeus)) were collected from two sites in the Solent, southern England, between 1972 and 1974 in order to determine the relationships between pea crab sex, size and occupancy, mussel size, time of year and position on beach. Larger mussels were more likely to be occupied by larger, female crabs, but pea crabs will occupy smaller mussels if fewer hosts are available. Mussel occupancy tends to increase from high to low water where food is more readily available. Pea crabs do not occupy mussels at random; there were more male/female pairs and fewer single males and pairs of females than expected. Possible mechanisms that explain these results are discussed. Berried females were found between April and October with a peak of 70% in berry in June and July. Larger females came into berry earlier, and may have been a year older, than smaller females. The association with mussels is best described as amensalism for male pea crabs and parasitism for females.

KEY WORDS: amensalism, host-parasite interaction, logistic modelling, pea crab-mussel association

INTRODUCTION

Pinnotheres pisum (Linnaeus) is a brachyuran crab found in the mantle cavity of bivalves, including the mussel *Mytilus edulis* (Linnaeus). Pea crabs have been recorded in the literature for over four hundred years (e.g. Rondeletius 1554) (Fig. 1), and from many different habitats such as the internal cavities of ascidians and oysters and the tubes of tubicolous polychaetes (Silas and Algarswami 1965, Warner 1977, Ingle 1980). Whilst resident within a mussel, pea crabs benefit from the relationship by feeding on strings of mucus collected from the mussel's gills (Orton 1920; pers. obs. CMCH).

The distribution and frequency of pea crabs in mussels has previously been studied in the English Channel by Houghton (1963) and Seed (1969) with very limited sampling, and by Huard and Demeusy (1968). In this study we selected two sites in the Solent where pea crabs occurred, one with a high, the other with a low density of mussels. Samples of mussels were collected with a view to exploring the factors influencing occupancy of mussels by pea crabs including size of mussel, time of the year and position on the beach.

MATERIALS AND METHODS

Sampling Sites

The results from a ten month pilot survey at Lee-on-Solent led to the choice of the site at Elmore. At this site (Grid reference SZ 566 997, Fig. 2) an intertidal raised mussel bed, referred to as 'the spit,' projected SW from the shore. The spit was the only intertidal mussel bed in the vicinity and arose in an area where the easterly and westerly currents in this region of the Solent converged. The mussel bed was on a substrate of shingle and sand overlying predominantly soft grey mud on the NW side and peat on the SE side. It was 60 m long, with a maximal width of 14 m and maximal height above the mud and peat of 0.2 m. At LWN, only the area

of maximal height was exposed, but at LWS the entire mussel bed was uncovered. The vertical distance between LWN and LWS was about one metre. The time of exposure varied with the strength and direction of the prevailing wind. The tidal range was from 2.5 to 4.5 metres.

Mussels were collected from the surface of the bed at monthly intervals from August 1972 to July 1973 with additional collections in September 1973 and March 1974. At each sampling time twenty-five mussels were collected from twelve stations at 5 metre intervals on a transect from HWN to LWN. All collections were made at low water spring tides.

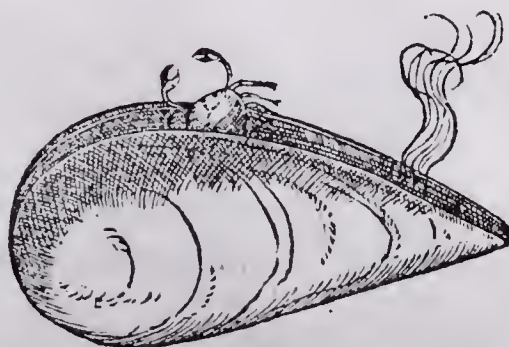
The site at Calshot (Grid reference SU 487 018, Fig. 2) was on the south-east side of a very narrow spit. The area studied extended 60 m seawards from HWN to midway between HWN and LWN. The site was more level than that at Elmore and the mussels were sparsely distributed. Samples were collected from twelve stations every second month from August 1973 to April 1974.

Treatment of Samples

Mussels were transported in polythene bags, kept cool in a refrigerator and examined the following day. If the mussels were placed in water prior to examination, many of the male crabs left the mussels, as was also reported by Huard and Demeusy (1968). All mussels were opened and any visible crabs removed. Mussel length and crab carapace width were measured with vernier callipers to the nearest 0.5 mm. The shell length ranges of the mussels collected from the two sites were similar, being 23 to 80 mm at Elmore and 23 to 75 mm at Calshot, although the mussels collected at Elmore were on average larger than those at Calshot (49.1 mm compared with 45.8 mm).

The sex of each crab was established by inspecting the width of the abdomen. Females in berry were also noted. Occasionally a mussel was found to be dead and filled with mud; these mussels have not been included in the subsequent analysis.

De cancris paruis qui in alienis testis viuunt.



CAPUT XXV.



ANCROS Paruos in alienis testis hospitari Aristoteles prodidit, & idem experientia docet, non tamen in omnibus testis sine discrimine eos reperiatis, non in le pade non in tellinis, non in conchulis, nunquam in mytulis marini stagni, sed in mitulis gurgitum, pinnis, pe-
CC

Figure 1. Copy of illustration of a pea crab from Rondeletius (1554, chapter XXV, p. 569).

Statistical Analysis

Within our analysis, basic statistical summaries were generated, and exploratory data analysis undertaken, using the Minitab statistical package (Ryan et al. 1985).

As part of a preliminary analysis the Poisson distribution was fitted to the frequency distributions of the number of crabs occupying mussels in order to investigate the hypothesis of random occupation of mussels by pea crabs. Integral parts of the Poisson model are: (i) the mean number of crabs occupying mussels is constant, and (ii) crabs occupy mussels independently of one another. Given differences in the observed frequencies for males and females and between the two sites, a separate Poisson distribution was fitted to the frequency distribution for each sex/site combination. The goodness of fit of the Poisson model was established using standard chi-squared procedures.

The GLIM statistical package (Aitken et al. 1989) was used to carry out logistic regression analysis in order to investigate the relationship between the probability of a mussel being occupied and various physical and environmental variables. Specifically, the fitted models were linear binomial response models with logistic link functions. Model fitting within GLIM is carried out via a maximum likelihood method. Subsequent, analysis of variance (ANOVA) based, cross-classification analyses to investigate the relationship between the carapace width of occupying pea crabs and environmental variables were also carried out using this piece of software. For both forms of analysis a step-down approach based on the criterion of deviance reduction was used to obtain parsimonious descriptions of the data structure.

RESULTS

Mussel Occupancy by Pea Crabs

2481 pea crabs (953 at Calshot and 1528 at Elmore) were found in the 5366 mussels collected at the two sites (1402 at Calshot and 3964 at Elmore). At Calshot, 45% of the crabs were males, while at Elmore only 28% were males. Table 1 provides a more detailed breakdown of mussel occupancy by pea crabs.

Investigating the Hypothesis of Random Occupation

The relevant data used in fitting the Poisson model of random occupation are given in Table 2.

Chi-squared goodness-of-fit statistics, calculated after combining categories for which the expected values were less than 5, were very highly significant ($p \leq 0.001$) for all but the males at Elmore. In the three significant cases the major disparities between the observed and expected frequencies arose because the Poisson model underestimated the frequencies of single occupancy, and overestimated the frequencies of multiple occupation, by crabs of the same sex. These disparities from the Poisson model could have been due either to crabs not locating themselves independently of one another or variations in the mean number of crabs occupying a mussel, or both. These possibilities were explored further, yielding the remaining results of this section.

Rejection of Independence

Chi-squared contingency table analysis rejected the hypothesis that males and females locate themselves in mussels independently

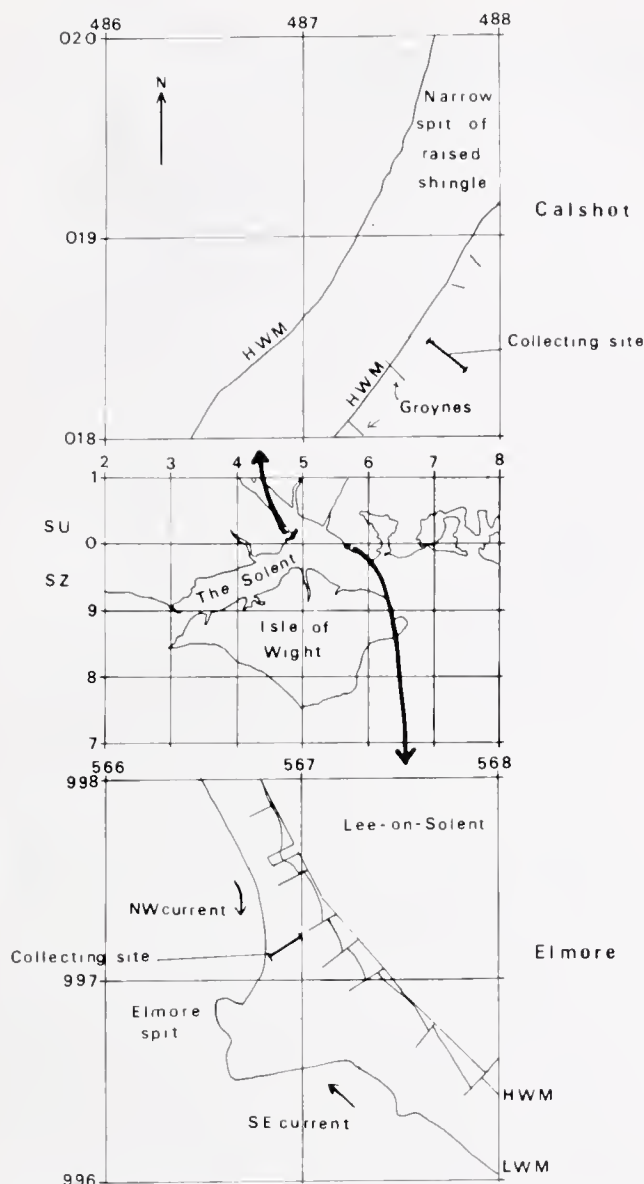


Figure 2. The collection sites in the Solent, southern England (centre) with detail of Calshot (above) and Elmore (below). Ordnance Survey National grid lines are shown giving 10 km squares (centre) and 0.1 km squares (above and below).

of one another ($p < 0.001$ at both sites). The relevant data is that given in Table 1. The predominant significant effect at Calshot resulted from the fact that no females were found to occupy mussels together with two or more males. A secondary significant effect was that more male/female pairings and fewer single males were found than would have been the case under the independence hypothesis. This latter effect was also found to be significant at Elmore.

Variables Influencing Occupancy

A much higher proportion of the sampled mussels were occupied by pea crabs at Calshot than at Elmore (54% compared with 34%). One-way ANOVA for mean mussel length with four cate-

TABLE 1.

Numbers of mussels at each site occupied by the indicated number of male and female pea crabs.

Number of Male Crabs	Number of Female Crabs		
	0	1	2
Calshot			
0	642	353	2
1	216	161	0
2	26	0	0
3	2	0	0
Elmore			
0	2601	954	0
1	245	147	0
2	16	1	0

For example, at Calshot 642 mussels contained no pea crabs and 161 mussels were occupied by male/female pairs.

gories of occupation gave highly significant results for both sites ($p \leq 0.001$ in both cases). Table 3 gives the sample mean and a 95% confidence interval for the population mean for each of the four categories of occupation at the two sites.

Allowing for multiple testing using the Fisher-Bonferroni method (Kotz et al. 1982) with an overall significance level of 5%, at both sites the mean length of mussels occupied by single males was not significantly different from that for unoccupied mussels, while the mean for mussels occupied by single females was significantly different; the mean for mussels occupied by more than one pea crab was significantly different from that for single females.

Logistic regression analysis was used to describe the relationship between the probability that a mussel would be occupied and the time at which sampling took place, the position on the beach and the shell length of the host mussel. The three occupancy categories of mussels occupied by single male pea crabs, single females and male/female pairings were considered individually at each of the two sites. At both sites, occupancy by single females and male/female pairs was found to increase with the size of the host mussel. Also, at Elmore, where the sampling stations covered the complete tidal range of the beach, the proportion of mussels occupied by crabs was higher near low water than near high water for all three categories of occupation.

TABLE 2.

Numbers of mussels occupied by specified number of pea crabs of the given sex (disregarding the number of occupying crabs of the opposite sex).

Number of Occupying Crabs of Specified Sex	Site Sex	Calshot		Elmore	
		Male	Female	Male	Female
0		997	886	3555	2862
1		377	514	392	1102
2		26	2	17	0
3		2	0	0	0

For example, at Elmore 392 mussels contained just one male (and unspecified numbers of females).

TABLE 3.
Mussel length (mm) for four categories of occupation.

	Calshot		Elmore	
	Mean	95% CI	Mean	95% CI
Unoccupied mussels	44.61	(44.1,45.1)	47.70	(47.4,48.0)
Mussels occupied by a single male	44.45	(43.5,45.4)	48.80	(47.9,49.7)
Mussels occupied by a single female	47.15	(46.5,47.8)	51.93	(51.5,52.3)
Mussels with multiple occupation	49.15	(48.0,50.3)	54.50	(53.4,55.6)

Relationship between Pea Crab Size and Environmental Variables

Table 4 shows that female crabs were on average nearly twice as large as males, and that the average size of each sex was similar at the two sites.

For each of four categories of pea crab occupation ANOVA was carried out for pea crab carapace width cross-classified according to three environmental variables. The four categories were single males, single females, males in male/female pairs and females in male/female pairs. The three environmental variables considered were sampling time, position on beach and shell length of the host mussel. From this analysis it was found that, across the two sites, the size of occupying females increased with the size of the host mussel, paired males were on average almost 1 mm larger than single males and paired females were on average 0.6 mm larger than single females.

Berried Females

In all, 203 female crabs were found to be berried at Elmore (181 single females, 21 in male/female pairs and 1 in a 2 male/1 female triple). Berried females were found only in the months April to October. Table 5 gives the proportion of berried females and the total number of females recorded for these seven months. It shows the proportion of berried females rising sharply from April and peaking at around 70% in June and July.

Very few berried crabs were found in the smallest mussels collected (with lengths in the range 22 to 42 mm), or in the quarter of the beach closest to high tide. Generally, the proportion of mussels occupied by berried females increased with the size of mussel and from high to low tide.

TABLE 4.
Carapace width (mm) of male and female pea crabs at Calshot and Elmore.

	Mean	SD	Range
Calshot			
Males	4.48	1.43	1.0–9.0
Females	7.82	2.09	2.0–13.0
Elmore			
Males	4.38	1.26	1.0–7.0
Females	8.13	1.79	1.5–13.0

The mean carapace width for the berried females was 8.80 mm whilst that for the unberried females was 7.98 mm. The difference between the two was very highly significant ($p \ll 0.001$) with a 95% confidence interval for the difference in population means being (0.60,1.05) mm. Overall, there was no significant difference between the mean shell length of mussels occupied by berried females compared to that for unberried females ($p = 0.11$).

ANOVA for the carapace width of berried females, cross-classified according to position on beach, sampling time (May to September) and shell length of the host mussel, showed that mussel size was the most important of these variables followed by the month in which sampling took place and then sampling position. Specifically, the mean carapace width of berried females increased with mussel size, was 0.75 mm larger in May than for the other four months and was 1.2 mm larger near low water than that near high water.

DISCUSSION

Occupancy

The marked difference in occupancy of mussels by pea crabs at the two sites (54% at Calshot, 34% at Elmore) was most likely due to the much greater density of the mussels at Elmore: if similar numbers of megalopae arrive at the two sites they are likely to enter a higher proportion and less optimal size of mussels at Calshot than at Elmore. This is supported by the data in Table 3 which show that for any given class of pea crab the mussels they occupy are smaller at Calshot than at Elmore.

Our various findings lead us to conclude that the Poisson model for random occupation is untenable. The results from the tests of randomness and independence, together with an inspection of the frequencies in Tables 1 and 2, indicate that for female pea crabs there exist mechanisms which inhibit co-occupation by two or more females and, at Calshot (where the average size of the sampled mussels was smaller than at Elmore), co-occupation by females with two or more males. Given the observed frequencies for the males, it is unlikely that similar mechanisms exist which have any strong effect on multiple occupancy by males. However, across the two sites there is evidence that mechanisms exist which promote occupation by male/female pairings and militate against single male occupation. These mechanisms could involve the behaviour of either full-grown crabs of one or both sexes, or megalopae and newly metamorphosed crabs which have just settled on the mussel bed.

The well camouflaged and tough carapace of mature male pea crabs, together with their swimming ability, would appear to enable them to survive outside a host for some time. Mature males in aquaria have been observed to leave mussels, live freely for over a month, and re-enter new mussels (pers. obs. CMCH). Mature males have also been collected from plankton hauls by Baan et al. (1972). Female crabs have a transparent, soft carapace and swim inefficiently (Hartnoll 1972; pers. obs. CMCH). Mature free-living females have not been found in nature. This suggests that female crabs normally remain inside bivalves.

Young crabs of both sexes settling on the mussel bed will occupy empty mussels. If they encounter an already occupied mussel their response would appear to depend on the number and sexes of the existing occupants. Immature single female crabs will enter mussels occupied by single males and cohabit, and *vice versa*. However, if the mussel is already occupied by a female (perhaps paired with a male) and another female encounters the

TABLE 5.
Proportion of berried females and total number of females recorded at Elmore

	Month						
	April 73	May 73	June 73	July 73	Aug. 72	Sept. 72	Oct. 72
Proportion of berried females	0.01	0.50	0.72	0.71	0.39	0.11	0.01
Total number of females recorded	80	70	83	70	116	104	93

mussel, then some form of interaction would appear to operate which results in one of the females (at the very least) abandoning the mussel. Similarly, if a male crab encounters a mussel occupied by a male/female pair then, as a result of some interaction, at least one of the crabs will abandon the mussel. The nature of these interactions is unknown to us but possibilities include: the prospective resident experiencing a lack of available space; aggressive behaviour resulting in occupation by the victor(s); the release by a paired female of a pheromone that deters other crabs from entering the host mussel. Two or more male crabs appear able to coexist, although presumably either, or both, of the first two possible sources of interaction mentioned above might apply when living space is found to be overly constrained. It is also possible that males move between mussels after occupation times of random length but they remain in a mussel longer if they are sharing it with a female. Carefully designed laboratory trials are required to explore these various possibilities.

From the results concerning the variables influencing occupancy and crab size it was found that the mussels occupied by single females were larger on average than those occupied by single males, and those occupied by more than one pea crab were larger still. Also, occupancy by single females and male/female pairs increased with the size of the host mussel, and the size of occupying female crabs increased with the size of the host mussel. These findings are no doubt all related to the lack of space available within smaller mussels to accommodate the larger size of the females and the combined size of multiply-occupying crabs. Houghton (1963) and Seed (1969) found a positive correlation between crab size and mussel size, but they did not distinguish between male and female crabs. Since it is likely to be the larger crabs that are sexually mature, this relationship may explain why we also found that paired males were larger on average than single males, and paired females were larger on average than single females.

At Elmore, where the sampling stations covered the complete tidal range of the beach, the proportion of mussels occupied by crabs was higher near low water than it was at high water for all three categories of occupancy (single male, single female and male/female pairs). This could be because mussels can only feed when covered by water, the pea crabs feed on the food collected by the mussels, and there is therefore more food available for crabs in the mussels found closer to low water. The lack of similar findings for Calshot could have been due to patchiness in crab occupancy within the more restricted sampling region at this site and/or the more level profile of the beach.

The higher proportion of male crabs found at Calshot than at Elmore was probably due to the fact that males tend to occupy smaller mussels than females, and more small mussels were sampled at Calshot than at Elmore (Table 3). However, these data together with those of Table 1 also indicate that, whilst being subject to the constraints of the interaction mechanisms between

crabs, pea crabs will occupy smaller mussels if the number of available hosts is limited.

Reproduction

Crabs have been observed mating inside hosts in February (pers. obs. CMCH). Mating may occur at other times, but, because berried crabs were only found from April through to October (with a peak in their numbers in June and July), fertilization is only likely to occur from February to May or June. Christensen and McDermott (1958) report that for *Pinnotheres ostreum* mating occurs in open water. Mature male *P. pisum* have been recorded swimming in plankton during June and July (Huard and Demeusy 1968) and September (Baan et al. 1972), but no free-living mature females have been found in nature, and this, together with the numbers of male/female pairs in our mussels and the observation of mating recorded above, indicate that for *P. pisum* mating probably occurs only inside hosts. One might therefore expect more male/female pairs to be found from February through to June. However, the seasonal occurrence of male/female pairs at Elmore does not support this expectation: they were found with more or less equal frequency throughout the year. One possible explanation for this is that the crabs face the same problem as dioecious parasites, namely, of finding a host that contains a potential mate out of a great many that do not. Selection will then favour any individuals which find a mate if they remain together, perhaps for several months. Our data also show that berried females are on average larger than unberried females, presumably reflecting the sexual maturity of larger females. Moreover, the larger females came into berry before the smaller ones, indicating that the former are likely to be the more mature females from the previous year's spawning.

Nature of Association

In the literature there is no consistency when defining the nature of the association between the pea crab and its habitat (or host). It is variously described as symbiotic (Anderson 1974), parasitic (Calman 1911), commensal (Huard and Demeusy 1968), or inquiline (Grassé 1960). A further problem is the lack of consensus as to what is meant by these terms. Following Odum (1971), mutualism and symbiosis are associations where both partners benefit; commensalism is where one partner benefits and the other neither benefits nor suffers harm; amensalism is where one animal benefits from the association whereas the other suffers, but the relationship is facultative for the amensal; parasitism is also a relationship where one animal benefits at the expense of the other, but it is obligatory for the parasite which usually lives in or on the other animal.

For *P. ostreum*, McDermott (1962) found that the oysters containing pea crabs often had damaged gills and palps. He attributed this damage to the crabs, which would indicate a parasitic asso-

ciation. For *P. maculatus*, mussels with pea crabs had lower filtration rates and lower oxygen consumptions than mussels without crabs (Bierbaum and Shumway 1988). In nutrient poor environments mussels with crabs had slower growth rates than mussels without crabs, but there was no such difference in nutrient rich environments (Bierbaum and Ferson 1986). *P. maculatus* collects food from the mussels's gills but does not appear to destroy the living tissues. For *P. pisum*, the observations of Orton (1920) and CMCH show that it too feeds on the food collected on the gill filaments of the mussel and does not eat the mussel tissue itself. Since the mussel loses some of the food it has filtered it must therefore ingest less than it would have done in the absence of the

crab. Given that no free-living mature females have been found in nature, their association with a host would thus appear to be akin to true parasitism. However, for mature males the association is best described as amensalism as they are able to survive outside hosts.

ACKNOWLEDGMENTS

CMCH is grateful to the late Dr. Vera Fretter for her supervision and encouragement during the initial stages of the research and to the Royal Society's Scientific Research in Schools Committee for their support.

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