Diversity gradients of marine Monogenea in the Atlantic and Pacific Oceans

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Summary. The number of species of Monogenea per marine fish species increases from high to low latitudes, but is much greater in the Pacific Ocean. It is suggested that the differences are due to the more advanced evolution at low latitudes and in the Pacific Ocean.

Latitudinal gradients in species diversity are nearly universal, and a recent review has shown that no general ecological explanation of the gradients can be given[2]. It seems likely that warm environments have more species because evolution there is more advanced, i.e. has had more 'effective' time to fill habitats due to greater evolutionary rates at high temperatures[2-4].

Such a time hypothesis implies that cold environments have relatively fewer species than warm environments in those parasite groups which have more species than their hosts at least in some regions, i.e. which diversify faster than their hosts. Increased evolutionary rates must lead to a relative increase in species numbers of such groups, and demonstration of gradients in relative species numbers of such parasites from polar to tropical regions, therefore, would support a time hypothesis. Further support would be given by the demonstration that the Atlantic Ocean has relatively fewer species of such parasites than the Pacific Ocean. The Atlantic Ocean, as a result of continental drift, began to form only approximately 150 million years ago with a narrow tropical connection to the Pacific closed several million years ago[5], and, thus, has had less time to fill habitats than the much older Pacific Ocean, although no differences between Atlantic and Pacific Oceans can be expected for those organisms which can easily be transferred over wide distances.

Monogenea were chosen for this study because there are more species of Monogenea than of hosts in the tropical Pacific[4], and because they are fragile parasites with thin-shelled eggs and a direct life cycle. Any passive transfer by birds or wind can therefore be excluded. Furthermore, most Monogenea are extremely host-specific and accidental transfer into another sea would normally not lead to infection of other host species. Only data from comprehensive surveys of the gills of marine teleosts are used for figure 1. They are from the Bering Sea[6], White Sea[7], Barents Sea[8], Gulf of Mexico[9], southeastern Australia[10], Great Barrier Reef[11], Argentina[12], and Brazil[13]. Data for fish of which less than 3 specimens were examined, are not included. Some small surveys are included in figure 2.

Figure 1 shows that there is a significant increase in relative species diversity of Monogenea towards low latitudes in the Atlantic Ocean, and that relative species diversity is distinctly greater in the Pacific Ocean.

A latitudinal increase in diversity also occurs in parasites of lower taxa of fish. The Carangidae comprise many species in the tropics and only a few in cold-temperate waters, and figure 2 shows that only one carangid species in cold waters had (2 species of) Monogenea, whereas all tropical species had at least 1 species.

All surveys of Monogenea used are incomplete. However, the smallest surveys are those in the Pacific Ocean and in warm waters. Hence, further studies will almost certainly show that the differences between low and high latitudes in the Atlantic and Pacific Oceans, and between the Pacific and Atlantic Oceans, are even more distinct.

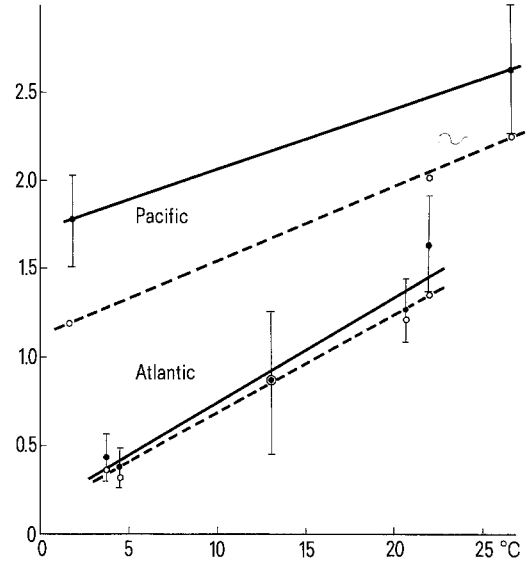

Fig. 1. Relative species diversity (= average species number of parasites per host species) of monogenean gill parasites of teleost fish in the Pacific and Atlantic Oceans. Abscissa: approximate means of annual sea-surface temperature ranges at various localities. Ordinate: mean numbers of monogenean species per host species. ●, means of individual diversity (= No. of monogenean species per host species, not corrected for lack of host specificity) ± SE. ○, total diversity at each locality (= total No. of monogenean species/total No. of host species examined at each locality). Localities from left to right in the Pacific: Bering Sea, southeastern Australia, Great Barrier Reef; in the Atlantic: White Sea, Barents Sea, Argentina, Gulf of Mexico, Brazil. Individual diversity is not given for southeastern Australia because only very few specimens were examined of most fish species. Atlantic (●): slope = 0.06, intercept = 0.15, r = 0.48, significance = 0.00001. Pacific (●): slope = 0.03, intercept = 1.74, r = 0.16, significance = 0.23.

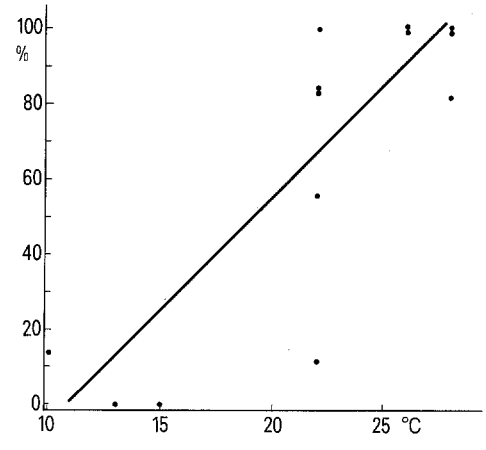

Fig. 2. Carangidae, infection frequencies with Monogenea. Each dot represents the frequency of infection of 1 host species with all Monogenea irrespective of species. Abscissa: approximate means of annual sea-surface temperature ranges at various localities. Ordinate: means of infection frequencies. Localities from left to right: Helgoland, Argentina, Chile, Brazil, Great Barrier Reef, Papua New Guinea[14]. Slope = 5.93, intercept = −65.62, r = 0.83, significance = 0.00004.

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10 Author's survey, most species near Coffs Harbour and Port Macquarie, northern New South Wales, 1 species at Melbourne (11 f.s., n = 180).
11 Author's survey, most species at Heron and Lizard Islands, 4 species near Port Moresby, Papua New Guinea. (28 f.s., n = 255.) 289 specimens of 16 species of very small Pomacentridae, Blenniidae and Gobiidae yielded 21 species of gill Monogenea. These are not considered because none of the other surveys include large numbers of small fish species.
12 Author's survey, Mar del Plata. (7 f.s., n = 404.)
13 Author's survey, Santos, Cananeia, Ubatuba (all in São Paulo State). (17 f.s., n = 414.)
14 Author's survey. Helgoland (10 °C, 1 f.s., n = 88); Argentina (13 °C, 1 f.s., n = 50); Valparaiso, Chile (15 °C, 1 f.s., n = 20); Brazil (22 °C, 5 f.s., n = 63); Great Barrier Reef (26 °C, 2 f.s., n = 21); Papua New Guinea (28 °C, 3 f.s., n = 39).

Host specificity indices of parasites and their application*

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Summary. Indices are defined which describe host specificity of parasites but can be applied to any association between organisms. The indices are used to analyze latitudinal differences in host specificity of marine Monogenea and Digenea.

Rohde[2] and Beaver[3] recently have compared host specificity of parasites at different latitudes. Such comparisons of parasite communities are difficult because indices which make use of all or much of the information, i.e. of intensities and frequencies of infection in different host species and of number of host species infected, do not exist. Akhmerov's[4] attempt to define host specificity as the reciprocal of the number of host species infected, uses only a minute fraction of this information and is, therefore, not satisfactory.

A good specificity index should use host numbers and the equitability (evenness) of infection, i.e. it should be inversely proportional to number of host species and evenness of infection of the hosts.

I propose the following 3 indices.

1. Index of host specificity based on intensities (densities) of infection.

$$S_i\,(\text{density}) = \frac{\sum \frac{x_{ij}}{n_j h_{ij}}}{\sum \frac{x_{ij}}{n_j}},$$ where S_i = host specificity

of i th parasite species, x_{ij} = number of parasite individuals of i th species in j th host species, n_j = number of host individuals of j th species examined, h_{ij} = rank of host species j based on density of infection x_{ij}/n_j (species with greatest density has rank 1). The specificity index of the whole parasite community can be defined as S_c (density) $= \sum (s_i/n_p)$, where n_p = number of parasite species in the community.

The disadvantage of the index is that no use is made of the number of host species examined. Therefore, in a small survey the indices often will be closer to 1 than in a large survey of the same population considering more host species. With regard to the index for the whole community, it will be changed not only by the enlarged host ranges of the species already recorded in the small survey, but also by the numbers and host ranges of additional parasite species found. Such changes are unpredictable and no correction for sample size can therefore be made, although such corrections are possible for individual indices. Correction for host species numbers, furthermore, is unrealistic because host species diversity is different at different localities and even complete surveys would have to be based on different species numbers. Errors due to sample size will be small if the surveys are of reasonable size, and comparisons of parasite populations from different localities should be made only on the basis of such large surveys. If there are several host species with equal rank, they should be treated as if they were species of subsequent ranks.

2. Index of host specificity based on frequencies (= prevalence = incidence) of infection (S_i (frequency)). This index uses the same formula as S_i (density), but x_{ij} = number of host individuals of j th species infected with parasite species i, n_j = number of host individuals of j th species examined, h_{ij} = rank of host species based on frequency of infection (species with highest frequency has rank 1).

3. Index of host specificity based on probability theory. If n_i = number of host species infected with parasite species