These conclusions are consistent with the observation of Schrauzer[3].

Our experimental results show that microstructures composed of molybdenum, iron and organic compounds can photocatalyze CO_2 reduction, N_2 reduction and water decomposition. In view of the abundance of reports in recent years which demonstrate that many transition metal complexes alone can perform these photocatalyses[12,13] and from the recent work of Yamase and Ikawa[14], it is not surprising that such catalysis is observed for these microstructures which use several transition metals as starting materials. However, this appears to be the first report for a photocatalytic role of molybdenum in carbon reduction[15]

The important concept which these observations lead to is *not* that these photocatalytic functions can be performed, but rather that these functions can take place concordantly in microstructures formed under geologically plausible conditions. These functions are characteristic of the procaryotes, in particular the blue-green bacteria, and our point is that mineral-organic microstructures can simulate these functions. Therefore, these microstructures clearly represent a likely metabolic stage between the nonliving and the living from the point of view of functional attributes. Hartman's[17] and Folsome's[18] conclusions that metabolism could have evolved from a simple rather than a complex environment is consonant with our findings.

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Niche width of parasites in species-rich and species-poor communities[1]

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Summary. Niche width of ectoparasites of marine fishes, as measured by host range and microhabitat width, is not affected by the number of species in a community. There is no reduction in species numbers of Monogenea due to greater numbers of other parasite species, and frequencies of infection with Monogenea are greater in tropical, species-rich communities.

Latitudinal gradients in species diversity are known for most groups of animals and plants[2]. Opinions differ about the mechanisms which allow so many tropical species to coexist. For theoretical reasons, it is usually assumed that in habitats with many species either the niches are narrower or they are more densely packed[3]. Recently, it has been suggested that a high diversity is maintained by frequent disturbances of intermediate severity[4], or by prevention of competitive equilibrium due to environmental fluctuations leading to periodic population reductions[5]. 'Solution of the problem is difficult because the niche is a highly abstract construct and to measure it is manifestly impossible'[6]. 'We can lower our sights, however, and, for suitably chosen organisms, make observations yielding quantitative measurements that can reasonably be interpreted as measures of niche width and overlap'[6].

In the following, ectoparasites of marine fishes and particularly Monogenea will be used as a model to study the mechanisms which permit coexistence of many species. Such parasites are an almost ideal model for several reasons. 1. The marine environment is more uniform than freshwater and terrestrial environments and gradients superimposed on latitudinal gradients are less important; 2. environmental variability can be further reduced by considering small habitats in the open water, i.e. the surface of fish; 3. the surface of fish and particularly the gills are habitats which can be examined accurately and quantitatively in a short time; 4. the distribution of ectoparasites in certain microhabitats can be accurately mapped; 5. many marine fishes are easily available in large numbers.

Evaluation of data from many surveys showed that there is an increase in species numbers of coastal marine fishes from high to low latitudes, and that species numbers are greater in the Pacific than in the Atlantic Ocean[2,7]. Species numbers of gill Monogenea increase even more strongly towards the equator, and they also are greater in the Pacific than the Atlantic[8]. Hence, communities of ectoparasites on tropical fish and particularly in the Pacific are generally richer in species than communities on cold-temperate fish.

In order to compare niche width of species in communities consisting of many and of few species of ectoparasites, 2 niche components are considered, 1. host range, and 2. size of microhabitat.

ad 1. Rohde[9,10] has shown that Monogenea have a similarly narrow host range at all latitudes, and there may even be a slight widening of the host range in warm Pacific waters, perhaps to be expected because of the large number of related host species in the tropical Pacific. No latitudinal differences are apparent, if host specificity is measured by the specificity index proposed by Rohde^{11,12}, which takes into account the equitability of infection in different host species.

ad 2. The microhabitats of all ectoparasites infecting the gills and the mouth cavity are considered, including those of the Didymozoidae, which - although endoparasitic - live close to the surface and are thus potential 'competitors' of ectoparasites. A diagram showing the parameters measured (or counted) is given in figure 1.

Pearson's correlation was used to test for a possible reduction in the number of preferred microhabitats due to 'competing' species. 'Preferred microhabitat' is a site which is preferred over all others at the 0.001 level (1 – sample χ^2). Nonparametric analysis of variance (Kruskal-Wallis test) followed by nonparametric multiple comparisons^{13} in some cases showed differences of increasing order of magnitude at the 0.05 level; such differences are not considered in figure 2 but would not affect the results. No correlation was found between the number of microhabitats and the number of parasite species, both when only gill parasites (figure 2, A) and when parasites on the gills and in the mouth cavity were considered (figure 2, B). This lack of correlation cannot be due to a sampling artefact, as indicated by the finding that fish species of which only a small number of specimens were examined, did not have fewer parasite species with smaller microhabitats than fish species of which many specimens were examined (Pearson's correlation, gill parasites of 1083 fish belonging to 32 species, parasites on the gills and in the mouth cavity of 1141 fish belonging to 29 species).

Reasons for the lack of correlation are that species in communities with few species do not expand into empty 'niche space', and conversely, that in multi-species communities there is often much overlap. Consequently, many potential niches are left empty, at least in those habitats which have one or few species only.

A possible objection to the assumption of 'empty' niches is that a host individual is a closely integrated unit which reacts as a whole to all parasites irrespective of their site. By this reasoning, only a certain number of parasite individuals and species can be carried and 'empty' microhabitats

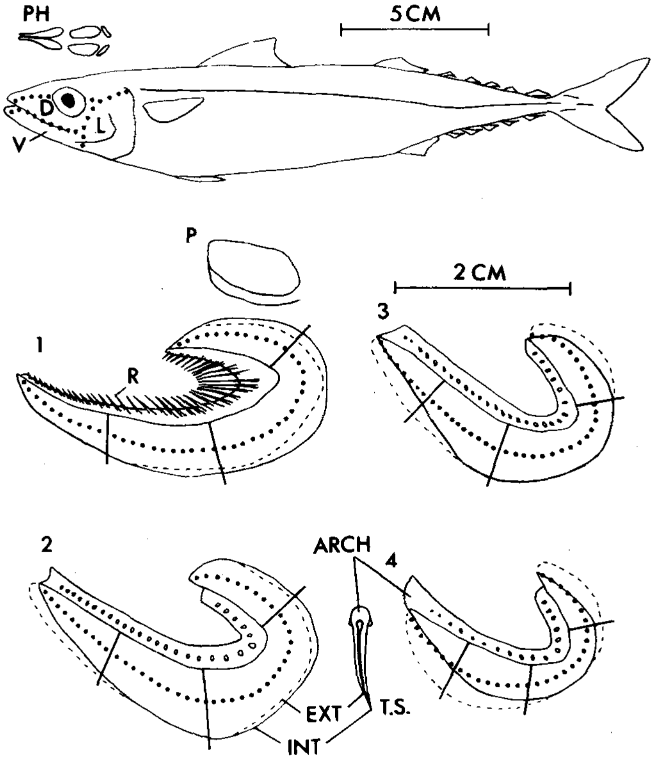

Fig. 1. Diagram showing microhabitats considered in the statistical evaluation. ARCH, gill arch; D, dorsal mouth cavity; EXT, external gill filament; INT, internal gill filament; L, lateral mouth cavity; P, pleurobranch; PH, pharyngeal plates; R, gill raker; T.S., cross section through gill; V, ventral mouth cavity. 1-4, Gills No. 1-4. The surface area of the external gill filaments is indicated by an interrupted line, that of the internal filaments by a continuous line, the border between basal and distal zone of the gill filaments by a dotted line (drawn only for the filaments with the largest surface area). The maximum number of preferred microhabitats is 1 dorsal mouth cavity + 1 ventral mouth cavity + 1 lateral mouth cavity + 1 pleurobranch + (1 gill arch × 4 gills × 4 longitudinal quarters × 2 internal or external surface) + (1 gill filament × 4 gills × 4 longitudinal quarters × 2 external or internal surface × 2 basal or distal half of filaments) = 1 + 1 + 1 + 1 + 32 + 64 = 100.

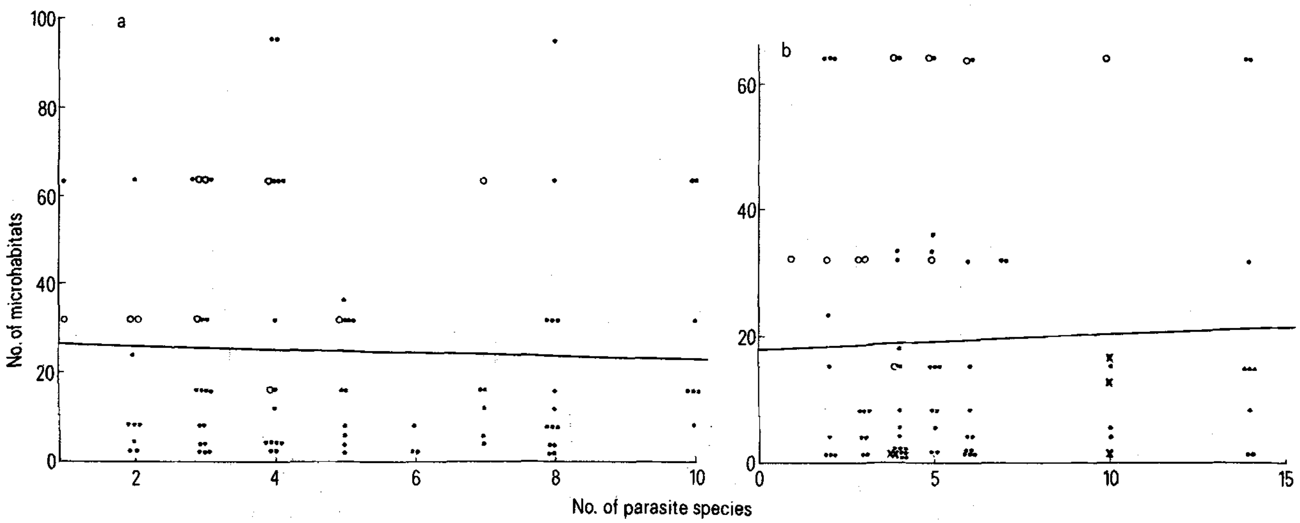

Fig. 2. Microhabitat width as a function of species numbers. 3A. Abscissa: No. of species of gill parasites per fish species. Ordinate: No. of preferred microhabitats. ○, cysts; ●, Copepoda and Monogenea. Slope = – 0.24, intercept = 25.95, r = – 0.024, sign. = 0.82. 3B. Abscissa: No. of species of parasites on the gills and in the mouth cavity. Ordinate: No. of preferred microhabitats. ×, Didymozoidae, ○, cysts, ●, Copepoda and Monogenea. Slope = 0.28, intercept = 17.63, r = 0.047, sign. = 0.67.

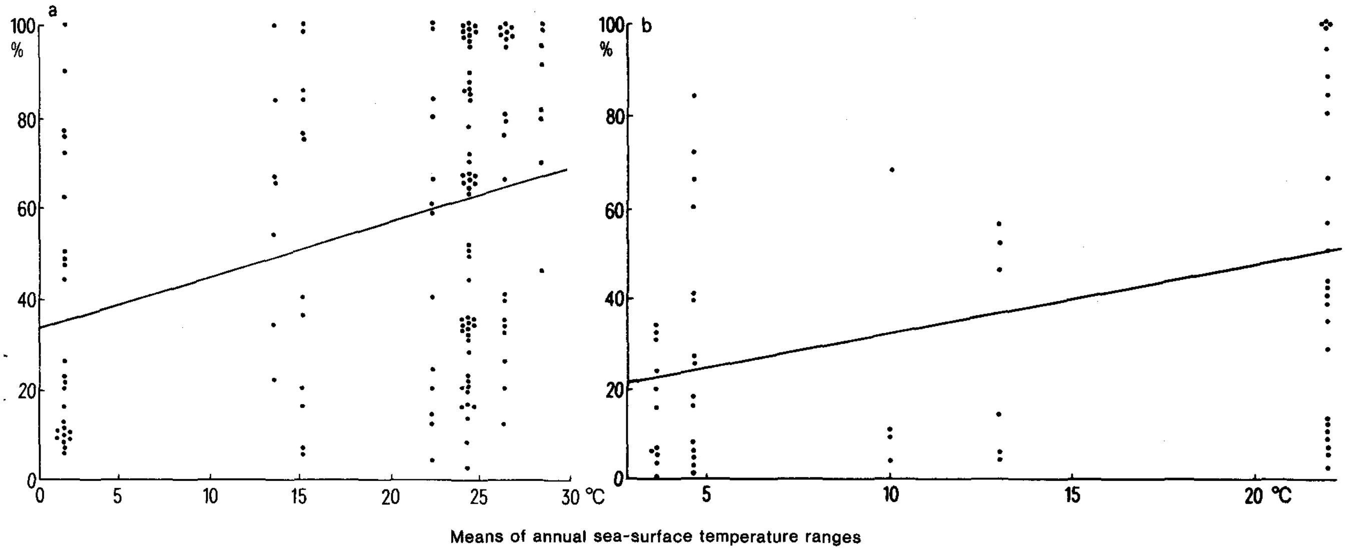

Fig. 3. Frequency of infection with Monogenea on the gills of marine teleosts at different latitudes in the Pacific (A) and Atlantic Oceans (B). Fish species without gill Monogenea not included. Abscissa: means of annual sea-surface temperature ranges. Ordinate: frequencies of infection (frequency = percent of individuals of a fish species infected with one particular species of Monogenea). *A*, Slope = 1.17, intercept = 32.81, r = 0.32, sign. = 0.0002. *B*, Slope = 1.44, intercept = 17.15, r = 0.38, sign. = 0.0026.

only seem to be empty, but the carrying capacity of the host is, in fact, utilized by species in other sites. If so, one would expect that host species with few species of Monogenea have a large number of other parasite species.

To examine this question, numbers of Monogenea species were compared by means of Pearson's correlation with numbers of other ectoparasitic species in the mouth cavity and on the gills (Copepoda, Isopoda, Didymozoa in Brazil, Argentina and southern Australia, 438, 424 and 285 fish of 17, 7 and 13 species respectively) and with numbers of all other species of ecto- and endoparasitic helminths (in the Barents Sea[14], White Sea[15] and Black Sea[16], 967, 1232 and 395 fish of 39, 25 and 30 species respectively). In no case was a negative correlation between number of Monogenea species and other parasite species found, although in some cases there was a positive correlation.

That habitats on fishes at least in cold-temperate seas are not filled to the limit, is further indicated by the finding that frequences of infection with gill Monogenea are even greater at low latitudes (figure 3). Intensities of infection are similar at all latitudes although the data for the Atlantic may indicate a possible reduction in infection intensities at low latitudes (Pacific, 138 values, slope 0.104, intercept 9.00, r = 0.033, sign. = 0.684; Atlantic, 59 values, slope = −0.95, intercept = 25.11, r = 0.33, sign. = 0.011). However, it has to be considered that most data at high latitudes were collected during the warm season when conditions for infection for most species are probably more optimal than during the cold season. Hence, intensities (and frequencies) of infection at high latitudes, measured over the whole year, are probably lower than the data indicate.

In summary, there is an increased relative species diversity (number or parasite species per host species) of Monogenea on the gills of marine teleosts in warm seas, and diversity is greater in the Pacific than in the Atlantic Ocean. Niche width, as measured by host range and number of microhabitats, however, is not affected by the number of species in the community. There is also no reduction in species numbers of Monogenea due to greater numbers of other parasite species, and frequencies of infection are even greater in warm seas. Infection intensities are usually very low, and similar at all latitudes. All this indicates that many potential 'niches', at least in cold waters, are not utilized, which is well in agreement with an evolutionary time hypothesis, according to which evolutionary rates are lower in cold environments and time has not been sufficient to fill all habitats[2].

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