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Effect of parasite infections on fish body condition: a systematic review and meta-analysis

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ABSTRACT

Using host body condition indices (BCIs) based on the relationship between host body mass and length is a general and pervasive approach to assess the negative effects of parasites on host health. Although many researchers, especially fish biologists and fisheries managers, commonly utilize BCIs, the overall general patterns among BCI – infection relationships remain unclear. Here, we first systematically reviewed 985 fish BCI – infection relationships from 216 publications and investigated the factors affecting the strength and directionality of effects in BCI – infection relationships. We specifically predicted that the BCI measure used, parasite taxonomic group, and the infection measure used would influence the observed effect size and directionality of BCI – infection relationships. We found that most studies were heavily biased towards specific BCI measures such as Fulton's BCI and Relative BCI. Furthermore, studies using Fulton's BCI were more likely to report significant results compared with those using other BCI measures, suggesting that index choice could lead to an overestimation of the negative effects of parasites. Our meta-regressions uncovered that the use of parasite intensity as an infection measure and studies based on experimental rather than natural infections were more likely to report significant negative effects, however there were no differences among parasite taxonomic groups. Surprisingly, many studies, especially field studies, did not report significant negative correlations between BCI and infection, contrary to widespread expectations among researchers that parasites would negatively affect fish health. We discuss potential mechanisms underlying these results. Finally, we make several recommendations for the use of BCI – infection relationships in future studies.

1. Introduction

Parasites, defined as organisms that exploit host energy for their development and survival (Crofton, 1971; Begon et al., 1996; Poulin, 2011), represent a significant proportion of global biodiversity and play pivotal roles in ecosystems (Poulin, 2011; Wood and Johnson, 2015). By definition, parasite infections generally reduce host energy reserves, body condition, and fitness (Begon et al., 1996; Sánchez et al., 2018). These negative effects of parasites can ultimately affect host population dynamics, species distributions, host community structure, and trophic interactions (Hudson et al., 1998; Krkošek et al., 2007; Wood et al., 2007; Hatcher et al., 2012; Friesen et al., 2020). Therefore, evaluating the negative effects of parasites in the wild is a crucial first step in many ecological studies.

Evaluating the host body condition index (hereafter BCI), based on host mass versus length relationships, is a pervasive and general approach to assess the negative effects of parasites on host health because this approach is easy to apply and cost-effective (Lagrue and Poulin, 2015; Maceda-Veiga et al., 2016; Sánchez et al., 2018). Several studies have found that BCIs are useful indicators of host health as they are well correlated with fitness-related traits such as lipid content (Neff and Cargnelli, 2004; Kaufman et al., 2007; Labocha et al., 2014; but see Wilder et al., 2016), growth rate (Bentley and Schindler, 2013), survival (Ben-David et al., 2002) and reproductive success (Chastel et al., 1995; Milenkaya et al., 2015). In BCI analysis, heavier hosts relative to the mass expected from their length are assumed to have better body condition (Jones et al., 1999; Wishart et al., 2024). To assess the negative effects of parasites using BCIs, researchers generally regress BCIs against parasite infection parameters (i.e., infection intensity and abundance) and/or compare BCIs among hosts of different infection status (i.e., infected versus uninfected individuals). In these analyses, negative relationships between BCIs and infection parameters are

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generally expected, however positive or statistically non-significant relationships between BCIs and infection have also been commonly reported in previous studies (reviewed by Sánchez et al., 2018; Shanebeck et al., 2022). The direction and strength of the relationships observed between BCIs and parasite infections are generally complex, and many possible mechanisms can produce these relationships (reviewed by Sánchez et al., 2018).

Despite the pervasive use of BCIs for evaluating the negative effects of parasites and the existence of potential biases governed by several factors affecting the detection of BCI – infection relationships, only two studies have comprehensively and quantitatively assessed the usage of BCIs in host-parasite interactions (reviewed by Sánchez et al., 2018; Shanebeck et al., 2022). Although their findings were novel and provided important insights into BCI – infection relationships, they mostly focused on studies using mammals and birds; datasets on other important taxa such as fish were largely missing from their analyses. Indeed, historically fish are probably the host taxon for which a BCI was used most frequently for assessing health (Le Cren, 1951; Cone, 1989; Murphy et al., 1991). Many types of BCIs have been developed in fish biology and fisheries (Le Cren, 1951; Nash et al., 2006), and the usage of BCIs has been widely discussed (Bolger and Connolly, 1989; Cone, 1989; Murphy et al., 1991; Blackwell et al., 2000). Therefore, a large number of studies exploring BCI – infection relationships in various fish host-parasite systems have been published, however overall general patterns have yet to be investigated.

Many factors not specifically considered in previous studies could affect BCI – infection relationships. One possible hypothesis is that the selection of BCI measures may influence the results of BCI – infection relationships. As pointed out by previous authors (Cone, 1989), many studies have used highly biased BCI measures for assessing fish health, especially Fulton's BCI, or K (Nash et al., 2006) and Relative BCI, or K_n (Le Cren, 1951). This biased use appears to be pervasive in studies investigating fish BCI-parasite infection relationships. Because both BCIs are easy to calculate (K: mass/length^3, K_n: observed mass/ length-specific expected mass predicted by the length-weight relationship in the focal fish population) and assume that fish with average (standard) health condition should show K and K_n = 1, they are very convenient for comparisons of fish health among different populations and species, and for quick assessments of fish health (Murphy et al., 1991). However, some fish species and populations violate the assumptions of these BCIs: many fish species have body shapes that do not follow the proportional length^3-mass relationship (Froese, 2006), which violates the assumption of K, and some fish populations show overdispersion and non-normal distributions (e.g., multimodal distribution) of body mass (Heath et al., 1991), which violates the assumption of K_n. Therefore, these BCIs might be insensitive indicators for evaluating the negative effects of parasites in some cases. However, these classical methods are still widely used, despite active discussion of these problems (Cone, 1989; Peig and Green, 2010; Wilder et al., 2016) and the proposal of new methods for inferring BCIs, such as Scaled Mass Index (SMI: Peig and Green, 2009, 2010). Previous meta-analyses have also considered the effects of different uses of BCI measures in BCI – infection relationships (Sánchez et al., 2018; Shanebeck et al., 2022), however they mostly focused on whether the metrics were determined qualitatively (e.g., subjective scoring of fat content) or quantitatively (e.g., length-weight relationships), and externally (e.g., visual assessment of fatness) or invasively (e.g., fat measurement by necropsy). Therefore, further exploration of the influence of the choice of BCI on a study's conclusion is warranted.

A second hypothesis is that the infection measure could affect BCI – infection relationships. Many types of infection measures such as abundance (the number of parasites per fish, including uninfected ones), intensity (the number of parasites per infected fish, i.e., excluding uninfected ones), and binary infection status (infected versus uninfected), have been used to assess BCI – infection relationships (Sánchez et al., 2018). However, the detectability and/or strength of BCI – infection relationships might vary depending on the measure used. In particular, the inclusion of uninfected fish might affect the outcomes of these relationships. Studies using binary infection status or abundance include uninfected hosts in their analyses, although uninfected hosts often show high variance in BCI for reasons other than parasite infections (e.g., O'Connell-Milne et al., 2016; Hasegawa et al., 2022); such high variance could obscure the actual negative effects of parasites. Studies using intensity as the infection measure would not suffer from this problem. An alternative hypothesis is that studies using intensity as a measure produce incorrect results, as the negative effects of parasites may not be intensity-dependent in some host-parasite systems (e.g., Franceschi et al., 2008), and BCI values for heavily and lightly infected hosts may not differ significantly.

A third hypothesis is that the strength and direction of BCI – infection relationships may vary depending on biological factors such as the parasite's taxon (i.e., nematodes, cestodes, isopods) and their associated ecological characteristics. For instance, while some parasites infect fish hosts through direct attachment to the fish's body surface, many helminth species such as nematodes and cestodes infect fish hosts through trophic transmission via ingestion of intermediate hosts. The negative effects of trophically transmitted helminths are generally chronic, and do not immediately cause significant loss of host body mass (Pedersen et al., 2007; Finnerty et al., 2018; Shanebeck et al., 2022). This can be particularly the case when these helminths use fish as paratenic hosts, where they neither develop nor consume host energy (e.g., Sabadel et al., 2025). Therefore, positive or neutral relationships can be expected in the case of trophically transmitted helminths such as nematodes.

Here, we systematically and quantitatively reviewed 985 fish BCI – infection relationships from 216 publications to critically examine the overall research findings in this study area and test the above hypotheses. Our main goal was to uncover general patterns of BCI – infection relationships in fish host-parasite systems and identify the key drivers of those relationships, with a particular focus on the selection of BCI measures, infection measures, and the parasite taxa investigated, as explained above. To accomplish these goals, we extracted fish BCI – infection relationships and performed a series of generalized linear mixed models (GLMMs) and meta-regressions. We successfully identified a highly biased usage of specific BCI measures and several key factors affecting the observed direction and/or strength of BCI – infection relationships. Based on our findings, we make several recommendations for future studies in this area.

2. Materials and methods

2.1. Literature search and data extraction

We retrieved studies examining fish host BCI – parasite infection relationships through a search of the ISI Web of Science (https://www.webofscience.com/wos/woscc/basic-search) on October 26, 2022. We used the following key word string: "fish*" AND ("parasit*" OR "infect*" OR "helminth*" OR "trematod*" OR "digenea*" OR "nematod*" OR "cestod*" OR "tapeworm*" OR "acanthocephala*" OR "monogenea*" OR "copepod*" OR "isopod*" OR "hirudin*" OR "branchiura*" OR "glochid*") AND ("condition ind*" OR "body condition*" OR "host condition*" OR "physiological condition*" OR "fish condition*" OR "condition factor*").

A total of 809 publications were identified through the above search, of which 242 were retained after the title, abstract and keywords were screened to confirm they were relevant (Supplementary Fig. S1). Then, we reviewed the full text of the remaining 242 publications and retained 216 of those after this further screening (Supplementary Fig. S1). In this process, we only retained publications that satisfied the following criteria: (i) publications focusing on macro-parasites (not micro-parasites such as protozoa and viruses) infecting fish (regardless of the host type such as intermediate, paratenic and definitive host), (ii) publications that examined the BCI – parasite infection relationship, (iii) BCIs used in the studies were calculated from host mass and length relationships (not physiological parameters such as blood cell counts, lipid content or water content), and (iv) publications were written in English. Conference proceedings or technical reports that might not have been peer-reviewed were also excluded. For criterion (iii), we included studies using the Hepatosomatic index (HSI: liver mass/body mass) because this is a well-known index for inferring overall fish health and similarly treated as other BCIs (e.g., Kelly et al., 2009). All screening described above was conducted by the first author (R. Hasegawa).

From these 216 publications, we extracted data for each reported BCI – infection relationship, with some publications providing several data points, i.e. when relationships were presented separately for different parasite species or fish species (in total, 985 data BCI – infection relationships). Specifically, we recorded the following information.

Parasite species and taxonomic group: we recorded the higher taxa for each parasite species (family, order, class, phylum) based on information in the publications and the Catalogue of Life (https://www.catalogueoflife.org). Based on these taxonomic categories, we lumped the parasites into the following parasite groups for the analysis described below: Acanthocephalan, Cestode, Copepod, Freshwater mussel (glochidium), Isopod, Monogenean, Nematode, Trematode metacercaria, Trematode adult, Numerous species, Other parasites. "Trematode" was divided into "trematode metacercaria" and "trematode adult" due to their different ecological characteristics (e.g., transmission modes). Some parasite taxonomic groups had small sample sizes (e.g., Branchiuran, $N = 9$; Pentastomid, $N = 2$), so we combined these as "Other parasites". Several studies investigated the BCI relationship against all found parasite species pooled together regardless of their taxa; we assigned these to the "Numerous species" category. Further, some studies pooled several species of parasites belonging to the same higher taxon in the same analysis (i.e., Acanthocephalan, Cestode, Copepod, Freshwater mussel, Isopod, Monogenean, Nematode, Trematode metacercaria, Trematode adult), due to difficulties in species identification (e.g., two species of nematodes that could not be distinguished). These BCI-infection relationships were placed in the relevant taxonomic category above due to the shared ecological characteristics of related parasites.

Host species and taxonomic group: we also recorded the fish's higher taxa (family, order, class, phylum) similarly to the parasite species. Similar to the cases with parasites, several studies investigated the BCI – parasite infections by analyzing all examined fish host species together regardless of their taxa, or pooling several host species belonging to the same higher taxon in the same analysis (e.g., two fish species from the same genus). As described above, we assigned these cases to the "Numerous host species" category or "relevant taxonomic category (e.g., the same genus)", respectively.

BCI measure: we recorded the BCI measure used in each study, as one of the following: Fulton's BCI (K: mass/length^3), Hepatosomatic index (HSI: liver mass/body mass), Relative BCI (K_n: observed mass/ length-specific expected mass predicted by the length-weight relationship in the focal fish population), residual index (RI: residuals calculated from the regression of mass against length), and length-mass comparison (L-M comparison: comparison of the mass-length regression intercepts among fish of different infection status). Other BCIs such as Scaled Mass Index (Peig and Green, 2009) and Relative weight (Wage and Anderson, 1978) rarely appeared among studies in the dataset, and hence these were grouped as "Other BCIs".

Infection measure: we recorded the infection measures used in each study, as follows: intensity (the number of parasites per infected fish), abundance (the number of parasites per fish, including uninfected ones), binary infection status (infected versus uninfected). These definitions follow Bush et al. (1997). Other infection measures such as repeated comparisons among different infection levels (i.e. heavily infected versus lightly infected) or parasite density (the number of parasites per gram of host mass), were rarely used, and thus were grouped as "Other infection measures".

Study design: earlier meta-analyses found an effect of study design on BCI – infection relationships (Sánchez et al., 2018; Shanebeck et al., 2022), and hence, we assigned each study to one of the following categories: (i) field study in which fish hosts were captured in natural environments, (ii) experimental study in which fish were experimentally infected under controlled conditions, and (iii) aquaculture study in which fish were obtained from aquaculture facilities such as fish farms, fish ponds, and marine fish cages.

Host sample size: the number of fish hosts used for statistical analyses in each study was also recorded for effect size calculation and meta regressions (see below). In the following GLMMs and meta-regressions, we excluded BCI – infection relationships calculated from extremely small sample sizes (i.e., $N < 20$) due to potential unreliability. Although some studies did not specify the specific sample sizes used in their focal analysis, we could reliably infer whether the sample sizes were greater than 20 based on their descriptions and figures. For these data, we recorded either "20 or more" or "20 or less" to increase the data for meta-regressions.

Statistical analysis types: the different BCI – infection relationships were divided into the following two categories: (i) correlative analysis that examined the correlation between BCI and infection, such as Spearman's rank correlations, and (ii) comparative analysis that compared BCIs among fish of different infection status such as infected versus uninfected, or among fish of different infection levels (i.e., heavily infected versus lightly infected). Some studies compared the Relative BCI (K_n, see above) with the mean value (i.e., $K_n = 1$), as parasite prevalence was 100% in their study systems, preventing any comparison of BCI among different infection levels. We included these cases as comparative analyses. Further, some studies made repeated comparisons of BCI among fish of multiple infection status (e.g., BCI in uninfected group versus lightly infected group; BCI in lightly infected versus heavily infected). We recorded each comparison as a separate case. Three studies did not perform statistical inferences, and these were categorized as other types.

Statistical significance and effect directionality: based on reported P-values, we recorded statistical significance for both correlative and comparative analyses. We set the significant level as $P < 0.05$, as most studies used this level. We categorized all BCI – infection relationships into the following three levels based on statistical significance and effect directionality: (i) significantly positive (i.e., positive correlation observed in BCI – infection relationship, or infected fish had a higher BCI compared with uninfected fish), (ii) significantly negative (i.e., negative correlation observed in BCI – infection relationship, or infected fish had a lower BCI compared with uninfected fish), and (iii) statistically non-significant.

Correlation coefficients (r): for studies that employed correlative analysis (see above), we recorded correlation coefficients. When a study reported the coefficient of determination (r^2), we converted it into a correlation coefficient. Effect directionality (i.e., positive or negative) and data accuracy were carefully determined from text and figures, where necessary.

Publication ID and publication year: we assigned a publication ID to each article because many publications reported multiple BCI – infection relationships, and possible non-independence was considered in the following analyses. We also recorded the year in which each study was published.

Overall, 561 BCI – infection relationships from 188 publications (including both correlative and comparative analyses) reported statistical significance, effect directionality and a sufficiently large host sample size (i.e., $N \geqq 20$). Therefore, these were used for the GLMM analyses below (Supplementary Fig. S1, see section 2.2). From those, 184 BCI – infection relationships from 63 publications had sufficient host sample sizes, and reported correlation coefficients (or coefficients of determination), and all other required data to be used for subsequent meta-regressions (Supplementary Fig. S1, see section 2.3).

2.2. Analysis of overall study trends

All statistical analyses were performed using R v. 4.1.1. (R core team, 2024). To investigate the overall patterns and factors potentially affecting the relationships' significance and effect directionality, we used a GLMM with the package "*glmmTMB*" v.1.1.8. (Brooks et al., 2017). Due to the high proportion of non-significant results (58% of 561 BCI – infection relationships), we employed a two-step hierarchical approach. First, we constructed a GLMM in which the response variable was a binomial variable that defined relationships as "statistically significant (including both positive and negative: 1)" or "statistically non-significant (0)". Then, we constructed a GLMM focused only on "statistically significant results", where the response variable was again a binomial variable (negative relationship as 1, positive relationship as 0). In both models, the explanatory variables were BCI measure (six levels: Fulton's BCI, Relative BCI, HSI, RI, L-M comparison, Others), parasite taxon (10 levels: Acanthocephalan, Cestode, Copepod, Freshwater mussel, Isopod, Monogenean, Nematode, Trematode adult, Trematode metacercaria, Others), infection measure (four levels: abundance, binary infection status, intensity and others), and study design (three levels: aquaculture study, experimental study, field study). In both models, we included "Publication ID" as a random effect since most publications reported more than two BCI – infection relationships (1–26, mean 2.98), in order to account for potential pseudo-replication and non-independence. We also included "host family" and "parasite phylum" as random effects to account for potential phylogenetic effects.

Our main initial interest concerned the effect of the highly biased usage of certain measures, such as Fulton's BCI, on the assessment of BCI – infection relationships. Therefore, we set Fulton's BCI as the baseline in the analysis (i.e., the reference level in the GLMMs). "Nematode" represented a large proportion of entries in our dataset, and thus, this group was set as the baseline. We also expected that BCI – infection relationships using intensity of infection would be more likely to report significantly negative relationships compared with other infection measures due to the exclusion of uninfected fish, which generally show high variance in BCI. Thus, we set this category as the baseline in the analysis. Finally, experimental studies are known to frequently report significant negative relationships in BCI – infections (Sánchez et al., 2018), and therefore, we set this category as the baseline in the analyses.

2.3. Meta-regression

For 184 BCI – infection relationships obtained from 63 publications that reported correlation coefficients (or coefficients of determination) calculated from a sufficiently large sample size (i.e., host sample size, $N \geqq 20$), we conducted meta-regressions using the R package "*metafor*" v. 4.6.0 (Viechtbauer, 2010) for a deeper exploration of the key drivers of the strength and direction of BCI – infection relationships. First, we transformed raw correlation coefficients into Fisher's *z*-transformed correlation coefficients, *Zr*, as an effect size using the function "*escalc*" in the "*metafor*" package, which allows us to incorporate sample size and variance for each study. Then, we constructed a mixed-effects model (MEM) fitted with a restricted maximum likelihood (REML) estimator using "*rma.mv*" function. In this model, we included the following moderators: BCI measure (six levels: Fulton's BCI, Relative BCI, HSI, RI, L-M comparison, Other BCIs), parasite taxa (10 levels: Acanthocephalan, Cestode, Copepod, Freshwater mussel, Isopod, Monogenean, Nematode, Trematode adult, Trematode metacercaria, Others), infection measure (four levels: abundance, binary infection status, intensity and others), and study design (three levels: aquaculture study, experimental study, field study). We also incorporated "publication ID", "host family", and "parasite phylum" as random effects for the same reasons as explained in the GLMM section (see above). Additionally, we also constructed the intercept-only MEM using "*rma*" function with REML function to examine overall mean effect sizes and obtain I^2, an indicator of heterogeneity among relationships (Nakagawa and Santos, 2012) using the same random effects. Finally, we constructed another MEM where only "publication year" was included as a moderator to explore the potential trends in effect sizes over time (i.e., testing for declining effect sizes; Costello and Fox, 2022). The same random effects described above were included in this model.

The potential publication bias was visually assessed using funnel plots (Egger et al., 1997). We discussed the effects of moderators for which 95% confidence intervals (CIs) did not overlap with zero (i.e., $P < 0.05$). All figures associated with meta-regressions were created by R package *orchaRd* v. 2.0 (Nakagawa et al., 2023).

2.4. Data accessibility

The data that support the findings of this study are openly available in Figshare at https://doi.org/10.6084/m9.figshare.28347155.v1.

3. Results

3.1. Overview

Our dataset retained after full-text screening consisted of 216 publications reporting 985 BCI – infection relationships (Supplementary Fig. S1). This included 194 species of fish hosts (147 genera, 71 families, 23 orders) and 172 species of parasites (129 genera, 76 families, 31 orders). Of the BCI-infection relationships, 855 (86.8%), 67 (6.8%) and 63 (6.4%) were reported from studies conducted in the field, aquaculture facilities, and experimental conditions, respectively. These relationships comprised 692 correlative analyses (70.3%) and 290 comparative analyses (29.4%). Three data points (0.3%) were identified as not involving any statistical analysis.

Across the dataset retained after full-text screening (i.e., 985 BCI – infection relationships), Trematode metacercaria was the most widely investigated parasite taxon (N = 191, 19.4%), followed by Cestode (N = 147, 14.9%), Numerous species (N = 143, 14.5%), Nematode (N = 137, 13.9%), Monogenean (N = 102, 10.4%), Copepod (N = 85, 8.6%), Acanthocephalan (N = 62, 6.3%), Isopod (N = 40, 4.1%), Freshwater mussel (glochidium) (N = 39, 4.0%), Trematode adult (N = 26, 2.6%), Others (N = 13, 1.3%).

Most of the studies used parasite abundance (N = 460, 46.7%) as the parasite infection measure, followed by parasite intensity (N = 111, 11.3%), binary infection status (N = 313, 31.8%), others (N = 99, 10.1%), and unknown (N = 2, 0.2%).

The use of specific BCI measures was highly biased (Fig. 1); Fulton's BCI was the most frequently used across all study years and accounted for almost half of the entries in the dataset (N = 441, 44.8%; Fig. 1), followed by Relative BCI (N = 248, 25.2%), HSI (N = 119, 12.1%), RI (N = 92, 9.3%), Others (N = 50, 5.1%), and L-M comparisons (N = 35, 3.6%). As expected, Fulton's BCI and Relative BCI made up more than half of entries in most year classes (Fig. 1). Although there were no clear temporal patterns in proportional changes for usage of each BCI, the proportion of Relative BCI tended to increase after the 2,000 s (Fig. 1).

3.2. Results of overall patterns in GLMM

In the first GLMM (using 561 BCI – infection relationships from 188 publications), where we investigated factors potentially affecting the relationships' significance, we found that several factors affected detectability in BCI – infection relationships (Supplementary Table S1). Studies using Fulton's BCI were more likely to report significant results compared with those using L-M comparisons or Relative BCI (Supplementary Table S1). Experimental studies were more likely to report significant results compared with studies conducted in aquaculture (Supplementary Table S1). Studies using cestodes were more likely to report significant results compared with those using nematodes (Supplementary Table S1).

In the second GLMM, where we investigated factors affecting the directionality of significant relationships, we found only differences among parasite taxa; studies examining trematode metacercaria were more likely to report significantly positive results compared with those examining nematodes (Supplementary Table S2).

3.3. Meta-regressions

In total, 184 effect sizes were collected from 63 publications and used in meta-regressions. The intercept-only MEM showed that heterogeneity was significantly high (I^2 = 91.98%) and the overall effect size (Fisher's Zr) was negative, but the effect was very weak (mean Zr = –0.069 [95% CI = –0.123 to –0.015], SE = 0.027, P = 0.013, k = 188; Fig. 2). There was no effects of publication year on the effect size (Zr = –0.003 [95% CI = –0.015 to 0.009], SE = 0.006, P = 0.618; Supplementary Fig. S2). Our funnel plots showed that points were distributed symmetrically in both tested models, and we consider there was little evidence of publication bias (Supplementary Fig. S3).

In a MEM including all moderators, we found experimental studies had significantly negative effect sizes, compared with other study types; however, this is based on a very small number of experimental studies (Fig. 3; Supplementary Table S3). Remarkably, field studies were equally likely to produce negative BCI – infection relationships as they were to produce positive ones (Fig. 3; Supplementary Table S3). As predicted, the effect size was more negative in studies using parasite intensity compared with other infection measures (Fig. 4; Supplementary Table S3). Contrary to our initial predictions, we found no evidence of different effect sizes among relationships based on different BCI measures (Fig. 5; Supplementary Table S3). Finally, among the parasite taxonomic groups, effect sizes were more likely to be positive in studies testing the effects of freshwater mussels' glochidia, although this was based on a very small sample size; all other parasite taxa did not show consistently negative nor positive effects on host BCI (Fig. 6, Supplementary Table S3).

4. Discussion

Evaluating the relationships between BCI and parasite infections is a historically pervasive approach for assessing the negative effects of parasites (Lagrue and Poulin, 2015; Sánchez et al., 2018), and countless studies have employed this approach in various host-parasite systems, especially for fish hosts infected by macroparasites (e.g., Lemly and Esch, 1984; Neff and Cargnelli, 2004; Lagrue and Poulin, 2015). Despite the universality of this approach, particularly in fish biology and fisheries, only two studies have critically reviewed the relationships between BCI and parasite infections (Sánchez et al., 2018; Shanebeck et al., 2022), however datasets in both of these studies are highly biased toward mammals and birds. Here, by conducting a systematic review and meta-analyses, we critically reviewed 985 fish BCI – infection relationships from 216 publications. We identified several factors, such as parasite infection measures (i.e., intensity, abundance) and BCI measures (i.e., Fulton's BCI), that can affect the outcomes of these relationships. Contrary to our initial expectations, although the mean correlation coefficients between BCIs and parasite infections were negative, they were very weak, indicating potential analytical artefacts in previous studies or much weaker negative effects of fish parasites on host health than previously assumed.

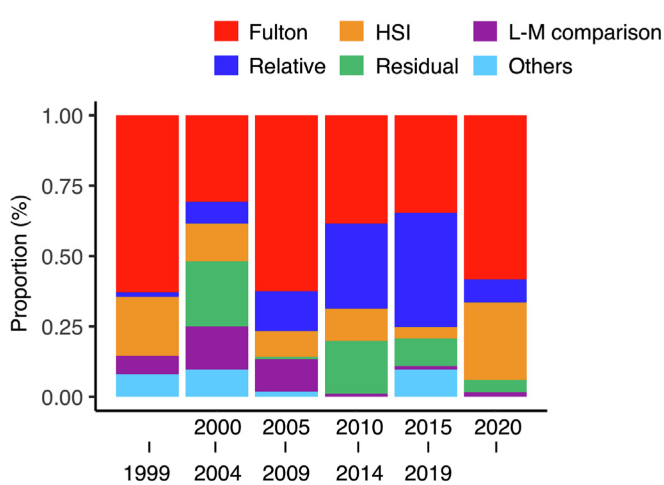

Fig. 1. The temporal trends in the use of host body condition indices (BCIs) in 5 year intervals over past decades. Fulton, Fulton's BCI; HSI, Hepatosomatic index; L-M comparison, length-mass comparision; Relative, Relative BCI; Residual, Residual index.

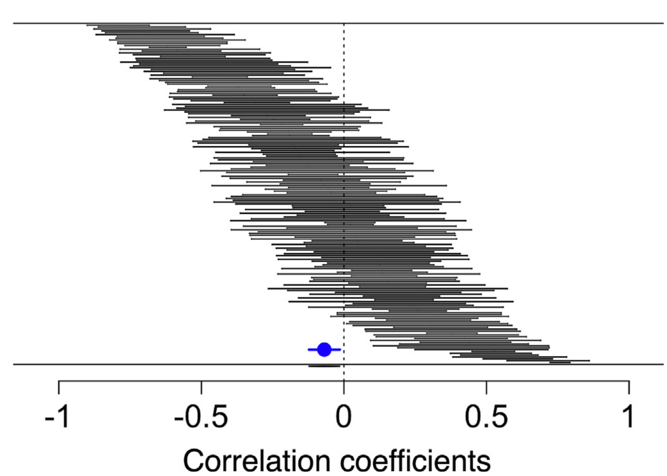

Fig. 2. The forest plot shows the 95% confidence interval (CI) of effect sizes for each study considered in the present paper, ranked from most negative (top) to most positive (bottom). The mean effect size and its 95% CI are represented by a blue dot and thick bar.

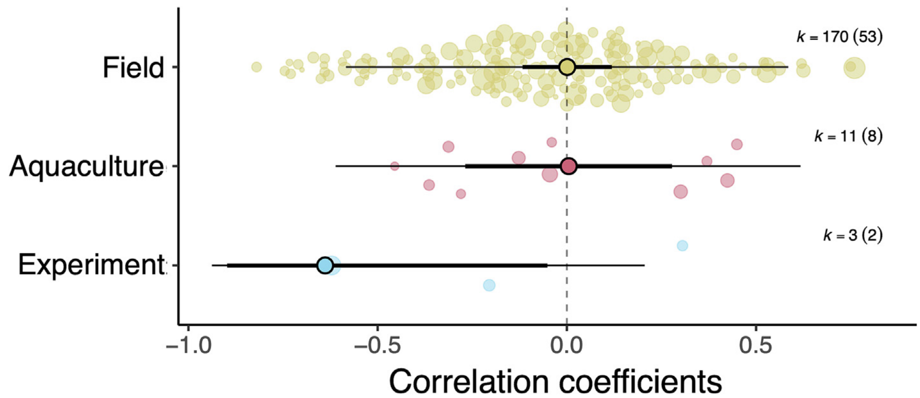

Fig. 3. Orchard plot showing the effect sizes for each study design (field study, aquaculture study, experimental study) estimated by *meta*-regressions. Each point represents a different body condition index (BCI)-infection relationship. The mean effect size and its 95% confidence interval (CI) are shown. The size of each plot indicates the relative host sample size used for each original analysis.

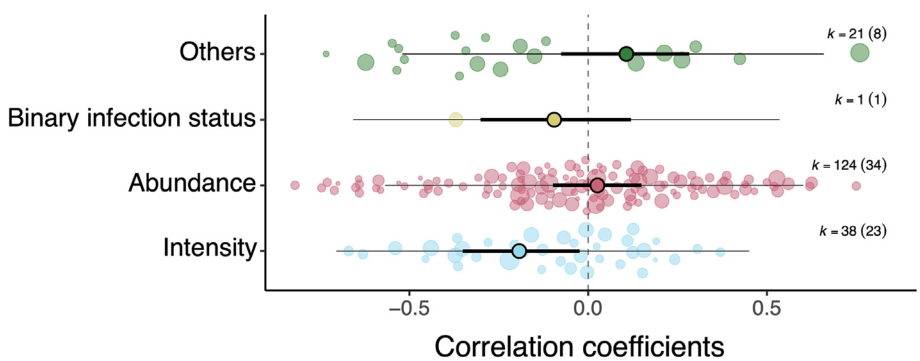

Fig. 4. Orchard plot showing the effect sizes for each parasite infection measure estimated by meta-regressions. Each point represents a different body condition index (BCI)-infection relationship. The mean effect size and its 95% confidence interval (CI) are shown. The size of each plot indicates the relative host sample size used for each original analysis.

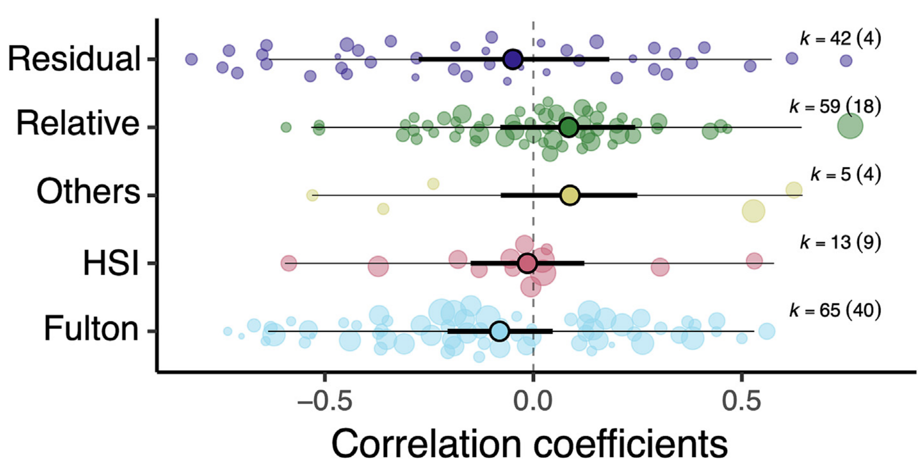

Fig. 5. Orchard plot showing the effect sizes for each host body condition index (BCI) measure estimated by meta-regressions. Each point represents a different BCI-infection relationship. The mean effect size and its 95% confidence interval (CI) are shown. The size of each plot indicates the relative host sample size used for each original analysis. Residual, Residual index; Relative, Relative BCI; HSI, Hepatosomatic index; Fulton, Fulton's BCI; Others, other BCIs.

As we predicted, Fulton's BCI was the most frequently used measure among all BCIs (more than 44% of BCI-infection relationships used this index; Fig. 1). Additionally, studies using this index were more likely to report significant results (either significantly negative or positive relationships; Supplementary Table S1) compared with those using other BCI measures such as L-M comparisons and Relative BCI (Supplementary Table S1). Given that these significant relationships consisted mostly of negative relationships (71% of the significant relationships using Fulton's BCI reported significantly negative correlations), this suggests that usage of this index may frequently overestimate the negative effects of parasites on host health. One possible reason is the violation of assumptions underlying the use of this index. Fulton's BCI is assumed to follow the principles of isometric growth (Cone, 1989), in which fish grow according to the equation; log (body mass) ~ a + 3log (body length). However, many fish species

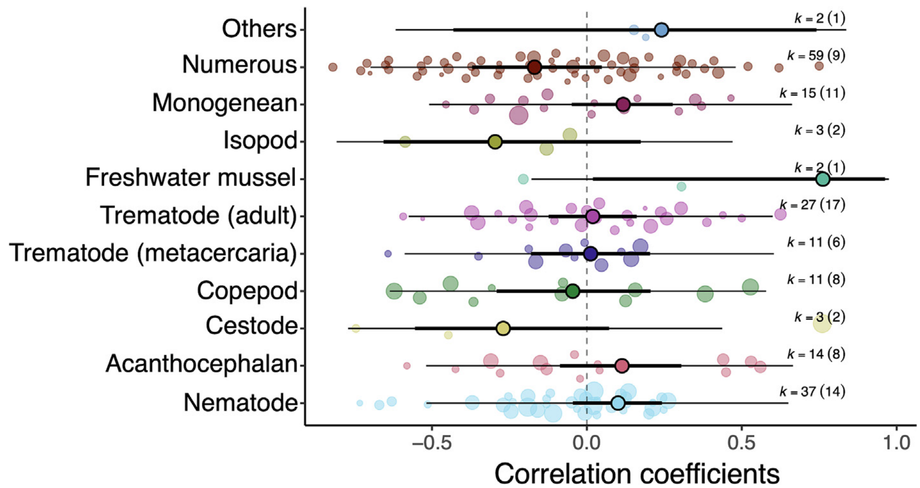

Fig. 6. Orchard plot showing the effect sizes for each parasite taxonomic category estimated by meta-regressions. Each point represents a different body condition index (BCI)-infection relationship. The mean effect size and its 95% confidence interval (CI) are shown. The size of each plot indicates the relative host sample size used for each original analysis.

do not grow isometrically but instead exhibit hyperallometric (i.e., positive allometry) or hypoallometric growth (i.e., negative allometry) (Froese, 2006). In either growth pattern, Fulton's BCI can become a function of body length, an issue that has been raised and criticized in many studies (Cone, 1989). Consequently, spurious correlations between Fulton's BCI and parasite infections are likely to arise, especially when correlations between parasite infections and fish body length exist, as is commonly observed in fish-parasite systems (Poulin, 2000). Indeed, some studies have discussed this possibility when they found strong positive or negative correlations between BCIs and parasite infections (Perrot-Minnot et al., 2019).

Our meta-regressions found no significant negative effects of parasite infections on BCI in field and aquaculture studies, whereas experimental studies showed significant negative effects. A note of caution is needed here as only three BCI – infection relationships from experimental studies could be obtained from two publications/host-parasite systems (Fig. 3; Supplementary Table S3). Nonetheless, since two previous meta-regressions reported similar results (Sánchez et al., 2018; Shanebeck et al., 2022), mostly for mammal and bird hosts, we can suggest that experimental studies are more likely to detect negative relationships, whereas those conducted in field and aquaculture conditions are not. An important finding, however, is that the overall mean effect size of field-based studies (Fig. 3) was essentially zero, and most field studies did not report significant results (Fig. 3; Supplementary Table S3). This was surprising because researchers almost always expect declines in BCIs in infected hosts; the more severe the infections, the lower the expected BCI (Sánchez et al., 2018; Shanebeck et al., 2022). Two potential reasons can explain our finding: artefacts in study design that mask any negative impacts of parasites, and the possibility that the actual negative effects of fish parasites on host health are negligible. One possible artefact is the usual reliance on cross-sectional evaluations. Field studies generally test for BCI – infection relationships cross-sectionally (Sánchez et al., 2018), however the negative effects of parasites may appear longitudinally, i.e. over time, as the BCI may decline only after prolonged periods of parasite attachment (Morton and Routledge, 2006) or within short time frames, such as during specific seasons or specific host life-history stages (McNew et al., 2019; Nakano et al., 2024). Furthermore, BCIs could be affected by various external and internal factors such as resource availability (Brosset et al., 2015; Pazianoto et al., 2016), population density (Casini et al., 2014; Kamimura et al., 2021) and host sex (Arnott et al., 2000; Lloret et al., 2002). Field studies, especially cross-sectional correlations, do not often control for these confounding factors and may frequently fail to detect negative effects of parasites, whereas experimental studies under highly controlled environments are more likely to detect these effects. Additionally, our datasets contained many studies that potentially examined the relationships between BCIs of paratenic hosts and parasite infections, resulting in no observable effects of parasites in field studies. Parasites generally neither develop nor derive energy from paratenic hosts, but instead just utilize these hosts as a means of transport to definitive hosts or temporary habitats (Anderson, 1984; Sabadel et al., 2025). Therefore, the negative effects on BCIs can be lower in these cases, compared with cases where parasites utilize fish hosts as definitive or intermediate hosts. These potential biases in our data may lead to non-significant results in our analyses, and future studies assessing the data separately for host type are required.

Another potential reason why many studies, field ones in particular, report unclear patterns between BCIs and parasite infections may be related to host resistance and tolerance strategies; the negative effects of parasites might be generally negligible, and tolerance might be the main host strategy to counter parasite infections in the wild. When hosts become infected by parasites, they defend themselves by either of two major strategies, resistance or tolerance (Råberg et al., 2007, 2009; Boots, 2008). While resistance is a strategy in which hosts try to kill or eliminate the infections per se (Råberg et al., 2007, 2009; Boots, 2008), tolerance is a strategy in which hosts try to reduce the damage caused by parasitic infections, without reducing the infection itself (Råberg et al., 2007, 2009; Boots, 2008). When the virulence of the parasites is low and chronic, tolerance would be the adaptive strategy because resistance is rather costly for hosts to develop and maintain, and could finally reduce body condition, growth, and survival (Weber et al., 2022). Consequently, positive correlations between parasite burdens and host fitness (or surrogates of fitness such as BCIs) emerge when hosts adopt a tolerance strategy (e.g., Budischak et al., 2018; Sánchez et al., 2018). Therefore, a high proportion of no or positive correlations between BCIs and parasite infections in our datasets suggest that many fish hosts may use a tolerance strategy against parasites in the wild.

Studies using infection intensity (the number of parasites per infected fish, i.e. excluding uninfected ones) as an infection measure generally had significant negative effects compared with those using other infection measures that include uninfected hosts, such as abundance and binary infection status. As we predicted, this may be due to the removal of uninfected fish from the analysis. The BCIs of uninfected hosts generally have higher variance compared with infected hosts (O'Connell-Milne et al., 2016; Hasegawa et al., 2022). This may be because many parasite species show negative-binomial distributions among individual hosts within host populations, in which most individuals are uninfected (Crofton, 1971; Poulin, 2007; Morrill et al., 2023), and BCIs of uninfected fish are affected by many factors (see discussion above). When uninfected fish account for a large proportion of individuals in the dataset, these may skew the data and mask the relationships between BCI and infection. Moreover, our results could also imply that negative effects of parasites on fish health are generally intensity-dependent. Many host behavioral and physiological alterations induced by parasites can result in a decline in BCIs (Lagrue and Poulin, 2015; Sánchez et al., 2018; Shanebeck et al., 2022), and these mechanisms may act in an intensity-dependent manner (Shirakashi and Goater, 2002; Bleay et al., 2007; Boltana et al., 2016; Filipsson et al., 2018). For instance, activation of immunity, an important cause of BCI declines (Sánchez et al., 2018; Shanebeck et al., 2022), is known to be intensity-dependent in some fish host – parasite systems (Bleay et al., 2007; Boltana et al., 2016). Host behavior, especially foraging behavior, which directly affects host BCIs (Cone, 1989), may also change depending on infection intensity (Crowden and Broom, 1980; Shirakashi and Goater, 2002; Filipsson et al., 2018). Indeed, several studies found clear intensity-dependent reduction of BCIs (Morton and Routledge, 2006). Thus, accounting for differences in infection intensity, rather than the simple comparison among different categories of individual hosts (i.e., infected versus uninfected), may be crucial to evaluate the negative effects of parasites (but see below).

Studies focusing on trematode metacercariae tended to report significant positive correlations between infection and BCI compared with other parasite taxonomic groups. This result is counterintuitive because parasites generally have negative effects on host health (Sánchez et al., 2018), however several explanations exist. Fish showing high activity and explorative behaviors are more likely to become infected with certain parasites, including skin-penetrating trematode metacercariae, because they have a higher probability of exposure to the infectious stages of these parasites (Marler and Moore, 1989; Poulin et al., 1991; Wilson et al., 1993). Since BCIs can correlate with host activity and explorative behaviors (Sih et al., 2015; Kanno et al., 2023), fish with higher BCIs may be more likely to become infected with metacercariae. Additionally, metacercarial infections are generally chronic (e.g., Vaughan and Coble, 1975; Johnson and Dick, 2001; Lagrue and Poulin, 2015), and their virulence may often be low; they do not cause a sudden decrease in host survival (e.g., Vaughan and Coble, 1975; Johnson and Dick, 2001). Thus, fish in better body condition may tolerate these infections, resulting in positive correlations between BCIs and metacercarial infections.

Overall, our current study has some important implications: the selection of BCI measures, parasite infection measures, and study design could affect the detectability of BCI-parasite infection relationships. Based on these results, we make several recommendations for future studies. First, researchers should carefully select appropriate BCIs. Although two major BCIs (Fulton's BCI and Relative BCI) are excellent indicators for rapid assessments and comparisons of fish health status among species, populations, and individuals (Bolger and Connolly, 1989), fish biologists should keep in mind that these BCIs are applicable to specific contexts and fish species, such as when (i) focal fish species show isometric growth (especially when using Fulton's BCI), and (ii) the body size (age) range of focal fish species/populations is narrow (Cone, 1989). Additionally, we recommend that researchers quantify the negative effects of parasites using more than two BCIs with their data to increase the reliability of their results. For instance, HSI could be superior to other BCIs for assessing the physiological costs induced by parasites, as the index is calculated from liver mass, an organ that plays pivotal roles in energy reserves and immunity (Copeman et al., 2017). The RI allows researchers to quantify host health, regardless of fish body length (Jakob et al., 1996; Schulte-Hostedde et al., 2005, but see Green, 2001), and this index will be useful when fish exhibit hyper- or hypo-allometric growth. Recently, new methods for evaluating host health have been developed. For instance, the SMI (Peig and Green, 2010) allows researchers to evaluate host body condition robustly, regardless of other host factors (i.e. body size). Indeed, this index has been shown to better predict host physiological states compared with other BCIs (Peig and Green, 2009, 2010). When multiple BCI metrics, including physiological ones, are available, the application of structural equation modeling (SEM) is an alternative approach for inferring BCIs by incorporating several related variables in the analyses and determining BCIs from multiple health perspectives (Frauendorf et al., 2021). Thus researchers should actively consider using these BCIs.

Second, researchers should consider host biological factors when assessing the relationships between BCIs and infections. Negative effects of parasites on fish health generally differ among sexes (Khan et al., 1997; Bagamian et al., 2004), developmental and maturity states (Kusterle et al., 2012; Carrassón and Cribb, 2014), ages (Parker and Booth, 2013), populations (Sala-bozano et al., 2012), and seasons (Nakano et al., 2024). However, we found many studies ignored these factors in their analyses, and some studies even combined data from several host and parasite species in the same analyses (as shown in the categories "Numerous host species" and "Numerous parasite species"), which might be one reason why we found no strong effect sizes. Thus, we strongly encourage researchers to include these biological factors in their analyses, such as by examining BCIs and infections separately for each category, and incorporating these factors as predictor variables into the analyses (e.g., GLMMs).

Third, in addition to BCI measures, researchers should use more than two parasite infection measures in their analyses, especially both infection measures that include uninfected hosts (e.g., abundance) and those that exclude uninfected hosts (e.g., intensity), as uninfected fish might be a key factor obscuring the outcomes of the relationships between BCIs and parasitic infections.

Fourth, researchers are encouraged to explore the negative effects of parasites under both experimental and field (or aquaculture) conditions to evaluate whether, how, and to what extent the focal parasite species has negative effects. Although field studies are important for describing patterns in the wild, it is difficult to capture the full picture of the relationships between host BCIs and parasite infections under natural conditions, as we discussed. Mechanisms of BCI reduction (including resistance or tolerance) are also difficult to disentangle in the field. In contrast, experimental infections under laboratory conditions can control initial BCIs and infection periods, and remove any potential effects of confounding factors. Additionally, these studies have the advantage of ascertaining the causality underlying the relationships between BCI and infections (i.e., whether parasites reduce host condition, or fish in poor condition are susceptible to infections) (Beldomenico et al., 2008; Beldomenico and Begon, 2010). However, experiments themselves tend to report negative correlations, as shown in the current study, possibly due to the unnatural environments. For instance, experimental studies tend to use higher doses of parasites than those seen in nature (Poulin, 2010), and as a consequence, higher infection success and infection levels are generally observed. On the contrary, experimental fish initially have better physiological conditions due to a higher amount of food and being free from competitors or predators, which may mitigate the negative effects of parasites. Therefore, researchers should carefully consider their experimental designs and associated outcomes. Another good option would involve experimental manipulation in the field. For instance, several previous studies conducted parasite removal experiments using anti-helminth drugs in the field, elegantly demonstrating the negative effects of parasites by comparing host health among control (parasites remained) and treatment groups (parasites removed by drugs) (Ezenwa and Jolles, 2015; Finnerty et al., 2018; Romano et al., 2021). This approach can be applied to parasite species with complex life cycles, for which it is difficult to conduct experimental infections in the laboratory.

In summary, we critically reviewed 985 published relationships between fish BCIs and parasitic infections. Evaluating these relationships remains a common method in the contexts of host conservation and fisheries management (Sánchez et al., 2018; Frauendorf et al., 2021) because this approach is simple and can be quickly applied to various systems without sacrificing hosts (Green, 2001). In addition to their usefulness and simplicity, BCIs are surrogate measures of host health and fitness-related traits (Neff and Cargnelli, 2004; Bentley and Schindler, 2013; Milenkaya et al., 2015), and therefore, many studies consider this approach to be a powerful method. However, as we have shown in this study, there are several pitfalls that might lead to erroneous conclusions. Therefore, based mainly on our recommendations, researchers should adopt a more cautious approach in future uses of fish BCI – parasite infection relationships.

CRediT authorship contribution statement

Ryota Hasegawa: Writing – original draft, Visualization, Validation, Software, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Robert Poulin:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization.

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Appendix A. Supplementary material

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