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# Aggregation and spawning by lampreys (genus *Ichthyomyzon*) beneath cover

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**Synopsis**

Lampreys are generally reported to spawn in shallow water on open, gravel bottoms. During surveys in Wisconsin and Minnesota, we regularly observed aggregations of adult *Ichthyomyzon* c.f. *gagei, I. castaneus,* and *I. fossor* beneath such cover objects as boulders, woody debris, and, at one site, vegetation. In some cases, observations of eggs or rapid quivering by individual lampreys indicated that spawning was occurring. The literature includes scattered anecdotal reports of similar behavior in other populations of *Ichthyomyzon.* Our data for *I.* c.f. *gagei* suggest that aggregations beneath cover objects occur at a greater range of depths than those in the open, but that aggregations in the open can contain greater numbers of individuals. Facultative spawning beneath cover objects may permit lampreys to spawn in deep waters with swift current where spawning could not otherwise occur. Moreover, this behavior may reduce the vulnerability of spawning lampreys to some types of predators.

## Introduction

Compared to other facets of their behavior, fishes display relatively little intraspecific variation in reproduction. This conservatism has fostered the classification of fishes into reproductive guilds (e.g., Balon 1975), a taxonomy proven useful for assessing impacts of environmental changes on fish assemblages (Berkman & Rabeni 1987). Nevertheless, some fish species are variable in their reproductive behavior. For example, Page & Simon (1988) discussed the potential for darters with specialized reproductive behaviors to revert to more primitive spawning behavior when suitable substrates are unavailable.

Spawning by lampreys (order Petromyzontiformes) is typically reported to involve construction of a shallow depression in open, gravel-bottomed habitat (Hardisty 1986, Malmqvist 1986, Moyle & Cech 1988), often in or just upstream from a stream riffle. This generalization is repeated in many synopses of regional ichthyofaunas (e.g., Harlan & Speaker 1956, Pflieger 1975, Smith 1979). On the basis of such descriptions, lampreys are assignable to the reproductive guild of nonguarding spawners on open, coarse bottoms (Balon 1975, Balon 1981).

During surveys for chestnut lampreys, *Ichthyomyzon castaneus,* southern brook lampreys, *I.* c.f. *gagei,* and northern brook lampreys, *I. fossor,* in Wisconsin and Minnesota, we regularly observed aggregations of these species associated with cover of various types, and there was evidence that in at least some cases these aggregations represented spawning groups. Furthermore, our review of the literature revealed anecdotal reports of spawning beneath cover objects by other populations of *Ichthyomyzon.*

## Materials and methods

Data on lamprey aggregations were collected between 23 May – 4 June 1988 at the localities listed in Table 1 and during previous surveys in Wisconsin (Cochran 1987) and Minnesota (Cochran & Pettinelli 1988). The primary purpose of these surveys was to refine the known geographic distribution of *Ichthyomyzon* c.f. *gagei* by surveying as many sites as possible. Therefore, surveys were planned to coincide with or slightly precede the lamprey spawning season, when brook lampreys are most readily detected, collected, and identified. However, because spawning occurs only briefly at any given site and is followed by the death of adult lampreys, it was not possible or desirable to make extended observations at every site where lampreys were detected.

At most sites, we detected lampreys visually by wading in shallow areas with open substrate or by snorkeling in areas of deeper, faster water over rocks and boulders. We enumerated individuals within aggregations when possible, and in most cases we measured the depths of aggregations with a meter stick. Samples of lampreys were collected at each site and preserved in formalin to permit laboratory confirmation of field identifications.

## Results

### *Ichthyomyzon* c.f. *gagei*

Cochran (1987) first reported *Ichthyomyzon gagei* from the St. Croix River drainage of Wisconsin and Minnesota, an area far removed from the main body of its range in the southern United States. Because recent analysis has revealed some morphological differences between northern and southern specimens (Sneen & Cochran 1990), we here refer to northern individuals as '*Ichthyomyzon* c.f. *gagei*' pending future studies to clarify their taxonomic status.

Prior to our 1988 survey, *I.* c.f. *gagei* was known in Wisconsin from only four locations (three along the Namekagon River and one on the Wood River) and a total of 21 specimens (Cochran 1987). During 1988, we surveyed 128 sites in and adjacent to the St. Croix River drainage and found *I.* c.f. *gagei* at seven, including six new localities (Table 1).

*Table 1.* Localities at which lampreys were observed during 1988. The letters 'c', 'o', and 's' refer respectively to aggregations of lampreys under cover, aggregations in the open, and single stragglers. All localities are in the St. Croix River drainage except for Bear Creek (Chippewa River drainage).

| River | Location | Dates | *Ichthyomyzon* species |
|---|---|---|---|
| 1. Namekagon | U.S. Highway 63 crossing, Sawyer County (T42N, R9W, Sec. 36) | May 24–June 5 | *I.* c.f. *gagei* – c,o, *I. castaneus* – c,o |
| 2. Namekagon | Larsen Road crossing, Sawyer County (T-42N, R8W, Sec. 20/21) | May 26 | *I.* c.f. *gagei** – c, *I. castaneus* – c |
| 3. Namekagon | Petersen Road crossing, Sawyer County (T-42N, R8W, Sec. 9/16) | May 23–31 | *I.* c.f. *gagei** – c, *I. castaneus* – c |
| 4. Namekagon | Squaw Bend Road crossing, Bayfield County (T43N, R8W, Sec. 26/35) | May 28 | *I.* c.f. *gagei** – o, *I. castaneus* – o |
| 5. Mackay Creek | U.S. Highway 63 crossing, Washburn County (T-40N, R11W, Sec. 28) | May 27 | *I.* c.f. *gagei** – c |
| 6. Bean Brook | County Road E, Washburn County (T40N, R11W, Sec. 35/36) | June 3 | *I.* c.f. *gagei** – s |
| 7. Yellow | State Highway 73 crossing, Washburn County (T39N, R13W, Sec. 32) | May 25 | *I.* c.f. *gagei** – c, *I. castaneus* – s |
| 8. Bear Creek | 26th Avenue crossing, Barron County (T36N, R11W, Sec. 19/30) | May 27 | *I. fossor* – c,o |

* New locality for *Ichthyomyzon* c.f. *gagei*.

Spawning *I.* c.f. *gagei* occurred at water temperatures of 15–22° C, within the previously reported range of 15–24° C (Cochran & Pettinelli 1988 and references therein).

Aggregations of *I.* c.f. *gagei* occurred both in the open on gravel substrate and beneath cover of various types (Table 1). Although some aggregations were located on gravel substrate only partially concealed by the overhanging edge of an adjacent boulder or log, we discovered many groups of lampreys in interstices beneath boulders and rocks where they could not have been detected before the overlying cover objects were removed. Even when an aggregation was only partially concealed, the actual number of individuals in the group was often greater than originally observed.

Rooted aquatic macrophytes did not typically occur where *I.* c.f. *gagei* were present. At the Yellow River, however, we found two spawning groups in beds of *Potomageton crispus,* where they had formed slight depressions partially obscured by the surrounding macrophytes. The leaves were roughly similar to the lampreys in size, shape, and color, and their movement with the current made the lampreys especially difficult to detect. One group was partially obscured by a rock in addition to macrophytes.

When aggregations of adult *I.* c.f. *gagei* beneath cover objects were previously noted (Cochran 1987, Cochran & Pettinelli 1988), it was not known whether the lampreys were engaged in spawning. During the present study, however, we obtained evidence that spawning may occur under cover. Although we could not always observe the behavior of lampreys in crevices, in several instances we witnessed the rapid quivering movements that are associated with the spawning act. In addition, we sometimes observed eggs in the water column immediately adjacent to the lampreys or sifted them from the underlying sediment.

We obtained sufficient data on *I.* c.f. *gagei* to suggest several trends. We emphasize, however, that complete samples were not obtained at all sites, and the patterns we describe below should be treated as hypotheses requiring verification with independent data.

(1) Aggregations beneath cover objects seemed relatively more common in the large swift-flowing Namekagon and Yellow rivers of Wisconsin (1988 data: 19 of 30 and 5 of 5 aggregations, respectively, were at least partially concealed) than in the smaller, shallower, and more slowly flowing Pine County streams of Minnesota (1986 data: 4 of 12 aggregations at least partially concealed).

(2) It was our impression that aggregations beneath cover tended to occur primarily in relatively deep, swift water. However, after pooling data for all sites, the mean depths for 24 aggregations beneath cover (41 cm; range = 10–70 cm) and 11 aggregations in the open (32 cm; range = 8.5–50 cm) were not significantly different (t-test, $p = 0.14$), nor were their respective variances (F-test, $p > 0.25$). A significant difference in variances might have resulted if aggregations beneath cover occurred over a wider range of depths. Although we did not collect enough data to make statistical comparisons for individual sites, the greatest depths at all sites were for groups of lampreys beneath cover objects, and these were all located in relatively swift current.

(3) The mean aggregation sizes for 28 aggregations beneath cover (6.9; range = 2–16) and 16 aggregations in the open (15.0; range = 2–45) were significantly different (t-test, $p = 0.05$). Because variances for the two groups were significantly different (F-test, $p < 0.005$), we compared the means with a t-test that did not require the assumption of equal variances (Ryan et al. 1985). Small groups beneath cover may simply reflect a physical limitation of space.

(4) At two sites on the Namekagon River (the U.S. Highway 63 and Petersen Road crossings), our observations spanned the spawning period for *I.* c.f. *gagei*. Aggregations beneath cover occurred throughout the spawning period, although the few lampreys observed on the last days appeared to be spent. By contrast, the spawning groups in the open at the Highway 63 crossing occurred only during the peak of spawning activity; only a few stragglers were observed in the open on later dates.

*Ichthyomyzon castaneus*

In 1988, we found adult *I. castaneus* in nine aggregations at four localities (Table 1), always with *I.* c.f. *gagei*. The number of *I. castaneus* in aggregations ranged from one to five, whereas the number of *I.* c.f. *gagei* in the same groups ranged from five to roughly 45. Both male and female *I. castaneus* occurred in aggregations, and we were able in one case to observe spawning-related activity. Four aggregations with *I. castaneus* were at least partially concealed by cover objects.

*Ichthyomyzon fossor*

During the present study, we found *I. fossor* spawning beneath rocks in Bear Creek, Barron County, Wisconsin (Table 1). We also found an aggregation of 8–10 individuals in the open at the same locality.

**Discussion**

We have observed three species of *Ichthyomyzon* in aggregations beneath cover objects. In at least some cases, each engaged in spawning beneath cover. Review of the literature has revealed scattered anecdotal accounts of aggregation or spawning beneath cover by other populations of *Ichthyomyzon* (Table 2), although many workers have also found these same species spawning in the open (e.g., Hankinson 1932, Case 1970, Pflieger 1975, Morman 1979, Robison et al. 1983). *Ichthyomyzon fossor* seems especially prone to spawning beneath cover. In their original description of the species, Reighard & Cummins (1916) reported that spawning in Michigan took place almost invariably when adults were hidden among or beneath stones 8–15 cm in diameter.

Reproductive and other behaviors may provide clues about evolutionary relationships among taxa (Page 1985). Our observations and literature review have focused on *Ichthyomyzon*. We have less evidence that spawning beneath cover objects occurs with regularity in other genera (Table 2). For example, in a recent detailed review of European

*Table 2.* Accounts of lampreys aggregating beneath cover. Cases in which the aggregated lampreys were reported to be spawning are listed separately (in at least some of the remaining cases, spawning beneath cover may have occurred but was not observed). In some cases, lampreys were only partly concealed by cover.

| Lamprey species | Aggregations beneath cover | Spawning beneath cover |
|---|---|---|
| *Ichthyomyzon* | | |
| *I. castaneus* | Cochran 1987, this study | Hall 1963, this study |
| *I. fossor* | Cochran & Pettinelli 1988 | Reighard & Cummins 1916 |
| | | Morman 1979 |
| | | Cooper 1983 |
| | | this study |
| *I.* c.f. *gagei* | Cochran 1987 | this study |
| | Cochran & Pettinelli 1988 | |
| | this study | |
| *I. gagei* | Dendy & Scott 1953 | |
| *I. greeleyi* | | Raney 1939 |
| *I. unicuspis* | | Morman 1979 |
| | | Greeley (in Smith 1985) |
| Other species | | |
| *Lampetra appendix* | | LeSueur 1827 (in Hubbs & Trautman 1937) |
| | | this study |
| *Petromyzon marinus* | | Applegate 1950 |
| | | Noltie & Robilliard 1987 |

lampreys (Holčík 1986), none of the ten species was reported to spawn beneath cover objects, although several were occasionally found spawning in the shade. It was generally reported that avoidance of daylight diminishes during the spawning season, so that even bright light is tolerated (e.g., Hardisty 1986). This response parallels the trend for *Ichthyomyzon* c.f. *gagei* to shift from cavities to open substrate as the spawning season progresses, and it is also consistent with Applegate's (1950) observations in Michigan and our own observations in Wisconsin that *Petromyzon marinus* which reach their spawning grounds prior to spawning spend daylight hours undercover. In addition to the accounts listed in Table 2, Martin Sneen (personal communication) observed two of seven spawning groups of *Lampetra appendix* in Jambo Creek, Manitowoc County, Wisconsin, on 3 May 1989 spawning beneath cover. One group was beneath the downstream edge of a stump, which formed a 'roof' 19 cm above the bottom in water 33 cm deep.

### *The significance of aggregations beneath cover*

It is possible that some aggregations have no functional significance per se but represent the collective result of habitat selection by individuals. As lampreys complete the transformation from the ammocoete stages, they are known to select coarser substrates (Hardisty 1986) and, except for spawning, they subsequently tend to be most active at night and to seek cover by day (Cochran 1986). Cochran & Pettinelli (1988) suggested that crevices among boulders in deep, fast water may provide overwintering habitat that is well oxygenated and protected from both ice scour and visual predators. Stream-dwelling parasitic lampreys may continue to use the same microhabitat during intervals between attachments to hosts (Cochran unpublished). Indeed, during this study, we occasionally found recently transformed *I. castaneus* beneath cover objects with mature conspecifics or mature *I.* c.f. *gagei,* associations that were probably coincidental.

As the spawning season approaches, it is likely that group-spawning lampreys are mutually attracted, probably through the action of sexual pheromones (Teeter 1980). As suggested by Cochran & Pettinelli (1988), crevice microhabitat may serve as a pre-spawning staging area, where individuals accumulate until an appropriate stimulus triggers the onset of nest construction and spawning. Mixed species aggregations in crevices (Cochran 1987) or spawning in the open (Huggins & Thompson 1970, Pflieger 1975, Morman 1979) possibly result from similarities in sexual pheromones of closely related species, as suggested by Cochran (1987) for *I. castaneus* and *I.* c.f. *gagei,* or from a propensity for smaller species to take advantage of the nest building activities of larger forms (Morman 1979). If only the latter hypothesis is correct, then nonparasitic species should be attracted by the pheromones of parasitic species, but not vice versa.

Our observations and literature review indicate that some aggregations of *Ichthyomyzon* beneath cover objects engage in spawning, contrary to typical accounts of lampreys spawning on open substrate. What are the possible selective advantages for this alternative behavior? We suggest two, which are not mutually exclusive.

First, the ability to spawn beneath cover objects may allow lampreys to reproduce in streams or reaches of streams where the current is too strong to permit successful spawning in the open. Similarly, cavity spawning may permit successful reproduction during years in which abnormally high discharges during the spawning season reduce the availability of suitable conditions in the open. Flexibility in spawning site use may be especially important to semelparous species, such as lampreys, which have only one opportunity to spawn. Often, but not always, aggregations of *Ichthyomyzon* beneath cover objects occurred in relatively deep, swift water. Swift current may limit the availability of suitably-sized substrate to pockets protected by boulders or other large objects, or it may be too strong for lampreys to hold position and complete the spawning act in the open. Thus, in some cases we have overturned boulders to reveal aggregations of lampreys which were then swept downstream, along with the underlying sediment.

Second, lampreys spawning beneath cover objects, especially in deep swift water, are undoubtedly less vulnerable to at least some types of visually hunting predators. It is very easy for human collectors to detect, approach, and capture lampreys spawning in shallow, open habitats, and they are quite vulnerable to such predators as gulls, herons, racoons, mink, and even dogs (Applegate 1950). Moreover, aggregations of lampreys spawning in the open are sometimes attended by schools of small cyprinids (Raney 1939, Case 1970, personal observations), which appear to be feeding on eggs. Spawning beneath cover would decrease mortality to these predators. However, other predators may occur in the crevice microhabitat. For example, we frequently have observed mudpuppies, *Necturus maculosus*, beneath cover objects at localities where lampreys also occur; a congeneric *N. lewisi* is known to prey on brook lampreys (Nickerson & Ashton 1983). Perhaps of greater significance, as potential predators of lamprey eggs, are crayfish. At some sites, we found numerous crayfish in crevices which earlier had concealed aggregations of spawning lampreys.

### *Implications of cavity spawning*

Cavity spawning by *Ichthyomyzon* must be taken into account when distributional surveys are planned. This is especially true for the nonparasitic species, which are difficult to identify as ammocoetes and are usually most easily collected as adults during their brief spawning season. To what extent a population in a particular locality relies on cavity spawning in swift, relatively deep water will affect the difficulty of detecting it with such traditional methods as seining or electrofishing, especially if these methods are applied only briefly at any site. Indeed, that *I.* c.f. *gagei* escaped detection in Wisconsin and Minnesota until only recently may be due at least in part to its propensity for cavity spawning. Hall's (1953) experience with *Ichthyomyzon castaneus* is instructive in this regard. His concerted effort during an extensive field study revealed only a single spawning group, which was concealed beneath a log, and he concluded that he would never have found it if he had not been snorkeling.

Regardless of whether cavities are used for overwintering, aggregation by pre-spawning adults, or spawning, cavity microhabitat may be just as critical to the persistence of lamprey populations as the microhabitats conventionally associated with spawning and rearing of ammocoetes. Future studies of cavity use by lampreys should include quantification of cavity versus open substrate spawning in a variety of natural situations, laboratory measurements of choice of spawning mode under controlled conditions, and assessment of cavity spawning by additional lamprey taxa.

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