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Reproductive Success, Relative Abundance and Population Structure of Two Species of *Nephtys* in an Estuarine Beach

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Abstract

During 1978 and 1979 specimens of *Nephtys hombergii* in the River Tyne estuary (North East England) became gravid during the winter but did not spawn in the spring breeding season; instead their gametes were resorbed. The drastic effects of these spawning failures were apparent in the population structure in 1980, when the 1978 and 1979 year-classes were shown to be virtually absent, by the size of the individuals in the population and the numbers of growth lines in their jaws. The population structure in 1975, by contrast, indicated that recruitment during the preceding 4 to 5 yr had been good. Spawning was also effective in 1980, and an 0 group was detected in August 1980. Comparable data has been obtained for *N. caeca*, which occurs in the same beach. It shows that recruitment of this species during 1976–1980 was consistently good, whereas analysis of the age-class frequencies suggests that recruitment of *N. caeca* was poor in 1973 and 1975. The dominance relationship of the two species in the beach has been reversed during the period 1975–1980. It is suggested that the sympatric distribution of the two species is maintained in part by periodic reproductive failure. The causes of this are not yet known; possible reasons, including the extremely cold conditions experienced in 1978–1979 are discussed. The difference in frequency of the 1978, 1979 and 1980 year classes will now permit a rigorous evaluation of the relationship between the number of growth lines in the jaws and age in *N. hombergii*.

Introduction

Nephtys hombergii and *N. caeca*, which dominate the community found in the sandy beach ("Black Middens") in the estuary of the River Tyne at North Shields (North England), do not seem to be spatially separated in the beach, and since both are thought to be non-discriminatory carnivores they may occupy very similar niches. The general characteristics of their life histories and reproduction in this locality have been described by Olive (1977a, 1978); both breed in late spring/early summer, releasing eggs of a similar size (ca. 200 μm) which develop into planktonic larvae. A brood of eggs may be produced each year for several years but, in the River Tyne, no specimens reach maturity before the end of their second year. Both species are potentially long-lived, with *N. caeca* having the greater longevity, reaching an age of up to 12 yr. The general similarity of habitat, life history, and so far as is known ecology, of the two species raises the question; "how is the balance between the two species maintained?". In *Nephtys* spp. it is possible to obtain an estimate of the age of individual worms by examining the growth lines in the jaws (Kirkegaard. 1970. 1978; Estcourt, 1975; Retière, 1976; Olive, 1977a, 1980a, and thus past variation in effective recruitment can be determined.

The populations of *Nephtys hombergii* and *N. caeca* have been used in studies of the physiology of reproduction (Olive, 1976, 1977a,b, 1978; Olive and Bentley, 1980) and have been kept under surveillance since 1973. We have noticed that, on several occasions, many specimens of *N. hombergii* have become gravid and apparently mature as usual, but that the gametocytes have not been spawned. Instead there has been a period of oosorption and the gametes have been ultimately resorbed. This phenomenon was particularly marked in 1979 when few, if any, of the oocytes produced by *N. hombergii* were released into the environment. This has led us to re-examine the population in the Tyne estuary to determine what effects repeated reproductive failure may have had on the balance between the two species.

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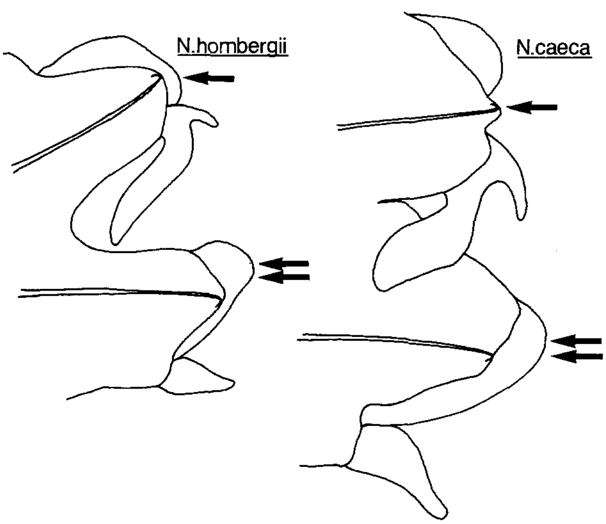

Fig. 1. *Nephtys hombergii* and *N. caeca*. Anterior views of mid-body parapodia of juveniles (both 0.5 mm body width). Individuals of this size can be distinguished by the position of the aciculum relative to the post-acicular notopodial lamella (single arrows) and by the shape of the post-acicular neuropodial lamella (double arrows)

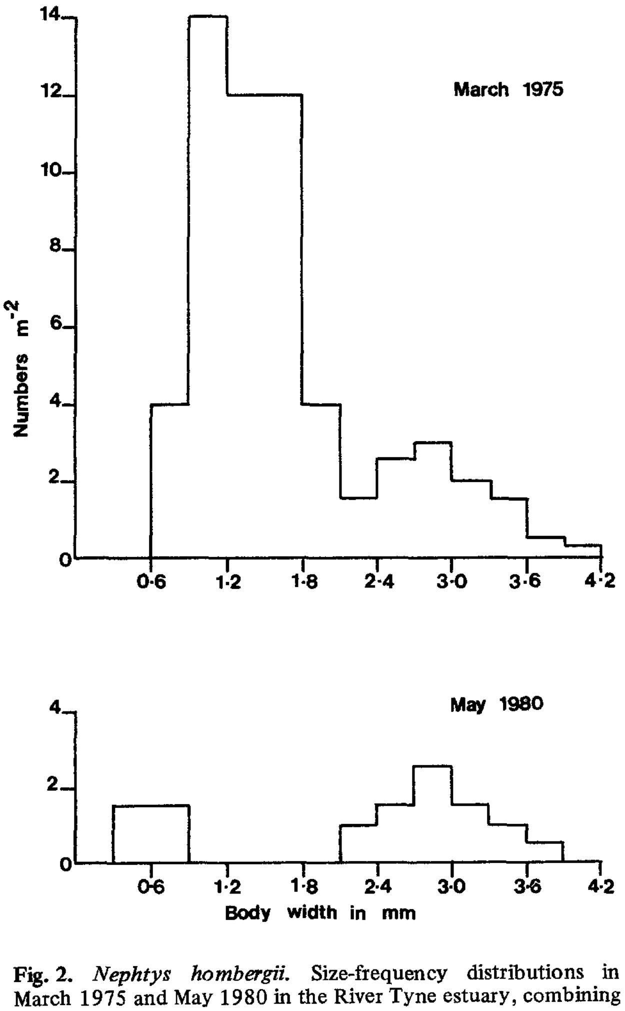

Fig. 2. *Nephtys hombergii.* Size-frequency distributions in March 1975 and May 1980 in the River Tyne estuary, combining the two sampling techniques

Materials and Methods

Nephtys hombergii and *N. caeca* were collected from the beach known as the "Black Middens" at North Shields in the estuary of the River Tyne at monthly intervals in 1973, 1974, 1975 and again in May and August 1980. Two sampling techniques were used:

(1) One-metre-square areas of sand were carefully dug and all the *Nephtys* spp. seen were collected; this method gives a good collection of the older individuals but misses the 0 group and, partially, the 1+ group during the first part of the second year of life.

(2) Samples of one-sixteenth of a m^2 were obtained, using a metal frame; the sand from this area was sieved through an 0.5 mm test sieve. This method gives a good estimate of the 0 and 1+ groups which are underestimated by the previous method. It does not permit the collection of adequate numbers of the older year-groups; therefore, both methods must be applied simultaneously to obtain a valid analysis of year-group frequency in the population.

After collection, the worms were narcotised in 5% ethanol sea water and fixed in 4% formalin. The body width in the post-pharyngeal region, Segments 30–45, was measured as a convenient parameter of size. The jaws were examined in transmitted white light at a magnification of x 40, using a stereoscopic dissecting microscope, after maceration in 1N sodium hypochlorite solution for 1 to 3 min, according to size (Olive, 1980a).

Results

Occurrence of Oosorption

A light microscopical study of the gametogenic cycles of *Nephtys hombergii* and *N. caeca* in 1977 revealed oosorption in *N. hombergii*, but not in *N. caeca*. In *N. hombergii*, numerous oocytes remained in the ovaries in the period June to October (Olive, 1978). Spawning could not be induced in such individuals by hormonal treatment (Olive and Bentley, 1980), and the oocytes were destined to be resorbed. The ovaries were invaded by phagocytic cells and the histological appearance of the ovaries became very complex due to the presence in the ovaries of (i) old oocytes, intact but destined to be resorbed; (ii) acellular masses of oocyte-derived cytoplasm; (iii) phagocytic cells, many of which had incorporated oocyte-derived cytoplasm into large vacuoles; (iv) pigmented cells; (v) young, newly developed oocytes, and associated follicle cells.

A study by N. Wright (unpublished) has shown that ovaries which contain degenerating oocytes are characterised by a very intense orange fluorescence when stained with Euschrysine 3R, which we interpret as indicating high levels of lysosome activity (see Allison and Young, 1969). The cytoplasm of normal oocytes displays a positive orange fluorescence only in the cortical granules and in small lysosome-like granules in the cytoplasm of a few of the follicle cells.

Table 1. *Nephtys hombergii*. Relative frequency of year-classes in River Tyne population, March 1975 and May 1980

Year-class	Ring No.	Age (yr)	Relative frequency
March 1975			
1974	0	1	0.46
1973	0	2	
1972	1	3	0.28
1971	2	4	0.22
1970	3	5	0.4
1969	4	6	0.02
May 1980			
1979	0	1	0.04
1978	0	2	
1977	1	3	0.43
1976	2	4	0.35
1975	3	5	0.10
1974	4+	6	0.81

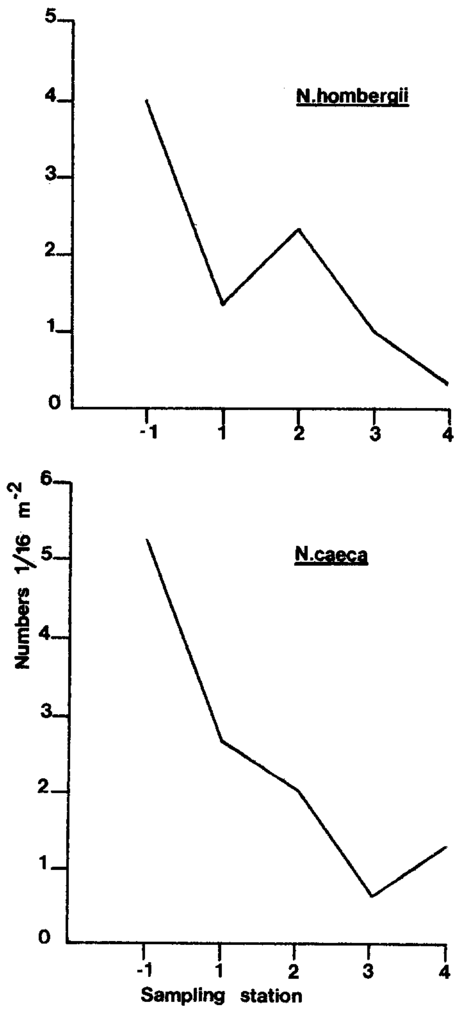

Fig. 3. *Nephtys hombergii* and *N. caeca*. Numbers of juveniles without rings in jaws, determined by Method 2 at 5 stations along a transect of beach at Black Middens, River Tyne, in August 1980. Station −1 was at extreme low-water spring tide level (0.3 m) and the transect rose to Station 4 (1.1 m)

Although it is difficult to quantify spawning success in *Nephtys hombergii*, it seems that complete shedding of the gametes (100% success) is rarely achieved in the River Tyne population. Spawning seems to have been relatively efficient in 1980, as in 1975 and 1976; it was less efficient in 1977 and 1978, and very poor in 1979. During the same period, *N. caeca* always spawned efficiently, and the ovaries of spent individuals did not contain relict resorbing oocytes. There are differences in the endocrinological control of oogenesis in these two species which may be related to the observed differences in oosorption. Hormonal deprivation of *N. hombergii* induces premature ovulation and oosorption in newly developing oocytes and so causes a complete dissolution of the ovaries (Olive and Bentley, 1980); however, this does not occur as a response to decerebration in *N. caeca*, in which species hormonal deprivation does not induce either ovulation or oosorption. Such differences in the endocrine control of oogenesis between species of *Nephtys* are being investigated further (Bentley and Olive, work in progress).

Population Structure

Juvenile specimens of *Nephtys hombergii* with a body width as small as 0.5 mm can be distinguished from juvenile *N. caeca* by microscopical examination of the parapodia, as seen in anterior view in Fig. 1; all juvenile *Nephtys* spp. were examined in this way. Samples were obtained in May and August 1980 which could be compared with those obtained previously in 1974/1975.

Nephtys hombergii

The population of *Nephtys hombergii* in May 1980 was very different to that in March 1975 (Olive, 1977a; Olive *et al.*, in press), as shown in Fig. 2. This was due to the absence of young individuals in 1980, when very few worms less than 2.4 mm body width were found, suggesting that individuals less than 2 yr old were not present, whereas such worms had represented the bulk of the population in March 1975. This was confirmed by examination of the jaws of the specimens, and Table 1 presents the relative abundance of the year-classes in the collections of March 1975 and May 1980, based on an analysis of the growth lines in the jaws. The population has clearly been affected by the reduced fecundity of 1978 and 1979. Despite this, the older individuals are present in numbers similar to those observed earlier, i.e., about 5 per m^2 (Fig 2), and since such worms have the capacity to produce large numbers of eggs, the potential fecundity of the population has not yet changed dramatically. Spawning in 1980 was, in fact, much more successful and, by August, the 0 group could be detected predominantly in the lower part of the beach (Fig. 3). The size-structure of the population in August 1980 is shown in Fig. 4. It is composed of the 0 group (3 months old), very few individuals in the next two year-groups, and a population of worms more than 3 yr old.

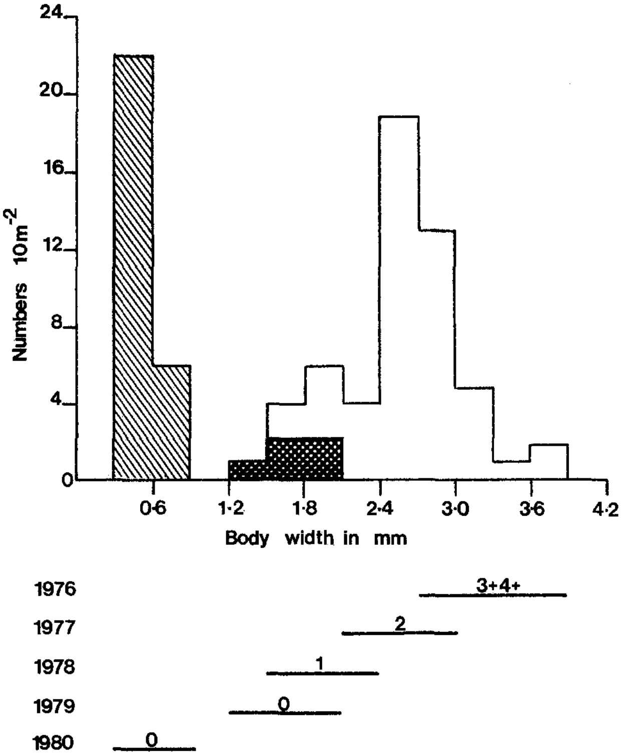

Fig. 4. *Nephtys hombergii*. Size-frequency distributions in August 1980 in the River Tyne estuary, combining the two sampling techniques. The 0 group (1980) individuals are represented by hatching and the 1+ group (1979) data is stippled. Ranges of sizes of worms grouped by reference to number of lines in jaws and inferred years of recruitment are also shown. Note that the 1979 and 1978 year-classes are very poorly represented

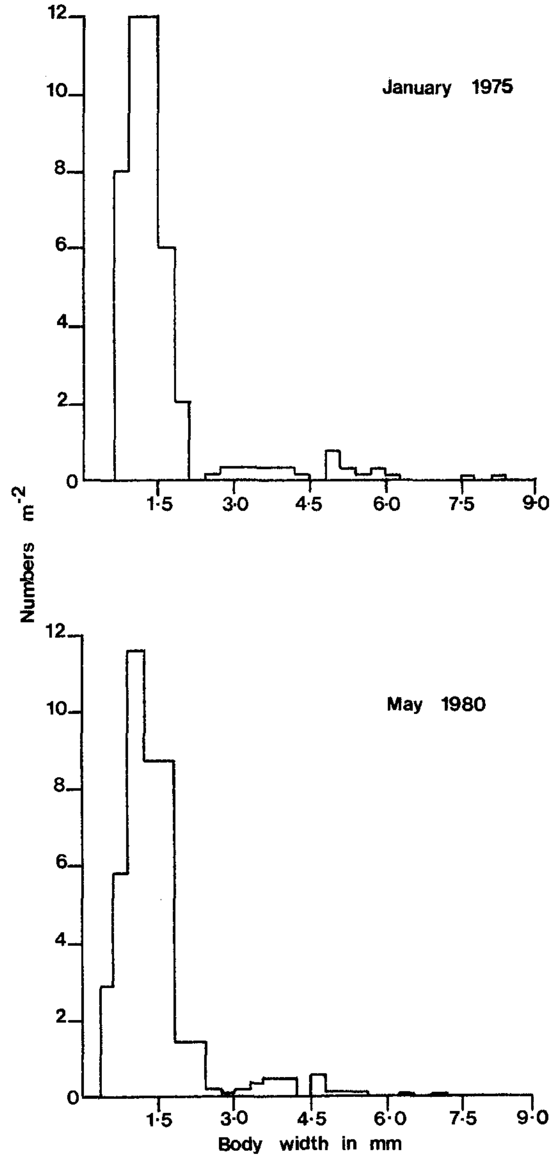

Fig. 5. *Nephtys caeca*. Size-frequency distributions in January ▶ 1975 and May 1980 in the Tyne estuary, combining the two sampling techniques

Nephtys caeca

Fig. 5 shows the structure of the population of *Nephtys caeca* in January 1975 and May 1980. The data for January 1975 demonstrates that there was a large 0 group, representing successful recruitment in 1974, but that there were very few individuals which could be attributed to the 1973 year-class. Both would, according to the hypothesis made at that time (Olive, 1977a), have had 0 rings in the jaws. The remaining part of the population consisted of relatively small numbers of older individuals, the eldest of which were about 10 yr old (8 rings in the jaws). A direct search for larvae suggested that recruitment of *N. caeca* in 1975 was also as poor as in 1973. A comparable sample obtained in May 1980 is also shown in Fig. 5; the large peak of individauls between 0.5 and 2 mm body width is composed of 2 year-classes: those recruited in 1979 (now about 11 months old) and those recruited in 1978 (now approaching 2 yr old). Confirmation of this can be obtained from an examination of the population structure in August 1980, as discussed below. Both year-classes have jaws without obvious rings, but only the older specimens have germ cells.

In addition to the 0 and I group individuals, there are a number of larger worms, resulting in a population showing positive skewness, which seems typical of this species and which indicates that it is potentially long-lived. The relative abundance of each year-class, based on an analysis of the growth lines in the jaws, is given in Table 2. Note that the year-group recruited in 1975, which has 3 rings in the jaws, is relatively poorly represented and that the population is dominated by the first 2 year-groups and those of 1976 and 1974. (At this time the last ring in the jaw was usually at a considerable distance from the edge of the jaw, but in a few specimens

Table 2. *Nephtys caeca*. Relative frequency of year-classes in River Tyne population, May 1980

Year-class	Ring No.	Age: yr (months)[a]	Relative frequency
1979	0	1 (0)	0.39
1978	0	2 (0)	
1977	1	3 (0)	0.09
1976	2	4 (0)	0.16
1975	3	5 (0)	0.09
1974	4	6 (0)	0.16
1973	5+	7 (0)	0.10

[a] Birth date assumed to be in May

Table 3. *Nephtys caeca*. Relative frequency of year-classes in River Tyne population, August 1980

Year-class	Ring No.	Age: yr (months)[a]	Relative frequency
1980	0	0 (3)	ni[b]
1979	0	1 (3)	0.46
1978	1	2 (3)	0.19
1977	2	3 (3)	0.12
1976	3	4 (3)	0.08
1975	4	5 (3)	0.04
1974	5	6 (3)	0.07
1973	6+	7 (3)	0.08

[a] Birth date assumed to be May
[b] ni: not included, numerous; sampled by the sieving method only

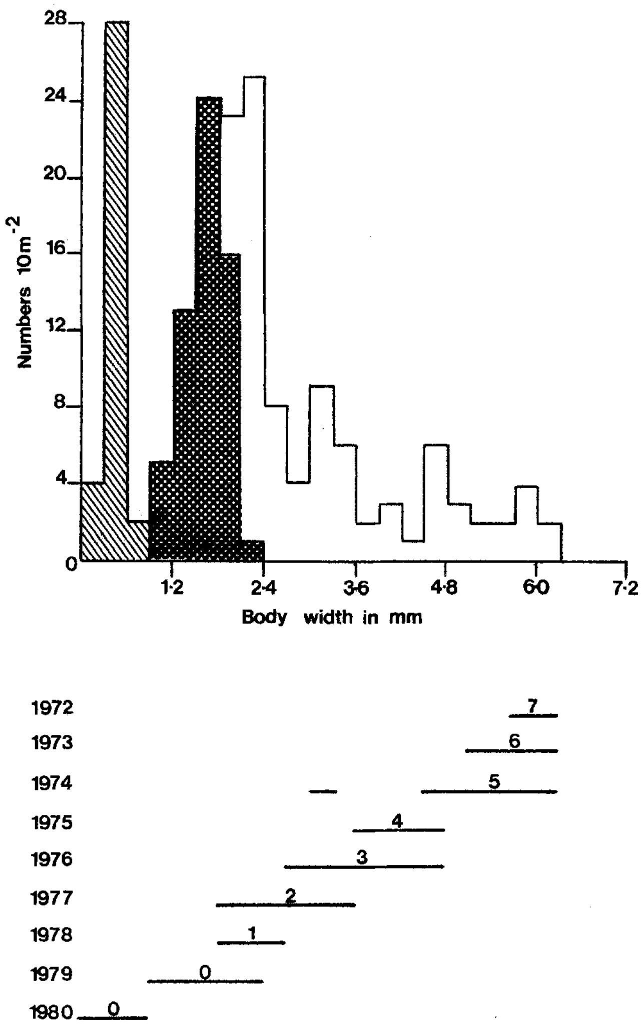

Fig. 6. *Nephtys caeca*. Size-frequency distributions in August 1980 in the River Tyne estuary, combining the two sampling techniques. The 0 group (1980) is represented by hatching and the 1+ group (1979) data is stippled. Ranges of sizes of worms, grouped by reference to number of lines in jaws and inferred years of recruitment, are also shown. Note that the 1978 group which had 0 rings in May (see Table 2) now appears as the group with 1 ring in the jaws

a new growth zone was forming; when this was the case the obviously newly developed growth line was not counted in assessing the ring number of the individuals, in order to achieve a homogeneous treatment of the growth lines.)

The *Nephtys caeca* population was examined again in August 1980. A careful search for new recruits was made, and these were found to be present predominantly in the lower part of the beach (Fig. 3). The structure of the *N. caeca* population at this time is represented in Fig. 6, together with an indication of the size range of each successive year-class. The 1980, 0 group (about 3 months old) of *N. caeca* did not overlap in size with the previous year-group, which also had jaws without rings. The relative abundance of each year class is given in Table 3; note that the poor year-class of 1975 now appears as the group with 4 rings in the jaws.

These observations provide confirmation that the ring in the jaws of *Nephtys caeca* forms after the breeding season, presumably with the renewal of somatic growth, and confirms that in this population the first ring is formed when the worms are 2 yr old and have produced germ cells for the first time; the observations also indicate that individual year-groups can be traced by the study of the rings in the jaws. Recruitment of *N. caeca* in the Tyne estuary population was good in 1976, 1977, 1978, 1979 and 1980, and there is a classical and complete series of year-classes, with the younger individuals predominating as expected. This contrasts with the situation in *N. hombergii*.

Balance Between the Two Species in the Tyne Estuary

The period of 2 or 3 yr up to 1980 has obviously been one which has favoured the reproduction of *Nephtys caeca* but not *N. hombergii* in the Tyne Estuary. It is possible to reconstruct, from direct observations on recruitment and from interpretation of the growth lines in the jaws, the relative success of recruitment in the two species during the period 1972–1980. The results of such an analysis are shown in Table 4; both species

Table 4. *Nephtys hombergii* and *N. caeca*. Effective recruitment in River Tyne Estuary during period 1972–1980

Year	*N. hombergii*	*N. caeca*
1972[a]	good	good
1973[a]	poor	poor
1974[b]	good	good
1975[b]	good	poor
1976[a]	moderate	moderate
1977[a]	moderate	moderate
1978[a]	poor	good
1979[b]	poor (nil)	good
1980[b]	moderate	good

[a] Inferred from relative frequency of year-classes, determined by examination of ring in the jaws
[b] Direct observation of recuitment class

Table 5. *Nephtys hombergii* and *N. caeca*. Dominance in River Tyne estuary, 1974/1975 and 1980. Values are numerical density (mean no. m^{-2} of post 0-group individuals)

Species	1974/1975	1980
N. hombergii	10.9	5.9
N. caeca	5.0	14.3

recruited intermittently; some years seem to have been unfavourable for one or both species. The poor recruitment of *N. hombergii* in recent years can be attributed directly to reduced fecundity caused by failure to release the gametes that have been developed; this coincides with a period of particularly effective recruitment by *N. caeca*. The poor recruitment of *N. caeca* which was sometimes observed during the earlier part of this study was not caused by spawning failure, but seems to have been due to mortality at some later stage. The numerical dominance of the two species in the beach has changed during the last 7 yr (Table 5), such that *N. caeca* is now the dominant species whereas *N. hombergii* was so previously. The reduced frequency of *N. hombergii* in the beach at present is due almost entirely to the absence of younger individuals; the density of the older year-classes is similar to that observed in 1974/1975. The growth records in the jaws suggest, however, that *N. hombergii* rarely live longer than 6 yr, and it will be interesting to observe how the events described so far effect the long-term structure of the populations of these two species.

Discussion

There are several accounts of reproductive failure in Polychaeta, which are of two kinds: (1) failure to develop gametocytes in a large part of a population (2) failure on the part of apparently gravid individuals to shed their mature gametes. The phyllodocid *Eulalia viridis*, like *Nephtys hombergii*, spawned inefficiently in North East England in 1978 and 1979 (Olive *et al.*, in press). The worms had become mature in an apparently normal manner, but did not shed their gametes, which were ultimately resorbed during a prolonged oosorptive phase following the normal breeding season. Hutchings (1973) described a similar, 'though more complex, situation in a population of *Melinna cristata* (also in North East England). The population was composed of juvenile worms, adults which failed to develop any gametocytes, and potential breeders in a gravid condition. Of the latter class, only a relatively small percentage actually spawned eggs, and the unspawned gametes were ultimately resorbed during the 3 months following the breeding season. In each of these three examples where spontaneous oosorption was observed, the population became one which was dominated by the older year classes. This suggests that there is, in these species, a direct relationship between spawning efficiency, effective fecundity and the level of recruitment into the population. Such a relationship suggests that the populations are self-maintaining and that either recruitment from neighbouring populations does not occur or that all the populations in the locality are similarly affected. Where populations are self-maintaining in this way and are not influenced by input of larvae from elsewhere, long-lived polytelic species have a clear advantage and can withstand periodic reproductive failure to a much greater extent than species with different reproductive strategies (Olive and Garwood, 1981; Olive *et al.*, in press). All the species of *Nephtys* investigated so far live for several years and are polytelic. Alheit (1979b) has remarked on the numerical stability of a population of *N. ciliata* in Kiel Bay (FRG) during the period 1968–1978. The population was composed predominantly of old individuals, and the occasional reproductive failures that were noticed had little effect on the overall density. Curtis (1977) suggested that in Arctic regions conditions which are suitable for reproduction may occur only rarely, and consequently there could be strong selection for increased longevity. While this is certainly true, the cause and effect in the relationship may not be as clear-cut, since the non-production of gametes may increase the competitive ability and probability of survival of the adults. The optimum strategy for such organisms is one which selects the best compromise between the need to produce gametes and the need to survive in order to make a further contribution to fecundity in the future.

This raises the question of whether spawning failure should be regarded only as an accidental occurrence caused by exposure to conditions which are unsuitable for reproduction, or whether reproductive failure could be regarded as part of the long-term reproductive strategy of a long-lived species in which the production of gametes each year is not essential. The causes of spawning failure in polychaetes are not yet known, but can be grouped into three general types, and it may be possible in some situations to determine which of these is the most likely:

(1) Restricted Energy Available for Reproduction. Several recent discussions have considered the premise that an organism has a limited energy resource and that this must be compartmentalised as energy available for

growth and energy available for reproduction (reproductive effort: see, for example, Calow, 1979). Under conditions where food input is restricted, there may be insufficient resources for the maintenance of somatic condition and the production of germ cells. Under these circumstances, sterile adults could develop as described by Curtis (1977). It is less easy to explain the observations on *Nephtys hombergii* in the present study and similar ones on *Eulalia viridis* (Olive *et al.*, in press) in this way, since a normal quantity of gametocytes seem to have been produced and then resorbed. Possibly the production of gametes reduced the condition of the adults below some critical level at which future survival would be severely reduced if the energy was lost as gametes – energy stored as gametes can be recouped through the process of oosorption.

(2) Unsuitable Environmental Conditions for Development of Gametes or their Release. Sterility or spawning failure could ensue if specific environmental conditions were not encountered. Our own laboratory studies (Garwood and Olive, 1978; Garwood, 1980; Olive, 1980b, and in press) are, however, revealing that the conditions under which gametes can develop are often very wide in the Polychaeta and that this type of restriction is perhaps only likely to apply where a species is near the limits of its range. Very little is known about the conditions which initiate spawning of marine invertebrates in nature; if they are very precise, unusual circumstances might inhibit spawning. The winter of 1978–1979 was, in fact, one of the coldest on record in North East England, and this was a year in which spawning failures have been reported. This represents circumstantial evidence for an influence of unusual environmental conditions, but the chain of causal relationships is not understood. Reproductive failure which is induced by abnormal conditions is likely to be non-adaptive in the sense that the conditions which are experienced during the period of egg development and spawning are unlikely to have a direct bearing on the conditions that would be experienced by the offspring several months later. Under these circumstances, selection of a genome which would be able to spawn under a wide range of conditions would seem to be most appropriate.

(3) Density-Dependent Inhibition of Egg Production or Release. There are many examples among higher organisms of situations in which the density of adults in a population has a direct influence on the fecundity (Wynne Edwards, 1962). Such mechanisms are able to maintain a population at a level which will not lead to over-utilisation of resources, but it is difficult to envisage how polychaetes inhabiting a sandy beach could gather the kind of information that would be necessary for a mechanism of this sort. However, there are some features of the biology of *Nephtys hombergii* which would suggest a high degree of control over the spawning process; spawning is induced by the release of a cerebral hormone (Olive, 1976) and, in 1979, the spawning hormone was present in the brains of the worms at the appropriate time, and the worms were physiologically able to respond to an injection of the hormone when, in nature, they did not spawn (Olive and Bentley, 1980). There is also reason to believe that for a population of *Nephtys* spp. the potential survivorship value of the offspring will be influenced by the density of the adults, since *Nephtys* species are cannibalistic (Clark, 1962; Scheibel, *in* Alheit, 1979a; and own personal observations). If very large numbers of *Nephtys* spp. juveniles are likely to be consumed by neighbouring individuals of the same or a competing species, resorption of the eggs may represent a theoretically "better choice" than spawning, but whether a mechanism for evaluating such a choice exists, is a separate issue.

Poor recruitment may be caused by other circumstances than spawning failure, for instance inefficient fertilisation, poor survival of the larvae, or their failure to recolonise the parental beach, and one of these seems to have been the cause of poor recruitment of *Nephtys caeca* observed in the Tyne Estuary in 1973 and 1975, when spawning was apparently successful. The Nephtyidae provide an especially valuable opportunity to evaluate the effects of periodic reproductive failure on population structure, since the growth lines in the jaws facilitate the recognition of individual year classes.

The interpretation of the growth lines in the jaws of Nephtyidae must be approached with caution. The major growth lines, which are thought to be related to annual events and thus to give an indication of age, are associated with many other minor growth lines – as shown by Olive (1977a, 1980a) and Kirkegaard (1978). A degree of subjectivity in recognising the status of annual growth lines is inevitable, and supporting evidence is desirable especially since Desbruyères (1977) has suggested that "disturbance lines" may develop as a consequence of major loss of posterior segments in *Aglaophamus ornatus*. Our observations on the growth lines in the jaws of successive year-classes in the population of *Nephtys caeca* confirms that, in this species, the method does permit the resolution of distinct year-classes. The first major growth line in the jaws of the specimens in the River Tyne population of *N. caeca* becomes apparent when the worms are a little more than 2 yr old. This may not be the case in all populations of *N. caeca*.

In his study of the reproductive biology of the subarctic polychaetes of the North Atlantic benthos, Curtis (1977) noticed that in many species the percentage of gamete-bearing individuals was low. His remarks on *Nephtys caeca* are particularly interesting: "A large number of apparently mature specimens did not develop gonads or sex cells during the field sampling period", and Kirkegaard's (1970) method for determining the age of *N. hombergii* did not work well for *N. caeca* near Godhåven, since the number of rings bore no apparent relation to the size of the individuals. This is certainly not the case for the Tyne Estuary population of *N. caeca* (Fig. 6), in which each ring was formed when somatic growth was resumed in the late spring after a period of germinal tissue production. If germ cells are not produced, as in many specimens in the Godhåven population, a distinct growth line may not be formed at this time and this would explain the lack of correlation noticed by Curtis.

The status of the growth lines in the jaws of *Nephtys hombergii* needs separate confirmation in each population studied. Retière (1976) suggested that each year-class in the population in the Rance Estuary became mature each year and that the growth line was strictly annual. Similarly, Kirkegaard (1970, 1978) found that the growth lines in North Sea *N. hombergii* are annual. This is not the case in the Tyne Estuary, where two quite distinct year-classes do not have rings in the jaws (Olive, 1977a). Furthermore, in some years a few specimens of *N. hombergii* may not become sexually mature when 2 yr old (Olive, 1978) and, in these circumstances, the ring number of the jaw minus 1 represents the minimum age of the specimens. A particularly favourable opportunity for the confirmation of this hypothesis now exists, due to the marked differences in the relative frequency of some successive year-groups.

The distribution of *Nephtys* species around the British Isles was discussed by Clark and Haderlie (1960) and Clark *et al.* (1962), although the North East of England was not included in their survey. They suggested that *N. hombergii* may experience greater competition with more arctic species (such as *N. caeca*) in the northern parts of the British Isles, although they found that *N. caeca* was not as common in Scotland as the available literature suggested. The present observations suggest that the two species do compete in the Tyne Estuary, and that the balance between the two species is partially maintained through periodic reproductive failures. A long-term investigation of the balance between these and other species of *Nephtys* in northern England and in Scotland will now be undertaken at this laboratory.

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