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BIODIVERSITY RESEARCH

Parasite species richness in New Zealand fishes: a grossly underestimated component of biodiversity?

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ABSTRACT

Estimates of total parasite species richness, for given host groups in given geographical areas, are always much higher than the numbers of known parasite species on which they are based. The discrepancy is a reflection of our limited current knowledge of parasite diversity. This is illustrated by a comparison of the parasite faunas of New Zealand fish species with those of Canadian fish; the latter have been well studied by fish parasitologists, and provide a standard for comparisons. More parasite species are known per host species for Canadian fish than for New Zealand fish, for both marine and freshwater fishes. This difference remains after correcting for differences in study effort, i.e. in the number of published studies per fish species. There are also more parasite species per fish species in Canada than in New Zealand when parasite species richness is expressed as number of species per unit of host body length. For freshwater fish, the difference can be explained by the restricted phylogenetic origins and geographical isolation of New Zealand fish species. For marine fish, however, there is no a priori reason to expect a difference in parasite species richness between fish in New Zealand and Canadian waters, and the observed difference probably results from a lack of appropriate parasitological surveys in New Zealand. If the true species richness of the parasite faunas of New Zealand marine fish species approaches that of their Canadian counterparts, then most of the diversity and ecosystem function of fish parasites in New Zealand remains unknown.

Keywords

Canada, helminths, host body size, marine conservation, New Zealand, study effort.

INTRODUCTION

At a time when the global loss of biodiversity is widely recognized as an urgent environmental issue, we are in a situation where we cannot say precisely how many species are being lost, or even how many currently exist. Estimates of existing biodiversity are difficult, because even among well-studied taxa such as terrestrial vertebrates, new species are still described each year (e.g. Hanken, 1999; Patterson, 2000). It is no surprise then that the true diversity of small-bodied or little-studied taxa is poorly known. Parasitic organisms fall within this category: they form an invisible fauna, most of them living inside other organisms. They can only be found after their host species are known to science, and after sufficient host individuals have been examined in detail; therefore, good estimates of parasite diversity for any geographical area always lag behind those of their hosts (Poulin & Morand, 2000). There have been few attempts to extrapolate the total diversity of parasites among certain taxa of hosts in given geographical areas (e.g. Cribb, 1998; Pérez-Ponce de Léon, 2001; Pérez-Ponce de Léon *et al*., 2002). These have suggested that metazoan parasites, which include several taxa of worms and arthropods, can represent a significant portion of the total metazoan biodiversity, but one that will remain unknown for the foreseeable future. Recently, the importance of parasites has been recognized in the context of several international initiatives calling for more extensive documentation of biodiversity (Brooks & Hoberg, 2000, 2001; Pérez-Ponce de Léon, 2001). Knowledge of parasite diversity opens a window into the evolutionary history and present-day ecology of free-living organisms, providing new perspectives on the biosphere (Brooks & Hoberg, 2000).

Here I take a look at the known diversity of parasites of New Zealand fish species, and try to evaluate how far we are from a full inventory of existing parasite species. Current compilations of known species, and estimates of what the New Zealand fauna includes, suggest that at best only 40% of free-living animal species in New Zealand have been described (Halloy, 1995); this value is lower if only marine habitats are considered. The decline in biodiversity in New Zealand is nonetheless obvious (Craig *et al*., 2000), prompting the government to launch its biodiversity strategy aimed at reversing the tide (Anon, 2000). In this context, parasite diversity can be very important. Parasites play key roles in ecosystems: they can regulate the abundance or density of host populations (Grenfell & Dobson, 1995; Hudson *et al*., 1998, 2002), stabilize food webs (Huxham *et al*., 1995; Combes, 1996), and structure animal communities (Minchella & Scott, 1991; Mouritsen & Poulin, 2002). A good knowledge of parasite diversity and whether or not it is declining is crucial for environmental management and conservation. Fish are a good host taxon to use in an assessment of the quality of our knowledge of parasite biodiversity in New Zealand. Because they are often caught and dissected in large quantities, for commercial or other purposes, their parasites are more likely to be found than those of other vertebrates.

Specifically, I contrast the parasite species richness of New Zealand fish species with that of Canadian fish species. Fish parasitologists in Canada have carried out extensive surveys of parasites of both freshwater and marine fish in Canadian waters, and the parasite faunas of Canadian fish are possibly the best known in the world (McDonald & Margolis, 1995). I use the known parasite biodiversity in Canadian fish as a benchmark for comparisons with the parasite diversity in New Zealand fish. The comparisons also control for differences in both host body size and study effort, and thus indicate whether New Zealand fish are currently known to host more or less parasite species, on average, than Canadian fish, per unit body size and for a given study effort.

METHODS

Lists of the parasite species known from New Zealand fish were obtained from the checklists of Hewitt & Hine (1972) and Hine *et al*. (2000), and those for Canadian fish from Margolis & Arthur (1979) and McDonald & Margolis (1995). The following taxa of metazoan parasites were included: Monogenea, Digenea, Cestoda, Nematoda, Acanthocephala, Copepoda, Isopoda, Branchiura, Mollusca (larvae or glochidia of certain bivalve taxa), and Hirudinea (leeches). The few metazoan parasite taxa excluded cause either rare or accidental infections in fish (e.g. Nematomorpha in New Zealand freshwater fish; Blair, 1983); unicellular parasite taxa were also excluded, because their detection often requires detailed surveys only carried out for commercially important fish species. The analyses included only actinopterygian (ray-finned) fish species for which at least one parasite species from the above metazoan taxa has been recorded. Among freshwater fish species, introduced fish species (e.g. *Salmo trutta* or *Perca fluviatilis* in New Zealand, and *S. trutta* or *Cyprinus carpio* in Canada) were excluded, given that the parasite fauna of exotic fish species is not the one they have acquired over evolutionary time in their area of origin.

In addition to parasite species richness (known number of metazoan parasite species), area of origin (New Zealand or Canada), and habitat (freshwater or marine), the maximum body length (in cm) of each fish species was recorded. This information was obtained from FishBase (*http://www.fishbase.org*); for a few fish species about which information was missing, standard fish guides were consulted to obtain length data (Scott & Crossman, 1973; Scott & Scott, 1988; McDowall, 1990; Paul, 2000).

As a measure of the extent of our knowledge about the different fish species, I used an index of study effort, taken as the number of publications on each fish species found in a combined search of two electronic data bases, the Aquatic Sciences & Fisheries Abstracts (1988–2003) and the Zoological Record (1978–2003). The Latin names, including all known synonyms, of each species were used as keywords during the searches. The publications that come up in a search for a given fish species include all kinds of research papers, not only parasite surveys; their number thus provides a relative index of how much we know about the general biology of that fish species. It also provides an indirect estimate of the number of fish individuals that were actually examined specifically for parasites: the more is generally known about a host species, the more individuals have probably been surveyed for parasitic infections. Host sample size if often an important correlate of known parasite species richness (Walther *et al*., 1995), and a correction for study effort can serve to control for spurious sampling effects.

The three continuous variables investigated here, i.e. parasite species richness, maximum host body length, and study effort, all required log-transformations ($\log(x + 1)$ in the case of study effort, because of several zero values) to meet the assumptions of parametric statistical tests.

RESULTS AND DISCUSSION

The data set included 5333 host–parasite associations involving 342 species of fish in Canada, and 772 host–parasite associations involving 149 species of fish in New Zealand. There were qualitative differences in the composition of these associations between Canada and New Zealand. For instance, ectoparasites represent approximately one quarter of all host–parasite associations in freshwater fish in Canada, but less than 10% in New Zealand freshwater fish, where branchiurans and leeches are absent and monogeneans are very rare (Fig. 1). In New Zealand freshwater fish, digeneans are relatively much more frequent among endoparasites than in Canadian freshwater fish. Differences also exist between the types of host–parasite associations found in marine fish of Canada and New Zealand (Fig. 1). For example, isopods and nematodes are more frequent as ectoparasites and endoparasites, respectively, in New Zealand marine fish than in Canadian ones. This does not mean that New Zealand marine fishes harbour more isopods and nematodes per host species than their Canadian counterparts; Fig. 1 simply illustrates the taxonomic composition of the host-parasite combinations reported to date, and not the average composition of the parasite fauna of a typical host species.

There were also quantitative differences between New Zealand and Canadian fish. A two-way ANOVA revealed that parasite species richness, i.e. the number of known parasite species per fish species, differed between the two countries ($F_{1,487} = 36.197$, $P = 0.0001$) and between marine and freshwater habitats ($F_{1,487} = 14.827$, $P = 0.0001$); there was a weak interaction between these

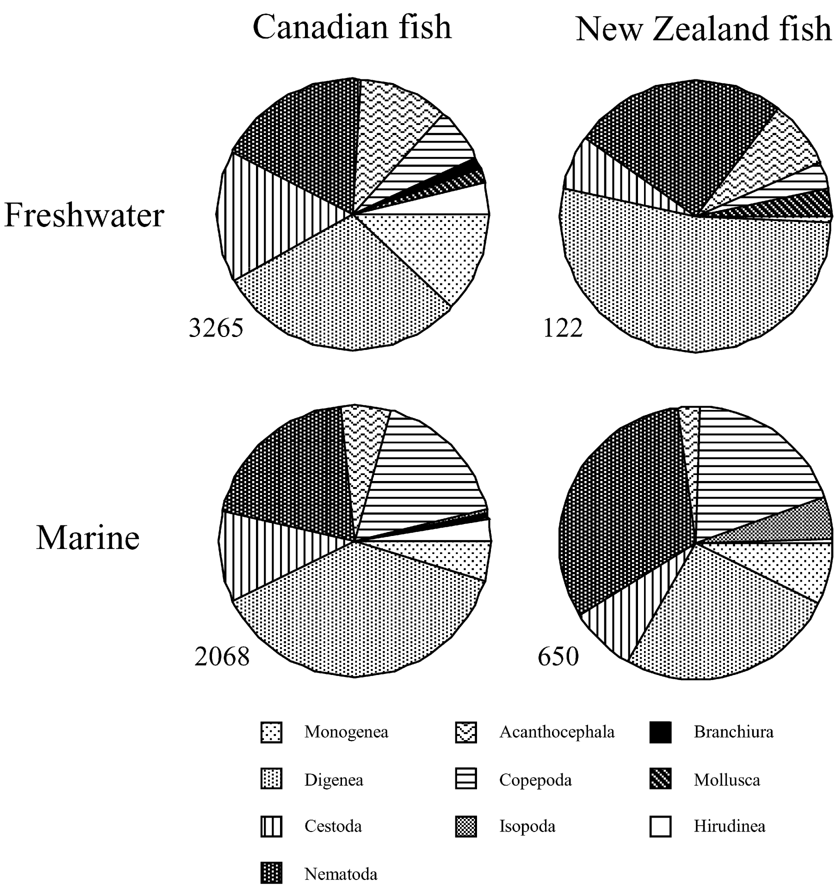

Figure 1 Distribution of host–parasite associations by parasite taxon, for both freshwater and marine fish species from Canada and New Zealand. The numbers beside the pie charts indicate the total number of host–parasite associations involved.

two factors ($F_{1,487} = 4.705$, $P = 0.0306$). On average, Canadian fish have a higher known parasite species richness (mean ± SD, back calculated from log-transformed data: freshwater species, 14.0 ± 3.2; marine species, 5.4 ± 3.3) than New Zealand fish (freshwater fish, 3.9 ± 3.0; marine species, 3.0 ± 2.7). The difference in parasite species richness observed between freshwater and marine fish species may in part be due to differences in body size between fish from these two habitats (two-way ANOVA, $F_{1,487} = 61.137$, $P = 0.0001$), with marine fish (47.0 ± 2.3 cm, $N = 336$ species) being larger than freshwater fish (19.4 ± 2.6 cm, $N = 155$ species), independently of their area of origin. There were indeed no differences in fish size between New Zealand and Canada, nor was there a significant interaction between habitat and area of origin (both $P > 0.17$).

In addition, there were differences in study effort between the different groups of fish. Across all fish species, study effort ranged from 0 to more than 10 000 published studies per fish species, with an average of 32 (back calculated from log-transformed data), according to the searches of the data bases. The number of published studies per fish species differed between Canadian and New Zealand fish species (two-way ANOVA, $F_{1,487} = 20.539$, $P = 0.0001$), and between freshwater and marine species ($F_{1,487} = 23.572$, $P = 0.0001$); the interaction term was not significant ($P = 0.3065$). Not surprisingly, our general knowledge of Canadian freshwater fish species is on average the best, and that of New Zealand marine fish species is on average the worst. Because of this and other differences mentioned above, comparisons between the parasite fauna of New Zealand and Canadian fish were made separately for freshwater and marine fish.

As a rule, the number of known parasite species per fish species increased with study effort (Fig. 2). Although the relationship is statistically significant for both freshwater and marine fish (linear regression, both $P = 0.0001$), the trend is stronger for freshwater fish, where study effort explains approximately 42% of the variance in parasite species richness compared with only 24% for marine fish (Fig. 2). If New Zealand and Canadian fish species are treated separately, we get slightly different slopes for the relationship (respectively, 0.522 and 0.424 for freshwater fish, and 0.204 and 0.322 for marine fish), but these do not differ from one another (F-test for difference between two slopes, Sokal & Rohlf, 1995: both $P > 0.60$), so all freshwater and all marine fish species are pooled for the regressions.

Residuals from the above regressions provide measures of parasite species richness corrected for study effort. Using these residuals, I found no relationship between parasite species richness and host body length for freshwater fish (all species: $r = -0.034$, $N = 155$, $P = 0.679$; Canadian species: $r = -0.056$, $N = 137$, $P = 0.515$; New Zealand species: $r = 0.150$, $N = 18$, $P = 0.552$). For marine fish, however, there was a weak but positive relationship between parasite species richness and host body length (all species: $r = 0.127$, $N = 336$, $P = 0.0196$), only seen in Canadian fish species if fish from the two different areas are separated (Canadian species: $r = 0.285$, $N = 205$, $P = 0.0001$; New Zealand species: $r = -0.068$, $N = 131$, $P = 0.439$). Host body length

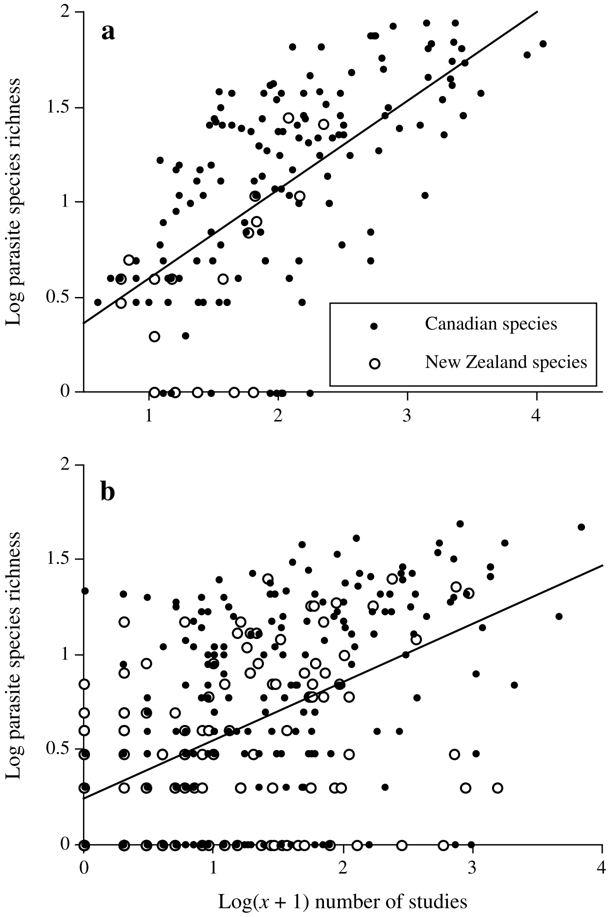

Figure 2 Known parasite species richness as a function of study effort (a) among 137 Canadian and 18 New Zealand species of freshwater fish ($y = 0.463x + 0.161$, $r^2 = 0.416$), and (b) among 205 Canadian and 131 New Zealand species of marine fish ($y = 0.300x + 0.249$, $r^2 = 0.235$).

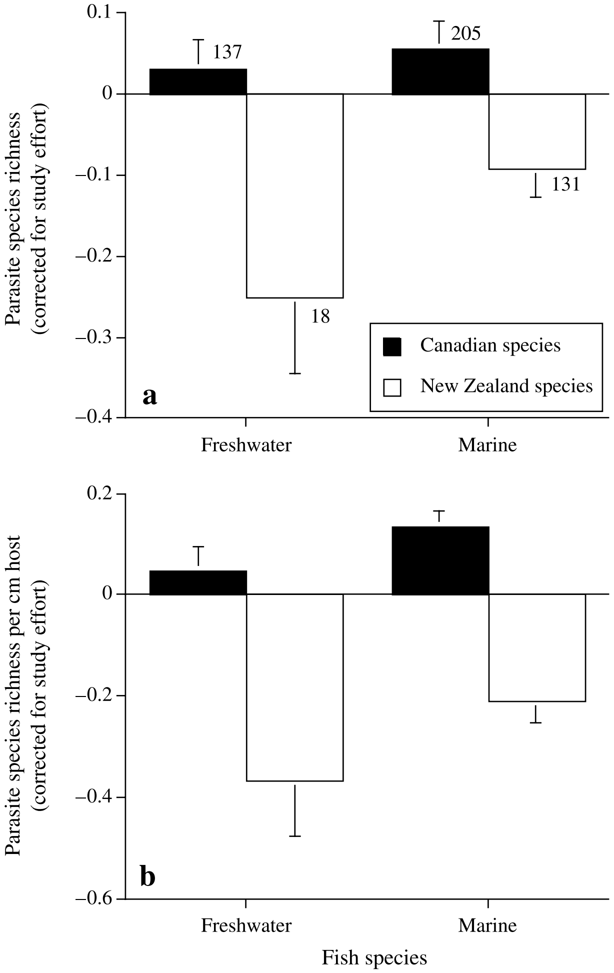

Figure 3 Mean (± SE) parasite species richness for freshwater and marine fish species from Canada and New Zealand: (a) species richness per fish species, where values are residuals from the regressions in Figure 2 and are thus values of parasite species richness corrected for study effort; (b) species richness per cm of host body length, where values are residuals of the regression between log (species richness/host body length) against study effort. Numbers above or below bars indicate sample sizes, and are the same for (a) and (b).

explained only about 8% of the variance in parasite species richness corrected for study effort among Canadian fish species, and it is therefore not a major determinant of parasite richness. In other comparative analyses of parasite diversity among fish species, host body size often but not always emerges as the best predictor of how many parasite species are harboured by a host species (see reviews in Poulin, 1997; Morand, 2000). While it is a better predictor than other host traits, host body size is not a reliable predictor: in other studies on fish hosts, it explained only an average of 12.5% of the variance in parasite species richness after correction for study effort and phylogenetic influences (Poulin, 1997), not much better than the 8% found in the present study.

Nevertheless, there are other ways of expressing parasite species richness that would take into account host length. The ratio of parasite species richness to host body length provides such as measure, where the number of parasite species known from a fish host is expressed as a number per unit host length. Just like 'raw' parasite species richness (see Fig. 2), parasite species richness per unit host length is positively related with study effort, but not as strongly (freshwater species: $r^2 = 0.078$; marine species: $r^2 = 0.036$; both $P < 0.0005$).

The true comparison of parasite diversity between Canadian and New Zealand fish species involves the above measures corrected for either or both study effort and host body length. Using residuals from the regressions in Fig. 2, I found differences in parasite species richness corrected for study effort between Canadian and New Zealand fish, for both freshwater (two-tailed *t*-test: $t = 2.822$, d.f. = 153, $P = 0.0054$) and marine species ($t = 3.055$, d.f. = 334, $P = 0.0024$). As seen in Fig. 3(a), on average Canadian fish species harbour more parasite species, and New Zealand fish harbour fewer, than expected based on our general knowledge of their biology. The exact same pattern emerges if parasite species richness per unit host length, corrected for study effort, is used instead of raw species richness (freshwater fish: $t = 3.017$, d.f. = 153, $P = 0.003$; marine fish: $t = 6.320$, d.f. = 153, $P = 0.0001$; Fig. 3b). Thus, for a given host body size and a given study effort, we have found more parasite species on Canadian fish than on New Zealand fish.

One possible confounding influence might come from the different phylogenetic origins of the New Zealand and Canadian fish fauna. Life history and ecological features of different host species are obviously linked with their phylogenetic relationships, with closely related host species likely to resemble each other more so than distantly related host species. Closely related host species are also likely to have similar parasite faunas, and it is crucial to take phylogenetic relationships into account when trying to determine which host features are associated with diverse parasite faunas (Poulin, 1995, 1997; Morand, 2000). Here, I am only trying to assess and compare the mean parasite species richness in fish species from different areas, and not to link it with any host traits. Still, a more conservative test would be to focus only on marine fish species common to both Canada and New Zealand. There were only 4 of those in the data bases searched: *Antimora rostrata*, *Mola mola*, *Xiphias gladius*, and *Thunnus alalunga*. More parasite species have been reported in Canadian than in New Zealand waters for the first three of these four species, but this does not allow for a robust statistical test. At the genus level, there are 18 genera of marine fish represented in both New Zealand and Canadian waters: *Anguilla* (only marine for part of their life cycle), *Alepocephalus*, *Antimora*, *Argentina*, *Bathylagus*, *Brama*, *Conger*, *Coryphaenoides*, *Lepidion*, *Macrourus*, *Merluccius*, *Mola*, *Nezumia*, *Notacanthus*, *Scomber*, *Thunnus*, *Trachyrhynchus*, and *Xiphias*. Most are only represented in one area by a single species, but taking average values computed across the two to three congeneric species present in some cases, we find a very weak tendency for Canadian fish to harbour more parasite species than their New Zealand counterparts (paired two-tailed t-test: $t = 1.928$, d.f. = 17, $P = 0.0707$). The average difference, back calculated from log-transformed data, is an extra two parasite species per host species in Canadian fish compared with New Zealand fish. However, using instead measures of parasite species richness corrected for unequal study effort among host species (i.e. the residuals from the regression in Fig. 2b), this small difference disappears ($t = 0.978$, d.f. = 17, $P = 0.3416$). Thus, the overall difference in parasite diversity between New Zealand and Canadian fish may be due, in part, to the different phylogenetic composition of their fish faunas.

This may be even more relevant to freshwater fish than to marine fish. Compared to that of Canada, the New Zealand freshwater fish fauna is not only poor in species, but it is also less taxonomically diverse. It is dominated by two families, the Eleotridae and Galaxiidae, neither of which occurs in North America. If, for whatever reason, these fish taxa are hosts to fewer parasites than Canadian freshwater fish taxa, then they cannot really be compared, and the differences reported here are merely artefacts. New Zealand freshwater fish are also geographically isolated compared to Canadian fish, another factor that may contribute to the low diversity of parasite they harbour, per unit of host length and for a given study effort.

In contrast, marine fish species of New Zealand and Canada consist of roughly the same higher taxa (orders and families), and their open habitat does not limit the spread and exchanges of parasites. The diversity of parasites harboured by New Zealand and Canadian marine fish should be approximately the same, unless there are fundamental differences between the two areas. One such difference may be the range of latitudes over which the two countries stretch: Canada (and the fish sampled along its coastline) extends to higher latitudes than New Zealand, about 45–70° N compared to 34–47° S. There is some evidence that marine fish species at lower latitudes harbour greater numbers of ectoparasite species (Poulin & Rohde, 1997; Rohde & Heap, 1998; Rohde, 2002), but this trend does not exist for endoparasites (Rohde & Heap, 1998; Rohde, 2002), nor is it apparent for any type of parasites in freshwater fishes (Choudhury & Dick, 2000; Poulin, 2001). If there were such a latitudinal gradient in parasite species diversity, it would act against the differences reported here, at least for ectoparasites. In any event, the results presented earlier, i.e. the higher parasite species richness in Canadian fish compared to New Zealand fish after correcting for both study effort and fish size, remain unchanged when ectoparasites and endoparasites are treated separately (unpubl. data). Therefore, the present results are not merely the product of latitudinal differences. Other biogeographical processes, however, may have shaped the parasite faunas of marine fish (see Hoberg & Klassen, 2002) and may be in part responsible for the differences observed between New Zealand and Canadian fishes.

The difference in parasite species richness between New Zealand and Canadian fish is corrected for study effort. Therefore, taking into account how much is known about the fish in general, more parasite species have been recorded on Canadian than on New Zealand fish species. The cause for the difference may be a discrepancy in the relative number of specific investigations of fish parasites between the two countries. Looking at the publication rate of records of fish parasites for Canadian fish (from Margolis & Arthur, 1979; McDonald & Margolis, 1995) and New Zealand fish (from Hewitt & Hine, 1972; Hine *et al*., 2000), it is clear that relatively more effort has gone into the study of Canadian fish parasites than their New Zealand counterparts (Fig. 4). The records listed in the checklists include not only surveys of parasites in wild fish populations, but also other types of investigations, such as studies of the pathological responses of fish to infection, or ultrastructural studies of the parasites themselves. Still, they reflect the effort that has gone in the study of the fish parasite fauna in the two countries. Because of its greater number of fish species and its larger human population (and thus larger pool of scientists), the number of records for Canada is higher than that for New Zealand (1573 and 211, respectively). But it is the shapes of the cumulative number of published records over time that show an unexpected difference (Fig. 4). The rate of studies on fish parasites in Canada has increased markedly in the 1970s, whereas that for New Zealand has not.

The known diversity of parasites in New Zealand freshwater fish is probably not too far off the real value; there are fewer parasite species per freshwater fish species in New Zealand than Canada, but geographical isolation and other factors can explain

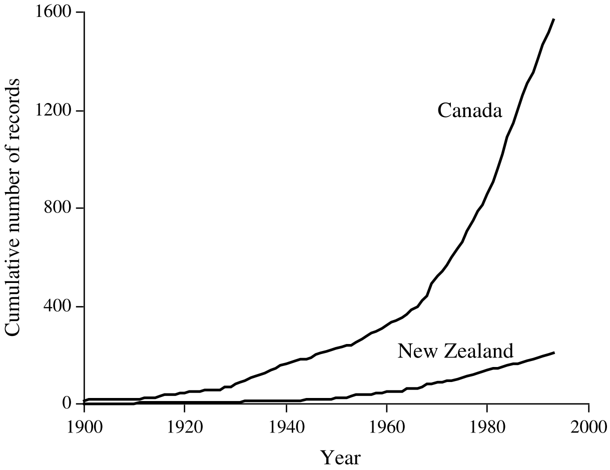

Figure 4 Cumulative number of published records of fish parasites as a function of time for both the Canadian and New Zealand fish fauna. Numbers of records for each year were obtained from checklists of parasites of Canadian (Margolis & Arthur, 1979; McDonald & Margolis, 1995) and New Zealand (Hewitt & Hine, 1972; Hine *et al*., 2000) fish species.

this. The parasite faunas of marine fish species, however, should be more comparable. Assuming that Canadian values apply to New Zealand fish species, we can extrapolate that, at a minimum, there are approximately two and a half species of parasites per marine fish species left to be discovered in New Zealand. In other words, we probably only know 55% of the parasite faunas of marine fish species that have been studied in New Zealand waters; of course, many fish species are yet to be examined for parasites, so this figure is a gross underestimate. At the present rate, it would take several centuries to achieve a more or less complete tally of all metazoan parasites of marine fish in New Zealand waters. If we were to archive this diversity, and understand its role in the functioning of marine ecosystems, in time to incorporate it in our plans to preserve marine biological resources, we would need to accelerate our rate of study by an order of magnitude. The situation is no doubt much worse with respect to the parasite faunas of coastal marine fish from many countries in Africa, Asia and Latin America, as well as most oceanic island nations, which do not have the resources necessary to survey the biodiversity of free-living organisms, let alone that of parasites. A huge international effort is required to properly document fish parasite biodiversity worldwide. Clearly, this will not happen in the near future, and we will have to tackle marine conservation issues with grossly incomplete information about fish parasites.

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