SIMPLE ECOLOGICAL SYSTEMS, SIMPLE SOLUTIONS TO COMPLEX PROBLEMS?

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ABSTRACT: Simple ecological systems, i.e. gills of marine fish, are used to look at some ecological patterns. Gills may vary in size, numbers of individuals and species of ectoparasites infecting them, and latitude where collected. All but one or a few of these variables can be kept constant in 'natural experiments'. The following conclusions are reached: many potential niches are empty, i.e. species have not yet evolved for them, since fish of similar size and habits in the same locality, or at different latitudes, or at different depths, contain different numbers of parasite species, and since only some parasite species harbour hyperparasites; microhabitat restriction may be stabilized or enhanced in order to facilitate mating of parasites; much of the evidence for the evolutionary significance of interspecific competition is doubtful, but whereas there is little or no evidence that interspecific competition has been an important evolutionary force leading to niche segregation, there is much evidence for the significance of mechanisms leading to reproductive isolation; by ruling out the effects of climatic stability, climatic predictability, spatial heterogeneity, productivity, stability of primary production, competition, rarefaction, predation, and ecological time, it is concluded that only an evolutionary time hypothesis can give a general explanation for latitudinal gradients in species diversity, although the other factors may have local effects or secondarily enhance the gradients; longer 'effective' evolutionary time at low latitudes is likely to be due to accelerated evolution as the result of faster selection and possibly faster mutation rates; a greater proportion of small species of marine teleost fish with their smaller microhabitats in tropical Pacific than in cool Atlantic waters indicates a possible reduction in niche width of tropical animals, however, there is no evidence for greater specialization and greater species packing of parasites in warm environments; no evidence was found that area per se is a primary force determining species diversity, an important factor determining species diversity of ectoparasites of marine fish, at least in some cases, is diversity of the host group; Thorson's rule, that non-pelagic development of marine benthic invertebrates increases with latitude, is shown to apply to a group of marine parasites, the Monogenea: the only explanation for the phenomenon consistent with characteristics of the Monogenea is suggested to be an effective method of getting to a host. It is stressed that conclusions based on the study of simple systems cannot be automatically applied to more complex ones, but simple systems must be understood if complex systems are to be understood. Some suggestions for future studies are outlined.

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Introduction: Can the Big Questions of Ecology and Evolution be Answered?

Numerous papers and some recent reviews show that community ecology has moved away from emphasis on a supposedly "well ordered equilibrium world" (Colwell 1984) to a more "pluralistic" theory (Schoener 1986a) (reviews in Price et al. 1984a; in particular Colwell 1984; Price 1984a,b; Price et al. 1984b; Schoener 1986a). Price et al. (1984b) and Price (1984a) emphasized

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that nonequilibrium conditions are common in which not interspecific competition but patchiness, disturbance, and other factors are important, and that alternative solutions to any problem exist in many species. Colwell (1984) stressed the significance of biological details of species, and according to Schoener (1986a) the new emphasis in community ecology is on differences, <u>not</u> similarities. We are heading towards a "pluralistic" theory of community ecology with a risk of becoming lost in a "vast encyclopedia of special cases"; at present, "both model construction and data gathering are too inchoate for any kind of empirical pronouncement, despite what we sometimes hear" (Schoener 1986a). In addition, theoretical considerations suggested that some of the earlier assumptions of ecological theory were tautological and as such could not make empirically testable predictions (e.g. Peters 1976; see also Slobodkin 1961, Armstrong and McGehee 1980 with regard to the competitive exclusion principle).

Certainly with all this in mind, Slobodkin (1986), in his plea for minimalism in science, pointed out that there is the "uncomfortable possibility that the "big questions" of ecology and evolution are simply too big to be answered", and "As science progresses, there may occur periods during which the imagination of investigators exceeds their capacity to acquire data and formally organize information. ... At these junctures, ... it may help to reconsider extremely simple situations in order to dispel the rhetorical clouds."

In the following I consider relatively simple ecological systems. I hope to show that even some "big questions" can be tackled by using such systems.

Data from studies of parasites, mainly copepods and monogeneans, on the gills of fish will be used to reach conclusions concerning some general ecological questions, including existence and number of empty niches, the relative significance of reinforcement of reproductive barriers and interspecific competition for niche segregation, the cause(s) of latitudinal gradients in species diversity and niche width, and the importance of area for determining species richness. Finally, a more special ecological phenomenon, the decrease of non-pelagic development of marine invertebrates with latitude (Thorson's rule), will be discussed.

The ecological systems considered are the gills of marine teleost fishes. Typically, there are four gills on each side of the head each consisting of a bony gill arch which may have or may not have gill rakers, and two rows of numerous gill filaments. In addition, there usually is one small pseudobranch consisting of a single row of filaments on each side of the head cavity. The surface area of the gills and the number of gill filaments tends to be larger in fast-swimming pelagic than in sluggish bottom-dwelling fish. The number of individuals and species of ectoparasites found on a single fish individual or species may vary; some may be without any parasites, others may have hundreds or even thousands of more than twenty species. Fish heads can be obtained easily in large numbers and the parasites fixed <u>in situ</u> by dropping the heads into 5% to 10% formalin. To study species diversity and microhabitat utilization of ectoparasites, gills are examined under a dissecting microscope and parasites mapped on drawings of the gills, which can be done within a short time: 1/2 hour to several hours, depending on the size of the gills and the number of parasites. Data can be evaluated quantitatively by dividing the gills into longitudinal sections and determining whether parasites occur on the gill arches or filaments, gills 1,2,3 or 4, the external or internal filaments, the basal or distal parts of the filaments, and the anterior or

posterior surface of the filaments (for details see Rohde 1978b, 1982) (Fig. 1). Number of filaments can be counted and the surface area of the gills measured with the aid of a planimeter. All parameters possibly affecting parasites except for one or a few can be kept constant, at least to a degree reasonably to be expected in biological studies, for instance by examining gills of several fish all belonging to one species in the same habitat differing in the number of parasite species or individuals. Such fish may not be exactly identical in some other parameters, but for the study of inter-actions between parasite species these parameters can be neglected, similar to physical experiments in which only those factors are kept constant considered relevant for the experiment.

The two major groups of ectoparasites are the Monogenea (flatworms) and Copepoda (crustaceans), and most studies have concentrated on these. This review also emphasises these two major groups. Occasionally Isopoda (crustaceans) and Protozoa are also found. There are very few ectoparasitic Digenea (flukes). Details of several studies of gill parasites have been published previously in specialized journals (e.g. Llewellyn 1956; Lambert and Maillard 1974, 1975; Rohde 1976a, b, 1977, 1978b, c, 1979b, 1980a, b, e, 1981a, 1982, 1984a, b, c, 1985, 1986, 1987b; Rohde and Hobbs 1986; Roubal 1981; Roubal et al. 1983; Ramasamy et al. 1985), and it is the aim of this review to make such data on ecological communities usually not considered by ecologists available to the non-specialist reader interested in general ecological questions, in the context of current ecological literature. Some important biological aspects of the two major groups of parasites are discussed in the following.

Monogenea are Platyhelminthes and have a direct life cycle, usually infecting gills and skin of fishes. There are no free-living species. They feed on blood and/or epithelial cells and mucus. Hatching is often induced by a factor produced by the host (e.g. Kearn 1986) and the probability of host infection may be enhanced by synchronization of hatching and host behaviour (review in Rohde, 1984a; Kearn 1986). Species have ciliated or, in some cases, non-ciliated larvae. All species of one family, the Gyrodactylidae, are viviparous producing non-ciliated juveniles, and infect other hosts by contact-transfer. Most Monogenea are specific to one or a few closely related host species (for details see Rohde 1984a, c). All species are hermaphroditic, but cross-fertilization (sometimes obligatory) has been demonstrated in some species (e.g. Kearn, 1965, 1970, in press). Copulatory organs (both male and female) are often of extraordinary complexity. All species show preferences for certain microhabitats which often are very narrow. Juveniles may slowly migrate to the site preferred by adults (e.g. Kearn, 1970).

Those Copepoda parasitic on fish infect their hosts as larvae, juveniles or adults. Adults of some species may leave a host and infect another. Even mating may sometimes occur in the free environment. Usually there is only one host in the life cycle, but there is evidence that some species have two (Kabata, 1981). Little is known on how copepods locate their hosts (Kabata, 1981). Species may have wide or very narrow microhabitats, microhabitats of juveniles and adults may be different, and adults may be very mobile or (the great majority) completely sessile. Food may be mucus, blood and epithelial cells, and even more internal tissue like connective tissue (Kabata 1970), 1981). All Copepoda are bisexual, sometimes with extreme sexual dimorphism.

Monogenea and Copepoda are of approximately equal significance as ectoparasites of fish.

Empty niches

The questions of whether and how many empty niches exist, what determines the selection and segregation of niches by animals, and the relative
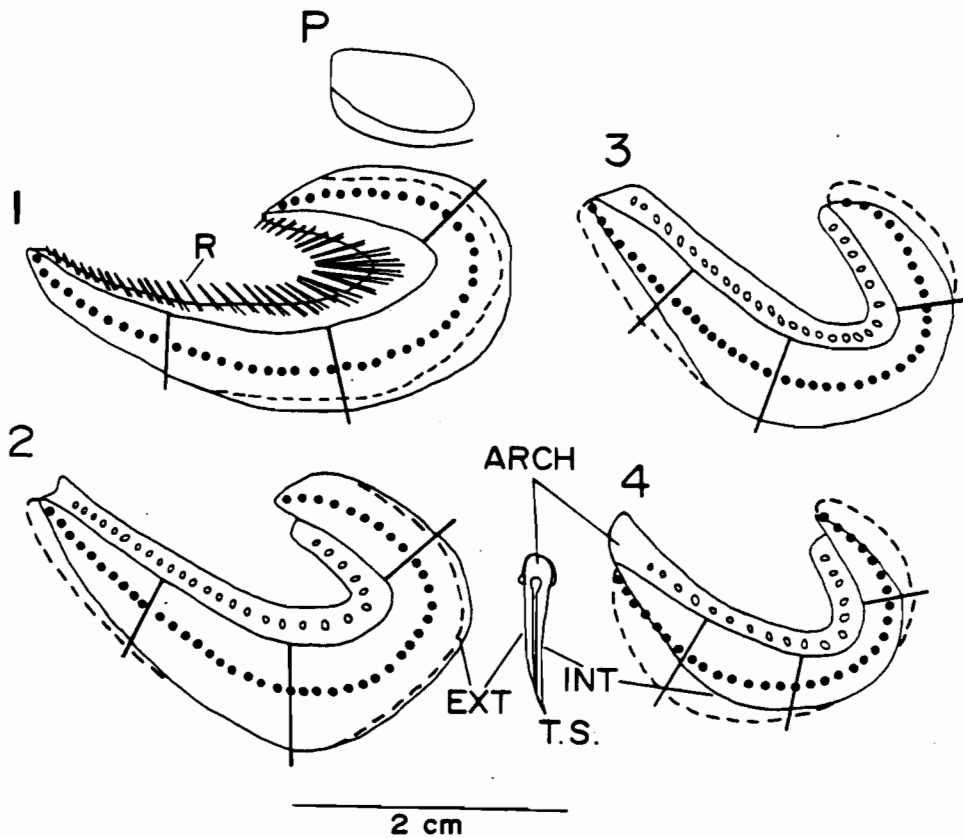

FIG. 1. - Diagram showing microhabitats on the gills of marine fish. ARCH = gill arch, EXT = external gill filament, INT = internal gill filament, P = pseudobranch, R = gill raker, T.S. = cross-section through gill, 1-4 = gills 1-4. The surface area of the external gill filaments is indicated by an interrupted line, that of the internal filaments by a continuous line, the border between basal and distal zones of the gills by a dark-dotted line, the border between the longitudinal quarters by continuous lines. The maximum number of microhabitats is (1 gill arch x 4 gills x 4 longitudinal quarters x 2 internal or external surfaces) + (1 gill filament x 4 gills x 4 longitudinal quarters x 2 external or internal surface x 2 basal or distal halves of filaments) + 1 pseudobranch = 97. Redrawn after Rohde (1982).   '
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significance of reinforcement of reproductive barriers and interspecific competition for niche segregation are all interconnected. Nevertheless, they will be treated separately to achieve greater clarity.

If niche is defined as "the sum total of the adaptations of an organismic unit" (Pianka 1983), there can be no "empty niches", since there can be no adaptations if there is no organism. If we adopt Hutchinson's (1957) definition of an ecological niche as a multidimensional hypervolume determined by a number of environmental (physical and biotic) variables within which a species can exist, the difficulty disappears, since the definition does not make reference to adaptations of an organism. Hutchinson's definition, as also accepted by Schoener (1986b) will be used here. Recent discussions of some aspects of the niche concept including "vacant" niches are by Herbold and Moyle (1986) and Walker and Valentine (1984).

Gills of fish, because of their relatively simple and uniform structure (compared for instance with complex habitats like forests or lakes), are uniquely suitable for estimating numbers of potential niches. Rohde (1979b, see also 1976a, b, 1977, 1978b), considered the most important niche dimensions of ectoparasites of (freshwater and marine) fish and calculated, mainly on the basis that many fish species harbour many species of ectoparasites in different microhabitats, that several 100,000 species of ectoparasites could exist on the more than 25,000 extant fish species. However, to date only approximately 5,000-6,000 species of ectoparasites have been described. Even if the assumption is made that there are 10 times as many undescribed species, only a very small proportion of all available niches is filled, i.e. species have not yet evolved for them. It must be stressed that even some very small fish species, e.g. Pomacentridae, were shown to harbour several species of ectoparasites, whereas other much larger fish harbour very few. Furthermore, some ectoparasites were shown to carry hyperparasites (examples in Rohde 1982), but most marine ectoparasites are without them; hence, there appears to be a vast reservoir of empty niches at this level, since it is highly unlikely that, for example, some parasitic nematodes or trematodes should be able to support hyperparasites, and others not, in particular if species are related and are of similar size. Further evidence for the availability of many empty niches comes from recent comparative studies of gill Monogenea of surface and deepwater fish in Australia. Rohde (1987b) examined the gills of 1862 fish of 46 species (26 families, 7 orders) from New South Wales coastal surface waters and recovered 72 species of Monogenea on those 37 fish species of which at least 10 fish were examined. He examined the gills of 1563 fish of 66 or 67 fish species (35 families, 15 orders) from deepwater in approximately the same region and recovered only 18 species of Monogenea on those 45 fish species of which at least 10 specimens were examined. Thus, relative species diversity (no. of Monogenean species/no. of fish species examined) is 1.95 and 0.40 respectively. Campbell et al. (1980) and Mamaev and Avdeev (1981) found similarly small numbers of Monogenea on deepsea fish of the north- eastern Atlantic and northwestern Pacific, respectively. Species numbers of other ectoparasites also were very small in the surveys of Rohde (1987b) and Campbell et al. (1980), they were not discussed by Mamaev and Avdeev (1981). Data available at present indicate that there are many empty niches on the gills of deepsea fish. If it should be shown that species richness in the deepsea only seems to be smaller because of the greater geographical patchiness in the distribution of parasites (which is not likely), the fact would remain that communities on the gills at least in large areas are not saturated with species (i.e. species for them might exist but for some unknown reason have not infected fish in some areas). As in the case of

hyperparasites, there is no evidence that deepsea fish are inherently incapable of supporting more species of parasites, and it certainly seems more likely that evolution has not overcome the difficulties in infecting fish in the vast volume of deeper water, and that this is responsible for the small number of parasitic species.

Finally, comparison of the ectoparasite faunas of related fish of similar size and habits in the same geographical area reveals that more species can be accommodated on at least some fish species. For example, there are three species of Sparidae in coastal New South Wales waters, i.e. Acanthopagrus australis (max. length 55 cm), Chrysophrys auratus (max. length 81 cm), and Rhabdosargus sarba (max. length 40 cm). Roubal (1981, see also Roubal et al., 1983) found 8 species of Monogenea, 1 species of Digenea and 11 species of Copepoda on the body and gills of the first species, and Roubal et al. (1983) found 6 species of Monogenea, 11 species of Copepoda and 2 of Isopoda on the second species. On the third species, I found only a single species of Monogenea, 5 of Copepoda, and 1 larval isopod (unpublished observations). Sample size of all three fish species was sufficient to permit the conclusion that their parasite faunas are more or less completely known, although an additional species has since been recovered from Acanthopagrus. There is no reason to assume that Rhabdosargus could not support as many parasites as the other two species, particularly in view of the fact that much smaller fish species were shown to carry up to 5 species of Monogenea and several copepod species (examples in Rohde 1979b).

A possible objection to the assumption that there are vacant niches is that a host is a 'closely integrated unit' which reacts as a whole to all parasites irrespective of their site, i.e. the carrying capacity of a host with apparent empty sites may in fact be fully utilized by parasites in other sites. To examine this question, Rohde (1981a) compared numbers of Monogenea species with numbers of other ectoparasite species on 438, 424 and 285 fish of 17, 7 and 13 species from Brazil, Argentina and southern Australia respectively, and with all other species of ecto- and endo-parasites on 967, 1232 and 395 fish of 39, 25 and 30 species in the Barents Sea, White Sea and Black Sea respectively. In no case was a negative correlation between number of Monogenea species and other parasitic species found, although in some cases there was a positive correlation. With regard to deepwater parasites, there is a general paucity of parasite species and not only of ectoparasites (e.g. Campbell et al. 1980).

Another possible objection to the existence of empty niches is that genetic differences between different host species (even closely related ones) determine the number of parasite species they can carry. Thus, the blood or mucus of a fish species with many parasite species, one might assume, somehow can support more species of blood or mucus-feeding Monogenea than the blood or mucus of a host species with a smaller number of parasite species. Although it is obvious that all species differ genetically in some way, there is no evidence for the assumption that such differences determine species numbers of parasites, and this seems highly unlikely in view of the fact that tropical fish with extremely different habits and corresponding differences in gill structure and probably blood etc. composition (e.g. fast swimming scombrids and sluggish sparids) have a similar parasite species richness, whereas fish from high latitudes but with similar habits, have a much poorer parasite fauna.

Several authors have concluded that there are many empty niches for other groups of animals (e.g. Bray 1987 for intestinal helminths of Anarhichas lupus in the North Atlantic; Kennedy et al. 1986 for freshwater fish of Jersey, Channel Islands; Lawton 1982 for herbivorous insects on the above- ground parts of bracken, Pteridium aquilinum; see also Price 1980, 1983, 1984; Simberloff 1981).

Vast numbers of vacant niches are likely to exist at least for parasites (see also Price 1984b), although evidence for the existence of empty niches in some groups of animals is ambiguous, as pointed out by Herbold and May (1986). An accurate estimate of the number cannot be given, but it may well be that several times as many species could exist as there are at present, because "the greater the number of species, the greater the potential for specialized predators and for colonization by parasites, hyperparasites, symbionts, commensals, etc...." (Rohde 1978b, see also 1977), i.e. niche diversification is self-augmenting, as pointed out by several earlier authors, (e.g. Dobzhansky, 1950; further references in Rohde 1978a). This leads to the apparent paradox that the tropics, because of their greater species diversity, may have more empty niches than temperate and cold environments (Rohde 1978b).

Some authors, e.g. May (1974) have concluded that ecological evidence favours the view of saturation of habitats with species ('every continent has a fauna reasonably proportionate to its area and climate, and each main fauna has a reasonable proportion of herbivores, carnivores, etc.', May 1974). Faunas considered in large-scale comparisons are usually mammals and birds, that is, vagile animals close to the top of the ecological hierarchy. It may well be that 'reasonably' similar faunas in different areas may simply mean that evolution has reached roughly the same stage in different areas at this particular point in time, at least for groups with great vagility or capacity for dispersal, or that a certain equilibrium between herbivores, carnivores, etc. is maintained at all stages of evolution, irrespective of the number of species.

The view that more species can be accommodated, should not be used as a justification for uninhibited introduction of foreign species into as yet undisturbed habitats. The fact that vacant niches exist does not mean that there is always room for more species of all kinds. It is likely that certain communities have all the species of certain (more likely large than small) sizes and kinds as they can accommodate. Furthermore, natural acquisition of additional species by communities may often be a slow evolutionary process.

The mating hypothesis of niche restriction

Rohde (1977) suggested that narrow habitats facilitate contact among individuals of a species and thus mating; selection may therefore have favoured niche restriction. Evidence given by Rohde (1976b, 1977, 1979b, 1980a, 1984c) is as follows: 1. Microhabitat restriction leads indeed to increased intraspecific contact; 2. adult stages typically have more restricted microhabitats than asexual larval stages or asexually reproducing species; 3. sessile and rare species have more clearly restricted micro-habitats (because it seems likely that mating becomes increasingly difficult with decreasing mobility and population density); 4. there is direct experi-mental evidence that microhabitats become more restricted at the time of mating.

Table 1 gives an example of microhabitat restriction in some Monogenea and Copepoda of one fish species (other examples in Rohde, 1977, 1980a,b, 1981a, 1984a) and Table 2 shows the obvious, that microhabitat restriction of para-

sites on fish species has a significant effect on intraspecific contact, and it must be stressed that, although Monogenea are hermaphodritic, the complexity of their copulatory organs (and direct cross-fertilization for most species is important. Even in monogenean species with simple copulatory organs which appear to permit self- fertilization, cross-fertilization may be obligatory (e.g. Entobdella soleae, see Kearn, in press). Copepoda are dioecious and therefore obligatory cross-fertilizers. With regard to the
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	Gill No.				Longitudinal			No.	Filament External	Internal
	1	2	3	4	1	2	3	4		
Gotocotyle bivaginalis	19	11	53	53	33	47	22	36	49	49
G. secunda	52	42	20	10	16	23	30	43	44	38
Pricea multae	31	41	49	35	44	16	30	51	60	51
Pseudothora- cocotyle indica	78	26	3	1	21	14	39	30	74	25
P. gigantica	0	11	23	0	0	7	27	0	25	11
Caligus infestans + C. asymmetricus	2	15	12	6	23	5	0	6	?	?
Pseudocycnoides armatus	20	10	6	5	0	0	0	44	?	?

TABLE 1. Number of parasites on the gills of 14 Scomberomorus commerson from Heron Island, Great Barrier Reef. Note: No preference for left or right gills. The first 5 species are Monogenea, the others Copepoda. Underlined data are significantly greater than the others. (One $-$ sample Chi^2 test and Mann-Whitney test for data pairs; one $-$ sample Chi^2 test, analysis of variance after logarithmic transformation of the data followed by a multiple range test, and non-parametric analysis of variance = Kruskal-Wallis test followed by a non-parametric multiple comparison for all other data.)
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second point, many examples can be given. For instance, adults of the digenetic trematode Stephanostomum baccatum live in the rectum (and lower intestine) of several marine fish species (Wolfgang 1955), whereas the larvae (metacercariae) are found in various somatic muscles, the operculum,skin, fins, pericardium, liver and mesentery of marine fish (Wolfgang 1954a,b, MacKenzie and Liversidge 1975). But even metacercariae may sometimes show at least a certain microhabitat restriction (e.g. Madhavi, 1986). Asexual cysts are usually randomly spread over all gills (several examples in Rohde 1980b).

Examples for the third point can be found in Rohde (1980b). Two species of sessile copepods on Trigla lucerna at Helgoland, Neobrachiella impudica and N. bispinosa, have much smaller microhabitats than the mobile copepods Caligus diaphanus and C. brevicaudatus on the same host, and a small ancyrocephaline monogenean occurring in large numbers on Hyporhamphus quoyi in New Guinea is randomly spread over all gills, whereas rarer species on other fish in the same region have clearly restricted micro- habitats.   In
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| | In contact with individual of: | | |
	same species	other species	none
Gotocotyla bivaginalis	92	15	33
G. secunda	71	9	42
Pricea multae	93	18	52
Pseudothoracocotyle indica	100	1	10
P. gigantica	33	0	1
Pseudocycnoides armatus	40	0	14

TABLE 2.   Intra- and interspecific contact among individuals of 6 species of gill parasites of Scomberomorus commerson at Heron Island, Great Barrier Reef.   Note: the first 5 species are Monogenea, the last species is a sessile copepod. Many of the specimens not in contact occurred in single or light infections. Data from Rohde (1977).
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considering such cases, it must be kept in mind, however, that some species occupy larger microhabitats when occurring in large numbers than when they are scarce (e.g. Ramasamy et al. 1985), which somewhat reduces the force of this argument.

The most dramatic evidence for the fourth point was recently provided by Kamegai (1986): juveniles (diporpae) of the monogenean Diplozoon nipponicum are spread over all gills of Carassius carassius auratus until the 4th day after infection.   They then gather on one gill and copulate for life (in Diplozoon two adults are fused permanently).   Experiments with cortisone acetate indicate that a chemotaxis is responsible for this "gathering phenomenon".   A less dramatic gathering of maturing monogeneans is also indicated by data given by Lambert and Maillard (1974, 1975): mapping of juveniles and adults of two species of the monogenean Diplectanum showed smaller microhabitats in the adults, apparently due to migration on the gills. Kearn (in press) observed that the monogenean Entobdella soleae, after transfer to another host individual (the sole Solea solea) migrates from the upper to the lower surface via the head; some transferred individuals, espec- ially adults, spend longer than others on the head, thereby improving the chances of meetings and spermatophore exchange between parasites arriving on the host at different times.   The behaviour of nonogeneans described here corresponds to a certain degree to that of the trypetid flies, the majority of

which use certain host plants to "rendezvous" for mating (Zwölfer 1974). It must be stressed, however, that microhabitats do not always become more rest-ricted at the time of mating. Many species have other means of mate-finding, and others have such narrow microhabitats that a further restriction for mating does not seem necessary.

Ward (1987) constructed a model to examine the optimal settling behaviour of organisms with a limited amount of time available for dispersal, in an environment containing two types of habitat or host. One prediction of the model was that, if mating occurs after settling (which, with very few exceptions, is always the case in parasites of fishes), males and females should be "equally and strongly habitat-specific. The prediction lends support to Rohde's (1979) conclusion that failure to find mates is an important factor limiting the host and site ranges of parasites." The model should also apply to the hermaphrodites among the parasites, since such species may be obligatory cross-fertilizers (see above).

Segregation of niches

We are here concerned not with how two species modify each other's microhabitat when they co-occur, but with the evolutionary causes of microhabitat and, more generally, niche segregation. Numerous observations of single-species infections of fish with ectoparasites have shown that preferences for certain microhabitats of ectoparasites, at least to a large degree, are not affected by the presence of other parasite species and therefore probably genetically determined, which does not exclude the possibility that different developmental stages select different sites and that site preference may sometimes also be partly determined by environmental conditions, such as crowding or O_2- saturation (shown for some freshwater Monogenea). Random selection of niches in a largely empty 'niche space' will often result in complete or partial niche segregation, even if species interactions have not occurred in evolutionary history and are not occurring now. Nevertheless, data like those in Table 1 for Gotocotyla bivaginalis - G. secunda and Pseudothoracocotyla indica - P. gigantica, indicating different microhabitat preferences of congeneric species on the same host, suggest that species interactions may have been responsible at least partially for segregation. The question arises whether interspecific competition or reinforcement of reproductive barriers has led to segregation in such cases. Frequently, the fact that segregation occurs is uncritically used as evidence that interspecific competition has occurred in the past, occasionally it is with equal lack of critical examination used as evidence for reinforcement. Thus, Sogandares-Bernal (1959) and Martin (1969) explained the segregation of trematodes in the intestine of their hosts as due to reinforcement, without giving evidence.

To study the question of whether competition or reinforcement has been responsible for segregation of species, Rohde and Hobbs (1986) examined the microhabitats of 35 species of ectoparasites of 6 fish species, 19 of them occurring in congeneric pairs or triplets on one host. Statistical analysis showed that congeners overlapped less than non-congeners. Many authors would explain this by the supposedly more intense competition between closely related species. However, ectoparasites of fish use the same resources, whether related or not, i.e. space for attachement and food provided by the host (for definition of 'resource' see Wiens 1984). Most polyopisthocotylean monogeneans, whether related or not, feed on blood, as shown by many histo-chemical and electron microscopic studies (e.g. Rohde 1980c). Other

monogeneans and copepods feed on mucus, epithelial cells, tissue fluid or blood, or a combination of these (Rohde 1984a, references therein). All these food sources are in unlimited ('infinite' in Thomson's 1980 sense) supply as long as the host is alive, i.e. they do not represent limiting factors. Furthermore, requirements for blood etc. on the gills and on other parts of the body cannot be responsible for spatial segregation because these resources can be obtained from all parts of the gills and body. As pointed out by Rohde and Hobbs (1986), this leaves only one niche dimension for which the parasites may 'compete' with resulting spatial segregation, that is space for attachment. 'Competition' for space, however, is not more severe in related species. For example, a copepod permanently attached at a certain site makes that site unsuitable for attachment by a monogenean. Greater segregation of congeneric species than of unrelated ones cannot therefore be the result of interspecific competition, which leaves reproductive isolation as the factor responsible. Rohde and Hobbs supported this conclusion by observations on copulatory organs of congeneric species with various degrees of overlap. They found that congeners entirely or largely segregated spatially, have more or less identical copulatory organs, whereas congeners which live in the same microhabitats and on the same host, have completely different copulatory organs (Figs. 2, 3). For example, the monogeneans Kuhnia scombri and K. sprostonae live on the gills and the pseudobranchs respectively, of Scomber scombrus in the North Sea; their male copulatory organs are almost identical. The monogeneans Lamellodiscus acanthopagri, L. squamosus and L. major live in the same microhabitats on Acanthopagrus australis (and only on that host species) on the coast of southeastern Australia (Fig. 4); their male and female copulatory sclerites differ strongly (Roubal 1981). It seems that reinforcement of reproductive barriers and not interspecific competition has led either to spatial or morphological segregation.

A critical examination of some reports using spatial segregation of parasites as evidence for interspecific competition shows that reinforcement of reproductive isolation may be a more likely explanation. For example, Schad (1962, 1963) examined in detail the distribution of 8 species of the nematode genus Tachygonetria (3 subsequently transferred to Mehdiella, see Petter 1966) in the intestine of the Greek tortoise, Testudo graeca. Four species have a paramucosal distribution, the other four are found in the lumen; species in each group are segregated to various degrees although all show some overlap. Species differ in body size, length of the male copulatory sclerites and male genital papillae, among other characters. If species occurring in the lumen are arranged in order of overlap, we obtain the series Tachygonetria numidica, T. macrolaimus, T. dentata, T. conica. These species differ in spicule length (measured on drawings in Petter 1966) as follows: approximately 55, 120, 40, 120 μm. It seems that species with the greatest spatial overlap are reproductively segregated by copulatory spicules of different size. The situation in paramucosal species is not as clear: M. uncinata, M. microstoma, T. robusta, M. stylosa, and 100, 100, 100, 550 μm. However, in addition to spicule length there are differences in body length and in genital papillae around the male gonopore which may lead to reproductive isolation, and the possibility must also be considered that unstudied chemical factors may contribute. Evidence, although not conclusive, shows that the interpretation

by Schad (1963) of segregation as the result of competition is at least doubtful.

The relative significance of interspecific competition and reinforcement of reproductive barriers has been discussed particularly with regard to the phenomenon of 'character displacement', divergence of two partly overlapping species in the area where both occur sympatrically (Brown and Wilson 1956; Miller 1967; recent discussion by Schoener 1986b; see also Grant's (1972) subsequent widening of the definition by excluding any reference to allopatric populations). Little is known about how common the phenomenon is (Arthur 1982), but many authors accept it uncritically as evidence that interspecific competition has occurred in the evolutionary past (e.g. Emlen 1973, Putman and Wratten 1984, Begon et al. 1986; Bradshaw and Mortimer 1986 for some cases), although already Brown and Wilson (1956), and in particular Miller (1967) have stressed that there may be two explanations for the phenomenon, i.e. competition ("ecological character displacement") or reinforcement of reproductive barriers ("Wallace effect", Grant 1966, see also Murray 1972 who questioned the validity of the distinction between the two aspects). Some studies seem to have provided conclusive evidence for the importance of competition in character displacement (e.g. Fenchel 1975a, b; Grant 1975), but several authors have pointed out that the ecological aspect of character displacement for many situations is weak (e.g. Grant 1972; Wilson 1975; Connell 1980; Arthur 1982). Concerning ectoparasites of fish, Rohde (1979a, b, 1981c) demonstrated that polyopisthocotylean monogeneans which use the same food (blood) may differ vastly in the light- and electron-microscopic structure and size of organs involved in blood-feeding, even if blood is obtained on the same hosts and in the same or widely overlapping microhabitats (see below). This casts further doubt on the assumption that such differences have evolved as the result of competition: they may be fortuitous.

The general conclusion, then, must be that there is little or no evidence for the view that interspecific competition has been an important evolutionary force leading to niche segregation in ectoparasites of fish, but that there is much evidence for the significance of mechanisms leading to reproductive isolation. The evolutionary significance of competition will be more fully discussed in the next section.

Evolutionary significance of interspecific competition.

The question of the ecological and evolutionary importance of interspecific competition has been central in ecological and evolutionary theory (for recent reviews see Schoener 1974, 1982, 1986, Tilman 1982, Lewin 1983, various papers in Kikkawa and Anderson 1986). Different authors have interpreted the significance of interspecific competition differently (e.g. Miller 1967, Lawton and Strong 1981, Schoener 1983, Connell 1983, Ferson et al. 1986, Schoener 1985, Underwood 1986). Parasites were very little considered in these discussions, although they represent the vast majority of animal species. Arndt (1940), including only 'classical' parasites, counted 10,000 parasites out of a total 40,000 animal species then known in Germany, and Price (1977), on the basis of a study of the British fauna, estimated that more than half of all animals are parasitic, excluding temporary parasites such as mosquitoes and leeches but including herbivorous insects associated over long periods with one host plant. Rohde (1976c) estimated the number of parasite species infecting the 1000 fish species in the southern part of the Great Barrier Reef to be close to 20,000, and seven animal phyla are comprised entirely of parasites (Rohde 1982). Many parasites are not likely to compete
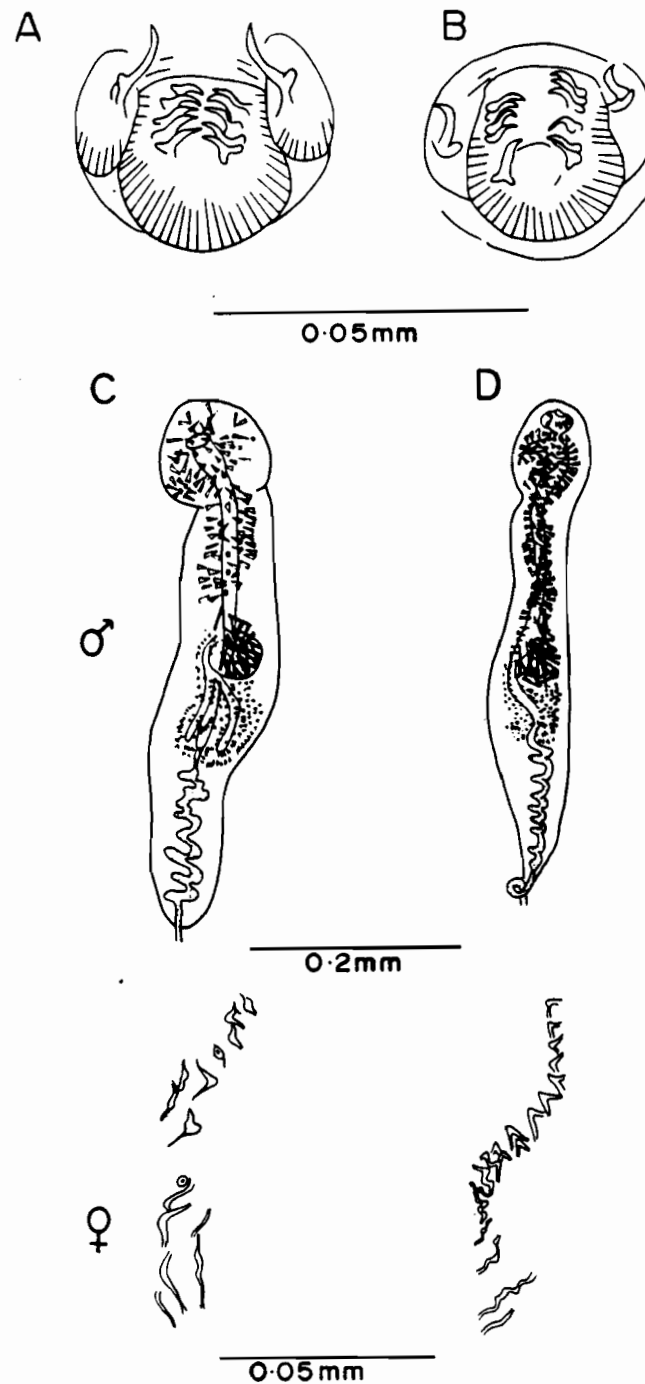
FIG. 2. - Copulatory organs of Monogenea with segregated microhabitats. A = Kuhnia scombri on the gills of Scomber scombri at Helgoland; B = K. sprostonae on the pseudobranchs of S. scombri at Helgoland; C = Vallisia sp. 1 on the gills of Oligoplites saliens in Brazil; D = V. sp. II on the pseudobranchs of O. saliens in Brazil. Modified acc. to Rohde and Hobbs (1986).
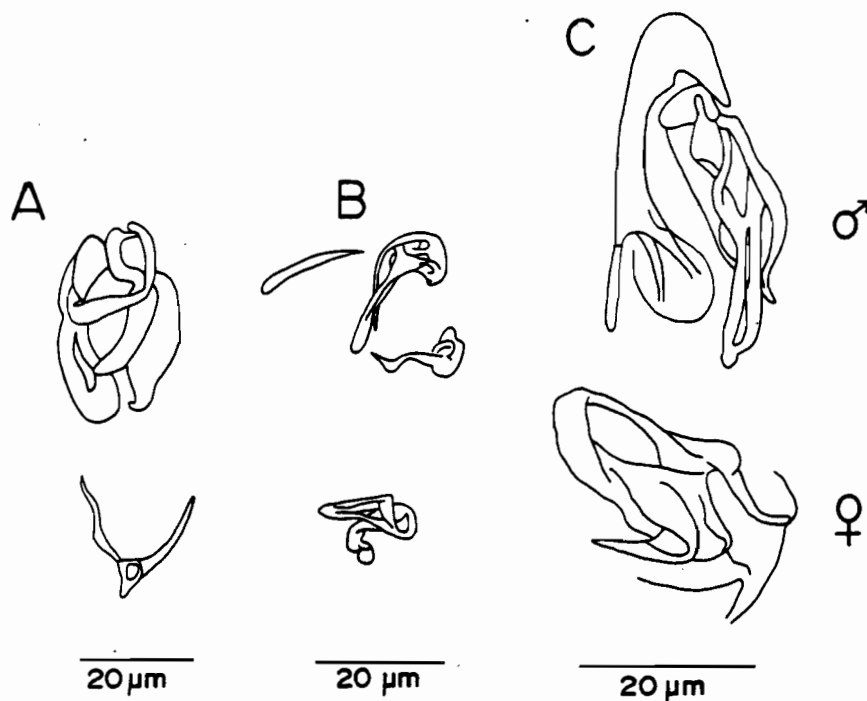***

FIG. 3. - Copulatory organs of Monogenea with identical microhabitats on the gills of Acanthopagrus australis in southeastern Australia. A = Lamellodiscus acanthopagri; B = L. squamosus; C = L. major. Modified acc. to Roubal (1981).
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with each other because they usually occur in very low population densities (e.g. Rohde and Hobbs 1988). It would be easy to provide numerous examples where a species does not expand into adjacent microhabitats even if 'competing' species are absent (see also Lawton 1982 for parasitic (phytophagous) insect communities), although competition in parasites has been demonstrated in some cases (e.g. Rohde 1982; Dobson, 1985; Holland 1987; Stock and Holmes 1988; review by Christensen et al. 1987 and is likely to be more prevalent in 'interactive' than 'isolationist' (non- interactive) helminth communities (Holmes 1986; Holmes and Price 1986; Stock and Holmes 1988).

One indicator for the evolutionary significance of interspecific competition that has been proposed is a reduction in the number of sympatric congeners compared with the number expected if sympatric congeners were randomly acquired (Pianka 1983; for negative results to find such a reduction in lizards see Pianka 1973; Terborgh and Weske 1969 for birds).

Congeneric species of ectoparasites infecting one species of marine fish are very common (e.g. Rohde 1976a, b, 1977, 1980b); I recovered six species belonging to the same genus of Monogenea from one fish species at Heron
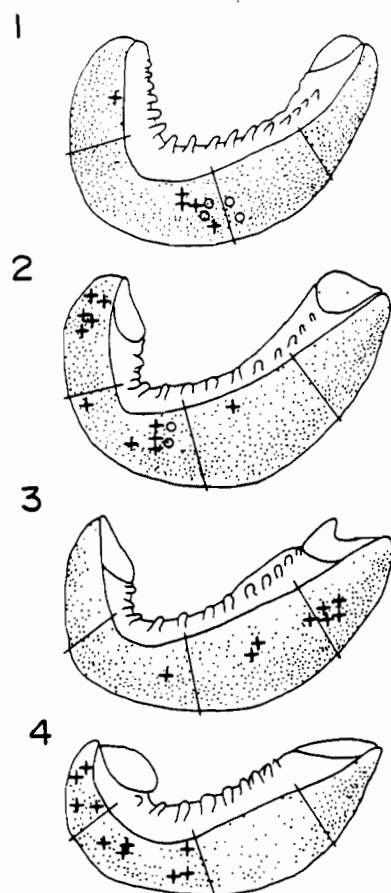
FIG. 4. – Distribution of the monogeneans <u>Lamellodiscus</u> <u>acanthopagri</u>
(●), <u>L</u>. <u>squamosus</u> (+), and <u>L</u>. <u>major</u> (O) on the gills of <u>Acanthopagrus</u>
<u>australis</u>. Data from Roubal, 1981.
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Island, Great Barrier Reef, and data from some surveys are presented in Tables
3 and 4. The data show that species of all groups of endo- and ectoparasitic
parasites examined can co-occur with species of the same genus in one fish
species. The best examined fish species in eastern Australia is the bream
<u>Acanthopagrus</u> <u>australis</u>. 16 of its 32 species of ectoparasitic copepods
andmonogeneans were found to co-occur in congeneric triplets and quintets, and
one third of its 24 species of endoparasitic helminths (Digenea, larval
Cestoda and Nematoda, Acanthocephala) co-occur in congeneric pairs. Even in
cold waters, i.e. the Barents and White Seas, with relatively few species of
parasites, almost half of all fish species harbour at least one congeneric
pair of ecto- or endoparasite, and one fish species harboured four congeneric

pairs. On the other hand, none of the deepwater fish examined in southeastern Australia had congeneric Monogenea, expected in view of the paucity of the deep sea monogenean fauna. Considering the fact that most surveys contain many fish species of which single or few specimens only were examined, it is certain that proportions of parasite species occurring in congeneric assocations and of fish species harbouring congeneric parasite species is much greater than indicated in Tables 3 and 4. In view of the great species diversity in tropical seas particularly of the Indo-Pacific, it seems likely that congeneric parasites are most common there. Although accurate estimates of fish harbouring congeneric parasites and of proportions of parasite species occurring as congeners are not possible on the basis of the scanty data available at present, especially for warm seas, it does not seem unlikely that fish species without congeners are the exception rather than the rule, and that a majority of parasite species co-occur with species of the same genus in one host species.

Although it is difficult or impossible to establish a null hypothesis, i.e. to predict what number of congeners could be expected, since many parasites are strictly host-specific and their presence in a particular area on certain fish species does not imply that they can infect others, the number of congeners infecting the same fish species is so great that a reduction of congeners occurring on the same host species due to competition must appear highly unlikely.

The argument could be widened, applying to any species of animal using the same limiting resource in a small habitat, for instance to multiple infection of snails with parasites (trematode larvae). Rohde (1981b) examined a population of the littoral snail __Planaxis__ __sulcatus__ at Heron Island, Great Barrier Reef, infected with seven species of trematode. Multiple infections in all combinations occurred as expected if infections were random. It has to be stressed, however, that randomness is difficult to define. Conceivably, infections of snails with certain parasites may be extremely localized within a snail population, due to particular behaviour patterns of the final hosts (e.g. birds or fish). Furthermore, several parasite species may be transmitted by the same final host making the likelihood of multiple infections very great. All this implies that a sensible null hypothesis can be established only on the basis of a sound knowledge of the biology of hosts and parasites. Other authors (references in Rohde 1981b) reported that multiple infections were sometimes more and sometimes less common than expected, although none of the authors analyzed data statistically. In spite of the caution necessary for interpreting the data, it seems that interspecific effects (in some cases due to predation of one species on the other) occur only rarely.

Much morphological evidence for an evolutionary effect of interspecific competition also is not convincing. For example, selection to avoid competition was held responsible for bringing about differences in size of feeding organs of sympatric species (the famous 1.3 ratio found by Hutchinson, see Christiansen and Fenchel 1977; Schoener 1986b; Eadie __et al__. 1987, for recent discussions and references). Different-sized feeding organs are thought to permit exploitation of differently-sized food and thus reduce niche overlap (for discussions see Schoener 1986b; Eadie __et al__. 1987). A simple model to examine the validity of the hypothesis would be to compare the feeding organs of co-occurring species using identical food. This was done by Rohde (1979b), who compared the size of the pharynx and buccal suckers of five species of Monogenea from the gills of the Spanish mackerel, __Scombero-__

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Host species (no. exam.) and locality	Number of congeneric parasite species	Total number of parasite species (% congeners)	Reference
Acanthopagrus australis (200)	5 Caligus (C) 3 Lernanthropus (C)	32 (ectoparasites only)	Byrnes (1985a,b, c, 1986a,b,c,d, 1987)
Eastern Australia	3 Polylabroides (M) 5 Lamellodiscus (M)	(50%)	Roubal (1981)
A. berda (320) Northern Australia	2 Ergasilus (C) 3 Caligus (C) 2 Lernanthropus (C) 2 Polylabroides (M) 4 Lamellodiscus (M)	29 (ectoparasites only) (45%)	Byrnes (1985a, b,c, 1986a,b,c, d, 1987)
A. butcheri (320) Southern Australia	4 Caligus (C) 2 Polylabroides (M) 3 Lamellodiscus (M)	23 (ectoparasites only (30%)	Byrnes (1985a, b,c, 1986, a,b, c,d, 1987)
A. latus (120) Northwestern Australia	5 Caligus (C) 2 Lernanthropus (C) 4 Lamellodiscus (M)	25 (ectoparasites only) (44%)	Byrnes (1985a, b,c, 1986a,b,c, d, 1987)
A. australis (449) Northern New South Wales	2 Digenea 2 larval Cestoda 2 larval Nematoda 2 Acanthocephala	11 Digenea 5 larval Cestoda 4 larval, 8 adult Nematoda 4 Acanthocephala (33%)	Bahrudin (1985a)
Chrysophrys auratus New Zealand (122) Southern and Southeastern Australia	4 Caligus (C) 2 Lepeophtheirus (C)	17 (ectoparasites only, excluding Isopoda)(35%)	Roubal et al. (1983)
15 species (130) Northern New South Wales	4 Eimeria	8 (Coccidia only) (50%)	Molnar and Rohde (1987)
66 or 67 species (1563) New South Wales deepwater	---	>19 (gill Monogenea only) (0%)	Rohde (1987b)
122 species (2097) Hawaii	60 species in congeneric pairs, triplets or quartets	147 (Monogenea only) (41%)	Yamaguti (1968) 1 record added from Rohde and Watson 1985b
62 species (3904) North Sea	8 Caligus in congeneric doublets and triplets	39 (Copepoda) only) (21%)	Boxshall (1974), 1 record added from Rohde 1980b

TABLE 3. Numbers of congeneric species of ecto- and endoparasites infecting marine fishes. Note that some of the surveys include many fish species of which only single or a few specimens were examined. Percentages of congeners are therefore certainly much greater than indicated. C - Copepoda, M - Monogenea.

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Number of fish species (locality)	Number of fish species with congeneric parasites (%)	Group of parasites	Reference
15 (Northern New South Wales	2 (13%) (2 pairs)	Coccidia only	Molnar and Rohde (1987)
66 or 67 (New South Wales, deepwater)	0 (0%)	Monogenea only	Rohde (1987b)
122 (Hawaii) (maximum 1 quartett)	35 (29%)	Monogenea only	Yamaguti (1968) 1 record added from Rohde and Watson, 1985b
46 Scombridae (mainly warm and warm-temperate oceans)	22 (48%) (maximum 1 quintett)	Copepoda only	Cressey and Cressey (1980) 1 record added from Boxshall (1974)
127 (Britain)	38–43 (30–34%) (Maximum 1 quintett + 1 triplet)	Copepoda only	Kabata (1979)
62 (North Sea)	12 (19%)	Copepoda only	Boxshall (1974)
29 (White Sea)	14 (48%) (including 1 species with 4 pairs, 2 with 3 pairs and 3 with 2 pairs of congeners)	Ecto- and endo-parasites	Shulman and Shulman-Albova (1953)
46 (Barents Sea)	20 (43%) (maximum 1 triplet + 1 doublet)	Ecto- and endo-parasites	Polyanski (1966)

TABLE 4   Numbers of marine fish species infected with congeners. Note that many fish were examined in very small numbers and percentages of species with congeners are therefore certainly much greater than indicated. For numbers of fish examined in some of the surveys see Table 3.
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morus commerson, on the Great Barrier Reef. All five species belong to the
Polyopisthocotylea which are known to be blood feeders (e.g. Rohde 1980c).
Size of the organs change with size of the parasites, but there are
considerable differences between maximum sizes both of pharynx and suckers of
the various species. The ratios for buccal suckers of the pairs closest to
each other, beginning with the largest suckers, are 1.2, 1.2, 1.2 and 1.4,
rather close to Hutchinson's ratio of 1.3. For pharynx the ratios are 1.0,
1.1, 1.3 and 1.0. Competition for food cannot explain the differences, and
preference for different microhabitats (Table 5) is an unlikely explanation in
view of the large overlap. Rohde (1979a, 1981d) also found differences at the
ultrastructural level between polyopistho-cotylean Monogenea using the same
food resource, blood.

As shown in the previous sections, evidence from gill parasites indicates
that many vacant niches are likely to exist, hence niches have probably
evolved largely at random without interference by other species. Selection
may enhance or stabilize niche restriction to facilitate mating, and
reinforcement of reproductive barriers probably has been responsible for niche
segregation in all or at least most of the cases of likely biotic interactions
which have been well analyzed. Our general conclusions then must be that
interspecific competition at least between ectoparasites of fish, is not the
predominant evolutionary force it is often thought to be, although it very
probably has some significance. This is well in agreement with the conclusion
reached by Connell (1980) that "the notion of co-evolutionary shaping of
competitors niches has little support at present" (see also Ramensky 1924,
Gleason 1926, Andrewartha and Birch 1954, Wiens 1977, Brooks 1985).
Interspecific competition is most likely to have evolutionary significance in
vagile animals of large body size, such as birds or mammals, or in animals
with great vagility, occurring in large populations such as free-living
insects (Rohde 1980a), because such animals are most likely to exhaust
limiting resources and overlap with species requiring similar resources.

Latitudinal gradients in species diversity

One of the most consistent and conspicuous latitudinal gradients in
nature, with few exceptions, is that of increasing species diversity towards
the equator (see reviews by Pianka 1966, 1983, Rohde 1978a; for fossil
examples Emlen 1973; recent studies of tropical insect faunas by Erwin 1982,
see also May 1986). Many explanations for the gradients have been given (see
Pianka 1983) but the prevalent view is that "Overall, the latitudinal gradient
lacks a clear and unequivocal explanation" (Begon et al 1986, p. 804). Pianka
(1983) and Rohde (1978a) stressed that one has to look for primary factors
(see Poulsen and Culver 1969), i.e. abiotic ones, as final causes.

In the following, I shall attempt to give a general explanation for the
latitudinal gradients in species diversity, mainly using data from gill
parasites of marine fish. There is an enormous increase in species numbers of
marine fish from high to low latitudes (Rohde 1978b, 1982 p.138), and since
most fish in warm waters have at least one and often several species of
Monogenea which are highly host-specific (Rohde 1978c, 1982 pp. 105, 144), it
is obvious that there must be a corresponding increase in absolute species
numbers of Monogenea towards the equator. Rohde (1980e) has shown that there
is not only an increase in absolute species numbers, but also in relative
species diversity, i.e. number of Monogenea species on the gills per host
species. To give some examples, Roubal (1981) and Roubal et al. (1983) found

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Species	Maximum diameter of pharynx (mm)	Maximum diameter of buccal suckers (mm)	Microhabitat (see also Table 1)
Gotocotyla bivaginalis	0.08	0.17	Filaments of gills 1-4, but gills 3 and 4 more strongly infected.
G. secunda	0.09	0.10	Filaments of gills 1-4, but gills 1 and 2 more strongly infected.
Pseudothoracocotyla indica	0.06	0.07	Base of filaments of gills 1 and 2, rarely of gill 3.
P. gigantica	0.09	0.12	Base of filaments of gills 2 and 3.
Pricea multae	0.06	0.14	Filaments of gills 1-4.

TABLE 5   Maximum size ((length + width)/2 in mm) and microhabitat preferences of five species of Monogenea Polyopisthocotylea on the gills of Scomberomorus commerson at Heron Island, Great Barrier Reef. Data from Rohde (1976a, 1979b).
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8 species of Monogenea on the gills and body of Acanthopagrus australis and 6 species on Chrysophyrys auratus, in warm-temperate coastal waters of northern New South Wales, Australia, and Rohde (1976a) found 5 species on the gills of Scomberomorus commerson in the southern part of the Great Barrier Reef. Cold-water fish, on the other hand, typically have not more than one species of Monogenea. Gradients may even be steeper than shown by Rohde (1980e), because surveys in the tropics are smaller than those at high latitudes, based on smaller samples per species. On the other hand, recent observations of additional gyrodactylid species in northern seas (Kulachkova 1985) may somewhat raise relative species diversity figures at high latitudes.

Characteristics of their habitat enable us to eliminate some of the explanations listed by Pianka (1983) for the Monogenea. Climatic stability and predictability do not differ consistently between cold and warm seas. Although temperature is more constant throughout the year in tropical and Arctic-Antarctic than in temperate waters, there are sometimes extreme temperature fluctuations in shallow tropical and subtropical waters (for instance on coral reefs) during the tidal and day-night cycles. Thus, temperature in small rock pools (without fish) at Heron Island, Great Barrier Reef (23° 27'S) was shown to fluctuate between approximately 25 and 40°C in a few hours (Rohde 1981b), and similar (or greater) fluctuations are likely to occur in some pools on reef flats which have permanent fish populations. Spatial heterogeneity also is not greater at low latitudes: counts of gill filaments and measurements of the surface area of 34 coldwater and 31

warmwater species of teleost fish showed that small territorial fish have the smallest gills with few filaments, and such fish are relatively more common in warm than in cold seas (see below; also Hughes 1984 for differences between fast and sluggish fish). It is well known that productivity is not greater in warm than in cold waters, and stability of primary production is not likely to be of great significance for the Monogenea, possibly excepting situations of fish mortalities due to algal bloom, etc. Since there are more species on the gills of tropical than of cold-water fish, greater competition might be expected. However, it has been shown in the previous sections that interspecific competition does not appear to be of great importance, and Rohde (1981a) has shown that intensities of infection with ectoparasites vary greatly at all latitudes and are not higher at low latitudes, although frequencies (prevalences) appear to be somewhat higher. This indicates that neither inter- nor intraspecific competition are likely factors responsible for greater species diversity in warm waters. Rarefaction depends on the effects of adverse conditions which certainly are not consistently greater for marine fish at low latitudes. Predation on ectoparasites is due to cleaning symbionts, which were reviewed by Rohde (1982). There are more studies of cleaning symbiosis in warm seas because of the more pleasant diving conditions, but cleaner fish, some of them highly gregarious and occurring in large numbers, are known from colder waters. There is insufficient evidence for assuming that cleaning is more important at low latitudes, and little is known about its ecological effects. Furthermore, as stated above, intensities of infection do not show a latitudinal trend, and frequencies of infection are even higher near the equator, which appears to indicate that both are not lowered more significantly in warm than in cold seas by cleaners.

This leaves two of the factors listed by Pianka, evolutionary and ecological time. Concerning the ecological time hypothesis, Rohde (1978a) referred to earlier publications by other authors and pointed out that temperate regions, particularly in the oceans, had a long undisturbed history and have probably been in existence as long as tropical ones. Furthermore, there is no reason why marine fish, except perhaps some territorial or highly specialized forms, and their parasites with them should not shift laterally during periods of temperature change (see Rohde 1986). Ecological time, therefore, is not a likely explanation for the gradient.

The only factor which is left as a general explanation for larger species numbers at low latitudes is evolutionary time. The conclusion reached here on the basis of studies of fish parasites was earlier reached by Rohde (1978a, b) using other evidence as well (see also Southwood 1961; Lawton and Price 1979). In particular, spatial heterogeneity, competition, rarefaction and predation, if they are indeed sometimes greater in the tropics, are the consequence and not the cause of greater species diversity. Thus, the great spatial heterogeneity on coral reefs is due to the great number of coral and other species. However, all this does not mean that these factors do not have any effect on diversity. All or some of them may well have local effects and enhance the latitudinal gradient secondarily: for example, more predatory species in the tropics may well keep population densities of prey down and conceivably accelerate speciation even further.

In conclusion, only a time hypothesis assuming longer 'effective' evolutionary time in warm environments, can give a general explanation of latitudinal gradients in species diversity, although other factors may

secondarily enhance the gradients. Since actual time available for evolution has been the same at all latitudes, the reason for longer 'effective' time is likely to be a greater evolutionary speed at low latitudes (Rensch, 1959), due to generally accelerated physiological processes and a greater number of generations per year leading to faster selection, and possibly due to faster mutation rates at high temperatures (Rohde 1978a,b, references therein; also Emlen 1973, references therein). The importance of temperature is also compatible with the finding of reduced species diversity of gill Monogenea on deepsea fish (see above). The statement that the greatest diversity in the sea is found at about 2000 m depth (Begon et al. 1986), although true for some groups, is certainly wrong if applied to all marine animals, particularly if one considers the great diversity on coral reefs.

The objection by Putman and Wratten (1984) to a time hypothesis, that it states the obvious, is observation rather than a true explanation and does not explain what allows communities to become more diverse, would be relevant only if all habitats at all latitudes were saturated with species. But we have seen above that there are probably many vacant niches, an upper limit of species numbers has not been reached at any latitude, and ecological 'explanations' for the differences, such as competition, predation, spatial heterogeneity etc., are therefore really only descriptions of what characterizes communities of different diversity, and not explanations.

The most convincing arguments against an evolutionary time hypothesis are based on paleontological evidence, for example the fact that Siluro-Devonian brachiopods replaced each other rather than partitioned niches (Boucot 1978), and that, more generally, benthic invertebrate communities have had rather have had rather fixed numbers of species over long periods. This is thought to indicate definite controls on rate and timing of allopatric speciation and not a random process in time, as well as a fixed carrying capacity for shell organisms (Boucot 1975, 1978). May (1974) concluded that paleontological evidence favours the view of a 'real constancy' of taxa over geological time, although the possibility cannot be ruled out that constancy in the number of taxa is an illusion and that there is no limit to the number of taxa in a given environment.

In considering paleontological evidence, it must be kept in mind that fossilizable organisms represent a minute proportion of all animal species. Hardly any of the parasitic species which represent over half of the animal species (see above 'Evolutionary significance of interspecific competition') and the large numbers of small insects recently discovered by insecticide fogging (see beginning of this section) can be expected to fossilize (in spite of the few amber fossils found). Even if some fossil groups appear to have constant species numbers over time, there may still be an overall effect of evolutionary time, particularly obvious in those groups which depend on others and lag behind in diversification, e.g. parasites.

Latitudinal gradients in niche width

Greater species numbers in the tropics are often thought to result in denser species packing (e.g. MacArthur and Wilson 1967; MacArthur 1972). Data from parasites of marine fish permit testing of this hypothesis. Niche dimensions tested are host range (host specificity), microhabitat width on the host, and equitibility of infection of host populations.

Rohde (1981a, 1982) distinguished host range and host specificity. Host range is the number of host species found to be infected with a parasite species irrespective of how heavily and frequently the various host species

are infected, whereas host specificity takes into account intensity and frequency (prevalence) of infection. Host specificity can be measured using the specificity index proposed by Rohde (1980d).

$$S_i \text{(density)} = \frac{\Sigma \dfrac{x_{ij}}{n_j h_{ij}}}{\Sigma \dfrac{x_{ij}}{n_j}}$$

where s_i = host specificity of the ith parasite species; x_{ij} = number of parasite individuals of ith species in jth host species; n_j = number of host individuals of jth species examined; h_{ij} = rank of host species j based on density of infection $\dfrac{x_{ij}}{n_j}$ (where highest rank is "1"). The same formula is used for calculating S_i (frequency) = host specificity based on frequency of infection (x_{ij} = number of host individuals of jth species infected with parasite species i; n_j = number of host individuals of jth species examined; h_{ij} = rank of host species based on frequency of infection). The closer to 1, the greater the host specificity.

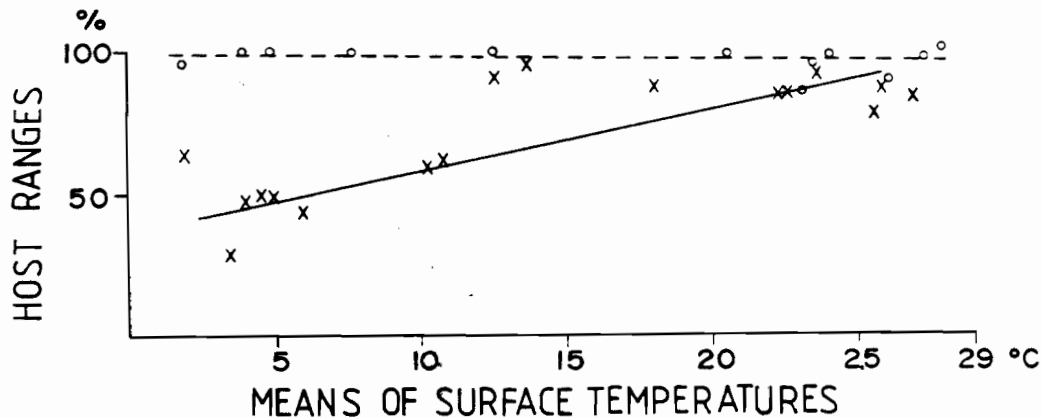Fig. 5 shows host ranges of Monogenea and Digenea (endoparasitic flukes)

FIG. 5. - Host ranges of marine Monogenea (o) and Digenea (X) at different latitudes. Abscissa: means of annual sea-surface temperature ranges ($^{\circ}$C). Ordinate: percent of parasite species infecting either 1 or 2 host species.
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at different latitudes. Whereas Monogenea have similarly narrow host ranges
at all latitudes, Digenea use considerably more hosts at high latitudes. This
could be interpreted as supporting the assumption of greater specialization
and niche packing by Digenea at low latitudes. However, host specificity of
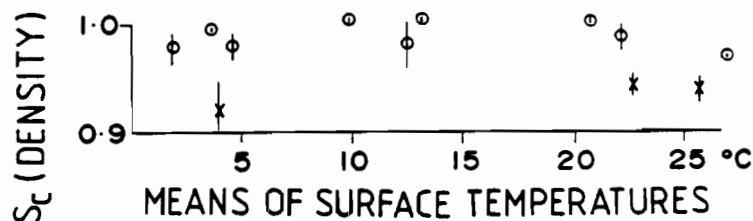both groups does not show a latitudinal trend (Fig. 6),

FIG. 6. – Host specificity S_c (density) of marine Monogenea (0) and Digenea
(X) at different latitudes. Abscissa: means of annual sea–surface temperature
ranges (°C). Note: Data by Zubchenko (1980, 1981) for 10 trematode species
of Macrouridae, Anarhichadidae and Pleuronectidae in the Northwest Atlantic
yielded a S_c (density) of 0.86, well in agreement with that in the White Sea.
It is not included in the diagram because of the small number of fish species
examined and the fact that some of the fish species are deepwater forms. S_c =
means of all S_1 (density) at each locality.
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because even Digenea of cold waters usually infect only one or very few hosts
heavily, and the others only lightly. For example, the digenean Lecithaster
gibbosus in the White Sea was found in 12 of 31 fish species examined, of
which 1 contained the vast majority of parasites. The parasite species
consequently had a host specificity index based on density of infection of
0.99 (Table 6). Rohde (1978c) explained the differences between Monogenea and
Digenea in terms of r- and K- strategy. Monogenea tend to follow a K-
strategy, which results in a high degree of host- and site specificity to
facilitate mating in low-density populations, whereas Digenea tend to infect
many ecologically suitable hosts. Host ranges in cold-temperate seas are
greater because of the less patchy and ecologically less restricted
distribution of hosts. More specifically, it may be that different modes of
infection of the two groups are responsible. Whereas Monogenea (at least some
species) can distinguish between °correct° and °wrong° hosts and hatching may
be induced by hosts in the vicinity of the eggs, hosts become infected with
Digenea by swallowing infective stages (e.g. Rohde 1984a). Perhaps host fish
in cold waters swallow the wrong prey containing larval digeneans more often
than in warm waters. An alternative explanation may be that more severe
stress in cold waters suppresses defense reactions to 'wrong' parasites.
Recent observations on herring parasites have shown that at very high (Arctic)
latitudes, host-specificity of gyrodactylid Monogenea of Clupea harengus also
breaks down to a certain extent (review in MacKenzie 1987).

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Fish species	1	2	3	4	5	6	7	8	9	10	11	12
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
No. of fish examined	21	95	15	7	83	32	84	21	82	64	3	117

$$S_i \text{ (density)} = 0.99$$
$$S_i^l \text{ (frequency)} = 0.54$$

TABLE 6. Host specificity of _Lecithaster gibbosus_ in the White Sea (data from Shulman and Shulman-Albova 1953).

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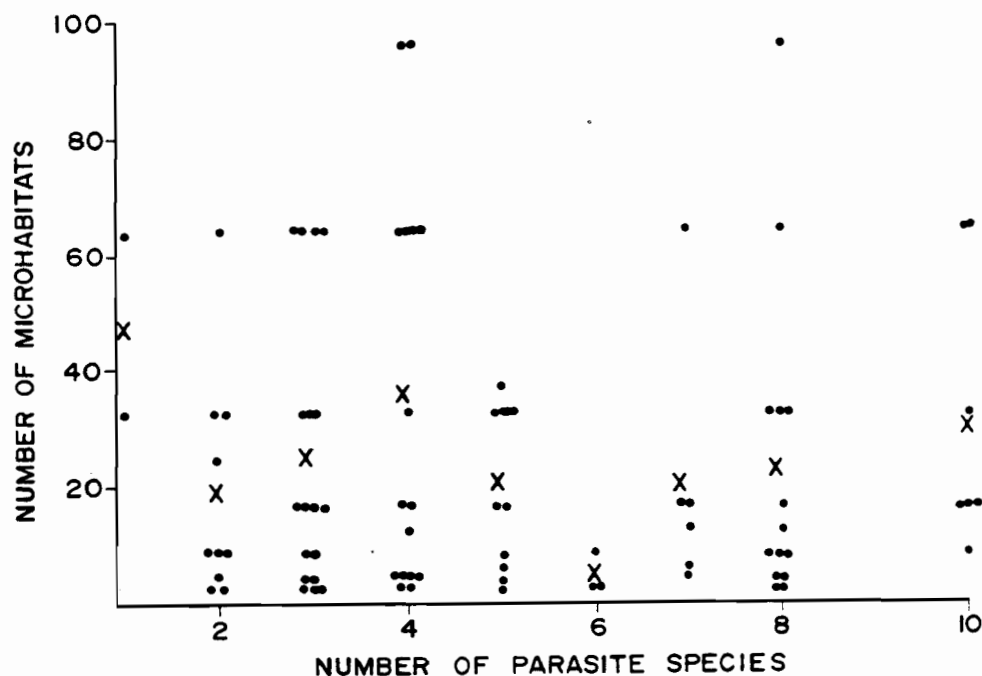

FIG. 7.- Numbers of gill microhabitats (see Fig. 1) of parasites in communities of different species diversity. Abscissa: number of species in the community; ordinate: number of microhabitats. x = means, ● individual data. Data from Rohde (1981a).

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There also is no inverse correlation between numbers of ectoparasitic species on marine fish and numbers of microhabitats (Fig. 7), and prevalence

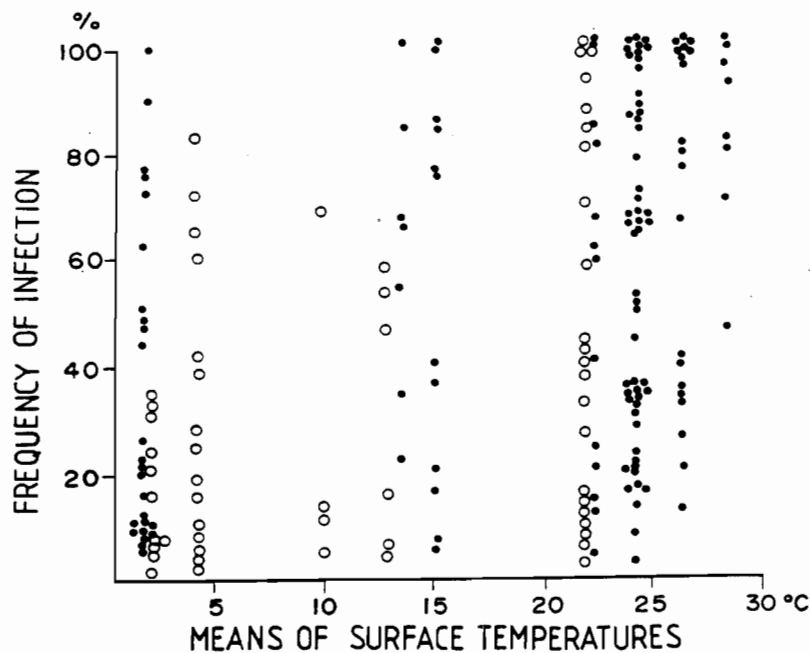(frequency) of infection with Monogenea is not smaller in warm seas (Fig. 8)

FIG. 8. - Prevalence (frequency) of infection of adult marine teleost fish with Monogenea in the Pacific ($\bullet$) ·and Atlantic (O) at different latitudes. Abscissa: means of annual sea-surface temperature ranges ($^{\circ}$C). Ordinate: frequencies of infection (%). Data from Rohde (1981a).
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i.e., the parasites are not more restricted to particular individuals or populations within species at low latitudes. Bark and ambrosia beetles (Beaver 1979) and butterflies (Price 1984) also do not show narrower host ranges in the tropics than in temperate regions, and in the former group temperate species are in fact more narrowly restricted to particular hosts. Stork (1987) concluded from arthropod samples collected by insecticide fogging ten Bornean lowland rain forest trees that for many insect groups there is less host-specificity in the tropics than in temperate regions.

A different and relatively easy approach to comparing width of niches at different latitudes may be a comparison of sizes of animals. The implication is that a large species will generally inhabit a larger habitat and feed on a larger range of differently sized food items than a small species. Such a comparison is attempted for marine teleost fishes in a species-poor environment, northern Europe, and a species-rich environment, New Guinea (Table 7). The data for northern Europe can be considered to be almost complete and definitive, both with regard to species numbers and maximum sizes of the fish. Unfortunately, data for New Guinea are far less complete. P. Kailola is presently compiling a checklist of fishes of New Guinea. In volume I of the checklist, 708 species are listed, only 275 of which are included in Munro (1967). In a more or less complete revision of the Scombridae, Collette and Nauen (1983) list 23 species, 14 of them longer than 1 m, for New Guinea, whereas Munro lists only 14 (put in several families), 8 of them longer than 1 m. Since samples used for descriptions by Munro were necessarily small, maximum sizes of species also can be expected to be somewhat larger than

Max. length (cm)	≤ 25	26-50	51-75	76-100	101-125	126-150	≥ 151
Northern Europe (247 species)	79 (32.7%)	61 (24.7%)	39 (15.8%)	22 (8.9%)	11 (4.5%)	15 (6.1%)	20 (8.1%)
New Guinea (980 species)	512 (52.2%)	274 (28.8%)	83 (8.5%)	62 (6.3%)	27 (2.8%)	1 (0.1%)	21 (2.1%)

TABLE 7. Numbers of marine teleost fish of different size classes in northern Europe (north of Biscay to the Barents Sea down to a depth of approximately 1000 m) and New Guinea. Data for northern Europe from Wheeler (1987), for New Guinea from Munro (1967). Note that the data for New Guinea are incomplete. Far more species probably occur in New Guinea, as indicated for instance by the data for scombrids in Collette and Nauen (1983), who recorded 14 large species (> 1 m), whereas Munro recorded only 8.
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given.   In spite of this incompleteness, data in Table 7 permit some
conclusions.   Firstly,   the   proportion   of   smaller   species   is
considerablygreater in New Guinea (many of the as   yet   unrecorded   species   are
probably small, and the underestimates of maximum sizes cannot significantly
affect numbers in the very large size classes (> 76 cm); secondly, the
absolute number of very large species (> l m) is greater in New Guinea (the
apparent similarity in numbers between Europe and New Guinea of 46 and 49
species is an illusion, see data on Scombridae above).

Our conclusion then, must be that there is some evidence that the
proportion of small animal species in the tropics is greater, indicating a
possible reduction in niche width because of the smaller habitats used by
small fish and the smaller microhabitats provided by small fish for parasites.
However, smaller habitats used by small fish and the smaller niches may simply
be a by-product of evolution, the result of faster speciation in small species
inhabiting smaller habitats than in wide ranging large species.   With regard
to parasites which all belong to approximately the same size class, evidence
available does not support the view of greater specialization in the tropics.

Species-area relationship

Pianka (1983; also Diamond and May, 1976; Connor and McCoy, 1979)
discussed the species-area relationship.

Parasite faunas on the gills of marine fish are ideal objects to study
species-area relationships, because gills of different fish with similar
habits do not differ in structural heterogeneity.   Three aspects will be
examined.   Firstly, the effect of gill size and number of gill filaments;
secondly, the effect of geographical range of hosts; and thirdly, the effect
of geographical area on a whole parasite fauna. Since there is an increase of
species diversity towards the equator, these three factors will be examined   in
species from particular latitudinal zones. Gill sizes (and numbers of gill
filaments) vary greatly among different fish.   For   example,   a   Gerres
subfasciatus (total length ll cm), had 590 gill filaments and a gill surface
area (measured with a planimeter, excluding the gill arches) of 3 cm^2, a
Scorpis lineolatus (total length 29 cm), had 884 filaments and a gill surface
area of 35 cm^2, and an Acanthocybium solandri (total length 160 cm), had 2766
gill filaments and a gill surface area of 527 cm^2.   In Fig. 9, total lengths
of fish are given as approximate indicators of gill sizes.

Fig. 9 shows that larger fish with larger gills do not have more species
of gill Monogenea than smaller fish in surface waters of northern New South
Wales and Canada.   Among the most throroughly examined fish in New South Wales
are the only three species of Sparidae found in that area.   The largest
species, Chrysophrys auratus (max. length 81 cm) has 6 species of Monogenea,
the middle sized one, Acanthopagrus australis (max. length 55 cm), has 9, and
the smallest, Rhabdosargus sarba, (max. length 40 cm) has one.   Of four
species of small Pomacentridae examined at Heron Island, southern Great
Barrier Reef, Pomacentrus wardi and P. popei had 5 species of gill Monogenea
and P. rhodonotus and Dascyllus aruanus had 2 each.   All fish are of
approximately the same size, a few cm long.   The scombrid Scomberomorus
commerson, examined in the same area, reaches a length of approximately 240 cm
and harboured 5 gill Monogenea.

Not much information is available on the effect of geographical range of
host species on parasite richness, because few fish species have been examined
throughout their area of distribution. Rohde and Watson (1985a, b) and Rohde
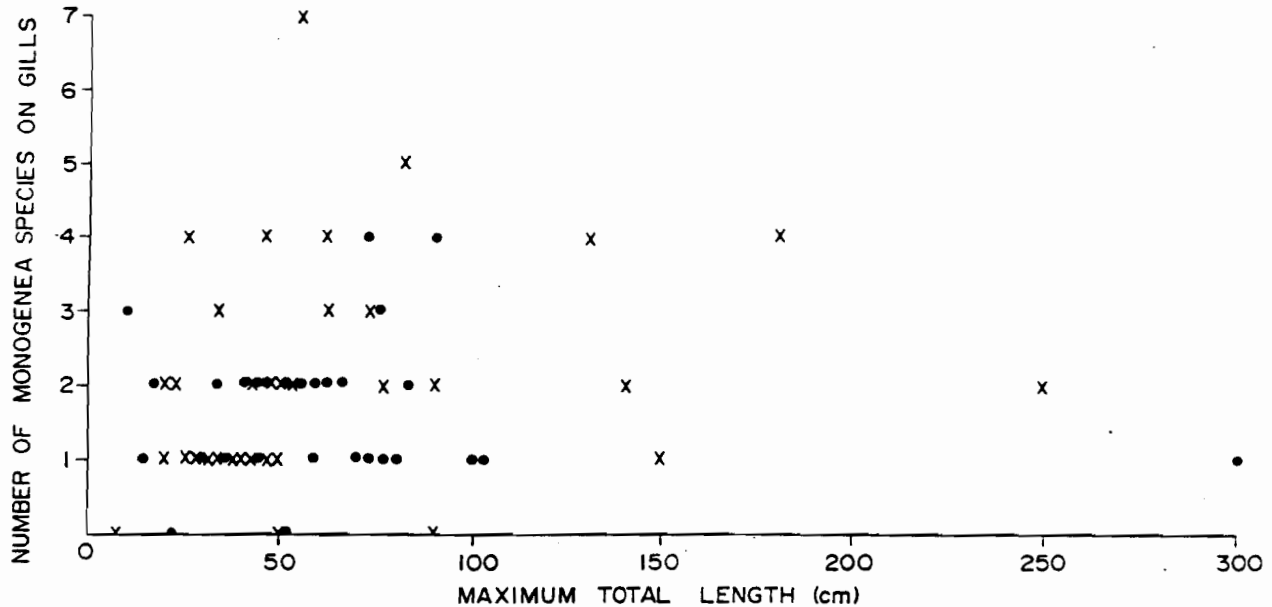
FIG. 9. Number of gill Monogenea on marine teleost fish of different total length. X = southeastern Australia; ● = Pacific coast of Canada. Only those fish included of which at least 20 specimens examined. Abscissa: maximum length reached by the fish species (data for Canada according to Pacific Biological Station, Nanaimo, B.C., Canada, and for southeastern Australia according to Scott et al., 1974, McCulloch, 1922, and Australian Museum, Sydney).

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(1987, and unpublished) made such a study of the Monogenea of the three species of Scomber, i.e. S. japonicus, S. australasicus and S. scombrus, based on large numbers of dissections from many localities. The three fish species are of approximately the same size. The first occurs in warm to temperate waters of the Indo-Pacific and the Atlantic and has five species of gill Monogenea. The second occurs in warm to cold- temperate waters of the Pacific only and has also five species. The third occurs in temperate to cold-temperate waters of the northern Atlantic and has four species. The data for parasitic copepods of Scomber given in Cressey et al. (1982) seem to indicate a correlation between geographical range of host species and number of copepod species. They found 5, 2, and 1 species on S. japonicus, S. australasicus and S. scombrus. More generally, according to these authors, wider ranging species required more specimens until all copepod species were collected, and scombrids with restricted distribution had lesser copepods. However, I have since collected a third copepod species from S. australasicus, and a second from S. scombrus. Each of the three species of Scomber has four (and one possibly five) monogeneans, whereas Acanthopagrus australis (family Sparidae), a fish restricted to southeastern Australia and New Zealand has 7 or 9 (on the gills). There does not appear to be a general correlation between geographical range of host fish and species numbers of parasites, although such a correlation may exist for certain smaller groups of hosts and

parasites. Because data are more reliable for genera than for species, Cressey's et al. (1982) data for copepods on scombrid genera were analyzed (Table 8). There is no correlation between length of fish and number of copepod species. Thus, the genera containing the largest species, Acantho-cybium (only 1 species with a maximum fork length of 210 cm) and Thunnus (7 species with a mean maximum fork length of over 200 cm) have 6 and 9 copepod species respectively, whereas Euthynnus (3 species with a mean maximum fork length of about 80 cm) has 11. There is a significant relationship between number of copepod species and number of geographical areas and also between number of copepod species and number of host species in the genus. However, the latter factor is far more important accounting for 93% of the regression sum of squares in sequential partitioning of sums of squares of a multiple linear regression analysis (for details see Table 8). At least in this case, not geographical range but diversity of the host group is the more important factor in determining species diversity of parasites, a phenomenon known as Eichler's rule (see Rohde 1982).

Concerning the third point, geographical area of parasite fauna, Rohde (1986) compared the Monogenea of fishes in the north Atlantic and north Pacific Oceans. Monogenea in these areas are predominantly represented by the Gyrodactylidae (see below: "Thorson's rule"), which occur in freshwater and in cold seas, but are practically absent from warm seas. Hence, it is unlikely that they have immigrated from more southern marine regions. Surveys in the northern cold Atlantic and adjacent seas have been underway for a longer period than in the northern Pacific, particularly by Russian workers. Nevertheless, a far greater number of monogeneans has been found in the northern Pacific than Atlantic (for references see Rohde 1986). Recent studies by Kulachkova (1985) on the herring, Clupea harengus, which has subspecies in the north Atlantic and Pacific, have added some gyrodactylids to the north-Atlantic and one to the north-Pacific records indicating the urgent need for up-to-date comprehensive surveys in both regions, but, in view of the much greater species richness of fish in the northern Pacific, there can be no doubt that the absolute species number of Monogenea in this region is much greater. Relative surface areas, measured with the aid of a planimeter on a zenithal equal area projection map, and data on number of 'main' islands, and length, discharge rates and annual discharge of major rivers (for methods see Rohde 1986) clearly indicate that the north Atlantic is not only larger and has a larger continental shelf area, but also has a greater 'complexity', as indicated by a greater total length of major rivers draining into it with a much greater annual discharge volume than the northern Pacific, and about an equal number of large islands. These data do not support the view that in this case, geographical area and structural complexity to any significant degree determine species richness. Rohde (1986) suggested that evolutionary time (older age of the Pacific) is responsible for greater species richness, although less glaciation during the last glacial also may have played a role, and factors related to area and complexity are apparently overridden by the time factor.

Our general conclusion must be that area as indicated by size of fish gills, geographical range of hosts and geographical area occupied by a fauna are not predominant in determining species richness. Effect of area, if it

exists at all, is overridden by other factors, such as evolutionary time,
possibly diversity of the group to which a host belongs, etc. This agrees
well with the conclusions of Kennedy (1978 also Kennedy et al. 1986) and Kuris
et al. (1980) that the species-area relationship, developed in the context of
island biogeography, is not a good predictor of parasite richness (see also
Strong and Levin 1979; Claridge and Wilson 1982; Blaustein et al. 1983;
Stevens 1986; but also Rey et al. 1981, 1982; McCoy and Rey 1983 who claimed
area as the most important indicator of species richness; also
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Host genus (no. of species/ no. of specimens examined)	Maximum fork length (cm)	No. of Copepod species	Total No. of geographical areas
Rastrelliger (3/155)	≥ 20–35	4	3
Scomber (3/614)	40–50	5	9
Acanthocybium (1/61)	210	6	7
Grammatorcynus (2/37)	60–110	2	3
Scomberomorus (18/663)	35–220	23	9
Sarda (4/195)	85–102	6	9
Gymnosarda (1/7)	150	3	3
Cybiosarda (1/8)	45	2	1
Orcynopsis (1/6)	130	1	1
Allothunnus (1/3)	96	1	5
Auxis (2/65)	50–58	6	9
Euthynnus (3/150)	65–100	11	9
Katsuwonus (1/132)	108	5	9
Thunnus (7/323)	100–>300	9	10
Gasterochisma (1/0)	≥ 164	?	6

TABLE 8. Number of copepod species on host genera of the family Scombridae.
Copepod data from Cressey and Cressey (1980), data on geographical
distribution of hosts from Collette and Nauen (1983). The following 10
geographical areas are considered: Western North Atlantic, Western South
Atlantic, Eastern North Atlantic, Eastern South Atlantic, Indian Ocean,
Western North Pacific, Western South Pacific including Australia and New
Zealand, Eastern North Pacific, Eastern South Pacific,
Antarctic-Subantarctic. Of Grammatorcynus and Auxis, only a single species
each was examined.

Note: A stepdown multiple linear regression analysis (Zar 1974) showed a
significant relationship of numbers of copepod species with numbers of host
species per genus and with numbers of geographical areas. The form of the
relationship was (if all host genera except <u>Gasterochisma</u> were included) y =
1.02 X_1 + 0.41 X_2, (r^2_{adj} = 0.95, df. 12), where y = no. of copepod species,
X_1 = no. of host species per genus, X_2 = no. of geog- raphical areas.   Maximum
fork length was found to be unimportant.   Of the two significant factors,
sequential partitioning of sums of squares showed that host species per genus
was the more important of the two, accounting for 93% of the regression sum of
squares. Exclusion of all genera of which less than 10 specimens were
examined, and of all these genera as well as <u>Grammatorcynus</u> and <u>Auxis</u>
practically gave the same result.
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Price and Clancy 1983). It should be noted that even for free-living animals
conclusions from the theory of island biogeography may vary between taxa.
Case   and   Cody (1987) have warned that great caution is necessary "in
generalizing beyond the bounds of their taxon and the island system in which
it has been studied."

Thorson's rule

Thorson's rule states that non-pelagic development of marine benthic
invertebrates increases with latitude.   It has been shown for many groups of
marine invertebrates that, whereas most warm water species have pelagic
planktotrophic larvae, most cold water species have viviparous/ ovoviviparous
development, development in egg capsules, and brooding (Thorson, 1950; reviews
by Mileikovsky 1971; Picken 1980; Jablonski and Lutz 1983). The most commonly
given explanation of the phenomenon is that planktotrophic larvae depend on
phytoplankton for food which, in Arctic and even more so in Antarctic waters,
blooms for only a few weeks; most species are unable to complete development
during this brief period (e.g. Thorson 1950; Picken 1980).   Other explanations
given were summarized in Rohde (1985).
Rohde (1985) demonstrated that Thorson's rule applies not only to marine
benthic invertebrates, but also to Monogenea on the gills of marine teleost
fish.   Most Monogenea have ciliated larvae which hatch from eggs and infect
other fish. One family, the Gyrodactylidae, is comprised exclusively of very
small viviparous species, and infection of hosts is by contact transfer.
There is a sharp increase in the proportion of Gyrodactylidae towards the
poles (Table 9). By considering characteristics of the Monogenea, some of the
'explanations' can be ruled out for this group.   In particular, free larvae
are without an intestine and are not planktotrophic, hence, any explanation
related to the phytoplankton bloom can be excluded.   Similarly, most other
explanations can be ruled out for the Monogenea on the basis of their biology,
and we are left with the explanation given earlier for some gastropods and
echinoderms (review by Jablonski and Lutz 1983), that non-pelagic offspring
can settle close to the parent in a favourable habitat, if suitable habitats
are difficult to find.   Apparently, at low temperatures, where production of
larvae is slowed down due to the generally reduced speed of physiological
processes, and where loss of pelagic larvae would be even greater than in warm
waters because of the reduced effectiveness of locating and infecting suitable
habitats (hosts) by free-swimming larvae due to the slow speed of physio-
logical processes, an effective method of getting to a host is imperative.
Gyrodactylidae have such a method: they infect hosts not by free larvae as
most other monogeneans do, but by contact transfer of juveniles or adults

(Bychowsky 1961; Scott and Anderson 1984). That this is indeed the likely explanation, is shown by observations on brooding in the Antarctic non-gyrodactylid monogenean Pseudobenedenia shorti. Whereas most monogeneans except the Gyrodactylidae have free-swimming ciliated larvae, this species has non-ciliated larvae already fully developed in egg clusters wrapped around the peduncle of the posterior attachment organ (Hargis and Dillon, 1968b; Gibson 1976); host infection is likely to be by contact transfer.
In both cases, that of the Gyrodactylidae and that of Pseudobenedenia, it is a particularly effective way of habitat (host) finding, and not correlation with the phytoplankton bloom, which appears to be important for life in cold waters. Since Thorson's rule describes a uniform trend of many unrelated groups in different marine habitats, it seems at least possible that the explanation given for Monogenea also applies to other groups (Rohde 1985). Assumption of such a general explanation does not rule out the possibility that other factors may have a modulating effect which perhaps enhances the phenomenon.

Concerning the special case of the Monogenea, it may be asked why viviparous species are so rare in warm seas. There is perhaps a historical answer: Gyrodactylidae may have invaded cold coastal waters from freshwater and have not had time to spread into warmer seas (and the deepsea). Alternatively, sluggish behaviour of fish in cold seas may make contact transfer of parasites feasible, whereas such a mode of infection is less successful between less sluggish fish at lower latitudes.

It could be argued that Gyrodactylidae are of freshwater origin and therefore not suitable for studying Thorson's rule. However, the freshwater origin of the family is by no means certain: they may also be of coastal origin and may have invaded freshwater secondarily and undergone adaptive radiation there. Furthermore and more importantly, Thorson's rule is a consequence of adaptations of animal species to a cold environment and it does not matter whether the adaptations were acquired in the sea or freshwater.

Do complex ecological systems have the same characteristics as simple ones?

The preceding sections have shown that simple ecological systems are well suited to examine factors responsible for certain characteristics because all but one or few parameters can be kept more or less constant, at least to a degree reasonably to be expected in biological studies, and the effect of a single or a few variables be examined, similar to the procedure in the physical sciences. The question arises whether characteristics of such simple systems can be expected to be applicable to more complex systems as well. The answer must be a conditional 'No'.
Dobson and May (1986) demonstrated for the case of certain nematodes infecting seal that tranformation of a simple linear relationship to a non-linear one leads to intuitively unexpected resuslts, and whereas most ectoparasites discussed in this paper have simple direct life cycles, parasites with more complex indirect life cycles may have different community patterns. The kind of life cycle, together with host vagility and complexity of the microhabitat (digestive tract) were among the factors identified by Kennedy et al. (1986) as being responsible for differences between patterns of helminth communities of fish and birds, although it is doubtful whether there are such differences at the level of overall patterns discussed here. In a more general way, May (1974) has demonstrated mathematically that complex ecological systems do not behave like simple ones, for example with regard to

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	LATITUDE	PROPORTION OF GYRODACTYLIDAE (%)
PACIFIC OCEAN		
Bering Sea	64° N	$\geq$ 88
Canada	$50-54^{\circ}$ N	50-54
U.S. Coast	$33-48^{\circ}$ N	22
Hawaii	20° N	0
Bay of Bengal	$13-22^{\circ}$ N	0
Northern Great Barrier Reef	15° S	0
Southern Great Barrier Reef	23° S	1-2
Northern New South Wales	30° S	1
New Zealand and South Australia	$38-46^{\circ}$ S	0
ATLANTIC OCEAN		
Barents Sea	70° N	75
White Sea	65° N	89
Gulf of Mexico	30° N	9
Brazil	23° S	0
Argentina	38° S	0
ANTARCTIC	$55-78^{\circ}$ S	33-41
DEEP SEA		
Northwestern Pacific	$40-50^{\circ}$ N	0
New York Bight	$39-40^{\circ}$ N	0
New South Wales	35° S	0

TABLE 9. Proportion of Gyrodactylidae on the gills of marine teleost fish at various localities. For details of no. of fish and fish species, and of references, see Rohde (1985).

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stability of the system, and it does not matter, in this context, whether complexity enhances or reduces stability (see discussion by Pimm, 1984).

Thus, conclusions from studying simple systems cannot be automatically applied to more complex ones. However, as in the physical sciences, they have to be understood if complex relationships are to be understood.

Concerning the question of whether results of studies on parasitic forms are applicable to other organisms: as pointed out above, parasites represent far more than half of all animal species, and a knowledge of population characteristics of parasites is therefore important per se. Furthermore, any organism occurring in low densities with little vagility can be expected to have ecological characteristics similar to those of parasites (Rohde, 1980a).

Summary and Suggestions for Further Studies

Simple ecological systems, i.e. gills of marine fish, are used to look at some ecological patterns. Gills may vary in size, numbers of individuals and species of ectoparasites infecting them, and latitude where collected and parasites may vary in the degree of phylogenetic relationship, microhabitats

and food used. All but one of these variables can be kept more or less constant in 'natural experiments'. The following conclusions are reached:

1. Many potential niches are empty, i.e. species have not yet evolved for them since different fish species of similar size and habits in the same locality, or at different latitudes, or at different depths, contain different numbers of parasite species, and since only some parasite species harbour hyperparasites.

2. Microhabitat restriction may be stabilized or enhanced in order to facilitate mating as indicated by the findings that microhabitat restriction leads indeed to increased intraspecific contact, sexually mature adults have typically more restricted microhabitats than asexually reproducing species or larvae, sessile and rare species have more restricted microhabitats, and microhabitats become more restricted at the time of mating.

3. Much of the evidence for the evolutionary significance of interspecific competition is doubtful. Thus, many studies that aim to demonstrate competition are biased because they select species which are likely to show interactions, and demonstration that interactions occur between extant species is not evidence for their underline evolutionary effect.
   There is no evidence for a reduction in the number of sympatric congeners or of congeners occurring on the same host, in gill parasites; likewise, multiple infections of snails with trematode parasites are as common as expected if infections were random. However, the difficulties in establishing null hypotheses (what is random?) for all these cases are stressed. Size differences in feeding organs occur also between species which use the same food resources, i.e. they are not unambiguous evidence for resource partitioning due to competition.

4. Whereas there is little or no evidence that interspecific competition has been an important evolutionary force leading to niche segregation, there is much evidence for the significance of mechanisms leading to reproductive isolation. This is , for example, indicated by the observation that congeneric species of gill parasites with identical resource requirements and identical or very similar copulatory organs are spatially segregated, whereas congeners with different copulatory organs may inhabit the same microhabitats.

5. Overall, evidence presently available indicates that interspecific competition does not have the predominant evolutionary importance often attributed to it, at least among ectoparasites of fish, although very likely it has some significance, particularly for large species and species with great vagility and occurring in large populations, because such animals are most likely to exhaust limiting resources and overlap with species having similar ecological requirements.

6. By ruling out the effects of climatic stability, climatic predictability, spatial heterogeneity, productivity, stability of primary production, competition, rarefaction, predation, and ecological time, it is concluded that only an evolutionary time hypothesis can give a general explanation for latitudinal gradients in species diversity, although the other factors may have local effects or secondarily enhance the gradients. Longer 'effective' evolutionary time at low latitudes is likely to be due to accelerated evolution as the result of faster selection and possibly faster mutation rates.

7. A greater proportion of small species of marine teleost fish in tropical Pacific than in cool Atlantic waters indicates a possible reduction in niche width of tropical animals. However, there is no evidence for

greater specialization and greater species packing of parasites in warm
environments, as indicated by similar host specificity of gill parasites
at all latitudes, by similar microhabitat width in communities of
different diversity, and by similar prevalences (frequencies) of infection
at different latitudes.

8. There is no evidence that area per se is a primary force determining
species diversity, as indicated by the findings that there is no
consistent difference in species numbers of ectoparasites on small and
large fish, on fish with wide and narrow geographical range, and between
parasite faunas of large and small areas (north Atlantic and north
Pacific). An important factor determining species diversity of
ectoparasites of marine fish, at least in some cases, is diversity of the
host group.

9. Thorson's rule, that non-pelagic development of marine benthic
invertebrates increases with latitude, is shown to apply to a group of
marine parasites, the Monogenea. The only explanation for the phenomenon
consistent with characteristics of the Monogenea is suggested to be as
follows. At low temperatures, where production of larvae is slowed down
due to the generally reduced speed of physiological processes, and where
loss of pelagic larvae would be even greater than in warm waters because
of the reduced effectiveness of locating and infecting suitable habitats
(hosts) by free-swimming larvae, an effective method of getting to a host
is imperative. In the Monogenea, such an effective method is contact
transfer. It is suggested that the same explanation may perhaps apply to
other marine invertebrates, since a general trend may have one general
explanation.

10. Conclusions based on the study of simple systems cannot be automatically
applied to more complex ones, but simple systems must be understood if
complex systems are to be understood.

11. A primary aim of future studies should be to collect more data on many of
the aspects discussed. We need comprehensive surveys in different seas
not only of ectoparasites, but also of endoparasites and their
hyperparasites for quantitatively more accurate conclusions concerning
numbers of empty niches and the latitudinal gradients in species diversity
and niche width. If possible, such surveys should include not only
helminths and crustaceans, but also viruses, bacteria and protozoans. To
test the views on niche segregation and the mating hypothesis of niche
segregation, microhabitats of many congeners and non-congeners on various
host species should be determined, as well as the structure of copulatory
and feeding organs of the parasites. Microhabitat width of asexual and
larval forms should be compared with that of sexually mature forms.
Complete surveys of fish in tropical waters including accurate size data
may make conclusions concerning denser niche packing in the tropics' more
secure, and comprehensive studies of parasites of whole fish families, as
done for copepods of Scombridae by Cressey and Cressey (1980) and Cressey
et al. (1982) may allow more reliable conclusions concerning the effect of
area on species numbers. With regard to Thorson's rule, Monogenea not
only of the gills but also of the body surface should be considered and
the phenomenon should be examined for other groups of parasites, such as
copepods and trematodes, as well. Some of these studies are already
underway; thus monogeneans of the genera of Scombridae and of the body
surface of various warm-water fish are being examined. However,
cooperation of many is necessary to gather the amount of data necessary,
using standardized methods for instance of microhabitat mapping (Fig. 1).

- Finally, the views presented here should be tested using different ecological systems. Some authors have already examined saturation of certain plants with insect parasite species, and the host specificity of insect parasites at different latitudes. However, other aspects should be considered and more studies of different groups are necessary for conclusions on how generally applicable are the ideas presented here.

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