ON THE PREFERRED FOODS OF SOME AUTOLYTOIDS (POLYCHAETA, SYLLIDAE).

by

Richard Hamond
Scaldbeck, Morston, Holt, Norfolk, England (1).

Résumé

Parmi les onze espèces d'Autolytinae des côtes du Norfolk, on peut constater que trois se nourrissent normalement, comme l'a décrit Okada (1928), de polypes d'Hydroïdes. L'hiver, lorsqu'ils ne peuvent pas vivre dans les polypes d'Hydroïdes détruits, les Vers recherchent une nourriture de remplacement encore inconnue ; au printemps et l'été, bien que mangeant plusieurs autres espèces de *Laomedea, Proceraea cornuta* et *Autolytus brachycephalus* évitent l'Hydroïde *Laomedea flexuosa* dont la chair, relativement dure, porte des nématocystes puissants. Parmi les représentants d'*A. brachycephalus*, espèce aux goûts éclectiques, ceux qui sont habitués aux *Eudendrium* ne mangent aucune *Laomedea*, bien que ce dernier genre soit bien accepté par ceux qui s'en sont nourris pendant toute leur vie. Par contre, *Procerastea halleziana* attaque seulement certains Gymnoblastiques. Quelques autres aspects de ces relations proie-prédateur sont brièvement discutés.

Introduction

During an investigation (Hamond, 1967) of the biology of the autolytoids found on the Norfolk coast (localities, Hamond 1963a), it was found necessary to feed the stocks in culture in order to rear the stolons for experimental work on the mating (described by Gidholm, 1965). Of the eleven Norfolk species of autolytoid (the sub-family Autolytinae, see Gidholm 1966), *Proceraea prismatica* (O. Fabricius) and *Autolytus* sp. aff. *langerhansi* Gidholm are known in North Norfolk waters only as planktonic stolons taken near the Blakeney Overfalls Buoy; *Autolytus* sp. (on *Hyas*-eggs), *A. quindecimdentatus* Langerhans (=*A. lugens* de Saint-Joseph), *A. edwardsi* de Saint-Joseph, *A. prolifer* (O.F. Müller), and *Proceraea picta* (Ehlers) were caught very rarely and always died before they could undergo a reasonable number of feeding trials; and *A. alexandri* Malmgren refused every food-organism offered it, although apparently in perfect health. Feeding was observed, therefore, in only three species, of which *Procerastea halleziana* Malaquin was available for a few trials,

(1) Present address: CSIRO, Fisheries Laboratory, Cronulla, Sydney, Australia.

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Proceraea cornuta (Agassiz) and *Autolytus brachycephalus* (von Marenzeller) were each available for many trials (Table 1). The above species are recorded in Norfolk waters by Hamond (1966), except for *P. prismatica* of which seven male stolons and one female stolon were taken in surface plankton near the Blakeney Overfalls Buoy on 10.2.1967.

TABLE 1
Results of feeding trials in the laboratory.

Hydroid	Autolytoid: *A. brachycephalus*	*P. cornuta*	*P. halleziana*
Clava multicornis	—	—	
Hydractinia echinata	—	—	—
Coryne muscoides	—	—	
Sarsia tubulosa	—		—
Tubularia larynx	—	—	+
Eudendrium rameum	—	—	
Halecium beani	?		
Filellum serpens	—		
Opercularella lacerata	—	—	
Campanularia verticillata		?	
Clytia johnstoni		—	
Laomedea dichotoma, var. *plana*	+	+	
L. bicuspidata	—		
L. gelatinosa	+	+	—
L. loveni	+	+	
L. flexuosa	?	—	
Abietinaria abietina	—		
Dynamena pumila	—	—	
Sertularia argentea		—	
Kirchenpaueria pinnata	—	—	
Plumularia setacea	—	—	

Autolytus alexandri was offered *Eudendrium rameum, Halecium beani, Filellum serpens*, and *Abietinaria abietina*, all of which it refused.
+: habitual feeding; ?: attempts to feed; —: refusal.

Material and methods

Potential food-organisms (hydroids, polyzoa, and algae) were collected either by dredging offshore or by hand in Blakeney Harbour; they were thoroughly washed on collection and were brought in a large excess of seawater back to the laboratory, where they were put under continuous (but not violent) aeration overnight in an enclosure, whose temperature was controllable to within a degree centigrade either way of the prevailing sea-temperature. Since the food-organisms did not usually reach the laboratory until late in the evening, the feeding trials were not held until next morning in most cases. Algae and polyzoa were invariably refused as food; hydroids (nomenclature in Tables 1 and 2 as in Hamond, 1957, 1963b) were sometimes acceptable.

Although this is the first time that the range of food eaten by any given species has been discussed, the method of feeding is well known; thus, *Proceraea cornuta* and *Autolytus brachycephalus* feed in exactly the manner described for *A. edwardsi* by Okada (1928), and for an un-named species of *Autolytus*, near to *A. brachycephalus*, by Hauenschild (1959). I was unable to observe *Procerastea halleziana* actually biting the prey (see below), but the method of feeding (described by Allen, 1921) does not differ in any essential respect from that practised by the above group of species.

Feeding trials

Trials were conducted by placing a clean branch of living hydroid in a small dish of filtered seawater under à binocular microscope, and by introducing the worms in such a way that they could creep onto the hydroid without being stung and could then feed or not as they chose. Worms which were stung before obtaining a hold on the colony very often gave up and crawled away, when in fact a successful introduction would normally have led to feeding; it was also necessary to ensure that the worms remained healthy in spite of having been kept without food for a day or two in order to make them hungry. In these circumstances, if a worm failed to feed within 15 minutes of being put onto the hydroid, it would not do so at all (see below, however, on *Procerastea*).

If the hydroid is acceptable the worm crawls along the hydrocaulus until it reaches a polyp, by which it is stung on the head or head appendages; the worm reacts to being stung by rearing backwards like a frightened horse shying, and by simultaneously curling its head appendages backwards for an instant, but if the food is suitable the worm usually persists in spite of being stung perhaps three or four times, and may by its repeated approaches cause the polyp to retract; the pharynx is then protruded and feeding begins. Thie applies to *P. cornuta* or to *A. brachycephalus* on a colony of *Laomedea* (any Norfolk species except *L. flexuosa*); *P. halleziana* (on *Tubularia larynx*) recoiled more than once from being stung but eventually crept up the stem to a position, on the lower side of the polyp, from which its head and first few segments reached through, between the bases of two adjacent aboral tentacles, to the neighbourhood of the gonophore clusters; in this position the worm remained motionless for more than an hour, almost certainly feeding either on the bodywall, or the contents, of the polyp or of the gonophores. It was impossible to observe feeding directly without moving the aboral tentacles, which on other occasions invariably led to withdrawal of the worm; my observations confirm those of Allen, that *P. halleziana,* even after several days' starvation, feeds only at long intervals and with extreme caution.

If the hydroid is unacceptable, the worms, when placed upon it, will crawl off it, either at once or after more or less roaming about without trying to feed; the response varies for different individuals of the same species of worm and for the same individuals when placed on different colonies of the same species of hydroid. Normally acceptable hydroids may sometimes be refused for no obvious reason (in September 1965, both *P. cornuta* and *A. brachycephalus* refused to feed on *Laomedea loveni*) and, of course, all hydroids were not quite fresh owing to the difficulties of collection and transportation; intertidal species survived better than those from dredgings, and hydroids of the family Plumulariidae survived worst of all, their polyps being completely shrivelled within an hour or two of collection. For all these reasons replicate trials were staged whenever possible, even on thoroughly familiar species.

The food in nature

Since worms can thus discriminate between acceptable and unacceptable foods, a species of hydroid found in nature to harbour autolytoids can be assumed to serve as their food, with a probability which increases with the number of individuals found on a given colony of that hydroid. Such finds, when not supported by feeding trials (Table 2), appear to indicate that:

a. *Procerastea halleziana* feeds habitually on *Sarsia eximia, Tubularia larynx, T. indivisa* and, occasionally, on *Eudendrium ramosum* ;

b. *Proceraea cornuta* feeds on *Eudendrium rameum, Opercularella lacerata,* and perhaps on *Halecium beani* ;

c. *A. brachycephalus* (with which the local form of *A. prolifer* appears to intergrade) feeds on *Sarsia tubulosa, Eudendrium rameum, Tubularia larynx, T. indivisa, Halecium halecium, H. beani,* and *Nemertesia ramosa.* On rare occasions, it may feed on *Laomedea flexuosa* or on *Kirchenpaueria pinnata,* both of which it normally avoids.

Instances (see Table 2) where very few of a species of autolytoid were found on a certain hydroid, have not been considered above. The data given in Table 2 are based on findings in the wild, whereas those in Table 1 are from feeding trials in the laboratory; until many more of both sorts of findings are available, it cannot be said that field and laboratory data contradict one another.

TABLE 2

Finds of autolytoids among hydroids in nature.

H stands for the inside of the "Hjördis" and S for Hunstanton Scaup (Hamond, 1963 a).

The volumes given are those of the collecting jars, into which the hydroids were packed fairly densely but without undue compression.

Sarsia eximia.
1. 8.1962. H. 1 litre of this and *Eudendrium ramosum*, mixed. 2 *A. prolifer*, ca. 10 each of *A. brachycephalus* and *P. halleziana.*
3. 9.1962. H. 100 mls. 2 *P. halleziana.*
15. 9.1962. H. 200 mls. 5 *P. halleziana.*

Sarsia tubulosa.
25. 2.1963. H. 300 mls. 21 *A. brachycephalus.*

Bougainvillia ramosa.
9. 9.1964. S. A litre, with a few very small colonies of this species, but mixed with *L. bicuspidata, E. rameum,* and *H. halecinum,* also 34 small *Ciona intestinalis.* 30 *A. brachycephalus,* 6 *A. prolifer,* 2 *P. cornuta.*

Eudendrium ramosum.
1. 8.1962. With *S. eximia* (q.v.).

Eudendrium rameum.
22. 6.1963. S. 5 colonies, each about 7 cm high (the usual size in Norfolk waters). 14 *P. cornuta,* 1 *A. brachycephalus.*
1.11.1963. S. 6 colonies. 3 *P. halleziana,* 3 small *P. cornuta,* 1 *A. brachycephalus,* 1 *Autolytus* resembling *edwardsi.*
9. 9.1964. S. 3 colonies, with *B. ramosa* (q.v.).
3. 4.1965. Dredge, close to Blakeney Overfalls Buoy. Several colonies each of this and of *H. halecinum.* 1 young *A. alexandri,* 15 *A. brachycephalus,* 1 *P. cornuta.*

Tubularia larynx.
14. 9.1962. H. 200 mls. 1 *P. halleziana,* 9 *A. prolifer,* 2 *A. brachycephalus.*
17. 9.1962. H. 800 mls. Myriads of *P. halleziana,* 6 *A. prolifer.*
26. 5.1963. H. 500 mls. 4 *A. brachycephalus.*
1. 7.1965. H. 800 mls. 3 *A. brachycephalus.*

Tubularia indivisa.
26. 4.1963. Dredged at 53°03′15″N. 01°00′15″E. 12 polyps. 1 small *Autolytus* sp. (as on *Hyas*-eggs), 6 tiny *P. cornuta.*
7. 9.1965. Dredged at 53°04′30″N. 01°03′E. A large clump of about ten polyps. 18 *A. brachycephalus* (very close to *prolifer*), ca. 40 *P. halleziana.*

Clytia johnstoni.
1.11.1963. H. 800 mls of *Ceramium* sp. covered with *Clytia* on its lower branches. 3 *P. cornuta,* 3 *A. brachycephalus.*

Laomedea bicuspidata.
9. 9.1964. H. With *B. ramosa* (q.v.).

Laomedea flexuosa.
16. 9.1962. Wells Rocks. 800 mls of *Fucus vesiculosus,* thickly covered with *L. flexuosa.* Many small *A. brachycephalus,* 2 *P. cornuta.*
5. 8.1963. Same place, similar sample. Ca. 90 *A. brachycephalus,* 5 *P. cornuta.*

Opercularella lacerata.
28. 1.1964. Site of Sheepbridge, Morston Quay. 800 mls of *Chondrus crispus* thickly covered with *O. lacerata.* Many *P. cornuta.*
8. 2.1964. Same place, similar sample. No autolytoids.
22. 2.1964. Same place, similar sample. About 100 *P. cornuta.*

Filellum serpens.
7. 9.1965. With four coppinias, thickly covering the stems of *Tubularia indivisia* (q.v.).

Halecium halecinum.
20. 8.1963. Cast ashore near Brancaster Golf Club. 800 mls. 2 *P. cornuta,* 20 *A. brachycephalus.*
9. 9.1964. With *B. ramosa* (q.v.).
3. 4.1965. With *E. rameum* (q.v.).

Halecium beani.
20. 8.1963. Cast ashore near Brancaster Golf Club. 500 mls. 15 *A. brachycephalus,* 8 *P. cornuta.*

Sertularia argentea.
26. 4.1963. Dredged with *T. indivisa* (q.v.).
30. 7.1963. Dredged at 53°01′35″N. 00°55′10″E. 800 mls. 2 small *P. cornuta.*

Kirchenpaueria pinnata.
17. 8.1962. Strond Pool. 800 mls of stones, shells, and algae, thickly overgrown with *K. pinnata.* 4 *A. prolifer.*
4. 8.1963. Strond Pool. 800 mls of *Fucus vesiculosus,* thickly covered with *K. pinnata.* 1 *P. cornuta,* 9 *A. brachycephalus.*
7. 9.1964. Strond Pool. 800 mls of brown alga with plenty of *K. pinnata.* 1 *A. prolifer,* 1 *A. brachycephalus.*

Nemertesia ramosa.
3. 4.1965. Dredged close to the Blakeney Overfalls Buoy. About a dozen tufts, up to 9 or 10 cms high, on a dead shell of *Ostrea edulis.* Ca. 50 *A. brachycephalus.*

Unsuccessful feeding

Only a few instances of this were observed; thus, *P. cornuta* from among *Laomedea* in Morston Creek, when offered some *Campanularia verticillata* cast ashore at Brancaster on 27.3.1964, bit hard at the polyps without causing noticeable damage, as if the polyps "tasted nice but were too tough". The same result is commonly obtained when *P. cornuta* or *A. brachycephalus* attempt to feed on the polyps of *L. flexuosa,* with the additional hazard that the nematocysts seem to be more potent in this species than in the other Norfolk species of *Laomedea* (see Hamond, 1957, p. 312), since the worms immediately beat a hasty retreat when stung, and very seldom make a further attempt to feed on the polyp in question. In *Laomedea* *loveni,* whose polyps are very much liked both by *P. cornuta* and by *A. brachycephalus,* the acrocysts containing the developing planulae are apparently resistant to attack owing to their tenacious and slippery outer surface; only once was an acrocyst seen being pierced, the embryos tumbled out without being eaten, and shortly afterwards the autolytoid (a young *P. cornuta*) abandoned the attempt and crawled away without eating anything.

Prey-predator relationships

Some hydroids are fed upon by more than one species of autolytoid; the dynamic aspects of this situation have not been investigated in detail, but it has been noticed more than once that very luxuriant growths of *Laomedea gelatinosa* in Morston Creek can support *P. cornuta, A. brachycephalus,* the nudibranch *Embletonia pallida,* and the pycnogonids *Achelia longipes, A. echinata,* and *Anoplodactylus petiolatus,* all simultaneously without detriment to the hydroid. This is especially noticeable during April and May, when *L. gelatinosa* has nearly attained its maximum colony size and before the rate of polyp decay and regeneration has begun to decline. Since the first sign of polyp decay is prolonged retraction, the sick or senescent polyps are the most likely to be eaten and hence the prey-predator relationship approaches the theoretical ideal, whose dynamic aspects determine the optimum number of autolytoids that a given colony can support at any one time.

Overwintering and individual preferences

In winter, almost all hydroids have died down; *A. brachycephalus* and *P. cornuta* are then found living among red algae in the lower part of Morston Creek; it was some of these individuals that refused to feed on *L. loveni* (see above), possibly because they were by then accustomed to a different diet. Also, it was repeatedly observed during the summer of 1965, that individuals of *A. brachycephalus* taken offshore (probably feeding on *Eudendrium rameum,* which was very common at that time) fed seldom or not at all on *Laomedea* spp., which were entirely acceptable to *A. brachycephalus* collected among *L. gelatinosa* in Morston Creek; morphologically, there was no difference between the dredged and the hand-collected specimens, whose stolons mated with one another freely either way, so that there is no evidence for the existence of distinct populations. It seems rather as if an individual worm has an exclusive taste for whatever species of hydroid it first lands on after hatching, assuming that this hydroid is in any case acceptable to the species as a whole. My very few winter records indicate that *P. cornuta* and *A. brachycephalus* are widely scattered in Blakeney Harbour during cold weather, but I have not been able to find out what they feed on at this time; Korringa (1951, p. 84) was unable to get *A. brachycephalus* to feed on oysters, barnacles, or the scyphistomes of *Aurelia,* and refused to believe that his specimens could live on the small quantities of *Laomedea* found by him at Yerseke.

Summary

Of the eleven Norfolk species of autolytoid, three were successfully used for feeding trials; all were found to feed exclusively on hydroid polyps under laboratory conditions, using the method of feeding described by Okada (1928) and others. Field observations confirm that, in summer, hydroid colonies are the normal habitat of these worms, but that they seek other (as yet unknown) sources of food in winter when the hydroid have died down. Further aspects of food selection by autolytoids are discussed.

Zusammenfassung

Unter den elf Norfolkschen Arten der Unterfamilie Autolytinae gibt es mindestens drei Hydropolypenfresser, wie Okada (1928) für eine anderer Art endeckt hatte. Da es im Winter keine lebenden Hydroiden bigt, müssen sich die Würmer andere Nahrungsmittel verschaffen. Diese Nahrung hat man bisher noch nicht entdeckt. *P. cornuta* und *A. brachycephalus* fressen die meisten Arten der Gattung *Laomedea*, aber vermeiden die zähe Fleisch und die besonders starken Nesselkapseln der Polypen von *Laomedea flexuosa*. Prinzipiell können *A. brachycephalus* viele Hydroidenarten fressen; eine einzige Individuum fresst aber nur die Art, an welche sie vom Geburt gewöhnt ist. *Procerastea halleziana* frisst nur Gymnoblastpolypen. Ausserdem werden noch andere Gesichtspunkte dieser Beute-Raüber Beziehung diskutiert.

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