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An assessment of parasite infestation rates of juvenile sockeye salmon after 50 years of climate warming in southwest Alaska

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Abstract Climate change has produced disproportionate levels of warming in high latitude ecosystems. A critical challenge is to understand how changes in temperature will mediate ecological processes, such as disease. Several authors have suggested that warming will increase prevalence of diseases at high latitudes, yet long-term studies are lacking. We evaluated how parasite abundance and prevalence in an ecologically and economically important species (juvenile sockeye salmon *Oncorhynchus nerka*) has changed in an Alaskan watershed that has experienced substantial climatic change over the past half-century. We hypothesized that the average increase in summer water temperature of 1.9°C over the past 46 years in our study system would have resulted in a corresponding increase in fish metabolism, and thus potential consumption rates, that would increase infestation rates of the tapeworm *Triaenophorus crassus*. However, our comparison of data from 1948–1960 to 2008–2009 provided no evidence that the parasite load in juvenile sockeye salmon has significantly changed and that there is no significant relationship between summer temperature and average infestation rates. Climatic projections for southwest Alaska forecast a continuation of the current warming trend, which could potentially have effects on our studied parasite-host interaction, but thus far we found no change in infestation rates over the last 60 years.

Keywords Climate change · Parasitism · *Triaenophorus crassus* · Bristol Bay · High latitude regions · Parasite-host interactions

Introduction

High latitude regions are experiencing accelerated rates of climate change with annual average temperatures 2-3°C higher than temperatures recorded in the 1950s and warming at rates higher than nearly all other regions of the globe; climate projections suggest a continuation of this strong warming trend (ACIA 2005). Despite the ability of landscape heterogeneity to buffer some of these effects, there already appear to be important ecological responses at population, community, and ecosystem scales (Post et al. 2009).

Over the past decade considerable attention has been given to the biological consequences of global warming, but little research has been done to evaluate the potential and observed changes in aquatic parasite fauna (Marcogliese 2001). Climate change in these high latitude regions has induced increased epidemic disease outbreaks in terrestrial species, which not only threatens ecosystem structure and function but also could impact food security and cultural activities of

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northern peoples (Kutz et al. 2009a). In areas where direct effects of climate change have been less obvious, parasite dynamics might provide an early warning signal of future environmental impacts (Poulin and Mouritsen 2006).

Aquatic systems in southwestern Alaska (USA) have been responsive to warming climatic conditions over the last century. Warmer spring temperatures have led to an average spring ice-breakup date that occurs 11 days earlier over the past 58 years in the Wood River system, Bristol Bay, Alaska (Fig. 1a; Schindler et al. 2005). This progression toward earlier spring breakup dates has also been associated with warmer summer water temperatures, which have increased by an average of 1.9°C over the past 46 years in epilimnetic waters of Lake Aleknagik (Fig. 1b), and has coincided with warmer summer air temperatures, which have increased by an average of 1.0°C over the past 62 years in southwest Alaska (Fig. 1c). Much of this shift has been a response to the warm phase of the Pacific Decadal Oscillation (PDO) that began in the mid-1970s, exaggerating the effects of warming (Mantua and Hare 2002; Schindler et al. 2005) and making this region a particularly valuable system to assess ecological responses to climate change.

Studies of Bristol Bay sockeye salmon *Oncorhynchus nerka* by the Fisheries Research Institute, University of Washington, were initiated in the mid-1940s and documented a high percentage of seaward-migrating sockeye salmon smolts bore cestode larvae encysted in their flesh (Burgner 1962). In 1952 this infestation was investigated more closely when it became apparent that the presence of the encysted larvae might be harmful to juvenile salmon. The parasite was identified as *Triaenophorus crassus* Forel, first described in Europe and commonly found encysted in the flesh of lake herring and whitefish *Coregonus* spp. of certain lakes in the prairie provinces of Canada and in the north central United States (Scheuring 1930; Miller 1952). Because sockeye salmon are the most abundant planktivore in the Wood River system, and because of their high commercial value, from 1948 through 1960, hundreds of emigrating sockeye smolts were evaluated for the parasite prior to leaving freshwater each year.

Over a half-century later, a time period during which there has been substantial climate change in this region, we had the unique opportunity to study how parasite abundance and prevalence has changed in a relatively pristine environment. Sockeye salmon are not only economically important to the region (Schindler et al. 2010) but also ecologically important

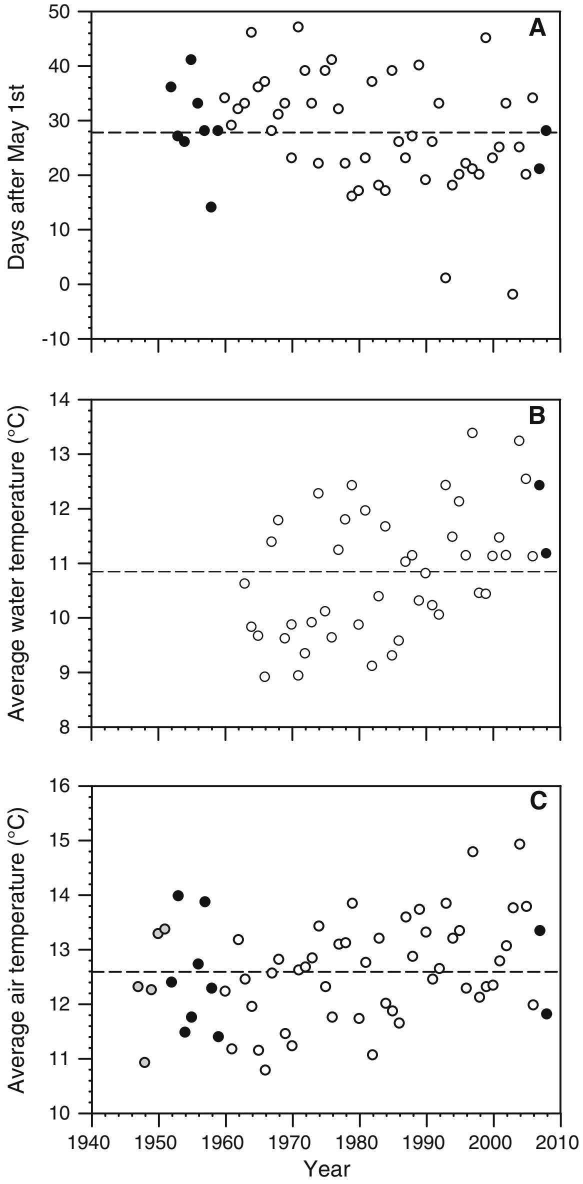

Fig. 1 **a** Spring ice-breakup date on Lake Aleknagik (southwest Alaska, USA) from 1952–2008. The breakup date is the first day enough ice has broken up that a boat can navigate the length of the lake. **b** Averaged July and August epilimnetic water (0–20 m) temperature (°C) of Lake Aleknagik from 1963–2008. **c** Averaged July and August air temperature (°C) taken at the King Salmon Airport from 1947–2008. Gray circles represent years with percent parasitized data, black circles represent years with infestation rates, and white circles are years with no parasite data. Dashed lines represent mean of data range

as they provide an annual pulsed subsidy of marine-derived nutrients to inland ecosystems, as adults return to their natal spawning grounds and die, which enhances the productivity of many plant and animal species (Naiman et al. 2002; Schindler et al. 2003). Because there is evidence that *T. crassus* can have deleterious effects on its second intermediate host (i.e., sockeye salmon; Rosen and Dick 1984; Pulkkinen et al. 1999) it is important to understand how accelerated rates of climate change might influence the interaction of sockeye salmon and *T. crassus* in the Bristol Bay region. To assess whether climate warming, which has affected the thermal environment of aquatic ecosystems in high latitude regions, is associated with the predicted change in parasite load we compared historical *T. crassus* infestation rate data collected during 1948–1960 with 2 years of samples from 2008 and 2009 from the Wood River system, Bristol Bay, Alaska.

Methods

Study system

The Wood River is a major tributary of the Nushagak River that flows into Bristol Bay in southwestern Alaska. The Wood River system consists of a chain of five large, deep, oligotrophic lakes that serve as a major nursery for sockeye salmon. Over the last 50 years, sockeye salmon escapement (run size after commercial fishing) to the Wood River system has averaged 1.1 million (Baker et al. 2006). Adult sockeye salmon return to the Wood River system and spawn between mid-July and mid-September. Embryos hatch in early spring and then proceed to emerge and migrate to their respective rearing lake during May and June where they feed in littoral regions prior to moving offshore into pelagic waters by mid-July (Rogers 1973). In the Wood River system, 90-95% of sockeye salmon spend one full growing season in freshwater prior to emigrating to salt water (referred to as one-check smolts; Crawford 2001).

Parasite

Cestodes, commonly referred to as tapeworms, have remarkable life-cycles that always involve two, and often three, hosts. Where present in Bristol Bay, *T. crassus* infects and uses copepod zooplankton as its first intermediate host. Infected copepods are then consumed by a planktivorous fish, most commonly juvenile sockeye salmon inhabiting freshwater lakes prior to smoltification, which feed primarily on zooplankton. Parasites bore their way from the fish's digestive tract into the musculature. After several months, *T. crassus* begins to form hooks on its scolex and become encysted in flesh by early fall where it can persist for the duration of the life of the host. To complete its life cycle, an infected fish must be consumed by the definitive host, native northern pike *Esox lucius*, where *T. crassus* uses its hooks to attach to the gut lining where it grows and matures prior to asexual reproduction the following spring (Miller 1952).

Data collection

Historic samples obtained for parasite evaluation were captured by fyke net during the course of the annual monitoring of seaward migrating sockeye salmon smolts at the Wood River system outlet located at Mosquito Point, Lake Aleknagik (59°16'26.37"N, 158°37'20.59"W). Random samples of 50–100 sockeye salmon smolts were collected weekly to biweekly throughout the 8–12 week migration time, which varied annually based on the timing of spring ice-breakup but typically occurred from late-May through early-August. From 1948–1952 smolts were dissected but only examined for parasite presence or absence. Beginning in 1953 smolts were dissected and individual parasites were enumerated.

In 2008 smolt migration monitoring at Mosquito Point was commenced with the same net and sampling design used in the historical time period. A total of 810 individuals were collected for parasite evaluation from 2008 and 2009 using a systematic sampling routine where every 2–6 days a random sample of all the fish caught, or 50 sockeye salmon smolts (whichever was smaller), was taken from the nightly catch. Individuals were weighed (g), measured (FL; mm), aged via scale annuli, and stored in 70% EtOH for later examination using a stereo microscope. Because 90-95% of the sockeye salmon juveniles collected in the Wood River system were age-1 fish, and because age-2 fish typically have 2-6X higher infestation rates compared to age-1 smolts, only age-1 smolts were used in this comparison between the historic and recent sampling periods. There have been no long-term changes in the proportion of age-1 and age-2 smolts in the system (Crawford 2001; McGlauflin 2010).

Data analyses

Because water temperatures were not consistently taken until 1963, we used the average summer (July and August) air temperature, which is significantly correlated with Lake Aleknagik average summer (July and August) water temperature using linear regression ($p<0.001$; $r^2=0.59$), taken from the King Salmon Airport, Alaska (58°41'N, 156°39'W), to evaluate the influence of temperature on the juvenile sockeye salmon and *T. crassus* interaction. Because age-1 fish acquired most of the detected parasites the year prior to emigrating we lagged the air temperature by 1 year in this comparison (e.g., 2009 parasitism rates compared with 2008 air temperature).

The parasite counts obtained for individually dissected fish were pooled by the year in which they were collected. Although parasite count data are often right-skewed and typically fail to meet the assumptions of normality and homoscedasticity of conventional statistics, by averaging the pooled data and evoking the Central Limit Theorem, the means from each of the years sampled will become approximately normally distributed. Using the pooled data, parasite prevalence (percentage of all fish per year with at least one parasite), abundance (average number of parasites per fish for all examined fish), and intensity (average number of parasites per infected fish) was calculated for each year. The sample means of the pooled data did not meet the assumption of normality required for simple linear regression, so a non-parametric Spearman's rank-correlation coefficient (r_s) was used to test the two null hypotheses that the relationship between (i) average summer temperature and parasite prevalence, abundance, and intensity in sockeye salmon juveniles, and (ii) time (year) and parasite prevalence, abundance, and intensity in sockeye salmon juveniles was less than or equal to zero ($\alpha=0.05$).

Results

Comparing the average summer air temperature to the parasite prevalence (i.e., percent examined with at least one parasite) of juvenile sockeye salmon, we found no significant relationship over the 15 years of collected data (Fig. 2a; $p=0.69$; $r_s=-0.136$). Evaluating the influence of average summer air temperature on the parasite infestation rates of juvenile sockeye salmon, we again found no significant relationship for either

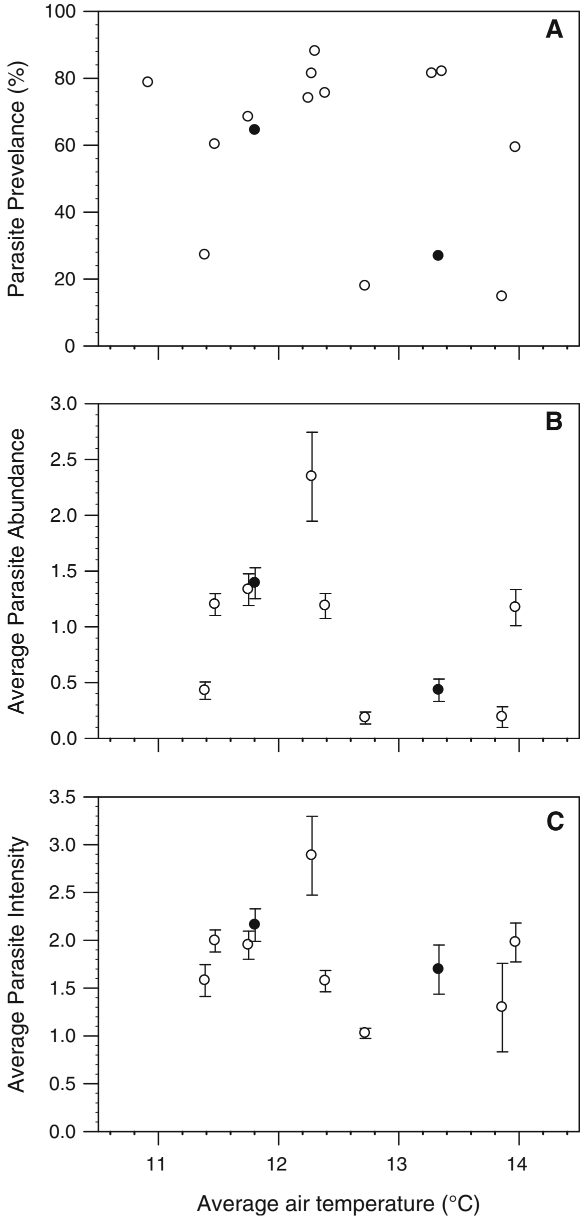

Fig. 2 Average summer air temperature (°C) versus the parasite (**a**) prevalence (percentage of juvenile sockeye salmon parasitized) (**b**) abundance (average number of parasites per host) ±95% confidence intervals and (**c**) intensity (the average number of parasites per infected host) ±95% confidence interval. Data from 2008 and 2009 are represented by the black circles

parasite abundance (Fig. 2b; p=0.87; r_s=−0.394) or parasite intensity (Fig. 2c; p=0.81; r_s=−0.309).

When we compared the 13 years of historic parasite prevalence to equivalent data collected in 2008 and 2009, we did not find a statistically significant positive long-term trend in the data (p= 0.99, r_s=−0.661). The magnitude of inter-annual variation in the percent of smolts parasitized, with the range of occurrence falling between 14.7% (1958) and 88.0% (1948), likely masked any longer term trend associated with warming (Table 1). The parasite abundance of examined sockeye salmon smolts also did not exhibit a statistically significant long-term trend using the 8 years of historic data and the 2 years of contemporary data (p=0.45, r_s= 0.042). Finally, evaluating the relationship between time and parasite intensity produced similar results as the other five comparisons with there not being a statistically significant positive relationship (p=0.29, r_s=0.200). Parasite abundances of juvenile sockeye salmon from 2008 (0.43 parasites/fish) and 2009 (1.39 parasites/fish) fell between the minimum rate observed in 1957 (0.18 parasites/fish) and maximum rate observed in 1959 (2.35 parasites/fish), with 2008 representing the fourth lowest rate and 2009 representing second highest rate in the 10 years of data (Table 1).

Discussion

Arctic and high latitude regions are good models for examining the effects of climate change on infectious diseases in wildlife because they are often relatively simple systems, free from confounding factors that complicate studies at lower latitudes (e.g., changing land-use, eutrophication, invasive species; Kutz et al. 2009b). In general, transmission rates of parasites and pathogens are expected to increase with increasing temperatures (Marcogliese 2008) as pathogen development and survival rates increase (Harvell et al. 2002), geographic range of parasites expand (Kutz et al. 2009b), and host susceptibility rises (Bruno et al. 2007). For example, Kutz et al. (2005) used an empirically based, predictive model to show that global warming in the Canadian Arctic has altered the transmission dynamics between an endemic parasitic nematode and its host the muskoxen, thereby escalating infection pressure on the muskoxen, and predicted this trend will continue. However, we did not detect a significantly altered relationship in parasite levels relative to temperature and time of sockeye salmon juveniles between historic (1948–1960) and contemporary (2008–2009) years, a time period characterized by substantial increases in growing season length and lake water temperatures.

Table 1 Year samples were collected, mean summer air temperature (°C), number of juvenile sockeye salmon examined (n), parasite prevalence (%), and the mean (x), standard deviation (SD), and 95% confidence intervals for parasite abundance and intensity

				Abundance			Intensity		
Year	Air temperature[a]	n	Prevalence	x	SD	95% CI	x	SD	95% CI
1948	12.3	100	88.0	-	-	- -	-	-	- -
1949	10.9	454	78.6	-	-	- -	-	-	- -
1950	12.3	294	74.0	-	-	- -	-	-	- -
1951	13.3	422	81.4	-	-	- -	-	-	- -
1952	13.4	449	81.9	-	-	- -	-	-	- -
1953	12.4	326	75.5	1.19	1.03	1.08 - 1.30	1.57	0.89	1.46 - 1.68
1954	14.0	302	59.3	1.17	1.44	1.01 - 1.34	1.98	1.38	1.77 - 2.18
1955	11.5	791	60.2	1.20	1.39	1.10 - 1.30	1.99	1.28	1.88 -2.11
1956	11.8	316	68.4	1.33	1.28	1.19 - 1.47	1.95	1.10	1.80 -2.10
1957	12.7	213	17.8	0.18	0.40	0.13 - 0.24	1.03	0.16	0.97 - 1.08
1958	13.9	184	14.7	0.19	0.64	0.10 - 0.28	1.30	1.17	0.83 - 1.76
1959	12.3	107	81.3	2.35	2.08	1.95 - 274	2.89	1.94	2.47 - 3.30
1960	11.4	472	27.1	0.43	0.86	0.35 - 0.51	1.58	0.95	1.41 - 1.74
2008	13.3	331	26.8	0.43	0.96	0.33 - 0.54	1.69	1.20	1.44 - 1.95
2009	11.8	479	64.4	1.39	1.69	1.25 - 153	2.16	1.67	1.99 - 2.33

[a] Air temperatures are lagged by 1 year (e.g., temperature listed for 1948 actually average from summer of 1947)

Although detection of subtle changes in this type of study is difficult due to low statistical power, as infection data tend to be non-parametric and sample sizes are typically small, since years are the appropriate unit of replication, our results are still important as this study spans a time period most other studies cannot and occurs at a spatial and temporal scale relevant to ecosystems and management. Because our data were not trending towards significance, or suggestive that there was in fact a biologically significant effect that could not be detected, suggests that our results were insignificant due to a lack of effect size, not due to limits of replication or variance in the data.

In our study system we expected *a priori* to see increases in prevalence, abundance, and intensity of the parasite *T. crassus* in sockeye salmon because of changes in consumption by salmon with warmer climates and more productive lakes. For poikilothermic animals metabolic demands increase as temperature increases thus increasing an individuals need to consume more calories (Brett 1971). Assuming that infestation rates in zooplankton have not declined, the caloric value of zooplankton has not changed per unit size, and the dietary composition of juvenile sockeye salmon has not changed, individual fish must increase the number of copepods (*T. crassus* first intermediate host) consumed to achieve equal levels of growth. Thus by increasing consumption they are more likely to consume an increased number of infected individuals thereby increasing their own infection rates. Likewise, since the PDO shift in 1977, age-0 sockeye salmon caught during annual tow net surveys on Lake Aleknagik are significantly larger than age-0 sockeyes prior to the shift given a specific density (Schindler et al. 2005). Thus, consumption rates of age-0 fish have not only increased sufficiently to match the metabolic demands of warmer water, but also provided greater surplus energy for growth. Therefore, we can conclude that given the observed increase in water temperature and growth rates of juvenile sockeye salmon, consumption rates have had to increase over this time period.

Given that increased consumption rates in juvenile sockeye salmon have not increased their infection rates, other factors must be influencing the interplay of *T. crassus* transmission into juvenile sockeye salmon. Over the past 42 years zooplankton densities have increased in Lake Aleknagik (Schindler et al. 2005), with non-significant but an increasing trend in *Bosmina*, *Daphnia*, *Cyclopoida*, and *Holopedium* (Carter 2010). However, only one out of the two identified species of cyclopoid *Cyclops columbianus* has been documented as the first intermediate host for *T. crassus* in the Wood River Lakes. Long-term historical records from the Wood River system have only identified groups of copepods to family and therefore we cannot make any concrete inferences regarding the population dynamics of the zooplankton host for this parasite. Warmer lake temperatures can influence community compositions at a local scale (Carter 2010) which could ultimately decrease the infestation rates of host species (Møller 2009). But even if *C. columbianus* densities increase with warmer temperatures, and the exposure rates of infected copepods increase as well, it is quite possible that infection levels in sockeye salmon could remain constant or even decrease. For instance, as water temperature increases the internal handling time of food for fish decreases (Elliott and Persson 1978) thereby potentially decreasing the time available for a parasite to infect its host.

While there are an endless number of hypotheses that can be conceived to explain our observed results, we were unable to detect a biologically significant change in juvenile sockeye salmon infestation rates of *T. crassus* in the Wood River system over the last 60 years despite a 1.9°C increase in lake water temperature. All things being equal, this increase in temperature and increases in juvenile growth rates should have increased the infestation rates from the food-borne parasite. In controlled experiments, researchers have demonstrated that increased temperature can promote increased parasite infection rates (Poulin and Mouritsen 2006). Our data demonstrate the necessity of validating this reductionist approach with observational studies at the spatial and temporal scales relevant to ecosystems and management. With projections of future climatic conditions in southwest Alaska predicting a continuation of warming trends for the next century (Christensen et al. 2007), it is possible that these ecosystems still might reach thermal thresholds needed to produce positive parasite infestation responses that have yet to occur. However, our data demonstrate that the complex effects of warming have not summed to generate a measurable change in the infestation rates of juvenile sockeye salmon in the Wood River system.

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