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Form and performance: body shape and prey-capture success in four drift-feeding minnows

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Abstract Identifying links between morphology and performance for ecologically relevant tasks will help elucidate the relationships between organismal design and fitness. We conducted a laboratory study to quantify the relationship between variation in body shape and prey-capture success in four drift-feeding minnow species. We offered drifting prey to individual fish in a test flume, counted successful strikes to measure prey-capture success and recorded the position (*X*, *Y* coor-

for most of the ontogenetic variation in capture performance, although other size-related, non-shape factors also seemed relevant. Fishes with deeper, shorter bodies, more caudally placed median fins and larger, more upward-pointing mouths exhibited greater capture success than more fusiform fish, suggesting that streamlining, which is energetically advantageous for sustained swimming, entails a cost in terms of prey-capture ability. Our findings demonstrate a strong connection

dinates) of ten landmarks on each fish's outline to delineate the specimen's form. We then quantified shape variation among species and related it to capture performance through thin-plate spline analysis. Body shape varied significantly among species and with specimen size and was the major determinant of capture success, explaining 45–47% of its variability. Prey-capture success at differing velocities differed among species, but once the effects of shape and size were accounted for, those differences were no longer significant. Allometric shape changes appeared responsible between organismal shape and performance and provide empirical evidence of the cost of morphological specialization for fishes in the drift-feeding functional guild.

Keywords Ecomorphology · Ecologically relevant tasks · Morphological costs · Stream fishes · Cyprinidae

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Introduction

The relationship between morphology and the use of trophic and spatial resources (i.e., ecological performance) has interested biologists since the time of Darwin (Lack 1947; Wainwright and Reilly 1994). Ultimately, morphology limits an organism's performance at ecologically relevant tasks, although morphology and behavior interact to form a feedback loop with reciprocal influences (Arnold 1983; Wainwright 1994; Ricklefs and Miles 1994). Therefore, establishing the relationship between organismal design and performance at important tasks provides (1) a mechanism for the abundantly reported correlations observed between morphology and ecological traits (Miles et al. 1987; Douglas and Matthews 1992; Norberg 1994) and (2) a basis for subsequent, detailed functional analyses

(Wainwright 1994). There are, however, relatively few explicit, experimental assessments of how morphology affects ecological performance in natural populations.

Organisms for which ecologically relevant tasks can be clearly identified and efficiently measured represent promising systems for elucidating morphology–performance relationships (Norberg 1994; Dewitt et al. 1999; Fulton et al. 2001), and drift-feeding stream fishes comprise just such a system. Drift-feeding fishes also are important components of stream fish faunas worldwide (Matthews 1998); thus, studies of their dynamics have the potential for generality. To briefly describe this system, drift-feeding fishes typically hold relatively stable foraging positions in running water from which they dash to strike at macroinvertebrates carried downstream by the current (i.e., drift) (Hughes and Dill 1990; Hill and Grossman 1993; Grossman et al. 2002). Swimming to hold position against a current may impose substantial energetic costs on drift-feeding fishes (Facey and Grossman 1990), and, at velocities higher than about 5–10 cm/s, current speed can negatively affect the ability of fishes to capture drifting prey (Hill and Grossman 1993; Tyler 1993; Grossman et al. 2002). However, fishes still occupy foraging positions with velocities higher than 10 cm/s because encounter rates with drifting prey generally increase with increasing current velocity (Hughes and fishes from a southern Appalachian stream. All species examined occupy positions in the water column in Coweeta Creek, N.C., and the influence of current velocity on prey-capture success is the dominant factor determining the focal-point velocities they occupy (Grossman et al. 2002).

Geometric morphometrics can elucidate subtle body shape differences in organisms and relate those to ecological factors (Rohlf and Marcus 1993; Bookstein 1996a; Monteiro et al. 2000). However, their use is not common in ecomorphology (Walker 1997; Adams and Rohlf 2000; Svanbäck and Eklöv 2002) and, to our knowledge, this tool has not previously been used to relate measurements of individual shape and performance. In this study, we utilized it to assess (1) intra- and interspecific variation in morphology and prey-capture performance, and (2) relationships between morphology and foraging success (i.e., ecological performance) of four syntopic drift-feeding minnows (Cyprinidae).

Materials and methods

Study species

Our study species were: rosyside dace (*Clinostomus*

Dill 1990; Grossman et al. 2002).

Prey capture is an ecologically relevant task for drift-feeding fishes that should be strongly linked to individual fitness, via its effects on growth. For example, spatial variation in prey-capture success is a major determinant of habitat selection and spatial distribution of individuals within habitat patches (Hughes and Dill 1990; Hill and Grossman 1993; Tyler and Gilliam 1995; Grossman et al. 2002). Spatial and temporal changes in prey-capture success also influence other ecological processes, including: (1) diel activity patterns (Fraser and Metcalfe 1997), (2) growth rates (Wilzbach and Cummins 1986) and (3) foraging mode shifts and niche segregation (Schaefer et al. 1999; Nakano et al. 1999). In addition, capture success of drift-feeding fishes can be measured with reasonable ease, accuracy and realism in the laboratory (Hill and Grossman 1993; Tyler 1993; Grossman et al. 2002).

To our knowledge, the relationship between body morphology and prey-capture success (i.e., ecological performance) has not been quantitatively assessed in drift-feeding fishes. Consequently, we used geometric morphometrics (Rohlf and Marcus 1993) and laboratory experiments on current velocity/prey-capture success to explore the link between morphology and ecological performance in a group of drift-feeding *funduloides*), warpaint shiner (*Luxilus coccogenis*), Tennessee shiner (*Notropis leuciodus*) and yellowfin shiner (*Notropis lutipinnis*). They are members of the "shiner clade", but yellowfin and Tennessee shiners are phylogenetically closest, both placed in the subgenus *Hydrophlox* within *Notropis* (Jenkins and Burkhead 1994; Mettee et al. 1996), and warpaint shiner is closer to them than to rosyside dace (Coburn and Cavender 1993). All four species are common and occur in syntopy in the middle reaches of Coweeta Creek (Little Tennessee River drainage, Macon County, NC, USA), although yellowfin shiner was introduced into the area by man approximately 15 years ago (Menhinick 1991).

The four study species are fairly similar in general external morphology and ecology. They are relatively small with most individuals being less than 80 mm in fork length (FL, length to the fork of the tail), although it is not uncommon for rosyside dace and warpaint shiner to reach lengths greater than 100 mm FL (Menhinick 1991; Jenkins and Burkhead 1994; Mettee et al. 1996). Typically, all four species consume drifting aquatic and terrestrial macroinvertebrates and occupy pools and runs with occasional warpaint and rosyside specimens in the tails or heads of riffles (Outten 1957, 1974; Reisen 1972; Grossman and Freeman 1987; Freeman and Grossman 1992a; Hill and Grossman 1993).

All four species forage both in groups (mono and multispecific) and solitarily (Freeman and Grossman 1992a, b).

Measurement of prey-capture success

The procedures used to assess prey-capture success have been described in detail by Grossman et al. (2002); hence, only the most relevant information is presented here. We captured fishes from Coweeta Creek during the summer of 1998 (water temperature 18–20°C) by seining. Fishes were taken to the laboratory and held in tanks at 18°C with water velocities of about 5 cm/s for 2–3 days before capture success measurements were taken. They were fed rations that approximated maintenance levels (Hill and Grossman 1993) using commercial trout pellets and live *Hyalella azteca* (Amphipoda) 4–7 mm long.

We measured prey-capture success of 107 individuals of the four species (*n*, mean length, range = rosyside dace, 28, 59.4, 40–76 mm; warpaint shiner 29, 64.5, 36–109 mm; Tennessee shiner 26, 51.8, 37–62 mm; and yellowfin shiner 24, 61.5, 42–75 mm) in a 90-cm-long by 35-cm-wide by 35.5-cm-deep test chamber with a Plexiglas viewing port. We recorded the exact positions of specimens during trials using grids marked on both sides and the bottom of the tank. We controlled veloc-

prey at approximately 20-s intervals until ten prey had been delivered. An observer recorded prey-capture data and noted both the holding and strike positions of the fish. After completion of the trial, we measured velocities at these locations with an electronic flow meter (Marsh-McBirney 201) accurate to ±0.01 cm/s. Each subject was tested at two or three velocities in a given day in combinations that minimized the effects of fatigue and satiation. Although capture success (proportion of prey captured) was measured at eight different velocities, in this study we only explored the general relationship between morphology and foraging performance at 10, 15, 10 and 25 cm/s and in more detail at 15 cm/s. We chose those velocities because capture success, although still reasonably high, exhibited sufficient variability to make statistical comparisons feasible. We selected 15 cm/s for more in-depth analysis because it is close to the optimal focal velocities used in the field by the four study species (Grossman and Freeman 1987; Hill and Grossman 1993; Grossman et al. 2002).

For a task to be ecologically relevant, individual differences in performance must show some temporal stability and, hence, individual scores in performance tests should be repeatable (Kolok 1999). We only tested fishes once at each velocity and, therefore, could not directly assess repeatability for our performance

ity in the tank using an electric trolling motor with variable speed controls (thrust = 37 lb) placed at the front of the chamber. A honeycomb collimator placed between the propeller and the chamber reduced turbulence in the tank. We conducted foraging trials at 18°C and used live *H. azteca* (4–7 mm long) as test prey. *H. azteca* is easily cultured and was readily consumed by the fishes. *H. azteca* always traveled the length of the chamber without sinking to the bottom and the fishes fed on it using behaviors similar to those exhibited under field conditions (Freeman and Grossman 1992a, b; G. Grossman personal observation). Live *H. azteca* were released into the current 5 cm below the surface via a piece of flexible plastic tubing attached at the upstream screen.

We measured capture success at the fish's focal position at velocities ranging from 5 cm/s to 40 cm/s at 5-cm/s intervals. Fishes always held position in the same area of the test chamber, and we used pilot trials to calibrate motor speeds to produce the desired velocities. A trial began by placing a single test fish in the chamber, allowing it to acclimate at 10 cm/s for 10 min and then delivering prey until it made one capture (a few fishes refused to feed and were not used in trials). We then gradually adjusted the apparatus until the desired velocity was obtained and began releasing measurement (capture success at 15 cm/s). However, capture success at 15 cm/s showed a high positive correlation with capture success at both 10 cm/s and 20 cm/s for all experimental subjects both within and among species ($r = 0.81$–0.90, all P values < 0.0001). Test subjects were never tested on the same day at adjacent velocities (e.g., 15 cm/s and 20 cm/s); hence, these data should not be serially correlated. Therefore, prey-capture success appears to meet the prerequisites for an ecologically relevant trait.

Morphological measurements

After the completion of capture success experiments, each fish was measured (fork length, mm) and euthanized with an overdose of MS-222. All experimental procedures were in compliance with the University of Georgia IAUAC policies. We then immediately collected ten landmarks on the profile of the fish (Fig. 1) by recording the position of the following points: (1) anterior-most point of jaw, (2) posterior-most point of neurocranium, (3) anterior insertion of dorsal fin, (4) posterior insertion of dorsal fin, (5) dorsal insertion of caudal fin, (6) ventral insertion of caudal fin, (7) anterior insertion of anal fin, (8) insertion of pelvic fin, (9) insertion of pectoral fin and (10) most posterior point

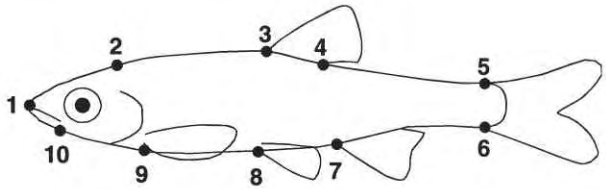

Fig. 1 Location of the ten landmarks used in the morphological analysis. See text for extended landmark definitions

of maxillary (Winans 1984; Wood and Bain 1995). For landmarks not on the outside of body form, we used the projection on the profile (perpendicular to the horizontal axis of the specimen). These, or very similar, landmark configurations can elucidate intra- and interspecific, ecologically relevant shape differences (Winans 1984; Wood and Bain 1995).

We measured landmarks by placing the specimen on its right side on a sheet of water-resistant paper set upon a Styrofoam board with the tip of the snout, the hypural bone and the caudal fin fork aligned along a straight line. We then used a needle to punch holes in the paper at the location of each landmark. A support was employed to ensure that the needle remained perpendicular to the paper (Winans 1984; Wood and Bain 1995). The paper sheets were then scanned and the *X*–*Y* coordinates of each landmark obtained from the digas implemented in the program TpsSpline (Rohlf 2002) to generate shape variables from the aligned specimens. The uniform component of shape variation expresses body shape changes such that sets of parallel lines on the form remain parallel after transformation. That is, shear or stretching occurs uniformly over the entire form. In contrast, non-uniform shape changes affect only localized areas of the landmark configuration (Bookstein 1991).

The TPS function depicts shape changes as deformations of the consensus configuration and yielded scores for a set of 14 partial warps (two times the number of original landmarks minus six), which represented non-uniform shape variation (Rohlf 1991), plus two additional uniform components, reflecting uniform shape changes (Bookstein 1996b). Together, the 16 shape variables accounted for total shape differences and located each specimen in shape space (Bookstein 1996a). This matrix of shape variables was then used in conventional statistical analyses to explore inter- and intraspecific patterns of shape variation and associated differences in prey-capture success (Adams and Rohlf 2000; Svanbäck and Eklöv 2002).

We tested for variation in shape among minnow species and by specimen size by conducting a multivariate analysis of covariance (MANCOVA) on the matrix of partial warp scores, with centroid size as a covariate.

itized images using TpsDig software (Rohlf 2001). To reduce measurement error, all landmark measurements and data analyses were made by one researcher (P.A. Rincón). Reliability of measurements, assessed by repeating the whole process on 20 randomly chosen specimens, was high (correlation between the two sets of inter-landmark distances: $r = 0.986$, $P < 0.0001$).

Statistical analysis

We used geometric morphometrics to quantify inter- and intraspecific variation in size and shape and the relationship between shape and prey-capture success (Bookstein 1991; Rohlf and Marcus 1993; Monteiro et al. 2000). To estimate the size of each fish, we used its centroid size—the square root of the sum of the squares of the distance of each landmark from the centroid (center of gravity) of all the landmarks, which summarizes the dimensions of a specimen in all directions (Bookstein 1991). We removed non-shape variation (location, orientation and scale) and generated a consensus shape for each species using Generalized Procrustes Analysis (Rohlf and Slice 1990) in MORPHEUS software (Slice 1998). We used the thin-plate spline (TPS) function (Bookstein 1991) and the standard formula for the uniform component (Bookstein 1996b) The statistical significance of shape differences between pairs of species was assessed with the generalized Mahalanobis distance (corrected for centroid size) between their centroids in multivariate space (Scheiner 1993). Interspecific differences were visualized by comparing the thin-plate spline deformation of each species' mean shape with the reference. Shape changes in relation to size were graphically depicted using multivariate regression of the shape variables matrix onto centroid size using the program TpsRegr (Rohlf 2000).

To elucidate the effects of fish morphology, size and species on prey-capture success, we used General Linear Models with capture success (arcsine square-root transformed) as the dependent variable and different combinations of predictor variables because predictor variables were not completely independent. For example, interspecific differences in performance may be due to variation among species in proximate determinants such as morphology, physiology and behavior. Analogously, changes in performance with size may be attributable to increases in sheer bulk and to size-related shape changes (i.e., allometry). By comparing the change in explanatory power of the whole model and of each factor in particular among models with different subsets of predictors, it is possible to obtain an idea of the relative importance of the potential

determinants of performance and the degree of redundancy between them (Myers 1990; Monteiro 1999). The reduction in the residual sum of squares (RSS) produced by a particular model relative to another was tested against the remaining RSS using the F statistic (Myers 1990; Dunham and Vinyard 1997; Rincón and Lobón-Cerviá 2002). Then, only for the data at 15 cm/s, the relationship between performance and shape was visualized by regressing partial warp scores against prey-capture success using the TpsRegr program (Rohlf 2000).

Prior to statistical analysis, variables were tested for significant departures from normality and homoscedasticity and none was found (Kolmogorov–Smirnov and Cochran's tests, all $P > 0.05$). Statistical analyses were performed with STATISTICA 6.0 (StatSoft 2001). Capture success was arcsine square-root transformed (Zar 1996), and all statistical results presented below are for the transformed data. However, we have presented untransformed values when they are more informative for the reader.

Phenotypic similarity between species in terms of morphology and performance may be the product of shared evolutionary history (Felsenstein 1985; Harvey and Pagel 1991). Diverse analytical procedures to estimate the effect of phylogenetic relatedness on the observed phenotypic patterns are available (Felsen-

cally from each other in shape and size, as shown by significant Mahalanobis distances (Table 1). Mahalanobis distances indicated that rosyside dace and Tennessee shiner differed the most morphologically, whereas Tennessee and warpaint shiners were most similar. Yellowfin shiner and rosyside dace were also fairly similar. The remaining differences were intermediate (Table 1). This pattern seemed largely due to morphological similarity rather than similarities in size, because the smallest Mahalanobis distance corresponded to the species pair with the largest size difference (warpaint and Tennessee shiners). Additionally, phylogenetic relatedness and phenotypic similarity (Table 1) were not concordant. For example, yellowfin shiner was most similar morphologically to rosyside dace and least to Tennessee shiner (Table 1). However, rosyside dace and Tennessee shiner are, respectively, the least and most phylogenetically close species to yellowfin shiner of the three species according to current taxonomy.

Most morphological variation, due to both species-specific differences and size-related changes, appeared related to changes in: (1) body depth, (2) length and depth of the caudal peduncle, (3) head size, (4) mouth size and orientation and (5) position and length of the dorsal fin (Fig. 2). Relative to the consensus shape, Tennessee shiner exhibited a marked reduction in

stein 1985; Martins and Hansen 1997). However, we have assessed the effect of phylogeny on our results non-mathematically because this is relatively straightforward with only four taxa with well-resolved relationships (see "Study species"), and our main interest lies in the functional consequences of morphological variation rather than its causal processes.

Results

Interspecific and allometric variation in morphology

Allometric patterns did not differ significantly among species, as demonstrated by the non-significant species × centroid size interaction in an initial full-factorial MANCOVA (Wilk's $\lambda = 0.6188$, $df = 48, 250.6$, $P > 0.63$). Consequently, the interaction term was removed and we explored morphological variation with a common slope model.

Total body shape (i.e., uniform and non-uniform components) varied significantly with centroid size (i.e., allometry) and among species (common slope MANCOVA, Wilk's $\lambda = 0.0604$, $df = 48, 259.5$ and Wilk's $\lambda = 0.4467$, $df = 16, 87$, respectively, both P values < 0.0001). The four species differed morphologi-

body depth over the whole configuration and a notable lengthening of the caudal peduncle. Also, the mouth was smaller and more downturned. Warpaint shiner displayed vertical compression only in the middle trunk area, although not as marked as in Tennessee shiner, and an anterior displacement of the dorsal fin (Fig. 2). In contrast, in yellowfin shiner, the middle trunk showed a marked increase in height. Yellowfin shiner also displayed shortenings of the caudal peduncle and of the dorsal portion of the head and elongation of the dorsal fin. Rosyside dace exhibited enlargement of the head in general (i.e., longer and deeper), and of the mouth in particular. Rosyside dace also showed a deepening of the trunk area immediately

Table 1 Morphological similarity among drift-feeding minnows. Squared Mahalanobis distances for pairwise comparisons between species centroids in multivariate shape space are presented above the diagonal and the associated F values below it. The corresponding P values are all <0.0001

Species	Rosyside dace	Yellowfin shiner	Warpaint shiner	Tennessee shiner
Rosyside dace	–	9.78	12.39	25.22
Yellowfin shiner	6.328	–	15.67	16.71
Warpaint shiner	9.254	10.468	–	7.21
Tennessee shiner	17.483	10.443	5.169	–

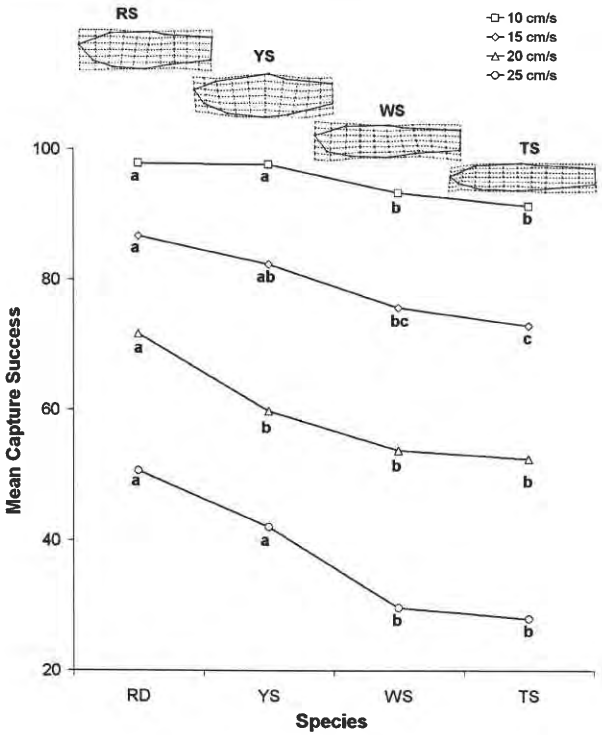

Fig. 2 Mean prey-capture success at 10, 15, 20 and 25 cm/s and average morphological configuration for: rosyside dace (*RD*), yellowfin shiner (*YS*), warpaint shiner (*WS*) and Tennessee shiner (*TS*). Species sharing a *letter* did not differ significantly (least

ANCOVA, $F_{3,102} = 4.922–10.051$, $P < 0.003$ and $F_{1,102} = 39.802–53.568$, $P < 0.0001$, in all cases, respectively). These two factors explained 41–47% of the variation in prey-capture success for the four species ($F_{4,102} = 17.995–23.013$, $P < 0.0001$). The use of a common slope model (hereafter Model I) was appropriate because the species × centroid size interaction was non-significant ($F_{3,99} = 1.229–2.118$, $P > 0.1$). A model with centroid size as the only predictor variable explained 30–34% of the variance in prey-capture success ($F_{1,105} = 46.075–53.675$, $P < 0.001$), whereas interspecific differences alone accounted for a lower, but still significant, 14–21% of the variance in foraging performance ($F_{3,103} = 5.827–9.034$, $P < 0.001$).

The pattern of interspecific differences in capture success remained essentially similar at all velocities. Rosyside dace exhibited the highest size-corrected mean capture success and Tennessee shiner the lowest (Fig. 2). Comparisons of least-square (LS) means indicated that rosyside dace mean capture success was always significantly greater than that of Tennessee and warpaint shiners ($t = 3.406–2.557$, $P < 0.02$ and $t = 2.786–3,123$, $P < 0.005$, respectively) and than that of yellowfin shiner at 20 cm/s ($t = 2.552$, $P < 0.02$). Yellowfin shiner exhibited significantly higher prey-capture success than Tennessee shiner ($t = 2.202–2,993$, $P < 0.03$) and warpaint shiner ($t = 2.215–2.894$,

squares comparisons) in mean prey-capture success at a given velocity. Shape changes have been magnified 3× for ease of interpretation. Confidence intervals have been omitted for clarity

anterior to the dorsal fin and, to a lesser extent, of the posterior end of the caudal peduncle, which also was shortened. The dorsal fin of rosyside dace was shorter and more posteriorly located (Fig. 2).

As centroid size increased, the body grew higher, except in the posterior end of the caudal area, for all four species. The mouth became larger and had a more upward orientation, the middle trunk expanded both vertically and horizontally, and the caudal peduncle displayed a marked contraction. The dorsal fin grew longer through a caudal displacement of its posterior insertion and the anal fin became more caudally placed (Fig. 3a). In comparison, smaller specimens showed more slender bodies, smaller, more terminal mouths, elongated caudal peduncles and more anteriorly placed anal fins (Fig. 3a).

Relationships between morphology, size, and prey-capture success

Capture success varied significantly among species and with size at all four velocities (common slope $P < 0.04$) at 10, 15 (Tennessee shiner only) and 25 cm/s. Similar to morphological analyses, patterns in prey-capture success were not concordant with phylogenetic patterns. For example, the two most closely related species (yellowfin and Tennessee shiner) differed significantly with respect to prey-capture success in three of four cases. By contrast, prey-capture success for Tennessee shiner never differed significantly from that of the more distantly related warpaint shiner.

Interspecific differences in capture success appeared largely attributable to differences in morphology. Incorporating the effects of variation in total shape into Model I by adding partial warp scores and uniform components as continuous independent variables increased the variance explained to 58–65% ($F_{16,86} = 1.829$–$2{,}674$, $P < 0.04$) at 15, 20 and 25 cm/s and to 51% at 10 cm/s (non-significant). In this augmented model (hereafter Model II), centroid size still displayed a significant effect on prey-capture success at all velocities ($F_{1,86} = 10.022$–21.141, $P < 0.0001$), but the species effect was no longer significant ($F_{3,86} = 0.002$–1.556, $P > 0.21$). Removal of the species term yielded Model III, which incorporated the effects of size and shape, and produced almost no reduction in explanatory power (51–57%), except at 25 cm/s (65–56%, although still non-significant). Shape variables

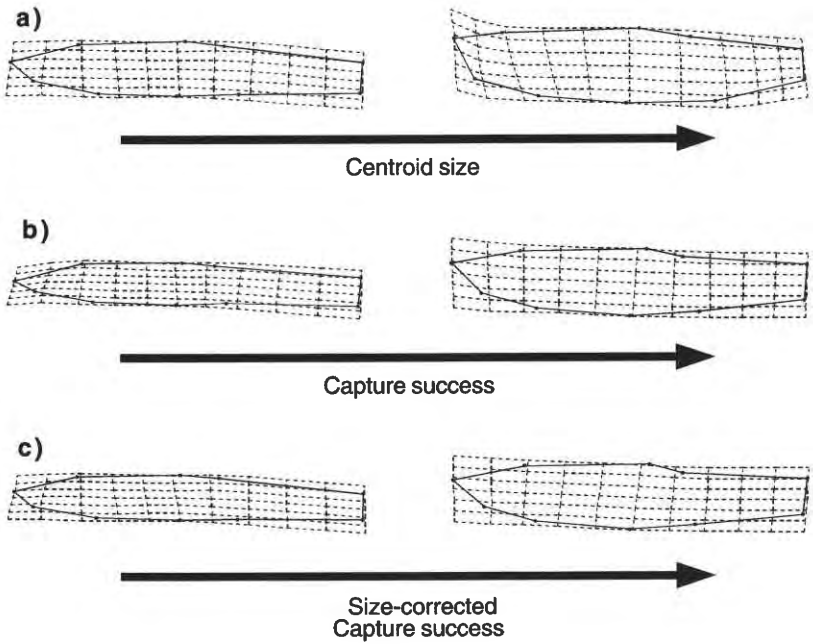

Fig. 3 Changes in morphology associated with variation in centroid size (increases to the *right*) (**a**), capture success (increases to the *right*) (**b**) and capture success after the effect of body size has been mathematically removed (increases to the *right*) (**c**). Shapes at the end of each axis are those corresponding to the lowest and highest values of the axis. Shape changes have been magnified 3× for ease of interpretation

alone (Model IV, no centroid size term) accounted for 45–47% of the variance in prey-capture success ($F_{16,90} = 4.525–6.339$, $P < 0.0001$) which represented a significant decrease in explanatory ability relative to Model III in all four cases ($F_{1,90} = 12.152–24.319$, $P < 0.0001$). Hence, morphological variation was the

variable (and, hence, acted as a partial surrogate for allometric shape variation), it explained 30–34% of the variance in prey-capture success. Consequently, it appears that allometric variation in shape actually was responsible for a greater proportion of the variation in prey-capture success than changes in sheer bulk. The

dominant factor affecting interspecific differences in prey-capture success and also appeared to explain a substantial amount of intraspecific variation (variance explained by size + species + shape = 51–65%, size + shape = 51–57%, size + species = 41–47%; shape alone = 45–47%, species alone = 14–19%, size alone = 30–34%).

Differences in total shape associated with variation in prey-capture success appeared to reflect both allometric and interspecific variation in form (Figs. 2 and 3a). Thus, as capture success increased, the body deepened anterior to the end of the caudal peduncle, and the mouth generally increased in size and was more dorsally oriented. In addition, the caudal peduncle decreased in length, and dorsal and anal fins were positioned more toward the posterior end of the body. Lower capture performance was associated with a slender body, extended caudal peduncle, smaller, more ventrally oriented mouth and more anteriorly placed dorsal and anal fins (Fig. 3b).

Allometric shape changes significantly affected prey-capture success. Centroid size accounted for 12–17% of the 51–57% of total variance explained by Model III (in which the size-free shape variables directly accounted for allometric shape changes). In comparison, when centroid size was the only independent relevance of allometric morphological variation to prey-capture success is well illustrated by the similarity in shape changes associated with larger size (Fig. 3a) and with increased capture success at 15 cm/s (Fig. 3b)

Discussion

Prey capture is an ecologically significant task with multiple, ecologically relevant consequences for a variety of organisms (Hill and Grossman 1993; Tyler and Gilliam 1995; Nakano et al. 1999; Grossman et al. 2002). To our knowledge, our results provide the first empirical evidence relating prey-capture success (ecological performance) to body shape at both inter- and intraspecific levels in stream fishes. Our data demonstrate that body shape is a major determinant of prey capture for four species of stream minnows. At current velocities between 10 cm/s and 25 cm/s, individuals with deeper bodies, more posteriorly positioned median fins and larger, more dorsally oriented mouths captured greater proportions of drifting prey than did more slender individuals with smaller, more ventrally oriented mouths. The observed morphology–performance link probably reflected the biomechanical consequences of body shape rather than phylogenetic relationships.

Three lines of evidence support this contention. First, species most similar in prey-capture ability were also most similar in shape, but were not most closely related phylogenetically (Harvey and Pagel 1991). Second, the relationship between morphology and performance was consistent whether shape varied between species or due to allometric growth (Ricklefs and Miles 1994). Third, the relationship agreed with biomechanical predictions derived from hydrodynamic theory (Webb 1984a, b; Vogel 1994; Walker 1997). However, although our results appear to represent true morphology–performance relationships, our four species were relatively close relatives, and phylogeny may play a greater role in a different, more varied assemblage (Douglas and Matthews 1992).

Our findings also suggest that prey capture may impose morphological constraints on drift-feeding fishes that differ from those of steady swimming (i.e., cruising or swimming to hold position against the current). We found that increased prey-capture success was associated with (1) deeper, shorter bodies, (2) more posteriorly placed median fins and (3) larger, more dorsally oriented mouths. Hydrodynamic theory and empirical evidence show that (1) and (2) improve maneuverability, but result in poorer steady swimming performance. Conversely, streamlining enhances steady swimming performance (Webb 1983, 1984a, b; to require much unsteady swimming (McLaughlin and Noakes 1998), more fusiform shapes should still result in lower energetic costs (Vogel 1994). Therefore, our results support Bisson's et al. (1988) suggestion that the morphology of drift-feeding fishes represents a compromise between the conflicting demands of prey capture (maneuverability) and holding position (sustained swimming).

The ecological consequences of this compromise (i.e., more streamlined individuals in areas of faster currents and deeper-bodied specimens in slower habitats) have been documented at both inter- and intraspecific levels and at multiple spatial scales (Thomas and Donahoo 1977; Taylor and McPhail 1985b; Taylor 1988; Bisson et al. 1988; Taylor and Foote 1991; McLaughlin 1994; Nicieza 1995). Some have argued that the costs of sustained swimming would exclude deep-bodied fishes from high-velocity areas, whereas more fusiform specimens would suffer a competitive disadvantage in slow-flowing water due to lower prey-capture efficiency (Bisson et al. 1988). Although, several studies have documented that more streamlined fishes have superior sustained swimming performance (Thomas and Donahoo 1977; Taylor and McPhail 1985b; Taylor and Foote 1991; Hawkins and Quinn 1996; Petterson and Brönmark 1999), our results provide the first evidence that more fusiform species also

Taylor and McPhail 1985a, b, 1986; Taylor and Foote 1991; Vogel 1994; Walker 1997). Maneuverability is defined as the ability to modify steady, forward locomotion rapidly and precisely and, thus, includes not just turning, but also accelerating, braking, etc. (Breder 1926; Walker 1997).

The spatial distribution and videographic analysis of the capture strikes of drift-feeding fishes clearly support our results because both show that swimming when striking at prey involves substantial turning and accelerating and is unsteady (Grant et al. 1989; Hughes and Kelly 1996; Rincón and Grossman 2001). Therefore, shapes favoring maneuverability should perform those attacks more efficiently. In contrast, using different experimental procedures, Schaefer et al. (1999) found that more fusiform longear sunfish *Lepomis megalotis* captured more prey than deeper bodied bluegill *L. macrochirus* as water velocity increased.

By showing that a more fusiform body shape reduces capture success, our results suggest that streamlining can have a cost for drift-feeding fishes. However, drift-feeding fishes often spend long periods of time holding position (i.e., presumably swimming steadily) against the current (Bachman 1984; Hughes and Dill 1990; Webb 1991; Hughes and Kelly 1996). Although holding position in a stream actually seems displayed reduced capture success.

Lower prey-capture success is not the only potential drawback of streamlining. For example, predator avoidance may also contribute to the trade off between streamlining and robustness. More fusiform shapes show lower burst swimming performance and, hence, probably reduced escape ability (Taylor and McPhail 1985a, b). Therefore, higher predation pressure may have constrained the emergence of more streamlined shapes in certain circumstances (Taylor and McPhail 1985a; Walker 1997).

We found that body shape varied significantly among species and with size, and that both types of variation affected foraging performance. Interspecific differences in morphology were the main factor influencing interspecific variation in capture success once the effect of size was removed mathematically. This result was surprising, because the four species appear superficially to be quite similar in morphology. In addition, our analysis did not take into account a number of non-shape traits (e.g., thermal physiology, muscle composition, etc.) that also may affect performance (Sidell and Moerland 1989; McLaughlin and Kramer 1991). The "species" term in Model I acted as a surrogate for differences in both morphology and these hypothetical factors and was statistically significant. However, once

the effects of morphology were explicitly incorporated (Model II), the species term was no longer significant and retained little explanatory power. Consequently, unmeasured, non-shape factors seemed to contribute little to the observed interspecific differences in capture performance.

Similarly, our results indicate that allometric shape variation was substantially more important for capture success than other potential, size-related factors. As size increases, both shape and non-shape traits (e.g., muscle properties and motor patterns) vary with it, and variation in both types of traits may produce size-linked changes in performance (Richard and Wainwright 1995; James et al. 1998; Hernandez 2000). Once the partial warp scores explicitly accounted for the effect of shape variation, centroid size represented the influence of those other, non-shape factors. The effect of centroid size remained statistically significant in Models II and III. However, its explanatory power decreased from 30–34% to 12–17%, and inclusion of this term into a model with only morphological variables produces a more modest increase in explanatory power than the addition of shape variables to a size-only model (7–11% vs. 21–24%). Therefore, larger size seems to result in increased prey-capture success mostly, though not exclusively, through size-related changes in shape.

Bisson et al. 1988; Walker 1997; Robinson et al. 2000; Svanbäck and Eklöv 2002). Our findings provide support for those claims and also suggest that the diverse demands placed on morphology by different ecological tasks and their evolutionary and ecological consequences deserve further attention; we showed drift-feeding fishes to be a promising system to further explore these questions.

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References

Adams DC, Rohlf FJ (2000) Ecological character displacement in *Plethodon*: biomechanical differences found from a geometric morphometric study. Proc Natl Acad Sci U S A 97:4106–

Because of the ability of geometric morphometrics to separate shape and non-shape variation in morphology, our results provide clear support for the hypothesis that allometric shape changes through ontogeny may play an important role in size-related variation in ecological performance (Emerson 1978; Galis 1993; Svanbäck and Eklöv 2002). The ecological effects of size variation have been abundantly documented (Peters 1983; Schmidt-Nielsen 1984; Werner and Gilliam 1984; Rincón and Lobón-Cerviá 2002) and allometric growth is the norm among animals (McMahon 1973). Therefore, the effects of allometric shape changes on performance are likely to be widespread and should receive attention in future studies of ontogenetic effects on resource use and ecological performance.

In summary, we have identified a strong relationship between body shape and prey-capture success (ecological performance) and have shown that morphological specialization in the form of streamlining incurs costs for drift-feeding fishes (i.e., reduced prey-capture success). Such costs, most likely the consequence of decreased maneuverability, were predicted by hydrodynamic theory and have been invoked to explain phenomena such as resource polymorphisms and spatial segregation in both lake and stream fishes (Webb 1983;

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Arnold SJ (1983) Morphology, performance and fitness. Am Zool 23:347–361
Bachman RA (1984) Foraging behavior of free-ranging wild and hatchery brown trout in a stream. Trans Am Fish Soc 113:1–32
Bisson PA, Sullivan K, Nielsen JL (1988) Channel hydraulics, habitat use, and body form of juvenile coho salmon, steelhead, and cutthroat trout in streams. Trans Am Fish Soc 117:262–273
Bookstein FL (1991) Morphometric tools for landmark data: geometry and biology. Cambridge University Press, Cambridge
Bookstein FL (1996a) Combining the tools of geometric morphometrics. In: Marcus LF, Corti M, Loy A, Naylor GJP, Slice DE (eds) Advances in morphometrics. Plenum Press, New York, pp 131–151
Bookstein FL (1996b) Standard formula for the uniform shape component in landmark data. In: Marcus LF, Corti M, Loy A, Naylor GJP, Slice DE (eds) Advances in morphometrics. Plenum Press, New York, pp 131–151
Breder CM Jr (1926) The locomotion of fishes. Zoologica 4:159–291
Coburn MM, Cavender TM (1993) Interrelationships of North American cyprinid fishes. In: Mayden RL (ed) Systematics, historical ecology and North American freshwater fishes, vol i-xxvi, 1-969. Stanford University Press, Stanford, pp 328–373
Dewitt TJ, Sih A, Hucko JA (1999) Trait compensation and co-specialization in a freshwater snail: size, shape and antipredator behaviour. Anim Behav 58:397–407
Douglas ME, Matthews WJ (1992) Does morphology predict ecology? Hypothesis testing within a freshwater stream fish assemblage. Oikos 65:213–224

Dunham JB, Vinyard GL (1997) Relationships between body mass, population density, and the self-thinning rule in stream-living salmonids. Can J Fish Aquat Sci 54:1025–1030
Emerson SB (1978) Allometry and jumping in frogs: helping the twain meet. Evolution 32:551–564
Facey DE, Grossman GD (1990) The metabolic cost of maintaining position for four North American stream fishes: effects of season and velocity. Physiol Zool 63:757–776
Felsenstein J (1985) Phylogenies and the comparative method. Am Nat 125:1–15
Fraser NHC, Metcalfe NB (1997) The costs of becoming nocturnal: feeding efficiency in relation to light intensity in juvenile Atlantic salmon. Funct Ecol 11:385–391
Freeman MC, Grossman GD (1992a) A field test for competitive interactions among foraging stream fishes. Copeia 1992:898–902
Freeman MC, Grossman GD (1992b) Group foraging by a stream minnow: shoals or aggregations? Anim Behav 44:393–403
Fulton CJ, Bellwood DR, Wainwright PC (2001) The relationship between swimming ability and habitat use in wrasses (Labridae). Mar Biol 139:25–33
Galis F (1993) Morphological constraints on behavior through ontogeny. The importance of developmental constraints. Mar Behav Physiol 23:119–135
Grant JWA, Noakes DLG, Jonas KM (1989) Spatial distribution of defence and foraging in young-of-the-year brook charr, *Salvelinus fontinalis*. J Anim Ecol 58:773–784
Grossman GD, Freeman MC (1987) Microhabitat use in a stream fish assemblage. J Zool 212:151–176
Grossman GD, Rincón PA, Farr MD, Ratajczak RE Jr (2002) A new optimal foraging model predicts habitat use by drift-feeding stream minnows. Ecol Freshw Fish 11:2–10
Harvey PH, Pagel M (1991) The comparative method in evolutionary biology. Oxford University Press, Oxford
information into the analysis of interspecific data. Am Nat 149:646–667
Matthews WJ (1998) Patterns in freshwater fish ecology. Chapman and Hall, London
McLaughlin RL (1994) Morphological and behavioural differences among recently-emerged brook charr, *Salvelinus fontinalis*, foraging in slow- vs. fast-running water. Environ Biol Fish 39:289–300
McLaughlin RL, Kramer DL (1991) The association between amount of red muscle and mobility in fishes: a statistical evaluation. Environ Biol Fish 30:369–378
McLaughlin RL, Noakes DLG (1998) Going against the flow: an examination of the propulsive movements made by young brook trout in streams. Can J Fish Aquat Sci 55:853–860
McMahon TA (1973) Size and shape in biology. Science 179:1201–1204
Menhinick EF (1991) The freshwater fishes of North Carolina. North Carolina Wildlife Resources Commission, Raleigh
Mettee MF, O'Neil PE, Pierson JM (1996) Fishes of Alabama and the Mobile basin. Oxmoor House, Birmingham
Miles DB, Ricklefs RE, Travis J (1987) Concordance of ecomorphological relationships in three assemblages of passerine birds. Am Nat 129:347–364
Monteiro LR (1999) Multivariate regression models and geometric morphometrics: the search for causal factors in the analysis of shape. Syst Biol 48:192–199
Monteiro LR, Bordin B, Furtado dos Reis S (2000) Shape distances, shape spaces and the comparison of morphometric methods. Trends Ecol Evol 15:217–220
Myers RH (1990) Classical and modern regression with applications. Duxbury Press, Belmont
Nakano S, Fausch KD, Kitano S (1999) Flexible niche partitioning via a foraging mode shift: a proposed mechanism for

Hawkins DK, Quinn TP (1996) Critical swimming velocity and associated morphology of juvenile coastal cutthroat trout (*Oncorhynchus clarki clarki*), steelhead trout (*Oncorhynchus mykiss*), and their hybrids. Can J Fish Aquat Sci 53:1487–1496

Hernandez LP (2000) Intraspecific scaling of feeding mechanics in an ontogenetic series of zebrafish, *Danio rerio*. J Exp Biol 203:3033–3043

Hill J, Grossman GD (1993) An energetic model of microhabitat use for rainbow trout and rosyside dace. Ecology 74:685–698

Hughes NF, Dill LM (1990) Position choice by drift-feeding salmonids: model and test for arctic grayling (*Thymallus arcticus*) in subarctic mountain streams, Interior Alaska. Can J Fish Aquat Sci 47:2039–2048

Hughes NF, Kelly LH (1996) A hydrodynamic model for estimating the energetic cost of swimming maneuvers from a description of their geometry and dynamics. Can J Fish Aquat Sci 53:2484–2493

James RS, Cole NJ, Davies MLF, Johnston IA (1998) Scaling of intrinsic contractile properties and myofibrillar protein composition of fast muscle in the fish *Myoxocephalus scorpius*. J Exp Biol 201:901–912

Jenkins RE, Burkhead NM (1994) Freshwater fishes of Virginia. American Fisheries Society, Bethesda

Kolok AS (1999) Interindividual variation in the prolonged locomotor performance of ectothermic vertebrates: a comparison of fish and herpetofaunal methodologies and a brief review of the recent fish literature. Can J Fish Aquat Sci 56:700–710

Lack D (1947) Darwin's finches. Cambridge University Press, Cambridge

Martins EP, Hansen TF (1997) Phylogenies and the comparative method: a general approach to incorporating phylogenetic coexistence in stream-dwelling charrs. J Anim Ecol 68:1079–1092

Nicieza AG (1995) Morphological variation between geographically disjunct populations of Atlantic salmon: the effects of ontogeny and habitat shift. Funct Ecol 9:448–456

Norberg U (1994) Wing design, flight performance and habitat use in bats. In: Wainwright PC, Reilly SM (eds) Ecological morphology: integrative organismal biology, vol i-viii, 1-367. University of Chicago Press, Chicago, pp 205–239

Outten LM (1957) A study of the life history of the cyprinid fish *Notropis coccogenis*. J Elisha Mitchell Sci Soc 73:68–84

Outten LM (1974) Additional comparative studies of Cyprinid fishes in the Southeast. J Elisha Mitchell Sci Soc 93:101–102

Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge

Petterson LB, Brönmark C (1999) Energetic consequences of an inducible morphological defence in crucian carp. Oecologia 121:12–18

Reisen WK (1972) The influence of organic drift on the food habits and life history of the yellowfin shiner, *Notropis lutipinnis*, (Jordan and Brayton). Am Midl Nat 88:376–383

Richard BA, Wainwright PC (1995) Scaling the feeding mechanism of largemouth bass (*Micropterus salmoides*): I. Kinematics of prey capture. J Exp Biol 198:419–433

Ricklefs RE, Miles DB (1994) Ecological and evolutionary inferences from morphology: an ecological perspective. In: Wainwright PC, Reilly SM (eds) Ecological morphology: integrative organismal biology, vol i-viii, 1–367. University of Chicago Press, Chicago, pp 13–41

Rincón PA, Grossman GD (2001) Intraspecific aggression in rosyside dace, a drift-feeding stream cyprinid. J Fish Biol 59:968–986

Rincón PA, Lobón-Cerviá J (2002) Non-linear self-thinning in a stream-resident population of brown trout (*Salmo trutta*). Ecology 83:1808–1816

Robinson BW, Wilson DS, Margosian AS (2000) A pluralistic analysis of character displacement in pumpkinseed sunfish (*Lepomis gibbosus*). Ecology 81:2799–2812

Rohlf FJ (1991) Relative warp analysis and an example of its application to mosquito wings. In: Marcus LF, Bello E, Garcia-Valdecasas A (eds) Contributions to morphometrics Museo Nacional de Ciencias Naturales, Madrid, pp 131–159

Rohlf FJ. TpsRegr, Version 1.26. [1.26] (2000) Stony Brook, New York, Department of Ecology and Evolution, State University of New York at Stony Brook

Rohlf FJ. TpsDig, Version 1.30. [1.30] (2001) Stony Brook, New York, Department of Ecology and Evolution, State University of New York at Stony Brook

Rohlf FJ. TpsSpline, Version 1.19. [1.19] (2002) Stony Brook, New York, Department of Ecology and Evolution, State University of New York at Stony Brook

Rohlf FJ, Marcus LF (1993) A revolution in morphometrics. Trends Ecol Evol 8:129–132

Rohlf FJ, Slice DE (1990) Extension of the Procrustes method for the optimal superimposition of landmarks. Syst Zool 39:40–59

Schaefer JF, Lutterschmidt WI, Hill LG (1999) Physiological performance and stream microhabitat use by the centrarchids *Lepomis megalotis* and *Lepomis macrochirus*. Environ Biol Fish 54:303–312

Scheiner SM (1993) MANOVA: multiple response variables and multispecies interactions. In: Scheiner SM, Gurevitch J (eds) Design and analysis of ecological experiments, vol i-xiv, 1-445. Chapman & Hall, New York, pp 94–112

Schmidt-Nielsen K (1984) Scaling: why is animal size so important? Cambridge University Press, Cambridge

Taylor EB, McPhail JD (1985a) Variation in body morphology among British Columbia populations of coho salmon, *Oncorhynchus kisutch*. Can J Fish Aquat Sci 42:2020–2028

Taylor EB, McPhail JD (1985b) Variation in burst and prolonged swimming performance among British Columbia populations of coho salmon, *Oncorhynchus kisutch*. Can J Fish Aquat Sci 42:2029–2033

Taylor EB, McPhail JD (1986) Prolonged and burst swimming in anadromous and freshwater threespine stickleback, *Gasterosteus aculeatus*. Can J Zool 64:416–420

Thomas AE, Donahoo MJ (1977) Differences in swimming performance among strains of rainbow trout (*Salmo gairdneri*). J Fish Res Board Can 34:304–306

Tyler JA (1993) Effects of water velocity, group size, and prey arrival rate on the capture efficiency of stream-drift by *Rhinichthys atratulus*. Can J Fish Aquat Sci 50:1055–1061

Tyler JA, Gilliam JF (1995) Ideal free distributions of stream fish: a model and test with minnows, *Rhinichthys atratulus*. Ecology 76:580–592

Vogel S (1994) Life in moving fluids. Princeton University Press, Princeton

Wainwright PC (1994) Functional morphology as a tool in ecological research. In: Wainwright PC, Reilly SM (eds) Ecological morphology: integrative organismal biology, vol i-viii, 1-367. University of Chicago Press, Chicago, pp 42–59

Wainwright PC, Reilly SM (1994) Ecological morphology: integrative organismal biology. University of Chicago Press, Chicago

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

Webb PW (1983) Speed, acceleration and manoeuverability of two teleost fishes. J Exp Biol 102:115–122:115–1222

Webb PW (1984a) Body form, locomotion and foraging in aquat-

Sidell BD, Moerland TS (1989) Effects of temperature on muscular function and locomotory performance in teleost fish. Adv Comput Environ Physiol 5:116–156

Slice DE. Morpheus et al.: software for morphometric research. Revision 01-30-98 (1998) Stony Brook, New York, Department of Ecology and Evolution, State University of New York

StatSoft I. *STATISTICA* (data analysis software system), version 6. http://www.statsoft.com (2001) Tulsa, StatSoft, Inc

Svanbäck R, Eklöv P (2002) Effects of habitat and food resources on morphology and ontogenetic growth trajectories in perch. Oecologia 131:61–70

Taylor EB (1988) Water temperature and velocity as determinants of microhabitats of juvenile chinook and coho salmon in a laboratory stream channel. Trans Am Fish Soc 117:22–28

Taylor EB, Foote CJ (1991) Critical swimming velocities of juvenile sockeye salmon and kokanee, the anadromous and non-anadromous forms of *Oncorhynchus nerka* (Walbaum). J Fish Biol 38:407–419

ic vertebrates. Am Zool 24:107–120

Webb PW (1984b) Form and function in fish swimming. Sci Am 251:58–68

Webb PW (1991) Composition and mechanics of routine swimming of rainbow trout, *Oncorhynchus mykiss*. Can J Fish Aquat Sci 48:583–590

Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. Annu Rev Ecol Syst 15:394–425

Wilzbach MA, Cummins KW (1986) Influence of habitat manipulations on interactions between cutthroat trout and invertebrate drift. Ecology 67:898–911

Winans GA (1984) Multivariate morphometric variability in Pacific salmon: technical demonstration. Can J Fish Aquat Sci 41:1150–1159

Wood BM, Bain MB (1995) Morphology and microhabitat use in stream fish. Can J Fish Aquat Sci 52:1487–1498

Zar JH (1996) Biostatistical analysis. Prentice Hall, New Jersey