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Effects of fish on the local abundance of crayfish in stream pools

Göran Englund

A survey of fish and crayfish distributions in pools in small Kentucky streams suggested that predatory fish have strong effects on the local distribution of crayfish. I tested this hypothesis by experimentally manipulating the density of fish in stream pools. The predator, green sunfish (*Lepomis cyanellus*), strongly reduced the density of crayfish (*Cambarus bartoni*). Prey movement rates into and out of pools were low compared to estimated predation rates; consequently, I concluded that observed reductions of crayfish densities by fish predators were due mainly to direct consumption. Estimated rates of predation and prey movements were combined into a model to simulate observed predator impact on crayfish in patches larger and smaller than the scale of the experiment. The simulation suggested that the results were robust to increases in spatial scale.

Data from the survey showed that crayfish densities in fish pools and fishless pools only differed for pools deeper than approximately 30–50 cm, probably because shallow pools had fewer and smaller fish. Thus, shallow pools provide a refuge for crayfish against fish. Very shallow pools (10–20 cm) generally had low densities of crayfish. Possible mechanisms that could explain the low density of crayfish in shallow pools include stronger effects of floods and higher predation pressure from terrestrial predators in these pools.

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Experimental studies indicate that effects of predators on prey densities are widespread but variable; comparisons across systems and across taxa within systems show that effects vary from trivial to overwhelming (Sih et al. 1985, Wilson 1991, Wooster 1994, Englund et al. in press). Understanding the mechanisms that produce this variation is crucial for our ability to build general models of the role of predation in natural communities (Osenberg et al. 1997, in press). Experimental studies have demonstrated particularly strong effects of variation in the size, morphology, and behavior of predators and prey (Zaret 1980, Sih 1992, Persson et al. 1996, Castell and Sweatman 1997, Osenberg et al. in press) and in environmental factors that cause physical disturbances or affect refuge availability (Bechara et al. 1993, Wootton et al. 1996, Carroll and Highsmith 1996). However, it is also clear that some variation in the

effects of predators on prey can be attributed to aspects of experimental design such as spatial and temporal scales and the influences of the surrounding unmanipulated habitat (Cooper et al. 1990, Hall et al. 1990, Peckarsky 1991, Wilson 1991, Englund 1997, Cooper et al. 1998).

Experiments addressing the influence of predators in streams also show quite variable effects of predators on prey densities, and there has been considerable debate about the sources of this variation (Allan 1983, Cooper et al. 1990, Sih and Wooster 1994, Englund 1997, Englund et al. in press). Empirical studies suggest that some variation can be explained by availability of different types of prey refuges, including those created by hydrological stress (Malmqvist and Sackmann 1996), secondary predators (Power 1987) or physical structures (Bechara et

al. 1993), or by different types of indirect effects (Power 1990, Soluk 1993). Other studies have emphasized that differences in predator and prey traits can cause variation in predator impacts across different taxa (Cooper 1988, Sih et al. 1988, Wooster 1996). Indeed, several recent meta-analyses have reported that predator impacts on prey densities vary between different categories of predators and prey, e.g., vertebrate vs invertebrate predators, drift feeding vs benthic feeding fish, and chironomids vs epibenthic prey (Wooster 1994, Dahl and Greenberg 1996, Englund et al. in press).

The interpretation of these patterns is complicated by the fact that most stream predator experiments are open, i.e., prey movements into and out of the experimental units are allowed. This means that differences between taxa or systems can be caused by variation in 1) predation rates, 2) movement responses of prey to predators, 3) predator-independent movement rates and/or 4) relative importance of movements and predation (Cooper et al. 1990, Englund 1997). In general, it is not possible to judge from prey density data which of these different mechanisms underlie observed patterns. This means that much insight can potentially be gained from experiments that, in addition to prey densities, also report movement and predation rates.

A crucial question, which until recently has received little attention, is whether or not the influence of prey movements on prey densities should be viewed as an artifact of the experimental design (Englund 1997, Cooper et al. 1998). Obviously, the influence of movements on prey densities inside experimental arenas must be regarded as an artifact if the objective is to estimate effects of predation on population vital rates, such as mortality or growth rates (Englund and Olsson 1996). Open experiments, however, may also be used to examine how predators affect the local distribution of prey across patches differing in predation intensity (e.g., Cooper et al. 1990, Sih et al. 1992). Depending on the scale of patchiness and the mobility of prey, such distributional patterns are often determined by a combination of direct predation and prey movements (Englund 1997). Thus, it is crucial to reproduce natural prey movement rates in examining predator effects on the local distribution of prey. Aspects of the experimental design that may influence movement rates are the size of the mesh used to enclose the predator and the spatial scale of the experiment. Published stream predation experiments vary tremendously in mesh size and spatial scale (mesh size: 0–14 mm, area: 0.01–70 m^2), and such variation can have strong effects on observed predator impact, even reversing the sign of the effect (Englund 1997).

Here I present experimental evidence that predatory fish can have strong effects on the local distribution of crayfish in stream pools. Because natural habitat patches, i.e., stream pools, were used as experimental units, it is likely that prey movement rates and predation rates were unaltered from natural levels. The experimental design allowed me to separate influences of consumption, predator-induced prey movements and predator-independent movements. I found that crayfish movement rates were low and, thus, that observed effects on crayfish densities were caused by consumption. Data from a field survey confirmed that fish strongly influence crayfish densities only in deep pools (>40 cm) where fish densities are highest.

Organisms and habitats

This study was performed in four small, central Kentucky streams (Raven Run Creek, Crayfish Creek, Fossil Creek, and Little Hickman Creek) located 25–35 km south to southwest of Lexington, Kentucky, USA. The streams have short riffles and runs alternating with pools of variable depth and area (ranges: 10–140 cm and 2–500 m^2). Flow is usually very low during summer and fall (June–November), and some pools dry up in the middle of summer. The dominating substrate in most pools is bedrock with scattered rocks of variable size. Some pools also have finer substrates (sand-silt) overlain by rocks along the margins. The fish fauna in these streams is diverse and include two abundant species, green sunfish (Lepomis cyanellus) and creek chub (Semotilus atromaculatus), which are large enough to be potential predators on crayfish. The distributions of these species are patchy. An upstream stretch typically has mostly ephemeral, fishless pools; a downstream stretch has fish in most pools; and an intermediate stretch has pools alternately containing and lacking fish.

Two species of crayfish, Cambarus bartoni and Oronectes putnami, are abundant in these streams. They can reach a large size (>10 cm body length) but most individuals are much smaller (15–35 mm body length). Cambarus hatchlings were observed in early fall (Sept.) while those of Oronectes occurred in early summer (May–June).

Methods

Field survey

I determined the abundances of crayfish in shallow and deep areas of pools differing in fish density and depth in September 1996, including pools in Raven Run Creek, Crayfish Creek, and Little Hickman Creek. Crayfish were sampled by sweeping a dipnet back and forth over an area (0.5 or 1 m^2) while overturning all the rocks in that area. The length of each crayfish from

the tip of the tail to the tip of the rostrum was measured to the nearest 5 mm. Two samples were taken in each pool: one in the shallow part (depth < 20 cm) and one in the deep part (depth > 20 cm). For each pool I also recorded total area and maximum depth, and I visually estimated the proportion of total area that was deeper than 20 cm. An average density of crayfish in each pool was calculated by weighting estimates from shallow areas by the proportions of the total pool area included in each depth category. After crayfish sampling, pools were electrofished once and the length of each captured fish was determined. Length measurements were transformed to biomass using length-weight regressions (Englund unpubl.).

Effects of fish on pool-to-pool distributions

An experiment was performed in order to test the hypothesis that the abundance of crayfish across pools is affected by fish predation. This experiment also allowed me to determine the relative contribution of predator-related mortality and prey avoidance responses to observed predator impacts on prey. I added green sunfish to four stream pools in the fishless upstream part of Fossil Creek, a tributary to Little Hickman Creek, and used four unmanipulated pools as controls for these fish additions. The pools were arranged in pairs, with a control pool a short distance downstream (1–5 m) from a fish pool. The two pools in such a pair were separated by a short riffle often including a small waterfall (height 30–50 cm). The distances between pair of pools ranged between 30 and 150 m. The pools were approximately 2–3 m wide, 4–12 m long, and 30–45 cm deep. The dominant crayfish species in these pools was *Cambarus bartonii*. The introduced fish ranged from 95 to 105 mm in total length, and fish density was 0.2 inds./m², corresponding to a biomass of 2.8 g wet weight per m². This density and biomass is well within the natural range for green sunfish in the studied streams. All introduced fish were recovered after the experiment. The entire flow into and out of each pool passed through one or two large drift nets (mesh 2 mm) that were placed in the riffles immediately upstream and downstream of each pool. The drift nets were in position during the entire experiment and were emptied every 24 h. To evaluate the effectiveness of the drift nets in intercepting all crayfish, I positioned two drift nets 2–3 m downstream of the nets placed at pool outlets after manually removing all crayfish in the riffle between the two sets of nets. No crayfish were caught in the downstream nets. Crayfish density and refuge use were determined visually before fish introduction and every other day during the 6-d experiment. During censuses, two people moved very slowly in an upstream direction and lifted every rock, counting crayfish and noting if they were under rocks or out in the open.

Because some pools had burrows in the bank and/or crevices under bedrock that could not be monitored, I also used a catch and removal method to estimate the total crayfish numbers in each pool. After the last visual count I searched through the pools, removed all rocks, and swept through each pool with a large dipnet, removing all crayfish that were captured. This procedure was repeated on the subsequent day with drift nets in place to prevent migration. Cumulative catch was regressed on catch per sampling occasion, and the y-intercept was used to estimate the total number of crayfish at the end of the experiment. For control pools, the estimated number of crayfish was approximately two times higher (1.8–2.6) than the numbers observed during the last visual count. These factors were used to adjust the visual counts (day 0–4) for each control pool. For one fish pool estimated and observed numbers did not differ. This pool did not seem to have any crevices under bedrock or burrows in the bank that could not be monitored and so visual counts were not adjusted. For the remaining three fish pools estimated numbers were 6.8–10.5 times higher than the final visual counts. I assumed that the probability that a crayfish should be spotted was lower in these pools because crayfish responded to fish addition by increasing refuge use (see results section). Thus, to adjust the counts made in fish pools before fish addition I used the mean of the adjustment factors for control pools. For days 2 and 4, I used the final adjustment factor for each fish pool multiplied with 0.4 and 0.7, respectively as an approximate correction for the increase in refuge use over time. These figures were chosen after inspection of the data on refuge use given in Fig. 10. For day 6, I used the numbers estimated with the catch and removal method for both types of pools.

Daily per capita emigration rates (m) were calculated using $m = \ln[N_t/(N_t - E)]$, where N_t is the number of crayfish in a pool on a certain day and E is the numbers emigrating from that pool during the next 24 h. Per capita mortality rates were calculated using a budget approach. For days 2, 4, and 6, I calculated a predicted abundance based on the numbers 2 d before and net migration (immigration – emigration) over the 2-d interval. The difference between predicted and observed numbers (c) was then used to calculate the per capita mortality rate per day (q) using $q = \ln[N_t/(N_t - c)]/2$. Cooper et al. (1990) suggested that the predator impact seen in open predation experiments could be quantified by a predator impact index, calculated as the natural logarithm of the ratio between densities in control and predator treatments. If initial density differences are considered, this index is given by PI = $\ln(N_{ct}/N_{pt}) - \ln(N_{c0}/N_{p0})$, where N_{c0} and N_{p0} are initial, and N_{ct} and N_{pt} are final densities in control and predator treatments. I also calculated the predator impact index if densities were only affected by mortality. The predicted abundance for each pool on days 2, 4,

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and 6 was calculated using $N_{t+2} = N_t e^{-2q}$, where q is daily per capita mortality rate.

To examine potential scale dependence of predator impact caused by the decreasing influence of prey movement as the spatial scale is increased, I used a model derived in Englund (1997). Where the background habitat is free of predators, the predator impact (PI) is given by

$$PI(t) = \ln[(m_p + q)/\{m_c + (m_p + q - m_c) e^{-(m_q + q)t}\}] \tag{1}$$

where q is the predation rate per prey per day, t is time (d), and m_p and m_c are the per capita migration rates per day out of predator and control units. Scale-dependence is introduced into this model by letting per capita migration rates be inversely proportional to the length of the experimental unit. The parameters q, m_p and m_c were estimated as the arithmetic means of the predation and migration rates calculated from the experimental results.

Statistical analyses

Statistical analyses were conducted using the general linear models module in SYSTAT 6.0 (SYSTAT 1996). Data were log-transformed to homogenize variances when visual inspection of raw data or residuals suggested that it was necessary. The field survey results included data for two crayfish species. To determine if relationships between crayfish density or size and fish density or depth differed between the two species, I ran ANOVAs or ANCOVAs including species identity as an independent variable, as well as the interaction effect between species and fish density or depth. Because none of these analyses produced a significant interaction between species identity and depth or fish density, I only present analyses where data for the two species are pooled. Data from the experimental manipulation of fish densities were analyzed using repeated measures ANOVA.

Results

Field survey

Fish pools had lower densities of crayfish than fish-free pools of comparable depth (Fig. 1, one-way ANOVA, $F_{1,18} = 10.9$, $P < 0.005$). However, there were strong effects of the maximum pool depth on crayfish densities (Fig. 2). Crayfish densities increased with maximum depth in fish-free pools but decreased with maximum depth in fish pools (linear regression, $t = 6.9$, df $= 24$, $P < 0.001$, for fish-free pools and $t = -3.2$, df $= 9$, $P < 0.01$, for fish pools). Fish biomass increased with maxi-
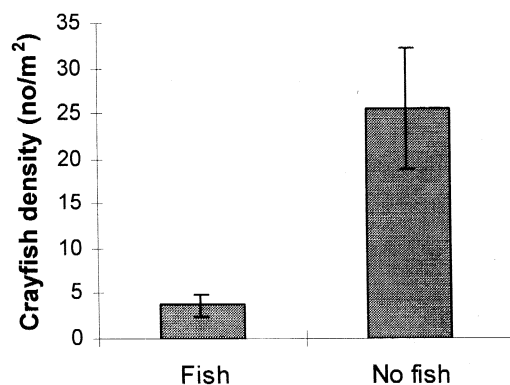

Fig. 1. Mean densities (± 1 S.E) of crayfish in pools deeper than 20 cm that contain or lack predatory fish.

mum depth (Fig. 3, $t = 2.9$, df $= 9$, $P < 0.05$) and there was a negative relationship between crayfish density and fish biomass in fish pools (Fig. 4, $t = -2.8$, df $= 9$, $P < 0.05$). Neither maximum depth nor the presence of fish was significantly related to mean crayfish size (ANCOVA, $F_{1,31} = 0.01$ for depth, $F_{1,31} = 0.36$ for fish presence, and $F_{1,31} = 1.97$ for depth $\times$ fish, all P's > 0.28).

Experimental manipulation of fish density

The addition of green sunfish significantly decreased crayfish abundance over time (Fig. 5, repeated measures ANOVA, fish $\times$ time interaction: $F_{3,18} = 7.7$, $P < 0.005$). Per capita mortality rates were also affected by the fish treatment (Fig. 6, effect of fish: $F_{1,6} = 12.1$, $P < 0.05$; effect of time: $F_{2,12} = 1.7$, NS; effect of time $\times$ fish: $F_{2,12} = 1.2$, NS). In fish pools per capita mortality rate was substantially higher (0.15–0.17 per day) than the mortality rate in fishless pools (-0.7–0.2 per day) suggesting that predation was by far the most important mortality factor (the negative mortality rate on day 2 in fishless pools was probably an artifact caused by increasing visibility as flow decreased). Esti-
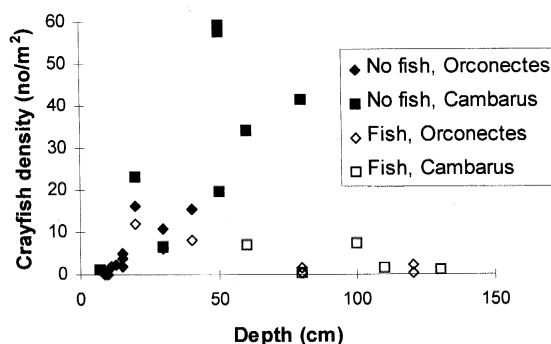

Fig. 2. Relationships between the densities of two species of crayfish, *Orconectes putnami* and *Cambarus bartonii*, and maximum depth in pools with and without predatory fish.
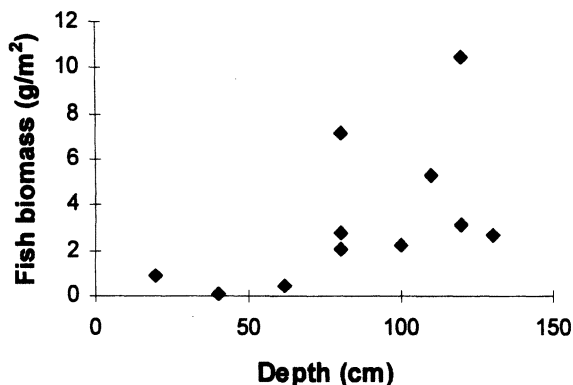
Fig. 3. Biomass of fish versus maximum depth (cm) of surveyed stream pools.

mated per capita emigration rates out of fish pools were slightly higher than emigration rates out of control pools; however, this difference was not significant (Fig. 7, effect of fish: $F_{1,6} = 3.5$, $P \geq 0.11$). The predator impact index (PI) increased over time (Fig. 8), and the inclusion of prey movements in calculating PI increased observed PIs slightly. The simulation based on the Englund (1997) model shows that the scale dependence of movement rates is expected to have little influence on PI over the scale range encountered during the survey (5–30 m, pool length) (Fig. 9). Mean size of crayfish did not differ between the two treatments (mean $\pm$ S.E. was 27.0 ± 0.8 mm in control pools and 30.2 ± 2.6 in fish pools, t-test with separate variances, $t_{3.6} = 1.13$, NS), indicating that size selective predation was not important. The proportions of crayfish populations that were in the open decreased over time in fish pools but stayed relatively constant in fish-free pools (Fig. 10, fish × time interaction, $F_{3,18} = 3.8$, $P < 0.005$). Note that these data probably underestimated the effect on refuge use because they are based on unadjusted visual counts. A much larger proportion of the crayfish population was overlooked in fish than fishless pools, probably because of their residence in refuges that could not be censused.
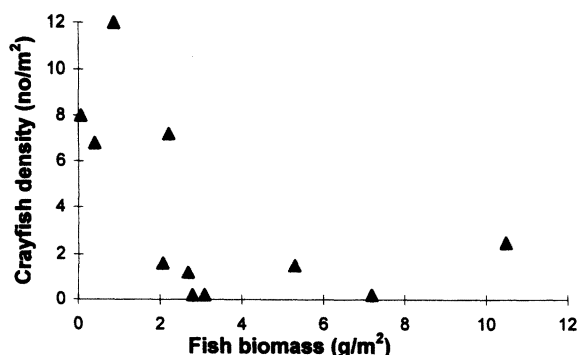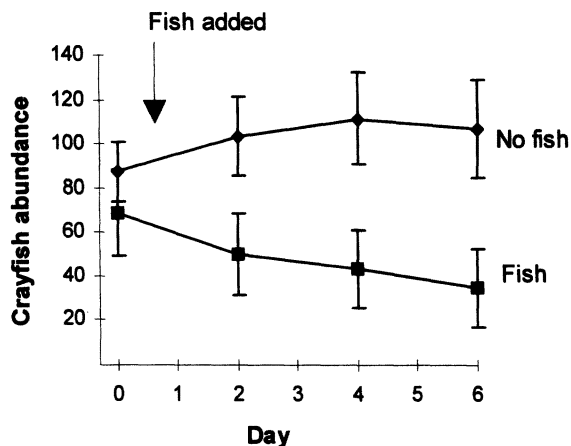

Fig. 5. Crayfish abundance (no./pool) over time in fish-free pools and in pools to which green sunfish were added. Error bars denote ± 1 S.E.

Discussion

Both the experiment and the survey indicated that fish have strong effects on the local distribution of crayfish. For example, a seven-fold difference in crayfish densities was observed between fish and fish-free pools deeper than 20 cm, and the predation rate calculated in the experiment was 10–15% per day. These effects are larger than those found in most earlier experiments addressing the effects of predatory stream fish (see reviews by Cooper et al. 1990, Wooster 1994, Englund et al. in press).

As a first step when comparing results between studies, it is useful to examine the relative influence of predation and movement rates on prey densities. Predation and prey movements are fundamentally different processes, and it may often be impossible to understand how the impacts of predators are modified by environmental factors unless we know if predator effects reflect movement or predation rates. Also, effects caused by movements and those caused by predation may often have different temporal dynamics (Englund unpubl.).
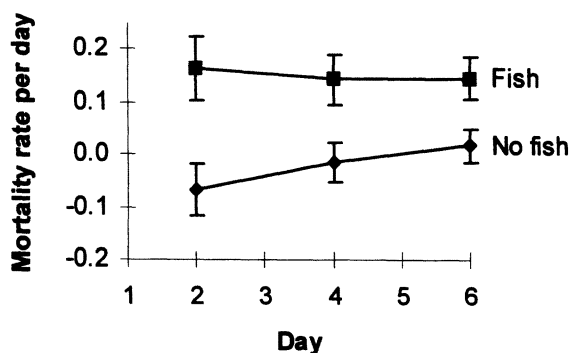

Fig. 4. Relationship between crayfish density and fish biomass in stream pools.

Fig. 6. Instantaneous per capita mortality rates for crayfish in stream pools with and without added green sunfish. Error bars denote ± 1 S.E.
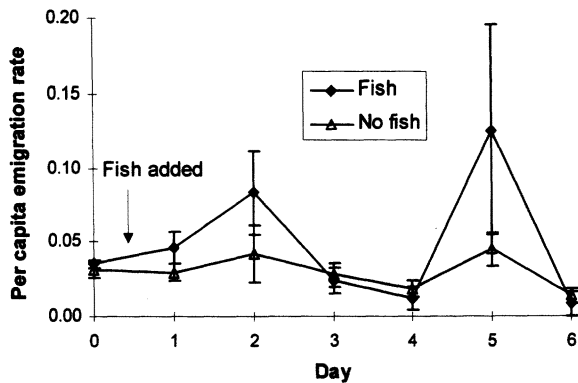
Fig. 7. Daily per capita emigration rates of crayfish out of pools with and without green sunfish. Error bars denote ± 1 S.E.

The metric appropriate for comparisons may thus depend on the relative influence of the two processes (Osenberg et al. 1997). In this study, predator impact primarily reflected the predation rate; overall prey movement rates were low, and the predator-induced emigration response was weak and statistically non-significant. In this respect, the studied system may differ from many other stream systems. Englund (unpubl.) analyzed data from seven stream studies that reported both predation and movement rates, and they concluded that predator-induced movements, rather than predation per se, were the most important mechanism for a majority of the investigated prey taxa. Furthermore, six of the seven studies were done on a much larger scale than a majority of the published stream studies, which suggests that movements may be even more important in most stream predation experiments.
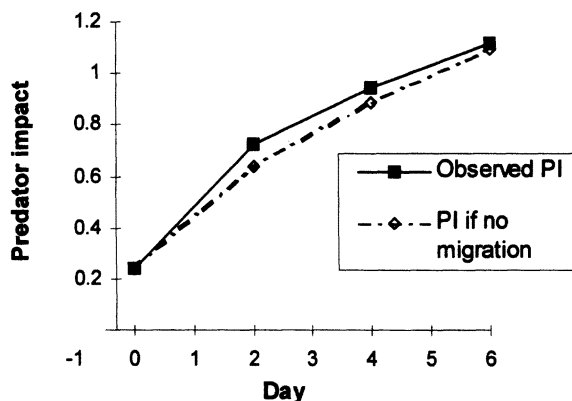

Fig. 8. Observed predator impact (PI) and the predator impact predicted if there were no crayfish movements into and out of pools. The observed predator impact was calculated as $PI = \ln(N_{ct}/N_{pt}) - \ln(N_{c0}/N_{p0})$, where N_{c0} and N_{p0} are initial densities in control and predator treatments and N_{ct} and N_{pt} are final densities. The predator impact predicted if there had been no movements was calculated as $N_{t+1} = N_t\, e^{-q}$ where q is daily per capita mortality rate.
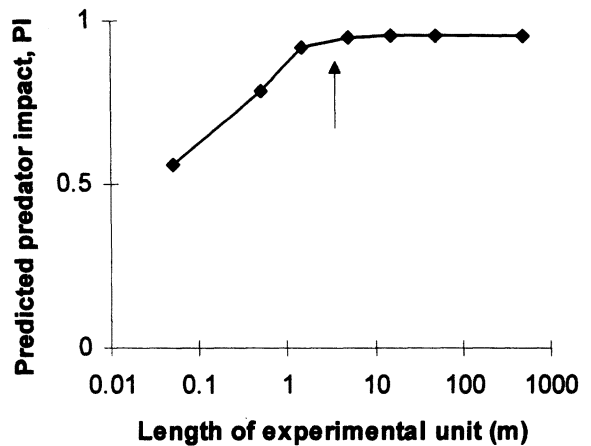

Fig. 9. Predicted relationship between predator impact and the size (length) of experimental arenas. Predictions were generated using eq. 1 in text, a time (t) of 6 d and estimated rates of predation and emigration. The predator impact index, PI, is given by the natural log of the ratio between densities in pools with and without fish added. The arrow indicates the scale of arenas (pools) used in the experiment.

When comparing the results of different studies, it is also important to consider the influence of experimental artifacts. In experiments addressing local distribution effects (as defined in the introduction), it is necessary to attain realistic predation and movement rates. Until recently stream ecologists have focused on the realism of predation rates while paying little attention to the realism of movement rates. For example, the choice of predator density is usually motivated with references to natural predator densities, while the choice of spatial scale and mesh size, which affect movement rates, usually is not considered. This lack of consideration of movement rates is an indication that unrealistic movement rates may have biased the results of many studies using cages or artificial channels. The present study and other studies that have used stream pools as experimental units should be less afflicted by this problem, since
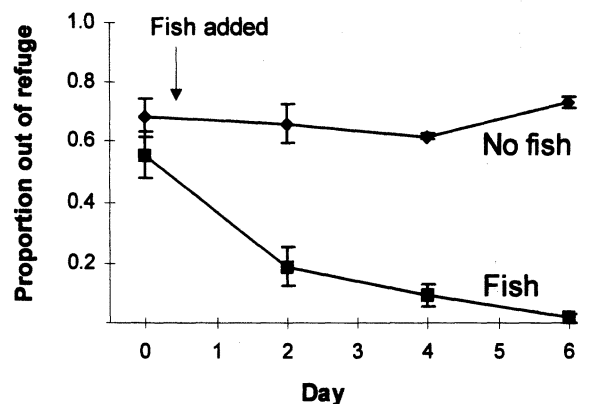

Fig. 10. The proportion of crayfish observed outside refuges in pools containing or lacking fish. Error bars denote ± 1 S.E.

mesh is not used to enclose predators and the spatial scale usually is similar to the scale of the patchiness that the experiment is meant to mimic (e.g., Cooper 1988, Sih et al. 1992, Wiseman et al. 1993). In this experiment the pools were slightly smaller than typical fish pools found in the survey (3–10 m vs 5–30 m, length), but the simulation indicated that the decreasing influence of movements at larger scales is expected to have little effect on the observed predator impact at these scales. Another mechanism that may bias movement rates in cages is that animals may be less likely to cross natural boundaries, such as those that separate different habitats (pools and riffles), than artificial boundaries (meshed cage sides) within a uniform habitat (cf. Holmqvist 1998).

Experimental conditions can also affect various types of predator and prey behaviors, resulting in unrealistic predation rates. For example, it has been suggested that small cages can affect predation rates because predator or prey movements are restricted or because prey become trapped in corners (Peckarsky 1991, Wilson 1991, McNally 1997). These types of artifacts should be less of a problem in experiments using natural habitat units. This experiment was performed in a previously fish-free stream which may have biased predation rates. Naïve prey typically have less efficient anti-predator responses, as exemplified by low refuge use during the first days after predator addition (e.g., Storfer 1997). Thus, it seems likely that the predation rates reported here were higher than would be observed in pools that have had fish for a long time. This may be regarded as an experimental artifact since the experiment was meant to mimic the situation in streams with fish.

An obvious disadvantage when using natural patches as experimental units is their relatively high variability compared to artificial units, particularly those stocked with uniform prey densities. Low power is a ubiquitous problem in experiments involving stream invertebrates owing to large sample-to-sample variation (e.g., Allan 1982, 1983). I considered variation among replicates by monitoring prey densities visually before and after predator addition. If I had not controlled for initial inter-replicate variation, the effect of fish on prey density would have been deemed non-significant (ANOVA of final densities, fish effect: $F_{1,6} = 3.8$, $P = 0.10$). At the same time, this experiment illustrates the danger of relying only on visual counts when the presence of a predator can influence the visibility of the response organism (Cooper 1988, Sih et al. 1992). Crayfish were 4–5 times less likely to be detected in fish than in control pools at the end of the experiment.

There are several lines of evidence suggesting that the effect of fish predation is larger in this system than in many other stream systems. Refuge availability is probably much lower in these stream pools than in many other stream habitats. Rocks that could provide cover were scarce in many pools and hydrological refuges,

i.e., areas where fish cannot feed due to high flow rates, are not found in these stream pools where flow is uniformly low. In fast-flowing streams with rocky substrate, I expect both interstitial and hydrological refuges to be more abundant. Second, fish in stream pools may rely on resources coming into the system, e.g., aquatic invertebrates and terrestrial insects trapped on the surface that drift into pools from upstream fish-free habitats. These allochthonous resources may increase the density of fish that can be sustained in a pool, thereby increasing the total predation pressure on invertebrates living in the pool (Englund 1993, Polis et al. 1995). This effect should be less pronounced in systems where fish have a more continuous distribution. Third, the low rates of prey movements that were independent of predators should also contribute to the strong effects on prey density. If prey exchange rates are high, the contrast between prey densities in fish and fish-free pools will decrease (Cooper et al. 1990).

Terrestrial predators and physical factors such as floods and pool depth may cause temporal and spatial variation in the impact of fish on crayfish. The survey showed that the effects of fish predation were strongest in the deepest pools where fish biomass was highest. The relationship between fish biomass and pool depth, where more and larger fish are found in deep relative to shallow pools, is very general, and it is believed to be caused by terrestrial predators (e.g., Power 1987, Harvey and Stewart 1991, Lonzarich and Quinn 1995). Wading and diving predators, e.g., birds and raccoons, typically prefer relatively large fish and their foraging efficiency decreases with increasing depth (Power 1987). This presumably causes larger fish to prefer deep pools. This reasoning suggests that the foraging activities of terrestrial predators create a refuge (shallow pools) for crayfish against fish predators. In a related study, I showed that this mechanism also affects the depth distribution of crayfish within pools (Englund unpubl.).

The finding that crayfish density in fish-free pools decreased with decreasing pool depth suggests that terrestrial predators may also partially determine the distribution of crayfish across pools of different depths. Experiments with tethered crayfish confirmed that the risk imposed by terrestrial predators is higher in shallow waters (5–15 cm) than in deep waters (40–70 cm) (Englund unpubl.). However, other factors may also influence this pattern. The risk of being displaced during floods is probably higher in shallow than deep pools. Many of the pools are separated by steep riffles or small waterfalls (0.2–1 m); consequently, current velocity can change from nearly zero during low flow to high levels during floods, and the substrate, which usually is smooth bedrock with a few scattered rocks, seems to offer little refuge from high flow disturbances.

Although low flow rates are typical for these streams during six months of the year (summer, fall), it is likely

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that occasional floods have important influences on the fish-crayfish interaction. Rainfall exceeding 25 mm per day, which often produces significant floods in these streams, occurs on average 5–6 times between May and November (University of Kentucky, Agricultural Weather Center). Data collected during an earlier experiment that was destroyed by a flood suggest that the drift of crayfish increases substantially during floods (Englund unpubl.). Thus, it is likely that crayfish movements during high flows tend to eliminate spatial patterns caused by predation during low flow (Cooper et al. 1990). This effect will be even more pronounced if crayfish use deep pools as flow refuge during flood events (cf. Lancaster et al. 1990, Lancaster 1996). Also, crayfish distributional patterns may be less pronounced during the wet season because crayfish movement rates are likely to be high and because fish can move between pools. Interestingly, high prey movement rates increase the proportion of the entire population that is exposed to predators, thereby increasing the predation rate on the entire prey population (Sih et al. 1988, Englund and Olsson 1996).

Several authors have found that different species of bass (*Micropterus* sp.) prey size-selectively on crayfish (e.g., Garvey et al. 1992, Rabeni 1992), and experiments with tethered crayfish suggest that this is also true for green sunfish and creek chubs (Englund unpubl.). Surprisingly, crayfish size differed very little between pools with and without fish, both in the experiment and in the survey. A possible explanation is that different sizes of crayfish show different propensities to migrate. If large but not small crayfish emigrate in response to fish, the weak effect of fish on crayfish size distributions could be explained.

In conclusion, this study shows that fish can have strong effects on the abundances and distributions of crayfish at the inter-pool scale in streams. Although this is the first experimental demonstration of such effects, other survey data suggest that similar effects occur on both smaller (Englund unpubl.) and larger spatial scales (Mather and Stein 1993). Because crayfish can affect the local densities of a wide array of stream-dwelling taxa, including a variety of macroinvertebrates and algae (Hart 1992, Creed 1994, Charlebois and Lamberti 1996, Perry et al. 1996), fish effects on crayfish distributions may have strong effects on entire stream communities.

References

Allan, J. D. 1982. The effects of reduction in trout density on the invertebrate community of a mountain stream. – Ecology 63: 1444–1455.

Allan, J. D. 1983. Predator-prey relationships in streams. – In: Barnes, J. R. and Minshall, G. W. (eds), Stream ecology: application and testing of general ecological theory. Plenum Press, New York, pp. 191–229.

Bechara, J. A., Moreau, G. and Hare, L. 1993. The impact of brook trout (*Salvelinus fontinalis*) on an experimental stream bottom community: the role of spatial and size refugia. – J. Anim. Ecol. 62: 451–464.

Carroll, M. L. and Highsmith, R. C. 1996. Role of catastrophic disturbance in mediating *Nucella-Mytilus* interactions in the Alaskan rocky intertidal. – Mar. Ecol. Prog. Ser. 138: 125–133.

Castell, L. L. and Sweatman, H. P. A. 1997. Predator-prey interactions among some iontertidal gatropods on the Great barrier reef. – J. Zool. 241: 145–159.

Charlebois, P. M. and Lamberti, G. A. 1996. Invading crayfish in a Michigan stream: direct and indirect effects on periphyton and macroinvertebrates. – J. N. Am. Benthol. Soc. 15: 551–563.

Cooper, S. D. 1988. Responses of aquatic insects and tadpoles to trout. – Int. Ver. Teor. Angew. Limnol. Verhandl. 23: 1698–1703.

Cooper, S. D., Walde, S. J. and Peckarsky, B. L. 1990. Prey exchange rates and the impact of predators on prey populations in streams. – Ecology 71: 1503–1514.

Cooper, S. D., Diehl, S., Kratz, K. and Sarnelle, O. 1998. Implications of scale for patterns and processes in stream ecology. – Aus. J. Ecol. 23: 27–40.

Creed, R. P. 1994. Direct and indirect effects of crayfish grazing in a stream community. – Ecology 75: 2091–2103.

Dahl, J. and Greenberg, L. 1996. Impact of stream benthic prey by benthic vs drift feeding predators: a meta-analysis. – Oikos 77: 177–181.

Englund, G. 1993. Effects of density and food availability on habitat selection in a net-spinning caddis larva, *Hydropsyche siltalai*. – Oikos 68: 473–480.

Englund, G. 1997. Importance of spatial scale and prey movements in predator caging experiments. – Ecology 78: 2316–2325.

Englund, G. and Olsson, T. I. 1996. Treatment effects in a predator caging experiment: influence of predation rate and prey movements. – Oikos 77: 519–528.

Englund, G., Sarnelle, O and Cooper, S. D. The importance of data selection criteria; meta-analysis of stream predation experiments., – Ecology (in press)

Garvey, J. E., Stein, R. A. and Heather, T. M. 1992. Assessing how fish predation and interspecific prey competition influence a crayfish assemblage. – Ecology 75: 532–547.

Hall, S. J., Raffaelli, D. and Turrell, W. R. 1990. Predator-caging experiments in marine systems: a reexamination of their value. – Am. Nat. 136: 657–672.

Hart, D. D 1992. Community organization in streams: the importance of species interactions, physical factors and chance. – Oecologia 91: 220–228.

Harvey, B. C. and Stewart, A. J. 1991. Fish size and habitat depth relationships in headwater streams. – Oecologia 87: 336–342.

Holmqvist, J. G. 1998. Permeability of patch boundaries to benthic invertebrates: influences of boundary contrast, light level, and faunal density and mobility. – Oikos 81: 558–566.

Lancaster, J. 1996. Scaling the effects of predation and disturbance in a patchy environment. – Oecologia 107: 321–331.

Lancaster, J., Hildrew, A. G. and Townsend, C. R. 1990. Stream flow and predation effects on the spatial dynamics of benthic invertebrates. – Hydrobiologia 203: 177–190.

Lonzarich, D. G. and Quinn, T. P. 1995. Experimental evidence for the effect of depth and structure on the distribution, growth, and survival of stream fishes. – Can. J. Zool. 73: 2223–2230.

Malmqvist, B. and Sackmann, G. 1996. Changing risk of predation for a filter-feeding insect along a current velocity gradient. – Oecologia 108: 450–458.

Mather, M. A. and Stein, R. A. 1993. Direct and indirect effects of fish predation on the replacement of a native crayfish by an invading cogener. – Can. J. Fish. Aquat. Sci. 50: 1279–1288.

McNally, R. 1997. Scaling artefacts in confinement experiments: a simulation model. – Ecol. Model. 99: 229–245.

Osenberg, C. W., Sarnelle, O. and Cooper, S. D. 1997. Effect size in ecological experiments: the application of biological models in meta-analysis. – Am. Nat. 50: 798–812.

Osenberg, C. W., Sarnelle, O., Cooper, S. D. and Holt, R. (in press). Resolving ecological questions through meta-analysis: goals, metrics, and models. – Ecology.

Peckarsky, B. L. 1991. A field test of resource depression by predatory stonefly larvae. – Oikos 61: 3–10.

Perry, W. L., Lodge, D. M. and Lamberti, G. A. 1996. Impact of crayfish predation on exotic zebra mussels and native invertebrates in a lake outlet stream. – Can. J. Fish. Aquat. Sci. 54: 120–125.

Persson, L., Andersson, J, Wahlström, E. and Eklöv, P. 1996. Size specific interactions in lake ecosystems: predator gape limitation and prey growth rate and mortality. – Ecology 77: 900–911.

Polis, G. A., Holt, R. D. Menge, B. A. and Winemiller, K. O. 1995. Time, space and life history: influences of food webs. – In: Polis, G. A. and Winemiller, K. O. (eds), Foodwebs. Chapman and Hall, New York, pp. 435–460.

Power, M. E. 1987. Predator avoidance by grazing fishes in temperate and tropical streams: importance of stream depth and prey size. – In: Kerfoot, W. C. and Sih, A. (eds), Predation: direct and indirect impacts on aquatic communities. Univ. Press of New England Hanover, NH, pp. 333–351.

Power, M. E. 1990. Effects of fish in river food webs. – Science 250: 811–814.

Rabeni, C. F. 1992. Trophic linkage between stream centrarchids and their crayfish prey. – Can. J. Fish. Aquat. Sci. 49: 1714–1721.

Sih, A. 1992. Integrative approaches to the study of predation. – Ann. Zool. Fenn. 29: 183–198.

Sih, A. and Wooster, D. A. 1994. Prey behavior, prey dispersal, and predator impacts on stream prey. – Ecology 75: 1207–1217.

Sih, A., Crowley, P., McPeek, M., Petranka, J. and Stroheimer, K. 1985. Predation, competition and prey communities: a review of field experiments. – Annu. Rev. Ecol. Sys. 16: 269–311.

Sih, A., Petranka, J. W. and Kats, L. B. 1988. The dynamics of prey refuge use: a model and tests with sunfish and salamander larvae. – Am. Nat. 132: 463–483.

Sih, A., Kats, L. B. and Moore, R. D. 1992. Effects of predatory sunfish on the density, drift, and refuge use of stream salamander larvae. – Ecology 73: 1418–1430.

Soluk, D. A. 1993. Multiple predator effects: predicting combined functional response of stream fish and invertebrate predators. – Ecology 74: 219–225.

Storfer, A. 1997. Gene flow and local adaptation in the streamside salamander (*Ambystoma barbouri*). – Ph.D. thesis, Univ. of Kentucky, Lexington, KY.

SYSTAT, 1996. Systat for Windows. – SPSS inc., Evanston, IL.

Wilson, H. W. 1991. Competition and predation in marine soft-sediment communities. – Annu. Rev. Ecol. Sys. 21: 221–241.

Wiseman, S. W., Cooper, S. D. and Dudley, T. L. 1993. The effects of trout on epibenthic odonate naiads in stream pools. – Freshwat. Biol. 30: 133–145.

Wooster, D. 1994. Predator impacts on stream benthic prey. – Oecologia 99: 7–15.

Wooster, D. 1996. Predator effects on stream prey behavior and local density. – Ph.D. thesis, Univ. of Kentucky, Lexington, KY.

Wootton, J. T., Parker, M. S. and Power, M. E. 1996. Effects of disturbance of river food webs. – Science 273: 1558–1561.

Zaret, T. M. 1980. Predation in freshwater communities. – Yale Univ. Press, New Haven, CT.