JOURNAL OF MORPHOLOGY 272:590–597 (2011)

Habitat-Specific Trends in Ontogeny of Body Shape in Stickleback From Coastal Archipelago: Potential for Rapid Shifts in Colonizing Populations

M.A. Spoljaric and T.E. Reimchen*

Department of Biology, University of Victoria, P.O. Box 3020, Victoria, British Columbia V8W 3N5, Canada

ABSTRACT We investigated ontogenetic trends in body shape of 54 freshwater (48 lake, seven stream) and six anadromous populations of threespine stickleback (*Gasterosteus aculeatus* L.) from the Haida Gwaii archipelago off the west coast of Canada. Multivariate analysis of covariance on the partial warp scores generated from 12 homologous landmarks on 1,958 digital images of subadult and adult male stickleback indicated that there was considerable variability of population ontogenetic slopes. We used discriminant function analysis to quantify body shape and determined that anadromous stickleback, which are ancestral to the freshwater populations, have a strongly negative ontogenetic slope (−5.62; increased streamlining with increased size). All freshwater populations exhibit a more positive slope (91% differed significantly from the marine slope), with the differences being most accentuated in populations from ponds and streams. In pristine lakes, ontogenetic slope could be predicted by lake volume as well as multivariate measures of habitat. Evidence from field transplant experiments of one of the intact populations indicates a rapid change (5 years) from allometric to isometric growth, equivalent to about half of the total slope variation among intact populations on the archipelago. We interpret this shift as developmental plasticity and suggest this may comprise the precursor for selection of optimal body shapes in these stickleback populations. J. Morphol. 272:590–597, 2011. © 2011 Wiley-Liss, Inc.

KEY WORDS: allometry; body shape; *Gasterosteus*; geometric morphometrics; ontogeny

INTRODUCTION

Physical and biological characteristics of the habitat structure the evolution of body shape in fishes (Walker, 1997; Guill et al., 2003; Klingenberg et al., 2003; Langerhans et al., 2003; McGuigan et al., 2003; Spoljaric and Reimchen, 2007). Body shape can develop isometrically or allometrically and if allometric,, through changes in position of characters (heterotopy) and changes in the timing or rate of development of a character (heterochrony; Gould, 1977; Zelditch and Fink, 1996; Klingenberg, 1998; Zelditch et al., 2000; Kimmel et al., 2005, 2008). Expression of isometric or allometric growth within and among species is associated with age-specific shifts in the ecological niche, which presumably optimizes attributes such as foraging efficiency (Werner et al., 1983a, 1983b; Werner and Gilliam, 1984) and movement (Aleev, 1977). Although there has been substantial historical interest in ontogeny and evolutionary change (Gould, 1977), the relationship between the extent of isometric or allometric growth and habitat attributes within a species has received less attention.

Following deglaciation in the Pleistocene of the northern hemisphere, marine stickleback (*Gasterosteus aculeatus* L.), which are highly conserved morphologically (Bell and Foster, 1994; Walker and Bell, 2000), colonized freshwater habitats and diversified in a broad range of lake and stream habitats (Bell 1976, 1984; Wootton, 1984; Bell and Foster, 1994; Reimchen, 1994). Stickleback from the Haida Gwaii archipelago (British Columbia, Canada) exhibit extensive interpopulation variation in morphology over short distances and inhabit geographically isolated, relatively pristine lakes and streams, which encompass a broad range of abiotic and biotic conditions (Moodie and Reimchen, 1976; Reimchen, 1994). We recently investigated body shape differences in these populations and found that the most derived shape and the lowest sexual dimorphism of body shape occurred in shallow ponds, which are least like the ancestral marine environment, whereas populations with a body shape similar to the marine form as well as a large sexual dimorphism occurred in large deep lakes (Spoljaric and Reimchen, 2007,

---

Contract grant sponsor: Natural Sciences and Engineering Council of Canada (NSERC) Operating Grant; Contract grant number: NRC2354 (to T.E.R.).

*Correspondence to: T.E. Reimchen; Department of Biology, University of Victoria, P.O. Box 3020, Victoria, British Columbia V8W 3N5, Canada. E-mail: reimchen@uvic.ca

Received 18 December 2009; Revised 19 September 2010; Accepted 27 September 2010

DOI: 10.1002/jmor.10939

2008). We also reported that approximately 10% of the total variation in adult male body shape and up to 15% of the sexual shape dimorphism in Haida Gwaii stickleback populations can be attributed to habitat-induced phenotypic plasticity.

In the current study, using geometric morphometrics on body shape of subadult and adult size classes of 54 freshwater populations and six marine "ancestral" populations, we assess the extent of isometric versus allometric growth and for the latter, the extent of differences among slopes. If population differences in ontogenetic slopes are detected, we predict that trajectories for marine populations will be conserved in large lakes and that populations in shallow ponds will be most dissimilar from slopes for marine populations. To evaluate the extent of stability in ontogenetic slopes, we also compare body shape ontogeny for an experimental pond population that was recently (1993) transplanted from a large-bodied melanistic stickleback in an adjacent large dystrophic lake (details in Spoljaric and Reimchen 2007).

METHODS

Sampling and Study Area

Samples of stickleback from 99 lakes, 19 rivers, and six marine/brackish localities from three major geographical zones (lowland, plateau, and mountain) on Haida Gwaii were collected from 1969–2003 (see Reimchen et al., 1985; Reimchen, 1989, 1992, 1994; detailed map in Spoljaric and Reimchen, 2007). Lakes in the plateau and mountain regions share similar ecology (Reimchen, 1992), so we combined the regions (plateau/mountain) to make comparisons to the lowland populations. Fish were anaesthetized (in accordance with University of Victoria animal care protocols), fixed in 10% formalin, and stored in 95% ethanol. Most of the sites are very remote and typically less than a day was spent at each site. Sampling was largely limited to shoreline habitats, which produced primarily reproductive adults with smaller numbers of subadult stickleback. Among the 124 localities ($n = 1,958$) originally sampled, we restricted our analyses to 54 populations, which had five or more individuals (total $n = 1,354$), for subadult and adult age classes, respectively. Adults are defined by nuptial colour and gonad condition. Typically, the samples had two size classes including reproductive adults (>50 mm and usually 3+ years) and secondly the subadults (usually 35–50 mm). Habitat physical data were also collected from a subset of localities and include lake area (ha), maximum depth (m), and volume (m^3; see Appendix). We previously reported a principal component (PC) analysis on the habitat physical data, where PC1 explains 39% of the variation among habitats and represents lake morphometry (shallow and stained ponds versus large, deep, and clear lakes; Spoljaric and Reimchen, 2007, 2008).

Multivariate Quantification of Body Shape

We used digital images of subadult and adult male stickleback ($n = 1,958$) in the program TPSDig (Rohlf, 2004) to produce shape data from 12 homologous landmarks (Fig. 1; Bookstein, 1991). We used discriminant function analysis and grouped the partial warp scores and uniform components of shape change (Rohlf, 1990, 1996, 1999), generated from the program TPSRegr (Rohlf, 2000), by population to quantify stickleback body shape along orthogonal canonical vectors (CV). Recently (Spoljaric and Reimchen 2007), we described the body shape of the putative marine ancestors of Haida Gwaii stickleback populations as streamlined, including narrower peduncles, anteriad and widely spaced dorsal spines, posteriad pelvis and longer dorsal and anal fins and the more derived stickleback shape as thicker peduncles, posteriad and closely spaced dorsal spines, more anteriad pelvis and shorter median fins. These shapes correspond to our most negative and most positive values of first CV (CV1) scores, respectively.

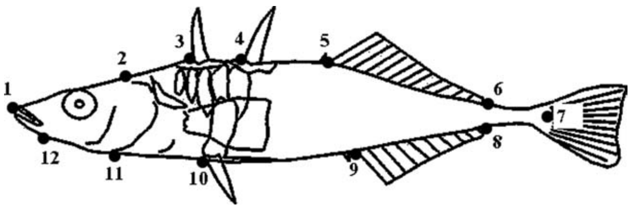

Fig. 1. Lateral view of stickleback showing the placement of landmarks used in the body shape analysis [1, anterior tip of premaxilla; 2, supraoccipital notch immediately left of the dorsal midline (DML); 3, anterior junction of first dorsal spine and basal plate along the DML; 4, anterior junction of the second dorsal spine and basal plate along the DML; 5, base of the first dorsal fin ray at the DML; 6, insertion of the dorsal fin membrane on the DML; 7, caudal border of hypural plate at lateral midline; 8, insertion of anal fin membrane on ventral midline (VML); 9, base of first anal fin ray on VML; 10, posterior tip of ectocoracoid; 11, anterior border of ectocoracoid on VML; 12, point of articulation between angular and quadrate].

To assess the ontogeny of shape change, comparisons among populations for shape trajectories were performed by testing the homogeneity of slopes using the interaction term from a multivariate analysis of covariance (MANCOVA) on the individual partial warp scores and uniform component scores from each stickleback (dependent variable), natural log of centroid size (covariate) and population name (fixed factor). To control for possible random effects due to different habitat types, we split the data (by marine, lake, and river) and performed the analysis on our groups. We use the natural log of centroid size because it is often used as an estimate of body size (Bookstein, 1991) and is tightly coupled to standard length within Haida Gwaii stickleback populations ($R^2 = 0.99$, $P < 0.001$; Spoljaric and Reimchen, 2007, 2008) as well as other west coast North American stickleback populations (see also Baumgartner et al., 1988; Walker, 1997).

We regressed the CV1 (32% of the total variation in body shape) against the natural log of centroid size and quantified the ontogenetic changes in shape through examination of each population's ontogenetic slope and mean square residuals. However, because allometric differences among populations may contribute to the discriminant function and inflate the differences in ontogenetic slope among populations, we also assessed the relationship between the first relative warp (PC analysis on the partial warp scores) and body size (ln centroid). Overall, the results were similar, and as such we present only the slopes for the CV scores. As well, the latter have better predictive power with biophysical data. The analysis was done for the whole archipelago ($n = 54$), and then separately for each geographical region (lowland, $n = 25$; plateau/mountain, $n = 29$).

We were not able to provide useful comparisons of heterochronic differences in body shape (see Zelditch et al., 2000) among populations, as in the majority of localities, we did not have an adequate time series to estimate explicit changes in developmental rate and timing of shape change among populations (Klingenberg, 1998).

Ontogenetic Slope and Habitat

We tested for any associations between ontogenetic trajectory and habitat. We determined that the ancestral ontogenetic trajectory from six Haida Gwaii anadromous stickleback populations were very similar [analysis of covariance (ANCOVA): anadromous population*ln centroid: $F_{5,69} = 0.66$, $P = 0.66$] and as such, we pooled these to generate a common slope (regression: degrees of freedom (DF) = 1, 80; slope = −5.62; $R^2 = 0.43$; $P < 0.001$), which we treat as the marine (ancestral) condition. We used ANCOVA to determine if a population's ontogenetic trajectory is the same as the slope from the pooled marine samples. ANOVA was used to determine if there are differences in the ontogenetic slopes between marine ($n = 6$), stream ($n = 7$), and lake ($n = 43$) stickleback populations, the latter partitioned into three volume categories (ponds: natural log of lake volume <11 m^3, $n = 11$; mid lakes: ln volume between 11 and 16 m^3, $n = 26$; large lakes: ln volume >16 m^3, $n = 6$) from pristine habitats. We also had four populations from artificial ponds (modified habitats from human activities). Linear regression allowed us to determine if there was relationship between ontogenetic slope and lake volume as well as our multivariate measures of lake morphometry (PC1) and chemistry (PC2). The analysis was conducted for the whole archipelago and then for each geographical region. We also progressively restricted our analyses to populations with the largest sample size and the greatest range of body size variation (ln centroid $s^2 > 0.02$) in an effort to compare ontogenetic slopes among our most substantial data.

To assess the stability in ontogenetic slopes, we also compared stickleback from an experimental pond (Mayer Pond) that was originally colonized from a 1993 transplant of stickleback (by TER) originating from an adjacent large lake (Mayer Lake) in which the stickleback exhibited all of the shape attributes typical for larger lakes. The habitat for the transplant population is a 0.07-ha (1 m depth) eutrophic roadside pond without piscivorous vertebrates, whereas the source population is an adjacent 490 ha (10 m max depth) dystrophic lake with a full suite of vertebrate predators (Moodie, 1972; details in Spoljaric and Reimchen, 2007). For Mayer Pond, we used samples from 2000 and 2002, whereas for Mayer Lake, we had samples from 1996 and 2002, all of which had two body size classes for estimating slopes. We used ANCOVA to compare the ontogenetic slopes from both the source and transplant populations.

RESULTS

Comparison of Ontogenetic Slope Among Populations

The null hypothesis for homogeneity of ontogenetic shape trajectories between stickleback populations on Haida Gwaii is rejected (MANCOVA: population*ln centroid: Pillai's Trace: $F_{53,1159} = 2.4$, $P < 0.001$). We split our data by habitat type (marine, lake, and river) and found that the results were concordant for both lake and river (lake: population*ln centroid: Pillai's Trace: $F_{45,1036} = 2.3$, $P < 0.001$; river: population*ln centroid: Pillai's Trace: $F_{7,123} = 2.1$, $P < 0.001$), but our marine populations had homogeneous slopes (population*ln centroid: Pillai's Trace: $F_{5,69} = 0.8$, $P = 0.9$). We quantified each of the 54 population's ontogenetic changes in shape by examining the direction of slopes between subadult and adult stickleback from the regression of the first shape variable (CV1: 32% of the total variation in body shape) against the natural log of centroid size. The slopes range in magnitude from −4.16 to 9.36 (Fig. 2). Twenty-two populations (41%) have near isometric changes in shape (range, −1.0 to 1.0) in which only small shape changes occur during growth, seven populations (13%) have a negative slope (<−1.0), whereas the remainder of populations ($n = 25$; 46%) exhibit a positive ontogenetic trajectory (>1.0). Negative slopes occur when younger stickleback shift toward an adult shape characterized by narrower peduncles, anteriad and widely spaced dorsal spines, posteriad pelvis and longer dorsal and anal fins. In contrast, positive slopes occur with a shift from a more ancestral body shape to adults characterized by thicker peduncles, posteriad and closely spaced dorsal spines, more anteriad pelvis and shorter median fins (Fig. 3).

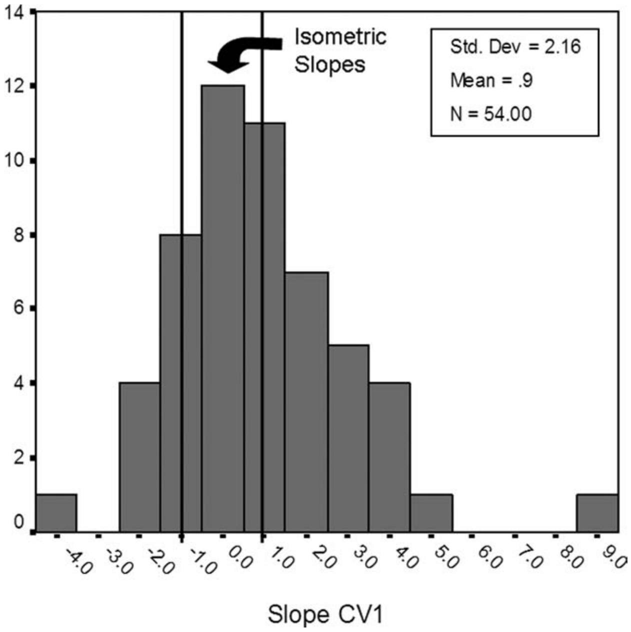

Fig. 2. Frequency distribution of ontogenetic slopes (CV1) for 54 freshwater stickleback populations from Haida Gwaii, British Columbia. Slopes (range, −1.0 to 1.0) were arbitrarily designated as "near isometric."

Ontogenetic Slope and Habitat

We examined ontogenetic trajectories in relation to habitat. All 54 fresh water populations have slopes that are more positive than the slope for the marine sample of which 49 slopes differed significantly (ANCOVA: all $P < 0.005$). We compared the slopes of the marine, stream, and lake populations; the latter separated into three size categories. On average, the stream populations had higher slope values than lake and marine samples (ANOVA: $F_{4,51} = 7.84$, $P < 0.001$; marine-large lakes difference = 3.5; marine-mid lakes difference = 4.1; marine-ponds difference = 6.0; marine-rivers difference = 6.5; Fig. 4).

Among lake stickleback, we found a relationship between ontogenetic slope and lake volume. Throughout the archipelago, populations with the

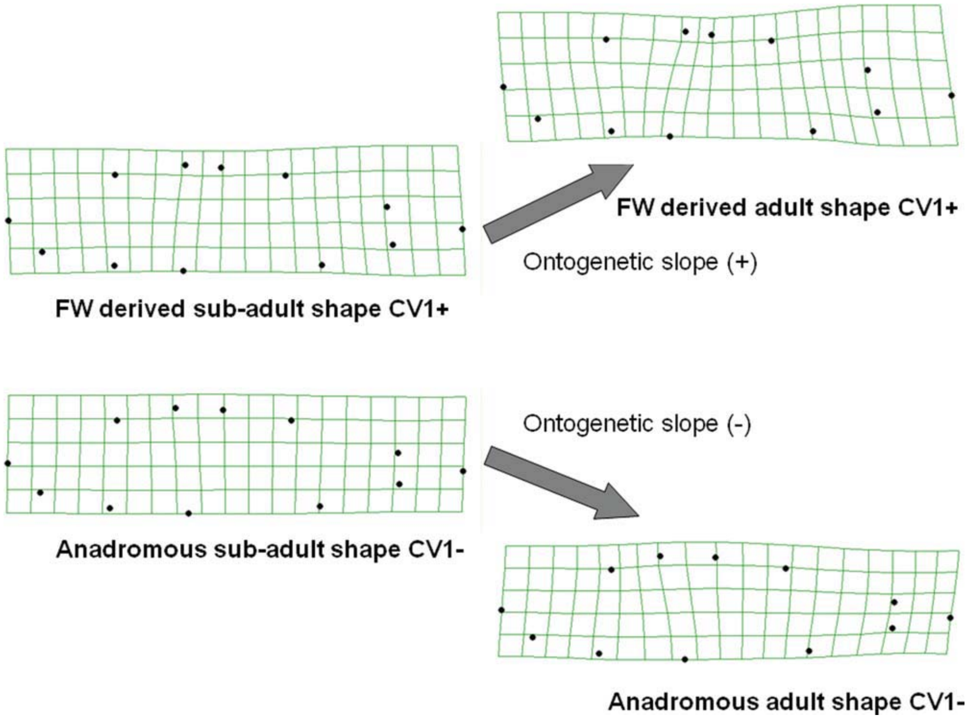

Fig. 3. Thin-plate spline plots showing hypothetical positive and negative slopes characterized by CV1 for the anadromous sample and a freshwater derived population from Haida Gwaii. Negative slopes occur when younger stickleback shift toward an adult characterized by narrower peduncles, anteriad and widely spaced dorsal spines, posteriad pelvis and longer dorsal and anal fins. Positive slopes occur with a shift in body shape, where adults are characterized by thicker peduncles, posteriad and closely spaced dorsal spines, more anteriad pelvis and shorter median fins. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

most positive slopes occur in smaller lakes, whereas those with the more streamlined ancestral shape (negative slope) are found in large deep lakes (regression: $R^2_{1,42} = 0.26$; $P < 0.001$). The relationship between slope and lake volume was replicated in each geographical region but only reached statistical significance in the lowlands (regression: slope $= -0.85$; $R^2_{1,16} = 0.72$; $P < 0.001$; Fig. 5). When we restricted our analysis to those populations with a greater variance in body size (ln centroid $s^2 > 0.02$), to increase confidence that the regression slope was based on a wide range in standard lengths, we found, with the smaller number of lakes, that ontogenetic slope could also be predicted by lake morphometry (PC1 regression: $R^2_{1,23} = 0.27$; $P < 0.05$) and lake chemistry (PC2 regression: $R^2_{1,23} = 0.26$; $P < 0.05$), suggesting that stickleback found in shallow stained ponds with low calcium, low conductivity, and low pH have a more derived ontogenetic trajectory than those stickleback found in habitats more similar to the ancestral marine environment. The results for lake morphometry were replicated in each geographical region (ANCOVA: geographic area*PC1: $F_{1,21} = 0.7$, $P = 0.41$; lowlands regression: $R^2_{1,9} = 0.52$; $P < 0.05$; plateau/mountain regression: $R^2_{1,13} = 0.35$; $P < 0.05$), whereas the relationship with lake chemistry indicated homogeneity of slopes between regions (geographic area*PC2: $F_{1,21} = 0.19$, $P = 0.67$).

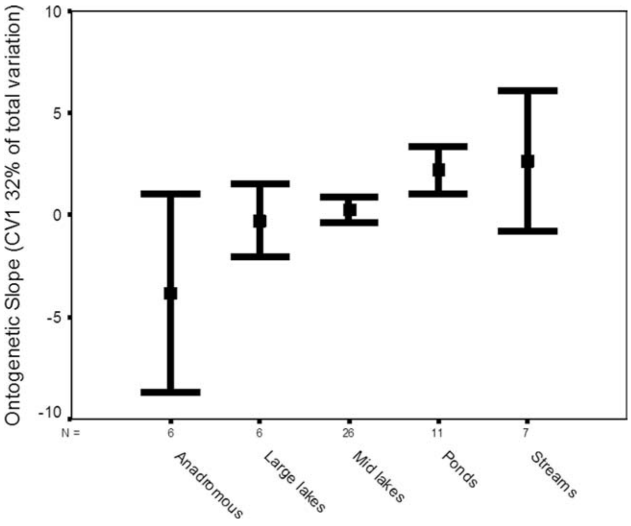

Fig. 4. Means and 95% confidence intervals of ontogenetic slope for stickleback populations found in different habitat types. Lakes were divided into three categories based on volume (ponds, ln volume less than 11 m^3; mid lakes, ln volume between 11 and 16 m^3; large lakes, ln volume greater than 16 m^3).

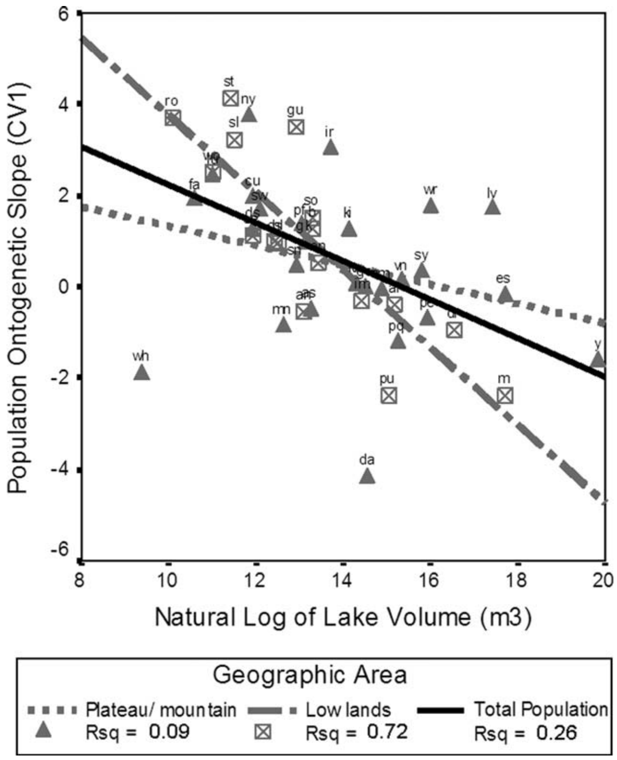

Fig. 5. Relationships between ontogenetic slope (CV1/ln centroid) and lake volume for the pristine localities for each geographical region within the Haida Gwaii archipelago. Site names listed here are abbreviated as follows: ai, Ain; am, Amber; as, Anderson South; an, Anser; b, Boulton; ce, Cedar; cu, Cumshewa; da, Darwin; ds, Desolate; dr, Drizzle; es, Escarpment; fa, Fairfax; gk, Goski; ge, Gowgaia; gu, Grus; hl, Harelda Lower; im, Imber; ir, Irridens; ki, Kiokathli; kr, Krajina; lv, Lower Victoria; lu, Lutea; m, Mayer; mn, Menyanthes; ny, New Years; on, OtterNorth; os, Otter South; pe, Peter; pq, Poque; pf, Puffin; pu, Pure; ro, Rouge; sl, Slim; sn, Snub; so, Solstice; st, Stellata; sy, Stiu; sw, Sundew; vn, Van Inlet; wh, White swan; wo, Woodpile; wr, Wright; y, Yakoun.

We also looked for differences in the ontogenetic slope between a transplanted population (Mayer Pond) and its source population (Mayer Lake). The two replicated samples from each population were homogenous (Mayer Pond ANCOVA: year*CV1: $F_{1,41} = 0.11$, $P = 0.74$; Mayer Lake ANCOVA: year*CV1: $F_{1,45} = 0.05$, $P = 0.82$). Highly significant differences occurred between the slopes of these two localities (ANCOVA: Mayer Lake/Mayer Pond*CV1: $F_{3,86} = 0.53$, $P < 0.003$). Although the source population yielded a highly negative slope, the transplanted population was isometric (Fig. 6). Using the common slope within each of these two groups (Mayer Pond, slope = 0.38; Mayer Lake, slope = −3.4), we determined that the differences in slope between the source and transplant (differences in slope = 3.8) represent 46% of the total variation in slopes among lake populations in the archipelago.

DISCUSSION

We have previously reported body shape variation among Haida Gwaii populations in which stickleback found in shallow ponds, habitats least like the ancestral marine environment, have a more derived body shape when compared with populations found in large deep lakes (Spoljaric and Reimchen, 2007). As well, those in ponds had reduced sexual dimorphism in shape when compared with populations in large lakes and marine habitats (Spoljaric and Reimchen, 2008) and cumulatively, these data indicate predictability between body shape and habitat. In this study, we show evidence that ontogenetic changes in shape also occur among these localities and that some of these changes can be predicted by the habitat type (lake or stream) and volume of the pond/lake. Our data suggest that the ancestral ontogenetic slope is negative with younger stickleback shifting toward an adult shape characterized by narrower peduncles, anteriad and widely spaced dorsal spines, posteriad pelvis and longer dorsal and anal fins. Among the 54 freshwater populations, seven exhibit a negative slope, 22 are largely isometric, whereas 25 have positive slopes with a body shape characterized by thicker peduncles, posteriad and closely spaced dorsal spines, more anteriad pelvis, and shorter median fins (Spoljaric and Reimchen, 2007). This indicates that in the majority of localities, body shape of stickleback during ontogeny shifts from a less derived (closer to the marine an-

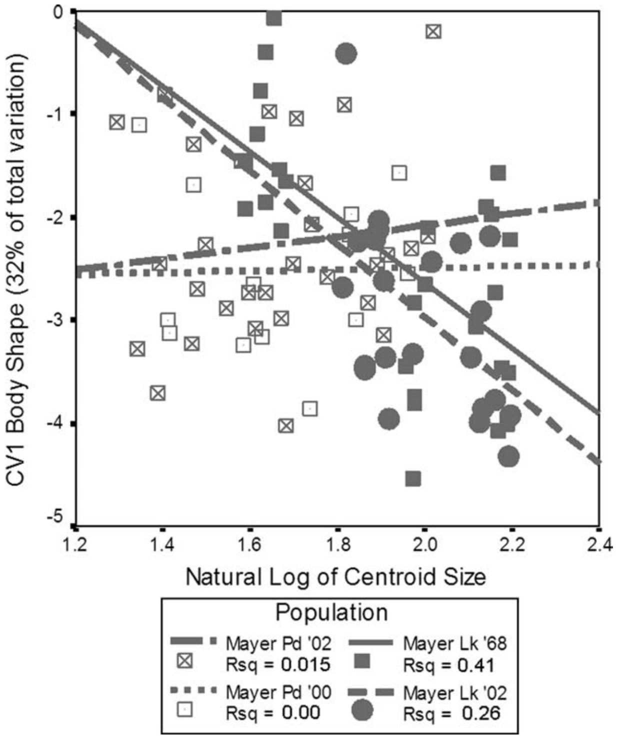

Fig. 6. Ontogenetic slopes of the source (Mayer Lake) and transplant populations (Mayer Pond). Mayer Lake is a 490-ha (10 m max depth) dystrophic lake with a full suite of vertebrate predators, whereas the adjacent Mayer Pond is a 0.07-ha (1 m depth) eutrophic roadside pond without piscivorous vertebrates.

cestral shape as quantified by CV1) to a more derived shape along this vector.

Ontogenetic slope of lake stickleback populations could be predicted by the physical characteristics of the habitat. Populations with a positive slope and derived shape are often found in shallow, stained ponds with low calcium, conductivity and pH, whereas populations with a negative slope and less derived shape are often found in large, deep, and clear lakes. Correlated with these physical differences are a broad range of predator assemblages that could be expected to influence the ontogeny of shape. Populations with very positive slopes, which occur in ponds, are characterized by macroinvertebrate piscivores on juveniles and avian piscivores on adults, whereas negative slopes occur in large lakes, where all size classes of stickleback are taken by predatory vertebrates (fish and birds; Reimchen, 1994). The relative contribution of hydrodynamic versus predator landscape to shape changes during ontogeny has not been determined. Our results are consistent with previous studies (see Walker, 1997; Walker and Bell, 2000; Spoljaric and Reimchen, 2007, 2008) that describe derived characteristics of body shape in stickleback populations found in shallow ponds, which are habitats least like the ancestral marine environment.

We found large differences between the ontogenetic trajectories in stickleback from a lake population (Mayer Lake) from that of a transplant population (Mayer Pond). Mayer Lake is large (490 ha) and dystrophic with a diversity of vertebrate predators (Moodie, 1972; Reimchen, 1992). Stickleback from this lake shift from littoral to open water habitats during growth (Moodie, 1972) and during this period they become more streamlined. The hydrodynamic features of an open water niche suggest that fish should have adaptations to reduce components of drag associated with steady swimming (Aleev, 1977; Webb, 1982, 1984) potentially accentuated by extensive exposure to fast swimming predatory vertebrates. Therefore, the ontogenetic shifts in body-shape detected in the Mayer Lake stickleback may represent size-specific adaptations to the ontogenetic change in the niche. Our results for the transplant population in Mayer Pond stickleback indicate a major shift from allometric growth in the source population to isometric growth. Mayer Pond has very limited space (0.07 ha) and is shallow (1 m) and it seems plausible that the isometric growth comprises a functional response to the restricted habitat.

The very rapid shift in the ontogenetic slope of the transplanted population, within two or three generations following the transplant, was surprising as we assumed that the trajectory of body shape (allometry) would be highly integrated and conserved (Albert et al., 2007). Virtually, all biophysical attributes of the pond including area, depth, spectra, productivity, and invertebrate assemblage are ecological opposites relative to the source locality (Spoljaric and Reimchen, 2007). Although it seems possible that rapid selection on heritable components of shape may structure these shifts, our results lead us to hypothesize that changes in ontogenetic trajectories in freshwater stickleback populations can occur very rapidly through strong developmental plasticity following abrupt exposure to large differences in the hydrodynamic, trophic, and predator landscape that would have occurred during postglacial colonization. Other evidence from lab-reared stickleback from Alaska under different dietary conditions suggests that populations may possess substantial ontogenetic plasticity and this presumably improves foraging opportunities in a trophically variable habitat (Wund et al., 2008). Neotropical cichlids exhibit functional phenotypic plasticity in trophic morphology that leads to phenotypic differences among individuals (Meyer, 1987). Stream dwelling salmonids exhibit plasticity in body shape in relation to stream velocity (Pakkasmaa and Piironen, 2000). If our suggestions are reasonable, plasticity could potentially comprise about one-half of the total variability in slopes among all fresh water populations in the archipelago. These effects may precede selection for alleles conferring optimal body shape (Albert et al., 2007) representing genetic accommodation (Baldwin effect; West-Eberhard, 2003; Wund et al., 2008).

In conclusion, this study yields four findings. First, our data indicate that there is considerable variability in the ontogenetic slopes in body shape among Haida Gwaii stickleback. Second, anadromous stickleback, which are ancestral to the freshwater populations, have a strongly negative ontogenetic slope (increased streamlining with increased size). Third, all freshwater populations exhibit a more positive slope, the differences being most accentuated in populations from ponds and streams. And finally, evidence from field experiments showing abrupt shifts in ontogenetic slopes following transplantation from a large dystrophic lake to a small eutrophic pond, lead us to hypothesize that about half of the total slope variation among intact populations on the archipelago might be because of plasticity. Functional plasticity of ontogenetic slopes to unpredictable habitats may be the precursor for selection of optimal body shapes in stickleback populations as proposed by West-Eberhard (2003).

ACKNOWLEDGMENTS

The authors thank Sheila Douglas for field assistance, and Dr. Michael Bell and Steve Leaver for discussion. This article is a component of an M.Sc Thesis by M.A.S.

LITERATURE CITED

Albert YKA, Sawaya S, Vines TH, Knecht AK, Miller CT, Summers BR, Balabhadra S, Kingsley DM, Schluter D. 2007.

The genetics of adaptive shape shift in stickleback: Pleiotropy and effect size. Evolution 62:76–85.

Aleev IUG. 1977. Nekton. Junk: The Hague. p 435.

Baumgartner JV, Bell MA, Weinberg PH. 1988. Body form differences between the Enos Lake species pair of threespine sticklebacks (*Gasterosteus aculeatus* complex). Can J Zool 66:467–474.

Bell MA. 1976. Evolution of phenotypic diversity in *Gasterosteus aculeatus* superspecies on the Pacific coast of North America. Syst Zool 25:211–227.

Bell MA. 1984. Evolutionary phenetics and genetics: The threespine stickleback, *Gasterosteus aculeatus*, and related species. In: Turner BJ, editor. Evolutionary Genetics of Fishes. New York: Plenum. pp 431–528.

Bell MA, Foster SA. 1994. The Evolutionary Biology of the Threespine Stickleback. Oxford; New York: Oxford University Press. p 571.

Bookstein FL. 1991. Morphometric tools for landmark data: Geometry and biology. Cambridge: Cambridge University Press. p 435.

Gould SJ. 1977. Ontogeny and Phylogeny. Cambridge: Harvard University Press. p 520.

Guill JM, Heins DC, Hood CS. 2003. The effect of phylogeny on interspecific body shape variation in darters (Pisces: Percidae). Syst Biol 52:488–500.

Kimmel CB, Ullmann B, Walker C, Wilson C, Currey M, Phillips PC, Bell MA, Postlethwait JH, Cresko WA. 2005. Evolution and development of facial bone morphology in threespine sticklebacks. Proc Natl Acad Sci USA 102:5791–5796.

Kimmel CB, Aguirre WE, Ullmann B, Currey M, Cresko WA. 2008. Allometric change accompanies opercular shape evolution in Alaskan threespine sticklebacks. Behaviour 145:669–691.

Klingenberg CP. 1998. Heterochrony and allometry: The analysis of evolutionary change in ontogeny. Biol Rev 73:79–123.

Klingenberg CP, Barluenga M, Meyer A. 2003. Body shape variation in cichlid fishes of the *Amphilophus citrinellus* species complex. Biol J Linn Soc 80:397–408.

Langerhans RB, Layman CA, Langerhans A, Dewitt TJ. 2003. Habitat-associated morphological divergence in two Neotropical fish species. Biol J Linn Soc 80:689–698.

McGuigan K, Franklin CE, Moritz C, Blows MW. 2003. Adaptation of rainbow fish to lake and stream habitats. Evolution 57:104–118.

Meyer A. 1987. Phenotypic plasticity and heterochrony in *Cichlasoma managuense* (Pisces, Cichlidae) and their implication for speciation in cichlid fishes. Evolution 41:1357–1369.

Moodie GEE. 1972. Morphology, life-history, and ecology of an unusual stickleback (*Gasterosteus aculeatus*) in Queen-Charlotte Islands, Canada. Can J Zool 50:721–732.

Moodie GEE, Reimchen TE. 1976. Phenetic variation and habitat differences in *Gasterosteus* populations of the Queen Charlotte Islands. Syst Zool 25:49–61.

Pakkasmaa S, Piironen J. 2000. Water velocity shapes juvenile salmonids. Evol Ecol 14:721–730.

Reimchen TE. 1989. Loss of nuptial color in threespine sticklebacks (*Gasterosteus aculeatus*). Evolution 43:450–460.

Reimchen TE. 1992. Naikoon Provincial Park, Queen Charlotte Islands: Biophysical Data for Freshwater Habitats. Victoria, British Columbia: Ministry of Environment.

Reimchen TE. 1994. Predators and evolution in threespine stickleback. In: Bell MA, Foster SA, editors. Evolution of the Threespine Stickleback. Oxford: Oxford University Press. pp 240–276.

Reimchen TE, Stinson EM, Nelson JS. 1985. Multivariate differentiation of parapatric and allopatric populations of threespine stickleback in the Sangan River watershed, Queen Charlotte Islands. Can J Zool 63:2944–2951.

Rohlf FJ. 1990. Morphometrics. Annu Rev Ecol Syst 21:299–316.

Rohlf FJ. 1996. Morphometric spaces, shape components and the effects of linear transformations. In: Marcus LF, Corti M, Loy A, Naylor GJP, Slice DE, editors. Advances in Morphometrics. New York: Plenum Press. pp 117–129.

Rohlf FJ. 1999. Shape statistics: Procrustes superimpositions and tangent spaces. J Classif 16:197–223.

Rohlf FJ. 2000. TPSRegr. Version 1.25. Stony Brook, NY: Department of Ecology and Evolution, State University of New York.

Rohlf FJ. 2004. TPSDig. Version 1.40. Stony Brook, NY: Department of Ecology and Evolution, State University of New York.

Spoljaric MA, Reimchen TE. 2007. 10 000 years later: Evolution of body shape in Haida Gwaii threespine stickleback. J Fish Biol 70:1484–1503.

Spoljaric MA, Reimchen TE. 2008. Habitat-dependent reduction of sexual dimorphism in geometric body shape of Haida Gwaii threespine stickleback. Biol J Linn Soc 95:505–516.

Walker JA. 1997. Ecological morphology of lacusterine threespine stickleback *Gasterosteus aculeatus* L (Gasterosteidae) body shape. Biol J Linn Soc 61:3–50.

Walker JA, Bell MA. 2000. Net evolutionary trajectories of body shape evolution within a microgeographic radiation of threespine sticklebacks (*Gasterosteus aculeatus*). J Zool 252:293–302.

Webb PW. 1982. Locomotor patterns in the evolution of actinopterygian fishes. Am Zool 22:329–342.

Webb PW. 1984. Body form, locomotion and foraging in aquatic vertebrates. Am Zool 24:107–120.

Werner EE, Gilliam JF. 1984. The ontogenetic niche and species interactions in size-structured populations. Annu Rev Ecol Syst 15:393–425.

Werner EE, Gilliam JF, Hall DJ, Mittelbach GG. 1983a. Experimental tests of optimal habitat use in fish: The role of relative habitat profitability. Ecology 64:1525–1539.

Werner EE, Gilliam JF, Hall DJ, Mittelbach GG. 1983b. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64:1540–1548.

West-Eberhard MJ. 2003. Developmental plasticity and evolution. New York: Oxford University Press. p 816.

Wootton RJ. 1984. A functional biology of sticklebacks. Berkeley and Los Angeles: University of California Press. p 265.

Wund MA, Baker JA, Clancy B, Golub JL, Foster SA. 2008. A test of the "Flexible Stem" model of evolution: Ancestral plasticity, genetic accommodation, and morphological divergence in the threespine stickleback radiation. Am Nat 172:449–462.

Zelditch ML, Fink W. 1996. Heterochrony and heterotopy: Stability and innovation in the evolution of form. Paleobiology 22:241–254.

Zelditch ML, Sheets HD, Fink W. 2000. Spatiotemporal reorganization of growth rates in the evolution of ontogeny. Evolution 54:1363–1371.

APPENDIX

Locality	n subadult	n adult	n Total	Range of SL (mm)	Mean SL (mm)	Habitat	Geographic area	Slope	Slope code
Ain	8	4	12	36.0–76.8	58.9	Mid lake	Lowlands	−0.4	Isometric
Amber	10	10	20	35.7–66.3	50.3	Mid lake	Plat/mtn	−0.07	Isometric
Anderson s	10	10	20	31.6–63.6	49.2	Mid lake	Plat/mtn	−0.53	Isometric
Anser	10	20	30	35.7–55.7	47.1	Mid lake	Lowlands	−0.56	Isometric
Boulton	22	27	49	31.7–62.0	49.7	Mid lake	Lowlands	1.26	Positive
Brent cr	10	10	20	30.5–48.8	40.0	Stream	Plat/mtn	3.04	Positive
Cape Ball	8	15	23	34.7–56.8	47.0	Artificial	Lowlands	1.27	Positive
Cedar	6	10	16	32.2–56.7	47.5	Pond	Lowlands	1.11	Positive
Chown	10	9	19	30.8–61.1	45.6	Stream	Lowlands	9.36	Positive
Cumshewa	7	9	16	34.4–54.4	46.2	Pond	Plat/mtn	1.94	Positive
Darwin	10	10	20	21.3–38.6	30.5	Mid lake	Plat/mtn	−4.16	Negative
Delkatla	10	9	19	31.1–52.3	40.8	Anadromous	Lowlands	−3.27	Negative
Desolate	7	9	16	32.7–52.7	45.1	Pond	Plat/mtn	1.23	Positive
Drizzle	33	21	54	36.2–79.1	61.1	Large lake	Lowlands	−0.95	Isometric
Entry pt		10	10	62.6–70.7	66.0	Anadromous	Lowlands	2.71	Positive
Escarpment	10	10	20	33.8–68.4	51.6	Large lake	Plat/mtn	−0.2	Isometric
Fairfax	8	9	17	33.2–50.4	42.7	Pond	Plat/mtn	1.89	Positive
Geike cr	6	10	16	28.3–56.1	45.8	Stream	Lowlands	4.69	Positive
Gold cr	9	8	17	33.9–64.1	46.7	Stream	Lowlands	−1.04	Negative
Goski	10	8	18	32.8–47.4	39.5	Mid lake	Plat/mtn	0.97	Isometric
Gowgaia	10	9	19	33.0–50.2	40.5	Mid lake	Plat/mtn	−0.04	Isometric
Grus	10	10	20	34.2–54.4	43.5	Mid lake	Lowlands	3.5	Positive
Harelda lower	9	10	19	32.8–62.9	48.6	Mid lake	Lowlands	0.97	Isometric
Imber	8	10	18	44.4–53.3	48.3	Mid lake	Lowlands	−0.32	Isometric
Inskip		21	21	44.8–49.6	47.1	Anadromous	Plat/mtn	0.45	Isometric
Irridens	10	10	20	33.4–49.2	42.2	Mid lake	Plat/mtn	3.02	Positive
Kiokathli	10	10	20	33.5–53.9	43.9	Mid lake	Plat/mtn	1.23	Positive
Krajina	10	9	19	35.4–50.2	41.8	Mid lake	Plat/mtn	0.05	Isometric
Low Victoria	9	11	20	34.8–57.0	47.0	Large lake	Plat/mtn	1.69	Positive
Lutea	10	20	30	32.7–53.7	44.5	Pond	Plat/mtn	2.44	Positive
Masset inlet		10	10	48.0–57.6	52.3	Anadromous	Lowlands	−8.54	Negative
Mayer	66	40	106	44.0–84.5	65.4	Large lake	Lowlands	−2.39	Negative
Mayer pd	52	38	90	33.0–68.3	53.9	Artificial	Lowlands	−0.31	Isometric
Menyanthes	10	10	20	34.2–57.1	44.5	Mid lake	Plat/mtn	−0.86	Isometric
Mollitors pd	10	10	20	34.7–53.2	43.7	Artificial	Lowlands	0.34	Isometric
New Years	10	10	20	37.5–68.7	51.7	Pond	Plat/mtn	3.75	Positive
Oeanda r	5	8	13	33.4–55.7	46.3	Stream	Lowlands	3.4	Positive
Otter s	10	10	20	35.3–63.7	50.0	Mid lake	Lowlands	0.52	Isometric
Otter n	10	10	20	34.5–57.5	45.3	Mid lake	Lowlands	0.98	Isometric
Peter	9	9	18	31.9–59.4	46.8	Mid lake	Plat/mtn	−0.7	Isometric
Poque	8	10	18	41.0–51.3	45.7	Mid lake	Plat/mtn	−1.24	Negative
Puffin	10	10	20	32.8–62.6	45.7	Mid lake	Plat/mtn	1.34	Positive
Pure	10	10	20	34.1–66.1	50.9	Mid lake	Lowlands	−2.37	Negative
Rouge	8	30	38	45.2–63.5	55.2	Pond	Lowlands	3.71	Positive
Sangan bk	9	8	17	35.2–47.5	40.8	Artificial	Lowlands	1.49	Positive
Sheldon		11	11	39.0–50.3	42.4	Anadromous	Plat/mtn	−7.56	Negative
Slim	9	10	19	33.3–61.8	49.8	Pond	Lowlands	3.21	Positive
Snub	5	7	12	35.5–53.8	44.4	Mid lake	Plat/mtn	0.45	Isometric
Solstice	10	10	20	36.0–51.6	44.6	Mid lake	Lowlands	1.5	Positive
Stellata	9	8	17	36.1–67.1	48.6	Pond	Lowlands	4.12	Positive
Stiu	10	15	25	35.5–66.4	52.0	Mid lake	Plat/mtn	0.31	Isometric
Sundew	10	10	20	35.0–51.4	43.4	Mid lake	Plat/mtn	1.65	Positive
Survey cr	9	8	17	33.9–44.3	39.8	Stream	Plat/mtn	−0.92	Isometric
Tlell est		10	10	41.8–46.3	44.2	Anadromous	Lowlands	−6.69	Negative
Van Inlet	10	10	20	33.4–50.6	41.2	Mid lake	Plat/mtn	0.1	Isometric
White swan	10	10	20	33.5–46.5	40.6	Pond	Plat/mtn	−1.92	Negative
Woodpile	10	10	20	35.3–61.2	48.6	Pond	Lowlands	2.5	Positive
Wright	8	10	18	35.0–50.4	42.7	Large lake	Plat/mtn	1.74	Positive
Yakoun lk	7	10	17	33.4–49.8	42.7	Large lake	Plat/mtn	−1.64	Negative
Yakoun r	10	10	20	33.3–50.0	41.3	Stream	Plat/mtn	−0.09	Isometric