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Study of *Caligus minimus* (Otto, 1821), (Caligidae Copepoda) infections of the sea Bass *Dicentrarchus labrax* (L.) in Bardawil lagoon

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SUMMARY. *Caligus minimus* (Otto, 1821) is a common parasite of *Dicentrarchus labrax* in Bardawil Lagoon and it also occurs sporadically on *D. punctatus* in this lagoon. It has also been found on *D. labrax* which were recently established in the Gulf of Suez. The incidence as well as the intensity of infection showed a distinct pattern of seasonal variation with maximum levels during winter and early spring and lowest levels of infection during summer and early autumn. Overall infection levels also showed distinct annual variation. Occurrence of larval stages on the fish followed the seasonal pattern observed in infections by adults copepods. The highest occurrence was observed every year in May. However, at any month of the year ovigerous females, and at least a few copepodites or chalimi may be found. Spatial distribution of infection among the fish was significantly contagious and with some exceptions followed the Poisson log normal distribution. However, the magnitude of overdispersion showed distinct seasonal fluctuations, with more extreme overdispersion in summer and autumn. These fluctuations apparently resulted from the diversity of temperature and salinity conditions in the lagoon which were most extreme during the summer and autumn. Positive correlation between host size and infection was evident only in the winter and spring months with highest levels of infection in the largest fish. Female copepods usually out number male copepods. The dominance of female over males was also exident in the preadult stages.

Etude des infections à **Caligus minimus** *(Otto, 1821) (Caligidae, Copepoda) chez* **Dicentrarchus labrax** *(L.) dans le lagon de Bardawill.*

RESUME. Caligus minimus (*Otto, 1821*) *est un parasite commun de* Dicentrarchus labrax *du lagon de Bardawill et on le rencontre parfois chez* D. punctatus *dans ce*

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même lagon. Il a également été trouvé chez D. labrax *récemment introduit dans le Golfe de Suez. L'incidence et l'intensité de l'infection varient suivant la saison avec un maximum au cours de l'hiver et au début du printemps, et un minimum pendant l'été et au début de l'automne. L'intensité de l'infection varie aussi d'année en année. La fréquence des stades larvaires chez le poisson correspond à la fréquence saisonnière observée dans les infections par Copépodes adultes. La plus haute fréquence a été enregistrée chaque année en mai. Cependant on peut rencontrer pendant toute l'année des femelles ovigères, et au moins quelques copépodites ou chalimi. La distribution de l'infection chez les hôtes est du type distribution contagieuse, et, sauf exception, suit la répartition log normale de Poisson. Cependant, l'ampleur de la surdispersion présente des variations saisonnières, avec une plus grande surdispersion en été et en automne. Ces fluctuations semblent être dues aux variations de température et de salinité dans ce lagon, qui atteignent leur maximum pendant l'été et l'automne. Une corrélation nette entre la taille de l'hôte et l'intensité de l'infection n'est mise en évidence que dans les mois d'hiver et de printemps. Les Copépodes femelles sont généralement plus nombreuses que les mâles. Cette prédominance des femelles sur les mâles est également observée chez les stades pré-adultes.*

Introduction

Caligus minimus (Otto, 1821) has been reported in sea bass *Dicentrarchus labrax* (L.) from the west Mediterranean, the Adriatic Sea, the north-east Atlantic and the North Sea (data compiled by Margolis *et al.*, 1965). Paperna and Lahav (1975) reported the occurrence of this copepod in the sea bass of Bardawil Lagoon, in the eastern Mediterranean basin. Caligid copepods are among the more pathogenic ectoparasites of cultivated marine fish (Kubota and Takakuwa, 1963 ; Paperna and Lahav, 1974 ; Hastein and Bergsjo, 1976). This parasite is a potential pathogen to cultured sea bass. Sea bass are cultivated in seawater in France, Italy and Israel. Infections were reported in caged cultured fish, in Southern France (Raibaut, A personal communication).

The sea bass is a eurohaline fish which readily enters coastal lagoons and estuaries. The population of Bardawil lagoons spawns during December-February. Sea bass spawns in the sea, however, it seems that the seaward migration is not simultaneous and some fish are caught in the lagoon also during December-February months. Fry appear in the lagoon by end of February and in early March (Blaushtein, 1976, and authors observations).

The habitat :

Bardawil Lagoon (the Sirbonian Sea) on the Mediterranean coast of Sinai Peninsula is a 650 km^2 perennially hypersaline water body with an average depth of about 1.1 m (*fig. 1*). The lagoon is interconnected with the sea through one natural and two man-made channels, constantly tended to avoid silting. Hydrographical data on the lagoon are fragmentary and are available only from annual reports (Roth, 1973 ; Ben Tuvia and Gilboa, 1974, 1975 ; Ben Tuvia, 1978). Seawater salinities off the Mediterranean coast of Israel are 38-39 ppt (Oren and Hornung, 1972 ; Roth, l.c.), while in the lagoon there is a clear gradient of increasing salinities from 38-42 ppt in the opening zone to 50-80 ppt in the inner sectors and up to 100 ppt in the most distant corners of the lagoon.

Salinities fluctuate within a range of 10-15 ppt between lowest values, at winter (February, March) to highest values during summer and autumn (August-October). During the latter season in some sectors of the lagoon there is also a distinct horizontal stratification with up to 20 ppt gradient. Climatic variations as well as the changing conditions of silting in the channels result also in annual variations in the overall salinity levels in the lagoon (*fig. 2*). Water temperatures fluctuate from 10-16°C in January to 28-34°C in July-August (*fig. 3*). These temperatures are far more extreme than in the nearby sea (16-17°C to 27-28°C, Oren and Hornung, l.c.). Dissolved oxygen levels demonstrated distinct seasonal fluctuations, with lowest recorded levels in summer and highest in Winter. Summer decline was more evident in the more inland sectors of the lagoon (*fig. 4*). Nevertheless, dissolved oxygen levels, 3-11 ppm/litre, are maintained throughout the seasons at close to saturation levels (88-98 %) with occasional oversaturations (up to 165 %) and with only rare declines below saturation (60 %). This is in spite of the prevailing eutrophic conditions, high salinities, and high summer temperatures.

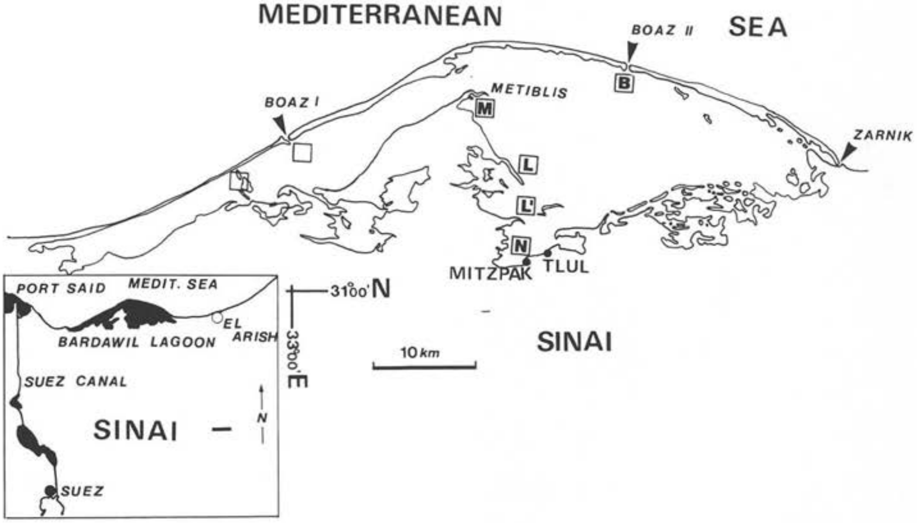

Fig. 1. Map of Bardawil Lagoon in north Sinai Peninsula.
Hydrographic sampling stations in squares.
B : « Boaz II ». L : « Lashon II ». L' : « Lashon I ». N : « Nahal Yam ». M : Metiblis.

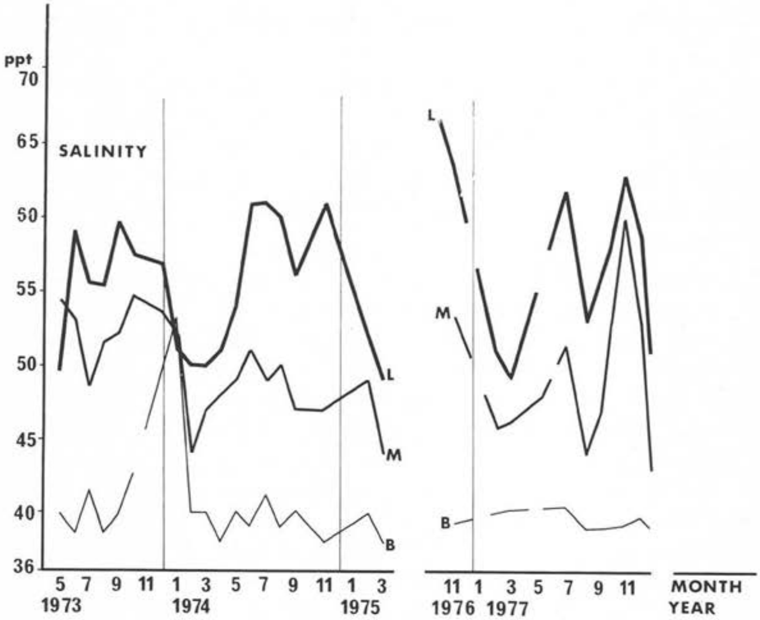

Fig. 2. Seasonal and annual fluctuation in salinity levels in three sampling stations in Bardawil Lagoon. B : « Boaz II ». L : « Lashon II ». M : Metiblis. (Data for late 1975 and 1976 are not available) (compiled from data of Ben Tuvia and Gilboa, 1974, 1975 and Ben Tuvia, 1977).

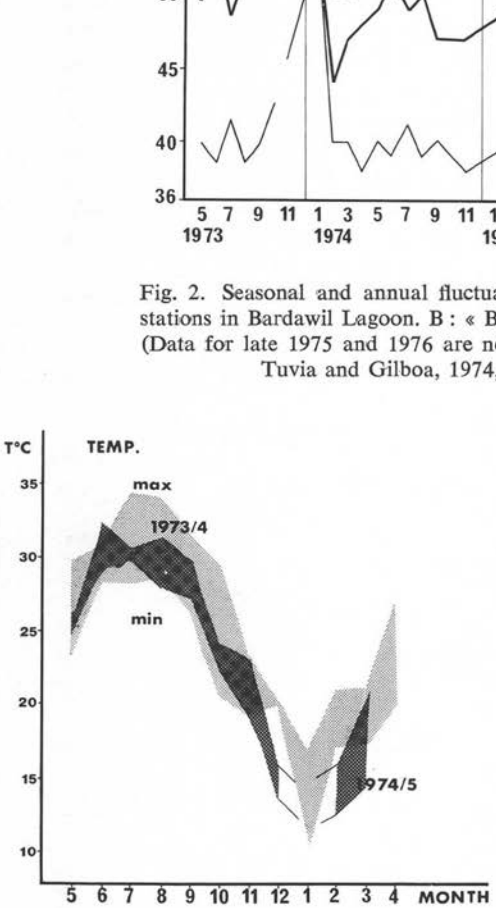

Fig. 3. Seasonal fluctuations in temperature in Bardawil Lagoon. Minimum - maximum levels from all sampling stations (see *fig. 1*). (Measurements were discontinued after May 1975) (compiled from data of Ben Tuvia and Gilboa, 1974, 1975).

Fig. 4. Seasonal fluctuation in dissolved oxygen values (in mg O_2/Lit.) for 1973-4. Sampling programme was discontinued after May 1974 (compiled from data of Ben Tuvia and Gilboa, 1974).

Methods (1)

For this study, fish were taken randomly from catches landed at the fishing station at Tlul. Samples were obtained from March, 1974 to September, 1976 with an additional sample in February, 1977. Altogether 480 fish were studied from 17 samples. Part of the collected fish were examined macroscopically. Only adult and subadult copepods could be counted by this method. Other fish were preserved in formalin 4 % for microscopic examination in the laboratory for recovery of adults as well as larval copepod stages. Sample size was limited by availability of fish in some seasons, but in certain seasons also by the marketing price of the fish. Fish size was determined by fork length (FL). Collected copepods were sorted by sex and stage of development.

Infection levels were recorded for each sample in terms of (*a*) incidence : % of infected fish in the sample and (*b*) intensity of infection : mean number of parasites per fish (x*t*) and mean number of parasites per infected fish (x*i*). The spatial distribution of the copepod infection among the fish was tested for agreement with poison distribution, by variance to mean ratio (Index of dispersion = I) when departure from unity was tested by X^2 test. The Morisita index of dispersion was employed for selected samples. Agreement with negative binomial distribution was tested by T statistic with moment estimate of k (Elliot, 1971).

Agreement with Poisson log normal distribution (Cassie, 1962) was tested by the significance (by X^2) of the proximity to unity of the variance to mean ratio of the ln $(x+1)$ transformed data (I*ln*).

Agreement with negative binomial and Poisson log normal distribution was also tested by X^2 test for « goodness of fit » of observed to expected values in each frequency class. However, this procedure could only demonstrate a general trend and was of limited accuracy in view of the small sample size usually available.

The overdispersed distribution of the infection was evident in all samples, mean (derived mean) and confidence intervals (Clt-95 %) were therefore computed from counts of parasites per fish, transformed to $\ln(x+1)$. Student t-test, as well as correlation and regression were computed from $\ln(x+1)$ transformed data. The validity of the $\ln(x+1)$ transformation was tested by Taylor's Power Law (Elliot, l.c.).

Seasonal changes in sample variance were demonstrated by the coefficient of variability, $C = 100\,SD/xt$.

Results

Data on host and distribution range in Near East waters.

In addition to sea bass (*D. labrax*), *C. minimus* also occurred sporadically in the spotted sea bass (*D. punctatus*) in Bardawil Lagoon : of 18, 180-315 mm long fish examined on 18.7.74 two were infected by copepods (1 F, 1 M and 1 F respectively) ;

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(1) Numerical data to figures 5 and 8 are deposited in authors laboratory and are available on request.

12 fish examined on 10.1.74 and 11 on 28.5.74 were all negative. Prevalence of infection of the sea bass at the same dates was 100 % and 58 % respectively. *C. minimus* was also found in the sea bass from the Mediterranean coast of Israel : heavy infection with both M and F copepods as well as larval stages was found on 430 mm long sea bass landed at Akkco (on the 23.3.76). Sea bass and spotted sea bass were recently also found in the Gulf of Suez : from a specimen of sea bass (*D. labrax*) caught in El Bilaim Lagoon on the 30.8.76 in the Suez Gulf 14 M and 13 F *C. minimus* were recovered as well as a few specimens of *Lernanthropus krøyeri*, v. Beneden, a common parasite of both sea bass and spotted sea bass in the Mediterranean, including Bardawil Lagoon. The two specimens of spotted sea bass (*D. punctatus*) caught in El Bilaim Lagoon in 1970, were only infected with *L. krøyeri.*

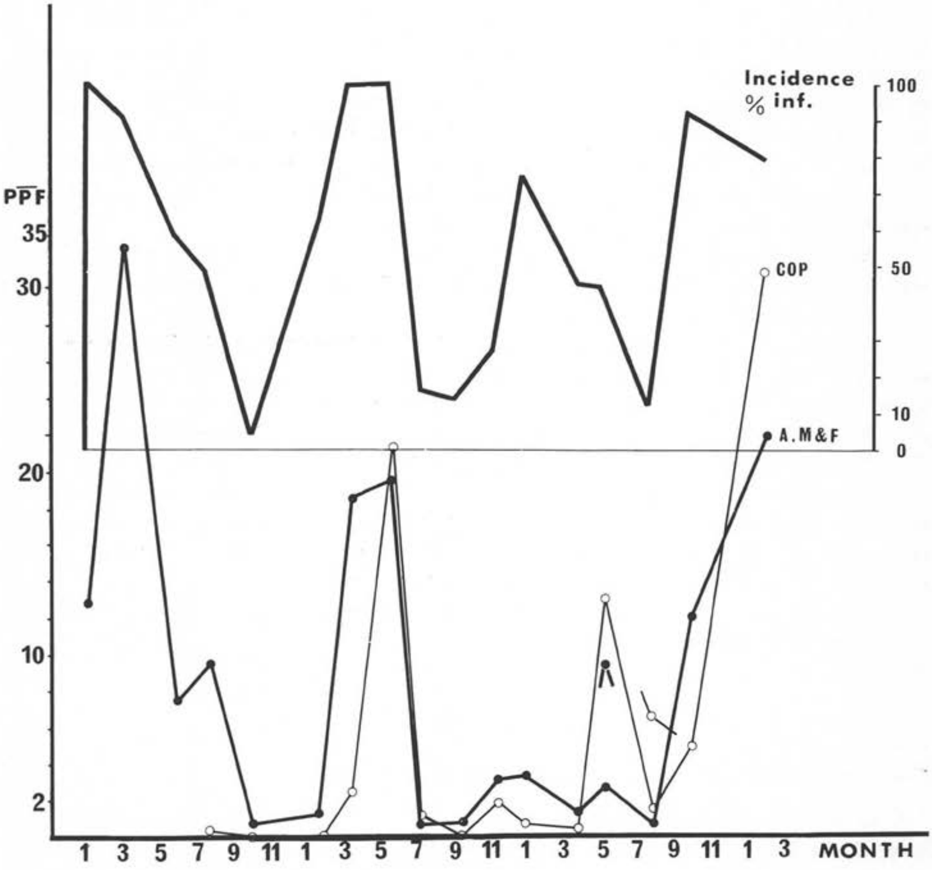

Fig. 5. — Seasonal fluctuation in the incidence of adult copepods and intensity levels (mean no. of parasites per fish) per sample of adult and larval *Caligus minimum* infection in *D. labrax* in fish landed at Tlul, Bardawil Lagoon. A.M and F : adult male and female copepods. COP : Copepodites. Disconnected points : infection levels in subsamples from different landings.

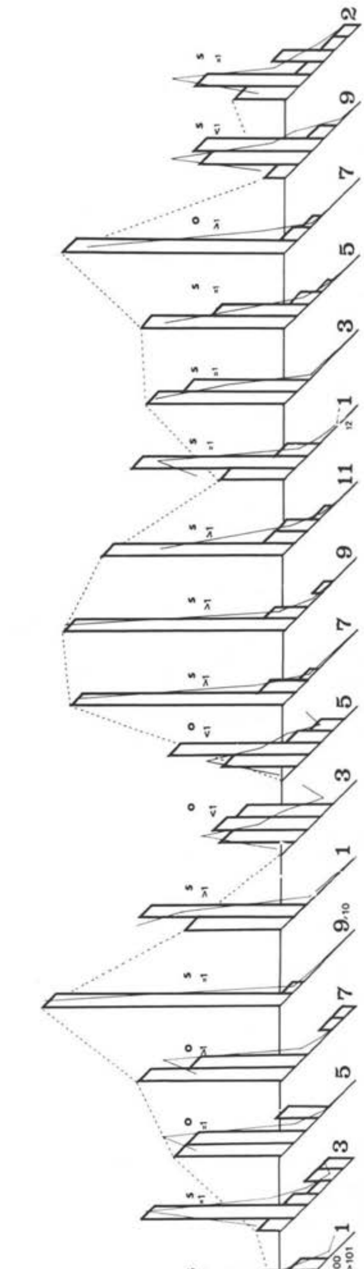

Fig. 6. — Relative frequency (RF) distribution of *C. minimus* in *D. labrax* landed at Tlul (p.p.f.: parasites per fish). s : significant « goodness of fit » (by X^2 test) with Poisson log normal distribution. o : « goodness of fit », not significant. < 1, $= 1$, > 1 : log variance to log mean ratio (I*n*) smaller, equals or higher than unity (by X^2 test). Distribution of the expected values of Poisson log normal distribution are represented by the narrow line graph. Dotted line unites the negative infection values of the samples.

Site of attachment on the host.

Adult copepods, of both sexes were found attached to the mucus integument of the mouth cavity. Parasites were only rarely found attached to the inner opercular integument and were never found on the gill filament or the skin. Larval stages — copepodites and chalimi — were found attached predominantly to the dental plates on the roof of the mouth, as well as to the gill arches among the gill rackers. Copepodites may also be found in other parts of the mouth cavity. However, attachment of the chalimus by the frontal filament appears to be effective only on dental and bony substrate.

Seasonal variation in the abundance and dispersal of infection by adult copepods.

Incidence as well as intensity of infection showed a distinct pattern of seasonal variation with maximum levels during winter and early spring and lowest levels of infection during summer and early autumn (*fig. 5, 6*). However, the magnitude of infection and the amplitude of the seasonal changes fluctuated considerably from year to year within the limited duration of our three year study. In 1976, infection levels were considerably lower than in the preceeding years of 1974/75, but unlike in previous years summer decline was brief and heavy infection was observed in fish already in September. The incidence (prevalence) values and amplitude showed on the other hand the least annual fluctuations and so were the computed values of the coefficient of variation (*fig. 7*) which were affected by the proportion of negative fish in the sample (this seasonal fluctuation pattern is however lost when coefficient of variation was computed from infected fish alone). Irrespective of season, contagious, or overdispersed distribution of the infection among the fish was evident in all samples.

Departure from randomness was demonstrated by the significantly (by X^2 test) higher than unity variance to mean ratio and by the Morisita index test. In all samples agreement with the negative binomial distribution was rejected at the 95 % probability level.

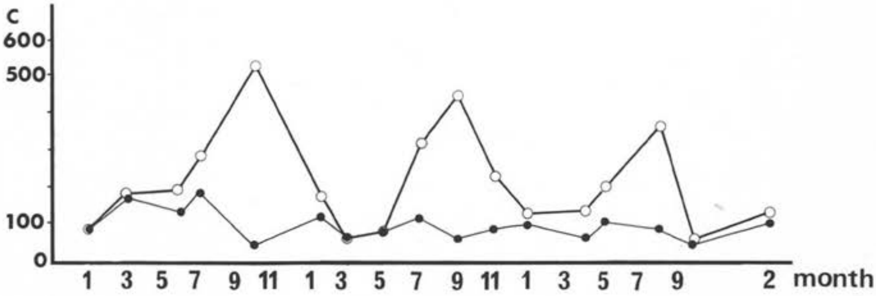

Fig. 7. Seasonal fluctuation of the computed values of coefficient of variation of infection of the samples. Dark dot : computed from all fish of the samples. Circle : computed only from the infected fish in the sample.

Taylor's Power Law parameter of 2 for log normal distribution was within the 95 % confidence limits of 1.24-2.02, computed from the samples data (from a regression line $\ln Y = -0.65 + 1.63 \ln X$).

Agrement with unity e.g. with the Poisson log normal distribution (at 95 % probability level by X^2 test) of variance to mean ratios of the log transformed data $(\ln + 1)$, was obtained in 8 out of 17 samples studied. X^2 test for goodness of fit of Poisson log normal distribution of expected frequencies to observed data yielded significant fit in 13 out of 17 samples, including samples showing significant departure from unity by log variance to log mean ratio test (*fig. 6*). However, in view of the relatively small samples to accuracy of the latter test is doubtful and discrepancies should be expected. Nevertheless, the computed indices of dispersion from the variance to mean ratio of the log transformed data (I*ln*) were found to be adequate parameters to demonstrate seasonal changes in the distribution of infection among fish in the samples. I*ln* values measuring dispersal pattern gave good measures of both prevalence and intensity of infection (*fig. 8*). I*ln* value approximated unity, or even declined below unity in heavily infected samples taken during January-May. In samples taken during July-September, or even November when infection is low or sporadic I*ln* value rose significantly above unity (approximating 2).

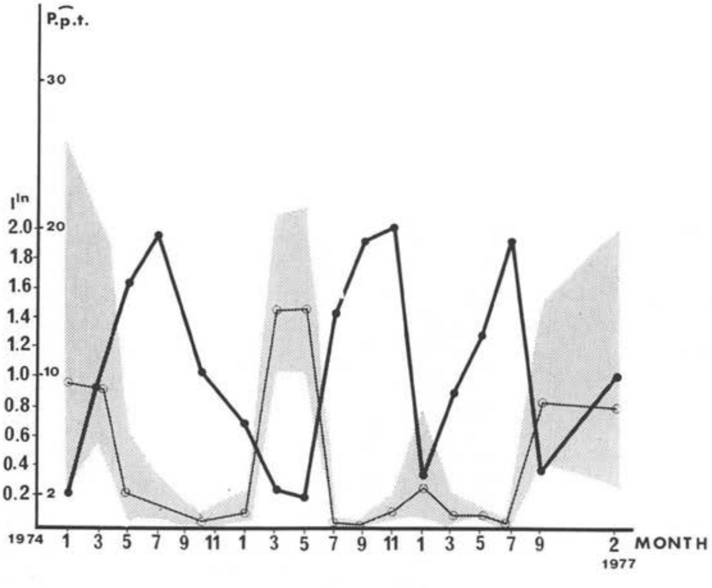

Fig. 8. Seasonal fluctuation in the computed sample I*ln* levels (log variance to log mean ratio) of the intensity of infection. Bold line : I*ln*. Narrow line : derived mean. Shadowed area : 95 % confidence limits for the derived mean.

Other factors affecting spatial distribution of copepods.

Sample site :

Differences in infection levels, incidence as well as intensity were noted between groups of fish obtained from catches landed by different fishing boats at the same sampling date (*Table I*). Each fishing boat usually operated in a specifically allocated sector of the lagoon.

Table I. *Differences in infection levels among fish landed by different fishermen groups at the same sampling date*

X_t mean parasite number per fish

X_i mean parasite number per infected fish

Sampling data	Group	Fish no.	Fish length	Prev. %	$X_t \pm SD$	$X_i \pm SD$
2.5.76	A	11	304 ± 54	18	0.27 ± 0.64	1.50 ± 0.70
	B	12	286 ± 57	91	8.25 ± 7.36	9.58 ± 7.17
	C	11	250 ± 35	9	0.27 ± 0.90	3 (1 fish)
	D	21	360 ± 78	47	2.00 ± 4.38	4.20 ± 5.69
20.7.76	E	20	366 ± 94	0	0	0
	F	23	298 ± 178	21	1.36 ± 6.59	6.60 ± 6.10
3.2.77	G	10	287 ± 36	80	8.10 ± 9.62	10.12 ± 9.77
	H	5	359 ± 69	80	49.00 ± 42.20	61.25 ± 37.07

t-tests : (*a*) fish length groups A/B = 0.77 ($p > 0.5$), B/D = 2.87 ($p < 0.5$), E/F = 1.52 ($p > 0,5$), G/H = 2.81 ($p < 0.5$).

(*b*) infection levels (X_t) A/D = 1.28 ($p > 0.5$), B/D = — 2.16 ($p < 0.5$), C/D = 1.28 ($p > 0.5$), G/H = 3.01 ($p < 0.5$), (X_i) B/D = 1.67 ($p > 0.5$).

Since most samples consisted of fish randomly obtained from all landings at the particular day of sampling the overdispersion in infection distribution observed in the samples could be attributed to the disparity in levels of infection between fish of the different landings. However, contagious distribution was evident even when fish of each landing were separately analysed.

Disparity in infection levels of fish from different landings of the same size range could be extreme, with incidence varying from 9-91 % and intensity of 1.5 to 9.58 parasites per fish (in May, 1975).

Size of fish factor however should not be overlooked. Differences in infection level between some landings also coincide with significant differences in fish sizes.

Relationship between host size and infection :

Copepods were absent from all 22 examined fingerlings, smaller than 50 mm in length (FL). Young of the year, 50-170 mm long fish were absent from our samples.

In the few fish occasionally checked from this size group infection was either absent or extremely low. In all other size groups, from 170 to 720 mm FL, incidence of infection increased significantly in the larger size classes (*fig. 9*). X^2 test departed significantly from homogenicity ($X^2 = 24.57$, = d.f. 7 p. $\leqslant 0.01$). Incidence of infection was above expected in the largest age classes (451-720 mm FL), and below expected in the smallest age classes (smaller than 250 mm FL). The relationship between host size and intensity of infection was tested in individual samples, by linear correlation. A significant positive correlation (at 95 %, and in many samples even at 99 % probability level) was usually only found in samples taken in May and July of every year, and in some years also the January and March samples, as well as the February, 1977 sample (*fig. 10*). In samples with a low level of incidence the relationship between host size and infection per individual samples was tested by t-test for significance of the difference in size (FL) distribution between infected and non-infected fish. Results confirm the trend observed above, of significant preference for infection in the larger fish in May-July samples.

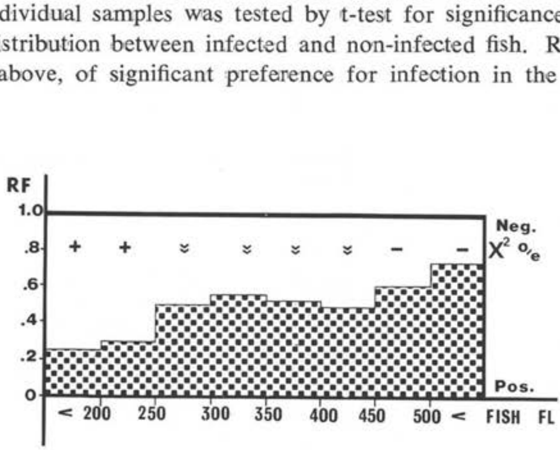

Fig. 9. Distribution of infection incidence in fish of different size classes. X^2 o/e : X^2 test for homogenicity. + : observed no. of negative fish is significantly higher than expected. — : observed no. of negative fish is significantly lower than expected. = : differences are insignificant.

In July samples the difference in infestation level between fishes of different size classes was particularly evident. While a gradual decline of infection was already evident by increasing numbers of fish in the sample free from infection, as well as overall decline in copepod numbers encountered per fish, heavy infection seemed to persist in the very large fish, 550-720 mm in length, of estimated age of 5-7 years. In these fish, infection load ranged from 30 to 110 copepods per fish and was also accompanied by numerous larval stages — copepodites as well as chalimi.

Sex ratio among copepods.

Female copepods generally outnumbered males (*Table II*). Although, on individual fish occasionally males outnumbered females. Calculated mean female-male ratio on

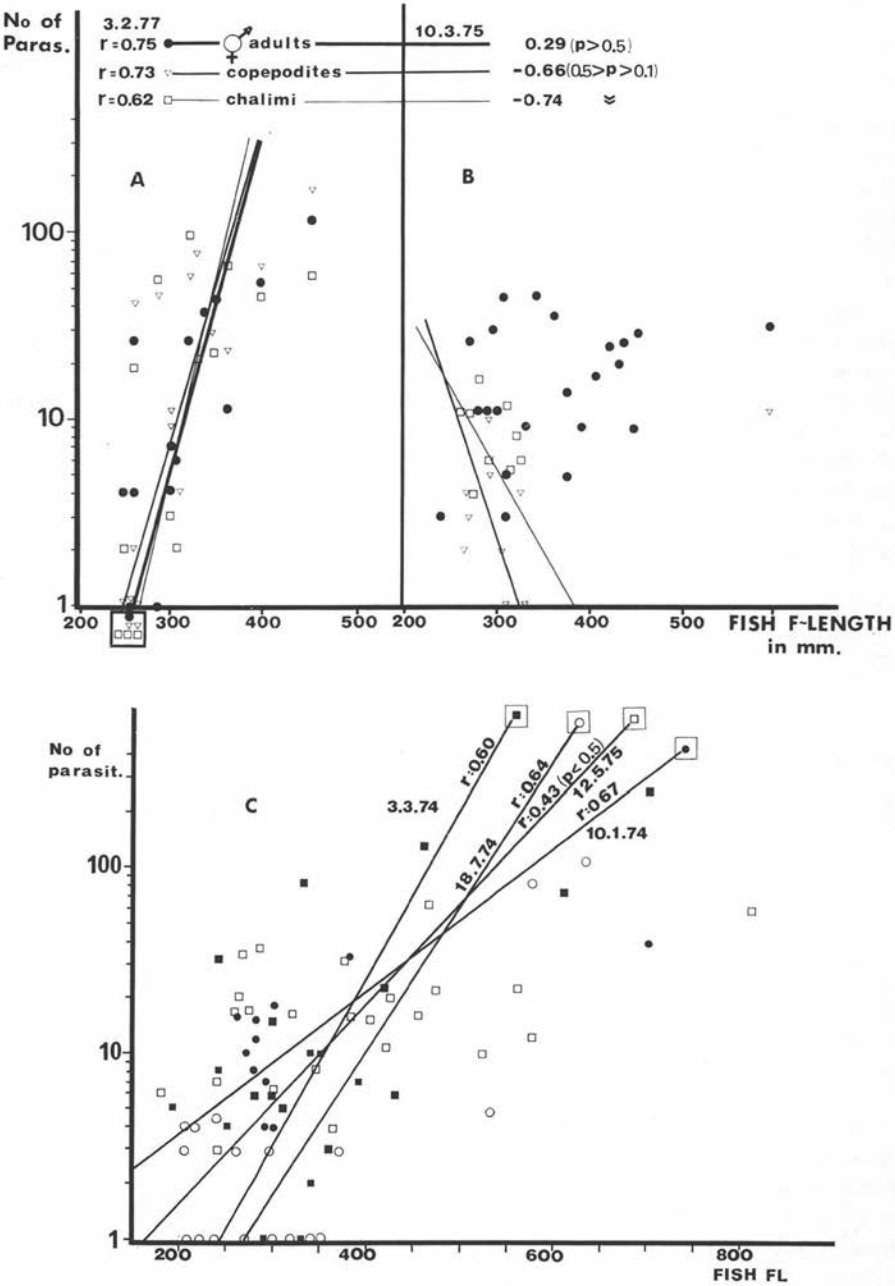

Fig. 10. Correlation between fish size (fork length) and no. of parasites infecting the fish. A. Sample of 3-2-77 ($n = 15$). Adult copepods: $y = 250.68 + 27.55 \ln X$. Copepodites: $y = 250.85 + 23.59 \ln X$. Chalimi: $y = 262.65 + 21.86 \ln X$.

B. Sample of 10-3-75, n (adult) $= 24$, n (copepodites and chalimi) $= 9$. Copepodites: $y = 317.41 - 27.58 \ln X$. Chalimi: $y = 386.38 - 51.46 \ln X$.

C. Adult copepods only. Sample of the 10-1-74: $y = 55.17 + 110.93 \ln X$ ($n = 13$); 3-3-74: $y = 242.88 + 47.47 \ln X$ ($n = 21$); 18-7-74: $y = 265.43 + 56.38 \ln X$ ($n = 23$); 12-5-74: $y = 166.37 + 79.37 \ln X$ ($n = 24$).

individual fish per samples (with one exception of December, 1975), was above unity (ranging from 1.15 to 3.80) and the overall mean from all samples was 2.14 (± 0.79). Similarly 95 % confidence limits of 0.89-2.63 for a mean of 1.74 was obtained for sex ratio of copepods infesting individual fish analysed from a random sample of 115 fish. Female predominance becomes even more evident when sex ratios are calculated from the overall crop of copepods collected from all fish per each bimonthly sample. In a random sample of 115 fish, a significant linear correlation (at 95 % probability level) could be demonstrated between female male ratio and the infection intensity level per individual fish (with 95 % confidence limits between 0.32 to 0.59 for computed $r = 0.47$). When overall sex ratio per sample was tested and correlated to the sample's mean intensity level of infection per fish, the correlation was below the 95 % significance level of acceptance (coefficient of determination $r^2 = 0.33$, from 17 samples). An increase in disparity between females and males was nevertheless evident throughout the 3 years study period in samples from either March or May. Thus, there is some evidence of a relationship between the male female ratio and seasonal fluctuations in infection. However, annual changes in overall sex ratio of the copepods were more pronounced than the seasonal fluctuations. Observations in the laboratory suggested that mature males and females are capable of resettling on new hosts. Sex ratio of premature copepods (5th stage chalimi, already differentiated sexually) per individual sample was 1.40 (± 0.80), or 1.27, for overall collected chalimi.

Table II. *Female/male ratio among copepods infecting sea bass (mean ratio and standard deviation ; n.a. - not applicable) and ratio of ovigerous females*

Date	Female - Male Ratio		
	Ratio per individual fish in each sample	Ratio for the total sample	% of females with egg sacs
10.1.74	2.20 ± 2.20	1.82	68 %
3.3.74	n.a.	n.a.	69 %
28.5.74	2.71 ± 3.10	3.80	61 %
18.7.74	2.10 ± 1.61	3.33	54 %
2.10.74	n.a.	3.00	2/3
20.1.75	1.37 ± 2.32	2.20	63 %
11.3.75	2.48 ± 1.76	2.17	65 %
12.5.75	2.88 ± 1.63	3.03	53 %
6.7.75	1.10 ± 1.03	1.15	57 %
8.9.75	1.80 ± 0.44	1.50	38 %
10.11.75	1.38 ± 1.46	1.50	82 %
23.12.75	1.00 ± 1.13	1.16	72 %
23.3.76	1.80 ± 1.92	2.50	80 %
2.5.76	1.80 ± 1.33	1.82	59 %
20.7.76	1.96 ± 1.22	2.30	47 %
22.9.76	1.77 ± 0.93	1.73	49 %
3.2.77	2.47 ± 2.08	2.83	45 %

These sex ratio values were somewhat lower than that of adult copepods obtained from the same fish (2.51 ± 1.49, with an overall value of 2.19). However, the significance of differences could not be confirmed by t-(dependent and independent) tests.

Seasonal abundance of ovigerous females.

Throughout the 3 years study period ovigerous females were present in all samples, in which fish were found infected, irrespective of the season. The percentage of females carrying egg sacs in the different samples ranged from 48 % to 82 %, with no correlation to the season during which the sample was taken (*Table III*).

Seasonal variation and dispersal pattern of larval copepods.

Copepodites, chalimi, or both, were present in samples taken at all seasons, but their abundance showed distinct seasonal variation (*Table III, fig. 5 and 11*). The highest number of copepodites, as well as chalimi were counted every year in May. A high level of infection was also observed in a sample taken in Frebruary, 1977 (and 1978). However, samples from earlier Februaries are not available, while levels of infection by larval copepods in January and March samples ranged from low to moderate. In samples taken during summer and autumn, infection by larval stages was generally low or occasionally even absent. Infection levels by larval copepods irrespective of the season closely followed infection levels by adult copepods. Thus, fish in the September, 1976 sample with an overall high infection level were also infested by large numbers of copepodites and chalimi, while winter samples with overall low numbers of adult copepods were infested with only a few larval stage copepods. In July samples the heavy infection by adult copepods was restricted to the very large fish of the sample (over 550 mm FL) and was accompanied by moderate or high infection by larval copepods. In the remaining smaller fish, infection by adult as well as larval copepods was low or absent altogether.

Larval stages with few exceptions (3 out of 480 examined fishes) were absent from fish not infected by adult copepods. This occurred irrespective of the season and the overall infection levels found in the other fish of the sample.

On the other and positive correlations (at 95 % probability level) between numbers of copepodites and adults infesting individual fish were evident only in 5 out of 8 samples and in neither of the May samples (*fig. 10*). Significant positive correlations between adults and copepodites as well as between chalimi and copepodites were found evident in 4 out of 8 samples. Correlations between numbers of chalimi and copepodites per individual fish were evident in 5 out of 9 samples including one of the May samples.

During the peak months of larval infection (e.g. February and May) larval copepods outnumbered adults and copepodites outnumbered or equalled that of chalimi (*fig. 11*). Inverse relations were evident in months of lower infection levels. Adult copepods then outnumbered the larval stages and chalimi usually outnumbered copepodites. During these months however larval infection was sometimes also found to consist entirely of copepodites (July 1976). These adult-larvae relationships were evi-

Table III. *Fish host sizes, incidence and intensities of infection by larval stages of* Caligus minimus *in samples taken during 1974-1977 in Bardawil Lagoon. * Calculated from the 5 only infected (500 mm FL) fish in the sample*

Sampling date	Fish no.	Copepodite infections per fish Mean (X_t)	Derived mean	95 % confidence limit	Chalimi infections per fish Mean (X_t)	Derived mean	95 % confidence limit
18.7.74	12	0.25	0.12	0 - 0.41	1.83	0.33	0- 1.39
2.10.74	47	0	0	0	0	0	0
20.1.75	8	0	0	0	0	0	0
10.3.75	9	2.44	1.70	0.56- 3.61	7.80	7.28	4.75-16.10
12.5.75	13	21.15	10.24	3.75-25.75	11.46	8.02	4.47-13.87
6.7.75	7	1.00	0.53	0.0 - 1.97	1.85	1.01	0.07- 3.57
8.9.75	13	0	0	0	0	0	0
10.11.75	9	2.00	0.47	0.0 - 2.06	1.57	0.87	0.0 - 3.48
23.12.75	11	0.90	0.73	0.28- 1.33	0.81	0.50	0.07- 1.11
23.3.76	11	0.45	0.23	0.0 - 0.69	0.72	0.50	0.07- 1.11
2.5.76	12	13.00	7.33	3.39-14.79	13.25	7.24	3.05-15.77
20.7.76	25	1.36	0.10	0.0 - 0.29	0.20	0.06	0.0 - 0.13
	5 *	6.80	1.31	0.0 -14.18	1.00	0.76	0.0 - 2.49
22.9.76	12	5.00	3.43	1.88- 5.82	11.75	6.84	3.61-12.32
3.2.77	15	34.80	11.93	3.95-32.78	24.26	8.20	2.52-23.04

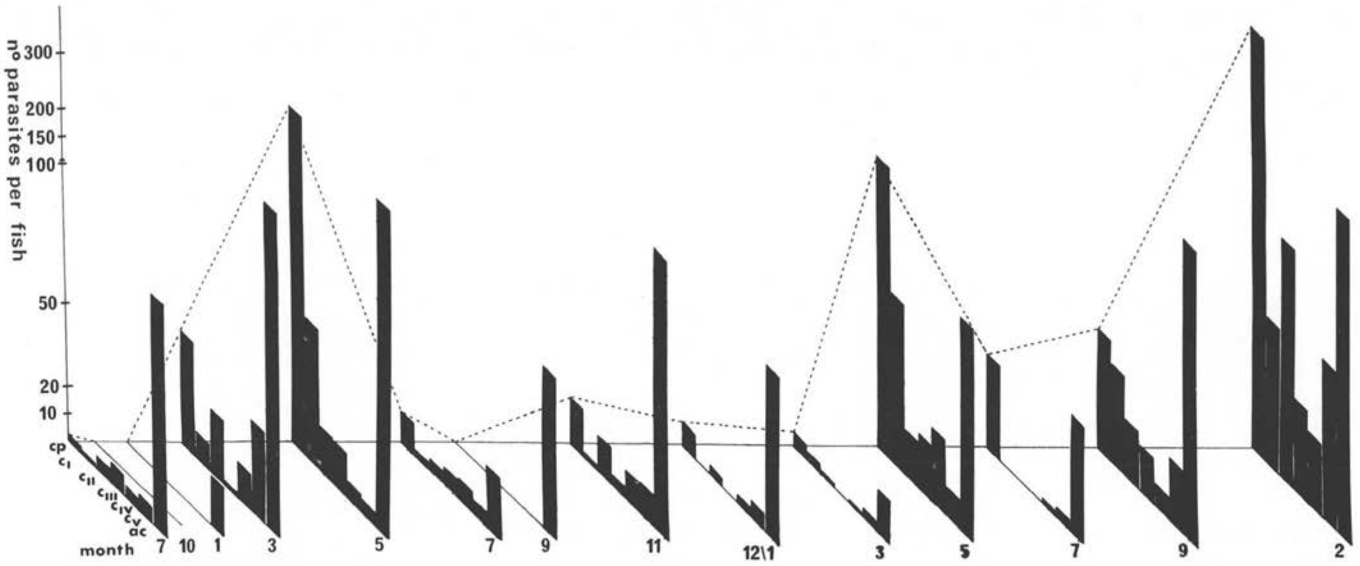

Fig. 11. Frequency distribution of the occurrence of larval copepods of different stages in the fish. cp : copepodites. cI : first stage chalimus. cII-V : second to fifth stage chalimi. ac : adult copepods.

dent only when age class distribution was analysed for copepods collected from the entire sample. However, when copepod populations of individual fishes of the sample were analysed these relationships were less evident, or were even non-existent.

The distribution pattern of the different developmental stages in each sample suggest the existence of several cohorts, e.g. repeated waves of infestation rather than a continuous settlement of larvae. However, accurate quantitative evaluation was not feasible from samples taken at bimonthly intervals.

The pattern of copepod larvae dispersal among individual fishes in each sample was of a similar pattern to that observed in adult copepods. Overdispersed distribution of infection of copepodites as well as chalimi was evident in all samples irrespective of the season. Agreement with Poisson log normal distribution, e.g. ratio variance to mean of ln transformed data (I*ln*) approximates unity, was evident in 7 out of the 12 copepodite and chalimi samples. This I*ln* parameter, like the case of adult copepods was also an efficient parameter to demonstrate seasonal fluctuation, e.g. demonstrating decreasing values (even significantly below unity) during peak occurrence season and increasing values coinciding with seasons when larval stages are rare.

Discussion

The highest levels of infection by *Caligus minimus* in sea bass of Bardawil Lagoon appear to occur in the winter and spring months and the lowest in the summer and autumn. This is in contrast to infections of fish by ectoparasites in northern latitude waters where their maximum abundance occurs during spring and summer and minimum abundance during the winter months (Gnadeberg, 1949 ; Bauer, 1959 ; Boxshall, 1974). These seasonal changes in infection levels of sea bass coincide with the fluctuating hydrographic conditions in the lagoon, which range between high temperatures (28-34°C), lower oxygen levels (3.6-5.7 mg/lit) and extreme hypersalinity (50-70 ppt) during the summer and early autumn months to low temperatures (10-16°C), higher oxygen levels (5.2-9.5 mg/lit) and moderate hypersalinity (43-55 ppt) during the winter.

In an inland lake in Tunis increase in salinity was suggested as the cause of depletion of infection in *Mugil cephalus* by *Ergasilus nanus* (Raibaut *et al.,* 1975). In Bardawil Lagoon temperature rather than salinity levels appear to be the more important factor affecting infection levels in sea bass. However, changes in infection levels are more likely to be determined by a complex of interacting a-biotic and biotic factors. Values of temperatures and salinities in the lagoon are also subjected to considerable annual variation (Ben Tuvia and Gilboa, 1975 ; Ben Tuvia, 1978), which apparently might be the cause of the observed annual changes in infection levels. In the laboratory. salinities above 55 ppt were detrimental to adult copepods, as well as to the free swimming stages of nauplii and copepodites in *in vitro* experiments (Paperna, 1977 and unpublished data). A temperature of 34°C was the upper tolerance limit for nauplii and free copepodites. Bauer (1959) reported that in parasitic copepods (*Ergasilus seiboldi*) temperatures above 30°C have a detrimental effect on the eggs, this effect was not checked in *C. minimus*. Survival and life span of nauplii was not affected by temperatures below 30°C, but their tolerance to salinity was apparently lowered particularly at temperatures approximating 30°C. At 15°C some naupliis survived even 60 ppt. The life span of the free copepodites which are the parasite's infective larva was temperature dependent, decreasing with the increase in temperature from 13 days in 15°C to 4 days in 29°C. The life span was further reduced when the rise in temperature was coupled to an increase in salinity from 30-40 to 50 ppt (Paperna, 1977 and unpublished data). No data are available on the effect of oxygen levels on *C. minimus* larval stages.

Occurrence of larval stages on the fish followed the seasonal pattern observed in incidence and intensity of adult copepod infections in fish. Thus, winter and spring conditions appear to be more favourable for transmission of infection, since the life span of the larval infection is extended and consequently the probability of successfully finding the fish host is increased. The high occurrence in May is however somewhat enigmatic since in some years, by May, temperatures in the lagoon may rise above 25°C.

Parameters measuring variability and spatial dispersion of infection among fishes demonstrated distinct seasonal patterns, and furthermore appeared to be less subjected to annual variation. Overdispersion measured by variance to mean ratio of log transformed data and coefficient of variation demonstrated regular seasonal amplitude, with peaks during summer and early autumn, when infection in the fish was on the decline. Increase in the magnitude of the overdispersion of the infection coincides with the increase in diversity of hydrographic conditions in the lagoon, particularly due to horizontal and vertical stratification of the water salinities in the lagoon during the summer and early autumn months (Roth, 1973 ; Ben Tuvia and Gilboa, 1975). Thus, during the summer months when conditions are generally unfavourable for transmission, prevailing temperatures below 30°C and salinities below 50 ppt in the deeper water zone and in the vicinity of the openings still facilitate effective transmission. In a diverse environment like Bardawil Lagoon, probability of infection is likely to be affected by the habitat preferences of the fish host. The mode of dispersal of infection among fishes will therefore result from the pattern of distribution of fishes among different habitats. Such distribution is affected by changes in schooling behaviour, migratory pattern or segregation to age classes. Fish of different ages are likely to have different habitat preferences.

Changes in infection levels and pattern of spatial distribution of infection in relation to the above mentioned factors were discussed by Boxshall (1974 *a*), Rawson (1977) and Tedla and Fernando (1970).

The occasionally extreme differences in infection levels found between groups of fish landed by different boats, presumably fished from different sectors in the lagoon apparently illustrates the combined effect of fish behavioural pattern and the environmental diversity. Differential distribution of infection along age classes has been reported by Tedla and Fernando (1970) from yellow perch infections by *Ergasilus confusus* in Lake Ontario, Canada, and *Mugil cephalus* infections by *Ergasilus nanus* in an inland lake in Tunis (Raibaut *et al.,* 1975). In the sea bass of Bardawil Lagoon a significant relationship between host length and the level of infection was observed only in May and July and in some of the winter month samples. Heavy infections in fish in July, were restricted to the largest size class fishes (about 500 mm FL), while in all other fish infection was low or absent. The differential distribution during the winter months when overall infection levels were high could be the result of the apparent segregation of the fishes of the lagoon to age classes during and after returning from spawning migration, rather than to the difference in habitat preferences of fish of different ages, since the conditions in the lagoon during the winters are relatively homogenous. Seaward migration may dilute infestation. However, heavy infection was also found in fish from the sea, as well as in spent fish near the opening to the sea. In May samples this segregation apparently still persists, but also the heterogenicity of the environment becomes more apparent. Seasonal changes in distribution of infection along age classes in relation to breeding seasons and migration were observed also in plaice infected by *Lepeophtheirus pectoralis* (Boxshall, 1974 *a*). The differential distribution of infection became more apparent outside the breeding season, while during the breeding season infection tended to be homogenously distributed.

Overdispersed distribution has been proposed as a characteristic feature of host parasite relationship (Crofton, 1971). The negative binomial distribution model was used to describe the dispersion pattern of some fish parasite populations (Pennycuick, 1971), including caligiids (Boxshall, 1974 *a*). The overdispersed distribution of *C. minimus* in sea bass which was evident in all samples, did not agree with the negative binomial model. On the other hand, log normal distribution (Cassie, 1965) was found to be a useful model to describe parasite dispersal pattern among fishes. Moreover, discrepancies from this model were employed to monitor seasonal variation in infection pattern. Decline in parasite abundance and increase in number of negative fish resulted in an increase in the overdispersion index of infection. Seasonal changes in pattern of dispersal of infection among fish were also evident in *Lepeophtheirus pectoralis* infections in plaice (Boxshall, 1974 *a*).

Sex ratio of adult copepods, as well as preadult chalimi was characterized by predominance of females over males. This ratio might well be a biological feature of caligiids in general. Same female predominance was observed in *L. pectoralis* (Boxshall, 1974). In *L. pectoralis* an increase in female to male ratio after October after the copepod breeding season suggested high male mortality following copulation. In *C. minimus* the highest discrepancies between female and male numbers were observed during the peak of the reproduction season in February and May. An increase in male ratio towards the summer months, while there is an overall decline of infection levels, suggests that females have a shorter life span than males and their numbers will deplete if they are not sufficiently replaced by new generations of copepods. Alternatively, females might also be less tolerant than males to higher salinities and temperatures which prevail in the lagoon in the summer months.

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