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Analysis of trait mean and variability versus temperature in trematode cercariae: is there scope for adaptation to global warming?

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ABSTRACT

The potential of species for evolutionary adaptation in the context of global climate change has recently come under scrutiny. Estimates of phenotypic variation in biological traits may prove valuable for identifying species, or groups of species, with greater or lower potential for evolutionary adaptation, as this variation, when heritable, represents the basis for natural selection. Assuming that measures of trait variability reflect the evolutionary potential of these traits, we conducted an analysis across trematode species to determine the potential of these parasites as a group to adapt to increasing temperatures. Firstly, we assessed how the mean number of infective stages (cercariae) emerging from infected snail hosts as well as the survival and infectivity of cercariae are related to temperature. Secondly and importantly in the context of evolutionary potential, we assessed how coefficients of variation for these traits are related to temperature, in both cases controlling for other factors such as habitat, acclimatisation, latitude and type of target host. With increasing temperature, an optimum curve was found for mean output and mean infectivity, and a linear decrease for survival of cercariae. For coefficients of variation, temperature was only an important predictor in the case of cercarial output, where results indicated that there is, however, no evidence for limited trait variation at the higher temperature range. No directional trend was found for either variation of survival or infectivity. These results, characterising general patterns among trematodes, suggest that all three traits considered may have potential to change through adaptive evolution.

1. Introduction

Species are being exposed to unprecedented rates and combinations of changes in environmental conditions (Vitousek et al., 1997; IPCC, 2007), to which a multitude of responses have already been documented (Walther et al., 2002; Parmesan and Yohe, 2003; Root et al., 2003; Parmesan, 2006). For example, natural populations are responding by shifting their geographic distributions or the timing of growth and reproduction, which due to differential sensitivity among species are bound to affect species interactions, including those between parasites and their hosts (Marcogliese, 2001; Harvell et al., 2002). Populations may also respond to environmental changes through phenotypic plasticity and/or undergo evolutionary adaptation through genetic changes (Bradshaw and Holzapfel, 2006; Gienapp et al., 2008; Hoffmann and Sgro, 2011; Donnelly et al., 2012). The influence of evolution on patterns of biological responses depends on the rate of evolutionary changes as well as the rate of environmental changes (Skelly and Freidenburg, 2010). Of crucial importance for adaptive evolutionary changes to occur is not only the generation time of a particular species, but also the degree of existing variation in critical traits (Houle, 1992; Skelly and Freidenburg, 2010).

High levels of variation for biological traits are common among individuals of the same population (e.g. Marras et al., 2010; Pistevos et al., 2011). This variability is a major determinant of physiological, ecological and behavioural diversity (Aldrich, 1989; Spicer and Gaston, 1999). When heritable, it represents the basis for natural selection processes occurring at the population or species level (Endler, 1986). Phenotypic variability is particularly important in enabling adaptation to changing conditions via natural selection without requiring mutational novelties, in particular when considering that mutational rates in metazoans are usually low (Huey et al., 1991; Hoffmann et al., 2003) and that the rates of on-going environmental changes are unnaturally high (IPCC, 2007). Even if reflecting non-adaptive cryptic genetic variation, phenotypic plasticity in response to altered conditions increases the variance in trait values and may thus facilitate adaptive evolution (Ghalambor et al., 2007).

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Concerns about the potential consequences of global changes for species have led to increased scientific interest in evolutionary adaptive potential and inter-individual variability (see reviews by e.g. Gienapp et al., 2008; Visser, 2008; Skelly and Freidenburg, 2010; Hoffmann and Sgro, 2011; Donnelly et al., 2012). Intraspecific variation has also been investigated in metazoan parasites such as trematodes. For example, intra-specific variation in emergence patterns of trematode transmission stages, i.e. cercariae, has been shown in *Schistosoma* spp. (Ngoran et al., 1997; Theron et al., 1997). Koehler et al. (2011) demonstrated that clones of the intertidal trematode *Maritrema novaezealandensis* have significantly different levels of phenotypic variability in terms of morphology, behaviour and survival (i.e. variability differed across different clones). It was also found that clones of *M. novaezealandensis* showed different levels of host specificity with regards to their ability to infect hosts or develop within them (Koehler et al., 2012a). In the context of climate change and increasing temperatures, Koprivnikar and Poulin (2009) demonstrated experimentally inter- and intra-specific variation in the emergence of intertidal cercariae from infected first intermediate snail hosts at different temperatures. For *M. novaezealandensis*, recent work has also shown genotypic differences in cercarial output from snail hosts, pointing toward temperature-clone-specific responses (Berkhout et al., unpublished data). Moreover, in a comparative analysis across several trematode species from a range of systems, inter- and intraspecific variation in responses of cercariae in relation to temperature was found to be common (Morley, 2011; Morley and Lewis, 2013).

As a straightforward index to anticipate the impacts of global change on a wide range of species, estimates of phenotypic variation may prove valuable for identifying species with greater or lower potential for evolutionary adaptation (Chown et al., 2009; Sunday et al., 2011). This should also be the case for parasites and pathogens. Usually, researchers are interested in mean responses and therefore variation in responses is often considered as noise (but see e.g. Aldrich, 1989; Chown et al., 2009; Pistevos et al., 2011; Sunday et al., 2011). However, while experimental error is probably responsible for some of that variation, some of it must be due to genetic differences among individuals (Sunday et al., 2011). Hence, these differences may reveal the “raw material” for natural selection (e.g. Whitehead and Crawford, 2006) and indicate the potential for evolutionary adaptation. This information, provided in published studies as measures of variability (e.g. S.E, S.D.), may therefore be used as an indicator of the scope for evolutionary adaptation.

Here, using the infective stage of trematodes that emerges from first intermediate hosts namely cercariae, we searched the literature to assess means and levels of variability in responses of cercariae to temperature. Cercariae are short-lived, non-feeding transmission stages which are directly exposed to environmental conditions during their search for a host (e.g. Pietrock and Marcogliese, 2003). This stage is a crucial step in the complex life cycle of trematodes. Trematodes typically rely on several hosts plus free-living stages to complete one generation; a fact that may make them particularly vulnerable to loss of species, changing species ranges, or altered environmental conditions directly affecting the parasite (Marcogliese, 2001).

Cercariae are produced asexually within first intermediate mollusc hosts (by intramolluscan stages, i.e. rediae or sporocysts) before leaving the host when conditions are suitable for transmission to the next host. Temperature has been shown to be an important factor affecting the production (i.e. development), emergence and functional aspects (i.e. survival and infectivity) of cercariae. In general, the number emerging is positively related to temperature up to an optimum range (Poulin, 2006; Morley and Lewis, 2013). The survival of cercariae generally decreases with increasing temperatures due to higher activity levels and the faster depletion of their limited energy reserves (Pechenik and Fried, 1995). Infectivity (the percentage of cercariae successfully infecting a host) usually also follows an optimum curve (e.g. Thieltges and Rick, 2006). However, trematodes are a diverse group of species occurring in different habitats and using different hosts to complete their life cycles and hence there are intra- and interspecific differences, e.g. for emergence of cercariae (Morley and Lewis, 2013) as well as for cercarial survival and metabolism (Morley, 2011), making the overall relationship between trematodes and temperature highly complex. Morley and Lewis (2013) also highlighted the importance of incorporating the latitude and acclimatisation regime of organisms into comparative studies of the thermal biology of trematodes, as temperature can have complex effects, especially on cercarial development and emergence, which depend on specific temperature ranges, latitude and the degree of acclimatisation to experimental conditions. While previous studies across trematode species from different systems (but see also Thieltges et al., 2008 for an assessment of cercarial emergence across marine species) analysed mean responses to temperature as Q10 values (i.e. a measure of the change in physiological rates per 10 °C increase in temperature) (Poulin, 2006; Morley, 2011; Morley and Lewis, 2013), the present study is concerned with the original data from the literature, in terms of the mean response, but importantly and as a novel approach, also in terms of the variability in those responses.

Our aim was to assess the mean and the variability of output, survival and infectivity of trematode cercariae (i.e. the expressed, phenotypic variability in those key traits) in relation to temperature, taking a range of factors into account including experimental acclimatisation, latitude, habitat and target host, and using General Linear Mixed Effect Models to analyse the data. For the means of the three response variables, we hypothesised cercarial emergence and infectivity data to follow an optimum curve, and survival of cercariae to decrease with increasing temperature. For the variability of responses, however, several outcomes were possible: (i) variability may increase with increasing temperatures, in particular for cercarial output and infectivity, possibly reflecting the potential for adaptation of trematodes to global warming; (ii) variability may decrease with increasing temperature, especially in the case of cercarial survival, suggesting that trematode parasites may only have limited ability to adapt to increasing temperatures, at least at this stage of their life cycle; (iii) variability may show no significant pattern across the range of temperatures covered, indicating that variability remains unaffected, especially at higher temperature levels. This may also be interpreted as potential scope for adaptation with increasing temperatures. Our study aimed at identifying general patterns that apply to trematodes as a group in order to contribute novel insights into the evolutionary potential of these parasites in the context of global warming.

2. Materials and methods

2.1. Data compilation

Data were obtained from experimental studies of cercarial output, survival and/or infectivity which included at least two temperature levels and which provided S.D.s for response variables (or other measures of variability from which the S.D. could be derived, i.e. S.E.s or confidence intervals (CIs)) (Table 1). The studies were compiled based on an online literature search (scholar.google.com, apps.webofknowledge.com) using several combinations and versions of the terms “cercariae”, “trematodes”, “output”, “emergence”, shedding”, “production”, “survival”, “longevity”, “infectivity”, “infection” and “temperature”, as well as by

Table 1

List of studies included in the analyses, showing the trematode species and their respective snail host species, shell length of the snail host (in mm), the temperature levels covered in the study and the respective analyses in which data were included (i.e. cercarial output, survival and/or infectivity).

Family/species	Snail host (1st intermediate)	Shell length (mm)	Temperature levels (°C)	Output	Survival	Infectivity	References
Cathaemasiidae							
Ribeiroia ondatrae	*Helisoma trivolvis*	15	17, 20, 26			x	Paull et al. (2012)
Diplostomatidae							
Bolbophorus confusus	*Helisoma trivolvis*	18	10, 23	x			Terhune et al. (2002)
Diplostomum spathaceum	*Lymnaea stagnalis*	36	4, 10, 20/7, 15		x	x	Lyholt and Buchmann (1996)
Diplostomum spathaceum	*Radix peregra*	22	5, 7.5, 10, 12.5, 15, 17.5, 20			x	Stables and Chappell (1986)
Echinostomatidae							
Acanthoparyphium sp.	*Zeacumantus subcarinatus*	12.5	15, 20, 25	x			Koprivnikar and Poulin (2009)
Echinostoma caproni	*Biomphalaria glabrata*	18	12, 35	x			Fried et al. (2002)
Echinostoma caproni	*Biomphalaria glabrata*	18	19, 25, 30, 36			x	Meyrowitsch et al. (1990)
Echinostoma caproni	*Biomphalaria glabrata*	18	12, 23/4, 12, 23, 28, 37.5		x	x	Fried and Ponder (2003)
Echinostoma trivolvis	*Helisoma trivolvis*	15	12, 22–24, 28–29, 37.5	x			Schmidt and Fried (1996)
Echinostoma trivolvis	*Helisoma trivolvis*	15	18, 24, 32		x	x	Pechenik and Fried (1995)
Echinoparyphium aconiatum	*Lymnaea stagnalis*	55	17.5, 22.5, 27.6	x			Sarounova, 2011 (thesis)[a]
Echinoparyphium recurvatum	*Lymnaea peregra*	17	15, 20, 25	x			McCarthy, 1989 (thesis)[b]
Echinostoma miyagawi	*Planorbis planorbis*	10	17.5, 22.5, 27.7	x			Sarounova, 2011 (thesis)[a]
Himasthla continua	*Hydrobia ulvae*	5	10, 14, 18, 22, 26, 30, 34	x			Kisielewski, 1998, (thesis)[c]
Himasthla rhigedana	*Cerithidea californica*	25	13, 14, 15, 16, 17, 18, 19	x			Fingerut et al. (2003)
Fasciolidae							
Fasciola gigantica	*Lymnaea natalensis*	4.5	19, 25, 30	x			Shalaby et al. (2004)
Fasciola hepatica	*Lymnaea viridis*	8	17, 22, 25	x			Lee et al. (1995)
Haploporidae							
Haploporida sp.	*Hydrobia ulvae*	5	10, 14, 18, 22, 26, 30, 34	x			Kisielewski (1998) (thesis)[c]
Hemiuridae							
Halipegus occidualis	*Helisoma anceps*	15.5	15, 20, 25, 30	x			Shostak and Esch (1990)
Heterophyidae							
Cryptocotyle concavum	*Hydrobia ulvae*	5	10, 14, 18, 22, 26, 30, 34	x			Kisielewski (1998) (thesis)[c]
Euhaplorchis californensis	*Cerithidea californica*	25	13, 14, 15, 16, 17, 18, 19	x			Fingerut et al. (2003)
Stictodora lari	*Velacumantus australis*	30	14.5, 19.5, 23.5	x			Appleton (1983)
Microphallidae							
Gynaecotyla adunca	*Ilyanassa obsoleta*	25	17, 22	x	x		Shim et al. (2013)
Gynaecotyla adunca	*Ilyanassa obsoleta*	25	17, 22	x			Koprivnikar et al. (2013)
Maritrema novaezealandensis	*Zeacumantus subcarinatus*	12.5	18, 25	x			Fredensborg et al. (2005)
Maritrema novaezealandensis	*Zeacumantus subcarinatus*	12.5	15, 20, 25	x			Koprivnikar and Poulin (2009)
Maritrema novaezealandensis	*Zeacumantus subcarinatus*	12.5	16, 20, 25, 30, 34	x	x	x	Studer et al. (2010)
Maritrema subdolum	*Hydrobia ulvae*	5	15, 20, 25	x	x		Mouritsen (2002)
Maritrema subdolum	*Hydrobia ulvae*	5	15, 20, 25	x			Mouritsen and Jensen (1997)
Microphallidae sp.	*Cerithidea californica*	25	13, 14, 15, 16, 17, 18, 19	x			Fingerut et al. (2003)
Philophthalmidae							
Echinostephilla patellae	*Patella vulgata*	60	10, 15, 20, 25		x		Prinz et al. (2010)
Parorchis acanthus	*Cerithidea californica*	25	13, 14, 15, 16, 17, 18, 19	x			Fingerut et al. (2003)
Parorchis acanthus	*Nucella lapillus*	30	10, 15, 20, 25	x			Prinz et al. (2011)
Philophthalmus burrili	*Velacumantus australis*	30	14.5, 19.5, 23.5	x			Appleton (1983)
Philophthalmus sp.	*Zeacumantus subcarinatus*	12.5	15, 20, 25	x			Koprivnikar and Poulin (2009)
Plagiorchiidae							
Neoglyphe locellus	*Planorbarius corneus*	13	17.5, 22.5, 27.5	x			Sarounova, 2011 (thesis)[a]
Renicolidae							
Renicola buchanani	*Cerithidea californica*	25	13, 14, 15, 16, 17, 18, 19	x			Fingerut et al. (2003)
Renicola roscovita	*Littorina littorea*	20	10, 15, 20, 25	x	x	x	Thieltges and Rick (2006)

(*continued on next page*)

Table 1 (*continued*)

Family/species	Snail host (1st intermediate)	Shell length (mm)	Temperature levels (°C)	Output	Survival	Infectivity	References
Schistosomatidae							
Austrobillharzia terrigalensis	*Velacumantus australis*	30	14.5, 19.5, 23.5	x			Appleton (1983)
Schistosoma haematobium	*Bulinus truncatus*	8	18, 19, 22, 25, 28, 31, 32	x			Pflüger et al. (1984)
Schistosoma mansoni	*Biomphalaria glabrata*	18	12, 35	x			Fried et al. (2002)
Schistosoma mansoni	*Biomphalaria glabrata*	18	15, 20, 25, 30, 35, 40		x		Lawson and Wilson (1980)
Schistosoma mansoni	*Biomphalaria glabrata*	18	15, 20, 25, 30, 35, 40			x	DeWitt (1965)
Trichobilharzia sp.	*Radix peregra*	22	15, 20, 25, 30	x			Rojo-Vazquez and Simon-Martin (1985)

[a] Sarounova, P., 2011. Effect of temperature on emergence of cercariae of model freshwater trematodes. BSc thesis, University of South Bohemia, Czech Republic.

[b] McCarthy, A.M., 1989. The biology and transmission dynamics of *Echinoparyphium recurvatum* (Digenea: Echinostomatidae). PhD thesis, King's College London, University of London, UK.

[c] Kisielewski, I., 1998. Caractéristiques de l'infestation de trois mollusques bivalves par des trématodes, dans le bassin d'Arcachon. MSc thesis, University of Bordeaux, France.

searching the reference lists of relevant papers, (i.e. Pietrock and Marcogliese, 2003; Poulin, 2006; Thieltges et al., 2008; Morley, 2011; Morley and Lewis, 2013). For cercarial output, data were extracted from the 22 studies for which data could be standardised, providing data on 30 trematode species from 11 families (total of $n = 179$ data points; see Table 1 for temperature levels covered in each study). For survival of cercariae, seven publications were included covering seven trematode species from five families (total of $n = 26$ data points). For infectivity, 11 publications provided data for nine trematode species from seven families (total of $n = 83$ data points). Data (means, measure of variability) were extracted from tables or figures, in the latter case by using the web-based application WebPlotDigitizer (arohatgi.info/WebPlotDigitizer/app/). For each response variable at each temperature, a coefficient of variation (CV) was calculated as S.D. divided by the mean.

The responses considered were: (i) mean cercarial output (i.e. mean number of cercariae emerging from individual hosts per unit time), (ii) CVs of cercarial output, (iii) mean cercarial age (in h) around 50% survival (i.e. mean cercarial half-life; see below), (iv) CVs of the cercarial age around the 50% survival mark, (v) mean infectivity (i.e. mean percentage of cercariae successfully infecting a host), and (vi) CVs of infectivity. Cercarial output data typically consisted of a mean ± some measure of variability for each of two or more temperatures, calculated across several snail hosts. As studies allowed for different time periods for cercariae to emerge from infected snails, the data were standardised to output per snail per 12 h to account for day-night and tidal cycles. In some experiments, batches of snails were moved from one temperature to another whereas in others different snails were kept at different constant temperatures. A preliminary analysis indicated this did not influence the model outcome and hence was not considered further. Data on cercarial survival are usually presented in a survival curve across time with limited variability at the beginning and towards the end of the curve. Only the data point closest to the 50% (±10%) survival mark was included in the analyses. This was done because the half-life of cercariae is related to the mean expected life span and can be a proxy for infection potential (Pechenik and Fried, 1995), and because this seems to be a good index of glycogen utilisation, i.e. the depletion of the limited energy source over the life span of the non-feeding transmission stage (Young et al., 1984). If no data point had been recorded within this range, the average of the two nearest points around 50% was calculated and used as the mean cercarial age for a particular temperature; the CV was calculated accordingly. For infectivity, the data consisted of, or were converted into, a percentage of cercariae out of a standardised dose that successfully infected a host, with means and CV calculated from several replicates at each of two or more temperatures. For studies showing a relationship between infectivity and age of cercariae, the data were averaged across groups of cercariae of different ages.

2.2. Factors considered

For each data point, the respective sample size included in the model was either the number of snails used times any temporal replication (output), the number of experimental units (survival), or the number of hosts or experimental units used (infectivity). For cercarial output, the size of the snail host has been found to be positively correlated with emergence (e.g. Thieltges et al., 2008) and hence snail size was included in the model, with data on the average size of snail hosts (shell length in mm) obtained from Poulin (2006), Thieltges et al. (2008) and Koehler et al. (2012b). For all responses, acclimatisation of study organisms to experimental temperatures was recorded as none, short-term (1–3 days) or long-term (>3 days). For output, the duration at which infected snail hosts were kept at the respective experimental temperature level prior to or during assessments of cercarial emergence was considered. For survival, only one study (Studer et al., 2010) used cercariae from snails acclimatised to the respective experimental temperatures for $\geqslant 1$ day (i.e. several weeks in this case). For infectivity, acclimatisation processes varied, either only considering acclimation of cercariae, second intermediate host or both. Exposure of organisms to experimental temperatures prior to a trial that lasted for only minutes was considered as short-term acclimatisation. Latitude of the study species (according to the collection site or origin of species) was recorded and categorised in accordance with Morley and Lewis (2013), i.e. as low for $\leqslant 35°$ and mid for 36–60° latitude. Habitat of the study species was categorised as freshwater, estuarine (for output only, data from Fingerut et al. (2003)) or marine. The target of the cercariae of a particular species was categorised as either an ectothermic host, an endothermic host (for Schistosomatidae; definitive host), or substratum (for Fasciolidae and Philophthalmidae which mostly encyst in the environment). For additional analyses of survival and infectivity for a subset of the dataset including only those trematode species targeting ectothermic hosts, the second intermediate hosts were categorised as either vertebrates or invertebrates.

2.3. Statistical analyses

Data were analysed with General Linear Mixed Effect Models (GLMMs) using the package *lme4* in the programme R 2.15.1

Table 2

Results from the General Linear Mixed Effect Models with output of trematode cercariae from infected snail hosts and their respective coefficients of variation, survival, i.e. mean cercarial age around the 50% survival mark and respective coefficients of variation, as well as infectivity, i.e. mean percentage of cercariae successfully infecting a host, and respective coefficients of variation as response variables. For survival and infectivity, also shown are model outputs of the analyses including species targeting ectothermic hosts only. Table showing parameter estimates, S.E.s and *t* values.

Response	Factors	Mean			CV		
		Estimate	S.E.	*t* Value	Estimate	S.E.	*t* Value
Output (12 h^{-1})	(Intercept)	2.15	0.64	3.35	0.25	0.18	1.37
	Temperature	0.30	0.03	10.58	−0.04	0.01	−3.05
	Temperature^2	−0.13	0.02	−5.52	0.02	0.01	2.29
	Snail host size	0.56	0.14	3.92	0.00	0.04	0.11
	Acclimatisation (none)	0.29	0.41	0.70	−0.08	0.12	−0.71
	Acclimatisation (short)	−0.20	0.54	−0.37	0.08	0.15	0.52
	Latitude (mid)	0.24	0.54	0.44	−0.02	0.15	−0.15
	Habitat (freshwater)	0.38	0.65	0.56	−0.17	0.19	−0.88
	Habitat (marine)	−0.14	0.80	−0.17	0.04	0.22	0.18
	Target (endotherm)	−0.25	0.50	−0.49	−0.02	0.10	−0.25
	Target (substratum)	−0.74	0.30	−2.48	0.04	0.06	0.75
	Mean output				−0.02	0.02	−1.16
Survival	(Intercept)	1.26	0.21	6.07	0.41	0.04	11.67
	Temperature	−0.27	0.03	−8.76	0.01	0.01	1.62
	Acclimatisation (none)	0.60	0.15	3.98	−0.27	0.02	−10.92
	Latitude (mid)	−0.43	0.16	−2.60	−0.20	0.03	−6.80
	Habitat (marine)	−0.32	0.14	−2.37	−0.08	0.02	−4.06
	Target (endotherm)	−0.60	0.20	−3.05	−0.38	0.03	−11.84
	Mean % survival				−0.02	0.01	−3.19
	Ectothermic hosts only						
	(Intercept)	1.29	0.30	4.34	0.41	0.04	11.47
	Temperature	−0.20	0.03	−5.82	0.01	0.01	1.16
	Acclimatisation (none)	0.63	0.22	2.86	−0.26	0.02	−10.77
	Latitude (mid)	−0.51	0.26	−2.00	−0.22	0.04	−6.08
	Habitat (marine)	−0.24	0.22	−1.08	−0.06	0.03	−2.39
	Target (vertebrate)	0.17	0.28	0.63	0.03	0.04	0.73
	Mean % survival				−0.03	0.01	−3.13
Infectivity	(Intercept)	0.93	0.23	4.11	−0.20	0.08	−2.44
	Temperature	0.06	0.02	2.63	0.01	0.01	1.15
	Temperature^2	−0.07	0.02	−3.99			
	Acclimatisation (none)	0.03	0.11	0.24	−0.03	0.04	−0.62
	Acclimatisation (short)	−0.13	0.15	−0.86	−0.15	0.05	−2.84
	Latitude (mid)	−0.26	0.23	−1.16	0.06	0.05	1.37
	Habitat (marine)	−0.20	0.17	−1.17	0.03	0.07	0.38
	Target (endotherm)	−0.40	0.27	−1.48	−0.04	0.11	−0.34
	Mean % infectivity				−0.12	0.01	−11.47
	Ectothermic hosts only						
	(Intercept)	0.93	0.26	3.59	−0.19	0.11	−1.70
	Temperature	0.05	0.03	1.62	−0.01	0.01	−0.78
	Temperature^2	−0.06	0.02	−2.60			
	Acclimatisation (none)	0.03	0.12	0.26	−0.03	0.04	−0.63
	Acclimatisation (short)	−0.14	0.15	−0.96	−0.13	0.05	−2.48
	Latitude (mid)	−0.37	0.33	−1.10	0.08	0.05	1.45
	Habitat (marine)	−0.09	0.27	−0.32	−0.01	0.12	−0.06
	Target (vertebrate)	0.12	0.30	0.38	−0.07	0.13	−0.50
	Mean % infectivity				−0.13	0.01	−10.43

(R Development Core Team; www.r-project.org). Normality was checked by visual inspection of histograms of residuals. Interactions among fixed effects were not included because our study sought general patterns only and there was no a priori biological reason to expect interactions. In all analyses, the publication from which the data originated, the trematode species nested within family (to account for phylogenetic relationships) and sample size were included as random factors. All continuous predictor variables were centred.

The fixed factors included in all analyses were temperature, acclimatisation, latitude, habitat and target host. For mean cercarial output 12 h^{-1} (log-transformed), the fixed factors also included in the model were temperature^2 to account for the non-linear nature of the response, and shell length of the snail host. The GLMM for CVs of cercarial output (log($x + 0.5$)-transformed) further included mean output as a fixed factor. From this dataset, one extreme outlier data point from the publication by Shostak and Esch (1990) was removed. For mean cercarial age around the 50% survival mark (in h; log-transformed), the predictors included were the ones stated above. The GLMM with CVs for survival (log($x + 0.5$)-transformed) as the response variable further included mean percentage survival as a fixed factor. For mean infectivity (arcsine-square root-transformed proportion), temperature^2 was additionally included as a fixed factor to account for the non-linear nature of the response. For the analysis of CVs (log-transformed; calculated based on arcsine-square root-transformed S.D.s and means), the quadratic term was not included as a predictor as it did not improve the model (based on Akaike Information Criterion values), whereas mean infectivity (%) was. For survival and infectivity, analyses for both means and CVs were repeated for a subset of the data only including cases with ectothermic target hosts.

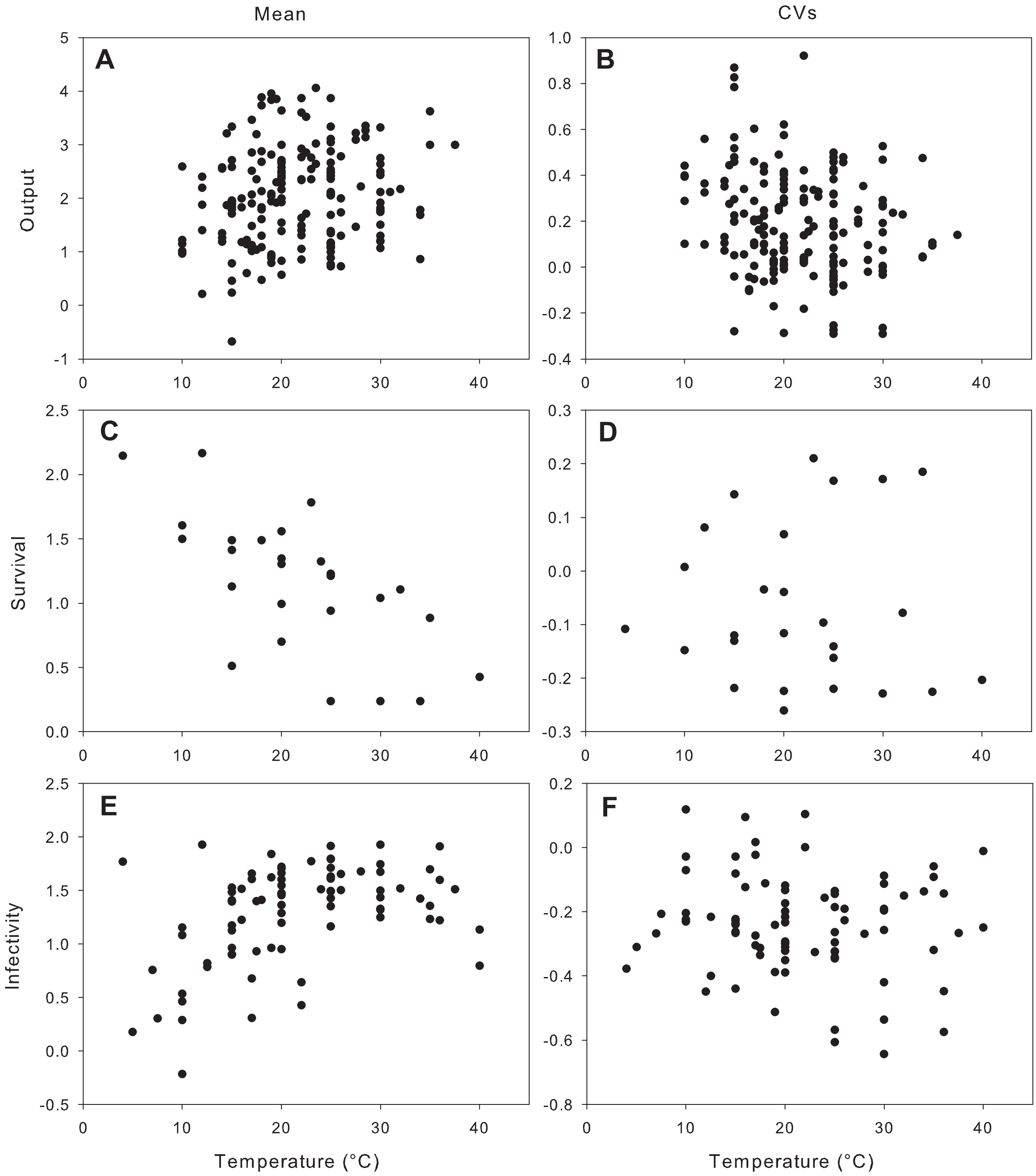

Fig. 1. Means and coefficients of variation (all log transformed) for output, survival and infectivity of trematode cercariae in relation to temperature. (A) Mean output 12 h^{-1}, (B) coefficients of variation for output, (C) mean cercarial age (in h) around the 50 ± 10% survival mark, (D) coefficients of variation for survival, (E) mean infectivity (mean proportion of cercariae successfully infecting hosts), (F) coefficients of variation for infectivity (based on arcsine square root transformed means and S.D.s).

3. Results

3.1. Cercarial output

Mean output of cercariae 12 h^{-1} from infected snail hosts was strongly affected by temperature, following an optimum curve with a significant quadratic term (negative parameter estimate) (Table 2, Fig. 1A). Output also increased with increasing snail host size (Table 2). Target also emerged as an important predictor with output of cercariae that encyst on substrate being significantly lower than output of cercariae that infect ectothermic hosts (Tables 2 and 3). None of the other predictors emerged as important (despite some relatively large differences in means for some categories according to the raw data, e.g. for acclimatisation; Table 3). CVs of output were also affected by temperature with the quadratic term emerging as marginally important with a slightly positive parameter estimate (Table 2, Fig. 1B). No other predictor was important (Table 2; Fig. 2A).

3.2. Cercarial survival

Mean cercarial age around the 50% survival mark was strongly affected by temperature, decreasing with increasing temperature (Table 2, Fig. 1C). Besides temperature, acclimatisation, latitude,

Table 3
Means and coefficients of variation, and respective S.D.s and sample sizes (*n*), for each response variable, i.e. output, survival and infectivity of trematode cercariae, categorised by acclimatisation (none, short or long), habitat (freshwater, estuarine or marine), latitude (low or mid) and target (ectotherm, endotherm, or substratum).

Response	Factor	Category	Mean	S.D.	CV	S.D.	*n*
Output (12 h^{-1})	Acclimatisation	None	1098.03	2310.21	1.31	1.17	90
		Short	387.22	584.24	1.51	1.30	49; 48
		Long	246.80	495.46	0.92	0.62	40
	Habitat	Freshwater	438.35	732.96	1.17	1.11	89; 88
		Estuarine	2143.94	3433.17	1.06	0.58	25
		Marine	539.33	1469.57	1.51	1.27	65
	Latitude	Low	915.10	2338.61	0.87	0.59	67
		Mid	592.47	1211.48	1.53	1.29	112; 111
	Target	Ectotherm	943.46	2008.53	1.50	1.30	105; 104
		Endotherm	776.44	1139.72	1.07	0.75	16
		Substratum	279.00	1128.81	0.94	0.71	58
Survival	Acclimatisation	None	33.59	38.89	0.29	0.25	21
		Long	2.69	1.46	0.91	0.14	5
	Habitat	Freshwater	41.40	45.79	0.33	0.30	14
		Marine	11.60	10.06	0.50	0.37	12
	Latitude	Low	37.29	47.76	0.30	0.40	8
		Mid	23.36	31.69	0.46	0.31	18
	Target	Ectotherm	31.39	41.28	0.51	0.33	20
		Endotherm	15.19	10.26	0.09	0.03	6
Infectivity	Acclimatisation	None	27.71	18.37	0.52	0.33	49
		Short	30.97	25.98	0.28	0.15	30
		Long	26.93	10.59	0.79	0.48	4
	Habitat	Freshwater	30.08	22.27	0.34	0.18	62
		Marine	25.23	16.86	0.75	0.43	21
	Latitude	Low	35.54	23.49	0.33	0.20	39
		Mid	22.92	16.74	0.55	0.37	44
	Target	Ectotherm	30.52	22.83	0.46	0.35	61
		Endotherm	24.21	14.49	0.41	0.20	22

habitat and target host all emerged as important predictors, with the half-life of cercariae being on average shorter after long compared with no acclimatisation, for species from mid compared to low latitudes, for marine compared with freshwater species and for those targeting endothermic compared with ectothermic hosts (Table 3). When only considering species infecting a second intermediate ectothermic host, temperature, acclimatisation and (marginally also) latitude remained important, whereas habitat did not. Additionally, no difference was found between the mean half-life of cercariae infecting vertebrate compared with those infecting invertebrate ectothermic hosts (Table 2).

In contrast to the effect of temperature on mean survival, temperature did not affect CVs (Table 2, Fig. 1D). Important predictors for CVs were, however, acclimatisation, latitude, habitat and target host. There was a negative correlation between the CV and the percentage survival indicating that variability decreases with increasing percentage of survival (50 ± 10%; i.e. lower variability closer to 60% survival, higher variability closer to 40% survival) (Fig. 2B). CVs were substantially higher when the target host was an ectotherm compared with endotherm. Note that patterns visible in the raw data (Table 3) are not always consistent with those revealed by the model output taking all factors into consideration; e.g. effects of latitude and habitat on CVs of survival. When considering only those species with an ectothermic target host, the results remained largely consistent, and no difference emerged between those species targeting a vertebrate compared with invertebrate ectothermic host (Table 2). For results regarding both mean and CVs for survival, note that the data set was very small and that data regarding endothermic hosts and long acclimatisation came from single studies (Lawson and Wilson, 1980; and Studer et al., 2010, respectively).

3.3. Infectivity

Considering all data points (i.e. species targeting endo- and ectothermic hosts), mean infectivity was only affected by temperature showing a slight optimum curve with a significant quadratic term (Table 2, Fig. 1E). When only considering species infecting ectotherms (i.e. removing data from a single study on *Schistosoma mansoni*), the effect of temperature disappeared (importance of the quadratic term remaining) (Table 2). None of the other factors emerged as important.

For the whole dataset, temperature also did not emerge as a strong predictor for CVs of infectivity (Table 2, Fig. 1F). Mean percentage infectivity was by far the most important predictor, with a negative correlation between increasing mean infectivity and CVs (Table 2, Fig. 2C). This indicates that when cercariae are successful at infecting a host, the variability of this success is small, while when success is low, then variability tends to be high. There was an effect of acclimatisation, with variability of infectivity being significantly lower after short compared with long acclimatisation (Table 3; note that acclimatisation was only long in one study, i.e. Studer et al. (2010)). These results were consistent when only considering species targeting ectothermic hosts. As for mean infectivity, no significant difference emerged for CVs between species infecting vertebrate or invertebrate ectothermic hosts. Note that data points regarding endothermic target hosts for both means and CVs came from a single study (DeWitt, 1965).

4. Discussion

Using data from the literature, we addressed the question of how trait means and variabilities of trematode cercariae are

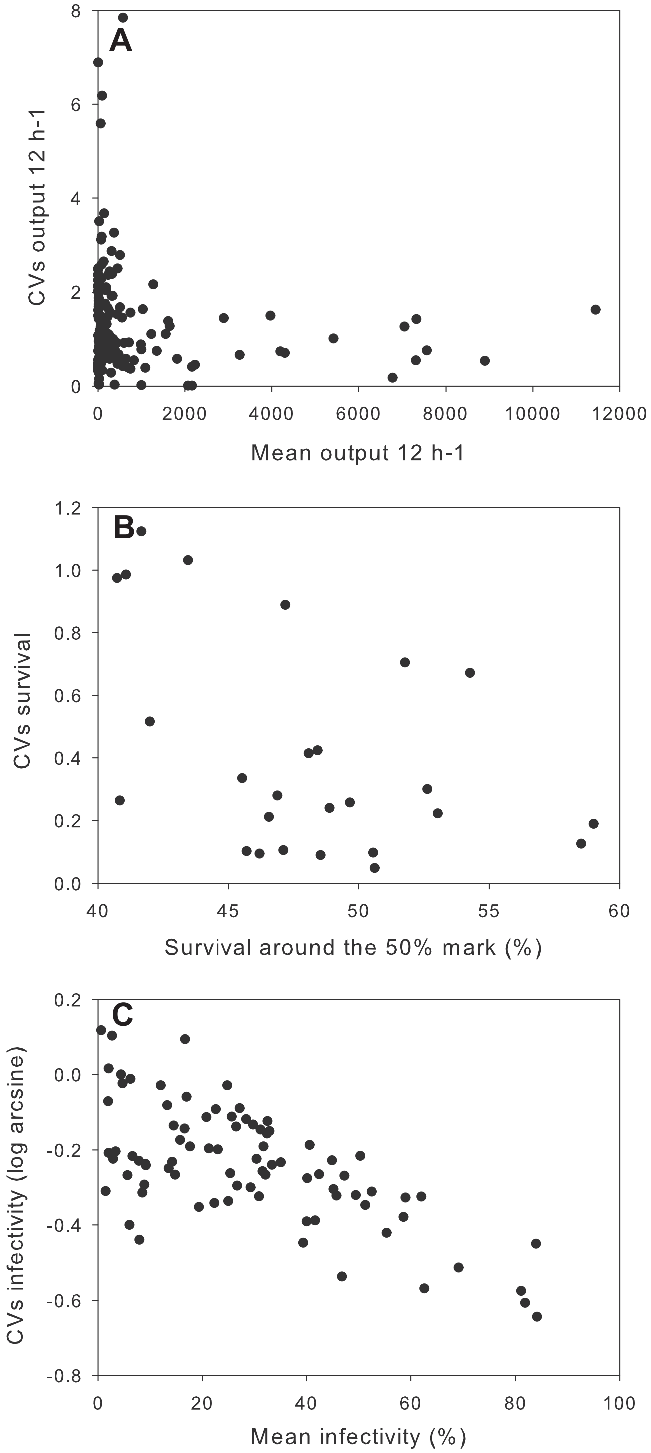

Fig. 2. Relationships between means and coefficients of variation for trematode cercariae (A) output from infected snail hosts, (B) survival and (C) infectivity (coefficients of variation log-arcsine square root transformed).

related to temperature. We were particularly interested in the variability of responses as they may reveal the potential for adaptive evolutionary change. Because our models included trematode species nested within family as a random factor, all our results control for species-specific idiosyncrasies and therefore represent general patterns among trematodes. While the results for mean responses were consistent with expected patterns, showing optimum curves for cercarial output and infectivity, and a linear decrease for cercarial survival, results for CVs were unexpected. Temperature was only an important predictor in the case of cercarial output, with variability increasing slightly at the higher temperature range, and no directional trend was found for the variability of cercarial survival and infectivity in relation to temperature.

Poulin (2006) indicated that in general, the number of cercariae being produced and emerging from mollusc hosts is strongly affected by temperature beyond what is normally expected from ectothermic physiology, with greater numbers emerging with increasing temperature. More recent work by Morley and Lewis (2013) has contrasted this pattern to some degree, indicating responses to temperature were largely within the ranges expected for ectotherms (e.g. Newell, 1973) and emphasising a relatively flat, constant response (i.e. thermostability) over optimum temperature ranges after the initial increase above the minimum thresholds for development and emergence. Over the low temperature range, a change from the production of daughter rediae or sporocysts to that of cercariae by the intramolluscan stages (i.e. rediae or sporocysts) is probably the main driver of the increasing output with increasing temperature (Dinnik and Dinnik, 1964; Wilson and Draskau, 1976). As cercarial emergence is also associated with the metabolic activity of the snail host, Morley and Lewis (2013) suggested that the decline in emergence rates at higher temperatures is unlikely to be due to a reduced capacity for cercarial development but rather associated with a decline in the physiological status of the molluscan host. Our results based on actual data from the original studies (rather than the physiological rates (Q10 values) used by Morley and Lewis (2013) and Poulin (2006)), confirm this optimum curve for output in relation to temperature, but more studies are needed to elucidate the actual mechanisms behind this pattern.

An analysis across marine trematode species found cercarial output to be positively correlated with snail host size, not correlated with latitude, negatively correlated with the size of cercariae (an aspect not considered here, but see also Koehler et al. (2012b)), and influenced by the type of target host, with output being highest for vertebrate targets and lowest for those species encysting on substrate (Thieltges et al., 2008). Our study, including trematode species from marine, freshwater and estuarine systems, only confirmed the importance of snail host size, consistent with Thieltges et al. (2008) and Poulin (2006), as well as the type of target. Our analysis, however, only confirmed that species targeting the substratum have a lower output than species targeting ectotherms. Trematode species at higher latitudes have also been suggested to show lower Q10 values than those at lower latitudes (Poulin, 2006), but the importance of latitude has been confirmed neither by Thieltges et al. (2008), Morley and Lewis (2013), nor the present study. Moreover, acclimatisation is a crucial component of thermobiological assessments and inter- and intraspecific comparisons, and has been highlighted to be of relevance for cercarial development and emergence (Morley and Lewis, 2013). However, despite relatively large differences between means (Table 3), the model results in the present study did not support a strong effect of acclimatisation on cercarial output.

Although the raw data for the variability of cercarial output (see Fig. 1B) does not provide an obvious directional pattern with increasing temperatures, the results from the statistical analysis indicated that the expressed phenotypic variability in this trait is not constrained at higher temperature levels. Indeed, with the quadratic term emerging as significant, the variability of cercarial output at the lower and higher temperature levels, i.e. with decreasing mean output (as opposed to the optimum range), increased. This indicates that when output is low (relative to optimum levels) variability tends to be high, whereas within the optimum range, variability tends to be lower. In contrast, neither acclimatisation, habitat, latitude, target host nor snail host size seem to be influencing the variability of this trait when considered in relation to temperature.

For survival, the linear decrease with increasing temperatures, also found in the present study, has been attributed to higher energy demands and hence the faster depletion of limited reserves at higher temperatures (Lawson and Wilson, 1980; Pechenik and Fried, 1995). In a comparative analysis across a range of trematode species, Morley (2011) found that temperature did not exert any disproportionate effect on the thermodynamics of cercarial metabolism and survival measured by temperature-driven reaction rates (i.e. Q10 and E^* (Arrhenius activation energy)); i.e. rates were within the ranges generally expected for ectotherms. Morley (2011) described substantial intra- and interspecific variation with some species or strains showing a relatively linear relationship of increasing mortality and glycogen utilisation rate with temperature, others showing a more convex relationship, and others again showing a thermostable zone with little change. Also, some species have peak metabolic activity that reflects the body temperature of the definitive host, rather than correlating with the molluscan host (Vernberg and Vernberg, 1963). Despite this variability, our analysis clearly identified a strong linear decline across the species included in the present study as a general pattern. Furthermore, the importance of acclimatisation in the context of cercarial survival (Morley, 2011) was confirmed in our model, but was based on data from a single study in which organisms were acclimatised for an extended period (Studer et al., 2010). For the full dataset, latitude and habitat also emerged as important predictors and species infecting ectothermic hosts had on average a longer cercarial half-life compared with those infecting endotherms (data for endothermic hosts, however, also originating from a single study). These differences did not persist when only considering species infecting ectothermic second intermediate hosts, and caution is needed with respect to these results due to the small data set used.

The strong decline in mean cercarial survival with increasing temperature was not accompanied by a decrease in variability. This indicates that while, on average, cercarial survival declines with increasing temperatures, the variability in this response remains high, i.e. without directional trend. In contrast, the percentage of survival (within the 40–60% range included in the dataset) did emerge as an important predictor of the variability in cercarial survival, with higher percentages of mean survival being associated with lower variability and the lower percentages of survival with higher variability. While temperature was not an important predictor in the model for CVs of survival, all other predictors emerged as important. In particular, there was a large difference between the variability in cercarial half-life of those species infecting endotherms compared with those infecting ectotherms, with variability in species infecting ectotherms being higher. The species infecting endotherms all belong to the family Schistosomatidae and thus variability is likely to be smaller due to the phylogenetic relationship among these species and the diversity of ectothermic hosts used by species from other trematode families, respectively. When only considering ectothermic hosts, no difference was found in the variability of survival for species infecting vertebrates compared with those infecting invertebrates. While acclimatisation, latitude and habitat remained important, the cautionary notes made above regarding the analyses of cercarial survival also extend to the variability of this trait; adding new data to this dataset is likely to change model outcomes and hence current results need to be treated with caution.

As a general pattern for trematodes, the functional trait of mean infectivity was shown to follow an optimum curve in relation to temperature. Up to the optimum range, increased infectivity is thought to be related to the higher activity of cercariae which leads to increased contact with potential hosts per unit of time. However, beyond the optimum temperature range, usage of the finite glycogen reserves may be too rapid to allow any successful transmission. It has also been suggested that host recognition mechanisms may be impaired at high temperatures (Evans, 1985; McCarthy, 1999), but direct effects on the behaviour or physiology of hosts themselves may also help explain a reduced infection success. This optimum curve for infectivity in relation to temperature was only apparent when considering all data; when only considering species targeting ectothermic hosts, the importance of temperature disappeared. This, however, is based on the removal of data from a single study (De Witt, 1965).

Temperature did not emerge as an important predictor for the variability in infectivity, despite the optimum relationship between the mean and temperature when considering data for species targeting ecto- and endothermic hosts. Variability, however, decreased strongly with increasing mean infectivity, with high infectivity being associated with low variability and low infectivity with high variability. Acclimatisation emerged as another relevant predictor with variability after short acclimatisation being on average lower than after long or no acclimatisation. These effects remained consistent after excluding the data from the only species in the dataset that targets endothermic hosts (i.e. *S. mansoni*). While this confirms the importance of acclimatisation in experimental procedures, the different approaches that were used in infectivity experiments included in the present study (see Section 2) prevent a straightforward interpretation of this result.

In general, variability of traits in relation to temperature may either increase with increasing temperatures, show no effect, or decrease. Assuming that the responses considered here have some genetic basis (see Koehler et al., 2011, 2012a; Berkhout et al., unpublished data), in the first two cases we might expect that this would indicate some scope for evolutionary adaptation based on a reasonable amount of genetic variation. In contrast, if variability decreases at higher temperatures, the trend would suggest that there is little scope for evolutionary adaptation. In the present analyses, we did not find any evidence for decreasing variation with increasing temperature; variation in all three traits remained virtually without a directional trend except for output showing even a slight increase in variability at higher temperatures. This possibly indicates relatively uncompromised adaptive potential of trematodes under increasing temperatures with regards to all three traits considered here.

One caveat of our study is that we examined only variability in some key traits, and not their heritability. However, our study was chiefly concerned with the question of whether and how the expressed phenotypic variability in those traits is related to temperature. As genotypic differences have been found for all three traits considered here (Berkhout et al. (unpublished data) for output; Koehler et al. (2011) for survival; Koehler et al. (2012a) for infectivity), strong evidence does exist that these traits are heritable and thus subject to selection. Our study also showed that the information encapsulated within a measure of variability can indeed be useful and should not only be treated as “noise”. In fact, providing such basic statistical information should be a standard requirement for publishing primary empirical studies (see Nakagawa and Poulin, 2012), as a range of studies could not be included in the present assessment due to the lack of these measures. Also, small and unbalanced datasets had to be used for some aspects of our study. As a consequence, some results are likely to change with the addition of new data. In particular, the survival and infectivity of cercariae remain understudied, as do other aspects of the transmission process and our general understanding of the thermal biology of trematodes and other parasites (see e.g. Bates et al., 2011). For example, future studies should include a wider range of temperatures than is commonly done, spanning the entire range relevant for a particular species in a given habitat, taking into account likely future scenarios of warming. Such knowledge is crucial for the development of predictive frameworks in the context of climate change.

Evolutionary processes in climate change – disease research have remained relatively unexplored (Rohr et al., 2011), despite existing evidence supporting the importance of evolution for disease processes on ecological timescales (Grenfell et al., 2004; Lebarbenchon et al., 2008; Morgan et al., 2012) and for various organisms as a consequence of contemporary climate change (Gienapp et al., 2008; Skelly and Freidenburg, 2010; Hoffmann and Sgro, 2011; Donnelly et al., 2012; Kelly et al., 2012). Albeit a very indirect way of assessing evolutionary potential, using the information provided by measures of variance seems a promising approach to assess the degree of variability for a given trait (Ghalambor et al., 2007). Although we cannot be certain that the traits considered in our study are in fact of high relevance for trematodes exposed to changing environmental conditions, the conclusions derived from our results are nonetheless useful as they identify general patterns governing the thermal biology of these parasites. However, the way trematodes will respond to global warming and other global changes is highly species-specific and effects are likely to be very localised. While it can be expected that some species will fare well whereas others might be very vulnerable (either due to direct effects or effects on hosts), our study suggests that trematodes in general may have, at least for the traits and the critical life cycle stage considered here, variability upon which selection may act. However, knowledge of genetic diversity of trematode and other parasite populations often remains limited and hence identifying changes in the genetic make-up of populations and species will be difficult. Moreover, modelling studies from intertidal systems have identified that increasing temperatures coupled with the increased impact of trematodes may lead to local extinction of affected host populations (Mouritsen et al., 2005; Studer et al., 2013). This is not only of concern for affected hosts, but ultimately also for the parasite species itself relying on these hosts to complete its life cycle. Local mortality events are likely to reduce the genetic diversity present in a system. Therefore, extreme events such as heat waves may result in local extinctions rather than allowing for selection to occur. Hence, besides assessments of potential consequences of long term changes allowing for selection, investigating the effects of extreme events should also be a priority for future investigations.

In conclusion, this study confirms optimum curves for mean output and infectivity and a linear decline for survival in relation to temperature. Our study is, to our knowledge, the first to assess the variability of these traits in relation to temperature; it revealed trait variability for all traits investigated, i.e. uncompromised variability for output, survival and infectivity of cercariae even at higher temperatures. This indicates temperature-independent variability within trematode species with respect to these traits, which may be important for selective processes under increasing temperatures due to global warming.

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