Chapter 1

General Introduction

The importance of studying marine parasites has been emphasised by Rohde (1976, 1981, 1993). Many marine parasites act as agents of disease in marine finfish, mammals, crustaceans and molluscs. Some of them can even be transmitted to man. Their importance has further increased with the development of commercial culture of marine animals (Rohde, 1984, 1993). Furthermore, marine parasites can be used as biological tags to study animal stocks and their migrations (Lester *et al.*, 1985), and also to solve phylogenetic problems (Cressy *et al.*, 1983; Rohde, 1993). Ectoparasites of marine fish serve as an ideal model to study ecological questions, because of the possibility of examining the body surface and gills of fish accurately and quantitatively in a short time, easy availability of fish in large numbers, and frequent occurrence on one individual of several and sometimes congeneric species of parasites (Rohde, 1981).

Scomber australasicus Cuvier and Valenciennes, known as either slimy mackerel, common mackerel or blue mackerel in Australia, is a pelagic, schooling fish in surface waters. It belongs to the family Scombridae which comprises 15 genera and 49 species and includes the mackerels, Spanish mackerels, bonitos and tunas (Collette and Nauen, 1983). The members of this family support very important commercial and recreational fisheries throughout tropical and temperate waters. Generally scombrids are appreciated for their high-quality flesh. Mackerels, tunas and Spanish mackerels are marketed fresh, frozen, canned, smoked and salted. The slimy mackerel is edible, but in Australia is mostly used as a live bait to catch larger and commercially more valuable fish.

There are three species in the genus *Scomber*: *S. scombrus*, *S. japonicus* and *S. australasicus*. *S. scombrus* is distributed in the North Atlantic and Mediterranean regions and *S. japonicus* in the North-east and North-west Pacific to the Philippines, Hawaii, East, Central and South-east Pacific, Mediterranean and Black seas, East and West Atlantic, Red and Arabian Seas. *S. australasicus* is distributed in the western Pacific Ocean from Australia and New Zealand, north to China and Japan and east to

the Hawaiian Islands. It is relatively rare in tropical waters. It also occurs around Socorro Island and off Mexico in the eastern Pacific Ocean (Collette and Nauen, 1983). There are important fisheries for this species in Japan, Australia and New Zealand. In Australia it is important in the southern parts of the country, from southern Queensland southward to New South Wales, Victoria and Tasmania and westward to South Australia and western Australia and also in northern Australia. As quoted by Collette and Nauen (1983) *S. australasicus* also bears synonyms: *Scomber tapeinocephalus* Bleeker 1854; *Scomber antarcticus* Castlenau 1872; *Pneumatophorus tapeinocephalus* Murakami and Hayano 1956; *Pneumatophorus japonicus tapeinocephalus* Abe and Takashima 1958.

Species composition

Parasites of *S. scombrus* and *S. japonicus* have been studied by several authors in the past. For instance, in 1985 Rego *et al.* reported the presence of two monogeneans, two digeneans, three cestodes, one acanthocephalan and three larval nematodes from *S. scombrus* off the coast of Portugal. Later, Romuk-Wodoracki (1988) observed eight species of endo- and ectoparasites from *S. scombrus* from the north-west Atlantic. Subsequently, Somdal and Schram (1992) detected eight species of ectoparasites on *S. scombrus* from Western and North Sea stocks. Twelve species of endo- and ectoparasitic helminths from *S. japonicus* were reported by Rego and Santos in 1983. Rohde and Watson (1985a,b) and Rohde (1987,1989) studied the morphology, microhabitats and geographical variation of monogenean parasites of *Scomber* species.

The endo- and ectoparasites of *S. australasicus* have also been surveyed by several authors. The gill monogeneans have been the most studied group of ectoparasites of *S. australasicus*. Three species of monogeneans, *Kuhnia minor*, *K. scombri* and *Kuhnia* sp. were detected by Korotaeva in 1974, but she did not describe the species. Later, five species of monogeneans, *K. scombri, K. sprostonae, K. scombercolias, Pseudokuhnia minor* and *Grubea australis* were recorded from *S.*

australasicus by Rohde (1987, 1989) and Rohde and Watson (1985a,b), of which *G. australis* was a new species (Rohde, 1987).

Studies on other parasite groups, particularly on didymozoids has been scarce. Although didymozoid trematodes are tissue parasites (endoparasites), some are sometimes considered as ectoparasites because they are externally visible, living close to the surface of the host body. Korotaeva (1974) observed one ecto- and one endo-parasitic didymozoid species, *Nematobothrium filiforme* (from the gills) and *Nematobothrioides australiensis* (from the gonads) from *S. australasicus*.

Copepods are another group of parasites found on *S. australasicus*. The parasites of this group so far reported are: *Euclavellisa australis* infecting the gills (Heegaard, 1940), *Clavellisa scombri* and *Pumiliopes capitulatus* (Cressey and Cressey, 1980) and *Pumiliopes jonesi* (Cressey *et al.*, 1983). The infection sites of the latter three species are unknown.

In addition to the above, one species of isopod, *Ceratothoa trillesi* observed in the buccal cavity of *S. australasicus* by Avdeev in 1979, four species of trematodes (*Lecithocladium excisum, Opechona bacillaris, O. orientalis* and *Stephanostomum scombri*), three species of cestodes (*Nybelinia* sp., Trypanorhyncha g. sp. and *Scolex* sp.), three species of nematodes (*Anisakis* sp., *Hysterothylacium aduncum* and *Thynnascaris legendrei*) and two species of acanthocephalans (*Rhadinorhynchus* spp.) have been reported as parasites of *S. australasicus* (Korotaeva, 1974; Beumer *et al.*, 1983).

It is noteworthy that some parasites (especially monogeneans, copepods and nematodes) are commonly found in all three species of *Scomber*. Some are found in two species of the genus. The monogeneans *K. scombri* and *K. sprostonae* infect all three species of *Scomber* (Rohde and Watson, 1985b), whereas *P. minor* and *K. scombercolias* are found in two species, *S. japonicus* and *S. australasicus* (Rohde and Watson, 1985a; Rohde, 1989). *Grubea cochlear* is a parasite of both *S. scombrus* and *S.*

japonicus, whereas *G. australis* is specific to *S. australasicus* (Rohde, 1987). Among copepods, *Clavellisa scombri* infects all three species of *Scomber* (Cressey and Cressey, 1980; Somdal and Schram, 1992). *Caligus pelamydis* was found in both *S. japonicus* and *S. scombrus* (Cressey and Cressey, 1980), while *Pumiliopes jonesi* and *P. capitulatus* were found in *S. japonicus* and *S. australasicus* (Cressey and Cressey, 1980; Cressey *et al.*, 1983). The nematode *Hysterothylacium aduncum* has been reported both from *S. scombrus* and *S. australasicus* (Beumer *et al.,* 1983; Romuk-Wodoracki, 1988).

Nikolaeva (1985) reported that some fishes of the family Scombridae can be infected with many species of didymozoids. For example, *Thunnus albacares* hosts 37 species of didymozoids. In contrast, Korotaeva (1974) reported only one ecto- and an endoparasitic didymozoid from *S. australasicus.* In many previous surveys on parasites of *S. australasicus,* the number of fish examined was less than 60 and in some cases only small fish were screened. In the present study, an attempt was made to detect the ectoparasitic fauna using a sample of 428 individuals of *S. australasicus,* of different lengths. The taxonomy of the didymozoids has been determined provisionally. Descriptions of those didymozoid species which have been examined for pathology are included, but taxonomic work continues in co-operation with Dr M. Murugesh of Andhra University, India.

Microhabitats

The microhabitat of a parasite is the site it occupies on or in the host. All ecto- and endoparasites show a preference for certain microhabitats (Rohde, 1993). A few studies on site or microhabitat preferences of ectoparasites in Australian fish have been carried out, including Rohde (1977, 1978) on *Carangoides emburyi* (Family Carangidae) and king fish (*Seriola grandis*; Family Carangidae), Armitage (1980) on snapper (*Chrysophrys auratus*; Family Sparidae), Byrnes (1980) on 4 species of bream (*Acanthopagrus* spp.; Family Sparidae), Roubal (1981) on black bream (*Acanthopagrus australis*; Family Sparidae), Roubal *et al.*, (1983) on snapper (*Chrysophrys auratus*;

Family Sparidae), and Rohde and Watson (1985b) on *Scomber* species (Family Scombridae). Rohde (1989) recorded microhabitats of five species of monogeneans on *Scomber australasicus* gills in south eastern Australia. The microhabitats of 13 ectoparasites of *S. australasicus* were examined in the present study.

Seasonal variation

Seasonal studies of parasitic infections of marine fishes are important because low intensities of a parasite observed at one time of the year can increase, leading to greater pathogenicity, at another time of the year. The biotic and abiotic factors influencing the seasonal abundance of parasites have been little studied (Valtonen *et al.*, 1990). Temperature is one of the abiotic factors determining seasonal patterns (Prost, 1963). Seasonal fluctuations in the population size of parasites in cold-temperate waters have been studied several times. In spite of distinct seasonality of temperature, parasite populations do not always fluctuate seasonally (Rohde, 1993), and although some parasites show seasonality, the fluctuation patterns of different parasite species vary. Some parasites become abundant in the warm season while some are more abundant during cold periods. Very little is known about parasite seasonality in tropical waters (Rohde, 1993).

There are two studies on seasonal variation of ectoparasites of Australian marine fish. Heath (1980) studied the seasonality of endo- and ecto-parasitic fauna of two species of whiting (*Sillago analis* and *S. maculata,* family Sillaginidae), and concluded that eight out of 18 species of parasites showed seasonal fluctuations (a myxosporean, a coccidian, two copepods, a cestode larva, an acanthocephalan and a nematode) during a nine month period of observation. Roubal (1990) studied seasonality in 17 species of ectoparasites of bream (*Acanthopagrus australis*, family Sparidae) and observed that only three showed seasonal fluctuations (a monogenean, a copepod, and an ectoparasitic digenean). The present study investigates whether significant seasonal fluctuations occur in the abundance of ectoparasites of *S. australasicus.*

Preference for host size

Some parasite species show a preference for hosts of a certain age (Rohde, 1993). Some species are more common in younger fish (Llewellyn, 1962) and some are more common in older fish (Paling, 1965). Age differences in infection with long-lived parasites may often be due to a simple accumulation. If the parasites are short-lived, other factors can influence parasite intensity (Rohde, 1993). Such factors include environmental ones that occur when and where a fish begin its life, the sequence of events that occurred in each habitat the fish encountered during its life, and the length of exposure. The present study involves an investigation of intensities of ectoparasites of *S. australasicus* of different lengths.

Host responses - (Effect of parasites on host)

Parasitism is a close association between two organisms, one of which, the parasite, depends on the other, the host, deriving some benefits from it without necessarily damaging it (Rohde, 1993). Some parasites and hosts are engaged in a continuous battle for survival. The parasites try to enter the host while the host tries to prevent infection. Mechanisms employed by the hosts to prevent infections can be either behavioural, or immune and tissue reactions (Rohde, 1993). The responses of the host may depend on the species of the parasite and the site of infection. The response of the host to ectoparasites can either be local or more widespread in the body. The second section of the current study is an attempt to understand tissue reactions of the host to didymozoid infections, considering only the local responses.

Studies of the pathology of metazoan parasites of fish in Australian waters are scarce. Roubal (1985) studied the histological, cytological and morphometric aspects of ectoparasite pathology on the marine bream, *Acanthopagrus australis*. However, several studies have been made of the pathology of protozoan parasites in Australia.

For example, Langdon *et al.* (1985) studied the pathology of some fish species parasitized by the ciliate *Chilodonella hexasticha.* Langdon (1991) also studied the pathology of milky flesh in the marine fish *Coryphaena hippurus* infected with the myxosporean *Kudoa thyrsites.* Philbey and Ingram (1991) examined the pathology of freshwater fish, *Maccullochella peeli* infected with the coccidian *Goussia lomi.* The pathological changes in fish gills due to the sarcodine *Paramoeba* sp. have been studied by Roubal *et al.* (1989) and Munday *et al.* (1990). Munday *et al.* (1993) studied amoebic gill diseases of sea-caged salmonids. Lom *et al.* (1992) examined four new myxosporean species and briefly described the histopathology of two. There have been no studies on the pathology of any parasite species of *S. australasicus.* For my pathological study, I selected three species of didymozoids because only a few studies of the pathology of didymozoids have been made.

Didymozoids are trematode flatworms of the family Didymozoidae, which is a widely distributed and diverse group of parasites, infecting mainly marine teleost fish. They are conspicuous among marine trematodes. The study of Didymozoidae began in 1819, when C. Rudolphi described the first species (Nikolaeva, 1985). Nikolaeva mentioned 212 species of didymozoids from over 100 species of fish of 32 families. Many more have been recorded recently (Nikolaeva and Tkachuk, 1986; Pozdniakov, 1987,1988,1989; Mordvinova, 1989; Abdul-Salam *et al.*, 1990a; Cribb and Williams, 1992; Murugesh *et al.*, 1992; Abdul-Salam and Sreelatha, 1993b). Most fish infected with didymozoids have only one species, but some fish, especially species of the family Scombridae, harbour many (Nikolaeva, 1985) (for example *Thunnus albacares* - 37 species; *Katsuwonus pelamis* - 33; *Thunnus obesus* - 25; *T. thunnus* - 19; *T. alalunga* - 16; *Euthunnus affinis* - 14; *Scomber japonicus* - 11; *Auxis thazard* - 9; *Seriola quinqueradiata* - 7; and *Makaira nigricans* - 6).

The distribution of didymozoids is mainly restricted to tropical and subtropical oceans around the world (Lester *et al.*, 1985; Nikolaeva, 1985; Williams *et al.*, 1993).

Only a few species have invaded temperate waters, and no didymozoids have been recorded in Arctic and Antarctic waters. According to Nikolaeva (1985), didymozoid faunas are richest and most diverse in the Pacific Ocean, where they probably originated.

Didymozoids infect a wide range of commercially important fish and may render them unsaleable (Lester, 1980; Williams *et al.*, 1993). The people of tropical and subtropical countries who eat raw fish such as tunnies, marlins, and flying fishes may ingest didymozoids along with other helminths (Nikolaeva, 1985). One study in Japan by Kamegai (1971) noted that the people excrete the eggs of the didymozoid *Gonapodasmius* when flying fish didymozoid maritae (adult stages) are eaten. The raw fish may have didymozoid metacercariae, which can acclimatise to human bowels, and begin the migrations peculiar to these larvae, possibly causing damage to human beings (Nikolaeva, 1985). However, Williams *et al.* (1993) reported that the didymozoid *Gonapodasmius williamsoni* was not likely to be pathogenic to human beings because only their non-infective adult stages occur in the snapper. Further, Gibson *et al.* (1981) stated that because of the absence of live didymozoid worms (*Halvorsenius exilis*) in older mackerel (*Scomber scombrus*), the worms themselves are probably rarely eaten by man, but residual eggs of *H. exilis* in the connective tissue of older *S. scombrus* may be ingested. Man is probably not an agent of transmission because processing procedures of fish, and modern sewage systems, kill the eggs (Gibson *et al.* 1981)

The complete life cycle of didymozoids is not yet fully known. Ishii (1935) proposed a direct life cycle. Self *et al.* (1963) studied the egg, miracidium and adult of *Nematobothrium texomensis* and attempted to determine the life cycle. They did not find evidence for a cycle with alternate hosts, and hence suggested a direct life cycle for *Nematobothrium texomensis*. However, they never found immature forms in either immature or mature host fish.

Nikolaeva (1965) suggested four alternate hosts, the first gastropod molluscs, the second crustaceans, the third small fishes (reservoir hosts) and the final large pelagic fishes. Yamaguti (1970) proposed a life cycle of Didymozoidae, on the basis of his observations on the adult and larval stages of didymozoids found in the Hawaiian fishes, as follows: " —> egg (usually ovoviparous) —> miracidium (hatching in molluscs which ingest egg) —> sporocyst-cercaria (in molluscs unknown as yet) —> premonilicaecum, pretorticaecum (postulated by Cable and Nahhas to develop in crustaceans) —> monilicaecum, torticaecum (free in proper and improper fish hosts) —> postmonilicaecum, posttorticaecum (developing and migrating in proper definitive fish hosts alone) —> juvenile (in definitive location in definitive fish hosts) —> adult (in particular teleosts)". Cable and Nahhas (1962) reported the presence of larval didymozoids in goose barnacles. They suggested that small fishes may acquire immature didymozoids by eating crustaceans, which serve as paratenic hosts. Madhavi (1968) and Køie and Lester (1985) found a didymozoid cercaria in the body cavity of a copepod, providing further evidence that crustaceans play at least an optional role in the life cycle. Larval or immature didymozoids have been observed in a number of small fish species by Fischthal and Kuntz (1964), Fischthal and Thomas (1968), Lester (1980), Køie and Lester (1985), Abdul-Salam *et al.* (1990b) and Abdul-Salam and Sreelatha (1993a,b). Køie and Lester (1985) studied larval didymozoids in fish from Moreton Bay but failed to correlate them with mature forms, because of the lack of information on adult didymozoids in fish from south-eastern Queensland.

Didymozoids are located in many parts of the fish body ranging from the very outer surface of the body (skin, fins) to the deep interior such as the connective or adipose tissue, muscles, and the digestive, respiratory, excretory or circulatory organs, even the palatal teeth or cranial bones. Because of the lack of knowledge of the didymozoid life cycle, it is not known how their larval stages enter the final host and reach their preferred site. According to Yamaguti (1970), larval stages are capable of

free migration in the body of their hosts. Hence, the family Didymozoidae exhibits a greater variety in microhabitats and morphology than other Digenea (Yamaguti, 1970). Some didymozoid species live in a capsule of host origin and some live free in host tissue without forming a capsule. The capsules completely enclose parasites without even permitting exit for the eggs, and the parasite is nourished by blood vessels of the host (Yamaguti, 1970). A new term, 'protected parasitism', was proposed by Yamaguti for this kind of parasitism. It is interesting to study the host-parasite association of such a specialized type of parasitism.

Only a few authors have described the histopathology or capsule structure of didymozoids, some of them with suggestions on how the species studied or their eggs leave the final host to continue the life cycle (Timon-David, 1937; Williams, 1959; Awachie, 1972; Noble, 1975; Gibson *et al.*, 1981; Lester, 1980; Eiras and Rego, 1987). Most of the studies are brief descriptions, all using light microscopy. Ultrastructural studies on didymozoid pathology have not been made. Timon-David (1937) studied the anatomy and pathology of *Didymocystis wedli* infecting the gill filaments of *Thunnus thunnus* from the Mediterranean. The parasite pair occupies the region between the marginal vein and the external margin of the gill filament. This positioning facilitates nutrition and oxygenation of parasites, and also dispersion of eggs. However, no evidence was found how this dissemination occurs, although the author presumed that the cysts attain a certain degree of maturity, open spontaneously and evacuate their contents to the exterior. Williams (1959) studied the anatomy of *Köllikeria filicollis* 'encysting' in the inner wall of the operculum of *Brama raii* caught on the north-west coast of Scotland. Each 'cyst' contained one to five male worms and one female worm. He believed that the 'cyst' is mainly a reaction product of the host tissue against secretions from some of the subcuticular gland cells of the female worm. He also observed some unidentified nucleated cells (degenerated macrophages, lymphocytes or host epithelial cells) associated with the inner layer of the 'cyst'. Awachie (1972)

reported a species of freshwater didymozoid of genus *Nematobothrium,* infecting three species of African carps, namely *Labeo pseudocoubie, L. coubie* and *L. senegalensis,* from Nigeria. The worms were coiled around the base of the eye ball and optic nerve without forming a capsule. The most commonly infected carp species was *L. pseudocoubie,* where both eyes were swollen and partly closed, and where also parts of the sclerotic coat were either swollen or eroded. However, the author did not know the exact action of the parasites, and believed that secondary bacterial infection of the area could be contributory to the generally poor and unhealthy condition of the infected eyes. In 1975 Noble studied the didymozoid *Nematobibothrioides histoidii* inhabiting the body wall tissues of the sunfish *Mola mola* caught in Californian coastal waters. He did not find any evidence of host reaction to this didymozoid, but he found small masses of eggs lying in the host connective tissue. The author did not know how these eggs get out of the host and presumed that they are released into water only when sunfish are attacked by their natural enemies and their tissues ruptured. Gibson *et al.* (1981) reported the didymozoid *Halvorsenius exilis* which infects the pericardium and the connective tissue of the anteriorly adjacent 'throat' region, along the kidney side of the dorsal peritoneum, in and around the obits of the eyes, and in the subcutaneous tissue of the opercula of the mackerel *Scomber scombrus* in the North Sea and English Channel. Live worms occurred only in young mackerel, but aggregation of eggs were found in older fish. The eggs appear to remain in the host's connective tissue, and are released only when the fish is eaten and digested, or dies and decomposes. According to the authors, one notable feature of the live worms is that, although they are in very close contact with the tissue of the fish host, there is no sign of a reaction against them, which suggests a long and close association with the host. Lester (1980) reported *Neometadidymozoon helicis* infecting the dermis of the buccal cavity and gill arches of the flathead *Platycephalus fuscus* from south-east Queensland, Australia. The parasites seemed to be encapsulated by a discrete "cyst", but sections stained for connective tissue

showed little more than a parting of the dermal fibres to accommodate them. *N. helicis* occurred seasonally, most of the parasites disappearing between September and December. At this time, 123 of 2041 capsules examined were red due to capillaries haemorrhaging around the worms. In the same period, 75 depressions in the mucosa, probably sites of former infection were found. Apparently, the capsule wall breaks down and the worms are released. Lester (1980) also observed another didymozoid, *Nematobothrium spinneri,* infecting the musculature of *Acanthocybium solandri*, which is enclosed by a thick wall of fibrous tissue. Connective tissue and blood capillaries are interdigitated between the coils so that the whole of the surface of the worm is in intimate contact with its host. He believes that this may facilitate the exchange of materials between the parasite and its host. Lester observed 21 capsules of *N. spinneri* and found only six of them with live worms. The other 15 were composed of masses of eggs within worm remains. He also examined a third didymozoid species, *Didymozoon brevicolle,* from the stomach wall of *P. fuscus*. Only two of 20 capsules of this species contained live worms. Therefore, he presumed that egg masses of *N. spinneri* and *D. brevicolle* are released into the environment only when the host is damaged or eaten by a predator. Eiras and Rego (1987) studied the histopathology due to *Nematobothrium scombri* living in nodules in the inner wall of the opercula of *Scomber japonicus* caught at Rio de Janeiro. The worms are surrounded by a thin layer of host dermal fibres, and no connective tissue of the host interdigitates with the coils of worms. Extensive masses of eggs were always observed. They noted haemorrhages and lymphocyte infiltration near the thick basal edge of some nodules, and to a lesser extent in the thinner parts of the nodules. According to the authors the cartilage contiguous with the nodule showed zones of destruction, with necrotic material and presence of macrophages and lymphocytes. Also, some condrocytes had pycnotic nuclei, and the cartilaginous matrix had an heterogeneous appearance. The above studies show that hosts react to some didymozoid parasites (Timon-David, 1937; Williams, 1959;

Awachie, 1972; Eiras and Rego, 1987; Lester, 1980), but not to others (Noble, 1975; Gibson, *et al.* 1981).

The present study examines host responses to three species of didymozoids infecting different parts of *S. australasicus* - *Nematobothrium filiforme* infecting primary gill filaments, *Allonematobothrioides scombri* infecting gill arches and *Nematobothrium* sp. infecting mouth tissue and skin of the operculum. Light microscopy (LM), scanning electron microscopy (SEM) and (for the first time) transmission electron microscopy (TEM) techniques were used to compare the responses of the host.

It is important to establish the nature of normal uninfected tissues to understand the host reactions. Information on the ultrastructure of normal gill filaments, skin of gill arch, skin of mouth tissue and skin of operculum in species of *Scomber* was lacking. Hence, the structures of these tissues in uninfected slimy mackerel are described with the aid of LM, SEM and TEM. Similarly, leucocytes are important elements in the teleost inflammatory response to many infections (Ellis, 1977). Since no information is available on leucocytes of fish of the genus *Scomber*, leucocytes in normal and in infected tissue of slimy mackerel are also described using LM and TEM.

Parasite responses - (Effect of host on parasites)

The effect of host size on the organs or the size of monogeneans may have significant implications for taxonomic studies of Monogenea, since many species are distinguished on the basis of hook size. Paling (1965) observed small worms of *Discocotyle sagittata* on juvenile *Salmo trutta* and large ones on adults. Gussev and Kulemina (1971a,b) found that the body size, sclerotized armature and copulatory complex increase with the size of the host in some monogeneans of the three genera *Dactylogyrus*, *Tetraonchus* and *Diplozoon*. Roubal *et al.* (1983) observed differences in the size of the body and sclerites of two monogeneans, *Lamellodiscus pagrosomi* and *Bivagina auratus* from large and small snapper, caught at the same locality in southern

Australia. Thoney (1986) found that body length and posterior clamp width of the monogenean *Microcotyle sebastis* were larger in naturally infested adult black rock fish, *Sebastes melanops* than in experimentally infested juveniles. Thoney (1988) also established a relationship between size of the monogenean *Heteraxinoides xanthophilis* and the length of its host *Leiostomus xanthurus.* Rohde (1991) observed a slight but significant correlation between lengths of hamuli of *Kuhnia scombri* and size of the host, *Scomber australasicus* caught at one location. In the present study, the length of large hamuli of the monogenean *Kuhnia scombri* were measured to determine whether there is a relationship with host size to examine possible effects of the host on its parasites.

In summary, the aims of the present study are:

1. to identify the ectoparasitic fauna of *Scomber australasicus*
2. to study the microhabitats of ectoparasites
3. to study seasonal variations in abundances of these parasites and to find a relationship between intensities of ectoparasites of *S. australasicus* with host lengths
4. to study the structure of uninfected gill filaments, skin of gill arches, mouth tissue and skin of operculum of *S. australasicus* as a basis for a study of the effects of parasites on the host
5. to study the effects of parasites on the host of three species of didymozoids, using light and electron microscopy (The three didymozoid species selected for the study are: *Nematobothrium filiforme* infecting primary gill filaments, *Allonematobothrioides scombri* infecting gill arches and *Nematobothrium* sp. infecting mouth tissue and skin of operculum.)
6. to study the host effect on parasites, by measuring the length of large hamuli of *Kuhnia scombri* on host fish (*S. australasicus*) of different lengths

References

Abdul-Salam, J. and Sreelatha, B. and Farah, M. (1990a). *Gonapodasmius epinepheli* n. sp. (Didymozoidae) from the grouper *Epinephelus tauvina* from the Arabian Gulf. *Systematic Parasitology*, **17**: 67 - 74.

Abdul-Salam, J. and Sreelatha, B. S. and Farah, M. (1990b). Surface topography and description of a larval didymozoid (Trematoda, Didymozoidae) from the threadfin bream *Nemipterus peronii*. *Japanese Journal of Parasitology*, **39**:369 - 375.

Abdul-Salam, J. and Sreelatha, B. S. (1993a). Description and surface topography of larval didymozoid (Trematoda) from *Apogon uninotatus* (Apogonidae) in Kuwait Bay. *Journal of Helminthological Society of Washington*, **60**: 211 - 215.

Abdul-Salam, J. and Sreelatha, B. S. (1993b). A survey of didymozoid trematodes of the barracuda *Sphyraena obtusata* from Kuwait Bay. *International Journal for Parasitology*, **23**: 665 -669.

Armitage, J. G. (1980). The Taxonomy, Zoogeography and Site Specificity of the Metazoan Ectoparasites of the Snapper, *Chrysophrys auratus*. M.Sc. (Prelim.) Thesis, University of New England, Armidale.

Avdeev, V. V. (1979). [Parasitic isopods of the genus *Meinertia* from Australian-New Zealand region.] *Biologiya Morya - Marine Biology*, **2**: 48 - 54. (Russian)

Awachie, J. B. E. (1972). On the didymozoid trematode parasitic in the eye socket of African carps *Labeo* spp. from area of the Kainji man made lake in Nigeria. *Acta Parasitologica Polonica*, **20**: 497 - 498.

Beumer, J. P., Ashburner, L. D., Burbury, M. E., Jetté, E. and Latham, D. J. (1983). *A checklist of the parasites of fishes from Australia and its adjacent Antarctic Territories.* Technical Communication No. 48 of the Commonwealth Institute of Parasitology, Commonwealth Agricultural Bureaux, Farnham Royal, Slough, England.

Byrnes, T. (1980). The Taxonomy, Site Specificity and Zoogeography of Metazoan Ectoparasites Infecting the Southern, Yellowfin and Tropical Black Bream. B.Sc. (Hons.) Thesis, University of New England, Armidale.

Cable, R. M. and Nahhas, F. M. (1962). *Lepas* sp., Second intermediate host of a didymozoid trematode. *The Journal of Parasitology*, **48**: 34.

Collette, B. B. and Nauen, C. E. (1983). "FAO Species Catalogue, Vol. 2 Scombrids of the World," FAO Fisheries Synopsis No. 125, Vl. 2, Rome, 137 pp

Cressey, R. and Cressey, H. B. (1980). *Parasitic copepods of mackerel- and tuna-like fishes (Scombridae) of the World.* Smithsonian Contributions to Zoology, No. 311. Smithsonian Institution Press, Washington.

Cressey, R. F., Collette, B. B. and Russo, J. L. (1983). Copepods and scombrid fishes: a study in host-parasite relationships. *Fishery Bulletin*, **81**: 227 - 265.

Cribb, T. H. and Williams, A. (1992). *Gonapodasmius williamsoni* sp. n. (Digenea: Didymozoidae) from the pink snapper, *Pagrus auratus* (Teleostei: Sparidae) in Western Australia. *Journal of Helminthological Society of Washington*, **59:** 153 - 158.

Eiras, J. C. and Rego, A. A. (1987). The histopathology of *Scomber japonicus* infection by *Nematobothrium scombri* (Trematoda: Didymozoidae) and of larval anisakid

nematode infections in the liver of *Pagrus pagrus*. *Memórias do Instituto Oswaldo Cruz, Rio de Janeiro*, **82**: 155 - 159.

Ellis, A. E. (1977). The leucocytes of fish: a review. *Journal of Fish Biology*, **11**: 453 - 491.

Fischthal, J. H. and Kuntz, R. E. (1964). Digenetic trematodes of fishes from Palawan Island, Philippines. IV. Some immature Didymozoidae, a bucephalid; a new hemiuroid genus and subfamily. *The Journal of Parasitology*, **50**: 253 - 260.

Fischthal, J. H. and Thomas, J. D. (1968). Trematodes of marine fishes from Ghana: families Acanthocolpidae, Bucephalidae, Didymozoidae. *Proceedings of the Helminthological Society of Washington*, **35**: 237 - 247.

Gibson, D. I., MacKenzie, K. and Cottle, J. (1981). *Halvorsenius exilis* gen. et sp. nov., a new didymozoid trematode from the mackerel *Scomber scombrus* L. *Journal of Natural History*, **15**: 917 - 929.

Gussev, A. V. and Kulemina, I. V. (1971a). [Taxonomic characters of some monogeneans from the hosts of different age.] *Parazitologiya,* (Leningrad), **5**: 162 - 171. (Russian)

Gussev, A. V. and Kulemina, I. V. (1971b). [Analysis of variability of characters, behaviour and development's cycle of monogeneans from the age of hosts.] *Parazitologiya,* (Leningrad), **5**: 320 - 329. (Russian)

Heath, B. M. (1980). Phenology of the parasites of two local species of whiting with respect to season and host age. B.Sc. (Hons.) Thesis, University of Queensland.

Heegaard, P. E. (1940). Some new parasitic copepods (Chondracanthidae and Lernaeopodidae) from Western Australia. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i København*, **104**: 87 - 101.

Ishii, N. (1935). Studies on the family Didymozooidae (Monticelli, 1888). *Japanese Journal of Zoology*, **6**: 279 - 335.

Kamegai, S. (1971). [The determination of a generic name of flying fishes' muscle parasite, a didymozoid, whose ova have occasionally been found in human feces in Japan.] *Japanese Journal of Parasitology*, **20**: 170 - 176. (Japanese)

Køie, M. and Lester, R. J. G. (1985). Larval didymozoids (Trematoda) in fishes from Moreton Bay, Australia. *Proceedings of the Helminthological Society of Washington*, **52**: 196 - 203.

Korotaeva, V. D. (1974). [Helminths of some commercial marine fish of the suborder Scomberoidei from the Australian region.] *Izvestiya Tikhookeanskogo Rybnogo Khozyaistva i Okeanografii (TINRO) (Parazity morskikh zhivotnykh)*, **88**: 61 - 66. (Russian)

Langdon, J. S. (1991). Myoliquefaction post-mortem ('milky flesh') due to *Kudoa thyrsites* (Gilchrist) (Myxosporea: Multivalvulida) in mahi mahi, *Coryphaena hippurus* L. *Journal of Fish Diseases*, **14**: 45 - 54.

Langdon, J. S., Gudkovs, N., Humphrey, J. D. and Saxon, E. C. (1985). Deaths in Australian freshwater fishes associated with *Chilodonella hexasticha* infection. *Australian Veterinary Journal*, **62**: 409 - 413.

Lester, R. J. G. (1980). Host-parasite relations in some didymozoid trematodes. *The Journal of Parasitology*, **66**: 527 - 531.

Lester, R. J. G., Barnes, A. and Habib, G. (1985). Parasites of skipjack tuna, *Katsuwonus pelamis*: fishery implications. *Fishery Bulletin*, **83**: 343 - 356.

Llewellyn, J. (1962). The life histories and population dynamics of monogenean gill parasites of *Trachurus trachurus* (L.). *Journal of the Marine Biological Association of the U.K.*, **42**: 587 - 600.

Lom, J., Rohde, K. and Dykova, I. (1992). Studies on protozoan parasites of Australian fishes I. New species of the genera *Coccomyxa* Léger et Hesse, 1907, *Ortholinea* Shulman, 1962 and *Kudoa* Meglitsch, 1947 (Myxozoa, Myxosporea). *Folia Parasitologica*, **39**: 289 - 306.

Madhavi, R. (1968). A didymozoid metacercaria from the copepod, *Paracalanus aculeatus* Giesbrecht, from Bay of Bengal. *The Journal of Parasitology*, **54**: 629.

Mordvinova, T. N. (1989). [A new Trematoda species *Nematobothrium atlanticus* (Didymozoidae), a parasite of flying fish.] *Zoologicheskii Zhurnal*, **68**: 135 - 137. (Russian)

Munday, B. L., Foster, C. K., Roubal, F. R. and Lester, R. J. G. (1990). Paramoebic gill infection and associated pathology of Atlantic salmon, *Salmo salar* and rainbow trout, *Salmo gairdneri*, in Tasmania. pp 215 - 222. In: F. O. Perkins and T. C. Cheng (Eds) *Pathology in Marine Science*. Academic Press, Inc. Harcourt Brace Jovanovich, Publishers, San Diego, California.

Munday, B. L., Lange, K., Foster, C., Lester, R. J. G. and Handlinger, J. (1993). Amoebic gill diseases of sea-caged salmonids in Tasmanian waters. *Tasmanian Fisheries Research*, number (#) **28**: 14 - 19.

Murugesh, M., Krishna Sai Ram, B. and Madhavi, R. (1992). Nematobothriine didymozoid trematodes from marine teleost fish of the coast of Visakhapatnam, Bay of Bengal. *Rivista di Parassitologia*, **9-**: 79 - 86.

Nikolaeva, V. M. (1965). [The developmental cycle of trematodes belonging to the family Didymozoidae (Monticelli, 1888) Poche, 1907.] *Zoologicheskii Zhurnal* **44**: 1317 - 1327. (Russian)

Nikolaeva, V. M. (1985). Trematodes - Didymozoidae Fauna, Distribution and Biology. pp 67 - 72. In: W. J. Hargis Jr (Ed) *Parasitology and pathology of marine organisms of the World Ocean.* Seattle, USA; US Department of Commerce, National Oceanic and Atmospheric Administration.

Nikolaeva, V. M. and Tkachuk, L. P. (1986). [A new species of didymozoids (Didymozoidae) from Japanese mackerel.] *Parazitologiya*, **20**: 219 - 221. (Russian)

Noble, G. A. (1975). Description of *Nematobibothrioides histoidii* (Noble, 1974) (Trematoda: Didymozoidae) and comparison with other genera. *The Journal of Parasitology*, **61**: 224 - 227.

Paling, J. E. (1965). The population dynamics of the monogenean gill parasite *Discocotyle sagittata* Leuckart on Windermere trout, *Salmo trutta*, L. *Parasitology*, **55**: 667 - 694.

Philbey, A. W. and Ingram, B. A. (1991). Coccidiosis due to *Goussia lomi* (Protista: Apicomplexa) in aquarium-reared Murray cod, *Maccullochella peeli* (Mitchell), (Percichthyidae). *Journal of Fish Diseases*, **14**: 237 - 242.

Pozdniakov, S. E. (1987). [*Didymonaja branchialis* sp. n. Gen. n. (Trematoda, Didymozoidae), a parasite of *Thunnus alalunga* from the north-western Pacific.] *Parazitologiya*, **21**: 755 - 757. (Russian)

Pozdniakov, S. E. (1988). [*Allonematobothrioides hirosaba* sp. n. (Trematoda, Didymozoidae) - a parasite of *Scomber japonicus* from north-western Pacific.] *Parazitologiya*, **22**: 187 - 190. (Russian)

Pozdniakov, S. E. (1989). [On the finding of didymozoids in pelagic sharks of the Pacific.] *Parazitologiya*, **23**: 529 - 532. (Russian)

Prost, M. (1963). Investigations on the development and pathogenicity of *Dactylogyrus anchoratus* (Duj., 1845) and *D. extensus* Mueller et v. Cleave, 1932 for breeding carps. *Acta Parasitologica Polonica*, **11**: 17 - 47.

Rego, A. A., Carvalho-Varela, M., Mendonca, M. M. and Afonso-Roque, M. M. (1985). Helmintofauna da sarda (*Scomber scombrus* L.) Peixe da costa continental Portuguesa. *Memórias do Instituto Oswaldo Cruz, Rio de Janeiro*, **80**: 97 - 100.

Rego, A. A. and Santos, C. P. (1983). Helmintofauna de cavalas, *Scomber japonicus* Houtt, do Rio de Janeiro. *Memórias do Instituto Oswaldo Cruz, Rio de Janeiro*, **78**: 443 - 448.

Rohde, K. (1976). Marine parasitology in Australia. *Search*, **7**: 477 - 482.

Rohde, K. (1977). Habitat partitioning in monogenea of marine fishes. *Heteromicrocotyla australiensis*, sp. nov. and *Heteromicrocotyloides mirabilis*, gen. and sp. nov. (Heteromicrocotylidae) on the gills of *Carangoides emburyi* (Carangidae) on the Great Barrier Reef, Australia. *Zeitschrift für Parasitenkunde*, **53**: 171 - 182.

Rohde, K. (1978). Monogenean gill parasites of the king fish *Seriola grandis* (Castlenau) from the Great Barrier Reef. *Publications of the Seto Marine Biological Laboratory,* **24**: 369 - 76.

Rohde, K. (1981). Niche width of parasites in species rich and species poor communities. *Experientia,* **37**: 359 - 361.

Rohde, K. (1984). Diseases caused by metazoans: Helminths. pp 193 - 320. In: Kinne, O. (Ed) *Diseases of marine animals.* Vol. 1V, part 1. Biologische Anstalt Helgoland, Hamburg.

Rohde, K. (1987). *Grubea australis* n. sp. (Monogenea, Polyopisthocotylea) from *Scomber australasicus* in southeastern Australia, and *Grubea cochlear* Diesing, 1858 from *S. scombrus* and *S. japonicus* in the Mediterranean and western Atlantic. *Systematic Parasitology*, **9**: 29 - 38.

Rohde, K. (1989). *Kuhnia sprostonae* Price, 1961 and *K. scombercolias* Nasir & Fuentes Zambrano, 1983 (Monogenea: Mazocraeidae) and their microhabitats on the gills of *Scomber australasicus* (Teleostei: Scombridae), and the geographical distribution of seven species of gill monogenea of *Scomber* spp. *Systematic Parasitology*, **14**: 93 - 100.

Rohde, K. (1991). Size differences in hamuli of *Kuhnia scombri* (Monogenea: Polyopisthocotylea) from different geographical areas not due to differences in host size. *International Journal for Parasitology*, **21**: 113 - 114.

Rohde, K. (1993). *Ecology of Marine Parasites - An Introduction to Marine Parasitology.* CAB International, Wallingford, Oxon, U. K.

Rohde, K. and Watson, N. (1985a). Morphology and geographical variation of *Pseudokuhnia minor* n. g., n. comb. (Monogenea: Polyopisthocotylea). *International Journal for Parasitology*, **15**: 557 - 567.

Rohde, K. and Watson, N. (1985b). Morphology, microhabitats and geographical variation of *Kuhnia* spp. (Monogenea: Polyopisthocotylea). *International Journal for Parasitology*, **15**: 569 - 586.

Romuk-Wodoracki, D. (1988). Parasitic fauna of Atlantic mackerel (*Scomber scombrus* L.) from the fishing grounds of Cape Hatteras. *Acta Icthyologica et Piscatoria*, **18**: 49 - 60.

Roubal, F. R. (1981). The taxonomy and site specificity of the metazoan parasites on the black bream *Acanthopagrus australis* (Günther 1859) in northern New South Wales. *Australian Journal of Zoology* Supplement **84**: 100p.

Roubal, F. R. (1985). Histological, cytological and morphometric aspects of ectoparasite pathology on the marine bream, *Acanthopagrus australis*. Ph.D. thesis, University of New England, Armidale.

Roubal, F. R. (1990). Seasonal changes in ectoparasite infection of juvenile yellowfin bream, *Acanthopagrus australis* (Günther) (Pisces: Sparidae), from a small estuary in northern New South Wales. *Australian Journal of Marine and Freshwater Research*, **41**: 411 - 427.

Roubal, F. R., Armitage, J. and Rohde, K. (1983). Taxonomy of metazoan ectoparasites of snapper, *Chrysophrys auratus* (Family Sparidae), from southern Australia, eastern Australia and New Zealand. *Australian Journal of Zoology* Supplement **94**: 68p

Roubal, F. R., Lester, R. J. G. and Foster, C. K. (1989). Studies on cultured and gill-attached *Paramoeba* sp. (Gymnamoebae: Paramoebidae) and the cytopathology of paramoebic gill diseases in Atlantic salmon, *Salmo salar* L., from Tasmania. *Journal of fish Diseases*, **12**: 481 - 493.

Self, J. T., Peters, L. E. and Davis, C. E. (1963). The egg, miracidium, and adult of *Nematobothrium texomensis* (Trematoda: Digenea). *The Journal of Parasitology*, **49**: 731 - 736.

Somdal, O. and Schram, T. A. (1992). Ectoparasites on northeast Atlantic mackerel (*Scomber scombrus* L.) from Western and North Sea stocks. *Sarsia*, **77**: 19 - 31.

Thoney, D. A. (1986). Post-larval growth of *Microcotyle sebastis* (Platyhelminthes: Monogenea), a gill parasite of the black rockfish. *Transactions of the American Microscopical Society*, **105**: 170 - 181.

Thoney, D. A. (1988). Developmental variation of *Heteraxinoides xanthophilis* (Monogenea) on hosts of different sizes. *The Journal of Parasitology*, **74**: 999 - 1003.

Timon-David, J. (1937). Les kystes á *Didymocystis wedli* du thon. Étude anatomo-pathologique. *Annales de Parasitologie Humaine et Comparee*, **15**: 520 - 523.

Valtonen, E. T., Prost, M. and Rahkonen, R. (1990). Seasonality of two gill monogeneans from two freshwater fish from an oligotrophic lake in northeast Finland. *International Journal for Parasitology*, **20**: 101 - 107.

Williams, A., Moran, M., Caputi, N. and Walters, C. (1993). Didymozoid trematode infection of snapper, *Pagrus auratus* (Sparidae), off Western Australia: parasite population biology and fishery implications. *Fisheries Research*, **16**: 113 - 129.

Williams, H. H. (1959). The anatomy of *Köllikeria filicollis* (Rudolphi, 1819), Cobbold, 1860 (Trematoda: Digenea) showing that the sexes are not entirely separated as hitherto believed. *Parasitology*, **49**: 39 - 53.

Yamaguti, S. (1970). *Digenetic Trematodes of Hawaiian Fishes.* Keigaku Publishing Co. Tokyo, Japan.

Chapter 2

Ectoparasitic fauna and description of three species of didymozoid trematodes (Nematobothriinae) from *Scomber australasicus* from the south-east coast of New South Wales

Chapter 3

Microhabitats of ectoparasites of slimy mackerel, *Scomber australasicus*

Chapter 4

No evidence for seasonality in the ectoparasitic fauna of slimy mackerel, *Scomber australasicus*

Chapter 5

Light microscopic study of the pathology of *Nematobothrium filiforme* from the gills of slimy mackerel, *Scomber australasicus.*

Chapter 6

Ultrastructure of the primary gill lamellae of *Scomber australasicus*

Chapter 7

Ultrastructure of the primary gill lamellae of *Scomber australasicus* infected by *Nematobothrium filiforme*

Chapter 8

Structure of the skin of the gill arch of the slimy mackerel, *Scomber australasicus* (Teleostei: Scombridae) as revealed by light and electron microscopy

Chapter 9

Light and electron microscopic study of the pathology of *Allonematobothrioides scombri* (Trematoda, Didymozoidae) infecting the gill arches of *Scomber australasicus* (Teleostei, Scombridae)

Chapter 10

Light and electron microscopic study of the pathology of *Nematobothrium* sp. (Trematoda: Didymozoidae) infecting the mouth tissue of *Scomber australasicus* (Teleostei: Scombridae)

Chapter 11

Pathology of a species of *Nematobothrium* (Trematoda, Didymozoidae) infecting the operculum of *Scomber australasicus* (Teleostei, Scombridae)

Chapter 12

The effect of host size on large hamuli length of *Kuhnia scombri* (Monogenea: Polyopisthocotylea) from Eden, New South Wales, Australia

Chapter 13

General Conclusions

Species composition

The metazoan ectoparasite fauna of slimy mackerel, *Scomber australasicus* from Eden, New South Wales, Australia is rich in species, consisting of altogether sixteen species, including monogeneans, trematodes (didymozoids - not strictly ectoparasites but close to the surface), copepods, isopods and cestodes. That species diversity is greater at lower latitudes has been known for a long time, but little attention has been paid to latitudinal differences in parasite species diversity. Rohde (1993) has shown that marine fish from warm waters harbour more species of gill parasites than cold water fish, and that Indo-Pacific fish harbour more parasite species than Atlantic fish. Thus, the richness of the ectoparasite fauna of *S. australasicus* from southern New South Wales is expected and could be enhanced by the influence of the east Australian current which carries warm water far down along Australia's east coast.

The monogeneans *Kuhnia scombri*, *K. scombercolias*, *K. sprostonae*, *Pseudokuhnia minor* and *Grubea australis* were observed in the present study. The same monogeneans were previously recorded from the same host by Rohde and Watson (1985a,1985b) and Rohde (1987,1989). Further, I observed a single polyopisthocotylean monogenean (Microcotylidae) on the gill filaments of one fish, similar to one previously observed on *Trachurus* sp. from Coffs Harbour by Rohde (unpublished). This may have been a chance infection, because *S. australasicus* tends to form mixed schools with *Trachurus* sp. (Rohde, personal communication). Among the monogeneans, *P. minor* is the most abundant species, followed by *K. scombri*, *K. scombercolias* and *G. australis*. *K. sprostonae* is the rarest monogenean parasitizing *S. australasicus*.

The number of didymozoid species observed is not definite because all of them could not be clearly identified. The two species *Nematobothrium filiforme* and *Allonematobothrioides scombri* occur in the gill filaments and the gill arch tissue, respectively. *N. filiforme* has been previously recorded by Korotaeva (1974) from the

same host and by Yamaguti (1934) from *Scomber japonicus*. *A. scombri* has not been previously recorded from *S. australasicus*, although it is known from the gill arches of *Scomber japonicus* (Yamaguti, 1970). It appears that the didymozoids *N. filiforme* and *A. scombri* are common parasites of both *S. australasicus* and *S. japonicus*. Another, possibly new and unidentified species of *Nematobothrium* (type 5a) was found in the fins, finlets, mouth tissue and skin of the operculum of the host. In addition, a didymozoid infecting the gill filaments (didymozoid type 4) and at least one other species infecting opercular bones, skull bones and the tissues around the eyes (didymozoid type 5b) remain to be identified. The most abundant didymozoid parasite of *S. australasicus* is *N. filiforme*.

Two species of copepods, *Brachiella magna* and an unidentified species of *Peniculus* were found for the first time on *S. australasicus*. Both occurred in small numbers. In addition, three species of caligid copepods were found in a single sample. These also remain to be identified. I did not find the previously recorded copepods of *S. australasicus*, *Euclavellisa australis* (see Heegaard, 1940), *Clavellisa scombri*, *Pumiliopes capitulatus* and *P. jonesi* (see Cressey and Cressey, 1980 and Cressey *et al.*, 1983).

I recovered one isopod, *Ceratothoa imbricata,* a new record from *S. australasicus* in Australia, although *Ceratothoa trillesi* was reported from the buccal cavity of the same host species by Avdeev (1979). Furthermore, a larval trypanorhynch (Cestoda), was found mostly in the sediments. Several unknown cysts were found on the primary gill filaments.

Microhabitats

The nature of the attachment organ determines the mobility of ectoparasites on the body of the host, and thus is a major factor influencing site specificity of ectoparasites. Most monogeneans have a narrow range of microhabitats because the

hooks and clamps of most polyopisthocotylean monogeneans permit attachment only to the gill filaments, and sometimes only to certain gill filaments (of a certain size) or to some parts of the filaments. All the monogenean parasites of *S. australasicus* were polyopisthocotyleans and were confined to restricted microhabitats on the gills. The monogenean *Kuhnia scombri* lives predominantly on the fifth and sixth longitudinal sections of the first gill and to a lesser degree on the second and third gills, (gill sections refer to eight longitudinal zones of a gill, numbered sequentially starting from the buccal end of the fish) almost exclusively at the base of the external gill filament. *K. sprostonae* lives on the pseudobranchs, and *Grubea australis* occupies mostly the seventh and eighth sections of the fourth gill and is rarely found on the other three gills. The microhabitats of the other two monogeneans, *Pseudokuhnia minor* and *K. scombercolias,* overlap. *P. minor* prefers the first six sections of the first gill and the first five sections of the third gill, and *K. scombercolias* prefers the fourth to seventh sections of the first and the third to seventh sections of the third gill. The distributions of monogeneans on the gills of *S. australasicus* in the present study agree with the results of Rohde (1989). However, he did not record *Kuhnia scombercolias* on the first gill, whereas I found this species there. This may be due to the large sample size I examined.

The didymozoid *N. filiforme* is encapsulated in the efferent side of the gill filaments of all four gills, large numbers occupying the seventh section of the second and third gills and the fourth section of the fourth gill. They usually prefer the proximal half of the gill filaments, mostly occupying the internal filaments of the first gill, and the external filaments of the fourth gill. No preference was seen for either external or internal gill filaments of the other two gills. Type 4 didymozoids occupy about two thirds of the gill filaments, toward the tip, mostly inhabiting the third to sixth longitudinal sections of the last three gills, and generally occurring in the external gill filaments. The didymozoid *A. scombri* is encapsulated in the gill arch tissue, attached

to the third or fourth gill arch by a short narrow stalk, often on the internal side of the gill arch. The didymozoids infecting the body (types 5a and 5b) were observed in the fins, finlets, mouth, operculum, skull bones and the tissue around the eyes. The distribution of didymozoids in the gills and external surface of *S. australasicus* has not been studied previously.

The copepod *B. magna* was mostly found attached to the gill arches and primary gill filaments of the first and third gills, and it prefers the external side of the gill arches. The copepod *Peniculus* sp. was usually found attached to the pectoral, pelvic fins or the dorsal finlets. The distribution of *B. magna* and *Peniculus sp.* on the gills and external surface of *S. australasicus* has not been studied previously.

The isopod *Ceratothoa imbricata* mostly occupies the mouth cavity, and sometimes occurs on the gills with no particular preference for any site on the gills because of their mobility. Trypanorhynch larvae were found in small numbers, mostly in the sediments, making it difficult to define the microhabitat. Unidentified cysts were found in small numbers usually occupying the third to seventh sections of the first gill. Their numbers decreased in successive gills (gills 1 to 4). The distribution of none of these species on *S. australasicus* has been studied previously.

Preferences for different microhabitats are consistent with several hypotheses explaining site preferences of ectoparasites of fish. According to Llewellyn (1956) and Wiles (1968), the differential spatial distributions of monogeneans on certain parts of the gills of their hosts are due to differences in the flow of water of the respiratory current over the different parts of the gill apparatus. The greatest volume of water in the gill ventilating current passes over the second and third gill arches, the first gill arch receives the next greatest volume and the fourth the least (Paling, 1969). Due to the greater volume of water flowing over the first three gills more parasites have the opportunity to attach to these gills. Wootten (1974) showed that more water passed over the distal halves than the basal halves of the gill filaments. The present

observations that *K. scombri*, *K. scombercolias* and *P. minor* are mostly present on the first three gills, whereas the fourth gills have very few monogeneans of these species, and that *P. minor* and *K. scombercolias* live on the distal zone of the filaments, partly agree with these hypotheses. Therefore, it appears that in this case the ventilation current indeed gives these parasites a greater opportunity to attach to these gills.

However, in the present study, more parasites were observed on the first gill than the second and third. This could be due to migration of parasites as suggested by Arme and Halton (1972) that the parasites may first randomly settle on the gills and then migrate to a particular microhabitat in response to unknown stimuli. The parasites may be migrating to specific attachment sites to minimise the resistance to the gill ventilation currents of their hosts (Llewellyn, 1956; Paling, 1969; Wootten, 1974). I found that *G. australis* lives mainly on the posterior quarter of the fourth gill and a few parasites were also recorded on the same location of the first three gills. *G. australis* is the largest among the monogeneans. Hence, this microhabitat attachment site may be an adaptation to reduce resistance to the gill ventilating current. Both *K. scombri* and *K. sprostonae* also have relatively large bodies. *K. scombri* is always attached to the basal part of the gill filaments and *K. sprostonae* was found only on the pseudobranchs. Again, this may be an adaptation to reduce resistance to the gill ventilating current.

Presence of more parasites on the first gill and decrease in their numbers on successive gills could also be due to size of the gill. The larger surface area of the first gill gives parasites more opportunity for attachment. The first gill is the largest and the fourth is the smallest.

The monogeneans *K. sprostonae* and *G. australis,* both species occurring in very low densities, have the most restricted microhabitats. This may facilitate mate finding. In contrast, *P. minor* and *K. scombercolias*, the most abundant monogeneans, show the lowest microhabitat restriction compared to the others. These results support Rohde's mating hypothesis (see Rohde 1977, 1978, 1979, 1980, 1989), in that the ability to

establish large populations and/or to move within the habitat means that cross-fertilizing species need not have as restricted microhabitats as less mobile and rarer species.

Congeneric species with similar copulatory organs, that is, *K. sprostonae*, *K. scombri* and *K. scombercolias* occupy different microhabitats without any overlap, whereas non-congeners found in considerable numbers, *K. scombercolias* and *P. minor,* overlap to a certain extent. All species of monogeneans studied by me are likely to be blood feeding (as indicated by haematin in their caeca) and its supply is not a limiting factor in living animals. Hence, competition for food cannot explain the spatial segregation of the three species of *Kuhnia*. It appears that reinforcement of reproductive barriers is the more likely cause of segregation as suggested by Rohde (1980) on the basis of the observation that species with dissimilar copulatory organs (*P. minor* and *K. scombercolias*) live in overlapping microhabitats, whereas congeners with identical copulatory organs (*Kuhnia* spp.) are spatially segregated.

Seasonal variation

Temperature has been considered to be a major factor regulating the seasonal abundance of fish ectoparasites and may act directly by regulating the rate of development or fecundity or indirectly through affecting host spawning behaviour and associated hormonal levels or host immune-responsiveness (Kennedy, 1975). However, environmental temperature does not appear to affect the seasonal abundance and prevalence of ectoparasites of *S. australasicus* greatly. Absence of clear seasonality indicates that ectoparasites of *S. australasicus* are unlikely to become particularly pathogenic at certain times of the year.

Although the results of the present study suggest that distinct seasonal fluctuations in abundance of ectoparasites of *S. australasicus* do not occur, the limitations of this investigation must be mentioned. Host samples were not received in regular intervals, and no samples were examined between November 1991 and June 1992. Samples frequently contained small fish only and only a few large fish were

examined from May 1990. Examination of regular and larger samples may perhaps show slight seasonal fluctuations.

Preference for host size

Some species of ectoparasites of *S. australasicus* (*K. scombri*, *P. minor*, *N. filiforme*, didymozoid type 4, didymozoids infecting the body, and unidentified cysts) were more frequently found on small than on large fish. *B. magna* occurred more frequently on larger fish. The remaining parasites did not show any significant relationship with fish length. According to Dogiel *et al.* (1958), the frequent increase in intensity and incidence of infection with the age of host, is to be expected merely on the basis of increase in size of surface available for attachment. Also, a longer life would provide more opportunity for infestation of gills. An increase in parasite numbers with age of the host may also result from the continuous infection with either short-lived or long-lived parasites, whereas the apparent independence between parasite numbers and host's age may be due to seasonal reinfection with short-lived parasites (Kennedy, 1970). Changes in the host's habitat, for example, migration to regions unfavourable for the parasite's development (Llewellyn, 1962), mucus production, tissue hypertrophy and immunity (Frankland, 1955; Kennedy, 1970), may lead to a decrease in parasite numbers. There are also environmental factors such as when and where a fish begin its life, the sequence of events that occurred in each habitat the fish encountered during its life, and the length of exposure that can influence the intensity of parasites (Rohde, 1993). However, factors responsible for heavier or lighter infections of small or large *S. australasicus* are not understood, and their study is beyond the scope of my work.

Host responses - (Effect of parasites on host)

The response of the host to the various didymozoid species depends on the type of tissue infected, the species of parasite, and the duration of parasite infection. It is also related to the size of the parasite. These responses of *S. australasicus* to

didymozoid parasites were studied in depth by T.E.M. observations of uninfected and infected tissues. This is the first electron microscopic study of the pathology induced by didymozoids.

The ultrastructure of uninfected gill epithelium and the scale-free epidermis of gill arch, mouth and operculum of *S. australasicus* agrees well with similar descriptions of other teleosts.

The three didymozoid species, *Nematobothrium filiforme*, *Allonematobothrioides scombri* and *Nematobothrium* sp. studied occupy three different sites on *S. australasicus*. *N. filiforme* (usually occurring in pairs) always infected the external side of both internal and external gill filaments, usually in the proximal half (close to the base of the gill arch) of the gill filament. The parasites always occupy a space between the basal lamina of the lateral epithelium and the efferent artery of the primary gill filament, where they are encapsulated by primary lateral epithelium and the efferent artery of the primary gill filament. The capsule of *A. scombri* is always attached by a stalk to the base of either the internal or external side of the gill arches, and usually sits on the primary gill filaments. The capsule itself is different from that of the didymozoid species infecting the primary gill filaments, as the worms are completely covered by the skin of the gill arch, and they do not have any contact with the rest of the gill arch tissue. *Nematobothrium* sp. infect the mouth tissues and the skin of the operculum and live in parted collagen fibres in the dermis. There is no overlapping of habitats between these three species. In contrast, Yamaguti (1970) observed sharing of microhabitats of the two didymozoid species *Didymocystis palati* and *D. superpalati* throughout their later larval and entire adult stages, in the palate of *Neothunnus macropterus*. They live as long as space is available and no displacement of one species by the other occurs throughout their parasitic life.

Some didymozoid species live in a capsule of host origin and some live free in the host tissue (Yamaguti, 1970). The formation of the capsule is the first visible

response of the host to capsule inducing didymozoids. Two ways of capsule formation were observed in the present study. In the first, the host tissue stretches to accommodate growing worms of the species *N. filiforme*. The capsules of very young *N. filiforme* were thread-like and whitish. When the parasites became larger, the capsule wall (lateral epithelium) stretched to accommodate them and the shape of the efferent artery also changed from round to oval, due to growth pressure of the parasite. Finally, the capsule became spindle shaped and yellowish due to mature worms with eggs. Timon-David (1937) also observed stretching of the epithelium due to growing *Didymocystis wedli* which occupies the same location as *N. filiforme* in the gill filaments of *Thunnus thunnus*.

In the second type of capsule formation, active tissue proliferation takes place resulting in complete encapsulation of worms. This was observed in *A. scombri* infections. The worm pair was completely covered by a thin-walled capsule of host origin (skin of gill arch), and a short and narrow stalk connected it to the gill arch. It appears that proliferation (hyperplasia) of epidermal cells and connective tissue occurs in the host tissue during infection. Yamaguti (1970) (on the basis of light microscopic observations) also reported that the didymozoid capsule is formed as a result of reactive tissue proliferation by the host. The structure of the capsule of *A. scombri* appears to be similar to the capsule of *Köllikeria filicollis,* described by Williams (1959) as a "cyst", where the worms were surrounded by the host tissue and attached to the epithelium inside the operculum near the posterior gill of *Brama raii*. According to his description, capsules are a reaction of the host tissue to secretions from some of the subtegumental gland cells of the female worm, and the inner layer of the capsule is of parasitic origin, derived from discharge products of 'subcuticular' (subtegumental) gland cells. The space between worms in the capsule of *A. scombri* is possibly filled with a liquid but its origin is not known. The larvae or juveniles of *A. scombri* may have some chemical substance to induce the proliferation of the skin of the gill arch but no evidence was

found to prove this. Since no developing capsules of *A. scombri* were observed during the study, the exact formation of this large capsule is not understood.

The free living didymozoid *Nematobothrium* sp. lives either parting the connective tissue of the mouth or freely between the connective tissue of the skin of the operculum. In the opercular tissue, the worms seem to be encapsulated, but closer examination reveals that they live between collagen fibres of the dermis. Similar (but light microscopic) observations have been made on didymozoids living in various tissues of fish by other authors (Self *et al.*, 1963; Nikolaeva and Korotaeva, 1970; Noble, 1975; Gibson *et al.*, 1981; Mordvinova, 1989; Cribb and Williams, 1992).

The presence of parasites results in some ultrastructural changes in the host tissue as well. The main change observed was cup-shaped electron-dense filamentous bands in the cytoplasm of the epithelial cells in the mature capsule wall of *N. filiforme.* These bands were not visible in developing capsules and they begin to appear in the cytoplasm of the epithelial cells after a certain stage in the development of *N. filiforme* capsule has been reached. Cup-shaped electron-dense filamentous bands were not conspicuous in the epidermal cells in the capsule wall of *A. scombri.* However, more cytoplasmic filaments not arranged in such dense bands were present in the cytoplasm of capsule epidermal cells of *A. scombri* than in those of the normal gill arch. Tissue changes were not observed in the epidermal cells of mouth tissue infected with *Nematobothrium* sp., but cup-shaped electron-dense filamentous bands were seen in some epidermal cells in the infected epidermis of the operculum. The worms occupy the dermal tissue that covers the opercular bone. The host tissue above the worms may be subjected to pressure produced by worms during their growth. The pressure on the opposite side may be limited by the bony parts of the tissue. The presence of cup-shaped electron-dense filamentous bands in the cytoplasm of the epithelial or epidermal cells and extra cytoplasmic filaments in the epidermal cells in the host are likely to be responses to resist the pressure exerted by growing parasites. The cytoplasmic

filamentous condensations and extra cytoplasmic filaments may give additional strength to the epithelial and the epidermal cells, and the epithelium and the epidermis may thus resist the pressure produced by the parasites during their growth. Cup-shaped electron-dense filamentous bands in the cytoplasm of epithelial or epidermal cells have not been recorded in previous pathological studies.

Worms of the species of *Nematobothrium* observed in the skin of the operculum were larger than those in the mouth tissue. The large size of the worms may also be responsible for formation of cup-shaped electron-dense filamentous bands in some epidermal cells.

The occurrence of large intercellular fluid filled spaces between epithelial or epidermal cells is another change common in the tissue infected with all three species of didymozoids, *N. filiforme*, *A. scombri* and *Nematobothrium* sp. Sometimes these spaces contain lymphocytes or granulocytes. The type and number of granulocytes present varied for different species of parasite and at various infection sites. Many epithelial or epidermal cells have pseudopodia-like cytoplasmic processes, which probably bind cells adjoining each other in the intercellular fluid. Similar observations have been made by Roubal (1985) in *Acanthopagrus australis* tissues due to ectoparasitic infections.

In the present study, mucous cells did not show any structural changes or increase or decrease in numbers due to the presence of didymozoid parasites. However, there are contrasting observations on the influence of ecto-parasitic infections on the density of mucus cells in the skin epidermis of fishes. According to some authors, ectoparasitic infections decrease mucous cell concentration in the skin epidermis and the gills of fishes [e.g., in the epidermis of salmonids infested with *Ichtyobodo necator* (Robertson *et al.*, 1981); the epidermis of *Salmo trutta* infested with the ciliates *Trichodina* and *Scyphidia*, the flagellate *Ichtyobodo*, the fungus *Saprolegnia* and the monogenean *Gyrodactylus* (Pottinger *et al.*, 1984); the skin and gills of salmonids infested with *Ichtyobodo necator* (Roubal *et al.*, 1987); the epidermis of fry of

Oncorhynchus mykiss infested with the monogeneans *Gyrodactylus colemanensis* and *G. salmonis* (Wells and Cone, 1990)]. In contrast, Benz (1980) reported an increase in mucous cell density in the epithelium of *Isurus oxyrinchus* due to infection with the ectoparasitic copepod *Nemesis lamna*. The absence of changes in the number of mucous cells in infected tissues could be due to the fact that the didymozoid species examined in the present study live in the tissues of the host.

The chloride cells remain unchanged in tissues infected with *A. scombri* and *Nematobothrium* sp. However, several chloride cells were seen in the capsule wall of *N. filiforme,* whereas chloride cells have not been observed in the lateral epithelium (near efferent blood vessel) of uninfected gill filaments. Langdon *et al.* (1985) described chloride cell hyperplasia in the gills of bony bream during an epizootic of a ciliate. The chloride cells are rich in mitochondria and the sodium pump enzyme Na^+ K^+ -adenosine triphosphatase and are thought to function in ionic regulation (Langdon *et al.*, 1985). The formation of additional chloride cells in the *N. filiforme* capsule is most probably due to didymozoid infection. The infection may change the permeability of the gill tissue, and this change is likely to be an attempt to restore ionic homeostasis.

T.E.M. observations of *S. australasicus* tissues in the present study revealed various blood and infiltrating cells in the host tissue due to didymozoid infections. Studies on pathological processes due to parasitic infections are relatively rare in fish, but leucocytes are known to be engaged (Fänge, 1992). Lymphocytes are common in both uninfected and infected tissues of *S. australasicus*, but are more common in infected tissues. Roubal (1986) also recorded lymphocytes as one of the most abundant infiltrating cells in gill pathogenic tissues of *Acanthopagrus australis*. Lymphocytes play a central role in the immune system of fish (Rowley *et al.*, 1988), but this was not studied by me.

A large number of erythrocytes, and a few monocytes and neutrophils were seen in the efferent blood vessel of the uninfected primary gill filaments of *S. australasicus*.

Extra-vascular neutrophils were only seen in the infected tissues of *S. australasicus*. Neutrophils participate in inflammatory responses in fish and sometimes they show phagocytosis (Rowley *et al.*, 1988). In the present study, neutrophils were mostly found in the capsule lumen of *N. filiforme*, the capsule dermis of *A. scombri*, and in the egg masses and near degenerating worms of *Nematobothrium* sp. as an inflammatory host response. Their phagocytic activity was observed only in the egg masses and near degenerating worms of *Nematobothrium* sp. Neutrophils are more abundant in infected tissue than in normal tissue of fish (Ellis, 1977; Roubal, 1986), and the present study agrees with this.

Some authors believe that the presence of a fibrillar substructure in granules of neutrophils is a typical feature of teleosts (e.g. Ferguson, 1976; Phromsuthirak, 1977; Bielek, 1980; Cannon *et al.*, 1980; Hawkins *et al.*, 1981; Hoole and Arme, 1982; Ferri and Macha, 1982). However, my observations did not reveal the presence of such in *S. australasicus*. Weinreb (1963) and Roubal (1986) also reported lack of substructures in the granules of neutrophils. Therefore, a fibrillar substructure cannot be regarded as typical of all teleost neutrophil granules.

Granulocytes function in fish by migrating to sites of inflammation and then destroying the invaders by phagocytosis or by a cytotoxic-like response (Rowley *et al.*, 1988). There are three types of granulocytes other than neutrophils in slimy mackerel tissue. The first type (Type 1) of granulocytes has moderately electron-dense granules with fibrillar substructure. These cells are similar to the type 1 wandering cell described by Roubal (1986) in *Acanthopagrus australis*, and the neutrophil described by Ferguson (1976) in *Pleuronectes platessa*, except for the absence of rough endoplasmic reticulum in the cytoplasm of the type 1 cell observed in the present study. Type 1 cells are common in uninfected primary gill filaments and in the uninfected epidermis of the operculum. They can be seen in the capsule lumen of *N. filiforme*, in the capsule wall (epidermis and dermis) of *A. scombri,* and in the epidermis of mouth and opercular

tissues infected with *Nematobothrium* sp. Although these cells are seen in both uninfected and infected tissues, these numbers are generally greater in infected tissues - indicating their accumulation as a response to parasite infection. However, phagocytic type 1 cells were not observed in the present study.

The second cell type (Type 2) has highly electron-dense granules. This cell type is similar to large granular leucocytes from circulating blood of the goldfish, described by Fujimaki and Isoda (1990), except for the absence of golgi complexes in the type 2 cells. The granules of the type 2 cell are ultrastructurally similar to those of eosinophilic granule cells described by Roberts *et al.*(1971) in the normal skin of plaice, and described by Powell *et al.*(1990) in the gills of rainbow trout. Type 2 cells are present in small numbers in uninfected and infected tissues, and a few were seen in the blood vessels. They are common in uninfected primary gill filaments and to a lesser extent in the dermis of uninfected opercular tissues. These cells were noted in the capsule lumen of *N. filiforme* and in the capsule wall of *A. scombri*. Type 2 cells were not associated with infection with *Nematobothrium* sp. Phagocytically active type 2 cells were not observed in the present study.

The third cell type (Type 4) has many moderately electron-dense granules without a fibrillar substructure. They were seen in the gill arch tissue. Cells of this type are rare in uninfected tissue but were common in the dermis of the capsule wall of *A. scombri*, indicating that their accumulation is a response to parasite infection. They were also noted in the small blood vessels of the capsule wall. On two occasions possible indications of phagocytosis were observed in the capsule dermis of *A. scombri*. However, the cells involved were not clearly identified.

The cells described as "type 3" in this study are rare and are mostly found at the surface of the primary epithelium of uninfected gill filaments. They could be developing stages of an acidophilic cell, because they contain prominent rER, and large electron-dense secretory granules that are similar to those of acidophilic cells. Small

desmosome-like structures were noted between "type 3" cells and epithelial cells. Hence, they are probably not a distinct type of free cell (granulocyte).

Macrophage-like phagocytic cells were observed in tissues affected by *Nematobothrium* sp. In particular they were seen around degenerating worms and masses of free eggs. Macrophages are the main cells responsible for phagocytosis in various tissues of fish (Fänge, 1992). The presence of macrophage-like cells in tissues affected by *Nematobothrium* sp. is either a response of the particular site of the host (mouth or operculum), because macrophage-like cells were not observed in infected gill filaments with *N. filiforme* and in infected gill arches with *A. scombri*, or a response to a particular species of parasite, because macrophage-like cells were not observed associated with *N. filiforme* and *A. scombri* infections. There presence also could be due to the duration of infection, as shown in the study of leucocyte responses during healing of an incision in the skin of *Gasterosteus aculeatus* (Phromsuthirak, 1977), where macrophages, neutrophils, eosinophils and lymphocytes were found accumulated in the skin. Leucocytes were found migrating into the skin from the blood. The number of neutrophils reached a peak after one day, that of macrophages after three days. Since the present study examined host responses of unknown duration, times of maximal cell abundance could not be determined. Future studies on the host response in experimental infections of known duration are important to determine the sequence, but the life cycles of didymozoids are not known.

In the present study, there was no sign of damage to the didymozoid parasites by the host, *S. australasicus*. Neutrophils and granulocytes were observed between worm sections of the capsules of *N. filiforme* but inflammatory cells of the host had never penetrated the tegument of the didymozoid worms. Neutrophils and granulocytes were not observed between worm sections of the capsules of *A. scombri*. A few infiltrated macrophage-like cells were observed near mature worms of *Nematobothrium* sp. in the skin of operculum, but none were observed near mature worms of *Nematobothrium* sp.

in the mouth tissue. No effect of host cells on mature worms was observed. This suggests that although the slimy mackerel reacts to the infection of didymozoids by an inflammatory response, it is not capable of rejecting the parasites, at least once they have reached an advanced stage of development.

The worms of *Nematobothrium* sp. infecting the mouth tissue and the skin of the operculum produce very little host response while a remarkable cellular response was noted around degenerating worms and free eggs. This situation may be similar to that shown by mammals against *Schistosoma* spp. where the parasites evade the immune response, while the eggs invoke a massive cellular response (Miyazaki, 1991). Once adult *Schistosoma* flukes are within the portal vein, they adopt a strategy so that the eggs laid there are able to leave the body of the host. First they migrate into small vessels and then lay eggs. The mechanical stimulus and metabolic substances excreted from eggs cause damage to the vascular wall, resulting in the rupture of the wall and the release of eggs to the outside of the vessel (into the intestinal wall). Inflammatory changes take place around the eggs, forming egg-nodules or papillomas. Tissue damage due to toxic products of the eggs and secondary bacterial infection will generate ulceration, which releases the eggs into the intestinal lumen. The eggs are shed in the faeces to start a new cycle of development (Miyazaki, 1991). In the present study the free eggs of the didymozoid *Nematobothrium* sp. invoke cellular response. Since no ulcerations or ruptures were observed in the surrounding host tissue, it is not clear how the free eggs of *Nematobothrium* sp. are released into the environment to continue the life cycle. The eggs are likely to be released when the host is dead or damaged or eaten by a predator (other larger fish) as suggested by previous studies (Noble, 1975; Lester, 1979,1980; Gibson *et al.,* 1981; Eiras and Rego, 1987). Further studies are needed for a better understanding of how the eggs of *Nematobothrium* sp. are released into the environment.

Nematobothrium sp. in the mouth had empty egg shells, and this is indicative but not conclusive evidence that these eggs have been destroyed by an immune response.

So far, not a single didymozoid life cycle is fully understood. Ishii (1935) suggest a direct life cycle for didymozoids, and Nikolaeva (1965) and Yamaguti (1970) believe that three or four alternate hosts are involved. Some information gathered from studies of the pathology may help to explain the part of the life cycle of the three didymozoids in the final host, *S. australasicus*. Some previous studies indicated that the life cycle of many didymozoids involves the death of the adult worm in the tissue and the release of the eggs to the environment when the host is dead or damaged or eaten by a predator [Noble (1975) for *Nematobibothrioides histoidii*; Lester (1979,1980) for *Nematobothrium spinneri* and *Didymozoon brevicolle*; Gibson *et al.* (1981) for *Halvorsenius exilis*; Eiras and Rego (1987) for *Nematobothrium scombri*]. *Nematobothrium* sp. infecting mouth and opercular tissues of *S. australasicus* examined in the present study evidently falls into this pattern because worms, degenerating worms and masses of didymozoid free eggs without traces of worms were observed. This contrasts with the observations on *N. filiforme* and *A. scombri* because all examined capsules of these two species contained worms. *N. filiforme* were more commonly found on smaller than larger fish, indicating that after some time, the worms either leave the host or die. Since no degenerating worms or free eggs were noted, the parasites may leave the host by breaking the capsule. However, partly broken capsules or scars of old capsules were not noted. Similarly, degenerating worms or free eggs in the capsules of *A. scombri* were not observed. Hence, this species may also leave the host after some time. Similar observations have been made by some authors for other didymozoid species. Timon-David (1937) suggested that the capsules of *Didymocystis wedli* after reaching a certain degree of maturity open spontaneously and evacuate their contents to the exterior. Awachie (1972) observed tissue erosion associated with *Nematobothrium* infection. Lester (1979,1980) also reported that most capsules of a

didymozoid species, *Neometadidymozoon helicis* examined disappear from the host tissue at a certain time of the year. He suggested that this may be related to sexual maturation of the host. In the light of previous literature and his own studies, Lester (1980) stated that the release of eggs through ulceration may be widespread among some didymozoid species. However, further studies are required to resolve how the worms or the eggs of *N. filiforme* and *A. scombri* are released into the environment.

The three parasites of *S. australasicus*, *N. filiforme*, *A. scombri* and *Nematobothrium* sp., only affect localized regions of the body, without causing significant injury to the host. This suggests the existence of a long standing, close association between parasites and host.

Parasite responses - (Effect of host on parasites)

Host-parasite interactions are not one-way, as shown by the effects that host size has on parasites. Larger *S. australasicus* have *Kuhnia scombri* with larger hamuli, corresponding to the findings of some other authors on the same and other parasite species (Paling, 1965; Gussev and Kulemina, 1971a,b; Roubal *et al.,* 1983; Thoney, 1986, 1988; Rohde, 1991). The effect of host size on the organs or the size of monogeneans may have significant implications for taxonomic studies of Monogenea, because many species descriptions are based upon differences in organ size.

Large *S. australasicus* have larger and wider gill lamellae than small fish, corresponding to the report by Hughes (1984) and Thoney (1988) that gill lamellae increase in size with fish size. The hamuli of *K. scombri* are used to attach to the gill filaments (Llewellyn, 1957). It is possible that the larger hamuli of worms on larger fish are an adaptation for attachment to the larger gill filament of such fish. Mechanisms responsible may be selection (i.e. worms with larger hamuli have a better chance of survival on larger fish) or direct adaptation (i.e. larger gill lamellae induce the formation of larger hamuli).

References

Arme, C. and Halton, D. W. (1972). Observations on the occurrence of *Diclidophora merlangi* (Trematoda: Monogenea) on the gills of whiting, *Gadus merlangus*. *Journal of Fish Biology*, **4**: 27 - 32.

Avdeev, V. V. (1979). [Parasitic isopods of the genus *Meinertia* from Australian-New Zealand region.] *Biologiya Morya - Marine Biology*, **2**: 48 - 54. (Russian)

Awachie, J. B. E. (1972). On the didymozoid trematode parasitic in the eye socket of African carps *Labeo* spp. from area of the Kainji man made lake in Nigeria. *Acta Parasitologica Polonica*, **20**: 497 - 498.

Benz, G. W. (1980). Tissue proliferation associated with *Nemesis lamna* Risso, 1826 (Copepoda: Endactylinidae) infestations on the gill filaments of shortfin makos (*Isurus oxyrinchus* Rafinesque). *Journal of Fish Diseases,* **3**: 443 - 446.

Bielek, V. E. (1980). Electron microscopical studies of blood cells in teleosts. III. Granulocytes. *Zoologische Jahrbücher Anatomie,* **103**: 105 - 121.

Cannon, M. S., Mollenhauer, H. H., Eurell, T. E., Lewis, D. H., Cannon, A. M. and Tompkins, C. (1980). An ultrastructural study of leucocytes of the channel catfish, *Ictalurus punctatus*. *Journal of Morphology,* **164**: 1 - 23.

Cressey, R. and Cressey, H. B. (1980). *Parasitic copepods of mackerel- and tuna-like fishes (Scombridae) of the World.* Smithsonian Contributions to Zoology, No. 311. Smithsonian Institution Press, Washington.

Cressey, R. F., Collette, B. B. and Russo, J. L. (1983). Copepods and scombrid fishes: a study in host-parasite relationships. *Fishery Bulletin*, **81**: 227 - 265.

Cribb, T. H. and Williams, A. (1992). *Gonapodasmius williamsoni* sp. n. (Digenea: Didymozoidae) from the pink snapper, *Pagrus auratus* (Teleostei: Sparidae) in Western Australia. *Journal of Helminthological Society of Washington*, **59**: 153 - 158.

Dogiel, V. A., Petrushevski, G. K. and Polyanski, Yu. I. (1958). *Parasitology of Fishes.* Leningrad University Press, Leningrad. (Translated (1961) by Z. Kabata. Oliver and Boyd Ltd., Edinburgh and London).

Eiras, J. C. and Rego, A. A. (1987). The histopathology of *Scomber japonicus* infection by *Nematobothrium scombri* (Trematoda: Didymozoidae) and of larval anisakid nematode infections in the liver of *Pagrus pagrus*. *Memórias do Instituto Oswaldo Cruz, Rio de Janeiro*, **82**: 155 - 159.

Ellis, A. E. (1977). The leucocytes of fish: a review. *Journal of Fish Biology*, **11**: 453 - 491.

Fänge, R. (1992). Fish blood cells. pp 1 - 54. In: W. S. Hoar, D. J. Randall and A. P. Farrell (Eds) *Fish Physiology.* Vol XII, Part B The Cardiovascular System. Academic Press, Inc. New York.

Ferguson, H. W. (1976). The ultrastructure of plaice (*Pleuronectes platessa*) leucocytes. *Journal of Fish Biology*, **8**: 139 - 142.

Ferri, S. and Macha, N. (1982). Ultrastructural and cytochemical identification of a granulocyte in a freshwater teleost epidermis. *Zoologische Jahrbücher Anatomie,* **107**: 281 - 287.

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

Fujimaki, Y. and Isoda, M. (1990). Fine-structural study of leucocytes in the goldfish, *Carassius auratus*. *Journal of Fish Biology,* **36**: 821 - 831.

Gibson, D. I., MacKenzie, K. and Cottle, J. (1981). *Halvorsenius exilis* gen. et sp. nov., a new didymozoid trematode from the mackerel *Scomber scombrus* L. *Journal of Natural History*, **15**: 917 - 929.

Gussev, A. V. and Kulemina, I. V. (1971a). [Taxonomic characters of some monogeneans from the hosts of different age.] *Parazitologiya,* (Leningrad), **5**: 162 - 171. (Russian)

Gussev, A. V. and Kulemina, I. V. (1971b). [Analysis of variability of characters, behaviour and development's cycle of monogeneans from the age of hosts.] *Parazitologiya,* (Leningrad), **5**: 320 - 329. (Russian)

Hawkins, W. E., Solangi, M. A. and Overstreet, R. M. (1981). Ultrastructural effects of the coccidium, *Eimeria funduli* Duszynski, Solangi and Overstreet, 1979 on the liver of killifishes. *Journal of Fish Diseases,* **4**: 281 - 295.

Heegaard, P. E. (1940). Some new parasitic copepods (Chondracanthidae and Lernaeopodidae) from Western Australia. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i København*, **104**: 87 - 101.

Hoole, D. and Arme, C. (1982). Ultrastructural studies on the cellular response of roach, *Rutilus rutilus* L., to the plerocercoid larva of the pseudophyllidean cestode, *Ligula intestinalis*. *Journal of Fish Diseases,* **5**: 131 - 144.

Hughes, G. M. (1984). General anatomy of the gills. pp1 - 72. In: W. S. Hoar and D. J. Randall (Eds) *Fish physiology.* Vol. X. Gills, part A. Anatomy, gas transfer and acid-base regulation. Academic Press, New York.

Ishii, N. (1935). Studies on the family Didymozooidae (Monticelli, 1888). *Japanese Journal of Zoology*, **6**: 279 - 335.

Kennedy, (1970). The population biology of heminths of British freshwater fish. pp145 - 159. In: A. E. R. Taylor and R. Muller (Eds) *Aspects of fish parasitology*. Symposium of the British Socity for Parasitology, Vol. 8. Blackwell Scientific Publications, Oxford.

Kennedy, C. R. (1975). *Ecological Animal Parasitology*. Halstead Press, New York.

Korotaeva, V. D. (1974). [Helminths of some commercial marine fish of the suborder Scomberoidei from the Australian region.] *Izvestiya Tikhookeanskogo Rybnogo Khozyaistva i Okeanografii (TINRO) (Parazity morskikh zhivotnykh)*, **88**: 61 - 66. (Russian)

Langdon, J. S., Gudkovs, N., Humphrey, J. D. and Saxon, E. C. (1985). Deaths in Australian freshwater fishes associated with *Chilodonella hexasticha* infection. *Australian Veterinary Journal*, **62**: 409 - 413.

Lester, R. J. G. (1979). Descriptions of two new didymozoids from Australian fishes. *The Journal of Parasitology*, **65** (6): 904 - 908.

Lester, R. J. G. (1980). Host-parasite relations in some didymozoid trematodes. *The Journal of Parasitology*, **66**: 527 - 531.

Llewellyn, L. (1956). The host specificity, micro-ecology, adhesive attitudes and comparative morphology of some trematode gill parasites. *Journal of the Marine Biological Association of the U.K.*, **35**: 113 - 127.

Llewellyn, J. (1957). The mechanism of attachment of *Kuhnia scombri* (Kuhn, 1829) (Trematoda: Monogenea) to the gills of its host *Scomber scombrus* L., including a note on the taxonomy of the parasite. *Parasitology,* **47**: 30 - 39.

Llewellyn, J. (1962). The life histories and population dynamics of monogenean gill parasites of *Trachurus trachurus* (L.). *Journal of the Marine Biological Association of the U.K.*, **42**: 587 - 600.

Miyazaki, I. (1991). *An Illustrated Book of Helminthic Zoonoses.* International Medical Foundation of Japan, Tokyo.

Mordvinova, T. N. (1989). [A new Trematoda species *Nematobothrium atlanticus* (Didymozoidae), a parasite of flying fish.] *Zoologicheskii Zhurnal*, **68**: 135 - 137. (Russian)

Nikolaeva, V. M. (1965). [The developmental cycle of trematodes belonging to the family Didymozoidae (Monticelli, 1888) Poche, 1907.] *Zoologicheskii Zhurnal,* **44**: 1317 - 1327. (Russian)

Nikolaeva, V. M. and Korotaeva, V. D. (1970). [*Nematobothrioides australiensis* sp. n., A new trematode of *Scomber australasicus.*] *Parazitologiya,* **4**: 330 - 333. (Russian)

Noble, G. A. (1975). Description of *Nematobibothrioides histoidii* (Noble, 1974) (Trematoda: Didymozoidae) and comparison with other genera. *The Journal of Parasitology*, **61**: 224 - 227.

Paling, J. E. (1965). The population dynamics of the monogenean gill parasite *Discocotyle sagittata* Leuckart on Windermere trout, *Salmo trutta*, L. *Parasitology*, **55**: 667 - 694.

Paling, J. E. (1969). The manner of infection of trout gills by the monogenean parasite *Discocotyle sagittata*. *Journal of Zoology London*, **159**: 293 - 309.

Phromsuthirak, P. (1977). Electron microscopy of wound healing in the skin of *Gasterosteus aculeatus*. *Journal of Fish Biology,* **11**: 193 - 206.

Pottinger, T. G., Pickering, A. D. and Blackstock, N. (1984). Ectoparasite induced changes in epidermal mucification of the brown trout *Salmo trutta* L.. *Journal of Fish Biology,* **25**: 123 - 128.

Powell, M. D., Wright, G. M. and Burka, J. F. (1990). Eosinophilic granule cells in the gills of rainbow trout, *Oncorhynchus mykiss*: evidence of migration? *Journal of Fish Biology,* **37**: 495 - 497.

Roberts, J. R., Young, H. and Milne, J. A. (1971). Studies on the skin of plaice (*Pleuronectes platessa* L.) 1. The structure and ultrastructure of normal plaice skin. *Journal of Fish Biology*, **4**: 87 - 98.

Robertson, D. A., Roberts, R. J. and Bullock, A. M. (1981). Pathogenesis and autoradiographic studies of the epidermis of salmonid infested with *Ichtyobodo necator* (Henneguy, 1883). *Journal of Fish Diseases,* **4**: 113 - 125.

Rohde, K. (1977). A non-competitive mechanism responsible for restricting niches. *Zoologischer Anzeiger*, **199**: 164 - 172.

Rohde, K. (1978). Monogenean gill parasites of the king fish *Seriola grandis* (Castlenau) from the Great Barrier Reef. *Publications of the Seto Marine Biological Laboratory,* **24**: 369 - 76.

Rohde, K. (1979). A critical evaluation of intrinsic and extrinsic factors responsible for niche restriction in parasites. *American Naturalist*, **114**: 648 - 671.

Rohde, K. (1980). Comparative studies on microhabitat utilisation by ectoparasites of some marine fishes from the North Sea and Papua New Guinea. *Zoologischer Anzeiger*, **204**: 27 - 63.

Rohde, K. (1987). *Grubea australis* n. sp. (Monogenea, Polyopisthocotylea) from *Scomber australasicus* in southeastern Australia, and *Grubea cochlear* Diesing, 1858 from *S. scombrus* and *S. japonicus* in the Mediterranean and western Atlantic. *Systematic Parasitology*, **9**: 29 - 38.

Rohde, K. (1989). *Kuhnia sprostonae* Price, 1961 and *K. scombercolias* Nasir & Fuentes Zambrano, 1983 (Monogenea: Mazocraeidae) and their microhabitats on the gills of *Scomber australasicus* (Teleostei: Scombridae), and the geographical distribution of seven species of gill monogenea of *Scomber* spp. *Systematic Parasitology*, **14**: 93 - 100.

Rohde, K. (1991). Size differences in hamuli of *Kuhnia scombri* (Monogenea: Polyopisthocotylea) from different geographical areas not due to differences in host size. *International Journal for Parasitology*, **21**: 113 - 114.

Rohde, K. (1993). *Ecology of Marine Parasites - An Introduction to Marine Parasitology.* CAB International, Wallingford, Oxon, U. K.

Rohde, K. and Watson, N. (1985a). Morphology and geographical variation of *Pseudokuhnia minor* n. g., n. comb. (Monogenea: Polyopisthocotylea). *International Journal for Parasitology*, **15**: 557 - 567.

Rohde, K. and Watson, N. (1985b). Morphology, microhabitats and geographical variation of *Kuhnia* spp. (Monogenea: Polyopisthocotylea). *International Journal for Parasitology*, **15**: 569 - 586.

Roubal, F. R. (1985). Histological, cytological and morphometric aspects of ectoparasite pathology on the marine bream, *Acanthopagrus australis*. Ph.D. thesis, University of New England, Armidale.

Roubal, F. R. (1986). Blood and other possible inflammatory cells in the sparid *Acanthopagrus australis* (Günther). *Journal of Fish Biology,* **28**: 573 - 593.

Roubal, F. R., Armitage, J. and Rohde, K. (1983). Taxonomy of metazoan ectoparasites of snapper, *Chrysophrys auratus* (Family Sparidae), from southern Australia, eastern Australia and New Zealand. *Australian Journal of Zoology* Supplement **94**: 68p

Roubal, F. R., Bullock, A. M., Robertson, D. A. and Roberts, R. J. (1987). Ultrastructural aspects of infestation by *Ichthyobodo necator* (Henneguy, 1883) on the skin and gills of the salmonids *Salmo salar* L. and *Salmo gairdneri* Richardson. *Journal of Fish Diseases*, **10**: 181 - 192.

Rowlay, A. F., Hunt, T. C., Page, M. and Mainwaring, G. (1988). Fish. pp 19 - 127. In: A.F. Rowley and N. A. Ratcliffe (Eds) *Vertebrate blood cells.* Cambridge University press, Cambridge.

Self, J. T., Peters, L. E. and Davis, C. E. (1963). The egg, miracidium, and adult of *Nematobothrium texomensis* (Trematoda: Digenea). *The Journal of Parasitology*, **49**: 731 - 736.

Thoney, D. A. (1986). Post-larval growth of *Microcotyle sebastis* (Platyhelminthes: Monogenea), a gill parasite of the black rockfish. *Transactions of the American Microscopical Society*, **105**: 170 - 181.

Thoney, D. A. (1988). Developmental variation of *Heteraxinoides xanthophilis* (Monogenea) on hosts of different sizes. *The Journal of Parasitology*, **74**: 999 - 1003.

Timon-David, J. (1937). Les kystes á *Didymocystis wedli* du thon. Étude anatomo-pathologique. *Annales de Parasitologie Humaine et Comparee*, **15**: 520 - 523.

Weinreb, E. L. (1963). Studies on the fine structure of teleost blood cells. I. Peripheral blood. *Anatomical Record,* **147**: 219 - 238.

Wells, P. R. and Cone, D. K. (1990). Experimental studies on the effect of *Gyrodactylus colemanensis* and *G. salmonis* (Monogenea) on density of mucous cells in the epidermis of fry of *Oncorhynchus mykiss*. *Journal of Fish Biology,* **37**: 599 - 603.

Wiles, M. (1968). The occurrence of *Diplozoon paradoxum* Nordmann, 1832 (Trematoda: Monogenea) in certain waters of northern England and its distribution on the gills of certain Cyprinidae. *Parasitology*, **58**: 61 - 70.

Williams, A., Moran, M., Caputi, N. and Walters, C. (1993). Didymozoid trematode infection of snapper, *Pagrus auratus* (Sparidae), off Western Australia: parasite population biology and fishery implications. *Fisheries Research*, **16**: 113 - 129.

Williams, H. H. (1959). The anatomy of *Köllikeria filicollis* (Rudolphi, 1819), Cobbold, 1860 (Trematoda: Digenea) showing that the sexes are not entirely separated as hitherto believed. *Parasitology*, **49**: 39 - 53.

Wootten, R. (1974). The spatial distribution of *Dactylogyrus amphibothrium* on the gills of ruffe *Gymnocephalus cernua* and its relation to the relative amounts of water passing over the parts of the gills. *Journal of Helminthology*, **48**: 167 - 174.

Yamaguti, S. (1934). Studies on the helminth fauna of Japan. Part 2 Trematodes of Fishes, I. *Japanese Journal of Zoology*, **5**: 249 - 541.

Yamaguti, S. (1970). *Digenetic Trematodes of Hawaiian Fishes.* Keigaku Publishing Co. Tokyo, Japan.