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On the biology of the Watchman prawn, *Anchistus custos* (Crustacea; Decapoda; Palaemonidae), an Indo-West Pacific commensal of the bivalve *Pinna*

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(With 10 figures in the text)

Anchistus custos Forskål is the only common prawn commensal with bivalves of the family Pinnidae in Singapore waters. The whole morphology shows pronounced modifications connected with the commensal mode of life. The second legs are large and massive and show marked positive allometry in the male but appear to have little function in the general life of the animal. The animal occurs wherever there are established populations of mature individuals of its host. Infestation rates are heavy and are affected by size of host and probably by competition with pinnotherid crabs. Multiple infestations are common and always involve individuals of both sexes and it has not been possible to demonstrate aggressive or territorial behaviour. Reproduction appears to occur throughout the year. Individuals are not normally found away from their hosts but rapidly abandon dead hosts. Location of the host depends in part on tactile stimuli and thigmotaxy and in part on pronounced positive rheotaxy. It has not been possible to demonstrate any distance chemical sense involved in host location but the prawn is repulsed by the presence of dead *Pinna* flesh. The prawn normally clings to the edge of the gill lamellae of its host and feeds by means of the highly modified first legs which are used as scrapers to remove mucus and entangled food particles from the gills of the host. Examination of gut contents of the prawn confirms this deduction. There is no evidence for any harmful effects on the host.

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Introduction

Various commensal prawns and crabs are common inhabitants of the mantle cavity of large bivalves of the genera *Pinna* and *Atrina*. The crabs belong to the family Pinnotheridae, especially the genus *Pinnotheres*, whilst the prawns are members of the subfamily Pontoniinae of the family Palaemonidae. The association between bivalves and pinnotherid crabs is relatively well known and has often been studied but little attention has been paid to the pontoniinid commensals.

Holthuis (1952) lists three genera of pontoniinid prawns which are known to occur in association with species of *Pinna* (including *Atrina*). In the same paper he described a new species of the genus *Paranchistus*, *P. ornatus* Holthuis, which is now known to be an associate of *Atrina* and less commonly of *Pinna* (Jacquotte, 1963). This is a species of the western Indian Ocean which is not known as yet from the central portion of the Indo-West Pacific. We have not found it in the few specimens of *Atrina vexillum* (Born) which we have been able to examine from the Singapore area. The other species of *Paranchistus*, whilst apparently bivalve commensals, are not found in association with members of the Pinnidae.

Of the remaining genera *Pontonia*, though represented in the Indo-West Pacific, does not there include commensals of *Pinna*, though it does so in other areas. Two genera, *Anchistus* and *Conchodytes*, remain which contain Indo-West Pacific species occurring regularly in association with species of *Pinna*.

In the latter genus there are three species which are recorded with some certainty as associates of *Pinna*. In addition both *C. meleagrinae* Peters and *C. tridacnae* Peters have been recorded as *Pinna* associates but Holthuis is probably correct in considering that such records are based on misidentified specimens of *C. biunguiculatus*. Of the other species *C. nipponensis* (de Haan) appears to be confined to Japanese waters. *C. monodactylus* Holthuis is apparently a rare species. Holthuis (1952) reported it from Formosa and the Lesser Sunda islands. It also occurs at Hong Kong (Bruce, pers. comm. and it has been reported from Singapore (Johnson, 1961*b*, 1962), although we did not find it in the present survey. Holthuis regards *C. biunguiculatus* (Paulson) as being a common and widespread species and there are certainly many specimens of this form in European museum collections. However we have failed to find any specimens in over 500 specimens of *Pinna* examined so that if not absent it is at least very rare in the Singapore area. A number of other common Indo-West Pacific decapod crustaceans are absent or rare at Singapore, a phenomenon which has already been commented on by Johnson (1961*b*, 1962, in press).

There is probably only one species of *Anchistus*, *A. custos* (Forskål), which occurs in association with *Pinna*. *A. miersi* (de Man) has also occasionally been reported but, as noted by Holthuis (1952), these records are most probably based on misidentified specimens of *A. custos*. Although *A. miersi* occurs at Singapore we have not found it in association with pinnid bivalves.

A. custos is a very common prawn, widely distributed in the Indo-West Pacific region (Fig. 1). The synonymy and distribution are reviewed by Holthuis (1952). More recent reports include those of Macnae & Kalk (1958), Jacquotte (1963), and Johnson (1961*b*, 1962). Holthuis regards it as being one of the two commonest prawns associated with *Pinna* in the Indo-West Pacific, the other being *Conchodytes biunguiculatus*. It is a very

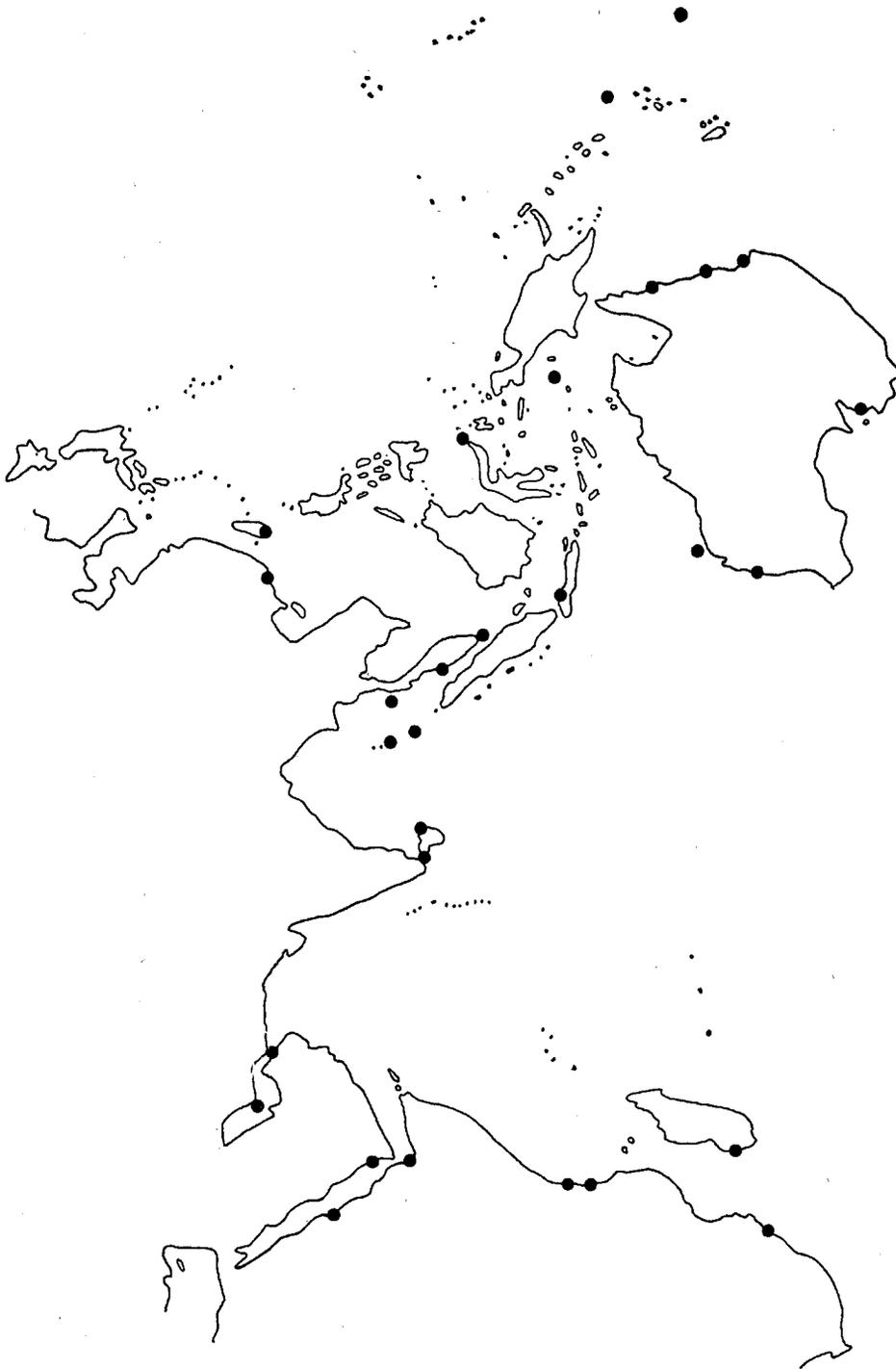


FIG. 1. Distribution of *Anchistus custos*.

common species in the Singapore area where it is the only common prawn associated with these bivalves. Although it is so common, and although its host is of some economic importance, little is known of the biology of *Anchistus custos*. Holthuis notes that it is a littoral species and lists several species of *Pinna*, including *P. vexillum* Born, now transferred to *Atrina*, with which it may be associated. Bruce (in Rosewater, 1961) also lists it as an associate of several species of *Pinna*. Jacquotte (1963) discusses its occurrence

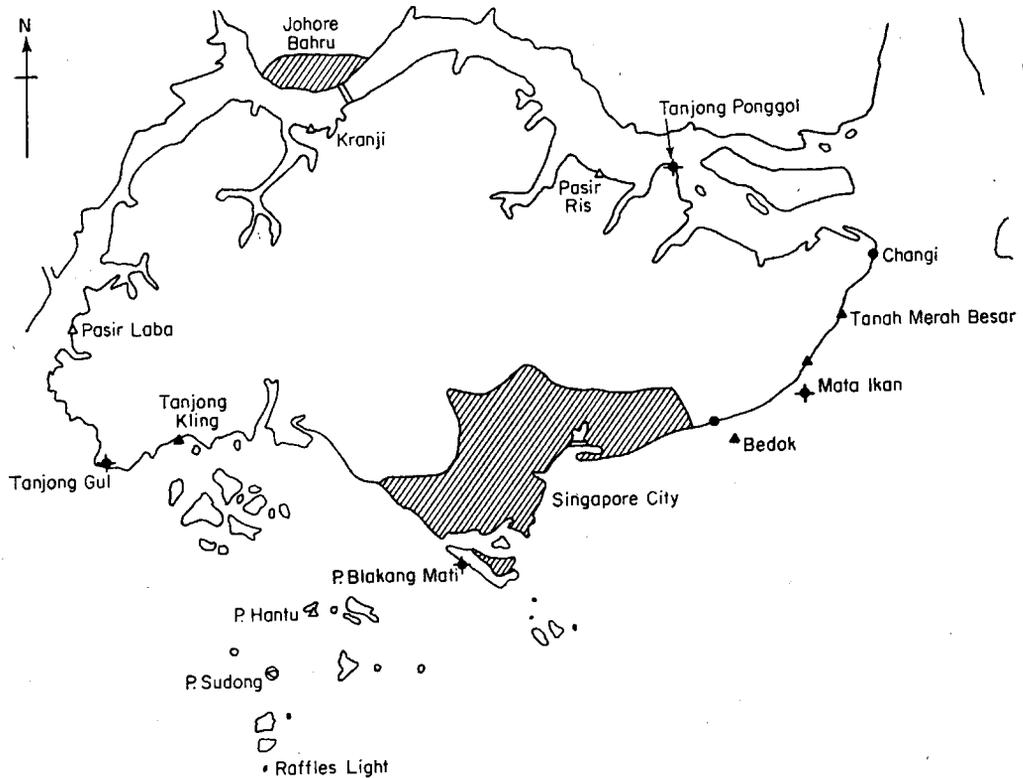


FIG. 2. Localities collected for *A. custos* at Singapore.

in two species of *Pinna* and *Atrina vexillum* at Tulear, Madagascar. Whilst most authors have treated *Anchistus custos* as a commensal of pinnid bivalves, Macnae & Kalk (1958) dissent from this view and report that free-living individuals are common at Inhaca island, Mozambique. The principal aim of our investigations has been the verification and investigation of this presumed commensal relationship between *Anchistus custos* and pinnid bivalves.

Material and methods

The material for the investigation has come from beaches around Singapore island where species of *Pinna*, especially *P. atropurpurea* (Sowerby), occur embedded in the sand and can be readily collected at low tide. Since the beach at Tanjong Ponggol (Fig. 2) was easily accessible and

comparatively undisturbed, investigations were concentrated on the population from that beach. In addition to beach populations samples of the offshore population were studied by employing local fishermen as skin-divers off Mata Ikan.

For studies on infestation rates the bivalves were brought back to the laboratory out of water but amongst damp seaweed. In the laboratory they were dissected as soon as possible and the associated prawns and crabs removed. All associates from any single individual were preserved in a single vial. Morphological studies were made on prawns freshly preserved in 70% alcohol. All measurements were made by means of vernier calipers.

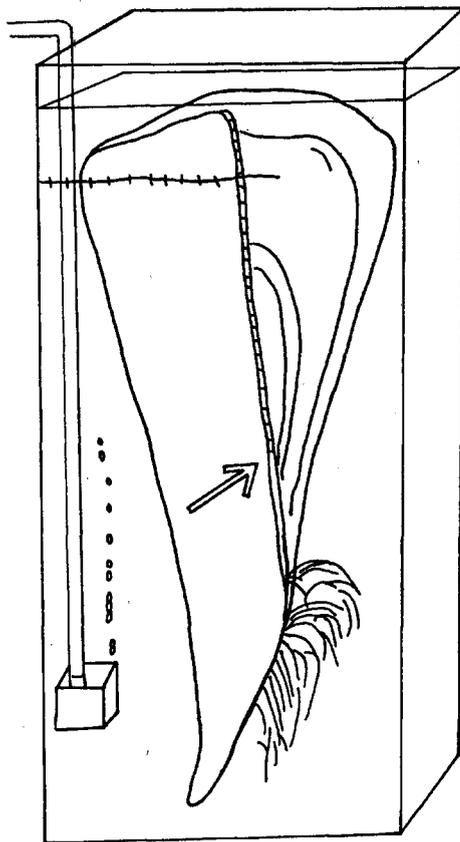


FIG. 3. Arrangement for observing commensals of *Pinna* under approximately natural conditions. Arrow indicates viewing direction.

For food studies the host bivalves were dissected in the field. The prawns were preserved immediately in 70% alcohol and the opened bivalves in 10% formalin.

For other studies living bivalves were brought back to the laboratory and maintained alive. It was found that the bivalves and associated prawns could easily be kept in good health for periods of up to a fortnight which was more than sufficient time for investigations to be made. The bivalves were kept in an air-conditioned room at an average temperature of about 23°C. Each was placed in a shallow dish containing fresh, unfiltered sea water. The water was aerated from a compressed air supply and was renewed from time to time. Prawns were kept under similar conditions away from their hosts and survived for several days.

In life individuals of *Pinna atropupurea* occur embedded in sand in a vertical position with only about 1 to 2 cm of the posterior end exposed, a position comparable to that figured for *P. muricata* Linnaeus by Jacquotte (1963). In order to obtain a close approximation to these conditions, bivalves containing prawns had part of one shell valve removed to serve as a window and were wedged firmly within narrow, vertical, plastic jars (Fig. 3). Unfortunately it was difficult to observe the prawns adequately with this arrangement. For ease in observation bivalves were placed horizontally in shallow glass troughs with the upper valve completely removed. The behaviour of the prawns could then be observed by means of a long-armed, stereoscopic microscope. Since the behaviour did not appear to be affected by this unusual orientation most of the observations were conducted with this arrangement, the arrangement with the vertical bivalve being used as a check.

General morphology

Kemp (1922) has produced a good taxonomic description of *Anchistus custos* and further details are given by Barnard (1950) and Holthuis (1952). Our specimens show good agreement with these descriptions. We will confine ourselves here to those features which are of special interest to the present study.

A. custos is a small prawn, though it is distinctly larger than are most free-living members of its subfamily. Large females may attain a length of about 34 mm but individuals more than 32 mm long are relatively uncommon. The build is clumsy but the body is not or only slightly depressed (Fig. 4); the general facies resembles that of other commensal pontoniinids. As compared with free-living pontoniinids the eyes are very small and the antennal flagellum is rather short. The rostrum is moderately long, though shorter than that of most free-living forms. It is unarmed, conical at the base, but compressed and downturned distally. This characteristic rostral form makes an easy recognition mark for the species. The legs are stouter than those of free-living species and the second legs are especially large and massive. Legs 3 to 5 end in short, strong, hooked dactyli. As in most other commensal pontoniinids the exoskeleton is smooth, polished, and spineless. The males do not attain as large a size as the females. Specimens with carapace length exceeding 7.5 mm are very rare, whereas females may have a carapace length of up to just over 9.0 mm. It is not known whether this difference represents a difference in growth rate or a difference in longevity. The male is also more slenderly built than the female and less clumsy in appearance. However the second legs are commonly relatively larger than are those of females of similar size.

The mouthparts and first legs will be discussed in the section on feeding. The second legs are always enlarged. In most of our specimens they are markedly unequal with one chela much larger and more massive than the other. This is in agreement with the material described by Kemp (1922). Holthuis (1952), however, finds that they are often equal or subequal. Subequal chelae occur in a few of our specimens, but only in those of small size, and with a frequency of less than 5%. The dactylus is strongly hooked and it is normally longer than the fixed finger. The fingers cross near to their tips, the dactylus passing externally to the fixed finger. Near its base the dactylus is produced into a very large, triangular, acute tooth lying internal to the fixed finger. Just distal to this there is a broader and lower tooth on the cutting edge of the fixed finger. In the smaller second leg the latter tooth is absent or vestigial and the tooth on the dactylus is absent or small. The second legs do not appreciably differ in the two sexes. It is difficult to suggest any functional

reason for this assymetry which is shown by many, but not all, pontoniid commensals. Similar assymetry is common amongst decapod crustaceans, including members of the Palaemonidae, and is perhaps best regarded as a heritage character. *A. custos* shows no tendency to be preferentially right-handed or left-handed. In two random samples of 20 individuals the numbers with the right or left second leg the largest were:

9 right, 11 left and
10 right, 10 left, respectively.

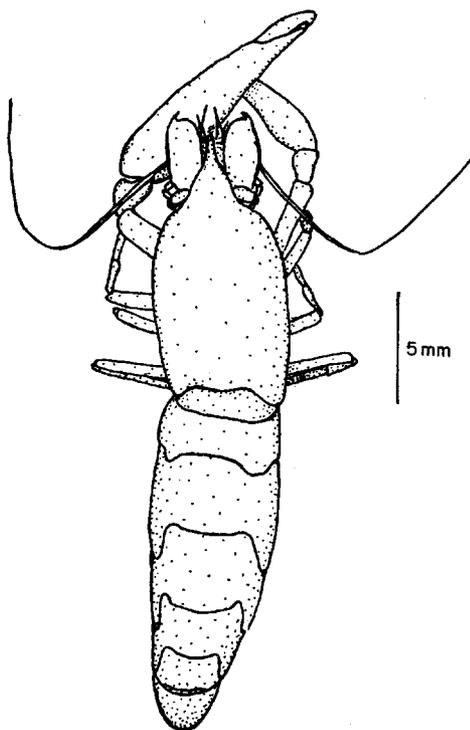


FIG. 4. Adult female of *Anchistus custos*.

Relative growth

In the male it is apparent, even on casual inspection, that the large second leg increases in relative size with increasing size of the individual. The first legs show no such obvious size increase and indeed appear to be relatively slightly smaller in large individuals.

In order to provide precise data detailed studies were carried out on the relative growth of these two limbs using a sample of 17 males and 19 females from Ponggol, Singapore. Measurements were restricted to chela length of the larger leg in each pair. This length was measured from the carpal articulation to the tip of the fixed finger.

In this species overall length does not provide a suitable independant variable since it is impossible to make precise, reproducible measurements. For this reason post-ocular carapace length was substituted. Since this length may itself show changes relative to

overall length (Johnson, 1961*a*) a preliminary check was carried out which revealed that there was no significant allometry in the present species. The results of the statistical analyses are given in Table I and the relationships are figured in Figs 5 and 6. Details of the measurements are deposited in the Zoology Department, University of Singapore.

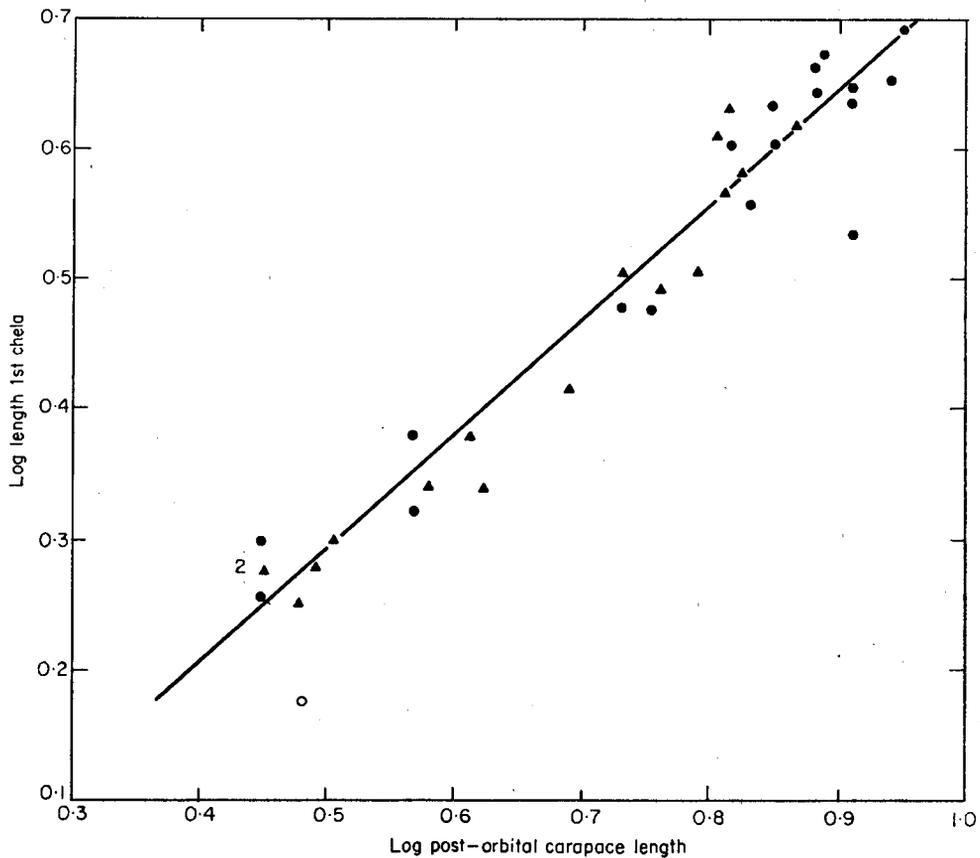


FIG. 5. Relation between length of carapace and length of chela of leg 1 in *A. custos*. —▲—, ♂; —●—, ♀.

TABLE I

Allometric growth of the 1st and 2nd chelae of the prawn Anchistus custos, log y = log a + b log x

Character	<i>N</i>	\bar{x}	\bar{y}	s^2y	<i>b</i>	Probability	<i>a</i>
1st chela male	17	0.6642	0.4348	0.00122	0.8887	0.0584	0.699
1st chela female	19	0.7714	0.5218	0.00215	0.8655	0.0616	0.715
1st chela both sexes	36	0.7208	0.4807	0.00163	0.8682	0.0388	0.716
2nd chela male	17	0.6642	0.9211	0.00074	1.2824	0.0455	1.173
2nd chela female	19	0.7714	0.9474	0.00091	0.9150	0.0402	1.744

N, No. of pairs of observations; \bar{x} , mean log *x*; \bar{y} , mean log *y*; s^2y , variance of *y*; *x*, post-ocular carapace length; *y*, overall length of chela.

For both legs the relationship between carapace length and chela length proves to be of simple allometric kind corresponding to the formula:

$$y = k + ax^b$$

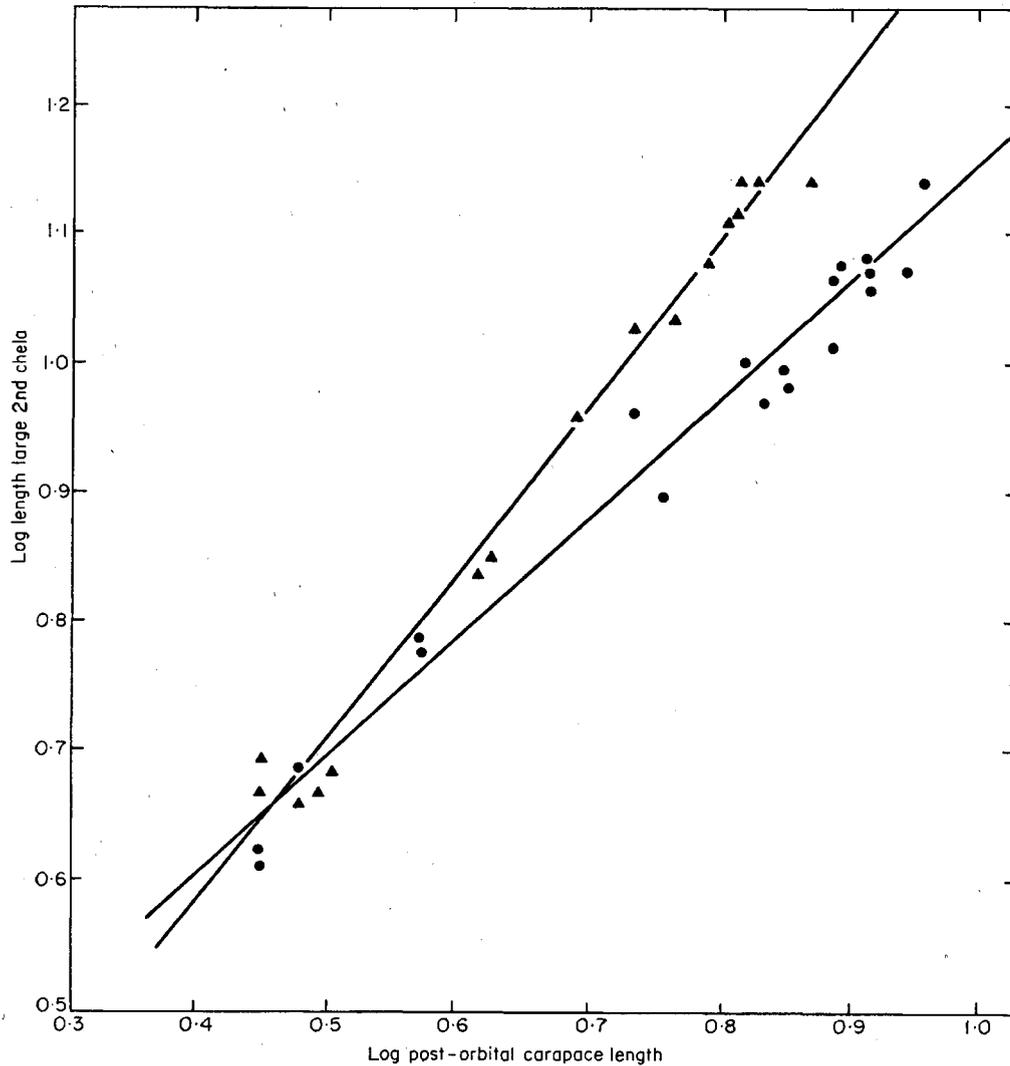


FIG. 6. Relation between length of carapace and length of chela of the larger 2nd leg in *A. custos*. —▲—, ♂; —●—, ♀.

where b is the allometric growth coefficient. The analyses confirm the somewhat surprising impression that the first legs become relatively smaller with increasing size of the individual. When the sexes are treated separately this negative allometry is not significant for the males and scarcely so for the females. However the coefficients show no significant difference between the two sexes so that the results can be pooled and the pooled results

give a growth coefficient which is considerably less than 1.0, the difference being highly significant.

In the male, as was expected, the chela of the large second leg shows marked positive allometry and the deviation of the growth coefficient from 1.0 is highly significant. In the female the growth coefficient is less than 1.0, indicating slight negative allometry, but this deviation is only probably significant so that the conclusion must be treated with caution. A sexual difference of this nature is not uncommon amongst palaemonid prawns and, indeed, decapod crustaceans in general.

Occurrence and infestation rates

In the Singapore area *A. custos* is found wherever there are established populations of the bivalve *Pinna atropurpurea*. It has not been reported from other pinnid bivalves in the waters of Malaya and Singapore and we have failed to find it in the five specimens of *P. hanleyi* (Reeve) and nine specimens of *Atrina vexillum* we have been able to examine. Holthuis does not include *Pinna atropurpurea* in his host list which contains seven others species of "Pinna" including *Atrina vexillum*. Thus our failure to find specimens in that species and *Pinna hanleyi* may merely reflect the small number of specimens available for examination. Nonetheless we would have expected to find specimens, at least in *Atrina vexillum*, had the infestation rates been as high as those for *Pinna atropurpurea*. Jacquotte (1963) found *Anchistus custos* in *Atrina vexillum* in addition to two species of *Pinna* but her figures show a clear preference for the *Pinna* species, especially for *P. bicolor* Gmelin. Thus, though the evidence is still inconclusive, there is a strong suggestion of host preference.

The localities from which we have obtained *Anchistus custos* are shown in Fig. 2. Infestation rates are given in Table II. It will be noted that we have failed to discover *A. custos* around or on the offshore islands. However we have only examined 12 specimens of *Pinna atropurpurea* and four of *Atrina vexillum* from all these localities, in all of which these bivalves are somewhat uncommon. Thus the absence of *Anchistus custos* may merely be apparent.

Pinna atropurpurea occurs around the shores of Singapore island and immediately adjoining islands in flats of muddy sand at depths of from about +0.5 to -20 m from chart datum. It is absent from flats of soft mud, mangrove swamps, reef edges and rocky shores.

Whilst the offshore populations appear to be permanent the beach populations tend to be temporary even on suitable beaches. Such beaches may have mature, flourishing stands or the species may be absent, or it may be represented entirely by dead shells or young individuals. These variations appear to result from human predation since the bivalve is popular and much sought after by the poorer seashore dwellers. Once mature populations have been discovered they are intensively collected and often completely exterminated. After some time a new population appears composed of young individuals. These are normally allowed to attain full size before collection is resumed. The offshore populations are difficult to collect and so are largely ignored. They act as permanent reservoirs for the species.

These aspects of host biology would be expected to affect the rate of infestation with *Anchistus custos* and our results agree with this prediction. The populations at Changi and Bedok consisted only of numerous small individuals and the infestation rates for

both *A. custos* and pinnotherid crabs proved to be nil. On the other hand small populations consisting, nonetheless, of mature individuals such as those at Pulau Blakang Mati and Tanjong Gul were heavily infested with both *A. custos* and pinnotherid crabs. Offshore populations and relatively undisturbed beach populations, such as that at Tanjong Ponggol during 1965, showed heavy infestation rates with *A. custos*, and moderate to heavy infestation with pinnotherid crabs. It thus appears that in the Singapore area any well established population of *Pinna atropurpurea* is likely to be heavily infested with *Anchistus custos*, with an infestation rate of between 20 and 60%. Pinnotherid crabs will usually

TABLE II

Infestation at Singapore of the bivalve Pinna atropurpurea with the prawn Anchistus custos and with pinnotherid crabs

Locality	Date	Bivalves examined	Single male	Nos with prawns			Nos with crabs
				Single female	Multiple	Ovigerous females	
Ponggol	17 March 1965	38	3	10	8	11	4
	8 April 1965	33	2	6	4	4	1
	29 August 1965	29	1	2	7	3	7
	24 October 1965	74	4	5	11	6	14
	7 February 1966	5	1	0	2	2	1
	Total	179	11	23	32	26	27
Mata Ikan offshore	5 March 1965	18	3	1	2	3	1
Bedok beach	25 October 1965	15*	0	0	0	0	0
Bedok offshore							
Changi beach	15 March 1965	20†	0	0	0	0	0
T. Gul	25 March 1965	5	1	1	0	0	0
Blakang Mati	3 July 1965	6	0	2	1	0	0
P. Sudong	29 March 1965	2	0	0	0	0	0

* All less than 150 mm long.

† All less than 125 mm long.

also be present; but the infestation rates are lower and probably never exceed 30%. When our figures are compared with those of Jacquotte (1963) it appears that *Pinna atropurpurea* at Singapore is more heavily infested than *P. muricata* but less heavily infested than *P. bicolor* at Tulear. Amongst Singapore forms *A. custos* appears as by far the commonest commensal of pinnid bivalves.

During the period March to October 1965 the populations of *Pinna atropurpurea* at Tanjong Ponggol was dense and consisted in large part of mature individuals. There was no intensive human predation. Heavy human predation commenced in October and the population was greatly reduced. By February 1966 the population was a very sparse one consisting mainly of moderately large individuals. The overall infestation rate with *Anchistus custos* showed a steady decline from March to October. During this period the percentage of small individuals of *Pinna atropurpurea* steadily increased suggesting a

causal connection. Analysis of infestation rates by size of host (Table III) shows that the larger the host individual the more likely it is to be infested with *A. custos*. When infestation rates were recalculated only for those host individuals which equalled or exceeded 200 mm in length the infestation rates for the four dates concerned became: 59, 69, 58 and 35%, respectively. These figures show no overall trend and it is thus apparent that the seeming regularity in change of infestation rate resulted from changes in host population structure. It is not possible at present to assign any cause to the remaining variation in infestation rate.

TABLE III

Size of host and infestation with the prawn Anchistus custos at Ponggol, Singapore

Size of <i>Pinna</i> (mm)	No. examined	No. with prawns	Infestation (%)
less than 100	2	0	0
100 to 149	45	10	22
150 to 199	72	22	31
200 to 249	48	24	50
250 and over	11	9	82

The infestation data suggest the occurrence of competition between *A. custos* and pinnotherid crabs. Where a specimen of *Pinna* is infested at all it normally contains either prawns or crabs but not both. Out of 240 individuals examined in the special survey only two contained both prawns and crabs. One of these was collected at Tanjong Ponggol on 17 March 1965 when all the specimens of *Pinna* of length above 150 mm which were examined contained either prawns or crabs. The nature of the exclusion mechanism is not clear since on the rare occasions when prawns and crabs were found together they appeared to be co-existing quite happily.

Multiple infestations are common. The largest number of specimens found in a single host during the present survey was four but one of us (D. S. Johnson) has previously observed as many as seven prawns (four males, three females) in a single host. The percentage of infested individuals of *Pinna* showing multiple infestation varies from 33 to 77%. The highest rates were found in the later collections from Ponggol.

We have found individuals of both sexes in all instances of multiple infestation. This agrees with the views of previous workers (Macnae & Kalk, 1958; Johnson, 1962; Jacquotte, 1963). With the exception of the last these do not give figures to support their statements. Jacquotte claims that, except in *P. muricata*, *Anchistus custos* always occurred in pairs. In *Pinna muricata* most specimens only included a single prawn though one held a pair. This does not agree with our experience at Singapore where it is not true to say that *Anchistus custos* normally occurs in pairs. Single occurrences are common, especially single occurrences of females. Even in multiple infestations odd numbers of prawns are common, especially associations involving one female and two males or *vice versa*. Where five or seven individuals are present these consist of two or three pairs and an extra individual whilst specimens with four individuals contained two pairs.

In view of the assertions of Macnae & Kalk (1958) we have made a special search for free living individuals at all localities which we have investigated. We have failed to find any such specimens. Moreover one of us (D. S. Johnson) has never found any free living specimens in many years of general collecting and no such specimens occur in the beach collections made by the former Singapore Regional Fisheries Research Station. This does not mean that individuals cannot occur away from their hosts, merely that such occurrence is rare. General and laboratory observations (see below) show that specimens quickly leave a dead host. Moreover the common occurrence of members of two sexes in the same host individual suggests that the males at least may wander in search of a new host from time to time. Presumably such migrations are of short duration or occur at night or both.

The smallest individuals of *A. custos* which we have found have carapace lengths of just over 2.5 mm. Such individuals are little larger than fully grown larvae. The observations suggest that early post-larvae seek out their hosts immediately so that any free living, post-larval phase will be of short duration.

Reproduction

The results in Table II, confirmed by general collecting over a period of years, indicate that ovigerous females can be found all the year round. There is some evidence for sporadic fluctuations in numbers of ovigerous females but none for any seasonal trends which can be readily correlated with major environmental changes. In all collections the ovigerous females showed considerable variation in the stage of development of the eggs which they carried. Thus *A. custos* appears to breed throughout the year at Singapore. Unfortunately we have not been able to observe mating behaviour in the laboratory and so cannot confirm this conclusion.

The eggs are produced in very large numbers. Total counts per ovigerous female gave a range from 700 to 1500. This compares with 400 to 500 for the large, free living pontoninid *Periclimenes dubius* Borradaile.

Behaviour

General observations

Anchistus custos is usually found in the infra-branchial chamber of the mantle cavity of the host though, especially in multiple infestations, individuals may occur in the supra-branchial chamber. Whilst they may occur almost anywhere in the mantle cavity, observations in the laboratory show that they spend most of their time clinging to the lower edge of the gill lamellae of the host (Figs 7 and 8). They are normally oriented so as to face towards the broad, open, posterior end of the bivalve shell. This orientation probably results from their marked positive rheotaxy (see below). In this position they move slowly along the edge of the gill and appear to be able to move with equal facility in forward and reverse directions. Both sides of the gill lamella are gripped by the dactyli of the third to fifth legs. During locomotion at least three legs (third and fifth on one side, fourth on the other) retain contact with the gill lamella. The pleopods beat slowly but continually and appear to provide most of the necessary propulsive force. In such undisturbed prawns locomotion is always slow and they spend considerable periods resting. During locomotion

and especially when the prawn is "resting" the second legs are normally carried with their tips applied to the gill lamella. They may thus give some assistance in holding on to the gill lamella though they are poorly designed for this purpose.

Individuals occasionally leave the edge of the gill lamella and make short excursions over the general surface of the lamella or the inner surface of the mantle, but they always

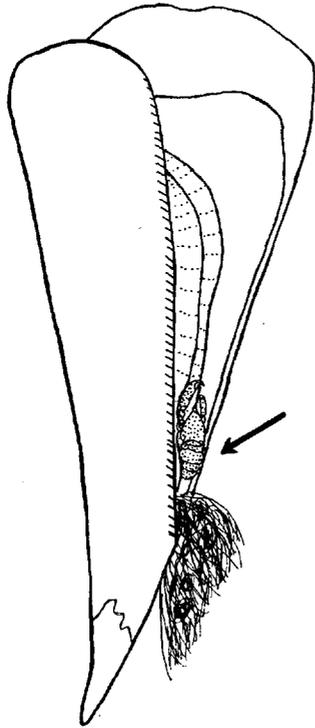


FIG. 7

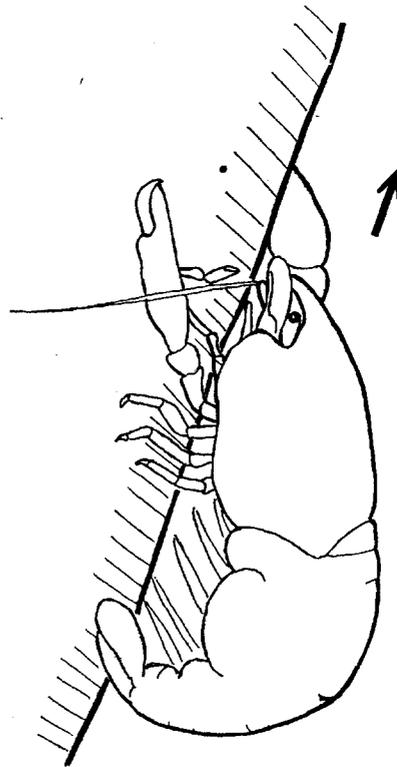


FIG. 8

FIG. 7. Position of feeding *A. custos* within the host.FIG. 8. Feeding *A. custos* on edge of gill lamella of host. The arrow points to the posterior (broad) end of the host.

return to the edge of the lamella after a short time. Prawns under observation in the laboratory showed a tendency to hide between the gill lamellae. The larger second leg was used to assist the prawn in pushing between two lamellae. It seems probable that this is a light avoidance reaction which would not occur in the intact host.

In view of the large size of the second legs and their differential development in the two sexes it was thought that they might be used either as weapons or in territorial and sexual behaviour. We have not been able to confirm these hypotheses. It was impossible to provoke any aggressive reaction to inanimate objects even when these were used to handle the prawn rather roughly. No interest was shown in living creatures of other species. Several

individuals of the same sex, even several males, can coexist peacefully in the same host. When individuals of the same sex meet they push past each other without showing any aggressive or flight responses. Individual males were transferred to occupied hosts to determine whether the occupant would show territorial behaviour. In all instances the intruder was ignored. It seems possible that this negative behaviour might change in the presence of receptive females but we have unfortunately been unable to obtain such females. It is at least clear that in ordinary circumstances these enlarged legs are not used in aggression or defence.

When and how mating takes place remains a mystery. Neither mating nor its preliminaries have occurred amongst those individuals which we have been able to observe. Normally individuals of different sex ignore each other when they meet. It thus appears that the female is only attractive to the male when in a receptive state, which is probably of short duration.

Location of the host

Since the larval stage of *A. custos* is planktonic it is necessary for post-larvae to locate their host after settling down. Similarly adults which are wandering abroad need some mechanism for host location. We have been able to make some observations aimed at elucidating the mechanisms involved.

When removed from their host individuals swim about clumsily and erratically. Movement appears to be random and there is no evidence for any directed searching behaviour. Individuals placed alone in a glass dish ultimately settled down aligned along the angle between bottom and side, an obvious thigmotactic response. However if specimens were left in a dish containing an intact specimen of *Pinna atropurpurea* they always succeeded in entering this within a few hours. Individuals left in a dish containing large, empty shells of any species of bivalve ultimately settled on the concave faces of these shells rather than in the dish. If shells of *Pinna* were mixed with other shells prawns settled on them more frequently than on those of other species. It is thus evident that *Anchistus custos* can discriminate between various surfaces presumably by means of tactile and/or chemical contact receptors. This discrimination would tend to cause individuals to settle on host shells if they contacted them.

We have been unable to demonstrate any distance chemical perception involved in host location. Prawns were made to swim in a dish containing an opened, living *Pinna*. They displayed the normal random swimming behaviour and showed no reaction to the presence of the host until they were almost in contact with it. Then they ceased random swimming and moved rapidly towards the gills of the host. This reaction only occurred when the prawn was within 10 to 20 mm of the edge of the *Pinna*. The exact course of the reaction was not easily observed, since it was very rapid, but we believe that it is initiated when the antenna of the prawn touches part of the host.

Settling experiments indicated that living hosts are more attractive than empty shells since where both are present the prawn always ultimately enters and settles in the living host. This suggested that chemical factors might be involved in host location. In order to test this prawns were placed in a dish containing portions of fresh *Pinna* flesh. Far from being attracted the prawns invariably showed pronounced avoidance reactions when they came close to these. Thus dead *Pinna* flesh repels *Anchistus custos*. A similar reaction

was shown to extracts made from *Pinna* flesh. Such avoidance reactions agree with the observation that prawns leave their host on its death, a behaviour pattern with obvious adaptive value.

These observations indicate that if any long distance chemical perception aids *Anchistus custos* in finding its host it is of minor importance. Nonetheless it was observed that sometimes a prawn would abandon random movement and swim directly and rapidly towards an intact *Pinna* even from a distance of 10 cm. It was found that this behaviour only occurred when sudden movements of the *Pinna* produced a jet of water which impinged on the prawn. The prawn then turned and swam rapidly upstream. The behaviour pattern could be duplicated by means of artificial jets of water produced by a bulb pipette. This pronounced positive rheotaxis is a specialization of a behaviour pattern which is widespread if not universal amongst palaemonid prawns. Individual bivalves in nature do suddenly open and close their shell valves from time to time, thus producing strong jets of water. This rheotactic behaviour is thus probably an important element in host location. Combined with thigmotaxy, light avoidance, and the ability to discriminate between surfaces on contact this would be sufficient to account for the known facts of host location in *Anchistus custos*. Possibly also this rheotaxy, combined with the tendency to settle on concave surfaces, accounts for some of the rare records of *A. custos* from "wrong" hosts, such as that of Lanchester (1901) from the mantle cavity of a large gastropod.

Food and feeding

The organs of feeding

The general pattern of the mouthparts and digestive system corresponds with that of other caridean prawns and especially of other palaemonids. The proventriculus is small and thin walled, whilst the mandibles are well developed for tearing and breaking up food particles.

The mouthparts, consisting of the mandibles, maxillae, and maxillipedes, have been described by Kemp (1922) and Holthuis (1952). Their descriptions are incomplete in several details, especially those concerning the distribution of setae; for this reason we have provided new figures (Fig. 9a to f). It will be seen that the mouthparts are of raptatory character and do not show filter-feeding adaptations. In this they contrast strongly with those of an undescribed *Conchodytes*-like pontoniid which is commensal with *Placuna* at Singapore and which possesses a well developed filtratory apparatus. In *Anchistus custos* the mouthparts are used in handling and breaking up food which has been collected by other limbs; but they are not themselves employed in food collection.

The peculiarly modified first legs have long attracted attention. Their structure is unique and is not even approached by other species which are currently placed in the same genus. Similar peculiarities are shown by *Anchistia aurantiaca* Dana and Holthuis (1952) has used this as evidence that that form is really a synonym of *Anchistus custos*. Most authors have not attempted to explain the function of these limbs. Tattersall (1921) suggested that they were modified for sexual purposes but gave no clear suggestion as to how they might be used. Neither did he attempt to explain why they were identical in size and structure in the two sexes. Barnard (1950) comments that their function is obscure.

The peculiarities which are most striking and most frequently noted are those of the face of the chela but the whole limb (Fig. 10) is unusual in structure and orientation.

The elongate carpus is slightly longer than the merus. The mero-carpal articulation is well developed and the whole distal portion of the limb pivots on this articulation and can be swung freely through a wide angle. Though the limb can be straightened at this articulation it is normally held in a strongly flexed position. At rest the merus points outwards and forwards whilst the distal portion of the limb points forwards inwards and somewhat

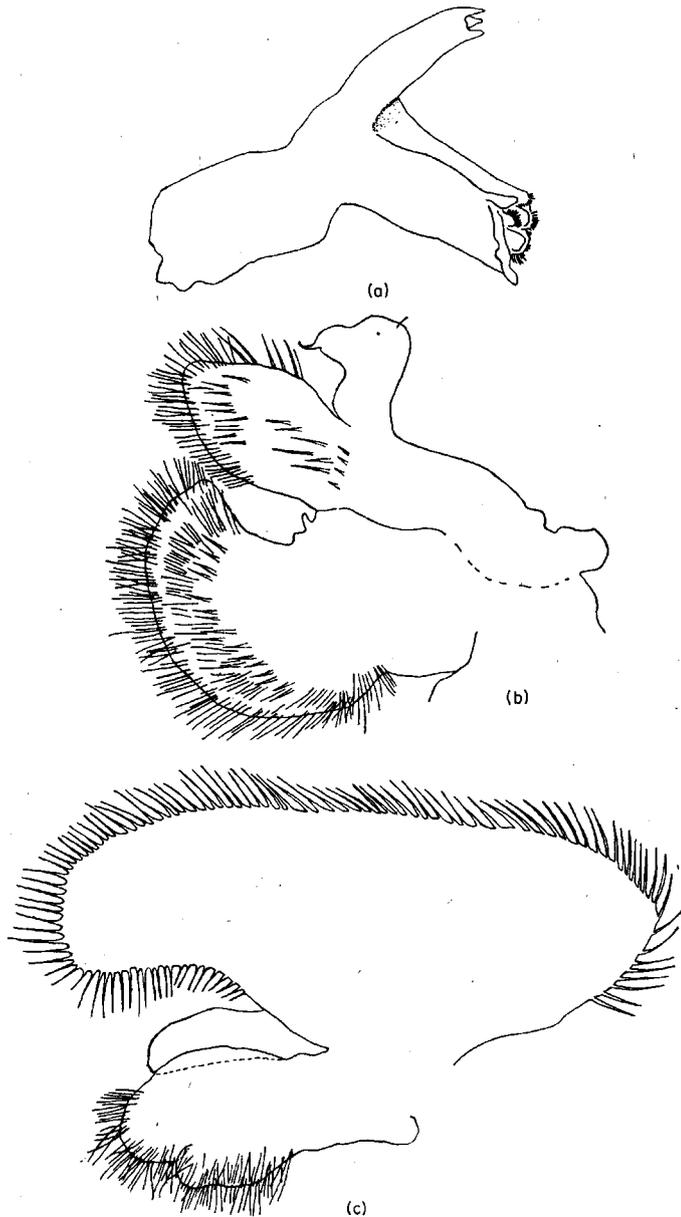


FIG. 9. Mouthparts of *A. custos*. (a) Mandible; (b) 1st maxilla; (c) 2nd maxilla.

downwards. The basal articulations of the limb also permit a wide range of movement. By contrast only a very restricted movement is possible at the carpopropodal articulation.

The ventral border of the chela is flat and straight. Along the whole posterior face there is a broad, deep groove. This is bordered by seta-bearing flanges from the dorsal and ventral margins. The function of this groove and the orientation of the limb in feeding will be considered below.

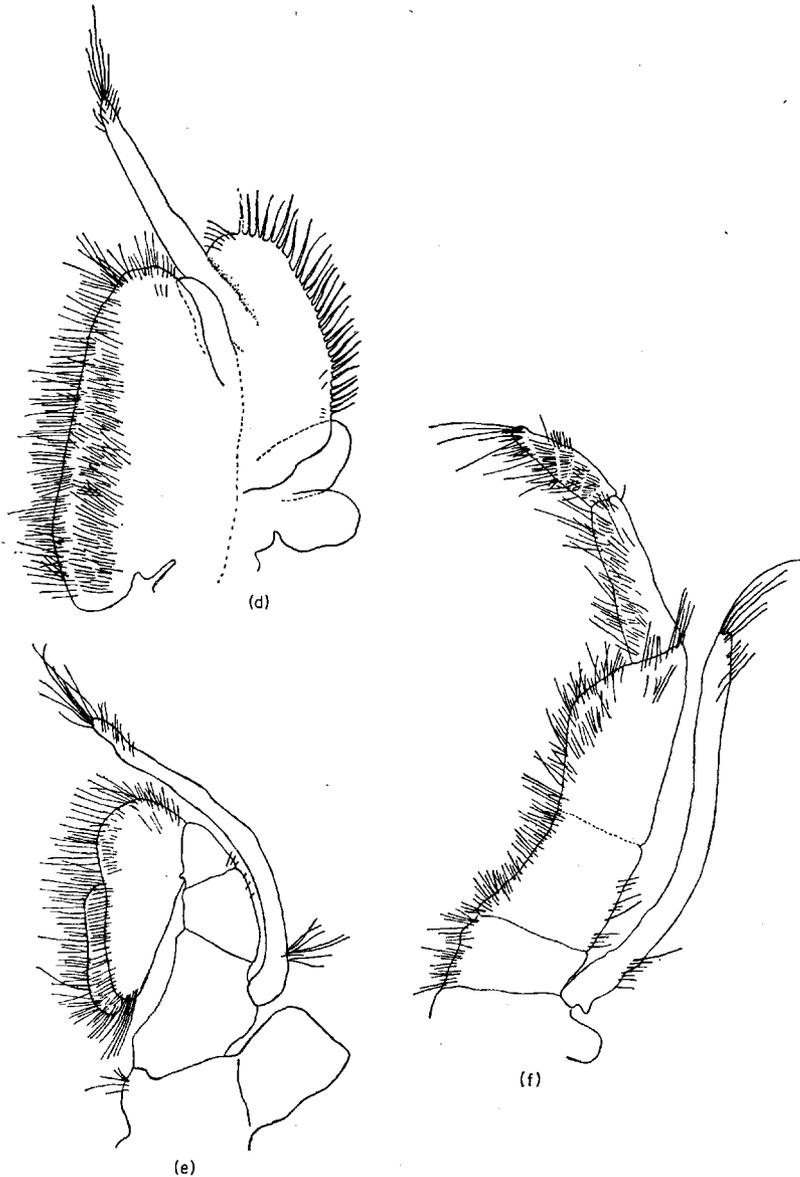


FIG. 9 (continued). Mouthparts of *A. custos*. (d) 1st Maxillipede; (e) 2nd maxillipede; (f) 3rd maxillipede.

In some palaemonid prawns the second legs may be used for seizing and holding food particles and food organisms. No such behaviour has been noted in *A. custos* where these limbs are not food collecting organs. Their structure has been dealt with above.

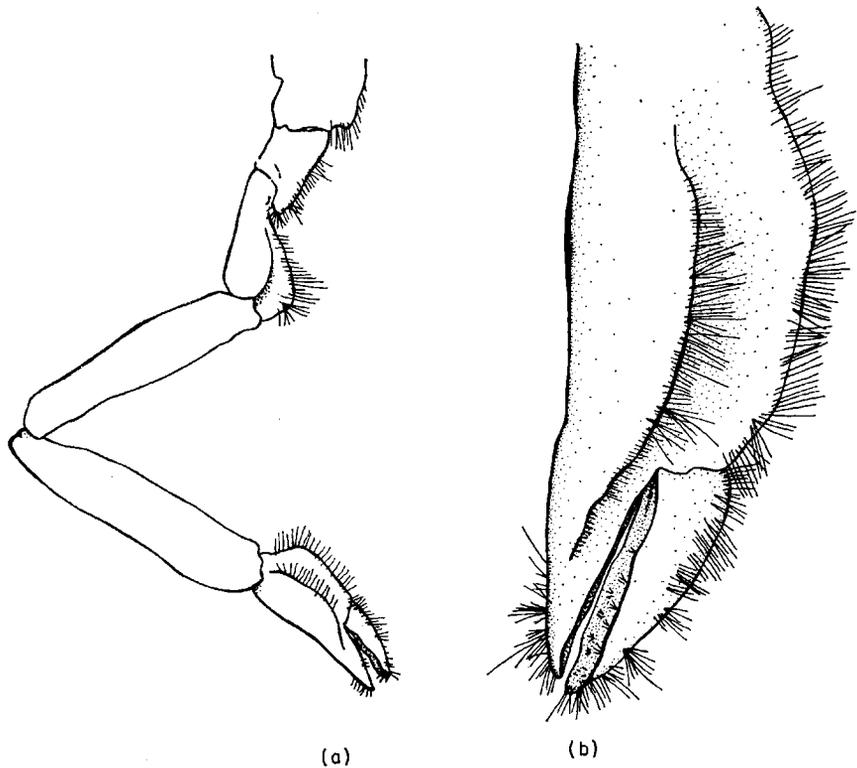


FIG. 10. 1st leg of *A. custos*. (a) Whole limb; (b) chela.

Mechanism of feeding

Our observations have revealed that the specialized first legs are used in food collection and are, indeed, the only important food-collecting organs. It has long been known that the first legs of palaemonid prawns may be used in food-collection; but the mode of operation as described by Borradaile (1917) is quite different from that found in *A. custos*. According to that author small particles of food are seized by the chelae and conveyed to the mouthparts, usually to the second maxillipedes. *A. custos* does not show such raptorial feeding.

In *A. custos* the chelae are used as scrapers to remove mucus and entangled food particles from the surface of the gill lamella of the host. As the prawn moves forwards along the edge of the gill lamella the first legs are continually in motion. The movements are somewhat difficult to observe since the distal part of these legs is directed inwards towards the gill lamella and is thus obscured by the body of the prawn in dorsal view and that of the host in ventral view. Our observations have been made in oblique, lateral view. Though a few details remain obscure it has been possible by this method to determine the main

outlines of the feeding process. Once the limb is in position for feeding, motion is largely confined to the distal portion. The laterally projecting merus acts as a gantry suspending the distal portion of the limb over the feeding surface. During the recovery stroke this distal portion swings backwards and upwards. As far as we can tell there is no contact with the gill lamella during this phase. At the end of this recovery stroke the chela is twisted so that its straight ventral edge is applied to the gill lamella with the concave posterior face facing forwards and downwards. The chela is then swung in an arc forwards

TABLE IV

Proventriculus and stomach contents of Anchistus custos and its host Pinna atropurpurea at Tg. Ponggol, Singapore

(Based on 26 specimens of *A. custos*)

	<i>Anchistus custos</i>		<i>Pinna atropurpurea</i> Occurrence in stomach
	No. of proventriculi in which present	Relative abundance	
General organic detritus	26	+++	—
Mucus	26	+++	p
<i>Coscinodiscus</i>	25	+++	p
<i>Navicula</i>	16	++	p
<i>Nitzschia</i>	10	+	p
Flagellates	16	+	p
Filamentous algae	14	+	p
Yeast	16	+++	—
Bacteria	25	+++	—

+++ , abundant; ++ , numerous × × ; + , not very numerous; — , absent; p , present.

and downwards towards the edge of the gill lamella and the mouthparts of the prawn. During this stroke mucus and food particles are scraped off the gill lamella and accumulate in the chela groove. The swing is continued so as to bring the chela into contact with the mouthparts. It is very difficult to observe what happens then but it appears that the mucus and food particles are scraped from the chela and transferred to the anterior mouthparts by means of the bristles on the second and third maxillipedes. It can be seen from this account that all the peculiarities of the leg can be accounted for as adaptations to this highly specialized feeding mechanism.

Food

If feeding occurs as described above then the food of *A. custos* should consist of materials obtained from the surface of the host gills. To check this the contents of the proventriculus of the prawn and the stomach of the host were examined.

Determination of the food of *A. custos* is complicated by the small size and thin walls of the proventriculus. Thus we were only able to obtain reliable results from 26 specimens.

Table IV gives the frequency in which the various food elements were encountered in these specimens. Mucus was not always immediately apparent but it could be demonstrated by staining with methylene blue. It was found that mucus and general detritus occurred in all specimens. Diatoms were also frequent and were often present in abundance. *Coscinodiscus* which occurred in all prawns save one was especially abundant. Flagellates and fragments of filamentous algae were not only less frequent but occurred in lesser abundance when present. The same food organisms were present in the stomach of the host. However bacteria and yeasts not found in the host were usually present in the proventriculus of the prawn. The yeast was an unusual one in which a large proportion of the population consisted of short filaments. Solitary cells exhibited characteristic yeast-like budding. As far as we can determine this form is an undescribed species. We were not able to find such bacteria and yeasts in water and mud samples from the locality nor in scrapings from the host gills. Thus there are grounds for regarding them as being commensal or symbiotic with the prawn.

The algae taken in by prawn and bivalve are all common at the collecting site. Carried on the feeding currents of the bivalve they are trapped in the mucus on its gills. A portion of this with the trapped algae is then scraped off by the prawn, and utilized as its principal food supply.

General discussion

Macnae & Kalk (1958) have propounded the view that *A. custos* is normally free living repairing to its host only for refuge and reproduction. The data which we have obtained on occurrence, behaviour, structure, feeding and food at Singapore, render this view untenable.

Our studies have provided a rational interpretation of the function of the peculiar first legs of this species. Other species assigned to the genus *Anchistus* do not have the first legs so modified and presumably do not possess such a specialized mode of feeding. It is probable that these forms should be removed from the genus. Certainly much less striking and fundamental distinctions have been used as a basis of generic separation elsewhere in the subfamily Pontoniinae. The genus *Anchistus* would then become a monotypic genus containing only *A. custos*.

The relations between *A. custos* and other commensals of *Pinna* is not fully clear. Jacquotte (1963) suggests, admittedly on incomplete evidence, that competition occurs between *Anchistus custos* and *Paranchistus*. Similarly our evidence suggests that pinnotherid crabs may also be competitors. Direct competition with species of *Conchodytes* appears to be unlikely. Unfortunately the rarity of that genus at Singapore has prevented us from testing this suggestion. However, if the species of *Conchodytes* have a biology similar to that of the obviously related form commensal with *Placuna* then they cannot be direct competitors for food.

Certain problems of behaviour and morphology remain obscure. In particular we have not been able to find any important use for the enlarged second legs or any behavioural mechanism which would account for the invariable presence of two sexes in multiple infections. The apparent absence of any aggressive or territorial behaviour is unexpected on both distributional and morphological grounds.

The occurrence of reproduction throughout the year is not unexpected in an equatorial

area. Incomplete unpublished evidence indicates that pan-seasonal reproduction is common amongst littoral crustaceans at Singapore. However, it is by no means universal. Hall (1962) has demonstrated pronounced seasonality in the reproduction of penaeids. Seasonal changes are quite pronounced in the Singapore littoral region and involve such factors as water temperature, salinity, rainfall and the amount of exposure to strong sunlight. This last factor is in part a consequence of the peculiar local tidal regime. For about half the year, April to September, the lowest tides occur in the early morning. For the remainder of the year they occur in the late afternoon. Thus continual reproduction in *A. custos* and other littoral crustaceans is evidence for a fairly pronounced eurytopy.

We have been unable to demonstrate damage caused by prawns to host tissues. This contrasts with the occasional reports of damage caused by pinnotherids (Silas & Alarga-swami, 1965). The amount of food consumed by the prawn is small. Thus even in multiple infections it is likely to be unimportant relative to the total food supply available to the bivalve. Thus *A. custos* appears to be a harmless commensal.

Summary

Anchistus custos is an abundant commensal of bivalves of the species *Pinna atropurpurea* at Singapore and is the only common prawn commensal with these bivalves in that area. Offshore populations of *Pinna* and mature beach populations, but not populations consisting of small individuals, are heavily infested with these prawns. The infestation rate increases with increasing average size of host individual.

Multiple infestations, which always involve members of both sexes, though not necessarily in equal numbers, are common.

Pinnotherid crabs are also commensal with *P. atropurpurea* and there is evidence for competitive exclusion between them and *Anchistus custos*.

A. custos does not normally occur away from its host.

A. custos shows pronounced structural modifications, especially of its first pair of legs, for its mode of life.

Individuals live in the host mantle cavity and spend most of their time clinging to the free edge of the gill lamella. The third to fifth legs are used for clinging whilst the pleopods give propulsive power in slow locomotion. Prawns leave their host immediately on its death and are repelled by dead *Pinna* flesh and extracts of *Pinna* flesh.

Location of the host appears to depend on a combination of random searching, positive rheotaxy, and contact stimuli. There is no evidence that any distance chemical perception is involved.

The highly modified first legs show slight negative allometry when compared with carapace length. They function as scrapers removing food organisms and mucus from the gills of the host and are the only important food collecting organs.

The proventriculus contains bacteria and yeasts in addition to food particles. These appear to be commensals or symbionts.

The function of the enlarged second legs remains obscure. Their size and form and marked positive allometry in the male suggest that they are used for sexual, aggressive, or territorial defence purposes; but these suggestions conflict with the apparent absence of such behaviour.

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