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The infection dynamics and dispersion pattern of *Lernaeocera branchialis* L. on 0+ whiting (*Merlangius merlangus* L.) in the Oosterschelde (SW Netherlands)

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Size and structure of the *Lernaeocera branchialis* population infecting 0+ whiting in the Oosterschelde were studied during 1989. Two periods of successful transmission were distinguished. The first transmission wave occurs in late spring when the post-larval whiting enter the Oosterschelde. A second wave occurs in autumn. This pattern in the infection dynamics is possibly related to seasonal variations in spatial overlap of the intermediate (*Platichthys flesus*) and the final host (*Merlangius merlangus*). The dispersion pattern of *Lernaeocera branchialis* within the whiting population can be described by the Poisson distribution. Possible explanations for the observed dispersion pattern are given. Evidence is presented that the rejection of pennella larvae is a key mechanism determining the abundance of *L. branchialis* in whiting. The potential impact of parasite-induced host mortality on population size and dispersion pattern of the parasite is discussed.

Key words: *Lernaeocera branchialis*; *Merlangius merlangus*; Oosterschelde; population dynamics; population structure; dispersion pattern.

I. INTRODUCTION

The abundance and distribution of crustacean ectoparasites on fish is chiefly determined by density-independent factors operating during and after the transmission process (Boxshall, 1974*a*, *b*; Hanek & Fernando, 1978; Poulin *et al.*, 1991*a*). The possible role of regulatory mechanisms in structuring crustacean ectoparasite populations is less well understood (Bortone *et al.*, 1978). There is some evidence from laboratory experiments that density-dependent mechanisms may be important (Poulin & Fitzgerald, 1987; Poulin *et al.*, 1991*b*) but convincing field data are absent. Kabata (1984) suggested that the regulatory role of density-dependent factors may be more important in crustacean mesoparasites, which are partially embedded in the host tissue.

One of the most widespread and best studied mesoparasites is the pennellid *Lernaeocera branchialis* L., a common parasite of gadoids in the North Atlantic and adjacent seas (Kabata, 1979). In the southern North Sea it infects commercially important fish species, such as *Merlangius merlangus* L. and *Gadus morhua* L. (Boxshall, 1971). As this parasite causes considerable pathological damage to the final host (Mann, 1952; Van den Broek, 1978; Guillaume *et al.*, 1985; Khan & Lee, 1989) and presumably also affects host population size and structure (Khan, 1988),

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it attracts the interest of an increasing number of ecologists and parasitologists. So far, comparatively few studies have been dedicated to the population dynamics of this parasite. Detailed information on frequency distributions of *L. branchialis* on their final hosts is scanty (Sproston & Hartley, 1941; Mann, 1952; Pilcher *et al.*, 1989).

In utilizing two hosts to complete their life cycle members of the genus *Lernaeocera* are probably almost unique among the parasitic Crustacea (Kabata, 1979). In the southern North Sea the common intermediate host of *L. branchialis* is the flounder *Platichthys flesus* L. (Boxshall, 1971; Whitfield *et al.*, 1988). After copulation on this host the inseminated females (called pennella larvae) leave the first host and infect gadoid final hosts. On the final host the adult female shows extensive metamorphosis by passing through a number of substages initially described by Sproston & Hartley (1941).

Previous studies on the seasonal pattern of occurrence of *L. branchialis* on *M. merlangus* have been limited in scope. Several authors found that 0+ whiting are infected with pennella larvae after entry into inshore or estuarine waters (Sproston & Hartley, 1941; Shotter, 1973; Van den Broek, 1979; Potter *et al.*, 1988). Recently Pilcher *et al.* (1989) studied the temporal patterns in infection of 1+ and 2+ whiting in the North Sea. Accounts of the temporal pattern in population structure and infection dynamics of *L. branchialis* were presented by Sproston & Hartley (1941) and Van den Broek (1979). Only a restricted number of fish was examined in both studies and some of their conclusions are not in agreement.

The aim of the present study is to examine the infection dynamics of *L. branchialis* in 0+ whiting. The specific objective is to identify the processes which generate the observed dispersion pattern of this parasite species in *M. merlangus*.

II. MATERIALS AND METHODS

The infection dynamics of *L. branchialis* in 0+ whiting were examined in the Oosterschelde, a marine bay in the southwest Netherlands (Fig. 1). For monitoring purposes monthly fish samples are taken by beam trawl in a number of subtidal stations [7 to 20 m below Nieuw Amsterdams Peil (NAP) = approx. Mean Tidal Level]. Details on the methodology of sampling and on the spatial structure of the fish fauna in the Oosterschelde are given in Hostens & Hamerlynck (1992).

In 1989 0+ whiting were first caught in the area in May. Sampling dates, numbers of fish caught and mean standard length are given in Table I. Fish were anaesthetized in a benzocaine solution and preserved in formalin 8% immediately after capture. After 3 months fish were transferred to 70% alcohol and measured (standard length, S.L.). The gill cavity was then checked for parasites.

Terminology was used according to the recommendations of Margolis *et al.* (1982).

The adult parasites present in the gill cavity of whiting were categorized into nine developmental stages. The staging is based on the nomenclature of Sproston & Hartley (1941) and Smith & Whitfield (1988), with some additions (Table II). The first three substages (P1, P2 and U) are characterized by the number of flexure points (Kabata, 1979). Besides, the P1 and P2 substages collected during the present study had a significantly different axial length (P1: 2·21 mm, S.D. = 0·53; P2: 5·62 mm, S.D. = 2·10) (*t*-test; $P < 0{\cdot}001$). As Whitfield *et al.* (1988) found that individual female *L. branchialis* can produce more than one set of egg-strings per season a new subdivision is introduced for the mature parasites: stages X1, X2 and Y (Table II).

Though strictly speaking not a stage of the parasite a further category (R) is distinguished. This ' stage ' is characterized by extensive proliferation of the gill arch tissue

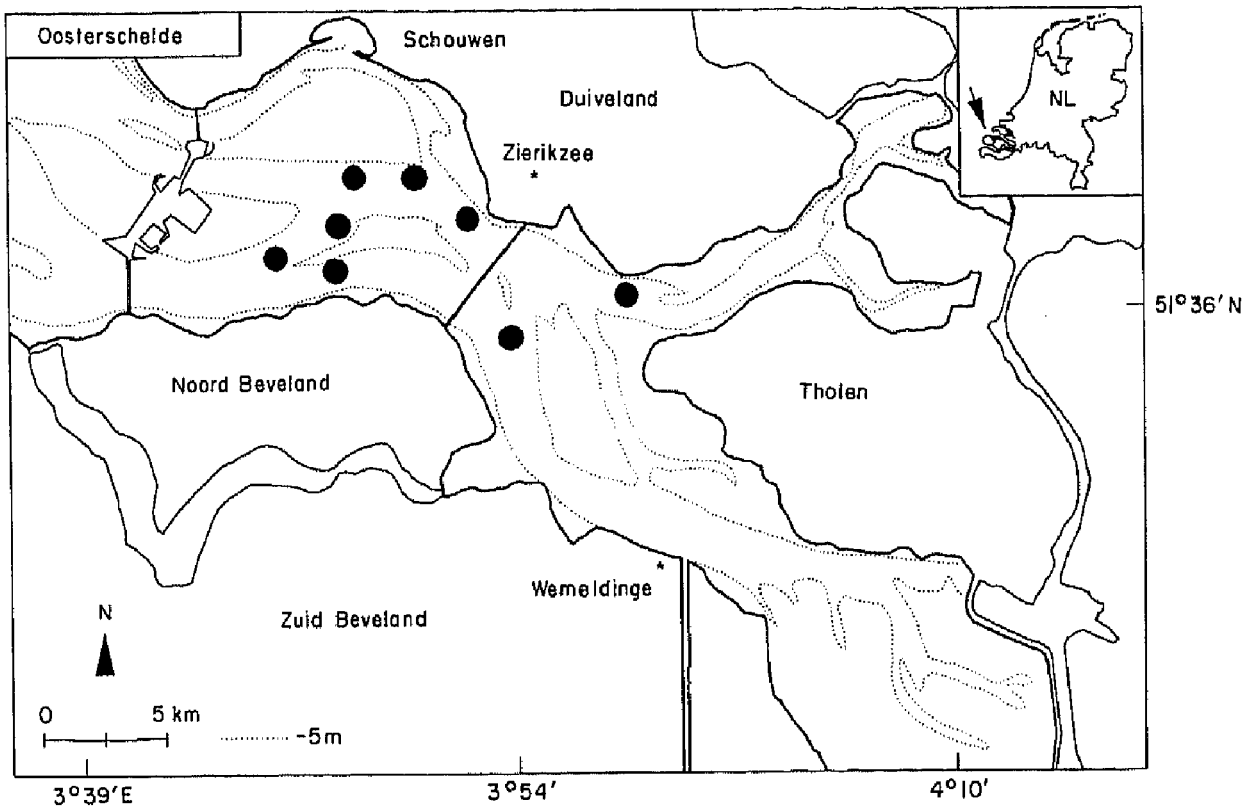

FIG. 1. Map of the study area. ●, Sampling localities.

TABLE I. Sampling dates, number of 0+ whiting caught and mean length of captured fish in the Oosterschelde (1989)

Sample	Sampling dates	No. caught	Mean standard length (mm) (S.D.)
May	16 May	80	64·2 (10·7)
	17 May	28	59·7 (10·9)
Jun.	14 Jun.	81	73·3 (15·8)
Jul.	5 Jul.	126	90·8 (18·1)
Aug.	3 Aug.	18	98·3 (22·6)
	7 Aug.	73	122·4 (20·7)
Sep.	5 Sep.	28	140·5 (18·4)
Oct.	3 Oct.	14	149·3 (26·8)
Nov.	31 Oct.	13	182·3 (16·9)
	6 Nov.	24	206·0 (18·5)
Dec.	4 Dec.	10	200·7 (18·1)

in the absence of a parasite specimen. As the site specificity of the R stage is similar to the distribution of P1 and P2 stages (Fig. 2) it is assumed that the R stage is a successful host tissue reaction to the parasite, resulting in parasite rejection. The R substage was only included in abundance and prevalence calculations when explicitly stated.

Site specificity of pennella larvae was studied by recording the gill arch where attachment occurred. The gills in the left (L) and right (R) gill cavity were numbered from 1 to 4, beginning with the most proximal gill arch (L1 to L4; R1 to R4).

TABLE II. Classification of adult female *Lernaeocera branchialis* on *Merlangius merlangus* (distinguishing characters are placed first)

Substage	Definition
Pennella (P1)	Straight body, no flexure Recently attached to the host Fully pigmented, copepod habitus
Pennella (P2)	One point of flexure Penetration of host tissue Rudiments of three holdfast processes present
Immature (U)	Two or three points of flexure Genital region not or partly swollen Elongating holdfast processes
Mature pregravid (W)	Genital region fully swollen Torsion of abdomen is complete Fully developed branched holdfast No external egg strings
Mature gravid (X)	External egg strings present
X1	Immature eggs
X2	Mature pigmented eggs
Y	External egg strings partly or completely spent
Dead parasite (Z)	Remains of holdfast embedded in host tissue
Rejected parasite (R)	Absence of parasite specimen Proliferation of gill arch tissue

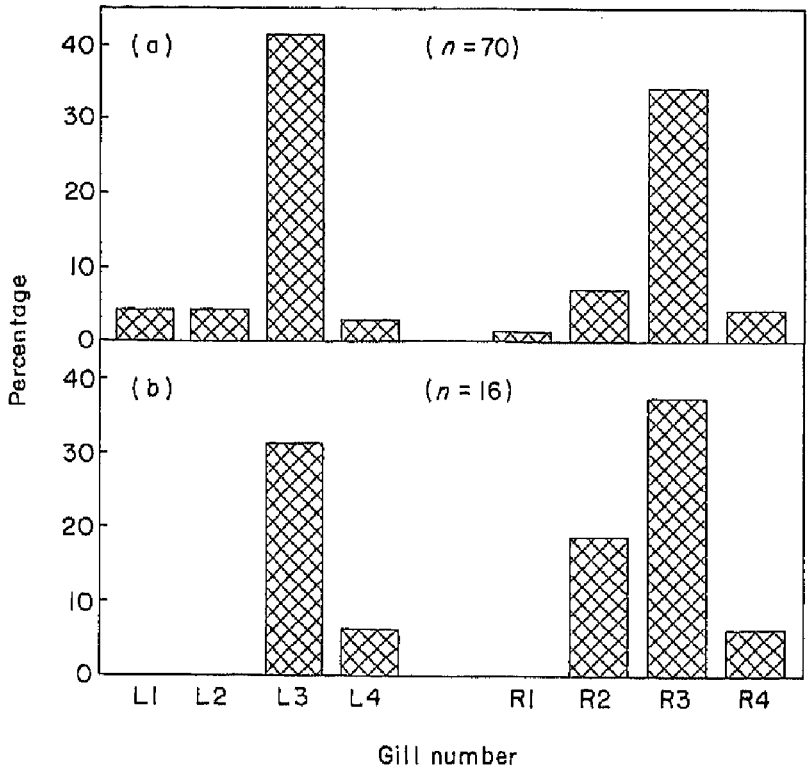

FIG. 2. (a) Site specificity of pennella substages of *Lernaeocera branchialis* on 0+ whiting in the Oosterschelde (1989). (b) Occurrence of R 'substages' on the gill arches of 0+ whiting.

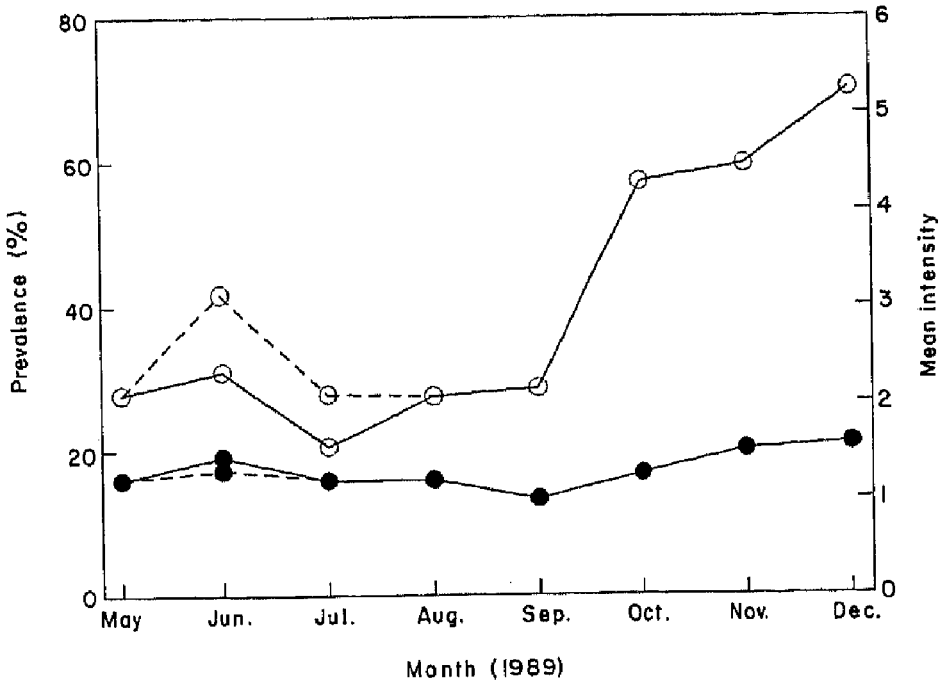

FIG. 3. Prevalence (○) and mean intensity (●) of *Lernaeocera branchialis* on 0+ *Merlangius merlangus* in the Oosterschelde (1989). The interrupted lines connect datapoints for prevalence and mean intensity when R substages are included.

Dispersion pattern was studied by calculating the variance to mean (V/m) ratio (Elliott, 1971) and the exponent b from Taylor's power function (Taylor, 1961). The observed distributions were compared with the Poisson series by χ^2 (goodness-of-fit) tests (Elliott, 1971).

III. RESULTS

The seasonal pattern in prevalence and mean intensity of infection of 0+ *M. merlangus* by *L. branchialis* is shown in Fig. 3. About 30% of the juvenile fish have already been infected with *L. branchialis* prior to first capture in May. The smallest fish infected by a P1 stage had a S.L. of 49 mm. The prevalence remained fairly constant until September. In the October sample a steep rise in prevalence to 60% was recorded. By December prevalence was about 70%. Mean intensity of *L. branchialis* infection fluctuates between 1 (September) and 1·6 (December).

Including the R stage in the prevalence calculation leads to a slightly different picture. In this case there is an initial rise in prevalence to 42% in June, followed by a decrease.

The temporal variations in the occurrence of the different parasite stages are shown in Fig. 4. There are clearly two peaks in the abundance of P1 stages: a first peak in May and a second peak in October–November. During summer and in December very few or no P1 stages were recorded, indicating low transmission levels. Stage X (mature) was first observed in July. The Z stage (dead parasite) was first observed in August. Within the X stage there is also a clear pattern in the succession of the substages X1, X2 and Y. In July and August all mature parasites were in substage X1. From September onwards X2 and Y substages were recorded together with X1 (Table III).

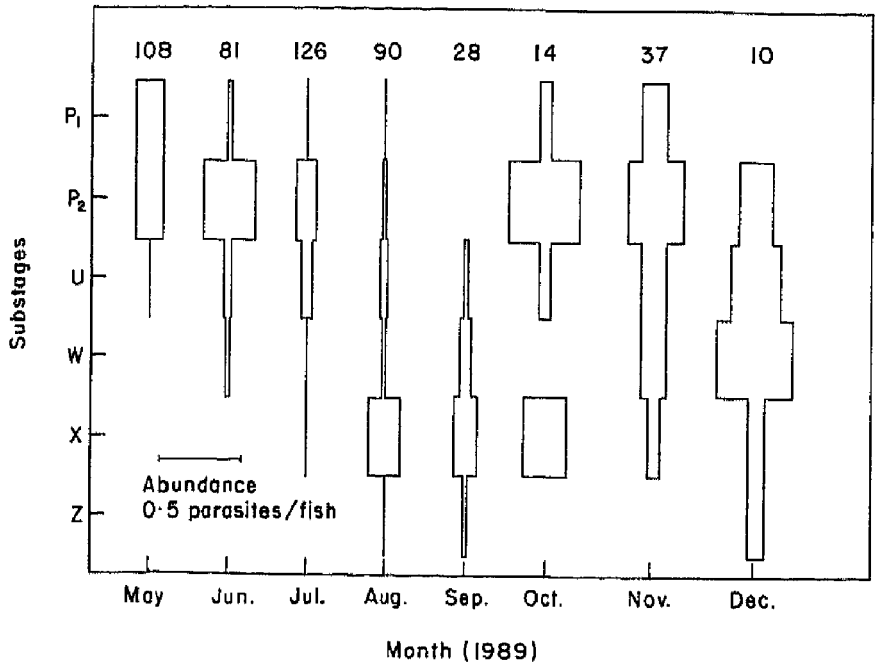

FIG. 4. Seasonal variations in population structure of *Lernaeocera branchialis* on 0+ whiting in the Oosterschelde (1989). The number of fish investigated is indicated.

TABLE III. Seasonal variations in the number of X1, X2 and Y substages infecting 0+ whiting in the Oosterschelde (1989)

	X1	X2	Y
May	—	—	—
Jun.	—	—	—
Jul.	2	—	—
Aug.	16	—	—
Sep.	3	1	—
Oct.	2	1	1
Nov.	2	—	1
Dec.	—	—	1

The seasonal pattern in the variance to mean (V/m) ratio is shown in Fig. 5. V/m ratios did not differ significantly from 1 (χ^2; $P>0{\cdot}05$), except in the sample taken on July 5 ($V/m=1{\cdot}28$, $\chi^2=160{\cdot}1$, $P<0{\cdot}05$). From September to October 1989, the V/m ratios are below 1. When the R stage is included in the calculations the V/m ratios for June and July approach 1 (respectively 1·04 and 1·12). Goodness-of-fit tests showed that there was good agreement ($P>0{\cdot}05$) with the Poisson series for all observed distributions. The temporal variance-mean regression equation was $\log V=0{\cdot}01+0{\cdot}99\log m$ ($r=0{\cdot}921$).

IV. DISCUSSION

Flounders (*P. flesus*) migrate to estuaries and coastal areas in early spring Hardisty & Badsha, 1986). In the Oosterschelde, high numbers of flounder are

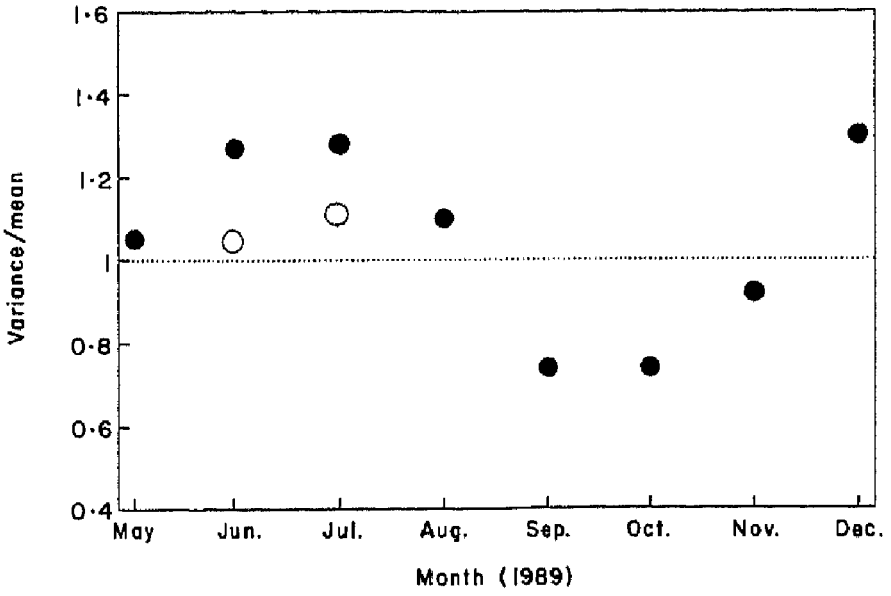

FIG. 5. Variance to mean ratios of *Lernaeocera branchialis* within a population of 0+ whiting in the Oosterschelde during 1989. ○, Variance to mean ratios when also R ' substages ' were considered.

present in the tidal gullies (between −30 and −6 m NAP) during immigration to the shallow waters (March–May) and during emigration to the open sea (October–November). In the summer months (from June to September) the flounders stay in shallow water (−0·5 to −4 m NAP) (P. A. Van Damme, unpubl.). In the Oosterschelde first-year class whiting on the other hand prefer the deeper gullies and do not migrate to shallow water (H. Hostens, pers. comm.). Consequently, 0+ whiting are out of the range of the intermediate host of *L. branchialis* during the hot summer months. Transmission of infective stages can only occur in spring and in autumn when both intermediate and final host are present in the gullies. The swimming abilities of pennella larvae are limited (Sproston, 1941) and the life span of this stage is assumed to be short (Stekhoven & Punt, 1937). The occurrence of pennella larvae (P1) on the gill filaments of whiting may therefore be a sensitive indicator for the degree of spatial overlap of flounder and whiting. Pilcher *et al.* (1989) likewise suggested that the degree of spatial overlap of intermediate and final host determines the infection level in 1+ and 2+ whiting in the North Sea. They found maximal *L. branchialis* infection levels in the winter months. This is in accordance with the migration pattern of flounder, which stay in deeper water during the winter.

The division of the pennella stage of *L. branchialis* in P1 and P2 substages is meaningful for the study of infection dynamics. The two substages can be easily distinguished by their distinct appearance and their significantly different length. Pennella (P) larvae were found on smaller whiting (5 cm) than as recorded by Shotter (1973) (10 cm), Sproston & Hartley (1941) (11 cm) and Potter *et al.* (1988) (9 cm). The autumn and winter prevalences in the Oosterschelde (60–70%) were higher than those recorded for 0+ whiting in the Bristol Channel (<11%) (Potter *et al.*, 1988) and for 0+ whiting from off the Isle of Man (<5%) (Shotter, 1973). The Oosterschelde is therefore an area where transmission of *L. branchialis* is highly successful. Parasite prevalence in the Oosterschelde is of the same magnitude as prevalences found in the Tamar estuary (Sproston & Hartley, 1941) and the

Medway estuary (Van den Broek, 1979). These estuaries are all characterized by high abundances of flounder, the intermediate hosts of *L. branchialis* (Van den Broek, 1979; Hardisty & Badsha 1986; Hostens & Hamerlynck, 1992; Hamerlynck & Hostens, 1992).

Sproston & Hartley (1941) found increased prevalences (up to 100%) in 0+ whiting collected in the Tamar estuary during the winter. They suggested that infected whiting do not migrate to the open sea in the winter but linger in the estuarine and inshore waters. Although the number of fish investigated during the present study is small, there is no indication that the same is true for the 0+ whiting population in the Oosterschelde: the high prevalences recorded on 31 October/6 November and on 12 December 1989 can adequately be explained by the second transmission wave in autumn (Fig. 3).

Estimates of the life span of individual *L. branchialis* vary from 8 weeks (Sproston & Hartley, 1941), over 9–10 months (Khan, 1988) to 1 year or more (Stekhoven & Punt, 1937; Capart, 1948). Kabata (1958) estimated the duration of substages of female *L. branchialis* f. *obtusa* on *Melanogrammus aeglefinus* L. by measuring the interval between the peak abundances of consecutive substages. His estimates for the duration of the P, U and W substages were 6, 8 and 8 weeks respectively. Although this method could not be applied during the present study, it is clear from Fig. 4 that the minimum development time from transmission of pennellae to the X-substage is 3 months. X2 and Y substages with mature eggs were found from September to December (Table III), making it possible for flounder to be infected with copepodid larvae during their autumn and winter migration to the open sea.

Crofton (1971) suggests that overdispersed distributions are a characteristic feature of host–parasite relationships. This type of distribution has been recorded for the majority of marine host–crustacean parasite relationships studied so far (Boxshall, 1974*b*; Borton *et al.*, 1978; Poulin & Fitzgerald, 1987). However, in the present study it was found that the distribution of *L. branchialis* within a whiting population from the Oosterschelde can be adequately described by the Poisson series during the major part of the year. Mann (1952) and Sproston & Hartley (1941) found overdispersed distributions of *L. branchialis* on 0+ whiting. Pilcher *et al.* (1989) also report aggregated distributions of this same parasite species on 1+ whiting. Thus, the dispersion pattern of *L. branchialis* on 0+ whiting in the Oosterschelde is clearly different from the patterns described for populations of the same parasite in other areas. In the present study a relatively high percentage of fish were infected with one parasite, and few fish harboured more than three parasites. As only a limited number of fish were investigated in this study the use of the V/m ratio, which is dependent on sample size, may be unreliable (Elliott, 1971). Therefore the use of Taylor's power law is more appropriate. The close approximation to 1 of the parameter b of Taylor's power law indicates that *L. branchialis* is randomly distributed on 0+ whiting. Scott (1987) and Nie & Kennedy (1991) however emphasize the occurrence of temporal changes in dispersion pattern and in the processes generating those patterns. In the present study the observed distributions may indeed result from the sequential and/or concomitant action of a range of biological processes in the course of the year. There are some indications that transmission success, parasite-induced host mortality as well as immunological factors can induce alterations in aggregation of *L. branchialis*.

The dispersion pattern of crustacean parasites is in the first place determined by the nature of the infection process (Boxshall, 1974*b*). Overdispersed distributions are commonly generated by a series of random waves of infection (Elliott, 1971; Boxshall, 1974*b*). In the present study however, the first transmission wave of pennella larvae was restricted to a relatively short time interval in spring. If this single transmission wave was a random process we could indeed expect a random distribution of *L. branchialis* on *M. merlangus*.

Secondly, immunological factors probably play an important role in summer: P2 substages were rejected from the gill arches, leading to the relatively high number of R 'substages'. Rejection of crustacean parasites by fish hosts is not well documented. Shields & Goode (1978) describe female *L. cyprinacea* being rejected from the tissue of *Carassius auratus* L. It may well be that this type of host effect is one of the key factors regulating abundance of adult mesoparasitic crustaceans. Rejection of juvenile parasites leads to more overdispersed distributions (Anderson & Gordon, 1982), an observation which was also made during the present study (Fig. 3).

A third factor which may influence the abundance and disperson of *L. branchialis* on 0+ whiting is parasite-induced host mortality. This factor lowers parasite abundance and tends to decrease the degree of aggregation (Anderson & Gordon, 1982). During the present study, the low variance to mean ratios and the low mean intensity recorded on 5 September and on 31 October/6 November may be due to higher mortality rates of infected whiting. The low number of X stage parasites in the winter may also result from host mortality but may also be a reflection of the low number of fish studied.

The efficiency of the fishing gear used was assumed to be 20% (Hostens & Hamerlynck, 1992). This estimated efficiency may be different for infected and uninfected fish. Sprengel & Lüchtenberg (1991) found that infection by endoparasites reduces maximum swimming speeds of *Osmerus eperlanus* L. and *Anguilla anguilla* L. Several authors have assumed that *L. branchialis* affects the swimming abilities of the final host (Sproston & Hartley, 1941; Mann, 1952; Khan, 1988) and some experimental evidence for this has been found recently (H. Möller, pers. comm.). If it is true that whiting infected with *L. branchialis* swim more slowly, they will be over-represented in samples collected by beam trawl. This may be an important source of error when calculating infection levels and frequency distributions of parasites. It may also hinder correct interpretation of the observed dispersion patterns during the present study.

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