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Variation in the intraspecific relationship between fish length and intensity of parasitic infection: biological and statistical causes

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In a meta-analysis, the overall mean correlation between fish length and the intensity of parasitic infections derived from 76 different host–parasite species was positive but weak and non-significant, following corrections for sample size. Whether the parasites were acquired by ingestion or by skin contact had no influence on the strength of the relationship. For cestodes, larval digeneans, and gnathiid isopods, however, the mean correlation between fish length and intensity of infection was significant. Some statistical parameters influenced the strength of the raw correlations computed within samples and thus led to over- or under-estimation of the true relationship. Sample size correlated negatively with the value of the correlation coefficients, whereas range in both fish lengths and intensities of infection correlated positively with the value of the correlation coefficients. Distinguishing between statistical noise and the biological processes shaping the size *v.* intensity relationship will be important if this relationship is to be incorporated into fish population models.

Key words: helminths; meta-analysis; parasitism; sample size; size-dependent infection.

INTRODUCTION

Empirical evidence supports a role for parasites in the population dynamics of their hosts (Scott, 1988; Scott & Dobson, 1989; Grenfell & Gulland, 1995). For metazoan parasites, often only the most heavily parasitized hosts incur higher mortality rates than do uninfected hosts. Models of host–parasite population dynamics are all based on the premise that parasite-induced host mortality is a function of the intensity of infection by metazoan parasites, or the number of parasites per host (Anderson & May, 1978, 1979; May & Anderson, 1978, 1979; Anderson & Gordon, 1982). It is common to infer that heavy parasite infections cause mortality from the truncated aggregated distribution of parasites among hosts, in which fewer heavily infected hosts are observed than are predicted by the negative binomial distribution (Crofton, 1971; Gordon & Rau, 1982; Adjei *et al.,* 1986; Rousset *et al.*, 1996). Understanding how parasites are distributed among hosts in a population, and which part of the population is more susceptible to infection, becomes crucial for building realistic population models. In particular, it is essential in population dynamics models to link parasite-induced mortality with age-specific mortality (Gulland, 1987; Lorenzen, 1996), because intensity of infection is usually associated with host age or size.

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Table I. Data used in the meta-analysis of the relationship between fish length and intensity of infection

Parasite species	Fish species	Mean length		Intensity range	Sample size	*r*	Sources*
		mm	(range)				
Acanthocephala							
Pomphorhynchus laevis	*Pleuronectes flesus*	133	(77)	217	74	0·550	1
Neoechinorhynchus rutili	*Culaea inconstans*	39	(14)	14	88	0·361	2
Pomphorhynchus laevis	*Leuciscus cephalus*	240	(419)	206	216	0·771	3
Corynosoma sp.	*Merluccius gayi*	440	(—)	—	1172	0·126	4
Echinorhynchus salmonis	*Oncorhynchus tshawytscha*	700	(580)	1276	101	0·521	5
Acanthocephalus lucii	*Anguilla anguilla*	—	(—)	—	148	0·063	6
Longicollum alemniscus	*Acanthopagrus australis*	52	(29)	34	16	0·130	7
Neoechinorhynchus pungitius	*Culaea inconstans*	30	(43)	34	221	− 0·005	8
Cestoda							
Proteocephalus sp.	*Culaea inconstans*	30	(43)	3	27	0·369	8
Clestobothrium crassiceps	*Merluccius gayi*	440	(—)	—	1172	0·226	4
Lacistorhynchus tenuis	*Mustelus canis*	900	(810)	144	49	0·354	9
Diphyllobothrium sp.	*Salvelinus alpinus*	210	(300)	295	131	0·311	10
Prochristianella tumidula	*Mustelus canis*	900	(810)	32	49	0·383	9
Grillotia dollfusi	*Merluccius gayi*	440	(—)	—	1172	0·161	4
Calliobothrium lintoni	*Mustelus canis*	900	(810)	57	49	0·122	9
Calliobothrium verticillatum	*Mustelus canis*	900	(810)	63	49	0·130	9
Nematoda							
Rhabdochona canadensis	*Rhinichthys cataractae*	60	(96)	—	313	0·449	11
Pseudoterranova decipiens	*Merluccius gayi*	440	(—)	—	1172	0·225	4
Raphidascaris acus	*Lota lota*	161	(207)	44	52	0·340	12
Proleptus acutus	*Schroederichthys chilensis*	400	(350)	275	54	0·490	13
Contraceacum sp.	*Merluccius gayi*	440	(—)	—	1172	0·299	4
Anisakis sp.	*Merluccius gayi*	440	(—)	—	1172	0·601	4
Capillaria wickinsi	*Pleuronectes platessa*	300	(220)	—	43	0·124	14
Camallanus lacustris	*Anguilla anguilla*	550	(550)	12	460	0·419	15
Anisakis sp.	*Pleuronectes platessa*	300	(220)	—	39	0·236	14

Table I. *Continued*

Parasite species	Fish species	Mean length		Intensity range	Sample size	*r*	Sources*
		mm	(range)				
Nematoda *continued*							
Rhabdochona cotti	*Cottus bairdi*	58	(73)	7	218	0·260	16
Anisakis sp.	*Merluccius gayi*	380	(320)	73	120	0·780	17
Spinitectus gracilis	*Salmo trutta*	220	(140)	29	53	0·280	18
Eustrongylides sp.	*Bagrus docmac*	430	(514)	125	47	0·783	19
Cystidicoloides tenuissima	*Salvelinus fontinalis*	220	(140)	277	154	0·420	18
Cystidicoloides tenuissima	*Salmo trutta*	220	(140)	194	142	0·290	18
Hysterothylacium sp.	*Merluccius gayi*	440	(—)	—	1172	0·109	4
Eustrongylides tubifex	*Lepomis gibbosus*	80	(101)	15	800	0·057	20
Eustrongylides tubifex	*Ambloplites rupestris*	90	(92)	3	435	0·026	20
Haplonema hamatulum	*Lota lota*	161	(207)	56	35	0·350	12
Cystidicoloides tenuissima	*Salvelinus fontinalis*	161	(123)	4	17	0·610	21
Cystidicola farionis	*Osmerus mordax*	175	(87)	—	32	0·610	22
Cystidicola farionis	*Coregonus clupeaformis*	365	(305)	—	75	0·343	22
Cucullanus heterochrous	*Pleuronectes platessa*	300	(220)	—	257	− 0·099	14
Cystidicola farionis	*Oncorhynchus gorbuscha*	401	(94)	—	17	− 0·480	22
Cystidicoloides ephemeridarum	*Salvelinus fontinalis*	130	(150)	380	20	0·720	23
Phocanema sp.	*Merluccius gayi*	380	(320)	21	120	0·675	17
Cystidicola farionis	*Coregonus artedii*	343	(71)	—	19	0·420	22
Adult Digenea							
Aporocotyle wilhelmi	*Merluccius gayi*	440	(—)	—	1172	− 0·036	4
Zoogonoides viviparus	*Pleuronectes platessa*	300	(220)	504	211	0·112	14
Brachyphallus crenatus	*Salvelinus fontinalis*	153	(107)	230	79	0·568	21
Crepidostomum cooperi	*Salvelinus fontinalis*	145	(90)	49	30	0·400	21
Bunodera lucioperca	*Culaea inconstans*	30	(43)	7	62	0·176	8
Bunodera eucaliae	*Culaea inconstans*	30	(43)	33	312	0·050	8
Digenean sp.	*Limanda limanda*	155	(—)	—	74	0·081	24

Table I. *Continued*

Parasite species	Fish species	Mean length mm	(range)	Intensity range	Sample size	*r*	Sources*
Larval Digenea							
Diplostomum spathaceum	*Aplodinotus grunniens*	—	(—)	260	101	0·113	25
Diplostomum sp.	*Salvelinus alpinus*	210	(300)	900	131	0·423	10
Telogaster opisthorchis	*Galaxias vulgaris*	66	(49)	62	52	0·734	26
Telogaster opisthorchis	*Gobiomorphus breviceps*	55	(38)	255	46	0·302	27
Uvulifer sp.	*Phoxinus* sp.	48	(53)	216	601	0·750	28
Neascus sp.	*Rhinichthys cataractae*	57	(107)	—	821	0·350	11
Posthodiplostomum minimum	*Rhinichthys cataractae*	53	(108)	—	977	0·620	11
Posthodiplostomum minimum	*Fundulus zebrinus*	62	(40)	—	1219	0·230	29
Monogenea							
Dactylogyrus sp.	*Rutilus rutilus*	—	(—)	—	22	0·475	30
Anoplodiscus cirrusspiralis	*Pagrus auratus*	233	(173)	93	56	0·260	31
Lamellodiscus acanthopagri	*Acanthopagrus australis*	60	(75)	499	649	0·253	32
Pseudodactylogyrus sp.	*Anguilla anguilla*	210	(95)	59	30	0·680	33
Salsuginus thalkeni	*Fundulus zebrinus*	62	(40)	—	1219	0·040	29
Gyrodactylus callariatis	*Gadus morhua*	150	(236)	—	41	0·500	34
Gyrodactylus bulbacanthus	*Fundulus zebrinus*	62	(40)	—	1219	0·060	29
Gyrodactylus stableri	*Fundulus zebrinus*	62	(40)	—	1219	0·120	29
Copepoda							
Thersitina gasterostei	*Gasterosteus wheatlandi*	17	(13)	11	303	−0·015	35
Thersitina gasterostei	*Gasterosteus aculeatus*	18	(11)	8	287	0·158	35
Kroyeria carchariaeglauci	*Prionace glauca*	2150	(750)	1134	5	0·877	36

Table I. *Continued*

Parasite species	Fish species	Mean length		Intensity range	Sample size	*r*	Sources*
		mm	(range)				
Isopoda							
gnathiids	*Thalassoma lunare*	116	(—)	—	47	0·515	37
gnathiids	*Hemigymnus melapterus*	181	(—)	—	62	0·690	37
gnathiids	*Siganus doliatus*	152	(—)	—	29	0·571	37
gnathiids	*Scolopsis bilineatus*	122	(—)	—	31	0·346	37
gnathiids	*Chlorurus sordidus*	117	(—)	—	27	0·560	37
gnathiids	*Ctenochaetus striatus*	138	(—)	—	26	0·559	37
Mollusca							
Margaritifera margaritifera	*Salmo salar*	605	(350)	450	136	−0·029	38

—, Data unavailable.

*1, Munro *et al.* (1989); 2, McLennan & Shires (1995); 3, Brown (1986); 4, George-Nascimento (1996); 5, Muzzall (1989); 6, Kennedy & Moriarty (1987); 7, Roubal (1993); 8, Font (1983); 9, Cislo & Caira (1993); 10, Frandsen *et al.* (1989); 11, Muzzall *et al.* (1992); 12, Muzzall *et al.* (1987); 13, George-Nascimento & Vergara (1982); 14, Wickins & Macfarlane (1973); 15, Nie & Kennedy (1991); 16, Muzzall & Whelan (1995); 17, Carvajal *et al.* (1979); 18, Muzzall (1986); 19, Paperna (1974); 20, Measures (1988); 21, Black (1981); 22, Lankester & Smith (1980); 23, Greenwood & Baker (1987); 24, Siddall *et al.* (1994); 25, Leno & Holloway (1989); 26, Poulin (1993); 27, James & Poulin (1998); 28, Paradis & Chapleau (1994); 29, Janovy *et al.* (1997); 30, Siddall *et al.* (1997); 31, West & Roubal (1998); 32, Roubal (1994); 33, Buchmann (1989); 34, Appleby (1996); 35, Poulin (2000); 36, Benz & Dupre (1987); 37, Grutter & Poulin (1998); 38, Cunjak & McGladdery (1991).

In fish populations, intensity of infection by metazoan parasites increases with the age or size of fish hosts (Dogiel *et al*., 1958). The increase sometimes stops beyond a certain host age or size, but the positive relationship generally holds when several size classes are pooled. Older fish have had longer to accumulate parasites than have younger ones. Being larger, they provide more internal and external space for parasite establishment, but incur higher infection rates because they eat more parasitized prey and offer a larger contact area for skin-attaching parasites. Simple mathematical models have been developed to describe this (des Clers, 1991).

It should therefore be relatively easy to incorporate fish size as a determinant of both age-specific and parasite-induced mortality in models of fish population dynamics. However, the relationship between fish size and intensity of parasite infection, although usually positive, varies from statistically non-significant to very strong and highly significant. This variation may result from: the exact measure of, or the range of, fish sizes used; whether uninfected fish are included in the computations [i.e. whether abundance or intensity is used as a measure of parasite numbers; Bush *et al*. (1997)]; or from biological differences between different types of parasites. Metazoan parasites of fish belong to several different taxa; they are acquired by fish in different ways, and settle in different organs within their host, with different consequences for fish health. It is important to elucidate the factors responsible for the different size *v*. intensity relationships reported in the literature if parasitism is to be included as a component in models of fish population dynamics.

This study aimed to determine which biological, methodological or statistical variables influenced relationships between fish size and intensity of parasitic infections, using a meta-analysis of published relationships. The results provide a clearer overall picture of size-dependent (or age-dependent) patterns of parasitic infections in fish.

METHODS

Pearson's or Spearman's correlation coefficients between fish length and numbers of parasites per individual fish were obtained from 38 studies (Table I). Correlations computed across average values for different size classes were excluded to ensure that variation among individual fish within each size class was retained, and to avoid the other problems associated with lumping fish into size classes (Pacala & Dobson, 1988).

Correlations were included in the data set only if (1) they were derived from fish samples obtained in natural populations or infected in semi-natural conditions; (2) the sample size was given; (3) the length (L_T, L_S, or L_F) of fish was specified (correlations using fish mass were rare and thus excluded); and (4) it was specified whether uninfected fish were included in the computations. When possible, the mean and range in fish sizes, the median intensity of infection (judged more representative than the mean given the aggregated distribution of parasites), and the range of infection intensities were also recorded.

Parasites were classified as either acquired by ingestion or by skin contact. Ingested parasites (nematodes, acanthocephalans, cestodes and adult digeneans) may settle in the gut, viscera, muscles or nervous system of their host. Parasites acquired by contact with external surfaces include larval digeneans (metacercariae), which usually migrate within the fish to encyst in a variety of locations, and ectoparasitic monogeneans, copepods, gnathiid isopods, and larval stages (glochidia) of some freshwater bivalves.

In the meta-analysis, each host–parasite species combination was treated as an independent observation. Phylogenetic influences may reduce the statistical independence of related species (Harvey & Pagel, 1991). For instance, the intensity of infection by parasite species of one family might be more likely to be linked to host size than that of parasites in another family. Also, size-dependent infections might be likely to develop in fish species from certain families but not from others. As there are currently no methods allowing simultaneous corrections for phylogenies of hosts and of parasites in statistical analyses, different host–parasite species associations were treated as independent since no fish or parasite taxa were over-represented in the data set.

The meta-analytical procedures used here follow Hunter & Schmidt (1990). The overall strength of the relationship between fish size and intensity of infection (mean correlation coefficient) was computed by weighting each correlation coefficient for sample size:

$$\bar{r}=\Sigma[N_i(r_i)](\Sigma N_i)^{-1}$$

where N_i is the number of fish examined in study i and r_i is the correlation coefficient between fish size and intensity of infection in that study. The variance of $\bar{r}$ is $S_{\bar{r}}^2$:

$$S_{\bar{r}}^2=\Sigma[N_i(r_i-\bar{r})^2](\Sigma N_i)^{-1}.$$

It is actually the sum of the true variance S^2 and the variance stemming from sampling error, S_{e}^2. The latter is estimated by:

$$S_{\mathrm{e}}^2=(1-\bar{r}^2)^2(\bar{N}-1)^{-1}$$

where $\bar{N}$ is the average sample size. The true variance, S^2 [the variance among correlations, as opposed to the variance in the individual study correlations stemming from sampling error (Hunter & Schmidt, 1990)], is the difference between $S_{\bar{r}}^2$ and S_{e}^2. From S^2 we obtain the standard deviation, S, of $\bar{r}$. The ratio of $\bar{r}$ to S (Z score) indicates how many standard deviations away from zero (null hypothesis) is situated the mean correlation coefficient, and hence, the probability of observing such a mean correlation coefficient. Since most of the correlation coefficients included in the analysis were positive and many were significant, this test in itself is not very useful. However, the significance of the variance can also be estimated using the following χ^2 approximation:

$$\chi^2_{k-1}=(\Sigma N_i)(S^2)(1-\bar{r}^2)^{-2}$$

where k is the number of correlation coefficients. If there is significant variation among correlation coefficients, then other variables may be at work. The correlations can then be subdivided with respect to a categorical variable, and $\bar{r}$ and S^2 recalculated for each subset. The categorical variable has an effect if either the different $\bar{r}$ vary among subsets, or the variance in the subsets is smaller than that of the entire data set.

Other statistical tests were standard parametric tests. When necessary, continuous variables were log transformed to meet the assumptions of normality.

RESULTS

Correlation coefficients between fish length and intensity of infection were obtained for 76 different host–parasite species associations (Table I). A total of 42 fish species, from 37 genera and 24 families, were represented in the data set. The 66 parasite species belonged to several genera (Table I), so that no host or parasite taxon was over-represented in the data set.

Not surprisingly, the mean correlation coefficient across all 76 relationships was positive, although not statistically significant ($\bar{r}=0{\cdot}240$, $P=0{\cdot}25$). Thus, despite many individual relationships being strong ($r\geq 0{\cdot}5$), the overall mean correlation coefficient was weak. This was no doubt due to the significant

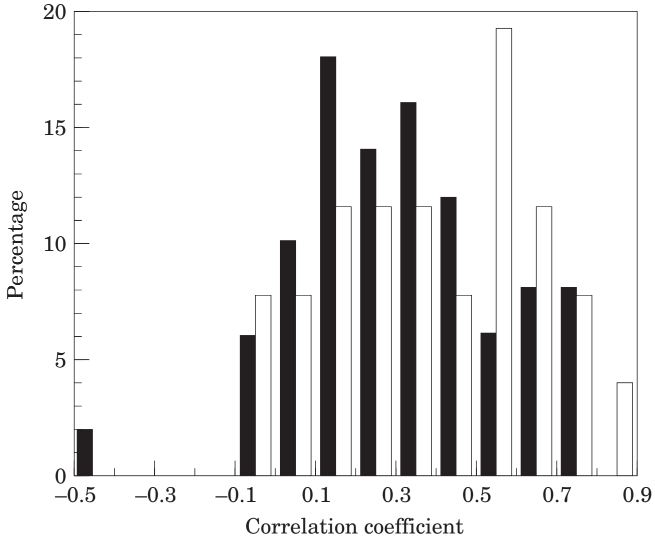

FIG. 1. Frequency distribution of correlation coefficient values among published relationships between fish length and intensity of parasitic infection. The 50 relationships involving ingested (■) parasites and the 26 relationships involving parasites acquired by skin contact (□) are presented separately.

variance among all correlations ($S^2=0{\cdot}044$, $P<0{\cdot}001$), suggesting that other variables affected the length *v.* intensity relationship. Raw correlations computed for parasites acquired by skin contact generally appeared stronger than those obtained for parasites acquired by ingestion (Fig. 1). However, after weighting for sample sizes, the mean correlation coefficients for these two groups of parasites were similar and not different from zero, again because of substantial variation among individual coefficients (Table II).

When parasites were grouped by taxa, the mean correlation between length and intensity was significant only where individual correlations varied little. Among ingested parasites, the mean correlation coefficient was significant only for cestodes (Table II), and among contact parasites, only for larval digeneans and gnathiid isopods (Table II). Insufficient information was available for molluscs and copepods for any definitive assessment. The final site of infection had no detectable influence on the correlation between fish length and intensity of parasitic infections.

Inclusion or not of uninfected fish, or the type of length measure used (L_T, L_S or L_F), did not influence the strength of the correlation between fish length and intensity of infection. However, log sample size (mean 319 fish examined per study, range 11–1219) correlated significantly and negatively ($r=-0{\cdot}332$, $P=0{\cdot}003$) with the strength of the raw correlation between fish length and infection intensity across all 76 coefficients (Fig. 2).

Across the 58 host–parasite combinations for which data were available, mean fish length and the range in fish lengths were strongly correlated ($r=0{\cdot}906$, $P<0{\cdot}0001$). Of these two variables, the log range in fish lengths correlated positively with the strength of the length *v.* intensity relationship [$r=0{\cdot}283$, $P=0{\cdot}031$; Fig. 3(a)]. Median intensity and the range in infection intensities were

TABLE II. Summary of the meta-analysis on the influence of mode of parasite acquisition and parasite taxonomy on the relationship between fish length and intensity of infection (see text for details)

Parasite type	No. of correlations	No. of species (no. of genera)	$\bar{r}$	S^2
Ingested parasites	50	43 (35)	0·229	0·0387**
Adult digeneans	7	7 (6)	0·037	0·0145**
Cestodes	8	8 (7)	0·205**	0·0003
Nematodes	27	21 (16)	0·285	0·0421**
Acanthocephalans	8	7 (6)	0·221	0·0500**
Skin-contact parasites	26	23 (15)	0·257	0·0508**
Larval digeneans	8	6 (5)	0·442*	0·0407**
Monogeneans	8	8 (6)	0·112	0·0078**
Molluscs	1	1 (1)	− 0·029	—
Gnathiids	6	6 (1)†	0·558**	0·0001
Copepods	3	2 (2)	0·076	0·0078

*$P<0·05$; **$P<0·001$.

†Species identity not available but likely to represent up to six species from at least one genus.

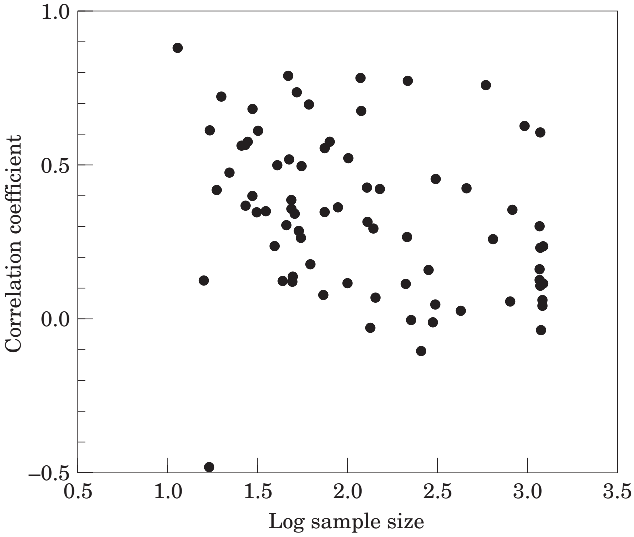

FIG. 2. Plot of correlation coefficients against log sample size (the number of fish examined) across published relationships between fish length and intensity of parasitic infection.

also highly correlated across the 44 host-parasite combinations for which data were available ($r=0·812$, $P<0·0001$). Of these two variables, only the log range in infection intensities correlated with the strength of the relationship between length and intensity [$r=0·302$, $P=0·047$; Fig. 3(b)].

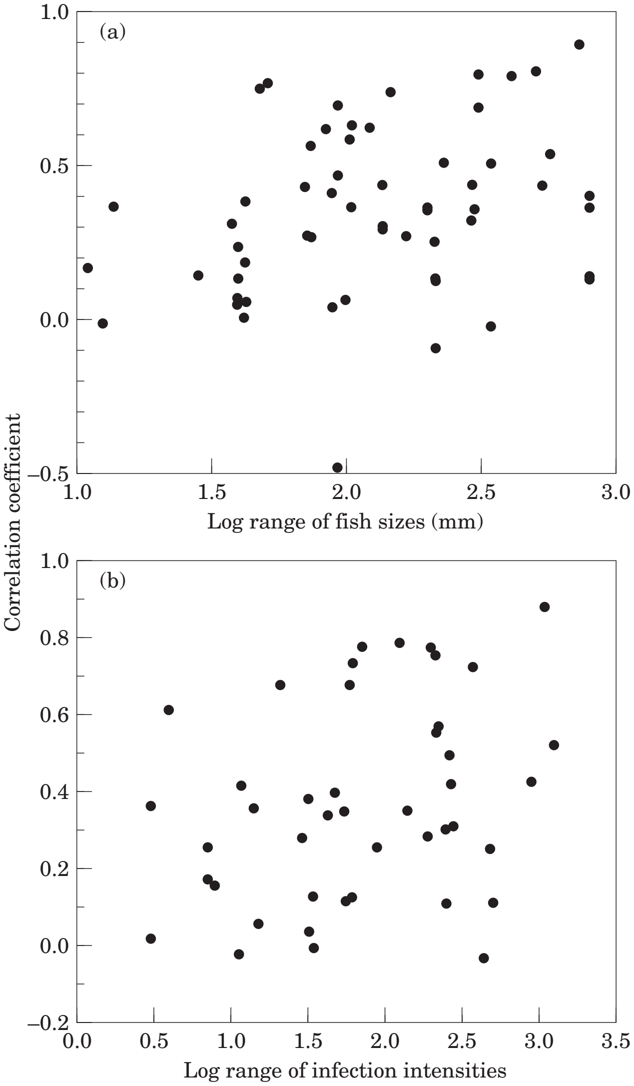

FIG. 3. Plot of correlation coefficients against (a) the log range in fish lengths in the sample, and (b) the log range of infection intensities among the fish examined, across published relationships between fish length and intensity of parasitic infection.

DISCUSSION

Within and among animal species, most physiological and ecological parameters covary with body size (Peters, 1983). Of particular interest in the context of fish population dynamics is the size dependence of mortality rates (Lorenzen, 1996). Because parasite-induced mortality rates, intensities of parasitic infection, and fish size are all interrelated, the relationship between fish size and intensity of infection must be incorporated into population models (Dobson & May, 1987). This relationship is highly variable, as illustrated in the present study. The correlations included here were a random sample of published ones; no doubt there exists a large number of non-significant correlations that have not been published. Among the mostly positive and often statistically significant relationships found in the literature, there is substantial variation in the size *v*. intensity relationship. The main findings of this meta-analysis were: (1) the overall, mean correlation between fish length and intensity of infection, weighted for sample size, was not significantly different from zero, independent of mode of infection; (2) the correlations were less variable and the mean correlation was clearly significant for some parasite taxa but not others; (3) correlations derived from small samples of fish were likely to overestimate the true relationship; and (4) correlations based on a narrow range of fish lengths or intensities of infection were likely to underestimate the true strength of the length *v*. intensity relationship.

Several biological parameters or ecological processes can determine which types of parasites are more likely to correlate closely with host size. Density-dependent regulation of parasite numbers, for instance, may obscure the relationship between fish length and intensity of infection by preventing the accumulation of large numbers of parasites even in the largest fish. Density dependence within hosts has been observed in fish endoparasites, whether they are acquired by ingestion (Brown, 1986) or through skin penetration (Lysne *et al*., 1997). Ectoparasites of fish, however, usually occur at intensities too low for any regulation to occur (Rohde, 1991). This basic ecological difference between external and internal parasites does not appear to influence the length *v*. intensity relationship in a consistent way. Other differences may explain why the relationship is stronger for certain parasite taxa than for others. For example, differences between taxa in life span within fish hosts could result in different rates of parasite accumulation as a function of fish age/size. Larval digeneans, for instance, are generally long-lived in fish hosts (Chubb, 1979) and their numbers correlate well with fish length (Table II). Also, parasite-induced mortality can weaken the size *v*. intensity relationship by removing large, heavily infected fish from the population; if parasite taxa differ in pathogenicity, the relationship may appear weaker for the most harmful parasites. These and other possibilities will require further study.

The important influence of sample size on the value of raw correlation coefficients is not surprising. The estimation of most population parameters in parasites is sensitive to sample size because of the aggregated distribution of parasites among their hosts (Gregory & Woolhouse, 1993; Poulin, 1996). The rare, heavily infected individuals in a natural host population are usually missed by inadequate sampling effort. The inclusion of these heavily infected individuals in computations of correlation coefficients has disproportionate effects on the strength of the relationship between size and intensity. Therefore, it would be preferable to use as many fish as possible, given logistical and ethical constraints, when attempting to quantify the size *v*. intensity relationship.

The ranges in both fish lengths and intensities of infection influenced the strength of the correlations between fish length and intensity. Obviously, it is preferable to sample the entire range of fish lengths in the population, rather than a portion of that range. This facilitates the detection of a relationship and allows non-linear relationships to be distinguished more readily. It is clear that the combined effects of sample size and the range in fish lengths and intensities of infection accounted for much of the variation in the published correlation coefficients. Future estimates will need to eliminate these sources of statistical noise if precise correlations are wanted.

Overall, the positive relationship between fish length and intensity of parasitic infection was more variable and not as strong as often assumed in the literature. Each specific relationship must still be evaluated on its own terms. Many studies have used size class averages and found strong, highly significant relationships between fish size and mean intensity of infection. The use of size class averages inflates the correlation coefficient by ignoring the variation in infection among fish within size classes (Pacala & Dobson, 1988). Some of the variation reported here originates from statistical artefacts, and some of it reflects biological differences among parasite taxa. If parasite-induced, size-dependent mortality is to be incorporated into future fish population dynamics models (Dobson & May, 1987), more effort will be required to quantify precisely the true size *v.* intensity relationship for targeted fish–parasite systems.

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