International Journal for Parasitology 50 (2020) 755–761

Contents lists available at ScienceDirect

International Journal for Parasitology

journal homepage: www.elsevier.com/locate/ijpara

Invited Review

Why ignoring parasites in fish ecology is a mistake

Juan T. Timi [a,*], Robert Poulin [b]

[a] Laboratorio de Ictioparasitología, Instituto de Investigaciones Marinas y Costeras (IIMyC), Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata- Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). Funes 3350, (7600) Mar del Plata, Argentina
[b] Zoology Department, University of Otago, PO Box 56, Dunedin 9054, New Zealand

ARTICLE INFO

Article history:
Received 28 January 2020
Received in revised form 8 April 2020
Accepted 18 April 2020
Available online 24 June 2020

Keywords:
Fish ecology
Parasites
Confounding effects
Biomarkers

ABSTRACT

Parasites are ubiquitous components of biological systems that have evolved in multiple independent lineages during the history of life, resulting in a diversity of taxa greater than that of their free-living counterparts. Extant host-parasite associations are the result of tight reciprocal adaptations that allow parasites to exploit specific biological features of their hosts to ensure their transmission, survival, and maintenance of viable populations. As a result, parasites may affect host physiology, morphology, reproduction or behaviour, and they are increasingly recognized as having significant impacts on host individuals, populations, communities and even ecosystems. Although this is usually acknowledged by parasite ecologists, fish ecologists often ignore parasitism in their studies, often acting as though their systems are free of parasites. However, the effects of parasites on their hosts can alter variables routinely used in fish ecology, ranging from the level of individual fish (e.g. condition factors) to populations (e.g. estimates of mortality and reproductive success) or communities (e.g. measures of interspecific competition or the structure and functioning of food webs). By affecting fish physiology, parasites can also interfere with measurements of trophic levels by means of stable isotope composition, or have antagonistic or synergistic effects with host parameters normally used as indicators of different sources of pollution. Changes in host behaviour induced by parasites can also modify host distribution patterns, habitat selection, diet composition, sexual behaviour, etc., with implications for the ecology of fish and of their predators and prey. In this review, we summarise and illustrate the likely biases and erroneous conclusions that one may expect from studies of fish ecology that ignore parasites, from the individual to the community level. Given the impact of parasites across all levels of biological organisation, we show that their omission from the design and analyses of ecological studies poses real risks of flawed interpretations for those patterns and processes that ecologists seek to uncover.

1. Introduction

Parasites represent one of the most successful modes of life in nature (Poulin and Morand, 2000) that has arisen on multiple independent occasions in many phyla (Poulin, 2011; Weinstein and Kuris, 2016). They are ubiquitous components of biological systems, comprising a significant proportion of world biodiversity (Dobson et al., 2008) and achieving substantial biomass, abundance and productivity in some ecosystems (Kuris et al., 2008; Hechinger et al., 2011). Extant host-parasite associations are the result of antagonistic interactions whose coevolution has led to tight reciprocal adaptations that allow parasites to exploit specific biological features of their hosts to ensure their transmission, survival, and maintenance of viable populations. As a result, parasites may affect the biology of their hosts in several ways and at different levels. They impose energetic demands on individual hosts and can affect their morphology, fecundity, reproduction, behaviour and survival (Marcogliese, 2004). Their impact extends beyond individual hosts to the levels of host populations, communities and even ecosystems. Indeed, parasites are able to regulate host populations (Anderson and May, 1979; May and Anderson, 1979; Hudson et al., 1998), structure free-living communities (Mouritsen and Poulin, 2002; Hudson et al., 2006; Lafferty et al., 2006, 2008; Dunne et al., 2013) and alter ecosystem function (Thomas, et al., 1999; Hatcher et al., 2012; Sato et al., 2012; Preston et al., 2016; Frainer et al., 2018).

Whereas the relevance of parasitic organisms in nature and their potential to provide important ecological information is acknowledged by parasite ecologists, ecologists studying free-living organisms often ignore parasitism in their studies, typically acting as though their systems are free of parasites, or as if para-

---

* Corresponding author.
E-mail address: jtimi@mdp.edu.ar (J.T. Timi).

https://doi.org/10.1016/j.ijpara.2020.04.007
0020-7519/

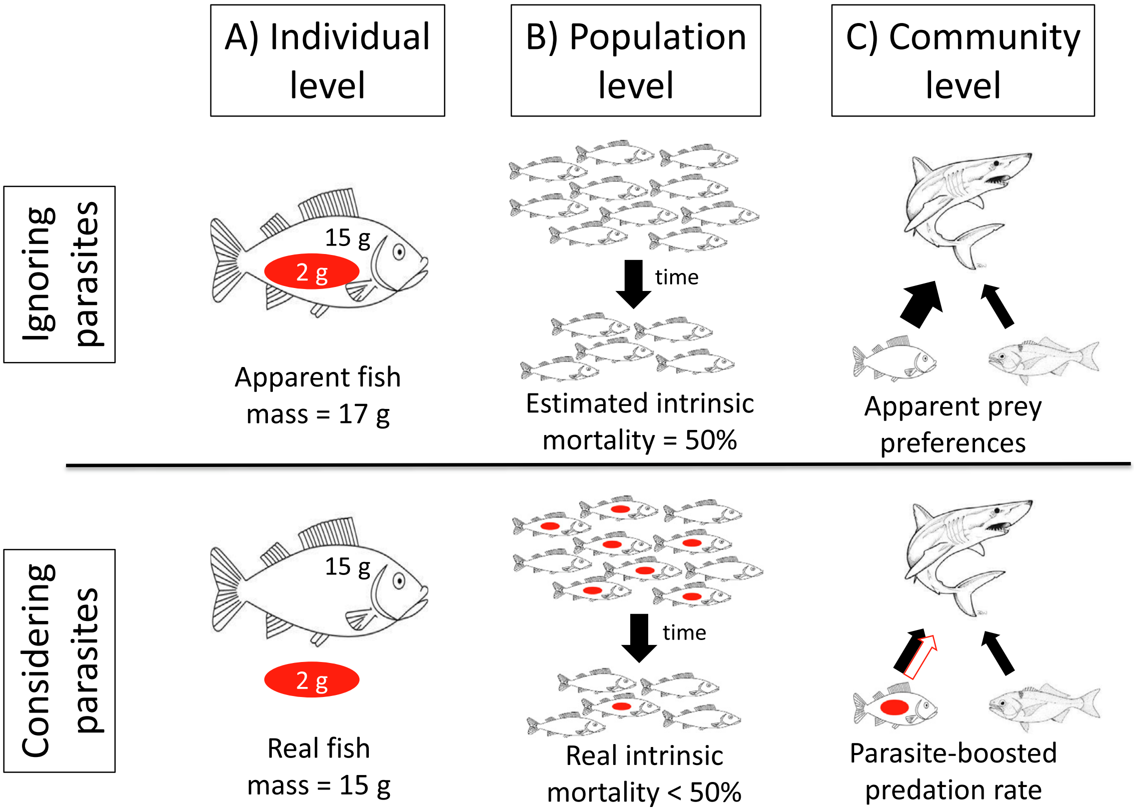

Fig. 1. Schematic illustration of the confounding effects of parasites on measurements of parameters at the individual (A), population (B) and community (C) level. In each hypothetical exmaple, the gross measurement (including the effect of parasitism) is contrasted with the net measurement (with the effect of parasites excluded), to highlight the estimate error obtained by ignoring parasites. (A) Overestimation of fish body mass when parasite mass (oval) is not deducted from the total (fish + parasites) mass, which can cause biases in calculations of condition factors. (B) Overestimation of the intrinsic mortality rate of a fish population during a given time interval when parasites (ovals) are ignored; infection by parasites raises the individual death rate, causing a greater proportion of fish to die than would have died in the absence of parasites. (C) Overestimation of true predator preference for one prey species relative to another due to parasite-induced alterations of host behaviour and susceptibility to predation; predation rates and the strength of trophic links and energy flow through a food web can be modified, in this example boosted (white arrow), by prevalent parasites of certain fish species in ways that are only recognised if parasites are considered in fish ecology studies.

sites exist in the system but do not matter (Minchella and Scott, 1991; Huxham et al., 1995; Lafferty et al., 2006; Wood and Johnson, 2015). Fish biologists are no exception and parasites are generally neglected in many studies, despite the fact they can alter variables routinely used in fish ecology and fisheries, and can have antagonistic or synergistic effects with host parameters normally used as indicators of physiological or reproductive status. Changes in host behaviour induced by parasites can also modify host distribution patterns, habitat selection, diet composition, sexual behaviour, etc., with implications for the ecology of fish and of their predators and prey. In this review, we summarise and illustrate (Fig. 1) the likely biases and erroneous conclusions that one may expect from studies of fish ecology that ignore parasites, and the need to incorporate them in the design and analyses of ecological studies based on natural systems or in experimental research using wild fish, to avoid misleading interpretations of patterns and processes from the individual to the community level.

2. Effect of parasites on fish condition

Parasites live in or on their hosts and, independent of any possible effect on host physiology and health, their mere presence alters the host's weight, sometimes substantially. Fish body mass, together with some linear measure, is routinely taken to calculate indices of "body condition" as snapshots of fish physiological state, i.e. as an estimate of nutritional state or relative "fatness" or "health". These serve as indirect indicators of past foraging success, fighting ability, ability to cope with environmental pressures, etc. (Jakob et al., 1996). In other words, they capture the general well-being or fitness of the population under consideration, with heavier fish of a given length considered to be in better condition (Jones et al., 1999).

However, and even when body condition indices are used to estimate the pathological effects of parasites on fishes, parasite mass is almost always ignored in such calculations, except in systems where relatively large parasites infect small fish (Lagrue and Poulin, 2015). For example, the larval tapeworm *Schistocephalus solidus* can attain 40% of the weight of its host, the threespine stickleback *Gasterosteus aculeatus*, and up to 92% of the host's mass in multiple infections (Hopkins and Smyth, 1951). However, most parasites are typically much smaller than their hosts (Lafferty and Kuris, 2002), although fishes can be infected by many parasites that contribute to a considerable total mass (Santoro et al., 2013). Consequently, a considerable proportion of fish mass can consist of parasite tissues, particularly for those hosts more heavily infected, and any detrimental effect induced by the parasite, measurable through host body condition indices, may be clouded by the effect of parasite mass (Fig. 1A).

Indeed, Lagrue and Poulin (2015) found that the inclusion or exclusion of parasite mass from fish body mass in calculation of the Residual Index (Jakob et al., 1996) significantly influenced correlation patterns between parasite load and fish body condition in the common bully *Gobiomorphus cotidianus*. Their results showed that a positive correlation between parasite load and fish body condition was observed when parasite mass was included, seemingly indicating that fish in better condition supported higher parasite loads. In contrast, when parasite mass was excluded, there was no detectable relationship between helminth parasite load and fish condition, indicating that fish body condition tends to be overestimated when parasite mass is not accounted for. Later, based on the Scaled Mass Index and Fulton's condition factor, Maceda-Veiga et al. (2016) found correlative evidence that parasite effects on the body condition of common bullies can range from positive to negative as parasite burden increases, both in models including or excluding total parasite biomass.

In the same way, other indices based on body mass are often used to evaluate the well-being or fitness of fish, such as the hepatosomatic index (liver weight as a percentage of whole body weight, Bolger and Connolly, 1989), or its reproductive condition, such as the gonadosomatic index (gonadal weight as a percentage of whole body weight, DeVlaming et al., 1982). Both indices are not only affected by the mass of parasites or their pathological effect on body mass, but also on the mass of individual organs. Indeed, some parasites have marked or specific tissue tropism and can also elicit tissular responses or pathologies that alter the target organ. For example, larvae of anisakid nematodes show preferences for the liver of *Merlangius merlangus*, reaching high burdens and provoking encapsulations and development of fibroses, altering the liver mass (Elarifi, 1982). Similar outcomes are produced by the coccidian *Goussia clupearum*, in the liver of *Micromesistius poutassou*, contributing to poor body condition as shown by changes in the hepatosomatic and body condition indices (Abollo et al., 2001) or by the nematode *Philometra floridiensis* in the ovaries of *Sciaenops ocellatus* (Bakenhaster et al., 2014).

Beyond a possible effect of parasite mass, different pathologies can also alter fish condition indices. For example, migration of larval parasites through fish tissues may cause a series of physical traumas that induce non-specific stress responses characterized by elevated oxygen consumption and increased metabolic rates with concomitant decreases in total body lipid content (Lemly and Esch, 1984). Furthermore, resource depletion by pathogens can be enhanced by the metabolic cost of mounting an immune response, given that the immune system competes for resources with pathogens (Cressler et al., 2014). The outcome of these interactions will depend on the host species, the parasite taxon, its level of infection, size, life stage and site of infection (Lagrue and Poulin, 2015), and variability in pathological effects is to be expected. For example, Santoro et al. (2013) found a strong negative correlation between body condition factor and parasite burden for only one of three antarctic fish species, which was the most heavily infected. On the other hand, no relationship between host condition factor was observed for a small freshwater fish in streams from Argentina, harboring high abundance of larval trematodes, after excluding the parasite mass from calculations (Taglioretti et al., 2018), which can account for between 4 and 20% of fish mass (personal observations). Also, at the intraspecific level, the growth rate, weight gain, food conversion efficiency and condition factor of Atlantic cod, *Gadus morhua*, experimentally infected with the hematophagous copepod *Lernaeocera branchialis*, varied with the age of both fish (young versus adults) and parasites (young versus post-mature) and the time post-infection (Khan and Lee, 1989).

Exposure to parasites, consequently, triggers cascades of metabolic responses in hosts, altering physiological variables that are also used as alternative biomarkers of an animal's body condition, such as white blood cell count, body water and glycogen content or stress and reproductive hormones (Maceda-Veiga et al., 2016). For example, infection by *L. branchialis* in Atlantic cod induces anorexia, stress and blood loss, eventually causing anemia, lethargy, emaciation and a decrease in metabolism (Khan et al., 1990). Parasite mass, therefore, should be excluded, or at least their effects considered, in any estimation of body condition, either directly when measuring fish mass or indirectly by considering physiological biomarkers.

3. Effects of parasites on biomarkers

Parasites may affect host biology in several ways, not only physiologically, but also reproductively, morphologically, or behaviourally (Marcogliese, 2004, 2005), potentially interfering with the interpretation of several variables of fish ecology. In that sense, it has been demonstrated that parasites alter the host's stable isotope composition (Dubois et al., 2009; Sánchez et al., 2013; Pulkkinen et al., 2016). Stable isotope analysis has become widely used in ecological studies, notably in those focusing on trophic webs (Post, 2002; Layman et al., 2011). Stable isotopes of carbon and nitrogen (δ^{13}C and δ^{15}N) can be used as natural tracers of energy transfers, providing medium- to long-term information on food assimilated by organisms (Dubois et al., 2009). The isotopic composition of a consumer is enriched δ^{13}C and δ^{15}N with respect to its food (Post, 2002), which is linked to the respiratory and excretory metabolisms, respectively (Checkley and Entzeroth, 1985). Differences in nutrient requirements create a potential imbalance in homeostatic needs between consumers (parasites) and resources (hosts) (Bernot and Poulin, 2018). Consequenty, as in the case of fish condition factors, parasites may induce shifts in stable isotope ratios between healthy and parasitized individuals in two ways, either by disturbing the metabolism of hosts (a 'pathologic' shift), or when the stable isotopic signature of parasites is very different from that of the host and their mass relative to host mass is large enough (a "mass-balance" shift) (Doi et al., 2008; Dubois et al., 2009).

The relation between the isotopic composition of parasites and hosts shows no general trend toward either depletion or enrichment in isotope values (Pulkkinen et al., 2016). This has been attributed to differences in life cycles, parasitised organ/tissue and trophic modes of parasites (Deudero et al., 2002), and to parasite-induced changes in habitat selection, feeding behaviour and/or niche specialization of the host (Miura et al., 2006; Sánchez et al., 2013; Pegg et al., 2017). Whether direct or indirect, the effect of parasites on fish isotopic composition should not be neglected.

In recent decades, parasites have been increasingly used as bioindicators of environmental impact of anthropogenic changes (Sures, 2003, 2004, 2006; Williams and MacKenzie, 2003; Marcogliese, 2005; Vidal-Martínez et al., 2010). In general, environmental parasitology includes the use of parasites as accumulation indicators for pollutants and as effect indicators (Sures et al., 2017). Several parasite taxa, especially cestodes and acanthocephalans, have a high potential for accumulation, bioconcentration and tolerance of chemicals, making them useful sentinels to monitor the biological availability of chemical pollutants (Sures, 2004, 2008a,b; Nachev and Sures, 2016; Sures et al., 2017). On the other hand, the use of parasites as effect indicators focuses on direct effects of pollutants on free-living stages or on changes in population and community structure (Sures et al., 2017). However, the use of parasite abundance has not always been demonstrated conclusively as an indicator of environmental impact, because numerical or physiological responses to pollutants vary depending on the species (Sures, 2008b; Blanar et al., 2009; Vidal-Martínez et al., 2010).

In nature, fish face both parasites and environmental pollution, both of which can affect their physiological homeostasis, sometimes simultaneously. Consequently, physiological, behavioral or molecular changes produced by pollutants or habitat disturbance, usually used as biological markers to indicate effects of pollution (Sures et al., 2017), can be clouded by the presence of parasites.

A direct effect of certain parasites on the pollutant metabolism of their host is mediated by the remarkable ability of certain helminth taxa to accumulate pollutants (Sures and Siddall, 1999). Several studies have reported lower heavy metal concentrations in wild fish infected with acanthocephalans and cestodes relative to uninfected counterparts, a phenomenon attributed to disturbance by parasites of the entero-hepatic cycling of metals by fishes (Sures and Siddall, 1999; Sures et al., 2017). Since some parasites act as pollutant sinks, resulting from contaminant uptake by parasites, pollutant concentration in fish can be underestimated if most analyzed hosts harbour parasites and the differences between parasitized and unparasitized hosts are not accounted for (Sures et al., 2017).

In ecotoxicological sciences, physiological responses of organisms to pollutants are also used as biomarkers and measured at a biochemical or molecular level to indicate the presence of contaminants and their possible detrimental effects on organisms (Forbes et al., 2006). Among the usually used biomarkers, oxidative stress, energy budgets, hormone regulation and genes and proteins involved in pollutant metabolism and excretion are not specific to pollutants, but might also be affected by parasitism, among other stressors (Marcogliese and Pietrock, 2011; Sures et al, 2017). Furthermore, parasites may influence the metabolism of pollutants, interact synergistically or antagonistically with them and induce physiological reactions in hosts which can be wrongly attributed just to pollution (Sures, 2006). Many studies on this topic, including different pollutants, host and parasite species (reviewed by Sures et al., 2017), have shown that the outcome of parasite-pollution interactions can be to either reduce or increase levels of biomarkers, underming the reliability of biomarkers as diagnostic tools. Consequently, it seems that parasites are, at least partially, the causative agents of many effects commonly attributed to environmental pollution, and that ecotoxicological research carried out on parasitized fish can lead to contradictory results if possible effects of parasites on biomarker responses are not considered.

4. Effects of parasites on fish behaviour

By definition parasites exert deleterious effects to their hosts, ranging from nutritional effects to more severe pathologies, altered physiological homeostasis or general malaise, wich may have consequences for almost every aspect of fish behaviour (Barber et al., 2000), from slight shifts in the time spent performing a given activity to the appearance of drastically new and strange behaviours (Poulin, 1995). Far from being merely side-effects of infection, many altered host behaviours are acually the product of natural selection acting on parasites to target particular neural pathways in the host and manipulate its behaviour to their advantage. Host manipulation by parasites has been reported in many host-parasite associations spanning all major phyla of living organisms (Moore, 2002; Poulin, 2010). Changes in foraging efficiency, time budget, habitat selection, competitive ability, predator–prey relationships, shoaling behaviour, swimming performance and sexual behaviour and mate choice have been related to parasitism; fish also adopt strategies to reduce their exposure to parasite infection (habitat avoidance, prey selectivity or avoidance of infected individuals) or to perform behaviours aimed at removing parasites (substrate scraping, visitation of cleaning stations) (see Barber et al., 2000 for a review).

Many parasites with complex, multi-host life cycles require their current hosts to be eaten by specific predators to complete their life cycle, and accordingly they modify their host's behaviour to increase its susceptibility to predation in different ways. Infected host behave differentially, are eaten more readily and are taken more frequently by predators than are unparasitized hosts (Lafferty and Morris, 1996). On the other hand, differences in diet composition and prey selection (i.e. prey size) between parasitized and unparasitized fish have also been observed (Barber et al., 2000). Therefore, changes in host behaviour induced by parasites can have implications for the ecology of both fish predators and fish prey. For example, the proportion of fish infected by larval cestodes or trematodes eaten by ichthyophagous birds was observed to be significantly higher than that of infected fish available in both natural and experimental studies (van Dobben, 1952; Lafferty and Morris, 1996; Lafferty, 2008), indicating that parasites determine not only how a fish behaves, but also what the birds eat. The results of many studies on the behaviour of fish, their prey and predators, may be largely influenced by parasitism; without accounting for the effects of parasites, the behaviours measured are not a true representation of fish behaviour.

5. Effects of parasitism beyond the individual host

Parasites impose energetic demands, affect the health, frequently increase the death rate, decrease the birth rate, and may alter the behaviour, nutritional status and growth of their individual hosts (Minchella and Scott, 1991). Thus, through direct or indirect effects on death rates of individual hosts, parasites can increase the mortality rate of fish populations above their intrinsic mortality determined by genetics and other environmental factors (Fig. 1B). These effects, which can be density-mediated (through mortality) or trait-mediated (physiological, developmental and behavioural), may be crucial to interspecific interactions and, via indirect interactions with non-host species, may play key roles in structuring communities (Hatcher et al., 2014). Consequently, parasites can substantially affect free-living communities, especially if the host is abundant or ecologically influential (Mouritsen and Poulin, 2005a,b; Wood et al., 2007). For example, parasites can alter the outcome of species interactions such as predator–prey relationships (Fig. 1C) and intraspecific and interspecific competition by weakening competitively dominant hosts (Hatcher and Dunn, 2011; Hatcher et al., 2012). Hence, parasites may shape the feeding ecology of predators (Fig. 1C), the population dynamics of prey, and the abundance, distribution and diversity of organisms in the environment (Minchella and Scott, 1991; Lafferty and Morris, 1996). Parasitic organisms also represent a substantial proportion of the biomass in some ecosystems (Kuris et al., 2008; Lambden and Johnson, 2013) and can modify the strength of competitive and trophic interactions among species (Fig. 1C), as well as their abundance and distribution. Consequently, parasites impact energy flow through the ecosystem (Hudson et al., 2006; Johnson et al., 2010; Preston et al., 2013; Britton and Andreou, 2016; Vannatta and Minchella, 2018), food web structure by increasing its complexity (Lafferty et al., 2006, 2008; Dunne et al., 2013) and the physical habitat available for other species (Thomas et al., 1998; Mouritsen and Poulin, 2002, 2005a,b), acting as ecosystem engineers (Hatcher et al., 2012).

In synthesis, parasites can play influential roles in ecosystem functioning, structure and stability (Hudson et al., 2006; Lafferty et al., 2008). They achieve this through their effect on biogeochemical cycles of water, carbon, nutrients and trace elements, and by affecting the fluxes of biomass and energy as well as temporal ecosystem dynamics including disturbance, succession and stability (Preston et al., 2016; Sures et al., 2017; Wood and Johnson, 2015). Therefore, the ecological importance of parasites for communities of free-living organisms and ecosystems should not be ignored for two main reasons. First, a complete picture of community and ecosystem structure and functioning cannot be achieved if the influence of parasites is overlooked. Secondly, their exclusion can lead to unrealistic interpretations of the metrics commonly used in ecological studies.

Indeed, although we are still a long way from having complete knowledge of the implications of parasitism (Sures et al., 2017), due, at least in part, to the heterogeneity in host traits (Tompkins et al., 2011) and to their interaction with parasite traits (Preston et al., 2016), other sources of variability should be considered in any study, ranging from the host population to the ecosystem level. These sources are mainly related to three key aspects of the distribution of parasitic organisms in natural host populations.

First, macroparasite infections are almost invariably overdispersed in host populations (Tinsley et al., 2020), a recurrent and almost universal distributional pattern of parasite ecology, in which the majority of host individuals harbour few or no parasites while a minority carry many parasites (Shaw and Dobson, 1995; Poulin, 2007). Consequently, the strength of any effect of parasitism on host traits, if density-dependent, will be naturally variable among individuals even in an otherwise completely homogeneous sample of hosts. For example, unexpected overdispersion can be obseved for given host traits affected by parasites. Alternatively, departures from expected linear relationships between host traits or host responses to other effectors can be induced by the over-dispersed nature of parasitism. Since variation in host characteristics related to sex, age, resistance or behaviour, in turn contribute to generate parasite aggregation (Warburton and Vonhof, 2018; Tinsley et al., 2020), the effect of parasite overdispersion will be even larger in heterogeneous host samples.

Second, variability in host traits can also determine the extent of parasitic infections, independent of their effect on parasite aggregation. Indeed, sex differences in parasite infection prevalence or intensity are commonly observed in a wide range of taxa (Duneau and Ebert, 2012). This effect has mainly been attributed to ecological causes such as differential exposure rates due to sex-specific behavior or morphology, and to physiological sex differences, usually hormonal in nature, and their interactions with immune responses (Poulin, 1996; Zuk and McKean, 1996; Duneau and Ebert, 2012). Therefore, sex differences in some host traits can be enhanced by parasitism or even caused by parasites through the effects of differential parasite loads.

Additionally, parasite burdens often increase with host age or size, especially for fishes (Dogiel et al., 1958; Poulin, 2000), resulting in cumulative patterns of parasite abundance as fishes grow. Nevertheless, decreasing levels of parasitic infection in the oldest age clasess have been observed in both freswater (Dogiel et al., 1958) and marine fishes (Brattey and Bishop, 1992), being attributed to the death of heavily infected individuals (Henricson, 1977; Lester, 1984). Cumulative patterns are reflected in ontogenetic changes in the structure of parasite assemblages in conspecific hosts in terms of abundance and species richness (Poulin, 2000, 2004; Timi et al., 2010; Valtonen et al., 2010; Timi and Lanfranchi, 2013). Larger hosts are able to accommodate more parasite species and sustain a greater absolute number of parasites than small ones, display larger surface areas for parasite attachment and can ingest larger quantities of food, resulting in a higher exposure to infective stages (Guégan et al., 1992; Poulin, 2000; Valtonen et al., 2010). Larger fish can also feed on larger prey items, increasing the number and broadening the set of potential parasites acquired (Timi et al., 2010, 2011). Cumulative processes are expected to be more pronounced for long-lived parasites such as larval stages, which persist for long periods in their hosts, depending, therefore, not only on fish size, but also on fish age and longevity (Cantatore and Timi, 2015). However, the functional relationship between fish length and age is not linear, as exemplified by the widely used von Bertalanffy and other growth models (Katsanevakis, 2006), with large increases in age not necessarily accompanied by proportional changes in size, especially in older fish. Thus, fish assigned to a given size class can belong to different cohorts and a sample can be heterogeneous in terms of parasite abundance, depending on the proportion of individual fish of different ages. Conversely, a sample of fish of homogeneous age, but with different sizes, can harbour variable parasite loads; in other words, for fish of similar age, larger ones are expected to harbour more parasites, whereas for fish of similar size, older ones will be more parasitized (Braicovich et al., 2016). Therefore, differences in some host traits, attributable to fish size, age or their combination, can be largely clouded by the effect of differential parasite burdens.

Third, fish are rarely infected by a single parasite species: several parasite taxa often co-exist within or on the same individual host (Cox, 2001; Wegner et al., 2003; Pedersen and Fenton 2007), sometimes reaching high species richness. Every effect of parasites on individual fish discussed in previous sections may be potentially induced, either independently, synergistically or antagonistically, by these many parasite species. By direct extrapolation, and depending on the co-occurrence patterns of parasite species in host populations, there will be a mosaic of possible multiple and combined effects of parasites on host traits for each host population under study.

6. Concluding remarks

Parasitism is one of the most common lifestyles on the earth (Poulin and Morand, 2000; Marcogliese 2005); parasites can be found on every free-living organism in every ecosystem, and fish in particular harbour considerable diversity (Poulin and Morand, 2000). Given the impact of parasites across all levels of biological organisation, their omission from the design and analyses of ecological studies poses real risks of flawed interpretations for those patterns and processes that ecologists traditionally seek to uncover. However, parasitism has been largely ignored in fish population and community ecology, as well as in research on biodiversity and ecosystem functioning, not only in their role as drivers of ecological processes, but as sources of variability for several metrics widely utilized to describe these patterns. These oversights should be amended by integrating parasitism into any research if fish ecologists hope to achieve a complete understanding of all aspects of fish biology. In this sense, researchers should either routinely conduct basic necropsies of their fish, or share all fish samples with parasitologists, in order to obtain parasite counts and identification from all individual fish in a study, or a subsample when relevant. This should be done prior to data analysis, to add parasites as extra predictors or confounding variables, if necessary. Alternatively, captive-free, laboratory-bred fish could be used in experiments to ensure that biological parameters relating to fish physiology or behaviour can be measured without the masking influence of parasitic infections.

Acknowledgements

Financial support was provided by grants from Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina (PIP No. 112-201501-00973); Fondo para la Investigación Científica y Tecnológica, Argentina (PICT 2015 No. 2013) and Universidad Nacional de Mar del Plata, Argentina (EXA 915/18).

References

Abollo, E., Calvo, M., Pascual, S., 2001. Hepatic coccidiosis of the blue whiting, *Micromesistius poutassou* (Risso), and horse mackerel, *Trachurus trachurus* (L.), from Galician waters. J. Fish Dis. 24, 335–343.

Anderson, R.M., May, R.M., 1979. Population biology of infectious diseases: part I. Nature 280, 361–367.

Bakenhaster, M.D., Lowerre-Barbieri, S., Kiryu, Y., Walters, S., Fajer-Avila, E.J., 2014. *Philometra floridensis* (Nematoda: Philometridae) damages ovarian tissue without reducing host (*Sciaenops ocellatus*) fecundity. Dis. Aquat. Organ. 108, 227–239.

Barber, I., Hoare, D., Krause, J., 2000. Effects of parasites on fish behaviour: a review and evolutionary perspective. Rev. Fish Biol. Fisher. 10, 131–165.

Bernot, R.J., Poulin, R., 2018. Ecological stoichiometry for parasitologists. Trends Parasitol. 34, 928–933.

Blanar, C.A., Munkittrick, K.R., Houlahan, J., MacLatchy, D.L., Marcogliese, D.J., 2009. Pollution and parasitism in aquatic animals: a meta-analysis of effect size. Aquat. Toxicol. 93, 18–28.

Bolger, T., Connolly, P.L., 1989. The selection of suitable indices for the measurement and analysis of fish condition. J. Fish Biol. 34, 171–182.

Braicovich, P.E., Ieno, E.N., Sáez, M., Despos, J., Timi, J.T., 2016. Assessing the role of host traits as drivers of the abundance of long-lived parasites in fish-stock assessment studies. J. Fish Biol. 89, 2419–2433.

Brattey, J., Bishop, C.A., 1992. Larval *Anisakis simplex* (Nematoda: Ascaridoidea) infection in the musculature of Atlantic cod, *Gadus morhu*a, from Newfoundland and Labrador. Can. J. Fish. Aquat. Sci. 49, 2635–2647.

Britton, J.R., Andreou, D., 2016. Parasitism as a driver of trophic niche specialisation. Trends Parasitol. 32, 437–445.

Cantatore, D.M.P., Timi, J.T., 2015. Marine parasites as biological tags in South American Atlantic waters, current status and perspectives. Parasitology 142, 5–24.

Checkley, D.M., Entzeroth, L.C., 1985. Elemental and isotopic fractionation of carbon and nitrogen by marine, planktonic copepods and implications to the marine nitrogen cycle. J. Plankton. Res. 7, 553–568.

Cox, F.E.G., 2001. Concomitant infections, parasites and immune responses. Parasitology 122, S23–S38.

Cressler, C.E., Nelson, W.A., Day, T., McCauley, E., 2014. Disentangling the interaction among host resources, the immune system and pathogens. Ecol. Lett. 17, 284–293.

Deudero, S., Pinnegar, J.K., Polunin, N.V.C., 2002. Insights into fish host-parasite trophic relationships revealed by stable isotope analysis. Dis. Aquat. Organ. 52, 77–86.

DeVlaming, V., Grossman, G., Chapman, F., 1982. On the use of the gonosomatic index. Comp. Biochem. Physiol. A 73, 31–39.

Dobson, A., Lafferty, K.D., Kuris, A.M., Hechinger, R.F., Jetz, W., 2008. Homage to Linnaeus: How many parasites? How many hosts?. Proc. Natl. Acad. Sci. USA 105, 11482–11489.

Dogiel, V.A., Petrushevski, G.K., Polyanski, Y.I., 1958. Parasitology of Fishes. Oliver & Boyd, London (Translated from Russian by Z. Kabata, 1961).

Doi, H., Yurlova, N.I., Vodyanitskaya, S.N., Kikuchi, E., Shikano, S., Yadrenkina, E.N., Zuykova, E.I., 2008. Parasite-induced changes in nitrogen isotope signatures of host tissues. J. Parasitol. 94, 292–295.

Dubois, S.Y., Savoye, N., Sauriau, P.G., Billy, I., Martinez, P., De Montaudouin, X., 2009. Digenean trematodes-marine mollusc relationships: a stable isotope study. Dis. Aquat. Organ. 84, 65–77.

Duneau, D., Ebert, D., 2012. Host sexual dimorphism and parasite adaptation. PLoS Biol. 10, e1001271.

Dunne, J.A., Lafferty, K.D., Dobson, A.P., Hechinger, R.F., Kuris, A.M., Martínez, N.D., McLaughlinm, J.P., Muritsen, K.N., Poulin, R., Reises, K., Stouffer, D.B., Thieltges, D.W., Williams, R.J., Zander, C.D., 2013. Parasites affect food web structure primarily through increased diversity and complexity. PLoS Biol. 11, e1001579.

Elarifi, A.E., 1982. The histopathology of larval anisakid nematode infections in the liver of whiting, *Merlangius merlangus* (L.), with some observations on blood leucocytes of the fish. J. Fish Dis. 5, 411–419.

Forbes, V.E., Palmqvist, A., Bach, L., 2006. The use and misuse of biomarkers in ecotoxicology. Environ. Toxicol. Chem. 25, 272–280.

Frainer, A., McKie, B.G., Amundsen, P.A., Knudsen, R., Lafferty, K.D., 2018. Parasitism and the biodiversity-functioning relationship. Trends Ecol. Evol. 33, 260–268.

Guégan, J.F., Lambert, A., Lévêque, C., Combes, C., Euzet, L., 1992. Can host body size explain the parasite species richness in tropical freshwater fishes?. Oecologia 90, 197–204.

Hatcher, M.J., Dunn, A.M., 2011. Parasites in Ecological Communities: From Interactions to Ecosystems. Cambridge University Press, Cambridge.

Hatcher, M.J., Dick, J.T.A., Dunn, A.M., 2012. Diverse effects of parasites in ecosystems: linking interdependent processes. Front. Ecol. Environ. 10, 186–194.

Hatcher, M.J., Dick, J.T.A., Dunn, A.M., 2014. Parasites that change predator or prey behaviour can have keystone effects on community composition. Biol. Lett. 10, 20130879.

Hechinger, R.F., Lafferty, K.D., Dobson, A.P., Brown, J.H., Kuris, A.M., 2011. A common scaling rule for abundance, energetics, and production of parasitic and free-living species. Science 333, 445–448.

Henricson, J., 1977. The abundance and distribution of *Diphyllobothrium dendriticum* (Nitzsch) and *D. ditremum* (Creplin) in the char *Salvelinus alp*inus. J. Fish Biol. 11, 231–248.

Hopkins, C.A., Smyth, J.D., 1951. Notes on the morphology and life history of *Schistocephalus solidus* (Cestoda: Diphyllobothriidae). Parasitology 41, 283–291.

Hudson, P.J., Dobson, A.P., Newborn, P., 1998. Prevention of population cycles by parasite removal. Science 282, 2256–2258.

Hudson, P.J., Dobson, A.P., Lafferty, K.D., 2006. Is a healthy ecosystem one that is rich in parasites? Trends Ecol Evol 21, 381–385.

Huxham, M., Raffaelli, D., Pike, A., 1995. Parasites and food web patterns. J. Anim. Ecol. 64, 168–176.

Jakob, E.M., Marshall, S.D., Uetz, G.W., 1996. Estimating fitness: a comparison of body condition indices. Oikos 77, 61–67.

Johnson, P.T., Dobson, A., Lafferty, K.D., Marcogliese, D.J., Memmott, J., Orlofske, S.A., Poulin, R., Thieltges, D.W., 2010. When parasites become prey: ecological and epidemiological significance of eating parasites. Trends Ecol. Evol. 25, 362–371.

Jones, R.E., Petrell, R.J., Pauly, D., 1999. Using modified length–weight relationship to assess the condition of fish. Aquacult. Eng. 20, 261–276.

Khan, R.A., Lee, E.M., 1989. Influence of *Lernaeocera branchialis* (Crustacea: Copepoda) on Growth Rate of Atlantic COD, *Gadus morhu*a. J. Parasitol. 75, 449–454.

Khan, R.A., Lee, E.M., Barker, D., 1990. *Lernaeocera branchialis*: a potential pathogen to cod ranching. J. Parasitol. 76, 913–917.

Katsanevakis, S., 2006. Modelling fish growth: model selection, multi-model inference and model selection uncertainty. Fish. Res. 81, 229–235.

Kuris, A.M., Hechinger, R.F., Shaw, J.C., Whitney, K.L., Aguirre-Macedo, L., Boch, C.A., Dobson, A.P., Dunham, E.J., Fredensborg, B.L., Huspeni, T.C., Lorda, J., Mababa, L., Mancini, F.T., Mora, B., Pickering, M., Talhouk, N.L., Torchin, M.E., Lafferty, K.D., 2008. Ecosystem energetic implications of parasite and free-living biomass in three estuaries. Nature 454, 515–518.

Lafferty, K.D., 2008. Ecosystem consequences of fish parasites. J. Fish Biol. 73, 2083–2093.

Lafferty, K.D., Kuris, A.M., 2002. Trophic strategies, animal diversity and body size. Trends Ecol. Evol. 17, 507–513.

Lafferty, K.D., Morris, A.K., 1996. Altered behaviour of parasitised killifish increases susceptibility to predation by bird final hosts. Ecology 77, 1390–1397.

Lafferty, K.D., Dobson, A.P., Kuris, A.M., 2006. Parasites dominate fod web links. Proc. Nat. Acad. Sci. 103, 11211–11216.

Lafferty, K.D., Allesina, S., Arim, M., Briggs, C.J., De Leo, G., Dobson, A.P., Dunne, J.A., Johnson, P.T.J., Kuris, A.M., Marcogliese, D.J., Martinez, N.D., Memmott, J., Marquet, P.A., McLaughlin, J.P., Mordecai, E.A., Pascual, M., Poulin, R., Thieltges, D.W., 2008. Parasites in food webs: the ultimate missing links. Ecol. Lett. 11, 533–546.

Lagrue, C., Poulin, R., 2015. Measuring fish body condition with or without parasites: does it matter?. J. Fish Biol. 87, 836–847.

Lambden, J., Johnson, P.T.J., 2013. Quantifying the biomass of parasites to understand their role in aquatic communities. Ecol. Evol. 3, 2310–2321.

Layman, C.A., Araujo, M.S., Boucek, R., Hammerschlag-Peyer, C.M., Harrison, E., Jud, Z.R., Matich, P., Rosenblatt, A.E., Vaudo, J.J., Yeager, L.A., Post, D.M., Bearhop, S., 2011. Applying stable isotopes to examine food-web structure: an overview of analytical tools. Biol. Rev. 87, 545–562.

Lemly, A.D., Esch, G.W., 1984. Effects of the trematode *Uvulifer ambloplitis* on juvenile bluegill sunfish, *Lepomis macrochirus*: ecological implications. J. Parasitol. 70, 475–492.

Lester, R.J.G., 1984. A review of methods for estimating mortality due to parasites in wild fish populations. Helgol. Meeresunters 37, 53–64.

Maceda-Veiga, A., Green, A.J., Poulin, R., Lagrue, C., 2016. Body condition peaks at intermediate parasite loads in the common bully *Gobiomorphus cotidianus*. PLoS ONE 11, e0168992.

Marcogliese, D.J., 2004. Parasites: small players with crucial roles in the ecological theatre. EcoHealth 1, 151–164.

Marcogliese, D.J., 2005. Parasites of the superorganism: are they indicators of ecosystem health?. Int. J. Parasitol. 35, 705–716.

Marcogliese, D.J., Pietrock, M., 2011. Combined effects of parasites and contaminants on animal health: parasites do matter. Trends Parasitol. 27, 123–130.

May, R.M., Anderson, R.M., 1979. Population biology of infectious diseases: part II. Nature 280, 455–461.

Minchella, D.J., Scott, M.E., 1991. Parasitism: a cryptic determinant of animal community structure. Trends Ecol. Evol. 6, 250–254.

Miura, O., Kuris, A.M., Torchin, M.E., Hechinger, R.E., Chiba, S., 2006. Parasites alter host phenotype and may create a new ecological niche for snail hosts. Proc. R. Soc. B 273, 1323–1328.

Moore, J., 2002. Parasites and the Behavior of Animals. Oxford University Press, Oxford.

Mouritsen, K.N., Poulin, R., 2002. Parasitism, community structure and biodiversity in intertidal ecosystems. Parasitology 124, S101–S117.

Mouritsen, K.N., Poulin, R., 2005a. Parasitism can influence the intertidal zonation of non-host organisms. Mar. Biol. 148, 1–11.

Mouritsen, K.N., Poulin, R., 2005b. Parasites boost biodiversity and change animal community structure by trait-mediated indirect effects. Oikos 108, 344–350.

Nachev, M., Sures, B., 2016. Environmental parasitology: parasites as accumulation bioindicators in the marine environment. J. Sea Res. 113, 45–50.

Pedersen, A.B., Fenton, A., 2007. Emphasizing the ecology in parasite community ecology. Trends Ecol. Evol. 22, 133–139.

Pegg, J., Andreou, D., Williams, C.F., Britton, J.R., 2017. Consistent patterns of trophic niche specialization in host populations infected with a non-native copepod parasite. Parasitology 144, 945–953.

Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83, 703–718.

Poulin, R., 1995. 'Adaptive' changes in the behaviour of parasitised animals: a critical review. Int. J. Parasitol. 25, 1371–1383.

Poulin, R., 1996. Sexual inequalities in helminth infections: a cost of being male?. Am. Nat. 147, 287–295.

Poulin, R., 2000. Variation in the intraspecific relationship between fish length and intensity of parasitic infection: biological and statistical causes. J. Fish Biol. 56, 123–137.

Poulin, R., 2004. Macroecological patterns of species richness in parasite assemblages. Basic Appl. Ecol. 5, 423–434.

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

Poulin, R., 2010. Parasite manipulation of host behavior: an update and frequently asked questions. Adv. Stud. Behav. 41, 151–186.

Poulin, R., 2011. The many roads to parasitism: a tale of convergence. Adv. Parasit. 74, 1–40.

Poulin, R., Morand, S., 2000. The diversity of parasites. Q. Rev. Biol. 75, 277–293.

Preston, D.L., Orlofske, S.A., Lambden, J.P., Johnson, P.T.J., 2013. Biomass and productivity of trematode parasites in pond ecosystems. J. Anim. Ecol. 82, 509–517.

Preston, D.L., Mischler, J.A., Townsend, A.R., Johnson, P.T., 2016. Disease ecology meets ecosystem science. Ecosystems 19, 737–748.

Pulkkinen, K., Aalto, S.L., Nykänen, H., 2016. Parasite infection alters host stable-isotope composition under controlled feeding. Freshwater Biol. 61, 1981–1990.

Sánchez, M.I., Varo, N., Matesanz, C., Ramo, C., Amat, J.A., Green, A.J., 2013. Cestodes change the isotopic signature of brine shrimp, *Artemia*, hosts: implications for aquatic food webs. Int. J. Parasitol. 43, 73–80.

Santoro, M., Mattiucci, S., Work, T., Cimmaruta, R., Nardi, V., Cipriani, P., Bellisario, B., Nascetti, G., 2013. Parasitic infection by larval helminths in Antarctic fishes: pathological changes and impact on the host body condition index. Dis. Aquat. Organ. 105, 139–148.

Sato, T., Egusa, T., Fukusima, K., Oda, T., Ohte, N., Tokuchi, N., Watanabe, K., Kanaiwa, M., Murakami, I., Lafferty, K.D., 2012. Nematomorph parasites alter the food web and ecosystem function of streams through behavioral manipulation of their cricket hosts. Ecol. Lett. 15, 786–793.

Shaw, D.J., Dobson, A.P., 1995. Patterns of macroparasite abundance and aggregation in wildlife populations: a quantitative review. Parasitology 111, S111–S133.

Sures, B., 2003. Accumulation of heavy metals by intestinal helminths in fish: an overview and perspective. Parasitology 126, 53–60.

Sures, B., 2004. Environmental parasitology: relevancy of parasites in monitoring environmental pollution. Trends Parasitol. 20, 170–177.

Sures, B., 2006. How parasitism and pollution affect the physiological homeostasis of aquatic hosts. J. Helminthol. 80, 151–158.

Sures, B., 2008a. Environmental parasitology. Interactions between parasites and pollutants in the aquatic environment. Parasite 15, 434–438.

Sures, B., 2008b. Host-parasite interactions in polluted environments. J. Fish Biol. 73, 2133–2142.

Sures, B., Siddall, R., 1999. Pomphorhynchus laevis: the intestinal acanthocephalan as a lead sink for its fish host, chub (Leuciscus cephalus). Exp. Parasitol. 93, 66–72.

Sures, B., Nachev, M., Selbach, C., Marcogliese, D.J., 2017. Parasite responses to pollution: what we know and where we go in 'Environmental Parasitology'. Parasit. Vectors 10, 65.

Taglioretti, V., Rossin, M.A., Timi, J.T., 2018. Fish-trematode systems as indicators of anthropogenic disturbance: effects of urbanization on a small stream. Ecol. Indic. 93, 759–777.

Thomas, F., Renaud, F., De Meeûs, T., Poulin, R., 1998. Manipulation of host behaviour by parasites: ecosystem engineering in the intertidal zone?. Proc. R. Soc. Lon. B: Biol. Sci. 265, 1091–1096.

Thomas, F., Poulin, R., de Meeüs, T., Guégan, J.-F., Renaud, F., 1999. Parasites and ecosystem engineering: what roles could they play?. Oikos 84, 167–171.

Timi, J.T., Lanfranchi, A.L., 2013. Ontogenetic changes in heterogeneity of parasite communities of fish: disentangling the relative role of compositional versus abundance variability. Parasitology 140, 309–317.

Timi, J.T., Luque, J.L., Poulin, R., 2010. Host ontogeny and the temporal decay of similarity in parasite communities of marine fish. Int. J. Parasitol. 40, 963–968.

Timi, J.T., Rossin, M.A., Alarcos, A.J., Braicovich, P.E., Cantatore, D.M.P., Lanfranchi, A. L., 2011. Fish trophic level and the similarity of larval parasite assemblages. Int. J. Parasitol. 41, 309–316.

Tinsley, R., Vineer, H.R., Grainger-Wood, R., Morgan, E., 2020. Heterogeneity in helminth infections: factors influencing aggregation in a simple host–parasite system. Parasitology 147, 65–77.

Tompkins, D.M., Dunn, A.M., Smith, M.J., Telfer, S., 2011. Wildlife diseases: from individuals to ecosystems. J. Anim. Ecol. 80, 19–38.

Valtonen, E.T., Marcogliese, D.J., Julkunen, M., 2010. Vertebrate diets derived from trophically transmitted fish parasites in the Bothnian Bay. Oecologia 162, 139–152.

van Dobben, W.H., 1952. The food of the cormorant in the Netherlands. Ardea 40, 1–63.

Vannatta, J.T., Minchella, D.J., 2018. Parasites and their impact on ecosystem nutrient cycling. Trends Parasitol. 34, 452–455.

Vidal-Martínez, V.M., Pech, D., Sures, B., Purucker, S.T., Poulin, R., 2010. Can parasites really reveal environmental impact?. Trends Parasitol. 26, 44–51.

Warburton, E.M., Vonhof, M.J., 2018. From individual heterogeneity to population-level overdispersion: quantifying the relative roles of host exposure and parasite establishment in driving aggregated helminth distributions. Int. J. Parasit. 48, 309–318.

Wegner, K.M., Reusch, T.B., Kalbe, M., 2003. Multiple parasites are driving major histocompatibility complex polymorphism in the wild. J. Evol. Biol. 16, 224–232.

Williams, N.H., MacKenzie, K., 2003. Marine parasites as pollution indicators: an update. Parasitology 126, S127–S141.

Weinstein, S.B., Kuris, A.M., 2016. Independent origins of parasitism in Animalia. Biol. Lett. 12, 20160324.

Wood, C.L., Johnson, P.T.J., 2015. A world without parasites: exploring the hidden ecology of infection. Front. Ecol. Environ. 13, 425–434.

Wood, C.L., Byers, J.E., Cottingham, K.L., Altman, I., Donahue, M.J., Blakeslee, A.M.H., 2007. Parasites alter community structure. Proc. Nat. Acad. Sci. 104, 9335–9339.

Zuk, M., McKean, K.A., 1996. Sex differences in parasite infections: patterns and processes. Int. J. Parasitol. 26, 1009–1024.