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Freshwater Mollusks Survive Fish Gut Passage

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ABSTRACT. Freshwater mollusks figure prominently in the diets of humpback whitefish (*Coregonus pidschian*) and broad whitefish (*C. nasus*), two benthic-feeding coregonid species. A recent examination of pea clams (Sphaeriidae), valve snails (Valvatidae), and pond snails (Lymnaeidae) from the lower digestive tracts of these fish found that many of the mollusks were alive. Survival completely through gut passage would indicate a dispersal mechanism for freshwater mollusks that has not been previously recognized. A field investigation was conducted with wild-caught humpback and broad whitefish to test the hypothesis that clams and snails are capable of surviving complete gut passage. Wild fish were captured alive and held in collection totes to obtain feces samples. Pea clams and valve snails were abundant in fish feces, and pond snails were present but not abundant. An average of 483 pea clams and 833 valve snails per fish were observed to have survived complete gut passage, while only a single surviving pond snail was found. These findings suggest that fish may play an important role in the dispersal of freshwater mollusks within freshwater systems.

Key words: Sphaeriidae, clams, Valvatidae, Lymnaeidae, snails, coregonid fish, gut passage

RÉSUMÉ. Les mollusques d'eau douce constituent une partie imposante du régime alimentaire du corégone à bosse (*Coregonus pidschian*) et du corégone tschir (*C. nasus*), deux corégonidés à alimentation benthique. L'analyse récente de pisidies (Sphaeriidae), de valvatidés (Valvatidae) et de lymnéidés (Lymnaeidae) provenant du tractus digestif inférieur de ces poissons a permis de constater que grand nombre de ces mollusques étaient toujours en vie. Le fait d'avoir entièrement survécu dans le passage digestif porterait à croire qu'il s'agirait là d'un mécanisme de dispersion des mollusques d'eau douce qui n'a jamais encore été reconnu. Une étude sur le terrain a été réalisée au moyen de corégones à bosse et de corégones tschir afin de mettre à l'épreuve l'hypothèse selon laquelle les pisidies, les valvatidés et les lymnéidés sont capables de survivre à travers tout le passage digestif. Des poissons sauvages ont été capturés en vie et conservés dans des sacs de prélèvement dans le but de recueillir des échantillons de fèces. Les pisidies et les valvatidés abondaient dans les fèces des poissons, tandis que les lymnéidés ne s'y retrouvaient pas en abondance. En moyenne, 483 pisidies et 833 valvatidés ayant survécu à travers le passage digestif ont été observés dans chaque poisson, tandis qu'un seul lymnéidé avait survécu. Ces constatations laissent croire que les poissons pourraient jouer un rôle important dans la dispersion des mollusques d'eau douce au sein des systèmes d'eau douce.

Mots clés : Sphaeriidae, pisidies, Valvatidae, Lymnaeidae, valvatidés, lymnéidés, corégonidés, passage digestif

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INTRODUCTION

Mollusks figure prominently in the diets of many fish species, including humpback whitefish (*Coregonus pidschian*) and broad whitefish (*C. nasus*), which are large, benthic-feeding salmonids in the subfamily Coregoninae (McPhail and Lindsey, 1970; Scott and Crossman, 1973). During recent coregonid sampling projects in Alaska, digestive tract contents were examined. Pea clams (Sphaeriidae) and valve snails (Valvatidae) were abundant throughout the digestive tracts of humpback and broad whitefish, and pond snails (Lymnaeidae) were present but not abundant. Intact shells and shell fragments of these organisms were present in both the stomach and hindgut regions. When intact clams and snails from the hindgut were rinsed and allowed to sit undisturbed, many clams opened their shells and extended a foot, and snails emerged from their shells and began moving about. It was apparent that many of these shelled organisms were surviving gut passage into the hindgut, and it was hypothesized that they would ultimately be expelled alive in feces.

Live gut passage of shelled organisms through predatory vertebrates has occasionally been documented in the past. In an experimental procedure, Vinyard (1979) showed that approximately 26% of the ostracods (*Cypridopsis vidua*) fed to bluegill sunfish (*Lepomis macrochirus*) survived gut passage. In a study of tadpoles of a bromeliad frog (*Scinaxax perpusillus*), Lopez et al. (2002) showed that bromeliad ostracods (*Elpidium* spp.) could pass through the amphibian gut unharmed. Conway et al. (1994) demonstrated that a majority of copepod eggs remained viable after two to seven hours of gut passage in larval turbot (*Scophthalmus maximus*, now known as *Psetta maxima*).

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Aarnio and Bonsdorff (1997) found that many ostracods and gastropods survived gut passage in juvenile flounder (*Platichthys flesus*). Haynes et al. (1985) were able to demonstrate that an invasive snail, *Potamopyrgus jenkinsi*, in the Thames River in England could survive at least a six-hour gut passage in rainbow trout (*Salmo gairdneri*, now known as *Oncorhynchus mykiss*). The ability to survive gut passage clearly provides a dispersal mechanism for some shelled invertebrates.

Pea clams are members of the family Sphaeriidae, which are self-fertilizing hermaphrodites (Thorp and Covich, 2001). They are viviparous, producing a small number of large young within the parent shell. The young are released as small, functional clams (Burky, 1983). Known geographic dispersal mechanisms for sphaeriid clams include passive dispersal in flowing water; aerial transport in hurricanes, tornadoes, and other twisters; and transport via animal vectors when valves close on duck feathers, insect limbs, or other animal parts (Rees, 1965; Mackie, 1979; Thorp and Covich, 2001). Dispersal of sphaeriid clams by surviving fish gut passage has not been documented.

Valve snails are prosobranchs in the family Valvatidae, and pond snails are pulmonates in the family Lymnaeidae. Young freshwater snails do not go through the pelagic stages that are common in marine snails, but emerge from eggs and quickly gain the appearance of miniature adults (Heard, 1963; Kozloff, 1990). Known geographic dispersal mechanisms include passive dispersal in flowing water; aerial transport in hurricanes, tornadoes, and other twisters; and transport via animal vectors when insects or birds carry individual snails or their eggs along with small bits of aquatic plants or mud (Rees, 1965; Clarke, 1981). Valve snails are capable of limited seasonal migrations between shallow and deep water (Aldridge, 1983) and tend towards upstream migration in flowing water (Haynes et al., 1985). Surviving fish gut passage has not been recognized as an important dispersal mechanism for freshwater snails, even though Haynes et al. (1985) documented the phenomenon for a single fish-snail pair.

This small field investigation of wild-caught adult humpback and broad whitefish was conducted during their spring feeding season. The objective was to test the hypothesis that freshwater clams and snails could survive fish gut passage.

METHODS

Feces were collected from humpback and broad whitefish in early summer 2004. Six humpback whitefish were examined in the Kanuti River drainage (66˚10.5′ N, 151˚45.0′ W) in interior Alaska during late May, and two broad whitefish were examined in the Selawik River delta (66˚26.5′ N, 159˚59.9′ W) in northwest Alaska in early June. Captured fish were held in floating feces collection totes anchored near the capture locations. Wire fence panels were installed on two sides of the totes to allow a continuous exchange of ambient water while preventing fish escape. A layer of similar wire fence suspended about 7 cm above the floor of the tote allowed feces to fall through, preventing fish from re-ingesting them. With this system no benthic feeding was possible, but pelagic invertebrates were available to detained fish. One fish at a time was placed in a tote, which was inspected for feces every 12 hours for 60 hours. At each inspection, all feces were removed from the tote and water temperature was recorded. Minimum passage time for each feces sample was recorded as the time elapsed from fish capture, when no more benthic feeding was possible, to the beginning of the 12-hour period preceding feces collection.

Feces were placed in a fine-mesh (0.5 mm) strainer to separate clams, snails, and shell fragments from other material. Light, soft organic material was removed from the heavier shells by progressive decanting in water. Once separated from other material, shells were placed in a glass plate with clear water and observed for 30 minutes. Clams that opened and extended a foot and snails that emerged from their shells and began moving were considered to be alive and were counted. Intact clams and snails that remained immobile throughout the observation period may also have been alive, but the determination could not be made. A sub-sample of the organisms was later examined for species identification by N. Foster, a specialist in Alaska mollusk taxonomy and the coordinator of the aquatic collection at the University of Alaska Museum in Fairbanks.

RESULTS

Feces were present in the collection tote at every 12-hourly inspection for every fish. All feces samples contained intact clams and snails, as well as shell pieces and fragments (Fig. 1). Live clams and snails were observed in every sample collected. Pea clams and valve snails survived gut passage times of at least 48 hours in water temperatures ranging from 4˚ to 13˚C. A single live pond snail survived a gut passage time of at least 12 hours.

Giant northern pea clams (*Pisidium idahoensis*) were identified in feces samples. They ranged in size from less than 1 mm to 12 mm across the long dimension of the shell. On average, 483 live clams were observed per fish (Table 1). An occasional clam was gaping, indicating that it had died but had not been digested. Additionally, a small number of clam valves were hinged open and empty, indicating that they had been either digested or consumed as empty shells.

Most snails observed in feces samples were identified as ribbed valve snails (*Valvata sincera*) and a small number were identified as Alaskan pond snails (*Lymnaea atkaensis*). Ribbed valve snails ranged in size from less than 1 mm to 6 mm across the longest dimension. On average, 833 live valve snails were observed per fish (Table 1). Alaska pond

FIG. 1. Shelled contents of a typical humpback or broad whitefish feces sample. The largest clam measures approximately 10 mm across the longest dimension. Note the range of sizes of clams and snails, as well as the presence of shell fragments. Two of the large clams in this image were extending a foot, demonstrating that they were alive.

snails were generally larger, ranging from 5 to 14 mm across the longest dimension. Pond snail shells were present in feces samples from every fish, but only a single live specimen was observed.

DISCUSSION

The gut-survival data from this study indicate that fish are dispersal agents for some freshwater mollusks. If fish predators were non-migratory or sedentary during feeding season, many mollusks would be expelled alive near the sites where they were initially ingested. But if fish migrated after feeding, they would transport the mollusks to more distant locations. In the lower Mackenzie River in northern Canada, Chang-Kue and Jessop (1992, 1997) found that both tagged lake whitefish (*C. clupeaformis*), which are closely related to humpback whitefish, and broad whitefish migrated as much as 500 km along the river during the course of a summer. These species could distribute ingested mollusks throughout a drainage system relatively quickly. Waterfowl, insects, and twisters may be needed to transport freshwater mollusks between drainages and into closed systems (Rees, 1965), but the present results indicate that fish are an important mechanism for distribution within drainage systems.

TABLE 1. Mean number (range) of live mollusks observed per fish, by species.

Mollusks	Humpback whitefish (n = 6)	Broad whitefish (n = 2)
Pea clams	442 (312–769)	604 (558–650)
Valve snails	873 (432–1212)	712 (591–833)
Pond snails	0	0.5 (0–1)

Valve snails, as members of the subclass Prosobranchia, are equipped with an operculum, a calcareous disk that seals the shell opening when the snail is withdrawn (Clarke, 1981; Thorp and Covich, 2001). Pond snails, as members of the subclass Pulmonata, do not have an operculum. Snails previously reported as surviving fish gut passage were members of the subclass Prosobranchia, like valve snails, and were thus equipped with opercula (Haynes et al., 1985; Aarnio and Bonsdorff, 1997). It is hypothesized that the operculum provides protection to the snail during gut passage, and that this anatomical feature could explain the high number of surviving valve snails and the apparent low survival rate of pond snails following gut passage.

The estimated energetic value of various fish prey organisms, including mollusks, has been calculated (Salonen et al., 1976) in attempts to compare energy consumed by the fish with energy costs for life history events, such as migration, growth to maturity, and spawning (Stein et al., 1984; Helminen et al., 1990; Lambert and Dodson, 1990). Energetics studies are based on the assumption that consumed prey are digested, even though it has been documented that different taxa are not equally vulnerable to digestion (Vinyard, 1979; Haynes et al., 1985; Aarnio and Bonsdorff, 1997; Sutela and Huusko, 2000). The present findings further highlight the need to confirm digestion of prey organisms in such studies, or to develop adjustment factors to account for partial or non-digestion.

This investigation was designed to document live gut passage of clams and snails through humpback and broad whitefish, but many important features of the phenomenon were not addressed and require laboratory study to resolve. For example, some clams and snails that are consumed may be digested, but this field investigation did not allow control of fish feeding, so it could not be determined if fish consumed live mollusks only, or a mix of live mollusks and empty shells. Temperature may be a factor in passage time and subsequent survival rates, as documented in a laboratory experiment with operculate snails consumed by juvenile flounder (Aarnio and Bonsdorff, 1997). Laboratory studies could easily be designed to determine normal gut-passage times for humpback and broad whitefish, survival rates of clams and snails during gut passage, size and temperature effects on survival rates, and differential survival rates of snails with opercula versus those without.

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