

Observations on the biology of the hermit crab, *Coenobita compressus* H. Milne Edwards (Decapoda; Anomura) on the west coast of the Americas*

by

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(Received for publication July 3, 1972)

ABSTRACT: The semi-terrestrial hermit crab, *Coenobita compressus*, is one of the most conspicuous supra-littoral invertebrates on the west coast of the American tropics. During Stanford Oceanographic Expedition 18, which sampled the intertidal flora and fauna at various points between Peru and California, information was collected on the natural history of this species over a wide range of latitudes and habitats. This information, which is summarized here, includes details on color, distribution, local names, type of shell occupied, percentage of females ovigerous at various localities, food and various aspects of behavior.

The semi-terrestrial hermit crab *Coenobita compressus* H. Milne Edwards is a conspicuous and frequently abundant inhabitant of the supra-littoral zone of the eastern tropical Pacific from Mexico to Peru. However, aside from brief mentions in the papers of GLASSELL (2), BRIGHT (1), and HAIG, *et al.* (3), there is little information available on the natural history of this species.

Considerable information on the biology of *Coenobita compressus* was obtained as part of a survey of the hermit crab fauna of the eastern tropical Pacific during Stanford Oceanographic Expedition 18 from April to June 1968. This expedition, aboard the RV Te Vega, sampled the intertidal fauna and flora from Paita, Perú (5°S) to Bahía Magdalena, Baja California (24°N). A map of this cruise and a station list are presented in Figure 1 and Table 1, respectively.

* This research was supported by NSF Grants GB6870 and GB6871 to Stanford University.

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TABLE 1

Station data, Stanford Oceanographic Expedition 18

Station	Locality	Date (1968)
1	Isla de Santa Clara, Golfo de Guayaquil, Ecuador	5—7 Apr.
2	Talara, Perú	8—9 Apr.
3	Paita, Perú	10—13 Apr.
4	Salinas and vicinity, Ecuador	15—18 Apr.
5	Manta, Ecuador	19—20 Apr.
6	Punta Galera, Ecuador	22 Apr.
7	Punta Sua, Ecuador	23 Apr.
8	Atacames Reef, Ecuador	23 Apr.
9	Punta Barca, Bahía de Buenaventura, Colombia	26 Apr.
10	Punta Mono, Isla Gorgona, Colombia	27 Apr.
11	Straits between Islas Gorgona & Gorgonilla, Colombia	28 Apr.
12	Bahía Solano, Colombia	30 Apr. 1 May
13	Bahía de Cupica, Colombia	2 May
14	Balboa, Canal Zone & Panama City, Panamá	5—6 May
15	Isla Taboguilla, Bahía de Panamá, Panamá	7 May
18—16	Isla Montuosa, Panamá	9 May
18—17	Area of Islas Negritos & Cedros, Golfo de Nicoya, Costa Rica	11—12 May
18—18	Bahía Brasilito, Costa Rica	13 May
18—19	Punta Chiquirin & vicinity, Golfo de Fonseca, El Salvador	15—16 May
18—20	Salina Cruz & vicinity, Oaxaca, México	20—22 May
18—21	Acapulco & vicinity, Guerrero, México	23—24 May
18—22	Bahía Tenacatita, Jalisco, México	27 May
18—23	Bahía Magdalena, Baja California, México	2 Jun.

Since the disproportionate amount of information collected on the biology of *Coenobita compressus* would not readily fit into a survey of the hermit crabs collected during the expedition (HAIG and BALL, in preparation) it is presented separately here.

MATERIAL AND METHODS

For length measurements and sex determination *Coenobita* had to be removed from their mollusc shells. This could usually be accomplished without damage by grasping all of the legs and exerting a steady pull. In some cases it was also necessary to tickle the crab's abdomen before the abdominal appendages would release their hold.

Feeding was studied by field observation and by fixing animals in the field and subsequently examining their gut contents.

Carapace length, as used in this paper, is the distance from the tip of the rostrum to the posterior margin of the carapace located between the membranous lobes. Crabs were weighed on a triple beam balance while at sea, so the weights given are approximate ($\pm 0.5g$).

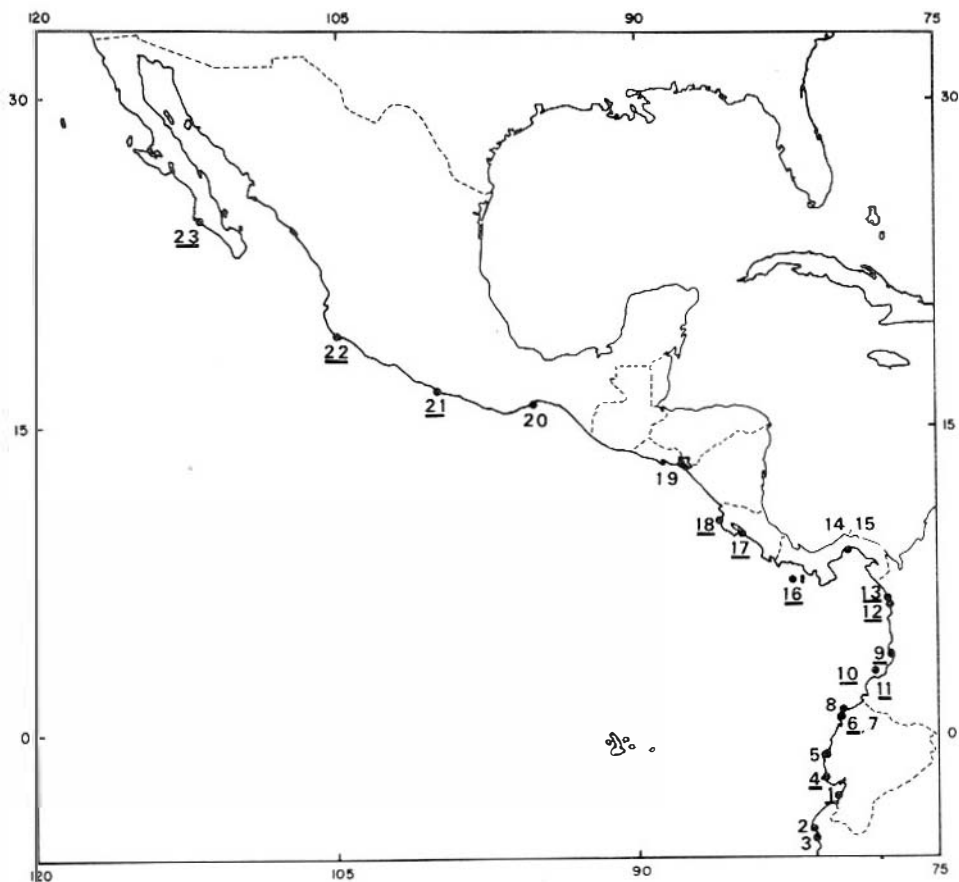


Fig. 1. Station map of Stanford Oceanographic Expedition 18. *Coenobita compressus* were collected at the underlined stations.

RESULTS

COLOR DESCRIPTION: This species exhibits considerable variability in color. Young animals range from blue-green to a gray-brown and their coloration is generally uniform. Larger animals vary from a very pale gray, to almost black, to brown and the coloration may be uniform or have considerable contrast. The following is a color description for a large male *Coenobita* from Punta Nabuga, Bahía Solano, Colombia (Station 12): eyestalks brown dorsally, white laterally and ventrally; antennules and antennae dark brown; chelipeds medium brown with lighter brown tubercles; ambulatories mottled light and dark brown; carapace mottled light and dark brown.

DISTRIBUTION: Stations where *Coenobita compressus* were collected during Stanford Oceanographic Expedition 18 are underlined in Figure 1.

- LOCAL NAMES (in some cases the spellings are phonetic):
 "ermitaño de la playa" - Paita, Perú
 "ki-ki" - Isla de Santa Clara, Manta, and Salinas, Ecuador
 "curicuaco" - Punta Galera, Ecuador
 "maricaco" - Isla de Gorgona, Colombia
 "cakire" - Muntas and Punta Nabuga, Colombia
 "calnegua" - Puntarenas, Costa Rica
 "ermitaño" or "cangrejo ermitaño" - Salina Cruz, México
 "chololo" - Bahía Tenacatita, México.

SIZE: Male *Coenobita* may grow considerably larger than the females. The largest male collected had a cephalothorax length of 38 mm (Station 23) while the largest female had a cephalothorax length of 28 mm (Station 22). Size data for samples of *Coenobita* collected at Punta Nabuga, Bahía Solano, Colombia (Station 12) and Bahía Tenacatita, México (Station 22) are presented in Table 2.

NATURAL HISTORY: *Coenobita compressus* are most active at night, and in arid areas (e.g. Stations 1 and 4) their activities are almost exclusively nocturnal. Activity usually begins in the evening shortly before sunset. About dawn the *Coenobita* begin seeking shelter and during the day great aggregations can frequently be found under ledges, in small rocky caves, under logs and driftwood or dug into the sand. In humid vegetated areas (e.g., Stations 6 and 9) many crabs remain active during the day; this being especially true of the smaller animals. At Bahía Tenacatita, México (Station 22) many *Coenobita* were active in a moist shaded area near a lagoon during the day and then spread out onto the beach at night.

TABLE 2

Size data for samples from two populations of *Coenobita compressus*

	males	all females	ovigerous females	non-ovigerous females
Punta Nabuga, Bahía Solano, Colombia				
N	47	69	51	18
Average carapace length (mm)	20.00	15.87	15.76	16.17
Range of carapace lengths (mm)	12-35	11-23	11-23	14-23
Bahía Tenacatita, México				
N	54	69	43	26
Average carapace length (mm)	18.89	18.04	19.95	14.88
Range of carapace lengths (mm)	11-35	10-28	13-28	10-22

It appears that small *Coenobita* are much more sensitive to desiccation than larger animals and at the two most arid stations where *Coenobita* were present (Stations 1 and 4) only large animals were found. In both of these areas there were extensive sandy beaches and it may be that young animals are restricted to certain small areas where there is slightly more moisture and small shells are more readily available.

Coenobita are frequently found in areas, such as sandy beaches, where shells are extremely scarce, and it appears likely that shell availability may be a major factor limiting populations in certain areas. Crabs with shells large enough that they can withdraw completely and block the shell aperture with a cheliped are much harder to extract from their shells than are crabs which are too large to withdraw completely, and for this reason they would presumably be less vulnerable to predators.

Since shells, especially large ones, are scarce in many of the areas inhabited by *Coenobita* it seems likely that many of the shells now occupied by hermit crabs have been passed around within the population over a period of many years. In this connection it is interesting to note that the majority of the shells occupied by *Coenobita* seem to be missing the columella. A similar observation has been made by KINOSITA and OKAJIMA (5) on shells of *Nerita striata* occupied by *Coenobita rugosus* from Japan. These authors attribute the absence of a columella to chemical effects and mechanical abrasion by the abdominal appendages.

The types of shells occupied by *Coenobita* at a number of localities are given in Table 3. At Station 1 no quantitative data were taken, while for Station 4 data are presented without regard to the size of the animal. At all other stations only hermit crabs with a cephalothorax length ≥ 11 mm were considered. Since the samples were sometimes collected by, or with the help of, others, no uniform sampling method was used. In several cases *Coenobita* were occupying shells of molluscs which did not appear to be common in the area. This is especially true of shells of *Turbo saxosus* which was collected alive, by members of the expedition working specifically on molluscs, only at Station 12. A small bright green alga was noted coating the inside of shells occupied by *Coenobita* at a number of localities. MAGNUS (6) reported an apparently similar alga coating the inside of shells occupied by *Coenobita jousseaumei* on the Red Sea.

Ratios of shell weight to crab weight were taken for 39 male *Coenobita* with the following results: minimum 0.28, median, 0.94, average 0.95, maximum 2.10. Crab weights ranged from 4.9-26.5 grams while shell weight ranged from 5.1-21.0 grams. Shell weight and volume measurements were taken for a number of *Turbo saxosus*, *Turbo fluctuosus*, *Thais biserialis*, *Thais melones*, and *Acanthina* sp. However, no large differences were found in their weight: volume ratios.

Table 4 gives the percentage of females ovigerous at a number of localities. At Station 4 all female crabs over 1.5 grams were considered, while at all other stations all females with a cephalothorax length ≥ 11 mm were used in the calculations. This figure was chosen because it was the size of the smallest ovi-

gerous female at any station. Eggs were not staged, but it was noted that they were in a number of different stages of development at any given locality. However, there was often a predominance of one stage. There does not appear to be any clear relation between latitude and the percentage of the population that is ovigerous.

TABLE 3

Types of shells occupied by Coenobita compressus at various localities (figures are %)

Mollusc species	1	4	6	11	12	16	17	22
<i>Turbo</i> cf. <i>T. saxosus</i> *	X**	37	66	7	3	2	60	13
<i>Turbo fluctuosus</i> *	X	5						
<i>Thais biserialis</i>	X	38	8					48
<i>Thais melones</i>	X	9	22	2	10	3	4	
<i>Nerita funiculata</i>				2				1
<i>Nerita scabricosta</i>				64	70	93	21	19
<i>Littorina zebra</i>					4			
<i>Littorina</i> sp.					6			
<i>Acanthina</i> sp.		5	1	4			2	
<i>Natica</i> sp.		1	1					
<i>Bulla</i> sp.				2				
<i>Purpura patula</i>				2	5			1
<i>Harpa crenata</i>				7			2	1
<i>Malea ringens</i>				4				
<i>Opeatostoma pseudodon</i>				2	1	1		
<i>Thais kiosquiformis</i>					1			
<i>Thais speciosa</i>							4	10
<i>Cantarus</i> sp.		3					2	
<i>Lutirus</i> sp.								3
<i>Cerithium</i> sp.								2
<i>Cymatium parthenopennae</i>								1
<i>Polynices</i> sp.		1						
muricid sp.							2	
unidentifiable		3	2	2			2	2
N		109	91	45	116	136	47	120

* These species are sometimes very hard to distinguish, so there may be some misidentifications.

** Indicates that this type of shell was occupied although percent occupancy was not recorded.

Coenobita appears to be a general scavenger. The following observations on feeding were obtained at various stations:

Salinas, Ecuador - fine organic material and sand (gut contents).

Punta Galera, Ecuador - fruit of the manzanillo tree (observation); wood fragments, eggs of a fish or crustacean (gut contents).

Punta Barca, Colombia - roots of a palm-like plant, bracket fungus, palm fronds or something growing on them (observation).

Isla Gorgona, Colombia - a mass of what appeared to be fish eggs, rotten wood, a dead leaf or something growing on it (observation).

Bahía Solano, Colombia - dead vespid wasp (observation - D.N. Rosenberg).

Bahía de Cupica, Colombia - "ciruela" (a small orange fruit), banana peelings (observation).

Isla Montuosa, Panamá - copra (observation).

Bahía Tenacatita, México - feces, probably human (observation).

TABLE 4

Percent female Coenobita compressus ovigerous at various stations

Location	Total Females Examined	% Ovigerous
Isla de Santa Clara, Ecuador	52	44
Salinas, Ecuador	30	87
Punta Galera, Ecuador	64	50
Isla Gorgona, Colombia	23	30
Punta Nabuga, Bahía Solano, Colombia	69	74
Isla Montuosa, Panamá	20	10
Puntarenas, Costa Rica	26	4
Bahía Tenacatita, México	66	65

People at various stations also told me that *Coenobita* eats such economically important foodstuffs as cacao, plátano and rice. The behaviour of *Coenobita* when locating food appears to depend to a large extent on environmental conditions. In humid, vegetated areas, where there is often a great deal of debris on the beach, the animals gave the appearance of wandering rather aimlessly with short, goal-directed journeys only when they were in the immediate vicinity of potential food. However, in arid regions where there is less debris on the beach and the animals are active only at night they appear to make more use of olfaction for long range orientation to food. At Isla de Santa Clara fermenting fruit was placed out at night and the behaviour of the crabs was observed by moonlight. Almost all approached the bait from downwind and many were headed directly for the bait from as far away as they could be seen. *Coenobita* appear to do a great deal of apparently "aimless" exploring and I several times found them climbing in trees or bushes with no apparent goal.

Shell fights between two *Coenobita* were observed several times. Since these encounters usually follow about the same pattern a single fight observed at Salinas, Ecuador will be described. Terms such as "ambulatory raise" and "cheliped extension" are discussed by HAZLETT (4). When first noticed, the two crabs were performing ambulatory raises. These soon changed to cheliped extensions with one of the animals being flipped away by the other. The crabs

then violently shoved at each other with their chelipeds until one animal withdrew into its shell. The other crab kept its cheliped in the aperture of the shell of the withdrawn animal. The two animals remained in this position for approximately fifteen minutes with the withdrawn animal periodically moving its ambulatories and stridulating frequently. Finally, the attacking animal attempted to move away and it became apparent that the tip of one of its ambulatories was held by the larger cheliped of the animal which had been withdrawn. A tug-of-war then ensued. This eventually ended and the two animals separated.

At Salinas, Ecuador (Station 4) *Coenobita* were observed allowing themselves to be caught by waves, presumably to replenish the water which they carry in their shells. They were always faced down the beach when the wave caught them and once it had passed they backed up the beach.

ACKNOWLEDGEMENT

I would like to express my thanks to all of the members of Stanford Oceanographic Expedition 18, without whose help specimens would not have been obtained at many localities. I am grateful to Judy Terry for help in identifying mollusc shells, and to Janet Haig for taxonomic help and for reading the paper.

RESUMEN

El cangrejo ermitaño *Coenobita compressus* es uno de los invertebrados supra litorales más comunes de las costas occidentales de los trópicos americanos. Durante la Expedición Oceanográfica No. 18 de Stanford, que tomó muestras de la flora y de la fauna de la zona entre marcas en varias localidades desde el Perú hasta California, el autor recogió gran cantidad de datos sobre la historia natural de esta especie en un amplio ámbito de latitudes y habitats. Estos datos, que aquí se consignan, incluyen observaciones sobre el color, la distribución geográfica, los nombres vernáculos, el tipo de conchas que ocupa, el porcentaje de hembras ovigeras en varias localidades, su alimentación y varios aspectos de comportamiento.

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