Ecology of marine parasites

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ABSTRACT: Important ecological aspects of marine parasites are discussed. Whereas effects of parasites on host individuals sometimes leading to death are known from many groups of parasites, effects on host populations have been studied much less. Mass mortalities have been observed mainly among hosts occurring in abnormally dense populations or after introduction of parasites by man. As a result of large-scale human activities, it becomes more and more difficult to observe effects of parasites on host populations under "natural" conditions. Particular emphasis is laid on ecological characteristics of parasites, such as host range and specificity, microhabitats, macrohabitats, food, life span, aggregated distribution, numbers and kinds of parasites, pathogenicity and mechanisms of reproduction and infection and on how such characteristics are affected by environment and hosts. It is stressed that host specificity indices which take frequency and/or intensity of infection into account, are a better measure of restriction of parasites to certain hosts than "host range" which simply is the number of host species found to be infected.

INTRODUCTION

The science of ecology is concerned with interactions of organisms and their biotic and abiotic environment. The environment of parasites differs from that of free-living organisms in having two components. One, the microenvironment, is the host itself; the other, the macroenvironment, is the environment of the host (Fig. 1). The macroenvironment affects parasites either indirectly through the host, or it affects them directly, for instance by providing a suitable salinity to ectoparasites. Direct effects of parasites on the macroenvironment are negligible, a consequence of the small size of parasites and the barrier between endoparasites and macroenvironment represented by the host. On the other hand, parasites and hosts affect each other in many ways. Such interactions, as well as the effects of the macroenvironment on parasites, will be discussed in the following, with special emphasis on characteristics of parasites and how they are affected.

EFFECTS OF PARASITES ON HOSTS

Parasites may affect individual hosts in a number of ways, by mechanical action, withdrawal or supply of substances, transfer of micro-organisms, possibly toxic effects, and effects on the host's immune responses (Fig. 1). The study of such effects is the task of pathology and not of ecology sensu stricto. Hence, only a few examples will be briefly mentioned. Acanthocephala may perforate the intestine of fish (mechanical action), cestodes may use up nutrients in the intestine of fish (withdrawal of substances), leeches may transmit protozoan blood parasites to fishes, and various helminths affect their hosts possibly by toxic excretions or secretions, although evidence is ambiguous. Finally,
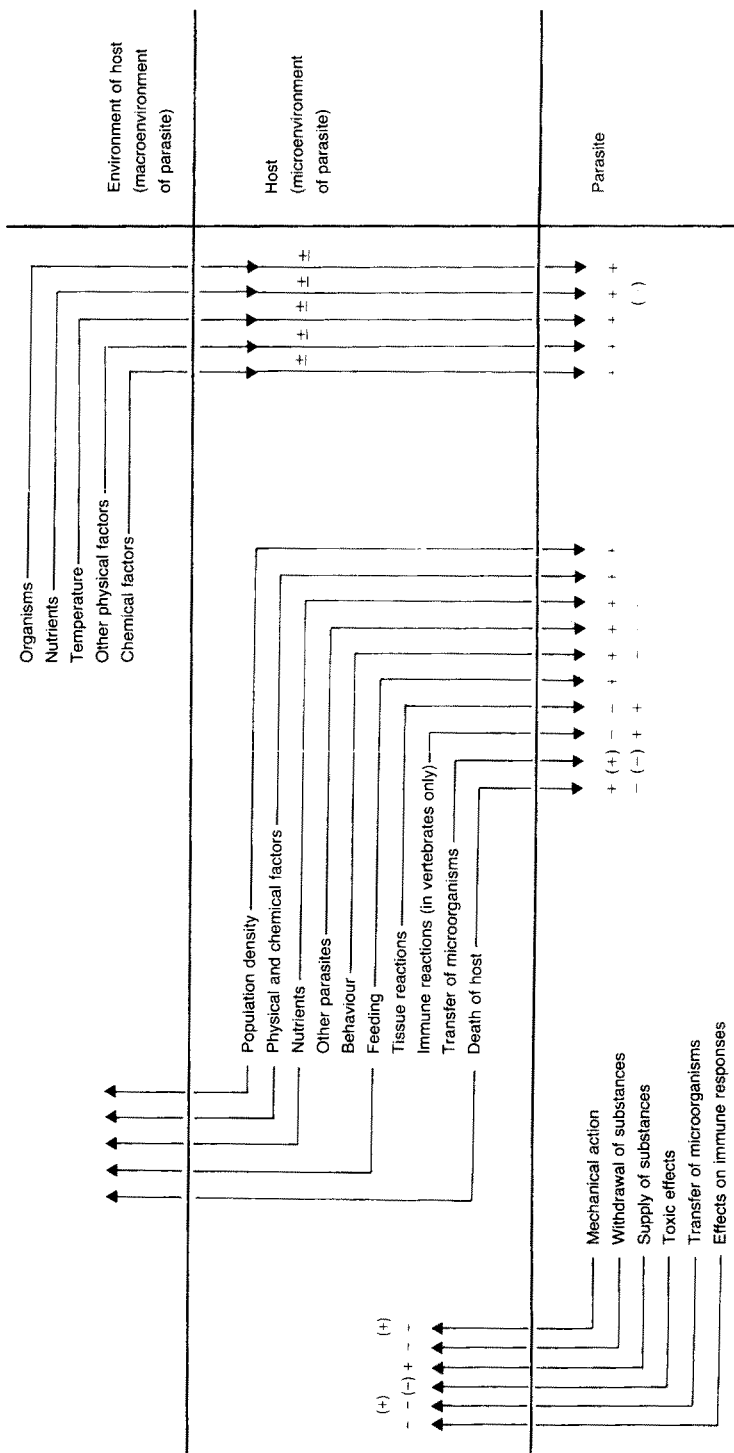
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Fig. 1. Diagram of interactions of environment, host and parasite. $+$ = positive effects; $-$ = negative effects; $(+)$ and $(-)$ = likely effects, but no evidence

"masking" of trypanosomes induces changes in the host's recognition of parasites and consequently its immune response. Marine examples of supply of substances and changes in the host's immune responses by parasites are not known. Direct observations in aquaria and sometimes in nature indicate that parasites may kill host individuals and circumstantial evidence from natural infections provides further evidence for fatal effects of parasites.

However, not all effects are negative. For example, Lincicome has shown that protozoan and helminth parasites may supply compounds lacking in a deficient diet and thus may be of benefit to the host (Rohde, 1982) and Berland (1980) suggested that ascaridoid nematodes in the stomach of fishes, marine birds, seals and whales may mechanically loosen and break up large food particles, permitting the digestive fluids to seep into the core quickly. This could be important because food is often ingested whole or in large chunks. Berland (1961) provided circumstantial evidence that char, *Salmo alpinus*, is lured to the mouth of the sluggish Greenland shark by copepods, *Ommatokoita elongata*, which live attached to the shark's eyes. Finally, animals living in the parasite's macroenvironment may harm it (e.g. cleaner fish) or be of benefit to it (e.g. as sources of food).

Effects of parasites on host populations in the sea are much less known. Only few cases of large-scale mortalities under apparently normal conditions have been recorded. For example, 500–600 dead mullet per km of shoreline, caused by infection with the myxozoan *Myxobolus exiguus* were observed in parts of the Black and Azov Seas (Petrushevsky & Shulman, 1961). Dogiel & Bychowsky (1934) and Dubinina (1949) reported mass mortalities of fish due to larval trematodes in brackish estuarine environments (Aral Sea, Volga delta).

Rohde (1982) reviewed the evidence for marine mass mortalities due to parasites. He concluded that parasite numbers under natural conditions are usually far below that which a host individual and population could carry, as evidenced by the heavy parasite loads occasionally observed, and "corresponding to the low infection rates of hosts with most parasites, observations of mass mortalities under natural conditions are rare. Even in cases where conditions seem to be normal, the effects of human activities, such as overfishing or removal of predators, cannot be ruled out".

Nevertheless, the fact that mass mortalities due to parasites have been observed so rarely under natural conditions, does not necessarily mean that mass mortalities are rare. It could also mean that fish weakened by disease are soon eaten by predators. Experiments under carefully controlled conditions simulating the natural environment, and extended observations in nature are necessary to improve our knowledge of this important aspect of marine parasitology. Unfortunately, increasing human activities make observation of diseases in the sea under "natural" conditions more and more difficult.

On the other hand, observations of mass mortalities under abnormal, crowded conditions, are not rare. Oyster beds have been devastated repeatedly by parasites, although other factors beside parasites may have been contributory factors (discussion in Rohde, 1982), and fish kept in tanks or aquaria are often killed by parasites, particularly by Protozoa and Monogenea. Directly traceable to human activities is the long-term destruction of sturgeon fisheries in the Aral Sea by the monogenean *Nitzschia sturionis*, which is well documented (e.g. Lutta, 1941a; Petrushevsky & Shulman, 1961). Dogiel &

Lutta (1937) reported that spiny sturgeon, *Acipenser nudiventris,* were dying in large numbers, due to the large (up to 2 cm long) gill-dwelling monogenean. In saltwater areas infection was 100 %, in areas with slightly reduced salinity almost 100 %. Maximum intensity of infection was 600. Worms did not only cover the gills, but also had spread to the lips and into the mouth. Some worms had even crept into the gut, where they remained active for some time. Fish with many worms had a reduced fat content, and there was a general emaciation of the body, as well as jaundice with yellowish-green colouration of the organs adjacent to the gall bladder, and wrinkling of the liver. No other parasites were present, nor was there any sign of bacterial disease. *Nitzschia sturionis* was not found during a previous examination in 1930, and local fishermen had not seen the parasite previously. It was apparently introduced into the Aral Sea from the Caspian Sea. In 1933, 350 000 larvae and in 1934, 7 million larvae of Caspian stellate sturgeon were introduced into the Aral Sea. In addition, 90 spawners were introduced in 1934 without previous inspection for fish disease, and *Nitzschia* was known to occur in the Caspian Sea (Dogiel & Lutta, 1937). According to Osmanov (1963) mortalities due to the parasite in the Aral Sea occurred in 1936, and sturgeon fisheries had no commercial significance for the next 20 years.

Lutta (1941b) made a detailed study of the effects of *Nitzschia sturionis* on *Acipenser nudiventris.* Its opisthaptor causes a mechanical irritation of the gill tissue. This and supposed action by toxic substances secreted by the worm, leads to an inflammation of the gills. "Histological examination revealed the following effects: mechanical destruction of the gill tissue; hyperplasia of the epithelium of the primary gill layers and to a lesser degree hypertrophy of the connective tissue; atrophy of the gill capillaries; and atrophy of the secondary gill layers. Morphological changes were so marked that gas exchange was apparently partially or completely impossible, leading to acute disease and mass mortality."

EFFECTS OF MACRO- AND MICROENVIRONMENT ON CHARACTERISTICS OF PARASITES

Main ecological characteristics of marine parasites (and any other parasites) are shown in Figure 2. That both macro- and microenvironment jointly or separately deter-

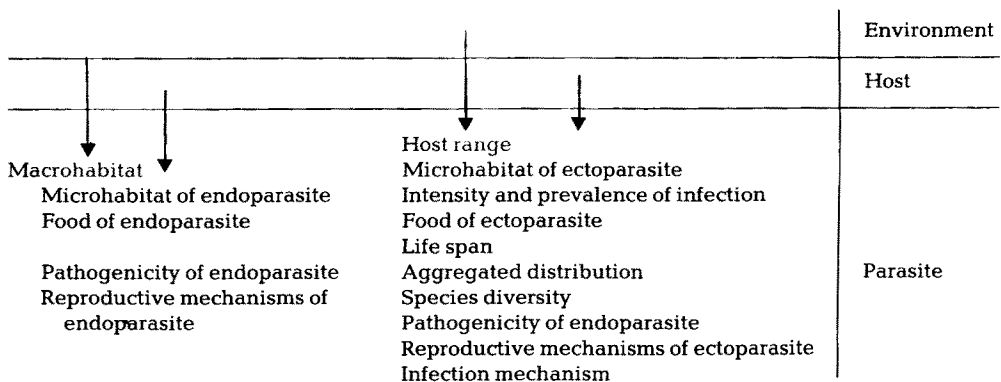|		Environment
		Host
Macrohabitat	Host range Microhabitat of ectoparasite Intensity and prevalence of infection	
Microhabitat of endoparasite Food of endoparasite	Food of ectoparasite Life span	
Pathogenicity of endoparasite Reproductive mechanisms of endoparasite	Aggregated distribution Species diversity Pathogenicity of endoparasite Reproductive mechanisms of ectoparasite Infection mechanism	Parasite

Fig. 2. Diagram showing the factors that determine ecological characteristics of parasites

mine some of the characters, will be illustrated by two examples (Fig. 2). The microhabitat of monogeneans on the gills of marine fish is characterized by certain physical parameters of the macroenvironment (e.g. strength and direction of water currents), but also by characteristics of the host (e.g. gill arch or filament for attachment). Microhabitats of nematode larvae in the mesentery of fishes, on the other hand, are entirely determined by characteristics of the host. Finally, the macrohabitat of a parasite, being the total of habitats occupied by the host species infected with a particular parasite, is entirely determined by factors in the macroenvironment, some affecting the host, others affecting free-living stages of the parasite, etc.

Examples will be taken from various groups of marine helminths and parasitic protozoans.

The relative importance of various groups of parasites of marine fishes, which have been studied best, is illustrated by Tables 1 and 2. Many studies have shown that digenetic trematodes have the greatest species diversity, followed by monogeneans and copepods.

HOST RANGE AND HOST SPECIFICITY

Rohde (1982) distinguished host range and host specificity of parasites. Host range is the number of host species infected by a certain parasite species irrespective of how heavily and frequently the various host species are infected, whereas host specificity takes intensity and/or prevalence (frequency) of infection into account. For accurate quantitative descriptions of host specificity, Rohde (1980a) developed specificity indices. One index is based on density of infection (total number of parasite individuals found in a host population/number of host individuals examined).

Table 1. Numbers of known parasites from mullets (after various authors, from Paperna & Overstreet, 1981)

Parasites	Eastern Mediterranean	Northern Red Sea	Black Sea	Mississippi	Additional reports from southeastern US
Blood Protozoa	0	1	0	2	0
Gill Protozoa	1	2	3	4	2
Microspora	0	1	0	0	0
Myxozoa	2	4	2	3	0
Monogenea	6	5	2	3	6
Digenea – adults	6	7	7	11	5
Metacercariae	12	2	2	6	3
Cestoda – larvae	2	0	1	3	0
Nematoda	4	0	1	3	4
Acanthocephala	2	1	1	1	0
Copepoda	4	4	1	6	11
Branchiura	0	0	0	1	4
Isopoda	0	2	0	1	1
Hirudinea	0	0	0	1	1
Total	39	29	20	45	37

Table 2. Host ranges of parasites of fish in the Barents Sea. Host records from other seas are considered, records of accidental hosts in which parasites do not mature are not (data from Polyansky, 1966)

Parasite group	Number of species	Percentage of species					
		In 1 host species	In > 1 species of 1 genus	In 1 family	Primarily in 1 family	In several families	Undeter-mined
Protozoa	25	21.7	4.3	17.4	21.7	8.7	26.2
Monogenea	21	52.4	9.5	33.3	4.8	0	0
Digenea	37	2.8	11.1	25.0	16.7	44.4	2.8
Cestoda	19	12.5	6.2	18.7	25.0	31.4	6.2
Nematoda	12	9.1	0	36.3	9.1	36.4	9.1
Acanthocephala	3	0	0	0	0	100.0	0
Hirudinea	3	33.3	33.3	33.3	0	0	0
Copepoda	15	6.7	20.0	27.0	33.2	6.7	6.7
Isopoda	1	0	0	0	100.0	0	0
Total	136	17.2	9.2	24.9	17.9	23.9	6.9

$$S_i \text{ (density)} = \frac{\sum \dfrac{X_{ij}}{n_j h_{ij}}}{\sum \dfrac{X_{ij}}{n_j}}$$

(S_i = host specificity of 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 $\dfrac{X_{ij}}{n_j}$, species with greatest density has rank 1).

A specificity index of all parasite species of a community can be defined as S_c (density) $= \dfrac{\Sigma S_i}{n_p}$

(n_p = number of parasite species in the community). The specificity index based on frequency (prevalence) of infection uses the same formula but the parameters in the formula are changed as follows: X_{ij} = number of host individuals of jth species infected with parasite species i, n_j = number of host individuals of the jth species examined, h_{ij} = rank of host species based on frequency of infection.

It is possible to take both intensity and frequency of infection into consideration, for instance by using S_i (density) + S_i (frequency) divided by a factor of two.

Values for both indices vary between 0 and 1. The closer to 1, the higher the degree of host specificity. An example is given in Table 3. *Lecithaster gibbosus* infects 12 of 31 host species in the White Sea. However, several host species are more frequently infected than others and S_i (frequency) is therefore 0.54. Most parasite individuals are found in one host species, and S_i (density) is therefore 0.99 indicating that one fish species serves as a more effective host than all the others combined.

Among parasites of marine fish, Monogenea have the most restricted host ranges and the greatest degree of host specificity. For instance, according to the data in Rohde

Table 3. Host specificity of some Digenea of marine fishes in the White Sea (data from Shulman & Shulman-Albova, 1953, after Rohde, 1980a). Total number of fish species examined = 31

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

(1978, 1979), of 435 species of marine Monogenea 78 % were restricted to one host species, 89 % to one genus, 96 % to one family, and 98 % to one order. However, all groups of parasites show host specificity of varying degrees. Sometimes, hosts belong to one taxon or to closely related taxa; in other words, parasites have a so-called phylogenetic host specificity. In other cases, ecological factors determine specificity and it is often reduced when ecological barriers are removed, for instance in aquaria.

Factors responsible for host specificity are little understood (see review by Rohde, 1982). In some cases, morphological adaptations of a parasite facilitate its attachment to a particular host in a lock and key pattern; in other cases certain physicochemical factors may induce hatching in one host species but not in another. Such factors may determine host as well as site specificity (see discussion of microhabitats). Often, differential mortality leads to host restriction. Thus, if monogeneans of the species *Entobdella soleae* are experimentally transferred to wrong hosts, worms become detached after 24–30 h, although they survive on glass for 2–6 days (Kearn, 1967, 1970). Serum factors were shown to be responsible for host specificity of the cestode *Acanthobothrium quadripartitum*. In vitro, it survives for more than 24 h in fish serum from its natural host, the ray *Raja naevus*, but 80 % of the worms are killed in serum from the "wrong" host, *Raja radiata*, within 2 h (McVicar & Fletcher, 1970). Presence of another parasite species may be a prerequisite for infection of a host. Thus, larvae of the bird schistosome *Austrobilharzia terrigalensis* occur only in snails of the species *Velacumanthus australis* on the New South Wales coast of Australia, which are also infected with other trematodes (Walker, 1979).

Ecological factors determining host specificity may be the feeding habits of the host(s). Thus, final hosts of the trematode *Paucivitellosus fragilis* on the coast of eastern Australia are several unrelated fish species, all of which are grazers (Pearson, 1968). The infective cercaria is attached to a substratum and ingested by feeding fish. Non-grazing fish have no chance of becoming infected although they are probably suitable hosts if artificially infected.

MICROHABITATS

There are no species of parasites that infect all tissues and organs of the host's body equally, i.e. all species show preferences for certain microhabitats of varying degrees. Examples are represented in Figures 3 and 4 and in Tables 4 and 5. On *Prionotus punctatus*, a teleost fish from the cold-temperate coast of Argentina, only three species of gill and skin parasites were found. An isopod was recovered only once from the fins and no statements other than that it is an ectoparasite are possible about its microhabitats. Cysts of unknown nature are restricted to the gill filaments which they appear to infect more or less at random. The copepod *Blias prionoti* also occurs only on the gill filaments but prefers the first three longitudinal quarters and the tips of the filaments (Fig. 3).

On *Scomber japonicus* in the warm waters off Sao Paulo State, Brazil, 10 species of parasites were found, on the gills and in the mouth cavity (Fig. 4; Table 5). Three species of didymozoid trematodes show the greatest site specificity. Two hundred and sixteen individuals (always encapsulated in pairs) were found only in a small site under the gill operculum. Two hundred and forty-four individuals of a different species of the same genus (*Nemathobothrium* sp. III) occurred in the dorsal roof of the mouth cavity, and 36

Table 4. *Prionotus punctatus*, Mar del Plata, Argentina. Distribution of ectoparasites on 32 fish

	Gill fila-ment	Gill arch	Gill no.				Longitudinal quarter no.				Exter-nal fila-ment	Inter-nal fila-ment	Fins
			1	2	3	4	1	2	3	4			
Blias prionoti (Copepoda)	*85*	0	18	27	26	14	*21*	*35*	*22*	*6*	25	59	0
Cysts	*22*	0	3	7	10	2	4	9	9	0	12	11	0
Isopod	0	0	0	0	0	0	0	0	0	0	0	0	1

individuals in the anterior and posterior ends of the arches of all four gills. A third species (*Nemathobothrium* sp. II) was restricted to the gill filaments, and particularly to the internal filaments of the first gill and the external filaments of the third gill. All other species on *Scomber japonicus*, for which sufficient data are available, show similar microhabitat preferences. Examples for microhabitat specificity of endoparasites and parasites of invertebrates were given by Rohde (1982).

Microhabitats frequently are not static, that is, they change with the age of the
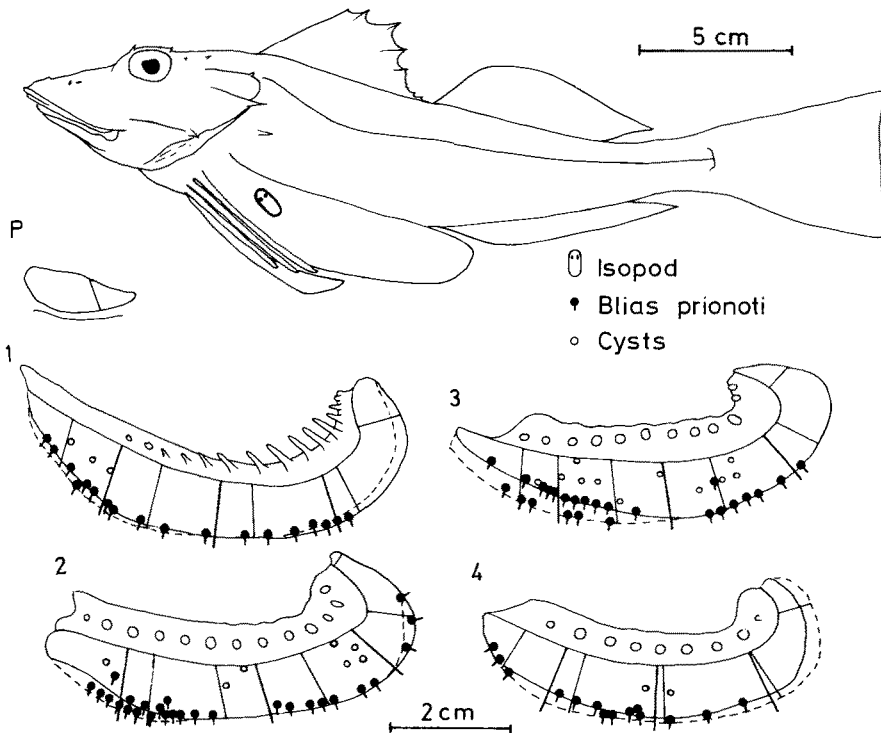
Fig. 3. *Prionotus punctatus*, Mar del Plata, Argentina. Distribution of ectoparasites on 32 fish

5 cm

P

2 cm

I

3

2

4

- • Nemathobothrium sp. I
- ▬   "   " II
- o   "   " II, single pairs
- ◊   "   " II, juv.
- ⊘   "   " III
- ❙ Kuhnia sp. I
- △   "   " II

- ❙ Grubea sp.
- ■ Caligus productus
- ✕ Caligus pelamydis
- ▲ Clavellisa scombri
- □ Cysts
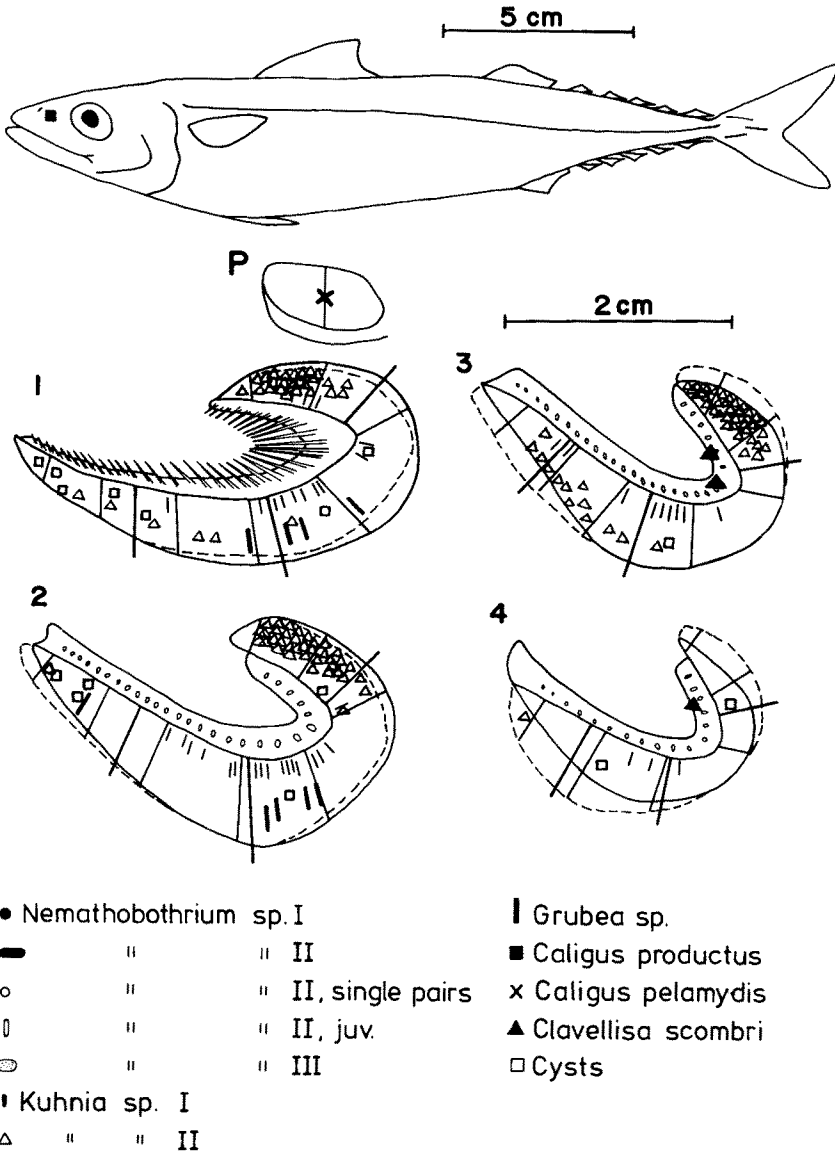
Fig. 4a. *Scomber japonicus*, São Paulo State, Brazil. Distribution of didymozoids and ectoparasites on 98 fish. Body surface examined in 50 fish and *Nemathobothrium* sp. III. recorded in 70 fish

parasites and/or with the age of the host. For example, larvae and young females and males of the copepod *Caligus diaphanus* live on the gill filaments of the gunard, *Trigla lucerna*, at Helgoland, whereas adults infect the inner wall of the opercular cavity (Rohde, 1980b). In some cases seasonal microhabitat changes have been demonstrated or changes due to the effect of other parasites. Thus, sites of the acanthocephalan
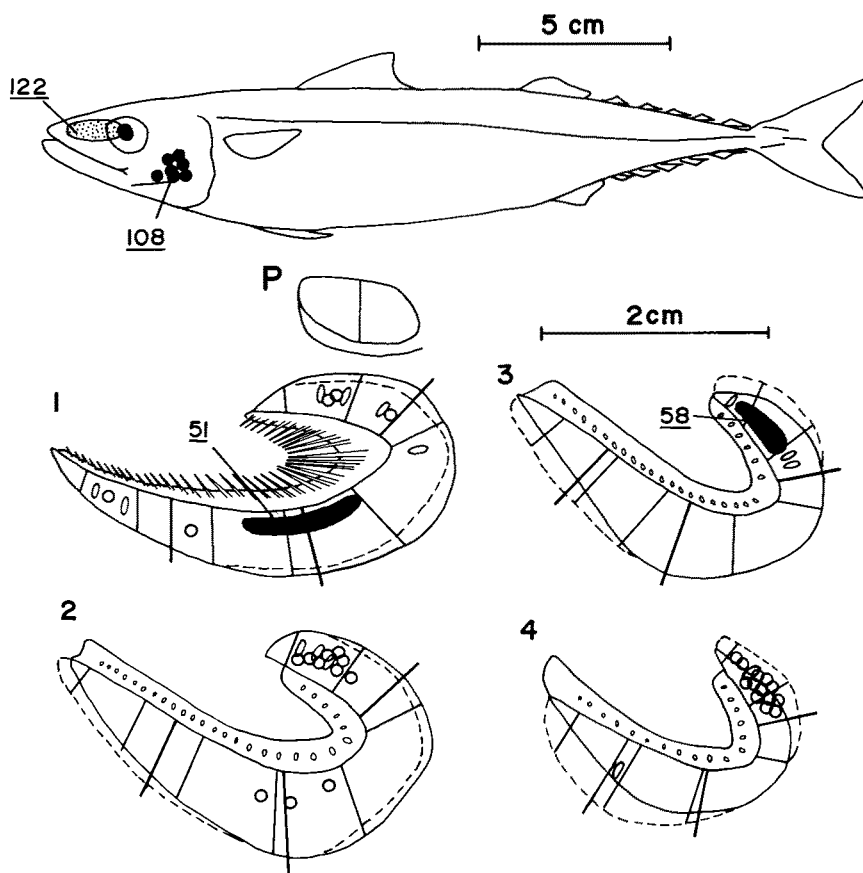
Fig. 4b. *Scomber japonicus.* Distribution of several parasites. For symbols see Fig. 4a

Echinorhynchus gadi in *Melanogrammus aeglefinus* undergo seasonal changes (Scott, 1981), and the same parasite is more restricted to the posterior intestine when the nematode *Hysterothylacium clavatum* is also present. Conversely, *H. clavatum* is more restricted to the anterior intestine in the presence of *E. gadi* (Shotter, 1976).

Very little is known about the reasons for site preferences (see review by Rohde, 1982). In some cases, morphological characteristics determine at least partly, whether a parasite can live in a certain microhabitat or not (Figs 5–8). For example, of three species of ectoparasitic helminths on the gills of *Seriolella brama* in New Zealand, *Syncoelium filiferum* is always attached to the spines of the gill rakers and arches by means of a stalked muscular ventral sucker which is not capable of attaching to gill filaments or smooth surfaces. The monogenean *Neogrubea seriolellae* has posterior clamps which consist of two valves suitable for grasping gill filaments but not spines or smooth surfaces. A second monogenean, *Eurysorchis australis* is always attached to the gill arches by means of modified clamps which do not act as grasping organs but as flat suckers for attachment to the smooth surface of the arches (Rohde et al., 1980). The

Table 5. *Scomber japonicus*, São Paulo State, Brazil. Distribution of didymozoids and ectoparasites on 98 fish. Body surface examined in 50 fish and *Nemathobothrium* sp. III recorded in 70 fish

Species	Gill filament	Gill arch	Gill no.				Longitudinal quarter no.				Ante-rior / Poste-rior surface of filament		External filament	Internal filament	Mouth cavity
			1	2	3	4	1	2	3	4	Ante-rior	Poste-rior			
Nemathobothrium sp. I (Didymozoida)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	216
Nemathobothrium sp. II	288	0	124	28	122	28	6	40	76	166	0	0	136 on gills Nos. 2–4	124 on gills No. 1; 24 on gills Nos. 2–4	0
Nemathobothrium sp. III	0	ca 36	8	14	8	6	18	0	0	18	0	0	0	0	ca 244
Kuhnia sp. I (Monogenea)	42	0	13	17	9	3	1	12	26	3	14	8	28	6	0
Kuhnia sp. II (Monogenea)	139	0	30	40	68	1	6	11	5	117	11	3	44	70	0
Grubea sp. (Monogenea)	9	0	4	5	0	0	1	1	7	0	3	0	1	1	0
Caligus productus (Copepoda)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Caligus pelamydis (Copepoda)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Clavellisa scombri (Copepoda)	0	3	0	0	2	1	0	0	1	2	0	0	0	0	0
Cysts	16	0	8	5	1	2	7	2	4	3	0	0	7	9	0
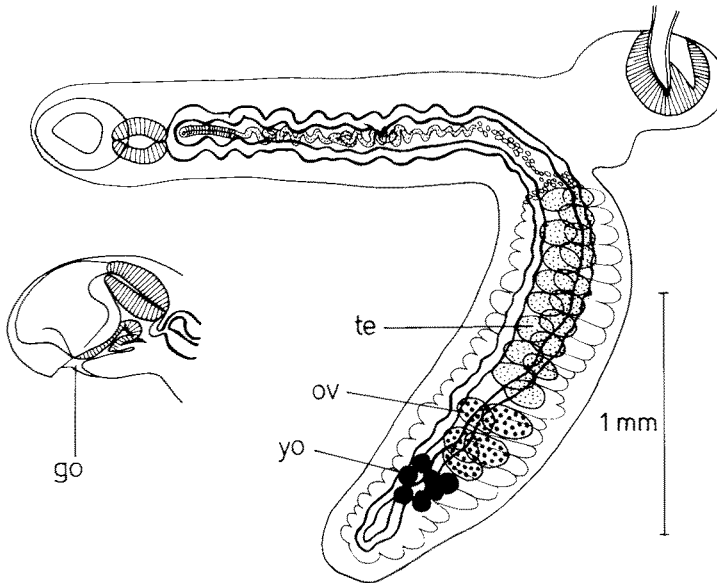
Fig. 5. *Syncoelium filiferum.* go = gonopore, ov = ovaries, te = testes, yo = yolk glands
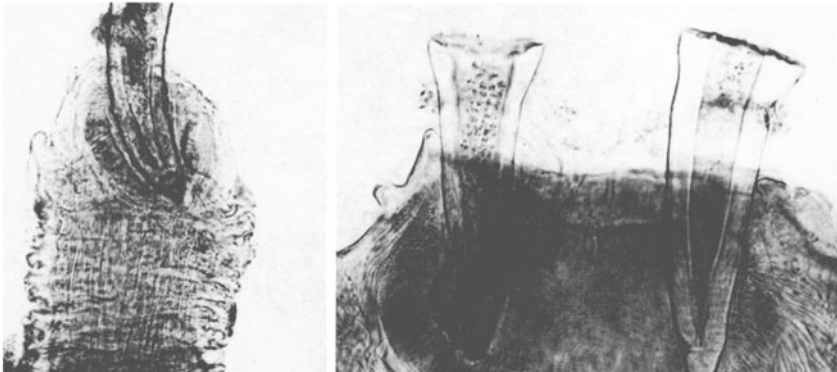
Fig. 6. Ventral sucker of *Syncoelium filiferum* grasping spines of gill arch

structure of the acetabulum in *Syncoelium* does not only determine the microhabitat of the parasite, but also its host range. A large variety of fish species were found to be infected, but only those with spines on the gill arches or rakers.

In other cases, physico-chemical host stimuli were shown to be at least partly responsible for site specificity. Thus, ex-sheathment and development of certain nematode species were shown to require host stimuli. Although the stimuli themselves may not be very specific, they may act on larvae of different species under different conditions of redoxpotential and pH and thus determine their microhabitats (and hosts)

(Rogers, 1957; Sommerville, 1957). However, all nematodes studied so far are non-marine.

    With regard to the biological function of microhabitat restriction, Rohde (1976a, b, 1977) suggested that enhancement of the chances to mate may be an important factor responsible for such restriction. Evidence is that sexually mature and sessile species as well as species occurring in low densities often have the most clearly restricted microhabitats.
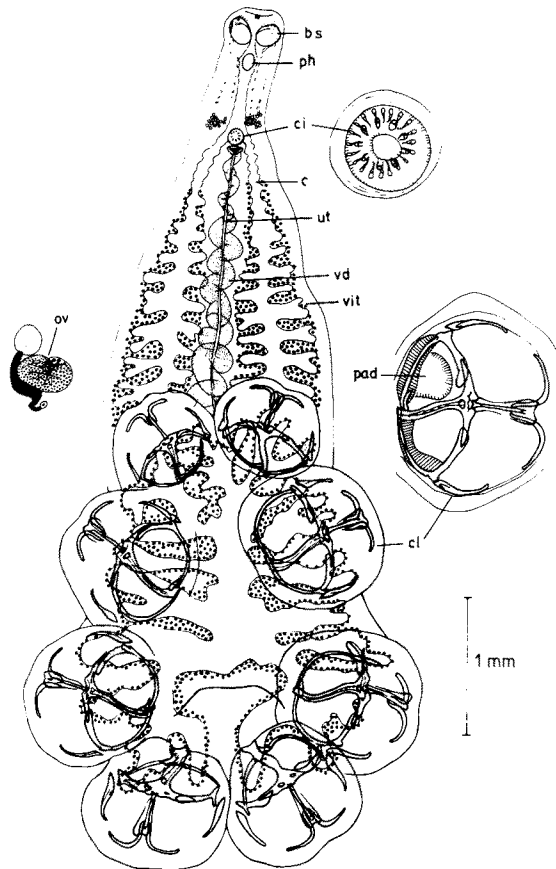
Fig. 7. *Eurysorchis australis* from the gill arches of *Seriolella brama* (after Rohde et al., 1980). bs = buccal sucker, c = caecum, ci = cirrus, cl = clamps ov = ovary, pad = clamp pad, ph = pharynx, ut = uterus, vd = vas deferens, vit = vitellaria

MACROHABITATS

    The macrohabitat of a parasite consists of those niche components which also represent the habitat of its host(s) (Rohde, 1982). For example, according to Cannon (1977a, b), among nematode larvae of marine fish in southeastern Queensland, *Anisakis* occurs only in open water fish, *Contracaecum* (probably *Hysterothylacium*) only in

inshore shallow water fish, and two others, *Phocanema* (= *Pseudoterranova*) and *Thyn-nascaris* (= *Hysterothylacium*) have intermediate distributions.

Russian authors have extensively studied the factors which affect the distribution of marine ,parasites in different macrohabitats. A review of this work was given by Polyansky (1961). The importance of chemical factors and particularly salinity was shown for parasites and especially ectoparasites in the Aral Sea. Some groups like Myxozoa and Ciliophora were absent in the saline part, and Monogenea and Trematoda were better represented in the freshwater part. Temperature affects, for instance, the trematode *Derogenes varicus*, which occurs in numerous fish species in cold surface
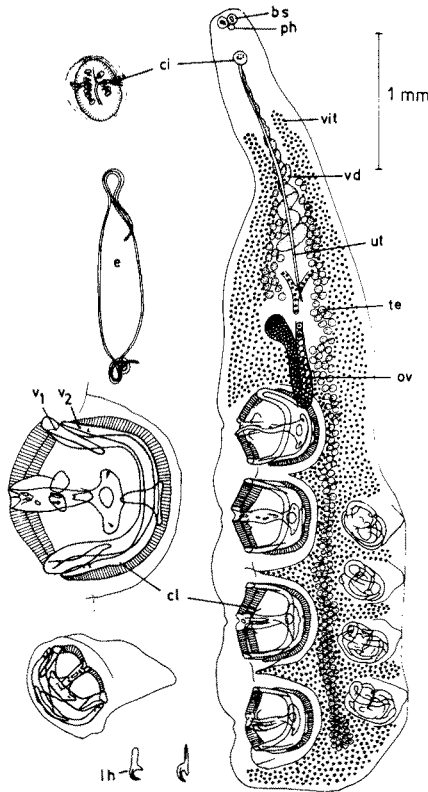
Fig. 8. *Neogrubea seriolellae* from the gill filaments of *Seriolella brama* (after Rohde et al., 1980). e = egg, lh = large hamulus, te = testes, v_1 = 1st valve of clamp, v_2 = 2nd valve of clamp. For further abbreviations see Figure 7

waters. At low latitudes, it occurs only in deeper cold waters or in areas with cold currents.

Ectoparasites sometimes must be able to withstand extreme conditions in the environment of their hosts, and sometimes rapid changes in those conditions. Thus, the louse *Antarctophthirus ogmorhini* on the Weddel seal, *Leptonychotes weddelli*, in Antarctica is exposed to extremely low temperatures and rapid pressure changes during diving of the hosts. It could be shown that the parasite survives cooling to −20 °C for 36 h, and diving to 600 m for 45 min (Murray, 1976).

PREVALENCE AND INTENSITY OF INFECTION IN HOSTS OF DIFFERENT AGE AND SEX, AND IN DIFFERENT SEASONS

In all host species which have been well examined, infections with parasites change with age. Some species are most common in juvenile hosts, others in hosts of middle or old age. Scott (1969) found that the trematode *Hemiurus levinseni* in 581 *Argentina silus* from the northwestern Atlantic had a high intensity and prevalence in young fish, both parameters decreasing with age. *Lecithophyllum botryophorum*, another trematode, on the other hand, had a higher intensity and prevalence of infection in larger fish. A third species, *Derogenes varicus*, was intermediate. Apparent reasons for the differences were migration of the fish with a corresponding change of diet. Young argentines feed heavily on planktonic copepods in shallow water and become infected with *Hemiurus*, whereas maturing fish move into deeper water and eat a higher proportion of near-bottom organisms which are second intermediate hosts of *Lecithophyllum*.

In long-lived parasites, higher infection may simply be due to a chance accumulation of parasites over time. Larger hosts, furthermore, eat more and come into contact with larger volumes of water which increases the chances of infection with endo- and ectoparasites, and they also represent a larger variety of larger microhabitats. Immune reactions which eliminate some parasites, as well as age resistance which may be due to thicker body layers preventing entry of parasites, counteract this to a certain degree. However, altogether an increase of parasite infections with age is more common than a decrease. A well-documented example is represented in Figure 9.

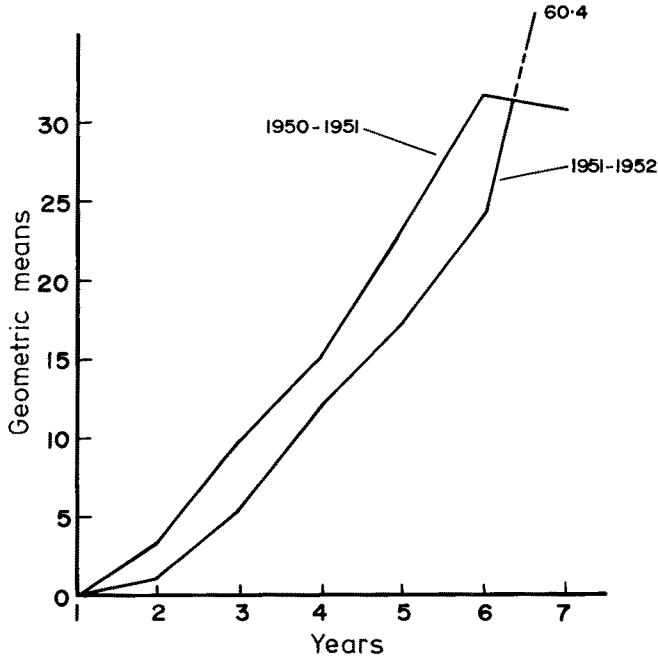Differences of infection between the two sexes of a host species are less common.

Fig. 9. Increase of mean level of infection of *Clupea harengus pallasi* with larval *Anisakis* in 1950–51 and 1951–52. Ordinate: geometric means of nematodes per fish. Abscissa: age of fish in years (redrawn after Bishop & Margolis, 1955)

Male walleye pollock, *Theragra chalcogramma*, in British Columbia, Canada, were more heavily infected with the third stage larvae of *Anisakis simplex* and plerocercoids of *Nybelinia surmenicola* than females of similar lengths, although prevalence of infection did not differ significantly. The other two helminth species examined, larval anisakids, infected both sexes equally (Arthur et al., 1982). According to Williams (1965), the monogenean *Calicotyle kroyeri* was never found in gravid female rays, *Raja radiata*, although non-gravid females may be infected. Male snails, *Hydrobia ulvae*, in Britain were much more commonly infected with larval trematodes than females, the ratio of infected males to infected females sometimes reaching 16 : 1 (Rothschild, 1938). Reasons for the differences may be of different kinds: different feeding habits of males and females (shown for some fish species), sexual differences in the composition of the skin (shown for freshwater trout), and possibly hormonal and tissue differences (snails?) (see review in Rohde, 1982).

Seasonal fluctuations are known for many parasite species of fish in cold-temperate seas. According to Möller (1974, 1975) most endoparasites of flounder, *Platichthys flesus*, and all of *Gadus morhua* in the Bay of Kiel showed seasonal fluctuations. Ectoparasites may show more distinct fluctuations. However, even in cold-temperate seas fluctuations are by no means universal, and very few studies in warm waters have been made. An example is the study of larval trematodes of two snail species on the Great Barrier Reef by Rohde & Sandland (1973) and Rohde (1981). Over two years, no seasonal fluctuations occurred in any of the trematodes.

Reasons for seasonal differences may be differences in feeding habits during the cold and warm months, changes in the composition of the skin of fishes (shown for freshwater trout), and seasonality of the infective stages of parasites (shown for many helminth species).

Table 6. Food of some marine helminths

Parasite	Food	Source
Monogenea Polyopisthocotylea	Blood, also low molecular organic compounds from water	Various authors Halton (1978)
Monogenea Monopisthocotylea	Mucus, epithelial cells, sometimes blood	Various authors
Didymozoida (Trematoda)	Blood and/or tissue fluid	Yamaguti (1970)
Aporocotyle simplex (Trematoda)	Blood	Thulin (1980)
Cestoda	Gut contents, tissue liquid	Various authors
Nematoda	Gut contents, host tissue, or blood	Various authors
Hysterothylacium bidentatum (Nematoda)	Fluid contents of stomach	Geller (1957)
Salvelinema walkeri (Nematoda)	Blood	Margolis (1967)
Acanthocephala	Contents of intestine, tissue liquid	Various authors
Hirudinea	Blood, some also prey	Various authors
Larval Gnathiidae (Isopoda)	Blood	Various authors
Copepoda	Blood, tissue, mucus	Kabata (1970)

FOOD

Some examples of food resources used by marine parasites are given in Table 6. Of particular interest is that species of ectoparasites may supplement host nutrients by compounds from the macroenvironment. Halton (1978) showed that *Diclidophora merlangi* can absorb L-alanine and L-leucine from the water through its tegument, although it feeds like all other polyopisthocotylean monogeneans also (and probably mainly) on the host's blood. The food may differ with the sex or age of the parasite. For example, the copepod *Lepeophtheirus salmonis* feeds on the blood of its host, the Atlantic salmon *Salmo salar,* but adult females do this to a greater extent than males and postchalimus larvae (Brandal et al., 1976).

LIFE SPAN

This aspect has been studied much less thoroughly than in parasites of man and domestic animals. It is known that human schistosomes may live for many years, whereas other human parasites are short-lived and infections are lost after short periods.

Seasonality of infection with many species of Monogenea indicates that the adults live less than one year (e.g. *Gastrocotyle trachuri,* according to Llewellyn, 1962, 1964). Time until maturation depends on temperature (*Benedenia seriolae:* 18 days at 21.8–26 °C, 45 days at 17–18 °C) and may be slow (*Diclidophora denticulata:* 180 days) (Table 7).

Table 7. Survival and maturation times of oncomiracidia of some marine Monogenea

Species	Survival time	Time until maturation (days)	Source
Benedenia seriolae	1 day	18 (21.8–26 °C) 45 (17 –18 °C)	Hoshina (1968)
Entobdella soleae	1 day	–	Kearn (1967)
E. hippoglossi	> 1 day	–	Kearn (1974a)
Neobenedenia melleni	≤ 6 h (loss of cilia)	–	Jahn & Kuhn (1932)
Diclidophora denticulata	1 day	180	Frankland (1955)
Diclidophora merlangi	12–15 h	(13 °C, end of active swimming)	MacDonald (1975)
	≥ 9 h	(18 °C, end of active swimming)	
	30 h	(18 °C, death)	
Gastrocotyle trachuri	> 1 day	–	Llewellyn (1964)

Examples of some marine hemiurid trematodes are given in Table 8. They show that even between species of one family there may be great differences in maturation time and life span. The acanthocephalan *Echinorhynchus lageniformis* lives for about one year in the final host, the starry flounder *Platichthys stellatus,* since older fish lose the parasites (Olson & Pratt, 1971). Among the leeches, the species *Johanssonia arctica* lives

Table 8. Survival and maturation time of some hemiurid trematodes of marine fishes

Parasite	Life span	Time until maturation	Source
Hemiurus communis	8 months (average) 15 months (maximum)	–	Meskal (1967)
H. communis?	Several years	–	Balozet & Sicart (1960)
Lecithophyllum botryophorum	8–10 months	–	Scott (1969)
Lecithaster sp.	3–9 months	–	Boyce (1967)
Tubulovesicula lindbergi	≥ 31 months	2–4 months	Margolis & Boyce (1969)
Lecithaster gibbosus	2–9 months	1–2 weeks	Margolis & Boyce (1969)

Table 9. Survival times of a marine metacercaria and some marine cercariae

Parasite	Survival time	Source
Bucephalus haimeanus (metacercaria)	≥ 10 months	Matthews (1973)
Paucivitellosus fragilis (furcocystocercous cercaria)	3–4 days	Pearson (1968)
3 species of cystophorous cercariae	2–5 days (locomotory activity) 2, 4–5, 20–25 days (medium life span) 6–7, 10–14, 35–40 days (maximum life span)	Timofeeva (1978)

$2^1/_2$ years at −1 to 2 °C (Khan, 1982), but others live less than one year. Thus, juvenile *Calliobdella carolinensis* attach themselves to fish in winter and die after cocoon deposition by May (Sawyer & Hammond, 1973). In *Hemibdella soleae,* maturity is reached in about 23 days after infection, and full size in about 37 days (Llewellyn, 1965).

Larval stages have vastly variable life spans (Table 9). Among trematode larvae, unencysted forms like miracidia or cercariae live only for hours (cercariae probably for > 1 day). Furcocystocercous and cystophorous cercariae, which are somewhat protected from the environment, may survive for several or many days, and in metacercariae with their effective cyst-wall, survival time may extend to many months. Some terrestrial and freshwater forms may even live for many years. In oncomiracidia of Monogenea, which are very small (< 1 mm long) and fragile, death occurs usually within 1 day (Table 7).

AGGREGATED DISTRIBUTION

Most parasite species are not randomly or uniformly distributed in host populations, they show an aggregated (overdispersed, contagious) distribution; that is, some individuals of a host population are more heavily infected than expected in a random distribution, and others are infected very little or not at all. Several theoretical distribu-

Table 10. Observed frequency distribution of *Stephanostomum baccatum* metacercariae in juvenile plaice from Firemore Bay, with negative binomial fitted to data (after MacKenzie & Liversidge, 1975). $X^2 = 11.386$, $P > 0.05$

Number of parasites	Observed number of plaice	Fitted negative binomial distribution
0	136	125.9
1– 5	164	154.9
6– 10	50	60.1
11– 15	35	33.2
16– 20	12	20.2
21– 25	16	12.8
26– 30	3	8.4
31– 35	6	4.6
36– 40	1	
41– 45	2	
46– 50	1	
51– 55	1	
56– 60	2	
61– 65	1	
66– 70	1	
71– 75	0 } 11	13.0
76– 80	0	
81– 85	0	
86– 90	0	
91– 95	0	
96–100	1	
101–145	0	
146–150	1	

tions have been used to describe aggregation in parasites, the most common one being the negative binomial. Table 10 contains data on frequency distribution of a larval trematode species in plaice. The data can be fitted almost perfectly to a negative binomial (other examples in Rohde, 1982). Crofton (1971) even used aggregated distribution as a characteristic of parasitism. However, as pointed out by Rohde (1982), such distributions are also common among free-living animals and plants.

Crofton (1971) has discussed the conditions which lead to non-randomness and aggregation in parasite distribution. These conditions are: (1) A series of exposures, each with a different chance of infections (e.g. numbers of cercariae shed by snails vary); (2) the infective stages are not randomly distributed (e.g. cercariae clustered close to snails); (3) an infection enhances the probability of further infection (e.g. decrease of host's resistance due to heavy helminth infection); (4) an infection decreases the probability of further infection (e.g. immunity); (5) variations in host individuals make the chances of infection unequal (e.g. different individuals with different food preferences); (6) the chances of infection of individuals change with time (e.g. age resistance).

Other conditions which contribute to aggregation are: (7) a single parasite individual may multiply on or in the host (e.g. gyrodactylid monogeneans); (8) host individuals prefer infected intermediate or transport hosts to uninfected ones (e.g. infection leads

to behaviour changes of intermediate hosts which expose them to predation by final hosts). Several of these factors will usually be jointly responsible for aggregated distributions of parasites.

Some authors have made suggestions concerning the biological function of aggregation of parasites. According to May (1977) it may bring about stabilization of the host-parasite association, and according to Kennedy (1975) because of aggregation only few heavily infected individuals of a host population usually die. Death of these hosts may ensure completion of the life cycle of a parasite which depends on being eaten by the next host, but the host population as a whole is not greatly affected. Kennedy (1976) also suggested that parasites in aggregated populations may have greater chances of contacting mating partners.

However, no empirical evidence in support of any of the suggestions is available.

NUMBERS AND KINDS OF SPECIES

Concerning the effects of ecological factors on the number of parasites in marine fish, Polyansky & Bychowsky (1963) summarized the results of extensive studies by Russian workers as follows: numbers of parasites are increased by (1) a great variety of food (and consequently of possible intermediate hosts); (2) a long life span; (3) a large area over which a fish migrates and consequently an increase in contacts with other final hosts (exchange of parasites with direct development) and intermediate hosts; (4) school formation; (5) a large body size.

The Atlantic cod, *Gadus morhua,* is a large fish occurring in dense populations; it migrates over long distances, has a long life (15 years) and a rich variety of food (in the Barents Sea more than 200 species of fish, benthos and plankton), and consequently a rich parasite fauna, Dollfus (1953) compiled data on its parasites and recorded 71 species.

Type of diet and habits determine which kinds of parasites are present. For example, the parasite fauna of mullet in the Black Sea (Reshetnikova, 1955) and the eastern Mediterranean (Paperna, 1975) changes throughout the life of the fish, corresponding to changes in habitat and feeding preferences. Fish smaller than 30 mm in coastal and estuarine waters have many didymozoid trematodes, cestodes and larval nematodes, acquired during planktonic feeding in the open water. They are replaced by trematodes and acanthocephalans acquired by benthic feeding and ectoparasites from older fish with whom young fish now share the same habitats. Fish returning for spawning to the open sea acquire deepwater trematodes.

According to Polyansky & Bychowsky (1963), generally fry of marine fish become infected first with parasites which use intermediate hosts, because schools of differently aged marine fish do not usually mix and exchange ectoparasites with direct life cycles. Freshwater fish of different ages, on the other hand, mix freely and acquire parasites by contact first.

PATHOGENICITY

Marine parasites show a wide range in their degree of pathogenicity. Various authors have reported that larvae of pseudophyllidean cestodes have little effect, and the same is true of many Monogenea. According to Kearn (1963), the skin monogenean

Entobdella soleae on *Solea solea* moves around frequently and the skin regenerates fast. Thus, little damage is done. On the other hand, *Neobenedenia melleni* on several fish species can severely harm its hosts, by destroying their eyes, etc., and lead to death. However, fish may acquire permanent or partial immunity after repeated exposures (e.g. Nigrelli, 1937). In trematode larvae, tissue reactions may depend on the species, the site of infection and on whether the larvae are dead or alive (see review in Rohde, 1982).

Effects may be aggravated when other parasites are present. Thus, Noble (1963) found a positive association between the ciliate *Trichodina* and the monogenean *Gyrodactylus* on *Gillichthys mirabilis*, i.e. intensity of infection with one species was greater when the other was present. Although no direct evidence was provided, the author suggested that the ciliate feeds on host tissue damaged by the monogenean (see also McVicar & MacKenzie, 1977).

Effects may also depend on environmental conditions. Paperna & Overstreet (1981) reported that adult trematodes probably cause little damage to mullet in their natural habitats, but effects may be very severe when fish are trapped in little water with many snails. Water quality was shown to affect pathogenicity of Monogenea. Thus, Skinner (1982) studied infections of the fish *Gerres cinereus, Lutjanus griseus* and *Strongylura timucu* with the monogeneans *Neodiplectanum wenningeri, Ancyrocephalus* sp. and *Ancyrocephalus parvus*, respectively, and the associated gill pathology. Fish were from two habitats in South Biscayne Bay, Florida, one heavily polluted with high amounts of ammonia, trace metals, and pesticides, and the other not polluted. Only fish from the polluted habitat were heavily infected and showed marked pathological effects. *Neodiplectanum wenningeri*, in light infections, caused mechanical damage by deflecting gill lamellae. In heavy infections, the lamellae were covered with the monogeneans, and there was increase in mucus production and clubbing of filaments where parasites were attached. Similarly, heavy infection with the two species of *Ancyrocephalus* caused pathological changes at the site of attachment. Localized host reaction to the parasites' hooks included epithelial hyperplasia and heavy mucus production, and the respiratory epithelium was lost in some instances. Often the side of the filament opposite the worm attachment was also affected. "In addition, the lamellae were deflected and adhered to each other, and in severe cases, clubbing of filaments was almost always present as was obliteration of normal filament structure." The affected filaments appeared white in fish preparations and the gills were congested with mucus. "Few fish from the non-polluted habitat had above-normal mucus, whereas all the fish from the polluted habitat had increased mucus production and moderate to severe pathological effects" (Skinner, 1982).

MECHANISMS OF REPRODUCTION

Compared with free-living relatives, parasites usually have a much increased reproductive potential (see review in Rohde, 1982). This is clearest in endoparasites with indirect life cycles. An excess of offspring is necessary to compensate for the hazards involved in the life cycle, particularly in finding the hosts. In addition to large numbers of eggs, parthenogenetic and/or asexual reproduction increases the number of offspring even further, and hermaphroditism enhances the chances to find mating partners in low-density populations (review in Rohde, 1982). Seasonality in egg production of many marine parasites indicates that temperature, either directly or indirectly via the host, has

an important effect on reproduction, and sometimes eggs are seasonally released from the host. Thus, according to Lester (1980), most didymozoid trematodes of the species *Neometadidymozoon helicis* in the dermis of the buccal cavity and the gill arches of flathead, *Platycephalus fuscus,* in Moreton Bay, Queensland, disappear between September and May, leaving behind depressions in the mucosa. Apparently, the capsule wall breaks down and releases the worms containing numerous eggs. It is known that immune responses affect egg production in various parasites, but no studies of marine parasites have been made in this regard.

MECHANISMS OF INFECTION

Infection of hosts by parasites may be by contact transfer, inoculation by a vector, ingestion of transport (paratenic) or intermediate hosts, by eggs, spores or cysts, or by free living larvae. Examples for each are shown in Table 11.

Contact transfer has been shown for small monogeneans of the family Gyrodactylidae, which are common on freshwater and marine fish. Leeches inoculate trypano-

Table 11. Some examples of infection mechanisms used by marine parasites

Means of infection	Group of parasites	Source
Contact transfer	Gyrodactylidae (Monogenea)	Bychowsky (1957)
Inoculation	Blood Protozoa of fish	Khan (1976, 1977a, b, 1978, 1980); Burreson (1979, 1982)
Ingestion of transport hosts	Anisakidae (Nematoda)	Several authors
Ingestion of intermediate hosts	*Pricea, Gotocotyla* (Monogenea)	Bychowsky & Nagibina (1967); Popova & Gitchenok (1978)
	Lobatostoma (Aspidogastrea)	Rohde (1973)
	Trypanorhyncha (Cestoda)	Several authors
Ingestion of eggs	*Lobatostoma* (Aspidogastrea) (by snail)	Rohde (1973)
Ingestion of cysts	Many Trematoda (metacercariae)	Many authors
Spores	Myxozoa	Several authors
Free larvae or juveniles	Many Monogenea	Many authors
	Many Trematoda (miracidia)	Many authors
	Leeches	Llewellyn (1965)

somes, piroplasms and probably haemogregarines into marine fishes, and larval nematodes of various genera belonging to the Anisakidae are accumulated through a food chain consisting of small invertebrates, large invertebrates, small and large fish, many of them serving as transport hosts in which no development of the parasites occurs. Final hosts (marine mammals, fish and birds) become infected by eating transport hosts close to the top of the food chain.

Intermediate hosts differ from transport hosts in that parasites develop in them. In

several cases, infection of a final host was shown to occur by ingesting intermediate hosts. Thus, the aspidogastrid *Lobatostoma manteri* develops to (almost) full size in snails, but maturity is reached only after ingestion of snails harbouring the parasite by fish, *Trachinotus blochi*. Elasmobranchs become infected by eating intermediate hosts containing the larvae of trypanorhynchs. Of particular interest is the finding that among the Monogenea, most of which have a direct life cycle, species of some genera *(Pricea, Gotocotyla)* apparently use smaller fish as "intermediate" hosts. Only juveniles are found on the gills of such fish, and maturation occurs only on the gills of large predatory fish. Infection of the latter appears to be by ingestion of the "intermediate" hosts. An example of ingestion of eggs leading to infection is the aspidogastrid *Lobatostoma* mentioned above. Snails ingest eggs containing infective larvae which hatch in their digestive tract. Trematode metacercariae are examples of cysts leading to infection when swallowed. Spores are the infective stages of Myxozoa, protozoan parasites common in many marine fish species.

Finally, free larvae or juveniles of many parasites are responsible for infecting the hosts. The leech *Calliobdella carolinensis,* for instance, dies after cocoon deposition in May. Juveniles hatch and attach themselves to the fish host the following winter (Sawyer & Hammond, 1973). Miracidia of numerous trematode species hatch, swim freely and infect snail hosts. Several detailed studies have been made on infection mechanisms of marine Monogenea involving free oncomiracidia.

In a simple case, the acanthocotylid *Acanthocotyle lobianchi* on the ray *Raja montagui*, the non-ciliated oncomiracidia hatch when the host settles on the eggs, induced by a specific substance (urea) in the mucus of the ray (Kearn & MacDonald, 1976) (Table 12). Where free-swimming larvae are involved, some "ingenious" infection mechanisms have evolved. This is necessary since oncomiracidia swim slowly compared with their fish host. Kearn (1967) measured the swimming speed of larval *Entobdella soleae* as 5 mm/sec, and Magnan (1930) found that the average cruising speed (lasting

Table 12. Hatching rhythms and stimuli in some Monogenea

Parasite	Host	Endogenous hatching	Hatching stimulus	Source
Entobdella soleae	Solea solea	Early morning	Non-specific urea	Kearn (1973, 1974b, 1975b); Kearn & MacDonald (1976)
E. hippoglossi	*Hippoglossus hippoglossus*	Early night	None	Kearn (1974a)
Acanthocotyle lobianchi	*Raja* spp.	None	Specific urea	Kearn & MacDonald (1976)
Dictyocotyle coeliaca	*Raja naevus*	None	None	Kearn (1975a)
Diclodophora merlangi (Scotland)	*Merlangius merlangus*	Morning	None	MacDonald (1975)
D. merlangi (England)	*Merlangius merlangus*	Late night	None	MacDonald (1975)

several hours) of some marine fish species was 3.2 body lengths/sec. Over short periods, fish may reach much greater speeds (e.g. Bainbridge, 1960). To overcome this discrepancy, endogenous hatching rhythms of some species are correlated with the host's behaviour and enhance the chances of infection (Table 12). Host-specific hatching factors produced by the host induce hatching of some species, and sometimes both endogenous rhythms and host induced hatching occur together.

There may even be differences in the behaviour pattern of different populations of one species of Monogenea, apparently an adaptation to differences in behaviour patterns of different host populations. Thus, according to MacDonald (1975), one population of *Diclidophora merlangi* hatched mainly during the first 4–6 h of the illumination period, another hatched mainly during the 2 h period before light. The host is the whiting, *Merlangius merlangus*, which undergoes vertical migrations under experimental conditions in relation to light. It is possible that different stocks of fish show different behaviour patterns and thus expose themselves to infection at different times of the light-dark cycle. However, such differences between host populations have not yet been demonstrated, but differences in parasite behaviour may give a clue concerning the host's behaviour and initiate its study.

LITERATURE CITED

Arthur, J. R., Margolis, L., Whitaker, D. J., McDonald, T. E., 1982. A quantitative study of economically important parasites of walleye pollock *(Theragra chalcogramma)* from British Columbian waters and effects of postmortem handling on their abundance in the musculature. – Can. J. Fish. aquat. Sci. *39*, 710–726.

Bainbridge, R., 1960. Speed and stamina in three fish. – J. exp. Biol. *37*, 129–153.

Balozet, L., Sicard, M., 1960. Un hemiuride parasite de l'anguille. – Archs Inst. Pasteur Algérie *38*, 44–49.

Berland, B., 1961. Copepod *Ommatokoita elongata* (Grant) in the eyes of the Greenland shark – a possible cause of mutual dependence. – Nature, Lond. *191*, 829–830.

Berland, B., 1980. Are parasites always harmful? – Proc. EMOP. Cambridge, *3*, 1–202.

Bishop, Y. M. M., Margolis, L., 1955. Statistical examination of *Anisakis* larvae (Nematoda) in herring *(Clupea pallasi)* of the British Columbia coast. – J. Fish. Res. Bd Can. *23*, 571–592.

Boyce, N. P., 1967. Some aspects of the biology of *Lecithaster* (Trematoda: Hemiuridae) of the West Coast of British Columbia. M. Sc. thesis, Dep. of Biology, Univ. of Calgary, 77 pp.

Brandal, P. O., Egidius, E., Romslo, I., 1976. Host blood: a major component for the parasitic copepod *Lepeophtheirus salmonis* Kroyeri 1838 (Crustacea: Caligidae). – Norw. J. Zool. *24*, 341–343.

Burreson, E. M., 1979. Structure and life cycle of *Trypanoplasma beckeri* sp. n. (Kinetoplastida), a parasite of the cabezon, *Scorpaenichthys marmoratus*, in Oregon coastal waters. – J. Protozool. *26*, 343–347.

Burreson, E. M., 1982. The life cycle of *Trypanoplasma bullocki* (Zoomastigophorea: Kinetoplastida). – J. Protozool. *29*, 72–77.

Bychowsky, B. E., 1957. Monogenetic trematodes. Am. Inst. Biol. Sci., Washington, 627 pp.

Bychowsky, B. E., Nagibina, L. F., 1967. On "intermediate" hosts in monogeneans (Monogenoidea). (Russ.) – Parazitologiya *1*, 117–123.

Cannon, L. R. G., 1977a. Some ecological relationships of larval ascaridoids from south-eastern Queensland marine fishes. – Int. J. Parasit. *7*, 227–232.

Cannon, L. R. G., 1977b. Some larval ascaridoids from south-eastern Queensland marine fishes. – Int. J. Parasit. *7*, 233–243.

Crofton, H. D., 1971. A quantitative approach to parasitism. – Parasitology *62*, 179–193.

Dogiel, V. A., Bychowsky, B. E., 1934. Parasite fauna of the fishes of the Aral Sea. (Russ.) – Parazit. Sb. *4*, 241–346.

Dogiel, V. A., Lutta, A. S., 1937. Mortality among spiny sturgeon of the Aral Sea in 1936. (Russ.) – Ryb. Khoz. *12*, 26–27.

Dollfus, R. P., 1953. Aperçu général sur l'histoire naturelle des parasites animaux de la morue Atlanto-Arctique *Gadus callarias* L. (= *morhua* L.) et leur distribution géographique. Lechevalier, Paris, 423 pp. (Encycl. Biol. 43).

Dubinina, V. B., 1949. Relation between the distribution of larvae of parasitic helminths in the fishes of the Volga delta and changes in concentration of birds. (Russ.) – Zool. Zh. *28*.

Frankland, H. M. T., 1955. The life history and bionomics of *Diclidophora denticulata* (Trematoda: Monogenea). – Parasitology *45*, 313–351.

Geller, E. R., 1957. Epizootiology of *Contracaecum* infection of sterlet, *Acipenser ruthenus*. (Russ.) – Zool. Zh. *36*, 1441–1447.

Halton, D. W., 1978. Trans-tegumental absorption of L-alanine and L-leucine by a monogenean, *Diclidophora merlangi*. – Parasitology *76*, 29–37.

Hoshina, T., 1968. On the monogenetic trematode, *Benedenia seriolae* parasitic on yellowtail. – Bull. Off. int. Épizoot. *69*, 1179–1191.

Jahn, T. L., Kuhn, L. R., 1932. The life history of *Epibdella melleni* MacCallum, 1927, a monogenetic trematode parasitic on marine fishes. – Biol. Bull. mar. biol. Lab., Woods Hole *62*, 89–111.

Kabata, Z., 1970. Diseases of fish I. Crustacea as enemies of fishes. T. F. H. Publ., Jersey City, 171 pp.

Kearn, G. C., 1963. The life cycle of the monogenean *Entobdella soleae*, a skin parasite of the common sole. – Parasitology *53*, 253–263.

Kearn, G. C., 1967. Experiments on host-finding and host-specificity in the monogenean skin parasite *Entobdella soleae*. – Parasitology *57*, 585–605.

Kearn, G. C., 1970. The physiology and behaviour of the monogenean skin parasite *Entobdella soleae* in relation to its host *(Solea solea)*. In: Ecology and physiology of parasites. Ed. by A. M. Fallis. Hilger, London, 161–187.

Kearn, G. C., 1973. An endogenous circadian hatching rhythm in the monogenean skin parasite *Entobdella soleae*, and its relationship to the activity of the host *(Solea solea)*. – Parasitology *66*, 101–122.

Kearn, G. C., 1974a. Nocturnal hatching in the monogenean skin parasite *Entobdella hippoglossi* from the halibut, *Hippoglossus hippoglossus*. – Parasitology *68*, 161–172.

Kearn, G. C., 1974b. The effects of fish skin mucus on hatching in the monogenean parasite *Entobdella soleae* from the skin of the common sole, *Solea solea*. – Parasitology *68*, 173–188.

Kearn, G. C., 1975a. Hatching in the monogenean parasite *Dictyocotyle coeliaca* from the body cavity of *Raja naevus*. – Parasitology *70*, 87–93.

Kearn, G. C., 1975b. The mode of hatching of the monogenean *Entobdella soleae*, a skin parasite of the common sole *(Solea solea)*. – Parasitology *71*, 419–431.

Kearn, G. C., MacDonald, S., 1976. The chemical nature of the host hatching factors in monogenean skin parasites *Entobdella soleae* and *Acanthocotyle lobianchi*. – Int. J. Parasit. *6*, 457–466.

Kennedy, C. R., 1975. Ecological animal parasitology. Blackwell, Oxford. 163 pp.

Kennedy, C. R., 1976. Ecological aspects of parasitology. North Holland Publ., Amsterdam, 474 pp.

Khan, R. A., 1976. The life cycle of *Trypanosoma murmanensis* Nikitin. – Can. J. Zool. *54*, 1840–1849.

Khan, R. A., 1977a. Susceptibility of marine fish to trypanosome. – Can. J. Zool. *55*, 1235–1241.

Khan, R. A., 1977b. Infectivity of *Trypanosoma murmanensis* to the leech, *Johanssonia* sp. – Can. J. Zool. *55*, 1698–1700.

Khan, R. A., 1978. Longevity of *Trypanosoma murmanensis* in the marine leech, *Johanssonia* sp. – Can. J. Zool. *56*, 2061–2063.

Khan, R. A., 1980. The leech as a vector of a fish piroplasm. – Can. J. Zool. *58*, 1631–1637.

Khan, R. A., 1982. Biology of the marine piscicolid leech *Johanssonia arctica* (Johansson) from Newfoundland. – Proc. helminth. Soc. Wash. *49*, 266–278.

Lester, R. J. G., 1980. Host-parasite relations in some didymozoid trematodes. – J. Parasit. *66*, 527–531.

Llewellyn, J., 1962. The life histories and population dynamics of monogenean gill parasites of *Trachurus trachurus*. – J. mar. biol. Ass. U.K. *42*, 587–600.

Llewellyn, J., 1964. The effects of the host and its habits on the morophology and life-cycle of a monogenean parasite. In: Parasitic worms and aquatic conditions. Ed. by R. Ergens & B. Rysavy. Czechoslovak. Acad. Sci., Prague, 147–152.

Llewellyn, L. C., 1965. Some aspects of the biology of the marine leech *Hemibdella soleae*. – Proc. zool. Soc. Lond. *145*, 509–528.

Lutta, A. S., 1941a. Infection of Aral Sea sturgeon *(Acipenser nudiventris)* with the gill trematode *Nitzschia sturionis*. (Russ.) – Trudý leningr. Obshch. Estest. *68*, 40–60.

Lutta, A. S., 1941b. Inflammation of the gills in *Acipenser nudiventris* caused by the monogenean *Nitzschia sturionis*. (Russ.) – Zool. Zh. *20*, 520–527.

MacDonald, S., 1975. Hatching rhythms in three species of *Diclidophora* (Monogenea) with observations on host behaviour. – Parasitology *71*, 211–228.

MacKenzie, K., Liversidge, J. M., 1975. Some aspects of the biology of the cercaria and metacercaria of *Stephanostomum baccatum* (Nicoll, 1907) Manter, 1934 (Digenea: Acanthocolpidae). – J. Fish Biol. *7*, 247–256.

McVicar, A. H., Fletcher, T. C., 1970. Serum factors in *Raja radiata* toxic to *Acanthobothrium quadripartitum* (Cestoda: Tetraphyllidea), a parasite specific to *R. naevus*. – Parasitol. *61*, 55–63.

McVicar, A. H., MacKenzie, K., 1977. Effects of different systems of monoculture on marine fish parasites. In: Origins of pest, parasite, disease and weed problems. Ed. by G. M. Cherrett & G. R. Sagar. Blackwell, Oxford, 163–182.

Magnan, A., 1930. Les caractéristiques géométriques et physiques des poissons. – Annls Sci. nat. *13*, 355–489.

Margolis, L., 1967. Blood feeding in *Salvelinema walkeri* (Nematoda: Cystidicolinae), a parasite of Coho salmon *(Oncorhynchus kisutch)*. – Can. J. Zool. *4*, 1295–1296.

Margolis, L., Boyce, N. P., 1969. Life span, maturation, and growth of two hemiurid trematodes, *Tubulovesicula lindbergi* and *Lecithaster gibbosus*, in Pacific salmon (genus Oncorhynchus). – J. Fish. Res. Bd Can. *26*, 893–907.

Matthews, R. A., 1973. The life cycle of *Bucephalus harimeanus* Lacaze-Duthiers, 1854 from *Cardium edule* L. – Parasitology *67*, 341–350.

May, R. M., 1977. Dynamical aspects of host-parasite associations: Crofton's model revisited. – Parasitology *75*, 259–276.

Meskal, F. H., 1967. Seasonal fluctuations in the population of two common trematode species from the stomach of the cod. – Sarsia *26*, 13–26.

Möller, H., 1974. Untersuchungen über die Parasiten der Flunder *(Platichthys flesus* L.) in der Kieler Förde. – Ber. dt. wiss. Kommn Meeresforsch. *23*, 136–149.

Möller, H., 1975. Die Parasiten des Dorsches *(Gadus morhua* L.) in der Kieler Förde. – Ber. dt. wiss. Kommn Meeresforsch. *24*, 71–78.

Murray, M. D., 1976. Insect parasites of marine birds and mammals. In: Marine insects. Ed. by L. Cheng. North-Holland Publ., Amsterdam, 79–96.

Nigrelli, R. F., 1937. Further studies on the susceptibility and acquired immunity of marine fishes to *Epibdella melleni*, a monogenetic trematode. – Zoologica, N.Y. *22*, 185–192.

Noble, E. R., 1963. The relations between Trichodina and metozoan parasites on gills of fish. In: Progress in protozoology. Ed. by J. Ludvik, J. Lom & J. Vavra. Czechoslovak. Akad. Sci., Prague, 521–523.

Olson, R. E., Pratt, I., 1971. The life cycle and larval development of *Echinorhynchus lageniformis* Ekbaum, 1938 (Acanthocephala: Echinorhynchidae). – J. Parasit. *57*, 143–149.

Paperna, I., 1975. Parasites and diseases of the grey mullet (Mugilidae) with special reference to the seas of the near east. – Aquaculture *5*, 65–80.

Paperna, I., Overstreet, R. M., 1981. Parasites and diseases of mullets (Mugilidae). In: Aquaculture of Grey Mullets. Ed. by O. H. Oren. Cambridge Univ. Press, Cambridge, 411–493.

Pearson, J. C., 1968. Observations on the morphology and life-cycle of *Paucivitellosus fragilis* Coil, Reid and Kuntz, 1965 (Trematoda: Bivesiculidae). – Parasitology *58*, 769–788.

Petrushevsky, G. K., Shulman, S. S., 1961. The parasitic diseases of fishes in the natural waters of the USSR. In: Parasitology of fishes. Ed. by V. A. Dogiel, G. K. Petrushevsky & Yu. I. Polyansky. Oliver & Boyd, Edinburgh, 299–319.

Polyansky, Yu. I., 1961. Ecology of parasites of marine fishes. In: Parasitology of fishes. Ed. by V. A. Dogiel, G. K. Petrushevsky & Yu. I. Polyansky. Oliver & Boyd, Edinburgh, 48–83.

Polyansky, Yu. I., 1966. Parasites of the fish of the Barents Sea. I.P.S.T., Jerusalem, 158 pp.

Polyansky, Yu. I., Bychowsky, B. E., 1963. Parasite fauna of sea fish. Results and perspectives of investigations by Soviet parasitologists on fish parasites in the seas of the U.S.S.R. (Proc. Conf. Fish Diseases). Israel Progr. Scient. Transl., Jerusalem, 187–193.

Popova, T. I., Gitchenok, L. A., 1978. On the question of the possibility of the existence of an intermediate host in the life cycle of monogeneans. In: Scientific and applied problems of helminthology. (Russ.) – Isd. "Nauka", Moscow, 79–84.

Reshetnikova, A. V., 1955. Parasite fauna of *Mugil cephalus* in the Black Sea. (Russ.) – Trudy karadap. nauch. Sta. T. I. Vyazems'koho *13*, 71–95.

Rogers, W. P., 1957. An alternative approach to the study of host-parasite specificity. – Int. Union Biol. Sci. Coll., *32*, 309–311.

Rohde, K., 1973. Structure and development of *Lobatostoma manteri* sp. nov. (Trematoda: Aspidogastrea) from the Great Barrier Reef, Australia. – Parasitology *66*, 63–83.

Rohde, K., 1976a. Monogenean gill parasites of *Scomberomorus commersoni* Lacépède and other mackerel on the Australian east coast. – Z. ParasitKde *50*, 49–69.

Rohde, K., 1976b. Marine parasitology in Australia. – Search *7*, 477–482.

Rohde, K., 1977. A non-competitive mechanism responsible for restricting niches. – Zool. Anz. *199*, 164–172.

Rohde, K., 1978. Latitudinal differences in host-specificity of marine Monogenea and Digenea. – Mar. Biol. *47*, 125–134.

Rohde, K., 1979. A critical evaluation of intrinsic and extrinsic factors responsible for niche restriction in parasites. – Am. Nat. *114*, 648–671.

Rohde, K., 1980a. Host specificity indices of parasites and their application. – Experientia *36*, 1369–1371.

Rohde, K., 1980b. Comparative studies on microhabitat utilization by ectoparasites of some marine fishes from the North Sea and Papua New Guinea. – Zool. Anz. *204*, 27–64.

Rohde, K., 1981. Population dynamics of two snail species, *Planaxis sulcatus* and *Cerithium moniliferum*, and their trematode species at Heron Island, Great Barrier Reef. – Oecologia *49*, 344–352.

Rohde, K., 1982. Ecology of marine parasites. Univ. Queensland Press, St. Lucia, 245 pp.

Rohde, K., Sandland, R., 1973. Host-parasite relations in *Lobatostoma manteri* Rohde (Trematoda: Aspidogastrea). – Z. ParasitKde *42*, 115–136.

Rohde, K., Roubal, F., Hewitt, G. C., 1980. Ectoparasitic Monogenea, Digenea and Copepoda from the gills of some marine fishes of New Caledonia and New Zealand. – N. Z. Jl mar. Freshwat. Res. *14*, 1–13.

Rothschild, M., 1938. Further observations on the effect of trematode parasites on *Peringia ulvae* (Pennant) 1777. – Novit. zool. *41*, 84–102.

Sawyer, R. T., Hammond, P. L., 1973. Observations on the marine leech *Caliobdella carolinensis* (Hirudinea: Piscicolidae), epizootic on the Atlantic menhaden. – Biol. Bull. mar. biol. Lab., Woods Hole *145*, 373–388.

Scott, J. S., 1969. Trematode populations in the Atlantic argentine, *Argentina silus,* and their use as biological indicators. – J. Fish. Res. Bd Can. *26*, 879–891.

Scott, J. S., 1981. Alimentary tract parasites of haddock (*Melanogrammus aeglefinus* L.) on the Scotian Shelf. – Can. J. Zool. *59*, 2244–2252.

Shotter, R. A., 1976. The distribution of some helminth and copepod parasites in tissues of whiting, *Merlangius merlangus* L. from Manx waters. – J. Fish Biol. *18*, 101–117.

Shulman, S. S., Shulman-Albova, R. E., 1953. Parasites of Fish of the White Sea. (Russ.) Isd. Akad. Nauk SSSR, Moscow, 199 pp.

Skinner, R. H., 1982. The interrelation of water quality, gill parasites, and gill pathology of some fishes from South Bsicayne Bay, Florida. – Fish. Bull. U.S. *80*, 269–280.

Sommerville, R. I., 1957. The exsheathing mechanism of nematode infective larvae. – Expl Parasit. *6*, 18–30.

Thulin, J., 1980. A redescription of the fish blood-fluke *Aporocotyle simplex.* Odhner, 1900 (Digenea, Sanguinicolidae) with comments on its biology. – Sarsia *65*, 35–48.

Timofeeva, T. A., 1978. The life-span of marine cystophorous cercariae in the external medium. (Russ.) – Parazitologiya *12*, 333–338.

Walker, J. C., 1979. *Austrobilharzia terrigalensis:* a schistosome dominant in interspecific interactions in the molluscan host. – Int. J. Parasit. *9*, 137–140.

Williams, H. H., 1965. Observations on the occurrence of *Dictyocotyle coeliaca* and *Calicotyle kroyeri* (Trematoda: Monogenea). – Parasitology *55*, 201–207.

Yamaguti, S., 1970. Digenetic trematodes of Hawaiian fishes. Keigaku Publ., Tokyo, 436 pp.