

# ON THE BIOLOGY OF *PONTOPHILUS SPINOSUS* (LEACH)

by

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## Résumé

*Pontophilus spinosus* occupe des zones sublittorales de sable et de cailloutis propres, couverts d'Hydres et de Bryozoaires. Les femelles mûres pondent une fois par an, entre la fin de novembre et le début de mars. Les larves éclosent en mai et les zoés apparaissent dans le plancton de mai à juillet. Les adultes arrivent sans doute à maturité 18 mois après l'éclosion, lorsque la carapace atteint respectivement 8 à 9 mm de long chez les femelles et 7 à 8 mm chez les mâles. Quelques femelles peuvent pondre une seconde fois l'année suivante, quand la longueur de la carapace a augmenté de 2 à 3 mm. Elles émettent de 200 à 600 œufs.

La plupart des adultes ont une livrée remarquable par sa couleur et par les taches blanc-verdâtre pâle qu'elle présente sur diverses parties de la surface dorsale. Les variations de la disposition des taches sont décrites et leur fréquence représentée par des figures.

*P. spinosus* semble se nourrir essentiellement de Polychètes Ampharetidae et Amphictenidae.

In the course of investigations of the sublittoral Caridea off the Northumberland coast (Allen 1959, 1960, 1963) approximately 200 specimens of *P. spinosus* were collected. Although this is a relatively small number, specimens were caught in each month of the year and examination of these has given information on the life history of this shrimp. Because the offshore sampling programme for this investigation has been completed and because there appears to be little account of the biology of *P. spinosus* in the literature, a record of this data would seem to be useful.

The methods used in this investigation have been fully reported in previous papers (Allen 1959, 1960). Briefly, sampling was carried out with a  $\frac{3}{4}$ " mesh, 9ft Agassiz Trawl, at four stations off the Northumberland coast (Allen 1963, fig. 1). Each haul was 20 minutes duration. The catch was sorted, a few specimens were kept alive for aquarium observations, the remainder measured and preserved. Carapace length (from the posterior rim of the eye socket to the posterior lateral edge of the carapace) and total length (from the tip of the rostrum to the tip of the telson in the extended animal) were measured to the nearest 0.1 mm. The shrimps were also examined for food contents of the stomach, maturity of the gonad, egg numbers, secondary sexual characters, larval development and colour variation.

*Pontophilus spinosus* occurs in the eastern Atlantic. Its northern limits are lat. 62° 35' off the Norwegian coast and off the south coast of Iceland. From here it is found southwards to the Bay of Biscay and the Mediterranean in depths ranging from 10 to 863 fathoms (Kemp 1910). It occurs off all British coasts. Off Northumberland, the adults are taken where the bottom has a covering of zoophytes. It occurred at two of the main collecting stations and of these it appears to favour the clean shell gravel of Station D (29 fm) rather than the muddy gravel of Station B (22 fm) (Table 1 and Allen 1963 fig. 1).

TABLE 1

Showing numbers of *P. spinosus* caught in each month of the year during the period 1958-1961. Also given is the total number of hauls in each month and the number of hauls with *Pontophilus* present.

	STATION D			STATION B		
	N° of <i>Pontophilus</i>	N° of hauls with <i>Pontophilus</i>	Total n° of hauls	N° of <i>Pontophilus</i>	N° of hauls with <i>Pontophilus</i>	Total n° of hauls
January.....	65	3	3	1	1	4
February.....	24	2	2	—	—	1
March.....	7	2	2	—	—	4
April.....	7	1	2	1	1	1
May.....	2	1	1	—	—	1
June.....	—	—	1	5	2	2
July.....	—	—	3	1	1	3
August.....	9	2	2	1	1	2
September.....	3	1	1	1	1	6
October.....	4	1	1	—	—	2
November.....	37	3	3	4	1	2
December.....	20	1	1	—	—	—
	178	17	22	14	8	28

Animals kept in the aquarium usually hold on to hydroids with their posterior pereopods. For long periods they remain motionless with the body flexed so that in lateral view the dorsal surface is markedly concave, i.e. the reverse of the normal body flexure of carideans. This motionless pose together with the characteristic greenish-white banding of the body makes an effective camouflage which is probably of considerable value in the capture of unsuspecting prey. This catalepsis also appears to be a fright reaction, for when the catches were being sorted *Pontophilus* frequently took up this pose and maintained it even though handled and narcotized. Aquarium specimens were also found on the surface of the gravel. Feeding was not observed.

There was considerable variation in the number of *P. spinosus* in each haul. Nearly 80 p. 100 of the specimens were collected between November and February (Table 1 and 2). Similar variation has been reported in the case of *Processa caniculata* and *Spirontocaris lilljeborgii* (Allen 1961, 1962). In the case of the two latter species

the largest numbers were caught immediately prior to egg laying. This was also true of *P. spinosus*, although relatively large numbers were also caught after egg laying had commenced, possibly because of the prolonged egg laying period. Gregariousness is no doubt an advantage at the time of copulation, particularly so when, as in the case of *S. lilljeborgii* females outnumber males by five to one. There is no such disparity in the case of *P. spinosus* in fact more males than females were caught in this investigation. The results show no evidence of migration in this species.

TABLE 2  
Analysis of the catches of *Pontophilus spinosus*

DATE	STATION	MALES	FEMALES - EGGS	FEMALES + EGGS	FEMALES TOTALS
23.1.58	B	0	1		1
23.4.58	B	0	1		1
18.6.56	B	3	1		1
29.6.59	B	1			0
9.7.59	B	0	1		1
4.8.59	B	0	1		1
1.9.59	B	1			0
10.11.59	B	3	1		1
11.11.59	D	15	10		10
23.11.59	D	2	2*	2	4
5.1.60	D	6	3	1	4
25.1.60	D	19	12*	8	20
4.8.60	D	3	1		1
18.8.60	D	4	1		1
15.9.60	D	2	1		1
17.10.60	D	4			0
15.11.60	D	6			0
13.12.60	D	12	7*	1	8
14.1.61	D	9	3	4	7
14.2.61	D	2		1	1
21.2.61	D	16	1	4	5
6.3.61	D	0		2	2
18.3.61	D	1	1	3	4
25.4.61	D	2		5	5
5.5.61	D	1		1	1
		112			80
*Specimens in breeding dress or that have lost eggs.					

### GROWTH AND BREEDING

The carapace measurements of the collected specimens are included in the histogram figure 1. It is probable that most of those caught between November and February belong to a single age group.

The average carapace length of the males of this group is 7.4 mm in November and 8.4 mm in February. Similarly, the average length of the females increases from 8.2 mm to 9.8 mm over the same period. Using this group of shrimps as a starting point, by inspection it is

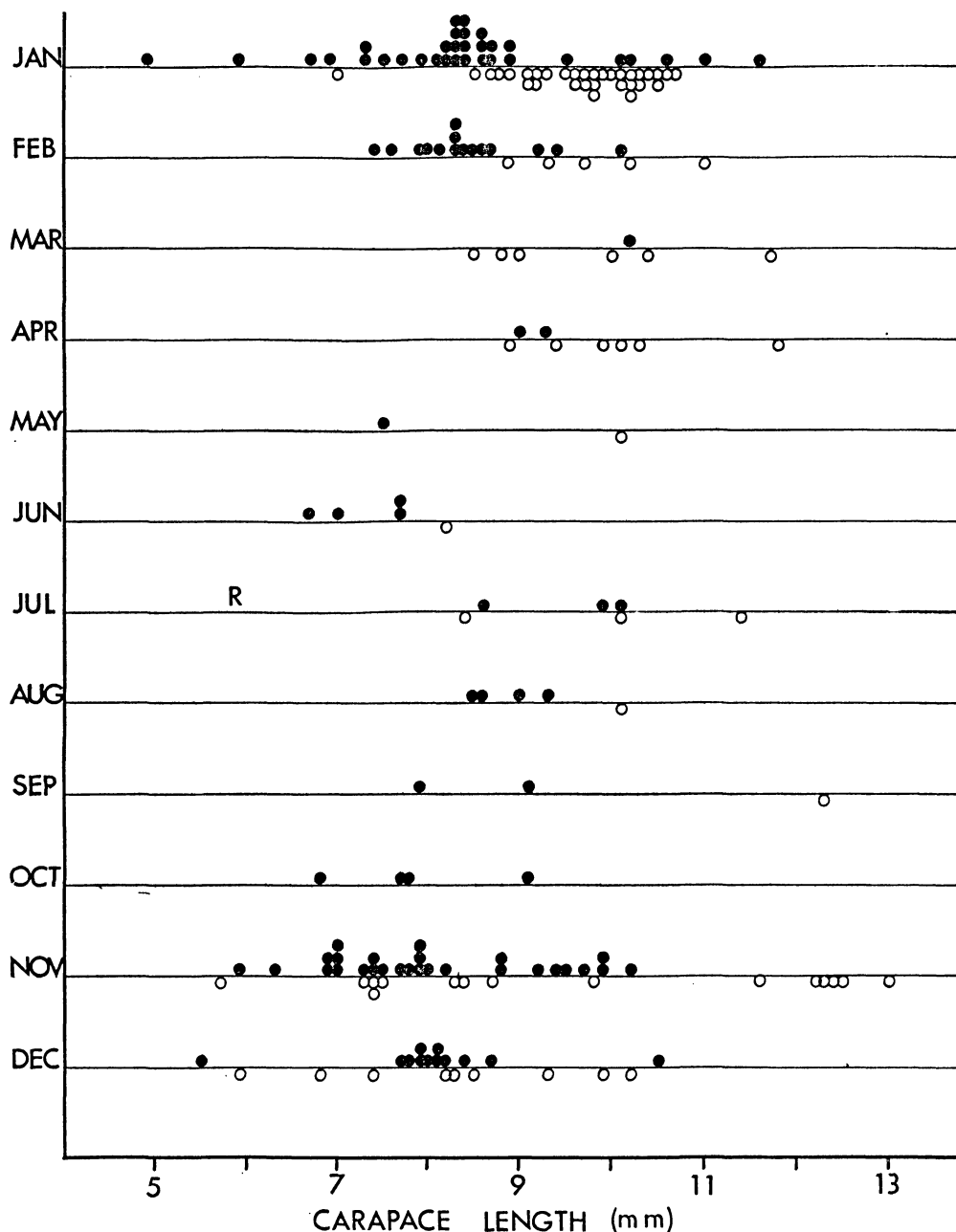


Fig. 1.—Monthly size/frequency histograms of those samples of *P. spinosus* collected between 1958-61.

Black circles above the line are males, open circles below the line, females.

possible to get some indication of the growth rate of *P. spinosus*. The results are shown as average growth rates at the top of figure 2. By extrapolation it is likely that most of those caught between November and February are 18 months old and the maximum life span of the Northumberland population will not be less than three years. The largest specimen collected was a female measuring 13.0 mm carapace length, the largest male measured 11.6 mm carapace length.

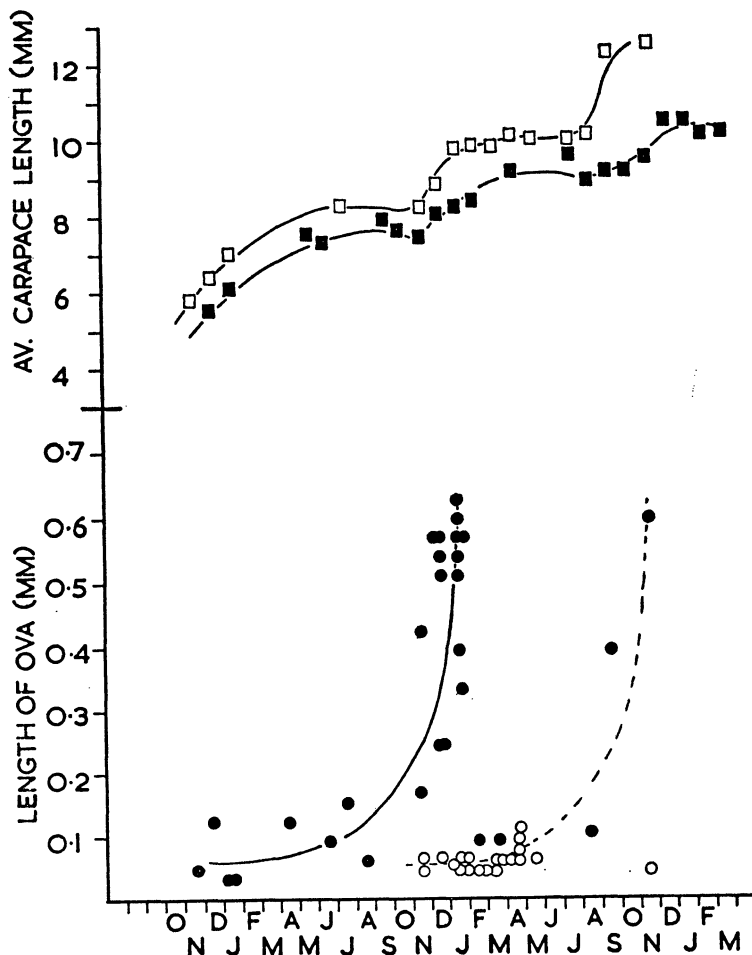


Fig. 2.—The upper graph shows the estimated average growth rate of male (black squares) and female (open squares) *P. spinosus*. The lower graph plots the growth of the ova in the ovary, open circles indicate ovigerous females. Both graphs are drawn to the same time scale.

*P. spinosus* is a dioecious species and no intersexes were found. As in most other carideans the male is smaller than the female of the same age (fig. 2). The body proportions of the two sexes are similar, growth is allometric and multiplication of carapace length by a factor of 3.45 will give total length.

Eggs are laid once a year and in this *P. spinosus* differs from other crangonids such as *Crangon vulgaris* and *C. allmani*. In the

case of the two latter species the oocytes in the ovary proliferate and mature while the first batch eggs are carried and immediately after the larvae are released, a second batch of eggs are laid. The gonads of *P. spinosus* show that there is no immediate development of the remaining oocytes after egg laying (fig. 2). Assuming that the suggested growth curve is correct, in the first winter after the release of the new year group (6 months) the ova in the ovary are small, less than 0.1 mm, and they do not begin to increase in size until the September of the second year (16 months). Between September and December the growth of the ova is very rapid and follow the typical exponential curve such as has been recorded for other carideans (Allen 1959, 1960, 1963). The testes and vas deferens show a similar development. The earliest date that ovigerous females were captured was 23rd November (Table 2). The ovigerous females were divided into three groups according to the stage of development of the embryo (a) recently laid eggs with early blastoderm, (b) early

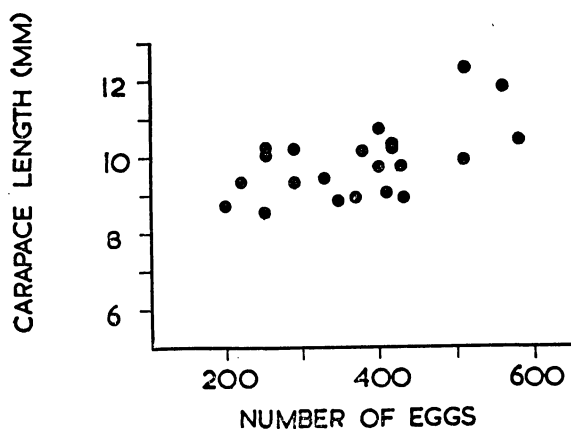


Fig. 3.—The variation of egg number with size in *P. spinosus*.

segmentation of the body and (c) well developed embryo within the abdomen free from the body and little yolk present. The eggs of the ovigerous females caught in November and December were at stage *a*, eggs at stage *b* were first recorded in January and those at stage *c* in April (Table 3). Recently laid eggs were recorded between November 23rd and March 6th but egg laying appears to reach a maximum in January. No ovigerous females were taken between June and October. A few females survive to breed a second time (fig. 2). Only two specimens were taken in breeding dress, one in December and one in January. However a number of specimens were recorded in which the eggs failed to attach to the pleopods and these, but for the lack of mature ova in the ovary, would have been classified as in breeding dress (Tables 2 and 3). Between 200 and 600 eggs are laid. Although there is a tendency for the larger females to carry more eggs (fig. 3) this is not so marked as in the case of other carideans (Allen 1959, 1960 and 1963). Thus the variation in eggs counts of ovigerous females measuring 10 mm carapace length almost covers the entire numerical range (fig. 3). The smallest ovigerous female

measures 8.5 mm carapace length. The eggs are spherical when first laid and are relatively small measuring approximately 0.6 mm in diameter. Immediately before release of the larvae, the length of the egg envelope measures about 0.9 mm.

TABLE 3  
Analysis of the condition of mature  
female *P. spinosus* during the breeding season

	Breeding Dress	Stages of Egg Development			Eggs lost	Without Eggs
		a	b	c		
November .....	—	2	—	—	—	13
December .....	1	1	—	—	—	6
January.....	1	8	5	—	8	9
February .....	—	2	3	—	—	1
March .....	—	2	3	—	1	—
April .....	—	—	3	2	—	1
May.....	—	—	—	1	—	—

The few records of breeding times for this species outside the Northumberland area fall within the period given above. The Marine Biological Association (1957) in addition to recording ovigerous females in these months also reports a record by Dr. Lebour for October. Zoea larvae have been recorded off the Northumberland coast in May and July by Jorgensen (1923) and in May and June by Bossanyi (1957). The latter author also recorded a postlarva in June and young adult stage in July. The smallest adult taken on the present survey was taken in January and measured 4.9 mm carapace length, other young immature adults less than 6.0 mm carapace length were taken in November and December. It seems probable that these specimens were hatched in the preceding May or June.

#### COLOUR VARIATION

Kemp (1910) describes the colour pattern of the adults, noting particularly the conspicuous greenish-white markings. Initially, little notice was taken of the colour pattern but later, when the first large winter sample was collected, it was noticed that there was considerable variation in the number and extent of the pale green markings and records were kept of the differences in the pattern. The results are analysed in figure 4 and Table 4. The pale green markings are found at nine main positions on the dorsal side of the shrimp. The maximum extent of these is shown in the composite figure 4A, but no specimen was caught that corresponded with this figure. The maximum number of positions recorded for any one shrimp was seven, and three specimens were taken without pale green markings. Eighteen different patterns were recorded (Table 4) and a selection of these is illustrated

in figure 4. The band stretching across the anterior half of the uropods and telson (position *h*), was recorded in all those with markings. Almost as frequent in occurrence is the band across the posterior edge of the 3rd abdominal segment. Least frequent were positions *b*

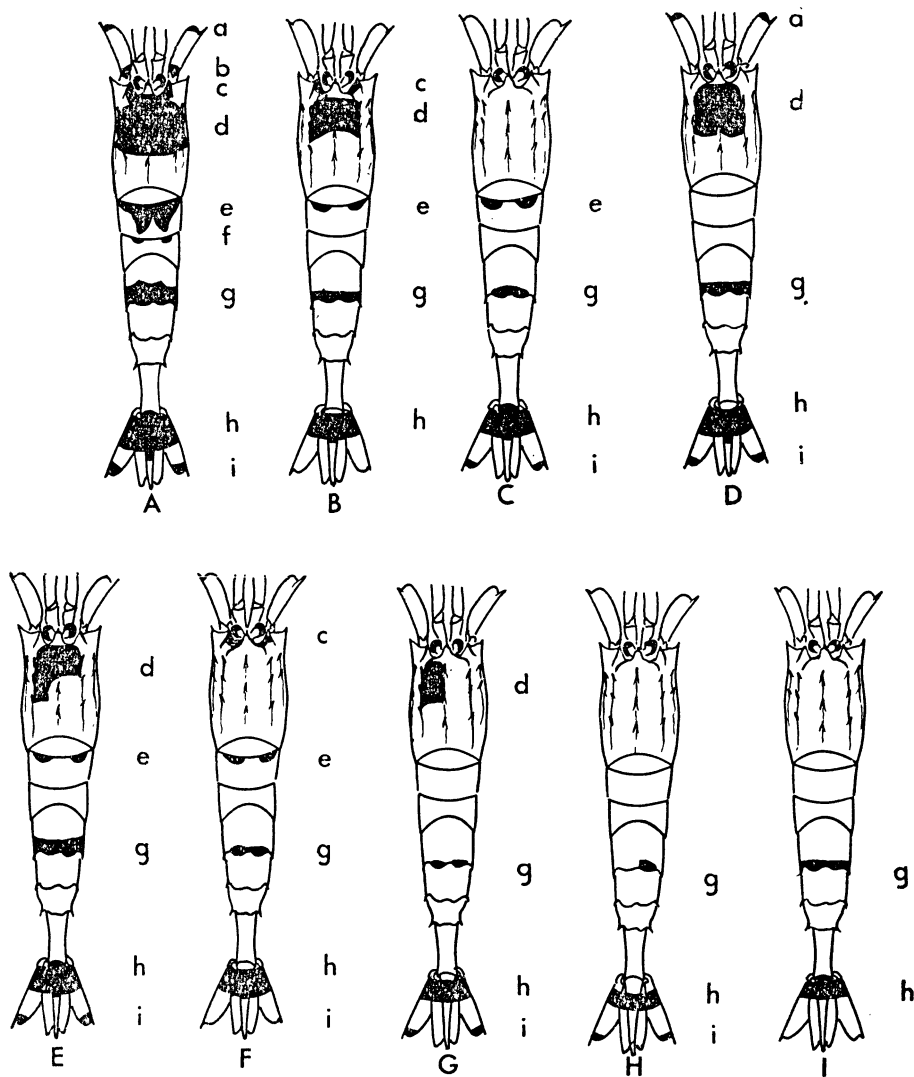


Fig. 4.—To show the range of variation of the pattern of the pale green markings of *P. spinosus*. The markings are shown as black areas. Figure A is a composite drawing to show the maximum extent of the green coloration, the remaining figures B - I are observed patterns.

and *f* (fig. 4) which were only recorded once. The majority of the specimens (68 p. 100) have four or more markings and correspond to the description given by Kemp (1910). The 'spectrum' of variation appears continuous and no colour varieties can be defined, even the extent of individual markings varies enormously and these may be



asymmetrical (fig. 4). There was no change in individual colour patterns during the relatively short periods that specimens were kept alive in the aquarium.

TABLE 4  
Analysis of the green colour pattern of *P. spinosus*  
for key to markings a - i see fig. 4.

Type of markings																	N° of Specimens		
a	+	+	+	-	-	-	-	-	+	-	+	-	-	-	-	-	15		
b	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	1		
c	-	+	-	+	-	+	-	+	-	-	-	+	-	-	-	-	18		
d	+	+	+	+	+	+	+	+	+	-	-	-	+	-	-	-	34		
e	+	+	+	+	+	-	+	+	-	+	-	+	+	-	-	-	29		
f	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1		
g	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+	48		
h	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	54		
i	+	+	+	+	+	+	+	-	+	+	+	-	-	+	+	-	40		
N° of Specimens	1	2	8	5	1	6	3	3	3	2	1	2	2	6	2	3	4	3	57 Total
N° of markings	7	7	6	6	6	5	5	5	5	4	4	4	4	3	2	2	1	0	
	3		14			15				7				6	5		4	3	

## FOOD

The stomachs of 109 specimens were examined for food contents. Of these, 68 had no food present and of the remaining 41, 29 contained annelid remains. The latter appeared to consist largely of unidentifiable ampharetids and amphictenids. Apart from the small ophiuroid fragment the only other recognizable remains were amphipod fragments which occurred in 6 stomachs. Invariably sand grains were mixed with the food. *P. spinosus* resembles the other crangonids of the area feeding predominantly on annelids. All have sharp toothed mandibles without incisor processes (Allen 1962). In the case of *P. spinosus* each mandible has two, pointed, terminal teeth.

## Summary

*Pontophilus spinosus* inhabits sublittoral clean sandy gravels which have a covering of hydroids and bryozoa. Mature females carry one brood of eggs each year these are laid between late November and early March. The larvae hatch out during May and zoea have been reported in the plankton from May to July. The adults probably come to maturity eighteen months after hatching when the females measure between 8 and 9 mm and the males between 7 and 8 mm carapace length respectively. Some may spawn a second time one year later when the carapace length has increased by a further 2 or 3 mm. They lay between 200 and 600 eggs.

Most adults have a striking colour pattern of pale greenish-white patches on various parts of the dorsal surface. The variations in this colour pattern are described and the frequency of their occurrence tabulated.

*P. spinosus* appears to feed mainly on ampharetid and amphictenid polychaetes.

### Zusammenfassung

*Pontophilus spinosus* lebt in sublittoralen sauberen Sand- und Schotterzonen, die mit Hydroiden und Bryozoen bedeckt sind. Reife Weibchen tragen jährlich eine Brut von Eiern, die zwischen Ende November und Anfang März gelegt werden. Die Larven schlüpfen im Mai und die Zoeae werden von Mai bis Juli im Plankton gefunden. Die Adulttiere erreichen die Geschlechtsreife wahrscheinlich achtzehn Monate nach dem Schlüpfen, d.h. wenn die Länge des Panzers der Weibchen zwischen 8 und 9 mm und diejenige der Männchen zwischen 7 und 8 mm erreicht. Einige Weibchen schreiten ein Jahr später, wenn die Panzerlänge um 2 bis 3 mm zugenommen hat, ein zweites Mal zur Eiablage. Sie legen zwischen 200 und 600 Eiern.

Die meisten Adulttiere haben auf verschiedenen Teilen der Dorsalfläche ein fleckenförmiges bleiches, weisslich-grünes Farbmuster. Die Variationen dieses Farbmusters werden beschrieben und die Häufigkeit seines Auftretens tabellarisch dargestellt.

Es scheint, dass *P. spinosus* sich vorwiegend von ampharetiden und amphicteniden Polychaeten ernährt.

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