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Are fish populations in temperate streams affected by crayfish? – A field survey and prospects

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Synopsis

Fish populations may be affected by predation and competition from various types of organisms, among which crayfish have been suggested as important actors. We here present results from stream surveys, suggesting that neither native noble, *Astacus astacus*, nor introduced signal crayfish, *Pacifastacus leniusculus*, necessarily affect fish population densities in temperate stream communities. Comparisons of fish densities within stream sites between years with absence and presence of crayfish showed no effect of either crayfish species. A further analysis of changes in fish densities between periods without and with crayfish in low, intermediate and high densities revealed that crayfish density did neither have an effect on fish densities. Our study is one of exceptionally few that consider the above aspects in long-term perspectives in natural systems, and we discuss that previously reported divergent results of crayfish effects on fish may be highly dependent on specific species and methods used, and that the effects of crayfish on fish populations deserve further attention to enable reliable predictions of community processes in streams.

Introduction

In many parts of the world fish species' distributions and numbers are declining due to for instance habitat destruction or environmental changes (e.g. Maitland 1995). Further, biotic interactions such as competition and predation from introduced species may fragment the distribution of native fish species (e.g. Townsend 2003). On the other hand, fish populations may increase population density and/or distribution with improved water quality or altered community composition (Eklöv et al. 1998, 1999). Simultaneously, inherent properties may cause population dynamics of different patterns and magnitudes (Begon et al. 1990, Hart & Reynolds 2002). Fish occurrence may hence vary both spatially and temporally for several biological and environmental reasons, and it is of utmost importance to assess these regulating factors to enable reliable predictions of population densities and species distributions.

Most fish species are susceptible to competition and predation, and both factors may have considerable direct and/or indirect effects on individuals and populations (Kerfoot & Sih 1987, Lima & Dill 1990, Hart & Reynolds 2002). As competition and predation would affect e.g. fish recruitment and survival, changes in competitive and predation pressure should create changes also in fish

population densities. Fish may be prey to a variety of predators, including larger fish, birds and invertebrates, all with potentially different predatory modes and effects on prey (O'Brien et al. 1990, Savino & Miller 1991, Maitland & Campbell 1992, Ogilvie & Pearson 1994). Similarly, fish experience competition for food, space and habitats from several types of organisms. The effects of competition and predation on fish populations may hence substantially depend on specific circumstances and species involved. In this study, we focus on the potential effects of native and introduced crayfish on population densities of fish in stream communities.

Crayfish may dominate the invertebrate biomass in streams and small rivers (Usio & Townsend 2001), and as omnivores they may significantly affect the biomass of their food sources, including detritus, algae, macrophytes and invertebrates, through both direct and indirect interactions (Nyström et al. 1996, Usio 2000, Stenroth & Nyström 2003). Crayfish are also preyed upon by many fish species, and fish may therefore affect crayfish abundance and behaviour (Englund 1999). On the other hand it has also been suggested that crayfish could affect the growth and densities of fish populations (Guan & Wiles 1997). Suggested mechanisms include crayfish predation on eggs and juveniles, modification of habitats, displacement from shelters, and competition for food (summarized in Dorn & Mittelbach 1999, Nyström 2002, Dorn & Wojdak 2004). The negative effects of crayfish on fish populations have been frequently discussed (Momot 1995, Dorn & Mittelbach 1999, Nyström 1999, Lodge et al. 2000), but the lack of field evidence and long-term field experiments makes the role of crayfish in structuring natural fish populations and communities largely unknown. Moreover, many lake and stream communities contain exotic crayfish species, such as the signal crayfish, *Pacifastacus leniusculus*, or the rusty crayfish, *Orconectes rusticus*. Both these crayfish species have been shown to be more aggressive and have higher consumption rates of invertebrates and macrophytes than many native crayfish, and in some cases also build up higher population densities than native crayfish (summarized in Lodge et al. 2000). It is therefore possible that introduced crayfish species may have greater impacts on fish communities than native crayfish. Introduced predators may be particularly important in determining the abundance of native fish. For example, the response of native fish assemblages to non-native fishes suggest that both predation and competition may be important mechanisms behind negative effects, but in most cases pre-disturbance data are lacking, making the evidence mostly circumstantial (Ross 1991). Likewise, the lack of pre-disturbance data has made evaluations of effects of native and non-native crayfish on fish populations largely impossible. In this study, densities of fish species in Swedish stream communities were compared between years with and without native noble crayfish, *Astacus astacus*, and introduced signal crayfish to evaluate effects of crayfish on fish densities under natural conditions in a longer-term perspective.

Materials and methods

Densities of fish and crayfish species were investigated at a total of 64 sites in 61 streams surveyed on a total of 478 occasions by the Swedish Board of Fisheries or the Regional County Administrations. These surveys are performed as parts of environmental surveillance and fish-stock assessment programs, and data are stored and quality controlled by the Swedish Electrofishing RegiSter[1] (SERS). The locations included in the analyses were selected to show changes in crayfish occurrence to enable comparisons of fish densities between crayfish presence and absence within a stream section. Only streams from the southern parts of Sweden (55.23N to 59.57N, Figure 1) with populations of noble crayfish and/or signal crayfish were selected. We only included sites that had at least two consecutive years with crayfish followed or preceded by a period of at least two years without crayfish. Thus, each site had been surveyed at least four consecutive years. In analyses, average densities of fish for years before and after appearance/disappearance of crayfish were used. Crayfish disappearance at sites where crayfish presence was followed by absence was most likely due to the crayfish plague, a major threat to crayfish (Vogt 1999, Lodge et al. 2000). All fishing

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[1] Swedish Electrofishing RegiSter, available from the Swedish Board of Fisheries internet URL http://www.fiskeriverket.se

Figure 1. Map of Sweden showing the geographical distribution of the 64 study sites in the investigation.

occasions were carried out when the water temperature was above 8°C and crayfish females were not carrying eggs (i.e. between June and September). As a consequence of this selection, the average water temperature during sampling was 14.3 ± 2.6°C (mean $\pm$ SD). Stream localities were also chosen to consist of comparable morphometries (width: 6.0 ± 3.9m, depth: 0.22 ± 0.07 m), and as different people carried out the surveys, we only used surveys performed by experienced personnel. Surveys were performed by electrofishing, an efficient practise for both fish and crayfish (Cowx & Lamarque 1990, Rabeni et al. 1997) and locally available equipment that follow guidelines for electrofishing in Sweden were used. Direct current (DC) was used at 81% of fishing occasions and pulsed DC at 19%. Catches were used to estimate fish and crayfish densities. 69% of the sites were fished two to four consecutive times on a survey occasion, and the remaining sites were fished only once per visit. When several fishing runs were performed, population densities (individuals 100m^{-2} for each species) were estimated according to Higgins (1985). When only one fishing run was performed, densities were estimated according to relations of catch efficiencies between single and depletion fishing presented in the Swedish Board of Fisheries' extensive data base (see also Kruse et al. 1998, Degerman & Sers 1999, Edwards et al. 2003).

The densities of all caught fish species were compared between survey occasions, within stream locality, when any of the two crayfish species was present and when no crayfish were present. Also, the effects of presence or absence of the separate crayfish species on fish species densities were analysed. Data remained non-normally distributed even after transformations (Kolmogorov-Smirnov tests: $Z > 1.942$, $p \leq 0.001$ in all cases), which is why non-parametric statistical analyses on non-transformed data were chosen. As the stream sections had been surveyed more than once during both presence and absence of crayfish, average fish densities from with and without crayfish were analysed and compared with Wilcoxon matched-pair signed-rank tests. Further, the effect of crayfish density on fish-density changes was analysed. Survey occasions with presence of any crayfish species were grouped into low ($>0-5$), intermediate ($>5-25$) and high crayfish density (>25 individual crayfish 100 m^{-2}). For each of the sites, the difference in density for each species of fish between absence and presence of any crayfish species was calculated (density without crayfish minus density with crayfish). The differences in fish densities between crayfish absence and presence were then compared between crayfish-density groups for each species of fish with Kruskal–Wallis H-tests.

Results

A total of eight fish species were caught in the surveys, forming commonly occurring fish communities in Swedish streams (Table 1). Brown trout, *Salmo trutta*, was found on all sites, and was divided into young-of-the-year fish (0+) and older (>0+). Trout did however not occur in the highest population densities, as bullheads, *Cottus gobio*

Table 1. Median densities (no. 100 m^{-2}), with 25–75% quartile ranges, of different fish species and age groups (for brown trout) at stream sites during years when crayfish were absent and when crayfish were present. Within-species densities from absence and presence of crayfish were compared with Wilcoxon matched-pair ranked tests.

	Number of sites	Density without crayfish	Density with crayfish	Wilcoxon z	Wilcoxon p
Noble and/or signal crayfish					
Brook lamprey	28	0.35 (0–1.5)	0.60 (0.04–1.2)	−0.40	0.69
Brown trout 0+	64	4.4 (0.4–22.3)	5.4 (0.5–22.6)	−0.45	0.65
Brown trout >0+	64	4.8 (1.2–12.1)	3.6 (1.6–13.9)	−0.64	0.52
Bullheads	14	18.2 (0.85–76.9)	13.5 (3.1–40.9)	−0.21	0.82
Burbot	38	0.88 (0.13–2.3)	1.6 (0.44–3.0)	−0.96	0.34
Eurasian perch	29	0.52 (0.10–1.7)	1.1 (0.04–2.1)	−0.70	0.48
European eel	18	0.60 (0.32–1.6)	1.0 (0.49–3.4)	−1.06	0.29
Minnow	33	5.0 (0–22.6)	4.3 (0.65–34.3)	−1.40	0.16
Northern pike	49	0.40 (0.09–0.85)	0.33 (0.08–0.70)	−0.02	0.82
Noble crayfish					
Brook lamprey	13	0.48 (0–3.9)	0.60 (0–1.4)	−1.38	0.17
Brown trout 0+	23	3.9 (0.22–9.9)	6.2 (0.80–20.4)	1.36	0.17
Brown trout >0+	23	4.8 (0.22–11.6)	3.6 (2.1–9.1)	−0.11	0.91
Bullheads	4	29.3 (0–83.9)	10.8 (3.0–16.3)	−1.07	0.28
Burbot	14	0.90 (0.03–2.6)	0.60 (0.1–2.9)	−0.28	0.78
Eurasian perch	10	0.92 (0.28–2.6)	0.73 (0–1.8)	−0.31	0.76
European eel	5	0.50 (0.06–0.83)	0.55 (0.28–2.2)	−0.67	0.50
Minnow	17	4.7 (0–20.6)	2.4 (0.50–29.3)	−1.13	0.26
Northern pike	18	0.65 (0.18–1.4)	0.53 (0–1.6)	−0.54	0.59
Signal crayfish					
Brook lamprey	15	0.20 (0–0.92)	0.75 (0.15–1.6)	−0.66	0.51
Brown trout 0+	41	9.8 (0.29–32.8)	5.0 (0.1–26.0)	−0.44	0.66
Brown trout >0+	41	4.7 (1.1–16.7)	3.4 (1.0–14.0)	−0.71	0.48
Bullheads	10	7.1 (0.85–83.9)	33.2 (2.8–79.1)	−1.12	0.26
Burbot	24	0.85 (0.23–1.9)	1.8 (0.80–3.1)	−1.33	0.18
Eurasian perch	19	0.40 (0–1.31)	1.2 (0.19–2.5)	−0.92	0.36
European eel	13	0.68 (0.34–6.9)	1.0 (0.52–4.8)	−0.70	0.48
Minnow	16	6.3 (0–22.6)	7.4 (0.85–50.8)	−1.07	0.28
Northern pike	31	0.40 (0.12–0.74)	0.33 (0.08–0.55)	−0.06	0.95

Comparisons were made for absence or presence of either noble crayfish or signal crayfish, and for absence and presence of each crayfish species separately.

and/or *C. poecilopus*, showed very high densities at some of the sites where they were found. On the contrary, northern pike, *Esox lucius*, occurred at many sites, but always in low densities. Other species found, brook lamprey, *Lampetra planeri*, burbot, *Lota lota*, European eel, *Anguilla anguilla*, minnow, *Phoxinus phoxinus*, and Eurasian perch, *Perca fluviatilis*, were moderately common and occurred in intermediate to low densities (Table 1).

The densities of the fish species found in the surveys did not differ between absence and presence of crayfish (Table 1). When comparing fish-species densities between absence and presence of noble crayfish and signal crayfish separately, no significant differences in densities were found

(Table 1). When comparing the change in fish population densities between years when crayfish were absent and when crayfish occurred in low, intermediate and high densities, density of crayfish had no significant effect (Table 2).

Discussion

Our results show no effects of crayfish presence, crayfish species or crayfish density on fish population densities in the investigated stream communities. Previous investigations on the topic have suggested divergent effects of crayfish on fish, where some report substantial effects (e.g. Guan &

Table 2. Average change in density (no. 100 m^{-2}) of different stream fish species and age groups (for brown trout) between years when crayfish were absent compared with when crayfish were present in low ($>0-5$ individuals 100 m^{-2}), intermediate ($6-25$) and high (>25) densities, respectively.

Species and age group	Number of sites	Average change in fish densities when crayfish density changed to			χ^2	p
		low	intermediate	high		
Brook lamprey	28	0.20	−0.10	2.20	0.72	0.69
Brown trout 0+	64	0.01	−3.00	5.00	0.86	0.65
Brown trout >+	64	−2.60	2.10	5.10	3.55	0.18
Bullhead	14	−8.00	−9.80	n.a.	0.32	0.57
Burbot	38	−0.72	0.66	−0.45	0.69	0.71
Eurasian perch	29	−0.57	0.63	0.15	1.12	0.57
European eel	18	−1.20	13.70	−1.80	1.27	0.53
Minnow	33	−8.40	−4.10	1.80	0.18	0.91
Northern pike	49	0.19	−0.27	0.32	1.03	0.60

The density changes were tested with Kruskal–Wallis non-parametric ANOVA.

Wiles 1997, Dorn & Wojdak 2004) while others correspond with our suggestion that crayfish have no or small effects on fish (e.g. Ilheu & Bernardo 1993, Xinya 1995, Stenroth & Nyström 2003). We argue that the discrepancies between studies originate from different methodological approaches, and possibly also from the presence of different fish species. Here, we discuss these differences in view of the potential for crayfish impact on fish population densities in streams, by briefly reviewing the potential effects of investigation set-up, predation, competition and habitat composition on the interplay between crayfish and fish.

Crayfish predation on fish

Several short-term tank or pond experiments have shown that crayfish such as *Orconectes virilis* and the noble crayfish may consume eggs and juvenile fish (Savino & Miller 1991, Miller et al. 1992, Rubin & Svensson 1993, Dorn & Wojdak 2004). On the other hand, other studies, using similar experimental designs, have shown that crayfish, *Procambarus clarki*, did not predate efficiently on fish (Ilheu & Bernardo 1993, Xinya 1995). These studies suggest that crayfish may predate on eggs and fish larvae in smaller experimental settings, but the predation effects depend on several factors such as habitat complexity, water temperature, if eggs are deposited in the gravel, and on the behaviour of the specific fish species. It can be argued that small experimental settings often

exaggerate predation effects, but that they are very useful in determining mechanisms or if predators can or cannot eat certain prey types (e.g. Diamond 1986). However, although useful for identification of potential mechanisms, smaller-scale, controlled experiments on crayfish effects on fish may be inappropriate for predictions of effects in nature, as we did not find any evidence of a negative effect of crayfish on fish densities.

Field experiments should better mimic natural conditions and interactions between organisms, but to our knowledge very few attempts have been made to evaluate crayfish effects on stream-living fish. However, Guan and Wiles (1997) found a negative correlation between the densities of the introduced signal crayfish and the benthic bullhead, *Cottus gobio*, and stone loach, *Barbatula barbatula*, in a British stream. Experimental results from an artificial stream confirmed that high densities of adult crayfish reduced the densities of both fish species. Dahl (1998), on the other hand, found that adult bullhead reduced the abundance of juvenile signal crayfish in a Swedish stream. Using an *in situ* smaller-scale experiment, Stenroth and Nyström (2003) did not find any evidence of signal crayfish affecting the survival and growth of juvenile brown trout, even though crayfish significantly reduced the abundance of benthic invertebrates. Rather, the survival of brown trout in this case was related to variations in water velocity. From the diverging results in the above studies, it is hence plausible to assume that experiments in

field circumstances may be relatively sensitive to specific conditions, such as size and foraging behaviour of the focal species used and/or temporal environmental parameters. It should also be noted that field investigations often by necessity lack the mechanistic components obtained in small-scale experimental set-ups (Diamond 1986).

Competition, habitat modifications and exotic crayfish species

When abundant, crayfish may play an important role in stream and river ecosystems by e.g. consuming invertebrates and by processing detritus (Momot 1995), but the potential for resource competition between crayfish and fish should be difficult to predict and is likely to vary depending for instance on specific food sources, dietary overlap and interactions between crayfish and fish (e.g. Carpenter 2005). Experimental studies using stream channels have for instance shown that crayfish may reduce the biomass of benthic invertebrates (Charlebois & Lamberti 1996, Usio 2000, Stenroth & Nyström 2003). Crayfish consumption of prey may, however, be affected by fish competitors. Stelzer & Lamberti (1999) found that crayfish, *O. propinquus*, effects on invertebrates were reduced in the presence of rainbow darters, *Etheostoma caeruleum*, and *O. virilis* consumed less fish eggs in the presence of sculpin, *Cottus cognatus*, whereas the feeding rate of sculpin was unaffected by crayfish presence (Miller et al. 1992). Likewise, Vaughn et al. (1993) found that algivorous minnows, *Campostoma anomalum*, negatively impacted *O. virilis* through resource monopolization. It should be noted, however, that crayfish and many fish species have different diet preferences, and direct competition for food resources may sometimes be weak (e.g. Olsson et al. 2006). For example, previous studies on crayfish suggest that crayfish are important predators on snails and less mobile prey, whereas many fish species prey upon more mobile but less protected prey such as amphipods or terrestrial prey (Dahl 1998, Nakano et al. 1999), that are not efficiently preyed upon by crayfish (e.g. Maitland & Campbell 1992, Nyström 2002). Also, because crayfish are consumed by many fish species (see summaries in Hogger 1988, Lodge & Hill 1994, Foster & Slater 1995, Dorn & Mittelbach 1999) crayfish may provide fish with

significant amounts of energy (e.g. Stenroth 2005). Based on the above examples, we conclude that crayfish may compete with fish for food, but that competitive strength and effect may vary substantially, especially under natural conditions where resources may be spatially and temporally separated.

Crayfish may also compete with fish for shelter, and such behavioural interactions may alter the involved species' vulnerability to shared predators. For example, crayfish, *O. putnami*, reduced the vulnerability of mottled sculpin, *Cottus bairdi*, to smallmouth bass, *Micropterus dolemieui*, probably by drawing the attention of the bass away from the sculpin (McNeely et al. 1990). In contrast, Rahel & Stein (1988), in a behavioural study, showed that the rusty crayfish increased the vulnerability of the johnny darter, *Etheostoma nigrum*, to smallmouth bass by evicting darters from shelters. Furthermore, bass also increased the vulnerability of darters to crayfish by forcing darters to seek cover under shelters occupied by crayfish. Based on these studies it is possible that crayfish affect the behaviour of some benthic fish species and thereby indirectly influence the vulnerability of these fish species to predation, but further studies are needed before any conclusions can be drawn on the importance of these mechanisms for fish populations.

Macrophyte beds may function as important juvenile habitats for fish in lakes and since crayfish may significantly reduce macrophyte abundance, fish recruitment may be affected. However, these ecological interactions have not been explored in detail (summarized in Dorn & Mittelbach 1999). Macrophyte beds are absent in many stream communities due to shading from surrounding trees, and we suggest that crayfish effects on fish recruitment due to macrophyte reduction are less important in streams than in e.g. the littoral zones of lakes. In rivers and streams, some crayfish species, such as the introduced signal crayfish and the native noble crayfish, may significantly affect bank stability through burrowing activities, and subsequently affect bank erosion (e.g. Holdich 1999). Such behaviour could potentially indirectly affect fish populations through e.g. increased turbidity and physical habitat alterations. Our study streams were however mostly located in forests with rather stable banks with coarse substrata, which are more difficult for crayfish to burrow in. Hence, fish popula-

tions in our study were probably not subjected to physical habitat alterations caused by crayfish.

The effects of introduced crayfish species on freshwater ecosystems have received much attention in recent years (e.g. Lodge et al. 2000), and our data are thus particularly interesting in this context since they include both native and introduced crayfish species and their overall influence on natural population densities of different fish species. The native noble crayfish has declined in numbers and distribution in Sweden since the outbreak of crayfish plague in 1907. Due to the decline of the native crayfish, the plague-tolerant signal crayfish was introduced into Sweden in 1960, and in 1996 signal crayfish occurred in more than 1000 lakes and more than 300 streams (Anonymous 1999). Although there are differences between signal and noble crayfish regarding behaviour and effects on prey and competitors (e.g. Nyström et al. 1999), our results show that neither species had a significant effect on stream fish populations in our study region.

Concluding remarks

In order to predict the effects of crayfish on fish in nature, natural population, community and habitat complexities should be considered, and the investigations should include long-term perspectives. However, as recently reviewed by Dorn & Mittelbach (1999), availability of such data is very limited and more such data as in this paper should be acquired, before conclusions can be drawn. Crayfish may interact with fish on an individual basis through competition and predation (e.g. in small scale experiments). However, these individual interactions between crayfish and fish did not cascade to population effects in our study. Even though these results originate from longer-term processes under natural stream conditions it may take more than two years to detect a change in fish population densities, since there is an inherent fluctuation in all fish populations between years. However, for a few streams, where there are longer time series with increasing crayfish densities, both trout and lamprey have stable populations sizes (SERS), indicating that the timespan in this study was sufficient. We suggest that negative effects of crayfish on stream-living fish populations should be expected only when the following assumptions

are met: (1) The fish species are limited by predation and/or food sources and not by other physico-chemical factors. (2) The fish species must be vulnerable to crayfish predation. (3) Shared limited food sources should be significantly reduced by crayfish. (4) The fish species should not utilize crayfish as a major food source. Specifically, we believe the direct predation by crayfish on fish, although likely to occur also in nature, was not frequent or important enough to scale up to population levels in our investigation. The combined effects of predation, competition and habitat modification from crayfish did hence not influence the study fish population densities.

Even though we found no effects of crayfish on fish population densities this does not mean that the lethal and non-lethal interactions between fish and crayfish at the individual level are unimportant. Also, other factors than crayfish, such as intra- and inter-specific competition, alternative predators, and physico-chemical properties, may be stronger regulators of fish population densities in temperate streams, potentially masking the effects of crayfish on fish. Before we know the relative effect sizes of these biotic and abiotic factors, it is hard to make conclusive predictions. We however stress that predictions of effects in nature demand investigations conducted under natural conditions, and the present study showed no real-life effects of the study crayfish species in our specific systems. Thus, although our findings suggest only minor effects at best, we emphasise the importance of further investigation into species- and habitat-specific effects of crayfish on for instance threatened or commercially important fish populations.

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