Encystment Discovered in a Marine Copepod

Abstract. *It has been believed that marine crustacea do not encyst as adults. The benthic copepod* Heteropsyllus nunni *has been found to encyst in intertidal sands in the summer; free-living forms are abundant in the winter. A unique platelike structure on the cephalothorax is thought to be the site of cyst formation.*

Encystment is rare in marine invertebrates and apparently unknown for marine crustacea (*1*). Encystment as adults was thought to be exclusively a freshwater phenomenon known only for a single genus of harpacticoid copepods (*2–5*). We have recently discovered encysted adults in a marine benthic harpacticoid, *Heteropsyllus nunni* Coull (*6*). This copepod is exclusively marine (*6*) and not related phylogenetically to the freshwater species (*7*, p. 1486). We document here the unexpected occurrence of copepod cysts in the marine environment and describe cyst morphology and the most probable mechanism of cyst formation. Furthermore, we provide preliminary data on the distribution and abundance of encysted and free-living *H. nunni* from a sand flat in North Inlet, South Carolina (33°19'N, 79°10'W).

Cysts were first discovered in intertidal samples collected (*8*) in August 1978 (sorted in May 1980) at a location 30 m shoreward from a site where we have been collecting monthly subtidal (1 m deep at mean low water) meiofauna samples for 8 years (1972 to 1980). Although free-living *H. nunni* occur at the subtidal site, cysts were not sought there before June 1980 and have not been found there subsequently; the cysts appear to be restricted to the intertidal zone.

Cysts are 0.42 ± 0.03 (mean ± standard error) mm in diameter, yellowish, and transparent. Each cyst is attached to a large (0.5 to 1.2 mm) sand grain or shell fragment and is covered with several smaller (0.21 to 0.32 mm) sand grains (Fig. 1A). We have found up to six cysts on one sand grain. In a sample of 50 individuals removed from cysts (Fig. 1B), we observed only adult females and males (ratio of 2.3:1), never nauplii or copepodites (*9*). No female dissected from cysts had attached spermatophores, egg sacs, or maturing ova, nor did any males have developing spermatophores. Because mated adults would show at least some of these characteristics, the encysted adults appear not to have mated. Each encysted adult was flexed, with its urosome recurved dorsally (Fig. 1C). Free-living *H. nunni* are not flexed; the urosome is simply a linear continuation of the main body axis. Observations on live encysted *H. nunni* preparing to excyst suggest that dorsal recurvature is necessary for emergence from the cyst. Prior to emergence, the copepod vigorously moves around in the cyst in the dorsally recurved state and uses its maxillipeds to work over the inner cyst surface, eventually "chewing" through the wall. If *H. nunni* were recurved ventrally, its mouthparts would be in an unsuitable position to abrade the cyst wall. All the encysted *H. nunni* that we examined contained numerous oil (fat) droplets; free-living forms have no such fat droplets.

In both encysted and free-living adults, an oblong platelike structure occupies the middorsal surface of the cephalon (Fig. 1, C and D). The structure does not occur in free-living copepodites of this species, and Coull did not include it in his original adult description (*6*). This structure is most likely the site of cyst formation. Out of the approximately 2500 known harpacticoid copepod species (*10*), this structure is known to occur in only two freshwater species, both of which encyst (*11*). Furthermore, it is reported as the cyst-forming gland in one of the two freshwater species (*4*) and in *H. nunni* is associated with various surface pores (Fig. 1E), suspected of being

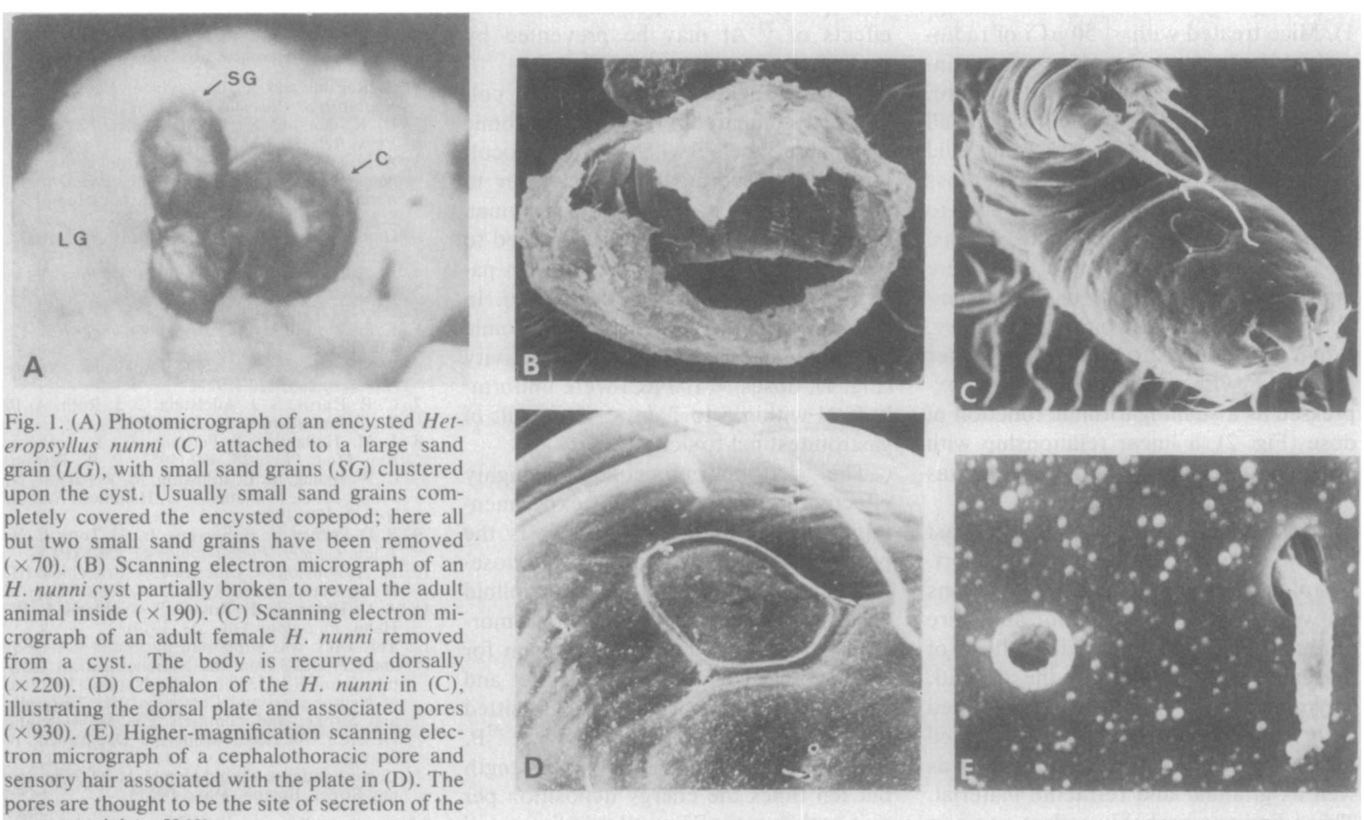

Fig. 1. (A) Photomicrograph of an encysted *Heteropsyllus nunni* (*C*) attached to a large sand grain (*LG*), with small sand grains (*SG*) clustered upon the cyst. Usually small sand grains completely covered the encysted copepod; here all but two small sand grains have been removed (×70). (B) Scanning electron micrograph of an *H. nunni* cyst partially broken to reveal the adult animal inside (×190). (C) Scanning electron micrograph of an adult female *H. nunni* removed from a cyst. The body is recurved dorsally (×220). (D) Cephalon of the *H. nunni* in (C), illustrating the dorsal plate and associated pores (×930). (E) Higher-magnification scanning electron micrograph of a cephalothoracic pore and sensory hair associated with the plate in (D). The pores are thought to be the site of secretion of the cyst material (×5360).

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Table 1. Mean number (per 10 cm^2) of free-living *Heteropsyllus nunni* taken each month over 8 years (September 1972 to September 1980) at the subtidal site (three replicates per month).

Year	Month											
	January	February	March	April	May	June	July	August	September	October	November	December
1972									0	1	2	1
1973	0	6	3	0	3	1	0	0	0	3	3	2
1974	5	7	4	0	1	0	0	0	0	1	10	3
1975	17	3	5	0	0	0	0	0	0	1	0	3
1976	2	9	6	0	0	0	0	0	0	0	0	1
1977	2	1	0	1	0	0	0	0	0	1	1	1
1978	0	1	3	9	1	0	0	0	0	1	0	3
1979	3	0	3	1	0	0	0	0	0	0	0	0
1980	0	1	1	0	0	0	0	0	0			
$\bar{X} \pm$ S.E.*	3.6 ± 1.8	3.5 ± 1.1	3.1 ± 0.6	1.4 ± 1.0	0.6 ± 0.3	0.1 ± 0.1	0	0	0	1.0 ± 0.3	2.0 ± 1.1	1.8 ± 0.4

*Mean ± the standard error of the mean.

the secretion site of cyst material. Recently, such surface pores have been shown to be the secretion sites of mucus used in feeding by the marine algal-dwelling harpacticoid *Diarthrodes nobilis* (*12*). Under Normarski differential interference microscopy the subplate material in *H. nunni* appears granular, whereas the subsurface material lateral to the plate is not. We also observed tubules connecting the subplate material to the anteriormost pores. The indications are that there is a gland underlying the plate in *H. nunni* and that this gland secretes the cyst. Confirmation must await the results of histological and transmission electron microscopy studies (*13*).

Encystment in freshwater harpacticoids has been reported as a response to environmental conditions, for example, warm temperatures (*5*), changing photoperiod (*5*), or anoxia (*3*). In all of these cases dormancy has been primarily a summer phenomenon, with free-living forms active at other times of the year (*5, 14*). *Heteropsyllus nunni* also encysts primarily in the summer, and free-living forms are most abundant in winter. After discovery of *H. nunni* cysts in May 1980, we sampled intertidally and subtidally in July, August, and September 1980 to confirm their occurrence, and in August to quantify the number of cysts and free-living forms. Intertidal cysts were abundant in the summer of 1980, and in August there were 21.8 ± 6.1 cysts and 4.3 ± 1.0 free-living forms per 10 cm^2 (N = 10). Fortuitously, we had four frozen January 1978 samples from the same site in which we found 0.5 ± 0.4 cyst and 3.9 ± 1.1 free-living forms per 10 cm^2. The proportion of cysts to free-living animals was significantly greater in August 1980 than in January 1978 ($P < .001$, Fisher's exact test). We found no subtidal cysts or free-living forms during the sampling from June through September 1980. During our 8 years of monthly subtidal sampling, we have never found cysts (before May 1980 we did not specifically search for them), and free-living forms occurred only in the colder months (Table 1). We do not know why there are no subtidal cysts, but we suspect that the subtidal site represents a "fringe" habitat for the species; *H. nunni*'s center of distribution is the intertidal zone. On the basis of the seasonal occurrence of intertidal cysts and the subtidal abundance data on free-living forms (Table 1), it appears that *H. nunni*, like its freshwater relatives, encysts in response to some summer environmental condition unique to the intertidal zone. Although encystment could be short (hours to days) or long (months), encystment of *H. nunni* appears to be a long-term phenomenon. The storage of fat droplets suggests preparation for an extended dormancy, and our field data, with cysts abundant in summer and free-living forms present in winter, suggests that encystment lasts for several months. The length of encystment, however, can only be determined by long-term studies (*15*).

The discovery of encystment in a marine crustacean indicates a unique life history among animals known to mate just as the female enters the adult stage (the chitin is still soft), to reproduce quickly, and to die. Mating (spermatophore placement) in *H. nunni* must take place in aged adults with hardened chitin since only sexually immature adults were found encysted, a unique occurrence in the Harpacticoida. As far as we know, this is the first case of a marine crustacean using adult encystment as a mechanism for weathering some unfavorable condition. The implications of the adaptive significance of encystment in marine invertebrate life histories are manifold and require long-term population studies. Nonetheless, it is apparent that encystment ensures the immediate availability of ready-to-mate adults when conditions improve. The occurrence of encystment in freshwater copepods is easily imagined as a relict adaptation to life in temporary ponds. The finding of the same phenomenon in an unrelated, strictly marine form is enigmatic.

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15. In September 1980 we initiated an experimental and regular sampling program to examine the causes of encystment and excystment and to determine the seasonal patterns of cysts at the intertidal site.
16. We thank D. Brambilla, J. Christy, R. Feller, P. Montagna, M. Palmer, S. Stancyk, J. Vernberg, D. Wethey, and S. Woodin for comments on earlier drafts of the manuscript and T. Bargar for assistance with the electron microscopy and photomicrography. This research was supported in part by NSF grant OCE78-09450. Contribution 382 from the Belle W. Baruch Institute for Marine Biology and Coastal Research, University of South Carolina.

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Cognitive Interaction After Staged Callosal Section: Evidence for Transfer of Semantic Activation

Abstract. *Sensory and cognitive functions were assessed in a right-handed male before and after partial and complete callosal commissurotomy. After the initial posterior section was made, there was no evidence of interhemispheric sensory transfer, although the left hemisphere did have access to stimulus-related semantic and episodic information from the right hemisphere. After the callosum was completely sectioned, this exchange was no longer observed.*

The splitting of mental unity following surgical section of the corpus callosum for seizure control demonstrates the importance of this fiber system for the normal interaction among the cortical areas subserving sensory, perceptual, and cognitive activity in each cerebral hemisphere (*1*). At the sensory level, a callosal "window" provides each hemisphere with a representation of the ipsilateral hemifield not available through primary afferent projections, which are almost exclusively contralateral (*2*). As sensory information undergoes further processing, it may gain access to referents in memory that contribute to recognition, comprehension, and a sense of episodic context. While internally represented referential information provides a basis for cognition in either hemisphere, the interhemispheric availability of such higher-order information has not been described under conditions in which the sensory window has been eliminated. Because of the recent modifications in the microsurgical technique of commissurotomy, the effects of partial as well as complete callosal section can now be examined in the same patient (*3*). The topology of callosal projection makes it possible to sever the interhemispheric connections between posterior cortical sensory areas while sparing the connections between more anterior areas that may be involved in cognition (*4*). We now describe what we believe to be the first observations of interhemispheric availability of higher-order information in the absence of sensory transfer after selective posterior callosal commissurotomy.

The patient, J.W., is a bright 26-year-old right-handed male with a history of staring spells, reportedly since grade school. After his first grand mal seizure at age 19, seizure frequency increased and remained intractable. Midline section of the corpus callosum was performed in two stages by D.H.W. The posterior half of the corpus callosum including the splenium was sectioned first, with the remaining anterior portion sectioned in a second operation approximately 10 weeks later because of a recurrence of seizures (*5*).

During the interoperative period, J.W. was evaluated for evidence of sensory transfer and for the status of perceptual and cognitive functions within each hemisphere (*6*). Tests for transfer indicated that after the initial posterior section, the primary visual, auditory, and somatosensory systems of the right hemisphere were disconnected from the expressive language system of the left hemisphere. For example, whereas J.W. named words presented to his left visual field with 63 percent accuracy before surgery, left-visual-field performance on this test (13 percent) was not significantly different from chance after posterior callosal section (*7*). In contrast, right-visual-field accuracy was unchanged after the initial surgery (93 percent preoperatively, 91 percent postoperatively) (*8*). Disconnection was also demonstrated on an interfield comparison test that required a same-different judgment of the simultaneous presentation of stimuli to each visual field. Although performance was nearly perfect (98 percent) before posterior section, it did not differ from chance (50 percent) after the initial surgery.

Table 1. J.W.'s left-visual-field performance (percent correct responses) on picture- and word-naming tests administered at each operative stage. The interoperative period refers to the interval following section of the posterior callosum but preceding complete section, which is represented at the postoperative stage. The initial surgery was performed on 10 August 1979, and the section was completed on 16 October 1979. The 20-questions interaction yielded above chance performance on pictures presented at the first interoperative session and aided both picture and word naming at the second interoperative session. By session 3, J.W. was using a self-generated inferential process.

Stage	Stimuli	
	Pictures	Words
Preoperative (8 August 1979)	93	63
Interoperative I (24 August 1979)	28	13*
Interoperative II (15 September 1979)	67	42
Interoperative III (27 September 1979)	83	58
Postoperative (9 November 1979)	20*	0*

*Not significantly better than chance.

The second phase of our evaluation revealed that although stimuli lateralized to the right hemisphere could neither be transferred to the left hemisphere for naming nor compared with left-hemisphere stimuli, they were being correctly interpreted within the right hemisphere. When the required response was pointing with the left hand rather than naming, the right hemisphere was 92 percent accurate at indicating picture-word correspondence for left-visual-field stimuli. Athough unable to provide a spoken description, J.W.'s ability to comprehend the meaning of words and pictures in the left visual field indicated the presence of a right-hemisphere semantic system, thus strongly suggesting that he could be included among the small subset of commissurotomy patients with language in the right hemisphere (*9*).

Despite the sensory disconnection that resulted from the posterior section, left-hemisphere verbal responses following right-hemisphere stimulation were unlike those of patients with a complete callosal section. While such stimuli could not be named, he did not deny having "seen" something. Instead, naming failures were accompanied by apologies for a poor memory and on occasion, an agitated state like that described in the tip-of-the-tongue phenomenon (*10*). At such times, the patient claimed to "see" the stimulus in his mind but was unable to name or describe it.

After several such incidents, the investigators initiated a game of "20 questions" whenever the patient felt that he had some sense of the left-visual-field information. This interaction would be-

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