Parasites as biological tags of fish stocks: a meta-analysis of their discriminatory power

ROBERT POULIN* *and* TSUKUSHI KAMIYA

Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand

(*Received 7 July 2013; revised 30 July 2013; accepted 31 July 2013; first published online 24 October 2013*)

SUMMARY

The use of parasites as biological tags to discriminate among marine fish stocks has become a widely accepted method in fisheries management. Here, we first link this approach to its unstated ecological foundation, the decay in the similarity of the species composition of assemblages as a function of increasing distance between them, a phenomenon almost universal in nature. We explain how distance decay of similarity can influence the use of parasites as biological tags. Then, we perform a meta-analysis of 61 uses of parasites as tags of marine fish populations in multivariate discriminant analyses, obtained from 29 articles. Our main finding is that across all studies, the observed overall probability of correct classification of fish based on parasite data was about 71%. This corresponds to a two-fold improvement over the rate of correct classification expected by chance alone, and the average effect size ($Zr = 0{\cdot}463$) computed from the original values was also indicative of a medium-to-large effect. However, none of the moderator variables included in the meta-analysis had a significant effect on the proportion of correct classification; these moderators included the total number of fish sampled, the number of parasite species used in the discriminant analysis, the number of localities from which fish were sampled, the minimum and maximum distance between any pair of sampling localities, etc. Therefore, there are no clear-cut situations in which the use of parasites as tags is more useful than others. Finally, we provide recommendations for the future usage of parasites as tags for stock discrimination, to ensure that future applications of the method achieve statistical rigour and a high discriminatory power.

Key words: biological tags, fisheries, stock discrimination, distance decay of similarity, meta-analysis, multivariate discriminant analysis.

INTRODUCTION

Discriminating between distinct populations of the same species of commercially-exploited fish is essential not only to work out their dynamics and manage their long-term sustainability, but also to identify violations of fishing rights (Hilborn and Walters, 1992; Evans and Grainger, 2002). Among other natural methods to discriminate between fish stocks, such as meristic analyses and genetic studies, the use of parasites as biological tags has gained wide acceptance in recent decades (Williams *et al*. 1992; MacKenzie, 2002). The rationale underlying the use of parasites as tags is that fish harbouring a given parasite species come from (or at least have spent some time in) geographical areas where this parasite is endemic. The more parasite species with different endemic areas are considered simultaneously, the more information can be obtained about the area of origin or past movements of fish hosts (MacKenzie and Abaunza, 1998).

Although now in wide usage in fisheries science, fish stock discrimination based on parasite infections is yet to come under close scrutiny in terms of its power and limitations. From an ecological perspective, and as explicitly acknowledged before (Timi *et al*. 2010; Vales *et al*. 2011; Braicovich *et al*. 2012), the reliability of parasites as biological tags is underpinned by the almost universal decay in the similarity of the species composition of assemblages as a function of increasing distance between them (Nekola and White, 1999). Although this pattern is seen across all taxa and biomes, its strength is known to be influenced by a range of factors (Soininen *et al*. 2007). Similarly, the usefulness of parasites as tags for stock discrimination is unlikely to be the same in all situations. Also, from a quantitative perspective, there has been no global synthesis of the discriminatory power of parasites to identify correctly which stocks individual fish come from. In other areas of applied or fundamental parasite ecology, comparative analyses and meta-analysis have been extremely useful by providing quantitative assessments of interspecific patterns and effect sizes, e.g. the overall strength of well-researched relationships between two variables (Morand and Poulin, 2003; Poulin and Forbes, 2012). We currently lack an overall assessment of the discriminatory power of parasites as biological tags for fish stocks, and of what factors can significantly influence this power.

* Corresponding author: Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand. Tel: +64 3 479-7983. Fax: +64 3 479-7584. E-mail: robert.poulin@otago.ac.nz

Parasitology (2015), **142**, 145–155.
doi:10.1017/S0031182013001534

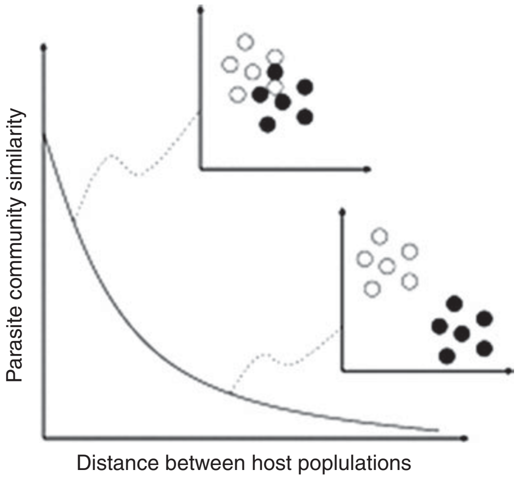

Fig. 1. Graphical representation of the exponential decay in parasite community similarity as a function of distance. Each point on the curve represents the pairwise similarity in species composition (based either on presence–absence data or on abundance data) between two parasite communities for a given geographical distance between them. The two smaller insets illustrate the expected outcomes of any type of discriminant analysis between fish from two populations that are either relatively close or distant to each other. The axes represent the main discriminant functions based on parasite community composition, and the symbols represent individual fish from the two populations.

Here, we address these general issues to offer an overview of the usefulness of parasites as tags for fish stock discrimination. First, we review the ecological basis for the use of parasites as reliable tags of fish populations. Our aim is to identify factors that should *a priori* influence how useful parasites can be and situations in which they should work best. Second, we conduct a systematic quantitative analysis of published studies using parasites as tags for the discrimination of marine fish populations. This was done by using a meta-analytical approach within a taxonomic framework, to account for the non-independence of different fish species based on their various levels of phylogenetic relatedness. This allowed us to determine if there are situations in which parasites are more useful, and which of the candidate factors identified in the first part of the article affect the discriminatory power of parasites. Our overall goal is to carry out a rigorous test of the usefulness of parasites as tags for fish stock discrimination and identify circumstances, if any, where their use is particularly recommended.

ECOLOGICAL BASIS OF PARASITES AS POPULATION TAGS

On any level, the similarity between two localities decreases with increasing distance between them. Thus, in both terrestrial and marine systems, the abiotic characteristics of a locality and the composition of its biota are generally very similar to those of nearby localities within a radius of a few kilometres, but very different from those that are hundreds or thousands of kilometres away. This obvious pattern is the foundation for the large-scale species turnover that accounts for the geographical distribution of living organisms (Nekola and White, 1999; Morlon *et al*. 2008). In quantitative terms, a decrease of similarity with distance corresponds to a decrease in the proportion of species shared by two communities as a function of the geographical distance between them (Fig. 1). The shape of this relationship is almost always exponential (or linear in log-space), such that the decrease in similarity is very steep initially but at greater distances similarity between two communities is almost invariably low.

There are no reasons to expect different patterns in parasite communities than those seen in free-living organisms. Most parasite species generally occur only in some populations of their host species. Also, among host populations where they do occur, their abundance can vary widely, especially if the host populations are distant from each other (Poulin, 2006). Pairwise distance between host populations is often the best predictor of the similarity between their parasite communities (Poulin and Morand, 1999). Therefore, not surprisingly, an exponential decay in similarity has been documented for the parasite communities of various host species, with this pattern being the general rule (Poulin, 2003, 2007; Krasnov *et al*. 2005; Poulin and Krasnov, 2010). The decay in similarity of parasite communities also applies to marine fish species, in spite of the open nature of oceanic environments (Oliva and González, 2005; Pérez-del-Olmo *et al*. 2009; Thieltges *et al*. 2010; Timi *et al*. 2010; Poulin *et al*. 2011). In the context of parasites as biological tags of fish stocks, the exponential decay pattern characteristic of parasite communities suggests that in a discriminant analysis (see Fig. 1), the power of parasites to distinguish accurately among fish from different populations would improve with increasing distances between those populations.

Several mechanisms can produce a decrease of the similarity in species composition between two communities with an increase of the distance between them. These fall into three general classes of mechanisms that are not mutually exclusive (Soininen *et al*. 2007). First, community similarity may decrease with distance simply because the similarity of climatic and physicochemical variables also decreases with distance (e.g. Steinitz *et al*. 2006). Different species have different ranges of abiotic factors that they can tolerate. The free-living infective stages of helminth parasites of fish, for instance, can only survive within narrow and species-specific ranges of environmental conditions such as water temperature or salinity (Pietrock and Marcogliese, 2003). This can lead to a gradual turnover of species in geographical space, with the species occurring in different localities reflecting the spatially changing local conditions. Importantly, because of the shape of the exponential decay curve (Fig. 1), similarity between two communities is more sensitive to the distance between them on smaller spatial scales, suggesting that there may be a minimum pairwise distance between localities below which fish parasites would be useless as biological tags of host populations.

Second, the physical nature of the environment can either facilitate or impede the dispersal of organisms among localities. Assuming that different parasite species have similar rates of dispersal, we would expect that similarity of parasite communities would decrease at a low and even rate in oceanic environments presenting no major physical barriers to dispersal. In contrast, community similarity should decrease more abruptly and rapidly in fragmented landscapes with major physical discontinuities, such as freshwater habitats where lakes and rivers are separated by land (Poulin and Krasnov, 2010). Thus, on small spatial scales, the dispersal of fish parasites, and therefore the homogenization of parasite communities over space, should be more likely in marine fish species, where populations are potentially connected. This again argues against the usefulness of parasites as tags on small spatial scales.

Third, even in environments with no barriers to dispersal, community similarity would also decrease with distance because of the limited dispersal of parasites, whether through their own power or via host movements. Different species have different dispersal capabilities. The free-living infective stages of parasites generally have extremely limited mobility, and on a geographical scale, their direct dispersal abilities are irrelevant. It is the indirect dispersal of parasites via host movements that vary greatly among species. For instance, parasite species using fish as intermediate hosts and birds as definitive hosts should achieve more extensive dispersal than those using the same fish as their final hosts. Parasites with simple (one-host) life-cycles, such as copepods or monogeneans parasitic on fish, have no dispersal route beyond that provided by their host's movements. We might thus expect different rates of decrease in community similarity with increasing distance for different subsets of parasite assemblages, depending on their life-cycle characteristics (see Karvonen and Valtonen, 2004; Fellis and Esch, 2005; Thieltges *et al*. 2009). Parasite taxa with limited dispersal potential and therefore greater endemicity would appear to be better candidates as tags for fish stocks, because similarity in their assemblages should decay rapidly as a function of distance. Interestingly, MacKenzie and Abaunza (1998) also recommend parasites with simple life-cycles, such as monogeneans or copepods, as ideal tags for fish populations, but for completely different reasons. However, it has been pointed out that monogeneans and copepods may be of limited value as biological tags, because they are generally short-lived and show marked temporal variation in abundance (Mosquera *et al*. 2003; Lester and MacKenzie, 2009), traits that may offset their limited dispersal. MacKenzie and Abaunza (1998) also point out that the parasites most widely used as tags are larval anisakid nematodes. Not only is the identification of these larval nematodes to the species level a real challenge (Mattiucci and Nascetti, 2008), they also use highly-mobile marine mammals as their definitive hosts, which *a priori* should improve their dispersal and limit their usefulness as discriminating tags. Nevertheless, larval anisakids still appear to be reliable tags in many studies.

The three general processes described above (species turnover along environmental gradients, dispersal constraints imposed by the environment, and species differences in dispersal) probably always combine to various degrees to generate observed patterns of distance decay in similarity. Soininen *et al*. (2007) have conducted a meta-analysis of the results of available studies on distance decay relationships (the vast majority on free-living organisms, mostly vascular plants in terrestrial systems), in order to identify key properties of organisms or environments associated with the rates of decrease of similarity with distance. They found that the observed rate of decay depends on the spatial scale of the study, the geographical area in which a study is performed, and the dispersal abilities of the organisms studied, although there were interactions among these factors and the resulting trends were complex. Nevertheless, these findings imply that using differences in community composition to distinguish between localities (or differences in parasite assemblages to distinguish between fish stocks) will not be equally effective under all circumstances.

Based on the universal decay in community similarity with increasing distance underpinning most biogeographical patterns, and the ecological processes summarized above and known to shape this decay, we can make two predictions about the usefulness of parasites as biological tags of marine fish populations. First, the type of parasites considered as tags should matter: studies including parasite taxa with simple one-host life-cycles (and limited dispersal) should yield more reliable results than those using solely helminths with complex life-cycles. Second, the spatial scale of a study should also matter: the greater the distance among fish populations, the more reliably parasites can be used to discriminate among those populations. In the following section, we address these predictions by performing a systematic, quantitative review of the literature on parasites as biological tags of fish stocks. Using a meta-analytical approach, we test the above two predictions as well as the influence of other potentially confounding variables, to assess the overall usefulness of parasites as tags, and identify the situations (if any) where they work best.

META-ANALYSIS OF STUDIES OF PARASITES AS TAGS

Methods: Data compilation

A dataset was compiled from published studies reporting results of multivariate discriminant analyses for the geographical separation of marine fish stocks using parasite communities as biological tags. The keywords 'parasit* AND stock* AND (tag* OR indicator* OR geographical variation* OR identification* OR segregation*)' were used for searches on ISI Web of Science in May 2013, which yielded 353 results. Articles were individually assessed for relevance to the present meta-analysis, firstly by their title and then by the content of their abstract. To be included, a study needed to have used multivariate discriminant analysis and to report the proportion of fish that could be correctly assigned to their original group based on parasite data. Articles on parasite tags of non-fish species that also used multivariate discriminant analysis were excluded as they were rare exceptions (e.g. Balbuena and Raga, 1994; Oliva and Sánchez, 2005). In the end, 29 studies on marine fish were retained. However, many of those studies provided more than one entry in the dataset, because either they examined more than one fish species, reported separate analyses on different subsets of parasites for the same fish species, or performed separate analyses before and after pooling fish from different localities. Therefore, the dataset included 61 effect sizes (see below).

In a multivariate discriminant analysis, the observed proportion of correct classification should be assessed in light of the probability of correct classification expected by chance alone. This issue has long been recognized in the ecological literature (Titus *et al*. 1984), but the probability of correct classification due to chance is rarely reported in studies of parasites as biological tags (only 10 out of 29 articles included in the present study). For our meta-analysis, the expected proportion of correct classification was therefore calculated using the proportional chance criterion, which is a simple method for accounting for differences in sample sizes between the groups being compared (see Tabachnick and Fidell, 2001, p. 489). Specifically, the expected proportion of correct classification by chance alone was computed as:

$$\frac{\sum_{i=1}^{G} n_i^2 / N}{N}$$

where n_i is the number of fish in group i, G is the number of fish groups corresponding to different sampling localities, and N is the total number of fish sampled. For each study, the overall proportion (across all localities) of correct classification (i.e. the proportion of all fish correctly assigned to their group of origin based on parasite data) was then compared against the expected proportion using the effect size calculator for proportional data provided by Lipsey and Wilson (2001). This computed a standard effect size r, i.e. a correlation coefficient, which in this case indicates how effective the observed classification is compared to random chance alone. The higher the value of r, the more accurate the classification of fish into their groups based on parasite data compared to the expected proportion of correctly assigned fish based on chance alone.

For each study, additional information was recorded on several other variables that were treated as moderators in the meta-regression analyses described below (which are equivalent to predictors in a multiple regression framework). These included the following seven variables: (1) the total number of fish sampled; (2) the number of parasite species used in the discriminant analysis; (3) the type of parasites involved, i.e. either endoparasites only or endo- and/or ectoparasites; (4) the number of localities from which fish were sampled; (5) the minimum distance between any pair of sampling localities; (6) the maximum distance between any pair of sampling localities; and (7) whether or not cross-validation was used for classification, which corresponds to classifying each fish by the functions derived from all fish other than that fish.

Meta-analytic procedures

Meta-analyses along with associated statistical analyses were carried out in R 2.15.1 (R Development Core Team, 2012). We used the *MCMCglmm* package (Hadfield, 2010) to account for correlated structures arising from study identity (Nakagawa and Santos, 2012); that is, we included study identity as a random effect in meta-analytic models because some studies contributed multiple effect sizes that may not always be independent of each other. Since higher-order taxonomy and phylogeny of fish, especially of Perciformes, are poorly resolved (Li *et al*. 2009), conducting a more robust phylogenetic meta-analysis proved difficult. Therefore, a random effect which contained fish species nested within fish family was included in the analysis in order to control for and assess the influence of taxonomic relationships between the fish taxa included. The raw correlation coefficients were transformed to Fisher's z-transformed correlation coefficients, Zr, and their sampling variances based on the number of fish sampled were computed using equations provided by Nakagawa and Cuthill (2007), thereby weighting for differences in sample sizes among studies. A measure of heterogeneity, I^2 (i.e. the degree of inconsistency among effect sizes)

Table 1. Summary of the dataset used in the meta-analysis. The proportion of correct classification is the observed one based on discriminant analysis using parasite data, with the correct classification expected by chance alone also shown

Family	Species	Proportion correct (by chance)	*r*	No. fish	No. parasite species	No. localities	Minimum – Maximum distance (km)	Reference
Atherinopsidae	*Odontesthes smitti*	0·5575[a] (0·335)	0·245	174	15[b]	3	65–814	Carballo *et al*. (2012)
Carangidae	*Trachurus lathami*	0·755[a] (0·397)	0·391	273	27[b]	3	136–2281	Braicovich *et al*. (2012)
Citharidae	*Citharus linguatula*	0·551 (0·333)	0·241	160	7[b]	3	64–457	Marques *et al*. (2006)
Eleginopidae	*Eleginops maclovinus*	0·975 (0·500)	0·71	40	24[b]	2	71–71	Brickle and MacKenzie (2007)
Eleginopidae	*Eleginops maclovinus*	0·897 (0·373)	0·595	192	7[b]	3	29–211	Henriquez *et al*. (2011)
Eleginopidae	*Eleginops maclovinus*	0·851 (0·373)	0·529	192	4[b]	3	29–211	Henriquez *et al*. (2011)
Eleginopidae	*Eleginops maclovinus*	0·727 (0·373)	0·382	192	4	3	29–211	Henriquez *et al*. (2011)
Eleginopidae	*Eleginops maclovinus*	0·527 (0·373)	0·17	192	2	3	29–211	Henriquez *et al*. (2011)
Gadidae	*Gadus morhua*	0·74[a] (0·500)	0·277	221	4	2	88–261	McClelland and Melendy (2011)
Gadidae	*Gadus morhua*	0·57[a] (0·500)	0·077	249	4[b]	2	98–175	McClelland and Melendy (2011)
Gadidae	*Gadus morhua*	0·52[a] (0·251)	0·308	249	4	4	88–492	McClelland and Melendy (2011)
Gadidae	*Micromesistius australis*	0·879[a] (0·504)	0·476	90	5	2	1105–1105	Niklitschek *et al*. (2010)
Gadidae	*Micromesistius australis*	1[a,c] (0·504)	0·709	90	17[b]	2	1105–1105	Niklitschek *et al*. (2010)
Hemiramphidae	*Hyporhamphus melanochir*	0·496 (0·111)	0·494	274	14[b]	9	22–302	Hutson *et al*. (2011)
Hemiramphidae	*Hyporhamphus melanochir*	0·383 (0·111)	0·404	274	4[b]	9	22–302	Hutson *et al*. (2011)
Macrouridae	*Nezumia pulchella*	0·72 (0·255)	0·486	217	18[b]	4	188–858	Salinas *et al*. (2008)
Macrouridae	*Nezumia pulchella*	0·79 (0·397)	0·433	217	18[b]	3	188–858	Salinas *et al*. (2008)
Merlucciidae	*Merluccius gayi*	0·582 (0·203)	0·424	922	18[b]	5	375–3302	Oliva and Ballon (2002)
Merlucciidae	*Merluccius gayi*	0·843 (0·483)	0·434	922	18[b]	3	529–3302	Oliva and Ballon (2002)
Merlucciidae	*Merluccius hubbsi*	0·7645 (0·261)	0·521	344	26[b]	4	246–1544	Sardella and Timi (2004)
Mullidae	*Mullus surmuletus*	0·803 (0·333)	0·501	300	17[b]	3	193–425	Ferrer-Castello *et al*. (2007)
Nototheniidae	*Dissostichus eleginoides*	0·55 (0·510)	0·044	629	9	2	707–1517	Oliva *et al*. (2008)
Percophidae	*Percophis brasiliensis*	0·8644 (0·266)	0·62	177	9	4	132–1207	Braicovich and Timi (2008)
Percophidae	*Percophis brasiliensis*	0·9322 (0·398)	0·641	177	9	3	245–1207	Braicovich and Timi (2008)
Phycidae	*Urophycis tenuis*	0·78[a] (0·520)	0·31	253	4[b]	2	160–353	Melendy *et al*. (2005)
Phycidae	*Urophycis tenuis*	0·72[a] (0·343)	0·402	396	5[b]	3	61–457	Melendy *et al*. (2005)
Pinguipedidae	*Pseudopercis semifasciata*	0·93 (0·380)	0·647	100	18[b]	3	136–836	Timi and Lanfranchi (2009)
Pinguipedidae	*Pinguipes brasilianus*	0·87 (0·334)	0·581	154	11[b]	3	87–739	Timi *et al*. (2008)
Pinguipedidae	*Pinguipes brasilianus*	0·7968 (0·294)	0·526	310	9[b]	4	87–920	Timi *et al*. (2009)
Pleuronectidae	*Reinhardtius hippoglossoides*	0·597[a] (0·112)	0·562	231	5	9	125–1938	Arthur and Albert (1993)
Pleuronectidae	*Reinhardtius hippoglossoides*	0·996[a] (0·332)	0·864	231	5	4	125–1938	Arthur and Albert (1993)
Pleuronectidae	*Reinhardtius hippoglossoides*	0·49 (0·167)	0·396	608	6	6	730–1972	Boje *et al*. (1997)
Pleuronectidae	*Reinhardtius hippoglossoides*	0·77 (0·391)	0·413	608	6	3	730–2373	Boje *et al*. (1997)
Pleuronectidae	*Hippoglossus stenolepis*	0·28[a] (0·080)	0·381	240	8	15	108–4291	Blaylock *et al*. (2003)
Pleuronectidae	*Hippoglossus stenolepis*	0·63[a] (0·276)	0·381	240	8	4	190–4291	Blaylock *et al*. (2003)
Pleuronectidae	*Hippoglossus stenolepis*	0·83[a] (0·428)	0·459	240	8	3	331–4291	Blaylock *et al*. (2003)
Pleuronectidae	*Hippoglossus stenolepis*	0·87[a] (0·567)	0·41	240	8	2	331–4291	Blaylock *et al*. (2003)
Pleuronectidae	*Hippoglossus stenolepis*	0·44[a] (0·211)	0·286	62	8	5	164–2862	Blaylock *et al*. (2003)
Pleuronectidae	*Hippoglossus stenolepis*	0·66[a] (0·394)	0·289	62	8	3	164–2862	Blaylock *et al*. (2003)
Pleuronectidae	*Hippoglossus platessoides*	0·79[a] (0·510)	0·334	232	2	2	121–279	McClelland and Melendy (2007)
Pleuronectidae	*Hippoglossus platessoides*	0·7[a] (0·531)	0·195	204	4	2	141–165	McClelland and Melendy (2007)
Pleuronectidae	*Hippoglossus platessoides*	0·48[a] (0·262)	0·255	437	4	4	121–497	McClelland and Melendy (2007)
Pleuronectidae	*Platichthys flesus*	0·663 (0·526)	0·156	160	15[b]	2	64–359	Marques *et al*. (2006)
Pleuronectidae	*Pleuronectes americanus*	0·84[a] (0·251)	0·604	190	7	4	94–526	McClelland *et al*. (2005)
Polynemidae	*Polydactylus macrochir*	0·83 (0·250)	0·59	265	9	5	198–1763	Moore *et al*. (2012)
Polynemidae	*Polydactylus macrochir*	0·445 (0·253)	0·231	252	9	5	73–695	Moore *et al*. (2012)

Table 1. (*Cont.*)

Family	Species	Proportion correct (by chance)	*r*	No. fish	No. parasite species	No. localities	Minimum – Maximum distance (km)	Reference
Polynemidae	*Polydactylus macrochir*	0·576 (0·249)	0·362	248	9	5	75–618	Moore *et al*. (2012)
Polynemidae	*Polydactylus macrochir*	0·784 (0·253)	0·547	342	10	6	122–2050	Moore *et al*. (2012)
Sciaenidae	*Micropogonias furnieri*	0·71 (0·220)	0·512	248	41[b]	5	689–3412	Luque *et al*. (2010)
Sciaenidae	*Micropogonias furnieri*	0·8 (0·405)	0·438	248	41[b]	3	764–3412	Luque *et al*. (2010)
Sciaenidae	*Cynoscion guatucupa*	0·753 (0·395)	0·391	299	18[b]	3	477–2139	Timi *et al*. (2005)
Sciaenidae	*Cynoscion guatucupa*	0·667 (0·397)	0·293	297	10[b]	3	477–2139	Timi *et al*. (2005)
Scophthalmidae	*Lepidorhombus boscii*	0·51 (0·372)	0·153	160	10[b]	3	64–457	Marques *et al*. (2006)
Sebastidae	*Helicolenus dactylopterus*	0·888[a] (0·439)	0·538	665	10[b]	3	966–1428	Sequeira *et al*. (2010)
Soleidae	*Microchirus azevia*	0·565 (0·500)	0·072	160	19[b]	2	97–304	Marques *et al*. (2006)
Soleidae	*Solea lascaris*	0·677 (0·334)	0·367	160	21[b]	3	64–457	Marques *et al*. (2006)
Soleidae	*Solea senegalensis*	0·507 (0·333)	0·195	160	22[b]	3	64–457	Marques *et al*. (2006)
Soleidae	*Solea solea*	0·446 (0·344)	0·117	160	12[b]	3	64–457	Marques *et al*. (2006)
Sparidae	*Boops boops*	0·93[a] (0·375)	0·649	100	6[b]	3	429–820	Power *et al*. (2005)
Sparidae	*Boops boops*	0·94[a] (0·375)	0·668	100	3	3	429–820	Power *et al*. (2005)
Triakidae	*Mustelus manazo*	0·92 (0·501)	0·558	25	8	2	579–579	Yamaguchi *et al*. (2003)

[a] Studies that used cross-validation.

[b] Ectoparasites included.

[c] Because the observed proportion was 1, it was adjusted to 0·975 for effect size calculation according to Fox and Weisberg (2011).

was also calculated from the meta-regression model. Based on *Zr* and the corresponding sampling variances, a random-effects meta-analysis was employed to estimate the overall effect size quantifying the proportion of correct classification relative to chance. Here, we note that *r* (*Zr*) values of 0·1 (0·1), 0·3 (0·31) and 0·5 (0·55) are considered as small, medium and large effects, respectively (Cohen, 1988) while I^2 values of 25, 50 and 55% are considered as low, moderate or high, respectively (Higgins *et al*. 2003).

A meta-regression model was then constructed in an attempt to account for the observed heterogeneity in the data and examine effect sizes at separate levels for each moderator listed above. As in a standard regression, this serves to determine whether any of the moderators (number of fish, number of parasite species, number of localities, minimum or maximum distance between localities, etc.) explains a significant amount of heterogeneity among studies, and thus affects the likelihood that parasites prove to be useful tags in any given situation. Finally, we checked for evidence of publication bias in our dataset. This could be manifested, for example, by under-representation of studies with weak effect sizes, as authors of such studies may decide not to attempt to publish them or editors may turn them down (the 'file drawer' effect). We assessed potential publication bias visually for asymmetry in funnel plots of both raw effect sizes and 'meta-analytic residuals' against the precision (or the inverse of sampling standard errors). We also quantitatively assessed publication bias using a rank correlation test between meta-analytic residuals and the inverse of sample variance (cf. Begg and Mazumdar, 1994).

RESULTS

Overall, the observed probability of correct classification was 71·08% across 61 effect sizes from 29 articles (Table 1). This marks a two-fold improvement over the rate of correct classification expected by chance alone, which was 35·32% on average. Furthermore, the average effect size was $r = 0{\cdot}414$ ($Zr = 0{\cdot}463$), which is indicative of a medium-to-large effect. In other words, using parasites provides a medium-to-large improvement on the correct classification of fish based on chance alone. However, there was overall a large amount of heterogeneity detected among effect sizes ($I^2 = 92{\cdot}56\%$), which was explained largely through study identity ($I^2 = 55{\cdot}70\%$) while taxonomic relationships explained little ($I^2 = 0{\cdot}59\%$); the residual heterogeneity, i.e. the unexplained inconsistency among data points, was 36·3%.

Weak effect sizes were frequently reported for studies in which the minimum distance between sampling localities was small (Fig. 2). However, the meta-regression models identified little contributions from any of the moderators, which indicates that the proportion of correct classification is affected little by the moderators included in our analysis (Table 2; Fig. 2). No publication bias was detected based on the residuals of the meta-regression model through visual inspection of the funnel plot and based on a correlation test (tau = 0·027, $P = 0·765$).

DISCUSSION

Our meta-analysis indicates that parasites are generally reliable biological tags that can improve understanding of many marine fish stocks. Using parasite data, the probability of correctly assigning a fish to its original stock is double what one can achieve by chance alone (71% *vs* 35%); in terms of formal effect sizes, this is a medium-to-large improvement over chance. We could not identify any significant moderator variables, i.e. any situations where, because of the details of a particular study, parasites would be more reliable tags than under other circumstances. It must be pointed out that heterogeneity among the effect sizes included in the analysis was fairly large (over 90%). Therefore, the results must be interpreted with some caution because when heterogeneity is substantial, the reliability of the mean effect size as an estimate is likely to be low. Nevertheless, as they stand, the findings suggest that parasites are useful and reliable stock indicators for marine fish under most circumstances.

The usefulness of parasites as biological tags can also be assessed by comparing their performance against that of other markers. For instance, in some studies there is good agreement between the stock delineation based on parasites and that based on genetic data (McClelland *et al*. 2005), suggesting that the two methods are equivalent in terms of their power to distinguish among fish stocks but this is not always the case. For example, based on parasitological studies of orange roughy, *Hoplostethus atlanticus*, Lester *et al*. (1988) discriminated five stocks from Australian waters and three from New Zealand waters. Using different genetic markers (microsatellites, cytochrome *c* oxidase subunit I and cytochrome *b* sequences), Varela *et al*. (2012, 2013) were unable to distinguish among orange roughy caught off the coasts of Australia and New Zealand, and only found genetic differentiation on a global scale, when comparing samples from the Atlantic with those from Australia and New Zealand. On small to intermediate

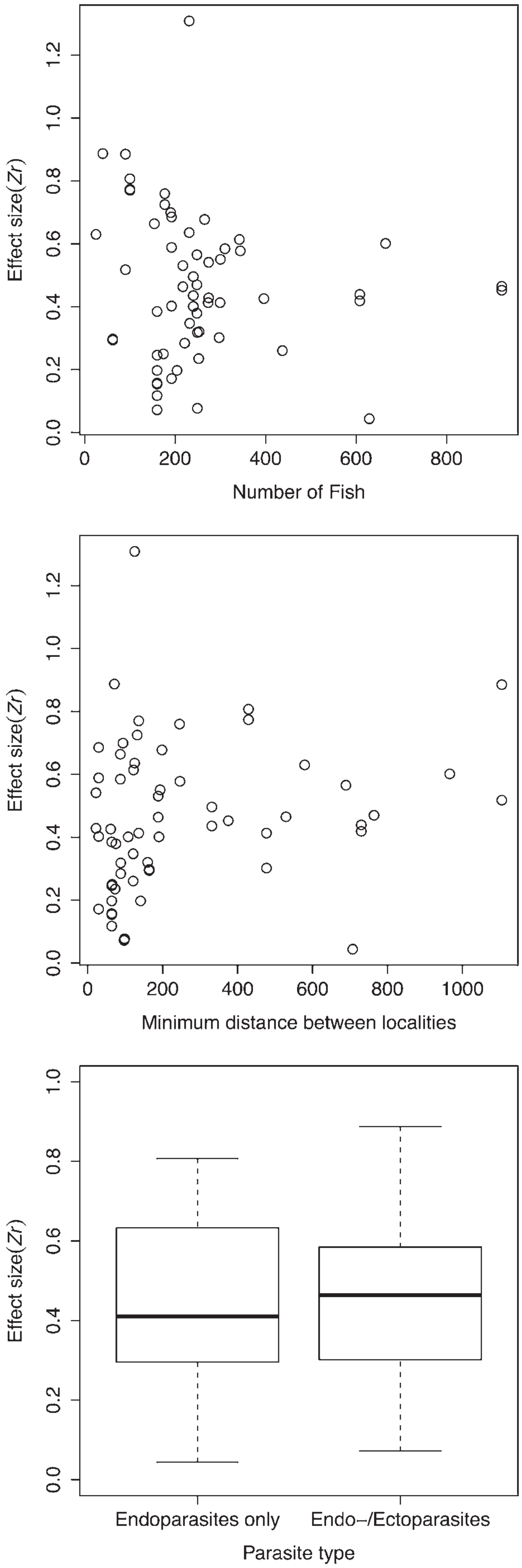

Fig. 2. Relationships between effect sizes (Fisher's z-transformed correlation coefficients, Zr) corresponding to the improvement in correct classification of fish using parasites compared to classification based on chance alone, and three potential moderators: the total number of fish sampled, the minimum distance between any pair of sampling localities, and whether the parasites used were endoparasites only ($N = 28$) or endo- and/or ectoparasites ($N = 33$).

Table 2. Results of a Bayesian linear mixed model (MCMCglmm) evaluating the relationship between the effect size of correct classification of fish based on parasite data, calculated as Zr, and potential predictors such as the number of fish examined, the number of parasite species included in analysis, the number of localities involved, whether or not ectoparasites were included, the minimum and maximum distance between sampled localities and whether cross-validation was used to compute the proportion of correct classification

	Posterior mean	Lower 95% CI	Upper 95% CI	MCMC *P*-value
(Intercept)	0·4657	0·3110	0·6083	< 0·0001
Number of fish	− 0·0727	− 0·1692	0·0127	0·1140
Number of parasite species	0·0054	− 0·0833	0·1002	0·9140
Number of localities	− 0·0042	− 0·0630	0·0479	0·8700
Ectoparasites	0·0716	− 0·0861	0·2147	0·3640
Minimum distance	0·0149	− 0·0909	0·1036	0·7430
Maximum distance	0·0894	− 0·0299	0·2222	0·1540
Cross-validation	0·0105	− 0·1738	0·2170	0·9290

Data points based only on endoparasites are included in the intercept. Posterior means are equivalent to regression coefficient estimates, 95% CI (credible intervals) are equivalent to 95% confidence intervals and MCMC *P*-values are comparable to standard *P*-values.

geographical scales (10^2–10^3 km), it seems that low-frequency dispersal of adult fish is enough to lead to genetic homogenization of different populations, whereas from an ecological perspective (as indicated by parasites) these may be considered as different stocks. Just as the use of parasites as biological tags is founded upon the distance decay of similarity in community composition, the use of genetic markers is founded upon the well-documented genetic isolation by distance, corresponding to a decrease in the genetic similarity between conspecific individuals with an increase in the geographic distance between their location. For marine fish, the 'isolation-by-distance' relationship is non-linear and dependent on the spatial scale considered (Bradbury and Bentzen, 2007), a pattern reminiscent of what is seen with distance decay of similarity (Soininen *et al.* 2007). It may be that at scales of 10^2–10^3 km, parasites are better to discriminate among stocks than genetic markers. Given some of the issues associated with the use of fish morphometry for stock discrimination (Cadrin, 2000), parasites may also be preferable to this method on most spatial scales.

We used the meta-analysis to test for the influence of several moderators, but in particular we wanted to test two predictions derived from ecological studies of the distance decay of community similarity. These were that studies including ectoparasites with simple life-cycles (and limited dispersal) should achieve more accurate classification of fish to their original groups than those using solely helminths with complex life-cycles, and that the greater the distance among fish populations sampled, the more reliably parasites can be used to discriminate among those populations. We found no strong support for either prediction. However, it must be noted that when ectoparasites are used in studies of parasites as biological tags, they are usually utilized in combination with endoparasitic helminths, with the latter group greatly outnumbering the former. It therefore becomes impossible to rule out that ectoparasites allow for better classification of their fish hosts. Thus we echo MacKenzie and Abaunza (1998) and recommend that whenever possible, parasites with simple life-cycles, such as monogeneans or copepods, should be used in stock discrimination studies, provided that the species in questions have a life-span long enough to dampen temporal fluctuations in abundance. With respect to distance among sampled localities, although the effect of the minimum distance between localities was not significant in the meta-analysis, most of the studies reporting weak effect sizes (small improvement in the correct classification of fish using parasites relative to chance alone) had small minimum distances among localities (see Fig. 2). It thus seems that the risk that parasites will be of little use as tags is greater when a study has a small spatial scale. We therefore encourage other researchers to use parasites with caution when some of their sampled locations are separated by 10^2 km or less.

Our systematic review of the literature on the use of parasites as biological tags to discriminate among fish stocks has also led us to consider making further recommendations for future research in this area. First, we suggest that all future studies should report the expected proportion of correct classification of fish based on chance alone. This is easy to compute (we provide the formula earlier), and yet it only appears in about one-third of the published studies included in our meta-analysis. The probability of correctly assigning fish to their original groups by chance is never zero. It is therefore important to present it as a benchmark against which the performance of the classification based on parasite data can be measured (see also Titus *et al.* 1984; Solow, 1990).

Second, and related to the above, it is common practice to lump fish from distinct areas into a single larger group following an initial analysis, and then repeat the discriminant analysis with fewer fish groups. Although there may be good biological or oceanographical reasons to justify the lumping, the statistical consequences are worth considering. For instance, the expected proportion of correct classification by chance alone generally increases *more* after lumping fish groups than that based on parasite data, due to increased inequality in sample sizes among groups. Thus any apparent improvement in discriminatory power when using fewer host groups may be an artefact. We therefore suggest that the results of discriminant analyses on a reduced number of fish groups be interpreted with caution.

Third, although the number of fish sampled was not a significant moderator in our meta-analysis (see Fig. 2), it is worth noting that the guidelines for multivariate discriminant analysis (see Tabachnick and Fidell, 2001) state that the sample size of each group, i.e. each locality sampled or fish stock, should exceed the number of parasite species included in the analysis. Some studies included in our compilation break this rule, or come very close to breaking it. As a rule of thumb, more than 50 fish per group would be needed to reliably estimate covariance (Tabachnick and Fidell, 2001), and we recommend that future studies of parasites as biological tags aim at this minimum sample size.

Fourth, in many studies, the level of taxonomic resolution for the parasites recovered is often limited, especially for larval helminths. This is not a problem unique to studies of parasites as biological tags of fish stocks, but applies more generally to all surveys of parasites (Poulin and Leung, 2010). However, in the context of stock discrimination, it seems that a greater effort to identify parasites to the species level could only improve the correct classification of fish into their respective stocks. We therefore encourage researchers in this area to make an extra effort toward full taxonomic identification of parasites.

In conclusion, the use of parasites as biological tags to distinguish among fish stocks has become a well-established and widely accepted methodology in fisheries management (Williams *et al.* 1992; MacKenzie, 2002). It is founded on a universal ecological phenomenon, the decay in the similarity of species composition among communities with increasing distance between them. Our meta-analysis validates the usefulness of parasites as tags of fish stocks, finding that this method allows a two-fold improvement in the rate of correct classification compared to random classification. Of course, it is not the perfect method: it requires the destructive sampling of many fish and is time-consuming but, regardless of these drawbacks, if the recommendations made above are followed, then the use of parasites as biological tags should continue to be the low-cost method of choice for the discrimination of marine fish stocks.

ACKNOWLEDGEMENTS

We thank Juan Timi and Ken MacKenzie for an invitation to contribute to this special issue. We are also grateful to Haseeb Randhawa, Juan Timi and an anonymous reviewer for constructive comments on an earlier version of this paper.

REFERENCES

Arthur, J. R. and Albert, E. (1993). Use of parasites for separating stocks of Greenland halibut (*Reinhardtius hippoglossoides*) in the Canadian northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 2175–2181. doi: 10.1139/f93-243.

Balbuena, J. and Raga, J. (1994). Intestinal helminths as indicators of segregation and social structure of pods of long-finned pilot whales (*Globicephala melas*) off the Faeroe Islands. *Canadian Journal of Zoology* **72**, 443–448.

Begg, C. B. and Mazumdar, M. (1994). Operating characteristics of a bank correlation test for publication bias. *Biometrics* **50**, 1088–1101. doi: 10.2307/2533446.

Blaylock, R. B., Margolis, L. and Holmes, J. C. (2003). The use of parasites in discriminating stocks of Pacific halibut (*Hippoglossus stenolepis*) in the northeast Pacific. *Fishery Bulletin* **101**, 1–9.

Boje, J., Riget, F. and Køie, M. (1997). Helminth parasites as biological tags in population studies of Greenland halibut (*Reinhardtius hippoglossoides* (Walbaum)), in the north-west Atlantic. *ICES Journal of Marine Science* **54**, 886–895. doi: 10.1006/jmsc.1997.0214.

Bradbury, I. R. and Bentzen, P. (2007). Non-linear genetic isolation by distance: implications for dispersal estimation in anadromous and marine fish populations. *Marine Ecology Progress Series* **340**, 245–257.

Braicovich, P. E., Luque, J. L. and Timi, J. T. (2012). Geographical patterns of parasite infracommunities in the rough scad, *Trachurus lathami* Nichols, in the southwestern Atlantic ocean. *Journal of Parasitology* **98**, 768–777. doi: 10.1645/ge-2950.1.

Braicovich, P. E. and Timi, J. T. (2008). Parasites as biological tags for stock discrimination of the Brazilian flathead *Percophis brasiliensis* in the south-west Atlantic. *Journal of Fish Biology* **73**, 557–571. doi: 10.1111/j.1095-8649.2008.01948.x.

Brickle, P. and MacKenzie, K. (2007). Parasites as biological tags for *Eleginops maclovinus* (Teleostei : Eleginopidae) around the Falkland Islands. *Journal of Helminthology* **81**, 147–153. doi: 10.1017/s0022149×07750514.

Cadrin, S. X. (2000). Advances in morphometric identification of fishery stocks. *Reviews in Fish Biology and Fisheries* **10**, 91–112.

Carballo, M. C., Cremonte, F., Navone, G. T. and Timi, J. T. (2012). Similarity in parasite community structure may be used to trace latitudinal migrations of *Odontesthes smitti* along Argentinean coasts. *Journal of Fish Biology* **80**, 15–28. doi: 10.1111/j.1095-8649.2011.03125.x.

Cohen, J. (1988). *Statistical Power Analysis for the Behavioral Sciences*. Lawrence Erlbaum Associates Inc., Hillsdale, New Jersey.

Evans, D. and Grainger, R. (2002). Gathering data for resource monitoring and fisheries management. In *Handbook of Fish Biology and Fisheries*, Vol. 2 (ed. Hart, P. J. B. and Reynolds, J. D.), pp. 84–102. Blackwell Publishing, Oxford.

Fellis, K. J. and Esch, G. W. (2005). Variation in life cycle affects the distance decay of similarity among bluegill sunfish parasite communities. *Journal of Parasitology* **91**, 1484–1486.

Ferrer-Castello, E., Raga, J. A. and Aznar, F. J. (2007). Parasites as fish population tags and pseudoreplication problems: the case of striped red mullet *Mullus surmuletus* in the Spanish Mediterranean. *Journal of Helminthology* **81**, 169–178. doi: 10.1017/s0022149×07729553.

Fox, J. and Weisberg, S. (2011). *An R Companion to Applied Regression*. Sage Publications, Thousand Oaks, California.

Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software* **33**, 1–22.

Henriquez, V. P., González, M. T., Licandeo, R. and Carvajal, J. (2011). Metazoan parasite communities of rock cod *Eleginops maclovinus* along southern Chilean coast and their use as biological tags at a local spatial scale. *Journal of Fish Biology* **79**, 1851–1865. doi: 10.1111/j.1095-8649.2011.03126.x.

Higgins, J. P. T., Thompson, S. G., Deeks, J. J. and Altman, D. G. (2003). Measuring inconsistency in meta-analyses. *British Medical Journal* **327**, 557–560. doi: 10.1136/bmj.327.7414.557.

Hilborn, R. and Walters, C. J. (1992). *Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty*. Chapman and Hall, New York.

Hutson, K. S., Brock, E. L. and Steer, M. A. (2011). Spatial variation in parasite abundance: evidence of geographical population structuring in southern garfish *Hyporhamphus melanochir*. *Journal of Fish Biology* **78**, 166–182. doi: 10.1111/j.1095-8649.2010.02849.x.

Karvonen, A. and Valtonen, E. T. (2004). Helminth assemblages of whitefish (*Coregonus lavaretus*) in interconnected lakes: similarity as a function of species-specific parasites and geographical separation. *Journal of Parasitology* **90**, 471–476.

Krasnov, B. R., Shenbrot, G. I., Mouillot, D., Khokhlova, I. S. and Poulin, R. (2005). Spatial variation in species diversity and composition of flea assemblages in small mammalian hosts: geographic distance or faunal similarity? *Journal of Biogeography* **32**, 633–644.

Lester, R. J. G. and MacKenzie, K. (2009). The use and abuse of parasites as stock markers for fish. *Fisheries Research* **97**, 1–2.

Lester, R. J. G., Sewell, K. B., Barnes, A. and Evans, K. (1988). Stock discrimination of orange roughy, *Hoplostethus atlanticus*, by parasite analysis. *Marine Biology* **99**, 137–143.

Li, B., Dettai, A., Cruaud, C., Couloux, A., Desoutter-Meniger, M. and Lecointre, G. (2009). RNF213, a new nuclear marker for acanthomorph phylogeny. *Molecular Phylogenetics and Evolution* **50**, 345–363. doi: 10.1016/j.ympev.2008.11.013.

Lipsey, M. W. and Wilson, D. B. (2001). *Practical Meta-analysis*. Sage Publications, Thousand Oaks, California.

Luque, J. L., Cordeiro, A. S. and Oliva, M. E. (2010). Metazoan parasites as biological tags for stock discrimination of whitemouth croaker *Micropogonias furnieri*. *Journal of Fish Biology* **76**, 591–600. doi: 10.1111/j.1095-8649.2009.02515.x.

MacKenzie, K. (2002). Parasites as biological tags in population studies of marine organisms: an update. *Parasitology* **124**, S153–S163.

MacKenzie, K. and Abaunza, P. (1998). Parasites as biological tags for stock discrimination of marine fish: a guide to procedures and methods. *Fisheries Research* **38**, 45–56.

Marques, J. F., Teixeira, C. M. and Cabral, H. N. (2006). Differentiation of commercially important flatfish populations along the Portuguese coast: evidence from morphology and parasitology. *Fisheries Research* **81**, 293–305. doi: 10.1016/j.fishres.2006.05.021.

Mattiucci, S. and Nascetti, G. (2008). Advances and trends in the molecular systematics of anisakid nematodes, with implications for their evolutionary ecology and host–parasite co-evolutionary processes. *Advances in Parasitology* **66**, 47–148.

McClelland, G. and Melendy, J. (2007). Use of endoparasitic helminths as tags in delineating stocks of American plaice (*Hippoglossoides platessoides*) from the southern Gulf of St. Lawrence and Cape Breton Shelf. *Fishery Bulletin* **105**, 180–188.

McClelland, G. and Melendy, J. (2011). Use of parasites as tags in delineating stocks of Atlantic cod (*Gadus morhua*) from the southern Gulf of St. Lawrence and the Cape Breton Shelf. *Fisheries Research* **107**, 233–238. doi: 10.1016/j.fishres.2010.10.022.

McClelland, G., Melendy, J., Osborne, J., Reid, D. and Douglas, S. (2005). Use of parasite and genetic markers in delineating populations of winter flounder from the central and south-west Scotian Shelf and north-east Gulf of Maine. *Journal of Fish Biology* **66**, 1082–1100. doi: 10.1111/j.1095-8649.2005.00659.x.

Melendy, J., McClelland, G. and Hurlbut, I. (2005). Use of parasite tags in delineating stocks of white hake (*Urophycis tenuis*) from the southern Gulf of St. Lawrence and Cape Breton Shelf. *Fisheries Research* **76**, 392–400. doi: 10.1016/j.fishres.2005.07.006.

Moore, B. R., Welch, D. J., Newman, S. J. and Lester, R. J. G. (2012). Parasites as indicators of movement and population connectivity of a non-diadromous, tropical estuarine teleost: king threadfin *Polydactylus macrochir*. *Journal of Fish Biology* **81**, 230–252. doi: 10.1111/j.1095-8649.2012.03335.x.

Morand, S. and Poulin, R. (2003). Phylogenies, the comparative method and parasite evolutionary ecology. *Advances in Parasitology* **54**, 281–302.

Morlon, H., Chuyong, G., Condit, R., Hubbell, S., Kenfack, D., Thomas, D., Valencia, R. and Green, J. L. (2008). A general framework for the distance-decay of similarity in ecological communities. *Ecology Letters* **11**, 904–917.

Mosquera, J., de Castro, M. and Gómez-Gesteira, M. (2003). Parasites as biological tags of fish populations: advantages and limitations. *Comments on Theoretical Biology* **8**, 69–91.

Nakagawa, S. and Cuthill, I. C. (2007). Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biological Reviews* **82**, 591–605. doi: 10.1111/j.1469-185X.2007.00027.x.

Nakagawa, S. and Santos, E. S. A. (2012). Methodological issues and advances in biological meta-analysis. *Evolutionary Ecology* **26**, 1253–1274. doi: 10.1007/s10682-012-9555-5.

Nekola, J. C. and White, P. S. (1999). The distance decay of similarity in biogeography and ecology. *Journal of Biogeography* **26**, 867–878.

Niklitschek, E. J., Secor, D. H., Toledo, P., Lafon, A. and George-Nascimento, M. (2010). Segregation of SE Pacific and SW Atlantic southern blue whiting stocks: integrating evidence from complementary otolith microchemistry and parasite assemblage approaches. *Environmental Biology of Fishes* **89**, 399–413. doi: 10.1007/s10641-010-9695-9.

Oliva, M. E. and Ballon, I. (2002). Metazoan parasites of the Chilean hake *Merluccius gayi gayi* as a tool for stock discrimination. *Fisheries Research* **56**, 313–320. doi: 10.1016/s0165-7836(01)00329-0.

Oliva, M. E., Fernandez, I., Oyarzun, C. and Murillo, C. (2008). Metazoan parasites of the stomach of *Dissostichus eleginoides* Smitt 1898 (Pisces : Notothenidae) from southern Chile: a tool for stock discrimination? *Fisheries Research* **91**, 119–122. doi: 10.1016/j.fishres.2007.11.012.

Oliva, M. E. and González, M. T. (2005). The decay of similarity over geographical distance in parasite communities of marine fishes. *Journal of Biogeography* **32**, 1327–1332.

Oliva, M. E. and Sánchez, M. F. (2005). Metazoan parasites and commensals of the northern Chilean scallop *Argopecten purpuratus* (Lamarck, 1819) as tools for stock identification. *Fisheries Research* **71**, 71–77.

Pérez-del-Olmo, A., Fernández, M., Raga, J. A., Kostadinova, A. and Morand, S. (2009). Not everything is everywhere: the distance decay of similarity in a marine host-parasite system. *Journal of Biogeography* **36**, 200–209.

Pietrock, M. and Marcogliese, D. J. (2003). Free-living endohelminth stages: at the mercy of environmental conditions. *Trends in Parasitology* **19**, 293–299.

Poulin, R. (2003). The decay of similarity with geographical distance in parasite communities of vertebrate hosts. *Journal of Biogeography* **30**, 1609–1615.

Poulin, R. (2006). Variation in infection parameters among populations within parasite species: intrinsic properties versus local factors. *International Journal for Parasitology* **36**, 877–885.

Poulin, R. (2007). Are there general laws in parasite ecology? *Parasitology* **134**, 763–776.

Poulin, R., Blanar, C. A., Thieltges, D. W. and Marcogliese, D. J. (2011). The biogeography of parasitism in sticklebacks: distance, habitat differences and the similarity in parasite occurrence and abundance. *Ecography* **34**, 540–551.

Poulin, R. and Forbes, M. R. (2012). Meta-analysis and research on host-parasite interactions: past and future. *Evolutionary Ecology* **26**, 1169–1185.

Poulin, R. and Krasnov, B. R. (2010). Similarity and variability of parasite assemblages across geographical space. In *The Biogeography of Host-Parasite Interactions* (ed. Morand, S. and Krasnov, B. R.), pp. 115–127. Oxford University Press, Oxford.

Poulin, R. and Leung, T. L. F. (2010). Taxonomic resolution in parasite community studies: are things getting worse? *Parasitology* **137**, 1967–1973.

Poulin, R. and Morand, S. (1999). Geographic distances and the similarity among parasite communities of conspecific host populations. *Parasitology* **119**, 369–374.

Power, A. M., Balbuena, J. A. and Raga, J. A. (2005). Parasite infracommunities as predictors of harvest location of bogue (*Boops boops* L.): a pilot study using statistical classifiers. *Fisheries Research* **72**, 229–239. doi: 10.1016/j.fishres.2004.10.001.

R Development Core Team (2012). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Salinas, X., González, M. T. and Acuna, E. (2008). Metazoan parasites of the thumb grenadier *Nezumia pulchella*, from the south-eastern Pacific, off Chile, and their use for discrimination of host populations. *Journal of Fish Biology* **73**, 683–691. doi: 10.1111/j.1095-8649.2008.01967.x.

Sardella, N. H. and Timi, J. T. (2004). Parasites of Argentine hake in the Argentine Sea: population and infracommunity structure as evidence for host stock discrimination. *Journal of Fish Biology* **65**, 1472–1488. doi: 10.1111/j.0022-1112.2004.00572.x.

Sequeira, V., Gordo, L. S., Neves, A., Paiva, R. B., Cabral, H. N. and Marques, J. F. (2010). Macroparasites as biological tags for stock identification of the bluemouth, *Helicolenus dactylopterus* (Delaroche, 1809) in Portuguese waters. *Fisheries Research* **106**, 321–328. doi: 10.1016/j.fishres.2010.08.014.

Soininen, J., McDonald, R. and Hillebrand, H. (2007). The distance decay of similarity in ecological communities. *Ecography* **30**, 3–12.

Solow, A. (1990). A randomization test for misclassification probability in discriminant analysis. *Ecology* **71**, 2379–2382.

Steinitz, O., Heller, J., Tsoar, A., Rotem, D. and Kadmon, R. (2006). Environment, dispersal and patterns of species similarity. *Journal of Biogeography* **33**, 1044–1054.

Tabachnick, B. G. and Fidell, L. S. (2001). *Using Multivariate Statistics*. Allyn and Bacon, Boston.

Thieltges, D. W., Dolch, T., Krakau, M. and Poulin, R. (2010). Salinity gradient shapes distance decay of similarity among parasite communities in three marine fishes. *Journal of Fish Biology* **76**, 1806–1814.

Thieltges, D. W., Ferguson, M. A. D., Jones, C. S., Krakau, M., de Montaudouin, X., Noble, L. R., Reise, K. and Poulin, R. (2009). Distance decay of similarity among parasite communities of three marine invertebrate hosts. *Oecologia* **160**, 163–173.

Timi, J. T. and Lanfranchi, A. L. (2009). The metazoan parasite communities of the Argentinean sandperch *Pseudopercis semifasciata* (Pisces: Perciformes) and their use to elucidate the stock structure of the host. *Parasitology* **136**, 1209–1219. doi: 10.1017/s0031182009990503.

Timi, J. T., Lanfranchi, A. L. and Etchegoin, J. A. (2009). Seasonal stability and spatial variability of parasites in Brazilian sandperch *Pinguipes brasilianus* from the Northern Argentine Sea: evidence for stock discrimination. *Journal of Fish Biology* **74**, 1206–1225. doi: 10.1111/j.1095-8649.2009.02190.x.

Timi, J. T., Lanfranchi, A. L., Etchegoin, J. A. and Cremonte, F. (2008). Parasites of the Brazilian sandperch *Pinguipes brasilianus* Cuvier: a tool for stock discrimination in the Argentine Sea. *Journal of Fish Biology* **72**, 1332–1342. doi: 10.1111/j.1095-8649.2008.01800.x.

Timi, J. T., Lanfranchi, A. L. and Luque, J. L. (2010). Similarity in parasite communities of the teleost fish *Pinguipes brasilianus* in the southwestern Atlantic: infracommunities as a tool to detect geographical patterns. *International Journal for Parasitology* **40**, 243–254.

Timi, J. T., Luque, J. L. and Sardella, N. H. (2005). Parasites of *Cynoscion guatucupa* along South American Atlantic coasts: evidence for stock discrimination. *Journal of Fish Biology* **67**, 1603–1618. doi: 10.1111/j.1095-8649.2005.00867.x.

Titus, K., Mosher, J. A. and Williams, B. K. (1984). Chance-corrected classification for use in discriminant analysis: ecological applications. *American Midland Naturalist* **111**, 1–7.

Vales, D. G., Garciá, N. A., Crespo, E. A. and Timi, J. T. (2011). Parasites of a marine benthic fish in the Southwestern Atlantic: searching for geographical recurrent patterns of community structure. *Parasitology Research* **108**, 261–272.

Varela, A. I., Ritchie, P. A. and Smith, P. J. (2012). Low levels of global genetic differentiation and population expansion in the deep-sea teleost *Hoplostethus atlanticus* revealed by mitochondrial DNA sequences. *Marine Biology* **159**, 1049–1060.

Varela, A. I., Ritchie, P. A. and Smith, P. J. (2013). Global genetic population structure in the commercially exploited deep-sea teleost orange roughy (*Hoplostethus atlanticus*) based on microsatellite DNA analysis. *Fisheries Research* **140**, 83–90.

Williams, H. H., MacKenzie, K. and McCarthy, A. M. (1992). Parasites as biological indicators of the population biology, migrations, diet and phylogenetics of fish. *Reviews in Fish Biology and Fisheries* **2**, 144–176.

Yamaguchi, A., Yokoyama, H., Ogawa, K. and Taniuchi, T. (2003). Use of parasites as biological tags for separating stocks of the starspotted dogfish *Mustelus manazo* in Japan and Taiwan. *Fisheries Science* **69**, 337–342. doi: 10.1046/j.1444-2906.2003.00626.x.