Acta Œcologica, 1995, **16** (3), 361-374

Comparative host-parasite relationship of two copepod species ectoparasitic on three fish species

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Abstract

The dispersal patterns of two sea lice species (*Lepeophtheirus thompsoni* and *L europaensis*) are analysed on their three Mediterranean teleost hosts (turbot for *L. thompsoni* and brill and flounder for *L. europaensis).* The influence of host age and ecology (marine for turbot and brill and brackish waters for flounder) is studied as well as are the differences in colonisation and diet strategies (blood for *L. thompsoni* and mucus for *L. europaensis)* displayed by these two copepod species. This study confirms the known differences in the degree of specialisation displayed by these two parasite species. It shows the influence of abiotic factors in determining parasite loads and localisation within the host. The spectacular differences found between *L. europaensis* on brill and on flounder show that the biotic factors (the host) have a considerable impact as well. Depending on the host-parasite pair involved and on the localisation of the parasite, differences are found concerning the impact on host population dynamics. We finally discuss these results in terms of plasticity, adaptation and divergence, in the light of previous work on the same or on closely related parasite species.

Keywords: Parasites, copepods, flatfishes, parasite distribution.

Résumé

Les schémas de dispersion de deux espéces de copépodes parasites (*Lepeophtheirus thompsoni* et *L europaensis*) sont analysés sur leurs trois hôtes téléostéens en Méditerranée (le turbot pour *L. thompsoni,* et la barbue et le flet pour *L. europaensis).* L'influence de l'âge de I'hôte, de son écologie (marine pour le turbot et la barbue, et eaux saumâtres pour le flet) est étudiée ainsi que les différences de strategies de colonisation et de régimes alimentaires de ces parasites (sang pour *L. thompsoni* et mucus pour *L. europaensis*). Cette étude confirme les différences déjà observées concernant le degré respectif de spécialisation de ces deux espèces parasites. L'influence des paramètres abiotiques apparaît dans le déterminisme des charges parasitaires et de la localisation sur l'hôte. Les facteurs biotiques (l'hôte) n'ont cependant pas un impact négligeable comme le montrent les fortes differences observées entre les *L. europaensis* prélevés sur barbue et ceux prélevés sur flet. En ce qui concerne l'impact possible des populations parasites sur la dynamique des populations de tents hôtes, des differences dépendantes de la nature du couple hôte-parasite et de la localisation du parasite sont mises en évidence. A la lumière de travaux précédents sur les mêmes espèces parasites et sur d'autres espèces proches, nous discutons ces résultats en termes de plasticité, d'adaptation et divergence.

INTRODUCTION

The role of biotic and abiotic factors in the Organisation of communities is a central theme in ecology, that unfortunately lacks field evidence (e.g. PRICE, 1987). In order to make powerful inferences about community Organisation, one needs either experimental tests or the use of biological models that enable comparative analysis. However, experimental manipulations are not often possible and thus, the use of closely related species, some of which may be exposed to different conditions, may be an alternative.

In the Gulf of Lions (French Mediterranean coast), *Lepeophtheirus thompsoni* Baird, 1850 and *Lepeophtheirus europaensis* Zeddam, Berrebi, Renaud, Raibaut and Gabrion, 1988 are two closely related caligid copepods that can hybridise in experimental conditions (DE MEEÜS *et al.,* 1990). These two species parasitise three different species of flatfishes (Heterosomata). *L. thompsoni* is specific to one host, the turbot *(Psetta maxima* (L. 1758)), a marine scophthalmid, and *L. europaensis* is found on both brill (*Scophthalmus rhombus* (L. 1758)), a marine scophthalmid, and flounder (*Platichthys flesus* (L. 1758)), a pleuronectid inhabiting lagoons. On each fish species, adult copepod females, once fertilised, colonise the gill cavity of the host where they lay their eggs. There, *L. thompsoni* females are mainly found on the gill filaments and are hematophagous, whereas *L. europaensis* females are mucophagous (ZEDDAM *et al.,* 1988). Other differences in specialisation between the two copepod species are known (diet, range of experimental host species, salinity tolerance) and discussed elsewhere (ZEDDAM *et al.,* 1988; DE MEEÜS *et al.,* 1990, 1992, 1993*a* and 1995).

In this paper, we present a field study of the dispersion patterns of these two copepod species on their hosts. Differences and similarities are observed in the ecologies of the two copepod species and within populations of *L. europaensis* found on brill and flounder. Such differences concern the location of copepods within the gill cavity, the within host parasite densities, the relation between host age and parasite abundance, the degree of aggregation and the pathogenic potentials of the parasites. These differences are discussed in the light of previous work on host ecology, host specificity, fecundity and plasticity of these parasites, and the age of each host-parasite association.

MATERIAL AND METHODS

Fishes

Flatfishes are asymmetric benthic predators. Turbot and brill are marine scophthalmids with the left side of their body being the zenithal one (side bearing the two eyes). Mating occurs during the coldest months and the fry colonise the shallower inshore waters. As they grow, young fishes occupy progressively deeper waters (Deniel, 1981, unpublished thesis, Université de Brest). Flounders are brackish water fishes with the right side of their body being the zenithal one. Mating occurs near the coasts during the coldest months. In the Gulf of Lions, young fishes colonise the lagoons and stream mouths where growth occurs. Adults then spend most of their time within those lagoons (Quignard *et al.,* 1984).

Sampling extended from the beginning of January to the end of June 1990. Non-commercialised fishes smaller than 190 mm (between 0 + and 1 + years old) were caught inshore (42 turbot, 11 brill) with a landing net. Larger fishes, caught in the offing, were examined at a fishing port (Grau-du-Roi, France) (179 turbot, 250 brill, 75 flounder). Hosts were measured, weighed and their copepods removed. It follows from the previous points that sample sizes critically depended on fishing performance. The absence of young flounders from samples resulted from our failure to capture them with the landing net.

To maintain homogeneity, only fishes of more than 190 mm, caught using the same technique (fishermen), were considered except when studying the relationships between parasitism and host size.

Copepods

The life cycle of these parasites is described in De Meeûs *et al.* (1990). It has a direct cycle with a fairly long free swimming phase (at least three days). Once attached to the host the parasite become mucophagous. Mating occurs on the body surface of the host and, once fertilised, females colonise the gill cavity where they lay eggs that develop and give birth to free swimming larvae. The natural specificity of *L. thompsoni* on turbot and of *L europaensis* on brill and flounder is known to mainly depend on the active preference of the infective stage (copepodid) (De Meeûs *et al.,* 1995). It should be noted that all stages of both species are mucophagous except *L. thompsoni* females which are mainly hematophagous (Zeddam *et al.,* 1988).

Males stay on the body surface of the host and can switch from one host to another (Anstensrud, 1990). They can also be removed or displaced while handled on fishing boats. Thus, only gravid females were sampled. The position of the parasite within the gill cavity of the host was noted. Females can indeed be found either on the gill filaments, on the inner surface of the operculum, on the floor of the gill cavity, or rarely on the body surface, each of these being either on the zenithal or the nadiral side of the fish.

Fishes and their parasites, parasite specificity and host biotopes are schematised in figure 1.

Data analysis

The nomemclature used to describe parasite distributions is that of Margolis *et al.* (1982). The mean abundance (*A*) corresponds to the total number of parasites sampled, divided by the total number of hosts. The prevalence (*Prev*) is the proportion of infected hosts. The mean intensity (*I*) is the mean number of parasites per infected host ($A = I.Prev$).

The influence of date of capture has been studied using the number of the day (e.g. 10 for the 10/01/90 and 173 for the 22/06/90) as a variable for Kendall's partial rank correlation tests. These correlation coefficients will be denoted $\tau_{Ab,T|L}$, where Ab is the parasite abundance, T the day of capture and L the length (held constant) of the host. The within host parasite repartition were tested with the Wilkoxon's signed-ranks tests for paired comparisons. These tests are described in Siegel & Castellan (1988).

Host size classes are used to study the relation between parasitism and host size. These classes consist of steps of at least 10 individuals, in such a way that hosts of equal size always belong to the same class. This is done in order to keep a high degree of homogeneity in host size within, and in number of individuals between, each class.

All homogeneity of proportions tests, which were made using Fisher exact tests on r x k contingency tables (Raymond & Rousset, in press), Kruskal-Wallis tests, Chi square tests, Kendall's

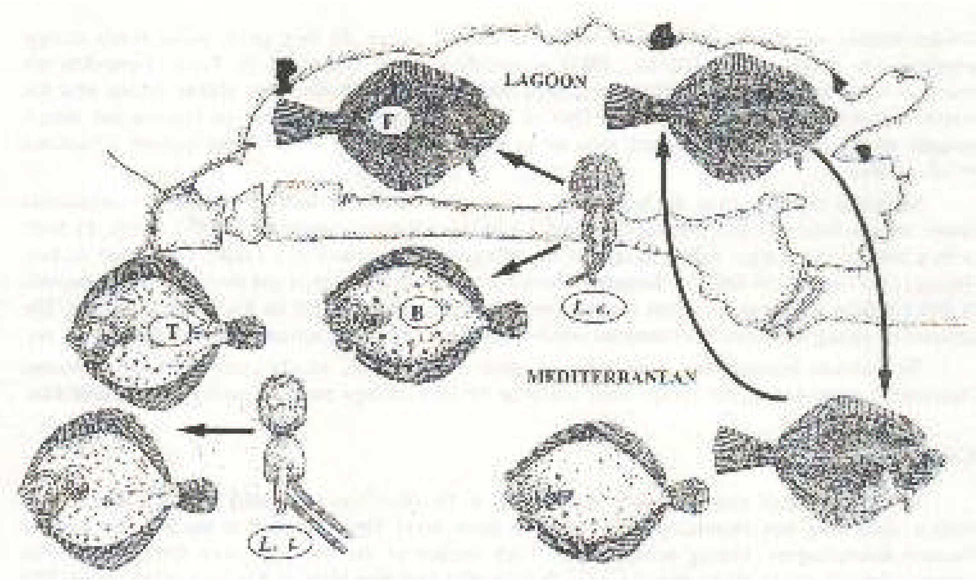

FIG. 1. - Summary of host parasite relationships encountered in the Gulf of Lions (France) between *L. thompsoni* (*L. t.*) and the turbot (T), and between *L. europaensis* (*L. e.*) and its two hosts: brill (B) and flounder (F). Turbot and brill are marine fishes while flounder inhabits lagoons and comes into the Mediterranean only during the coldest months for its reproduction (curved arrows).

partial rank correlation tests and Wilkoxon's signed-ranks tests for paired comparisons were computed with the package NPSTAT 2.5^{TM} (Praxème *R&D*).

All other tests (three way G-test, Homoscedasticity) were made using the program Logitheq-5.1 (BOY, 1994, Station Biologique de la Tour du Valat, Le Sambuc, 13200 Arles, France).

The description of these tests can be found in SOKAL & ROHLF (1981).

For mean comparisons we used the non-parametric test of Kruskal-Wallis because in each case the homogeneity of variances was rejected, even on log transformed data.

To account for type I error in multiple tests, we used the sequential Bonferroni procedure (described in RICE, 1989), where the desired significance level (α) is divided by the number of remaining comparisons.

In order to test the effect of parasitism on host survival, we applied the ANDERSON & GORDON (1982) test to our data. This test allows for inferences on host mortality due to parasite accumulation through time. Both parasite abundance and aggregation must increase with host age and then decrease as a result of the death of the most heavily infected hosts. The severity of the phenomenon is described by the intensity of such decrease.

RESULTS

Within host distribution

Within each host species, the distribution of copepods (table 1) is not random. There are significant effects of host species, side of the host and position in the gill cavity (three way *G*-test, $P<0.001$ for each pair of factors). On turbot, *L. thompsoni*

TABLE I. - *Within host distribution of each copepod species* (L. t. *and* L. e. *for* L. thompsoni *and* L. europaensis) *on turbot (T), brill (B) and flounder (F). Z and N stand for zenithal and nadiral sides. 0, F, G and S stand respectively for the inner surface of the operculum, the floor of the gill cavity, the gills and the body surface.*

		ZO	ZF	ZG	NO	NF	NG	Zs	NS	Total
L. t.	T	0	62	418	0	98	443	3	1	1025
L. e.	B	121	190	2	228	367	2	0	1	911
L e.	F	66	475	2	65	322	1	4	1	936
	Total	187	727	422	293	787	446	7	3	2872

are mainly found on the gill filaments (85% out of 1 025 females) (Wilcoxon's signed-ranks tests for paired comparisons, $z=8.5$, $P=O$). Parasites appear to be distributed at random on the zenithal (47%) and nadiral sides ($z=1.7$, $P=0.1$). However, when sampled on the floor of the gill cavity, parasites are more often observed on the nadiral side (61%) ($z=2.2$, $P=0.032$). *L. thompsoni* was never found on the inner surface of the operculum. On brill, *L. europaensis* are rarely found on the gills (0.4% out of 911 females), and the nadiral side is preferred (66%) ($z=7.7$, $P=0$) as is the floor of the gill cavity (61%) ($z=5.5$, $P=0$). On flounder, the floor of the gill cavity is also preferred (86% of 936 females) ($z=6.2$, $P=0$) by *L. europaensis,* but here it is the zenithal side which is the most often colonised (58%, $z=3.5$, $P=0$), gill filaments appearing to be neglected (0.3%). The colonisation of the body surface is very rare for each host (0.4, 0.1 and 0.5% respectively). This last result was expected from previous experimental observations (DE MEEÜS *et al.,* 1990, 1993*b*).

Even when the data concerning gill filaments are removed, the differences in the distribution of parasites between host species cannot be explained by chance ($P=0$, Fisher exact test on a 3 x 6 contingency table) (table II). Each kind of paired comparison is significant ($0 \leq P \leq 0.0014$, table II), except for the comparisons between the distributions of parasites infecting turbot and brill outside the gill filaments and/or outside the operculum (table II). For all other comparisons, the probabilities remain significant at the 95% level after the Bonferroni procedure (dividing 0.05 by the number of tests gives 0.0016). Thus, all fish display a different distribution of parasites, but when considering parasites found on the floor of the gill cavity, *L. thompsoni* colonises turbot's sides in the same proportions as *L. europaensis* does on brill, while on brill and flounder, *L. europaensis* displays very different distribution patterns.

TABLE II. - *Probability obtained during Fisher exact tests for multiple comparisons. - G stands for the removal of data on gills. The sign/stands for the pair of locations compared and & stands for the hosts that are compared.*

	Tot-G	Z/N	O/F	Z/N-G	Z/N on F	Z/N on O	O/F on Z	O/F on N
All	0	0	-	0	0	-	-	-
T & B	0	0	-	0.18	0.3	-	-	-
T & F	0	0	-	0	0	-	-	-
B & F	0	0	0	0	0	0.0014	0	0

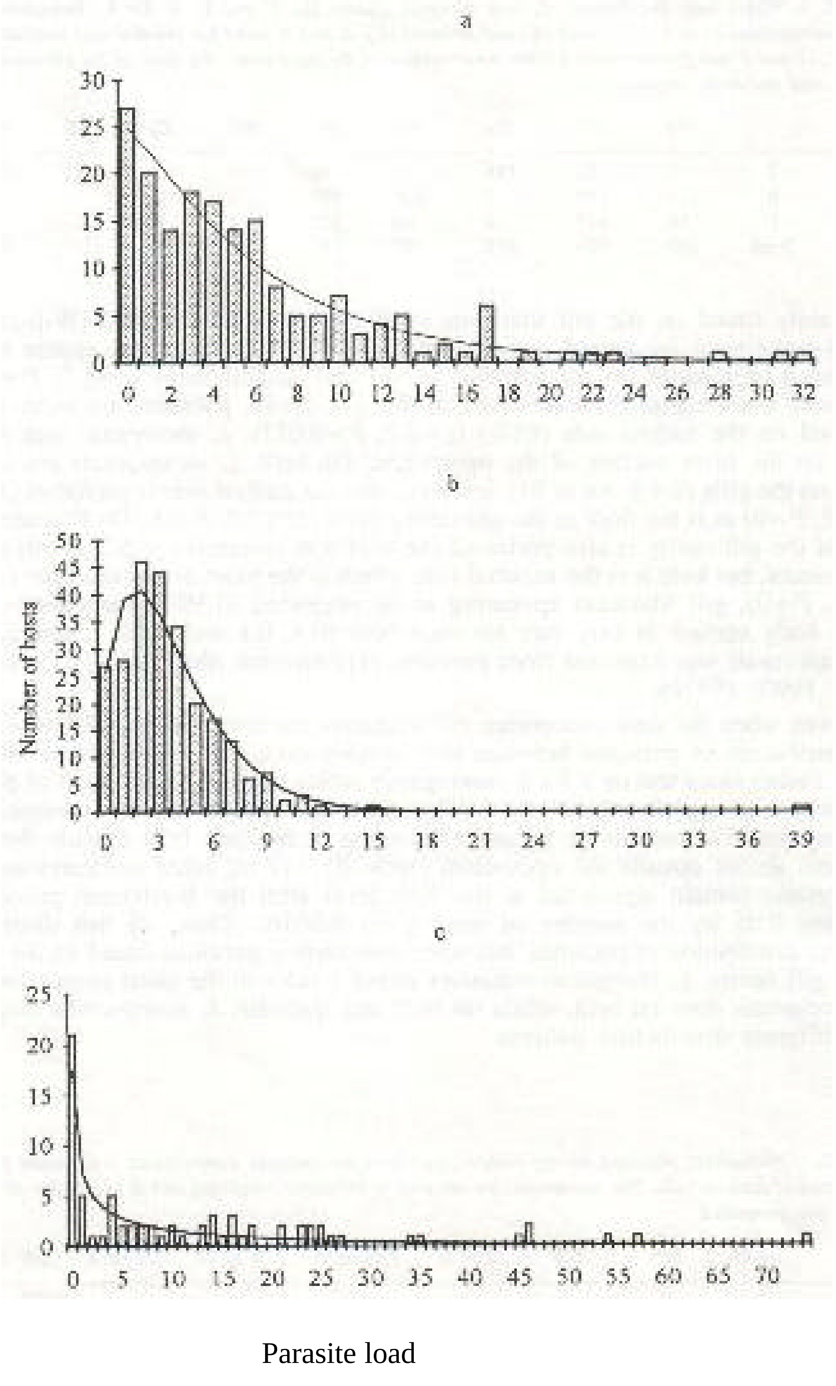

FIG. 2. - Frequency distribution of parasites on their host and adjustment to the negative binomial distribution: (a) ***L. thompsoni*** on turbot (k = 1.07), (b) ***L. europaensis*** on brill (k = 2.55) and (c) on flounder (k = 0.43).

Distribution on host populations: influence of date of capture

Fixing the effect of host size, Kendall's test of partial rank correlation between parasite abundance and date of capture appeared positive for all fishes and significant (two tailed tests) for turbot ($\tau_{Ab,T|L}=0.1$, $P=0.048$) and flounder ($\tau_{Ab,T|L}=0.2$, $P=0.013$) and not significant for brill ($\tau_{Ab,T|L}=0.08$, $P=0.059$) (note that none of these tests stay significant at the 1% level). There is thus a slight increase of parasitism from January to June, at least on flounder populations.

Distribution on host populations: influence of host species

The two copepod species, *L. thompsoni* on turbot and *L. europaensis* on brill or flounder, display various aggregated dispersal patterns on their hosts ($\beta = s^2/mean > 1$) (fig. 2). The most aggregated parasite is *L. europaensis* on flounder ($\beta = 19.5$), while the same parasite species displays a much weaker level of

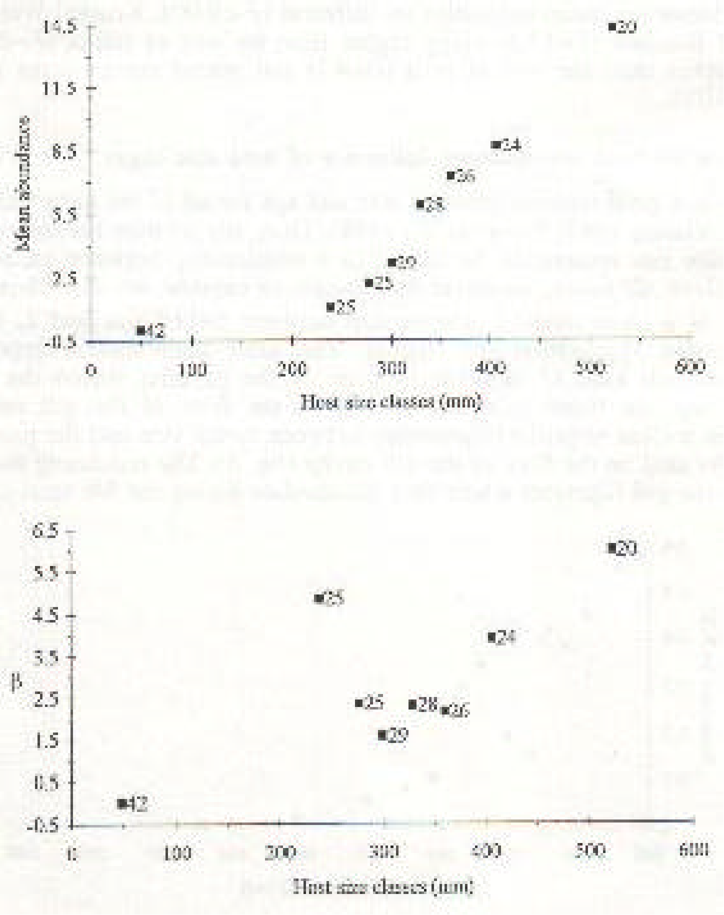

FIG. 3. - Relation between turbot size and *L. thompsoni* abundance and degree of aggregation (β). The number of hosts is indicated on the right of each square.

aggregation on brill (β=3.3). *L. thompsoni* on turbot occupies an intermediate position (β=6.2). These distributions can be adjusted to negative binomial distributions with k=1.07 (P=0.84, χ^2=6.5, 11 d.f.) for *L. thompsoni*, k=2.55 (P=0.56, χ^2 =8.7, 10 d.f.) for *L. europaensis* on brill and k=0.43 (P=0.49, χ^2 = 1.4, 2 d.f) for *L. europaensis* on flounder. The mean abundances on the three hosts are different (P<0.001, Kruskal-Wallis, 2 d.f.). This is mainly due to differences between *L. thompsoni* on turbot (Abundance A=5.7) and *L. europaensis* on brill (A=3.6) and between *L. europaensis* on brill and on flounder (A=12.5) (paired comparisons, P<0.05 and P<0.01 respectively), while the differences between turbot and flounder are not significant (P>0.05). Prevalences are significantly different among the three host species (P=0.0022, Fisher exact test). This mainly comes from the differences between prevalences on brill (*Prev*=0.89) and on flounder (*Prev* = 0.72) (P = 0.0007). The prevalence observed on turbot (*Prev* = 0.85), when compared to the two other fishes, loses significance at the 95% level after the Bonferroni procedure (i.e. α=0.017) (P=0.24 with brill and P=0.02 with flounder). However, mean intensities are different (P<0.001, Kruskal-Wallis, 2 d.f.), the one of flounder (I=17.3) being higher than the one of turbot (I=6.7) which is itself higher than the one of brill (I=4.1) (all paired comparisons significant with P<0.01).

Distribution on host populations: influence of host size (age)

There is a good relation between size and age for all of the three hosts studied (Robert & Vianet, 1988; Vianet *et al.*, 1989). Thus, any relation between parasitism and host size can reasonably be linked to a relationship between parasitism and host age. Here, all fishes, whatever their origin of capture, are considered.

There is a clear positive relationship between turbot size and *L. thompsoni* abundance and aggregation (β) (fig. 3). The same phenomenon appears when considering each kind of possible location of the parasite within the host (not shown) except for those parasites located on the floor of the gill cavity. This comes from a clear negative relationship between turbot size and the proportion of copepods located on the floor of the gill cavity (fig. 4). The remaining parasites are located on the gill filaments where they accumulate during the life span of the host.

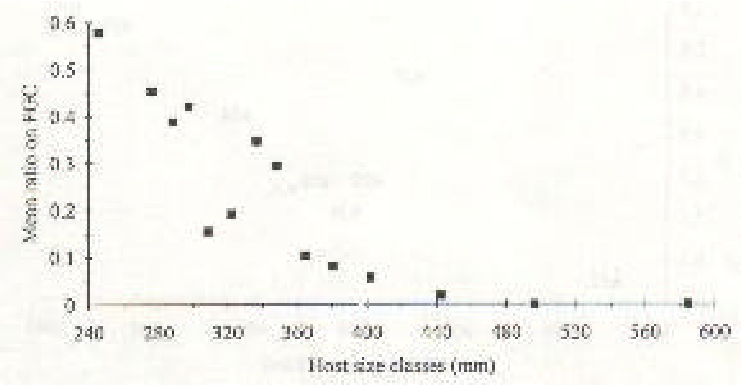

FIG. 4. - Relation between turbot size and the proportion of *L. thompsoni* located on the floor of the gill cavity (FGC).

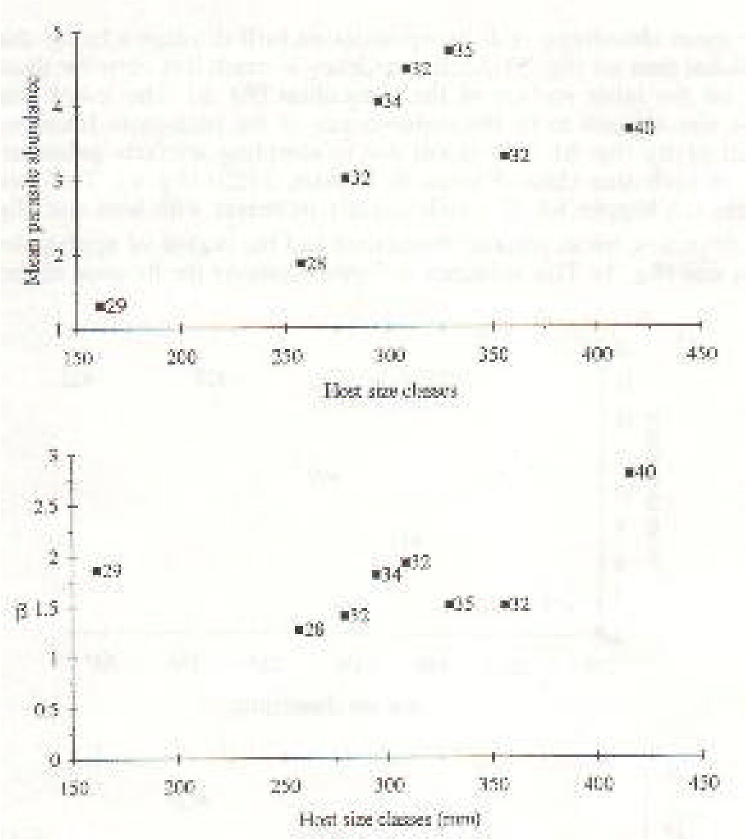

FIG. 5. - Relation between brill size and *L. europaensis* mean parasite abundance and degree of aggregation (β). The number of hosts is indicated on the right of each square.

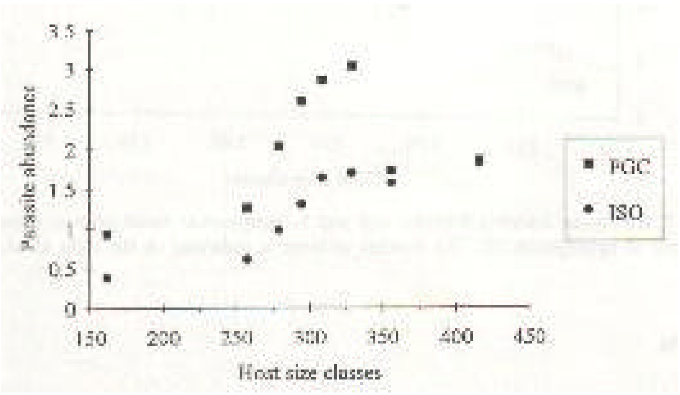

FIG. 6. Relation between brill size and *L. europaensis* mean parasite abundance for parasite located on the inner surface of the operculum (ISO) or on the floor of the gill cavity (FGC) (number of hosts as in fig. 5).

The mean abundance of *L. europaensis* on brill displays a bump-shaped curve for the global data set (fig. 5). Such a tendency is much less clear for those parasites sampled on the inner surface of the operculum (fig. 6). The lower abundance at high host size appears to be the consequence of the parasitism found on the floor of the gill cavity (fig. 6). This is not due to sampling artefacts generated by small samples of each size class (PACALA & DOBSON, 1988) (fig. 6). This bump-shaped curve does not happen for 13, which slightly increases with host size (fig. 5).

On flounders, mean parasite abundance and the degree of aggregation increase with host size (fig. 7). This tendency is found whatever the location of the parasites.

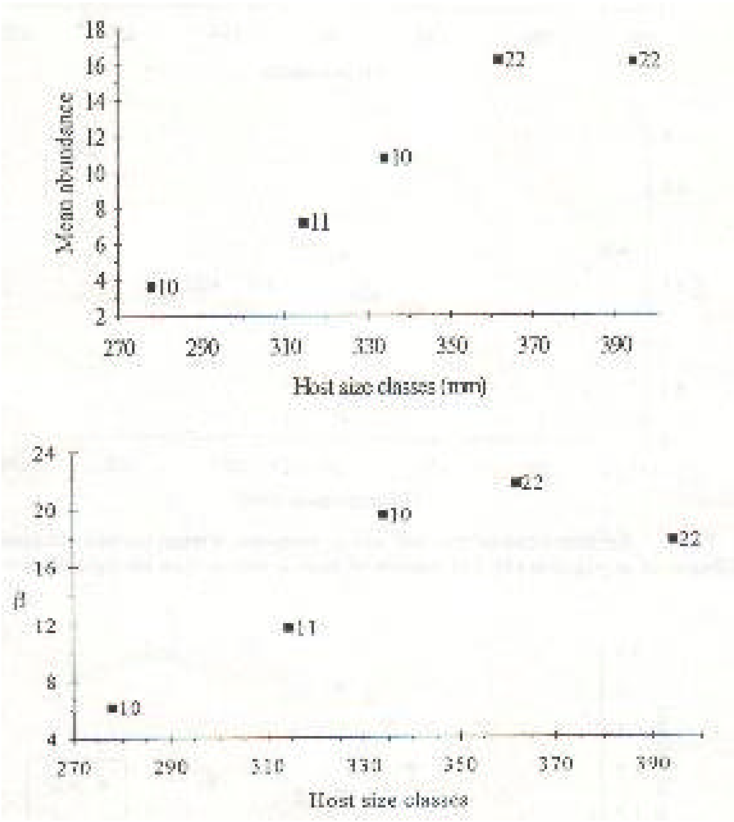

FIG. 7. - Relation between flounder size and *L. europaensis* mean parasite abundance and degree of aggregation (β). The number of hosts is indicated on the right of each square.

DISCUSSION

The results obtained here illustrate the influence of biotic (host) and abiotic (sea and lagoons) factors in determining parasite loads and localisation within the host. We found that abiotic factors appear predominant.

In the Mediterranean, *Lepeophtheirus europaensis* displays an increase in abundance from January to June on flounders. This result is in slight accordance with what is described for the closely related *L. pectoralis* (Müller, 1776) on plaice (*Pleuronectes platessa* (L. 1758)) in the North Sea (Boxshall, 1974*a*) where such an increase appeared more pronounced. This may be mainly attributable to temperature (Boxshall, 1974*a*), which covaries with the climate much more in brakish than in marine waters. However, parasite abundance on flounders can critically depend on the type of lagoon from where the fishes came when captured by the fishermen (see below). Such an uncontrolled factor might have unfortuitiously lead to the observed pattern. Alternatively, we did not observe any change in egg production of females as Boxshall (1974*a*) did for *L. pectoralis* since *L. thompsoni* and *L. europaensis* females where found gravid during all the sampling period.

L. thompsoni on turbot and *L. europaensis* on brill (marine environment) display more similar distribution patterns when compared to each other than when compared to *L. europaensis* on flounder (lagoons). In the marine environment (*L. thompsoni* on turbot and *L. europaensis* on brill), copepods prefer the nadiral side of host gill cavity when sampled outside the gill filaments, and are found in much lower densities within parasitised hosts than for *L. europaensis* on flounder (lagoons), on which they are mainly found on the zenithal side. Interestingly, the nadiral side of turbot and brill and the zenithal one of flounder actually correspond to the biological right side of each of those fishes, suggesting a common physiological mechanism (mucus, respiratory flow?). This may also be due to differences in abiotic factors (oxygen, substratum?) between the marine and the brackish water environments. The differences in the degree of aggregation observed between the marine (lower aggregation) and the lagoon (higher aggregation) environments can easily be explained by the opposite degree of heterogeneity of each. The marine environment is open and stable while lagoons are isolated and can display highly variable conditions (e.g. salinity) in space and time. Flounder can colonise lagoons of highly varying salinity (Hartley, 1940), while *L. europaensis* from flounder, even if more euryhaline than those parasitising marine hosts, cannot survive at a salinity lower than 20‰ (De Meeûs *et al.,* 1992, 1993*a*). Thus, in some lagoons where conditions are suitable, high degrees of parasitism can occur while in others *L. europaensis* is absent from flounders. As a consequence, aggregation can mainly be explained by a heterogeneity of parasitism from one host cohort to the other one for turbot and brill, but not for flounder.

The observed increase of parasite burden with host age is a frequent observation in ecological parasitology (e.g. Anderson & Gordon, 1982), even in parasitic copepods of marine fishes (e.g. Boxshall, 1974*b*; Van Den Broek, 1979; Nagasawa, 1987; Etchegoin & Sardella, 1990; Poulin *et al.,* 1991; see Kabata, 1981 for review). This is sometimes explained by increases in the available space within the host and/or in the probability of encounter with infective stages (Van Den Broek, 1979; Etchegoin & Sardella, 1990; Poulin *et al.,* 1991). This hypothesis is difficult to reject, but fails to explain the concomitant increase in the degree of aggregation $\hat{a}$ that is clearly observed here on turbot and flounder. Furthermore, this is not compatible with the decline of parasite abundance observed for the oldest brills in our work, and in other studies on parasitic copepods (Bortone *et al.,* 1978). Another explanation relies on host changes in behaviour with ageing that would render the oldest hosts more susceptible to parasitic infection (Anderson

& GORDON, 1982). This is possible for turbot and brill where the different cohorts are not sympatric. Indeed, individuals tend to migrate from shallow to oreat depth with ageing (DENIEL, 1981, unpublished thesis, Université de Brest). This could be correlated to a gradient in the probability of infection. However, such an explanation seems incompatible with flounder sedentary behaviour during the major part of its life cycle (DE MEEÜS *et al.,* 1993*a*), with the differences observed on brill between parasites located on the floor of the gill cavity and those located on the inner surface of the operculum, and with the differences observed between brill and turbot in the marine environment. Another alternative is parasite accumulation through time. Indeed, the life span of these copepods seems long enough (DE MEEÜS *et al.,* 1993*b*; ANSTENSRUD, 1990) to accumulate on hosts. This hypothesis is compatible with the simultaneous increase of parasite abundance and aggregation in our data.

The differences observed may be correlated to differences in strategy previously described for *L. thompsoni and L. europaensis* (DE MEEÜS *et al.,* 1990, 1992, 1993*a*, 1993*b* and 1995). In the sea, *L. thompsoni* is a specialist that colonises its host (turbot) more efficiently than *L. europaensis* does on its host (brill). Such differences may be due to a much lower reproductive output of *L. europaensis* (mucophagous) as compared to *L. thompsoni* (hematophagous) (DE MEEÜS *et al.,* 1993*b*). In contrast, *L. europaensis* is a generalist that is able to colonise a much wider range of hosts (even turbot in the laboratory), in a much wider range of abiotic conditions (i.e. salinity, DE MEEÜS *et al.,* 1992, 1993*a*) than *L. thompsoni,* which is only able to exploit turbot, even in the laboratory (DE MEEÜS *et al.,* 1990, 1993*a* and 1995). Such a strategy leads *L. europaensis* to experience very different conditions. Abiotic factors like salinity are known to induce differences in developmental capabilities of eggs and free swimming stages (DE MEEÜS *et al.,* 1992, 1993*a*). The distribution of females within the gill cavity (zenithal-nadiral, floor-operculum) strongly discriminates brill and flounder. The flounder, which is a recent host for *L. europaensis* (DE MEEÜS *et al.,* 1990, 1992, 1993 a) appears as a very favourable resource for this parasite, since much higher densities (the present study) of more fecund females (DE MEEÜS *et al.,* 1993b) are found on it as compared to brill. All these observations support the potential for an adaptive divergence currently occurring in the Mediterranean between *L. europaensis on* brill and on flounder (DE MEEÜS *et al.,* 1993*a*).

Based on the ANDERSON and GORDON (1982) model, host mortality by parasite accumulation does not appear to play a role in turbot. Parasitism and aggregation always increase with age, except for *L. thompsoni* located on the floor of the gill cavity where the relation is bump-shaped, because of the negative relationship between host age and the proportion of parasites located there. This last point can be explained either by the death of the youngest turbot when gill-infected, or by the size of the gill filaments, too small in the youngest turbot to allow for the attachment of copepod females. The latter hypothesis seems more likely in the light of the behaviour displayed by gravid *L. thompsoni* females bred on young turbots (DE MEEÜS, personal observations). For *L. europaensis,* the shape of the curve for parasite abundance as a function of host size can be explained by the differentially high mortality of the most heavily infected hosts. Interestingly, this phenomenon appears much less pronounced when considering the inner surface of the operculum and much more pronounced for parasites found on the floor of brill gill cavity. This cannot be simply due to a reversal in site preferences of copepods, since parasitism decreases when all sites are taken into account. It may be due, rather, to acquired immunity on the part of the host. However, data obtained on the inner surface of the operculum and those observed on the two other fishes do not support this argument. Such a phenomenon more likely reflects a differential pathological effect depending on parasite location, more injurious on the floor than on the operculum. Following ANDERSON & GORDON (1982), the fact that such a bump-shaped curve does not affect , which slightly increases with host size, implies that the mortality induced may not be very severe. On the other hand, no such parasite-induced host mortality was found for flounder, where parasite abundance and aggregation increase constantly with host size.

In support of these ideas, copepods are much more likely to be found on the floor than on the operculum in any of the three hosts. This is always true for turbot and flounder where the parasite is not injurious and in which parasites are rarely found on the operculum. This appears to be the reverse for older brill where the accumulation of copepods on the floor of the gill cavity seems to induce host mortality. Here, the floor of the gill cavity may be more favourable than the operculum for these copepods, but more prone to injury for brill. Surprisingly, the hematophagous *L. thompsoni* does not seem to injure the gills of turbot, at least enough to induce observable effects on turbot populations. Furthermore, *L. europaensis* appears more injurious to its ancestral host (brill) than to the derived one (flounder). Thus, the dogma of higher virulence associated with a recent association between a host and its parasite is not confirmed by our results, in accordance with EWALD's (1994) views on the evolution of infectious diseases.

Sea lice can play a role in the structuring of wild populations of fishes (POULIN & FITZGERALD, 1987) and are the major pathogens of farmed salmons (PIKE, 1989). The plasticity *(sensu lato)* that such ectoparasites can display, when faced with new hosts and/or new external environments, suggests that long-term control programmes against such organisms might be faced with a daunting task.

ACKNOWLEDGEMENTS

We thank M. E. HOCHBERG for very useful comments on the manuscript.

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