Assessing niche differences of sex, armour and asymmetry phenotypes using stable isotope analyses in Haida Gwaii sticklebacks

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Summary

Identifying phenotype-specific selective landscapes within populations continues to challenge evolutionary biologists in studies of adaptive variation. We explore here the potential application of carbon and nitrogen stable isotope ratios of tissues as time-integrated proxies of niche space among sex, armour and asymmetry phenotypes within an endemic population of giant threespine stickleback from Haida Gwaii, western Canada. Muscle tissues were extracted from 289 stickleback collected from Drizzle Lake, taken in transects during June 1981, June 1982, September 1982 and June 1983 and isotopic ratios of $\delta^{15}N$ ($\delta^{15}N$) and $\delta^{13}C$ ($\delta^{13}C$) determined by continuous-flow isotope ratio mass spectrometry. Among all fish, $\delta^{15}N$ values, which reflect relative trophic level, ranged from 6.5‰ to 10.6‰, while $\delta^{13}C$, which reflects reliance on different carbon pathways of primary producers, ranged from $-30.5$‰ to $-27.5$‰. The sexes did not differ in $\delta^{15}N$ but females were significantly enriched in $\delta^{13}C$ relative to males among all samples. In each transect, lateral plate phenotypes differed in $\delta^{15}N$, with higher plate counts generally enriched in $\delta^{15}N$. $\delta^{13}C$ did not vary among plate phenotypes. Approximately 50% of the adult population exhibit lateral plate asymmetries usually with one plate different between sides. Sticklebacks that were asymmetric (absolute asymmetry) did not differ from symmetric fish for either $\delta^{15}N$ or $\delta^{13}C$ signatures. However, this result masked a significant and consistent effect of signed asymmetries (right side − left side), with $\delta^{15}N$ enrichment among right-biased compared to left-biased asymmetric. These unexpected results indicate the presence of subtle and previously unrecognized niche differences in lateral plate number and asymmetry phenotypes and are consistent with the predictions of niche-width and adaptive variation hypotheses. The results also suggest the wider application of isotopic techniques to elucidate phenotype-specific ecological and selective landscapes.

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Introduction

In spite of the central importance of the multi-dimensional niche, evolutionary biologists have not readily incorporated niche dimensions into studies of phenotypic variability and adaptive variation within populations. Part of this is due to the challenge in quantifying phenotype-specific niches over the life history of organisms. As such, niche differences within species are not well documented and their extent or importance is not well established. Initial formulation of hypotheses addressing intraspecific niche variation were advanced by Levene (1952) on multi-niche polymorphisms who modeled an equilibrium in which two genotypes would be preserved in a population if each occupied different niches. Van Valen (1965) formulated hypotheses on the relationship between niche width and morphological variance in which individuals along a phenotypic continuum exhibit niche specialization over a resource axis. In addition to early field tests on polymorphic taxa (e.g., Reimchen, 1979; Jones & Probert, 1980), more extensively studied were quantitative traits involving trophic axes in which niche diversification may be a natural extension of intraspecific competition (Grant et al., 1976; Grant & Price, 1981; Robinson & Wilson, 1994; Ackermann & Doebeli, 2004; Egas et al., 2005). Recent efforts to manipulate intraspecific competition lead to disruptive selection at higher densities (Bolnick, 2004) consistent with the importance of phenotype-specific trophic differentiation.

To provide a test of the adaptive variation hypothesis using quantitative traits, a field study was initiated in 1976 on the Haida Gwaii archipelago in British Columbia, Canada. This study has investigated the morphological variability in predator defenses within several insular lake populations of threespine stickleback (*Gasterosteus aculeatus*). Previous investigations in this archipelago had shown that populations differ in the average number, variance and asymmetry of their bony lateral plates in relation to predation regime among localities (Moodie, 1972; Moodie & Reimchen, 1976). Assessment of sources of mortality on stickleback demonstrated taxonomic diversity of predators and an associated diversity in foraging methods (Reimchen & Douglas, 1984; Reimchen, 1994). Some of the intrapopulation variation in lateral plates and other defense structures was predictably associated...