

The Breeding Biology of two Sympatric Species of Tropical Intertidal Hermit Crabs, *Clibanarius chapini* and *C. senegalensis*

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Abstract

A one-year study of breeding in the two intertidal hermit crabs *Clibanarius chapini* Schmitt and *C. senegalensis* Chevreux and Bouvier showed that both species maintain a high reproductive activity throughout the year. Brief low reproductive activities, found in both species, occurred in different months: *C. chapini* in November, *C. senegalensis* in May. While these drops cannot be attributed to any recognisable environmental factor, it is suggested that such pattern may result from competition between the two species. Sex-ratio studies indicated slightly more females than males in both species. The maximal size attained by males of both species is considerably greater than that of the females; in *C. senegalensis* this is very marked. It is suggested that it may be selectively advantageous for a female to attain a smaller maximal size since her brood must also be accommodated within the shell. As expected for continuously breeding species, recruitment of young into the population is also continuous.

Introduction

There has been considerable interest in the reproductive cycles of tropical marine invertebrates with regard to some environmental factors. Thorson (1946, 1950), Gunter (1957), Moore (1958) and Giese (1959) emphasize temperature as an important controlling factor. Sandoz and Rogers (1944), Knight (1967), and Buchanan and Milleman (1969) consider the effects of salinity, while Knowlton (1965) shows the importance of food. However, complete studies of breeding cycles of marine invertebrates have been fragmentary (Goodbody, 1965).

Among crustaceans, continuous breeding cycles have been reported in *Puggetia producta* (Booolootian *et al.*, 1959), *Mysidium columbiae* and *Emerita portoricensis* (Goodbody, 1965), *Petrolisthes elongatus* (Greenwood, 1965), *Calcinus laevimanus* and *C. latens* (Reese, 1968) — both with brief quiescent periods, and *Clibanarius zebra* (Reese, 1968). As will be brought up later, all these species show breeding peaks and it is questionable as to the relevant trigger or triggers from the environment which might be involved.

Among the non-continuous breeders, Booolootian *et al.* (1959) provide data on *Pachygrapsus crassipes* and *Emerita analoga* from the Californian coast. *Palaemonetes pugio* is a summer breeder (Little, 1968), so is *Palaemon macrodactylus* (Little, 1969). *Uca pugilator* breeds actively between May and October (Herrnkind, 1968). *Carcinus tibicensis* and *Clibanarius tricolor* from Barbados, West Indies, are both seasonal breeders (Lewis, 1960).

In this work, the breeding biology of two species of *Clibanarius*, *C. chapini* and *C. senegalensis*, has been investigated to add to our knowledge in this area of crustacean biology.

Material and Methods

Hermit crabs were obtained at Tenggobo, a fishing village near Prampram (ca. 6°N), about 60 km to the east of Accra, Ghana. Two-meter quadrat samples were collected from late September, 1969 to June, 1970. Thereafter, non-quantitative observations were made up to September, 1970 so as to complete a whole year of observations. The collected crabs were taken to the Department of Zoology, University of Ghana, Legon. Various methods employed are described under each subtopic.

Observations

Breeding Period

Throughout the sampling period, ovigerous females of both species were present in all samples. During the first 6 weeks, sampling was done weekly; thereafter, samples were taken once a fortnight or once a month.

Tables 1 and 2 show the numbers of female crabs in berry in each sample; places and dates of sampling are also given.

Fig. 1 illustrates the percentages of females in berry in monthly samples. In both species there was a consistently high percentage of females in berry throughout the period of sampling, except for a sharp drop in the case of *Clibanarius chapini* in November, 1969 and in *C. senegalensis* in May, 1970.

Table 1. *Clibanarius chapini*. Percentage females in berry and those with and without ovarian eggs collected at Tengpobo, Ghana

Date	Distance from MLT mark; seaward (m) ^a	No. of females collected	No. with eggs	% total with eggs	No. in berry	% total in berry	% total with ovarian eggs only
1969							
24 Sept.	10	16	16	100.0	14	87.5	12.5
4 Oct.	10	14	12	85.7	11	78.5	7.2
24 Oct.	10	63	58	92.0	47	75.0	17.0
	100	137	109	79.5	82	60.0	19.5
31 Oct.	50	2	2	100.0	2		
	beyond 100	60	58	96.0	57	95.0	1.0
12 Nov.	10	71	69	97.2	29	41.0	56.2
	50	36	28	77.8	20	55.8	22.0
	100	18	10	55.6	4	22.3	33.3
28 Nov.	10	21	12	57.1	5	24.0	33.1
	50	16	14	87.5	7	43.8	43.7
12 Dec.	10	234	212	90.0	152	65.0	25.0
	50	64	41	64.0	29	45.4	18.6
1970							
23 Jan.	10	78	63	81.0	61	78.2	2.8
	50	315	275	87.3	252	80.0	7.3
	100	106	86	81.0	79	75.0	6.0
11 Feb.	10	113	108	95.6	49	43.5	52.1
	50	40	34	85.0	29	72.5	12.5
	100	54	53	98.0	53	98.0	98.0
27 Feb.	10	76	50	65.8	47	62.0	3.8
	50	72	67	93.1	63	87.5	5.6
	100	54	54	100.0	48	88.9	11.1
20 March	10	121	117	96.7	109	90.1	6.6
	50	74	70	94.6	66	89.2	5.4
	100	42	42	100.0	42	100.0	0.0
20 April	10	136	131	96.3	124	91.2	5.1
	50	70	67	95.7	66	94.3	1.4
23 May	10	29	26	89.5	23	79.5	10.0
	50	132	125	94.5	121	91.5	3.0
20 June	10	152	139	91.4	130	85.5	5.9

^a10, 50 and 100m are distances from MLT (mean low tide) mark, seaward, to points of collection. All collections were made at low tide, and the areas were covered by no more than 25 cm water.

Table 2. *Clibanarius senegalensis*. Percentage females in berry and those with and without ovarian eggs collected at Tengepobo, Ghana

Date	Distance from MLT mark; seaward (m) ^a	No. of females collected	No. with eggs	% total with eggs	No. in berry	% total in berry	% total with ovarian eggs only
1969							
29 Sept.	10	158	137	86.7	111	69.8	16.9
4 Oct.	10	54	47	87.0	30	55.8	31.2
	50	32	27	84.5	22	69.0	15.5
15 Oct.	10	75	66	88.0	46	61.3	26.7
24 Oct.	10	320	280	88.5	250	78.0	10.5
	50	26	19	73.0	16	61.6	11.4
	100	9	8	89.0	4	44.5	44.5
31 Oct.	10	61	53	87.0	34	56.0	31.0
	50	67	60	90.0	45	67.3	22.7
	100	54	48	89.0	41	76.0	13.0
	beyond 100	19	15	79.0	15	79.0	0.0
12 Nov.	10	7	6	85.8	5	71.5	14.3
	50	34	31	91.2	25	73.5	17.7
	100	2	2	100.0			
28 Nov.	10	53	37	69.7	25	47.3	22.4
	50	301	281	93.3	208	69.0	24.3
12 Dec.	10	125	92	73.8	72	57.8	16.0
1970							
23 Jan.	10	96	81	84.3	77	80.0	4.3
	50	200	173	86.5	162	81.0	5.5
	100	21	8	38.2	5	23.8	14.4
11 Feb.	10	44	39	88.6	32	73.0	15.6
	50	39	35	90.0	29	74.5	25.5
	100	84	82	98.0	82	98.0	0.0
27 Feb.	10	104	80	76.9	68	86.4	11.5
	50	22	21	95.5	18	81.8	13.7
	100	64	62	96.9	58	90.6	6.3
20 March	10	50	46	92.0	45	90.1	1.9
	50	28	24	85.7	23	82.1	2.6
	100	87	84	96.6	77	88.5	8.1
20 April	10	70	58	82.9	55	78.6	4.3
	50	73	68	93.2	63	86.3	6.9
23 May	10	161	111	69.0	63	39.0	30.0
	50	168	162	96.5	82	48.8	47.7
20 June	10	95	89	93.7	64	67.4	26.3

^a10, 50 and 100m are distances from MLT mark, seaward, to points of collection. All collections were made at low tide, and the areas were covered by no more than 25 cm water.

Table 3. *Clibanarius chapini* and *C. senegalensis*. Total numbers of females with single and double batches of embryonic stages

Date	Distance from MLT mark; seaward (m)	<i>C. chapini</i>					<i>C. senegalensis</i>				
		No. with eggs	No. with 1 batch		No. with 2 batches		No. with eggs	No. with 1 batch		No. with 2 batches	
			No.	% total	No.	% total		No.	% total	No.	% total
1969											
29 Sept.	10	16	2	12.5	14	87.5	137	26	18.0	111	82.0
4 Oct.	10	12	1	8.3	10	91.7	47	23	49.0	24	51.0
	50						27	6	22.3	21	77.7
24 Oct.	10	58	11	19.0	47	81.0	280	30	10.8	250	89.2
	50	9	4	44.5	5	55.5	19	5	26.4	14	73.6
	100	109	27	24.8	82	75.2	9	4	44.5	5	55.5
31 Oct.	10						53	20	37.8	33	62.2
	50						60	27	45.0	33	55.0
	100						48	9	18.8	39	81.2
	beyond 100	58	57	98.5	1	1.5	15	3	20.0	12	80.0
12 Nov.	10	69	42	61.0	27	39.0	6	2	33.3	4	66.7
	50	28	8	28.5	20	71.5	31	9	29.0	22	71.0
	100	10	6	60.0	4	40.0					
28 Nov.	10	12	11	92.0	1	8.0	37	25	67.5	12	32.5
	50	14	7	50.0	7	50.0	281	90	32.0	191	68.0
12 Dec.	10	212	78	36.7	134	63.3	92	27	29.4	65	70.6
	50	41	18	44.0	23	56.0					
1970											
23 Jan.	10	63	8	12.7	55	87.3	81	4	5.0	77	95.0
	50	275	25	9.1	250	90.9	173	11	6.4	164	93.6
	100	84	9	10.5	75	89.5	8	3	37.5	5	62.5
11 Feb.	10	108	78	72.2	30	27.8	39	17	43.6	22	56.4
	50	34	5	14.7	29	85.3	35	18	51.4	17	48.6
	100	53	15	28.3	38	71.7	82	28	34.1	54	65.9
27 Feb.	10	50	11	22.0	39	78.0	80	14	17.5	66	82.5
	50	67	15	22.4	52	77.6	21	4	19.0	17	81.0
	100	54	7	13.0	47	87.0	62	7	11.3	55	88.7
20 March	10	117	10	8.5	107	91.5	46	2	4.3	44	95.7
	50	70	4	5.7	66	94.7	24	1	4.2	23	95.8
	100	42	0	0.0	42	100.0	84	9	10.7	75	89.3
20 April	10	131	21	16.0	110	84.0	58	4	6.9	54	93.1
	50	67	3	4.5	64	95.5	68	7	10.3	61	89.7
23 May	10	26	3	11.5	23	88.5	111	50	43.5	61	56.5
	50	125	6	4.8	119	95.2	162	90	55.5	72	44.5
20 June	10	139	14	10.1	125	89.9	89	28	31.5	61	68.5

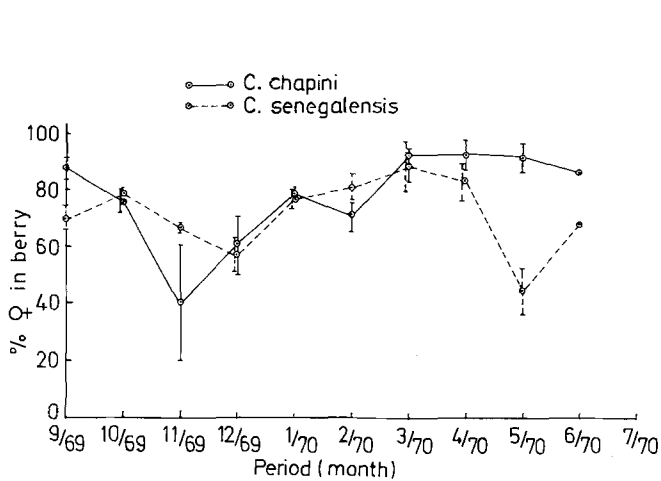


Fig. 1. *Clibanarius* spp. Percentages of females in berry in monthly samples, 1969 and 1970

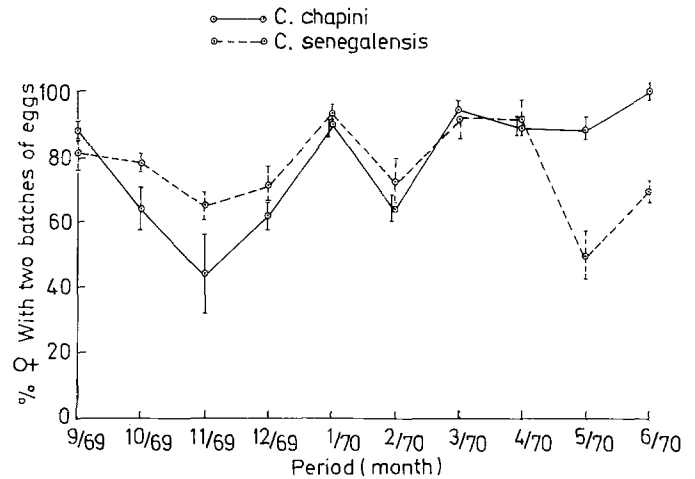


Fig. 2. *Clibanarius* spp. Total numbers of females with two batches of embryonic stages in monthly samples, 1969 and 1970

A single female may have two batches of embryonic stages at the same time, one batch developing oocytes in the ovary, and the second embryos (dividing eggs or larvae) on the 3 abdominal appendages. Table 3 shows the percentages of females with one batch and those with two batches of embryonic stages. In Fig. 2 the percentages of females with two batches of embryonic stages in monthly samples are illustrated. Most females had two batches of embryonic stages. Batch ratio reflects the drops in percentage females in berry recorded in November, 1969 and in May, 1970 for *Clibanarius chapini* and *C. senegalensis*, respectively. Both species breed throughout the year.

Fecundity

As indicated previously, a single female may possess two batches of embryonic stages, one in the ovary and the other on the pleopods. In egg counts, the two batches were considered separately. Crabs in berry were carefully removed from their shells after being narcotized to prevent loss of eggs or larvae from their appendages; 5-15 crabs of each species were used from each sample. The ovaries were dissected out, and the eggs separated and counted in small quantities (≈ 100), using a dissecting microscope. The appendages to which the eggs and larvae were attached were cut off, and the eggs or larvae separated.

In Table 4, the numbers of eggs in the ovary and on the abdominal appendages of individual females are shown. From this table, the following conclusions can be drawn: (1) Within the same size group there is considerable variation in the total number of eggs produced; (2) for each individual, the number of eggs in the ovary may differ markedly from the number on the abdominal appendages; (3) fecundity is consistently high throughout the year.

Egg Size

Measurements were made of the diameter of ovarian and pleopodal eggs. Three females of each species were used and 200 eggs were considered from each area. Fig. 3 shows typical histogram plots. A population of eggs from each area had about the same size, indicating that eggs from each location are most probably of the same age.

Mating Behaviour and Mode of Fertilization

Mating behaviour was observed twice in *Clibanarius chapini* and once in *C. senegalensis*. I could see no obvious differences between the two species. The following series of events were observed: Through some unknown mechanism, the male recognises the female (Hazlett, 1970, 1972, in a more detailed treatment of this topic, discusses the visual, chemical and behavioural orientational components involved.) The male faced the female and gripped the aperture of the female's shell with his ambulatory legs. He then pushed his chelipeds into the shell of the female, touching her legs in so doing. Then, at regular intervals, the male made pecking movements at the legs of the female with his chelipeds. He did not however grasp the female's legs. The pecking movement was periodically interrupted by a "shell-rocking" pattern. The male withdrew his chelipeds to grasp the edge of the female's shell. He then flexed and extended his chelipeds symmetrically so as to move the female's shell backwards and forwards. During this process a nubile female suddenly emerges from her shell as also does the male, and the two make ventral contacts for a few seconds. This is the copulatory act and, at the end of it, spermatophores are left at the genital openings of the female. The times recorded for this act for the three observations was between 4 and 7 sec. The basic pat-

Table 4. *Clibanarius chapini* and *C. senegalensis*. Numbers of eggs or larvae on abdominal appendages and numbers of eggs in ovaries from individuals of various size groups

Species	CL (mm)	No. of eggs/larvae on abdominal appendages ^a				Embryonic stage	No. of ovarian eggs ^b	Total	Species	CL (mm)	No. of eggs/larvae on abdominal appendages ^a				Embryonic stage	No. of ovarian eggs ^b	Total	
		1	2	3	Total						1	2	3	Total				
3 Oct. 1969								28 Nov. 1969										
<i>C. chapini</i>	4.0	ns	ns	ns	449	Old eggs	None	449	<i>C. chapini</i>	5.0	273	278	138	689	Old eggs	nc	689+	
	5.0	ns	ns	ns	403	Old eggs	None	403		5.5	176	187	103	466	Hatched larvae	nc	466+	
	5.0	301	311	269	881	Young larvae	None	881		5.5	166	178	91	435	Old eggs	nc	435+	
	5.0	138	122	94	354	Eggs about to hatch	None	354		5.5	ns	ns	ns	627	Old eggs	nc	627+	
	5.0	99	170	84	353	Eggs about to hatch	313	666		5.5	202	241	139	582	Old eggs	nc	582+	
	5.0	128	210	99	437	Old eggs	140	577		5.5	ns	ns	ns	299	Hatched larvae	319	618	
	5.0	163	277	224	664	Old eggs	nc	664+		<i>C. senegalensis</i>	3.0	ns	ns	ns	166	Hatched larvae	135	301
	6.0	ns	ns	ns	495	Larvae, just hatched	889	1384			4.5	195	271	182	648	Old eggs	nc	648+
4.5	ns	ns	ns	624	Old eggs	712	1336	4.5	192		240	132	564	Old eggs	nc	564+		
5.0	ns	ns	ns	439	Larvae, just hatched	910	1349	4.5	271		334	228	833	Old eggs	nc	833+		
5.0	178	287	90	555	Eggs about to hatch	1004	1559	5.0	153		149	48	350	Old eggs	274	624		
5.0	137	287	224	648	Eggs about to hatch	580	1228	5.0	127		154	60	341	About to hatch	682	1023		
5.0	224	352	146	722	Old eggs	nc	722	5.5	ns		ns	ns	654	Hatched larvae	497	1148		
5.5	237	280	181	698	Old eggs	604	1302	5.5	454		596	434	1484	Old eggs	nc	1484+		
5.5	ns	ns	ns	479	Larvae, just hatched	549	1028	5.5	468	631	339	1438	Old eggs	nc	1438+			
<i>C. senegalensis</i>	6.0	ns	ns	ns	1182	Old eggs	712	1894	6.5	ns	ns	ns	910	Hatched larvae	564	1474		
	6.0	85	269	148	502	Eggs about to hatch	nc	502+	12 Dec. 1969									
	6.0	ns	ns	ns	614	Larvae, just hatched	305	919	4.5	186	249	222	657	Old eggs	None	657		
									5.0	329	373	158	860	Old eggs	None	860		
<i>C. chapini</i>	5.0	ns	ns	ns					5.0	ns	ns	ns	472	Hatched larvae	None	472		
	5.5	347	508	392	1247	Old eggs	nc	1247+	5.5	357	471	263	1091	Old eggs	nc	1091+		
	5.5	280	313	183	776	Old eggs	None	776	5.5	280	313	183	776	Old eggs	None	776		
	6.6	442	466	240	1128	Old eggs	None	1128										

^ans: not separated; ^bnc: not counted.

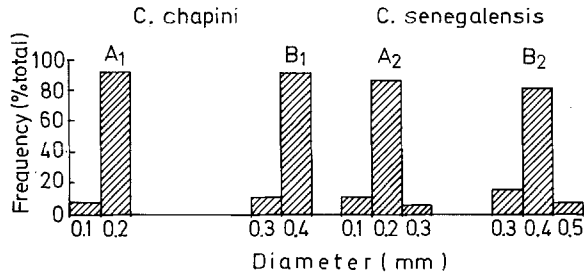


Fig. 3. *Clibanarius* spp. Histograms of egg sizes; A₁ and A₂: ovarian eggs; B₁ and B₂: pleopodal eggs

Table 5. *Clibanarius chapini* and *C. senegalensis*. Larval release

Species	Date (May, 1970)	Time (hrs)	No. of larvae released
<i>C. chapini</i>	21	21.30	160
	22	No release	-
	23	13.00	22
	24	22.30	178
	25	11.00	16
<i>C. senegalensis</i>	1. 21	21.00	86
	22	11.00	14
	23	22.00	172
	2. 21	20.00	90
	22	13.00	25
	24	23.00	243

terns observed are thus similar to those described for other diogenids (Hazlett, 1966, 1972).

Although the mode of fertilization is not clearly understood, presumably, as in other spermato-phore-carrying decapods, fertilization is internal (see Ryan, 1967), the sperm moving along the female's oviduct and fertilizing the eggs before oviposition.

Larval Release

Some observations were made in the laboratory on larval release. Zoea larvae were released in batches of 10 to 200. The time interval between any two successive batches can be as short as 5 min or as long as 24 h. Individuals in each batch were carried out of the female's shell in the exhalent current which passes ventral to the head,

in groups of 3, 4 or 5, at intervals of only a few seconds.

Larval release in both species occurs in the night. Observations were made on two females of *Clibanarius senegalensis* and one of *C. chapini* over a number of days. The times of release of batches and the number of larvae released in each batch was noted (see Table 5).

Observations made on females releasing their larvae revealed that batches of larvae do not necessarily all come from the same pleopod. A female which has almost completed releasing her larvae may still have some larvae in scattered areas on all three abdominal appendages.

The exact stimuli which lead to the release of these batches of larvae, apart from a diurnal variation, are not known. This is a question of some interest since the population of larvae are all seemingly at the same stage of development and yet are released over a period of as long as 5 days.

Sex Ratio and Size Groups

In the course of the study, observations were made on the sex ratios in the population. The size groups within the populations were analysed to obtain some idea of population dynamics of the two species.

In Tables 6 and 7, the sex ratio is recorded for each collection from different places on different dates. Although there are some cases which show a sex ratio of 1:1, in most cases there is a statistically significant deviation from this.

Fig. 4 presents histograms of size groups, as determined by cephalothorax length, of female and male *Clibanarius chapini*. There are two general features demonstrated by these histograms. First, there is a dominant size group amongst females which is not found amongst males. Second, the maximum size of the males in the samples is only slightly greater than that of the females.

In *Clibanarius senegalensis* a dominant size group is present among the females, but again absent in the males (Fig. 5). The males of this species attain much greater maximum size than in *C. chapini*.

Discussion

The almost constant states of the three factors presumed to be important in breeding of tropical marine invertebrates (temperature, salinity, and food), have led to the axiom that these species breed continuously. Whether or not these factors operate exclusively or together remains a matter of controversy (see Reese, 1968). The breeding cycles of the few species investigated reveal that peaks and dips in the cycles are common (Table 8).

Both *Clibanarius chapini* and *C. senegalensis* display high reproductive activity throughout the year (lowest, 40%; highest, 90%). An interesting feature is that both species have their lowest reproductive activities at different times of the

year, *C. chapini* in November and *C. senegalensis* in May. These dips cannot be attributed to changes in availability of food, nor to temperature or salinity changes. Both temperature and salinity display negligible variations on the beach throughout the year and there is an overabundance of food for the hermit crabs (Ameyaw-Akumfi, in preparation). While it can be suggested that such differential dipping in the cycles may result from competition, the factors involved are not known.

Giese (1959) points out that an extended breeding season may indicate that "the individuals of a species are producing several successive broods during the year or that they are breeding asyn-

chronously i.e. some are in earlier stages of maturation, some are getting ready to spawn, some are spawning and still others are already spent." Fig. 2, which illustrates the occurrence of two batches of embryonic stages, one in the ovary and one on the abdominal appendages, follows the same pattern as the plot illustrating only females in berry (Fig. 1). This suggests that there may be a production of several successive broods during a year. No studies were made on how many broods are produced by an individual female.

For a continuous breeder, one might predict continuous recruitment. Such is the case for both species in the present study. The marked differ-

Table 6. *Clibanarius chapini*. Sex ratio in individual samples

Date	Distance from MLT mark; seaward (m)	No. of males	No. of females	Total	% males	% females	Sex ratio (male: female)	P
1969								
29 Sept.	10	14	16	30	46.7	53.3	1:1.0	
4 Oct.	10	22	14	36	61.0	39.0	1:0.7	<0.95>0.05
24 Oct.	10	45	63	108	41.7	58.3	1:1.4	<0.95>0.05
	100	48	137	185	26.0	74.0	1:2.8	<0.001
31 Oct.	beyond 100	16	60	76	21.0	79.0	1:3.7	<0.001
12 Nov.	10	31	71	102	30.5	69.5	1:2.3	<0.001
	50	33	36	69	48.0	52.0	1:1.1	<0.95>0.05
	100	20	18	38	52.8	47.2	1:0.9	<0.95>0.05
28 Nov.	10	33	21	54	61.1	38.9	1:0.6	<0.95>0.05
12 Dec.	10	100	234	334	30.0	70.0	1:2.4	<0.001
	50	32	64	97	34.6	65.4	1:2.0	<0.001
1970								
23 Jan.	10	30	78	108	27.8	72.2	1:2.6	<0.001
	50	178	315	493	36.1	63.9	1:1.8	<0.001
	100	61	106	167	36.5	63.5	1:1.7	<0.005
11 Feb.	10	43	113	156	27.5	72.5	1:2.6	<0.001
	50	25	40	65	38.5	61.6	1:1.6	<0.1
	100	22	54	76	29.0	71.0	1:2.6	<0.001
27 Feb.	10	52	76	128	40.6	59.4	1:1.5	<0.05
	50	27	72	99	27.3	72.7	1:2.6	<0.005
	100	32	54	86	37.2	62.8	1:1.7	<0.05
20 March	10	30	121	151	19.9	80.1	1:4.0	<0.001
	50	46	74	120	32.3	61.7	1:1.6	<0.05
	100	15	42	57	26.3	73.7	1:2.5	<0.025
20 April	10	68	136	204	33.3	66.7	1:2.0	<0.005
	50	25	70	95	26.3	73.7	1:2.8	<0.005
23 May	10	12	29	41	29.3	70.7	1:2.3	<0.005
	50	33	132	165	20.0	80.0	1:4.0	<0.005
20 June	10	49	152	201	24.4	75.6	1:3.0	<0.005

ences in size patterns of males and females raise the question of their significance. One interpretation, that there was a highly successful "class" of females which dominate all samples seems untenable; samples had been collected at monthly intervals, and the modal size of the females remained effectively constant over a period of 9 months (Figs. 4 and 5). Although no direct information upon growth rates is available, it seems improbable that so stable a situation would have persisted for so long a period.

The data are more easily interpreted as indicating that the growth rate of the female slows mar-

kedly on attainment of sexual maturity. The inhibitory effect of egg-carrying on moulting in the female has been discussed by Passano (1960). It is possible that there is a direct selection for a check in growth rate independent of any nutritional drain. Unlike the males, females have to accommodate not only themselves, but also their brood within the confines of a gastropod shell and, should the female continue to grow beyond sexual maturity, she might be unable to find a suitable shell to accommodate herself and her brood. In fact, a survey of available empty shells of the species used by these crabs provided no evidence for a re-

Table 7. *Clibanarius senegalensis*. Sex ratio in individual samples

Date	Distance from MLT mark; seaward (m)	No. of males	No. of females	Total	% males	% females	Sex ratio (male:female)	P
1969								
29 Sept.	10	93	158	251	37.0	63.0	1:1.7	<0.001
4 Oct.	10	70	54	124	56.4	43.6	1:0.6	<0.95>0.05
	50	55	32	87	63.2	36.8	1:0.6	<0.95>0.05
24 Oct.	10	169	320	489	44.6	55.4	1:1.9	<0.001
31 Oct.	10	34	61	95	35.8	64.2	1:1.8	<0.01>0.001
	50	38	44	82	46.5	53.5	1:1.2	<0.95>0.05
	100	29	23	52	56.0	44.0	1:0.8	<0.95>0.05
12 Nov.	50	37	34	71	52.1	47.9	1:0.8	<0.95>0.05
28 Nov.	10	29	53	82	35.5	64.5	1:1.8	<0.01>0.001
	50	44	145	189	23.3	76.7	1:3.3	<0.001
	100	56	156	212	26.5	73.5	1:2.8	<0.001
12 Dec.	10	75	125	200	37.5	62.5	1:1.7	<0.01>0.001
1970								
23 Jan.	10	70	96	166	42.2	57.8	1:1.4	<0.1
	50	87	200	287	30.3	69.7	1:2.3	<0.001
	100	16	21	37	43.2	56.8	1:1.3	<0.1
11 Feb.	10	28	44	72	39.0	61.0	1:1.5	<0.1
	50	26	39	65	40.0	60.0	1:1.5	<0.1
	100	14	84	98	14.0	86.0	1:5.7	<0.001
27 Feb.	10	50	104	154	32.5	67.5	1:2.1	<0.005
	50	10	22	32	31.2	68.8	1:2.0	<0.001
	100	51	64	115	44.3	55.7	1:1.3	<0.5
20 March	10	45	50	95	47.3	52.6	1:1.1	
	50	13	28	41	31.7	68.3	1:2.1	<0.1>0.25
	100	31	87	118	26.3	73.7	1:2.8	<0.1>0.025
20 April	10	75	70	145	51.7	48.3	1:0.9	
	50	50	73	123	40.7	59.3	1:1.5	<0.100>0.25
23 May	10	153	161	314	48.7	51.3	1:1	
	50	54	168	222	25.3	75.7	1:3	<0.005
20 June	10	46	95	141	32.6	67.4	1:2	<0.005

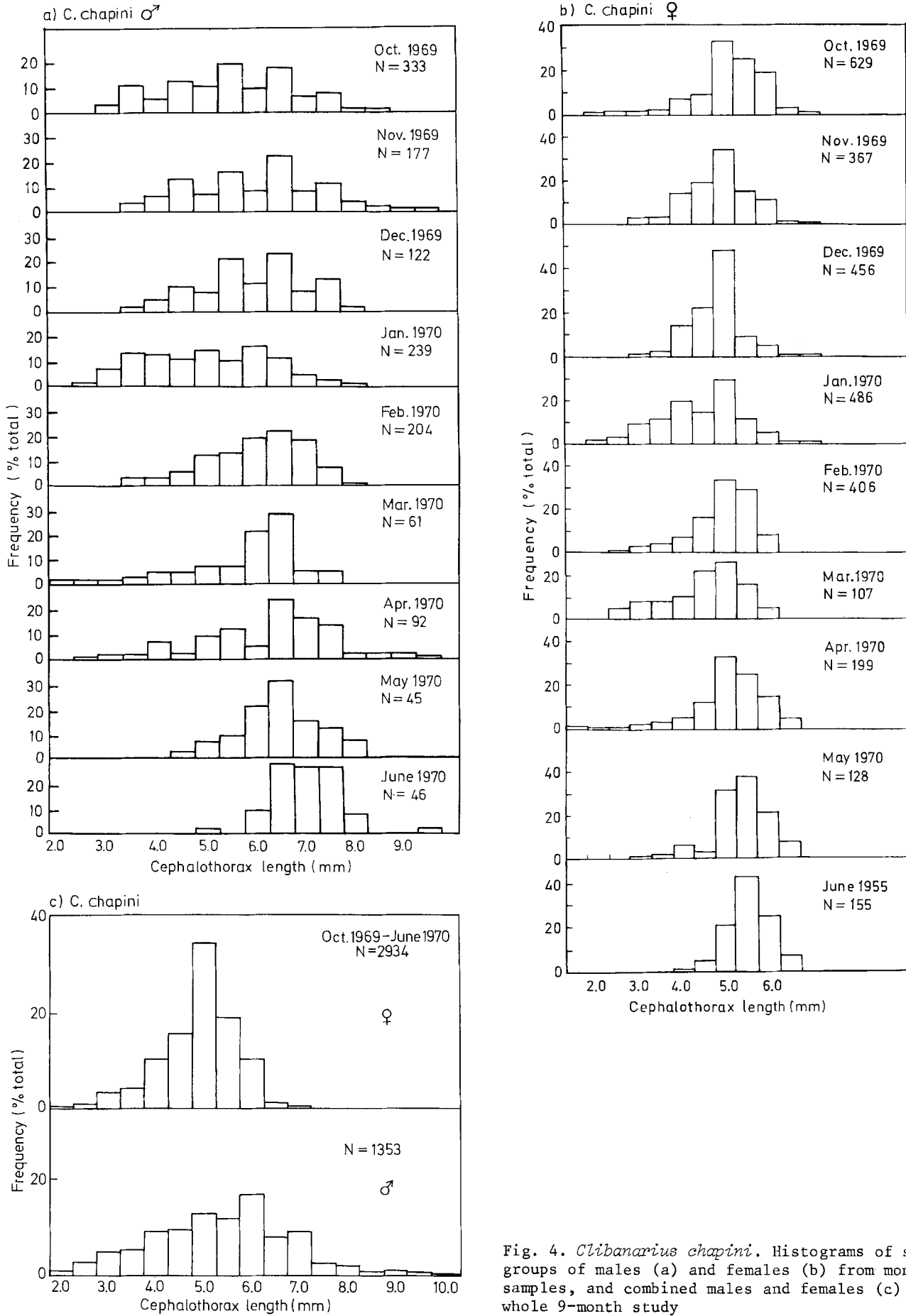


Fig. 4. *Clibanarius chapini*. Histograms of size groups of males (a) and females (b) from monthly samples, and combined males and females (c) for whole 9-month study

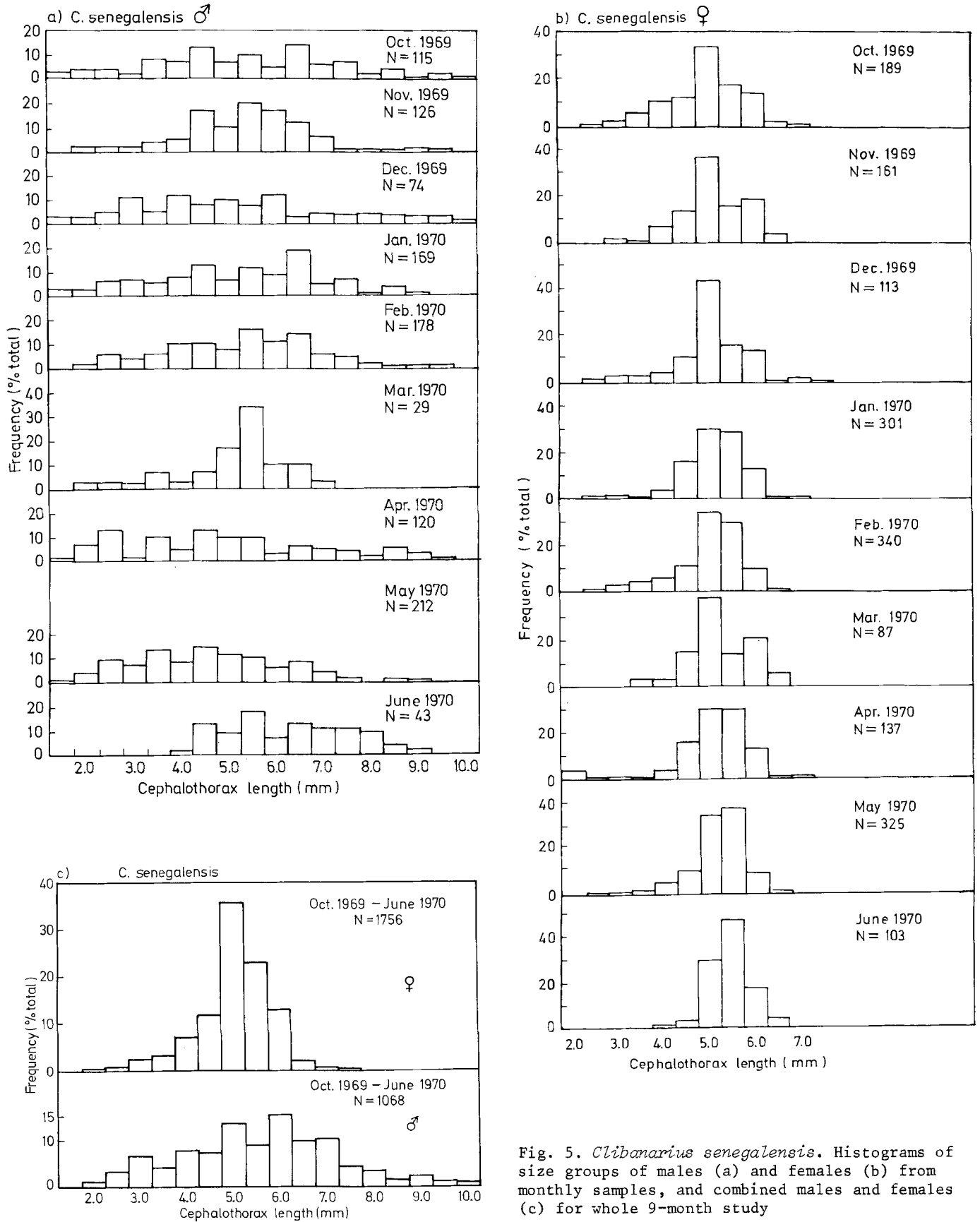


Fig. 5. *Clibanarius senegalensis*. Histograms of size groups of males (a) and females (b) from monthly samples, and combined males and females (c) for whole 9-month study

serve of large, unused shells. In other words, the adults attain as great an adult size as can be tolerated in the snail shells which they occupy (Markham, 1968) and, in these circumstances, we might indeed expect females to be smaller than males. This, however, does not explain why both male and female *Clibanarius chapini* grow to almost the same size.

Finally, a word about the time of larval release. This occurred in the night in both species in the laboratory, and most probably also occurs in nature. Fabre Domergue and Biatrix (1903) described hatching in the lobster *Homarus gammarus* (L.) (= *H. vulgaris* Milne Edwards), stating that it occurred during the early hours of the night. Fullarton (1896), in the same species, described the total time required for hatching of a brood to vary from 3 to 5 weeks or even longer. Recently, Ennis (1973) described such nocturnal larval release in *H. gammarus* lasting 2 to 6 weeks. In the sand lobster *Scyllarus americanus*, Robertson (1968)

also reported nocturnal larval release. Locomotor activity studies on both *Clibanarius* species revealed that both *C. chapini* and *C. senegalensis* are nocturnal, although the former also showed considerable activity in the day time (Ameyaw-Akumfi, unpublished data). Since larvae are released in the expiratory current, it is reasonable to assume that the larval releasing mechanism might be contingent to the general activity of the adult female.

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Table 8. Recorded breeding activities of some tropical invertebrates

Species	Reproductive pattern	Reproductive peak	Lowest reproductive activity level	Locality	Source
<i>Pugettia producta</i>	Continuous	Fairly constant level throughout year		Central Californian coast (36°30'N)	Booolootian <i>et al.</i> (1959)
<i>Petrolisthes cinctipes</i>	Continuous	Jan.-March	Oct.-Nov.	Central Californian coast (36°30'N)	Booolootian <i>et al.</i> (1959)
<i>Hemigrapsus nudus</i>	Continuous	Nov.-Jan.	March-Sept.	Central Californian coast (36°30'N)	Booolootian <i>et al.</i> (1959)
<i>Pachygrapsus crassipes</i>	Seasonal (March-Aug.)	June-July	March, April and August	Central Californian coast (36°30'N)	Booolootian <i>et al.</i> (1959)
<i>Emerita analoga</i>	Seasonal (April-Oct.)	June-July	April-May, Sept.-Oct.	Central Californian coast (36°30'N)	Booolootian <i>et al.</i> (1959)
<i>Mysidium columbiae</i>	Continuous	Nov. (1960), Aug. (1961)	Jan. (1960), Oct. (1961)	Jamaica (18°N)	Goodbody (1965)
<i>Emerita portoricensis</i>	Continuous	Feb., May-Sept.	April, Oct.-Dec.	Jamaica (18°N)	Goodbody (1965)
<i>Petrolisthes elongatus</i>	Continuous	Winter and early spring	Fall and summer	Hauraki Gulf, New Zealand (35°S)	Greenwood (1965)
<i>Calcinus laevimanus</i>	Continuous	May-Aug.	Nov.-Dec.	Kaneohe, Oahu Bay, Hawaii (21°30'N)	Reese (1968)
<i>Calcinus latens</i>	Continuous	Feb.-March, Aug.	Oct.-Dec.	Kaneohe, Oahu Bay, Hawaii (21°30'N)	Reese (1968)
<i>Clibanarius zebra</i>	Continuous	Feb.-April, Aug.	May-July, Sept.-Nov.	Kaneohe, Oahu Bay, Hawaii (21°30'N)	Reese (1968)

Literature Cited

- Booolootian, R.A., A.C. Giese, A. Farmanfarmian and J. Tucker: Reproductive cycles of five west coast crabs. *Physiol. Zoöl.* 32, 213-220 (1959)
- Buchanan, D.V. and R.E. Millemann: The prezoal stage of the Dungeness crab, *Cancer magister* Dana. *Biol. Bull. mar. biol. Lab., Woods Hole* 137, 250-255 (1969)
- Ennis, G.P.: Endogenous rhythmicity associated with larval hatching in the lobster *Homarus gammarus*. *J. mar. biol. Ass. U.K.* 53, 531-538 (1973)
- Fabre-Domergue et E. Biatrix: Le mecanisme de l'emission des larves chez la femelle du homrad europeen. *C. r. hebd. Séanc. Acad. Sci., Paris* 136, 1408-1409 (1903)
- Fullarton, J.H.: The European lobster: breeding and development. *Rep. Fishery Bd Scotl.* 14, 186-222 (1896)
- Giese, A.C.: Comparative physiology: annual reproductive cycles of marine invertebrates. *A. Rev. Physiol.* 21, 547-576 (1959)
- Goodbody, I.: Continuous breeding in populations of two tropical crustaceans *Mysidium columbiae* (Zimmer) and *Emerita portoricensis* Schmitt. *Ecology* 46, 195-197 (1965)
- Greenwood, J.G.: The larval development of *Petrolisthes elongatus* (H. Milne-Edwards) and *Petrolisthes novaezelandiae* Filhol (Anomura, Porcellanidae) with notes on breeding. *Crustaceana* 8, 285-307 (1965)
- Gunter, G.: Temperature. *In: Treatise on marine ecology and paleoecology. Vol. 1. Ecology*, pp 159-184. Ed. by J.W. Hedgpeth. New York: Geological Society of America 1957
- Hazlett, B.A.: Social behaviour of the Paguridae and Diogenidae of Curaçao. *Stud. Fauna Curaçao* 23, 1-143 (1966)
- Tactile stimuli in the social behaviour of *Pagurus bernhardus* (Decapoda, Paguridae). *Behaviour* 36, 20-48 (1970)
- Shell fighting and social behaviour in the hermit crab genera *Paguristes* and *Calcinus* with comments on *Pagurus*. *Bull. mar. Sci.* 22, 806-823 (1972)
- Herrnkind, W.: The breeding of *Uca pugilator* (Bosc) and the mass rearing of the larvae with comments on the behaviour of the larval and early crab stages (Brachyura, Ocypodidae). *Crustaceana (Suppl.)* 2, 214-224 (1968)
- Knight, M.D.: The larval development of the sand crab *Emerita rathbunae* Schmitt (Decapoda, Hippidae). *Pacif. Sci.* 27, 58-76 (1967)
- Knowlton, R.E.: Effects of some environmental factors on the larval development of *Palaemonetes vulgaris* (Say). *J. Elisha Mitchell scient. Soc.* 81, p. 87 (1965)
- Little, G.: Induced winter breeding and larval development in the shrimp *Palaemonetes pugio* Holthuis (Caridae, Palaemonidae). *Crustaceana (Suppl.)* 2, 19-26 (1968)
- The larval development of the shrimp *Palaemon macrodactylus* Rathbun, reared in the laboratory, and the effect of eyestalk extirpation on development. *Crustaceana* 17, 69-87 (1969)
- Lewis, J.B.: The fauna of the rocky shores of Barbados, West Indies. *Can. J. Zool.* 38, 391-435 (1960)
- Markham, J.C.: Notes on growth patterns and shell utilization of the hermit crab *Pagurus bernhardus* (L.) Ophelia 5, 189-205 (1968)
- Moore, H.B.: Marine ecology, 493 pp. New York: John Wiley & Sons 1958
- Passano, L.M.: Molting and its control. *In: The physiology of Crustacea, Vol. 1.* pp 473-536. Ed. by T.H. Waterman. New York: Academic Press 1960
- Reese, E.: Annual breeding seasons of three sympatric species of tropical intertidal hermit crabs, with a discussion of factors controlling breeding. *J. exp. mar. Biol. Ecol.* 2, 308-318 (1968)
- Robertson, P.B.: The complete larval development of the sand lobster *Scyllarus americanus* (Smith) (Decapoda, Scyllaridae) in the laboratory, with notes on larvae from the plankton. *Bull. mar. Sci.* 18, 294-342 (1968)
- Ryan, E.P.: Structure and function of the reproductive system in the crab *Portunus sanguinolentus*. *Proc. Symp. Crustacea (Mar. biol. Ass., India)* 2, 506-521 (1967)
- Sandoz, M. and R. Rogers: The effect of environmental factors on hatching, moulting and survival of zoea larvae of the blue crab, *Callinectes sapidus* Rathbun. *Ecology* 25, 216-228 (1944)
- Thorson, G.: Reproduction and the larval development of Danish marine bottom invertebrates. *Meddr Kommm Danm. Fisk.-og Havunders. (Ser. Plankton)* 4, 1-523 (1946)
- Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.* 25, 1-45 (1950)

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