Order in ectoparasite communities of marine fish is explained by epidemiological processes

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SUMMARY

Two kinds of community structure referred to, nestedness and bimodal distribution, have been observed or were searched for in parasite communities. We investigate here the relation between these two kinds of organisation, using marine fishes as a model, in order to show that parasite population dynamics may parsimoniously explain the patterns of ectoparasite species distribution and abundance. Thirty six assemblages of metazoan ectoparasites on the gills and heads of marine fish showed the following patterns: a positive relationship between abundance and the variance of abundance; a positive relationship between abundance and prevalence of infection; a bimodal pattern of the frequency distribution of prevalence of infection; nestedness as indicated by Atmar and Patterson's thermodynamic measure (a mean of 7·9°C); a unimodal distribution of prevalence in parasite assemblages with a temperature lower than the mean, and a bimodal distribution in assemblages with a temperature higher than the mean. We conclude that patterns are the result of characteristics of the parasite species themselves and that interspecific competition is not necessary to explain them. We emphasize that a holistic approach, taking all evidence jointly into account, is necessary to explain patterns of community structure. Ectoparasite assemblages of marine fish are among the animal groups that have been most thoroughly examined using many different methods, and all evidence supports the view that these animals live under non-equilibrium conditions, in largely non-saturated niche space in which interspecific competition occurs but is of little evolutionary importance.

Key words: Ectoparasites, fish parasites, community ecology, nested patterns, epidemiology, bimodal distribution, species coexistence, competition.

INTRODUCTION

The search of order is intricately linked with the development of ecological theories, and investigating patterns (of distribution and abundance of species, for example) is considered as one way to highlight the existence of order. Processes are inferred from observed patterns (May, 1976; Brown, 1995). Within this context, insular biogeography was and still is the paradigm in evolutionary and ecology research (at least in a macro-perspective approach). Patterns of species richness and distribution among islands, and adaptive radiation and character displacement through competition between species on islands have been investigated by many authors (e.g. Grant, 1968, 1975; Brown, 1995).

The concepts developed in insular biogeography were directly applied to parasites based on the simple analogy that hosts are islands for parasites (Dritschilo *et al*. 1975; Kuris, Blaustein & Alió 1980). Thus, arguments of insular biogeography were invoked to predict that parasite species richness should be positively linked with host body size (Kuris *et al*. 1980; Guégan *et al*. 1992; Morand, 2000, and further references therein). However, the dynamics of species diversity, i.e. extinction and colonisation processes, which are the core of the theory of insular biogeography, were not taken into account. Moreover, geographic distance, which is an important feature of the theory, was also ignored, i.e. no analogy was proposed to adapt some of the hypotheses of insular biogeography to the case of host-parasite systems.

The analysis and interpretation of community structure were influenced by the hypothesis of competitive exclusion, according to which species may coexist only if they differ in certain characters, e.g. body size or trophic structures (Hutchinson, 1959; MacArthur, 1972; Simberloff & Boecklen, 1981). More specifically, the coexistence of insular free-living organisms seems to be favoured by divergence in morphology, especially the morphology of specialised organs such as the feeding apparatus (Grant & Schluter, 1984). Accordingly, it was proposed that parasite communities are also structured by competition (Holmes, 1990). However, although restriction of niche size by competing species is observed in the case of some endoparasites

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and mostly in species-rich communities, this is not the case for most ectoparasites, and there is no evidence for parasite species exclusion (Rohde, 1977, 1979, 1991).

Free-living coexisting species usually do not live in random assemblages. Nested subset structures in ecological communities are commonly found, that is, communities with successively lower species richness tend to be subsets of richer assemblages (Patterson & Atmar, 1986). Nested subset structure is often interpreted as the effect of highly predictable colonisation/extinction processes that determine the composition of communities (Brown, 1995). Hence, the search for nested patterns in parasite communities was the subject of several studies, and emphasis was placed on either the role of hosts and/or competition (Guégan & Huguený, 1994; Huguený & Guégan, 1997; Poulin & Guégan, 2000). The intrinsic character of parasites, i.e. their dynamics, was rarely taken into account when explaining nestedness patterns (but see Worthen & Rohde 1996; Rohde *et al*. 1998).

A different kind of community order investigated in free-living organisms is core-satellite organisation (Hanski, 1982). The core-satellite hypothesis is included in metapopulation theory (Hanksi & Gyllenberg 1993). The core-satellite hypothesis predicts a bimodal distribution of organisms in their environment, that is, the majority of species is present in most patches, or in only a small fraction of patches. The core-satellite hypothesis does not invoke competition but a rescue effect, i.e. the ability to re-colonize empty patches after extinction. It is based on the character of species, i.e. their population dynamics, and does not need an explanation based on competition and/or special attributes of the environment, nor the patch or the host.

The two kinds of community structure referred to, nestedness and bimodal distribution, have been observed or were searched for in parasite communities. However, nobody has investigated the relation between these two kinds of organisation. Here, using marine fishes as a model, we show that epidemiology, i.e. parasite population dynamics, parsimoniously explains the patterns of parasite species distribution and abundance.

METHODS

Core-satellite hypothesis and the distribution and abundance of parasites

Morand & Guégan (2000) have investigated the patterns of abundance and distribution of mammalian nematodes. They found a bimodal distribution of worm prevalence and a positive relationship between abundance and prevalence. They argued that these patterns are not the result of host specialisation but simply the results of demographic and stochastic processes.

Here we propose to reinvestigate this pattern for the case of fish ectoparasites. We use the data of Rohde, Hayward & Heap (1995 and unpublished records of Hayward) on 36 communities of gill and head ectoparasites of marine fish (only fish species with at least 5 ectoparasite species were included in the analyses, a further 97 fish species had fewer ectoparasite species).

Epidemiological modelling shows that the mean worm burden $\mathrm{M}(t)$ is linked to the prevalence of infection $\mathrm{P}(t)$ at time t according to:

$$P(t) = 1 - [1 + \mathrm{M}(t)/k]^{-k}$$

where k is the parameter of the negative binomial distribution.

Perry & Taylor (1986) emphasised that k is linked to the mean worm burden M:

$$1/k = a\ \mathrm{M}^{\mathrm{b}-2} - 1/\mathrm{M}$$

with a and b the two parameters of

$$\mathrm{s}^2 = \mathrm{a} \times \mathrm{M}^{\mathrm{b}}$$

where a represents a constant parameter, b an index of spatial heterogeneity, M the mean abundance and s^2 its variance (Taylor, Woiwod & Perry 1978, Taylor *et al*. 1983)

Measure of order

Several problems may arise when testing for nested patterns. For example, the lack of a significant nested pattern does not necessarily imply a random organisation (Poulin & Guégan, 2000). Atmar & Patterson (1993) have proposed to use a direct measure of order, which is based on entropy. As emphasised by Atmar & Patterson (1993): "statistical stochasticity is a concept closely related to heat, information, noise, order and disorder". They proposed the use of a metric that measures the *heat of disorder* inherent in the historical biogeography of an archipelago (i.e. historical organisation of communities). We use this method because it provides a simple thermodynamic measure of the order and disorder to describe nested patterns. A matrix temperature of perfect order assumes the attributes of a frozen liquid, where complete order exists only at 0 °C. As the temperature rises, turbulence is imposed on the system, at 100 °C no discernible extinction order remains, the presence-absence matrix has assumed the attributes of a free gas. The temperature of a matrix is inherent in the manner in which species are distributed throughout the matrix. Changes in temperature between 0 °C and 100 °C are assumed to be continuous.

RESULTS

Abundance–variance relationship

Treating each ectoparasite population as an independent observation, we found a positive re-

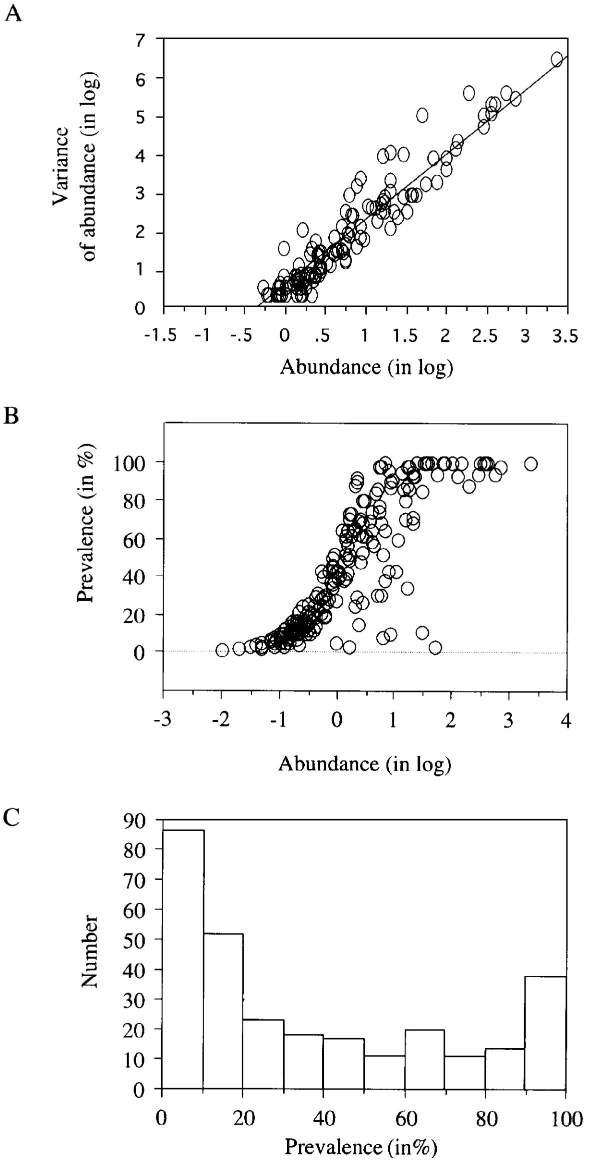

Fig. 1. (A) Relationship between the logarithms of the variance (s^2) and abundance (M), across populations of fish ectoparasites, fitted to a power-function with the intercept $a = 0{\cdot}57 \pm 0{\cdot}04$ and the slope, $b = 1{\cdot}71 \pm 0{\cdot}04$ ($r^2 = 0{\cdot}92$; $P < 0{\cdot}0001$; $n = 171$ populations). (B) Relationship between abundance (average parasite burden) and prevalence of fish ectoparasites (171 populations). (C) Bimodal distribution of prevalence of fish ectoparasites.

lationship between the mean abundance (in log) and the variance of abundance (in log) (Fig. 1A), with estimates of parameters $b = (1{\cdot}71 \pm 0{\cdot}04)$ and $a = (0{\cdot}57 \pm 0{\cdot}04)$. The values of these estimates are within the ranges typically observed in various assemblages of parasites (Morand & Guégan, 2000).

Bimodal distribution

A positive relationship between abundance and prevalence of ectoparasites was observed (Fig. 1B). The frequency distribution of ectoparasite prevalence showed a bimodal pattern (Fig. 1C).

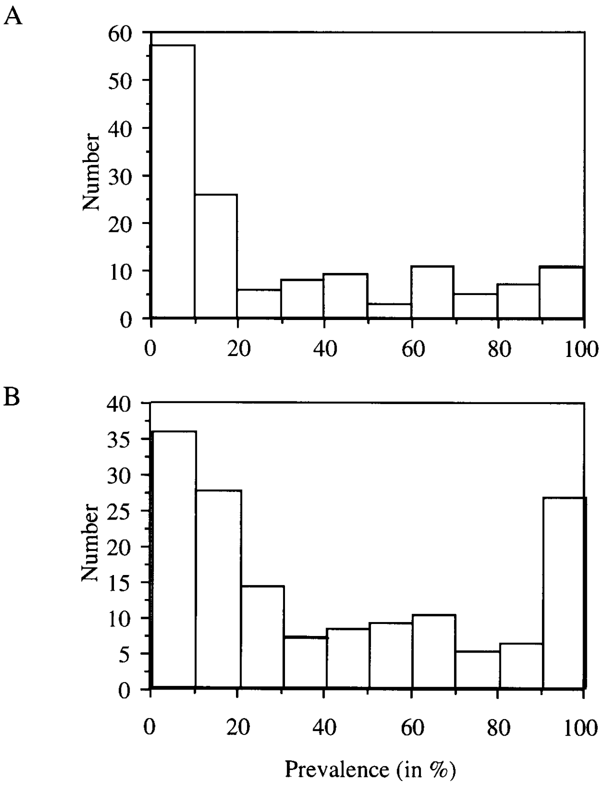

Fig. 2. (A) Unimodal distribution of prevalence of ectoparasite populations in assemblages characterized by a low temperature matrix (see Methods). (B) Bimodal distribution of prevalence of ectoparasite populations in assemblages characterized by a high temperature matrix (see Methods).

Temperature of ectoparasite assemblages

The temperatures of ectoparasite assemblages ranged from 4·9 °C to 43 °C with a mean value of 7·9 °C ± 0·5. The assemblages with a temperature lower than the mean value of 7·9 showed a unimodal distribution of prevalence (Fig. 2A), whereas the assemblages with a temperature higher than the mean value showed a bimodal distribution of prevalence (Fig. 2B). This suggests that increase of temperature, i.e. increase in disorder, leads to a core-satellite distribution of parasites within the assemblage.

DISCUSSION

Epidemiological processes appear to be the most parsimonious explanation for the diversity, abundance and distribution of ectoparasite species infecting fish.

Distribution and abundance of ectoparasites on marine fish

As predicted by the core-satellite model, rare (satellite) ectoparasite species were observed to be more frequent in the environment (host) than locally abundant (core) species. According to Morand & Guégan (2000), a positive relationship between abundance and prevalence is purely the result of epidemiological processes. Demographic explanations may therefore explain the observed patterns of bimodality of prevalence when making Monte-Carlo simulations using epidemiological modelling frameworks (Anderson & May, 1985; Morand & Guégan, 2000).

Nestedness is the result of epidemiological processes

Nested patterns, mostly investigated in biogeographical studies, are said to be the result of extinction/colonisation events on archipelagos or isolated habitats (Atmar & Patterson, 1993). The observation of nested patterns in ectoparasite assemblages of tropical fish was explained by considering host body size as the determinant (Guégan & Hugueny, 1994), leading to the conclusion that hosts are a major determinant of parasite infracommunity structure (Guégan & Hugueny, 1994). But it was also suggested that competition between species may lead to non-randomness (see Poulin, 1996). Poulin (1997) emphasised that the nested structure of parasite communities may be the result of interspecific competition, but found no empirical support. In contrast, Rohde *et al*. (1998) emphasised that nestedness structure of parasite communities is not a proof for the existence of interspecific competition, since it may also (and more likely) result from different colonisation sequences, as suggested by the observation that nestedness in populations of a marine fish species was found only when juvenile and adult fish were tested jointly, but not when they were tested separately (Kleeman, 1996). Host specificity determines if a parasite is able to colonize a host and then may affect the nestedness structure parasite communities (Matejusova, Morand & Gelnar, 2000). However, there is not sufficient information on host specificity concerning marine ectoparasites to investigate this effect.

Nested patterns were observed in some studies (Guégan & Hugueny, 1994; Hugueny & Guégan, 1997), but in the majority of cases nested patterns were rarely observed and ectoparasite communities of fish seem to form random, unstructured assemblages (Rohde *et al*. 1994, 1995, 1998; Poulin, 1996; Worthen & Rohde, 1996).

Rather than using a dichotomic classification of nestedness (nested versus non-nested) as done in previous studies, we preferred here to use a measure of order following Atmar & Patterson (1993) that permits a continuous gradation from 0-nestedness to 100% nestedness. We found that each assemblage of ectoparasite species is characterized by a temperature cooler than expected by chance. We also found that assemblages characterized by a low temperature form unimodal distributions and that assemblages characterized by a hot temperature form bimodal distributions (i.e. core satellite pattern) (Fig. 3). We suggest that nestedness is the result of differential colonisation/extinction processes acting at the level of each parasite species. These differential colonisation/extinction processes are attributes of species and related to birth and death processes in population dynamics, i.e. they are not the consequence of interspecific competition, as further discussed below.

Competition is not important

A large number of field observations indicate that interspecific competition does not affect the ''structure'' of ectoparasite assemblages (Rohde, 1979, 1989, 1991, 2001; Rohde & Heap, 1998; Simkova *et al*. 2001; Lo & Morand, 2000, 2001). Morand *et al*. (1999) showed a lack of saturation of fish ectoparasite communities suggesting that infracommunities of parasites are not saturated by local parasite residents. This implies that resources provided by the fish are far from being totally exploited by parasites, as previously shown by Rohde (e.g. 1979, 1989, 1998, 2001).

Coexistence of ectoparasites is favoured by intraspecific aggregation, which is the common feature of parasite distribution (Morand *et al*. 1999; Lo & Morand, 2001). The increase of intraspecific aggregation compared with interspecific aggregation when total parasite species richness increases facilitates ectoparasite species coexistence (Morand *et al*. 1999). However, this does not suggest that interspecific aggregation is a response to interspecific competition, for which there is no evidence. Rather, interspecific aggregation is likely to be the result of behavioural characteristics of each ectoparasite species.

In conclusion, epidemiology is the most parsimonious explanation of the order that may be observed in ectoparasite assemblages. The observation of pattern (or the lack of pattern) is simply the result of demographic characteristics of each ectoparasite species in an assemblage, and competition does not need to be invoked. The assemblage pattern that can emerge may be the consequence of many different factors that affect the probability of a given host of being infected by a particular parasite.

A holistic approach to understanding parasite assemblages

We have shown above that ectoparasites of marine fish do not live in entirely random assemblages. Core and satellite species can be distinguished and some degree of nestedness occurs. However, these patterns can be explained by epidemiological processes, i.e. by characteristics of the various parasite species. It is not necessary to invoke interspecific interactions to explain them. Nevertheless, we wish to emphasize that different methods and different approaches may lead to different conclusions. Therefore, a holistic

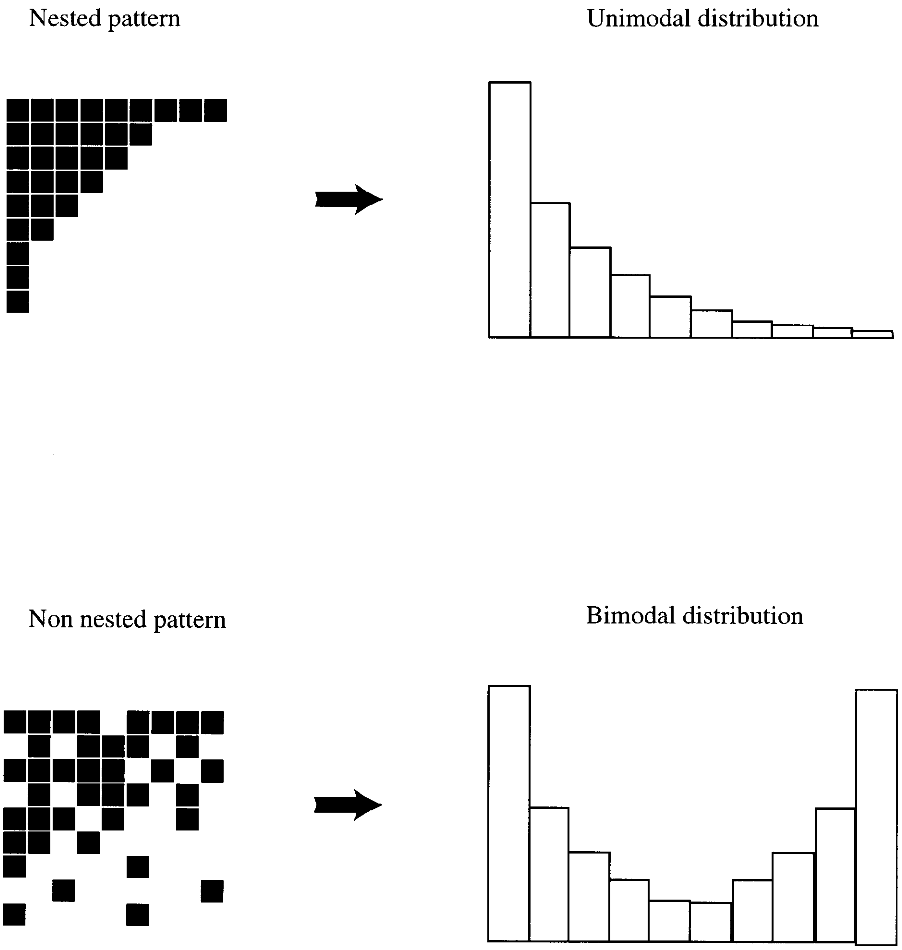

Fig. 3. Link between nested structure and prevalence distribution of parasites. (A) a nested structure, generally characterized by a low temperature, leads to a unimodal distribution of ectoparasite prevalence values. (B) a non nested structure, generally characterized by a high temperature, leads to a bimodal distribution of ectoparasite prevalence values.

approach is necessary, an approach that takes all evidence jointly into account, as suggested by Rohde (in press) when considering evidence for the mating hypothesis of niche restriction, that is, for the hypothesis that facilitation of mating is of great importance in restricting niches of parasites.

Assemblages of ectoparasites (and to a lesser degree of endoparasites) of marine fishes are now among the best known animal groups that have been studied with regard to the question of whether equilibrium or non-equilibrium conditions prevail. The evidence given by various authors for equilibrium conditions is complete or partial competitive exclusion or habitat shifts in the presence of other species, character displacement and particularly differences in the size of feeding organs of species using similar food resources (e.g. Krebs, 1997), as well as an asymptotic relationship between local and regional species richness (Cornell & Lawton, 1992). Many studies have shown that, for marine parasites, all evidence very strongly suggests that these animals live under non-equilibrium conditions. Evidence is as follows: (1) there is a high degree of non-saturation, i.e. many habitats are empty, as shown by comparison of host species of similar size and from similar habitats with few and many parasite species (e.g. Rohde, 1979); (2) many species are little or not affected by the presence of other potentially competing species (e.g. Rohde, 1991 and further references therein); (3) differences in the size of feeding organs do also occur when resources are in unlimited supply, suggesting that such differences may be fortuitous (Rohde, 1991); (4) many examples of character displacement (of reproductive organs) can best be explained by reinforcement of reproductive barriers, and niche restriction may often be the result of selection to facilitate mating and not of competition (Rohde, in press); (5) an asymptotic relationship between local and regional diversity may be a consequence of differential likelihoods of species to appear in a community because of different colonization rates and life spans, and interactions between species are not necessary to explain the relationship (Rohde, 1998); (6) interspecific aggregation is reduced relative to intraspecific aggregation (Morand *et al.* 1999); (7) positive associations are much more common than negative ones (Rohde *et al.* 1994); (8) hyperparasites of various degrees are very rare, i.e. many habitats (hosts) are empty for future colonization (e.g. Rohde, 1989); (9) parasites do not conform to the packing rules derived from spatial scaling laws (fractional geometry) (Rohde, 2001); (10) nestedness, when it occurs, is not the result of interspecific competition but of characteristics of the various species themselves (this paper).

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