Host-parasite interactions and global climate oscillations

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SUMMARY

It is suspected that host-parasite interactions are influenced by climatic oscillations such as the North Atlantic Oscillation (NAO). However, the effects of climatic oscillations on host-parasite interactions have never been investigated. A long-term (1982–1999) dataset of the host snail *Lymnaea stagnalis* and trematode metacercariae infection has been collected for Lake Chany in Western Siberia. Using this dataset, we estimated the impact of the NAO on the population dynamics of hosts and parasites as well as their interactions. The results of general linear models showed that the abundance of dominant parasite species and the total parasite abundance significantly increased with NAO, with the exception of *Moliniella anceps*. Other climatic and biological factors were relatively weak to explain the abundance. There was no significant relationship between NAO and the population density of host snails. The prevalence of infection was related to the total abundance of parasites, but not to the NAO. Thus, the responses to the NAO differed between the host and parasites, indicating mismatching in host-parasite interactions. Therefore, climatic oscillations, such as the NAO, influence common parasitism.

Key words: long-term data set, NAO, parasitism, trematoda, snail.

INTRODUCTION

Host-parasite interactions are an important component of community and food web structure, and have been the focus of many recent ecological studies (e.g. Lafferty *et al*. 2006; Kuris *et al*. 2008; Sukhdeo, 2010). Parasites can augment the energy flow of food webs, alter the strength of interactions, and cause trophic cascades. The inclusion of infectious agents in the fundamental ecological concepts might allow for a better understanding and mitigation of human impacts on ecosystems, such as global climate change (Lafferty *et al*. 2008).

Inter-specific interactions like those of hosts and parasites should be influenced by climate change. In fact, human-induced climate change has recently been reported to impact ecological interactions. Many studies have concurrently documented changes in intra- and inter-specific interactions, and community structure caused by climate change (e.g. Post and Stenseth, 1999; Gordo and Sanz, 2005; Chiba *et al*. 2006). For parasitology, McCarthy (1999) reported that the survival and infectivity characteristics of cercariae changed under different air temperatures. Mouritsen and Poulin (2002) reported potential links between host-parasite interactions and global climate oscillations. They summarized host-parasite systems influenced by temperature in particular, but also by precipitation and ocean currents. Thus, they expected that Atlantic and other climatic oscillations indirectly influenced the dynamics of parasite and the host in a region throughout changes in temperature, precipitation and other environmental factors.

In the northern hemisphere, the North Atlantic Oscillation (NAO) is an important index of climatic oscillation (Hurrell, 1995). An extended version of the index can be derived for the winter months of the year using a station in the southwestern part of the Iberian Peninsula (Hurrell, 1995). The NAO is a major driving force in the climate system of the northern hemisphere and determines most of the inter-annual variation in winter temperatures in the northern hemisphere including the northern Atlantic Ocean (Hurrell, 1995). A highly positive NAO index (measured as the deviance from the average sea level pressure difference between the Azores and Iceland) is associated with high temperatures, strong winds, and high levels of precipitation in northern Europe. Conversely, a low NAO index gives rise to the opposite conditions (Hurrell and van Loon, 1997). The NAO impacts ecological processes such as population and community dynamics and specific interactions (e.g. Post and Stenseth, 1999; Ottersen *et al*. 2001; Blenckner and Hillebrand, 2002; Stenseth *et al*. 2003; Schindler *et al*. 2005; Chiba *et al*. 2006). Hence, it was concluded that the NAO might strongly affect host-parasite interactions in aquatic

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and terrestrial habitats in northern regions (Mouritsen and Poulin, 2002). In addition, the authors suggested that host-parasite interactions are influenced by climatic oscillations. However, they also reported that no study has directly considered the importance of climatic oscillations in host-parasite interactions.

In Lake Chany, western Siberia, researchers have collected a long-term dataset on density of host snail populations, prevalence and mean abundance of metacercariae infection. Using this long-term dataset, we can test the hypothesis that the NAO influences host and parasite interactions. In this study, we estimated the impact of the NAO as well as local environmental factors on the host and parasite interactions using the 17-year dataset of the population dynamics of host snail and trematode parasites (i.e. metacercariae infections) in Lake Chany. Hence, we can test whether NAO and local environmental factors influence host-parasite interactions. Moreover, many waterbird species breed and stop over at Lake Chany during spring migration from wintering in Africa, Western Europe and the Middle East (Yurlov, 1981; Veen *et al*. 2005). NAO influences the bird population size and distribution during breeding and wintering (e.g. Zalakevicius *et al*. 2006; Gordo, 2007), and most waterbird species are the final hosts of trematoda in this area (e.g. Yurlova *et al*. 2006). Thus, indirect effects of NAO through birds would influence interactions of snail hosts and trematode cercariae and metacercariae in the lake.

MATERIALS AND METHODS

Dataset for host and parasite densities

The datasets created by Yurlova *et al*. (2006) were used for this study. Detailed descriptions of the study area and collections are provided in Yurlova *et al*. (2006). Briefly, sample collection was conducted at the littoral zone of Lake Chany (54°30′–55°09′ N, 76°48′–78°12′ E) in Russia. Three sampling sites were chosen, each separated by 0·5–1·0 km (see Yurlova *et al*. 2006). *Lymnaea stagnalis* comprises the dominant species within the pulmonate snail assemblage (Yurlova and Vodyanitskaya, 2005). Specimens of *L. stagnalis* and their parasites were sampled annually from 1982 to 1999, with the exception of 1983. Sampling was conducted approximately every 10 days between 20 May and 20 August of each year, and the annual mean data are provided in Yurlova *et al*. (2006). Snails were collected by hand at a depth of 0·1–0·5 m. The sample from each sampling site contained 4–6 subsamples (depending on the density of snails), each obtained from an area of 0·25 m^2.

Snails were counted, and shell length was measured from the apex to aperture to study snail density and population structure. The snails were dissected and examined for both primary (asexual in digestive gland) and secondary infections (metacercariae). In parasitological analyses to estimate prevalence (%) and mean abundance of metacercariae and prevalence of parthenitae infection, mature individuals (shell length >15 mm) were used, because for juvenile snails, metacercariae infection is very rare and parasites are practically absent in snails with 2–10 mm shell length.

In total, 18 species of metacercariae belonging to 6 families were found in *L. stagnalis* with *Moliniella anceps*, *Cotylurus cornutus*, and *E. aconiatum* and *E. recurvatum* (*Echinoparyphium* spp.) being the dominant parasite species found in 70–90% of the samples, common in all years, seasons and sites (Yurlova *et al*. 2006). The metacercariae of the Echinostomatidae family (*E. aconiatum*, *E. recurvatum* and *Moliniella anceps*) were encysted in mantles and lung cavities, and that of *Cotylurus cornutus* were in the hepatopancreas. We calculated the mean abundance as the number of parasites per host snail, and used abundance of these dominant species and total parasite abundance of all 18 spp. per host snail for our analysis. We also calculated the prevalence of infection (%) with metacercariae species in the snail population.

Life cycle of parasite and host

According to our previous data, the first intermediate hosts for *E. aconitum* in Lake Chany are *L. stagnalis* and *L. palustris*, those for *E. recurvatum* are primarily *L. tumida*, *L. auricularia* and rarely *L. stagnalis*, those for *M. anceps* are *L. stagnalis* and *L. palustris*, and for *Cotylurus* spp. are *L. stagnalis*, *L. tumida*, and *L. auricularia* (Yurlova, 2003). Second intermediate hosts for all 4 dominant trematode spp. in Lake Chany included several Pulmonata and Prosobranchiae snail species (Yurlova *et al*. 2006). The final hosts for *Echinoparyphium* spp. are Anatidae, Rallidae, Scolopacidae, Laridae bird species, and those for *C. cornutus* are Anatidae, Rallidae, Scolopacidae, Laridae, Accipitridae and Charadriidae birds (Yurlova *et al*. 2006). In contrast, the final host for *M. anceps* is only the coot *Fulica atra* (Filimonova and Shalyapina, 1975).

L. stagnalis is the dominant species in Lake Chany with a 2-year life span (Yurlova, 2003). Reproduction age is 1 year (shell length: >20 mm). The optimal water temperature for snail reproduction is 18–30 °C. The reproduction period is from May to August.

Climate dataset

We used the mean water temperature, water level, and ice-melting date of the lake as local climate indicators. The relative water level of the lake and ice-melting date were obtained from the local hydrological station maintained by the West

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Siberian Hydrological and Meteorological Service, Novosibirsk, Russia. Water temperature was measured at a depth of 0·3–0·4 m at the shoal of the Kargat River close to the sampling site from May to August.

In this study, we used NAO as the climatic oscillation index. NAO was defined as the normalized air-pressure difference between a station on the Azores and one on Iceland. An extended version of the index can be derived for the winter half of the year by using a station in the southwestern part of the Iberian Peninsula (Hurrell, 1995). Kitaev and Kislov (2007) reported that in west Siberia, NAO circulation influenced regional and local meteorological regimes, especially snow cover and air temperature. Hence, from the evidence, we can assume that the local climate around Lake Chany was also influenced by NAO. NAO measured by The NAO index was provided by the Climatic Research Unit, School of Environmental Sciences, University of East Anglia, UK (data available online: http://www.cru.uea.ac.uk/~timo/projpages/nao_update.htm). We used the annual mean NAO from 1982 to 1999.

Statistical analysis

To estimate the role of climatic and ecological factors in host and parasite dynamics, we used generalized linear models (GLMs) based on a Gaussian distribution with $\log_{10}(x+1)$-transformation. Before analysis, we checked Variance Inflation Factors (VIF) among the explanation factors and also tested time-series autocorrelation using Durbin-Watson test. The VIFs for the factors were <3 (not shown), and time-series autocorrelation was not significant ($P>0{\cdot}05$). The models were selected by a stepwise procedure based on the Akaike information criterion (AIC) to determine the best model for the relationships. Given that the climatic dataset was annual, we used the annual mean of the dataset collected at Lake Chany from May to August for the GLM. The models used for the GLM were as follows. For parasite species [*Echinoparyphium* spp. (*E. aconiatum* and *E. recurvatum*), *M. anceps*, and *C. cornutus*] and total parasite abundance:

$$\begin{aligned}\text{Mean abundance} = {} & \text{ß NAO} + \text{ß host density} \\ & + \text{ß WT} + \text{ß WL} + \text{ß icemelt} \\ & + \text{ß snail density infected by} \\ & \quad \text{parthenitae of each species} + \alpha.\end{aligned}$$

For the host snail (*L. stagnalis*):

$$\begin{aligned}\text{(Density)} = {} & \text{ß NAO} + \text{ß WT} + \text{ß WL} + \text{ß Ice melt} \\ & + \text{ß prevalence} + \text{ß total parasite abundance} \\ & + \text{ß shell size} + \alpha.\end{aligned}$$

$$\begin{aligned}\text{(Prevalence)} = {} & \text{ß NAO} + \text{ß WT} + \text{ß WL} + \text{ß ice melt} \\ & + \text{ß total parasite abundance} \\ & + \text{ß host density} + \text{ß snail density infected} \\ & \quad \text{by parthenitae of each species} \\ & + \text{ß shellsize} + \alpha,\end{aligned}$$

where ß indicates the coefficient of factors and α indicates the constant. WT, WL, and Ice melt indicate water temperature, water level in summer, and the day of the year when the lake ice melted, respectively. The factors for the GLMs are provided in Appendix 1. The mean water temperature did not change markedly from 1982 to 1999, whereas the water level of the lake significantly increased (see Appendix 1; simple regression, $R^2=0{\cdot}32$, $P<0{\cdot}01$, slope: 0·38 m per decade). The annual mean of the NAO fluctuated between the years 1982 and 1999.

To estimate the importance of each factor for hosts and parasites, we also performed a simple linear regression. All statistical analyses were performed using R ver. 2.12.0 (R Development Core Term, 2011).

RESULTS

Changes in mean abundance of metacercariae and prevalence of parthenitae and cericariae for 4 dominant trematoda species in *L. stagnalis* from 1982 to 1999 are shown in Table 1, and the correlations between both variables were significant in the species; *C. cornutus*, *M. anceps*, and *Echinoparyphium* spp. ($r>0{\cdot}46$, $P<0{\cdot}05$ Pearson's correlation coefficients).

The best GLM for *C. cornutus* included only NAO (Table 2), whereas those for *Echinoparyphium* spp. contained other factors including density of snails infected by the parthenitae; however, NAO was the only significant indicator ($P<0{\cdot}05$). Mean abundances of *C. cornutus* and *Echinoparyphium* spp. significantly increased with NAO (simple regression in Fig. 1, $R^2=0{\cdot}30$ and 0·49, $P<0{\cdot}01$). Conversely, for *M. anceps*, among other variables, ice melting date and water level were included in the best GLM (Table 2). Also, single regression indicated no relationship between the mean abundance of *M. anceps* and NAO ($R^2=0{\cdot}004$, $P=0{\cdot}81$). For total parasite abundance, the best GLM included NAO among other variables; however, NAO was the only significant factor. Mean abundances of the total parasite species significantly increased with NAO (Fig. 1, $R^2=0{\cdot}44$, $P<0{\cdot}01$).

With respect to the density of the host snail *L. stagnalis*, the best GLM included only NAO, but was not significant (Table 3). Regarding prevalence of metacercariae infection, the factors in the best GLM included NAO, total parasite abundance, and other factors, but total parasite abundance was

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Table 1. Mean abundance of metacercariae and prevalence (%) of cercariae for dominant trematode species in *Lymnaea stagnalis* from 1982 to 1999

	C. cornutus		*M. anceps*		*Echinoparyphium* spp.	
Year	Metacercariae, mean abundance	Cercariae, prevalence (%)	Metacercariae, mean abundance	Cercariae, prevalence (%)	Metacercariae mean abundance	Cercariae prevalence (%)
1982	28·57	0·00	12·72	3·57	37·24	0·77
1984	17·84	0·00	4·35	0·42	14·97	1·04
1985	1·21	0·00	1·55	3·56	4·97	0·16
1986	74·81	0·58	2·42	0·58	35·32	0·44
1987	17·14	0·00	3·68	0·00	0·82	0·00
1988	42·32	1·40	1·59	1·40	0·28	0·08
1989	240·00	5·97	10·57	1·01	24·79	0·20
1990	191·4	1·34	11·55	1·34	198·14	3·94
1991	115·7	2·77	0·78	0·15	129·84	0·69
1992	158·0	0·94	3·81	0·94	81·64	0·39
1993	68·59	0·69	1·19	3·09	31·59	1·37
1994	76·28	0·70	7·99	2·61	18·01	0·78
1995	51·67	0·00	4·71	1·89	9·45	0·79
1996	57·21	0·42	19·53	5·88	28·88	0·21
1997	39·54	0·00	13·51	3·26	8·57	0·00
1998	39·55	0·87	12·73	13·58	18·67	0·87
1999	45·07	0·81	11·99	0·00	43·80	1·22

Table 2. Coefficients and R^2 values for the best GLMs for parasite abundance

(The coefficients are expressed as mean ± S.E., and the asterisk (*) indicates significance ($P<0·05$). NAO indicates the North Atlantic Oscillation and snail density with trematode parthenitae means snail density, which is infected by trematode parthenitae of each species.)

Factors	*C. cornutus*	*M. anceps*	*Echinoparyphium* spp.	Total parasite abundance
Annual NAO	0·593 ± 0·163*		0·67 ± 0·164*	0·653 ± 0·129*
Host snail density				
Ice melting date		0·023 ± 0·013	0·022 ± 0·016	0·013 ± 0·011
Water level		0·381 ± 0·259	1·18 ± 0·43*	0·443 ± 0·273
Water temperature				−0·133 ± 0·088
Snail density infected by parthenitae			0·183 ± 0·43	
(Intercept)	1·262 ± 0·103*	−890·5 ± 487·1	−843·8 ± 605·6	−491·8 ± 402·6
R^2	0·487*	0·227	0·717*	0·703*

the only significant factor ($P<0·05$, Table 3). The relationship between prevalence and total parasite abundance was significantly positive (Fig. 1, $R^2=0·47$, $P<0·01$). Conversely, the regression between prevalence and NAO was not significant, but followed a positive trend (Fig. 1, $R^2=0·18$, $P=0·10$).

DISCUSSION

Our results showed that the abundance of most of the dominant metacercariae species might be influenced by the NAO. Stenseth *et al*. (2003) suggested that biological effects might be more strongly related to global climate indices than to any single local climate variable. However, the mean abundance of *M. anceps* was not influenced by the NAO but was impacted by the ice period of the lake as well as the water level. Global climatic oscillations influence the population dynamics of terrestrial and aquatic organisms (e.g. Post and Stenseth, 1999; Schindler *et al*. 2005; Chiba *et al*. 2006), but only in localized areas of lakes (e.g. Schindler *et al*. 2005). Our results support these previous studies, despite the small sampling area of this study.

Straile (2002) suggested that inter-annual variability in the timing of clear water phases in lakes was strongly related to the NAO. Given that the NAO is responsible for inter-annual and decadal fluctuations in winter air temperatures (Hurrell and van Loon, 1997), it may reflect the annual climatic and limnological conditions of West Siberia and Lake Chany. Indeed, a significant correlation between the NAO and the temperature in western Siberia was observed from 1900 to 2000 (Vaganov *et al*. 2000;

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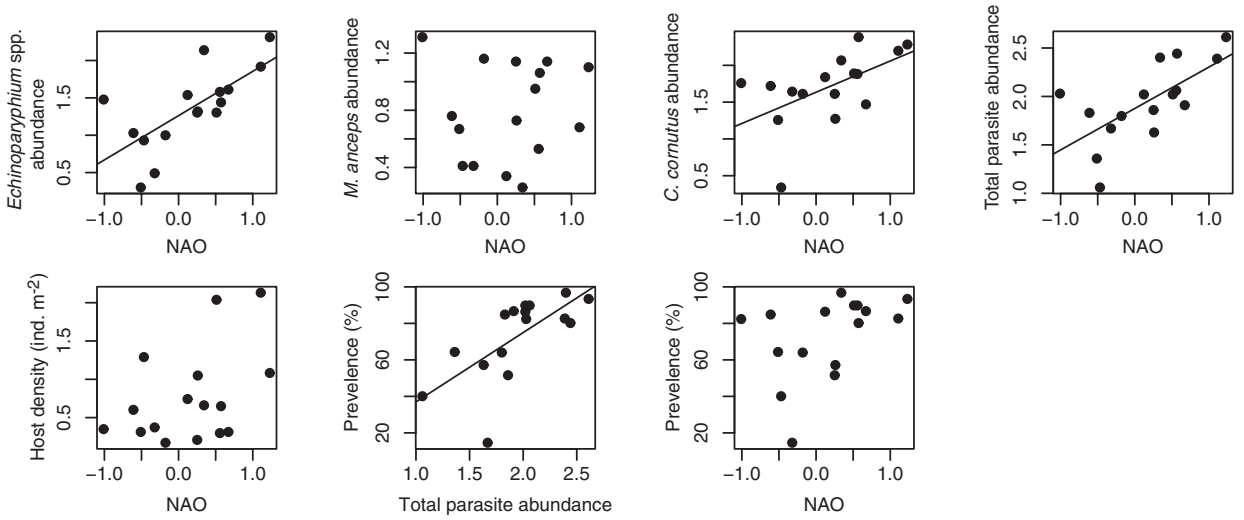


Fig. 1. Relationships between NAO and mean parasite abundance, host density, and prevalence of metacercariae infection, and the relationships between total parasite abundance and prevalence of metacercariae infection. Values on the y-axis were $\log_{10}(x+1)$-transformed. The lines indicate the simple linear regression lines.

Table 3. Coefficients and R^2 values for the best GLMs of host density and prevalence

(The coefficients are expressed as mean ± S.E., and the asterisk (*) indicates significance ($P<0{\cdot}05$). NAO indicates the North Atlantic Oscillation and snail density with trematode parthenitae means snail density, which is infected by trematode parthenitae of each species.)

Factors	Host density	Prevalence
Annual NAO	0·428 ± 0·233	−0·17 ± 0·13
Ice melt date		−0·01 ± 0·01
Water level		0·10 ± 0·06
Water temperature		
Host density	—	
Prevalence		—
Total parasite abundance		0·56 ± 0·17*
Snail density infected by parthenitae	—	
Shell size		
(Intercept)	0·699 ± 0·147*	396·0 ± 249·4
R^2	0·195	0·603*

Ippolitov *et al*. 2007). Thus, the NAO is an important factor in determining the densities of host and trematode parasite populations during the summer.

Mouritsen and Poulin (2002) suggested that host-parasite interactions are influenced by climatic oscillations. However, in this study, the abundances of parasites (metacercariae) were not significantly related to host density, and the density of *L. stagnalis* was not influenced by metacercariae infections. The asexual stages of the parasite (parthenitae) influence host reproduction (Sorensen and Minchella, 2001; Gutiérrez *et al*. 2002; Yurlova, 2003; Negovetich and Esch, 2008) and host density (Yurlova *et al*. 2000). However, there is little understanding of the influence of metacercariae infection on the reproduction of snails. Our data indicated that the population dynamics of hosts and parasites were not strongly influenced by host-parasite interactions in the 'snail-metacercariae' host-parasite system. The density of *L. stagnalis* was not influenced by the metacercariae infection, probably because the infection was not caused by host castration like parthenitae. Thus, global climatic oscillation, such as NAO, may indirectly affect host-parasite interactions through the independent population dynamics of the hosts and parasites, for example, the differences in the temperature responses in populations of host and parasite. In this case, climatic conditions of the lake may exert a greater effect on recruitment of *L. stagnalis* than changes in metacercariae infection rate of the species.

The trematode species found as metacercariae in *L. stagnalis* also infect snails as first intermediate hosts and various water birds as definitive hosts (Yurlova *et al*. 2006). Thus, the population dynamics of the parasites would also be related to the first intermediate hosts and the migration of birds, as well as their density, distribution, and other population parameters such as the timing of spring migration and breeding success, all of which are influenced by the NAO (Nott *et al*. 2002; Hechinger and Lafferty, 2005; Marra *et al*. 2005). However, in this case, our analyses found no relationship between the density of the infected snails and the abundance of metacercariae. Thus the linkages between primary (snail) and secondary (snail) hosts for metacercariae populations are not detected from our dataset. Although our dataset did not directly support this hypothesis, but climate effects on the linkages between secondary and primary hosts for parasite would be not related and probably climate effects on the particular host-parasite interaction is more important and stronger

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than the effect on linkages of hosting. The hypothesis of host-linkage effect on host-parasite dynamics would be very important to consider the whole cycle of parasitism, thus, further study is needed to test the hypothesis using direct evidence.

We estimated the effects of the NAO and local climate factors on host snail and parasite interactions. Our data indicated that the NAO influenced common parasitism in an aquatic ecosystem. Host-parasite interactions indirectly influence food webs and community structures (Mouritsen and Poulin, 2002; Lafferty *et al*. 2008; Sukhdeo, 2010). Thus, we conclude that the indirect effect of parasitism is important when evaluating the impact of climate change on ecosystems. However, in this study, we were not able to estimate the indirect effects of parasites on the other species, given the limitations of the dataset used. Thus, it would be worthwhile to address the indirect effects of climatic oscillations on ecosystems in future studies.

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