Evidence that Parasitic and Nonparasitic Life History Types are Produced by One Population of Lamprey

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A population of lamprey in a small stream on Vancouver Island, British Columbia, Canada, was shown to contain the nonparasitic *Lampetra richardsoni* and a parasitic variety.

L'auteur montre que la population de lamproies d'un petit cours d'eau de l'île de Vancouver (Colombie-Britannique) se compose de l'espèce non parasite *Lampetra richardsoni* et d'une variété parasite.

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Recently, it was reported (Beamish 1985; Beamish and Withler 1986) that a lamprey in Morrison Creek on Vancouver Island, British Columbia (Fig. 1), was a parasitic variety of the nonparasitic *Lampetra richardsoni*. The variety was parasitic in the laboratory, was unable to survive in seawater, and it lived 1 yr longer than the nonparasitic variety. During that year the parasitic variety increased in size by an average 6.3 cm and 8.0 g (Fig. 2). Allelic frequencies of the parasitic variety were identical to the variety that was believed to be the nonparasitic *L. richardsoni*. The allelic frequencies between the Morrison Creek varieties differed slightly from *Lampetra ayresi* and *L. richardsoni* from other rivers, but the differences were within the range of frequencies observed among the populations sampled. The identical allelic frequencies of the two varieties in the creek suggested that the parasitic variety was not a distinct species. Thus, two distinct life history types appeared to be produced by one population (Fig. 2). I named the parasitic variety *Lampetra richardsoni* var. *marifuga* Beamish, 1985, to facilitate discussion of the two life history types.

Although the presence of the *L. r.* var. *marifuga* was clearly shown, the presence of a nonparasitic variety was not proven. The lamprey identified as *L. richardsoni* could have been spawning individuals of *L. r.* var *marifuga* which in spawning condition could not be separated from spawning *L. richardsoni*. Proof that nonparasitic varieties existed required collecting lampreys in an early stage of metamorphosis and maintaining them in the laboratory until they spawned. Typical *L. richardsoni* would be lamprey that metamorphosed in the summer of one year and matured in the spring of the following year. The parasitic variety would not spawn at this time and would be silver in appearance with prominent dentition.

This note describes the maturation of metamorphosing lampreys collected in Morrison Creek in August 1985. Despite the small size of the sample, the results are reported now, because they confirm that a nonparasitic variety exists in Morrison Creek.

Materials and Methods

Lampreys at an early stage of metamorphosis were collected in Morrison Creek in early August 1985 using electroshockers. They were maintained in a sand substrate in an 800-L tank with flowing fresh water without feeding. Visual examinations were conducted occasionally over a 10-mo period. In early June 1986 they were measured, photographed, examined for sex and maturity, and preserved in Bouin's fixative for 24 h and then transferred to 70% ethyl alcohol. Histological sections were made to confirm the stage of maturity of the parasitic variety.

Results and Discussion

Only four metamorphosing lampreys were collected despite an intensive effort. All four lampreys were at an early stage of metamorphosis. Eyes were developed, but there was no iris. The mouth was oval and contained fimbria. Using the criteria of Potter et al. (1982), these lampreys were about stage 2–3. The lampreys were not examined frequently, to reduce the chance of mortality. At the time of next examination on October 6, 1985, their metamorphosis was completed. They were examined again in early November 1985, March 1986, April 1986, May 1986, and June 1986. Early signs of maturation were first observed in April; by early May, three were mature. One of the lampreys was becoming silver in early March. By early June 1986, three lamprey were in spawning condition and one had the silver coloration of the parasitic variety. The three mature individuals (Fig. 2) were a uniform dark olive brown, had enlarged, closely spaced first and second dorsal fins, and had obsolete dentition. One of the mature lampreys had eggs that were visible through the body wall, another was a mature male, and the third was a maturing female. Since they were obviously mature and ready to spawn, they were preserved as was the silver colored individual.

Histological examination of the silver specimen confirmed the external observations. This male had maturing sperm but no external signs of maturation. The intestine was fully functional, as described in Beamish and Withler (1985) and Beamish and Youson (unpubl. data). Teeth were prominent and well developed. This "silver"form was identical in appearance to the silver-colored lamprey that were parasitic in the laboratory (Beamish 1985; Beamish and Withler 1986). Although this fish was not allowed to feed, there was no doubt that it was the parasitic variety.

The existence of the nonparasitic life history type was demonstrated by the three lampreys that started metamorphosis in late July or early August 1985 and matured and would have spawned in 1986. In the sample of 18 metamorphosed lampreys collected in February 1981 (Beamish 1985), 2 became silver. One of them was preserved and one allowed to feed and the other 16 matured and spawned. While the observations of maturation from both these samples were similar, the February 1981 sample of mature lampreys had completed metamorphosis and theoretically could be the silver or parasitic variety in its second year as an adult. The present study confirms that two distinct varieties occur.

The presence of two life history types, even though *L. r.* var. *marifuga* may feed very little in the stream (Beamish and Withler 1986), and the identical allozyme allelic frequencies strongly suggest the existence of gene flow between the two varieties. Gene flow between the two varieties indicates that one population is producing both nonparasitic and parasitic lamprey. The existence of morphologically distinct varieties with different life history types produced by one population has not been reported for other lamprey populations. It is possible that natural hybridization between *L. ayresi* and *L. richardsoni* had occurred (Beamish and Withler 1986). However, *L. ayresi* is not found anywhere in the Morrison Creek watershed. If natural hybridization occurred, it must have occurred some time ago because the parasitic variety has been observed in the stream each year since 1977. The present population, therefore, must have as part of its genotype the ability to produce both life history types.

The population is considered to be *L. richardsoni* because the nonparasitic variety has a typical *L. richardsoni* life history and normal gonad development, while the parasitic variety has an abnormal sex ratio and abnormal gonad development (Beamish 1985; Beamish and Withler 1986).

The theory that nonparasitic lamprey evolved from parasitic lamprey (Zanandrea 1959; Hardisty and Potter 1971; Vladykov and Kott 1979) is based on the morphological similarity of these paired or satellite species and an overlapping distribution. Recently, I proposed (Beamish 1985) that some nonparasitic species evolved from an intermediate freshwater, parasitic stage, rather than directly from anadromous species. If the theory of an intermediate stage is correct, then it is to be expected that there will be populations of lamprey that produce both parasitic and nonparasitic life history types. The popula-

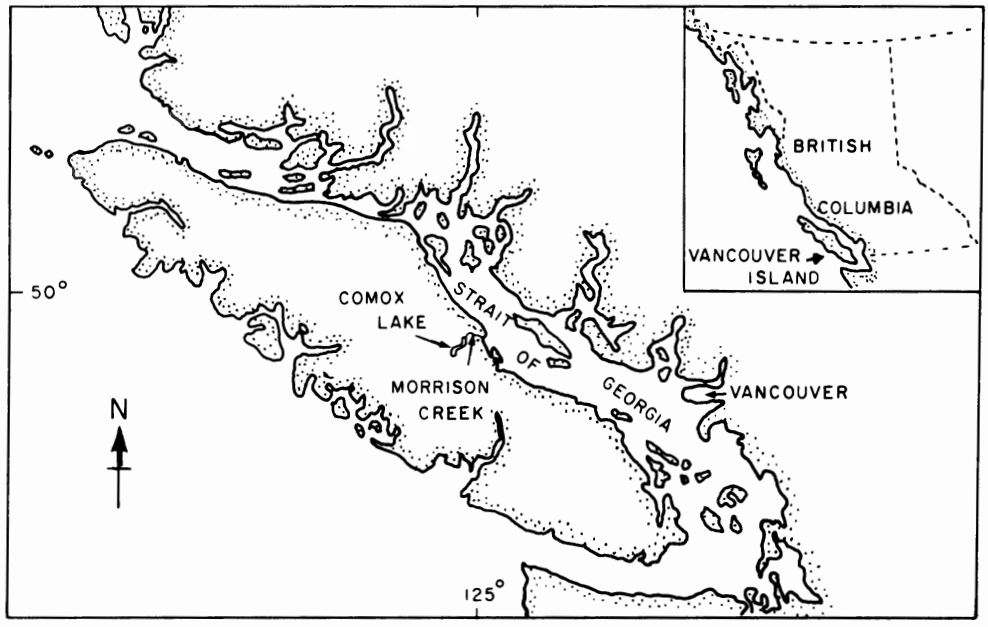

FIG. 1. Location of Morrison Creek.

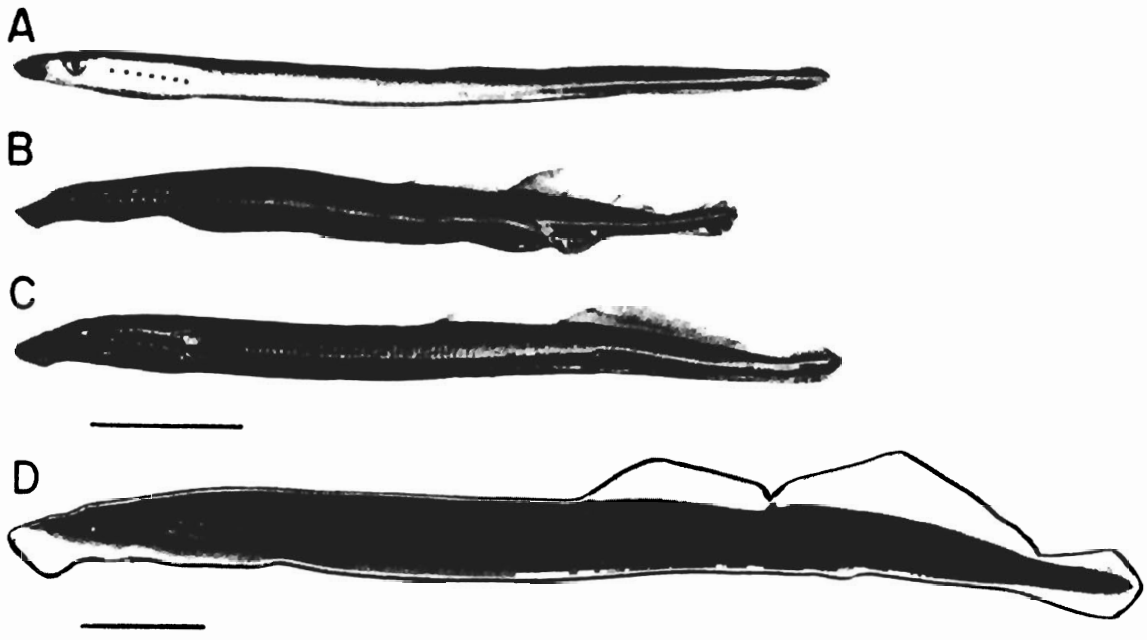

FIG. 2. (A) Male, parasitic variety, showing silver colour and no external signs of maturation. (B) Mature female and (C) mature male *L. richardsoni* from Morrison Creek. Bar = 2 cm. A, B, and C were photographed June 1986 after being held in the laboratory since August 1985. (D) Mature male, parasitic variety, brought into the laboratory in June 1981 and reared to maturity in 1982. Bar = 2 cm.

tion of lamprey in Morrison Creek is the first example of such a population.

There is another study that may be a second example of a population that produces parasitic and nonparasitic life history types. Kux (1965) described *Lampetra* (*Eudontomyzon*) *gracilis* as a new species of nonparasitic lamprey that was paired with the parasitic *Eudontomyzon danfordi*. Kux (1967) maintained ammocoetes in aquaria until they metamorphosed, and in some cases fed, to confirm that two life history types existed. He found that 55% ($n = 16$) matured without feeding and 45% ($n = 13$) fed. The lamprey that fed lived 1 yr longer than those that did not. Kux (1967), therefore, used the diameter of the gut and the development of the gonad to separate the parasitic and nonparasitic species.

Recently, Renaud and Holčík (1987) found that *E. gracilis* is indistinguishable from *E. danfordi* and is a junior synonym of *E. danfordi*. They speculated that the proven, nonparasitic behavior of a parasitic species in Kux's experiments was the result of poor feeding conditions. Another explanation is that the population of lampreys sampled by Kux (1965, 1967) was capable of producing both life history types.

In addition, it appears that aspects of the biology of the parasitic *E. danfordi* are similar to the biology of typical nonparasitic species. It is known that the parasitic *E. danfordi*

have large ammocoetes, up to 245 mm (Vladykov 1931). Large ammocoetes are characteristic of nonparasitic species (Vladykov and Kott 1978, 1979). There is no doubt that *E. danfordi* feeds; however, there does not appear to be much growth, suggesting that the amount of feeding is quite limited. Kux (1965) indicated that the size of wild prespawning adult *E. danfordi* ranged from 160 to 245 mm and from 184 to 205 mm in the laboratory (Kux 1967). Renaud and Holčík (1987) recorded the lengths of 90 adults as ranging from 136 to 241 mm. They recorded the lengths of the oldest age groups of ammocoetes as ranging from 166 to 216 mm. Thus, the size of ammocoetes and adults is quite similar. This limited amount growth was confirmed in one of Kux's (1967) experiments in which one *E. danfordi* increased in length from 198 to 203 mm and in weight from 7.8 to 9.2 g during the period of feeding from June until September. The large size of the ammocoetes and the limited amount of feeding on both live and dead fishes (Grossu et al. 1962; Kux 1965, 1967) may be an indication that the *E. danfordi* population is closer to a nonparasitic life history type than a parasitic life history type.

The inability to differentiate adults of either life history type, morphometrically or meristically, the similarity in size, the common occurrence of both life history types in the laboratory experiments, and the apparent similarity in spawning times all indicated that interbreeding could occur. If it occurs, then this is a second example that parasitic and nonparasitic life history types are produced by one population of lamprey.

It is interesting that one female lamprey that spawned but did not feed in Kux's (1967) study was reexamined by Renaud and Holčík (1987) and found to have no secondary sex characteristics. The absence of secondary sex characteristics was observed in silver-colored male *L. r.* var. *marifuga* that, despite the presence of maturing sperm, fed in the laboratory and did not spawn for almost a year (Beamish and Withler 1986).

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