

Fast-start swimming performance and reduction in lateral plate number in threespine stickleback

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Abstract: Threespine stickleback (*Gasterosteus aculeatus*) have colonized freshwater habitats in circumboreal coastal regions, resulting in populations with variable but generally reduced lateral plate numbers compared with marine ancestors. Several abiotic and ecological factors associated with variation in lateral plate number among freshwater populations of *G. aculeatus* have been found, including large-scale climatic effects, variation in water-flow rates and levels of dissolved calcium, and the presence or absence of predatory fish. In addition, it has been proposed that plate reduction might be an adaptation for evading predator pursuit that enhances fast-start performance. If this hypothesis is correct, one would predict that fast-start performance would improve as lateral plate numbers decrease. I tested this prediction by comparing fast-start performance among stickleback with different numbers of lateral plates within two freshwater populations. Fast-starts of individual stickleback were video-recorded at 60 Hz and maximum velocity, maximum acceleration, displacement, and body curvature were calculated for each fish. Lateral plate number was significantly negatively correlated with velocity and displacement but not with acceleration or curvature. These results suggest that reduction in lateral plate number has the potential to be advantageous in some predation regimes because of its association with enhanced fast-start performance.

Résumé : Les épinoches à trois épines (*Gasterosteus aculeatus*) ont colonisé les milieux d'eau douce des régions côtières circumboréales, donnant ainsi naissance à des populations dont les plaques latérales sont présentes en nombre variable, mais généralement réduit, comparativement aux formes marines ancestrales. La variation du nombre de plaques latérales chez les populations dulcicoles de *G. aculeatus* est associée à plusieurs facteurs abiotiques et écologiques, tels les effets climatiques sur une grande échelle, les variations du débit de l'eau, les concentrations de calcium dissous et la présence ou l'absence de poissons prédateurs. De plus, il a été émis en hypothèse que la réduction des plaques est peut-être une adaptation qui permet aux épinoches d'échapper aux prédateurs en optimisant leur performance de départ précipité. Si cette hypothèse se vérifie, on peut prédire que la performance de départ précipité s'améliore lorsque le nombre de plaques latérales diminue. J'ai testé cette prédiction en comparant la performance de départ précipité chez des épinoches à nombres de plaques latérales différents provenant de deux populations d'eau douce. Les départs précipités ont été enregistrés sur bande vidéo à 60 Hz et la vitesse maximale, l'accélération maximale, le débattement et la courbure du corps ont été calculés pour chaque poisson. Le nombre de plaques latérales s'est avéré être en corrélation négative avec la vitesse et le débattement, mais pas avec l'accélération, ni avec la courbure du corps. Ces résultats indiquent que la réduction du nombre de plaques latérales peut être avantageuse dans certains régimes de prédation, parce qu'elle est reliée à une meilleure performance lors des départs précipités.

[Traduit par la Rédaction]

Introduction

The reduction of defensive armour in derived groups can evolve as a result of historical factors, limiting nutrients, or decreases in predation intensity. In addition, armour reduction may result in biomechanical benefits that are specific to a recently colonized habitat. Marine threespine stickleback (*Gasterosteus aculeatus*) have colonized freshwater habitats across the northern hemisphere, resulting in large numbers of isolated populations in coastal regions (Bell 1976; for a review see Wootton 1984). Stickleback have a predation-defence apparatus consisting of dorsal and pelvic spines as well as a series of heritable, bony lateral plates (Hagen 1973; Hagen and Gilbertson 1973; Avise 1976). The plates are used for protection against punctures from predatory fish

(Reimchen 1992), and support the adjoining dorsal and pelvic spines (Reimchen 1983). This allows the spines to remain erect and deflect lateral pressure during manipulation by predators (Hoogland et al. 1957).

Freshwater stickleback exhibit immense variation in lateral plate number, ranging from none to the complete set of 30–35 (Hagen and Gilbertson 1972; Moodie and Reimchen 1976; Gross 1977; Reimchen et al. 1985; Reimchen 1994). There are three widely recognized lateral plate morphs in stickleback: low-plated morphs, which possess a low number of anterior plates and no caudal keel; partially plated morphs, which possess anterior and some abdominal plates and a caudal keel; and completely plated morphs, which possess the entire suite of anterior and abdominal plates as well as a caudal keel (Bell 1976; Hagen and Moodie 1982; Wootton 1984). Variation in plate number, even within lateral plate morphs, is in contrast to the homogeneous presence of the completely plated phenotype among marine ancestral stickleback (Bell 1976; see review in Wootton 1984).

At a climatic scale in fresh water, low plate numbers are associated with higher temperatures and reduced annual tem-

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perature fluctuations (Hagen and Moodie 1982; Baumgartner and Bell 1984). Within drainages, low-plated stickleback tend to reside in slow-moving, low-gradient habitats, while completely plated stickleback are associated with fast-moving, high-gradient habitats (Hagen 1967; Bell 1982; Baumgartner and Bell 1984; Baumgartner 1992). At smaller scales, localized environmental and selective forces have been shown to be predictors of lateral plate expression. A low level of dissolved calcium is associated with reduced armour (Giles 1983; Francis et al. 1986; Bell et al. 1993), and the absence of fast predatory fish is associated with fewer lateral plates (Hagen and Gilbertson 1972; Moodie and Reimchen 1976; Gross 1977; Bell and Richkind 1981). Reimchen (1992) proposed that plate reduction might be an adaptation to predation regimes where the chances of escape during pursuit are high if it improves fast-start performance. There is evidence that plate numbers decrease as the dominant predators shift from salmonids, which have high pursuit efficiency, to diving birds, which have low pursuit efficiency, both among and within lakes on the Queen Charlotte Islands, British Columbia, Canada (Reimchen 1994, 1995). Experimental demonstration of a negative relationship between swimming performance and lateral plate number in stickleback would support the hypothesis that plate reduction improves the hydrodynamic efficiency of stickleback in the wild.

Several studies have addressed trade-offs between body armour and hydrodynamic performance in stickleback. Nelson (1969) suggested that short spines in brook stickleback (*Culea inconstans*) could be the result of natural selection for escape during pursuit. Experiments have confirmed that *C. inconstans* with reduced pelvic spine development have superior burst velocity and acceleration both among populations (Andraso and Barron 1995) and within populations (Andraso 1997). A comparison of swimming performance between anadromous and freshwater threespine stickleback showed that the freshwater fish, presumably with fewer lateral plates, had better fast-start performance than anadromous completely plated fish (Taylor and McPhail 1986). The low-plated limnetic and benthic stickleback species in Paxton Lake, British Columbia, both had significantly greater burst velocities than completely plated marine stickleback (Law and Blake 1996).

However, none of these studies have specifically addressed the effect of lateral plate expression on swimming performance, and the studies with *G. aculeatus* have not compared swimming performance among individuals within populations. Variation in swimming performance among lateral plate number phenotypes from different populations is likely to be confounded by other morphological and behavioural effects. Comparing swimming performance among individuals within populations would minimize variation due to these factors. It is the purpose of this study to assess variation in swimming performance within two populations of *G. aculeatus* that are polymorphic for lateral plate number.

Materials and methods

Sample collections and experimental protocol

Gasterosteus aculeatus were collected from Fairy Lake, Vancouver Island, British Columbia, and Tlell Pond, Queen Charlotte Islands, British Columbia, on 15 May 1999 and 12

June 2000, respectively. Fish from each locality were trapped with baited minnow traps within 3 m of shore. This restricted the analysis primarily to stickleback with benthic feeding modes and reduced the risk of confounding the study with variation in swimming performance between benthic and pelagic stickleback. Locality samples were kept in separate 50-gallon holding tanks in the aquatic facility at the University of Victoria.

The experimental tank was a 45 by 35 cm fibreglass container filled with 5 cm of dechlorinated water and with a laminated 1.0-cm² grid placed on the bottom. A Hi-8 Sony Sports video camera was erected 1.5 m directly above the centre of the tank. Stickleback were randomly selected from the collected samples and placed individually in the experimental tank. Fish that had obvious injuries and females that were visibly ripe were excluded from the experiment. After placement in the experimental tank, the fish were allowed to acclimate for 5 min. After this time had elapsed, I waited until the stickleback were stationary and facing away from the side of the tank, started the camera, and then thrust the handle of a fish net directly towards the fish's head to initiate a flight response. This technique has been used in other studies of burst-flight performance in fishes and has produced conclusive results (Harper and Blake 1990; Brainerd and Patek 1998). The startle response in teleosts is an all or nothing response activated by one Mauthner cell and its spinal motor neurone pool (Eaton et al. 1977). Therefore, because of the threshold nature of the response, there should not be a graded relationship between the degree of the response and the intensity of the stimulus.

After the flight response had ceased, the video recorder was turned off and the fish were allowed 3 min to recover before being given the visual stimulus again. If the stickleback became unresponsive to the stimulus, no more replicates were performed for that individual. Between 1 and 4 replicates were performed per fish. Twenty-one fish were tested from Tlell Pond and 42 from Fairy Lake. All individuals were tested at water temperatures of 18–19°C.

After the burst-swimming tests were completed, the fish were removed from the tank and lightly anaesthetized. Standard length (SL; mm), body depth (mm), and the average number of lateral plates per side $((R + L)/2)$ were recorded using a dissecting microscope, after which the fish were returned to their holding tank. Body depth was measured at the point of maximum dorsoventral depth of each fish and did not include spine or fin size. In stickleback, this is at the point just anterior to the base of the second dorsal spine. Mean lateral plate number was square-root transformed. Means and variances of SL, body depth, and lateral plate number did not differ significantly between the Fairy Lake and Tlell Pond samples (Table 1). Minimum SL was 38.5 mm in the Fairy Lake sample and 45.1 mm in the Tlell Pond sample, both of which were above the minimum SL at which lateral plate development is complete (Bell 1981). All fish were handled and cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care.

Video and statistical analysis

Video data were digitized and split-frame images were deinterlaced, allowing for an image frequency of 60 frames/s. Video-image analyses were completed in Scion Image.

Fig. 1. Calculation of the curvature coefficient (CC), modified from Webb (1978). BL, bent length, or chord distance, from the snout to the posterior tip of the caudal peduncle of the flexed fish; SL, standard length of the straight fish at rest.

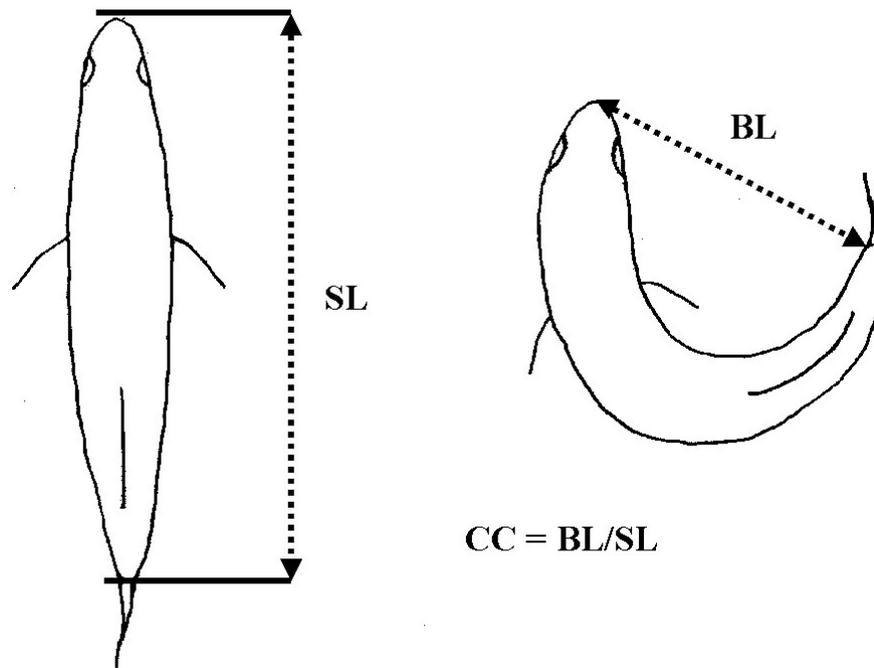


Table 1. Mean and variance of standard length (SL), body depth, and lateral plate number for Fairy Lake and Tlell Pond stickleback samples.

	Fairy Lake (mean \pm SD)	Tlell Pond (mean \pm SD)	Levene's test		<i>t</i> test	
			<i>F</i>	<i>P</i>	<i>t</i>	<i>P</i>
SL	53.03 \pm 6.72	56.16 \pm 6.95	0.001	0.977	1.902	0.061
Depth	12.78 \pm 1.70	12.96 \pm 1.60	0.480	0.491	0.448	0.655
Lateral plate no.	9.83 \pm 6.88	12.80 \pm 8.11	1.971	0.165	1.667	0.100

Maximum velocity and maximum acceleration reached during the Mauthner-initiated flight response were calculated for each individual fish replicate, as well as the distance travelled (displacement) in millimetres in the first 6 frames (0.100 s). Other studies of burst-swimming performance in *G. aculeatus* have shown that maximum velocity and acceleration were reached in the first 0.040–0.050 s (Taylor and McPhail 1986; Law and Blake 1996).

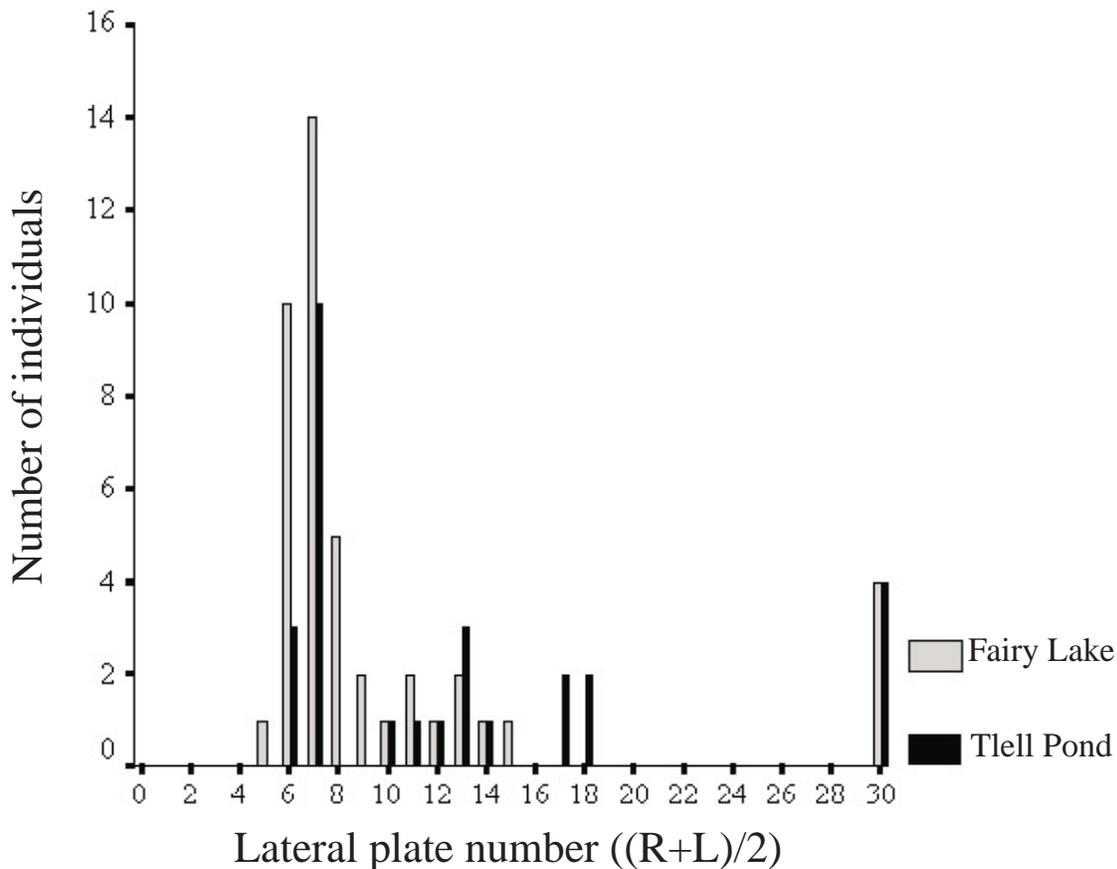
Mauthner-initiated startle responses are preceded by curvature of the body (Eaton et al. 1977). The initial angle of this curvature is positively correlated with burst velocity in *C. inconstans* (Andraso and Barron 1995; Andraso 1997). It is conceivable that additional plates could reduce the angle of curvature and thus affect swimming performance in threespine stickleback. Therefore, curvature was measured in each individual replicate in this study. The curvature coefficient (CC) was measured as the chord distance from the snout to the posterior tip of the caudal peduncle when the stickleback assume their c-shape (the bent length) divided by SL of the fish when straight (Webb 1978; Fig. 1). Smaller CC values indicate greater curvature.

The collection of replicate performance data allowed me to determine if variation within individuals (among replicates) was significantly larger than among individuals. The numbers of replicates were low and varied among individu-

als (from 1 to 4), resulting in significant heteroscedasticity in performance variance among individuals for all performance variables. Therefore, non-parametric Kruskal–Wallis (K-W) tests were run on individuals \times maximum velocity, maximum acceleration, displacement, and CC. There was significantly greater variation among than within individuals for maximum velocity (K-W test, $\chi^2 = 59.944$, $P = 0.028$), maximum acceleration (K-W test, $\chi^2 = 59.079$, $P = 0.033$), and displacement (K-W test, $\chi^2 = 61.088$, $P = 0.017$). The curvature coefficient did not have significantly greater variance among than within individuals (K-W test, $\chi^2 = 48.548$, $P = 0.079$), although significance was approached.

Analysis of covariance (ANCOVA) was performed to determine if the relationships between the 4 performance variables and the factors (SL, body depth, and lateral plate number) were similar enough between the two lakes for their samples to be pooled in multiple regression analyses. Multiple regression analyses were used to assess the residual effects of each of the factors on the performance variables. Distributions of the 4 performance variables did not differ significantly from normality (Kolmogorov–Smirnov test, $P > 0.200$ for each variable).

Lateral plate numbers ranged from 5 to 30 per side in Fairy Lake and from 6 to 30 in Tlell Pond. The combined lateral plate number phenotypes from the two samples formed

Fig. 2. Frequency distribution of lateral plate number phenotypes in Fairy Lake and Tlell Pond.**Table 2.** Correlation-coefficient matrix showing levels of correlation (r) among the 4 performance variables.

	Velocity	Acceleration	Displacement
Acceleration	0.673**	—	—
Displacement	0.869**	0.642**	—
Curvature coefficient (CC)	-0.318*	-0.177	-0.151

* $P < 0.050$ (two-tailed).** $P < 0.001$ (two-tailed).

a roughly continuous distribution from 5 to 18 only, which included both the low-plated and the partially plated morph (Fig. 2), followed by a group of outliers composed of 8 completely plated individuals (with 30 plates per side). Performing regression analyses on data containing outliers is a serious violation of the underlying assumptions of most parametric tests (Zar 1999). I therefore ran the multiple regression analyses both excluding and including this group of outliers to determine if there were incongruities in the results. All statistical analyses were performed in SPSS-10.0.

Results

There was a high degree of correlation among the 4 performance variables (Table 2). Velocity, acceleration, and displacement all had a strong positive correlation with each other and were significant at $\alpha < 0.001$ in each case. The CC was negatively correlated with each of the other 3 variables but was significant only with velocity at $\alpha < 0.050$.

All ANCOVAs passed Levene's test for homogeneity of

variation. None of the slopes between the factors and performance variables differed significantly between Fairy Lake and Tlell Pond (Table 3). This allowed me to test whether the adjusted means of the variables were similar enough between the two populations to pool them into one sample. The adjusted means of the performance variables differed significantly between Fairy Lake and Tlell Pond for maximum acceleration and displacement, approached significance for maximum velocity (Fairy Lake fish showed greater performance for all 3 variables), and were insignificant for CC (Table 3). I therefore included location as a factor in the regressions to account for the variance in adjusted means between samples.

Lateral plate number was significantly correlated with maximum velocity after the effects of SL, body depth, and sample locality were removed (Table 4). Stickleback with fewer plates achieved greater maximum velocity. However, this association only applied to the low-plated and partially plated stickleback. When the completely plated outliers were included in the regression analysis, the correlation remained

Table 3. Test for homogeneity of slopes and differences of adjusted means (ANCOVA) between lake samples for each of the performance variables (maximum velocity, maximum acceleration, displacement, and CC) and 3 factors (SL, depth, and lateral plate number).

Dependent variable	SL		Depth		Lateral plate no.		Adjusted means	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Velocity	0.813	0.371	0.032	0.858	0.374	0.543	3.451	0.068
Acceleration	0.914	0.343	0.002	0.962	0.001	0.972	8.925	0.004*
Displacement	0.927	0.340	0.079	0.779	0.144	0.706	7.191	0.009*
CC	0.007	0.934	2.872	0.096	0.121	0.730	0.036	0.851

Note: Lateral plate number is square-root transformed.

**P* < 0.050.

Table 4. Partial correlations and significance levels from multiple regression analyses.

Dependent variable	Factor	Partial <i>r</i>	<i>P</i>
Velocity	SL	0.032 (0.018)	0.816 (0.893)
	Depth	0.037 (0.017)	0.788 (0.898)
	Lateral plate no.	-0.267 (-0.232)	0.049* (0.074)
	Sample	-0.140 (-0.180)	0.310 (0.169)
Acceleration	SL	0.152 (0.151)	0.269 (0.249)
	Depth	-0.118 (-0.113)	0.390 (0.388)
	Lateral plate no.	-0.023 (-0.131)	0.865 (0.318)
	Sample	-0.351 (-0.356)	0.009* (0.005)*
Displacement	SL	0.016 (0.003)	0.908 (0.979)
	Depth	0.057 (0.054)	0.680 (0.782)
	Lateral plate no.	-0.290 (-0.315)	0.033* (0.015)*
	Sample	-0.221 (-0.262)	0.108 (0.045)*
CC	SL	-0.186 (-0.173)	0.180 (0.195)
	Depth	0.127 (0.153)	0.358 (0.253)
	Lateral plate no.	0.057 (0.055)	0.676 (0.684)
	Sample	0.103 (0.071)	0.453 (0.595)

Note: Values in parentheses reflect inclusion of outliers in the analysis.

**P* < 0.050 (two-tailed).

negative but became insignificant. SL, body depth, and location had no significant effect on maximum velocity, with or without the outliers.

Maximum acceleration had no significant correlation with SL, body depth, or lateral plate number, with or without the outliers (Table 4). However, sample location was a significant predictor of acceleration in both cases.

Displacement increased significantly as lateral plate number decreased, both with and without the outliers (Table 4). None of the other 3 factors had a significant effect when the outliers were excluded, but sample location was a significant predictor of displacement with outliers included.

There were no significant correlations between any of the factors and CC, regardless of the inclusion or exclusion of the outliers (Table 4).

Discussion

In freshwater threespine stickleback, lateral plate number was negatively associated with maximum velocity and displacement but not with maximum acceleration or minimum CC. These results suggest that while lateral plate number was negatively associated with some components of fast-start performance as predicted, it did not appear to affect performance by limiting flexibility (CC) or acceleration. In addition, flexibility was not strongly correlated with the other

performance variables, and had only a weak significant association with velocity (Table 2). Hence, flexibility itself was not a good predictor of fast-start performance in these two populations.

There could be two explanations for this. The first is that the error variance of CC may have been too great for significant correlations to be detected between it and other factors. While the variance of CC was greater among than within individuals, it was not significantly so (*P* = 0.079). Measurement error in the extraction of data from the video could have swamped correlations, if present, between lateral plate number and curvature as well as between curvature and the other performance variables. Problems with accurate extraction of video data have been demonstrated, and instantaneous information such as minimum body curvature or maximum acceleration is frequently "smoothed over" when using frame-by-frame analysis with low film speeds (Harper and Blake 1989).

Secondly, associations between swimming performance and lateral plate number may have been confounded by other morphological or behavioural factors that directly affect swimming performance. Taylor and McPhail (1986) found that stream-dwelling stickleback, presumably with fewer plates, had superior fast-start performance to marine stickleback, and attributed this to differences in body shape. The benthic stickleback of Paxton Lake have fewer plates than the limnetic

stickleback, but there are other morphological differences between them that are correlated with lateral plate morph (McPhail 1992). If body form is correlated with lateral plate number in stickleback in Fairy Lake and Tlell Pond, this could have produced complex and unresolved interaction effects on swimming performance. However, all of the stickleback used were taken from benthic littoral regions of the lakes, reducing the likelihood of confounding the results with differences in body shape associated with microhabitat use. Nonetheless, subtle body-shape variation among benthic stickleback from these lakes, as well as behavioural differences correlated with lateral plate morph, could have contributed to unexplained variance in swimming performance in this study, confounding the weak associations between lateral plate number and performance variables (Table 4).

Lateral plate number may have directly affected velocity and displacement by generating drag. The effect of drag on hydrodynamic performance in fishes is well documented (Webb and Skadsen 1979; Vogel 1981; Webb 1982), and projections or "roughness" of the surface can reduce fast-start performance. The lateral plates of stickleback form slight lateral projections at their posterior edges. The length of these projections was very close to but slightly greater than the largest admissible size before disruption of the boundary layer occurs (Schlichting 1960; Aleyev 1977), raising the possibility that the lateral plates may have generated enough drag to affect performance.

The group of outliers in this study was composed entirely of the completely plated morph, the exclusion of which had some subtle effects on the results (Table 3). The completely plated morphs attained slightly higher velocities than predicted by the regression of fish with 18 plates or fewer, reducing the negative partial r value to just below significance. It is conceivable that other behavioural or morphological traits which also affect swimming performance could be associated with this phenotype. For example, the reduction of the negative effect of lateral plate number on burst velocity in the completely plated morph could reflect a plateau in the accrual of the hydrodynamic costs of adding more than 18 plates. The inclusion of the completely plated outliers also resulted in a significant effect of sample locality on displacement (Table 3). Interestingly, the inclusion of completely plated morphs resulted in higher partial r values for sample effects for every performance variable except CC, suggesting that the completely plated morphs in Fairy Lake may have other behavioural or morphological attributes that enhance their burst-swimming performance which are lacking in the completely plated morphs from Tlell Pond.

The demonstration of a negative relationship between swimming performance and lateral plate number in this study supports the hypothesis that plate reduction is associated, either directly or indirectly, with improved hydrodynamic efficiency. This association is predicted by Reimchen's (1992) hypothesis that plate reduction is a defensive adaptation for evading predators with low pursuit efficiency. Estimates of relative pursuit and handling efficiencies suggest that there may be stronger selection for fast-start performance in stickleback subject to predation by diving birds than in those subject to predation by trout (Reimchen 1988, 1991, 1992, 1994; C.A. Bergstrom, unpublished data). If this is the case, reduction in lateral plate number may be advantageous in avian predation

regimes as a result of its association with enhanced fast-start swimming performance.

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