
Habitat-dependent reduction of sexual dimorphism in geometric body shape of Haida Gwaii threespine stickleback

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We investigated the extent of sexual dimorphism in body shape in adult threespine stickleback (*Gasterosteus aculeatus*) from 39 lakes, eight streams, and five marine (two brackish, three full marine) localities on the Haida Gwaii archipelago off the mid-coast of British Columbia, as well as three lakes from southern British Columbia with benthic–limnetic species pairs. Based on digital images of 709 males and 593 females, body shape was quantified using discriminant function analysis on partial warp scores generated from twelve homologous landmarks. All populations showed males with higher positive values for canonical vector 1, which are characterized by larger heads, larger gape, posteriad dorsal spines, posteriad pelvis, longer anal fin, and deep posterior caudal depth relative to those in females. Geographical variability was present, with the highest dimorphism occurring in two of the marine habitats in addition to large lakes, whereas reduced dimorphism occurs in small shallow dystrophic ponds. We suggest that this reduction is the derived condition and is primarily due to loss of niche breadth and convergence in body shape between the sexes in pond habitats. Analyses of two experimental pond populations indicate that up to 15% of the shape dimorphism can be attributed to habitat-induced phenotypic plasticity. © 2008 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2008, **95**, 505–516.

ADDITIONAL KEYWORDS: adaptation – archipelago – *Gasterosteus aculeatus* – geometric morphometrics – niche – Queen Charlotte Islands – species pairs.

INTRODUCTION

Patterns of population variation play an important role in evolutionary diversification, and many insights into evolutionary processes have come from studies of within-population variation over a broad geographical range of the species (Badyaev *et al.*, 2000). A source of intrapopulation variation is sexual dimorphism, which continues to be extensively studied in multiple taxa not only for the role of sexual selection (Andersson, 1994), but also for ecological processes that can amplify, constrain, or reduce morphological and behavioural differences between the sexes (Selander, 1966; Schoener, 1969; Lande, 1980; Slatkin, 1984; Shine, 1989; Bonnet *et al.*, 2001; Butler & Losos, 2002; Bolnick & Doebeli, 2003).

One of the least investigated components of sexual dimorphism is body shape. Within a species, adult shape is conserved and phenotypically integrated (Strauss & Bookstein, 1982; Rohlf, 1990; Bookstein, 1991), often persisting throughout the geographical range of the species and over extended geological time (Walker & Bell, 2000). Different reproductive life histories between males and females could constrain the extent of shape dimorphism among populations (Rolf, Armitage & Coltman, 2005). However, diversifying selection can facilitate subtle morphological differences between the sexes (Shine, 1989).

Threespine stickleback (*Gasterosteus aculeatus*) are a useful taxon to investigate the potential for shape dimorphism between the sexes and the potential for population variability in this trait. After deglaciation in the Pleistocene, the highly morphologically conserved marine stickleback (Bell & Foster, 1994; Walker & Bell, 2000) colonized freshwater habitats

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and diversified in a broad range of lake and stream habitats (Münzing, 1963; Bell, 1976; Wootton, 1976, 1984). Previous investigations of stickleback have detected sexual dimorphism in defence structures (Penczak, 1965; Moodie, 1972; Potapova, 1972; Moodie & Reimchen, 1976a; Reimchen, 1980; Reimchen, Stinson & Nelson, 1985; Fernández *et al.*, 2000; Reimchen & Nosil, 2006) and additional morphometric characters including vertebral number, median fin size and trophic structures (Wootton, 1976; Bentzen & McPhail, 1984; Mori, 1984; Reimchen & Nelson, 1987; Caldecutt & Adams, 1998; Caldecutt, Bell & Buckland-Nicks, 2001; Kristjánsson, Skúlason & Noakes, 2002a; Reimchen & Nosil, 2006), body size (Moodie, 1972; Kitano, Mori & Peichel, 2007) and body shape (Leinonen *et al.*, 2006).

Stickleback populations from the Haida Gwaii archipelago (previously Queen Charlotte Islands), western Canada, provide a novel opportunity for investigations of sexual dimorphism. As well as marine habitats, populations inhabit geographically isolated, pristine lakes and streams, which encompass a broad range of biotic and abiotic environmental variation and provide natural replicated experiments because many of the divergent and endemic lake populations appear to be independently derived from marine ancestors (Moodie & Reimchen, 1976b; Reimchen, 1994). We recently investigated body shape in male stickleback from these populations and found that the most derived shape relative to marine stickleback occurred in ponds and small lakes that are least like the open marine environment of the ancestral populations (Spoljaric & Reimchen, 2007). Based on establishment of an artificial population in a barren pond, we determined that, on average, less than 10% of the total variation in body shape could be attributable to phenotypic plasticity and that the ecomorphological associations reflect adaptation to local selective landscapes. The present study investigates the extent of sexual dimorphism in body shape using geometric morphometrics and tests for associations to habitat. If body shape differences between the sexes are phenotypically constrained, we predict few if any differences among the populations. Alternatively, because Haida Gwaii lakes have low diversity of fish species (Carl, Clemens & Lindsey, 1959), we predict there could be extensive ecological opportunities for shape differentiation between the sexes within lakes due to a lack of interspecific competition. Given the diversity of biophysical variability on Haida Gwaii, we also predict that the degree of shape dimorphism will be enhanced in larger lakes with more ecological opportunity and reduced in small and shallow ponds with less breadth in niche space (Nosil & Reimchen, 2005). We examined several fully-plated marine populations from adjacent marine waters

because these represent the putative ancestral condition to Haida Gwaii freshwater populations (Moodie & Reimchen, 1976b; Deagle, Reimchen & Levin, 1996). We also compared the dimorphism in two experimental populations that were established in 1992 and 1997 from two different source populations to determine whether the sexual dimorphism had varied with respect to the source populations. As a further comparison, we investigated four of the benthic and limnetic species pairs from the Strait of Georgia, southern British Columbia (Larson, 1976; McPhail, 1984), predicting that the level of dimorphism would be reduced for each species pair relative to Haida Gwaii populations because the within-lake resource spectrum is restricted by the presence of other species (Vamosi, 2003).

MATERIAL AND METHODS

SAMPLING AND STUDY AREA

Samples of predominantly sexually mature and sub-adult stickleback from 99 lake, 19 stream, and six marine localities on Haida Gwaii were collected by T.E.R. from 1969–2003 (Figs 1, 2). These comprise three major geographical zones (lowland, plateau, and mountain) on the archipelago. Collection, scoring methods, and site descriptions are provided elsewhere (Reimchen *et al.*, 1985; Reimchen, 1989, 1992, 1994). Following anaesthetics, fish were fixed in 10% formalin, and stored in 95% ethanol. Fish gonads were removed and stained with methylene blue, and sex was determined under a dissecting microscope. Habitat physical data were also collected by T.E.R. during the fish collection from a subset of localities [pH, specific conductance, calcium concentration (mmol), T400 (percent 400 nm light transmission), lake area (ha), maximum depth (m), volume (m³), elevation (m), and distance to the ocean (m)]. We recently reported a principal component analysis on the habitat physical data where PC1 explains 39% of the variation among habitats and represents lake morphometry (small, shallow, and stained ponds versus large, deep, and clear lakes) and PC2 explains 25% of the variation and represents lake chemistry (low in calcium, conductivity, and pH; Spoljaric & Reimchen, 2007).

QUANTIFICATION OF BODY SHAPE

Digital photographs were made of 1958 males and 1850 females. To minimize potential ontogenetic effects, only adult male and female stickleback (1303 males and 1216 females) were used. We excluded populations with less than five adults of either sex to reduce spurious sampling effects. Gravid females, which are readily identified by a distended abdomen, were also excluded from the quantification of shape.

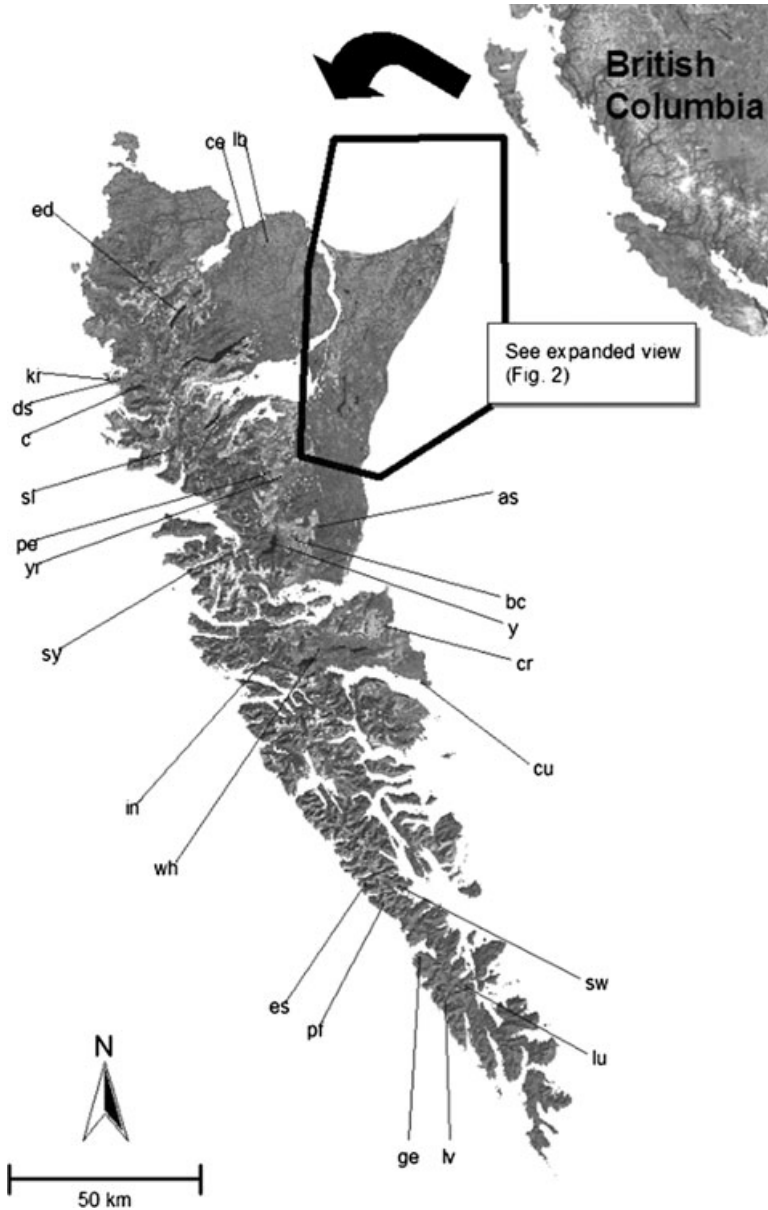


Figure 1. Localities of stickleback collections on Haida Gwaii. Site names: as, Anderson south; bc, Brent creek; c, Coates; ce, Cedar; cr, Copper river; cu, Cumshewa; ds, Desolate; ed, Eden; es, Escarpment; ge, Gowgaia; in, Inskip lagoon (marine); ki, Kiokathli; lb, Labrador creek; lv, Lower Victoria; lu, Lutea; pe, Peter; pf, Puffin; si, Seal Inlet; sy, Stiu; sw, Sundew; wh, White swan; y, Yakoun; yr, Yakoun River.

Of the 52 remaining populations (lake, $N = 39$; river, $N = 8$; and marine, $N = 5$), 709 adult males and 593 adult females were used in the shape analysis. Digital images were analyzed with the program TPSDig (Rohlf, 2004) to produce shape data from 12 homologous landmarks (Fig. 3) (Bookstein, 1991). We used the program TPSRegr (Rohlf, 2007) to align and scale the data in concordance with the generalized-least squares orthogonal Procrustes method and to generate partial warp scores (corresponding to variation in

body shape at smaller scales), and the uniform components of shape change (large-scale variation in shape from the alignment procedure) (Rohlf, 1990, 1996, 1999).

Discriminant function and relative warp analysis (Rohlf, 2002) on the partial warp scores and uniform components of shape were used to quantify male and female stickleback body shape. The uniform component was included to attain the total within population variation of body shape differences (Rohlf, 1993;

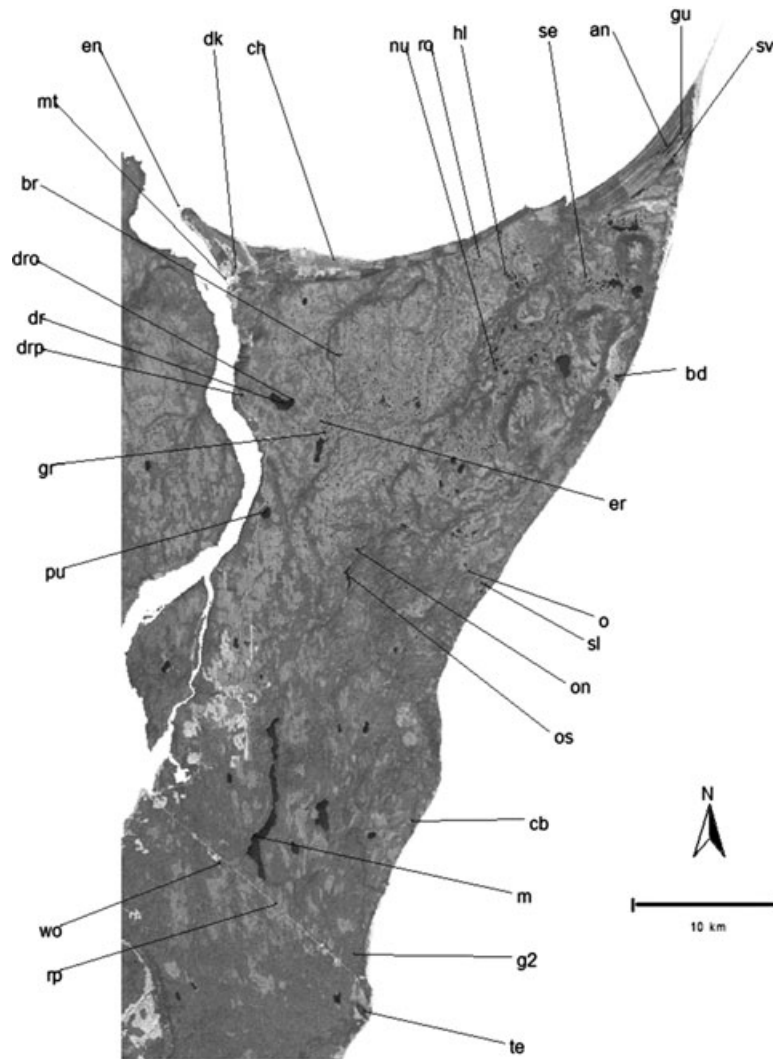


Figure 2. Stickleback localities from north-east Haida Gwaii. Site names: an, Anser; bd, Blue Danube; br, Branta; cb, Cape Ball; ch, Chown creek; dk, Delkatla (marine); dr, Drizzle; dro, Drizzle outlet creek; drp, Drizzle pond; en, Entry point (marine); er, Eriophorem; g2, Geike #2 Creek; gr, Gros; gu, Grus; hl, Harelda Lower; mt, Masset Inlet (marine); m, Mayer; nu, Nuphar; o, Oeanda river; on, Otter north; os, Otter south; pu, Pure; rp, Mayer pond; ro, Rouge; se, Serendipity; sv, Silver; sl, Slim; te, Tlell estuary (marine); wo, Woodpile.

Bookstein, 1996). The discriminant analysis produced one canonical vector (CV1) that captured 100% of the variation in male and female shape. The relative warp analysis produced twenty shape vectors, with the first five accounting for 80% of the total variation in the archipelago. The two multivariate methods yielded largely concordant results with respect to the dimorphism and biophysical associations and, as such, we report only the discriminant functions.

Pearson correlation was used to describe body shape along the vector from log linear regression transformed measures of standard morphometric variables calculated from the digital images of each fish (Table 1; also Spoljaric & Reimchen, 2007). These

morphometric measurements were standardized to remove any effects of allometry using the equation:

$$\log Y'_{ij} = (\log Y_{ij} - [v_j(\log x_i - \log x)])$$

where Y'_{ij} is the adjusted value of character j for individual i , Y_{ij} is the original value, v_j is the average allometric coefficient, x_i is the standard length of individual i and x is the mean standard length averaged over all individuals in the study (Reimchen *et al.*, 1985; Reimchen & Nosil, 2006). Maximum negative CV1 values contrasts stickleback with small heads, anteriad dorsal spines, anteriad pelvis, shallow posterior caudal depth, small gape, and

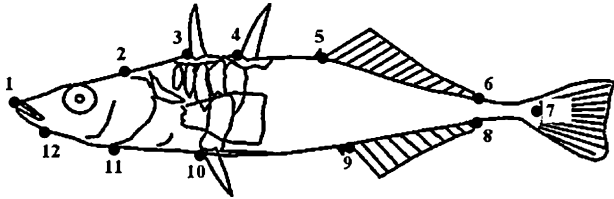


Figure 3. Lateral schematic of stickleback showing the placement of landmarks used in the body shape analysis. 1, anterior tip of premaxilla; 2, supraoccipital notch immediately left of the dorsal midline (DML); 3, anterior junction of first dorsal spine and basal plate along the DML; 4, anterior junction 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.

shorter anal fin against maximum positive CV1 values with large heads, posteriad dorsal spines, posteriad pelvis, deep posterior caudal depth, large gape, and longer anal fin.

SEXUAL DIMORPHISM OF SHAPE

Based upon the differences from the mean CV scores for males and females from each locality, we computed a dimorphism index. Wilcoxon signed rank tests were used on the mean CV scores to test for trends in dimorphism throughout the archipelago. Independent sample *t*-tests were used on the mean male and female CV scores from each of the 52 stickleback populations to calculate the proportion in which mean male and female body shape differed significantly. These tests were also performed on the size-adjusted mean morphometric measures for male and female stickleback from each locality on Haida Gwaii. We also looked at two experimental pond stickleback populations (Spoljaric & Reimchen, 2007) and compared the amount of sexual shape dimorphism with that of their source populations.

As a geographically independent test of sexual dimorphism, we extended our shape analysis to benthic–limnetic species pairs from the Strait of Georgia in southern British Columbia (McPhail, 1984). Using the same landmarks, we analyzed male and female stickleback from three lakes: Enos Lake benthic stickleback (nine males and 11 females), Paxton Lake benthic (14 males and eight females) and Paxton Lake limnetic (15 males and six females) stickleback, and Priest Lake benthic stickleback (11 males and 12 females).

Table 1. Wilcoxon signed rank test for sexual dimorphism (mean trait size in male – mean trait size in female) of morphometric characters for 52 stickleback populations from Haida Gwaii

Trait	Z	Bias	P
Standard length (unadjusted)	2.31	Female	< 0.03
Pelvis	6.28	Female	< 0.001
Pelvis position	6.26	Male	< 0.001
Head length	6.28	Male	< 0.001
Head depth	6.06	Male	< 0.001
Gape	6.28	Male	< 0.001
Dorsal spine 1 (D1) position	6.17	Male	< 0.001
Distance between D1 and D2	0.64	Male	0.52
Body depth (anterior)	6.04	Male	< 0.001
Body depth (posterior)	4.16	Male	< 0.001
Dorsal fin length	4.54	Male	< 0.001
Anal fin length	6.27	Male	< 0.001
Caudal depth (anterior)	3.54	Male	< 0.001
Caudal depth (posterior)	5.73	Male	< 0.001

Characters for each stickleback were transformed using log-linear regression to remove any effects of allometry.

We standardized CV values and used *Z*-scores (*Z*-CVs) in analysis of covariance to investigate potential relationships between shape dimorphism and body size. The natural log of centroid size was used as the size reference (see also Baumgartner, Bell & Weinberg, 1988). The centroid size is the square root of the sums of squared distances of a set of landmarks from the mathematical center (i.e. centroid) of a configuration of landmarks (Bookstein, 1991). The analysis was performed for populations throughout the whole archipelago, and then separately for populations in each geographical area (combining plateau/mountain) to determine whether there were consistent associations in each region between shape and habitat.

DIMORPHISM AND HABITAT

The degree of sexual-shape dimorphism was compared (analysis of variance) among lake, river, and marine populations of stickleback on Haida Gwaii. These tests were also conducted on the Procrustes dimorphism (population mean male configuration minus population mean female configuration) and on each of the standardized morphometric variables. We also looked at specific habitat variables to further partition the data. Pearson's correlation was used to examine the association between the degree of sexual-shape dimorphism and a multivariate measure of lake habitat for the whole archipelago and each geographical region. Shape was quantified from the canonical vector (CV1) as well as the Procrustes

dimorphism, and habitat was quantified from a principal component analysis of lake physical data. We looked for trends in populations throughout the whole archipelago and then separately for lake populations in each geographical area.

RESULTS

SEXUAL DIMORPHISM OF BODY SHAPE

Our canonical vector data yielded geographically widespread body shape differences between the sexes. Each population exhibits a male bias towards positive values of CV1 and a female bias towards negative values of CV1 (Wilcoxon signed rank test, CV1: $Z = 6.28$, $P < 0.001$; independent samples t -tests: 98% differed significantly).

Individual characters were examined for potential dimorphism between the sexes. Wilcoxon signed rank tests on mean morphometric measurements for each population indicate differences between males and females for most characters. Apart from maximum standard length and the length of the pelvic girdle, which were larger in females, the majority of size-adjusted shape traits were significantly larger in males than in females (Table 1). Our results suggest that, compared with females, male stickleback tend to have longer heads (52 of 52 populations concordant; 94% of these differ significantly between the sexes), deeper heads (49 of 52 populations; 69% significantly), larger gape (52 of 52 populations; 89% significantly), posteriad dorsal spines (49 of 52 populations; 65% significantly), deeper bodies (47 of 52 populations; 44% significantly), a longer dorsal fin (44 of 52 populations; 21% significantly), and a longer anal fin (51 of 52 populations; 79% significantly).

In the experimental populations, there was a marginal reduction in the extent of shape dimorphism compared with the source populations. In Drizzle Pond (CV1 dimorphism = 2.41), there was a 13% reduction in the dimorphism after 6 years relative to the shape dimorphism in Drizzle Lake (CV1 dimorphism = 2.76). In Mayer Pond (CV1 dimorphism = 2.63), there was a reduction of 15% of the shape dimorphism after ten years relative to the dimorphism in Mayer Lake (CV1 dimorphism = 3.11).

The results from our comparisons with the benthic limnetic species pairs from southern British Columbia were very similar to those from Haida Gwaii. Relative to females, male stickleback had greater values for CV1. There were differences among the three lakes in the extent of the shape dimorphism but these values were distributed throughout the range of differences found on Haida Gwaii (Fig. 4). Similar to female stickleback from Haida Gwaii, the southern females had greater maximum standard length

(t -test: 4 of 4 populations; 3 of 4 significant), greater length of the size-adjusted pelvic girdle (3 of 4 populations; 2 of 4 significant), shallower heads (3 of 4 populations; 2 of 4 significant) and also greater distance between the first two dorsal spines (3 of 4 populations; none significant) than males.

Standardized CV scores were used to examine the relationship between sexual shape dimorphism and adult body size. There was a slight positive relationship between CV1 and size (Z -CV1, sex \times ln centroid: $F_{1,1298} = 3.6$, $P < 0.06$). We partitioned for geographical region and a significant relationship was present in the lowland populations for CV1 (Z -CV1, sex \times ln centroid: $F_{1,867} = 5.1$, $P < 0.03$) but not the plateau/mountain region.

SHAPE DIMORPHISM AND HABITAT

We compared the extent of sexual dimorphism among habitats on Haida Gwaii. There were no overall statistical differences among the three main habitat types ($F_{2,49} = 0.24$; $P = 0.79$; lake: $N = 39$; mean difference = 3.3; river: $N = 8$; mean difference = 3.3, marine: $N = 5$; mean difference = 3.6). Populations from clear water habitat (T400 > 85%) showed a slightly greater CV1 dimorphism ($N = 16$; mean difference = 3.6) than those found in moderately stained habitat (T400 = 70–85%; $N = 10$; mean difference = 3.4) and deeply stained habitat (T400 < 70%; $N = 18$; mean difference = 3.1; $F_{2,41} = 2.04$; $P = 0.14$). When dimorphism was evaluated using Procrustes distance between mean male and female configurations, the relationship with water clarity was highly significant ($F_{2,41} = 4.5$; $P < 0.003$). The greatest difference in the expression of dimorphism occurred between clear and deeply stained habitats (Procrustes, t -test: $t = -2.9$, $N = 34$, d.f. = 32, $P < 0.007$; CV1, t -test: $t = 1.9$, $N = 34$, d.f. = 32, $P = 0.06$).

We also examined individual trait differences between the sexes (mean male minus mean female) and habitat type. Among the fourteen characters (Table 1), twelve showed no significant associations ($P > 0.05$) between the extent of dimorphism and habitat. However, of the two remaining traits, size-corrected dorsal fin length was greater in males than females in most populations (Table 1) but the extent of dimorphism differed among the three habitat types ($F_{2,49} = 5.0$; $P < 0.02$). The dimorphism was most expressed in lake populations and least expressed in river and marine habitats. In eight populations, including two in marine habitat, females had slightly larger dorsal fin lengths than that of males but this reached significance (t -test: $t = -2.32$, $N = 20$, d.f. = 18, $P < 0.04$) only for one of the marine populations. Size-corrected posterior caudal depth also differed between the three habitat types with the greatest dimorphism

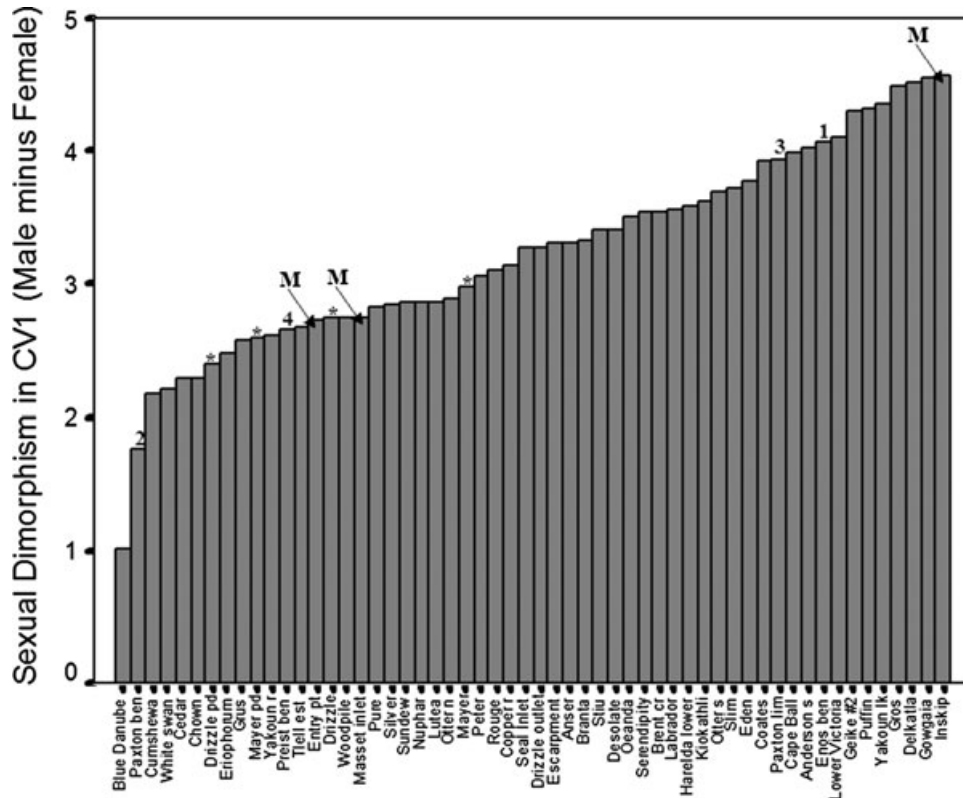


Figure 4. Bar graph of the sex differences in body shape (CV1 male minus CV1 female) from 52 stickleback populations from Haida Gwaii and four populations from the Strait of Georgia, southern British Columbia (1, Enos benthic; 2, Paxton benthic; 3, Paxton limnetic; 4, Priest benthic). Largest positive values on y-axis indicate male bias with large heads, large gapes, deep bodies and posterior dorsal spines. 'M', fully plated marine ('trachurus') populations. *Experimental pond and their source populations.

in lake habitats and the least in river and marine populations ($F_{2,49} = 3.83$; $P < 0.04$).

We further evaluated the relationship between the extent of sexual dimorphism and multivariate measures of lake habitat. Throughout the archipelago, we found a significant relationship between shape CV1 and lake morphometry (PC1: $N = 26$; CV1: $r = 0.56$, $P < 0.004$; Fig. 5), suggesting the observed body shape dimorphism decreases in populations found in small and shallow ponds. There was no association between the dimorphism of shape quantified by CV1 and lake chemistry PC2 (CV1: $r = -0.12$, $P = 0.56$).

The data were also partitioned between the two major geographical regions. In the lowlands, shape dimorphism was not associated with lake morphometry (PC1: $N = 15$; CV1: $r = 0.03$, $P = 0.91$), nor with lake chemistry (PC2: $N = 15$; CV1: $r = 0.31$, $P = 0.26$). In the plateau/mountain populations, we detected a relationship between body shape and lake chemistry (PC2: $N = 11$; CV1: $r = -0.60$, $P < 0.05$) and we observed the lowest dimorphism in populations found in small shallow ponds (PC1: $N = 11$; CV1: $r = 0.69$, $P < 0.02$).

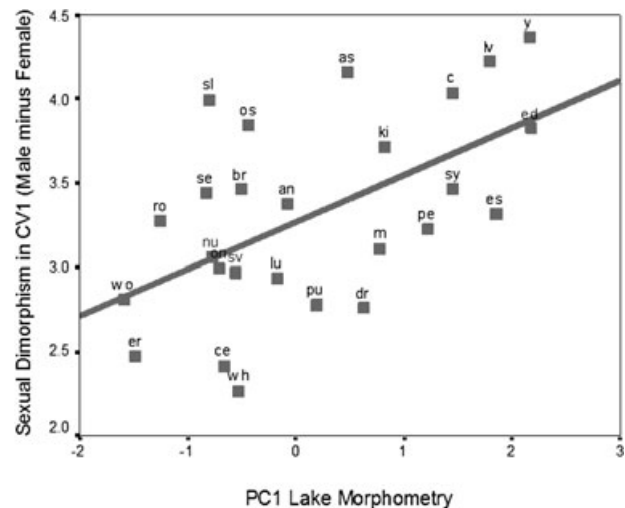


Figure 5. Scatterplot of the general sex differences in body shape of stickleback (CV1 male minus CV1 female) from 26 lakes on Haida Gwaii against lake morphometry (area, depth and volume). Positive PC1 values indicate large and deep lakes, whereas negative values indicate small and shallow ponds. For site names, see Fig. 2.

DISCUSSION

Although threespine stickleback have been extensively studied throughout their circumboreal distribution for the remarkable morphological and behavioural variability (Wootton, 1976, 1984; Bell & Foster, 1994), the extent of sexual dimorphism in adult shape among populations has received limited attention. Previous investigations have shown that, relative to females, males tend to have smaller body size, larger head, and larger median fins (Moodie, 1972; Reimchen *et al.*, 1985; Caldecutt & Adams, 1998; Kristjánsson *et al.*, 2002a; Reimchen & Nosil, 2006; Kitano *et al.*, 2007). In our study of marine and freshwater stickleback populations from the Haida Gwaii archipelago, we have found widespread concordance to these trends but major variability in the extent of the dimorphism among and within the three habitat types. Even in the marine ancestral groups, which are morphologically conserved (Bell & Foster, 1994; Walker & Bell, 2000), we found examples of both low and high shape dimorphism, which limits our ability to characterize any single ancestral condition among freshwater colonists. The male's deeper body, longer median fins, and deeper peduncle suggests an adaptation for rapid acceleration and manoeuvrability (Webb, 1984; Taylor & McPhail, 1986; Domenici & Blake, 1997; Walker, 1997; Spoljaric & Reimchen, 2007), possibly facilitated by divergent predation regimes between the sexes (Reimchen, 1980, 1994; Reimchen & Nosil, 2004).

Sexual selection has often been implicated as the basis for sexual dimorphism (Darwin, 1874; O'Donald, 1967). Greater standard length of females could result from male preference (Baker, 1994) because a larger size in fishes including stickleback is associated with increased fecundity and ability to assimilate large amounts of nutrients (Wootton, 1973; Bagenal, 1978; Baker, 1994; Bonnet *et al.*, 2001). Recent evidence suggests that the dimorphism in adult length may be environmentally determined (Kitano *et al.*, 2007). Female stickleback evaluate males based on multiple criteria including performance of the zig-zag dance during courtship (Wootton, 1976; Bakker & Mundwiler, 1999; Östlund-Nilsson, 2007), which could be influenced by one or more of the body shape differences between the sexes. The posteriad position of the male's spines in many populations may influence dorsal pricking, which is also important in courtship (Wilz, 1970). A greater body depth of males in most populations could confer an advantage in male–male interactions, whereas the larger median fins may facilitate trunk stability during egg fanning, all of which may be attractive to females (van Iersel, 1953; Wootton, 1976, 1984; Bakker, 1994; Foster, 1994; Kraak, Bakker & Mundwiler, 1999).

Ecological factors including intraspecific competition for resources and habitat use may provide additional selective pressures for shape differences between the sexes (Selander, 1966; Slatkin, 1984; Shine, 1989; Bolnick & Doebeli, 2003). During reproduction, male stickleback are benthic and littoral (Wootton, 1976) and this influences both trophic and defense attributes. Gape, dentition, head size, head shape, and body depth indicate adaptation by males to a benthic trophic niche (Bentzen & McPhail, 1984; Caldecutt & Adams, 1998; Caldecutt *et al.*, 2001; Kristjánsson, Skúlason & Noakes, 2002b; Reimchen & Nosil, 2006; Kitano *et al.*, 2007; present study). The larger head proportions would maximize buccal volume and suction velocity as an adaptation for feeding on macrobenthos (Caldecutt & Adams, 1998), whereas deep bodies should increase manoeuvrability (Webb, 1982, 1984) and facilitate foraging in the structurally complex littoral zone (Hart & Gill, 1994). By contrast, the smaller head of the female suggests reduced ability to generate suction (Caldecutt & Adams, 1998), whereas their more fusiform bodies would contribute to lower drag during steady swimming in open waters, comparable to that described in multiple taxa (Aleev, 1977; Vogel, 1981; Webb, 1984; Domenici & Blake, 1997; Walker, 1997). Further evidence for niche differentiation between the sexes occurs from direct analyses of diet and parasite infections. On Haida Gwaii, males from Boulton Lake are more littoral than are females, have an increased frequency of benthic items in their stomachs, and were more heavily infected with the tapeworm *Cyathocephalus truncatus* and the trematode *Bunodera*, whereas females have an increased frequency of pelagic items and a higher infection of the tapeworm *Schistocephalus solidus* (Reimchen, 1982; Reimchen & Nosil, 2001). The general littoral and benthic habitat of male sticklebacks and limnetic habitat of female sticklebacks also structures differential exposure to a diversity of predators, including macroinvertebrates, fish, and diving birds (Reimchen, 1994; Reimchen & Nosil, 2002), some of which could influence defense adaptations associated with body shape, including body depth and spine positions.

As a comparison with the sexual dimorphism in Haida Gwaii stickleback, we examined the benthic–limnetic species pairs from southern British Columbia. Within these lakes, benthics and limnetics exhibit behavioural and morphological foraging adaptations to their respective habitats in which benthics have larger gape and deeper body compared with limnetics (Larson, 1976; Bentzen & McPhail, 1984; McPhail, 1984, 1992; Schluter, 1993). Dietary differences between the sexes within each species from Enos Lake suggest that female limnetics were more planktivorous than limnetic males, which had mod-

erate success feeding on both benthos and plankton (Bentzen & McPhail, 1984). Recent investigations of a highly variable freshwater stickleback population from Benka Lake, Alaska, suggest that both sexes of the benthic morphotype forage on macrobenthos and both sexes of the limnetic morphotype forage on plankton (Baker *et al.*, 2005). On Haida Gwaii, benthic–limnetic species pairs within lakes have not been identified. As such, we predicted that for the species pairs in southern British Columbia, there would be only limited sexual dimorphism within each species as the benthic and limnetic trophic niches were occupied. However, contrary to our predictions, we found that the extent of the shape dimorphism and direction of individual trait comparisons between sexes within each species pair were representative of that found on lakes of Haida Gwaii. More explicitly, one of the species pairs (Enos Lake benthics) exhibited some of the highest dimorphism (CV1) for all populations. This suggests either that insular populations of Haida Gwaii stickleback have less available niche space within each lake than their southern counterparts, perhaps due to the general lower taxonomic diversity of prey on archipelago (MacArthur & Wilson, 1967), or that other processes associated with sexual selection and a wider resource base in the southern populations may accentuate the dimorphism in habitats within each species pair.

Given the general associations between deep-bodied stickleback in littoral habitat and fusiform shapes in limnetic habitats (McPhail, 1994; Walker, 1997; Hermida *et al.*, 2005; Spoljaric & Reimchen, 2007), we expected that the degree of sexual dimorphism in shape would also vary with habitat as the sexes differ in their littoral and limnetic distribution (Reimchen, 1980; Reimchen & Nelson, 1987; Nosil & Reimchen, 2005). The pristine lakes and streams on Haida Gwaii provide a diverse range of biophysical features that could act differentially on male and female stickleback morphology and we predicted, and observed, that large lakes would have greater shape dimorphism than small lakes and ponds. Previous studies of character variance in stickleback from the nearby Banks-Dewdney archipelago provide evidence for ecological release in large lakes (Nosil & Reimchen, 2005). Among all of the Haida Gwaii freshwater populations, those found in large lakes, which usually have high water clarity, tended to have high CV1 shape dimorphism, whereas the most divergent body shape in freshwater populations relative to marine stickleback occurred in small, shallow, and stained ponds, usually with low conductivity (Spoljaric & Reimchen, 2007), and it is in these habitats where the shape dimorphism decreases. We consider that the presence of higher dimorphism in large lakes and the reduction of dimorphism in small pond habitats

represents differences in ecological opportunity (Nosil & Reimchen, 2005) and is consistent with broader conceptual contexts of the ecology of sexual dimorphism (Selander, 1966; Shine, 1989).

Our assumption is that the dimorphism that we are describing has high heritability. We are partially able to evaluate this assumption from our data on the two small and shallow experimental ponds. These (Mayer Pond and Drizzle Pond) were established in 1992 and 1997, respectively, from adjacent large and deep lake source populations (Mayer Lake and Drizzle Lake). Both experimental populations show a modest reduction in dimorphism relative to the source populations and this has occurred within 10 years. Although some of this might comprise genetic responses, we currently suspect that these small differences in shape represent primarily phenotypic plasticity given the rapidity of response following colonization (Spoljaric & Reimchen, 2007). If this is the case, and these are representative, up to 15% of the differences in dimorphism among populations on Haida Gwaii may originate from nonheritable effects.

In conclusion, the present study yields two general findings. First, sexual dimorphism in body shape occurs in the majority of marine and freshwater populations and is characterized by males with smaller adult body size but relatively larger heads, deeper bodies, and longer median fins than those of females. Because marine populations are widely recognized as the ancestral colonists to freshwater habitats (Bell, 1976), the persistence of the dimorphism in a broad diversity of freshwater stream and lake habitats indicates continuity to the evolutionary processes structuring the shape dimorphism, such as constraints, sexual selection, and diversifying selection through niche differentiation. Our second finding demonstrates that CV1 shape dimorphism is geographically variable and tends to be more expressed in populations from large lakes and least expressed in small shallow ponds. This general reduction in shape dimorphism suggests that this derived condition is an adaptation that develops following colonization of habitats with limited niche space.

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