

# B A S T E R I A

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## Some Observations on the Ecology of *Hydrobia stagnorum* (Gmelin) and *H. ulvae* (Pennant), and the Relationship Ecology - Parasitofauna (continued)

by

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### PART II. *Hydrobia ulvae* (Pennant)

Under the heading of 'Materials and Methods' above, eight different „habitats” were referred to on the island of Terschelling where specimens of *Hydrobia ulvae* were collected. These „habitats” can be typified as follows:

Habitat 1. An old cart-track, well overgrown with plants belonging to the „*Salicornieto-Spartinetum*” association. The bottom of the cart-track was of mud, but not covered with an algal layer.

Habitat 2. In a dense *Spartina townsendi* growth. There was a dense carpet of light green algae covering the bottom of fine mud.

Habitat 3. A mudflat, with very sparse, widely scattered plants of *Salicornia*. The mud was slippery and sticky and covered with a dark algal layer.

Habitat 4. A cart-track with only a few scattered plants. The condition of the track indicated that it was fairly new (and in any case, not so old as the cart-track in Habitat 1.) The section chosen had a clean mud bottom with no algal growth.

Habitat 5. The same type of habitat as in 4 above, but older and with a dense algal growth over the bottom. Some 70% of the snails collected here were found on clear areas of mud between the growth of alga. The vegetation was of scattered *Salicornia* plants and a small group of three *Spartina* plants.

Habitat 6. This was an area of very dense *Spartina* growth on the very edge of the creek (near low water mark). The bottom here was of very dense, fine mud, with no algal growth.

Habitat 7. A narrow track, not in the *Spartina* zone, but rather isolated from it. There was a fairly dense growth of *Salicornia*, on the other hand. The bottom was muddy, with a tendency for algal growth, but this was not well-developed.

Habitat 8. An island of dense-growing *Spartina townsendi* actually in the water of the creek (i.e. always, or nearly always, submerged). The bottom of a rich, soft mud with a light green algal layer approximately 0.5 cm. thick. *H. ulvae* was found both in and on the algal layer.

In each case the snails were counted, measured (length and breadth), weighed (living, but with shells dried externally) and then taken to the laboratory where the infection rates were determined. All observations were examined statistically and are shown in Table III.

TABLE III

Table showing the analysis of the populations of *H. ulvae* from the 8 different „habitats” described in the text. The explanation of the symbols is as follows: a/m<sup>2</sup> gives the number of snails found per square meter, and b/m<sup>2</sup> the biomass of these snails in grams. The terms %x and %y are explained in the text. M(length) is the mean length of the population and d, its standard deviation; M(breadth) is the mean breadth of the population, and d, its standard deviation.

Habitat Number	a/m <sup>2</sup>	b/m <sup>2</sup>	%x	%y	M (length)	d	M (breadth)	d
1.	35	0.504	10.40	31.3	4.78	6.59	2.06	0.97
2.	788	11.832	14.72	39.6	4.86	6.12	2.23	3.06
3.	3	0.023	12.50	12.5	4.18	8.65	2.03	2.50
4.	1,220	17.40	14.75	41.0	4.93	5.92	2.30	3.42
5.	480	6.58	10.40	28.0	4.69	6.14	2.38	3.52
6.	436	5.42	5.40	55.0	4.73	4.24	2.15	1.78
7.	340	3.42	0.0	0.0	4.16	4.54	2.18	1.20
8.	2,250	23.23	1.33	62.0	4.43	2.96	2.12	1.64

The first column in the Table (Table III) gives the number of *H. ulvae* per square meter and it will be seen that there is a wide range from 3 in „habitat” 3 to 2,250 in „habitat” 8. Field observations show that this snail does not favour a bottom of thick sticky black mud, covered by a thin layer of algae, especially when many gas-bubbles are trapped in this layer. These gas-bubbles are probably derived from decomposition in the mud. When the habitats were arranged in the order of decreasing occurrence of this gas-filled mud and algal layer, it was found that this agreed with the number of snails per square meter, as shown in the graph, Figure 5.

The study most directly comparable with that described here is one carried out by ROTHSCHILD (1941), in which the *H. ulvae* population of a pool near Plymouth, England, was sampled over two years, to examine growth rates and their connection with infection.

In this particular pool, ROTHSCHILD described growth conditions as „maximum”, with infected snails displaying gigantism and reaching a length of 9 to 10 mm, although these large forms were probably not older than uninfected snails 6.75 mm long. The average length over the whole series of snails collected in Terschelling was found to be approx. 4.6 mm (in August) - which is smaller than the length given by ROTHSCHILD (loc.cit.) for her snails in July, when they were about 5.75 mm long.

If we accept the statement by ROTHSCHILD (loc. cit.) that uninfected snails do not in general grow to a length greater than 6.75 mm, we can assume that all snails above the length of 6.75 mm are probably infected. This was, in fact, confirmed by the survey carried out on Terschelling, although the bulk of infection was found in snails much smaller than this and below the mean for the whole population. This is illustrated by the figures given in the column „%y” in Table III, which should be read in conjunction with the column of values „%x”. This column gives the percentage of the population above the length of 5.5 mm, which was taken as a reasonable „threshold value” for size, above which one might expect most snails to be infected. It will be seen that in all cases, with the exception of 3 and 7, the actual infection is much higher than the „%x” value. The discrepancy between the value chosen for the „%x” and the value given by ROTHSCHILD (loc. cit.) for the maximum length attained by uninfected snails is due to the fact that the average length of snails on Terschelling was about 1 mm shorter than the value given by ROTHSCHILD for the month (August) in her observations. The „%x” value gives, then, a rough and ready method of expressing the expected rate of infection in the populations, but it must be remembered that it is arbitrarily derived.

#### CONSIDERATION OF EACH POPULATION OF SNAILS AND ITS INFECTION RATE

„Habitat” 1. Only number 3 was considered as less favourable for *H. ulvae*, on the basis of field observations on the type of bottom and algal growth, etc., as described above. As seen in Table III, 35 snails were collected per sq. meter and 10.4% of these were longer than 5.5 mm. The infection rate, determined by dissection, was found to be 31.3%, i.e. three times as great as the „%x” value.

„Habitat” 2. Here 788 snails were found per sq meter, 39.6% of which were infected, somewhat less than three times the value of „%x”.

„Habitat” 3. The number of infected *H. ulvae* agrees with the percentage above the 5.5 mm level, but it should be remembered that few snails were found on this mudflat, as shown by the low value of  $a/m^2$ .

„Habitat” 4. The value of „%x” is somewhat more than three times the value of „%y”. This area, which is very similar to that chosen as number 1, differs only in that the cart-track was made in 1960, while number 1 was made earlier, 1958 or 1959.

„Habitat” 5. The value of „%x” is identical with that for number 1; although this cart-track is a continuation of that considered as number 4, it is much older, having been joined on to number 4 subsequently. Once again, the value of „%y” is slightly less than three times the value of „%x”.

„Habitat” 6. In the order of favourability, this was more or less centrally placed (see the graph, Figure 5). 436 snails were found per sq. meter and only 5.4 % of these exceeded the 5.5 mm level. The infection rate, however, is 10 times the „%x” value.

„Habitat” 7. This is strictly comparable with numbers 1, 4 and 5. It is, however, a much older track and situated further away from the edge of the creek. Although 340 snails were found per sq. meter, none were above the 5.5 mm level and none were infected.

„Habitat” 8. This was the most densely populated area examined in this survey. 2,250 snails were found per sq. meter and although only 1.33% were above the 5.5 mm level, some 62% proved to be infected, i.e. more than 47 times the value of „%x”.

We can divide the 8 „habitats” into three groups:

- a). Where „%x” = „%y” - i.e. numbers 3 and 7
- b). Where „%x” = approx.  $\frac{1}{3}$  of „%y” - i.e. numbers 2, 4 and 5
- c). Where „%x” is much smaller than „%y” - i.e. numbers 6 and 8.

Group a) „Habitats” 3 and 7.

Although both these „habitats” show an agreement between „%x” and „%y”, this agreement arises for two different reasons. On the bare, open and exposed mudflat of number 3, only a few snails were to be found. The mudflat itself is near the central channel of the creek and readily accessible to birds in the area. It was noted during the survey that larger specimens of *H. ulvae* have a tendency to creep out into the open, avoiding the cover of vegetation, which would make them easy prey for birds; here, only 10.4% of the snails were larger than the threshold value chosen for this survey, which may have been due to a recent feeding period of sea-birds on the mudflat, for a characteristic pattern of feet and beak-marks could

be seen in the soft mud. The chance of infection for snails on the mud is surely not high, as it seems unlikely that any snails live permanently on the mudflat, but that they creep there during high water, avoiding vegetation. It may be more correct to say that not only larger snails creep into the open, but that infected snails creep into the open, but this could not be established during this survey.

In the case of „habitat” number 7, a different explanation can be offered for the agreement of „%x” and „%y”. 7 is a more or less permanent pool in an old cart-track, high above the water-mark. Here the population is most certainly built up from spat, which is carried here during spring tides. The mean size of these snails was also the lowest found: 4.16 mm. It was observed that birds did not come into the neighbourhood of this or other similar pools, high above the water-mark. This may be due to the ample food supply nearer at hand and to dense reed growths which border this region.

Group b) „Habitats” 1, 2, 4 and 5.

These are all similar habitats, which differ from each other only in their distances from the edge of the creek. An examination of Table III shows that the percentage of infection is between 28% and 41%. These differences appear to reflect the accessibility of the habitats to the birds, which settle on small temporary islands in the middle of the creek opposite the area under consideration. This question of accessibility can be illustrated by „Habitats” 4 and 5 - the same cart-track, which is divided into an older and a younger section. The values of „%y” are 41% and 28% respectively. The older section is further away from the edge of the water and contains smaller and fewer snails than the other; these are also derived mainly from spat (480 snails per sq. meter compared to 1,220 snails per sq. meter). The younger section of 4 - 5 is lower and longer under water, has more snails and a higher percentage of these are above the 5.5 mm level.

„Habitat” 1 is strictly comparable to 5 above, being also an older cart-track; the percentage of snails above the 5.5 mm level is identical and the percentage of infected snails nearly so (31.3% and 28.0%, respectively). The main difference, in the number of snails per sq. meter, could not be accounted for in any other way than by the occurrence of a mudtype which appears to be avoided by *H. ulvae* in number 1, and the occurrence of free mud and the light green alga in number 5.

Group c) „Habitats” 6 and 8.

The occurrence of high percentages of infection in these two „Habitats” - much higher than the percentages of larger snails can be accounted for in the same way as in the consideration of habi-

tats 1, 2, 4 and 5. Both numbers 6 and 8 are close to the areas favoured by birds and near water; number 8, for example, is submerged under at least 3 cm of water (observed at low tide, August). The presence of fresh green alga and a soft, rich mud layer and a continual supply of organic detritus combine to make this a thriving habitat for the snails. There is probably also a continual supply of spat, which is shown by the low „%x” figure.

#### PART IIa. THE PARASITES OF *Hydrobia ulvae*.

These were trematode larvae only. One of the more interesting features was the finding of *Cercaria lebouri* Stunkard 1932 once more. (This cercaria was also found in the sample of *H. ulvae* from Texel). This also confirms the findings of MARKOWSKI (1936).

In addition to *C. lebouri*, a cercaria was found which appears to be new to the literature, and for which the name *Cercaria angularis* n. sp., is proposed.

#### *Cercaria angularis* n. sp. (Figure 6)

A small cercaria, 242  $\mu$  long (maximum), characterised by constant, angular outlines to the body — a feature observed in all specimens. The tail  $1\frac{1}{2}$  to twice the length of the body, thin, pointed and without appendages, hairs or spines. Anterior sucker rounded, large and muscular, with 8 orifices for gland-ducts. One pair of well-developed eyespots (black in ripe specimens) situated behind the posterior rim of the oral sucker. Penetration glands simple, running from oral sucker to 4 large nucleated cells on either side of the body, situated central and somewhat ventral. The oral sucker opens ventrally and sub-terminally. No pharynx or other traces of alimentary system. Acetabulum represented by a rudiment only. Excretory bladder large, with two lateral sacs. Median caudal excretory canal runs the length of the tail, opening at the tip. No flame cells seen, owing to the high content of cystogenous cells, which obscure most of the internal structures. The acetabulum rudiment is situated anterior to the excretory bladder and between the laterally placed gland cells.

Location: Rediae in hepato-pancreas.

Locality: Island of Terschelling, The Netherlands.

Measurements in  $\mu$  (range of 20 living specimens):

Cercaria Length of body:	98 - 41	Breadth of tail	19 - 8
Breadth of body:	68 - 24	Oral sucker, length:	30 - 18
Length of tail:	144 - 39	Breadth of tail	19 - 8

Redia Length: 330 - 237  
 Breadth: 75 - 63

Pharynx length: 23 - 19  
 Pharynx width: 16 - 14

The redia is characterised by paired lips anteriorly and a small, ringlike collar. The anterior sixth of the redia is annulated. Gut short, projecting to just below the annulated region and bent sharply to one side. 8 cercariae found per redia (average). Unpigmented, no daughter rediae seen.

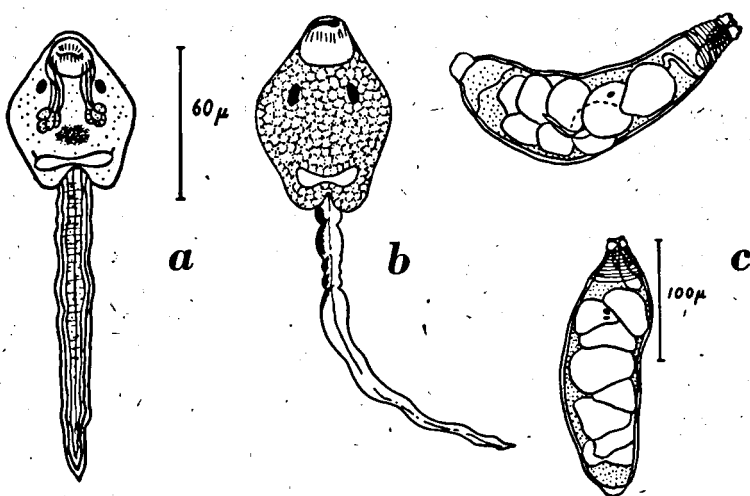


Figure 6. a: *Cercaria angularis* n. sp. Appearance of cercaria when obscuring cystogenous glands are not represented; b: natural appearance of *C. angularis* n. sp.; c: rediae of *C. angularis* n. sp.

In general appearance and the fact that it possesses no acetabulum, this cercaria resembles *C. grisea* Markowski 1936 and *C. ubiquitous* Stunkard 1932. Both of these are Xiphidiocercariae, however, and can be called „monostomes” in the sense employed by SEWELL (1922) only. Despite extensive examination of several scores of cercariae, no stylet could be found in *C. angularis* n. sp. This, combined with the angular appearance of the latter cercaria, would appear to warrant its description as a new species.

*C. angularis* n. sp. was found mainly in snails further away from the creek - while *C. lebouri* occurred mostly in „habitats” nearer to the main body of water.

## GENERAL DISCUSSION

„Since trematodes use invertebrates as the first and often also as the second intermediate host, it seems justified to deduce that the trematodes must play an important role in population dynamics and to some extent also in the distribution of invertebrate species. The number of miracidia and cercariae per unit volume of water rises to a considerable value, especially in pools with their limited space, and hence the effect of trematodes, especially in pool faunas, must be taken into account.” From WIKGREN (1956).

The distribution of parasites is determined by many factors and it is practically impossible to analyse them all in such a simple survey as this. It is possible, on the other hand, to obtain some indication of the most important if we examine some of the conclusions drawn above in the consideration of both Terschelling and the Hondsbossche Zeewering.

In both areas the avian hosts are abundant and can be considered as a constant supply of infection. The nature and degree of this infection will be determined, then broadly speaking, by the following factors:

- 1) The environmental requirements and behaviour of the snails,
- 2) The accessibility of the habitat for the definitive hosts,
- 3) The behaviour of the trematode parasites.

#### 1. The Environmental Requirements and Behaviour of the Snails.

It was long supposed that the distribution of *H. ulvae* was determined by the distribution of the sea-lettuce, *Ulva lactuca* Le Jol. (ROBSON, 1920), but as VAN BENTHEM JUTTING (1923) has pointed out, this is not so in the Netherlands, for although large numbers of *H. ulvae* were found on Terschelling during this survey, *Ulva lactuca* was very rarely seen, and then mostly as a part of the washed-in debris. VAN BENTHEM JUTTING (1933) pointed out the large numbers of this snail which occur in connection with *Zostera* and *Enteromorpha*, which was confirmed by this survey. *Hydrobia ulvae* is a detritus-feeder, and is dependent upon a supply of rich mud and a layer of gas-free alga on the mud, as seen in this survey. Otherwise, the nature of the surrounding vegetation does not appear to be important.

The environmental requirements of *Hydrobia stagnorum* would seem to be somewhat different; mention has been made of a simple experiment carried out with the miracidia of *Fasciola hepatica*, at the same time a similar experiment was carried out with specimens of *Hydrobia stagnorum*, to determine its requirements. The results are shown in Graph 2, Figure 7. It can be seen that the „optimum activity” occurred at a dilution of 75% sea-water (as calculated from



the area of the Hondsbossche Zeewering), controlled by the  $\text{AgNO}_3$  precipitation test. The term „optimum activity” is a somewhat vague term, but it was taken here as meaning the greatest activity as determined 2-hourly over a period of 20 days. Almost immediate

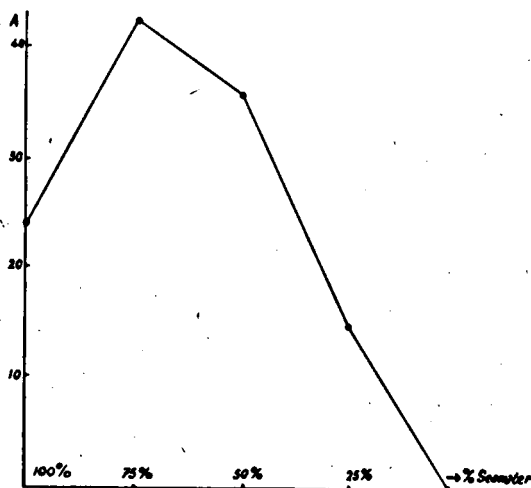


Figure 7. Graph number 2, showing the activity of specimens of *Hydrobia stagnorum* collected from the Hondsbossche Zeewering in various concentrations ranging from pure water to sea-water. A is the number of snails showing „activity”. It will be seen that the optimum for *H. stagnorum* is at a concentration of 75% of the sea-water in the vicinity of the collection point.

death occurred in 100% sea-water. Behind the Hondsbossche Zeewering the supply of brackish water occurs by seepage below the sea-wall; dilution in the habitat of the snails occurs during snow, rainfall etc., in the winter, but in summer the concentration of chloride will increase by evaporation. In the photograph, Figure 2, a salt-pan can be seen at „C”, where large crystals of salt were, in fact, found. Here the water was a more or less saturated salt solution and it is significant that no specimens of *H. stagnorum* could be found there. This can be correlated with the rapid death of the snail in the 100% solutions. While this does give an approximate indication of the requirements for the snail, it tells us little about the requirements of the miracidia of the trematode larvae in those habitats. It was observed that *C. lebouri* Stunkard, 1932, continued swimming for periods of up to 43 minutes in the 75% solution, while

in higher concentrations, although death did not immediately follow, decaudation occurred very rapidly, and this was followed in a few minutes by encystment. Whether these cysts were infective could not be determined.

## 2. The Accessibility of the habitat for the definitive hosts.

It was assumed at the beginning of the General Discussion that the avian population formed a constant supply of infection. This is justified, however, only when the habitat to be infected is accessible to the definitive hosts. That this „accessibility” may operate within very precise limits has been seen from the eight „habitats” examined on Terschelling. It can be summarised as - the closer to the creek (and thus to the milieu favoured by the birds), the greater the chance of infection. Even in the case of number 7, where the snails occurred in an environment apparently „favourable” for them, none were infected, because of the unfavourable accessibility factor. The actual size of snails in a flourishing population on Terschelling appears to be a less important characteristic for the probable infection-rate of the population than the situation of that population in the environment as a whole.

We have to deal in parasitology with a complex interplay of factors which involve both the population of hosts and intermediate hosts and their parasites, in reality a „feed-back” situation. In the case of the populations considered here, the snail population is limited by the suitability of the environment (which suitability overlaps with the requirements of the avian hosts and those of the larval parasites) and by the presence of birds and very probably also by the degree of parasitism that the snails undergo. The parasite population, in its turn, is determined by the presence of both birds and snails etc. ROTHSCHILD (1941) has pointed out that so high is the incidence of parasitism in some populations of *H. ulvae* that if this phenomenon was of general occurrence throughout the total population, a reduction would occur in the numbers of the snail. She further states (loc. cit.) that mud-flats, which are „teeming” with *H. ulvae* do not favour such a heavy incidence of parasitism. That the situation is otherwise on the island of Terschelling can be attributed to the habits of the waders and other birds which populate the area. Their feeding-grounds are restricted for a large part to the creek and its immediate surroundings, and isolated pools and bodies of water further away on the banks of the creeks do not appear to be visited.

### 3. The Behaviour of the Trematode Parasites.

This has already been mentioned under section 2. and can be dealt with rather briefly here. Both snails and birds are required, as intermediate and final hosts in the life-cycles. The cysts on the shells of *Hydrobia stagnorum* from the Hondsbossche Zeewering have already been dealt with, but the advantage of this method for the parasite has not been mentioned. When a bird eats a specimen of *H. stagnorum* from one of the habitats shown in the photograph, Figure 2, then it takes in automatically a dose of between 11 and 20 cysts - a sufficient number under most circumstances to ensure an infection. What is striking, is that only two snails from Terschelling were found to have cysts of this monostome and then only 1 and 3 cysts respectively. It is difficult to account for this exactly, but it may be that the main period of emergence of the monostome cercariae was already over when the survey was carried out, or, and this appears to be more likely, that it had not yet begun, since so few cysts were found, and it is improbable that no cysts would have remained over from an earlier period of cercarial emergence.

### SUMMARY

A survey is given of the parasites found in two species of *Hydrobia*, *H. stagnorum* from the Hondsbossche Zeewering in Noord-Holland and *H. ulvae* from the island of Terschelling.

In *H. stagnorum*, *Cercaria lebouri* Stunkard, 1932, was found together with cysts of the same, and *Cercaria markowskii* n. sp. Both species are described.

In *H. ulvae*, *C. lebouri* Stunkard, 1932, was re-discovered and *C. angularis* n. sp. described.

An analysis is given of a simple survey of eight „habitats” on Terschelling where *H. ulvae* and its parasites were examined and the complexity of the ecology involved is emphasised.

From this survey, the following tentative conclusions can be drawn:

1. Accessibility is probably the most important factor which determines whether the final hosts are infected from a population of intermediate hosts, and whether this population receives a further infection from the definitive hosts.
2. The behaviour of host, intermediate host and parasite is such that in a given environment their habits must sufficiently overlap to allow any life-cycles to be completed. Further, larval parasites have more requirements than either final or intermediate host, since both of

these can live without the parasite (see „habitat” 7 for an example of this).

3. It does not seem likely, from the results obtained for the island of Terschelling, that parasites form a „limiting factor” for the populations of *Hydrobia ulvae*.

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## SAMENVATTING

In dit artikel wordt het verband tussen milieu en besmettingsgraad behandeld bij twee soorten van *Hydrobia*, n.l. *Hydrobia stagnorum* (Gmelin) en *H. ulvae* (Pennant) van de Hondsbossche Zeewering resp. het eiland Terschelling. In *H. stagnorum* zijn *Cercaria lebouri* Stunkard, 1932 en *C. markowskii* n. sp. gevonden, in *H. ulvae* nogmaals *C. lebouri* en *C. angularis* n. sp.

Op het eiland Terschelling werden acht verschillende „milieus” gekozen en onderzocht op het aantal slakken, hun lengte en breedte, graad en aard van besmetting, hetwelk wordt weergegeven in Tabel III.

Het bleek mogelijk om de volgende conclusies te trekken:

1) Accessibiliteit blijkt de beperkende faktor te zijn van de besmetting, d.w.z. de afstand tussen het milieu van de tussengastheer en de definitieve gastheer is meer van belang dan men tot nu toe dacht.

2) Het gedrag van de tussengastheer resp. definitieve gastheer en parasiet moet zo gecoördineerd zijn dat een „overlap” bestaat binnen het hele milieu om een bepaalde levenscyclus mogelijk te maken.

3) Het lijkt niet waarschijnlijk dat parasieten een „limiting factor” van de populaties van *H. ulvae* op het eiland Terschelling zijn. De nadruk wordt gelegd op het samenspel tussen verschillende factoren binnen een bepaald milieu hetwelk leidt tot een „terugkoppeling”.