



Effects of parasites on fish behaviour: a review and evolutionary perspective

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Contents

Abstract	page 132
1. Introduction	133
1.1 Scope of the review	
1.2 The ubiquity and importance of fish parasites	
1.3 Essential terminology	
1.4 Predictable pathological side effects of infection: the behaviour of 'sick' individuals	
2. The evolution of host behaviour change	135
2.1 Parasite life cycle diversity: the potential for infection-associated behaviour change	
2.1.1 Direct life cycles	
2.1.2 Indirect life cycles: the manipulation hypothesis	
2.1.3 Evidence for parasite increased trophic transmission (PITT)	
2.2 Predation by hosts and non-hosts	
2.3 Parasite location and possible mechanisms of manipulation	
3. Infection-associated changes in behaviour	138
3.1 Altered foraging behaviour	
3.1.1 Altered time budgets	
3.1.2 Reduced ability to compete for food	
3.1.3 Diet composition and prey selection	
3.2 Altered locomotion	
3.2.1 Reduced swimming performance	
3.2.2 Conspicuous locomotion	
3.3 Altered anti-predator behaviour	
3.3.1 Avoiding encounter	
3.3.2 Avoiding detection	
3.3.3 Avoiding selection	
3.3.4 Evading a predatory strike	
3.3.5 Post-capture escape	
3.3.6 Effects of parasite infectivity and host age	
3.4 Altered habitat selection	
3.4.1 Effects of infection on the horizontal distribution of fish hosts	
3.4.2 Effects of infection on the vertical distribution of fish hosts	
3.4.3 Changes in vegetation / cover preferences	
3.5 Altered sexual behaviour	
3.5.1 Effects of parasites on reproductive development in fishes	
3.5.2 Consequences of parasitism for courtship, mate choice and parental care	
4. Parasite avoidance and infection-reducing mechanisms	150
4.1 Avoidance of infected prey	
4.2 Avoidance of habitats associated with infection risk	
4.3 Infection reduction behaviours	
5. The influence of parasites on shoaling behaviour: a case study in parasite-associated behaviour change	152
5.1 Mode of parasite transmission and host shoaling behaviour	
5.2 The costs and benefits of association for and with parasitised fish	
5.2.1 Competition	

5.2.2 Predation	158
5.3 Shoaling preferences	159
5.4 Recognition of parasitised individuals	160
5.5 Parasite-assortative shoaling under natural conditions	
6. Conclusions and directions for future research	
Acknowledgements	
References	

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Abstract

Fish serve as hosts to a range of parasites that are taxonomically diverse and that exhibit a wide variety of life cycle strategies. Whereas many of these parasites are passed directly between ultimate hosts, others need to navigate through a series of intermediate hosts before reaching a host in (or on) which they can attain sexual maturity. The realisation that parasites need not have evolved to minimise their impact on hosts to be successful, and in many cases may even have a requirement for their hosts to be eaten by specific predators to ensure transmission, has renewed interest in the evolutionary basis of infection-associated host behaviour. Fishes have proved popular models for the experimental examination of such hypotheses, and parasitic infections have been demonstrated to have consequences for almost every aspect of fish behaviour. Despite a scarcity of knowledge regarding the mechanistic basis of such behaviour changes in most cases, and an even lower understanding of their ecological consequences, there can be little doubt that infection-associated behaviour changes have the potential to impact severely on the ecology of infected fishes. Changes in foraging efficiency, time budget, habitat selection, competitive ability, predator-prey relationships, swimming performance and sexual behaviour and mate choice have all been associated with – and in some cases been shown to be a result of – parasite infections, and are reviewed here in some detail. Since the behavioural consequences of infections are exposed to evolutionary selection pressures in the same way as are other phenotypic traits, few behavioural changes will be evolutionarily neutral and host behaviour changes that facilitate transmission should be expected. Despite this expectation, we have found little conclusive evidence for the Parasite Increased Trophic Transmission (PITT) hypothesis in fishes, though recent studies suggest it is likely to be an important mechanism. Additionally, since the fitness consequences of the many behavioural changes described have rarely been quantified, their evolutionary and ecological significance is effectively unknown.

Potential hosts may also change their behaviour in the presence of infective parasite stages, if they adopt tactics to reduce exposure risk. Such ‘behavioural resistance’, which may take the form of habitat avoidance, prey selectivity or avoidance of infected individuals, can be viewed as behavioural change associated with the threat of being parasitised, and so is included here. Actually harbouring infections may also stimulate fishes to perform certain types of simple or complex behaviours aimed at removing parasites, such as substrate scraping or the visitation of cleaning stations, although the efficacy of the latter as a parasite removal strategy is currently subject to a good deal of debate.

The effects parasites have on shoaling behaviour of host fish have attracted a good deal of attention from researchers, and we have provided a case study to summarise the current state of knowledge. Parasites have been shown to affect most of the antipredator effects of shoaling (such as vigilance, co-ordinated evasion and predator confusion) and can also impair an individual’s foraging ability. It therefore seems unsurprising that, in a number of species avoidance of parasitised individuals has evolved which may explain the occurrence of parasite-assorted shoals in the field. Parasitised fish are found more often in peripheral shoal positions and show a reduced tendency for shoaling in some fish species. Given the array of host behaviours that may be changed, the fitness consequences of shoal membership for parasitised hosts and their parasites are not always easy to predict, yet an understanding

of these is important before we can make predictions regarding the ecological impact of infections on host fish populations.

Clearly, there remain many gaps in our knowledge regarding the effects of parasites on the behaviour of host fish. We believe that a much greater understanding of the importance of infection-associated behaviour changes in fish could be gained from high quality research in comparatively few areas. We have completed our review by highlighting the key research topics that we believe should attract new research in this field.

1. Introduction

Despite the fact that parasites are usually much smaller than their hosts, infections often have significant consequences for host biology, and the idea of harm caused to the host is a concept central to the many definitions of parasitism that have been proposed. Parasites, then, are not passive organisms simply 'hitching a ride' with their hosts; to be classified as a parasite, a commensal organism must fulfil criteria that include the fact that its presence has a negative effect on its host (Begon et al., 1990). Since parasites generally utilise host energy resources these deleterious effects are frequently nutritional, but it is rare for this to be the only consequence of infection. Any deleterious effects parasites have as they invade, move around or grow inside or on the host may – through associated pathology, physiological imbalance or general malaise – have consequences that affect the growth, survival and, ultimately, reproductive 'fitness' of the host (i.e. its capacity to contribute genes to the next generation). Many of the consequences suffered by infected individuals are associated, in one way or another, with altered behaviour.

1.1 *Scope of the review*

Depending on the specific definition of parasitism adopted, the term 'parasite' may be used to describe many kinds of organism – from viruses to vertebrates. We have largely restricted our review to the effects of macroparasites on teleost fish hosts. The macroparasites (May and Anderson, 1979) are an artificial group of metazoan parasites, composed mainly of members of the Platyhelminthes (flatworms, including monogenean and digenean trematodes and cestodes), Nematelminthes (roundworms and allies, including nematodes and acanthocephalans), annelids (such as leeches) and Arthropods (true lice and parasitic copepods).

Although parasite infections are likely to affect the behaviour of fish in all aquatic environments, the majority of studies examine freshwater species. Consequently, infection-associated changes in the behaviour of marine fishes (and other vertebrates) are not well understood (Rohde, 1993, p. 92). There are likely to be many reasons for this bias. Probably the most important are the relative ease with which freshwater fish are maintained in the laboratory, and the lack of basic knowledge of both 'normal' behaviour patterns of host species and the natural history of parasites, including life cycle details, from other habitats. Our review inevitably reflects this literature bias, but an effort has been made to include under-represented groups where possible. Obviously, infection-associated behavioural changes have the potential to be enormously important for our exploitation of marine fish through fisheries and aquaculture, and their further study would be of clear benefit.

The format of our review reflects an attempt to maximise its heuristic and practical value. We begin with an analysis of the evolutionary basis and potential evolutionary consequences of parasite-mediated behaviour change in fishes (section 2). We then move on to review the findings of laboratory and field studies that have investigated the effect of parasites on various aspects of fish behaviour (sections 3). In section 4, we review the various behavioural mechanisms employed by actual and potential fish hosts to avoid parasites, or reduce infection levels. In the final section (section 5) we offer a case study of infection-associated change in the shoaling behaviour of fishes. Shoaling behaviour is believed to have evolved mainly as an anti-predator strategy, but also has important consequences for foraging behaviour (Pitcher and Parrish, 1993). As such, it provides a good system for the study of parasites with indirect life cycles, some of which apparently manipulate their intermediate hosts to increase predation and thus transmission to their final host. Shoaling behaviour is also of great interest to the study of directly transmitted parasites, because the temporal

and spatial proximity of individuals within shoals – like any social group – potentially facilitates their transmission. In section 6, we conclude our review and detail areas that we believe currently offer the most exciting and ecologically relevant opportunities for research in this field.

1.2 *The ubiquity and importance of fish parasites*

Aquatic habitats offer ideal conditions for the maintenance and evolution of parasite life cycles. Water provides a physiologically stable, buffered environment, and its viscosity facilitates the dispersal and survival of eggs and fragile free-living stages. Food webs are also relatively long and intricate and this has, in many cases, enabled the development of complex parasite life cycles. Because of the central role played by teleost fishes in such ecosystems – especially with respect to their role as consumers in food chains, but also because they offer a large surface area for encounter and colonisation – they are frequently utilised as hosts by parasitic organisms. In addition, fishes are highly mobile and this may be attractive to certain kinds of parasites since they create the potential for further dispersal. Probably for all of these reasons, fish that live in natural ecosystems are rarely found to be free from infections. Even in artificial aquaculture environments fish are at risk from acute outbreaks of parasite infections, resulting from the maintenance of high stock densities.

The study of fish parasitology has importance for many reasons. Fish parasites cause commercial losses in both the aquaculture and fisheries industries and may have human health, as well as socio-economic, implications both in developing and developed countries. A full understanding of the diverse effects of fish parasites on their hosts is therefore central to the development and maintenance of fisheries worldwide. The effect of parasites on the behaviour of fish hosts is clearly an important aspect of this understanding. The subject is also of academic interest, as recent advances in the disciplines of behavioural and evolutionary ecology have given insight into the potential roles that parasites play in shaping the evolution and ecology of host species. Furthermore, and of current importance, parasites clearly have a role in the maintenance of biological and behavioural diversity of their hosts (Combes, 1996; Renaud et al., 1996).

In recent years, new applications of fish parasitology have been developed. In both freshwater and marine systems, parasites may potentially be used as

bio-indicators of pollution (Poulin, 1992; MacKenzie et al., 1995; though such use is not without its problems (Rohde, 1993)), and also as biological tags for stock separation (e.g. MacKenzie and Longshaw, 1995). Infection-associated changes in host behaviour may be important in determining the efficacy of such uses.

1.3 *Essential terminology*

[In an attempt to maximise the value of this review, we have kept our use of technical terminology to a minimum. However, certain terms that have practical value have been used, and are introduced here. For further terminology the reader is referred to Dobson (1988) and Margolis et al. (1982)].

Infecting organisms may live inside a host, in which case they are termed **endoparasites**, or on the external surface as **ectoparasites**. (In fishes, the gill surfaces are usually classified as external environment since they are in constant contact with the external medium, even in species where they are enclosed within opercula). Parasites exhibit a variety of life cycle types. Those that are transmitted from one **definitive** host (in which they reach sexual maturity) to another are described as having **direct** life cycles. Parasites that use at least one **intermediate** host (which harbours sexually immature forms of the parasite) to transfer between definitive hosts are said to have **indirect** or **complex** life cycles.

The extent of parasite infection can be expressed in terms of an individual host as the **intensity** of infection (the number of individual parasites of a particular species harboured) and in terms of host populations as the *prevalence* (the proportion of hosts harbouring at least one individual parasite of a particular species).

1.4 *Predictable pathological side effects of infection: the behaviour of 'sick' individuals*

The 'normal' behaviour of an individual under a given situation may be explained conveniently as a result of motor responses brought about by the complex integration and neurological processing of inputs from many sensory systems. Since any or all of these factors may be damaged by parasites, altered behaviour may sometimes be coincidental to infection (Poulin, 1998) and infection-associated pathology may be an inevitable consequence ('side-effect') of being colonised or inhabited by another organism (Minchella, 1985). Moreover, since parasites generally exhibit an overdispersed (or 'aggregated') distribution amongst

their host populations, the majority of host individuals harbour no or few individuals of one parasite species, whereas a few harbour a disproportionately high number of them (Anderson, 1994). Heavily infected hosts are often reported to behave oddly, and such density-dependent effects may be expected if individual parasites are even mildly pathogenic.

However, since behavioural changes inevitably have implications for the ecology of host organisms and consequently for the parasites they harbour, these changes are unlikely to be evolutionarily neutral, and adaptive explanations for their existence frequently need to be sought.

2. The evolution of host behaviour change

The behaviour of parasitised individuals has been described as a 'mixed phenotype' (Dawkins, 1982) since it exhibits characters that result from both host and parasite genotypes. Since an individual's behaviour determines the way in which it interacts with its environment, alterations inevitably have consequences for the ecology of both the host and the parasite. Clearly then the parasite (within the host) is exposed to selective pressures in exactly the same way as the host it infects, and if the behavioural change results in improved transmission success, the parasite phenotype that brought it about will be selected for. In these cases, behavioural changes associated with infection may be interpreted as adaptations of the parasite, rather than simple pathological effects associated with infection.

2.1 *Parasite life cycle diversity: the potential for infection-associated behaviour change*

Parasitic animals have evolved from free-living ancestors. Current evolutionary theory suggests that this is most likely to have occurred when individuals, pre-adapted for some other purpose, gained a selective advantage over other conspecifics by initial close association with, and subsequent exploitation of, a larger host organism (Poulin, 1998). Many parasite species have, so far, progressed no further along the scale of life cycle complexity and employ only a single host species as a host that supports the complete life cycle (often interspersed with a free-living stage). Other parasites have acquired successive hosts, apparently added sequentially to the life cycle as a result of historical chance events that allowed individuals

acquiring more hosts to gain reproductive, dispersal or other fitness advantages (see Poulin, 1998, for a recent review of parasite life cycle evolution). The precise nature of the parasite life cycle is important in predicting, interpreting, and evaluating the consequences of, host behaviour change.

2.1.1 *Direct life cycles*

Directly transmitted parasites may benefit from host behaviour changes that bring their current host into contact with other host individuals, or that maximise the probability of other hosts being present when infective stages are released. In addition, mechanisms that increase the success of parasite offspring finding hosts may also be expected, and there is a good deal of evidence that parasites have evolved this type of mechanism. Tinsley (1990) has reviewed studies demonstrating both host-finding behaviour of free-living stages and spatio-temporal synchronisation of the release of infective stages with host presence. For example, the common sole (*Solea solea*, Soleidae) is frequently infected with a directly transmitted skin parasite (*Entobdella soleae*). Eggs released from the parasite stick to the sandy substrate, the favoured habitat of the host fish, and only hatch during the first few hours of daylight. Since sole are typically active during the night, and rest in the sand during the day, the hatching period matches the period of minimum host activity, and is likely to be adaptive (Kearn, 1986). The fact that a related parasite, *E. hippoglossus*, exhibits the opposite periodicity supports the hypothesis that such mechanisms may have evolved to enhance transmission, since this parasite infects the halibut (*Hippoglossus hippoglossus*, Pleuronectidae), which is diurnally active. However, this is an example of parasites exploiting normal host behaviour patterns, and not altering host behaviour *per se*.

In fact, since most direct parasites require their hosts to remain alive long enough for them to reproduce, and will usually die if ingested by a predator, large deviations from 'normal' host behaviour – which is already assumed to be adapted for survival – are not expected. Vaughan and Coble (1975) showed that three directly transmitted ectoparasites did not increase the risk of predation of their fish hosts, despite the presence of conspicuous characters such as black spots. Vaughan (1979) found that predatory largemouth bass (*Micropterus salmoides*, Centrarchidae) did not selectively predate bluegill sunfish (*Lepomis macrochirus*, Centrarchidae) following experimental infection with lymphocystis, despite the growth of

large tumours on host fish. However, while the received wisdom is that, in order to prevent host predation or accidental death, directly transmitted parasites should be largely avirulent (Smith Trail, 1980) there are of course exceptions. A single *Argulus* louse might not have much effect on its host, but 50 would. In populations where hosts harbour unnaturally high levels of infections as a consequence of some other factor, such as artificially high densities or pollution levels, otherwise avirulent parasites could affect behaviour as a result of their increased numbers. Herting and Witt (1967) found various centrarchid and cyprinid forage fishes infected with the directly transmitted monogenean *Dactylogyrus* sp. to be more susceptible to bowfin (*Amia calva*, Amiidae) predation, apparently due to their sluggish movements. This indicates that increased predation is not necessarily a functional adaptation, but may arise simply as a side effect of pathology even when it is costly to the parasite.

2.1.2 Indirect life cycles: the manipulation hypothesis

Parasites that utilise more than one host in their life cycle have a greater potential, and in some circumstances possibly even a requirement, to evolve strategies of host manipulation that enhance their probability of transmission. Although the acquisition of successive hosts has clearly been beneficial to these organisms, increasing the number of hosts intuitively reduces the probability of any one offspring navigating successfully through one life cycle. Parasites acquiring successive hosts probably overcame the problem of multiple transmissions initially by being massively fecund; however, since it is energetically expensive to increase egg load, parasites that produce offspring that are transmitted more efficiently should be at a selective advantage.

There is a wealth of data concerning the pathological consequences of parasitic infections in fish, and many altered behaviours have been described that appear to be the result of parasitism. Studies have increasingly examined the possibility that manipulation of host behaviour is a parasite adaptation, serving to facilitate transmission. Parasite-mediated behavioural changes in a variety of taxa have been reviewed (e.g. Holmes and Bethel, 1972; Dobson, 1988; Moore and Gotelli, 1990; Moore, 1995; Combes, 1991; Poulin, 1995) but as yet the evidence for increased transmission in fish remains somewhat equivocal. In addition, there is still some debate as to what constitutes behaviour 'modification' or 'manipulation', the terms most frequently used to describe this phenomenon. The essence of the problem is that observed behavioural differences may have arisen as a result of four types of mechanism (after Poulin, 1994a):

ulation', the terms most frequently used to describe this phenomenon. The essence of the problem is that observed behavioural differences may have arisen as a result of four types of mechanism (after Poulin, 1994a):

- (1) the observed behaviour may be an adaptive response of the host to infection; or,
- (2) the observed behaviour may be adaptive for the parasite, for example increasing transmission by predation by the definitive host; or,
- (3) the observed behaviour may be a result of the pathology due to infection, without being adaptive for either parasite or host; or,
- (4) the observed behaviour may reflect the struggle between host and parasite genetic interests.

The various explanations, and the problems in distinguishing between them, may be illustrated with a brief example. Three spined sticklebacks (*Gasterosteus aculeatus*, Gasterosteidae) are frequently infected with the plerocercoid larvae of the avian cestode *Schistocephalus solidus* – parasites that grow rapidly in the body cavity of the fish and make massive demands on host energy reserves (Orr and Hopkins, 1969; Walkey and Meakins, 1970). Infected fish exhibit altered prey preferences both in the laboratory (Milinski, 1984; Ranta, 1995) and in field studies (Tierney, 1994), generally feeding on smaller prey items than uninfected conspecifics. It has been suggested that such a preference may serve to reduce competition with uninfected fishes. The behaviour may therefore be alternatively viewed as:

- (a) a host-induced behavioural change, serving to maximise the chances of host survival until the breeding season by optimising energy intake; or
- (b) a parasite-induced behavioural change that maximises energy uptake by the host, facilitates parasite growth and reduces the chances that the fish should die of starvation before the parasite attains infectivity; or
- (c) a consequence of the debilitating nature of *Schistocephalus* infection, which may make infected fish less able to pursue, catch and handle larger prey; or
- (d) an enforced compromise reflecting the requirements of both host and parasite systems.

In the absence of data regarding the ultimate effect of a particular parasite-associated behaviour change on host survival and parasite transmission, it is often extremely difficult to suggest whether an observed altered behaviour is more likely to be a host- or parasite-mediated change or a neutral side-effect.

Although examples of behavioural changes adaptive for parasites have been demonstrated in some invertebrate hosts (see Holmes and Bethel, 1972), attempts to examine the extent of the manipulation hypothesis in different taxa have not been wholly successful (e.g. Poulin, 1994a), and it remains to be seen whether this is an important process in parasitised fish.

2.1.3 Evidence for parasite increased trophic transmission (PITT)

A number of studies have reported increased predation on parasitised animals including invertebrates (Holmes and Bethel, 1972; Moore, 1983) and mammals (Hoogenboom and Dijkstra, 1987; Rau and Caron, 1979). The advantage for the parasite in such cases is intuitively clear: parasites ingested by definitive hosts have the chance to reproduce whilst those that are not effectively have a fitness of zero. Any parasite that can increase the likelihood of reaching its definitive host will increase its fitness, and selection for such mechanisms is expected to be strong. Lafferty (1999) has termed this 'parasite increased trophic transmission' (PITT) to distinguish the process from other behaviour changes. It follows that demonstrating increased predation of parasitised individuals is an essential step in understanding parasite-mediated behaviour.

However, although studies on fish hosts often suggest that parasitised individuals may suffer increased predation, only very few studies have demonstrated unambiguously increased susceptibility of fish intermediate hosts to definitive host predators. van Dobben (1952) reported that 30% of roach (*Rutilus rutilus*, Cyprinidae) captured by cormorants were infected with *Ligula intestinalis* from a population where only 6.5% of roach carried the parasite, and this study strongly supports selective predation of parasitised fish by a definitive host under natural conditions. The best evidence that parasitised fish are subject to greater predation by definitive hosts is from Lafferty and Morris's (1996) study of California killifish (*Fundulus parvipinnis*, Cyprinodontidae), intermediate hosts of a brain-encysting trematode (*Euhaplorchis californiensis*) that increases the frequency of conspicuous behaviours fish hosts perform. Enclosed pens in a natural lagoon were stocked with mixed groups of parasitised and unparasitised fish, and one pen was covered with netting to prevent predation. After twenty days, predation by herons and egrets (definitive hosts of the parasite) was assessed by

counting the remaining fish, and birds were found to be 30 times more likely to eat infected fish than uninfected ones. The magnitude of selective predation in this example suggests that PITT may well occur in other parasitised fish, where more extreme effects on behaviour have been recorded.

Indirect evidence also supports a role for PITT in other parasite systems, although predation experiments are required to confirm transmission in most cases. Some parasitised fish have been recorded swimming closer to the water surface than uninfected conspecifics, including ninespine sticklebacks *Pungitius pungitius*, Gasterosteidae) with *Schistocephalus* (Smith and Kramer, 1987) and fathead minnows (*Pimephales promelas*, Cyprinidae) with *Ornithodiplostomum* sp. (Radabaugh, 1980). Laboratory experiments using a heron as a predator confirm the suggestion that the risk of predation increases for fish nearer the surface (Kramer et al., 1983). Yet Lemly and Esch (1984) found no evidence of selective predation by kingfishers on bluegill sunfish infected with a trematode, despite significant increases in host oxygen demand (the mechanism responsible for surface-swimming behaviour in other systems; Lester, 1971).

2.2 Predation by hosts and non-hosts

As parasitised fish may be eaten by both definitive hosts and by non-host predators, infections that increase susceptibility to all types of predation will not necessarily increase transmission rates to definitive hosts. For example, avian predators are the definitive hosts of *Schistocephalus*, but to date increased predation has only been demonstrated for non-host predators (Jakobsen et al., 1988). Similar predation by non-hosts has been found in guppies infected with *Diplostomum* sp. and roach infected with *Ligula* (Brassard et al., 1982; Sweeting, 1976; but see also Coble, 1970). General increases in predation may still increase parasite fitness, as long as relatively more parasites are eaten by suitable hosts than would be if no behavioural alteration took place. However, as all parasites eaten by non-hosts are lost from the population, we might expect mechanisms that direct prey animals harbouring infective stages explicitly towards predators that are suitable subsequent hosts to be more widespread than they appear to be. Other factors may prohibit the evolution of such specific mechanisms. For example, indirectly transmitted fish parasites often have a number of potential final hosts – such as the

wide range of piscivorous birds that are susceptible to certain helminth infections (Smyth, 1985). Piscivorous birds have a variety of foraging strategies, including diving from above (kingfishers and terns), swimming beneath the surface (cormorants and mergansers) and stalking in shallow water (herons). Specialisation to increase predation by one of these predators would probably restrict transmission to another group – and may also make fish vulnerable to non-host predators – and so be selected against.

Some directly transmitted parasites may alter host behaviour to actually reduce their hosts' risk of 'fatal' predation. Milinski (1985) showed that although sticklebacks infected with *Schistocephalus* fed closer than uninfected fish to a potentially-predatory cichlid, those individuals infected with the directly-transmitted microsporean *Glugea anomala* avoided the cichlid more than uninfected fish. Although the mechanism bringing about this behaviour change is unknown, the consequences are likely to favour this particular parasite.

2.3 Parasite location and possible mechanisms of manipulation

An important factor in the alteration of host behaviour by parasites is the site they occupy within a host. Examples of parasite presence in areas that are likely to affect anti-predator behaviour are not in themselves proof of adaptation for transmission, but can indicate systems warranting closer study. Metacercariae of diplostomatid trematodes are common, globally distributed parasites of freshwater fish that frequently migrate to the brain or eyes of their fish hosts following invasion via the skin. The occupancy of such sites probably evolved initially for protection against immune responses and stomach secretions of the final host (Szidat, 1969; Ratanarat-Brockelman, 1974; Cox, 1994), with organ impairment (and potential effects on transmission) being a side effect of potential benefit to the parasites. For example, *Diplostomum spathaceum* metacercariae grow in the lens of the eyes causing parasitic cataract and eyefluke disease (Chappell et al., 1994). However, there may be more directly adaptive explanations for small-scale site selection within organs. There is evidence that *D. spathaceum* metacercariae aggregate in areas of the lens receiving minimum illumination, when more extensive migration through the lens would result in greater damage and more severe effects on vision that may be harmful to the parasite as well as the host (Gaten, 1987).

Diplostomum phoxini metacercariae, in contrast, are found in the brain tissues of minnows (*Phoxinus phoxinus*, Cyprinidae). Within the brain, metacercariae aggregate in specific lobes concerned with vision and motor control (Barber and Crompton, 1997), sites that once damaged are likely to alter escape responses from predators, supporting the idea that behavioural alteration by this parasite may be under active selection.

Parasites have traditionally been proposed to alter the behaviour of hosts by one of two types of mechanism (Milinski, 1990). Manipulation may occur via direct mechanisms, for example by affecting the neuro-endocrine system of the host by the release of hormone or neurotransmitter analogues, or may alternatively alter host behaviour in a more indirect manner, by changing some other physiological parameter that invokes a certain behavioural response in the host. An example of indirect manipulation would be the increased feeding of fish infected with nutritionally demanding parasites such as larval cestodes, induced by the low levels of circulating nutrients in the host. However, although cases of indirect and direct manipulation of host behaviour are sometimes easily distinguished, to separate one from the other requires a level of detail regarding the host-parasite interaction that is not often understood. For instance, it is not known whether the altered swimming behaviour of cyprinid fishes harbouring heavy infections of diplostomatid trematodes is caused by physical damage to the brain itself, a build up of metabolic compounds from the parasites affecting muscle function, or the secretion of behaviour modifying chemicals. Of course the elucidation of the precise mechanisms by which infections are associated with host behaviour change would give a great deal of insight into the adaptive nature of the interaction (Poulin, 1998). Unfortunately the nature of such mechanisms has only rarely been discovered, and usually in invertebrate, and not fish, hosts (e.g. Helluy and Holmes, 1990; Maynard et al., 1996) and this remains a potentially fruitful area for new research.

3. Infection-associated changes in behaviour

Fishes perform a wide variety of behaviours over different temporal scales. On a day-to-day basis, individuals need to locate and compete for food and avoid predators; over longer time periods, they need to find mates and spawn successfully, which may require long-distance migrations or fighting over a territory or limited resources. Infections potentially affect the

ability of individuals to carry out these, and many other, behaviours.

3.1 Altered foraging behaviour

Parasites utilise energy reserves of their hosts; this is most obvious in species that undergo some visible growth or development within their fish host, but even those that encyst or apparently lay dormant use host-derived energy for the maintenance of vital functions. Energy expended by the host in maintaining parasites may be drained further if the infection increases the metabolic cost of locomotion, or is associated with an increase in energetically demanding immune function. Conversely, fishes infected with strongly debilitating parasites may exhibit markedly reduced activity levels and therefore have a lower energy requirement. Either way, the effects of parasite infection in fishes are frequently manifest as a change in energy expenditure and, subsequently, appetite and feeding behaviour. The stickleback – *Schistocephalus* system has been a valuable tool for researchers investigating the various effects parasites may have on the nutrition, behaviour and ecology of hosts. Much of our knowledge of behavioural changes in this area has come from studies of this system, which has been reviewed by Milinski (1990) and Barber and Huntingford (1995).

3.1.1 Altered time budgets

If parasitised fish have increased energy requirements there are several ways in which foraging behaviour could be modified to meet the extra demands of coping with parasite infection. Most intuitively, infected fish could modify their time budget to increase the proportion of time spent foraging. Giles (1987b) demonstrated this in three-spined sticklebacks harbouring *Schistocephalus solidus* plerocercoids. However, since increases in foraging time must be made at the expense of some other behaviour, they unbalance the presumably adaptive former time budget. In the case of sticklebacks infected with *Schistocephalus*, the increase in foraging time appears to be made at the expense of anti-predator behaviour (Giles, 1983; Milinski, 1985). Interestingly, the strategies employed by infected sticklebacks are similar to those documented for salmonids injected with a growth hormone supplement (Jönsson et al., 1998), which also increases energetic demand.

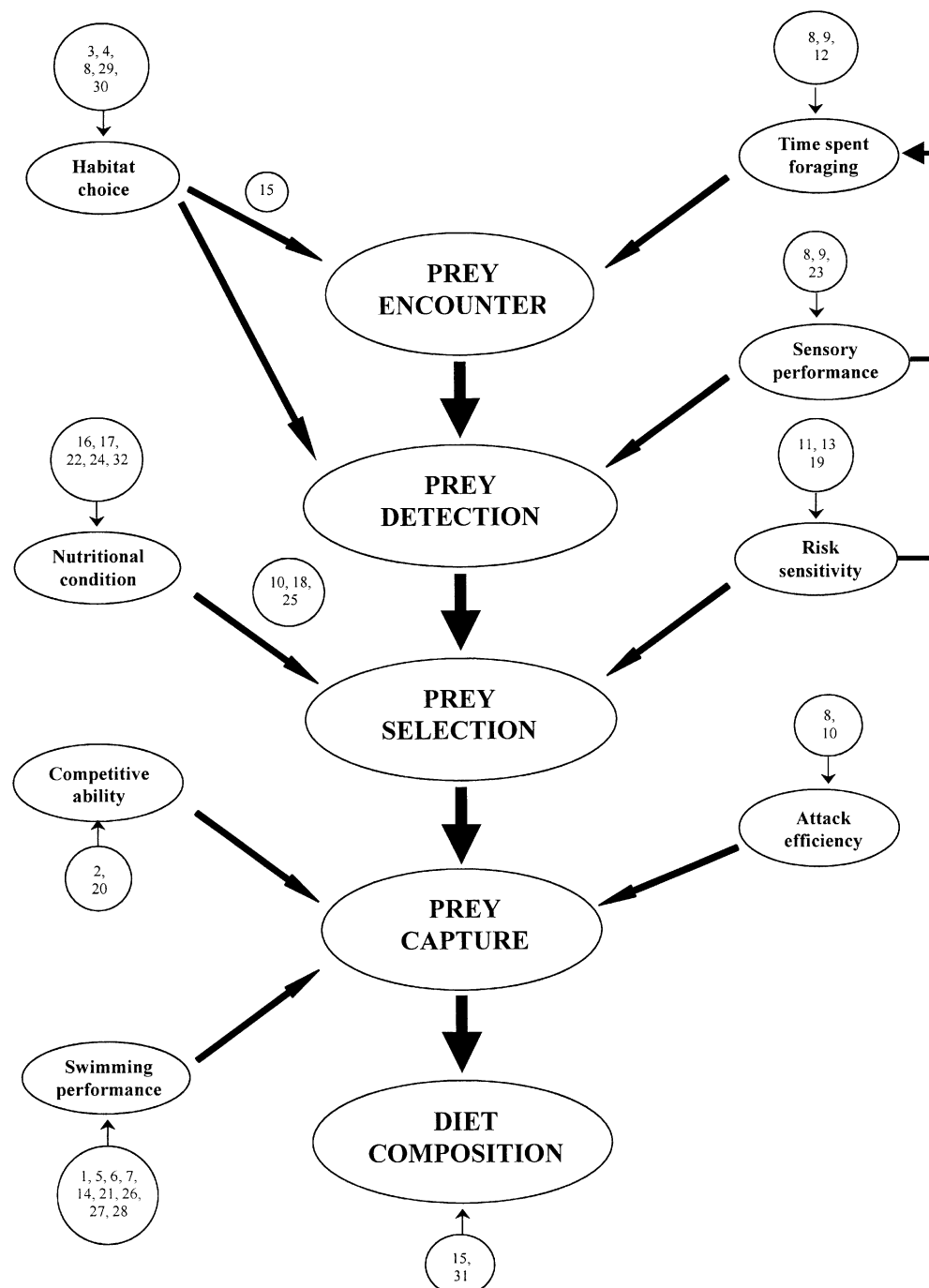
However, parasites that make only marginal demands on host energy reserves may also alter host foraging behaviour profoundly if they occupy sites

that impair the normal functioning of sensory or motor systems. Many parasites, such as trematode metacercariae, have a predilection for sites such as the brain, eye or nervous tissue, and such infections often impair sensory function (Holmes and Zohar, 1990). *D. spathaceum* infections in the eye lenses of dace (*Leuciscus leuciscus*, Cyprinidae) and sticklebacks reduce reactive distances to prey (Crowden and Broom, 1980; Owen et al., 1993) and impair foraging efficiency. Heavily infected fish therefore need to spend a greater proportion of time foraging to attain a rate of food intake equivalent to uninfected conspecifics.

3.1.2 Reduced ability to compete for food

Many fish parasites affect their hosts in ways that may impair competitive ability. The most obvious ways in which foraging ability can be constrained are through reductions in prey detection, swimming speed and manoeuvrability. For example, the *Diplostomum*-infected dace described above make a higher proportion of failed attacks whilst foraging (Crowden and Broom, 1980), which would inevitably reduce their success in competition with uninfected fish. For fish competing for food with other conspecifics the ability to move quickly to a prey item once detected is important, and Milinski (1982) showed that, among sticklebacks feeding on cladocerans, the fastest swimmer in a group obtained the most food. We may predict that the many and varied parasite infections that reduced host swimming performance (see section 3.2) should also reduce host competitiveness under such conditions.

However, there is evidence that the effects of such infections on competitive ability are rarely straightforward. Particular characteristics of the foraging habitat may interact with infection status to determine the relative success of infected individuals in natural populations. For instance, the ability of infected sticklebacks to compete for food is dependent on the type of competitive environment experienced. Infected fish in competition with an uninfected conspecific for temporally spaced food items (which generates 'contest' competition) fare better than they do if food items are presented simultaneously (which generates 'scramble' competition) (Barber and Ruxton, 1998). Whereas in the first situation poor competitors may be able to invest more heavily in competition to mediate their disability, in the second situation success depends on efficient prey handling, something infected fish are not good at (Cunningham et al., 1994).



(1) Baldwin *et al.*, 1967 (2) Barber and Ruxton 1998 (3) Bean and Winfield 1989 (4) Bean and Winfield 1992 (5) Brassard *et al.*, 1982 (6) Butler and Millemann 1971 (7) Coleman 1993 (8) Crowden and Broom 1980 (9) Crowden 1976 (10) Cunningham *et al.*, 1994 (11) Giles 1983 (12) Giles 1987 (13) Godin and Sproul 1988 (14) Harris and Wheeler (15) Jakobsen *et al.*, 1988 (16) Lemly and Esch 1984 (17) Lester 1971 (18) Milinski 1984 (19) Milinski 1985 (20) Milinski 1990 (21) Moles and Heifetz 1998 (22) Orr and Hopkins 1969 (23) Owen *et al.*, 1993 (24) Pascoe and Matthey 1977 (25) Ranta 1995 (26) Smith 1973 (27) Smith and Margolis 1970 (28) Sprengel and Luchtenberg 1991 (29) Sproston and Hartley 1941 (30) Szidat 1969 (31) Tierney 1994 (32) Walkey and Meakins 1970

Figure 1. Simplified summary flowchart documenting the foraging sequence in fishes and how parasite infection may influence foraging behaviour at each stage. Studies that have demonstrated infection-associated effects on components of foraging behaviour in fishes are shown (numbers refer to references shown at the foot of the figure), as are other uninvestigated areas of potential interest ('?').

3.1.3 Diet composition and prey selection

In a series of elegant experiments, Milinski (1984) demonstrated that where prey items differing in size were available, sticklebacks infected with *Schistocephalus* preferred lower quality items (small *Daphnia*), whereas uninfected conspecifics ingested more of the higher quality prey (large *Daphnia*). Parasitised individuals may therefore mediate their reduced competitive disability by selecting apparently sub-optimal prey items, for which there is less competition. However, the different preferences may be equally well explained by simple optimal foraging rules; since the parasite restricts prey handling and ingestion, the profitability of small items (which are more easily handled) may actually be higher for infected fish on an energetic basis (Cunningham et al., 1994). This view is supported by the analysis of diet data gathered by Jakobsen et al. (1988), who found that whereas uninfected female sticklebacks fed primarily on planktonic cladocerans, *Schistocephalus*-infected females from the same population fed mainly on benthic invertebrates. The latter may have been preferred despite their lower gross energetic value because they are easier for the debilitated fish to catch, and so offer a higher foraging return.

Tierney (1994), who studied a park pond population of sticklebacks in Scotland, provides further evidence for infection-associated differences in diet quality. Seasonal analysis of stomach contents showed that *Schistocephalus*-infected individuals fed on items of lower nutritional value during periods when food was scarce, when they also tended to have less full stomachs than uninfected fish. Given the additional energy requirements of sticklebacks infected with this parasite (Lester, 1971) the fact that hosts only secure poor quality food may mean that their foraging periods are extended even further, potentially exposing them to still higher risks of starvation or predation.

Observations of foraging behaviour in parasitised fish may be complicated by the energetic constraints of infection, and this may contribute to the contradictory results obtained from apparently similar studies. In the example cited above, Milinski (1984) found that infected sticklebacks, starved for two days prior to testing, ate more small, suboptimal sized prey than uninfected fish. Ranta (1995), however, used fish deprived of food for only four hours before testing, and his infected fish ate fewer food items but were more selective in consuming larger prey, resulting in a slightly higher energy gain. One explanation for the discrepancy is that infected individuals subject to starvation develop

a greater hunger than uninfected fish as a result of the energetic demand of supporting the *Schistocephalus* larva, and reduce their prey selectivity accordingly (see further discussion in Barber and Huntingford, 1995).

Parasites – or more correctly the risk of infection – also have the potential to alter prey selection if fish have evolved to avoid either prey items that contain infective parasite stages, or whole prey taxa, if their consumption is associated with subsequent infection. This is discussed further in section 4.1.

3.2 Altered locomotion

The swimming behaviour of fish has been studied extensively and many different aspects of swimming may be quantified (Blake, 1983; Videler, 1993). Different types of infection-associated effects on the swimming behaviour of fish hosts have been documented. Such effects can be conveniently separated into quantifiable reductions in some aspect of the swimming performance of infected fish, and increases in ‘conspicuous’ swimming behaviour, which are more difficult to measure and therefore generally take the form of descriptive or anecdotal accounts.

3.2.1 Reduced swimming performance

Parasitic infections are known to affect many aspects of host physiology that have the potential to alter locomotion (see Holmes and Zohar, 1990). Effects such as atrophy of the musculature (Sweeting, 1977) and pathology of the nervous system are likely to interfere with normal swimming movements of fish. Other, less obvious, pathology may also reduce swimming performance. The trematode *Ascocotyle pachycystis* encysts in the bulbus arteriosus of infected sheephead minnows (*Cyprinodon variegatus*, Cyprinodontidae) and obstructs blood flow, significantly decreasing the time infected fish are able to swim at their maximum sustainable velocity before becoming exhausted (Coleman, 1993). Waste products from parasites may also interfere with host physiology and reduce swimming performance. Anisakid nematodes encyst in the flesh of gadoid fish and secrete metabolic compounds (alcohols and ketones) that appear to have an anaesthetic effect on the surrounding musculature (Ackman and Gjølstad, 1975). McClelland (1995) speculates that such compounds secreted by the nematode *Pseudoterranova decipiens* may be responsible for the slow swimming speed of infected smelt (*Osmerus eperlanus*, Osmeridae) and eels

(*Anguilla anguilla*, Anguillidae) recorded by Sprenkel and Lichtenberg (1991). Since the definitive hosts of these indirectly transmitted parasites are marine mammals (phocid seals), which acquire the worms after eating infected fish, reduced swimming performance could conceivably enhance transmission.

Butler and Millemann (1971) found that the 'salmon poisoning' trematode *Nanophyetus salmonicola* had more severe effects on the swimming performance of coho salmon (*Oncorhynchus kisutch*, Salmonidae) and steelhead rainbow trout (*Oncorhynchus mykiss*, Salmonidae) smolts when water velocity was increased suddenly than when the increase was incremental. This suggests that burst-swimming performance (which is most likely to alter the outcome of predator-prey interactions) would be markedly reduced by infections. However, the importance of the behaviour change on transmission to definitive hosts (fish-eating birds and mammals) is unclear, since these changes are only apparent during the migration phase of the parasite (Holmes and Zohar, 1990).

Experimental infection studies provide the strongest evidence for infection-mediated behaviour change, and several have been undertaken to examine changes in swimming performance. Baldwin et al. (1967) infected salmonids with trematodes and reported a subsequent reduction in swimming performance. Guppies (*Poecilia reticulata*, Poeciliidae) infected with small numbers of trematode cercariae exhibit reduced activity (Brassard et al., 1982), apparently increasing their susceptibility to predation by brook trout (*Salvelinus fontinalis*, Salmonidae).

However, reduced swimming ability as a result of pathology is not confined to infection with indirectly transmitted parasites. The myxosporidian parasite *Myxobolus arcticus* significantly reduces swimming speed in infected sockeye salmon (*Oncorhynchus nerka*, Salmonidae), where transmission is not a factor (Moles and Heifetz, 1998). For parasites that use fish as definitive hosts, it is even more difficult to see an advantage in reducing host swimming performance. Nonetheless, Smith and Margolis (1970) demonstrated that sockeye salmon smolts infected with adult *Eubothrium salvelini* cestodes fatigued after swimming only 2/3rds the distance of uninfected smolts. In a later study of infection in migrating sockeye, Smith (1973) found that numbers of infected fish were concentrated towards the end of the run, probably as a result of their impaired swimming ability.

As with other behaviours, there is no reason for all parasite infections to bring about measurable changes in host swimming behaviour. Directly-transmitted nematodes inhabiting the gastro-intestinal tract of rainbow trout do not affect sustained, critical or burst swimming speed of the host under experimental conditions (Russell, 1980); this may be a result of the site inhabited, or the life cycle of the parasite (which may of course be linked). Despite thorough examination, Klein et al. (1969) could determine no effect of *Crepidostomum farionis*, an intestinal digenean trematode, on swimming in salmonids.

3.2.2 Conspicuous locomotion

Parasites that damage parts of the nervous system essential for the control of swimming behaviour may cause effects over and above simple reductions in swimming speed or stamina. Although these changes are difficult to quantify, they have frequently been described as being 'conspicuous' to human observers (and hence probably to other predators) and these, often erratic, swimming movements may be very important in determining predation pressure on hosts. For example, when the brains of European minnows (*Phoxinus phoxinus*, Cyprinidae) are invaded by large numbers of *Diplostomum phoxini* metacercariae (but not otherwise; Ashworth and Bannerman, 1927) fish exhibit 'intermittent swimming movements' (Rees, 1955). *Myxosoma cerebralis* – the protozoan causative agent of 'whirling disease', which is of economic significance in the cage aquaculture of salmonids – destroys the cartilage of the inner ear of host fish, which subsequently display erratic circular swimming movements (Uspenskaya, 1957; Kreirer and Baker, 1987; Markiw, 1992).

Heavy infections of adult and plerocercoid cestodes grossly distend the abdomens of host fish (e.g. Smith, 1973; Barber, 1997). Such changes increase cross-sectional area, flow resistance and frictional drag (Rodewald and Foster, 1998), reduce the body flexibility necessary for fast starts and are costly in terms of locomotory speed and efficiency (Blake, 1983; Videler, 1993). The 'jerky' swimming movements, characterised by increased lateral amplitude relative to swimming speed, reported from bleak (*Alburnus alburnus*, Cyprinidae) infected with *Ligula intestinalis* (Harris and Wheeler, 1974), and the 'sluggish' movements of common shiners (*Notropis cornutus*, Cyprinidae; Dence, 1958) probably result from such mechanisms. However, although infection-associated modifications in the swimming movements

(‘kinematics’) of host fish are likely to be important mechanisms in determining detection and selection by predators, this area has so far attracted little attention from researchers, and few quantitative studies have been undertaken.

3.3 Altered anti-predator behaviour

In order to contribute genes to future generations, free-living individuals need to avoid becoming prey for animals higher up the food chain before they are able to reproduce. Many of the behavioural strategies of fish – especially of small fishes that frequently fall prey to larger animals – have evolved to avoid predation. There is clearly strong selection for morphological and behavioural phenotypes that enable individuals to survive to sexual maturity and, consequently, against those that do not. As discussed in Section 2, infection-associated anti-predator behaviour of host organisms is of special interest since predation has serious, and often conflicting, fitness consequences for hosts and parasites. In this section we deal with the behavioural changes that may contribute to the patterns of predation observed in laboratory and field studies.

Just as the foraging behaviour of fish can be subdivided into separate stages and the success of infected and uninfected fishes examined under each, so can anti-predator behaviour. Fish show many behavioural adaptations to the threat of predation, and these can be separated for convenience into behaviours that have evolved to reduce the frequency of detection, those that reduce the chance a predator will attack and those that reduce the success of a predatory strike.

3.3.1 Avoiding encounter

A primary anti-predator strategy of vulnerable fish is the reduction of spatio-temporal overlap with their predators. Any of the changes to the habitat selection of parasitised individuals covered in Section 3.4 may consequently change the frequency with which hosts come into contact with their predators. Similarly, alterations to time budgets such as those detailed in Section 3.1.1, where foraging time is increased at the expense of vigilance or increased proximity to danger, may also have implications for predator avoidance. The reduced propensity for infected fish to join and remain with shoals (dealt with in Section 5 below) may also reduce predator avoidance, since groups of animals have better ability to detect predators than lone individuals. Similarly, parasites that

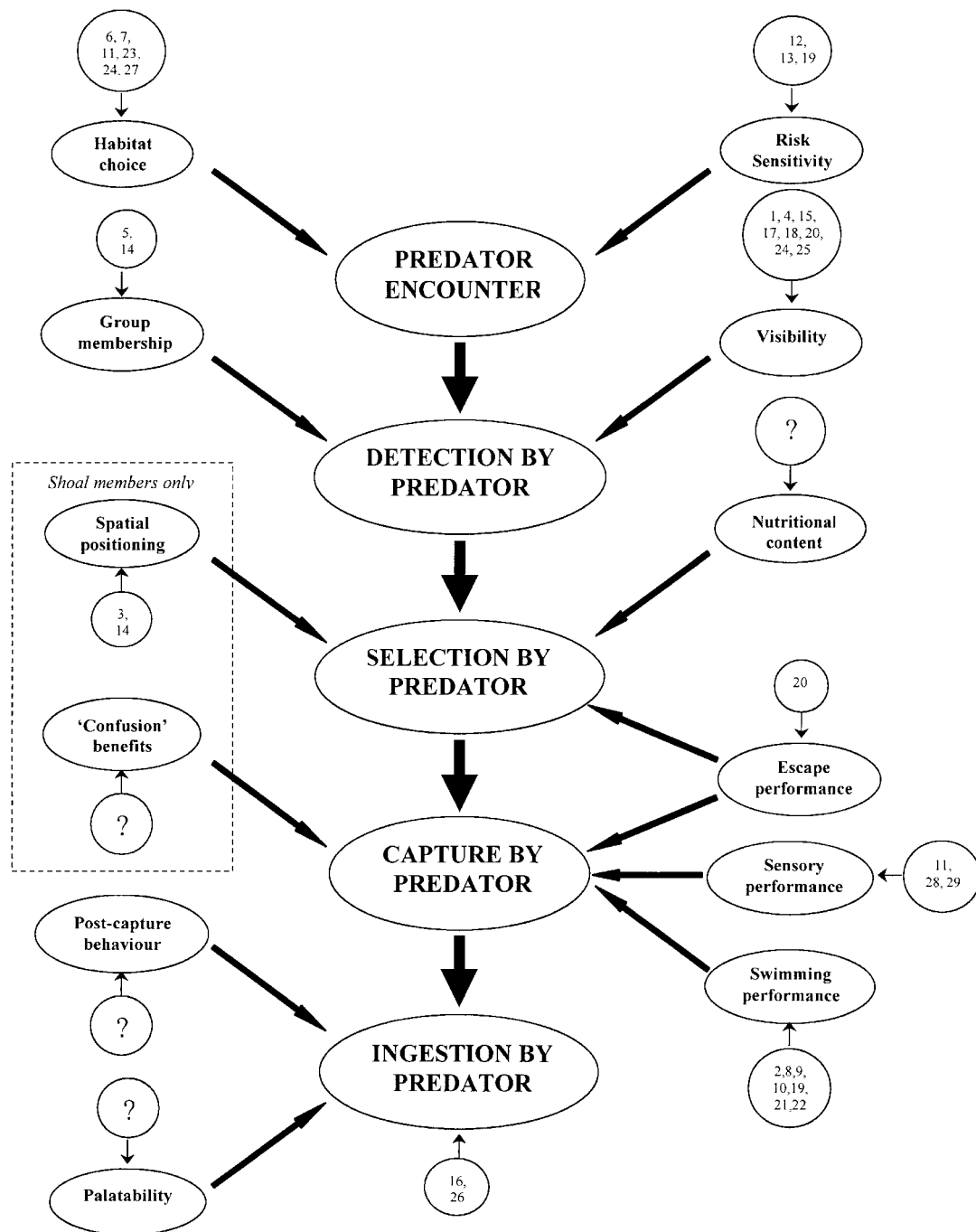
impair host sensory capability may reduce the probability that a predator will be discovered at an early stage. Some parasites seem to increase the risk taken by their hosts by increasing the time spent close to predators. Sticklebacks infected with *Schistocephalus* fed closer than uninfected fish to a potentially predatory cichlid (Milinski, 1985), and returned quicker to a food patch following disturbance by a model predator (Giles, 1987b). Godin and Sproul (1988) showed that the degree of risk taken by infected sticklebacks under such conditions was closely linked to both the size of the infection harboured and the availability of prey. Although the ecological consequences of these behaviours are unclear, similar increased risk-taking in fish given supplementary growth hormone does increase susceptibility to avian predators in the wild (Jönsson et al., 1996, 1998).

3.3.2 Avoiding detection

Even if prey fish are in spatio-temporal overlap with their predators, they are frequently adapted to avoid detection. Fishes are often cryptically coloured, patterned or counter-shaded in a way that makes it difficult for predators to detect them visually (Wootton, 1990; Bone et al., 1995). Morphological changes, such as black or white spots (Milinski, 1985; Krause and Godin, 1996), swellings (Barber, 1997) or colour changes resulting from demelanisation (LoBue and Bell, 1993; Ness and Foster, 1999) associated with infection by certain parasites may disrupt this camouflage and make host fish more visible. Odd spatial positions occupied by infected fish in compact schools (Krause and Godin, 1994a; Barber and Huntingford, 1996) may also predispose them to predation by certain types of predators. Non-visual changes may also be important, yet have received little attention in the literature. For example, it is possible that physiological changes in hosts or waste products from parasite metabolism may provide chemical cues to predators with well-developed olfactory systems. Even changes in the normal ‘sounds’ (fast pressure pulses) made by fish whilst swimming (Hawkins, 1993) may be expected if infection alters the hydrodynamics of infected fish.

3.3.3 Avoiding selection

Prey items are generally selected on the basis of their net energetic value to a predator, in other words their nutritional value after allowance has been made for capture success, handling time and digestive efficiency. If infected prey can be recognised by predat-



(1) Arme and Owen 1968 (2) Baldwin *et al.*, 1967 (3) Barber and Huntingford 1996 (4) Barber 1997 (5) Barber *et al.*, 1995 (6) Bean and Winfield 1989 (7) Bean and Winfield 1992 (8) Brassard *et al.*, 1982 (9) Butler and Millemann 1971 (10) Coleman 1993 (11) Crowden and Broom 1980 (12) Giles 1983 (13) Godin and Sproul 1988 (14) Krause and Godin 1994a (15) Krause and Godin 1996 (16) Lafferty and Morris 1996 (17) LoBue and Bell 1993 (18) Milinski 1985 (19) Moles and Heifetz 1998 (20) Ness and Foster 1999 (21) Smith and Margolis 1970 (22) Sprengel and Luchtenberg 1991 (23) Sproston and Hartley 1941 (24) Szidat 1969 (25) Tierney *et al.*, 1993 (26) van Dobben 1952 (27) Jakobsen *et al.*, 1988 (28) Crowden 1976 (29) Owen *et al.*, 1993.

Figure 2. Simplified summary flowchart documenting the sequences of predation avoidance strategies in fishes and how parasite infection may influence anti-predator behaviour at each stage. Studies that have demonstrated infection-associated effects on components of anti-predator behaviour in fishes are shown (numbers refer to references shown at the foot of the figure), as are other uninvestigated areas of potential interest ('?').

ors, they may be taken if the advantages of including them in the diet outweigh the costs. This will often depend on whether the predator is susceptible to the infections harboured by the prey, but where they are not suitable hosts infected fish may be preferred (Lafferty, 1992). Alternatively, predators may have evolved strategies for detecting and avoiding infected fish if their ingestion has serious fitness consequences.

If infections themselves are not directly detectable by predators, infection-associated behaviour may predispose infected fish to predator selection, especially when prey items are aggregated. Although being a member of a group generally provides anti-predator benefits (Hamilton, 1971), large aggregations also attract certain predators, and when these predators attack the level of protection is not shared equally amongst group members (Krause, 1994a). Individuals that 'stand out from the crowd' are particularly susceptible (e.g. Landeau and Terborgh, 1986). Infected fish may appear 'odd' for a variety of reasons, discussed above and in section 5 of this review, and it is likely that they suffer a higher predation risk than uninfected group members, although definitive experiments are needed to confirm this.

3.3.4 *Evading a predatory strike*

Once a predator attacks, fishes have various strategies to maximise their chances of escape. These escape responses may be separated into individual-level behaviours, or complex group responses. The infection-associated reductions in burst swimming speed detailed in section 3.2.1 are clearly of ecological importance here, but few studies have examined more complex escape behaviours. The kinematics of fast-start responses, fleeing to cover, freezing, or carrying out protean (unpredictable) swimming behaviour are all likely to be of importance in determining the outcome of predator-prey interactions and there is a need for studies in this area. The proficiency of parasitised individuals in complex group manoeuvres (which are an important anti-predator response of many prey fish species (Pitcher and Parrish, 1993)) is not known. However, it is likely that at least some types of parasites reduce such performance, since *L. intestinalis*-infected minnows are unable to maintain close spatial positions – which are essential for the maximisation of group synchrony (Partridge and Pitcher, 1980; Gray and Denton, 1991) – within polarised schools (Barber and Huntingford, 1996).

3.3.5 *Post-capture escape*

Many predators handle prey prior to ingestion, and this may present prey with an opportunity to undertake what has been termed a 'secondary escape', that is escaping after having been captured (Blake and Hart, 1995). Cod foraging on brown shrimp *Crangon crangon* may lose up to 75% of their prey this way (S.A. Arnott, pers. comm.), and sticklebacks caught in sampling programmes often carry scars from failed attacks (e.g. Reimchen, 1988), suggesting that post-capture escape of prey is likely to be an important, though often overlooked, ecological process. Parasites may have effects at this late stage in the predation process if they affect the type or degree of struggle shown by fish hosts following capture by predators. In addition, some fish have spines or other appendages that may be raised as an effective deterrent to ingestion (e.g. Hoogland et al., 1957; Wootton, 1990). Infections that alter the efficacy of such mechanisms could also be important in determining relative predation pressure on differentially infected fish, even in the absence of predator selection. Although these mechanisms may be important in determining precise predation pressures on uninfected and infected fish within a population, we are aware of no studies that have examined the effect of parasite infection on such behaviour.

3.3.6 *Effects of parasite infectivity and host age*

Anti-predator effects are often linked to both parasite burden and to parasite age. Studies examining the onset of 'risky' host behaviour have found that it is often associated with the parasite reaching a size at which it is transmittable, giving strong indications that those behaviours are an adaptive mechanism to increase transmission, rather than a side effect of pathology. Szidat (1969) reports that *Diplostomum mordax* metacercariae remain in the brain cavities of host pejerrey (*Basilichthys bonariensis argentinensis*, Atherinidae) without causing noticeable pathology until they reach an infective stage, when active secretions of the parasite attack brain tissues and begin to impair vision and movement. A similar relationship has been found in *Schistocephalus*, where only infective plerocercoids (those over 50 mg) affect the anti-predator behaviours of stickleback hosts (Tierney and Crompton, 1992; Tierney et al., 1993).

For fish species that undertake sequential reproductions (either long-lived annual spawners, or short-lived species with long breeding seasons and multiple spawning), infection-associated reduced anti-predator

behaviour should have a higher fitness cost for young fish (with high expected future reproductive success) than for older individuals. We therefore expect any resistance to such changes to be more marked in young individuals. In a laboratory study, Poulin (1993a) showed that negative effects of the trematode *Telogaster opisthorchis* on the anti-predator responses of upland bullies were more pronounced in 2+ and 3+ age-group fish than in 1+ fish. These results are consistent with the theory that fish with more to lose in terms of future reproductive success invest more heavily in opposing the effects of infection.

3.4 Altered habitat selection

As discussed in section 3.3.1, individuals under the threat of predation may reduce the chance of encountering predators by spending time in regions such that their distributions do not overlap. Predator avoidance is, however, only one of the criteria used by fish when making habitat selection decisions. The needs to find suitable food and, at particular times of the year, to locate mates and to spawn also determine the type of habitats required, and therefore the extent to which fish are exposed to the threat of predation. Since parasites have the potential to affect discriminatory ability, foraging behaviour and reproductive behaviour, infections are frequently associated with altered habitat selection. The presence of parasites in the environment may also alter the distribution of fish hosts if a lower level of infection can be achieved by occupying a particular type of habitat, and this is discussed in section 4.2.

Observed distributional contrasts between parasitised and non-parasitised individuals may relate to the depth of water in the habitat in which they are found, their position in the water column, avoidance of currents, preference for open water or inshore habitats, and for the presence or absence of surface or in-water cover. However it is frequently difficult to distinguish between cause and effect of the observed spatial differences. For example, do individual fish become infected with a parasite because they naturally occupy a high-risk habitat (for whatever reason), or does the parasite alter host behaviour to make them move into such areas?

3.4.1 Effects of infection on the horizontal distribution of fish hosts

Shallow inshore areas are associated with an elevated predation risk (Adams et al., 1994), yet they

offer good foraging and growing conditions, favourable O₂ levels and a light environment that is essential for courtship in certain kinds of fish. Consequently, many freshwater and marine fish undergo seasonal or diurnal migrations into and out of such areas to fulfil these vital requirements. In a study of the biological and ecological effects of *Ligula intestinalis* infection on cyprinid hosts in Lough Neagh, Northern Ireland, Bean and Winfield (1989) found that *Ligula* infection was associated with changes in the horizontal distribution of larger gudgeon (*Gobio gobio*, Cyprinidae) hosts at certain times of year. During the summer both uninfected and infected fish occupied the shallower inshore waters, and the proportion of infected fish was found to be independent of site depth. However, during the autumn, when uninfected fish moved offshore and were found in deeper water sites, infected fish were randomly distributed, and much the more common class in shallow water. The most likely explanation for this is that some infected fish, which presumably have a higher nutritional requirement, delay their autumnal offshore migration to take advantage of the high quality foraging environment offered by the inshore waters. Sproston and Hartely (1941) gave a similar explanation for their observations of disproportionately high levels of ectoparasite infections amongst individual whiting (*Merlangius merlangus*, Gadidae) and pollack (*Pollachius pollachius*, Gadidae) that delayed annual seaward migrations in an English estuary at the end of the winter. The prevalence of the ectoparasitic copepod *Lernaeocerca branchialis* amongst these “lingering” individuals was found to approach 100%, whereas typically only 10–20% of all of the overwintering population was infected. The authors suggest that the delay in migration may be a result of either chronic anaemia associated with infection or a result of a physiological response to ionic imbalance and subsequent avoidance of higher salinity water to which migrations normally are directed. Unusually for such an early study, they also suggest that the delayed migration may be adaptive for the parasite. Larvae from eggs released from adult parasites first need to infect flounders (*Platichthys flesus*, Pleuronectidae), a species that is found in the over-wintering areas, but not in the open sea. The eggs from parasites on hosts that delay their migration will therefore be deposited in shallow water, where conditions are optimal for development, and suitable hosts are abundant.

Another reason for differential habitat preferences of parasitised fishes may be a result of debil-

itated individuals selecting the optimal habitats in which to recover or recuperate from their infections. Guthrie and Kroger (1974) showed that although adult menhaden (*Brevoortia* spp., Clupeidae) captured in commercial offshore fishing waters were rarely debilitated, the vast majority of adults captured schooling with juveniles in traditional estuarine nursery areas were either injured or infected with the isopod *Olencira praegustator* or the ectoparasitic copepod *Lernaenicus radiatus*. Since even non-parasitised adults schooling with juveniles showed signs of having recovered from either injury or parasitic infection, the authors suggest that debilitated adult menhaden recuperate from their ailments by staying with and schooling with slower swimming juveniles until these schools leave the estuaries.

However, the abundance of other hosts in complex life cycles will also influence parasite distribution between habitats and populations. Coleman (1993) reports that sheepshead minnows in isolated estuarine sloughs have a high prevalence and intensity of parasites because parasites and fish are in close proximity during periods of cercarial release from snail intermediate hosts. Balling and Pfeiffer (1997) suggest that the increased occurrence of the eyefluke *Tylodelphis clavata* at certain sites within one lake may be explained by the local abundance of the final host, a heron (*Ardea cinerea*). A similar correlation has been proposed between the distribution of piscivorous birds and local levels of infection with *Schistocephalus* amongst a lacustrine stickleback population (Gilbertson, 1979). If fish occupying certain habitats or regions of a water body are more or less likely to pick up infections, observational studies alone will be insufficient to demonstrate parasite-associated habitat shifts.

3.4.2 Effects of infection on the vertical distribution of fish hosts

In Lough Neagh, large gudgeon and roach infected with *Ligula* plerocercoids were both found to swim significantly higher in the water column than uninfected conspecifics (Bean and Winfield, 1992). However, there were no differences between the horizontal and vertical distributions of smaller infected roach and gudgeon when compared with healthy individuals of the species. These results suggest that the observed distribution is more likely to be an effect of infection than a cause: one explanation could be that only fish with larger worms exhibit the behavioural modifications. Anecdotal reports suggest that in the analogous *Schistocephalus*-stickleback system, infec-

tion is similarly associated with an increase in the swimming height of host fish, with infected sticklebacks frequently being observed swimming at the water surface (Arme and Owen, 1967; Lester, 1971; Meakins and Walkey, 1975; Giles, 1983, 1987a; but see Ness and Foster, 1999). Although it has been suggested that such observations may be biased because the abdominal swelling of infected fish makes them appear higher in the water than they actually are (McPhail and Peacock, 1983), there are other reasons why infected fish might occupy upper layers of the water column. Experimental investigations suggest that infected fish may be more buoyant than uninfected conspecifics (LoBue and Bell, 1993), causing them problems when they attempt to dive. In addition, the combined effects of an increased resting metabolic rate and the greater energetic costs of locomotion suffered by infected fish may force them into surface water to exploit favourable oxygen tensions (Walkey and Meakins, 1970; Lester, 1971; Giles, 1987a).

Other parasites alter the height at which their hosts swim in the water column in different ways. Infection with the metacercariae of diplostomatid trematodes, which invade the central nervous systems and peripheral sensory organs of a wide range of fishes, is frequently associated with changes in swimming height. Fathead minnows (*Pimephales promelas*, Cyprinidae) infected with brain-dwelling *Ornithodiplostomum ptychocheilus* metacercariae swam closer to the water surface in experimental trials (Radaburgh, 1980), as did dace (*Leuciscus leuciscus*, Cyprinidae) infected with *Diplostomum spathaceum*, which inhabit the lens of the eye (Crowden and Broom, 1980). Whereas brain-dwelling parasites such as *O. ptychocheilus* are likely to alter motor control by direct interference, *D. spathaceum*-infected dace probably spend more time at the water surface, where they forage on drift items, to compensate for their reduced visual acuity (Crowden, 1976).

3.4.3 Changes in vegetation / cover preferences

Jakobsen et al. (1988) describe the change in cover preferences of three spined sticklebacks, infected with *Schistocephalus*, that occurred following the introduction of Atlantic salmon (*Salmo salar*, Salmonidae) into a Norwegian lake. The proportion of infected sticklebacks caught in traps positioned far from vegetation exceeded that of uninfected individuals during the autumn, when competition for benthic organisms (the preferred prey items in this population) was greatest. Selective predation on infected sticklebacks by the

salmon is also attributed to this change in habitat selection, which takes infected fish away from safe vegetated inshore areas and into risky exposed regions and, in their study, resulted in a dramatic reduction in the parasite prevalence in the stickleback population.

3.5 Altered sexual behaviour

Read (1990) specifies two broad mechanisms by which parasites may alter the sexual behaviour of their hosts. Firstly, many infections impair reproductive development of hosts or have other effects that prevent hosts engaging in reproduction at all, and this interference will be of benefit to the parasite if some degree of host 'castration' improves parasite growth or transmission success. Secondly, for hosts that are capable of reproduction and attempt it, parasites may have a role in determine their mating success. Infection may influence intrasexual competition for limiting resources essential to courtship, or affect sexual attractiveness, and thereby intersexual choice, in some way. Although it is indisputable that castration effects occur and are important, no consensus has yet emerged amongst studies examining the second type of mechanism, despite enormous research effort in recent years (Andersson, 1994; Hamilton and Poulin, 1997).

3.5.1 Effects of parasites on reproductive development in fishes

Energy taken in by animals that reproduce sexually can be channelled into one of three sinks: the basic maintenance of vital systems, somatic growth or sexual development. Clearly priority lies with the first system; animals must always maintain sufficient input of energy for the support of vital systems. Any extra energy input above that required for basic maintenance may therefore be used for the other two systems. Which system is the beneficiary of this extra energy depends on the age of the individual fish and the stage of reproduction (Wootton, 1990). If a fish harbours parasites, these are also likely to drain host energy reserves and may be thought of as a fourth sink into which host energy may be channelled. Whereas some parasites are probably only a minor drain on energy reserves, others that live in the gut, grow in the body cavity, or absorb nutrients from an invasive connection from the externa (such as lice etc.) probably redirect a significant proportion of host-derived nutrients.

Interference with host reproductive effort (RE) may be adaptive for the parasite, if it increases the availability of utilisable energy, or if resulting

increases in somatic growth of the host frees the parasite from deleterious predation by non-susceptible predators (see reviews by Dawkins, 1982; Barnard, 1990). Many fish parasites are associated with a reduction in host RE, and they appear to achieve this either through the energetic demand they place on their host or by the release of hormone analogues that block sexual maturation. Cyprinid fish infected with *L. intestinalis* plerocercoids do not undergo changes associated with the sexual phase, and it appears that gonad development is suppressed by modifications to the host pituitary that interferes with normal gonadal hormone production (Arme, 1968; Thompson and Kavaliers, 1994). However, the nature of such a chemical stimulus is unclear. Sticklebacks infected with *Schistocephalus* are rarely found to be reproductively active and have small gonads (Arme and Owen, 1968).

However, care must be taken when interpreting infection-associated reductions in host RE as adaptive parasitic castration. Forbes (1993) outlines various mechanisms by which it may be adaptive for hosts to reduce RE whilst infected (for example, to channel energy reserves into immune function).

3.5.2 Consequences of parasitism for courtship, mate choice and parental care

Even in systems where parasites do not interfere with host sexual behaviour through castration mechanisms, it is probable that infections reduce the sexual success of hosts in other ways, and many of these results probably have their basis in modified host behaviour. The mechanisms by which evolution may proceed through sexual selection rather than natural selection have recently received unprecedented coverage in the behavioural ecological and evolutionary literature (see review by Andersson, 1994). Parasites have been widely implicated as a force in the evolution of mate choice, and one of the most influential theories has been that provided by Hamilton and Zuk (1982). The Hamilton-Zuk (H-Z) hypothesis states that since parasites are debilitating, the level of infection should be reflected in the extent of elaboration of 'costly' secondary sexual characters, since parasitised individuals would not be able to develop such ornaments. Because the heritability of host resistance mechanisms are expected to be maintained as a result of genetic cycling with parasite virulence, then the degree of elaboration should be a reliable ('honest') indicator of an individual's infection status and – assuming exposure levels are equal – its genetic suitability to a particular environment. So females choosing males

with brightly coloured, or otherwise ornamented, traits as mates may be selecting healthy males, and possibly 'good genes' (including those for parasite resistance) for their offspring. However, there may be other, more direct, benefits associated with the avoidance and rejection of males that have high levels of infections, such as the avoidance of potentially harmful directly-transmitted contagious parasites (e.g. Hillgarth, 1996) and a reduced chance of passing viral and micro-parasites to offspring through vertical transmission. Additionally, for species that provide some level of parental care, choosy individuals may avoid selecting mates that have a reduced chance of surviving to raise (or help raise) the brood, or those that may have a reduced effectiveness as a carer for eggs or young (e.g. Møller, 1994; Haakarainen et al., 1998).

Fishes have proved popular models for the examination of the H-Z and other hypotheses in sexual selection theory, since they display a wide variety of nuptial decoration and mating systems, offer relatively short generation times, frequently display parental care and may be kept in the laboratory with relative ease. Although we do not intend to provide exhaustive coverage here, the main advances in our knowledge resulting from this research are detailed below.

In many fish species sexual selection is a two-stage process, with the chosen sex (generally males) initially competing between themselves over limited resources that are essential pre-requisites to breeding (such as nest sites). This battle for resources is termed 'intra-sexual selection' and those successful individuals are then assessed and chosen between by the choosing sex (generally females) in a process termed 'inter-sexual selection'. Infection has the potential to alter the success of hosts at both stages, though evidence for clear effects of the former is scarce. Hamilton and Poulin (1995) examined the effects of the digenean trematode parasite *Telogaster opisthorchis* on aggression and competition over nest sites in male upland bullies (*Gobiomorphus breviceps*, Eleotridae). Parasite load had no significant effect on male aggression or success in dyadic contests, nor was aggression a predictor of the likely winner of these contests. In a laboratory study examining sexual selection in sand gobies (*Pomatoschistus minutes*, Gobiidae), neither male success in competition for nest sites, nor selection by females in mate choice trials could be linked to parasite infection status, despite infection levels with six different macroparasites being quantified (Barber, unpublished ms).

If variation exists in the level of important parasites amongst the sexually active male population, females should have been selected to identify infected individuals and select against them (Andersson, 1994). But how can they detect infected males? Some infections are visible, and fish are known to base decisions about with whom to associate on visual cues (see section 5.5). Male deep-snouted pipefish (*Syngnathus typhle*, Sygnathidae) – a sex role-reversed species – avoid mating with females parasitised with the trematode *Cryptocotyle*, which induces visible black spots on the skin but is not directly contagious between fish (Rosenqvist and Johansson, 1995). Discriminating males may gain direct reproductive benefits, as heavily infected females have a lower fecundity. Milinski and Bakker's (1990) study demonstrated elegantly that female three-spined sticklebacks use male coloration to select mates, and that their preference for brighter red males reduced their chance of mating with a fish harbouring *Ichthyophthirius multifiliis* ('whitespot') infection. Kennedy et al. (1987) found the rate of display to be the important factor in determining mate choice in Trinidadian guppies, and the fact that males infected heavily with nematode and trematode parasites displayed less frequently resulted in them being selected less often by females than males with fewer parasites. Aspects of courtship dance are also important in determining the reproductive success of male sticklebacks (Rowland, 1994) and it is likely that reported changes in the size of the pectoral fins associated with various infections change various dance parameters (Brønseth and Folstad, 1997). In this way courtship dance may be acting as an 'amplifier' (*sensu* Hasson, 1990) of fin size, and hence of infection status and male quality.

Despite evidence for infection-associated mate preferences, in most cases, the fitness consequences of choosing males differing in infection status has not been quantified, and there are reasons to believe that infection-based mate choice may not always have predictable results. For example, Stott and Poulin (1996) found that parasitised upland bullies spent more, not less, time fanning eggs (i.e. provided more parental effort), possibly in an attempt to maximise survival of their current (and probably final, because of their infection status) reproductive attempt. In this way, females choosing them may have benefited from improved levels of offspring hatching.

Additionally, if parasites infect females as well as males then the selection force driving parasite-mediated sexual selection (female choice) may be

weakened, since such infections may affect the discriminatory performance of females, or reduce the effort that they invest in mate selection (Poulin and Vickery, 1996). There is experimental evidence in support of this hypothesis. In a study examining mate choice in upland bullies, Poulin (1994b) found that females infected heavily with encysted larval trematodes invested less time in mate inspection and consequently were more likely to choose lower-quality males as mates. Such mechanisms may slow down processes of sexual selection (Vickery and Poulin, 1998).

4. Parasite avoidance and infection-reducing mechanisms

The relationship between parasite and host is one of constant evolution, described classically as an 'arms race' (Dawkins and Krebs, 1979) or 'Red Queen' effect (e.g. Ridley, 1993), with both parties attempting to gain the evolutionary advantage. Selection therefore acts on hosts to resist infection and to survive to reproductive age, in order to produce as many viable offspring as possible (Poulin et al., 1994). The threat posed by the mere existence of parasites in the environment may therefore alter the behaviour of potential hosts even before they become infected. Lozano (1991) outlined mechanisms by which the threat extended by the presence of infective parasites may influence the behaviour of actual or potential fish hosts. Firstly, the avoidance of free-living parasite stages, of other individuals carrying contagious infections, or of prey harbouring potentially infective parasites may be predicted. Secondly, parasite-reducing behaviours, such as the visitation of cleaning stations or scraping the body against the substrate to remove ectoparasites or the ingestion of potential prophylactic, anti-parasitic compounds, may occur.

If infection with a specific parasite reduces host fitness because it directly affects survival, fecundity or growth, then individuals that are able to avoid becoming infected, or at least reduce infection levels, should be favoured by selection. Variation in the immune responses of hosts, which allow some individuals to either resist infection, to fight parasite invasion or substantially reduce its effects, is probably important in generating observed patterns of infection amongst populations. However, observed patterns of distribution of parasites amongst host populations may also be affected by variation in exposure to infective stages,

brought about by different host behaviour patterns. If the risk of infection is associated with the occupancy of specific habitats, the consumption of infected prey or with any particular social habits such as grouping, then by avoiding such behaviours potential hosts may prevent, or at least reduce, their chances of becoming infected. Such 'behavioural resistance' (*sensu*; Wedekind and Milinski, 1996) is therefore the first line of defence in countering parasite invasion (Nelson et al., 1975) and should reduce the demands on the immune system (Hart, 1994). Behavioural resistance can evolve if the costs of its employment are less than the costs associated with infection to overall reproductive success (Minchella, 1985; Keymer and Read, 1991). Hart (1990) outlined the major types of behavioural resistance, which he separated into two functional groups; (1) the avoidance, repelling or removal of parasites and (2) preferences for mates with low levels of parasite infections. Both types of behavioural resistance have been examined in teleost fishes.

4.1 Avoidance of infected prey

In natural habitats, which present animals with a range of potential prey items, individual foragers are expected to select an optimal diet – that is one composed of items that yield the best nutritional return for the effort expended to locate, acquire, handle and digest them (Stephens and Krebs, 1986). Whether or not the avoidance of either individual infected prey items, or of whole taxa that frequently harbour infective parasite stages, is a feasible evolutionary option will therefore depend on many factors. Especially important are the prevalence of the infection in the prey population, how infection alters prey conspicuousness, escape ability (for motile prey) and nutritional value and also the cost of infection to the potential host (Wedekind and Milinski, 1996). If the fitness cost of infection is negligible, yet prey items containing infective parasites are much easier to catch (because they are more easily detected, or have impaired escape responses) and have equivalent nutritional value to uninfected prey, then avoidance is unlikely to evolve, and such prey may even be preferred (Lafferty, 1992). If infection has either more severe effects on subsequent survival or, for instance, reduces the nutritional value of the prey item sufficiently, then selective foraging on uninfected individuals is predicted (Wedekind and Milinski, 1996). However, a proviso must also be added: foraging predators must also be able to recognise parasitised prey if they are to avoid them. Experimental evid-

ence so far has not been supportive. No evidence for avoidance of infected individuals has been found in two experimental tests of behavioural resistance using sticklebacks feeding on copepods infected with larval cestodes (Urdal et al., 1995; Wedekind and Milinski, 1996). The fact that in one study increased predation on them was recorded (Wedekind and Milinski, 1996) suggests that the impaired escape responses of infected copepods (Urdal et al., 1995; Pasternak et al., 1995; Wedekind and Milinski, 1996) may instead facilitate transmission.

4.2 Avoidance of habitats associated with infection risk

Certain microhabitats may be associated with a higher risk of infection than others, and if they can be avoided, hosts may benefit in terms of reduced exposure to parasites. Poulin and FitzGerald (1988) investigated daily fluctuations in the extent of infection with the mobile ectoparasitic crustacean *Argulus canadensis* amongst juvenile three-spined and black-spotted sticklebacks (*Gasterosteus wheatlandi*, Gasterosteidae) in estuarine tide pools in Canada. Both species harboured twice as many of these parasites in the afternoons (when water temperatures were higher and fish swam close to the substrate) as they did in the mornings (when water temperatures were lower and fish swam close to the surface). The authors also demonstrated that water temperature itself did not influence the success of parasite attacks. Their results suggest that diurnal changes in stickleback distribution, brought about by daily fluctuations in water temperature and oxygen tensions, probably cause the observed temporal patterns of infection. In a subsequent laboratory study, Poulin and Fitzgerald (1989c) demonstrated that proximity to both substrate and vegetation is important in determining infection levels, and also that – when freed from the tide pool environmental regime – sticklebacks may change habitat preferences to avoid parasites. Juvenile three-spined and blackspotted sticklebacks preferred to swim close to the bottom of the tank when there were no *Argulus* present, but began swimming at the surface (away from the substratum) and reduced their preference for vegetation when parasites were added.

Parasite infections that are transmitted directly between fish hosts may be effectively avoided through more direct, discriminatory mechanisms, such as shoal choice and mate selection. In addition, shoaling may also provide protection against certain types of para-

sites that act as predators (e.g. Poulin and FitzGerald, 1989a). These mechanisms of infection avoidance are examined in the relevant sections elsewhere in this review (Sections 3.5.2 and 5).

4.3 Infection reduction behaviours

Even after infections have been acquired, fish may still be able to reduce their impact or severity by performing certain types of behaviour. A simple behavioural response to ectoparasite infection is observed both in wild fish populations and in farmed aquaculture species, in which infected individuals attempt to remove parasites by scraping their body against the available substrate (e.g. Urawa, 1992). In natural populations this ‘flashing’ behaviour is highly visible and is likely to increase predation risk, whereas in aquaculture damage caused by scraping against nets may both facilitate the development of secondary infections and severely reduce product marketability. Perhaps the best known infection-reducing mechanism, however, is the visitation of cleaning stations in tropical reef systems, where station-holding species pick ectoparasites and necrotic tissue from the surfaces of client fish (Gorlick et al., 1978; Poulin, 1993b). Recent interest in the use of wrasses (Labridae) and other proposed cleaner species as a non-chemical parasite-control strategy in both temperate (Costello, 1996) and tropical aquaculture (Cowell et al., 1993) has renewed interest in this field. However, while these so-called ‘cleaning symbioses’ are regular textbook examples of highly evolved, mutually beneficial interspecific interactions, there are major gaps in our understanding of their evolution and current adaptive value (Poulin and Grutter, 1996). In particular, recent research has questioned the value of cleaning stations for the reduction of infections. It is now unclear whether the visitation of cleaning stations is actually beneficial for the host in terms of reducing infection load (e.g. Grutter, 1996), and ultimately whether such interactions are truly mutualistic, or are actually rather more one-sided ‘parasitic’ interactions themselves.

Other mechanisms have been suggested by which fish may exhibit resistance or ‘self-cure’ from parasite infections. Lozano (1991) suggested that animals might forage selectively on specific foods to protect themselves against parasites, by eating prophylactic food items, and also rid themselves of parasites by eating anti-parasitic food items. Although we are aware of no specific examples in fishes, birds are known to use similar mechanisms; starlings (*Sturnus*

vulgaris) line their nests with particular herbaceous plants that appear to improve the ability of nestlings to withstand parasitic infections (Gwinner et al., 2000). An interesting current debate is in the value of carotenoid pigments in providing protection against parasitic and other diseases. These compounds – which need to be taken in the diet yet have no nutritional value – are the precursors of Vitamin A and have both antioxidant and immunostimulant properties in fishes (e.g. Christiansen et al., 1995), making them of considerable interest. They are also the group of compounds primarily responsible for sexual coloration in fish, and there is evidence that in male Arctic charr (*Salvelinus alpinus*, Salmonidae) the intensity of sexual coloration co-varies with immune status (Skarstein and Folstad, 1996). Although it is likely that carotenoid-based signals in fishes indicate some aspect of infection status or immune capacity (Folstad and Karter, 1992), the mechanisms by which they may do so are likely to be complex and are so far unclear (Olsen and Owens, 1998).

5. The influence of parasites on shoaling behaviour: a case study in parasite-associated behaviour change

Many teleost fish form loose aggregations ('shoals') or more polarised swimming groups ('schools') under certain circumstances, and the costs and benefits of group membership in fish have been widely studied (reviewed in Pitcher and Parrish, 1993). The most important factors regulating the composition of fish shoals are considered to be foraging efficiency and predation risk (Pitcher and Parrish, 1993), and these are dependent not only on the number of individuals in the group, but also on individual traits such as size (Krause and Godin, 1994b; Krause et al., 1996; Ranta et al., 1992), competitive ability (Krause, 1994b) and hunger state (Krause, 1993; Reeb and Saulnier, 1997; van Havre and Fitzgerald, 1988). Since parasitism may be expected to alter many of these traits (see section 3), infections may have important consequences for individual fish as members of shoaling groups. In addition, fish (regardless of their infection status) may behave differently in the presence of parasites. Any such changes may alter the dynamics of group membership; yet understanding the exact nature of these effects requires a close consideration of different types of host-parasite systems. In particular it is essential to realise the importance of the mode of transmission

of the parasite when interpreting infection-associated changes in shoaling behaviour.

5.1 Mode of parasite transmission and host shoaling behaviour

Increased opportunity for transmission of parasites that have direct life cycles has been cited as a common cost of group living (Alexander, 1974) and positive correlations between infection with such parasites and group size have been shown for birds and mammals (Brown and Brown, 1986; Hoogland, 1979; Moore et al., 1988; Poulin, 1991b). However, the evidence for a similar relationship in fishes is less compelling. Poulin (1991a) found no evidence that shoaling freshwater species in Canada had a higher richness of parasite fauna, for either contagious ectoparasites or other types of parasite. A reanalysis of this data by Ranta (1992) found that, for some groups of parasites, solitary host species harboured significantly lower parasite diversity than shoaling host species, but this pattern did not hold for directly transmitted parasites. Shoaling may still have costs arising from increased parasite transmission, but they are presumably generally outweighed by the benefits of group living for some species. When these costs become significant they may constrain group size or influence the shoaling decisions of individuals, and there is some evidence that this does occur.

The transmission of contagious parasites is facilitated by close proximity between hosts. If infection reduces host fitness we may expect active avoidance behaviours to evolve, if the mechanisms required to detect and avoid parasitised individuals are not themselves too costly. Individual juvenile three-spined sticklebacks avoid schools of conspecifics carrying the contagious ectoparasite *Argulus canadensis*, and prefer to shoal with uninfected fish (Dugatkin et al., 1994). *Argulus* has been shown to reduce growth and increase mortality of infected sticklebacks (Poulin and Fitzgerald, 1987), and if individual fish regularly have a choice between joining different groups, the ability to recognise and avoid parasitised shoals may be an important factor in decision making. This example also illustrates the difficulty of trying to make broad classifications of parasite types; although *Argulus* is capable of being transferred directly between hosts, it can also rest on the substrate and attack passing fish much in the same way as a sit-and-wait predator. Grouping is often an effective strategy against this latter strategy; for example increasing shoal size

lowers the risk of infection by reducing the average number of parasite attacks per stickleback (Poulin and Fitzgerald, 1989a). In the laboratory sticklebacks form larger shoals when exposed to the parasite, suggesting that shoaling can be an effective anti-parasite mechanism in this case. Grouping as a response to parasites is also seen in mammals, where an increase in group size results in fewer attacks by biting flies, (Freeland, 1977; Rubenstein and Hohmann, 1989; Mooring and Hart, 1992). Other examples show that group living can confer other, indirect, advantages with regard to infection reduction. In the bluegill sunfish, colonial nests are less prone to infection with fungus than are solitary nests (Cote and Gross, 1993). Colonial males are able to spend more time engaged in egg fanning, which reduces infection, and grouping may also 'dilute' the risk from fungal spores, lowering the encounter rate for individual nests.

Two prerequisites for the evolution of avoidance of parasitised fish are that infection with the parasite constitutes a significant cost, and that other fish can readily identify infected individuals. Monogenean parasites of the genus *Gyrodactylus*, which are widespread on marine and freshwater fish, are directly contagious between hosts, and infections can result in severe pathology and even death (Cusack and Cone, 1986; Lester and Adams, 1974). Anecdotal evidence suggests that detection of this parasite may be a limiting factor in the evolution of discrimination. Scott (1985) observed that for guppies with the ectoparasite *Gyrodactylus bullatarudis* "heavily infected fish become lethargic and the fin rays often stick together resulting in abnormal swimming behaviour. Such differences do attract the attention of other guppies and do increase the number of contacts". Uninfected fish do not show the avoidance behaviour we might expect given the possible consequences of infection. This may in part be due to the fact that the parasite itself is not conspicuous. The behaviour of infected fish may also not be a reliable or specific indicator of infection status of the sort that gives rise to discrimination responses. Thus healthy fish may approach individuals showing unusual behaviours to gain more information on their condition and assess their value as shoal mates.

While the risk of infection seems an obvious and direct cost of shoaling with fish carrying contagious parasites, the costs and benefits of shoaling are less readily predictable if parasites have complex, or indirect, life cycles. Such parasites are not transmitted between fish, but the effects they have on parasitised

individuals, which often include altered foraging and anti-predator behaviour (section 3), may translate into indirect costs of association for uninfected shoal-mates. Here we outline the ways in which parasitism can potentially affect shoal membership (and hence group composition) and then review the shoaling decisions that have been documented to date.

5.2 *The costs and benefits of association for and with parasitised fish*

5.2.1 *Competition*

Competition for food within a shoal is likely to be altered by the presence of parasitised individuals. Shoaling fish locate patchy food sources faster than individuals, but are then subject to competition from other members of the group when feeding (Pitcher and Parrish, 1993). Individuals vary in their competitive ability, however, and Metcalfe and Thomson (1995) have shown that European minnows can recognise poor competitors and prefer to shoal with them. If parasitism reduces the ability of hosts to compete for food (as discussed in section 3 above), healthy fish may benefit from associating with and exploiting such fish in competitive foraging situations, provided that the costs of association are not too high. However, parasitised individuals may often be poor at detecting food, thus not increasing the encounter probability with food for other group members in the first place. In addition, parasitised fish also make decisions about shoal membership, and if their food intake is severely reduced, fish infected with nutritionally demanding parasites such as *Schistocephalus* (Pascoe and Matthey, 1977) may do better to leave shoals and forage on their own. *Schistocephalus*-infected three-spined sticklebacks have a reduced shoaling tendency even when satiated (Barber et al., 1995). Shoaling will only be profitable for parasitised individuals if the costs of competitive interactions are outweighed by the anti-predator benefits of being in a group.

5.2.2 *Predation*

Predation is often cited as a major force driving the evolution of shoaling behaviour, and the benefits of reduced predation for individual fish within shoals have been reviewed by a number of authors (see Magurran, 1990; Pitcher and Parrish, 1993). Individuals spend more time foraging with increasing shoal size, which appears to be related to higher levels of vigilance in larger shoals. Shoaling fish may also benefit from a reduced *per capita* risk of predation

The reported effects on vision associated with even low levels of infection with the lens-dwelling metacercariae of trematode parasites such as *Diplostomum* spp. (Crowden and Broom, 1980; Owen et al., 1993) are not only likely to reduce vigilance, but may impair the ability of parasitised fish to shoal closely and evade predator attacks. Radabaugh (1980) demonstrated that fish parasitised with *Ornithodiplostomum* sp. formed less compact shoals that were divided more frequently than uninfected shoals. Shoal cohesion has been positively correlated with survival time in interactions with predatory pike (*Esox lucius*, Esocidae; Mathis and Smith, 1993), and parasitised fish may increase the vulnerability to predation of uninfected shoal-mates by compromising anti-predator evasion behaviour. Furthermore it has been shown that phenotypically odd individuals reduce the predator confusion effect of the entire group thus putting not only themselves, but all shoal members, at a higher risk (Landeau and Terborgh, 1986). The latter has, however, only been described for differently coloured fish and remains to be tested for a species in which strong parasite-associated phenotypic changes occur.

The impaired swimming behaviours discussed in section 3.2 above are likely to increase the predation susceptibility of infected fish. There are also examples of parasites that seem to act directly on anti-predator behaviour. Szidat (1969) reported very conspicuous ‘tumbling’ behaviour at the water surface in pejerrey (*Basilichthys* sp.) infected with *Austrodiplostomum mordax*, an extreme case of behavioural alteration that seems very likely to increase predation of infected fish. *Ligula intestinalis* is a common cestode parasite in cyprinid fishes (Kennedy, 1974) that has been shown to alter the spatial positioning of infected European minnows in polarised schools (Barber and Huntingford, 1996). Parasitised fish occupied peripheral positions more often than expected and exhibited increased nearest neighbour distances. Given that *Ligula* infection also results in a marked distension of the body (Arme and Owen, 1968), infected fish are expected to be more susceptible to predation as a result of oddity and deviant positioning within the school. Other parasites such as *Psilostomum* sp. encyst in and damage the lateral line (Beaver, 1939) – an organ that is important in detecting objects and in schooling in particular (Bleckmann, 1993) – and these infections potentially reduce host ability to form cohesive schools and participate in co-ordinated group manoeuvres.

5.3 Shoaling preferences

The effects of *Schistocephalus solidus* on the behaviour of its intermediate host the three spined stickleback, *Gasterosteus aculeatus*, have been well documented (Milinski, 1990; Barber and Huntingford, 1995). This pseudophyllidean cestode grows in the body cavity of the fish and completes its life cycle when eaten by its avian definitive host. In the stickleback the parasite may grow to an enormous size, in some cases weighing as much as the host (Arme and Owen, 1967), and this results in a gross distension of the abdominal cavity. This distension is particularly visible from above, increasing the dorsal profile of the host (Barber, 1997) and presenting parts of the pale ventral surface, and may make parasitised individuals stand out as ‘odd’ in a group of unparasitised sticklebacks. Some populations show other phenotypic differences as a result of infection, such as reduced pigmentation (LoBue and Bell, 1993), which is also associated with decreased anti-predator responses (Ness and Foster, 1999). Infected sticklebacks also show reductions in specific anti-predator behaviour, swimming shorter distances and returning to feed sooner than uninfected fish after a simulated predatory attack (Giles, 1987b; Godin and Sproul, 1988). It appears that energetic demands and reduced competitive ability force parasitised fish to take greater risks of predation which alter their shoaling behaviour (Barber et al., 1995).

Infected sticklebacks may reduce the anti-predator benefits of shoaling through lower vigilance and greater risk taking, as well as reducing the phenotypic uniformity of the shoal, and recent evidence shows that these factors may be important to fish making shoaling decisions. In laboratory tests, uninfected sticklebacks given a choice of joining two equal-sized shoals preferred to associate with uninfected conspecifics over *Schistocephalus*-infected fish (Barber et al., 1998). Test fish were from a population with no prior experience of the parasite and thus lacked information about relative competitive ability and behaviour of parasitised fish. Therefore preferences should have been solely based on the minimisation of oddity using morphological cues. When the size of the infected shoal was increased to three times that of the uninfected shoal, however, test fish preferred to join the larger group. In large shoals the number of fish may swamp phenotypic differences, reducing the importance of oddity effects. Alternatively, the anti-predator benefits afforded by a large number of fish may simply

outweigh the disadvantages of associating with parasitised individuals.

The influence of parasitism on shoal choice has been investigated in one other host-parasite system. The banded killifish (*Fundulus diaphanous*, Cyprinodontidae) is an intermediate host of the digenean trematode *Crassiphiala bulboglossa*, and parasitised fish show altered anti-predator behaviours similar to those of the sticklebacks discussed above. Transmission of the parasite to its definitive avian host, the belted kingfisher (*Megaceryle alcyon*), requires predation on infected killifish, which spend less time shoaling, occupy peripheral shoal positions more often than uninfected fish and show reduced responses to a simulated predator (Krause and Godin, 1994a). Infected fish can be identified by the presence of black spots visible on the skin, as a result of parasite encystment. Both parasitised and unparasitised killifish prefer to shoal with unparasitised stimulus shoals, if those shoals are phenotypically uniform (Krause and Godin, 1996). Test fish did not prefer unparasitised shoals over mixed shoals of parasitised and unparasitised fish, but did demonstrate a significant preference for shoals containing a single parasitised fish. This gives rise to the interesting suggestion that a parasitised fish in a shoal may be more vulnerable to predator attack as a result of the oddity effect, and that this could increase the chances of survival for the uninfected shoal members. The costs and benefits of shoaling in mixed-phenotype groups are likely to change with the ratio of phenotypes (see discussion of confusion effect above), and this complex area is worthy of further research.

5.4 Recognition of parasitised individuals

A prerequisite for the evolution of partner choice and the discrimination of parasitised fish is the ability to reliably identify and react to parasitised individuals. A number of studies have shown that fish have the sensory ability and cognitive skills to discriminate amongst conspecifics based on a variety of cues. There is now good evidence that some species prefer to shoal with similar sized conspecifics (Pitcher and Parrish, 1993; Ranta et al., 1992). Fish are also able to recognise and make choices about shoaling partners on the basis of prior experience. European minnows prefer to shoal with poor competitors, (Metcalf and Thomson, 1995) and sticklebacks choose particular partners during predator inspection based on their behaviour during earlier encounters (Milinski et al., 1990). In addition,

fish can recognise familiar conspecifics (Brown and Colgan, 1986; Magurran et al., 1994) and even unfamiliar kin (van Havre and Fitzgerald, 1988; Fitzgerald and Morissette, 1992).

Although olfactory cues have been shown to be important in some shoaling preferences (Brown and Smith, 1994), there is as yet no evidence that fish use them in the detection of parasitised conspecifics. Dugatkin et al. (1994) found that the presence of the ectoparasite *Argulus* alone did not elicit an avoidance reaction in sticklebacks, but that it was some combination of the parasite and its infected host that caused discrimination. This suggests that, in this case at least, fish are reacting to the effect of the parasite on its host rather than to chemical cues from the parasite itself. It was noted that "parasitised fish swam in an erratic fashion", and although in many cases these effects remain to be quantified, the fact that such altered behaviours are apparently widespread provides a potential cue to parasite presence for fish making shoaling decisions.

Visual signals are important in shoal formation (Guthrie and Muntz, 1993), and discrimination based on visually conspicuous parasites has been demonstrated (see also mate choice based on cues from visible parasites in section 3.5.2). Magurran et al. (1994) showed that female guppies can distinguish familiar shoal mates using only visual information, apparently from subtle morphological or behavioural cues. It would be surprising therefore if fish were not able to identify parasitised conspecifics given the often striking morphology of infected individuals. In cases where discrimination of parasitised fish has been demonstrated, visual and morphological cues appear to be most important. Barber et al. (1998) used fish with no experience of parasitised individuals to show that sticklebacks could identify conspecifics infected with *Schistocephalus* solely on immediate morphological cues (probably abdominal distension), without recourse to learned information on the behaviour of parasitised fish. Krause and Godin (1996) injected black ink into the epidermis of killifish to simulate the metacercarial cysts of *Crassiphiala bulboglossa*. Test fish showed a significant preference for shoaling with unparasitised fish sham-injected with water rather than those marked with black ink spots. This suggests that killifish use the presence of black spots as a direct visual cue indicating parasitism in conspecifics, although it does not preclude the use of additional cues, such as behaviour, under natural conditions. Furthermore, test fish presented with parasitised indi-

viduals increased their shoaling preference for unparasitised individuals with increasing parasite load in stimulus fish, possibly because parasite status became easier to detect.

Fish could also use general body condition as a guide to the infection status of shoal mates: Lemly and Esch (1984) found that body condition of juvenile bluegill sunfish was negatively correlated with the intensity of parasitism by the trematode *Uvulifer ambloplitis*. Condition factor, however, may vary with other factors such as food availability, and will not be a specific indicator of parasite presence. Indeed, low body condition is not necessarily a result of parasitism although fish that are already in poor condition due to other factors may be more susceptible to infection. Assessments of length-weight relationships will also be unreliable in cases where the parasite constitutes a significant mass, in *Schistocephalus* infections for example (Arme and Owen, 1967).

An interesting problem that arises during investigations of shoal choice is the consideration of how much information fish have regarding their own condition; specifically, do fish 'know' that they are parasitised? If shoaling choices are driven by predation pressure, and fish join groups on the basis of minimising phenotypic oddity, a parasitised fish carrying a conspicuous mark on its flank may actually *increase* its risk of predation by joining a group of unparasitised, 'unmarked' individuals. Krause and Godin (1996) found that parasitised killifish chose to shoal with unparasitised conspecifics despite their resultant oddity. The observation that fish may apparently make erroneous decisions that do not appear to maximise their fitness suggests that a fish's knowledge of its infection status may be limited. Yet it is still an intriguing question. Similarly, despite several studies demonstrating that fish know what size they are and choose to associate with groups best matching their own length (e.g. Ranta et al., 1992), it is still not fully understood quite how a fish is able to compare its own body size with that of conspecifics.

5.5 Parasite-assortative shoaling under natural conditions

The effects of parasitism observed in various fishes under laboratory conditions may have important consequences for natural shoals. Fish in the laboratory show preferences for associating with fish of similar body size (Krause and Godin, 1994b; Ranta et al., 1992), and evidence suggests that free-ranging

shoals may often be size-assorted, possibly as a result of differential swimming speeds and/or active shoal choice (Krause et al., 1996, 1998; Svensson et al., 2000). Similarly, reduced swimming ability, selective predation or active shoal choice may give rise to parasite-assortative shoaling in the wild.

Positive correlations have been found between group size and the prevalence and intensity of contagious parasites across animal groups (Cote and Poulin, 1995), but there is as yet no good evidence that fish species pay a similar cost of grouping. Mobile ectoparasites can stimulate fish to form larger groups under laboratory conditions (Poulin and Fitzgerald, 1989a), and may play an important role in habitat choice and community structure, especially where parasites affect different host species to varying degrees (see Poulin and Fitzgerald, 1987, 1988). Assortative shoaling may arise simply as a side-effect of pathology: injured menhaden (*Brevoortia* spp.) or those carrying ectoparasites tend to be found in estuarine nursery areas associated with juvenile shoals, while adults caught offshore are rarely infected (Guthrie and Kroger, 1974), possibly because debilitated fish remain with slower swimming juveniles to recuperate.

In experimental trials, unparasitised fish preferred to associate with healthy conspecifics but so did parasitised individuals (Krause and Godin, 1996). Therefore the occurrence of parasite-assorted shoals in the field probably depends on other factors constraining choice behaviour (such as differential swimming speeds in parasitised and unparasitised fish). Detailed analyses of shoal composition in the wild (Hoare et al., 2000) have revealed that a complex suite of pressures including parasitism shape the formation of natural killifish shoals. The parasite *Crassiphiala bulboglossa* was not randomly distributed between groups, with shoals assorted by both parasite load and parasite prevalence. *C. bulboglossa* has an indirect life cycle, so the observed pattern is not due to direct transmission of parasites. Instead it appears that active shoal choice with regard to parasitism (Krause and Godin, 1996) is responsible for structuring free-ranging fish shoals in this example. For parasites with indirect life cycles, prevalence and intensity of infection in one host depend upon transmission rates in other hosts, and correlations between parasite levels and group size are likely to be weak (Cote and Poulin, 1995). The results of Hoare et al. (2000) support this prediction, finding no strong relationship between shoal size and either parasite load or prevalence.

Parasitism is only one of the factors influencing shoal formation, and it may be outweighed by other considerations depending upon the severity of the infection. In shoals that contain heterotypic phenotypes (e.g. size or species based differences) foraging considerations may be stronger than predation factors in selecting for assortiveness (Krause et al., 1998). Parasite-assorted shoals may also arise for reasons other than active shoal choice. The way in which fish become infected can affect parasite distribution within and between shoals. Mobile ectoparasites often exhibit aggregated distributions in which a few fish are heavily parasitised and most fish harbour few parasites. Poulin and Fitzgerald (1989c) showed that sticklebacks infected with a single *Argulus* parasite were more likely to acquire further parasites than uninfected fish. Positioning within shoals is also likely to be related to parasitism, but it may be difficult to separate cause and effect in such instances. Parasitised fish may take up positions on the periphery of shoals to take advantage of foraging benefits if parasitism increases energetic demand or reduces competitive ability. However, edge individuals may be more exposed to certain types of mobile parasites that act like predators than those in the centre (Krause, 1994a; Mooring and Hart, 1992). In contrast, if anti-parasitism is the main function of grouping, *per capita* parasitism rates should not exceed those of solitary individuals.

Parasite assortative shoaling and altered behaviour in parasitised individuals could result in a sampling bias that must be considered in studies of fish distribution and shoal composition even if parasitism is not an explicit concern. For example, seine nets catch significantly more fish infected with *Schistocephalus* than minnow traps (Reimchen, 1982), and trout infected with *Diplostomum* spp. are under-represented in angling catches (Moody and Gaten, 1982). If parasitism increases susceptibility of fish to predation, it may also make infected fish more likely to be sampled by humans.

6. Conclusions and directions for future research

In our review, we have attempted to present the current status of knowledge regarding the influence of parasite infections on fish behaviour, its possible evolutionary basis and ecological consequences. The area of research is one of interest to both evolutionary and behavioural ecologists, who frequently use fish as models because they are convenient vertebrates to

study, and to fish biologists with either species-based or ecological interests. As such the research described has often approached the relevant issues from disparate viewpoints, and it is possible, even likely, that studies by one group of researchers have been missed by researchers in other fields – we of course may also be guilty here. From the studies we review, it is clear that while parasites have effects on the behaviour of fish hosts, there are large gaps in our understanding of the mechanistic basis of these behavioural modifications. Even less is known about their importance in ecological processes and with respect to how, or even whether, these changes have ecological consequences in terms of the survival and fitness of hosts or of parasites. Below we have summarised the main areas we believe will be most productive and useful in developing our understanding of these fascinating, complex and ecologically important systems.

Mechanisms of behavioural change

Currently little is known about the causal mechanisms of proposed parasite-manipulation of host behaviour in fishes. There is a clear need to examine infection-associated behaviour change in light of detailed knowledge of the mechanisms that bring them about. The adoption of an interdisciplinary approach is probably prerequisite to the realisation of these goals.

Parasite increased trophic transmission (PITT)

Although recent studies have begun to examine predation by susceptible hosts on infected fish there is a need for more definitive tests of the increased transmission hypothesis in natural habitats, which have a variety of predators (many of which are non-susceptible). Experiments to investigate predation by definitive hosts and non-host predators are still required in most systems where fish are the intermediate hosts. There are both ethical and scientific difficulties associated with examining the consequences of these behavioural changes in terms of increased mortality or susceptibility to predators, and as yet few studies have demonstrated experimentally the effects of altered behaviour on predation. Even where parasite infections are associated with increased predation by hosts, there is scant evidence linking this increased predation directly with specific behaviour patterns, and in many cases other correlates of infection (e.g. non-visual cues) cannot be ruled out. In the future the use of video / computer imaging techniques may make it possible to examine the effect of behaviour

change alone. In addition, many of the studies regarding PITT have given conflicting evidence, and it may be that more attention needs to be paid to the type of host-parasite systems examined. It is likely that there are good reasons why parasites may not always be associated with behaviour change, or even why they change behaviour in ways that have opposite host fitness consequences to those predicted.

Ecological consequences of infection-associated behaviour change

Do changes in host behaviour observed in the laboratory translate into larger scale changes in host ecology in natural habitats? We have reviewed a large body of work regarding the effects of parasites on various behaviours, yet the majority of these studies have been undertaken in the laboratory under controlled (yet essentially unnatural) conditions. So far we have little knowledge regarding how these altered behaviours of infected fish impact on their ecology in natural environments. Before we can begin to understand the ecological importance, and ultimate fitness consequences, of any of the infection-associated behaviour changes covered in this review it is essential that studies be designed to collect such data from fish populations in natural aquatic habitats.

Multiple infections

Within natural fish populations it is rare to find individuals to be infected with a single parasite species. The majority of fishes carry a diverse parasite community, frequently composed of multiple representatives of a large number of species. For many of the parasites harboured by an individual fish the ultimate fate of their host will determine their fitness, and one type of event (e.g. predation by another fish) may have completely opposite fitness effects for different co-infecting parasite species. When hosts are infected with more than one parasite, there is scope for competition between parasite species for control of their host's behaviour. In addition, where large numbers of a single parasite species occupy one host there is also scope for intraspecific competition for host control, if those parasites differ in their development stage with respect to their infective status. And if there also exists some degree of genetic relatedness between co-existing parasites, this also leads to intriguing concepts such as the possibility for social facilitation in host behaviour change, inclusive fitness and 'suicide'. This is a fascinating area, which links

well with contemporary key topics in evolutionary ecology.

Behaviour change and host conservation

Many of the examples cited in our review demonstrate that parasites very often change the behaviour of hosts in a density-dependent manner. Frequently it is only those individuals carrying very heavy parasite burdens that exhibit significant behaviour change. Since the majority of infections exhibit an over-dispersed distribution amongst host populations, heavily infected, behaviourally altered individuals are likely to comprise only a small proportion of the population. Since the level or pattern of infection is generally determined at least in part by environmental conditions, mean infection levels may be susceptible to perturbations resulting from pollution events, habitat degradation, or longer-term global change. If such events lead to higher general levels of infection, behavioural change may occur in a larger proportion of hosts and may have far more severe population-level consequences. Typically, tolerance of species to ecological parameters are tested using LD₅₀ or similar tests, whereas – through behavioural mechanisms such as those outlined above – fish in parasitised populations may be sensitive to far lower perturbations than imagined. Studies examining the interaction between environmental factors (such as elevated temperature, increased levels of pollution or habitat degradation) intrinsic levels of infection and density-dependent behaviour change would provide a good deal of insight into the population-level consequences of habitat perturbations.

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