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Variation in larval sea lamprey demographics among Great Lakes tributaries: A mixed-effects model analysis of historical survey data

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ABSTRACT

Understanding variation in fish populations is valuable from both a management and an ecological perspective. Great Lakes sea lampreys are controlled primarily by treating tributaries with lampricides that target the larval stage. Great Lakes streams were divided into four categories based on their regularity of parasitic lamprey production inferred from the historic regularity of chemical treatments. This categorization was intended to direct future assessment efforts, but may also reflect differences in early demographics. We analyzed assessment data collected from 1959 to 2005 using mixed-effects models and variance components analyses to test for differences in recruitment and growth to age 1 among stream categories. Recruitment was twice as large in regularly treated streams as in irregularly treated streams, indicating that age-1 year-class strength is correlated with consistent chemical treatments. We found no differences in length at age 1 among stream categories; however, Lake Superior streams with irregular treatment histories exhibit more variation in length at age 1 than streams that are treated regularly. The majority of variation in length at age 1 was due to within-year variation, which was fairly consistent across stream types within each lake. Our results indicate that early life history differs among subsets of the Great Lakes sea lamprey population, and management practices should be modified to account for these differences. Mixed-effects models and variance components analyses are useful tools for analyzing large historical datasets for patterns of demographic variation within and among populations, whether the ultimate goal is pest control, harvesting, or conservation.

Introduction

Many fish species show wide variation in demographic parameters among populations (e.g., Hutchings and Jones, 1998; Shuter et al., 1998; Winemiller and Rose, 1992), and nearly all populations exhibit such variation over time (Ricker, 1954; Hilborn and Walters, 1992). Both spatial and temporal variations in demographic parameters have implications for management. If not properly accounted for, this variability can cause high inter-annual variation in yield or catch rates in the case of desired fisheries, and high annual variation in control success in pest species such as sea lampreys (*Petromyzon marinus*). Across space, stocks with differing demographic characteristics have differential vulnerability to similar levels of exploitation (Shuter et al., 1998; Hilborn et al., 2005; Purchase et al., 2005), while variation over time increases the need to devise management strategies that respond effectively or are robust to unplanned variations in abundance (e.g., Beddington and May, 1977; Walters and Pearse, 1996; Engen et al., 1997). In addition, understanding the relationship between growth rates and later abundance and the identification of spatial and temporal patterns in recruitment variation have long been central goals of fisheries ecology (Ricker, 1954; Anderson, 1988). The historical importance of variation in fish populations suggests that studies which describe and increase mechanistic understanding of demographic variation in fish populations are valuable from both a managerial and ecological perspective.

Fish population dynamics are principally determined by the net effect of three demographic processes: recruitment, which for this discussion we define to include reproduction and early survival; growth; and mortality. Management strategies for exploited stocks can depend on which of these demographic processes have the greatest influence on spatial and temporal variation in abundance. For example, in lake trout (*Salvelinus namaycush*) populations, spatial variation in growth and mortality rates is thought to determine the differential vulnerability of populations to exploitation. Shuter et al. (1998) used an analysis of this variation to argue for different sustainable lake trout exploitation rates in lakes of differing size. In contrast, the dynamics of many other fish species are strongly influenced by the irregular occurrence of very large recruitment events. For example, large recruitment events in Lake Erie walleye

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(*Sander vitreus*) in 1984, 1988, and 2003 have overwhelmingly influenced yields in both commercial and recreational fisheries for this species (Thomas et al., 2007). As well, understanding spatial variation in recruitment dynamics helps managers to determine the degree to which models of recruitment developed for a subset of populations are suitable for application to other populations (Myers et al., 1997; Peterman et al., 1998). Variation in recruitment and other demographic rates is also common among vertebrate pest species (e.g., Twigg and Williams, 1999; Brown et al., 2005). Demographic variation is particularly important for the control of invasive sea lampreys in the North American Great Lakes, where empirical research and modeling have shown that recruitment variation can have a large effect on the success of control tactics that target reproductive success (Jones et al., 2003). However, as in desired fish populations, the causes of variation in recruitment are often poorly understood.

Sea lampreys are invasive pests in the Great Lakes that parasitize other fishes during their juvenile stage. Larval sea lampreys (known as ammocoetes) are stream-dwelling filter feeders (Applegate, 1950). Sea lampreys in the Great Lakes are controlled primarily through the periodic treatment of streams with the lampricide 3-triflouromethyl-4-nitrophenol (TFM), and successful treatments kill from 95%% to 100% of sea lampreys present in the stream at the time of treatment (Smith and Tibbles, 1980; Christie et al., 2003; Heinrich et al., 2003). Streams are not treated annually, because ammocoetes remain in their natal streams for 3 to 7 years before becoming parasitic. Ideally, the frequency of treatment should match the cycle of recolonization, growth, and maturation of sea lampreys following treatment events (hereafter referred to as “parasitic lamprey production”) in individual streams. However, spatial and temporal variability in demographic processes results in inconsistency in parasitic lamprey production, both within and among streams, and hinders the ability of managers to predict the timing of stream treatments that would optimally prevent the escapement of parasitic sea lampreys. This variability has necessitated the use of costly assessments of larval sea lamprey populations to aid the selection of streams for treatment (Slade et al., 2003), with assessment accounting for roughly one third of the total sea lamprey control budget since 1995.

Identification of the demographic processes responsible for variation in parasitic lamprey production within and among streams is of considerable practical interest. Recent studies have drawn attention to the uncertainty inherent in the current methods used to select streams for lampricide treatment. In particular, these studies have demonstrated uncertainties in estimates of parasitic lamprey abundance due to imprecise estimates of ammocoete abundance (Steeves et al., 2003), and uncertainties regarding growth rates and prediction of metamorphosis (Hansen et al., 2003). It is doubtful that increases in assessment resources could fully resolve these uncertainties in the assessment and stream selection process (Hansen et al., 2003; Slade et al., 2003). A better understanding of the demographic processes that influence treatment cycles could point to more efficient assessment strategies that focus on these processes, and potentially provide a means to incorporate prior information on stream-specific demographic processes into the stream selection process.

In this study, we used data from larval sea lamprey assessment surveys conducted between 1959 and 2005 to estimate recruitment and growth to age 1 for a number of sea lamprey-producing streams. Our objective was to determine whether variation in treatment regularity among streams was correlated with measurable differences in recruitment or growth. We tested for differences in both the mean and the variance of these rates among streams with differing treatment histories to determine 1) if recruitment to age 1, growth to age 1, or both were correlated with differences in the regularity of historical stream treatment, and 2) if mean rates, variation in rates, or both differed among streams with different regularity of treatment. We hypothesized that sea lamprey ammocoetes in streams with irregular treatment histories would have more variable demographic rates, and possibly lower mean rates, than those in streams with regular treatment histories. We used mixed-effects statistical models and variance components analysis to analyze historical assessment data to test this hypothesis, despite the fact that the data were not collected with this objective in mind. A secondary goal was to demonstrate the utility of these statistical methods for opportunistic exploration of similar questions for other desirable and damaging fish species. These methods are particularly useful for situations where data are unbalanced and non-independent, as is often the case when data are collected across a broad spatial and temporal range.

Methods

Study area

Survey data used for these analyses were collected from throughout the Laurentian Great Lakes basin, excluding Lake Erie (Fig. 1). Only two streams from the Lake Erie basin had more than 1 year of data that fit the timing criteria required for this analysis (described below). This paucity of data made the establishment of patterns in variation of population-level processes among stream categories impossible for this lake. For the purposes of these analyses, we considered larval sea lampreys within different streams to be distinct populations. Parasitic sea lampreys mix as one population within the lake environment and do not home to natal streams (Bergstedt and Seelye, 1995); however, mixing does not occur during the ammocoete phase, and growth and timing of metamorphosis are known to differ among streams (Hansen et al., 2003).

Stream categorizations

Most lamprey-producing streams are treated on a 3–5 year cycle, but streams differ in the regularity with which large populations of transformers develop (Heinrich et al., 2003; Lavis et al., 2003; Morse et al., 2003). Some streams are highly regular in their cycles of parasitic lamprey production and need for treatment (i.e., they require chemical treatments at fixed intervals), while others vary widely. Previous authors have suggested that differences in recruitment, growth, and survival following lampricide treatments contribute to differences in treatment regularity (Heinrich et al., 2003; Lavis et al., 2003); however, the relative role of each of these processes in determining treatment regularity is unknown. Researchers and sea lamprey managers have divided streams considered for chemical control into four categories based on their regularity of parasitic lamprey production inferred from the historic regularity of chemical treatments and from the expert opinion of assessment biologists who work on these streams. Stream treatment decisions are based on both the assessed abundance of stream-dwelling larval populations as well as the cost of treating a stream, and stream categories were developed based on the history of stream treatments. Survey data were not analyzed prior to categorizing streams.

The purpose of the four stream categories developed prior to this analysis was to guide future assessment efforts. Category 1 streams are highly predictable in their parasitic lamprey production cycle and their treatment schedule; that is, the same number of years consistently separates chemical treatments. The actual number of years between treatments varies *among* Category 1 streams, but is consistent *within* streams; that is, some are treated on a 3 year cycle while others are treated on a 4 or 5 year cycle. Category 2 streams are somewhat variable in their parasitic lamprey production cycle and treatment schedule, but show some signs of patterns in the length of time between treatments. For example, a Category 2 stream may have 4 years between some treatments and 3 years between others. Category 3 streams are highly variable in their production of sea lampreys and treatment schedule. For example, a Category 3 stream may have 4 years between some treatments and 10 years between