MORPHOLOGICAL AND ECOLOGICAL STUDIES OF *CLAVELLA ADUNCA* (COPEPODA, LERNAEOPODIDAE) ON POLAR COD, *BOREOGADUS SAIDA*

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Clavella adunca (STRØM, 1762) from the Barents Sea polar cod was studied. The general appearance and morphology of the appendages were similar to *C. adunca* f. *iadda* LEIGH-SHARPE, but the size of the trunk and cephalothorax were greater than those in other populations (mean trunk length 3.8 mm, width 3.0 mm, mean cephalothorax length 4.3 mm). Most of the parasites (94 %) were found on the fins.
Parasites were found in the whole distribution area of the polar cod, but were most frequent in the eastern part of the Barents Sea. Of 42 samples 39 contained infected fishes. The distributions of the parasites on the hosts were always overdispersed and negative binominal distributions proved to be a good empirical model of the observed distributions. The infection rate was higher during winter than during summer. No correlation between the infection rate and the age of the host was observed.

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INTRODUCTION

Since *Clavella adunca* (STRØM, 1762) was described, the species has been the subject of much controversy. LEIGH-SHARPE (1925, 1933) divided it into six separate species, based mainly on morphometric differences. Later authors disagreed with his view, and currently LEIGH-SHARPE's species are regarded as ecotypes of *C. adunca* (see NUNES–RUIVO 1957; KABATA 1960, 1963a, b). The general distribution of *C. adunca* is very wide both in the North Atlantic and in the North Pacific (POLYANSKII 1955; YAMAGUTI 1963). It has also been recorded from the Antarctic (KABATA & GUSEV 1966). SCHRAM (1980) observed *C. adunca* on polar cod in the Barents Sea.

Aspects of the biology and ecology of *C. adunca* from cod and whiting have been studied by POULSEN (1939), POLYANSKII (1955), SHOTTER (1971, 1973), and JANUSZ (1979). SHOTTER (1971) found that *C. adunca* f. *scientaria* from temperate waters is a shortlived species. SHOTTER (1973) and POULSEN (1939) observed that *C. adunca* are most abundant in more or less closed waters. Most authors seem to agree that the infection rate decreases with the age of the fish. POLYANSKII (1955) found pronounced seasonal variations in the infection rate, while SHOTTER (1971, 1973) and BOXSHALL (1974a) found no variation.

The frequency distribution of number of *C. adunca* per host has not been described in statistical terms BOXSHALL (1974a) stated that the distribution was overdispersed and SCHRAM (1980) stated that the parasites were aggregated, probably with a negative binominal distribution.

In the present paper some aspects of the morphology and ecology of *Clavella adunca* from Barents Sea polar cod are studied. Both ecological and morphological data are used to give a description of the population.

MATERIAL AND METHODS

Samples of polar cod were caught by pelagic or bottom trawls. From each sample 100 or more fish were used. The percentage of fish infected by *C. adunca* was recorded for all samples (Table 1). In some samples the length of the fish, number of parasites on each fish, and site of infection were recorded.

From some samples the parasites were dissected out, and brought to the laboratory for study. Morphology was examined on entire and dissected specimens. Most specimens were cleared in lactophenol and stained by lignin pink. In some cases, phase contrast illumination was used. All measurements were made using a binocular microscope with ocular micrometer. Weights of parasites were recorded using a Sauter micro balance.

The negative binominal distribution was fitted to the observed frequencies of *C. adunca* per polar cod, using the method of maximum likelihood (BLISS & FISHER 1953).

RESULTS

The general appearance of the observed specimens was similar to that of *C. adunca* f. *iadda* LEIGH–SHARPE. The morphology of the appendages was studied in both males and females and compared with the descriptions and figures given by NUNES–RUIVO (1957) and KABATA (1960, 1963a, b). No differences of taxonomic significance were found.

Length and weight were recorded of 26 females taken from polar cod from various parts of the

Table 1. Distribution of *Clavella adunca* on polar cod in the Barents Sea.

Sample number	Month	Year	Position N	Position E	Number of fish examined	Percentage of infection
1	8	1970	74°14′	38°46′	100	3.0
2	11	1970	77°00′	38°02′	112	1.8
3	5	1971	73°50′	47°20′	100	3.0
4	6	1971	73°43′	49°50′	100	0.0
5	6	1971	72°20′	43°30′	126	3.2
6	6	1971	73°00′	45°10′	349	16.1
7	7	1971	75°10′	50°00′	100	0.0
8	12	1971	72°23′	38°19′	108	41.7
9	12	1971	74°12′	36°58′	100	18.0
10	5	1972	72°50′	38°20′	103	33.0
11	5	1972	71°31′	48°26′	100	5.0
12	5	1972	72°30′	47°45′	109	5.5
13	5	1972	72°34′	48°22′	103	3.0
14	5	1972	73°05′	45°34′	102	3.0
15	5	1972	73°05′	45°25′	101	6.0
16	5	1972	73°56′	48°10′	141	22.0
17	6	1972	73°47′	48°22′	110	14.0
18	6	1972	73°45′	48°20′	121	5.0
19	6	1972	73°56′	47°32′	111	13.0
20	6	1972	74°20′	46°06′	120	7.0
21	6	1972	73°40′	50°17′	120	28.0
22	6	1972	73°30′	51°30′	112	11.0
23	6	1972	73°00′	49°10′	115	2.6
24	8	1972	76°41′	32°00′	93	0.0
25	8	1972	76°30′	42°00′	101	7.0
26	8	1972	77°08′	48°00′	100	3.0
27	8	1972	76°04′	48°00′	98	25.5
28	8	1972	76°30′	52°00′	108	18.5
29	8	1972	77°01′	57°26′	97	20.6
30	8	1972	77°56′	58°50′	50	20.0
31	2	1973	72°52′	37°12′	55	33.0
32	2	1973	72°20′	38°50′	82	27.0
33	9	1973	77°50′	28°00′	148	4.1
34	9	1973	77°30′	28°00′	155	3.9
35	9	1973	79°04′	34°00′	216	1.4
36	9	1973	78°40′	42°00′	300	1.7
37	10	1973	77°10′	56°07′	6	83.0
38	10	1973	77°06′	60°00′	100	18.0
39	10	1973	76°30′	56°25′	28	46.4
40	10	1973	75°00′	52°55′	100	22.0
41	10	1973	74°50′	47°07′	100	35.0
42	6	1974	75°53′	27°23′	131	7.6

Table 2. Size (mm) and weight (g) of *Clavella adunca* from polar cod.

	N	Mean	95 % Confidence limits (±)	Range
Trunk, length	26	3.80	0.22	2.9–5.3
Trunk, width	26	2.99	0.10	2.5–3.6
Cephalothorax, length	26	4.29	0.23	3.4–6.0
Ovisacs, length	24	5.34	0.49	3.9–6.8
Total weight	20	0.0305	0.0035	0.017–0.043
Ovisacs, weight	20	0.0156	0.0023	0.008–0.024

Barents Sea (Table 2). The mean length of the trunk was 3.8 mm and the mean width 3.0 mm. The mean length of the cephalothorax was 4.3 mm. Ranges and confidence limits are given in Table 2. There was no significant correlation between the length and the width of the trunk ($r = 0.15$) or between the length of the cephalothorax and the length of the trunk ($r = 0.29$).

Body proportions were variable, but the length of the trunk was always greater than the width (Table 3). The cephalothorax was usually longer than the trunk. The mean total weight was 0.031 g, and the ovisacs constituted 49 % of this (range 37–63 %). Only two males have been measured, and both were 0.51 mm long.

Eggs from 8 females were counted and fecundity ranged between 493 and 1 227 eggs, with a mean of 786 eggs per female. There was no significant correlation between the trunk size and the fecundity.

Geographical distribution

Clavella adunca was recorded from all parts of the Barents Sea where polar cod have been found. During the years 1970–1974 polar cod from 42 stations were studied and infected specimens were recorded from 39 of these stations. The infection rate was highest in the eastern Barents Sea and lower in the Spitsbergen area, where the population density of polar cod is lower. The host spends most of its life in waters with temperatures below 0° C. Only during the spawning period (December–February) temperatures above 0° C are preferred.

Distribution of Clavella adunca *on the host*

The site of attachment of *C. adunca* was recorded from 126 infected polar cod in 9 samples from September to October 1973 and June 1974. Of 255 parasites 26 % were found on the pectoral fins and 22 % on the first dorsal fin (Table 4). Only 6 % were not associated with the fins. Most of these were attached to the skin on various parts of the fish. Only two out of 255 parasites were found in the mouth cavity of the host and one was found attached to the eye.

Size distribution of the infected polar cod

Length distribution of infected and uninfected polar cod was studied in 11 samples. As the length distribution was often bimodal or highly skewed, only mean lengths and ranges are given (Table 5).

No infection of polar cod smaller then 8.5 cm has been observed. Fish smaller than 12 cm were never infected with females bearing ovisacs. In fish longer than approximately 12 cm and 2 years old, there was no correlation between the length and infection rate.

Seasonal variation

Ten of the 42 samples studied were taken during the

Table 3. Body proportions of *Clavella adunca*.

Host species	Area of infection	Geographical area	Author	Trunk length/ trunk width Mean	Range	Cephalothorax length/ trunk length Mean	Range
Polar cod	Mainly fins	Barents Sea	This paper	1.28	1.01–1.91	1.01	0.77–1.50
Cod	Fins	Greenland	NUNES–RUIVO (1957)	1.40		1.19	
Cod	Mainly mouth	Barents Sea	Own unpubl. results	0.99	0.79–1.26	1.49	1.16–2.22

Table 4. Site of attachment of *Clavella adunca* on 121 polar cod.

Site of attachment	N	%
First dorsal fin	57	22.3
Second dorsal fin	42	16.4
Third dorsal fin	31	12.1
Pectoral fin	66	25.8
First anal fin	20	7.8
Second anal fin	13	5.1
Caudal fin	10	3.9
Ventral fin	1	0.4
Operculum, side etc.	12	4.7
Eye	1	0.4
Mouth	2	0.8
	256	100.0

winter (October–April). The mean infection rate for this period was 32.7 %. The mean infection rate for 32 samples taken during the summer (May–September) was 9.3 %. A Mann–Whitney test showed that the difference in infection rate between winter and summer samples was highly significant ($U = 50$, $Z = -3.25$). No seasonal variation in the proportion of females carrying ovisacs was observed.

Frequency distribution of C. adunca *on the host*

The frequency distribution of parasites per host was studied in 17 of the samples collected in February, June, August, September, and October (Tables 6 and 7).

The sample means ($\bar{x}$) varied between 0.032 and 1.178 and the variance (s^2) between 0.097 and 3.263. The variance was always greater than the mean, and they were closely correlated. There was also a very close correlation between sample mean and infection rate (I).

The negative binominal distribution is given by the expansion of the expression $(q-p)^{-k}$ where $q = 1 + p$ and $k > 0$. The parameters p and k were estimated by the maximum likelihood method (BLISS & FISHER 1953) and the fit was tested using second $(\frac{\Delta U}{SE\ U})$ and third moment $(\frac{\Delta T}{SE\ T})$ tests (ANSCOMBE 1950). The results are listed in Table 6; observed and expected frequencies are given in Table 7.

There was no significant difference between the third moments of the observed and the fitted distributions. The second moment was significantly different in one of the 17 samples ($P < 0.05$). The sign of ΔT and ΔU was negative in 16 of the samples. If pkq, which is more efficient measure for second moment than $(x + \frac{\bar{x}}{k})$, is used, the sample second moments are always lower than expected.

The parameter k, and the mean number of parasites per fish ($\bar{x}$), were significantly correlated with the infection rate (I), (Table 8). The relation between $\bar{x}$ and I was nearly linear, while that between k and I was slightly concave upwards. The

Table 5. Length (mm) of polar cod from the Barents Sea.

	Total measured			Infected, total			Infected with mature females		
Sample number	N	l	Range	N	l	Range	N	l	Range
31	155	13.4	10.5–19.0	19	13.2	10.5–19.0			
32	182	15.8	12.5–21.0	22	15.4	12.5–18.5			
33	148	11.6	6.0–22.0	6	15.2	8.8–19.6	5	16.5	15.3–19.6
34	155	11.1	7.0–23.0	6	15.6	8.6–21.1	3	20.2	21.1–18.3
35	216	13.5	6.0–21.0	3	18.0	16.4–20.2	2	18.3	16.4–20.2
36	139	12.0	8.0–19.0	5	14.3	11.5–19.0	3	16.0	12.8–19.0
38	126	18.6	9.0–24.0	18	17.7	11.8–22.6	11	19.0	13.5–21.9
39	28	9.9	5.0–19.0	13	11.6	9.6–18.7	2	15.2	12.3–18.0
40	116	20.9	15.0–24.0	22	19.3	16.0–23.4	15	19.1	16.0–21.6
41	117	17.1	12.0–21.0	35	17.3	14.5–20.4	26	17.2	14.5–20.4
42	131	16.0	9.0–24.5	9	17.3	15.5–19.0			

Table 6. Negative binomial distributions fitted to the data. N = number of parasites, $\bar{x}$ = mean number of parasites per fish, s^2 = variance, s^2/x = overdispersion, I = infection rate, p, k and q are parameters of the negative binomial distribution, $\frac{\Delta T}{SE\ T}$ and $\frac{\Delta U}{SE\ U}$ is difference between observed and expected third and second moments divided by their standard error.

Sample number	N	$\bar{x}$	s^2	s^2/x	I	p	k	pkq	$\frac{\Delta T}{SE\ T}$	$\frac{\Delta U}{SE\ U}$
6	349	0.292	0.730	2.500	16.1	1.587	0.184	0.755	−0.359	−0.168
25	101	0.139	0.381	2.746	6.9	2.286	0.061	0.457	0.224	−0.265
26	100	0.060	0.138	2.296	3.0	2.400	0.025	0.204	−0.103	−0.340
27	98	0.490	0.974	1.989	25.5	1.527	0.321	1.238	−0.437	−0.708
28	108	0.528	2.755	5.256	18.5	4.364	0.121	2.832	−0.403	−0.044
29	97	0.515	1.587	3.076	20.6	3.066	0.168	2.094	−0.298	−0.603
30	50	0.400	1.102	2.755	20.0	1.896	0.211	1.158	−0.620	−0.097
31	55	0.491	0.810	1.650	33.0	0.640	0.767	1.050	−0.203	0.020
32	82	0.720	2.081	2.892	27.0	3.365	0.214	3.142	−0.184	−0.851
33	148	0.0743	0.192	2.579	4.1	1.930	0.0385	0.218	−0.218	−0.187
34	155	0.0451	0.056	1.249	3.9	0.285	0.158	0.058	−0.235	−0.110
35	216	0.0324	0.097	2.990	1.4	3.484	0.0093	0.145	−0.089	−0.312
36	300	0.0967	1.014	10.491	1.7	16.390	0.0059	1.682	−0.139	−4.789*
38	100	0.330	0.728	2.207	18.0	1.514	0.218	0.830	−0.309	−0.355
39	28	1.178	3.263	2.768	46.4	2.146	0.549	3.705	−0.418	−0.253
40	100	0.580	1.761	3.037	22.0	4.143	0.140	2.983	−0.177	−0.934
41	100	0.740	2.033	2.747	35.0	1.770	0.418	2.050	−0.392	−0.031

* $P < 0.05$

correlation between k and $\bar{x}$ was highly significant, while there was no correlation between p and I. The parameter p was closely correlated with overdispersion ($\frac{s^2}{x}$), while the correlation between k and overdispersion was significant but poor. Both were nonlinear.

IWAO (1970) and IWAO & KUNO (1971) have shown that mean crowding, $\overset{*}{x} = \bar{x} + \frac{\bar{x}}{k}$, is usually linearly related to mean density, $\bar{x}$. In the case of *Clavella* on polar cod, there was no significant correlation between these variables ($r = -0.092$).

Since the variables studied in Table 8 are not mutually independant, the probabilities given must, however, be treated with caution.

DISCUSSION

C. adunca from polar cod in the Barents Sea was larger than all other populations studied. Nearest in size is *C. adunca* f. *iadda* LEIGH-SHARPE from Greenland cod. These have a mean trunk length of 3.20 mm, width 3.32 mm, and cephalothorax length 3.76 mm (NUNES-RUIVO 1957). These measurements fall within the ranges but outside the confidence limits of *C. adunca* from polar cod.

The body proportions of *C. adunca* from polar cod are rather close to those from fins of cod from Greenland and from the Barents Sea (see Table 3). *C. adunca* associated with gill- or mouth cavities is smaller and also differs in body proportions (see Table 3 and JANUSZ 1979).

SCHRAM (1980) found that *C. adunca* most frequently was associated with the fins of the polar cod, and the results of the present study fit closely with his results (Table 4). According to POLYANSKII (1955) *C. adunca* from Barents Sea cod was most frequently associated with the gill- or mouth cavity. On cod caught off Labrador and New Foundland JANUSZ (1979) found that 50 % of the parasites were attached in the gill cavity, 37 % at the anus, and 13 % at the fins. KABATA (1960) and BOXSHALL (1974a) studying *C. adunca* from gadoids in British waters and in the North Sea also stated that they were usually found in the mouth cavity.

There also seems to be other ecological differences. Both POULSEN (1939), POLYANSKII (1955), KABATA (1960), and SHOTTER (1973) observed a decrease in infection of *C. adunca* with increasing fish age. JANUSZ (1979) found that the infection on cod increased up to an age of 7 and 8 years, and then decreased. SCHRAM (1980) also found the highest rate of infection on polar cod of middle age. In the present study no clear relation between fish age and infection rate was found.

POLYANSKII (1955) showed that the incidence of infection with *C. adunca* on cod was considerably higher during the summer than during the winter. SHOTTER (1971, 1973), who studied *C. adunca* from *Merlangius merlangus* (L.) from the Irish Sea, found no seasonal variation in the infection rate. In the present study the highest infection rate was found during the winter. The differences between the population on cod and polar cod from the Barents Sea, may be caused by their different behaviours.

Table 7. Frequency distribution of *Clavella adunca* on polar cod. O = observed frequency, C = frequency calculated from the negative binomial distribution.

Station number	6 O	6 C	25 O	25 C	26 O	26 C	27 O	27 C	28 O	28 C	29 O	29 C	30 O	30 C
	293	293.0	94	93.9	97	97.0	73	72.8	88	88.1	77	76.6	40	40.0
1	33	33.1	1	4.0	1	1.7	12	14.1	10	8.7	7	9.7	5	5.5
2	12	12.0	3	1.5	1	0.6	5	5.6	5	4.0	6	4.3	3	2.2
3	5	5.4		0.7	1	0.3	6	2.6		2.3	2	2.3	1	1.1
4	3	2.6		0.4		0.2	2	1.3	1	1.4	2	1.4		0.1
5	1	1.3		0.2		0.1		0.7		0.1	1	0.1		
6	1	0.7		0.1		0.1		0.4	1	0.1	2	0.1	1	
7	1	0.4		0.1				0.2		0.1				
8		0.2		0.1				0.1	1					
9		0.1						0.1	1					
10		0.1							1					

Station number	31 O	31 C	32 O	32 C	33 O	33 C	34 O	34 C	35 O	35 C	36 O	36 C	37 O	37 C
0	37	37.6	60	59.8	142	142.0	149	149.0	213	213.0	295	295.0	82	81.8
1	13	11.3	9	9.9	4	3.6	5	5.2	1	1.5	2	1.6	9	10.7
2	3	3.9		4.6		1.2	1	0.7	1	0.6		0.8	6	3.4
3		1.4	6	2.6	1	0.1		0.1		0.3		0.5	1	1.8
4	2	0.1	3	1.6	1				1	0.2		0.4	1	0.9
5			2	1.1						0.1	1	0.3	1	0.4
6				0.1						0.1		0.2		0.2
7				0.1						0.1		0.2		0.1
8												0.1		0.1
9											1	0.1		
10											1	0.1		

Station number	39 O	39 C	40 O	40 C	41 O	41 C
0	15	14.9	78	79.5	65	65.3
1	6	5.6	8	9.0	20	17.5
2	2	3.0	2	4.1	4	7.9
3	1	1.7	6	2.4	6	4.1
4	2	1.0	4	1.5	1	2.2
5		0.6	1	1.0	2	1.3
6	1	0.4		0.7	1	0.7
7		0.3	1	0.5		0.4
8		0.2		0.4	1	0.3
9		0.1		0.3		0.2
10		0.1		0.2		0.1

Cod are usually found in warmer water during summer than during winter, while polar cod prefer the highest temperatures during winter when they are spawning. Differences in feeding habits may also be of importance, but the available material does not allow a close analysis of this.

Only few attempts have been made to fit theoretical distributions to ectoparasites on fish. WILLIAMS (1964) used log series to describe the relationship between Copepoda and Branchiura on fish. The log series are the limiting form of the negative binomial,

Table 8. Correlation matrix for some characteristics of original and fitted negative binomial distributions. For explanation see Table 6.

	lg x	lg s^2	lg I	lg k	lg p
lg x					
lg s^2	0.936***				
lg I	0.804***	0.776***			
lg k	0.780***	0.505*	0.924***		
lg p	0.055 ns	0.400 ns	−0.233 ns	−0.582**	
lg $\frac{s^2}{\bar{x}}$	–	–	−0.249 ns	−0.505*	−0.929***

*** $p < 0.001$ △, ** $p < 0.01$ △, * $p < 0.05$ ○, ns not significant $p < 0.05$.

in which the zero observation is excluded, when $k = 0$.

BOXSHALL (1974b) studied the numerical relationship between a population of *Lepeophtheirus pectoralis* (MÜLLER) and its host population and found it to be a good fit to a negative binomial distribution. JOHANNESSEN (1975) fitted a negative binomial distribution to *Caligus elongatus* NORDMANN and *Lepeophteirus salmonis* (KRØYER) on their hosts.

CROFTON (1971) proposed the negative binomial distribution to be a fundamental model for parasite-host distributions, although he admits that many different biological situations may lead to this distribution.

The free-swimming stages of *Clavella* are very short (KABATA 1970) and will therefore not disperse randomly in the water masses. The chances that the larvae will settle on the host parasitized by the mother seem to be great, and this can cause a negative binomial distribution.

The close fit between observed and calculated frequencies, seems to indicate that the distribution of *Clavella* is not pronouncedly truncated (sensu CROFTON 1971). The difference between the second and third moment of the observed and the fitted binomial distribution may, however, indicate that heavily infected polar cod have a higher death rate than the others, and therefore are removed from the population at a higher rate.

The quantitative relationship between *Clavella* and polar cod differs in several ways from that of *Lepeophtheirus* on plaice. The most fundamental difference is possibly that $\overset{*}{x}$ and $\bar{x}$ were closely correlated in the case of *Lepeophtheirus* (see BOXSHALL 1974b), but not in *Clavella.*

In *Clavella* k ranges between 0.006 and 0.767, while the range is 0.28–9.80 in *Lepeophtheirus*. The ranges of $\bar{x}$ were 0.032–1.178 and 0.32–5.26 respectively.

PENNYCUICK (1971) fitted negative binominal distribution to *Echinorhynchus* and *Diplostomum* parasitizing *Gasterosteus aculeatus* L., and she found good correspondance between observed and theoretical frequencies. She also investigated the relationship between the parameters of the original distribution on those of the negative binomial and her results were rather similar to those from the study. For *Echinorhynchus,* however, she found no systematic difference between s^2 and pkq, while s^2 was usually greater than pkq for *Diplostomum.* For *Clavella* pkq was always greater than s^2.

It appears that *Clavella adunca* from the Barents Sea polar cod differs from other populations in the same area in size, body proportions, and preferred site of attachment. There also seems to be other ecological differences. No morphological differences could be observed in the appendages, which are usually considered to be most reliable as taxonomic characters. It therefore seems most convenient to refer the population on polar cod as *C. adunca* f. *iadda* LEIGH-SHARPE, until more data are available.

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REFERENCES

Anscombe, F.J. 1950. Sampling theory of the negative binomial and logarithmic series distributions. – *Biometrika* 37:358–382.

Bliss, C.I. & R.A. Fisher 1953. Fitting the negative binomial distribution to biological data and a note on the efficient fitting of the negative binomial. – *Biometrics* 9:176–200.

Boxshall, G.A. 1974a. Infection with parasitic copepods in North Sea marine fishes. – *Journal of the Marine Biological Association of the United Kingdom* 54:355–372.

— 1974b.The population dynamics of *Lepeophtheirus pectoralis* (Müller): dispersion pattern. – *Parasitology* 69:373–390.

Crofton, H.D. 1971. A quantitative approach to parasitism. – *Parasitology* 62:179–193.

Iwao, S. 1970. Problems of spatial distribution in animal population ecology. – Pp. 117–149 in: Patil, G. (ed.). *Random Counts in Scientific Work,* 2. University Park and London.

Iwao, S. & E. Kuno 1971. An approach to analysis of aggregation pattern in biological populations. – Pp. 461–513 in: Patil, G., E.C. Pielou & W.E. Waters (eds). *Statistical Ecology* 1. University Park and London.

Janusz, J. 1979. Occurrence of the parasite *Clavella adunca* (Strøm, 1762) (Copepoda parasitica: Lernaeopodidae) in the cod (*Gadus morhua* L.) from North Atlantic waters. – *Acta Ichthyologica et Piscatoria* 9:37–54.

Johannessen, A. 1975. Lakselus, *Lepeophtheirus salmonis* Krøyer (Copepoda, Caligidae). Frittlevende larvestadier, oppdrettsanlegg og kommersielle fangster i vestnorsk farvann 1973–74. Cand.real. thesis. Univ. Bergen, Bergen. 113 pp.

Kabata, Z. 1960. Observations on *Clavella* (Copepoda) parasitic on some British Gadoids. – *Crustaceana* 1:342–352.

— 1963a. The second antenna in the taxonomy of Clavellinae (Copepoda, Lernaeopodidae). – *Crustaceana* 5:5–14.

— 1963b. Clavella (Copepoda) parasitic on British Gadidae: one species or several? – *Crustaceana* 6:64–74.

— 1970. Crustacea as enemies of fishes. – Pp. 171 in: Snieszko, S.F. & H.R. Axelrod (eds). *Diseases of fishes.* Book 1. T.F.H. Publ., Jersey City.

Kabata, Z. & A.V. Gusev 1966. Parasitic Copepoda of fishes from the collection of the Zoological Institute in Leningrad. – *Journal of the Linnean Society. (Zool).* 46:155–207.

Leigh-Sharpe, W.H. 1925. A revision of the British species of *Clavella* (Crustacea, Copepoda) with a diagnosis of new species, *C. devastatrix* and *C. invicta.* – *Parasitology* 17:194–200.

— 1933. A second list of parasitic Copepoda of Plymouth with a description of three new species. – *Parasitology* 25:113–118.

Nunes-Ruivo, L. 1957. Contribution à l'étude des variations morphologiques de *Clavella adunca* (H. Strøm). Copépode parasite de *Gadus callarias.* Considérations sur quelques *Clavella* parasites des Gadidae. – *Revista da Faculdade de Ciencia Universidade de Lisboa* (2) (C) 5:229–256.

Pennycuick, L. 1971. Frequency distributions of parasites in a population of threespined sticklebacks, *Gasterosteus aculeatus* L., with particular reference to negative binomial distribution. – *Parasitology* 63:389–406.

Polyanskii, Yu. I. 1955. *Parasites of the fish of the Barents Sea.* Translated 1966, Israel Program for Scientific Translations, Jerusalem. 158 pp.

Poulsen, E.M. 1939. Investigations upon the parasitic copepod *Clavella uncinata* (O.F. Müller) in Danish waters. – *Videnskabelige meddelelser fra Dansk naturhistorisk forening i København.* 102:223–244.

Schram, T.A. 1980. The parasitic copepods *Clavella adunca* (Strøm), *Haemobaphes cyclopterina* (Fabricius), and *Sphyrion lumpi* (Krøyer), on Polar cod, *Boreogadus saida* (Lepechin) from Spitsbergen. – *Sarsia* 65:273–286.

Shotter, R.A. 1971. The biology of *Clavella uncinata* (Müller) (Crustacea: Copepoda). – *Parasitology* 63:419–430.

— 1973. Changes in the parasite fauna of whiting *Odontogadus merlangus* (L.) with age and sex of host, season, and from different areas in the vicinity of the Isle of Man. – *Journal of Fish Biology* 5:559–573.

Williams, C.B. 1964. *Patterns in the Balance of Nature.* Academic Press, London, New York. 324 pp.

Yamaguti, S. 1963. *Parasitic Copepoda and Branchiura of Fishes.* Interscience Publishers, New York. 1104 pp.

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