Parasites as biological indicators of the population biology, migrations, diet, and phylogenetics of fish

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Introduction, and guidelines for the use of parasites as biological indicators

Parasites have been used for almost a century as biological 'indicators', 'tags' or 'markers' to provide information on various aspects of host biology. One of the first attempts to employ parasite indicators in a study of fish biology was that of Dogiel and Bychovsky (1939) to distinguish between stocks of sturgeon (*Acipenser* spp., Acipenseridae) in the Caspian Sea. The most promising parasite indicators in this study were the monogeneans *Diclybothrium circularis* and *Nitzschia sturionis* (Fig. 1). Since then a wide range of parasites from several different taxonomic groups have been found to be suitable biological indicators (Table 1 and Fig. 2).

In some circumstances parasite tags may be better than artificial (mechanical) tags for

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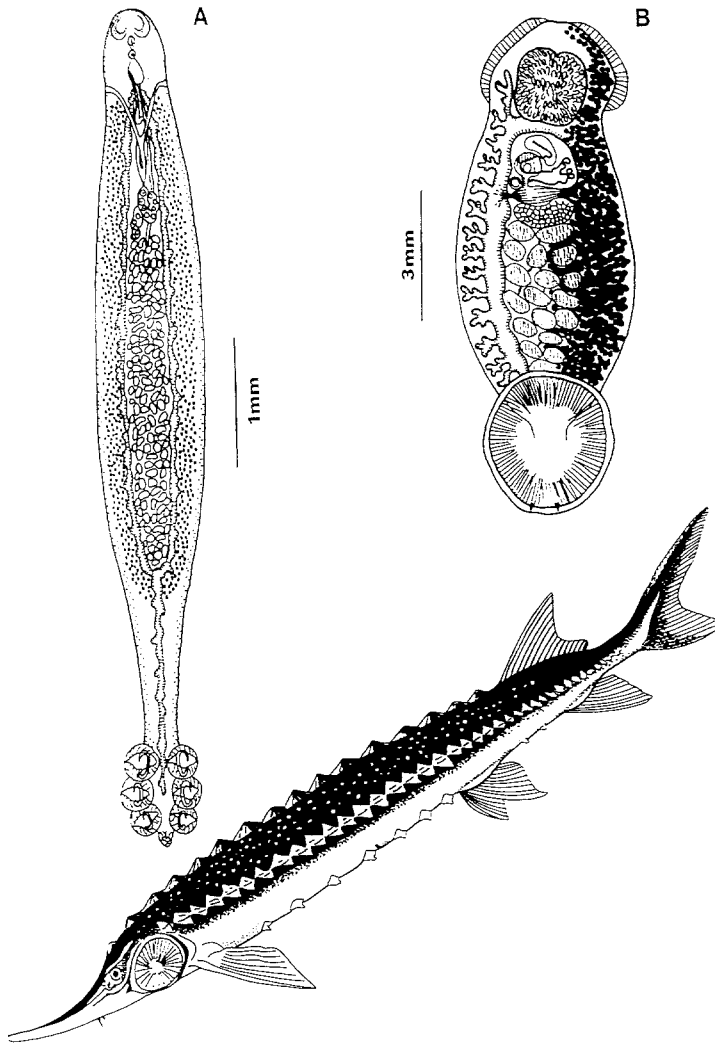*Author to whom correspondence and reprint requests should be addressed.

Fig. 1. The monogeneans *Diclybothrium circularis* (A) and *Nitzschia sturionis* (B) were among the helminth parasites used by Dogiel and Bychovsky (1939) to separate shoals of sturgeon, e.g. *Acipenser stellatus* in the Caspian Sea. (Parasites redrawn from Beverley-Burton, 1984, and Bychovsky, 1961; fish redrawn from Bristow, 1987.)

population studies. They are most appropriate, for example, in studies of delicate or deepwater species, including crustaceans which may shed their artificial tags when they moult. Redfish of the genus *Sebastes* (Scorpaenidae) were amongst the first fish to be studied with parasite tags (Herrington *et al.*, 1939). This was partly because of their high mortality on being trawled from deep water and returned to the sea. Artificial tags are clearly not appropriate for such delicate species.

Fish for parasitological examination may be obtained from routine sampling programmes and so are less expensive than specialized artificial tagging experiments.

Table 1. Some examples of parasites from the major taxonomic groups that have been used as biological indicators in fish and fisheries research.

Parasite	Host	Reference
PROTOZOANS		
Apicomplexa		
Eimeria sardinae	Herring, *Clupea harengus*	McGladdery (1987)
Microspora		
Glugea atherinae	Smelt, *Atherina boyeri*	Berrebi and Britton-Davidian, (1980)
Myxozoa		
Myxobolus aeglefini	Blue whiting, *Micromesistius poutassou*	Karasev (1988)
Sarcomastigophora		
Trypanosoma murmanensis	Cod, *Gadus morhua*	Khan *et al.* (1980)
METAZOANS		
Platyhelminthes		
Aspidogastrea		
Multicalyx cristata	Bullnose ray, *Myliobatis freminvillei*	Thoney and Burreson (1986)
Cestoda: metacestodes		
Grillotia smaris-gora	Mackerel, *Scomber scombrus*	MacKenzie (1990)
Cestoda: adults		
Proteocephalus sp.	Sockeye salmon, *Oncorhynchus nerka*	Bailey *et al.* (1989)
Monogenea		
Kuhnia scombri	Pacific mackerel, *Scomber australasicus*	Rohde (1987)
Digenea: metacercariae		
Cryptocotyle lingua	Cod, *Gadus morhua*	Buchmann (1986)
Digenea: adults		
Hemiurus levinseni	Cod, *Gadus morhua*	Boje (1987b)
Nematoda		
Larvae		
Anisakis sp.	Herring, *Clupea harengus*	Chenoweth *et al.* (1986)
Adults		
Cystidicola farionis	Sockeye salmon, *Oncorhynchus nerka*	Butorina and Shedko (1989)
Hysterothylacium aduncum	Cod, *Gadus morhua*	Boje (1987a, b)
Acanthocephala		
Larvae		
Polymorphus botulus	American lobster, *Homarus americanus*	Brattey and Campbell (1986)
Adults		
Neoechinorhynchus salmonis	Sockeye salmon, *Oncorhynchus nerka*	Bailey *et al.* (1989)

Table 1 *continued*

Crustacea		
Copepoda		
Neobrachiella robusta	Pacific Ocean perch, *Sebastes alutus*	Leaman and Kabata (1987)
Isopoda		
Epipenaeon elegans	Shrimp, *Penaeus semisulcatus*	Mathews *et al.* (1988)

Studies involving parasite tags also eliminate doubts concerning the possible abnormal behaviour of artificially tagged hosts. Ideally the use of parasite tags and artificial tags should be seen as complementary methods. Several examples exist of studies which have combined parasite tagging data with other methods of stock discrimination such as artificial tagging, together with meristic, morphometric, biochemical and genetic data (Danilevski and Kamburov, 1969; Konovalov, 1975; Hislop and MacKenzie, 1976; Berrebi and Britton-Davidian, 1980; Brunenmeister, 1980; Gaevskaya and Shapiro, 1981; Bugaev, 1982; Heath and Baird, 1983; Margolis, 1984; Quinn *et al.*, 1987; Shandikov and Paruhkin, 1987; Wood *et al.*, 1987, 1989; Bishop *et al.*, 1988; Moles and Short, 1989).

Research on parasites as biological indicators for aquatic hosts is increasing at a remarkable rate. MacKenzie (1987a) revealed only nine papers for the 1950s, whereas there were more than 30 from the 1960s and more than 50 from the 1970s. For this review we found over 140 relevant papers for the 1980s. Our main aim in the present work is to review these in order to update previous works by MacKenzie (1983a, 1987a). From 1980 to 1991 most studies have been concerned with using parasite tags in population studies of fish species of commercial importance. Much of this review will therefore be devoted to this aspect. As a preliminary indication of the scope for further work, other sections will mention the use of parasites in studies of marine invertebrates, as indicators of host diet and feeding behaviour, and as indicators of host phylogenetics and systematics.

The following general guidelines for work on parasites as indicators of aquatic host populations are taken from Kabata (1963), Sindermann (1961, 1983), MacKenzie (1983a, 1987a), Lester (1990) and Moser (1991b).

1. The parasite should have significantly different levels of infection in the subject host in different parts of the study area, i.e. differences in prevalence and/or mean intensity of infection between samples. This may seem an obvious requirement, but there have been at least two studies in which the relative levels of infection were irrelevant. Beverley-Burton and Pippy (1977) suggested that the mean body lengths of anisakid nematode larvae could be used to test hypotheses that two or more samples were drawn from the same host population, and Beverley-Burton (1978) investigated the acid phosphatase polymorphism of the same group of parasites as a possible means of distinguishing between populations of their fish hosts. These are rare exceptions, however, and biological tag studies are usually based on differences in prevalence and/or mean intensity of infection between samples.

2. Kabata (1963) considered that a tag parasite should include only one host in its life

cycle, and Sindermann (1983) preferred parasites with single-host life cycles. They did not, however, discount the use of parasites with complex life cycles, but pointed out that they involved more work and a wider study. Although parasites with single-host life cycles are the simplest to use, to restrict one's choice to this group would eliminate many potentially useful tags. Many successful studies include parasites with more than one host in the life cycle, and the associated background research has often made an important contribution to our wider knowledge of host–parasite relationships.

3. The parasite should have a life span, or remain in an identifiable form, in the subject host long enough to cover the time scale of the investigation. The minimum acceptable life span will vary depending upon the type of population study, as discussed below. Lester (1990) considered this to be the most important criterion for judging the suitability of a parasite as a tag.

4. Both Kabata (1963) and Sindermann (1983) suggested that the prevalence of a tag parasite should remain relatively stable from season to season and from year to year. Seasonal variations, however, can determine seasonal migrations of the subject host. As far as longer-term variations are concerned, there is good evidence that many populations of aquatic parasites are basically unstable (Kennedy, 1977, 1985). Problems posed by annual fluctuations can be overcome by following infections in single year classes of the subject host and by avoiding comparisons of data from mixed year classes.

5. Kabata (1963) suggested that the environmental conditions throughout the area studied should preferably be within the physiological range of the parasite intended as a tag. The condition is certainly applicable to ectoparasites which are directly exposed at all times to the external environment. On the other hand a biological tag study usually depends on the fact that the distribution of the parasite is limited, directly or indirectly, by environmental conditions. Unfavourable conditions act directly on free-living larval stages of endoparasitic helminths and/or dispersal stages of protozoans. They may also act indirectly by limiting the distributions of other hosts which are essential to the completion of the parasite's life cycle. A good knowledge of the ranges of tolerance of the different stages of a proposed tag parasite, and of its hosts, to various environmental factors is important.

6. The parasite should be easily detected and identified. For example very small metazoan parasites which do not produce obvious lesions or other signs of infection should be avoided if possible. If a parasite is easily confused with other species, the time taken to confirm the identity of each specimen may become a limiting factor.

7. Examination of the host for a tag parasite should involve the minimum of dissection. A high degree of site specificity is an advantage.

8. Although pathogenic parasites can sometimes make good tags (Lester, 1990), those which affect host behaviour should be avoided.

Fig. 2. Some parasites used as biological indicators in fish biology and fisheries research. (A) Oocyst of the protozoan *Eimeria sardinae* (see McGladdery, 1987). (B) Aspidogastrean *Multicalyx cristata* (see Thoney and Burreson, 1986). (C) Monogenean *Kuhnia scombri* (see Rohde, 1987). (D) Digenean *Aponurus laguncula* (see Bray and MacKenzie, 1990). (E) Plerocercoid of the cestode *Diphyllobothrium* sp. (see Frechet *et al.*, 1983). (F) Plerocercoid of *Lacistorhynchus* sp. (see MacKenzie, 1985). (G) Acanthocephalan *Neoechinorhynchus salmonis* (male) (see Bailey *et*
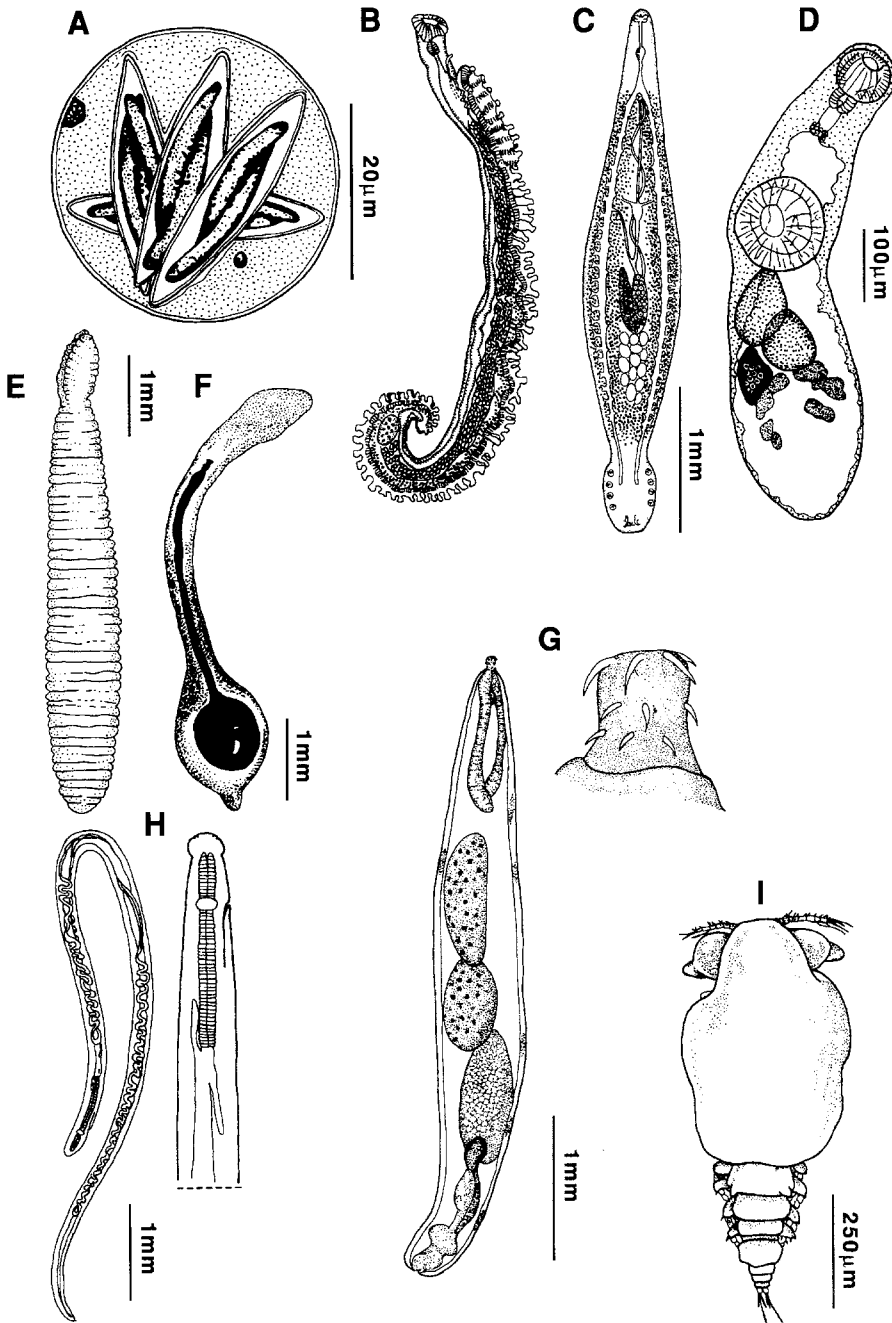
al., 1989). (H) Nematode *Hysterothylacium aduncum* (female) (see Boje, 1987a, b). (I) Crustacean *Ergasilus nerkae* (female) (see Groot *et al.*, 1989). (A) Redrawn from Möller and Anders (1986); (B) Redrawn from Caira (1990) after Manter (1954); (C) Redrawn from Beverley-Burton (1984); (D) Redrawn from Bray and MacKenzie (1990); (E) Redrawn from Smyth (1976); (F) Drawn from photo in MacKenzie (1985); (G) Redrawn from Arai and Arai (1989); (H) Redrawn from Möller and Anders (1986); (I) Redrawn from Kabata *et al.* (1988b).

Population studies

These studies may be conveniently grouped into the following categories: fish stock separation; fish recruitment migrations; fish seasonal and/or age-related migrations; marine invertebrates. Certain studies simultaneously provide information on more than one of the above categories.

FISH STOCK SEPARATION

These studies aim to identify within a host population intraspecific groups (stocks) which are distinguished by different patterns of behaviour at certain stages of their life history. Stocks may differ from one another in having different nursery, feeding, or spawning grounds, or possibly in some other forms of behaviour. As noted by MacKenzie (1987a), several different groups of parasite are appropriate for use as tags in stock separation since it is not usually necessary to select parasites with long life spans in the host. For convenience of presentation we shall discuss studies on freshwater and anadromous fish and those on marine fish separately.

Freshwater and anadromous fish

The literature on stock separation of freshwater and anadromous fish is dominated by the work of the Soviet school of ecological parasitology founded by V.A. Dogiel in the first half of this century. This work was the subject of a major review by Shul'man and Shul'man (1983). These authors used *Diphyllobothrium* plerocercoids (Fig. 2(E)) to study stock separation in *Oncorhynchus* and *Salvelinus* spp. (Salmonidae), and adult hemiurid digeneans, juvenile and adult acanthocephalans and ascaridoid nematode larvae to investigate *Salvelinus* and *Coregonus* spp. (Salmonidae). Margolis and his co-workers have also made major contributions to stock separation of North American salmonids, especially the sockeye salmon (*Oncorhynchus nerka*) (Margolis, 1982a,b, 1984, 1985; Bailey and Margolis, 1987; Bailey *et al.*, 1988, 1989).

    Stock separation studies of the 1980s include those on *Oncorhynchus* and *Salvelinus* using *Diphyllobothrium* plerocercoids as tags (Butorina and Kuperman, 1981; Bugaev, 1982; Konovalov and Butorina, 1985). *Diphyllobothrium* plerocercoids have also been used to discriminate between stocks of rainbow smelt (*Osmerus mordax*, Osmeridae) in the St. Lawrence estuary (Frechet *et al.*, 1983). Butorina and Shedko (1989) have recently used the parasitic nematode *Cystidicola farionis* as an indicator to distinguish between stocks of sockeye salmon fry in Lake Azabache in the U.S.S.R.

    Analysis of different parasite assemblages has been shown to provide a potentially efficient means of stock separation in certain anadromous fish species. Using this method Frandsen *et al.* (1989) differentiated four intraspecific stocks (or sympatric morphs) of freshwater resident Arctic charr (*Salvelinus alpinus*, Salmonidae) in Thingvallavatn Lake, Iceland. Preliminary evidence provided by Groot *et al.* (1984) that different parasite assemblages of juvenile *O. nerka* in the Fraser River System, British Columbia, Canada could be used as a means of stock segregation was confirmed by Bailey and Margolis (1987), who presented detailed parasitological data for stocks of different origin in this system. Bailey *et al.* (1988) showed that the same approach could be used to resolve the stock composition of *O. nerka* smolts caught during their seaward migration in the Strait of Georgia. In this latter study, Bailey *et al.*, (1988) used a versatile multivariate maximum likelihood model originally designed by Fournier *et al.* (1984). This model of

analysis was later used effectively by Wood *et al.* (1987) to differentiate stocks of maturing *O. nerka* during their homing migration off south-eastern Alaska. In addition to parasite infection data, Wood *et al.* (1987) also employed scale, meristic and electrophoretic data in their analyses.

Bailey *et al* (1989) examined the survival of freshwater parasites of juvenile *O. nerka* in the Fraser River System with the aim of determining their potential as biological indicators once the fish had entered seawater. Their results suggest that some species of parasite, such as the cestodes *Eubothrium* sp. and *Proteocephalus* sp., the acanthocephalan *Neoechinorhynchus salmonis* (Fig. 2(G)), and metacercariae of the digenean *Diplostomum* sp., are all potentially useful as indicators due to their long-term survival in marine conditions. Others, such as the myxosporean *Myxidium salvelini*, the copepod *Salmincola californiensis*, and the digenean *Phyllodistomum umblae*, were judged to be unsuitable for extended use as biological tags because of their relatively low tolerance of high salinity.

A number of recent papers refer to the use of parasite tags for discrimination between intraspecific anadromous and freshwater resident forms of fish species occurring together in mixed populations. Stock separation studies of this type concentrate on the fact that when feeding in estuaries or in the sea, the anadromous forms become infected with marine parasites, some of which they retain when they return to fresh water. They can therefore be separated from freshwater resident forms of the same species by their marine parasites. These anadromous forms also tend to have significantly lower levels of infection with freshwater parasites than the freshwater resident forms. Several of the most useful tags to have been used in this type of study are marine helminths which are acquired by anadromous fish when they feed on marine crustaceans. They include adult hemiurid digeneans, metacestodes, juvenile and adult acanthocephalans and anisakid nematode larvae (Black, 1981; Butorina and Kuperman, 1981; Dick and Belosevic, 1981; Awakura and Nomura, 1983; Frechet *et al.*, 1983; Frimeth, 1987a,b; Bouillon and Dempson, 1989; Urawa, 1989).

Studies of this type have focussed mainly on salmonid fish, notably charr (*Salvelinus* spp.). Frimeth (1987a,b), for example, differentiated anadromous and non-anadromous stocks of the brook charr (*Salvelinus fontinalis*) by surveying their parasite faunas. Anadromous charr could be differentiated from non-anadromous charr in fresh water by the presence of their marine parasites. High prevalences of infection with metacercariae of the marine digenean *Cryptocotyle lingua* resulted in the well-known disease of 'black spot' which proved to be the best indicator of anadromous charr in fresh water. (Fig. 3). Metacercariae of the digenean *Diplostomum* sp. were characteristic of freshwater resident charr. A similar study by Bouillon and Dempson (1989) showed that freshwater resident forms of Arctic charr (*Salvelinus alpinus*) could be identified by their high infection levels of *Diplostomum* sp. metacercariae, *Diphyllobothrium ditremum* plerocercoids, and adults of the digenean *Crepidostomum farionis*, and the absence of marine and brackish water parasites such as *Brachyphallus crenatus* and *Bothrimonus sturionis*.

Marine fish

Recent papers include the following: Arthur and Arai (1980a,b), Kulachkova (1989) and Moser (1991a,b) on Pacific herring (*Clupea pallasi*, Clupeidae); Burn (1980) on smooth flounder (*Liopsetta putnami*, Pleuronectidae); Siegel (1980) on four species of Antarctic channichthyids; Scott (1981) on haddock (*Melanogrammus aeglefinus*,
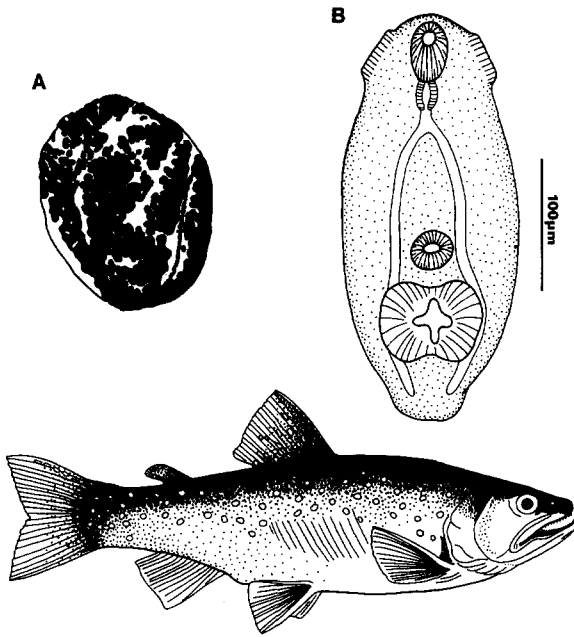
Fig. 3. Frimeth (1987a,b) was able to distinguish anadromous from non-anadromous brook charr (*Salvelinus fontinalis*) by the presence of metacercarial cysts of the marine digenean *Cryptocotyle* (A) which produce a condition known as 'black spot'. Metacercariae of *Diplostomum* (B) were characteristic of non-anadromous charr. (Parasites redrawn from Grabda, 1991, and Kakacheva-Avramova, 1983; fish redrawn from Bristow, 1987.)

Gadidae); Scott (1982) on four species of flatfish; Lardeaux (1982), Aloncle and Delaporte (1983) and Jones (1991) on albacore (*Thunnus alalunga*, Scombridae); MacKenzie (1983b) on bluefin tuna (*Thunnus thynnus*, Scombridae), Manooch and Hogarth (1983) on wahoo (*Acanthocybium solanderi*, Scombridae); Sankurathri *et al.* (1983) on Pacific hake (*Merluccius productus*, Merlucciidae); Timofeeva and Marasaeva (1984) and Hemmingsen *et al.* (1991) on cod (*Gadus morhua*, Gadidae); Arthur (1984) and Kabata and Whitaker (1984) on walleye pollock (*Theragra chalcogramma*, Gadidae); Avdeev (1985) and Avdeev and Avdeev (1989) on Sea of Okhotsk pollock (*Laemonema (= Podonema) longipes*, Gadidae); Shandikov and Parukhin (1987) on *Nototheniops tchikh* (Nototheniidae); and Moser and Cowen (1991) on *Trematomus bernacchi* (Nototheniidae).

MacKenzie (1987a) stated that the most commonly used parasites in this type of study were larval stages of anisakid nematodes, probably because they are amongst the most common helminths of marine teleost fish. Larval anisakid nematodes have been used as biological tags for North Atlantic redfish (*Sebastes* spp.), herring (*Clupea harengus*, Clupeidae) and mackerel (*Scomber scombrus*, Scombridae) (e.g. Kuehlmorgen-Hille, 1983; Bourgeois and Ni, 1984; Scott, 1985; Chenoweth *et al.*, 1986; Dumke, 1988; Eltink, 1988; Scott, 1988; Avdeev and Avdeev, 1989; Lang *et al.*, 1990; Moser, 1991a,b). In contrast, studies using adult nematodes as biological tags are rare although they

do exist. For example, Boje (1987a,b) used adults of *Hysterothylacium aduncum* (Fig. 2(H)) as tags to separate stocks of cod.

Køie (1983) and MacKenzie (1987a) suggested that digeneans have advantages as tags over other types of parasite since they tend to be highly specific to the primary host, which is usually a mollusc. The geographical distribution of the molluscan host largely determines the area within which a fish second intermediate host can become infected, and also, more or less, the area within which a fish definitive host can become infected, depending on the sedentary or migratory nature of the intervening intermediate host.

Several digenean species, notably those of the families Acanthocolpidae, Acanthosto-matidae, Bucephalidae, Diplostomatidae, and Heterophyidae, use fish as intermediate hosts. The metacercariae of these digeneans have been used in a number of tagging studies (Szuks, 1980; Turnpenny *et al.*, 1981; Bamber *et al.*, 1983; Køie 1983, 1984; Karasev, 1984; Bamber and Henderson, 1985; Buchmann, 1986). Adult digeneans of several species have also proved useful. For example, Boje (1987a,b) was able to discri-minate inshore and offshore stocks of cod in Greenland waters using an adult hemiurid digenean *Hemiurus levinseni*, along with the nematode *Hysterothylacium aduncum*. Cod of the inshore stock were characterized by their high levels of *H. levinseni* and low levels of *H. aduncum*. Conversely, cod of the offshore stock could be discriminated by their high levels of *H. aduncum* and low levels of *H. levinseni*.

The giant digenean *Hirudinella ventricosa* has shown some potential as a stock discri-minator for scombrid fish (Manooch and Hogarth, 1983; Eggleston and Bochenek, 1990). Where adults of several species of digeneans are found in one host species, they can be divided into ecologically based groups to indicate differences in host diets and the extent of stock separation (Gaevskaya and Kovaleva, 1980, 1985; Scott, 1982; Køie, 1983, 1984; Zubchenko, 1985a). Kabata *et al.* (1988a) used seven species of intestinal digeneans belonging to five families (Fellodistomatidae, Acanthocolpidae, Hemiuridae, Derogenidae, Opecoelidae) to distinguish between offshore seamount stocks and a continental slope stock of the sablefish (*Anoplopoma fimbria*, Anoplopomatidae) off the west coast of Canada.

Metacestodes, particularly those of the order Trypanorhyncha, have been used as effective biological indicators in stock separation studies on several species of marine teleost fish. An example of this type of study is that of MacKenzie and Mehl (1982, 1984), in which the plerocercoid of *Grillotia smaris-gora* (= *G. angeli*) was used to identify mackerel in the North Sea which had originated from waters south of Ireland. The study was based on the fact that the elasmobranch definitive host of *G. angeli*, the monkfish (*Squatina squatina*, Squatinidae) is rare in the North Sea and to the north of Ireland. Infected mackerel in northern waters could only have originated from southern waters.

Other studies using trypanorhynch metacestodes include those of MacKenzie *et al.* (1984), Avdeev (1985), Lester *et al.* (1986), Brill *et al.* (1987), Avdeev and Avdeev (1989), MacKenzie (1990) and Moser (1991b). It is noticeable that marine metacestodes have more often been used as biological indicators than adult cestodes. This might be due in part to the fact that adult marine cestodes occur more commonly in elasmobranch fish, and to date only one biological tag study has been concerned with the population biology of elasmobranch fish (Watson and Thorson, 1976).

Parasitic copepods were used in stock separation studies on marine fish in the 1980s by Walters (1980a,b), Kabata and Ho (1981) and Leaman and Kabata (1987). Two host-

parasite relationships dominate the use of parasitic copepods for stock separation: cod (*Gadus morhua*) with *Lernaeocera branchialis*, and redfish (*Sebastes* spp.) with *Sphyrion lumpi* (Fig. 4). However, despite their extensive use, certain features of the biology of both copepod species lessen their value as biological tags. *L. branchialis* is highly pathogenic to its definitive host (Kabata, 1970), while its intermediate and definitive hosts are known to vary geographically. The prevalence of *S. lumpi* has been shown to vary markedly with host age, host sex, season, and depth (Gaevskaya, 1984). Since earlier workers were unaware of such variations they could not take them into account when collecting the data or interpreting their results in terms of stock separation.

Fungi, protozoans, monogeneans, acanthocephalans, and isopods have all been used with varying degrees of success to separate stocks of marine fish (MacKenzie, 1983a). Some of the most successful studies have used protozoans as indicator parasites. For example, Khan *et al.* (1980) used the trypanosome *Trypanosoma murmanensis* in Atlantic cod as a stock separator. Khan *et al.* (1982) used two species of blood protozoa, the trypanosome *T. murmanensis* and the piroplasm *Haemohormidium terraenovae* to separate stocks of Greenland halibut (*Reinhardtius hippoglossoides*, Pleuronectidae). MacLean (1980) used *Haematractidium scombri*, a species of blood protozoan, to examine stock separation in mackerel. Other studies using protozoans include those of
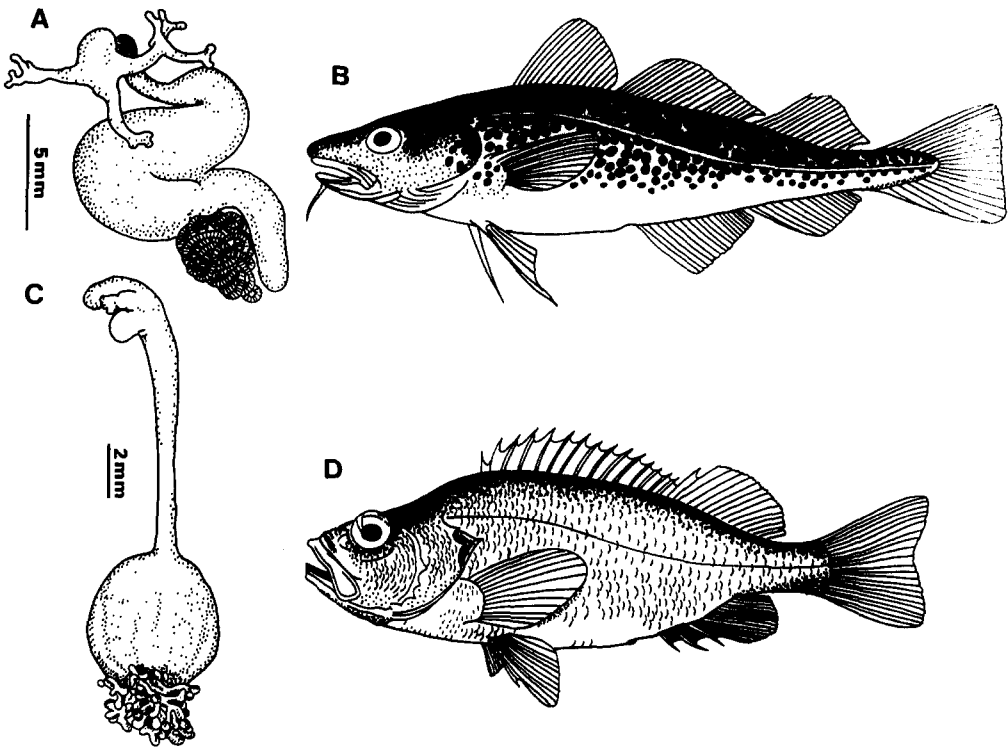

Fig. 4. (A) and (C) Females of two species of parasitic copepod used as indicators in stock separation studies on marine teleost fish. (A) *Lernaeocera branchialis* on (B) cod, (*Gadus morhua*). (C) *Sphyrion lumpi* on (D) redfish, *Sebases* sp. (Parasites redrawn from Kabata, 1979; fish redrawn from Bristow, 1987.)

Berrebi and Britton-Davidian (1980), who used the microsporidian *Glugea atherinae*, in addition to electrophoretic methods, to differentiate four discrete populations of *Atherina boyeri* (Atherinidae), Karasev (1984, 1988), who used the myxosporean *Myxobolus aeglefini* as a stock separator for blue whiting (*Micromesistius poutassou*, Gadidae), McGladdery (1987), who used the coccidian *Eimeria sardinae* to differentiate between different spawning groups of Atlantic herring *C. harengus* (Fig. 2(A)), and Hemmingsen *et al.* (1991), who suggested myxosporeans of the genus *Myxidium* as tags for cod in northern Norway.

The value of monogeneans as stock separation indicators has been realized in a number of studies, for example Gaevskaya and Kovaleva (1980), Walters (1980a,b) and Oliver (1981). Detailed studies of two species of *Diclidophora (D. esmarkii* and *D. luscae*) which were previously thought to be morphologically indistinguishable, were used by Llewellyn *et al.* (1980) to make interesting observations on the potential of these monogeneans as biological tags to study the immigration of Norway pout (*Trisopterus esmarkii*, Gadidae) (normally found in more western and northern waters) into the Plymouth area. An unusual study of this type is that of Rohde (1987), who found that sclerites of the marine monogenean *Kuhnia scombri* (Fig. 2(C)) from the mackerel *Scomber australasicus* from New Zealand and New South Wales differed significantly with respect to the length of the hamuli. From this it was concluded that different populations of *S. australasicus* may exist at the two localities. However, these results should be interpreted with caution in the light of recent research showing significant intraspecific variation in the sizes of monogenean hamuli and hooks with respect to season and temperature (Kulemina, 1987; Mo, 1991)

Stock separation of deep-water marine fish using parasites as biological indicators has been an interesting development of the 1980s. Studies of this type have been carried out on the grenadier fish (*Coryphaenoides rupestris*, Macrouridae) by Szuks (1980) and Zubchenko (1985b). Others are those of Zubchenko (1981, 1984), Houston and Haedrich (1986) and Lester *et al.* (1988). An important aspect of some of these studies, and that of Tkachuk (1985), has been to show that parasite faunas vary significantly with depth. This suggests that parasites provide a potential means of separating stocks restricted to different vertical zones of the water column.

FISH RECRUITMENT MIGRATIONS

Parasites provide valuable information on recruitment migrations, which involve the movement of adolescent fish from their nursery grounds to join the adults on the feeding and spawning grounds. The choice of parasite indicators in studies on fish recruitment migrations is much more limited than the range available for stock separation investigations. The parasite must fulfil two additional important requirements. Firstly, it must infect young fish on the nursery ground and ideally the adult host should not be susceptible to further infection. If it is, then research should be directed towards determining the geographical distributions of the hosts of other stages in the parasite's life cycle. This may lead to identification of parts of the study area within which infection could not occur because it would be impossible for the life cycle of the parasite to be completed. A second important requirement is that the parasite must have a life span long enough for it to remain identifiable in the fully mature adult host. In the 1980–91 period parasite indicators have been used to provide information on recruitment migrations of several species of both anadromous and marine fish.

Anadromous fish

Several studies focus on a range of parasites acquired by the young of anadromous fish in fresh water to provide information on their migrations to the sea. All parasites used are capable of surviving the transition from fresh to salt water and include myxosporeans, protozoans, digenean metacercariae, metacestodes and nematodes.

Pippy (1980) assessed the value of parasites as indicators of Atlantic salmon (*Salmo salar*, Salmonidae) migrations in Greenland coastal waters and the open Atlantic. Black *et al.* (1983) used the copepod *Salmonicola edwardsii* to indicate the movements of anadromous brook charr *Salvelinus fontinalis* to the sea. Boyce and Clarke (1983) examined the migration of sockeye salmon (*Oncorhynchus nerka*) using the cestode *Eubothrium salvelini*, and found that infection with this cestode impaired adaptation of migrating yearlings to saline conditions. Margolis (1982a,b) used two species of myxosporean to separate stocks of *O. nerka* recruited from different parts of the same river system in British Columbia, Canada. Further studies by Margolis (1984, 1985) used two digeneans to demonstrate the North Pacific oceanic range of steelhead trout (*O. mykiss*, Salmonidae) from freshwater systems in North America. Metacercariae of diplostomatid digeneans have been suggested by Jennings and Hendrickson (1982) as potential indicators of the nursery origin of *O. tschawytscha* and *O. kisutch* in a California river system.

Groot *et al.* (1989) used variations in parasite assemblages among Fraser River and Lake Washington stocks of sockeye salmon smolts to investigate their migratory patterns in the Strait of Georgia, Canada. The following twelve parasite species were used: *Myxobolus neurobius, Diplostomum* metacercariae sp. 1 and 2, *Tetracotyle* sp. metacercaria, *Phyllodistomum umblae, Diphyllobothrium* plerocercoids, a dilepidid cysticercoid, *Philonema agubernaculum, P. oncorhynchi, Neoechinorhynchus* spp., *Ergasilus nerkae* (Fig. 2(1)) and *Salmincola californiensis*. The results indicated that most smolts migrate northward via both the eastern and western routes through the Strait of Georgia. Smolts of the Lake Washington stock were found to use the western migration route more frequently than the eastern. It was suggested that the Lake Washington smolts were transported westward when attempting to cross the Fraser River plume.

Bouillon and Dempson (1989) examined metazoan parasites as indicators of the seaward migration of young anadromous Arctic charr (*Salvelinus alpinus*). A comparison of the parasites of freshwater resident and sea-run charr showed that land-locked fish were most heavily infected by *Diplostomum* sp. metacercariae, *Crepidostomum farionis* adults and *Diphyllobothrium ditremum* plerocercoids. In the sea-run charr, *Bothrimonus sturionis* and *Brachyphallus crenatus* adults were dominant (Fig. 5). At age 1+ years, 43% of the charr collected in the Ilkraut River were infected with marine or brackish water parasites. This suggested that some young charr, although not yet ready for the annual seaward migration, were making short feeding excursions into salt water.

Marine fish

Species of marine fish often have nursery areas that are separated geographically from one another, and also from the feeding and spawning grounds of the adults. Recruitment migration studies have centred largely upon identifying the adults of different nursery origin in mixed populations. The parasites for this type of work must be characteristic of a particular nursery area and also be long lived.

A range of parasite types has been employed in this form of study. MacKenzie and Mehl (1984) looked at the plerocercoid of the trypanorhynch cestode *Grillotia smaris-*
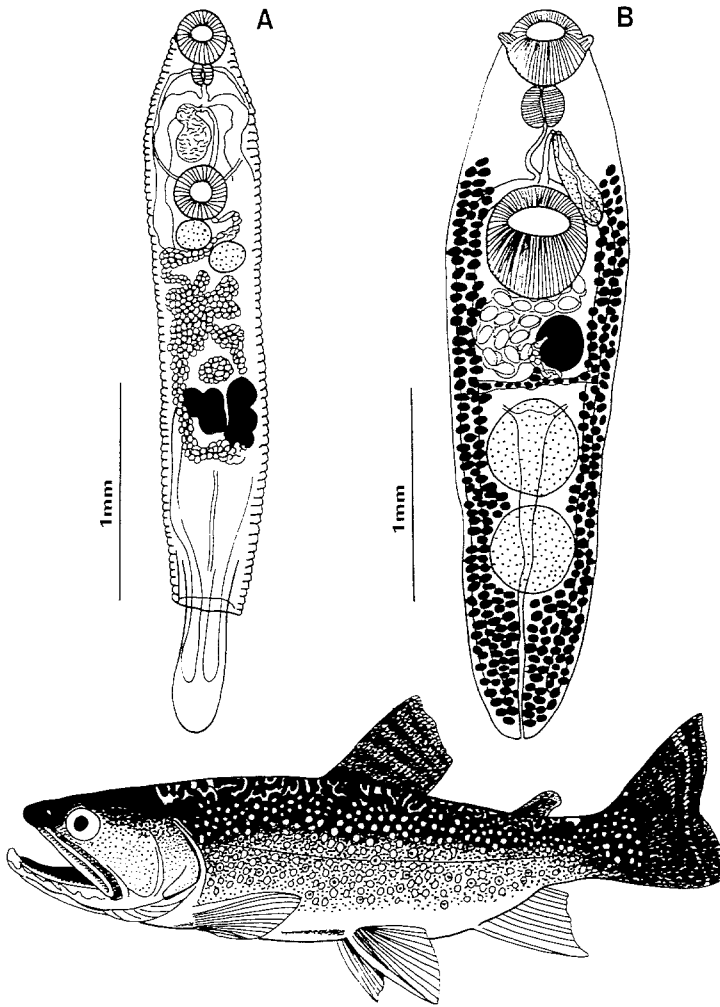
Fig. 5. Adults of the marine digenean *Brachyphallus crenatus* (A) and the freshwater digenean *Crepidostomum farionis* (B) were among the parasite indicators used by Bouillon and Dempson (1989) in their study which examined seaward migration of Arctic charr (*Salvelinus alpinus*). (Parasites redrawn from Dawes, 1947, 1968; fish redrawn from Bristow, 1987.)

gora (= *G. angeli*) to estimate proportions of mackerel (*Scomber scombrus*) of different nursery origin in mixed populations of adult fish in the North-east Atlantic. Two species of renicolid metacercariae and the plerocercoid of the trypanorhynch cestode *Lacistorhynchus* sp. (Fig. 2(F)) allowed MacKenzie (1985) to trace recruitment migrations of herring in the North Sea and adjacent waters. Heath (1984) used the same parasite indicators to examine recruitment migrations of herring in the North Sea. McGladdery and Burt (1985) found that two anisakid nematode larvae, one metacercarial and two adult digeneans, one cestode plerocercoid and a coccidian protozoan were effective indicators in a study of migration, feeding and spawning behaviour in herring in the North-

west Atlantic. A number of parasites, but in particular a myxosporean protozoan and an adult cestode, were employed in a study by Zubchenko (1985b) to show the recruitment migrations of the rock grenadier (*Coryphaenoides rupestris*) in the North-east Atlantic. Jones (1991) investigated a variety of parasites to trace the recruitment migrations of albacore tuna (*T. alalunga*) between the tropics and the New Zealand area.

FISH SEASONAL AND/OR AGE-RELATED MIGRATIONS

The adults of many species of fish undergo seasonal migrations to and from spawning and feeding grounds. Parasites have been good indicators in several investigations on such migrations. A basic requirement in this type of study is that the parasite be acquired by the fish host in certain parts of the migratory range but not in others. Since the time scale of seasonal migration studies is less than 1 year, longevity of the parasite is not an important factor in most instances. Indeed, as MacKenzie (1987a) has suggested, a short life span measured in weeks or months may be advantageous.

Seasonal spawning and feeding migrations of herring (*C. harengus*) and garfish (*Belone belone*, Belonidae) have been investigated in the Baltic Sea. Both species of fish spawn in areas of low salinity and some stocks migrate seasonally to feeding grounds further west in areas of higher salinity. These migratory stocks can be identified on their low-salinity spawning grounds by their infections of characteristically marine anisakid nematode larvae, adult hemiurid digeneans and trypanorhynch metacestodes (Gaevskaya and Shapiro, 1981; Grabda, 1981). Other studies in the Baltic Sea have included those of Rautskis (1983) on *Vimba vimba* (Cyprinidae), and Fagerholm and Valtonen (1980) on whitefish (*Coregonus lavaretus*, Salmonidae).

Seasonal migrations of stocks of North Sea herring between their summer feeding grounds and their autumn/winter spawning grounds were studied by MacKenzie (1988) using five digenean parasites: *Brachyphallus crenatus, Derogenes varicus; Hemiurus luehei, Lecithaster gibbosus* and *Aponurus laguncula* (Fig. 6). Each species of digenean was suspected of having a different enzootic area in the North Sea and therefore they had potential as indicators for identifying the summer feeding grounds of different stocks of herring. Bray and MacKenzie (1990) showed how *A. laguncula* (Fig. 2(D)) in particular could be used to identify the summer feeding grounds of herring in the southern North Sea and English Channel. Other marine fish species on which information regarding migration biology has been made available by the use of parasite indicators include cod. Timofeeva and Marasaeva (1984) used the myxosporean *Myxobolus aeglefini* to provide evidence that the White Sea winter cod (*Gadus morhua hiemalis*) undergoes considerable migrations and goes beyond the limits of the White Sea.

Occasionally parasites provide supplementary information to confirm the results of more standard population studies on the seasonal migrations of host fish species. For example, in the Elbe River the presence of the copepod *Lernaeocera branchialis* on the gills of flounder (*Platichthys flesus*, Pleuronectidae) was noted far upstream in the freshwater regions of the river in the spring of 1982 (Wichowski, 1983). This discovery supported a previous suggestion that during the winter most flounders had migrated from the freshwater reaches of the river toward the estuary due to severe ice conditions. When the flounder re-entered the river after the water temperature had increased they retained the marine copepod.
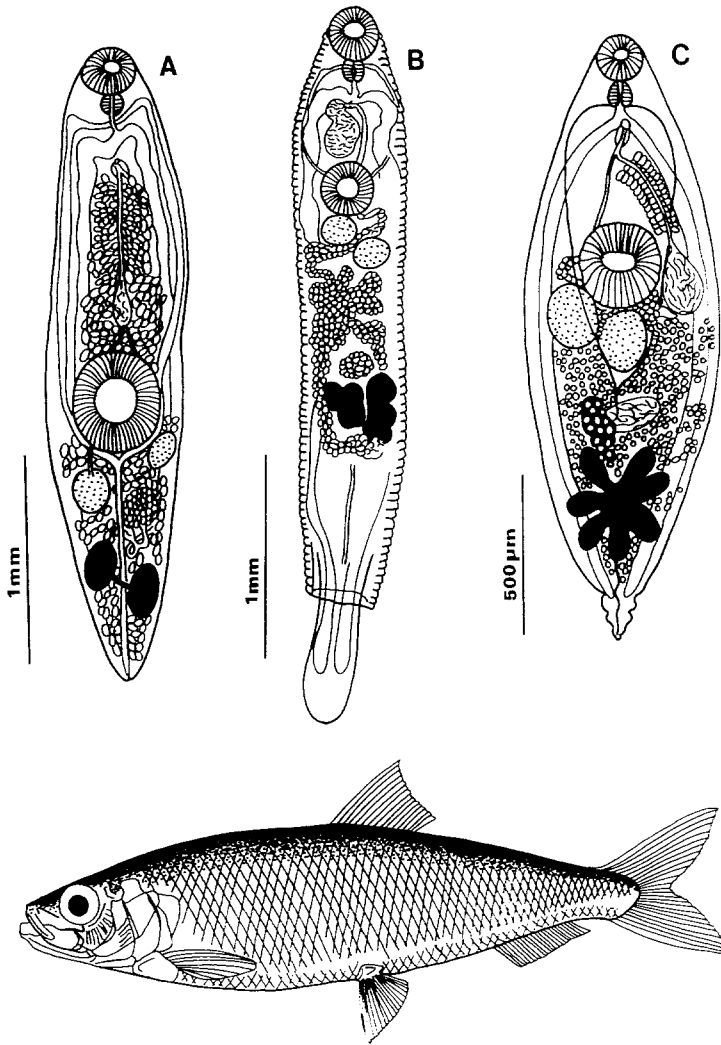
Fig. 6. Adults of three of the five species of digeneans used by MacKenzie (1988) as indicators to study seasonal migrations of herring (*Clupea harengus*) in the North Sea: (A) *Derogenes varicus*, (B) *Brachyphallus crenatus* and (C) *Lecithaster gibbosus*. (Parasites redrawn from Dawes, 1947; fish redrawn from Bristow, 1987.)

MARINE INVERTEBRATES

Commercially important marine invertebrates are infected by a number of protozoan and metazoan parasites. Marine crustaceans, for example, are particularly important as intermediate hosts for helminths (Couch, 1983; Hochberg, 1983; Kinne, 1983; Overstreet, 1983). The use of parasites as biological tags should be just as applicable to aquatic invertebrates as it is to fish. However, despite this obvious potential only one study of this type was published prior to 1980. Uzmann (1970) showed how coastal and offshore stocks of the lobster *Homarus americanus* could be separated by both qualitative and

quantitative differences in their parasite faunas. A larval nematode was almost exclusively restricted to the offshore stock, and a juvenile acanthocephalan to the coastal stock. Since 1980 eight papers have been published.

Smith *et al.* (1981) provided evidence for the existence of two species of arrow squid in the cephalopod genus *Notodarus* from New Zealand waters. They found that squid from western areas had high levels of infection with larvae of the trypanorhynch cestode *Nybelinia* sp. In contrast, squid from southern and eastern areas were uninfected. Parasite data corresponded closely with the results of electrophoretic and morphological studies on the two squid species, and allowed them to be differentiated from each other in sea areas where overlap occurred. Bower and Margolis (1991) suggested that meta-cestodes of *Nybelinia surmenicola* and larvae of the nematode genera *Hysterothylacium* and *Contracaecum* could prove useful as tags for stock differentiation of North Pacific flying squid, *Ommastrephes bartrami*.

Owens (1983, 1985) used a parasitic isopod together with a lecanicephalid meta-cestode in a stock separation study on the banana prawn *Penaeus merguensis* in a gulf of Carpentaria, northern Australia. Brattey and Campbell (1986) examined coastal and offshore populations of the American lobster *Homarus americanus* in the region of Nova Scotia, Canada. They found the acanthocephalan *Polymorphus botulus* in lobsters from both the coastal and offshore populations. Since it was known that the primary hosts of *P. botulus* occurred only in coastal waters, acquisition of the parasite by lobsters was consid-ered to be possible only in these areas. The presence of *P. botulus* in both coastal and offshore lobsters therefore indicated that some degree of mixing had occurred between the population of lobsters inhabiting coastal waters and the lobster population living offshore.

Two digenean metacercariae, *Neolebouria tinkerbellae* and an unidentified species (Metacercaria A) in the marine shrimp *Pandalus jordani* and 'Metacercaria A' in *Pandal-opsis dispar*, were used by Thompson and Margolis (1987) to determine intraspecific population discreteness in these two species from areas off the coast of British Columbia. Dolshenkov *et al.* (1987) used gregarine protozoans as indicators to provide information on the population biology of the shrimp *Euphausia superba*. A bopyrid parasite *Epipen-aeon elegans*, was used by Mathews *et al.* (1988) to provide information on migration patterns of the commercially important shrimp species *Penaeus semisulcatus* in Kuwait waters. The results of this study agreed closely with the migratory patterns deduced from the movements of conventionally tagged shrimp in the same area.

Fish diet and feeding behaviour

In addition to their usefulness as indicators of stock composition and migration patterns, some species of parasite also provide information on fish diet and feeding behaviour. To become infected with most helminth parasites with more than one host in the life cycle, fish must eat the intermediate hosts of these parasites. Since many helminth parasites exhibit some degree of specificity to their intermediate hosts, the presence of such para-sites in fish indicates predation on particular organisms. Whereas examination of stomach contents shows only the very recent food items eaten by the fish, parasites give an indi-cation of the diet over a much longer period of time. Studies on helminths to provide information on diet and feeding behaviour have been carried out on a variety of fresh-water, anadromous and marine fish species.
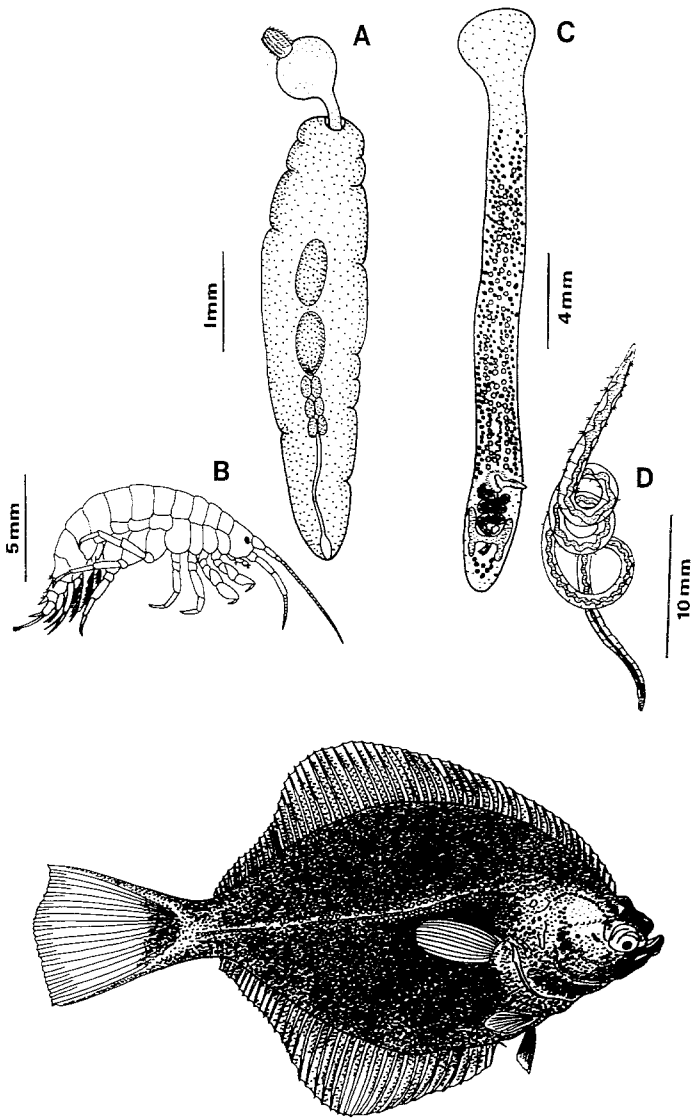
Fig. 7. Infection of flounder (*Platichthys flesus*) from one region of the River Elbe with the acanthocephalan *Pomphorhynchus laevis* (A) indicated to Möller (1984) that the fish had been feeding on the amphipod intermediate hosts *Gammarus* sp. (B) Infection of flounder from a different region of the Elbe with the cestode *Caryophyllaeus* sp. (C) indicated extensive feeding on the oligichaete intermediate hosts of this worm, e.g. *Tubifex* sp. (D) The information provided by the parasite indicators on host diet was later confirmed by stomach contents analysis. (Parasites redrawn from Kakacheva-Avramova, 1983; *Tubifex* and *Gammarus* redrawn from Fitter and Manuel, 1986; fish redrawn from Bristow, 1987.)

A good example is that carried out by Möller (1984), who discovered significant local differences in the prevalences of two intestinal parasites of flounder (*Platichthys flesus*) in the Elbe River: the acanthocephalan *Pomphorhynchus laevis* and the cestode *Caryophyllaeus* sp. This indicated that amphipods, infected with the larvae of *P. laevis*, were the main food items in areas where this acanthocephalan was dominant, whereas oligochaete worms were the main food items where *Caryophyllaeus* sp. predominated (Fig. 7). The pattern of food consumption suggested by the parasite indicators was later confirmed by analysis of stomach contents of flounders from the two areas.

Intestinal helminths were also used by Rydlo (1985) to investigate the feeding behaviour of three fish species: *Chalcalburnus chalcoides mento* (Cyprinidae), *Vimba vimba elongata* and *Salvelinus alpinus*. Frandsen *et al.* (1989) used intestinal helminths as indicators to illustrate significant differences in the feeding ecology of four sympatric morphs of Arctic charr (*S. alpinus*) in Thingvallavatn Lake, Iceland. In similar studies on monomorphic populations of Arctic charr from northern Canadian lakes, Curtis (1985) and Bérubé and Curtis (1986) also found significant associations between occurrence in the stomach of parasites and of food items which were serving as intermediate hosts. This indicated that some individual fish were specialized on particular types of food. From their respective parasite faunas, Permyakov and Rumyanstev (1982) identified two separate stocks of *Coregonus lavaretus* with distinct dietary differences from a lake in the U.S.S.R. However, the presence of *Diplostomum* metacercariae in both the littoral and deep-benthic forms suggested that both forms had a common origin in the littoral regions of the lake, to which the primary hosts were restricted. In the same paper these authors examined populations of *C. lavaretus* from two oligotrophic lakes. High levels of infection with *Eubothrium salvelini*, a cestode transmitted by zooplankton, were found in one lake. In the other, infection levels with this cestode were low. This was interpreted by the authors as an indication that zooplankton did not form an important part of the diet of *C. lavaretus* in the latter lake.

Studies on parasites to provide information on the diet and feeding behaviour of marine fish have also been carried out. Houston and Haedrich (1986), for example, used intestinal helminths to examine the feeding behaviour of deep demersal fishes of the upper continental slope east of Newfoundland. MacKenzie (1987b) discovered significant differences between the intestinal parasite faunas of Atlantic and Pacific herring. These differences provided evidence for a more demersal pattern of feeding by the Pacific herring. In addition to indicating geographical differences in feeding behaviour, intestinal helminths have also been used to provide information on age-related dietary changes in marine fish. This type of study is illustrated by the work of Thoney and Burreson (1986), who discovered that in the bullnose ray (*Myliobatis freminvillei*, Myliobatidae) infections of the aspidogastrean *Multicalyx cristata* (Fig. 2(B)) occurred only in individuals with a disc diameter greater than 68 cm. This provided evidence that the rays feed on the mollusc intermediate hosts (or teleost paratenic hosts) of *M. cristata* only after they have reached a certain minimum size. A similar type of study on the ray *Dasyatis americana* (Dasyatidae) has provided information on size-related feeding behaviour in this species. Details of this unpublished work are given by Caira (1990).

Host phylogenetics and systematics

Parasitology often illuminates host phylogeny and systematics, especially if used in conjunction with more standard methods such as enzyme electrophoresis and comparative morphology. Euzet *et al.* (1989) investigated the value of branchial monogeneans of the genus *Protoancylodiscoides* as phylogenetic indicators of their tropical catfish hosts (*Chrysichthyes* spp. Bagridae). Forty sympatric host individuals were analysed for their electrophoretic polymorphism and also for their branchial monogeneans. The electrophoretic study identified three distinct species, *C. auratus, C. maurus* and *C. nigrodigitatus*, and each of these host species was characterized by its own species of *Protoancylodiscoides*. It was therefore concluded that the gill monogeneans provided as good an indication of the phylogenetic relationships of their fish hosts as did the electrophoretic studies on the hosts themselves.

Lambert and Romand (1984) investigated the specificity of dactylogyrid monogeneans on cyprinid fish hosts (Fig. 8). They found that, on a regional scale, groupings of parasites corresponded closely with taxonomic groupings of host cyprinid species. The taxonomic groupings for the fish had originally been suggested by ichthyologists and were based on studies of the production of hybrids. Rokicki (1983) found that ectoparasites could be used to differentiate two subspecies, *Merluccius merluccius capensis* and *Merluccius merluccius paradoxus* (Merlucciidae).
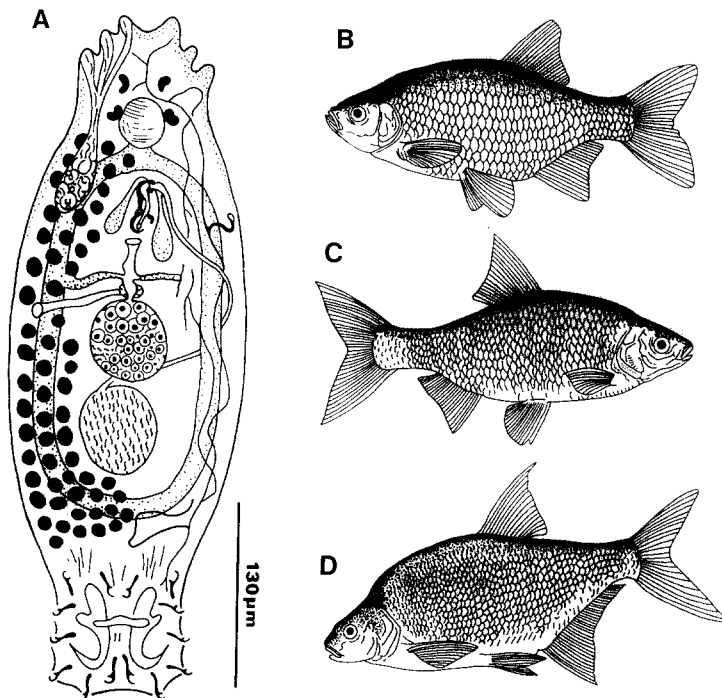

Fig. 8. Species of dactylogrid gill monogenean (A) were used by Lambert and Romand (1984) as indicators to examine the phylogenetic interrelationships of their cyprinid fish hosts, e.g. rudd (*Scardinius erhythrophthalmus*) (B), roach (*Rutilus rutilus*) (C) and bream (*Abramis brama*) (D). (Parasite redrawn from Lambert and Romand, 1984; fish redrawn from Bristow, 1987.)

Brooks *et al.* (1981) used six species of cestodes in the genera *Potamotrygonocestus,* *Acanthobothrium* and *Eutetrarhynchus,* and two nematode species, to investigate phylogenetic origins of, and interrelationships between, four species of South American freshwater elasmobranchs (stingrays) in the genus *Potamotrygon* (Potamotrygonidae): *P.* *magdalene, P. yepezi, P. cicularis* and *P. motoro.* Phylogenetic branch diagrams for the *Potamotrygon* species were constructed using cladistically generated parasite phylogenies in combination with parasite 'presence/absence' data (Fig. 9). Mainly from these data, they concluded that potamotrygonid stingrays represent a monophyletic group whose ancestor was a marine stingray from the Pacific which was trapped in South America by Andean orogeny. A similar study by Brooks and Deardorff (1988) on tetraphyllidean cestodes of the genus *Rhinebothrium* and nematodes of the genus *Echinocephalus* also provided support for the hypothesis of a Pacific origin for potamotrygonid stingrays. However, the work of Brooks *et al.* (1981) has recently been the subject of part of a major review by Caira (1990), who criticized the bases on which the final conclusions were made. She suggested that the system should be reevaluated prior to any general acceptance of the conclusions offered.

Since it was developed by Brooks *et al.* (1981), the technique of using cladistically generated parasite phylogenies in conjunction with parasite 'presence/absence' data to provide information on the phylogeny of aquatic hosts has been used in a number of studies, some of which have made suggestions for improvements, e.g. O'Grady and Deets (1987). Recent studies in this area have involved the use of parasitic copepods on elasmobranch and teleost fish (Deets, 1987; Deets and Ho, 1988; Dojiri and Deets, 1988).

Previous sections of this review have given examples of how parasites have been used to provide information on relatively short-term migrations of freshwater and anadromous fish. An exception is the work of Black (1983), in which a nematode was used to study the migration or dispersion of an anadromous fish species over a much longer time scale, providing valuable phylogenetic information on the geographical origins of the host. The nematode *Cystidicola farionis* was used to trace the migration of lake trout *Salvelinus* *namaycush* originating from an ancestral stock that had survived glaciation in a Bering refugium in the unglaciated parts of the Yukon River system. Present day parasite distribution data suggests that *S. namaycush* had dispersed across northern British Columbia and the coastal mainland of the Northwest Territories in Canada during the glacial retreat.

A similar type of study to that of Black (1983) was carried out by Ibragimov (1987), who suggested that colonization of brackish and salt water environments by the Danube bleak (*Chalcalburnus chalcoides,* Cyprinidae) in the region of the Caspian Sea was a comparatively recent event on the geological time scale. His suggestion was based on the absence of marine parasites specific to *C. chalcoides* and also on the fact that the monogenean *Dactylogyrus chalcalburni,* the only species of parasite known to be specific to *C. chalcoides,* is a freshwater form only poorly adapted to saline conditions.

In contrast to the relatively large number of papers on parasites as indicators of fish phylogeny, only one focuses on an invertebrate. Smith *et al.* (1981) used parasite data, in conjunction with results from electrophoretic and morphological studies, to show that there are two sibling species of a cephalopod, the arrow squid *Notodarus sloani,* in New Zealand waters. Previously it had been thought that there was only one species of arrow squid in this area.

A   PARASITES   **D**

	1	2	3	4	5	6	7	8
E. spinicaudata	−	+	−	−	+	+	−	−
P. magdalenae	−	−	−	+	−	−	−	−
P. yepezi	+	−	−	−	−	−	+	−
P. circularis	+	+	+	−	−	+	−	+
P. motoro	−	+	+	−	−	+	−	−

B   PARASITES

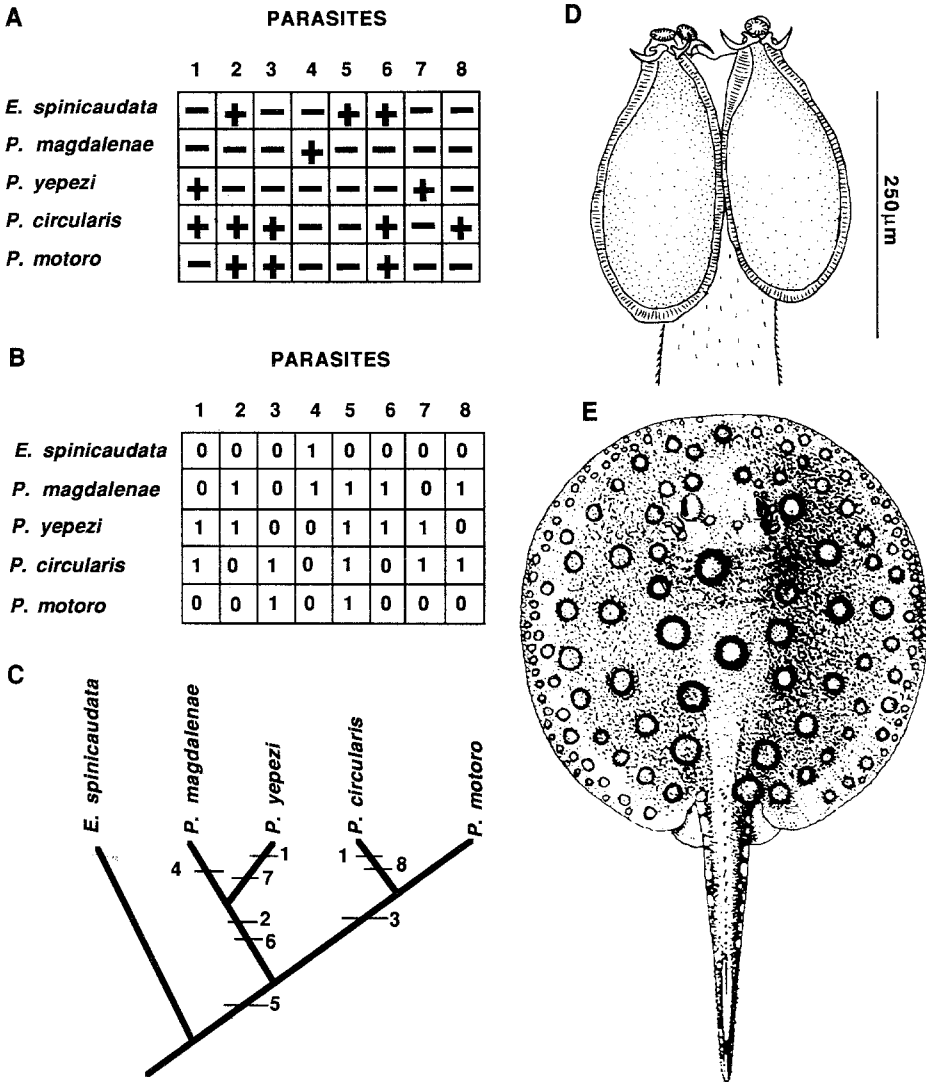|	1	2	3	4	5	6	7	8
E. spinicaudata	0	0	0	1	0	0	0	0
P. magdalenae	0	1	0	1	1	1	0	1
P. yepezi	1	1	0	0	1	1	1	0
P. circularis	1	0	1	0	1	0	1	1
P. motoro	0	0	1	0	1	0	0	0

E

C

Fig. 9. Diagram to illustrate the generation of a phylogenetic tree for four species of South American freshwater stingray in the genus *Potamotrygon* based on cladistic analysis of a presence/ absence matrix constructed for eight species of helminth parasite by Brooks *et al.* (1981). (A) A host-parasite presence/absence matrix where + indicates present and − absent. Parasites are numbered as follows: 1, *Echinocephalus daileyi*; 2, *Rhinebothrium paratrygoni*; 3, *Eutetrarhyn-chus araya*; 4, *Acanthobothrium quinonesi*; 5, *A. terezai*; 6, *Rhinebothroides scorzai*; 7, *Potamo-trygonocestus amazonensis*; 8, *Terranova edcaballeroi*. Host genera: E., *Elipesurus*; P., *Potamotrygon*. (B) A binary presence/absence matrix polarized using parasites in the outgroup elasmobranch host species *Elipesurus spinicaudata*. Codes as in (A). (C) A branch diagram produced by cladistic analysis of matrix B which illustrates the hypothetical relationships among the four species of *Potamotrygon*. Codes as in (A). (D) The scolex of *Potamotrygonocestus amazon-ensis*, one of the cestodes used in the cladistic analysis. (E) A potamotrygonid stingray. (A, B, C Redrawn from Caira, 1990, based on Brooks *et al.*, 1981; D redrawn from Mayes *et al.*, 1981; E reproduced with permission from Wheeler, 1985.)

Summary and conclusions

A main aim of this paper was to review work published in the last decade or so, with emphasis on those reports directly concerned with fish population studies in relation to fisheries research. With regard to research on parasites to indicate fish diet and feeding behaviour, or to illuminate host phylogenetics and systematics, a limit on the length of the review prevented us from citing a number of other papers relevant to these topics. These and other areas in which parasites have been used to further our knowledge of fish biology will be the subject of a separate review.

MacKenzie (1987a) concluded that the following fish parasites were worthy of further research as biological indicators: (i) Haematozoa, (ii) intestinal helminths in seasonal migration studies, and (iii) trypanorhynch metacestodes in recruitment studies of marine teleosts. There is also considerable potential for more population studies based on parasitological work on: (i) invertebrates, particularly crustaceans and cephalopods, (ii) deepwater marine fish, and (iii) elasmobranch fish.

It is expected that the recent increased interest in the parasites of deep-sea fish (Campbell, 1990) will lead to more research in this area and that this will identify potential indicators for studying aspects of the biology of deep-water fish. There has been only one study on the population biology of elasmobranchs (Watson and Thorson, 1976), but the increasing market for elasmobranchs for human consumption, and their importance as predators of commercially important teleosts and invertebrates, demands a better understanding of their population biology. Elasmobranchs carry a range of host-specific parasites, many of which would be ideal tags.

The scope for further work on parasites beyond that which is of immediate value in fisheries research is infinite because, in general, fish parasites are very host-specific. Often a particular species may be specific to a mollusc, arthropod, fish or any other group of invertebrates or vertebrates, depending on the stage of its life cycle. Of the 5000 or so known species of fish helminths, we have estimated that there is a good understanding of only about 200 life cycles. In only a few of these have the data been used to enhance knowledge of host biology, although the key to a life cycle is often the food and feeding habits of its host. Since the host specificity of a parasite is now generally thought to be dependent on four groups of factors, namely morphological, ecological, physiological and phylogenetic, then it follows that any parasite study will illuminate these aspects of the biology of the host. For these basic reasons it is not surprising that fish parasites are being used increasingly to enhance our knowledge of the following and other aspects of host biology: phylogeny, biogeography, seasonality, age, length and growth rates, life history, schooling and other forms of behaviour, ecology, stress and immunology. The two last named topics are of particular interest and value because it is now thought that some fish helminths are good indicators of stress through pollution (Khan and Thulin, 1991; MacKenzie *et al.*, unpublished data).

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