Starfish encounters: An experimental study of its advantages

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Summary. The predatory starfish *Crossaster papposus* exploits a chemically mediated escape response in another predatory starfish *Asteria rubens* when a common food resource is available to both species. Intraspecific avoidance among *C. papposus* is strong and functions in dispersal. Responses to inter- and intraspecific encounters among starfish may be important to the predatory ecology of species in high positions in their food webs.

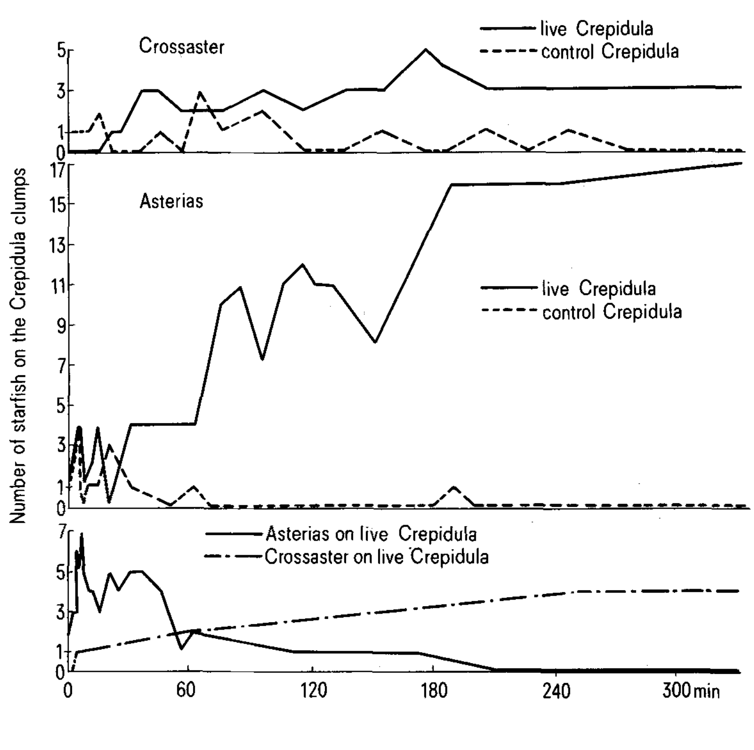
In Puget Sound, Washington State, the sunstar *Crossaster papposus* (L.) is a generalist, non starfish-eating, predator which is eaten by another solasterid starfish, *Solaster dawsoni* Verrill[1,2]. In European waters, however, *C. papposus* is a predator of another predatory starfish *Asterias rubens* (L.) as well as molluscs and other groups. *C. papposus* in this community has no known predators[3-5], although it can occasionally be cannibalistic[5,6]. Laboratory experiments on European *C. papposus* suggest that both intraspecific and interspecific encounters with *A. rubens* may aid in maintaining the status of *C. papposus* as a predator in its local community.

Whole *C. papposus* elicit escape responses in *A. rubens* upon contact[4] and at a distance due to olfaction[7]. Extracts of its tissues have a similar effect[8]. *C. papposus* will strongly avoid extracts of and contact with conspecifics[8]. This unsociability was predicted long ago[9]. By contrast, *A. rubens* has long been known as a gregarious species[10].

Intraspecific avoidance is a new phenomenon in echinoderm literature which has been described in predatory starfish[1,2,8,11,12], ophiuroids[13,14], and echinoids[15,16]. Dispersal would seem to be the main function of intraspecific avoidance. The tendancy to aggregate is, on the other hand, widespread throughout the Echinodermata[17,18].

The duration of inter- and intraspecific contacts between *C. papposus* and *A. rubens* gives a useful indication of their basic tolerance of the presence of others. The table lists the means and ranges of the contact durations. *A. rubens* so strongly avoided *C. papposus* that none were captured, even when *A. rubens* was smaller than the sunstars. Intraspecific avoidance among *C. papposus* was strong and consistant as it was in situ in the Crouch estuary, Essex, England[20]. By comparison, *A. rubens* showed much more intraspecific tolerance.

Tests were carried out to quantify the different intraspecific behaviour of individuals of *C. papposus* and *A. rubens* taken from co-existing populations in the Crouch estuary. The experiments attempted to induce aggregation first in 36 individuals of *C. papposus* and then in 36 *A. rubens* using a shallow, 0.88 m^2 parabolic shaped arena[19]. The arena contained 2 clumps, 12–15 cm in diameter, of *Crepidula fornicata* (L.) - a prey species of both starfish. 1 clump had only the live gastropods while the other had only cleaned, empty shells as a control. Finally 36 *A. rubens* and 12 *C. papposus* were put with the *C. fornicata* and observed for the effects of *C. papposus* on the aggregating behaviour of *A. rubens*. All these experiments were monitored by time-lapse cinematography and run up to 6 h. The figure shows that *A. rubens* will readily aggregate on the food locus while *C. papposus* did not display such a tendancy, although it was attracted to the food. Once a few *C. papposus* began feeding, access to the food was denied to non-feeding conspecifics who would flee from contact with the feeding ones. Once *C. papposus* was feeding, contact with conspecifics did not cause the feeding individual to flee. This suggests a higher priority of the feeding stimulus to that of close proximity of conspecifics. Cannibalism, which is common in predatory starfish[20], only occurred in *C. papposus* in the laboratory after a period of starvation[20]. Cannibalism was never observed among *A. rubens* although it has been



Settlement of *C. papposus* and *A. rubens* on food stimuli.

reported elsewhere[3]. The presence of the 12 *C. papposus* among the 36 *A. rubens* and food dramatically reduced the feeding activity in *A. rubens*. Individuals of *A. rubens* were quicker to begin feeding but they were soon displaced by contact with *C. papposus* when it began to feed on the *C. fornicata*. Once the sunstars became established on the food, all *A. rubens* attempting to feed were prevented from doing so by contact with the *C. papposus*. *C. papposus* effectively exploited the avoidance behaviour of *A. rubens* to gain access and reserve the same food resource for itself. Actual attacks on *A. rubens* by *C. papposus* were very rare during the experiments.

The extensive starfish dredging surveys of the Crouch have revealed that the 2 species have a discrete distribution[6,21,22]. This has been related to different recruitment strategies of the species and heavy predation by *C. papposus* on newly settled *A. rubens*[6,22]. Interspecific avoidance among adults should now be considered an important factor also. The gut contents of adult *C. papposus* in the Crouch overlapped considerabley with that of *A. rubens*, especially on molluscan prey, and *C. papposus* showed little evidence of starfish predation[20,21]. Indeed, recent work by Hancock[5] has suggested that *C. papposus* will very readily take molluscs and that it is not such a specialized predator on *A. rubens* as previously thought[6,22].

From the experiments reported here and accumulated field evidence, it is suggested that *C. papposus* in the Crouch is not so much an active predator of *A. rubens* but could be an active competitor with *A. rubens*. *C. papposus* exploits its fright substance in excluding *A. rubens* from a common food source. Also, *C. papposus* disperses its own population to perhaps decrease intraspecific competition for food and exclude *A. rubens* from the immediate area. In a detailed field study[23] the importance of aggression in the competitive co-existance of 2 starfish species has been clearly shown. The dominant competitor decreased the feeding rate and affected the distribution of the other species after aggressive encounters. Non-predatory encounters between starfish[11,23] require further study as their effects may alter starfish predatory activities and thus may be important to the ecology of some benthic communities. These encounters reveal an interesting behavioural complexity of these animals.

Starfish contact durations

Contact type	n	Mean (sec)	Range (sec)
Asterias–Asterias	100	39.8	3–291
Crossaster–Crossaster	100	9.0	1– 27
Crossaster–Asterias	100	6.1	1– 22

The ranges do not include the single longest contact in all cases (n = 99). The temperature during tests varied between 11 and 13 °C.

* Present address: Bermuda Biological Station, St. George's West 1-15, Bermuda. I thank the MAFF. Fisheries Lab., Burnham-on-Crouch for hospitality and facilities, Prof. N.B. Marshall, F.R.S. and Dr A.C. Campbell for laboratory facilities at Q.M.C.

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Studies on the cytochemical localization of adenylate-cyclase activity in *Dugesia lugubris* s.l.[1]

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Summary. The localization of adenylate-cyclase activity in *Dugesia lugubris* s.l. has been investigated cytochemically using 5'-adenylyl-imidodiphosphate as substrate. The enzyme was localized in mucous gland cells, in rhabdite cells, in intercellular spaces and also in nerve endings of this planarian. The presence of adenylate-cyclase on the membrane suggests that it might mediate different stimulus-secretion coupling by increasing cyclic AMP synthesis in specialized areas of the planarian.

Adenylate-cyclase has been found in a very wide variety of organisms, ranging from bacteria to mammals. It appears to occur throughout the animal kingdom and in most cases a major regulatory role has been established for the enzyme[4]. A number of systems have been studied in higher animals, in which the enzyme mediates the action of many hormone messengers[5]. The adenylate-cyclase of neuronal tissue has been shown to be sensitive to a number of putative neurotransmitters, including norepinephrine, dopamine, serotonin, histamine and octopamine[6]. A number of similarities have been found between the physiological receptor for a particular neurotransmitter and the regulatory subunit of the adenylate-cyclase.

Such similarities constitute important evidence that a par-