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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

Host specificity of some Digenea of marine fishes in the White Sea. Data from Shulman et al.[5]. Total number of fish species examined = 31

Fish species	1	2	3	4	5	6	7	8	9	10	11	12	S_i (density)	S_i (frequency)	S_i ($1-P_{ij}$)
Lecithaster gibbosus															
No. of parasites found	14	12	4379	3	1	2	16	32	6	1	1	13			
No. of fish infected	10	5	11	1	1	2	3	7	5	1	1	2	0.99	0.54	0.61
No. of fish examined	21	95	15	7	83	32	84	21	82	64	3	117			
Hemiurus levinseni															
No. of parasites found	1	18	4	1	651	13	93	–	–	–	–	–			
No. of fish infected	1	1	3	1	51	10	13						0.77	0.64	0.77
No. of fish examined	15	1	83	38	83	143	21								
Prosorhynchus squamatus															
No. of parasites found	48	4000	11	2	1										
No. of fish infected	2	35	3	1	1	–	–	–	–	–	–	–	0.98	0.84	0.84
No. of fish examined	41	83	38	68	143										
Crepidostomum farionis															
No. of parasites found	6	1													
No. of fish infected	2	1	–	–	–	–	–	–	–	–	–	–	0.99	0.97	0.94
No. of fish examined	12	117													
Anisorchis opisthorchis															
No. of parasites found	2														
No. of fish infected	2	–	–	–	–	–	–	–	–	–	–	–	1	1	0.97
No. of fish examined	3														

i, and n_j = number of host species examined, the probability of finding a host species infected with i among n_j (assuming that sufficient individuals of each species are examined to detect the infection) is $P_{ij} = (n_i/n_j)$. There are 2 possibilities to use this probability for defining host specificity.

Firstly, host specificity could be defined as the reciprocal of P_{ij}, but to compensate for the number of host species examined, n_j would have to be introduced into the equation. Hence

$$S_i = \frac{1}{P_{ij}/_{nj}} = \frac{1}{n_i}$$

No use is made in this formula of host species numbers, frequency and intensities of infection, and the definition of host specificity is reduced to that of Akhmerov[4]. This index will not be used in the following.

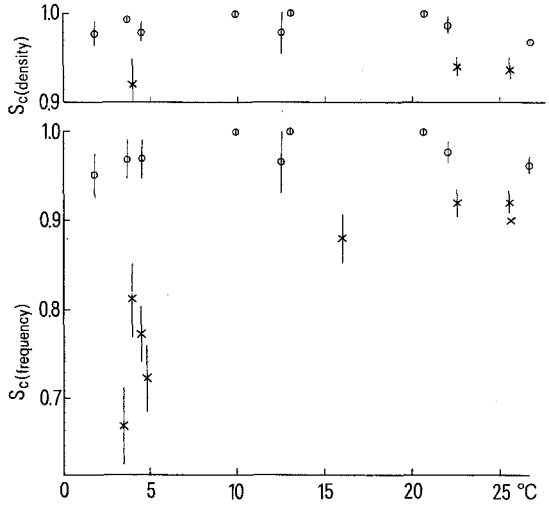
Secondly, host specificity could be defined as the probability of not finding an infected host species among all the host species examined:

$$S_i = 1 - P_{ij}.$$

In large samples (many host species examined), S_i approaches 1 for parasites restricted to a single host species. The disadvantage of this index is that, although host species numbers are used, no use is made of intensities and frequencies of infection. Furthermore, it is strongly affected by the number of species examined. For example, a parasite species occurring in 2 host species has a $S_i(1-P_{ij})$ of 0.99, if a total of 150 species has been examined, and of 0.90, if 20 species have been examined. The index is useful for comparison of populations only if sample sizes are almost identical, which is rarely the case, and it is therefore not used in the following.

Application of the first 2 indices to communities of marine Monogenea and Digenea shows that Si(density) is in most cases closer to 1 than Si(frequency). The reason is that, even though several host species may be infected, only 1 or a few usually are heavily infected (table). Among 25 species of Monogenea from 7 surveys, which had more than 1 host species, S_i(density) was larger than S_i(frequency) in 20 cases. Among 68 species of Digenea from 3 surveys with more than 1 host species, S_i(density) was largest in 53 cases. The figure shows specificity indices based on frequency and density of infection for marine Monogenea and Digenea at different latitudes. Both indices indicate a similar high specificity for Monogenea at all latitudes, whereas Digenea have a reduced host specificity at high latitudes, as indicated by smaller values of S_c(frequency). Nevertheless, Digenea in cold waters, in spite of the larger number of hosts, have clear preferences for some of these hosts and the values for S_c(density) therefore are similar at all latitudes.

All indices discussed above can be applied to higher taxa of parasites and hosts, e.g. to genera and families. The indices do not take into consideration whether different host



Host specificity of marine Monogenea (○) and Digenea (×) at different latitudes. Abscissa: means of annual seasurface temperature ranges. Ordinate: host specificity indices: S_c(density) and S_c(frequency). Data from various authors[6]. Note: parasite numbers are not given and S_c(density) can therefore not be calculated for some localities.

species belong to different genera and families, but normally there is a high degree of correlation between range of host species and range of higher host taxa, and an index based solely on species is therefore fully satisfactory.

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Cone mosaics in a teleost retina: Changes during light and dark adaptation

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Summary. The square mosaic pattern of retinal cones in the guppy, *Poecilia reticulata,* changes during dark adaptation into a row mosaic. The functional significance of this change is discussed.

In most teleosts, the visual cells show a mosaic-like arrangement, with cones the dominating elements and rods interspersed at random[2,3]. There are 2 standard types of mosaic: in the row mosaic the contact zones between the partners of double cones are linearly arranged; in the square mosaic, the double cones form a zig-zag pattern, with the contact zones of 2 adjoining double cones forming an angle of 60 or 90°. In both types of mosaics, single cones usually occur. They are spaced at equal distances, forming rows parallel to, or intersecting with, rows of double cones[4,5-7]. A change from row to square pattern occurs during the ontogeny of a few teleosts[8-10]. Row and square patterns are also found in the same retina, occurring each in a different region[11,12].

In the guppy, *Poecilia reticulata* P., the square mosaic extends over the whole bulbus, except for a narrow peripheral growth zone[13]. However, when retinal fragments, obtained by immersing the eyes in calcium-free Ringer solution, were examined, they invariably showed a row mosaic (results unpublished). It was therefore decided to establish whether the entire retina, on being subjected to Ca-free Ringer, reveals a row mosaic, and if so, to investigate the causes of this pattern change.

Materials and methods. Adult fish (eye diameter > 1.6 mm), kept under a 12-h day and night cycle, were used. Light and dark adapted retinae were obtained by microdissection in Ringer solution either with or without Ca. For light microscopical analysis, whole intact retinae were mounted on slides and viewed with a Nomarski differential interference microscope (Zeiss), with Polaroid camera attachment. For electron microscopy, retinae were fixed in glutaraldehyde, postfixed in osmium tetroxide and embedded in araldite[17]. Ultrathin sections were stained with uranylacetate and lead citrate and viewed with a Philips 201C electron microscope.

Results and discussion. Light microscopy of whole light adapted retinae, freed in Ca-free Ringer, revealed that the cones over the whole eye bulbus had assumed a row mosaic pattern (figure 1). The occurrence of a row mosaic, in place of the square mosaic, could be attributed to the incubation medium used. Ca-free Ringer is used for retinal preparations, because it facilitates the detachment of the sensory retina from the adjoining interdigitating pigment epithelium and the pigmented chorioid[14]. Similarly, the absence of calcium may loosen the contacts between the different types of cones, thereby causing the disintegration of the square mosaic. The square mosaic in the guppy consists of double cones and long single cones in close apposition, whereas the short single cones are relatively isolated. The ellipsoids of long single and double cones show subsurface cisterns along the contact zone. Subsurface membranes also characterize the contact zone between the double cone partners (figure 2A). More vitreally, double and long single cones gear with each other by so-called fins (villous expansions of the cell membrane in the myoid region)[15].

Retinae treated with Ca-containing Ringer gave varying results. With this method, laborious microdissection is needed to separate the pigment epithelial processes which

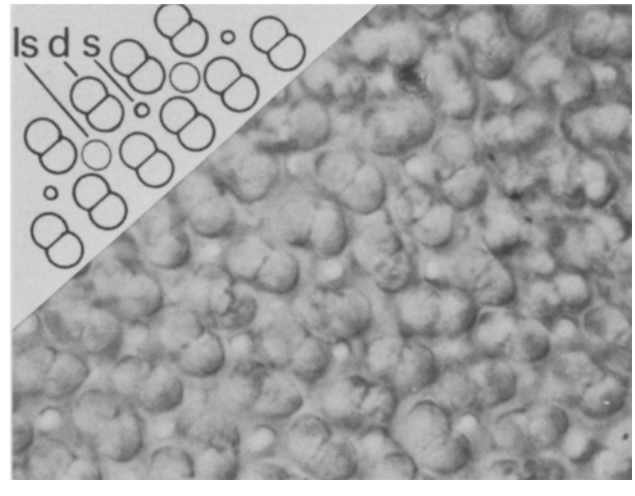

Fig. 1. Visual cell layer of the guppy, *Poecilia reticulata* (eye diameter > 1.6 mm). Photomicrograph taken by polaroid camera attached to Nomarski differential interference microscope, focussed to the level of double cone ellipsoids. Retina freed from pigment layers in calcium-free Ringer solution. Double cones are arranged in a row pattern, separated by rows of alternating long and short single cones. Abbreviations: d, double cone; ls, long single cone; s, short single cone. Magnification × 900.