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MORE THAN PREDATOR AND PREY : A REVIEW OF INTERACTIONS BETWEEN FISH AND CRAYFISH

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FISH
CRAYFISH
PREDATION
BENTHOS
ECOSYSTEM ENGINEERING
COMPETITION

ABSTRACT. – Crayfish are a major constituent of benthic invertebrate production in both lentic and lotic habitats. Crayfish also provide an important food resource for many fish. Because of their abundance and relatively large body size, the interactions between fish and crayfish can have profound effects on the rest of the benthic community. In this paper we will 1) review the well-studied trophic and ecological relationships between fish and crayfish and 2) posit other potentially important but less-studied interactions. Fish and crayfish have generally been viewed as predator-prey. Crayfish are not easy prey for many fish because of their large size and defensive armor, and a number of studies have shown that the relative size of fish and crayfish is a major factor affecting the predator-prey interaction between these species. Crayfish may also compete with small benthic fish for food and shelter. Further, crayfish have been implicated in the declines of fish populations due to direct predation on fish eggs, and crayfish may indirectly affect fish populations through their destruction of macrophyte beds, which are important juvenile fish habitats. Many of these more subtle interactions between fish and crayfish were first observed when exotic species of crayfish were introduced to a new system (either intentionally or accidentally). More experimental work and long-term data sets are necessary to discover the importance of these less-studied interactions between crayfish and fish. Careful consideration should be given to the multiple pathways of fish-crayfish interactions when managing, farming, introducing, or studying these aquatic macroconsumers.

POISSONS
ÉCREVISSES
PRÉDATION
BENTHOS
INGÉNIERIE D'UN ÉCOSYSTÈME
COMPÉTITION

RÉSUMÉ. – Les Ecrevisses sont un constituant majeur de la production des invertébrés benthiques dans les habitats lentiens et lotiens. Elles représentent aussi une importante ressource nutritive pour nombre de Poissons. En raison de leur abondance et de la taille relativement élevée de leur corps, les interactions entre les Poissons et les Ecrevisses peuvent avoir de profonds effets sur le reste de la communauté benthique. Nous présentons ici 1) une synthèse à propos des relations trophiques et écologiques déjà bien connues entre les Poissons et les Ecrevisses, 2) d'autres interactions potentiellement importantes mais moins bien étudiées. Les Poissons et les Ecrevisses ont été généralement perçus comme prédateurs-proies. Les Ecrevisses ne sont pas des proies faciles pour de nombreux Poissons à cause de leur forte taille et de leur armement défensif, et nombre d'études ont montré que la taille relative Poisson-Ecrevisse est un facteur majeur affectant l'interaction prédateur-proie entre ces espèces. Les Ecrevisses peuvent aussi entrer en compétition avec de petits Poissons benthiques pour la nourriture et l'abri. En outre, elles ont été impliquées dans le déclin des populations de Poissons en raison de la prédation directe sur les œufs de Poissons qu'elles exercent et elles peuvent affecter indirectement les populations de Poissons par la destruction des herbiers de macrophytes qu'elles provoquent, ces derniers constituant des habitats importants pour les Poissons juvéniles. Nombre de ces interactions subtiles entre Poissons et Ecrevisses ont été tout d'abord observées lorsque des espèces exotiques d'Ecrevisses ont été introduites dans un nouveau système (intentionnellement ou accidentellement). De nouveaux travaux expérimentaux et des données à long terme sont nécessaires pour découvrir l'importance de ces interactions Ecrevisses-Poissons peu étudiées. Une attention particulière devrait être accordée aux multiples possibilités d'interactions en ce qui concerne l'aménagement, l'élevage, l'introduction ou les études de ces macro-consommateurs aquatiques.

Table I. – Annual production (kg/ha/yr) of crayfish and percentage consumed by predatory fish in four natural systems.

System: lotic/lentic	Crayfish Annual Production (kg/ha/yr)	Percent of Annual Production consumed by fish	Fish species	References
Lentic				
3 Michigan lakes	17-141.8	1-40 ^a	<i>Salvelinus fontinalis</i>	Gowing and Momot 1979
Lotic				
Missouri stream	415-505	33 ^b	<i>Ambloplites rupestris</i> and <i>Micropterus dolomieu</i>	Rabeni 1992
Michigan stream	415	15 >35 ^c	<i>Micropterus dolomieu</i> <i>Ambloplites rupestris</i>	Vannote and Ball 1972
West Virginia stream	70	31 35 10	<i>Ambloplites rupestris</i> <i>Micropterus dolomieu</i> <i>Pylodictis olivaris</i>	Roell and Orth 1993, Roell 1989 (from Rabeni 1992)

^a dependent upon fish density, ^b converted from g dry wt/m² (from Momot 1995), ^c estimated value from Vannote and Ball (1972).

INTRODUCTION

Recent research in freshwater systems has documented a rich array of ecological interactions between fish and benthic invertebrates. These interactions include top-down effects of fish on benthos; e.g., effects of fish on invertebrate densities (Diehl 1995, Batzer 1998), invertebrate size-structure (Mittelbach 1988), species composition (Power 1992, McPeck 1990), behaviour (Wooster & Sih 1995, Lima 1998), and morphology (Johansson & Samuelsson 1994). Similarly, bottom-up effects of benthic invertebrates may significantly influence fish diets (Crowder & Cooper 1982), habitat use (Werner *et al.* 1983a), growth rates (Diehl & Kornijów 1998), and abundances (McIvor & Odum 1988). In many of these interactions, body size plays an important role. For example, most freshwater fish are size-selective foragers (Wootton 1990, Gerking 1994), often feeding preferentially on large invertebrates (Mittelbach 1988). Consequently, intense fish predation may shift the size-structure of benthic invertebrate communities towards smaller individuals and smaller species (Strayer 1991).

In most cases, fish are much larger than the benthic invertebrates they feed upon. When this is true, the relationship between invertebrate size and fish foraging preference is relatively simple – bigger is better. Larger invertebrate prey generally provide the highest energetic gain (Mittelbach 1981, Persson & Crowder 1998), and fish growth rates have been shown to be positively correlated with the abundance of large, benthic invertebrates (Mittelbach 1988). However, some benthic invertebrates may reach large enough

sizes, or may be sufficiently well armored, that larger individuals are no longer vulnerable to most fish predators. When this is the case, trophic interactions between fish and benthos become more complex.

Crayfish (Decapoda) are among the largest freshwater benthic invertebrates. As they often dominate benthic invertebrate biomass, crayfish provide a rich prey resources for some freshwater fish. Due to their large size and defensive armor, crayfish are not easy prey for all fish which complicates the trophic interactions. In this paper, we first document the importance of crayfish to benthic invertebrate production in many freshwater systems, and the importance of crayfish to the diets of benthic-feeding fish. We then examine predator-prey interactions between fish and crayfish. Lastly, we explore some less-well studied direct and indirect interactions between these two freshwater macroconsumers.

TROPHIC RELATIONSHIPS

Crayfish are often significant components of benthic invertebrate production (Rabeni *et al.* 1995, Momot 1995), and many studies report crayfish dominating benthic standing stock biomass (Huryn & Wallace 1987, Griffith *et al.* 1994, Momot 1995). Because crayfish are omnivores, they provide direct links from both primary production and detrital-based food webs to fish (Vannote & Ball 1972, Rabeni 1992, Roell & Orth 1993). Fish have been shown to be important consumers of annual crayfish production in many systems (Table I), and fish predation may provide

Table II. – Results of gut content analyses in several freshwater systems where fish were found eating crayfish.

System and location	Crayfish Species	Fish species	Proportion of diet (wt mass)	frequency in diet ^a	Reference
Lentic					
Kansas, USA	<i>Orconectes nais</i>	<i>Micropterus salmoides</i>		0.6-0.85	Rickett 1974 ^b
Illinois, USA	<i>Orconectes virilis</i>	<i>Micropterus dolomieu</i>	44-49		Ross et al. 1995
Manitoba, Can	<i>Cambarus sp.</i>	<i>Micropterus dolomieu</i>		0.68	Fedoruk 1966
Michigan, USA*	<i>Orconectes virilis</i>	<i>Ambloplites rupestris</i>		0.42	Chircinske et al. unpub. data
Manitoba, Can	<i>Cambarus sp.</i>	<i>Stizostedion vitreum</i>		0.03	Fedoruk 1966
Michigan, USA	<i>Orconectes virilis</i>	<i>Salvelinus fontinalis</i>	10-70		Gowing and Momot 1979
Michigan, USA ⁺	<i>O. virilis, O. propinquus</i>	<i>Perca flavescens</i>		0.45	Quinn and Janssen 1989
Michigan, USA ⁺	<i>Orconectes propinquus</i>	<i>Perca flavescens</i>	2-60		Wells 1980
Michigan, USA*	<i>Orconectes virilis</i>	<i>Perca flavescens</i>		0.3	Chircinske et al. unpub. data
Norway	<i>Astacus astacus</i>	<i>Perca fluviatilis</i>		0.93	Dehli 1981
Kansas, USA	<i>Orconectes nais</i>	<i>Ictalurus melas</i>		0-0.16	Rickett 1974 ^b
Lotic					
Michigan, USA	<i>Orconectes propinquus</i>	<i>Micropterus dolomieu</i>		0.97	Vannote and Ball 1972
W. Virginia, USA	various ^c	<i>Micropterus dolomieu</i>	60-85		Roell and Orth 1993
Michigan, USA	<i>Orconectes propinquus</i>	<i>Ambloplites rupestris</i>		0.66	Vannote and Ball 1972
W. Virginia, USA	various ^c	<i>Ambloplites rupestris</i>	55-80		Roell and Orth 1993
W. Virginia, USA	various ^c	<i>Pylodictis olivaris</i>	70-95		Roell and Orth 1993
s. England, UK	<i>Asticus pallipes</i>	<i>Esox lucius</i>		<0.1	Mann 1976

^a proportion of fish found with at least one crayfish in their gut contents (empty stomachs excluded when possible). ^b experimental ponds stocked with fish and crayfish. ^c mixed diets of *Orconectes sanbornii*, *Orconectes virilis*, and *Cambarus sciotensis*. ⁺ Lake Michigan ^{*} Lake Huron

top-down control on crayfish densities. For example, Mather & Stein (1993) and Lodge & Hill (1994) found a significant inverse relationship between densities of predaceous fish and crayfish. Svärdson (1972) further showed that in Sweden, where eels (*Anguilla anguilla*) and crayfish (*Astacus astacus*) are largely allopatric, that the introduction of eels generally leads to the local extermination of crayfish. Largemouth bass (*Micropterus salmoides*) have also been shown to significantly reduce or eliminate crayfish from aquaculture ponds (0.04-1 ha) (Rickett 1974, Taub 1972). In contrast to the above studies, Gowing & Momot (1979) concluded that predation by brook trout (*Salvelinus fontinalis*) had little control of crayfish production in an inland Michigan (USA) lake. However, due to gape limitation, brook trout in this study were only able to feed upon juvenile crayfish, limiting their ability to control crayfish numbers. Additional long-term experimental studies using natural densities of crayfish and their predators are needed to determine the extent of "top-down" influences on crayfish abundances.

The importance of crayfish in diets of several fish species is summarized in Table II. Some fish

species feed heavily on crayfish (e.g., smallmouth bass, *Micropterus dolomieu*, rock bass, *Ambloplites rupestris*, and flathead catfish, *Pylodictis olivaris*), while other fish are more opportunistic and consume crayfish infrequently (e.g., walleye, *Stizostedion vitreum*, black bullhead, *Ictalurus melas*, northern pike, *Esox lucius*). Small, gape-limited fish or fully-pelagic fish, are likely to feed on only the smallest crayfish.

The importance of crayfish in fish diets increases with fish age and size. In general, YOY (young of the year) fish rarely consume crayfish due to limitations in fish mouth gape (Roell & Orth 1993, Rabeni 1992). For those fish species that feed extensively on crayfish, the percentage of crayfish in the diet increases during ontogeny (Keast 1977, Dehli 1981, Roell & Orth 1993). These ontogenetic diet shifts are due to changes in the relative vulnerability of crayfish as fish size increases (Stein 1977). The proportion of crayfish in a species' diet may also vary widely among systems (Table II). For example, Gowing & Momot (1979) found that trout from lakes with high trout stocking densities consumed more crayfish than trout stocked into lakes at low density. Wells (1980) found that perch foraging over rocky

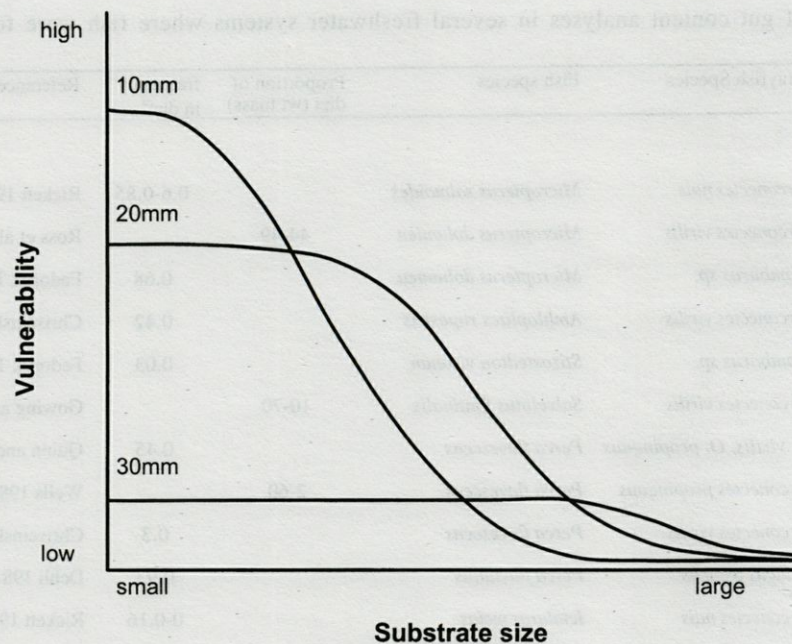


Fig. 1. – Hypothetical relationship between crayfish size (10-30 mm CL), substrate size, and vulnerability to fish predation.

substrate in Lake Michigan utilized crayfish to a greater degree than perch foraging over sandy bottoms. Crayfish are generally more common in rocky substrate (Janssen & Quinn 1985, Kershner & Lodge 1995) and therefore perch may consume crayfish in proportion to their abundance. Ward & Neumann (1998) suggested that largemouth bass consumption of crayfish changes with seasons (most eaten during summer-fall), and that bass consume more crayfish in systems where forage fish are scarce. Seasonal variation in average crayfish size and molting stage also affects their vulnerability to fish predation. Most crayfish molt 1-3 times per growing season. Following a molt, even a large crayfish can be extremely vulnerable to predation (Stein 1977). Below we consider in more detail the factors that influence the predator-prey interaction between fish and crayfish.

TRADITIONAL PREDATOR-PREY STUDIES

Effects of body size and substrate

A number of studies have examined interactions between predatory fish and their crayfish prey. Stein & Magnuson (1976) and Stein (1977) report a series of experiments in which smallmouth bass preyed upon crayfish (*Orconectes propinquus*). In these experiments, crayfish size was inversely related to feeding preference with the smallest crayfish eaten first. Reproductive (F1) males and gravid females were the least

vulnerable life stages, while recently molted crayfish were the most vulnerable. Stein (1977) also found that the interaction between fish and crayfish size was influenced by substrate size. If we assume that absolute vulnerability to fish predation cannot increase above that experienced on bare sand, we can hypothesize the interaction between crayfish size and substrate size looks something like Fig. 1. At small substrate sizes (sand), small crayfish have the highest vulnerability to predation. When substrate (rock) size increases to a threshold value, the smallest crayfish (10 mm) experience a refuge from predation by using the substrate as shelter. Consequently, intermediate-sized crayfish (20 mm) are most vulnerable and eaten first. As substrate size increases still further, a greater number of these intermediate size crayfish can utilize the substrate. Large crayfish (30 mm) can utilize only large rocks for shelter but maintain relatively low vulnerability regardless of the substrate size. Although this relationship is consistent with experimental evidence in gravel bottom pools, the ability of crayfish to burrow in soft sediments or clay may change the interaction substantially (see Vorburger & Ribic 1999).

Effects of fish on crayfish behaviours

In the presence of predatory fish, crayfish alter their microdistributions (Stein 1977, Hill & Lodge 1994) and activity levels (Stein & Magnuson 1976, Resetarits 1991). Field studies and experiments indicate crayfish use more cobble habitat (or otherwise structured habitat) and use less open

sand in the presence of predaceous fish (Stein & Magnuson 1976, Stein 1977, Hill & Lodge 1994, Lodge & Hill 1994, Kershner & Lodge 1995, Mather & Stein 1993). In the absence of predatory fish, crayfish tend to prefer the substrate which provides the greatest food availability, while in the presence of predators crayfish prefer substrate with the most available refuge (Hill & Lodge 1994). Regardless of the presence of fish predators, crayfish become more evenly distributed across sand, cobble, and macrophyte habitats at night (Hill & Lodge 1994).

Crayfish foraging activity is generally suppressed in the presence of predatory fish (Stein & Magnuson 1976, Resetarits 1991), while chelae displays and other behaviours reducing vulnerability increase (Stein & Magnuson 1976). Crayfish with large chelae (males) seem to be affected least by the presence of fish predators (Stein 1977, Stein & Magnuson 1976). Blake & Hart (1993) studied the effects of chemical and visual predator cues on crayfish activity levels. Crayfish (*Pacifastacus leniusculus*) given chemical stimuli of either perch (*Perca fluviatilis*) or eels (*Anguilla anguilla*) reduced activity levels during both night and day periods. When given visual stimuli without prior chemical cues, crayfish only changed behavioural patterns during the day. Hamrin (1987) also found that patterns of crayfish diel activity levels were altered by the presence of fish predators. However, in Hamrin's study, total crayfish activity actually increased in the presence of crepuscular fish predators. Hamrin's (1987) result runs counter to the findings of Stein & Magnuson (1976), Resetarits (1991), and Blake & Hart (1993). This result was probably due to predatory treatments that did not involve both visual and chemical cues. In the predator treatments, perch were placed in plexiglass tubes, which likely limited the chemical signals necessary for crayfish to alter (decrease) nighttime activity levels. In summary, the presence of predatory fish has negative effects on crayfish activity levels. Further, these reductions in activity have been shown to have significant negative effects on crayfish growth rates (Resetarits 1991, Hill & Lodge 1998). In addition, Hill & Lodge (1995) found increased macrophyte and macroinvertebrate densities in mesocosms where crayfish experienced the presence of bass.

Crayfish species are differentially susceptible to fish predation (Didonato & Lodge 1993, Garvey *et al.* 1994), and fish predation may facilitate invasions by exotic crayfish species (Hill & Lodge 1998, Söderbäck 1994). For example, in northern Wisconsin (USA) *Orconectes rusticus* (the rusty crayfish) has invaded lakes previously occupied by two congeners (*O. propinquus* and *O. virilis*) (Olsen *et al.* 1991, Hobbs *et al.* 1989). *O. rusticus* has excluded the native crayfish in these lakes

and the evidence suggests that fish predation is a significant mechanism involved in the replacement of the native crayfish species by *O. rusticus* (Didonato & Lodge 1993, Garvey *et al.* 1994, Hobbs *et al.* 1989, Hill & Lodge 1998). In mixed species assemblages, *O. rusticus* are more successful at obtaining available shelters and are relatively less vulnerable to fish predation in open sand (Garvey *et al.* 1994). As a result, bass selectively feed on the exposed and relatively more vulnerable *O. virilis* and *O. propinquus*, while *O. rusticus* are avoided (and thereby persist). Overall, *O. rusticus* is able to maintain higher growth and lower mortality than the two native *Orconectes* in the presence of predaceous fish (Hill & Lodge 1998). This example is likely analogous to the replacement of *Astacus astacus* by the introduced *Pacifastacus leniusculus* in Swedish lakes where the data indicates preferential perch predation on the native *A. astacus* (Söderbäck 1994).

INTERACTIONS BETWEEN CRAYFISH AND SMALL BENTHIC FISH

Although small benthic fish like sculpins (European bullheads -*Cottus* spp.) or darters (*Etheostoma* spp.) are generally too small to feed on crayfish, these fish species share common adult sizes, food resources, and predators with crayfish. Therefore, crayfish and smaller benthic fish may interact competitively. However, these interactions are less well-studied than the standard predator-prey interactions of fish and crayfish. Studies of interactions between small benthic fish and crayfish include competition for limited shelters (Guan & Wiles 1997), competition for food (Miller *et al.* 1992), behavioral interactions in the presence of predators (McNeely *et al.* 1990), and combinations of these interactions (Rahel & Stein 1988, Wojdak & Miner unpubl manuscr).

In studies of competition for shelters, the results are mixed and dependent upon the species of fish and crayfish studied. Guan & Wiles (1997) found significant competition for shelter between the introduced crayfish *Pacifastacus leniusculus* and two benthic fish (*Cottus* sp. and *Neomacheilus* sp.) in a British lowland river. In laboratory experiments, crayfish excluded fish from shelters, and field surveys showed inverse correlations between fish and crayfish abundances (Guan & Wiles 1997). Rahel & Stein (1988) found similar results with darters (*Etheostoma* sp.) and the crayfish *O. rusticus*. In the laboratory, crayfish evicted darters from shelters and caused them to increase overall activity; this increased darter susceptibility to smallmouth bass predation. Wojdak and Miner (unpubl manuscr) found that an introduced fish species, the round goby (*Neogo-*

bius melanostomus) had the opposite effect on crayfish (*Orconectes rusticus*). In laboratory experiments, gobies competitively excluded crayfish from shelters and exposed the crayfish to increased bass predation. Thus, results of competition for shelter seem dependent upon the specific pair of species under study.

McNeely *et al.* (1990) found a complex behavioral interaction between *O. putnami* and the mottled sculpin (*C. bairdi*). In the presence of bass and crayfish, sculpins experienced less predation. This interaction involved a change in predator-avoidance behavior by the sculpin, dependent upon crayfish presence or absence. When crayfish were absent the sculpin utilized few shelters and employed a stationary behavior to avoid predator detection. In the presence of crayfish, sculpin increased use of shelter to avoid predation. The crayfish in this study were relatively invulnerable to predation and did not alter shelter use dependent upon bass presence or absence. However, the increased benthic activity of crayfish was thought to « draw the attention of the bass away from the sculpin » (McNeely *et al.* 1990).

Crayfish and equivalent-sized small benthic fish share common predators and shelters. From the above studies it is clear that competitive outcomes for common refugia are less than predictable. Complex behavioral interactions and agonistic exclusions act to make the outcomes of these interactions specific to particular fish-crayfish pairs. If introduced species of benthic fish and crayfish competitively exclude natives, this could lead to restructuring of the benthic food web as carnivorous benthic fish and omnivorous crayfish replace each other. Competition between benthic fish and crayfish for common food resources is a virtually unstudied area that deserves future research.

Trophic energy transfer, predator-prey interactions, and competition are the most obvious ways which fish and crayfish may interact. However, there are a number of other potential pathways by which fish and crayfish populations may be linked. In the next section, we outline a few of the more subtle interactions that may occur between fish and crayfish. Much of the impetus for this section comes from studies that have examined the effects of exotic crayfish introductions (Hobbs *et al.* 1989) which have led to many insights about the roles of crayfish in freshwater communities (Lodge *et al.* 1998).

POTENTIAL NEGATIVE EFFECTS OF CRAYFISH ON FISH

Egg predation

In some northern Wisconsin lakes (USA), the decline of gamefish populations has been attrib-

ted to the invasion of the exotic crayfish *O. rusticus* (Hobbs *et al.* 1989). Egg predation has been proposed as one mechanism causing declines in bass, other sunfish (Centrarchidae), walleye, and lake trout (*Salvelinus namaycush*). Observations indicate that sunfish only nest in areas where *O. rusticus* have been experimentally removed (Wilson, University of Wisconsin, Madison, USA pers comm). In experiments, crayfish (*Orconectes* spp.) ate lake trout eggs (Savino & Miller 1991, Horns & Magnuson 1981), and rates of egg-predation ranged from 2-5 eggs/crayfish/day, depending upon temperature, substrate, and crayfish species. Given this rate of predation, Savino & Miller (1991) concluded that predation by crayfish on lake trout eggs will only be important over a restricted set of conditions; high crayfish density and/or low egg density within cobble habitat.

The potential for crayfish to consume the eggs of warmwater fish may be greater. Bass and sunfish spawn at much warmer temperatures than lake trout, and Horns & Magnuson (1981) have shown that the rate of egg consumption by crayfish increases with temperature. Further, most bass and sunfish concentrate their eggs in shallow, littoral zone nests, which may make them more vulnerable to crayfish predation than the widely scattered eggs of trout or walleye. If crayfish can infiltrate these nests and/or feed unnoticed at night, egg predation on warmwater gamefish may be significant.

Destruction of macrophyte beds and effects on fish recruitment

Macrophytes are known to disappear in the presence of crayfish (Feminella & Resh 1989, Matthews & Reynolds 1992, Lodge *et al.* 1994, Olsen *et al.* 1991, Chambers *et al.* 1990). Some of the macrophyte destruction is due to active crayfish feeding, while a substantial amount is apparently due to non-consumptive fragmentation (Lodge & Lorman 1987, Olsen *et al.* 1991). In this manner, crayfish may be viewed as ecosystem engineers – modifying the structural complexity of littoral zones through non-consumptive means (Lawton 1994, Jones *et al.* 1994).

For many fish species, macrophyte beds serve as important juvenile habitat (Mittelbach 1981). Dense stands of littoral-zone macrophytes provide shelter from predatory fish (Werner *et al.* 1983b), and also provide a source of vegetation-dwelling invertebrate prey (Osenberg & Mittelbach 1989, Persson & Greenberg 1990). Complex structural habitats (macrophyte beds) decrease the efficiency of piscivorous fish (Persson & Crowder 1998), affording protection for growing juvenile fish. When juveniles of different fish species take advantage of this littoral vegetated habitat, com-

petition may occur (Mittelbach 1984, 1988). If macrophyte beds shrink following crayfish introductions, competition between juvenile fish for the remaining macrophyte refuge or associated invertebrate prey may increase. A loss of vegetated habitat may also lead to changes in competitive advantage between fish species (Persson 1991).

When exotic crayfish species such as *O. rusticus* and *Procambarus clarki* were introduced to water bodies, large losses in macrophytes were observed (Lodge & Lorman 1987, Lodge *et al.* 1994, Feminella & Resh 1989). Additional studies of *P. leniusculus* and *O. virilis* in Sweden and Canada respectively, support the hypothesis that exotic crayfish species will have large effects on macrophyte biomass, species richness, and associated invertebrate community structure/abundance when introduced (Nyström & Strand 1996, Chambers *et al.* 1990, Hanson & Chambers 1995). The links between macrophyte losses and effects on fish recruitment are logically sound, yet remain unexplored.

CONCLUSIONS

Fish and crayfish have traditionally been viewed as predator and prey. Recent studies, however, document a wealth of potential interactions between these macroconsumers. Many of these interactions were first observed when an exotic species of crayfish entered a system. Although predatory fish generally suppress crayfish activity, growth, and population densities, there are a number of examples where fish have been shown to have much smaller impacts on exotic crayfish. In one well-documented example, fish were found to accelerate the rate at which the exotic crayfish, *O. rusticus*, invades new lakes (Hill & Lodge 1998).

Although conclusive data is lacking, introduced benthic fish (eg., gobies) and crayfish (*P. leniusculus*), may competitively exclude native fish and crayfish with potentially important consequences for structuring of benthic food webs. Future work in this area should 1) investigate the invasion ecology and competitive arenas between benthic fish and crayfish, and 2) examine the trophic effects of swapping carnivorous benthic fish and omnivorous crayfish in benthic food webs.

While most studies have focused on the predatory effects of fish on crayfish, there are a number of ways in which crayfish may negatively effect or control fish production. For example, crayfish eat fish eggs, and warmwater fish species may be especially vulnerable to crayfish egg predation. Crayfish also destroy macrophytes, which in turn

reduce important habitat for juvenile fish (Mittelbach 1984, Persson & Crowder 1998). Future research in these areas should concentrate on the consequences of egg predation and macrophyte destruction (ecosystem engineering) for warmwater fish production. Between species differences in egg predation and macrophyte destruction should be examined to highlight potential consequences of crayfish introductions. Understanding the mechanisms of interaction between fish and crayfish is crucial if we are to be able to predict the consequences of species introductions, both intentional and accidental (Lodge *et al.* 1998).

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