

Zoogeography

The geographical distribution of marine parasites has not been well studied and is largely, although not entirely, limited to some aspects of the zoogeography of parasites of marine fishes. Some effort has gone into studying latitudinal, longitudinal and depth gradients of fish parasites. Interestingly, ectoparasites and endoparasites of marine fishes show different latitudinal patterns. Whereas the relative species richness (number of parasite species per host species) increases markedly from high to low latitudes for ectoparasites, this is not the case for endoparasites. The latter also show greatest diversity in the tropics, but this is entirely due to an increased diversity of host species at low latitudes. Thorson's rule, which states that benthic marine invertebrates tend to produce large numbers of small pelagic larvae in warm waters, but small numbers of large offspring by various mechanisms at high latitudes, applies to monogenean gill parasites of marine fishes. Furthermore, host ranges (but not host specificity) are greater for digeneans at high than at low latitudes, whereas monogeneans do not show differences between latitudes.

Concerning longitudinal gradients, a study of scombrid ectoparasites has shown that there is a primary centre of diversity in South-East Asian waters, and a secondary one in the Caribbean, with diversity decreasing with distance from these centres.

Concerning gradients with depth, relative species diversity of monogeneans is several times greater in surface than in deep waters off eastern Australia. Parasites can be used to study host populations and their migration, not only of marine fish but also of various invertebrates. Such parasite tags are much cheaper than other methods, such as comparative genetic studies, as discussed (on pages 351–355). The section discusses general methodology, selection criteria for tag parasites and application of the method to different host groups. Parasites also are useful for making inferences about long-term historical dispersal. The relevant section describes the only two examples studied (i.e. that of scombrid dispersal with emphasis on the role of oceanic barriers, and that on the historical migrations of Indo-Pacific whiting, Sillaginidae). The section on introduced marine parasites addresses a very important problem (i.e. that of the many parasites introduced into new regions, where they have become important pests). It also discusses the use of deliberately introduced parasites to control introduced free-living pest species, such as crabs or echinoderms. The Chapter concludes with a concise discussion of deep-sea parasites. Very little is known about the diversity and distribution of free-living deep-sea organisms (probably more than 99% of invertebrates have not yet been described), and deep-sea parasites have been studied even less. They are of great importance, considering the huge spaces of the deep-seas, and the many species of fish and invertebrates found there.

Latitudinal, longitudinal and depth gradients

Klaus Rohde

Introduction

Most plant and animal species are most diverse at low latitudes. Differences in species richness between latitudes are often truly amazing. Thus, there are about 150 species of marine fish in the North Sea, but there are thousands in tropical seas of much smaller areas. But even at a particular latitude, differences exist along longitude. For example, the south-east Asian waters are particularly rich in faunal diversity, whereas the eastern Pacific is much poorer. Little is known about species numbers in the deep sea, but the few studies that have been conducted suggest that diversity at least of some groups (e.g. nematodes) is very great in the deep-sea benthos. This section evaluates evidence for gradients not only in marine parasite diversity, but also for gradients in reproductive strategies, host specificity and latitudinal ranges.

Latitudinal gradients in species richness

Latitudinal gradients in species richness of marine parasites were last reviewed by Rohde (2002). They have not been studied for most marine groups, but are well documented for metazoan ectoparasites and endoparasites of marine fishes. In both groups of parasites, species richness is much greater in the tropics than at high latitudes. However, ectoparasites and endoparasites differ significantly in one important aspect, that is, species richness of ectoparasites increases at a greater rate towards the equator than that of host species, whereas relative species richness (number of parasite species per host species) of endoparasites is more or less the same at all latitudes. The great number of endoparasite species in tropical seas is entirely (or almost entirely) due to greater species numbers of hosts. The differences between ectoparasites and endoparasites remain after correction for phylogeny, using the method of phylogenetically independent contrasts (Poulin and Rohde 1997). The same difference is shown by two major groups of ectoparasites and endoparasites, the monogeneans and digeneans (Fig. 9.1). Consequently, infracommunity richness of ectoparasites but not of endoparasites is greater in the tropics (Rohde and Heap 1998).

Rohde (1992, 1999) and Willig (2001) have reviewed the various hypotheses proposed as explanations for the gradients. Most of them are either circular or insufficiently supported by evidence. Importantly, most of the explanations are based on the assumption that habitats are saturated with species and that species richness is determined by limiting factors (i.e. that equilibrium conditions prevail). Rohde (1992, 1999) proposed an alternative hypothesis, that the gradients can best be explained by a gradient in 'effective evolutionary time' modulated by several factors. He defined effective evolutionary time as the composite of two factors (i.e. evolutionary speed and evolutionary time under which communities have existed under relatively constant conditions). Evolutionary speed, according to Rohde (1992, 1999, references therein) is determined by mutation rates, generation times and the speed of physiological processes. These parameters are correlated with temperature: mutation rates and the speed of physiological processes are increased, and generation times are reduced in the tropics. Because niche space is largely empty, the net effect will be a faster accumulation of species at low latitudes. The possibility cannot be ruled out that different limits to species richness in different habitats do exist, but they have not been reached at this point in evolutionary time.

Several recent studies deal with the effects of temperature on generation times and the effect of generation time on speed of evolution (for a full discussion and references see Rohde 2005). Gillooly *et al.* (2002) described a general model, based on first principles of allometry and biochemical kinetics, that predicts generation time ('time of ontogenetic development') as a function of body mass and temperature. Development time of species in all groups tested is

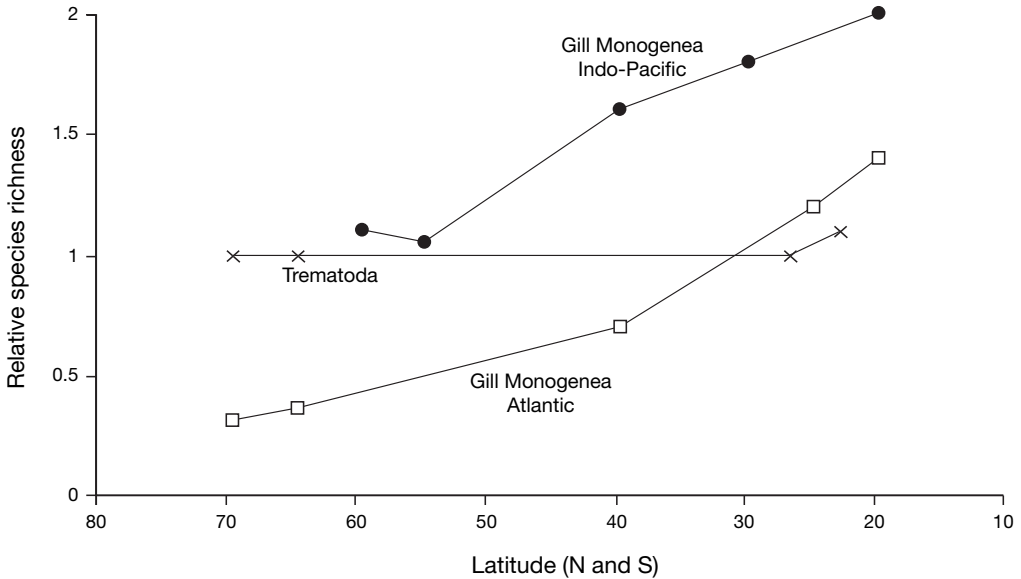


Figure 9.1 Relative species diversity (number of parasite species per host species) of digeneans and monogeneans of marine teleosts at different latitudes. Data from various sources (e.g. Rohde and Heap 1998).

negatively correlated with temperature. Mutation rates are greater at higher temperatures (references in Rohde 1992), and an acceleration of physiological processes with temperature is well documented. However, experimental evidence for direct temperature effects on speed of selection is not available. Such evidence is urgently needed.

Fossil evidence supports the view that speciation rates are higher in the tropics, but molecular evidence that relative rates of diversification per unit time increase towards the tropics is controversial (references and discussion in Rohde 2005). Of very great importance, the study of Allen *et al.* (2002) has shown that species diversity, including those of marine fish parasites, can be predicted from the biochemical kinetics of metabolism. Their model predicts quantitatively how species richness increases with environmental temperature. Allen *et al.* (2002) conclude that evolutionary rates are constrained by generation times of individuals and mutation rates, both of which are correlated with metabolic rates and show the same Boltzmann relation to temperature. The authors concluded that their results support the hypothesis that increased temperatures accelerate the biochemical reactions that control speciation rates and thereby increase the standing stock of species.

Latitudinal gradients in reproductive strategies

Thorson (1957) demonstrated that many marine benthic invertebrates in warm waters produce large numbers of small pelagic planktotrophic larvae, whereas high latitude species tend to produce fewer and larger offspring, often by viviparity or ovoviviparity, and larvae develop in egg capsules or by brooding (Thorson's rule). Many subsequent studies have confirmed this generalisation. Rohde (1985) provided evidence for a similar phenomenon in the gill Monogenea. Most species in warm or temperate seas produce numerous eggs from which free-swimming larvae hatch. In contrast, most species infecting coldwater fish (particularly in the northern hemisphere) belong to the Gyrodactylidae, all of which reproduce by viviparity (Fig. 9.2). Juveniles are transferred to other fish by contact transfer.

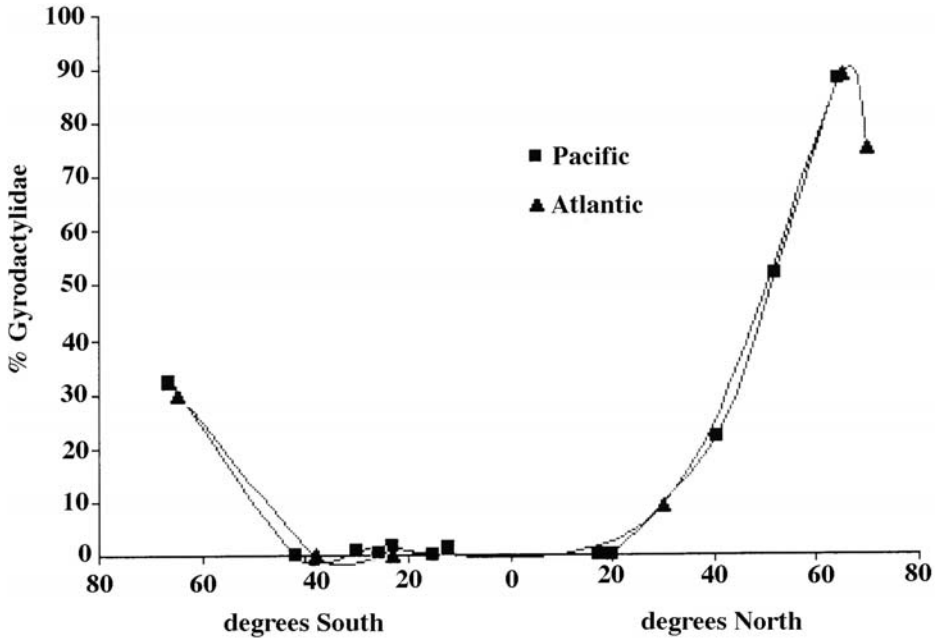


Figure 9.2 Percentage of marine Gyrodactylidae on the gills of marine teleosts at different latitudes. Data from various sources including Ernst *et al.* (2001).

Several explanations for Thorson's rule have been given; the most widely accepted one is that phytoplankton blooms at high latitudes do not last long enough to permit development of small planktotrophic larvae. This explanation does not hold for the Monogenea, because monogenean larvae do not feed on phytoplankton. Rohde (1985, 1999) suggested that the most likely explanation is direct temperature effects. The number of pelagic larvae that can be produced at low temperatures is too small to guarantee infection by host searching, and small larvae cannot locate hosts in the huge spaces of the ocean at temperatures where physiological processes are greatly slowed down. Hence, selection has led to a strategy that guarantees a suitable habitat by remaining on the same host individual. Since the trend in the Monogenea and free-living benthic invertebrates is so similar, Rohde (1985) suggested a similar explanation for the latter.

Latitudinal gradients in host ranges and host specificity

The host range of a parasite species is the number of its recorded host species, whereas host specificity takes intensity and/or prevalence of infection in each host species, and the phylogenetic relationship of hosts into consideration (for details see pp. 286–293). There is little information about latitudinal differences in host ranges and specificity for most parasite groups, but studies of monogeneans and digeneans of marine teleosts along latitudinal gradients in the Indo-Pacific and Atlantic oceans have shown that host ranges are very narrow for monogeneans at all latitudes, whereas host ranges for digeneans are much greater at high than at low latitudes (Rohde, 1978, 1980). However, host specificity is similarly great for both groups at all latitudes, if specificity is measured using prevalences and intensities of infection (Rohde 1980). Apparently, digeneans in cold waters, in spite of the greater number of hosts, infect only some host species heavily. However, only one large survey at high latitudes permits calculation both of host ranges and host specificity for Digenea. More studies are necessary, and latitudinal gradients in host ranges and specificity in other parasite groups should be assessed.

Longitudinal gradients and geographical ranges

Longitudinal differences in species diversity of marine parasites have been little studied. Rohde and Hayward (2000) studied monogenean and copepod ectoparasites of the scombrid genera *Scomberomorus* and *Grammatorcynus*, and found that the tropical/subtropical western Pacific is the primary centre of diversity, and that the tropical/subtropical western Atlantic is a secondary centre. Coastal scombrid fishes and their parasites spread between the Indo-West Pacific and Atlantic oceans via the Tethys Sea, and between the western Atlantic and the eastern Pacific, before the Central American landbridge was established. As the result of this dispersal, fish species in low diversity seas have relatively more parasite species than those found in high diversity seas. When considering only endemic fish and parasite species, however, the Indo-West Pacific and the West Atlantic (i.e. the primary and secondary centres of diversity) have parasite-host ratios of 1.75 and 1.25, respectively, versus a ratio of 1.00 for all other seas.

Studies of parasites of rabbit fish, *Siganus* spp., from the coasts of eastern Australia and East Africa have shown a much greater species richness of ectoparasites, but not of endoparasites, in Australian waters. Kleeman (2001) found 19 species of metazoan ectoparasites on *Siganus doliatus* on the Great Barrier Reef, whereas Martens and Moens (1995) and Geets *et al.* (1997) found only seven or eight species on *S. sutor* from the western Indian Ocean. Endoparasite richness did not show significant differences: seven versus five species.

The effects of geographical ranges of hosts on species richness of parasites have been little studied. There is some, but ambiguous, information that fish species with the widest geographical distribution have the greatest number of parasites species (Rohde 1989).

Depth gradient

Deep-sea parasites are discussed in detail in the section on Deep sea parasites (pp. 366–369). Relative species diversity of Monogenea is about five times greater in surface than in deepwater fish off the coast of south-eastern Australia (see Rohde 1993).

Important references

Reviews on latitudinal diversity gradients and their explanations are by Rohde (1992, 1999) and Willig (2001). Rohde (1993, 2002), Poulin and Rohde (1997) and Rohde and Heap (1998) discussed latitudinal gradients in species richness of marine parasites, in particular of gill parasites of teleost fish, Rohde and Hayward (2000) evaluated longitudinal gradients of gill monogeneans of scombrid fishes. Discussions of latitudinal gradients in host specificity and reproductive strategies can be found in Rohde (1978) and Rohde (1985), respectively. Recent evidence on a non-equilibrium explanation of latitudinal diversity gradients was presented by Allen *et al.* (2002), Gillooly *et al.* (2002) and Rohde (2005). Our knowledge of depth gradients was reviewed by Rohde (2002).

Parasites as biological tags

Ken MacKenzie

Introduction

An important applied aspect of marine parasitology is the use of parasites as biological tags to investigate the population structure of marine organisms, particularly commercially important species of fish. Different components, distinguished by varying degrees of separation, can be recognised within populations of most marine organisms. For example, two sympatric components may have a common feeding area but separate spawning areas, while others may be separated to a greater extent. The efficient and sustainable management of a commercially exploited

marine species depends on a sound knowledge of its population structure. Various methods can be used to investigate this structure, including the use of naturally occurring parasites as biological tags.

The basic principle underlying this method is that the host can become infected with a particular parasite species only within the endemic area of that parasite. The endemic area is that geographical region in which conditions are suitable for transmission of the parasite and the completion of its life cycle. It is determined by the existence of suitable environmental conditions, primarily temperature and salinity for marine organisms, and the presence of all required host species for different stages of the parasite's life cycle. If an infected host is found outside the endemic area of the parasite, it can be inferred that that individual had been within the endemic area at some time.

Methods

A biological tag study should preferably begin with a survey of the entire parasite fauna of the target host in the area under study. Two different approaches can then be applied to the resultant data. First, a small number of parasite species are selected according to established criteria (see below). A large number of host individuals are then examined specifically for these species and the data are compared using fairly simple tests of statistical significance such as Fisher's Exact Test and ANOVA. Second, entire parasite assemblages are analysed using more advanced statistical methods such as a multivariate maximum likelihood model, non-parametric discriminant analysis and canonical multivariate analysis. This approach is of particular value in studies of large valuable host species that are not available for examination in large numbers. It is less applicable to studies of smaller species of fish, particularly pelagic species, because many of these do not have the diverse parasite faunas and high intensities of infection necessary for such analyses. A useful recent development (Lester *et al.* 2001, Moore *et al.* 2003) has been to divide the parasite fauna of the target host into temporary and permanent groups, depending on their life spans in that host, and to analyse the two groups separately. With large fish it may be prohibitively time consuming to count all the parasites present in individual hosts, but this problem can be minimised by subsampling the more numerous parasite taxa.

Selection criteria for tag parasites

The ideal tag parasite should satisfy the following criteria. However, parasites fulfilling all of these are rarely encountered, so compromises usually have to be made. Also, new variations in the way parasite data are analysed are continually appearing in the literature, so these criteria should be regarded as guidelines rather than hard-and-fast rules.

- The parasite should have significantly different levels of infection in different parts of the study area. Exceptions are studies using geographical variations in parasite genetics, which up to now have been applied mostly to larval anisakid nematodes (Pascual *et al.* 1996, Mattiucci *et al.* 2002).
- The parasite should have a long life span in the target host. For studies of stock identification and recruitment, parasites with life spans similar to those of the host itself are usually necessary, but for studies of seasonal migrations parasites with shorter life spans, such as adult digeneans, can be used. Encysted larval or juvenile stages of helminths, such as digenean metacercariae (Fig. 9.3) and cestode plerocercoids (Fig. 9.4) often have life spans measured in years in their fish hosts.
- Parasites with direct single-host life cycles are the simplest to use. Those with complex life cycles involving two or more stages in different hosts are more problematic because more information is required on the various biotic and abiotic factors that influence

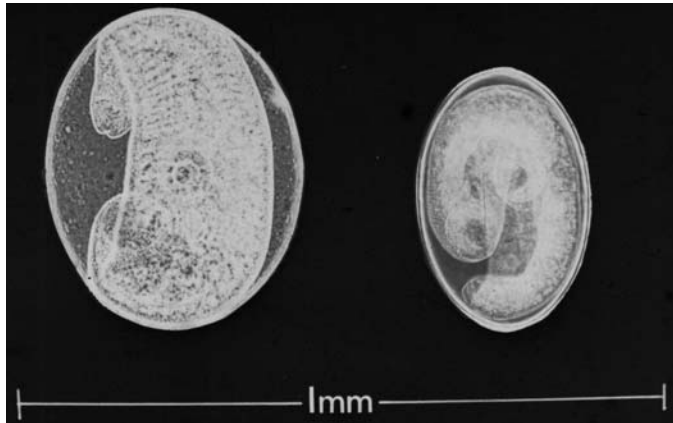


Figure 9.3 Metacercariae of *Renicola* spp. from the visceral cavity of herring, *Clupea harengus*. These infect herring in the first year of life and have life spans of many years in the fish host.

parasite transmission. Given adequate information they can, however, be used just as effectively, and continuing research on the biology and ecology of marine parasites is improving the efficiency of biological tagging.

- The level of infection should preferably show no significant variation from year to year, but the effects of annual variations can be nullified by following infection levels in single year classes of the target host over several years.
- The parasite should be easily detected and identified. Examination of the host should involve the minimum of dissection, so highly visible and site-specific parasites are particularly useful (Fig. 9.5).
- Seriously pathogenic parasites, and those that affect host behaviour, should not be considered for use as tags.

Advantages of biological tagging

The most efficient approach to a population study is the multidisciplinary one, in which several different tagging methods are used to complement one another. Each method has its own strengths and weaknesses and the use of parasites as tags is recognised as having the following advantages over other widely used methods such as artificial tagging and genetic studies.

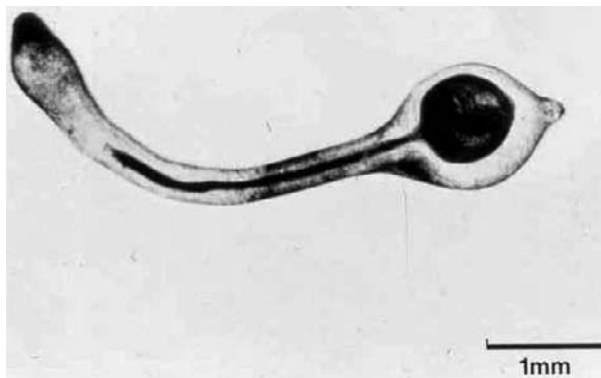


Figure 9.4 Plerocercoid of the trypanorhynch cestode *Lacistorhynchus tenuis* from the visceral cavity of teleost fish. These plerocercoids have life spans of many years in the fish host.

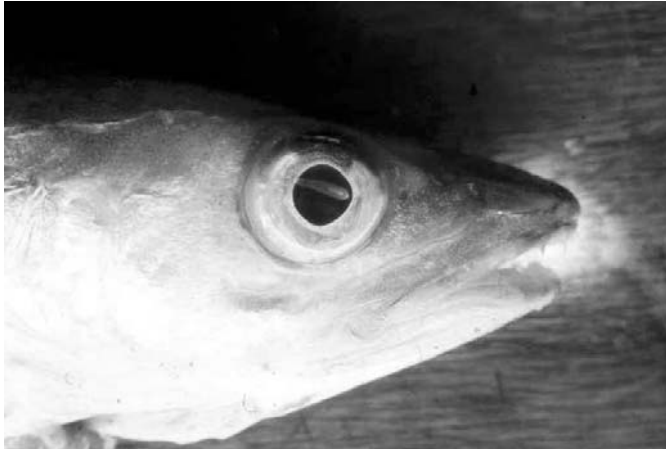


Figure 9.5 A good example of a highly visible and site-specific parasite: the plerocercoid of the trypanorhynch cestode *Gilquinia squali* *in situ* in the humour of the eye of whiting, *Merlangius merlangus*.

- Parasite tags are more appropriate for small, delicate and deepwater species of fish that suffer high mortality rates following artificial tagging. They are also more appropriate for crustaceans that lose artificial tags when they shed their old carapace.
- Each host specimen sampled represents a valid observation, whereas with artificial tags each individual must be sampled, tagged and recaptured to obtain a single valid observation.
- Parasites are less expensive to use because samples can be obtained from routine sampling programs or from commercial catches, rather than from dedicated tagging cruises.
- The use of parasites eliminates doubts concerning possible abnormal behaviour of artificially tagged hosts.
- Biological tagging and genetic studies operate over different time scales. Genetic studies operate over an evolutionary time scale and thus are less likely to identify population components that are at an early stage in the process of separating into subspecific groups variously known, for example as 'strains' or 'races'. Parasites, however, can often be used to identify host population components distinguished by behavioural differences, but between which there is still a considerable amount of gene flow ('ecological stocks').

Parasites as tags for different taxonomic groups of host

Crustaceans

Crustaceans are important intermediate hosts for many species of marine helminths, which can be used effectively as biological tags. Good examples are the stock identification studies of Owens (1983, 1985) and Thompson and Margolis (1987). These authors used metacestodes, digenean metacercariae and a bopyrid isopod as tags to distinguish between stocks of commercially important shrimps and prawns.

Cephalopods

The use of parasites in population studies of cephalopod hosts was reviewed by Pascual and Hochberg (1996), who discussed the problems peculiar to this host group. These included short life spans, variable growth rates and protracted spawning seasons, the latter giving rise to multi-

ple cohorts in a single population at any given time. These factors, together with the importance of squid as intermediate and paratenic hosts for marine helminths, led these authors to recommend the use of genetic studies of selected helminth larvae, particularly anisakid nematodes.

Pelagic fish

Most studies on pelagic fish have been carried out on herring, *Clupea harengus* and *C. pallasii*, and on carangid fish of the genus *Trachurus* (see MacKenzie 1987b, Williams *et al.* 1992, MacKenzie 2002). The most frequently used parasites have been larval nematodes of the genus *Anisakis*, but trypanorhynch metacestodes, digenean metacercariae and parasitic isopods have also featured prominently.

Demersal fish

The commercial importance of Atlantic cod, *Gadus morhua*, hake, *Merluccius* spp., and rockfish, *Sebastes* spp., has led to many population studies of these species using parasites as tags. Demersal fish tend to have richer and more varied parasite faunas than pelagic species and this is reflected in the wide variety of parasites that have been used as tags. Although considerable potential exists for the use of parasites as biological tags for elasmobranch fish, the only studies that have attempted to realise this potential so far have been those of Moore (2001) and Yamaguchi *et al.* (2003).

Marine mammals

The use of parasites as biological tags for marine mammals was reviewed by Balbuena *et al.* (1995), who gave examples to illustrate both the value and limitations of the method. In the few studies carried out so far, acanthocephalans have proved particularly useful for identifying stocks of cetaceans.

Important references

The first publication describing the use of a parasite as a biological tag for a marine host was that of Herrington *et al.* (1939). General accounts including reviews are by Sindermann (1961, 1983), Kabata (1963), MacKenzie (1983, 1987a, 2002), Lester (1990), Moser (1991), Williams *et al.* (1992), Balbuena *et al.* (1995), Pascual and Hochberg (1996) and Arthur (1997). MacKenzie and Abaunza (1998, 2004) provided a guide to procedures and methods for stock discrimination of marine fish by parasite tags.

Parasites as indicators of historical dispersal

Craig Hayward

Introduction

Parasites have been employed often in the study of migrations of hosts, and to distinguish different host populations (Rohde 2002). The use of parasites as biological tags in the discrimination of host stocks, for example, is considered above (pp. 351–355). Such studies are concerned with relatively small scales of distance and time. In contrast, studies using parasites as indicators of larger-scale patterns in the zoogeography of host animals, and historical dispersal in evolutionary time, are less common. This approach, dubbed the von Ihering method, was first used in the late 1800s (von Ihering 1891). In biogeography, this technique can test hypotheses about the role of particular barriers in limiting the continental distribution of living species, and also higher groups. However, studies using this approach in the marine environment are much fewer than

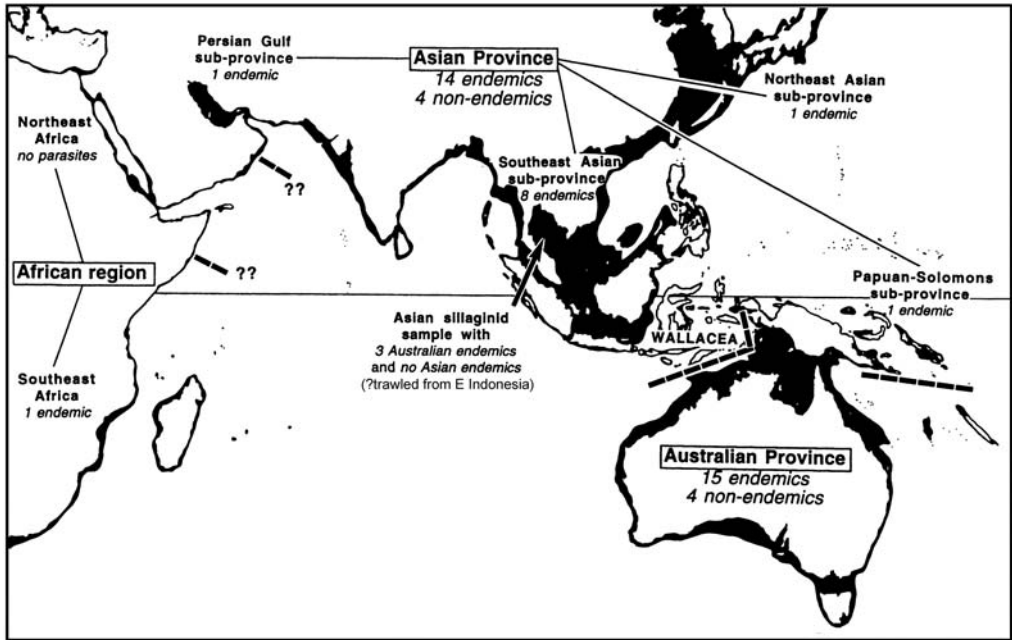


Figure 9.6 Provinces of ectoparasites of Indo-Pacific whiting (Sillaginidae), and proposed position of barriers to dispersal of these fishes. Reproduced from Hayward CJ, Distribution of external parasites indicates boundaries to the dispersal of sillaginid fishes in the Indo-West Pacific. *Marine and Freshwater Research* **48**, 391–400, with permission from CSIRO Publishing (1997).

in terrestrial and freshwater realms. This is largely because marine parasites are still relatively less well known than those in other environments.

Two recent studies have analysed the ranges of parasites of perciform fishes to investigate historical dispersal across oceanic barriers. These studies focused on external parasites having high host specificity, as the planktonic larval stages of such parasites are usually very brief, and so their long-range dispersal accurately reflects historical movements of their host fishes. The first study (Hayward 1997) dealt with the distribution of copepods and monogeneans on Indo-Pacific whiting (Sillaginidae), and the second study, by Rohde and Hayward (2000), considered the distribution of copepods and monogeneans on four genera of Scombridae.

Dispersal history of Indo-Pacific whiting

Indo-Pacific whiting are benthic schooling fishes with small, elongate bodies belonging to Sillaginidae, a family related to croakers (Sciaenidae). Most have limited regional distributions in the tropics. They live in shallow, inshore marine waters over sandy and silty substrates from Australia northwards to Asia, and westwards to eastern Africa. Hayward (1997) examined over 1500 individuals belonging to 26 species (out of 27) in three genera from throughout this region for parasites.

The distribution patterns of ectoparasites specific to these fishes lead to recognition of two provinces (regions of endemism) with high parasite diversity: one on the continental shelf of Australia, and one on the shelf of Asia (Hayward 1997; Fig. 9.6). The Australian province has 15 endemics (five monogeneans, one leech and nine copepods), and the Asian province 14 endemics (two monogeneans and 12 copepods). These provinces are separated by a region with coastlines that descend very steeply to the ocean floor (with few substrates suitable for these fishes),

and by deep ocean waters that must largely inhibit sillaginid movements. This region, known as Wallacea, is already well known as a boundary region for terrestrial animals, plants, freshwater fishes and assorted inshore marine fishes.

Some sillaginids must have dispersed across this barrier in eastern Indonesia in recent geological time, leading to the occurrence of four parasites (three monogeneans and a copepod) in both provinces. At least one other less-recent invasion of Australian waters by Asian sillaginids would account for the occurrence of six pairs of copepod congeners that have one member in each province. Presumably, such dispersal occurred some time since the mid Miocene (about 15 million years ago), when the modern configuration of islands in eastern Indonesia began to form. Dispersal of sillaginids in the opposite direction seems unlikely, as a genus of polyopisthocotylean monogeneans common among Australian sillaginids, *Polylabris*, would also be expected to be present in Asia, but this is not the case.

Three species of Australian parasites also appear to be presently encroaching onto the periphery of the Asian shelf, because they were found in just a single sample of sillaginids, *Sillago aeolus*, collected from a fish market along the Gulf of Thailand (Fig. 9.6). (However, although it was assumed that the fish in this sample had been fished locally, they may have been trawled remotely in eastern Indonesia, on or near the Australian continental shelf, by long-distance trawling vessels based at Bang Saen, Thailand).

The most widespread sillaginid, *Sillago sihama*, also seems to have dispersed to African shores from the Arabian Sea as planktonic larvae only (as no Asian parasites were present in samples of 29 hosts), and relatively recently (as only one locally endemic parasite appears to have been acquired, Fig. 9.6).

Dispersal history of Spanish mackerels and mackerels

Scombrid fishes (mackerels, tunas and bonitos) are relatively large, epipelagic fishes of the tropics and subtropics. Rohde and Hayward (2000) compiled previously published and new data on the distribution of ectoparasites of four scombrid genera (*Scomberomorus*, *Grammatorcynus*, *Scomber* and *Rastrelliger*) belonging to 26 species. The distributions of 32 copepods and 25 monogeneans on these fishes were then analysed to investigate the hypothesis that the wide stretch of deep ocean between the East and West Pacific (the East Pacific Barrier) is responsible for the pronounced break in the circumtropical warm water fauna of the continental shelves. An alternative boundary to historical dispersal that is often considered important is the New World Land Barrier, which emerged to join the continents of North and South America several million years ago.

At the level of parasites species, analysis showed that there is a primary centre of diversity in the West Pacific, and a secondary centre in the West Atlantic (Rohde and Hayward 2000, Fig. 9.7). The West Pacific centre shares its species of the largely coastal *Scomberomorus* and *Grammatorcynus* and their parasites almost entirely with seas located to the west. Predominantly coastal fish species and their parasites have not dispersed across the eastern Pacific, but rather dispersed across the New World Land Barrier, before the Central American land bridge was formed. The only species of parasites shared by the western and eastern Pacific (four copepods) also have a circumtropical distribution, and may have dispersed to the Eastern Pacific through the Western Atlantic. In contrast with the West and East Pacific areas, all four other neighbouring areas (West Pacific–Indian, Indian–East Atlantic, East Atlantic–West Atlantic, West Atlantic–East Pacific) share species, indicating that the Eastern Pacific Barrier has been highly effective in limiting dispersal.

In contrast with the parasites of the relatively near-shore *Scomberomorus* and *Grammatorcynus*, the parasites of the more pelagic *Scomber* spp. in the West Pacific share species with seas both to the east and west, although at the genus level, only two circumtropical monogenean

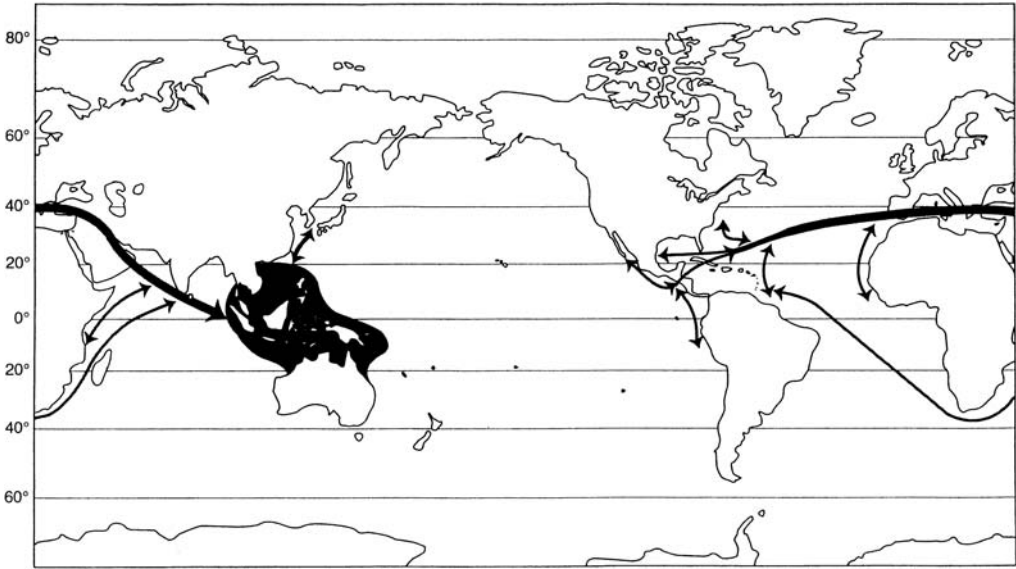


Figure 9.7 Geographical relationships of scombrids, *Scomberomorus* and *Grammatocygnus*, and their copepod and monogenean ectoparasites. Note the primary centre of species richness in the western Pacific; the East Pacific Barrier has been an effective barrier to dispersal. Reprinted from *International Journal for Parasitology* 30, Rohde K, Hayward CJ, Oceanic barriers as indicated by scombrid fishes and their parasites, pages 579–583, Copyright (2000), with permission from Elsevier.

genera are shared by the East and West Pacific (Rohde and Hayward 2000). Extant distribution patterns are probably also affected by the fragmentation of habitats at the time the Tethys Sea closed, during the Miocene (5–25 million years ago), as a result of changes in plate tectonics. (The Tethys was a large ancient sea that existed between Europe–Northern Asia and the African and Indian continents, and once connected the Atlantic and Pacific oceans.) In conclusion, the East Pacific Barrier has been thoroughly effective as a barrier to dispersal of species of *Scomberomorus*, *Grammatocygnus* and their parasites, whereas it has been less effective for species of *Scomber* and their parasites.

Important references

Von Ihering (1891) pioneered this approach, postulating ancient relations between New Zealand and South America. The only recent work done in this area using marine parasites is by Hayward (1997) on ectoparasites of sillaginid fishes, and Rohde and Hayward (2000) on oceanic barriers as indicated by scombrid fishes and their parasites. Rohde (2002) reviewed the work.

Introduced marine parasites

Mark E Torchin and Armand M Kuris

Introduction

The deleterious effects of introduced species on biodiversity, ecosystem function and human economies are becoming increasingly apparent (Elton 1958, Vitousek 1990, Wilcove *et al.* 1998, Ruiz *et al.* 1999, Chapin *et al.* 2000). While marine and estuarine environments are among the most heavily invaded systems on earth (Ruiz *et al.* 2000, Grosholz 2002), surprisingly little is known about introduced marine parasites. Undoubtedly, more introduced marine parasites

exist than are reported. Parasites are common and important components of natural communities including marine environments (this volume). Yet, unlike the recent increase in reports of introduced free-living marine species (Cohen and Carlton 1998, Ruiz *et al.* 2000, Grosholz 2002), reports of parasites invading marine environments are relatively uncommon (Torchin *et al.* 2002). Partly, this may be because, unlike their introduced hosts, parasites are often difficult to observe and thus some exotic parasites go unreported. However, introduced 'hosts' also escape their native parasites, often resulting in significantly reduced parasite species richness and prevalence in the introduced populations compared to their native populations. Parasites from a host's native range may never reach the novel region due to stochastic processes or, if they do, stochastic and/or demographic processes may prevent their establishment (Torchin *et al.* 2002), such that, only a subset of the host's native suite of parasites actually establish introduced populations (Torchin *et al.* 2003). Escape from parasites appears to be a general phenomenon across taxa and habitats (Mitchell and Power 2003, Torchin and Mitchell 2004). Evidence from molluscs, crustaceans and fishes (Kennedy 1993, Torchin *et al.* 2003) indicate that introduced aquatic species escape most of their native parasites. Nevertheless, since parasitism is probably the most common consumer strategy, and since free-living species generally host at least one parasite species, and more commonly several (Price 1980, Toft 1986), the paucity of reported marine parasite invasions is intriguing.

Modern shipping and transport have made the global movement of ballast water a primary vector for introducing marine organisms to novel regions (Carlton and Geller 1993, Ruiz *et al.* 1997, Drake and Lodge 2004). The transport of planktonic larval life history stages in ballast water is a key invasion route (Carlton and Geller 1993). Although larval organisms can be infected by parasites and pathogens, they are often lost postrecruitment and are typically not the same types of parasites that infect adult populations (Rigby and Dufour 1996). Hence, introduced species that arrive as larvae in ballast water are presumably rarely parasitised (Lafferty and Kuris 1996, Torchin *et al.* 2002). Thus, in marine systems, invasions resulting from the release of ballast water may filter out potential introduced parasites. Although many microorganisms, including potential pathogens, have been recovered from ballast water, the extent to which this leads to successful establishment of introduced marine pathogens is uncertain (Ruiz *et al.* 2000). However, even though marine parasites may face significant obstacles to invasion compared to free-living species, some parasites do establish populations in new regions. These introduced parasites often affect native species and have deleterious consequences in their new habitat (Table 9.1).

Protozoan parasites

Protistan parasites have often caused significant and widespread effects in marine systems and aquaculture operations. Some of these pathogens are likely to be introduced species. However, for other pathogens there is limited evidence for an exotic source. Many of these are parasites of oysters, often considered to have been introduced with infected stocks. MSX disease, caused by *Haplosporidium nelsoni*, has caused massive mortalities of native oysters in Delaware and Chesapeake Bay since 1957. *Haplosporidium nelsoni* was probably introduced from Asia (Andrews 1980, Barber 1997) resulting from undocumented introductions of the Japanese oyster, *Crassostrea gigas* (Barber 1997). Recent molecular evidence supports this hypothesis and suggests that the parasite was initially introduced from Japan to California and subsequently, to the East Coast of the United States with importations of *C. gigas* from California (Friedman 1996, Burrenson *et al.* 2000). Another possible introduction, *Perkinsus marinus*, agent of Dermo disease in oysters may have been introduced with infected *C. virginica* (Ruiz *et al.* 1999). The recent range extension of this oyster pathogen is a result of repeated introductions of infected native oysters to the north-eastern United States of America (USA) (Ford 1996). Both of these pathogens have

Table 9.1 Introduced parasites

Parasite taxon	Parasite	Host	Native/introduced region	Method of introduction	References
Protozoa	Haplosporidia	Oysters, bivalves	JAP/PNA	Aquaculture	Friedman (1996)
	* <i>Haplosporidium nelsoni</i>		ASI/ANA	Aquaculture	Barber (1997), Andrews (1980)
	* <i>Bonamia ostreae</i>		PNA/EUR	Aquaculture	Minchin (1996), Chew (1990)
	* <i>Perkinsus marinus</i>		S. ANA/N. ANA	Aquaculture	Ford (1996)
	* <i>Paramoeba invadens</i>	Sea urchin	Unknown/N. ANA	Unknown	Scheibling and Hennigar (1997)
Monogenea	<i>Gyrodactylus anguillae</i>	Eels	EUR?/AUS, ASI, ANA	Aquaculture	Hayward <i>et al.</i> (2001a), Ernst <i>et al.</i> (2000)
	<i>Pseudodactylogyrus anguillae</i>		ASI/EUR, ANA	Aquaculture	Hayward <i>et al.</i> (2001b)
Trematoda	<i>Pseudodactylogyrus bini</i>		ASI/EUR, ANA	Aquaculture	Hayward <i>et al.</i> (2001b)
	<i>Gyrodactylus salaris</i>	Salmon	—/NOR	Stocking	Johnsen and Jensen (1991), Hastein and Lindstad (1991)
	* <i>Neobenedenia melleni</i>	Marine fishes	HKG, HAN/JAP	Aquaculture	Ogawa <i>et al.</i> (1995)
Nematoda	<i>Nitzschia sturionis</i>	Sturgeon	CAS/ARA	Stocking	Osmanov (1971), Zholdasova (1997)
	* <i>Austrobilharzia variglandis</i>	Asian mud snail	ASI/PNA	Aquaculture	Torchin <i>et al.</i> (in press)
Polychaeta	<i>Anguillicola crassus</i>	Atlantic mud snail	ANA/PNA	Aquaculture	Grodhaus and Keh (1958)
	* <i>Spirocamallanus istiblenni</i>	Eels	ASI/EUR, ANA	Aquaculture	18 Barse and Secor (1999)
Copepoda	<i>Terebrasabella heterouncinata</i>	Marine fishes	FRP/HAW	Stocking	Font and Rigby (1999)
	<i>Mytilicola orientalis</i>	Abalone, snails	SAF/PNA	Aquaculture	20 Kuris and Culver (1999), 21 Culver and Kuris (2000)
Rhizocephala	<i>Mytilicola intestinalis</i>		ASI/EUR, PNA	Aquaculture	His (1977), Stock (1993), Bernard (1969), Holmes and Minchin (1995)
	<i>Mycicola ostrae</i>		MED/N. EUR	Fouling	Minchin (1996), Stock (1993)
Mollusca	<i>Loxothylacus panopaei</i>	Mud crabs	ASI/EUR	Aquaculture	Stock (1993)
	<i>Heterosaccus dollfusi</i>	Swimming crab	GOM/ANA	Aquaculture	van Engel <i>et al.</i> (1965), Hines <i>et al.</i> (1997)
Asterisks indicate suspected introductions. Regions are: ANA Atlantic North America, EUR Europe, PNA Pacific North America, AUS Australia, ASI Asia, NOR Norway, JAP Japan, ARA Aral Sea, GOM Gulf of Mexico, RED Red Sea, HKG Hong Kong, HAN Hainan, CAS Caspian Sea, SAF South Africa, FRP French Polynesia, HAW, Hawaii. After Torchin <i>et al.</i> (2002).					

been a serious source of mortality for native oysters in the mid Atlantic and may limit oyster populations in the Chesapeake Bay (Ruiz *et al.* 1999). Oyster translocations may have also resulted in the introduction of *Bonamia ostreae* from California to Europe (Chew 1990). A shipment of the European flat oyster, *Ostrea edulis*, cultured in California from broodstock originating in the Netherlands (Barber 1997) may have initiated the spread of epizootics of this parasite throughout Europe (Barber 1997). Recent outbreaks of the marine amoeba, *Paramoeba invadens*, have caused mass mortalities in the sea urchin, *Strongylocentrotus droebachiensis*, in the North Atlantic coast of Canada. *Paramoeba invadens* may be an exotic species, but further research is needed to determine its origin (Scheibling and Hennigar 1997).

Monogeneans

Although typically restricted to the freshwater portions of their hosts' life cycles, monogeneans introduced with catadromous and anadromous fishes have also been accidentally imported along with their hosts. Stocking Norwegian rivers with infected salmon may have introduced *Gyrodactylus salaris* to wild Atlantic salmon stocks. This monogenean now causes heavy mortality in salmon parr (Johnsen and Jensen 1991). *Gyrodactylus salaris* was geographically isolated in rivers because it could not survive in brackish or marine water but the movement of infected fish among hatcheries enabled its spread (Johnsen and Jensen 1988). Introduced monogeneans are common pests in the eel trade. They often cause mortality and are capable of infecting native eel species (Hayward *et al.* 2001a, b). *Pseudodactylogyrus anguillae* and *P. bini* were introduced from Asia to North America and Europe with the importation of the Japanese eel, *Anguilla japonica* (Hayward *et al.* 2001a). Both species now infect wild populations of the native North American eel, *Anguilla rostrata* (Cone and Marcogliese 1995, Hayward *et al.* 2001a) and wild populations of the native European eel, *Anguilla anguilla* (Gelnar *et al.* 1996, Hayward *et al.* 2001a). Another probable invader, *Gyrodactylus anguillae*, occurs on four continents. It was likely introduced from Europe through the importation of infected European eels (Hayward *et al.* 2001b). Yet another monogenean introduced with the importation of fish is *Nitzschia sturionis*. Stocking stellate sturgeon from the Caspian into the Aral Sea introduced this monogenean which caused massive mortality of the native ship sturgeon in the 1930s (Osmanov 1971, Zholdasova 1997). The monogenean, *Neobenedenia melleni* (= *girellae*), is a pest in marine fisheries in Japan. Ogawa *et al.* (1995) suggest that this parasite was introduced to Japan with amberjack, *Seriola dumerili*, imported from Hainan and Hong Kong and spread to other fishes due to its unusually low host specificity. It causes mortality in heavily infected fish. Other parasite introductions, primarily monogeneans, resulting from fish releases have also been reported from the land-locked seas in the Ponto-Caspian region (Grigorovich *et al.* 2002).

Trematodes

Introduced to the West Coast of North America with the importation of oysters from Japan, the mud snail, *Batillaria cumingi* (= *atramentaria*), brought with it the Japanese trematode *Cercaria batillariae* (Torchin *et al.* in press). Both the snail host and parasite now occur in several estuaries from Vancouver, British Columbia to central California (Ching 1991, Torchin *et al.* in press). *Cercaria batillariae*, a heterophyid whose adult form has still not been described nor is its life cycle fully known (Shimura and Ito 1980), infects at least three native fish species as second intermediate hosts and native birds as final hosts in its introduced range (Torchin *et al.* in press). An additional consequence of this invasion is that at the southern end of its introduced range, the Japanese mud snail is outcompeting and locally extirpating populations of the California mud snail, *Cerithidea californica* (Carlton 1975, Byers 2000, Byers and Goldwasser 2001). *Cerithidea californica* serves as first intermediate host for at least 18 native trematode species throughout its range in California (Martin 1972) and, at least 10 trematode species where the

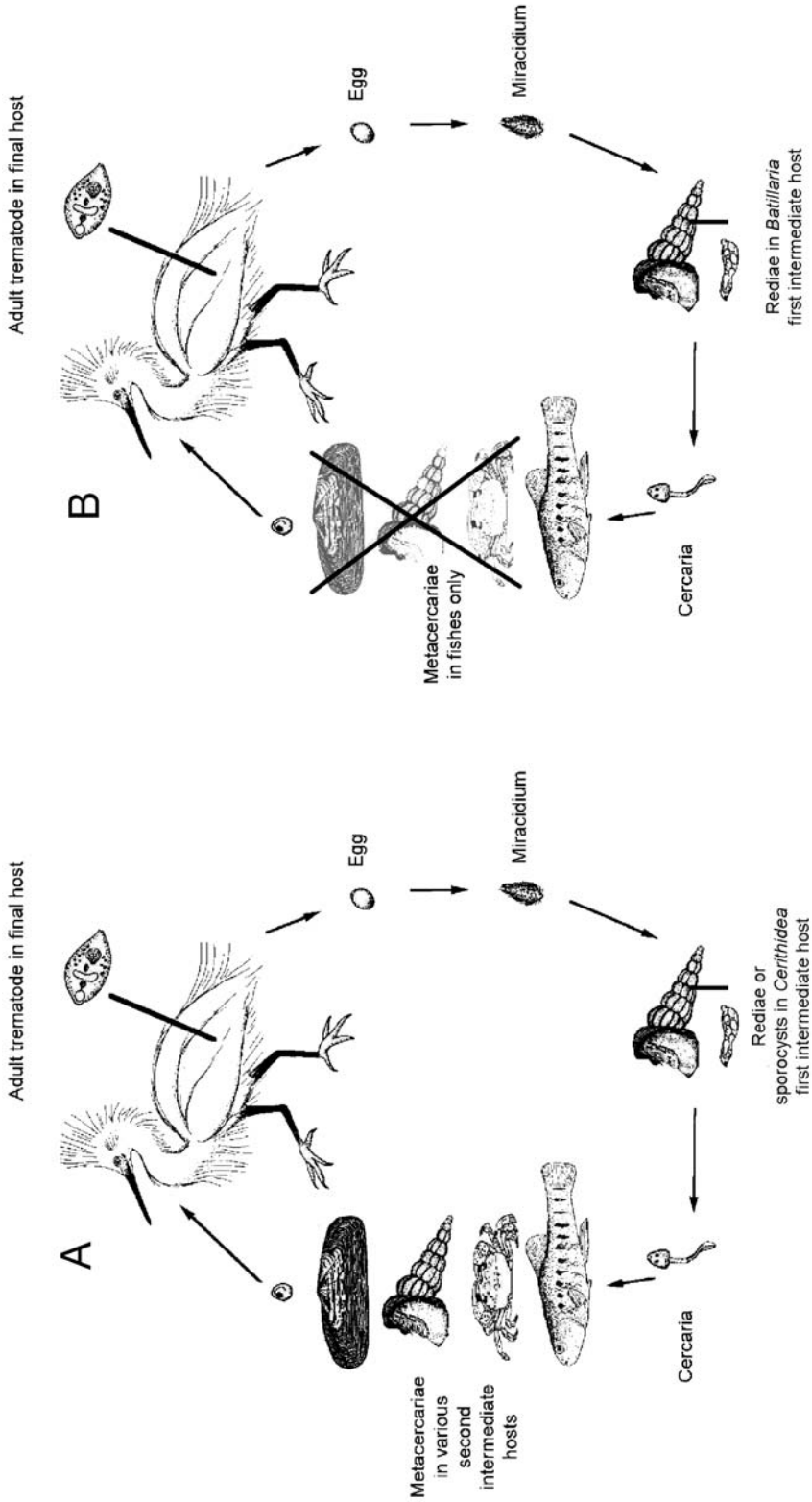


Figure 9.8 Generalised life cycle for trematode species. **A.** *Cerithiidea californica* as first intermediate host. **B.** *Cercaria batillariae* using *Batillaria cumingi* as a first intermediate host. The particular type of second intermediate host used (e.g. a fish or a crustacean) depends upon trematode species, and *Cercaria batillariae* uses several native fish species as second intermediate hosts (Torchin *et al.* in press). Figure adapted from Huspeni and Lafferty (2004).

two snail species overlap (Torchin *et al.*, in press). Most of these trematodes are trophically transmitted through the marsh community, infecting multiple hosts during their life cycle. As *C. californica* is replaced by *B. attramentaria*, its parasites will also become locally extinct since none are known to infect alternative first intermediate hosts, including *B. attramentaria*. Although the precise consequences of these local extinctions on the marsh community remain unclear, the removal of several native trematode species due to local extinction of their first intermediate host will eliminate infection by the trematodes in the second intermediate host molluscs, crustaceans and some fishes. In turn, the several native trematode species will be replaced with a single introduced trematode species (Fig. 9.8). Because some of these trophically transmitted parasites can alter foraging dynamics in these systems (Lafferty 1992, Lafferty and Morris 1996, Lafferty 1999), the replacement of this native parasite fauna may have indirect effects, potentially altering the abundances of intermediate and final hosts (Torchin *et al.* in press).

Another snail introduced with the importation of oysters is the Atlantic mud snail, *Ilyanassa obsoleta* (Demond 1952, Carlton 1999). In its introduced range, *I. obsoleta* is reported to be infected with five species of larval trematodes (Grodhaus and Keh 1958). One of these, *Austrobilharzia variglandis*, initially described from the snail's native range in coastal estuaries in eastern North America, causes swimmer's itch in humans (Miller and Northup 1926, Stunkard and Hinchliffe 1952, Grodhaus and Keh 1958). Although identifications of the four other species are not reported (Grodhaus and Keh 1958) they are possibly a subset of *I. obsoleta*'s native suite of parasites (Torchin *et al.* 2002). Studies comparing these trematodes to those in the native range are required to resolve this issue.

Nematodes

A serious pest in eel fisheries is the swim bladder nematode, *Anguillicola crassus*. Native to Asia, *A. crassus* has been introduced to Europe and North America where it now infects native eels in both in nature and in culture (Barse and Secor 1999). *Anguillicola crassus* can reach high prevalences in native eel populations and it can cause severe pathology in European and North American eels (Barse and Secor 1999).

Although the origin of the nematode, *Spirocamallanus istiblenni*, is still uncertain, Font and Rigby (1999) present evidence that this nematode may have been introduced to the Hawaiian Islands along with its host, the blue-lined snapper, *Lutjanus kasmira*. Further investigation may reveal whether this nematode, which also infects endemic Hawaiian fishes, is an introduced species (Font and Rigby 1999).

Polychaetes

In the 1980s, a polychaete worm, *Terebrasabella heterouncinata*, was accidentally imported to California from South Africa with infested abalone. It rapidly became a major pest in abalone mariculture facilities in California (Kuris and Culver 1999). Although it does not derive any nutrition from its host, it induces severe deformation of the host's shell. This reduces the market price of infested animals and may make them more susceptible to shell-cracking predators (Kuris and Culver 1999). This worm was accidentally released from a mariculture facility into the wild where it infested abalone and other susceptible native gastropods. This wild population has since been eradicated by culling potential host snails below the density threshold for transmission (Culver and Kuris 2000).

Copepods

The global transport of marine bivalves for aquaculture has led to widespread introductions of parasitic copepods. Native to Asia, *Mytilicola orientalis* and *Myicola ostrae* are both parasitic

copepods of the Pacific oyster, *Crassostrea gigas*. *Mytilicola orientalis* has been accidentally introduced to Europe and the Pacific Coast of North America, while *Myicola* has only been reported from Europe (His 1977, Stock 1993, Holmes and Minchin 1995, Minchin 1996). Both species infect native bivalves and *M. orientalis* is considered a serious pest (Holmes and Minchin 1995). *Mytilicola intestinalis*, which was presumably introduced to northern Europe from blue mussels originating in the Mediterranean Sea, may have been transported in its host, *Mytilus galloprovincialis*, on the hulls of ships (Minchin 1996). In the early 1950s an epidemic of *M. intestinalis* caused considerable damage to mussel fisheries and infections spread to other native bivalve species in the Netherlands (Stock 1993).

Rhizocephalans

Another putative aquaculture-related parasite introduction is the rhizocephalan barnacle, *Loxothylacus panopaei*. First reported in Chesapeake Bay in 1964, it was presumably introduced with infected mud crabs associated with oysters transplanted from the Gulf of Mexico (Van Engel *et al.* 1965). It now parasitises three crab species in its introduced range, including two which only appear to be infected within the introduced range (Hines *et al.* 1997). This barnacle is a parasitic castrator and anecdotal information suggests that after its introduction to Chesapeake Bay, its two primary hosts became rare. Recently this has been supported by documentation of a negative association between the prevalence of this parasite and the biomass of its host, *Rhithropanopeus harrisi* within Chesapeake Bay (ME Torchin unpublished data, summer 2002–summer 2003). Another introduced rhizocephalan barnacle, *Heterosaccus dollfusi*, recently invaded the Mediterranean Sea through the Suez Canal, even though its crab host, *Charybdis longicollis*, invaded before 1954 and is now well established (Galil and Lützen 1995, Galil and Innocenti 1999). This parasite has not been recovered from any species of native crab, nor from other introduced species of portunids, including *Charybdis hellerii*, also native to the Red Sea. Other reports of rhizocephalans introduced with their hosts are anecdotal and lack confirmation (e.g. Boschma 1972, Kinzelbach 1965).

Controlling introduced pests with parasites

The reduction or absence of parasites in introduced pest species, (Torchin *et al.* 2003) may explain why some introduced species proliferate in their new environment and become destructive invaders (Torchin *et al.* 2001). Thus, replacing some key parasites in introduced pest populations may mitigate the damage they cause. The use of biological control in marine environments, where introduced species increasingly pose ecological and economic threats (Cohen and Carlton 1998, Ruiz *et al.* 1997), has only been proposed recently (Lafferty and Kuris 1996, review by Secord 2003). Lafferty and Kuris (1996) developed a model for the use of natural enemies, including parasites, as biological control agents against introduced marine pests. Basing the strategy on successful examples of terrestrial biocontrol, Lafferty and Kuris (1996) emphasise the key differences between marine and terrestrial ecosystems crucial for evaluating the safety and efficacy of this approach. Kuris and Lafferty (2000) relate the concerns of safety of marine biological control to terrestrial weed pest control identifying the need for high host specificity of the proposed control agent. In contrast, the efficacy, particularly of parasitic castrators or parasitoids used as marine biological control agents, is comparable to insect pest biological control due to the regulatory similarity of these and terrestrial parasitoids (Kuris and Lafferty 2000, Kuris *et al.* 2002).

Serious consideration of marine pest biological control is relatively new and most research has been directed towards the control of the European green crab, *Carcinus maenas*. The green crab is a benthic marine predator and usually considered a pest where it is introduced (Lafferty and Kuris 1996, Grosholz *et al.* 2000). Additionally, the introduced populations of green crabs

lack most of parasites common in their native range (Torchin *et al.* 2001). In particular, parasitic castrators were not present in any of the introduced populations. In Europe, however, the prevalence of parasitic castrators (which block reproduction and growth) was negatively associated with demographic success (biomass and body size) of green crabs, suggesting that these parasites may partially control green crabs in Europe. While several factors could interact with parasitism and influence this result, Torchin *et al.* (2001) found that factors such as latitude, environmental quality, limb loss (a proxy for predation) and other types of parasites had no significant effect in their analysis. Furthermore, uninfected introduced green crab populations were significantly larger and had a greater biomass compared to European populations (Torchin *et al.* 2001). Recent models also indicate that parasitic castrators, under a range of larval recruitment dynamics, have the potential to control introduced host populations (Kuris and Lafferty 1992, Lafferty and Kuris 1996). The rhizocephalan barnacle, *Sacculina carcini*, a parasitic castrator of *C. maenas* in Europe, is a candidate biological control agent of introduced green crab populations in Australia and the West Coast of North America (Lafferty and Kuris 1996). However, host specificity trials indicate that *S. carcini* is able to settle on, infect, but not complete development in non-host crabs native to Australia and the West Coast of North America (Thresher *et al.* 2000, Goddard *et al.* in press). Sands (1998) suggested that the ability to complete development and reproduce in non-target hosts is the standard for unacceptable risk of a biological control agent. However, Goddard *et al.* (in press) demonstrated that settlement of *S. carcini* on non-host native crabs often results in an infection lethal to the host but the parasite does not successfully develop. Hence, safety and efficacy of the control agent are inversely associated (Goddard *et al.* in press). Because native crabs can be infected but do not serve as hosts, they act as population sinks for the parasite. An evaluation of these impacts, plus those estimated for other species of crabs not included in the testing, could be weighed against the benefit of controlling green crabs and releasing California native crabs and other native species from predation by *C. maenas*.

The parasitic larval sea anemone, *Edwardsia liniata*, which infects the north-western Atlantic ctenophore, *Mnemiopsis leidyi*, has been proposed as a possible biological control agent for invasive populations of *M. leidyi* in the Black Sea (Bumann and Puls 1996). While the parasitic planula larvae of this anemone reduce growth rates and may control *M. leidyi* populations in their native range, they can also infect other ctenophore species. Additionally, they may cause seabather's eruption (dermatitis) in humans and the sessile benthic adults may alter benthic community structure (Bumann and Puls 1996).

Biological control has also been proposed for the Asian seastar, *Asterias amurensis* (Kuris *et al.* 1996). Of four candidate species listed, the ciliate *Orchitophyra stellarum* has received the most attention (Kuris *et al.* 1996, Goggin and Bouland 1997). However, more research is needed to examine its ability to control host populations and determine its host specificity (Goggin and Bouland 1997).

Conclusion

Although introduced marine species often escape their parasites, some parasites manage to invade with their hosts and establish populations in the new region. Once established, they can spread and impact native species. Still, reports of introduced marine parasites remain limited. Undoubtedly more introduced marine parasites exist than are reported, partly because parasites are often difficult to observe and with increased attention, more introduced parasites will be inevitably be revealed. It is often difficult to determine the origin of parasites of introduced hosts (Font and Rigby 1999) and of newly discovered parasites (Scheibling and Hennigar 1997) and these should not, *a priori*, be considered exotic. Comparing parasite faunas of native and introduced hosts and native and introduced populations of the exotic species (Torchin *et al.* 2002, Torchin and Mitchell 2004) and by using historic evidence (Font and Rigby 1999) it is possible

to make strong inferences as to the origins of emerging diseases and cryptogenic parasite species. Marine parasites encounter several obstacles to introduction especially if 'hosts' are introduced as larvae. Interestingly, evidence suggests that most of the exotic marine parasites in Table 9.1 resulted from aquaculture or fisheries related introductions. It is not surprising that adult hosts transferred from one aquaculture area to another (where population densities are often unnaturally high) would facilitate the introduction and transmission of parasites. It is notable, however, that most of these historical introductions often occurred without quarantine or screening for parasites and pathogens and that most current aquaculture practices account for this. Introduction of parasites can have serious impacts on native marine communities. More research is needed to discover exotic parasites and their effects as well as investigate the consequences of exotic species that lack many or all of their infectious natural enemies. In certain cases in which destructive marine invaders lack infectious agents, replacing key parasites may mitigate the damage they cause. Thus, further research is needed to fully evaluate the potential for safe and effective marine biological control.

Important references

General texts and papers on biological invasions are by Elton (1958), Dobson and May (1986), and Byers and Goldwasser (2001). Important work on marine invasions is by Chew (1990), Carlton and Geller (1993), Ruiz *et al.* (2000) and Grosholz (2002).

Drake and Lodge (2004) discussed global hotspots of biological invasions: evaluating options for ballast-water management. Eradication of introduced marine pests, their management and control were discussed by Lafferty and Kuris (1996), Culver and Kuris (2000) and Secord (2003). Minchin (1996) gave an account of management of the introduction and transfer of marine molluscs.

Deep-sea parasites

Rodney A Bray

Introduction

The deep sea has been 'loosely' defined as the part of the ocean below the epipelagic zone (Herring 2002), that is, all of the ocean below the level of the continental shelf margin or shelf-slope break. In most of the ocean this, in effect, means the ocean deeper than about 200 m, although the shelf can be deeper, particularly around the Antarctic continent (Fig. 9.9). The bottom drops away to the abyssal plain at 4000 m to 6000 m, with occasional trenches reaching deeper than 11 000 m. By the definition given here, the deep sea covers about 65% of the Earth's surface and over 50% is covered with water more than 3000 m deep (Gage and Tyler 1991). This vast area is not uniform and the character of the fauna of the shallower parts of the zone differs markedly from the deep areas such as the abyssal plain and, probably, the trenches. At high latitudes the typical shelf fauna may reach down the slope to more than 1000 m, and in polar regions typical deep-sea parasites may be encountered in depths of a few hundred metres. The mid-ocean ridge and hydrothermal vent fauna and cold-seep faunas probably also have a distinct character (de Buron and Morand 2004). Cold seeps occur widely, from shallow water to trenches, where methane seeping from the rocks of the sea floor nourishes bacteria and their symbiotic organisms.

Virtually everything known about deep-sea parasites is of the stages infesting fishes. The fish fauna of the deep sea is depauperate in members of the largest fish order Perciformes, and this is reflected in the parasite diversity in the deep sea. Gadiforms of the family Macrouridae constitute a major part of the deep-sea fauna in much of the world's ocean. Other gadiform families such as the Ophidiidae and Moridae and other orders such as the Scorpaeniformes, Osmeriformes, Notacanthiformes, Anguilliformes and Aulopiformes are well represented in the deep sea.

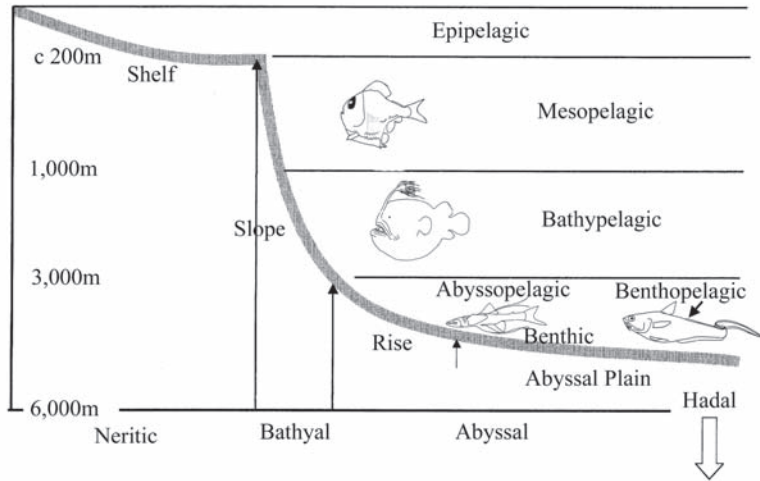


Figure 9.9 Diagram of certain oceanographic features and the terminology used.

Conditions in the deep sea

Pressure: Pressure increases by one atmosphere (0.101 megapascals) for each 10 m of increased depth (Tyler 1995). This is a problem to the fauna only when there are gas-filled cavities (e.g. swim bladder), and only then if the pressure (i.e. depth) changes rapidly. The density of water (830 times that of air) increases only by 0.5% per 1000 m. Nevertheless, this is enough to materially affect the rate of reactions involving a change in volume, such as those using enzymes. Deep-sea animal enzymes generally have reduced pressure sensitivity and reduced efficiency (relative to shallow water animals), rather than a series of sensitive enzymes relating to the pressure changes with depth (deep-sea animals normally inhabit a much greater depth range, *eurybathy*, than shallow forms, *stenobathy*).

Temperature: Temperature variation below the thermocline (800–1300 m) is low. At the thermocline the temperature is just below 4°C and decreases only slightly below that depth. Although the deep-sea fauna must be adapted to cold, the temperature is not highly variable. Cold tolerance, however, is not adequate to adapt animals to life in deep water.

Light: Photosynthesis is not well sustained below 200 m and sunlight cannot be detected below 1000 m. Bioluminescence and glow from black-smoker vents are the only sources of light in the deep sea.

Energy availability and food supply: For most of the deep sea, food descending from the photic zone supplies energy. This can be descending phytodetritus (deep-sea ‘snow’) or remains of animals, which may be tiny zooplankton or massive whales or fishes. The seasonal pulse of phytodetritus imposes seasonality on deep-sea communities.

Patchiness – mate finding and parasite transmission: Large food-falls attract many organisms and it is likely that these are the venues for mating and transmission. The attractiveness to animals of hydrothermal vents and cold seeps may also serve to concentrate parasite stages and their hosts.

What parasites are known

De Buron and Morand (2002) found that 57% of metazoan parasites reported in waters deeper than 1000 m were digeneans, 25% crustaceans (80% copepods), 10% cestodes, 4% acanthocephalans, 2% nematodes and 2% monogeneans. Protistans (in which they included the myxozoans) make up less than 17% of parasite records.

Protistans

This covers a wide variety of organisms, whose relationships are now being elucidated. Few have been reported from deep waters. A few blood parasites, such as haemogregarines and coccidians, are known from deep-sea fishes (Davies and Merrett 2000). One *Eimeria* species is known to damage the swim bladder of macrourids (Grabda 1983). Moreira and Lopez-Garcia (2003) surveyed protist diversity at hydrothermal vents using rDNA and identified sequences of several parasitic protist lineages, including Apicomplexa, Perkinsozoa, Syndiniales and Kinetoplastida. They concluded that many vent organisms must be infested.

Myxozoa

Identified myxosporean members of the families Myxobolidae, Auerbachiiidae, Alatosporidae, Ceratomyxidae and Myxidiidae are known. *Myxidium* species are commonly found in macrourids and have been used as an indicator to separate stocks (Szuks 1980).

Platyhelminthes

Monogenea: Most records are members of the family Diclidophoridae, which are frequently found on macrourids. There are also records of Acanthocotylidae, Capsalidae, Chimaericolidae, Dactylogyridae, Discocotylidae, Hexabothriidae, Mazocraeidae, Microcotylidae, Monocotylidae, Plectanocotylidae and Tetraonchoididae. Monogeneans are successful until the lower slope where, apparently, fish densities are too low for successful transmission (Campbell *et al.* 1980).

Cestoda: The unsegmented 'cestodian' *Gyrocotyle* is common in holocephalans, most of which occur in deep water, and numerous trypanorhynch and tetraphyllideans are reported from deep-sea elasmobranchs. All reports of adult cestodes from deep-sea teleosts are of members of the order Pseudophyllidea, from the families Bothriocephalidae, Philobythiidae, Echinophallidae and Triaenophoridae. Members of the latter family show some predilection for deep-sea fishes.

Digenea: This group is probably the largest group of metazoan parasites in deep-sea fishes, but only 17 families out of about 150 known are reported. Depth profiles are marginally better known for this group (Bray 2004). Four families, the Derogenidae, Fellodistomidae, Hemiuridae and Lepocreadiidae, have species reaching to abyssal depths (i.e. about 5000 m). Three further families, the Lecithasteridae, Opecoelidae and Zoogonidae, reach below 3000 m, one, the Gorgoderidae, deeper than 2000 m and three, the Acanthocolpidae, Accacoeliidae and Sanguinicolidae, just deeper than 1000 m. Four further families, Bucephalidae, Cryptogonimidae, Faustulidae and Monorchiiidae, reach below the shelf break at 200 m. Two further families, Bivesiculidae and Hirudinellidae, include species reported from deep-sea fishes, but with no detailed bathymetric data. It is apparent that the Bucephalidae are common parasites in cold-seep regions as Powell *et al.* (1999) found that the prevalence of 'Bucephalus-like trematodes' in cold-seep mussels at a depth of 550 m to 650 m was 70% or more at three sites.

Nematoda

Relatively few nematodes are known from the deep sea. The families Capillariidae (Enoplida), Anisakidae and Cucullanidae (Ascaridida) and Philometridae, Rhabdochoniidae and Cystidicolidae (Spirurida) are reported from fishes. Many anisakids are larval forms, which are likely to be found as adults in cetaceans and pinnipeds. One cystidicolid species is reported from a hydrothermal vent fish (Justine *et al.* 2002).

Acanthocephala

Adult palaeacanthocephalans of the families Echinorhynchidae and Rhadinorhynchidae are most commonly reported. Less common are members of the families Heteracanthocephalidae

and Hypoechinorhynchidae. Several polymorphid larvae are reported in deep-water fishes, presumably as adults these are cetacean or possibly pinniped parasites. One species is described from a hydrothermal vent fish (de Buron 1988).

Crustacea

A few families of copepods have exploited deep-sea demersal fishes. According to Boxshall (1998) two families of the order Poecilostomatoidea and five of the order Siphonostomatoidea are reported. Three families are commonly encountered, the Sphyrriidae, Lernaepodidae and Chondracanthidae, and members of four others, the Hatschekiidae, Pennellidae, Philichthyidae and Hyponeoidea, are occasionally found. Several copepod species are reported from hydrothermal vent fishes (see de Buron and Morand 2004).

Areas of ignorance

A huge proportion of the area covered by the deep sea has not been sampled, let alone for parasites. No data are available from trenches. The data from hydrothermal vents and cold seeps are rudimentary. The life cycles, host relationships, distribution and zoogeography of deep-sea parasites have not been studied.

Important references

Important general texts on deep-sea biology are those by Marshall (1979), Gage and Tyler (1991) and Herring (2002), and those on deep-sea fishes by Merrett and Haedrich (1997) and Randall and Farrell (1997). Klimpel *et al.* (2001) produced a checklist of the 'metazoan' parasites of deep-sea fishes, including Myxozoa. Major review articles on deep-sea parasites include those of Noble (1973), Campbell (1983) and Bray *et al.* (1999). The most important paper on deep-sea parasite ecology is Campbell *et al.* (1980). For speculations on the parasite fauna of hydrothermal vents, see de Buron and Morand (2004).