

although no attempts have been made to identify the bacterial species. The calculated yield, in grams of cells per gram of cellulose used, was 0.29. When the medium was not supplemented with corn steep liquor, cell yield was 0.19.

A second experiment was conducted (Figure) in which the non-utilized paper of the previous experiment was reused with fresh fermentation medium, which included all the components except newspaper. The object was to determine if cellulose consumption in experiment 1 was stopped by the deficiency of some nutrient. As can be observed, the values of biomass produced and cellulose utilized were very small. According to AMEMURA and TERUI<sup>9</sup>, the amorphous regions in the fringe micelles of pulp cellulose are first attacked, leading to an enrichment of crystalline segments, the latter being the most difficult to solubilize. The resistance of the newspaper to further degradation can probably be explained by the fact that the cellulases produced by the Y-11 culture could only

attack the sites more accessible, leaving undegraded most of the crystalline regions.

The conversion of cellulosic wastes into microbial protein is attracting attention. Further studies for the improvement of the substrate utilization are being carried out.

*Resumen.* Se aisló un cultivo mixto denominado Y-11 con el cual se estudió la conversión de papel periódico a biomasa. Los trabajos se llevaron a cabo a nivel de fermentador. El residuo sólido no degradado de una fermentación previa, fué reutilizado con nuevo medio de cultivo con objeto de determinar si la hidrólisis de esta fuente celulósica se detenía por el agotamiento de algún nutriente o por otros factores.

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<sup>9</sup> A. AMEMURA and G. TERUI, J. Ferment. Technol. Osaka 43, 281 (1965).

## Direct Shell Acquisition by Hermit Crabs from Gastropods

Hermit crabs commonly live in and carry about 'empty' gastropod shells. Acquisition of these shells by means of shell exchange between individuals has been well documented<sup>1-4</sup>. However, for years, biologists have wondered how 'new' gastropod shells (i.e., from freshly killed gastropods) are introduced into the hermit crab population. MAGELHAES<sup>5</sup> hypothesized that hermit crabs prey on gastropods for the shell, while BRIGHTWELL<sup>6-7</sup> gave evidence from laboratory work that the hermit crab *Pagurus bernhardus* acquires shells by removing gastropods injured by predatory fishes. No one

to date, however, has observed the acquisition of 'new' gastropod shells in the field or described the mechanisms by which this essential resource enters the hermit crab community. This is of obvious importance to a basic understanding of the structure of any marine ecosystem in which hermit crabs are found. This paper presents the first account of the acquisition of new shells from gastropods just killed by natural predators.

Four species of hermit crabs, *Pagurus pollicaris* SAY, *P. longicarpus* SAY, and *P. annulipes* (STIMPSON) from St. Joseph Bay, Gulf Co., Florida, and *Paguristes grayi*

Sites of predation on gastropods attended by *Pagurus pollicaris*, species of predator and prey gastropods and outcome of competition for prey shell

No. and type of site	No. and species of crabs present	Predator species	Prey species	Rank of crab getting new shell and outcome of competition for shell
1 Prepared	5 <i>Pagurus pollicaris</i>	<i>Fasciolaria tulipa</i>	<i>Fasciolaria hunteria</i>	1, Dominant acquired shell
2 Prepared	6 <i>Pagurus pollicaris</i>	<i>Pleuroploca gigantea</i>	<i>Fasciolaria hunteria</i>	1, Dominant acquired shell
3 Prepared	7 <i>Pagurus pollicaris</i>	<i>Pleuroploca gigantea</i>	<i>Fasciolaria hunteria</i>	1, Dominant acquired shell
4 Prepared	10 <i>Pagurus pollicaris</i>	<i>Pleuroploca gigantea</i>	<i>Fasciolaria hunteria</i>	1, Dominant acquired shell
5 Natural	3 <i>Pagurus pollicaris</i>	<i>Pleuroploca gigantea</i>	<i>Fasciolaria hunteria</i>	1, Dominant acquired shell
6 Natural	3 <i>Pagurus pollicaris</i>	<i>Pleuroploca gigantea</i>	<i>Fasciolaria hunteria</i>	2, Dominant rejected small shell
7 Prepared	14 <i>Pagurus pollicaris</i>	<i>Pleuroploca gigantea</i>	<i>Fasciolaria hunteria</i>	3, Dominant rejected small shell
8 Prepared	12 <i>Pagurus pollicaris</i>	<i>Pleuroploca gigantea</i>	<i>Fasciolaria hunteria</i>	3, Dominant rejected small shell
9 Prepared	4 <i>Pagurus pollicaris</i>	<i>Pleuroploca gigantea</i>	<i>Fasciolaria hunteria</i>	0, <sup>1</sup> Dominant rejected small shell
10 Prepared	5 <i>Pagurus pollicaris</i>	<i>F. tulipa</i>	<i>Fasciolaria hunteria</i>	0, <sup>2</sup> Dominant rejected small shell
11 Prepared	4 <i>Pagurus pollicaris</i>	<i>F. tulipa</i>	<i>Fasciolaria hunteria</i>	2, Dominant rejected small shell
	1 <i>Pagurus longicarpus</i>			
12 Prepared	6 <i>P. pollicaris</i>	<i>F. tulipa</i>	<i>Fasciolaria hunteria</i>	4, Dominant lost shell while fighting
13 Prepared	4 <i>P. pollicaris</i>	<i>Pleuroploca gigantea</i>	<i>Fasciolaria hunteria</i>	3, Dominant lost shell while fighting
14 Prepared	11 <i>P. pollicaris</i>	<i>F. tulipa</i>	<i>Fasciolaria hunteria</i>	2, Dominant not near enough to prey
	1 <i>P. longicarpus</i>			
15 Prepared	4 <i>P. pollicaris</i>	<i>F. tulipa</i>	<i>Fasciolaria hunteria</i>	4, Dominant not near enough to prey
16 Natural	4 <i>P. pollicaris</i>	<i>P. gigantea</i>	<i>Fasciolaria hunteria</i>	3, Dominant not near enough to prey
17 Natural	6 <i>P. pollicaris</i>	<i>F. hunteria</i>	<i>Polinices duplicatus</i>	0, Gastropod not completely eaten
	2 <i>P. longicarpus</i>			
18 Prepared	1 <i>P. pollicaris</i>	<i>P. gigantea</i>	<i>F. hunteria</i>	0, Only one crab present
19 Prepared	1 <i>P. pollicaris</i>	<i>P. gigantea</i>	<i>F. hunteria</i>	0, Only one crab present
20 Natural	1 <i>P. pollicaris</i>	<i>P. gigantea</i>	<i>F. hunteria</i>	0, Only one crab present

<sup>1</sup> Shell too small for use. <sup>2</sup> Shell dragged from site, abandoned, then occupied by crab not present at site.

BENIDICT from Bimini, Bahamas, have been observed to aggregate around various gastropods being eaten by other predatory marine snails. Of the 3 Florida species, *P. longicarpus* occurs together with either *P. pollicaris* or *P. annulipes*. These hermit crabs establish a dominance hierarchy and compete for the freshly emptied shell when it is dropped by the predator.

In this paper, the behavior of one of the above hermit crabs, *P. pollicaris*, at these predation sites is described. The role of a dominance hierarchy in acquiring shells is described and the possible benefits to the hermit crabs are discussed.

**Materials and methods.** The natural predation sites involved the gastropods *Pleuroploca gigantea* (KIENER) and *Fasciolaria hunteria* (PERRY), which preyed on the gastropods *F. hunteria* and *Polinices duplicatus* (SAY), respectively. Other predation sites were established by feeding *F. hunteria* to the predatory gastropods *P. gigantea* and *Fasciolaria tulipa* (LINNÉ) (Table). To reduce ingestion time and insure prey capture by the predator, part of the foot of the prey was excised in 10 of 15 cases. All observations were made at St. Joseph Bay by snorkeling in shallow water in areas where predators, prey and the hermit crab, *P. pollicaris*, occur naturally. Since the hermit crabs generally oriented towards the predation sites from downcurrent (Figure 1), the observer was stationed 1.5–2.0 meters from the predation site and at a 90° angle to the current flow. The approach direction was noted and the temporal sequence of behavior of

each crab was recorded on a plastic slate and, where possible, on 16 mm movie film.

**Observations.** There are 6 main stages in the temporal sequence of behavior of the hermit crabs at predation sites: 1). orientation towards the site; 2. accumulation of the crabs at the site; 3. agonistic interaction of the crabs resulting in a dominance hierarchy; 4. quiescent period during which crabs may bury themselves; 5. intense agonistic interaction and rapid shell exchange after the freshly emptied shell is dropped; and 6. rapid dispersal of the hermit crabs.

A total of 115 hermit crabs came to 5 natural and 15 prepared predation sites for an average of 4.2 and 6.4 crabs per site, respectively. I was present on 15 occasions at the initiation of predation. On 13 of these occasions, the first hermit crabs appeared within 15 min. On the remaining two occasions they appeared within 45 min. All of the first arrivals came from downcurrent as did approximately 90% of the remaining crabs that arrived. Hermit crabs crossing downcurrent of the site often turned and proceeded directly upcurrent to the site. Crabs crossing upcurrent seldom changed direction (unless within approximately 1 m of the site) and rarely attended the predation site. This suggests that the cue used by the crabs to reach the site is chemical. Studies are in progress to determine the nature of the attractant stimulus.

The first hermit crabs to arrive always touched the predator or prey, then usually remained within 0.5 m from them (Figure 2). The crabs already present immediately interacted with successive arrivals in the form of agonistic behavior typical of that reported for hermit crabs of the genus *Pagurus*<sup>8,9</sup>. This consisted of cheliped presentations, cheliped extensions, shell grabs and a mutual exchange of blows with the chelipeds, termed 'wild fighting' after SHÖNE<sup>10</sup>. This resulted in an eventual dominance hierarchy in which the dominant individual was that crab whose approach elicited retreat on the part of any other crab at the predation site. Since a new arrival may assume any position in the hierarchy, dominance was not correlated with arrival time. However, dominance was correlated with size, the dominant animal being the largest in 12 of the 15 sites where this was noted.

At 50% of the sites observed, after the initial interaction, over 45% of the crabs present (but not the dominant) generally buried themselves in the substrate, leaving only the eyestalks exposed. Burial of the crabs often corresponded to a quiescent period characterized by at least 30 min of little interaction between the crabs of any kind (0.32 acts/min for active period and 0.04 acts/min for quiescent period).

The quiescent period, however, was interrupted by 2 events. First, any intense agonistic interaction (i.e., wild fights) between crabs resulted in the buried animals leaving the substrate and coming directly to the prey to rapidly make contact with any occupied or empty shell in the area. If the prey shell was not yet available, the crabs again buried themselves within 1–2 min. Second,

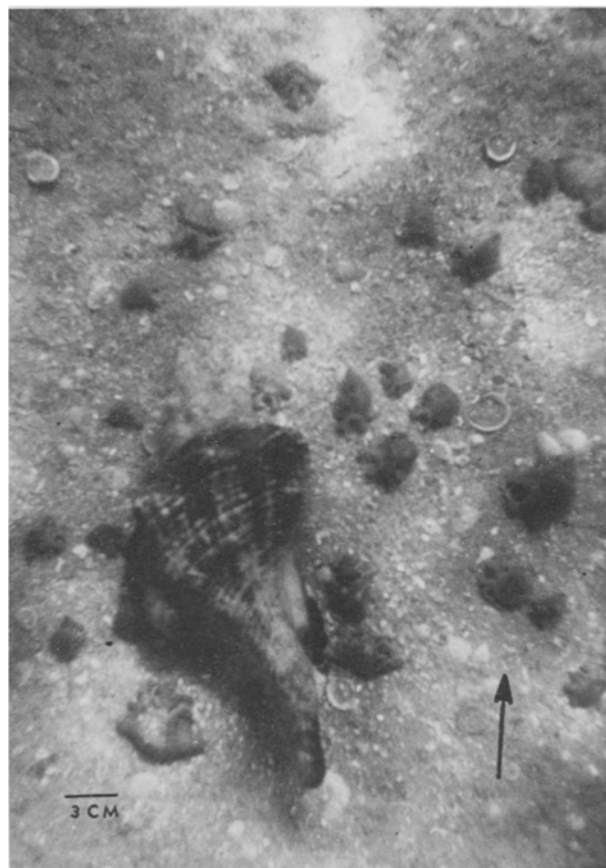


Fig. 1. *Pagurus pollicaris* hermit crabs attracted to a natural predation site. The gastropod *Pleuroploca gigantea* is preying on the snail *Fasciolaria hunteria*. Note the positioning of the crabs with respect to current flow (arrow).

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<sup>3</sup> B. A. HAZLETT, Bull. mar. Sci. 16, 76 (1966).

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<sup>8</sup> B. A. HAZLETT and W. H. BOSSERT, Anim. Behav. 13, 357 (1965).

<sup>9</sup> B. A. HAZLETT, Ecology 49, 573 (1968).

<sup>10</sup> H. SHÖNE, Am. Zoologist 8, 641 (1968).



Fig. 2. *Pagurus pollicaris* hermit crabs gathered around the gastropod *Pleuroploca gigantea* preying on the snail *Fasciolaria hunteria* in the laboratory.

dropping of the prey shell by the predator resulted in those hermit crabs in the immediate vicinity (probably within sight of the shell) and those crabs downcurrent quickly emerging (less than 5 sec) from the sand and approaching the prey. The dominance hierarchy at this point began to break down and the general movement of the crabs became very rapid. If the now empty shell was of the appropriate size, the first crab reaching it quickly changed shells. Due to its close proximity to the prey, this was usually the dominant crab. However, if the shell was much too small it was rejected and sized by other high ranking members of the hierarchy (Table). Old shells vacated as a result of this initial shell exchange were also quickly entered by the subordinate crabs. A total of 38 exchanges (an average of 1 for every 3 crabs present) occurred before the crabs dispersed from the site (usually in less than 1 min).

This rapid shell exchange was strikingly different from that usually seen in *P. pollicaris* and *Pagurus* hermit crabs in general. Acquisition of another shell usually involves a complicated set of behavioral acts such as positioning of the shell, exploration by insertion of the chelipeds and the first pair of walking dactyls into the aperture, and, after shell exchange, alternately pulling the body back into and extending the body from the shell in a ducking motion. The entire process usually takes several minutes. At predation sites, however, shell exchange was a two step process taking 1–2 sec: 1. grasping the new shell and 2. immediately changing into it. Any preliminary sizing of the shell was brief and apparently visual, occurring during the short period between shell contact and shell exchange.

Crabs acquiring the prey shell always attempted to immediately leave the site, but were often hampered by other crabs in the vicinity. Harassment involved grasping the prey shell and initiation of shell exchange behavior by such means as shell rapping<sup>4</sup>. Harassment, even by crabs not originally at the predation site, continued until after the crab left the immediate vicinity. The prey shell occupant, however, was never observed to give up its shell during this period. The continued harassment suggests that the freshly emptied prey shell, even away from the site, is extremely attractive to hermit crabs. The attractant stimulus resulting in this behavior

is probably chemical, rather than the physical newness of the shell, since this behavior was observed at no other time regardless of shell condition.

**Discussion.** Acquisition of a new shell may be important to the hermit crab in several ways. First, shell destroying organisms such as the boring sponge *Clione celata* GRANT and *Hyella* algae are prevalent in the shallow inshore areas of the northeastern Gulf of Mexico. Any shell affected by these organisms is often porous and easily broken. I have seen predators of hermit crabs, such as the oxystomatid crab *Calappa flammea* HERBST and the spiny lobster *Panulirus argus* (LATREILLE), break open a fragile shell very easily, but be deterred by a new stronger shell.

Secondly, two shells acquired at predation sites, *F. hunteria* and *P. duplicatus*, provide a preferred substrate for attachment of the sea anemone, *Calliactis tricolor* LÉSEUR. In over 85% of the cases observed, when associated with *P. pollicaris*, *C. tricolor* was found only on these two shell types. This association is beneficial to the hermit crab in that *Calliactis* sea anemones can protect the crabs from such predators as *C. flammea* and *Octopus vulgaris* LAMARCK<sup>11, 12, 13</sup> and therefore confers additional selective value to these shells.

**Zusammenfassung.** Freilandbeobachtung des Erwerbs von Schalen einer durch Raubschnecken frisch getöteten Schnecke durch Einsiedlerkrebse.

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