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Meta-analysis of seasonal dynamics of parasite infections in aquatic ecosystems

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ABSTRACT

Seasonal infection dynamics characterise many host-parasite interactions, as abiotic conditions drive fundamental biological processes in both hosts and parasites. The extent to which seasonal cycles in parasite abundance are universal, and whether the same underlying mechanisms are responsible for seasonality across different host-parasite associations, have received little attention to date. Here, global patterns of seasonal infection dynamics are tested using a meta-analysis of 693 seasonal contrasts in the local abundance of metazoan parasites in aquatic vertebrates, representing 343 parasite species and 148 host species. These include both contrasts between winter and summer in temperate systems, and between wet and dry seasons in tropical systems. Overall, the analysis found no evidence that seasonal infection dynamics are universal, nor that they are controlled by the same factors. More specifically, the results indicate no overall effect of the magnitude of local seasonal differences in abiotic conditions (temperature or precipitation), type of host (amphibian or fish), habitat (freshwater, coastal marine or deep-sea), host body length, or mode of transmission (skin contact or trophic) on the extent of seasonal differences in parasite infections. Instead, the results revealed many clear taxon-specific or habitat-specific patterns of seasonal infection dynamics, with some parasite or host taxa generally showing distinct peaks in infections in summer or dry seasons, and others showing no seasonal changes. The present findings serve to identify empirically which host-parasite associations are most likely to respond to changing climatic conditions, and thus provide useful information for fisheries and aquaculture.

1. Introduction

Seasonal fluctuations in abiotic conditions are cyclic, largely predictable and global drivers of a range of biological processes across multiple ecosystems. They are major forces regulating population dynamics (Fretwell, 1972) and strong agents of natural selection (Varpe, 2017; Williams et al., 2017). They also affect interspecific interactions and species diversity within communities (Tonkin et al., 2017). Seasonality of infectious diseases is of particular interest, with the dynamics of many pathogens following seasonal changes in external conditions (Dowell, 2001; Altizer et al., 2006). Identifying the processes linking seasons with infections is necessary to better forecast the future impact of climate change on disease. Climate change is altering seasonal cycles (Parmesan, 2006). This will lead to changes in, and possible mismatches between, host physiology and phenology on the one hand, and temporal peaks in parasite epidemiological dynamics on the other hand (Lafferty, 2009). These impacts may be particularly pronounced in aquatic ecosystems (Marcogliese, 2001; Paull et al., 2012; Barber et al., 2016).

Seasonal differences in the prevalence and abundance of metazoan ecto- or endoparasites of aquatic vertebrates (fish and amphibians) have long been recognised (e.g., Chubb, 1977, 1979, 1980, 1982). However, although they have been documented in multiple host-parasite associations, there has been no attempt to identify global patterns and test broad-scale hypotheses regarding the underlying processes responsible for differences in seasonality of infection risk among host-parasite systems. One obvious hypothesis is that across the globe, the magnitude of local seasonal differences in abiotic conditions correlates with the local seasonality of infection. This hypothesis is based on the reasonable assumption that abiotic factors are key drivers of host physiology and phenology, and/or of parasite multiplication and transmission. In ectotherms, temperature almost universally correlates positively with physiological rates such as metabolism, digestion, cell division and growth (Sibly and Calow, 1986; Willmer et al., 2000). Indeed, there is strong evidence that temperature regulates the asexual multiplication of trematodes within their snail intermediate host before infective stages exit the snail to seek fish or

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amphibian hosts (Poulin, 2006), as well as regulating the production of eggs and infective stages in fish ectoparasites (e.g., Johnston and Dykeman, 1987; Buchmann, 1988; Tubbs et al., 2005) and the growth rates and maturation times of endoparasites in both intermediate and final fish hosts (e.g., Studer et al., 2010; Franke et al., 2017). Also, ambient temperature affects the metabolism of ectothermic animals such as fish and amphibians (Sibly and Calow, 1986), and therefore their feeding rates and exposure to trophically transmitted parasites. The net result of all these accelerated processes should be higher infection risk by more parasites passing through more generations during summer than winter. Thus, in temperate regions, greater local differences in temperature between winter and summer should correspond to more pronounced seasonal variation in infection levels. In the tropics, however, where temperatures vary less throughout the year, the same may not be true of localities characterised by greater differences in precipitation, as opposed to temperature, between the dry and wet seasons.

A second hypothesis is that different types of aquatic habitats provide different levels of buffering against seasonal changes in temperature and precipitation. Freshwater habitats, especially the littoral zones of lakes and the small and easily accessible rivers where many parasitological studies are conducted, are affected by changes in air temperature and precipitation (Wetzel, 2001). For instance, the droughts and spates typical of many rivers illustrate the extremes to which freshwater habitats are subjected. Coastal marine habitats, in contrast, represent larger volumes of water that are open and well-mixed, making them less sensitive to atmospheric influences, although they do experience seasonal variation in factors such as pH and dissolved oxygen concentrations. Finally, deep-sea habitats are characterised by mostly stable temperatures through the year, with little variation between seasons (Knauss and Garfield, 2017). Therefore, we might predict that seasonal differences in infection levels would be more pronounced in freshwater habitats, followed by coastal habitats, and finally deep-sea habitats, matching the relative magnitude of seasonal abiotic variation in those habitats.

The above hypotheses focus on the effects of factors associated with where hosts and parasites live; however, intrinsic properties of hosts and parasites themselves can also influence the magnitude of seasonal variation in their abundance. For instance, different parasites use different routes to infect their hosts, and a reasonable hypothesis would be that transmission mode influences the extent to which seasonal variation in external conditions affects infection levels. In temperate areas, differences in temperature between winter and summer may have similar impacts on infection dynamics regardless of a parasite's mode of transmission. In parasites transmitted by free-swimming infective stages via contact with the host's skin or gills (i.e., copepods, monogeneans, trematode metacercariae), the positive effect of temperature on the production and activity of infective stages (Johnston and Dykeman, 1987; Buchmann, 1988; Tubbs et al., 2005; Poulin, 2006) should result in summer peaks in infections. Trophically transmitted helminths, which are acquired through the ingestion of infected prey, should also reach higher infection levels in summer months since metabolic rates and prey ingestion rates of fish and amphibians increase in the warm summer months (Sibly and Calow, 1986). In contrast, in the tropics, differences in precipitation between the dry and wet seasons can have different impacts on infection dynamics depending on a parasite's mode of transmission. Freshwater habitats expand in volume during the wet season, and undergo contraction in the dry season. The flow rates of streams and rivers also increase greatly during the wet seasons. Given that temperatures do not vary very much between those seasons, the production of transmission stages in parasites infecting hosts via skin contact should remain roughly the same. Therefore, all else being equal, for the density-dependent transmission of free-living infective stages, target hosts will be easier to find when concentrated in small bodies of water in the dry season, but harder to find when diluted in larger water volumes or in high water flow conditions (e.g., Barker and Cone, 2000) during the wet season, leading to higher infection risk in the dry season. Trophically transmitted parasites may experience similar boom-and-bust cycles of abundance, but to a lesser degree. The small temperature variation between tropical seasons should not cause substantial changes in fish and amphibian feeding rates. However, if infection levels by certain larval helminths in prey species peak in the dry season for the reasons outlined above, there may be cascading consequences for fish definitive hosts.

Other properties of hosts and parasites may influence seasonal patterns of infection levels. For example, the lifespan of parasites in fish and amphibian hosts, from infection to death, can either negate or exacerbate seasonal infection dynamics. Long-lived parasites that persist across seasons should present more stable infection levels over time compared with species in which individuals live for only a few months and go through population expansions and crashes every year. However, although juvenile helminth stages seem to be longer-lived than adult stages, there is very little accurate information available on parasite lifespan. Host lifespan can also influence seasonal infection dynamics. Assuming they cannot clear infections, long-lived hosts, i.e. larger species, are more likely to carry over infections from previous seasons or years, whereas small-bodied species that live only one or 2 years are more likely to only harbour parasites acquired in the months prior to sampling. All else being equal, we might thus expect larger-bodied species to show less pronounced seasonal variations in infection levels than small-bodied species.

Here, I conduct a meta-analysis of published data on seasonal differences (winter versus summer for temperate systems, wet versus dry seasons for tropical systems) in infection levels by metazoan parasites of fish and amphibians. The analysis specifically tests the predictions detailed above: (i) seasonal variation in infection levels should increase with the magnitude of local seasonality in abiotic conditions; (ii) seasonal differences in infection levels should be more pronounced in freshwater habitats, followed by coastal habitats and deep-sea habitats; (iii) parasites transmitted by infective stages contacting host skin should peak in abundance in the dry season in tropical freshwater systems, but not those transmitted trophically; (iv) the mode of transmission should have little influence in temperate systems, where all parasites should peak in abundance in summer; and (v) seasonal variation in infection levels should decrease with increasing host body size. In recognition that ecological patterns may be phylogenetically constrained (Harvey and Pagel, 1991), the analysis also considers host and parasite taxonomic affiliations, and reveals some idiosyncratic and taxon-specific patterns. Overall, the present findings represent the first attempt to provide a global, empirical synthesis of seasonal dynamics in parasite infections, serving both as a test of specific ecological predictions as well as a basis for predicting the future impacts of global climate change on particular groups of hosts and parasites.

2. Methods

2.1. Dataset assembly

A search of the ISI Web of Science was conducted for the years 2008–2018, inclusively, using the keyword string: (fish* or amphibia* or frog* or toad*) and (parasite* or helminth* or trematod* or digenea* or nematod* or cestod* or tapeworm* or acanthocephala* or monogenea* or copepod*) and (season* or temporal* or winter or summer or wet or rainy or dry) and (prevalence* or "infection level*" or abundance* or intensit*). Given how frequently infection data are reported separately for different seasons in the parasitological literature, this time period provides a large and representative sample of studies. A total of 1133 studies were returned by the search of the Web of Science, of which 264 were retained after their abstract was read. Only populations of teleost fish or amphibians exposed to natural parasite infections were considered, and thus several studies of captive fish populations maintained under natural conditions (e.g., in sea cages) were included. Populations of amphibians in which seasonal samples focused on different life stages (e.g. tadpoles versus adults) were excluded. A total of 234 (out of 264) of the articles could be obtained, either directly via Otago University's (New Zealand) library, which subscribes to an extensive range of scientific publishers (https://www.otago.ac.nz/library/databases/index.php), or by requesting a copy from the authors. Finally, 133 of these 234 articles provided all the necessary information (see below) and were used to construct the dataset.

Each entry in the dataset consists of one parasite species on one host species in one locality over one annual cycle, for which data were available on either prevalence or abundance in both winter and summer (temperate zone up to 70°N or S) or in both the wet and dry seasons (tropics). Therefore, for studies conducted over several years, i.e. studies with paired replicate samples for both seasons, different years of sampling were considered distinct and entered separately in the dataset. The definitions of winter and summer samples, or wet season and dry season samples, were taken as stated in each original article. Samples from other seasons (spring, autumn) were ignored to focus on the contrast between the two most extreme seasons. A few exceptions were made in cases where spring samples were taken as soon as possible (e.g., after ice cover was gone) following the end of winter, and counted as winter samples. Many studies contributed multiple entries to the final dataset. For each entry, the following information was recorded from the study, or from other sources:

Parasite species and host species: the higher taxa (family, order, class, phylum) to which they belonged were also recorded, following the taxonomic classification in the Catalogue of Life (www.catalogueoflife.org).

Host body length and seasonal size difference: the maximum body length (cm) of adult individuals in each host species was obtained from a standard source: FishBase (www.fishbase.org) for fish (total length), and AmphiBIO (Oliveira et al., 2017) for amphibians (snout-vent length). Also, when the data were available in the original study, hosts were categorised as either showing no size difference between seasons, or as being significantly longer in winter, summer, the wet season or the dry season; if no information was provided, it was assumed there was no clear size difference between seasons. Because the authors of the original studies aimed to capture hosts of similar sizes across seasons, in the few cases where differences in host sizes were observed, these tended to be small in absolute terms and probably not biologically relevant, despite statistical significance. A preliminary analysis indicated that categorising studies based on whether or not small differences in host sizes between seasons were found had no impact on the main results of the meta-analysis, therefore this factor was not included in the main analyses (see below).

Habitat: the habitat in which the host population was sampled was classified as freshwater, coastal marine, or deep-sea (offshore, >250 m).

Locality and climatic variables: the name of the sampling locality was recorded, as were its latitude and longitude. If not given in the original study, the latter were obtained from Google maps (https://maps.google.com). Using these coordinates, the following climatic variables were extracted for each locality from the MERRAclim database, which provides high-resolution (2.5 arc-minutes) data from satellite-based remote sensing information (Vega et al., 2017): temperature seasonality (variable code BIO4, reported as standard deviation * 100) and precipitation seasonality (variable code BIO15, reported as the coefficient of variation). These quantify the extent of annual variation in temperature and specific humidity based on monthly minimum and maximum local values. Although these are measures of atmospheric conditions, air temperature relates to water temperature of coastal and freshwater ecosystems, and precipitation determines the input of rain water to aquatic habitats.

Mode of transmission: parasites were classified either as acquired via contact with the host's external surfaces, regardless of whether or not penetration ensued (copepods, monogeneans, trematode metacercariae), or acquired trophically, i.e. by ingestion of infected prey (cestodes, nematodes, acanthocephalans, adult trematodes).

Host sample sizes: the numbers of individual hosts examined for parasites in each season (winter versus summer, wet versus dry) were recorded. Cases where the sample size was ≤ 5 individuals in one season were not included.

Parasite infection parameters: the prevalence (proportion of infected host individuals) and the abundance of infection (the mean number of parasite individuals per host, including uninfected hosts in the calculation) were recorded separately for each season. In addition, the standard deviation of abundance was also recorded, if given; if the standard error (*SE*) was given instead, the standard deviation was calculated as $SE\sqrt{N}$, where N is the number of hosts examined. When necessary, these data were extracted from figures in the original articles. Host-parasite associations in which a single host was found infected across both seasons were excluded, to avoid cases of accidental infection.

Study year and ID: to account for potential global-scale, interannual variation and for the non-independence of multiple entries coming from the same study, both the year of study and study ID were included in the dataset. When samples from one season and from the following opposite season were collected across consecutive calendar years (e.g., summer = July 2010, winter = January 2011), year of sampling was recorded as the year in which the first sample was taken. Preliminary analysis indicated that year of study had no influence on seasonality of infections, and it was therefore not included in the main analyses.

2.2. Effect sizes

For each seasonal contrast, up to three different effect sizes were calculated to measure seasonal differences in infection levels. First, seasonal differences in parasite abundance were measured using a *corrected difference in abundance*, which is basically Cohen's *d* (Hedges and Olkin, 1985), the classical measure of effect sizes in meta-analysis (Nakagawa and Santos, 2012):

$$\frac{\overline{Y}_s - \overline{Y}_w}{s} J$$

Where $\overline{Y}_s$ and $\overline{Y}_w$are, respectively, the mean abundance of parasites per host in summer and winter, and s is the pooled standard deviation across both seasons:

$$s = \sqrt{\frac{(N_s - 1)(s_s)^2 + (N_w - 1)(s_w)^2}{N_s + N_w - 2}}$$

Where s_s and s_w are, respectively, the standard deviation of mean abundance, and N_s and N_w the host sample sizes in the summer and winter seasons. Host sample size affects estimates of parasite infection levels (Gregory and Blackburn, 1991; Gregory and Woolhouse, 1993). Therefore, the correction factor J serves to correct for small sample sizes by giving more weight to comparisons based on large samples; it approaches one as total sample size increases, and is calculated as:

$$J = 1 - \frac{3}{4(N_s + N_w - 2) - 1}$$

Second, an *uncorrected difference in abundance* was also calculated, because standard deviations were often not reported in the original studies and using a different measure not incorporating the pooled standard deviation allowed many more comparisons to be included. Although not adjusted for the standard variation, the uncorrected effect size in abundance is expressed as a proportion of the average abundance across both seasons, a necessary standardisation as mean seasonal abundance values range over more than one order of magnitude among host-parasite combinations:

$$\frac{\overline{Y}_s - \overline{Y}_w}{(\overline{Y}_s + \overline{Y}_w)/2} J$$

Third, because some studies reported only prevalence and not abundance of infection, a *difference in prevalence* was also computed as follows:

$$(P_s - P_w)J$$

Where P_s and $P_w$are, respectively, the prevalence of infection in summer and winter. Effect sizes were computed such that positive values indicate greater infection levels in summer, and negative values indicate greater infections in winter. The exact same effect sizes were computed for comparisons of infection levels between wet and dry seasons, with positive values indicating greater infection levels in the wet season, and negative values indicating greater infections in the dry season.

2.3. Statistical analysis

Most surveys of fish parasites report seasonal differences in infections as a routine procedure, i.e. as a secondary result and not as a test of specific hypotheses. Therefore, no publication bias (i.e., a tendency for findings showing higher infections in one season in particular to be preferentially published) was expected among effect size estimates in the dataset. Nevertheless, funnel plots were used as a visual test for apparent biases.

Temperature seasonality and precipitation seasonality were positively correlated across all study localities ($r = 0.505$, $P < 0.0001$). Generally, seasonality in temperature is pronounced in temperate areas and minimal in the tropics, whereas seasonality in precipitation shows the inverse trend (Lisovski et al., 2017). Therefore, they were not used in the same models (see below), with temperature seasonality included as a predictor in analyses of infection seasonality in temperate zones (summer-versus-winter comparisons), and precipitation seasonality included in analyses of infection seasonality in the tropics (wet-versus-dry comparisons).

Seasonal differences in infection levels were analysed using a series of generalised linear mixed models (GLMMs) implemented in JMP v.14 (SAS Institute Inc.). Separate models were run for each of the three effect sizes as response, using a Gaussian error structure as effect size values approximated normal distributions in all cases. To account for the possible non-independence of effect sizes coming from the same study, all models included study ID as a random factor (Nakagawa and Santos, 2012). In addition, to control for non-independence due to shared phylogenetic history, both host taxonomy (family nested within order) and parasite taxonomy (family nested within phylum) were included as additional random factors in all models. Other taxonomic levels, e.g. genus, were not included due to frequent discoveries of cryptic taxa, possible misidentifications, and/or unresolved classification.

The first set of models tested for different patterns between amphibian and freshwater fish hosts; this included only summer-versus-winter comparisons, since the dataset did not include any tropical amphibian species. Fixed factors included whether the host was a fish or an amphibian, host body length, mode of transmission (skin contact or trophic), and temperature seasonality. Note that host taxonomy was not included as a random factor in these models, since they were comparing two distinct host groups.

The second set of models focused on fish only (not amphibians) in temperate zones (summer-versus-winter comparisons). Fixed factors included habitat (freshwater, coastal or deep-sea), host body length, mode of transmission, and temperature seasonality.

The final set of models focused on fish in the tropics (wet-versus-dry season comparisons). Fixed factors included habitat (freshwater and coastal only; no data from deep-sea in the tropics), host body length, mode of transmission, and precipitation seasonality.

3. Results

A total of 693 combinations of one parasite species in one host species in one locality over one annual cycle were compiled from the 133 articles. These comprise 141 species of fish (114 genera, 62 families, 19 orders), seven species of amphibians (seven genera, five families, one order) and 343 species of helminth and copepod parasites (223 genera, 101 families, 28 orders). The number of parasite species may in fact be greater, because several studies only identified parasites to the genus level (e.g. *Anisakis* sp. for nematodes, *Diplostomum* sp. for trematodes, etc.). The full dataset and list of original sources are available as Supplementary Data S1.

Of the 693 entries in the dataset, 36 entries involve amphibian hosts, 322 involve freshwater fish hosts, 294 involve coastal marine fish hosts, and 41 involve deep-sea fish hosts. Geographically, they cluster in several regions of active parasitological research, but still show a good spread across the world (Fig. 1). Overall, 486 entries involve seasonal contrasts in infection between summer and winter in temperate hosts, and 207 contrasts between wet and dry seasons in tropical hosts. With respect to mode of parasite transmission, 343 contrasts involve parasites acquired via contact with host skin, and 350 involve parasites acquired trophically. The number of entries included in each analysis for different host and parasite taxa, different habitats and for the three different effect sizes considered, are given in Supplementary Tables S1–S6. Funnel plots showed a roughly symmetrical distribution of points around the mean effect size (e.g., Supplementary Fig. S1), and little evidence of publication bias.

3.1. Seasonal infections in freshwater fish and amphibians

The analyses revealed no significant overall differences between freshwater fish and amphibians in seasonal patterns of parasite infections, for any of the three effect sizes considered (Supplementary Table S7). However, the relatively small number of data points for amphibians relative to fish may limit the power of this comparison. Nevertheless, when looking separately at different groups of parasites, one difference becomes apparent: the prevalence of nematode infections rises significantly during summer in amphibian hosts, but not in freshwater fish (Supplementary Table S3). Other potential differences for particular groups of parasites cannot reliably be assessed due to a limited number of contrasts. The overall analysis also indicated that, based on uncorrected differences, summer-biased peaks in parasite abundance increased with increasing temperature seasonality, as expected, and with

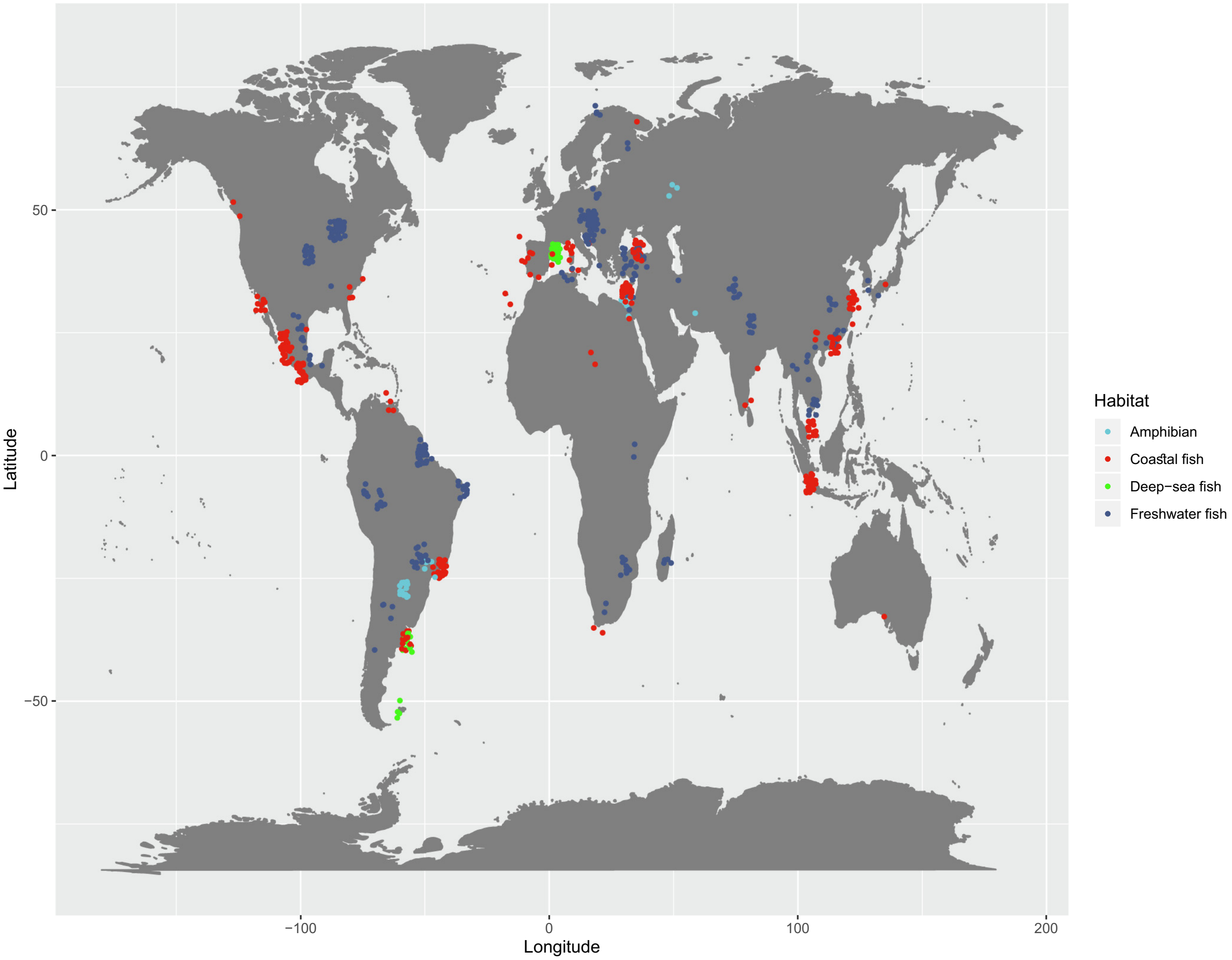

Fig. 1. Geographical distribution of the 693 seasonal contrasts in helminth parasite infection levels in amphibian hosts (N = 36), freshwater fish hosts (N = 322), coastal marine fish (N = 294) and deep-sea fish (N = 41), in the data set compiled from articles published between 2008 and 2018.

increasing host body size, contrary to the original prediction (Supplementary Table S7). However, both these effects were quantitatively very weak.

3.2. Seasonal infections in temperate fish

The second set of GLMMs was designed to test for overall effects of habitat (freshwater, coastal or deep-sea), host body length, mode of transmission, and temperature seasonality on summer-versus-winter contrasts in parasite infections, and it revealed no significant effects of any of these factors (Supplementary Table S8). Here again, however, some patterns emerge when looking separately at different parasite groups. For example, whatever the effect size considered, infections by monogeneans tend to peak significantly in summer in freshwater fish, but not in marine fish (Fig. 2; Supplementary Tables S1–S3). For copepods, which have a similar mode of transmission (contact with host external surfaces), the pattern is the opposite: infections tend to peak significantly in summer for marine fish, but not for freshwater ones (Fig. 3; Supplementary Tables S1–S3). The same is true for trematode metacercariae, which also infect fish via skin contact, but only when differences in prevalence are used as effect size (Supplementary Table S3).

There were also inconsistent patterns for trophically transmitted parasites. Cestode infections showed a general tendency to peak in summer for both freshwater and marine coastal fish hosts (Supplementary Tables S2 and S3). Acanthocephalan infections generally peaked in summer for freshwater fish, with no similar evidence for marine fish (Supplementary Tables S2 and S3). In contrast, nematode infections were higher in summer than winter for coastal marine fish hosts, but not for freshwater or deep-sea fishes (Fig. 4; Supplementary Tables S1 and S3). Finally, adult trematode infections showed no overall significant summer-versus-winter differences for any of the habitats (Supplementary Tables S1 and S3).

3.3. Seasonal infections in tropical fish

The final set of GLMMs were designed to test for overall effects of habitat (freshwater or coastal), host body length, mode of transmission, and precipitation seasonality on wet-versus-dry season comparisons in parasite infections. The analysis indicated that, based on corrected differences, wet season peaks in parasite abundance increased with increasing precipitation seasonality, and also with decreasing host body size, in line with the original prediction (Supplementary Table S9). However, both these effects were quantitatively very weak. When looking separately at different parasite

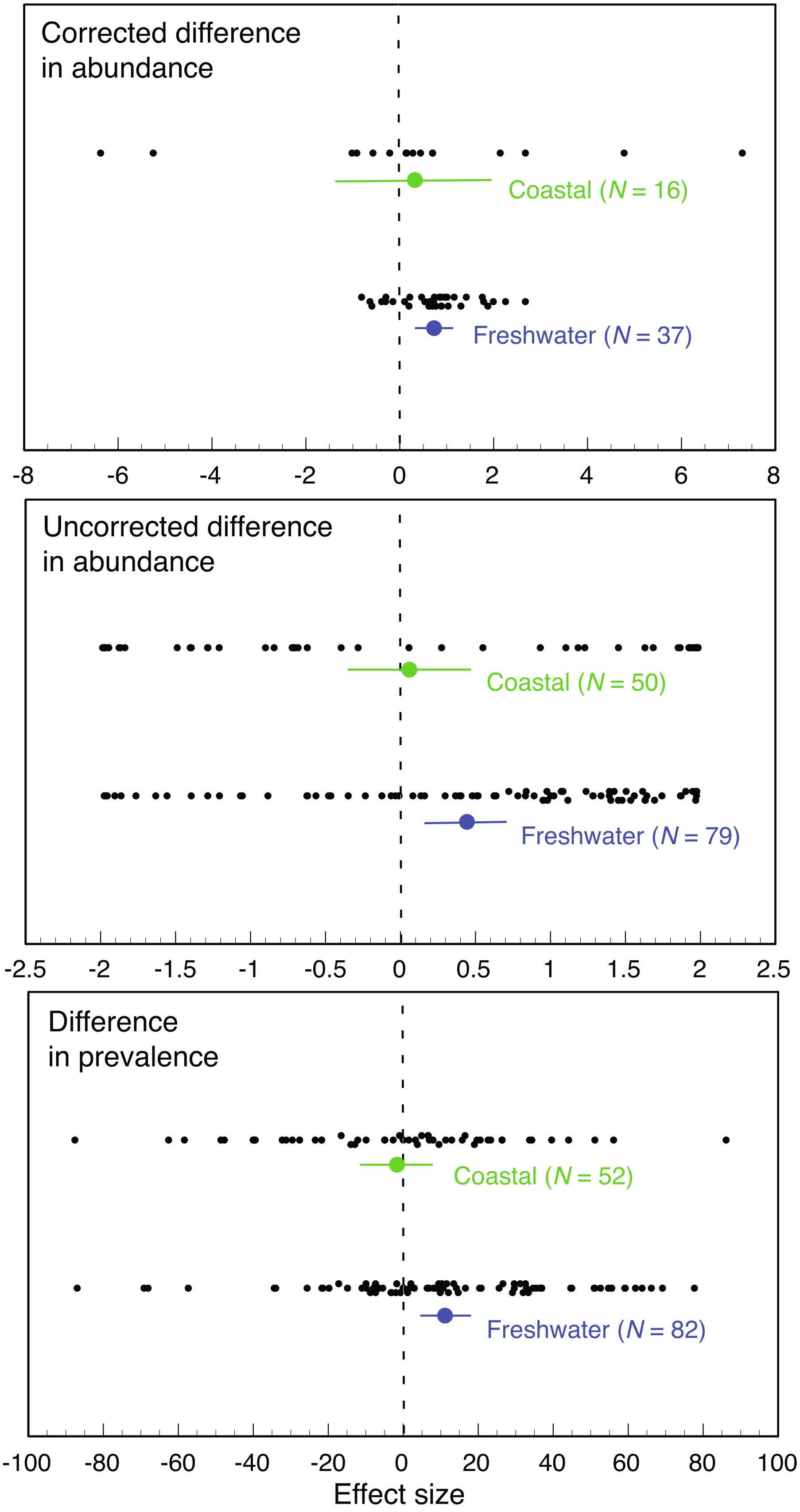

Fig. 2. Seasonal contrasts between winter and summer in monogenean infections on fish hosts, based on three different effect sizes. Data are presented separately for fish from freshwater and coastal marine habitats (data from the deep sea were not included due to small sample sizes). Shown are individual contrasts (black) as well as the overall mean effect size and its 95% confidence interval (colour); effects sizes with confidence intervals that do not cross zero are considered significant. Positive values indicate higher infections in summer; points are jittered where necessary to minimise overlap.

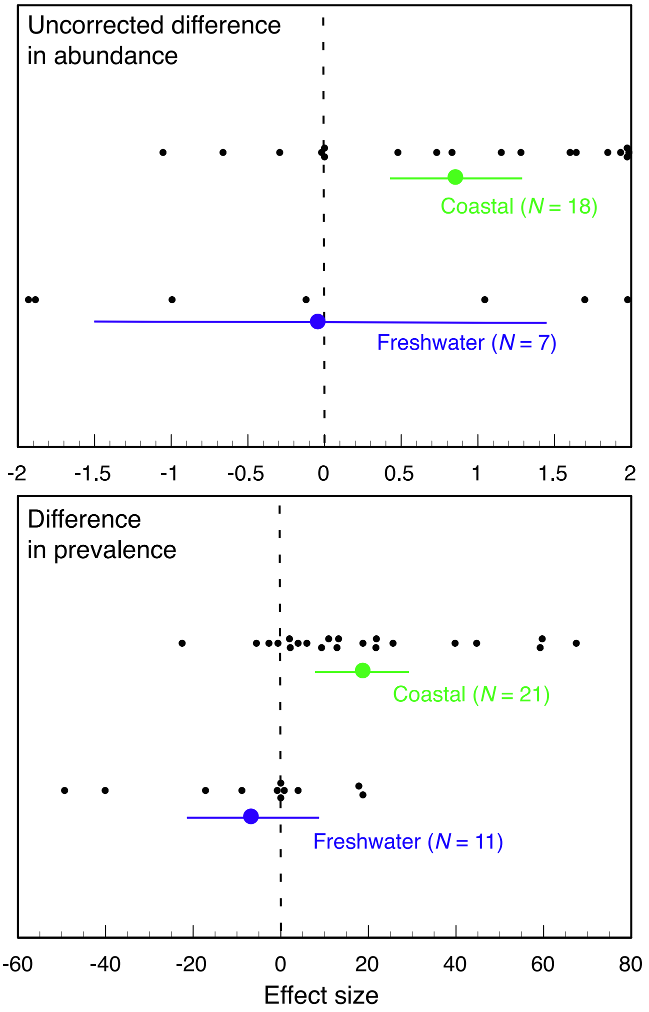

Fig. 3. Seasonal contrasts between winter and summer in copepod infections on fish hosts, based on two different effect sizes (data on corrected differences in abundance were not included due to small sample sizes). Data are presented separately for fish from freshwater and coastal marine habitats (data from the deep sea not included because of small sample sizes). Shown are individual contrasts (black) as well as the overall mean effect size and its 95% confidence interval (colour); effects sizes with confidence intervals that do not cross zero are considered significant. Positive values indicate higher infections in summer; points are jittered where necessary to minimise overlap.

groups, only two patterns become apparent, neither of which supports the original hypotheses: trematode metacercariae showed generally higher corrected abundance during the wet season in freshwater fishes (Supplementary Table S4), and monogeneans showed generally lower prevalence during the wet season in coastal marine fishes (Supplementary Table S6).

In all above GLMMs, study ID accounted for very little of the unexplained variance (Supplementary Tables S7–S9). In some cases, parasite taxonomy did; the taxon-specific patterns highlighted above probably account for this. Host taxonomy also accounted for much variance in some models (Supplementary Tables S8 and S9), and this is reflected in the different effect sizes associated with different fish families. For example, among the marine fish families best represented in the dataset, parasite infections showed a general tendency to peak significantly in summer in some families such as Mugilidae and Trichiuridae, but not in other families (Fig. 5). The same is true for freshwater fish families (data not shown), indicating that host taxonomy may influence the seasonality of parasite infections.

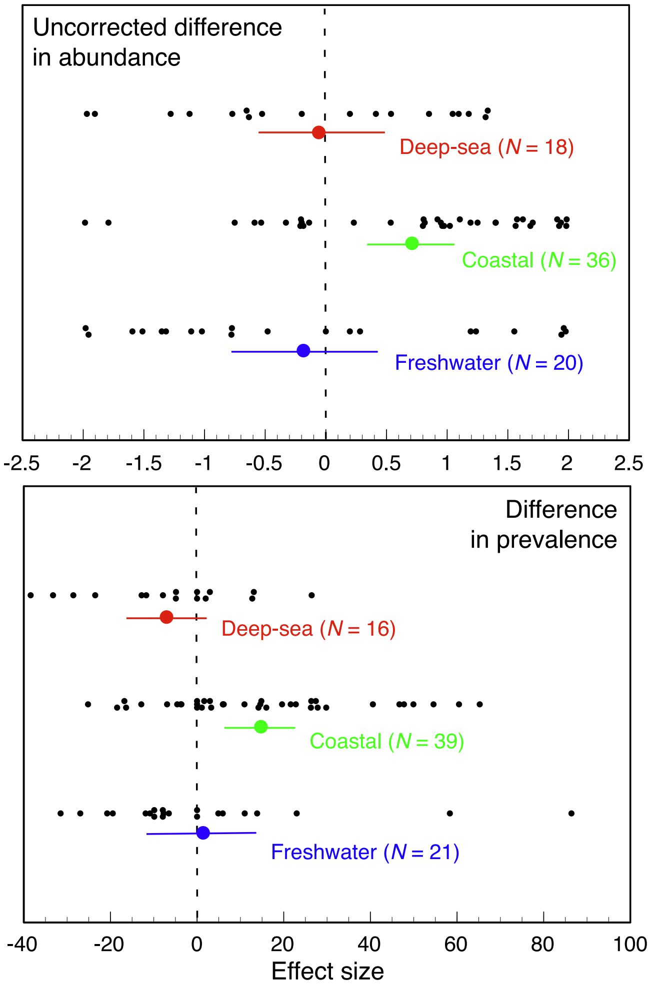

Fig. 4. Seasonal contrasts between winter and summer in nematode infections of fish hosts, based on two different effect sizes (data on corrected differences in abundance were not included due to small sample sizes). Data are presented separately for fish from freshwater, coastal and deep-sea marine habitats. Shown are individual contrasts (black) as well as the overall mean effect size and its 95% confidence interval (colour); effects sizes with confidence intervals that do not cross zero are considered significant. Positive values indicate higher infections in summer; points are jittered where necessary to minimise overlap.

4. Discussion

The tacit, and admittedly reasonable, assumption that infections peak in summer months pervades the literature on the ecology of parasite epidemiology, particularly in the case of fish parasites. Here, using a meta-analytical approach, this assumption and several hypotheses related to it were put to the test. The findings suggest that seasonal dynamics of infections are far from universal among parasites of fish and amphibians, and that no single factor drives seasonality of infections across all host-parasite systems. The only consistent patterns emerge within certain parasite taxa, indicating that the particular biology of some parasites but not others makes them sensitive to abiotic conditions, linking their population dynamics to seasonal variation in external conditions.

The first prediction tested here was that seasonal variation in infection levels should increase with the magnitude of local seasonality in abiotic conditions. It seems plausible that if, for instance, temperature is a key determinant of parasite reproduction and growth (Johnston and Dykeman, 1987; Buchmann, 1988; Tubbs et al., 2005; Poulin, 2006; Franke et al., 2017) as well as host feeding activity, greater summer increases in temperature

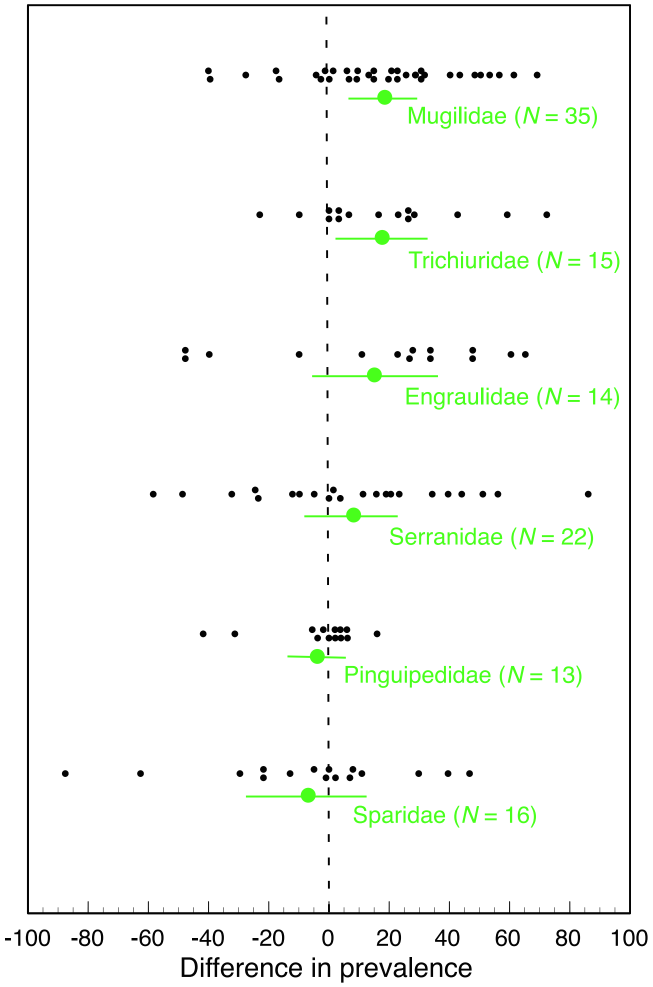

Fig. 5. Seasonal contrasts in prevalence of parasite infections between winter and summer in coastal marine fish hosts belonging to different families (only families for which at least 12 contrasts in prevalence were available are included). Shown are individual contrasts (black) as well as the overall mean effect size and its 95% confidence interval (green); effects sizes with confidence intervals that do not cross zero are considered significant. Positive values indicate higher infections in summer; points are jittered where necessary to minimise overlap. Families are ranked from greatest (top) to smallest (bottom) mean effect size.

should lead to greater infection risk. Similar mechanisms are not so clear regarding the effects of precipitation in the tropics, but nevertheless more pronounced seasonal differences in precipitation seem likely to affect seasonal infection dynamics. The results of two of the generalised linear mixed models support the prediction, in one case for temperature seasonality and in the other precipitation seasonality. However, the coefficient estimates associated with these factors were low and therefore the effects of seasonality were small, and they were not significant in the other mixed models with different effect sizes as response variables. Therefore, the analyses provide very weak support for the prediction that greater seasonality in abiotic conditions drives greater seasonality in infections. It must be noted that magnitude (or amplitude) of abiotic differences between seasons is only one component of the degree of seasonality; the other is their predictability, i.e. the consistency of seasonal variation across years (Lisovski et al., 2017). Conceivably, low seasonal predictability of abiotic conditions can act as a selection force on the phenology of host and parasite populations. Incorporating this component as a predictor in future analyses might uncover effects of local seasonal variation not revealed by the present analyses.

The meta-analysis also tested whether seasonal differences in infection levels were more pronounced in freshwater habitats, followed by coastal habitats and deep-sea habitats, based on the broad patterns in abiotic seasonality in those environments (Wetzel, 2001; Knauss and Garfield, 2017). None of the generalised linear mixed models provided support for this prediction across all host-parasite systems. However, several taxon-specific patterns were observed. For example, in temperate systems, monogenean infections generally peak in summer in freshwater habitats but show no seasonality in marine ones, whereas the exact opposite is observed for copepods. Similarly, among trophically transmitted parasites, acanthocephalan infections are generally highest in summer in freshwater habitats but show no overall significant seasonality in marine ones (coastal or deep-sea), whereas nematodes show the opposite pattern, peaking in summer in coastal marine habitats but not in freshwater ones. To some extent, these contrasting findings may arise from the phylogenetically determined biological properties of the species making up those parasite groups. As an example, two families (Gyrodactylidae and Dactylogyridae) make up a large fraction of freshwater monogeneans in the dataset, but are poorly represented among the marine species. If species in either of these families are unusually sensitive to temperature, this could explain the difference between habitats observed here, without being a consequence of the habitats themselves. Gyrodactylids are unique among monogeneans for their viviparous mode of reproduction with new embryos already growing within unborn embryos, which contrasts with the simple oviparous (egg laying) reproduction of other monogeneans (Kearn, 1994). This mode of reproduction allows for rapid population growth, and if it is particularly temperature-sensitive, combined with the clear sensitivity of egg production in dactylogyrids (see Buchmann, 1988), this may account for the widespread summer rise in freshwater monogenean abundance revealed by the analysis. Other taxon-specific patterns may have similar underlying causes, i.e. peculiarities of certain families associated with a given habitat and not others.

Mode of transmission was also investigated as a factor modulating seasonal variation in infection levels. In temperate systems, both parasites transmitted by free-swimming stages contacting host skin and those transmitted trophically were expected to show similar seasonal dynamics, with abundances peaking in summer. The generalised linear mixed models confirmed that there was no overall difference in effect sizes between the two types of parasites. Significant summer peaks (i.e., effect size with 95% confidence intervals not overlapping zero) were observed for particular parasite taxa, but not others. Different habitat-specific patterns were observed for parasite taxa with similar transmission modes (e.g., copepods versus monogeneans, or acanthocephalans versus cestodes). For tropical systems, parasites transmitted by infective stages contacting host skin were expected to peak in abundance in the dry season in tropical freshwater systems, due to the concentration of hosts in contracted water bodies. No significant seasonal variation in freshwater monogenean or copepod infections was observed in the present study. The analysis did reveal lower prevalences of infection by monogeneans in the wet season, but in coastal marine fishes only; the reasons for this are unclear, but unlikely to relate to the mode of transmission per se. Since many coastal marine localities involved in the original studies were lagoons or inshore embayments, it may also be that the greater freshwater runoff during the wet season leads to a decrease in salinity, which possibly reduced the survival of marine ectoparasites.

In the present analyses, only seasonal differences in temperature and precipitation were considered. However, aquatic habitats undergo seasonal changes in other physico-chemical variables, many of which can influence the survival and transmission success of parasite free-living stages (Pietrock and Marcogliese, 2003). Furthermore, the free-swimming infective stages of many parasites can be consumed and destroyed by non-host organisms (Thieltges et al., 2008). If predation rates on transmission stages by non-host organisms also increase at higher temperatures, for instance, then they could potentially offset in part the increased output and activity of these free-living stages during summer months, thus dampening the increase in infections of target hosts. Indeed, consumption rates of trematode free-swimming cercarial infective stages by filter-feeders and other predators are generally temperature-dependent (Studer et al., 2013; Goedknegt et al., 2015). This may explain the limited evidence (only one of the three effect sizes, and only for coastal marine fish hosts) found here indicating that infections by trematode metacercariae rise significantly in summer months.

Finally, the meta-analysis also investigated the influence of host-related factors on seasonal parasite dynamics. There was no evidence that whether the host was a fish or an amphibian had any effect on the magnitude of seasonal differences in infections, although it must be noted that relatively few data points were available for amphibian hosts. With that caveat, no pattern seemed to be specific to one host type only. Nematode infections showed a significant tendency to peak in summer in amphibians, but they did so in fish too based on other effect sizes. The prediction that seasonal variation in infection levels would decrease with increasing host body size received no real support across all generalised linear mixed models. There were, however, differences among host families, with parasites of all kinds more likely to show significant seasonal dynamics in some fish families than others. Seasonal fluctuations in parasite infection may be driven by endogenous processes related to host biology. Many host species display annual cycles in their reproductive biology, and these are associated with physiological, endocrinological and behavioural changes. These intrinsic biological rhythms can generate seasonal variation in immunity, causing hosts to become more susceptible to infection in certain seasons (Martinez-Bakker and Helm, 2015). Seasonal timing of reproduction can also lead to a predictable pulse of new susceptible hosts recruited into the host population, with consequent impacts on parasite transmission and infection success (Altizer et al., 2006). Although the studies included here sampled fish in different seasons but from roughly the very same locality, small-scale seasonal migrations may also affect parasite infections and confound attempts to isolate pure seasonality effects. It is very likely that these processes vary in importance among fish families, which would explain the results obtained here and indicate that host phylogenetic factors also shape parasite temporal dynamics.

The data analysed here may not allow for a test of subtle seasonal dynamics, but only test for strong seasonality. Individual studies generally report data pooled for a whole season; in reality, some parasites may show peaks of abundance within a season, i.e. early or late summer. Combining data across an entire season would miss such finer-scale temporal fluctuations. The present meta-analysis therefore reveals only broad seasonal trends; detailed field studies remain essential to uncover more complex dynamics.

The findings summarised here provide the first known global, empirical assessment of seasonal dynamics of parasite infections in aquatic ecosystems. They reveal that summer peaks in parasite infections are common (but not universal) in temperate systems, but that differences in infections between the wet and dry seasons in the tropics are much less pronounced. The results also show that there is no universal driver of infection seasonality: neither the magnitude of local abiotic variation, the type of habitat, nor the parasite's transmission mode had an overall effect on infection seasonality. Instead, what the meta-analysis found was that taxon-specific and even habitat-specific patterns were the norm: seasonal dynamics are strong and clear for some parasite taxa and some host taxa in certain habitats, but not for others. These idiosyncratic patterns suggest that sensitivity to abiotic conditions varies widely among host-parasite systems. The consequences of climate change for parasite infections are expected to be particularly severe in aquatic ecosystems (Marcogliese, 2001; Barber et al., 2016). In this context, the present findings provide an empirical basis to identify the type of host-parasite associations most likely to respond to changing climatic conditions, based on their sensitivity to seasonal effects, and thus have relevance for fisheries and aquaculture as well.

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Appendix A. Supplementary data

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References

Altizer, S., Dobson, A., Hosseini, P., Hudson, P., Pascual, M., Rohani, P., 2006. Seasonality and the dynamics of infectious diseases. Ecol. Lett. 9, 467–484.

Barber, I., Berkhout, B.W., Ismail, Z., 2016. Thermal change and the dynamics of multi-host parasite life cycles in aquatic ecosystems. Integr. Comp. Biol. 56, 561–572.

Barker, D.E., Cone, D.K., 2000. Occurrence of Ergasilus celestis (Copepoda) and Pseudodactylogyrus anguillae (Monogenea) among wild eels (*Anguilla rostrata*) in relation to stream flow, pH and temperature and recommendations for controlling their transmission among captive eels. Aquaculture 187, 261–274.

Buchmann, K., 1988. Temperature-dependent reproduction and survival of Pseudodactylogyrus bini (Monogenea) on the European eel (*Anguilla anguilla*). Parasitol. Res. 75, 162–164.

Chubb, J.C., 1977. Seasonal occurrence of helminths in freshwater fishes, part I. Monogenea. Adv. Parasitol. 15, 133–199.

Chubb, J.C., 1979. Seasonal occurrence of helminths in freshwater fishes, part II. Trematoda. Adv. Parasitol. 17, 141–313.

Chubb, J.C., 1980. Seasonal occurrence of helminths in freshwater fishes, part III. Larval Cestoda and Nematoda. Adv. Parasitol. 18, 1–120.

Chubb, J.C., 1982. Seasonal occurrence of helminths in freshwater fishes, part IV. Adult Cestoda, Nematoda and Acanthocephala. Adv. Parasitol. 20, 1–292.

Dowell, S.F., 2001. Seasonal variation in host susceptibility and cycles of certain infectious diseases. Emerg. Infect. Dis. 7, 369–373.

Franke, F., Armitage, S.A.O., Kutzer, M.A.M., Kurtz, J., Scharsack, J.P., 2017. Environmental temperature variation influences fitness trade-offs and tolerance in a fish-tapeworm association. Parasit. Vectors 10, 252.

Fretwell, J.R., 1972. Populations in a Seasonal Environment. Princeton University Press, Princeton, NJ.

Goedknegt, M.A., Welsh, J.E., Drent, J., Thieltges, D.W., 2015. Climate change and parasite transmission: how temperature affects parasite infectivity via predation on infective stages. Ecosphere 6, 96.

Gregory, R.D., Blackburn, T.M., 1991. Parasite prevalence and host sample size. Parasitol. Today 7, 316–318.

Gregory, R.D., Woolhouse, M.E.J., 1993. Quantification of parasite aggregation: a simulation study. Acta Trop. 54, 131–139.

Harvey, P.H., Pagel, M.D., 1991. The Comparative Method in Evolutionary Biology. Oxford University Press, Oxford, UK.

Hedges, L., Olkin, I., 1985. Statistical Methods for Meta-Analysis. Academic Press, New York.

Johnston, C.E., Dykeman, D., 1987. Observations on body proportions and egg production in the female parasitic copepod (*Salmincola salmoneus*) from the gills of Atlantic salmon (*Salmo salar*) kelts exposed to different temperatures and photoperiods. Can. J. Zool. 65, 415–419.

Kearn, G.C., 1994. Evolutionary expansion of the Monogenea. Int. J. Parasitol. 24, 1227–1271.

Knauss, J.A., Garfield, N., 2017. Introduction to Physical Oceanography. Third ed. Waveland Press, Illinois, USA.

Lafferty, K.D., 2009. The ecology of climate change and infectious diseases. Ecology 90, 888–900.

Lisovski, S., Ramenofsky, M., Wingfield, J.C., 2017. Defining the degree of seasonality and its significance for future research. Integr. Comp. Biol. 57, 934–942.

Marcogliese, D.J., 2001. Implications of climate change for parasitism of animals in the aquatic environment. Can. J. Zool. 79, 1331–1352.

Martinez-Bakker, M., Helm, B., 2015. The influence of biological rhythms on host-parasite interactions. Trends Ecol. Evol. 30, 314–326.

Nakagawa, S., Santos, E.S.A., 2012. Methodological issues and advances in biological meta-analysis. Evol. Ecol. 26, 1253–1274.

Oliveira, B.F., São-Pedro, V.A., Santos-Barrera, G., Penone, C., Costa, G.C., 2017. AmphiBIO, a global database for amphibian ecological traits. Sci. Data 4,. https://doi.org/10.1038/sdata.2017.123 170123.

Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Syst. 37, 637–669.

Paull, S.H., LaFonte, B., Johnson, P.T.J., 2012. Temperature-driven shifts in a host-parasite interaction drive nonlinear changes in disease risk. Glob. Change Biol. 18, 3558–3567.

Pietrock, M., Marcogliese, D.J., 2003. Free-living endohelminth stages: at the mercy of environmental conditions. Trends Parasitol. 19, 293–299.

Poulin, R., 2006. Global warming and temperature-mediated increases in cercarial emergence in trematode parasites. Parasitology 132, 143–151.

Sibly, R.M., Calow, P., 1986. Physiological Ecology of Animals: An Evolutionary Approach. Blackwell, London.

Studer, A., Thieltges, D.W., Poulin, R., 2010. Parasites and global warming: net effects of temperature on an intertidal host-parasite system. Mar. Ecol. Progr. Ser. 415, 11–22.

Studer, A., Kremer, L., Nelles, J., Poulin, R., Thieltges, D.W., 2013. Biotic interference in parasite transmission: can the feeding of anemones counteract an increased risk of parasitism in amphipods at higher temperature? J. Exp. Mar. Biol. Ecol. 445, 116–119.

Thieltges, D.W., Jensen, K.T., Poulin, R., 2008. The role of biotic factors in the transmission of free-living endohelminth stages. Parasitology 135, 407–426.

Tonkin, J.D., Bogan, M.T., Bonada, N., Rios-Touma, B., Lytle, D.A., 2017. Seasonality and predictability shape temporal species diversity. Ecology 98, 1201–1216.

Tubbs, L.A., Poortenaar, C.W., Sewell, M.A., Diggles, B.K., 2005. Effects of temperature on fecundity in vitro, egg hatching and reproductive development of *Benedenia seriolae* and *Zeuxapta seriolae* (Monogenea) parasitic on yellowtail kingfish *Seriola lalandi*. Int. J. Parasitol. 35, 315–327.

Varpe, Ø., 2017. Life history adaptations to seasonality. Integr. Comp. Biol. 57, 943–960.

Vega, G.C., Pertierra, L.R., Olalla-Tárraga, M.A., 2017. MERRAclim, a high-resolution global dataset of remotely sensed bioclimatic variables for ecological modelling. Sci. Data 4,. https://doi.org/10.1038/sdata.2017.78 170078.

Wetzel, R.G., 2001. Limnology. Third ed. Academic Press, San Diego, USA.

Williams, C.M., Ragland, G.J., Betini, G., Buckley, L.B., Cheviron, Z.A., Donohue, K., Hereford, J., Humphries, M.M., Lisovski, S., Marshall, K.E., Schmidt, P.S., Sheldon, K.S., Varpe, Ø., Visser, M.E., 2017. Understanding evolutionary impacts of seasonality: an introduction to the symposium. Integr. Comp. Biol. 57, 921–933.

Willmer, P., Stone, G., Johnston, I., 2000. Environmental Physiology of Animals. Blackwell Science, Oxford.