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THE AGGRESSIVE BEHAVIOR OF *MUNIDA SARSI* (CRUSTACEA : GALATHEIDAE)

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ABSTRACT

Munida sarsi is a deep water, bottom-living galatheid. Its aggressive behavior was observed for several weeks in aquaria that could only partially mimic its natural habitat. It threatens by extending its chelipeds, snapping its pincers, and raising its abdomen off the mud. The cheliped extension appears to be the indispensible part of the display. Threatening individuals spar with each other, and though such bouts are unpredictable in occurrence, duration, and outcome, they are mutually stimulating, harmless, and involve a series of stereotyped movements. The aggressive behavior of *M. sarsi* seems primarily to ensure each its private space of mud on which to dig and feed.

INTRODUCTION

Munida sarsi is a galatheid whose behavior, like that of most galatheids, is little known. It is a deep water, bottom-living animal that appears to be non-social and indiscriminately aggressive. A study of its aggressiveness provides a useful way of determining what some of its natural behavior is like and how it compares with other decapod crustaceans.

Aggressive behavior of some sort is characteristic of many reptant decapods. Threat and combat have been analysed extensively in hermit crabs (REESE 1962, HAZLETT 1966a), fiddler crabs (SALMON 1967, CRANE 1967), ghost crabs (HUGHES 1966, BOVBJERG 1956), and in stomatopod crustaceans (DINGLE & CALDWELL 1969), but they are undescribed in galatheids.

Galatheids are best known from deep-water collecting expeditions, but shallow water species do exist. For example, PIKE (1947) described the morphology of *Galathea squamifera*, and BRYAN (1965) has shown it to be a truly marine decapod lacking osmoregulatory capability. BOURBON (1962) noticed that it migrated into inshore bays during the winter months when its eggs were developing to maturity, and PEREZ (1927) has given fine accounts of the morphological changes that occur in it when it becomes sexually mature.

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Only NICOL (1932) has observed galatheid behaviour in any detail. She described the modified third maxilliped of *Galathea dispersa*, and showed that it was specialized for sweeping up mud particles, and hence that galatheids, like most anomurans, are primarily deposit feeders.

The ecology and morphology of *Munida sarsi* were discussed briefly by BRINKMANN (1936) who was more specifically interested in the parasites it and other *Munida* species were hosts to. It lives in abundance at moderate depths of one to four hundred meters along the Norwegian coast.

METHODS AND MATERIAL

I collected and observed *Munida sarsi* during August 1969 while working at the Biological Station of the University of Bergen at Espegrend, Norway. They were gathered by otter trawl from 240 meters in Raunefjorden, south-west of Bergen (collection reference numbers E233–69 and E236–69). A total of 45 individuals, sexually mature though not sexually active, were kept in aquaria for two to three weeks without any mortality.

I kept *Munida sarsi* in groups of five to eight per aquarium, in running water at 6–12°C, on a mud substrate. I observed their movements, confrontations, and responses under natural daylight, and photographed them by electronic flash. Their environment in captivity was therefore but a rough approximation of their natural one.

OBSERVATIONS

Unaggressive behavior

The unaggressive *Munida sarsi* usually squatted in a depression in the mud that it had scooped out, feeding by scraping and picking intermittantly at the mud around it, and cleaning itself almost continually with its modified fifth pair of legs. I found no patterns or organization to the feeding behavior. The durations of the periods between the various feeding actions were as impredictable as the sequence of those actions.

Digging

An undisturbed *Munida sarsi* generally remained in its scooped depression until some stimulus provoked its departure. It tended to squat with its back against an object, like a rock if one were present, and it let its long chelipeds lie unraised out in front of it (Fig. 1).

It dug its depression by scraping the mud away from under it. For example, it would scrape with the third and fourth appendages on one side, pushing mud forward and out to that side. Then it would shift its position so that its abdomen was over the scraped mud, clap its abdomen rapidly against its thorax several times, and so blow the loosened mud forward in front of it. Thus by a combination of scraping with unilateral pairs of legs and clearing out loose mud by a modification of its escape response, *Munida sarsi* could dig a depression large and deep enough to hide it at least partly from view.

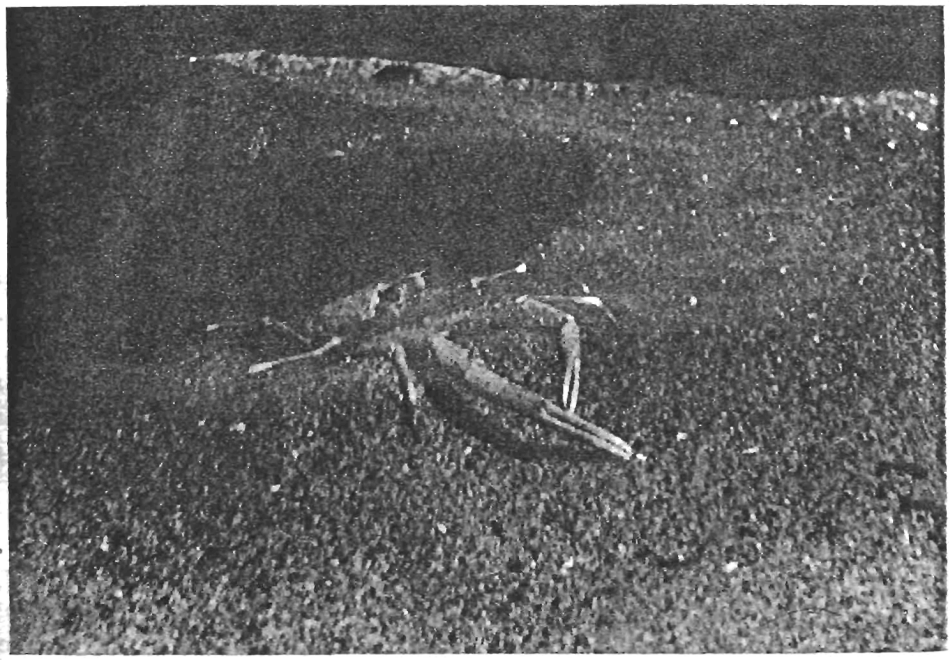

Fig. 1. An unaggressive *Munida sarsi*, sitting in the shallow depression it has dug for itself.

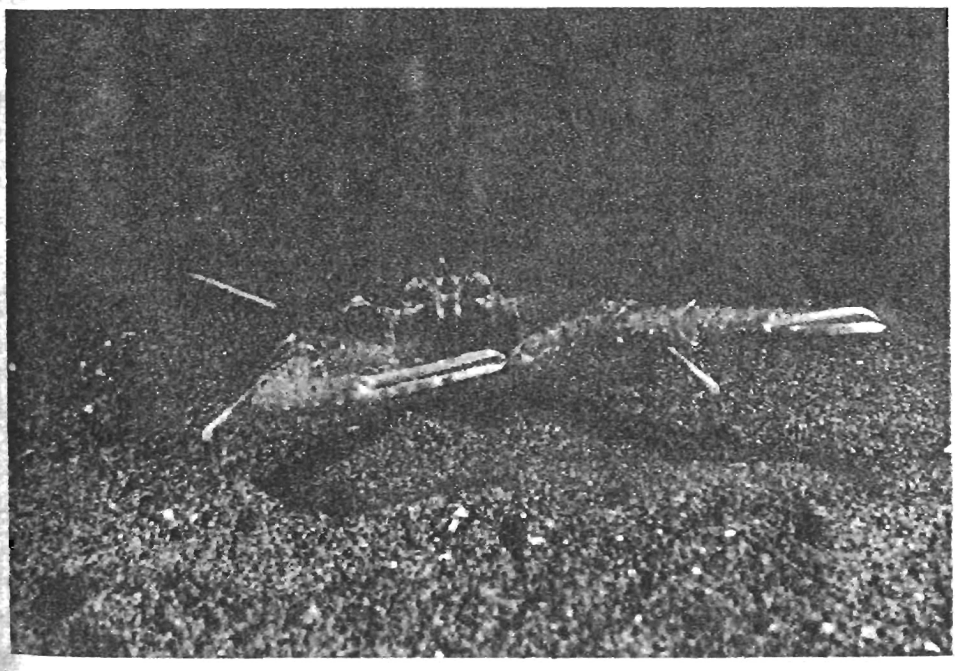

Fig. 2. *Munida sarsi* about to eat a small bit of mud it has picked up in the pincers of one cheliped, still threatening with the other cheliped.

Feeding

Cleaning. The fifth pair of legs is typically abbreviated and modified among anomurans, and that of galatheids is no exception. *Munida sarsi* cleaned itself with these legs which could act independently or in unison, reaching up under the carapace, under the abdomen, cleaning the surface of the body, scraping the legs and antennae and eyes. Always, after one of these extraordinarily prehensile legs cleaned some part of the body exo-skeleton it reached to the mouth parts where it was itself cleaned off.

Scraping. *Munida sarsi* sometimes scraped mud forward with one or two of its second, third or fourth pairs of legs on one side at a time. If it scraped with two legs, they were always adjacent ones. Instead of scraping the mud away to the side as it did when digging, however, it scraped it forward to the maxillipeds which cleaned off the legs. Occasionally, it would pump its abdomen to disturb the mud before it scraped one or two of its legs through it.

Picking. *Munida sarsi* also fed by picking up bits of mud with the pincers of its chelipeds, and passing the bits to its maxillipeds and mandibles (Fig. 2).

Scavenging. When *Munida sarsi* found or was offered a piece of mollusk tissue, it would grab the piece and tear it apart with its maxillipeds or the pincers of its chelipeds. When an individual was put in water containing snail juice, it became hyperactive and snapped away at the elusive juice.

Aggressive behavior

The threat and conflict activities of *Munida sarsi* stood out in stark contrast to this general picture of a quiet, solitary existence. Their variation in degree, duration, stimulation, and situations in which they occurred were again as variable as they were unpredictable.

Degree of threat

Munida sarsi threatened by raising and extending its chelipeds and raising its body up off of the substrate, and the height to which it raised them indicated the intensity or aggressiveness of its threat.

Starting from the unaggressive stances involved in feeding, digging, and resting, an individual that extended and raised one of its chelipeds with its pincer open exhibited minimum threat. If it extended and raised its other cheliped as well, and raised its abdomen off the substrate, tilting its body so that its chelipeds were raised even higher, it then exhibited moderate threat. It achieved maximum threat by raising its abdomen so far off the substrate that its fourth pair of legs and perhaps one of its third pair no longer reached the ground, and it then strutted slowly forward, backward or sideways, its appendages extended as far as possible short of collapse (Figs. 3, 4, and 5).

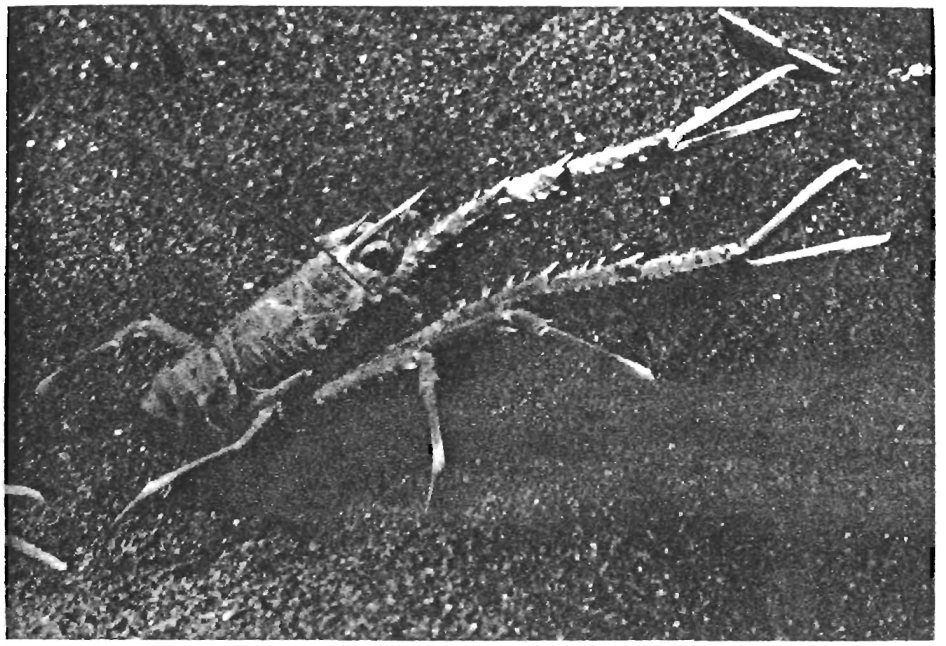

Fig. 3. *Munida sarsi* threatening from its scooped depression.

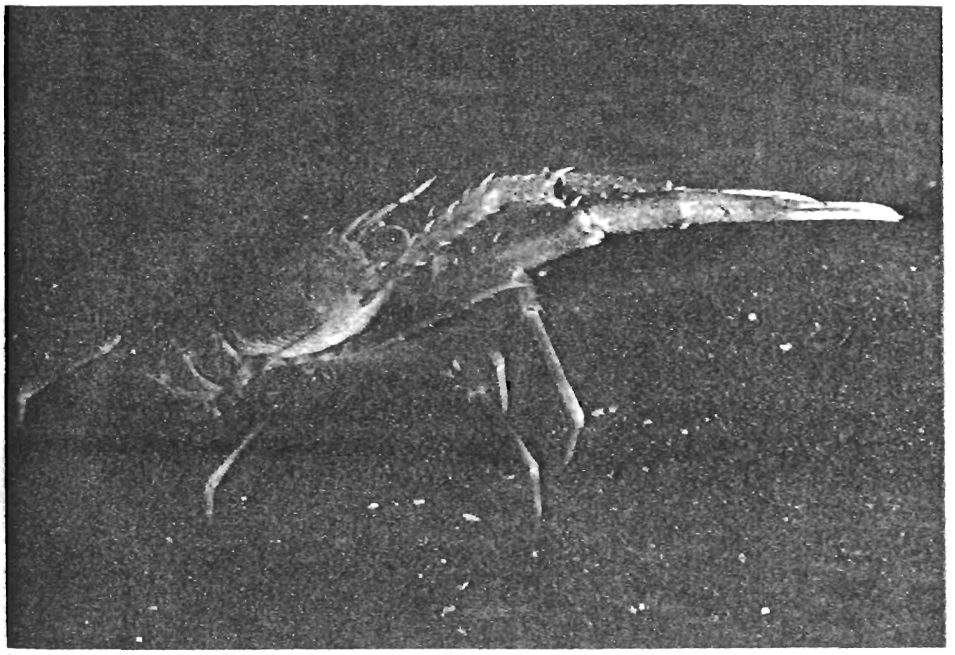

Fig. 4. *Munida sarsi* in moderate threat, chelipeds extended, abdomen partly raised, but pincers closed.

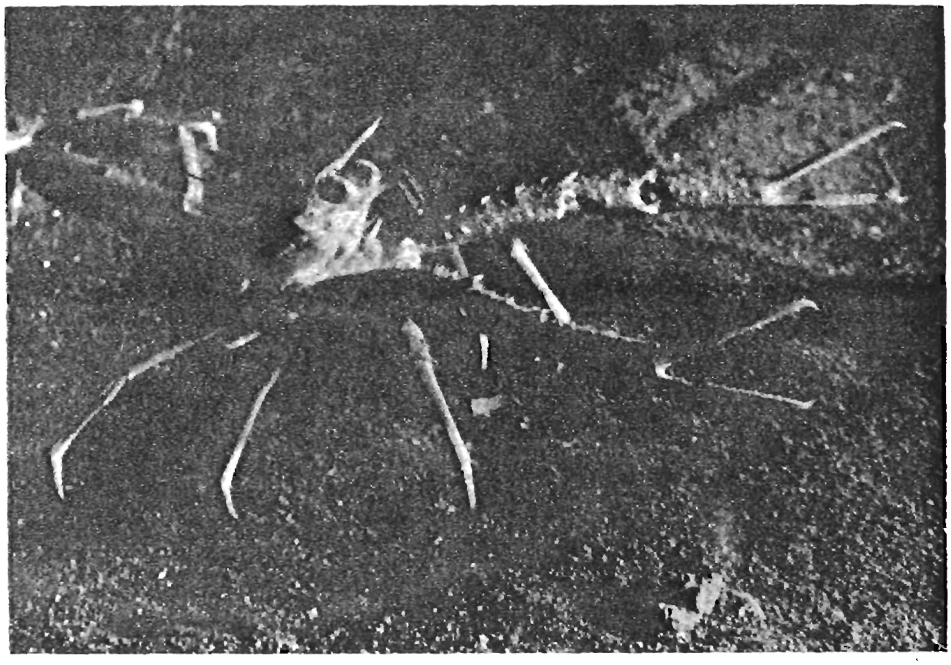

Fig. 5. *Munida sarsi* in maximum threat, abdomen raised high off the mud, chelipeds extended and pincers gaping.

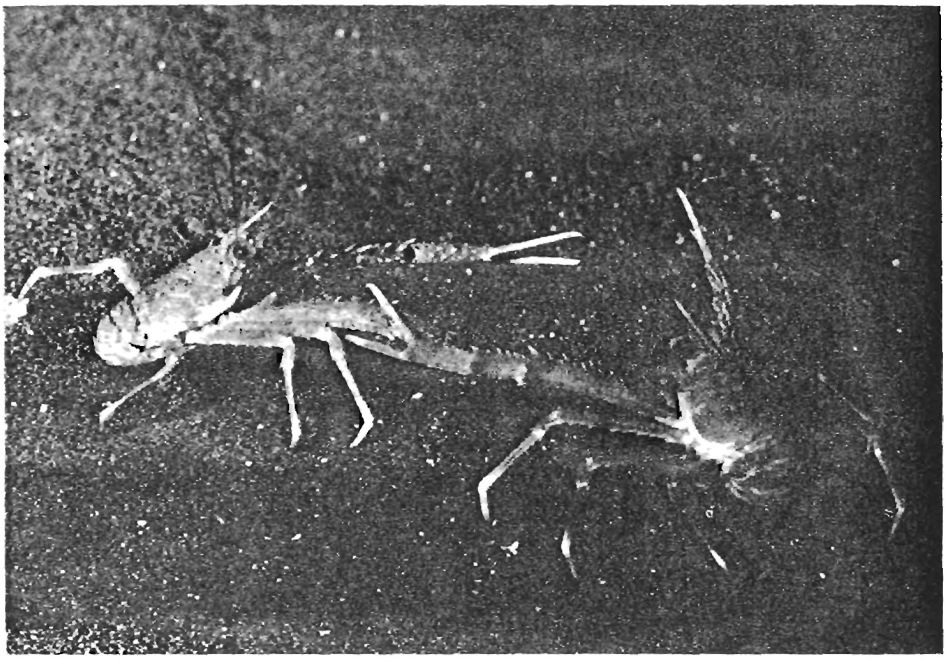

Fig. 6. Two threatening *Munida sarsi* sparring with one another.

Combat

When two individuals in moderate or maximum threat positions faced each other, one of them usually initiated a sparring match. With pincers snapping, each would attempt to grab a cheliped of the other near one of the joints, though occasionally they locked pincers instead. Their cheliped thrusts were always abrupt and quick, almost jerks, and the thrusts of one appeared to induce the other to thrust back. Two individuals remained clutching and jerking in mutual threat for as long as 30 minutes if neither one had the advantage, but most confrontations were quickly decided and lasted for but a few seconds (Fig. 6).

Even during combats, however, the behavior of a single individual varied greatly. In a brief encounter it might not even raise its abdomen off the ground, or on the other hand it might rise immediately to maximum threat, snapping and sparring instantly. During prolonged encounters the extent of threat and combat rose and fell and never stayed at just one level.

Escape

Munida sarsi avoided or escaped encounters in typical decapod fashion by clapping its abdomen against its thorax and spurting away backwards. This avoidance maneuver was rapid, moving the animal 10–20 cm away in a fraction of a second, and the clapping of the abdomen stirred up a mud screen that made subsequent detection possibly even less likely. The escaping individual invariably came to rest facing and threatening whatever had made it move off.

This avoidance behavior commonly ended a combat. For example, in a sparring match if one animal was grabbed at one of its cheliped joints, it could jerk itself free only by spurting backwards violently. An escaping individual was never followed or chased by the individual it had been in conflict with.

Submission

When two *Munida sarsi* met, each would have to threaten the other for any kind of encounter or combat to arise. If a marauding, threatening individual met another which did not threaten back, it simply ignored it and passed on. In an encounter between two threatening individuals, if one did not clutch, jerk and spar, the other ceased these actions as well, and the threat of both slowly faded. If one ceased threatening abruptly in an encounter, the other either ceased as well, or moved on still threatening.

In other words, no combat developed or continued when only one individual threatened, and the normal positions of feeding, digging, and resting were recognized as unaggressive ones. Submission here then was identical to not threatening.

Natural threat situations

Munida sarsi threatened in at least three types of situations. When sitting in its scooped depression and approached by another individual, it threatened and usually drove off the intruder in a few seconds without even leaving the depression. This could be similar to the territorial defense typical of other decapods.

It also threatened in defense of food it had found. When a scavenging *Munida sarsi* found a piece of snail tissue, for example, it held and tore it up with its maxillipeds, and at the same time extended its chelipeds in a threat posture that intensified whenever another individual approached. It could therefore eat and threaten at the same time.

Quite a different situation from that of food or home defense was that of defense against potential predators. In several instances, *Munida sarsi* threatened and snapped at small fish that attacked it. Faced with persistent attack, from a large crab for example, it backed off slowly, always facing and threatening the attacker, a guarded avoidance. Whenever attacked abruptly, *Munida sarsi* immediately swung to face the attacking source, its chelipeds and abdomen raised in maximum threat. It used its spurting avoidance behavior only when it was actually grasped or it had no space behind it to back into.

There were instances also when *Munida sarsi* threatened for no apparent reason. On one occasion an individual stood on top of a rock for almost 8 hours, in maximum threat the whole time although it was undisturbed by other *Munida sarsi* or by potential predators.

Damage in conflicts

In the more than 100 intraspecific encounters that I recorded, never did one *Munida sarsi* harm another. Either the conflict faded out, or one individual did not threaten, or one spurted away, always before one had hurt the other.

In interspecific encounters, *Munida sarsi* scared off fish of moderate size, simply avoided large decapods like *Nephrops norvegicus*, and threatened other decapods of about its own size.

Dominance

Although most conflicts had a winner, a group of captive *Munida sarsi* did not establish any sort of dominance hierarchy. Size was the only characteristic that predictably determined the victor in a conflict, and only then when the size disparity was great. Every encounter was a new one, and an individual that seemed particularly aggressive and possessive on one day might appear quiet and unaggressive the next. A complex interaction of internal and external factors must have been involved in determining aggressive levels.

Releasing stimuli

Despite this complex interaction of factors, it should be possible to isolate and identify those factors which *Munida sarsi* makes most use of in recognizing and responding to the threat of other individuals.

All attempts involving artificial models either failed or were merely ambiguous. Though *Munida sarsi* sparred with each other, they chewed on or ignored models made of stone, wood or clay, even when the models were of appropriate colors, size, shape, and postures to induce conflict. Only when the models were made to move, like puppets, did *Munida sarsi* threaten them, but they did not spar with them and there is no reason to believe they recognized them as their own kind. This does, however, again emphasize the importance of movement in inducing and maintaining any sort of threat or conflict.

On the other hand, some natural experiments suggest that the actions of the chelipeds are of primary importance in stimulating conflicts. Many *Munida sarsi* were injured by the otter trawl that caught them, and a number of these, missing one or more appendages, were kept in aquaria with intact animals.

Individuals lacking antennae appeared to be as successful in conflicts as those not lacking them. Similarly, those missing one or more walking legs could still spar effectively provided they had enough legs left to balance on. Individuals missing one cheliped were also apparently unaffected by the loss. The loss of an appendage is not irrevocable, for several individuals had begun regenerating new chelipeds two weeks after they had lost them.

Those missing both chelipeds, however, were ignored by other *Munida sarsi*. Though they raised their abdomens so high that they walked on only three legs, they never induced others to threaten back at them, and intact threatening individuals walked past them unnoticing.

DISCUSSION AND CONCLUSIONS

Although the water temperatures and the substrates in the aquaria in which *Munida sarsi* lived were approximately like those of their natural habitat, I did not attempt to give them their natural conditions of space, light, and pressure. I have assumed that, despite their naturally dim environment, vision is the primary sense involved in their threat behavior. With their normal-sized eyes, adaptive coloration, as well as the obvious visual elements of posture, patterns, and movement that characterize their threat displays, it is difficult to assume otherwise. HAZLETT (1966b) similarly found that the displays of deep-water pagurids appeared to be visually oriented. Most crustaceans also possess an acute chemical sense, yet the role of chemoreception in determining threat behavior has been generally ignored, and I have not attempted to include it.

Despite these qualifications, it is possible to deduce from its behavior in captivity a general picture of the natural behavior of *Munida sarsi*. It is well adapted to living on mud, for its appendages are modified for digging, for supporting it on a loose mud substrate, and for scraping and filtering food particles from that substrate. It partially hides itself in its depression in the mud, and it is normally solitary and quiet, scavenging for food only when the rare opportunity presents itself.

Munida sarsi is, moreover, a highly coordinated animal. For example its modified cleaning legs are remarkable in their dexterity, it can pick up a small pinch of mud with the pincers of either cheliped, and it directs its snapping thrusts at the joints of an opponent's chelipeds. It is therefore capable of the refinements of action which are vital to the development of complex behavior.

Although its aggressive and unaggressive activities appear to be unpredictable in occurrence, sequence, and duration, it may with slight modifications use the same action in a variety of situations. For instance, it uses much the same scraping motions in both digging and feeding, and it claps its abdomen against its thorax in much the same way to assist it in digging, feeding or escaping. It also responds to a great variety of disturbing stimuli by threatening in precisely the same way. Its moderately complex behavior is, in other words, derived from a limited number of simple actions.

Though *Munida sarsi* indiscriminately threatens any attacking or disturbing source, and may even threaten in an apparent absence of stimulation, it reserves its sparring behaviour solely for intraspecific conflict. The stimulation of such sparring conflict is no doubt complex, involving physiological states as well as external releasing signals, yet certain elements are more important than others. Body posture is never enough to induce a conflict by itself, whereas possession of a single cheliped is, provided it is used correctly. The special jerking movements of the chelipeds of one of the protagonists in a conflict may be the specific cues which stimulate the other to return in kind, for when one ceases to jerk and spar, the other does as well, and the conflict fades. Body posture, though not vital, still plays an important role, for by raising and tilting its abdomen, *Munida sarsi* emphasizes the extension of its chelipeds.

The aggressive conflicts of *Munida sarsi* thus involve stereotyped postures and movements. Moreover, an animal need only escape or become unaggressive for the conflict to end, and so the conflicts are harmless. These features of stereotyped movement and postural emphasis of the chelipeds, together with their harmlessness, are generally characteristic of decapod aggressive behavior (DINGLE & CALDWELL 1969). *Munida sarsi* differs from many other decapods, however, in its apparent lack of any predictable dominance hierarchy, a lack perhaps associated with its solitary, relatively stationary and non-scavenging existence.

Despite the wealth of accounts of the ritualized aggression of animals, the functions of aggression remain a matter for debate. CRANE (1967) in an attempt

to account for the high frequency of conflicts in the special case of fiddler crabs, suggested ritualization might function in actually shortening the duration of their conflicts. The more commonly accepted functions of defense of territory and competition for mates seem to apply to most other decapods, however.

In the case of *Munida sarsi*, food is abundant in the mud and certainly not something to compete for. Sexual competition might be important in the breeding season, but early August is not the season. Nevertheless, the conflicts of *Munida sarsi* are ferocious though harmless, and may simply be a way of ensuring each individual its private space of mud on which to dig and feed.

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