

Predicting harvest of non-native signal crayfish in lakes — a role for changing climate?

Patrik Bohman, Lennart Edsman, Alfred Sandström, Per Nyström, Marika Stenberg, Pia Hertonsson, and Jacob Johansson

Abstract: The signal crayfish (*Pacifastacus leniusculus*) was introduced to Sweden in 1960, and it has a high commercial and recreational value, but it may also have negative effects on native ecosystems. To better predict how climate warming will affect population dynamics of this cool-water crayfish, we explored the role of temperature and density dependence as explanatory factors of the subsequent years' catch rates of commercially sized signal crayfish in four Swedish lakes. We found air temperatures to be good proxies for water temperatures in all lakes, except during winter. We could only obtain water temperature data for Lake Vättern, and winter temperature data were therefore only included in the analysis of catch-per-unit-effort patterns in this lake. Our results indicate that increasing mean air temperatures will potentially affect the population dynamics of cool-water freshwater crayfish species such as the signal crayfish. Based on data from four lakes, it seems that the population dynamics of signal crayfish are lake-specific and could be affected by either recruitment during the juvenile stage, the survival and growth of adults, or both. Increased fluctuations in water temperature during winter may potentially influence adult survival. To better predict the effects of global warming on the dynamics of cool-water crayfish populations, we suggest that future studies should investigate recruitment in crayfish along temperature gradients and the influence of variations in water temperature on winter mortality.

Résumé : L'écrevisse signal (*Pacifastacus leniusculus*) a été introduite en Suède en 1960 et, si elle présente une valeur commerciale et sportive élevée, elle pourrait également avoir des effets négatifs sur les écosystèmes indigènes. Afin de mieux prédire l'incidence des changements climatiques sur la dynamique des populations de cette écrevisse d'eau froide, nous avons examiné le rôle de la dépendance sur la température et la densité comme facteurs explicatifs des taux de prises d'écrevisses signal de taille économique durant les années subséquentes dans quatre lacs suédois. Nous avons constaté que la température de l'air est une bonne variable substitutive pour la température de l'eau dans tous les lacs, sauf en hiver. Comme nous n'avons pu obtenir des données sur la température de l'eau que pour le lac Vättern, ce lac est le seul pour lequel l'analyse des motifs de les captures par unité d'effort incluait des données sur les températures hivernales. Nos résultats indiquent que l'augmentation des températures de l'air aura potentiellement une incidence sur la dynamique des populations d'espèces d'écrevisses d'eau froide comme l'écrevisse signal. À la lumière de données sur quatre lacs, il semble que la dynamique des populations d'écrevisses signal soit propre au lac et pourrait être influencée par le recrutement durant le stade juvénile, la survie et la croissance des adultes, ou les deux. Des fluctuations accrues des températures de l'eau durant l'hiver pourraient influencer la survie des adultes. Pour mieux prédire les effets du réchauffement planétaire sur la dynamique des populations d'écrevisses d'eau froide, nous proposons que des études futures se penchent sur le recrutement chez les écrevisses le long de gradients de température et sur l'influence des variations de la température de l'eau sur la mortalité hivernale. [Traduit par la Rédaction]

Introduction

Understanding fluctuations in population size is fundamental in ecology. In applied ecology, population fluctuation typically holds for species that are of high commercial value or that pose a threat to native biodiversity, such as non-native species. Identifying the mechanisms causing these fluctuations requires long-term data, which are typically very rare for non-native species (Strayer et al. 2006). Furthermore, in many instances non-native populations show an initial rapid increase followed by either a stable or more oscillating phase (Crooks 2005). These population patterns and the lack of long-term data challenge our abilities to understand the population dynamics of non-native species (e.g., Dörr and Scalici 2013; Sandström et al. 2014a).

Non-native freshwater crayfish species have received much attention in fisheries and community ecology and conservation biology.

Fishing of non-native crayfish species can be of great economical and recreational value (Holdich 1993; Ackefors 1999), but these species simultaneously have negative impacts on native fauna and flora worldwide (e.g., Nyström 1999; Lodge et al. 2000; Bohman et al. 2006; Holdich et al. 2009). To be able to successfully manage non-native crayfish populations both at present but also in the future, we urgently need to identify the factors affecting their population growth rates in different aquatic habitats and during different climatic scenarios.

In this study, we use time series analyses (16–37 years) to explore long-term catch data of non-native North American signal crayfish (*Pacifastacus leniusculus*) in four Swedish lakes with different abiotic and biotic characteristics. We fitted the best model by combining density dependence and seasonal variations in temperature during previous years to predict subsequent years' catches of

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P. Bohman, L. Edsman, and A. Sandström. Swedish university of Agricultural Sciences, Department of Aquatic Resources, Institute of Freshwater Research, Stångholmsvägen 2, SE-17893 Drottningholm, Sweden.

P. Nyström, M. Stenberg, and P. Hertonsson. Ekoll AB, Majgatan 17b, 215 65, Malmö, Sweden.

J. Johansson. Theoretical Population Ecology and Evolution Group, Department of Biology, Lund University, SE-22362 Lund, Sweden.

Corresponding author: Patrik Bohman (email: patrik.bohman@slu.se).

Table 1. Selected physicochemical and biological characteristics of the study lakes.

	Year	Area (km ²)	Mean depth (m)	MSL (m)	Alkalinity (mequiv·L ⁻¹)	Total P (µg·L ⁻¹)	Color (mg Pt·L ⁻¹)	No. of fish species
L. Erken	1966	24	9.1	11	1.70	34	32	8
L. Hövern	1970	6	6.2	65	0.67	31	63	8
L. Vittsjön	1991	2	2.9	100	0.16	27	345	10
L. Vättern	1969	1835	35.0	89	0.52	7	7	26

Note: Data were compiled from different Swedish databases and monitoring surveys and with respect to water chemistry presented as mean values from various measurements conducted in 2000–2008. Data on stocking year of signal crayfish and height above mean sea level (MSL) is also given.

commercially sized crayfish in these lakes. The potential mechanisms causing population fluctuations in non-native crayfish species is not yet fully understood. There are some studies, however, where the dynamics have been studied in more detail that suggests that temperature variation as well as predation rates could have important roles (e.g. Hein et al. 2006; Olsson et al. 2010; Hansen et al. 2013).

The signal crayfish is currently the most widely spread non-native crayfish in Europe. The species is found in 27 countries, but it has also been introduced to Japan and outside its native range in the USA (summarized in Capinha et al. 2013). It is a long-lived species (up to 18 years old) that in lakes typically reaches its commercially harvestable size (≥10 cm total length (TL) in Sweden) 5–8 years after hatching, depending on population density, temperature, food supply, and sex (summarized in Lewis 2002). It was first introduced to Sweden in 1960, where it has negative effects on the native noble crayfish (*Astacus astacus*), mainly by transferring the oomycete causing crayfish plague (*Aphanomyces astaci*; Bohman et al. 2006), but also on other flora and fauna through predation and competition (summarized in Nyström 1999; Ruokonen et al. 2014). Today the signal crayfish can be found in at least 4000 localities in Sweden, and the commercial catch of this species has been estimated to be worth more than US\$40 million yearly (Bohman and Edsman 2011). It has, however, recently been shown that some populations of signal crayfish in Sweden and Finland have collapsed, and the value of the fisheries has dropped substantially in those lakes (Sandström et al. 2014a; Jussila et al. 2014). Time series analysis of a vital signal crayfish population in Lake Bunn, Sweden, suggests that air temperatures and density in previous years explain population fluctuations (Olsson et al. 2010). Temperature may affect cool-water crayfish species in many ways and during their entire life cycle (summarized in Lodge and Hill 1994). At some stages, high temperatures may promote individual growth rates and reproductive success in species such as the signal crayfish, but in other situations variations in temperature may potentially cause stress and susceptibility to crayfish plague and other diseases (Söderhäll and Cerenius 1999; Aydin et al. 2014; Edsman et al. 2015). In addition to this, even though high temperatures may promote individual growth rates and rapid embryonic development, increasing temperatures may also substantially increase mortality rate during moulting in freshwater crayfish (Brewis and Bowler 1983). In an era of global warming and a changing climate, more long-term studies are needed before it is possible to predict how further climate change will affect the population dynamics of cool-water crayfish species. To achieve this goal, it is crucial to correctly specify the most important temperature bottlenecks affecting different life stages of crayfish and to include these in a predictive analysis.

The overall aim of this study was to further explore the complex role of temperature and population densities as explanatory factors of the subsequent years' catch rates of commercially sized signal crayfish (≥10 cm TL) in four Swedish lakes. Based on the previous work on cool-water crayfish biology cited above, we identified the temperature bottleneck periods and formulated the following assumptions: (i) direct negative density dependence is important in crayfish populations, (ii) high yearly temperature but low amplitudes in temperature during winter in a given year has positive effects on recruitment to commercially sized crayfish, with time lags of

5–8 years, and (iii) high yearly temperature but low amplitudes in temperature during winter has positive effects on growth and survival of harvestable sized crayfish (≥7–9.9 cm TL), having positive effects on subsequent years' catches of commercially sized crayfish (time lags of 0–2 years).

Materials and methods

Study lakes

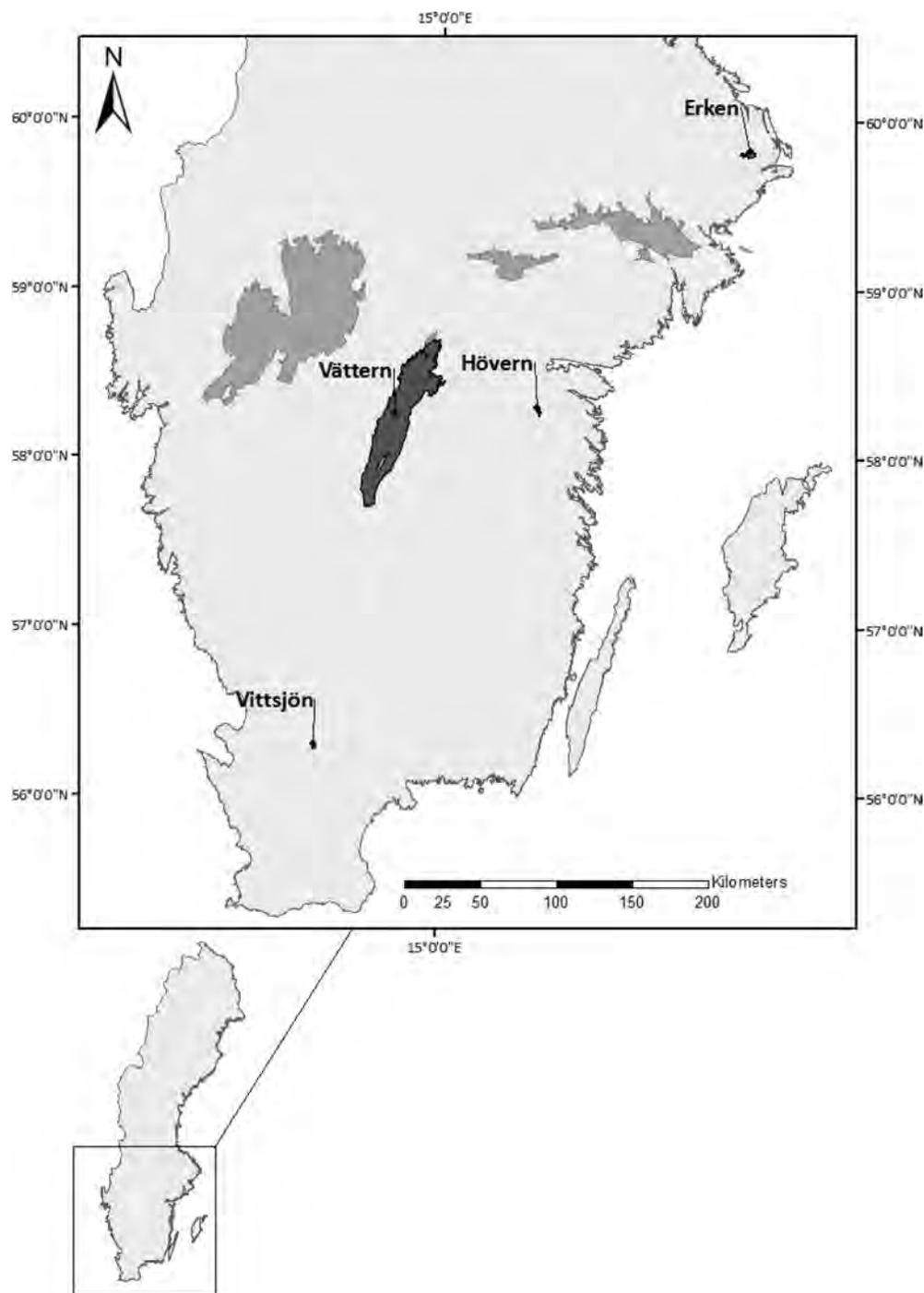
Time series data on catch statistics of signal crayfish in Sweden can be found in a database administered by Swedish University of Agricultural Sciences. From this database we selected four lakes encompassing a south–north gradient of signal crayfish occurrence in Swedish lakes (Fig. 1). All lakes had reliable data on crayfish fisheries (consecutive years with data on catch, efforts, and landings) and a catch time series of at least 16 years. The lakes varied in several physicochemical and biological characteristics (Table 1), as well as in fisheries management regulations and fishing pressure. Lake Vättern is the second largest lake in Sweden with a commercial fishery of signal crayfish. This lake is ultra-oligotrophic with a maximum depth of 120 m. In the other range of the spectrum we included the comparatively small Lake Vittsjön, with brown water and a maximum depth of 9 m.

Catch and temperature data

All four lakes had harvested populations of signal crayfish. The catch statistics from the lakes were based on reports of catch per unit of effort (CPUE) of commercially sized signal crayfish in baited traps (e.g., Edsman and Söderbäck 1999). In three of the lakes (L. Hövern, L. Erken, L. Vittsjön) CPUE was given in numbers, and in L. Vättern it was given in biomass (kg). According to subsamples from the commercial catch in L. Vättern (years 2009–2014; $n = 11\,000$ individuals), 1 kg of crayfish corresponds to 21.6 individuals. In all four lakes the lower size limit for commercially sized crayfish is 10 cm TL.

Lake Erken has a limnological research station, which has contributed to make it one of Sweden's most extensively studied freshwater environments. Both noncommercial and commercial fishing for signal crayfish occur in L. Erken. Our data are derived from the main commercial fishing company (Naturvatten i Roslagen AB), and we used fishing data from a specific site in mid-August – early September. In the much smaller Lake Hövern, we used CPUE data from the main fishing rights owner. Fishing is conducted at the same sites during a short period of time (early August – early September). CPUE has been more or less stable in recent years, and the catch is on average 1.5 t per year. The fishing for signal crayfish in L. Vittsjön is not conducted by professional fishermen, but the entire shore of the lake is fished at least twice a year during August. During this event, all trapped crayfish ≥10 cm TL are removed for human consumption. In the years 2000–2013, the median numbers of crayfish removed yearly was about 6800 individuals. In L. Vättern (Sweden's second largest lake), a major commercial fishery on signal crayfish has developed with annual catches increasing from about 20 t in the year 2000 to more than 140 t in 2008. We have used CPUE data from commercial fisheries in L. Vättern. All fishermen are obliged to report their catches and efforts. We only used data from July to August,

Fig. 1. Map of Sweden with the location and names of the four study lakes. The four largest lakes in Sweden are also shown in the map (Lake Vänern, Lake Vättern, Lake Mälaren, and Lake Hjälmaren).

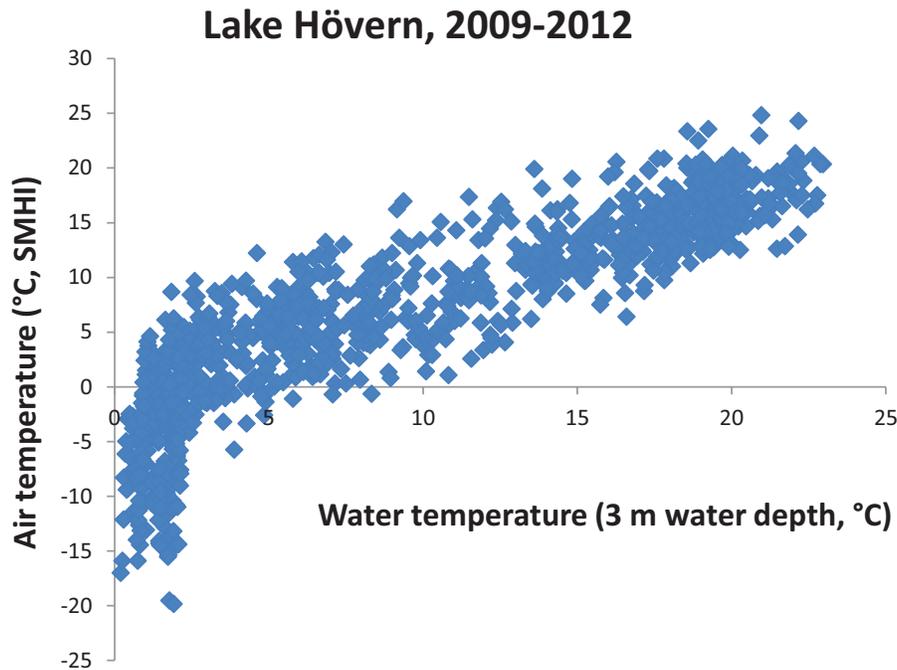


which is the most intense fishing period. This dataset includes fishing on private as well as common waters. After 2008, the total catch (of crayfish >10 cm) has dropped at several sites in the northern parts, probably due to high fishing pressure (P. Bohman, L. Edsman, A. Sandström, P. Nyström, M. Stenberg, P. Hertonsso, and J. Johansson, unpublished data). In other parts of the lake, CPUE is more stable.

Previous studies involving signal crayfish and population fluctuations have successfully used air temperature from local weather stations as a proxy for water temperature in the lakes (Olsson et al. 2010). Since we wanted to link water temperature in the lakes to population fluctuations, we collected additional measurements on

water temperature in some of the lakes in 2009–2013 to further explore the strengths of relationship between water temperature and air temperature. In L. Erken, we used water temperature data from a permanent weather station. In L. Hövern and L. Vittsjön, we used TidbiT v2 Water Temperature Data Loggers (UTBI-001) to register water temperature with a 4 h interval. In these lakes, we used one logger for each lake (from a depth of ~3.0 m where crayfish are caught). The data logger software HOBOWare Pro was used to manage the logged temperature data from these lakes. In L. Vättern, water temperature data were obtained from Motala waterworks (where water temperature is registered on different depths

Fig. 2. Correspondence between mean daily air temperature and mean daily water temperature (at 3 m water depth) in Lake Hövern, 2009–2011. Air temperatures were provided by the Swedish Meteorological and Hydrological Institute and water temperatures from our own temperature logger in the lake.



several times each day). In L. Hövern, for example, there was a good correspondence between mean daily air temperature and mean daily water temperatures in 2009–2012, except during the winter period (Fig. 2). A closer examination of the data showed that the mean daily water temperature (9.5 °C) is slightly higher than the mean daily air temperature (6.5 °C) in 2009–2012. This is mainly because the water temperature does not drop as much during the winter months in comparison with the air temperature. Furthermore, variations in the duration of the ice cover period will substantially influence the water temperature in lakes, and we therefore only included winter water temperatures in our analysis for L. Vättern (from a water depth of 5 m). This was the only lake for which we had water temperature data for the whole time series of crayfish catches. However, the small discrepancy between air and water temperatures during the rest of the year in the other three lakes should not cause confounded effects in our analyses of signal crayfish population dynamics. This is because we included temperature periods with warmer temperature (i.e., the majority of the growing season and the season for egg development). We therefore used the data for L. Vättern to test if the amplitudes in water temperature during winter (called “Winter Stress”; see Identifying temperature bottlenecks below) could explain crayfish population dynamics.

Identifying temperature bottlenecks

Water temperature plays a crucial role by affecting the entire life cycle and growth of freshwater crayfish. In their study of signal crayfish population dynamics in the Swedish Lake Bunn, Olsson et al. (2010) transformed air temperature data into more ecologically relevant parameters. To predict the subsequent years’ catches of commercially sized signal crayfish, we used a similar yet modified approach. Firstly, we used only air temperature data as a proxy for water temperatures outside the winter season (three lakes), and we included water temperatures from the entire year in one lake (L. Vättern). Secondly, we specifically analyzed the effects of temperature on (A) recruitment of juveniles to harvestable sized crayfish (time lags of 5–8 years were expected, but we extended the analysis to the range of 2–9 years) and (B) growth and survival of

trappable but not yet commercially harvestable adult crayfish (i.e., $\geq 7\text{--}9.9$ cm TL, time lags of 0–2 years). We identified three potential temperature bottlenecks. The first bottleneck was named “Winter Stress” (WS). This included the variation in water temperature in L. Vättern during winter (standard deviation; November–March), and high variation was expected to negatively affect adult crayfish (WSa) survival but also the ability of egg bearing females (WSe) to keep their eggs vital and free from fungus and oomycetes. Our longtime experience in signal crayfish culture is that stress in winter often induces a high mortality, sometimes because of outbreaks of diseases such as crayfish plague. There are few literature studies on this topic; however, Taugbøl and Skurdal (1992) and Brewis and Bowler (1983) mention this phenomena. WS could only be evaluated for L. Vättern, since this was the only lake with long time series with water temperature measurements. Temperature variation in the winter is potentially high in L. Vättern, since it is only occasionally covered by ice (11.8 days per year during our study period; Sandström et al. 2014b).

For all four study lakes, we assumed that embryonic development of crustaceans is influenced by temperature (Styf et al. 2013). At low spring temperature the egg development and hatching of young-of-the-year crayfish will be delayed and juvenile survival may be low that year. We named this bottleneck “Egg Development” (ED), and it included the sum of the daily mean air temperature between April and June. Mass-specific respiration and consumption rate in signal crayfish is highly temperature-dependent (Karjalainen et al. 2015). The number of days with at least 8 °C (April–October) was the third bottleneck, since that is the growth season for all crayfish in a lake. We named this period “Growth” (G). For clarification, ED was only included when testing scenario A recruitment of juveniles.

Model selection

Our starting point was the modified Ricker model applied by Olsson et al. (2010) to explain observed fluctuations in catches of harvestable sized (≥ 10 cm TL) signal crayfish and noble crayfish (*Astacus astacus*) in L. Bunn. In our case, we applied the modified temperature bottleneck periods defined above for scenario A juveniles:

Table 2. Calculated values from the best models ($\Delta AIC_c < 2$) for the four different study lakes.

Lake	<i>n</i>	AIC_c	ΔAIC_c	CPUE (mean)	CI	Scenario	Growth rate <i>a</i>	Density dependence <i>b</i>	Egg Develop. <i>d</i>	Growth <i>e</i>	Winter Stress <i>c</i>	Time lag <i>k</i>
L. Erken	29	-10.13		3.477	1.559	B	0.082	-0.161	—	0.117	NA	1
	29	-9.906	0.224	3.477	1.565	B	0.081	-0.162	—	-0.108	NA	3
	29	-8.757	1.373	3.477	1.598	A	0.112	-0.222	0.103	—	NA	6
L. Hövern	37	-35.958		2.408	1.154	A	0.139	-0.362	—	0.101	NA	7
	37	-35.022	0.940	2.408	1.146	A	0.133	-0.371	-0.057	0.135	NA	7
L. Vittsjön	16	18.839		8.808	3.190	B	0.242	-0.318	-0.231	—	NA	2
L. Vättern	18	-106.451		0.147*	0.076	B	0.055	-0.103	—	—	-0.223	2
	18	-106.436	0.015	0.147*	0.072	B	0.036	-0.097	—	-0.104	-0.204	2

Note: NA, not available; —, not included in model. Included are length of time series (*n*), corrected Akaike information criterion (AIC_c), ΔAIC_c , mean catch per unit effort (CPUE) of signal crayfish, confidence interval (CI), modelled scenarios affecting juveniles (A) or adults (B), values for the included variables (*a–e*), and time lag (*k*). ΔAIC_c values are given for the second-, third-, and fourth-best models (if applicable). Models with $\Delta AIC_c < 2$ were considered as equally good as the best model for L. Erken, L. Hövern, L. Vittsjön, and L. Vättern. Note that “Winter Stress” only was tested in the model of L. Vättern (where data was based on water temperature data, in contrast with the other lakes where air temperature data were used). CPUE is given in numbers, but for L. Vättern (*), it is given in kilograms.

$$N_{t+1} = N_t \times e^{(a+bxN_t+cxWSe_{t-k}+dxED_{t-k}+exG_{t-k})}$$

where N_t is the catch per unit of effort in the year *t*, *a* is the intrinsic growth rate, *b* is the density dependence, *c* is the influence of winter stress on egg-bearing females (WSe) at lag *k* ($k = 2–9$; note in this case only tested for L. Vättern), *d* is the influence of egg development (ED) at lag *k* ($k = 2–9$), and *e* is the influence of growth (G) at lag *k* ($k = 2–9$). Furthermore, since experimental studies have shown that density of adult signal crayfish does not negatively affect survival and recruitment of juvenile signal crayfish (Olsson and Nyström 2009), we did not find any reason at this stage to test different combinations of time lags of density dependence besides the bottleneck periods defined above.

For scenario B adults, the temperature variable ED was excluded. The resulting model was as follows:

$$N_{t+1} = N_t \times e^{(a+bxN_t+cxWSa_{t+j}+exG_{t-k})}$$

with the same definitions as above except that here *c* is the influence of winter stress on adult crayfish (WSa) at lag *j* ($j = 0–1$; note in this case it is only tested for L. Vättern), and *e* is the influence of growth (G) at lag *k* ($k = 0–1$).

We used the Akaike information criterion corrected for small sample size (AIC_c ; Burnham and Anderson 1998) to select the best model and determine which temperature bottleneck periods should be included in the model. A forward selection procedure was used starting with the growth rate parameter *a* and the density dependence parameter *b* and successively adding the other variables one at a time in all possible combinations. The procedure was repeated for the different years ($k = 2–9$) to find the model with the lowest AIC_c . We also provide ΔAIC_c to interpret and compare model results. Models where $\Delta AIC_c < 2.0$ can be considered as almost equally important. All covariates were standardized (normalized value characterized by the mean and standard deviation) to be able to be directly compared. All calculations were conducted using Solver in Microsoft Excel for Windows.

Results

We found a strong direct negative influence of density dependence on subsequent years' catches of harvestable sized signal crayfish in all four lakes (Table 2; Fig. 3). We also found a positive influence of intrinsic growth rate on catches in all four lakes. Our models tested the influence of three different temperature bottleneck periods. We could not find any consistent and general pattern with respect to these temperature bottleneck periods that could explain the population dynamics in the four lakes. For L. Erken, for example, the two best models applied temperature periods potentially affecting the survival and growth of adult crayfish (scenario B; $k = 1$ and 3), whereas the third-best model applied to

periods potentially affecting the survival and growth of juvenile crayfish (scenario A; $k = 6$). In L. Vittsjön, the best model included temperature potentially co-occurring with the period for egg development (scenario B; $k = 2$). The variation in water temperature during winter (WS) was only tested in L. Vättern where it appeared to be a significant factor contributing to the performance of the best models (scenario B; $k = 2$; Table 2). The only lake where the best model contained a longer time lag was L. Hövern (scenario A; $k = 7$).

Lake Erken

The best model for L. Erken had a time lag of 2 years ($t - 1$) and included density dependence, intrinsic growth rate, and the temperature variable G. The number of days with temperatures above 8 °C between April and October had a positive influence on CPUE (0.117) of trappable but not yet commercially harvestable adult crayfish (scenario B; $t - 1$; Table 2). For L. Erken, the second-best model included the same variables as the first one but with a time lag of 4 years (scenario B; $t - 3$; Table 2) and a negative (-0.108) instead of positive influence on CPUE. The third-best model had a time lag of 7 years (scenario A; $t - 6$; Table 2) and a positive effect (0.103) of temperatures during ED on CPUE.

Lake Hövern

The best model for L. Hövern included density dependence, intrinsic growth rate, and the temperature variable G with a time lag of 8 years ($t - 7$; Table 2). There was a positive influence (0.101) on CPUE from an increasing number of days with temperatures above 8 °C (April–October; scenario A; $t - 7$; Table 2). The second-best model for L. Hövern, with a time lag of 8 years, showed a positive effect (0.135) of the variable G, with ED (the sum of the daily mean air temperature between April and June) having a negative influence (-0.057) on CPUE (Table 2). This model also included density dependence and intrinsic growth rate.

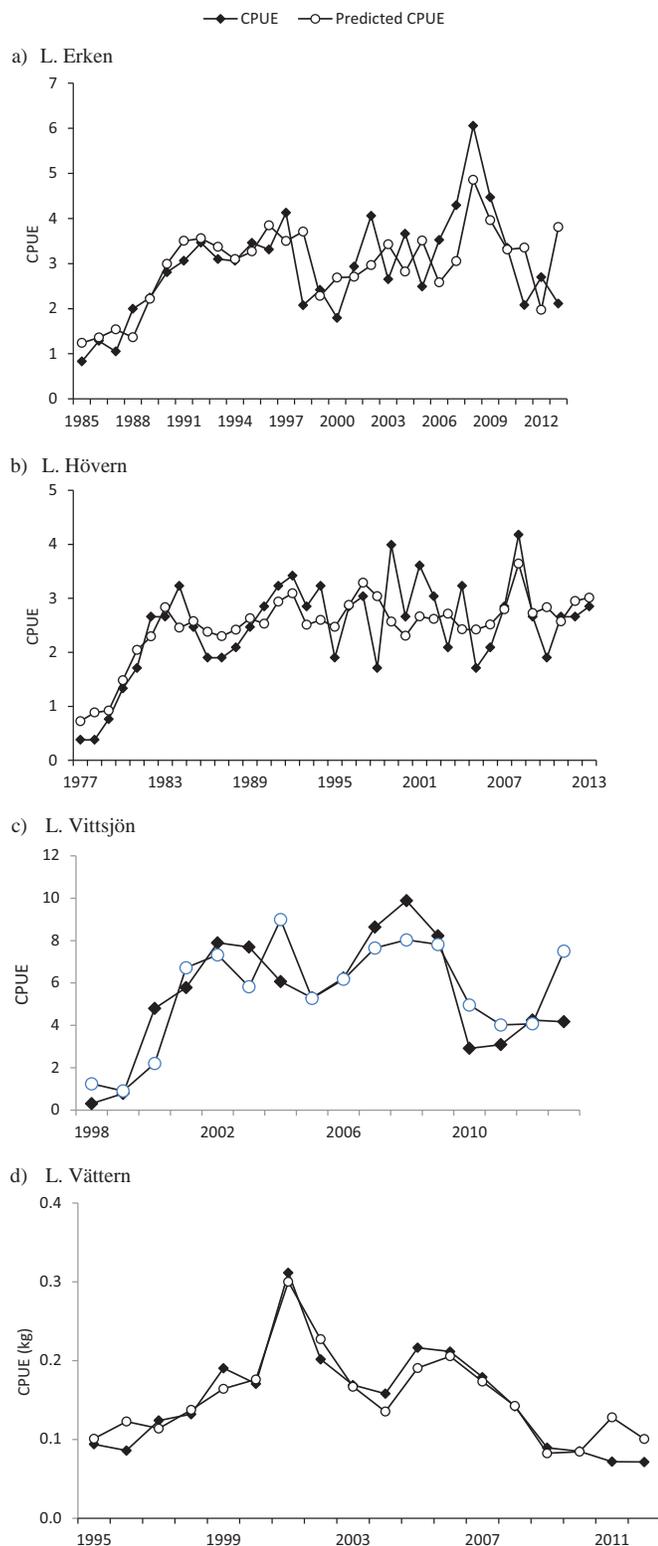
Lake Vittsjön

The best model for L. Vittsjön had a time lag of 3 years ($t - 2$) and included density dependence, intrinsic growth rate, and the temperature variable ED. There was a negative influence (-0.231) of the sum of the mean daily temperatures during ED between April and June on CPUE (scenario A; $t - 2$; Table 2).

Lake Vättern

Lake Vättern was the only lake with data on water temperatures and where we tested all three temperature bottleneck scenarios, including WS. The best model for L. Vättern had a time lag of 3 years ($t - 2$) and included density dependence, intrinsic growth rate, and the temperature variable WS (variation in winter temperature, standard deviation; November–March). There was a negative influence (-0.223) on CPUE from an increasing variation in winter temperatures (scenario B; $t - 2$; Table 2). The second-best

Fig. 3. (a–d) Observed and predicted (best-fitted model) of catches per unit effort (CPUE) of harvestable sized (≥ 10 cm TL) signal crayfish for four Swedish lakes: (a) Lake Erken, (b) Lake Hövern, (c) Lake Vittsjön, and (d) Lake Vättern. Note that in L. Vättern CPUE is measured in kilograms (numbers were not available for this fishery), and the model is based on predictions from water temperature data and CPUE.



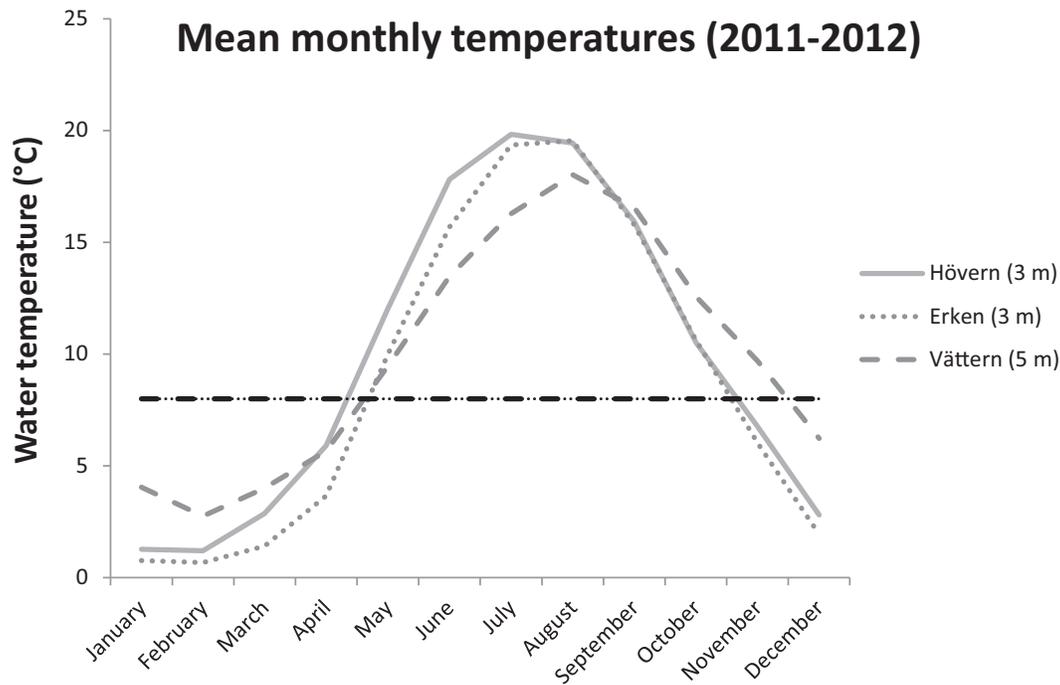
model in addition to negative influence of WS (-0.204) also included an influence of the variable G. There was a negative influence (-0.104) of an increasing number of days with at least $8\text{ }^{\circ}\text{C}$ (April–October; scenario B; $t = 2$; Table 2).

Discussion

Our time series analyses indicate that climate factors (ambient air and water temperatures) can be used to predict the subsequent years' catches of harvestable (by size) signal crayfish in four different Swedish lakes. In accordance with previous studies on freshwater crayfish, the results also show that a large catch in one year has a negative influence on the catch in the following year (i.e., negative density dependence; Olsson et al. 2010; Zimmerman and Palo 2012). We included three different bottleneck periods in our analyses, and the relative importance of these periods seemed to vary among lakes, but also within the same lake. Nevertheless, the best models indicated that two different scenarios could be important. Either scenario A, temperature conditions for juveniles (L. Hövern) and egg development (L. Vittsjön) were important, or scenario B, temperature effect on growth and survival of the adult stages was important (L. Erken and L. Vättern). Even though the direction of the influence of the different temperature bottlenecks (G, ED, or WS) on CPUE varied among lakes, we found that for the only lake where we had data on water temperature (L. Vättern), the best models both included negative effects of WS on CPUE. A high variation in water temperature during winter had negative effects on CPUE with a time lag of 3 years. Thus, overall our results indicate that mortality associated both with the growth period and the winter period can be important when explaining the dynamics of naturally occurring freshwater crayfish populations. Similar conclusions were made by Brewis and Bowler (1983). They found that both overwinter mortality and moult-associated mortality affected population survival in the cool-water crayfish *Austropotamobius pallipes*.

In accordance with our results, previous work suggests that understanding population dynamics of harvested crayfish populations can be complicated because of counteracting factors and time lags (Sadykova et al. 2009; Olsson et al. 2010; Zimmerman and Palo 2012). Many freshwater crayfish species are long-lived with slow growth rates and have a low reproductive output (Holdich 1993). Responses to perturbations may therefore take time (Momot 1991). For example, harvest may reduce the number of large crayfish in a population, leading to positive density-dependent effects on growth rate and survival of smaller-sized crayfish (Moorhouse and Macdonald 2011). We found significant negative effects of density dependence in all four studied lakes, but the influence of harvest was hard to interpret. We did not find any specific patterns related to fishing pressure, since the magnitude of the effect of density dependence did not appear to be related to fishing pressure. In parallel, it has been argued that changes in growth and fecundity in response to exploitation are limited for slow-growing cool-water crayfish species (Momot 1991). In some models there was a positive effect on catch from higher summer temperatures in previous years, potentially caused by faster individual growth rates. Increased temperature has been shown to significantly increase individual growth rates, the proportion of sexually mature females, and recruitment of freshwater crayfish (Scalici et al. 2008; Sadykova et al. 2009; Skurdal et al. 2011). In some of the lake models we had negative influence of increased temperatures on CPUE (e.g., the second-best models of L. Erken and L. Vättern; Table 2). Elevated temperatures may also cause physiological stress and reduced resistance to disease (Söderhäll and Cerenius 1999; Shields 2012), as well as increased mortality associated with growth and moulting (Brewis and Bowler 1983). We found that temperatures during the years when juveniles hatch and grow could potentially be important in two–three of our four study lakes. At low temperatures the development and subsequent survival of young-of-the-year crayfish is expected to be impaired (Abrahamsson and Goldman 1970; Abrahamsson 1973).

Fig. 4. Two years of mean monthly water temperatures from three out of our four study lakes. The horizontal dashed line indicates lower temperature limit for egg development and growth of signal crayfish. Temperature was measured on a daily basis at water depths where commercially sized crayfish are caught in the lakes.



Abrahamsson and Goldman (1970) found that the eggs of signal crayfish in Lake Tahoe (in North America) could not develop at all when the water temperature was below 7 °C. Thus, if lake temperature increases during our identified bottlenecks of ED and G, we would expect climate change to have positive effects on recruitment of the signal crayfish in lakes with colder temperatures. In the case of L. Erken, this was the scenario supported by the best model. However, it should also be stressed that the scenarios with elevated temperatures may have negative effects (see below and the second-best model in L. Erken; Table 2). Lake Vättern resembles the large, deep, and ultra-oligotrophic L. Tahoe. In L. Vättern we found water temperature time lags of up to 3 years to be important when predicting subsequent years' catches of signal crayfish. Here, WS and the number of days with temperatures above 8 °C when crayfish grow (April–October) were important. The best catches of signal crayfish in L. Vättern are typically from water depths between 8 and 15 m. In L. Vättern, L. Erken, and L. Hövern, the monthly water temperatures (at 3 m depths for the smaller lakes) is often much below 7–8 °C (Fig. 4). It is possible that increases in temperature during egg development and growth period may potentially negatively affect recruitment of signal crayfish in some lakes.

Some of the collapsing signal crayfish populations in Sweden have been linked to lower altitudes and warmer mean yearly temperatures than the more stable populations in other lakes (Sandström et al. 2014a). With a time lag of 3 years, our analyses indicate that a greater magnitude of temperature fluctuations during winter (WS) could help explain the subsequent years' catches of commercially sized signal crayfish. This pattern could be a result of increased stress and mortality of adult, but not yet harvestable sized, crayfish. Most populations of signal crayfish in Sweden (including the ones studied here) have been shown to be carriers of crayfish plague, potentially affecting the growth, overall performance, and survival of different life stages in changing environments (discussed in Sandström et al. 2014a). We speculate that crayfish plague could be an important component and a complicating factor affecting North American spe-

cies of crayfish, species that are otherwise rather tolerant to this disease, a situation that may shift with changing climate.

Some recent studies point in the direction that temperature and global warming may have important effects on crayfish distribution. In areas with high introduction efforts (e.g., Sweden), the climate suitability is the most important factor behind invasion success of signal crayfish (Capinha et al. 2013).

Our results indicate that the positive influence from summer temperature (number of days with temperature above 8 °C during April–October) on CPUE can probably be used to predict subsequent years' catches of harvestable sized signal crayfish in some temperate lakes. The time lags may differ among lakes, in our case between 2 and 8 years. The length of the time series varied considerably among our study lakes, as did the predictions of the best-fitted models. For example, the time series for L. Vittsjön was only 16 years and the confidence interval of the best-fitted model was relatively high. In such situations the risk of spurious correlations (i.e., falsely identified dependences) could be high. The length of time series for L. Vättern was similar (18 years) and the confidence interval for the best model was also comparatively high. Here we only modelled how population densities are affected by temperatures in one single previous year. However, the catch in a given year most likely consists of individuals of different ages and whose egg development (or other critical stages) consequently have occurred in different years. To deal with this, future investigations could develop and analyse age-structured models (e.g., matrix population models; Caswell 2001) that can accommodate temperature effects distributed over several years.

To conclude, our study implicates that it is possible to predict future catches of signal crayfish quite well, using temperature data and assumptions on density dependence. This could provide a valuable tool for the management of the fisheries of signal crayfish and potentially also other crayfish species. We included lakes with different characteristics, considering abiotic and biotic factors as well as exploitation. In three of the lakes, models including temperature effects on adults were selected. This finding could

potentially be relevant for other species of crayfish as well. But to predict the effects of global warming on the dynamics of cool-water crayfish populations, we suggest that future studies should investigate recruitment in crayfish along temperature gradients. Furthermore, because increased temperature and higher amplitudes in water temperature may affect adult survival and their individual growth rates, this may also be an important topic for future mechanistic studies.

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