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ZOOLOGY

Life in the flow lane: differences in pectoral fin morphology suggest transitions in station-holding demand across species of marine sculpin

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ARTICLE INFO

Article history:

Received 28 September 2011
Received in revised form 27 February 2012
Accepted 7 March 2012

Keywords:

Benthic fishes
Scorpaeniformes
Flow regime
Functional regionalization
Station-holding

ABSTRACT

Aquatic organisms exposed to high flow regimes typically exhibit adaptations to decrease overall drag and increase friction with the substrate. However, these adaptations have not yet been examined on a structural level. Sculpins (Scorpaeniformes: Cottoidea) have regionalized pectoral fins that are modified for increasing friction with the substrate, and morphological specialization varies across species. We examined body and pectoral fin morphology of 9 species to determine patterns of body and pectoral fin specialization. Intact specimens and pectoral fins were measured, and multivariate techniques determined the differences among species. Cluster analysis identified 4 groups that likely represent differences in station-holding demand, and this was supported by a discriminant function analysis. Primarily, the high-demand group had increased peduncle depth (specialization for acceleration) and larger pectoral fins with less webbed ventral rays (specialization for mechanical gripping) compared to other groups; secondarily, the high-demand group had a greater aspect ratio and a reduced number of pectoral fin rays (specialization for lift generation) than other groups. The function of sculpin pectoral fins likely shifts from primarily gripping where demand is likely low, to an equal dependence on gripping and negative lift generation where demand is likely high. Specialization of the ventral pectoral fin region for gripping likely contributes to the recent diversification of some species into high-demand habitats.

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1. Introduction

Benthic aquatic organisms that live in areas susceptible to displacement by high water flow, such as fast flowing streams or wave-swept intertidal regions, often display morphological and behavioral adaptations to decrease drag and increase friction with the substrate (Koehl, 1984). For example, aquatic vertebrates often exhibit drag-reducing changes in overall body size and shape (Webb, 1989; Kerfoot and Schaefer, 2006; Langerhans, 2008; Rivera, 2008; Carlson and Lauder, 2011). Additionally, behavioral responses, such as changes in body and pectoral fin posture, can also enhance station-holding capability by altering drag and/or lift (Webb, 1989; Gerstner and Webb, 1998; Wilga and Lauder, 2001; Blake, 2006; Carlson and Lauder, 2010). However, the relevant studies typically focused on the whole organism, and the understanding of how the morphology of specific structures, such as pectoral fins of fishes, can adapt to flow regimes is minimal. Structural adaptability could create new ecological opportunities for species, as is the case with pharyngeal jaw modifications in cichlids (Hulsey et al., 2006). Alternatively, tradeoffs between different

behaviors could potentially constrain the ability of a structure to adapt (Blake, 2004; Kane and Higham, 2011). For example, the pectoral fins of scorpaeniform fishes can be used for steady swimming, maneuvering, station-holding, perching, walking, digging, predator deterrence, and sensory input, and some species show specializations for certain behaviors (Gosline, 1994). Therefore, understanding the contribution of individual structures, such as pectoral fins, to the evolution of diversity among fishes is necessary.

For benthic fishes in areas of high flow, modifications to increase friction with the substrate are necessary for counteracting the dislodging effects of drag (Webb, 1989). This can include postural modifications that generate a negative lift force into the substrate (Wilga and Lauder, 2001; Coombs et al., 2007) as well as morphological and behavioral modifications for gripping the substrate (Carlson and Lauder, 2010, 2011). The pectoral fins of fishes in Scorpaeniformes, Blennioidea, and Cirrhitidae (among others) are modified for gripping, and have protrusions of the ventral pectoral fin rays beyond the webbing (Fig. 1), termed “fin hooks” in blennies (Brandstätter et al., 1990). Modifications of the ventral fin rays in some groups may be key for explaining the diversity of species among habitats where high flow demands are common (Webb et al., 1996).

Sculpins (Scorpaeniformes: Cottoidea) are benthic fishes known for their ability to hold position in high water flow (Gosline, 1994;

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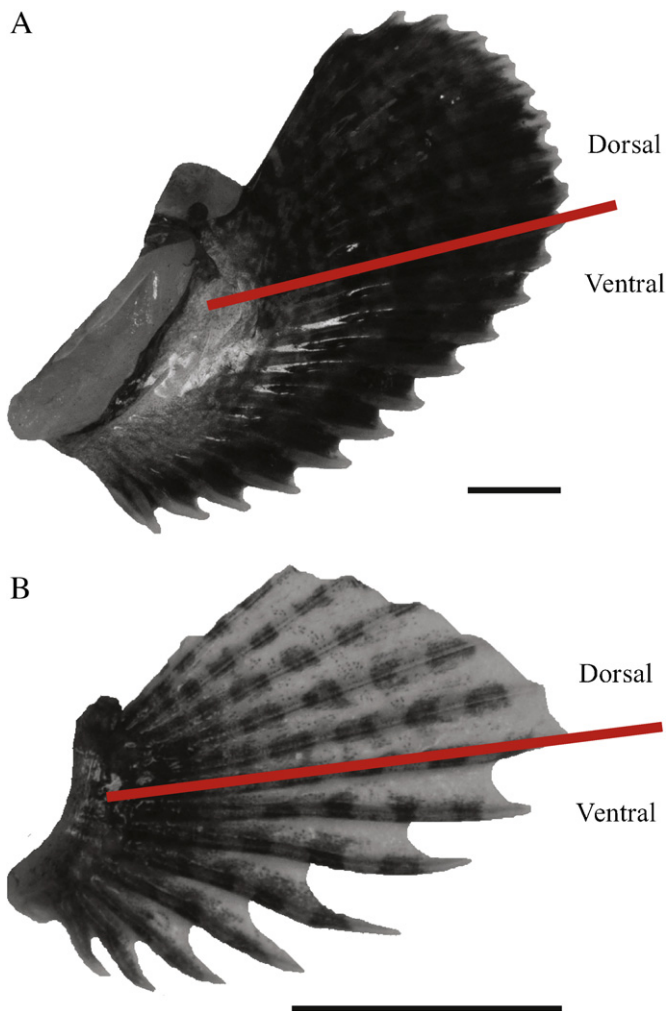


Fig. 1. Morphology of (A) *Dasycottus setiger* and (B) *Oligocottus maculosus* pectoral fins and regionalization into a relatively unmodified dorsal region that contributes to lift generation (positive and negative) and a highly modified ventral region that is used for gripping. Differences between species are apparent in the degree of specialization of the ventral region of the fin. Images have been scaled to the same length. Scale bar = 1 cm.

Webb et al., 1996; Kerfoot and Schaefer, 2006; Coombs et al., 2007). To accomplish this, sculpin pectoral fins are regionalized (Fig. 1), so that the relatively unmodified dorsal region contributes to lift generation (positive and negative), whereas the ventral region is highly modified for gripping (Webb et al., 1996; Coombs et al., 2007; Taft et al., 2008). The functional significance of the ventral fin rays has been demonstrated by reduced station-holding performance when pectoral fins were ablated in *Myoxocephalus scorpius* (Webb, 1989). Alternatively, station-holding performance was not affected when fins were ablated in *Etheostoma flabellare* and *Percina roanoka* (Matthews, 1985), which are benthic station-holding darter species that do not have regionalized pectoral fins. Additionally, greater station-holding performance in *M. scorpius*, compared to other teleost species, is attributed to increased friction performance as a result of their ability to grip the substrate with the distal tips of the ventral fin rays (Webb, 1989). This gripping behavior present in sculpins is likely accomplished by ventral fin rays that are stiffer proximally and flexible distally so that they are strong but flexible for grasping the substrate (Taft et al., 2008; Taft, 2011). Combined, these studies indicate the significance of pectoral fin regionalization, more specifically the contribution of ventral fin ray modifications, to the station-holding capability of sculpins in high flow demand habitats.

Sculpins demonstrate an intraspecific response to flow regimes in freshwater systems, and a similar trend may also be apparent on larger scales. For some species, populations in higher flows exhibit decreased body size, decreased head and body depths, and increased caudal peduncle depth compared to populations from lower flows (Kerfoot and Schaefer, 2006; Bogdanov, 2007). These changes represent plasticity of general body form in response to flow regime so that there is an overall reduction in frontal area and a more streamlined body in high flow habitats. The transition from deeper water (>100 m) to shallower water (intertidal) in sculpins (Ramon and Knope, 2008; Mandic et al., 2009) indicates that species may have been exposed to variation in flow regime across their evolutionary history. Specifically, intertidal organisms are exposed to increasingly unsteady water flow as a result of increased wave action (Koehl, 1984; Denny et al., 1985). Intertidal species are also typically smaller in body size than their subtidal counterparts (Eschmeyer et al., 1983), a morphological change that is associated with high flow in sculpins (Kerfoot and Schaefer, 2006; Bogdanov, 2007). Therefore, demand for station-holding may increase across these evolutionary transitions. Although pectoral fins contribute significantly to station-holding performance in sculpins (Webb, 1989), little is known about how these structures might also reflect evolutionary transitions.

To determine whether morphological divergence is significantly different across species of sculpins, we examined pectoral fin morphology across 9 species collected from diverse habitats. We hypothesize that varying degrees of pectoral fin morphological specialization are present among sculpins, and that these specializations might represent functional specialization for station-holding. Additionally, we quantified body morphology of these species (following Kerfoot and Schaefer, 2006) to determine whether sculpins from these habitats are likely exposed to differences in flow regime demand. We predicted that (i) a lower-profile head and body depth (as observed in freshwater systems) would indicate increases in demand for station-holding across species, and (ii) species would separate in multivariate space to indicate morphological transitions in specialization of pectoral fin morphology. Specifically, we expected that highly specialized species would have pectoral fins with thicker ventral rays and less webbing.

2. Materials and methods

Specimens were collected near Bamfield, BC, Canada from marine (deep subtidal, shallow subtidal, and intertidal) and freshwater habitats (Table 1 and Fig. 2) under Fisheries and Oceans Canada license XR 80 2010 and all collection and experimental procedures were approved by the Animal Care Committee at the Bamfield Marine Sciences Centre. Collection technique varied by habitat, and included trawls of the deep channels in Barkley Sound, beach seines, minnow traps, and dipnetting in tidepools. Specimens were collected over 9 weeks (summer 2010 and summer 2011) and represented a diversity of morphology, habitat, and ecology among sculpins. The focus was on members of the superfamily Cottoidea (sculpins, including true sculpins of the family Cottidae) with morphological and functional similarities for pectoral fin station-holding. Non-cottid sculpins (*Dasycottus setiger* and *Blepsias cirrhosus*) display regionalized pectoral fin morphology, indicating some degree of selection for pectoral fin station-holding, and were included in the analysis. With the exception of *B. cirrhosus*, which is typified by epi-benthic sculling behaviors (Marliave, 1975), all species are benthic. Despite our attempts, only 1 individual each of *Hemilepidotus spinosus* and *H. hemilepidotus* were obtained. These individuals were similar to each other and were considered on a genera rather than a species-level basis.

Table 1
 Species collection information and descriptive characteristics.

Species	Family ^b	n	Collection technique	Depth range ^c (m)	Depth collected (m)	Max. size ^c (cm)	Mean total length (cm)	Mean mass (g)
<i>Blepsias cirrhosus</i> ^a	Hemitripterae	4	Seine	Intertidal-37	0-1	19	4.15 ± 0.2	0.9 ± 0.1
<i>Dasycottus setiger</i>	Psychrolutidae	5	Trawl	18-122	60-100	23	13.4 ± 2.3	47.62 ± 21.0
<i>Leptocottus armatus</i>	Cottidae	1	Trawl	Freshwater-91	60-100	46	21.7	114.9
<i>Chitonotus pugetensis</i>	Cottidae	5	Trawl	Intertidal-142	60-100	23	10.84 ± 0.6	11.54 ± 1.8
<i>Cottus asper</i>	Cottidae	9	Minnow traps	Freshwater	0-1	13	11.22 ± 0.5	18.07 ± 2.4
<i>Scorpaenichthyes marmoratus</i> ^a	Cottidae	3	Seine	Intertidal-76	0-1	99	6.23 ± 0.1	3.2 ± 0.1
<i>Hemilepidotus</i> sp. ^a	Cottidae	2	Seine	Intertidal-97	0-1	30	14.4 ± 0.4	38.05 ± 2.0
<i>Artedius fenestralis</i>	Cottidae	5	Seine	Intertidal-55	0-1	14	7.92 ± 0.8	5.82 ± 1.5
<i>Oligocottus maculosus</i>	Cottidae	7	Seine and dipnet	Tidepools	0-1	8.9	5.29 ± 0.3	1.79 ± 0.4

^a Specimens were juveniles.

^b Taxonomy follows Nelson et al. (2004).

^c Data are taken from Eschmeyer et al. (1983).

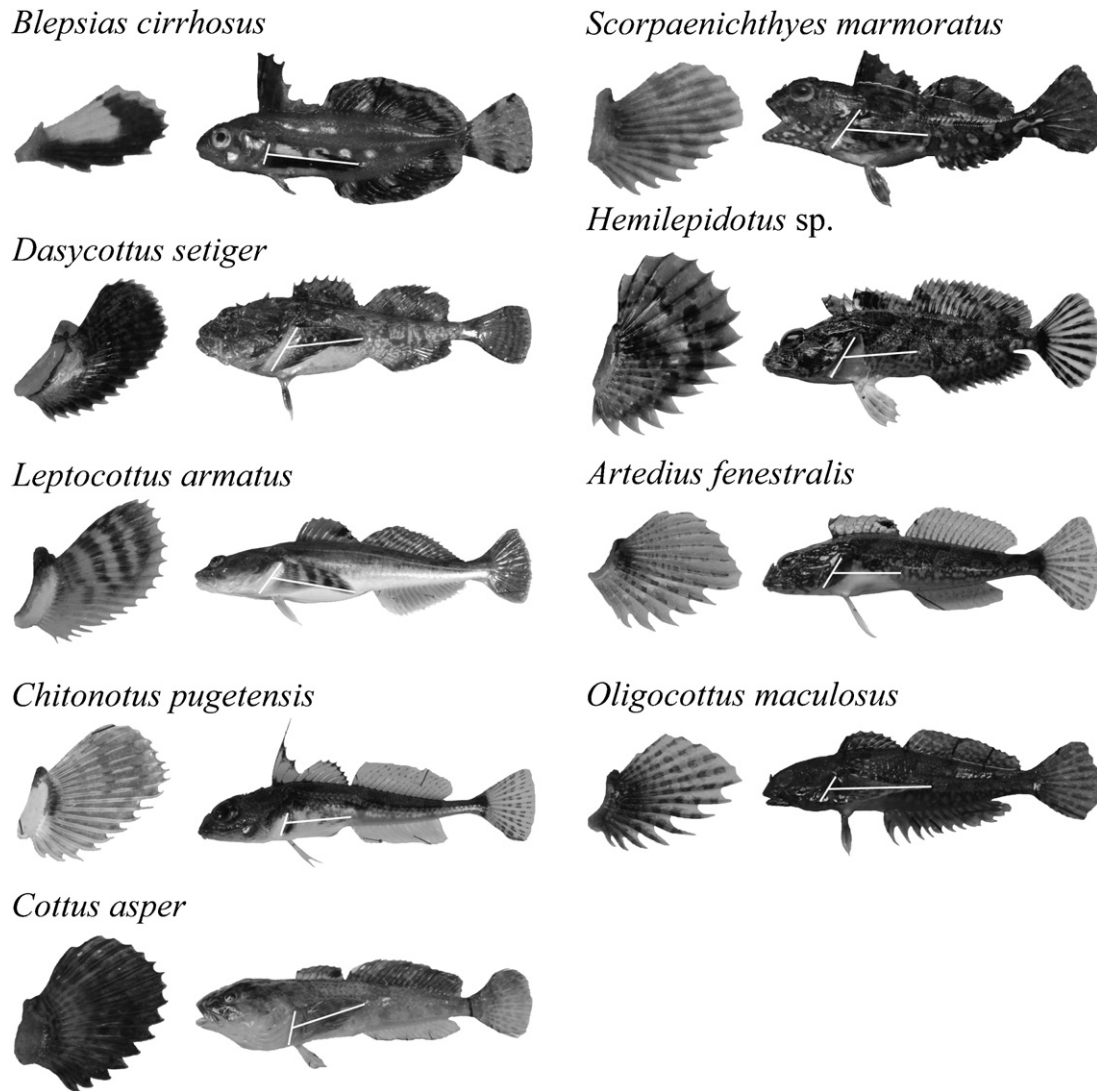


Fig. 2. Representative photographs of fin and body morphology for the species listed in Table 1. Pectoral fin insertion and length are marked by oblique and horizontal (respectively) white lines on the body. Images have been scaled to the same total length. Mean specimen size is given in Table 1.

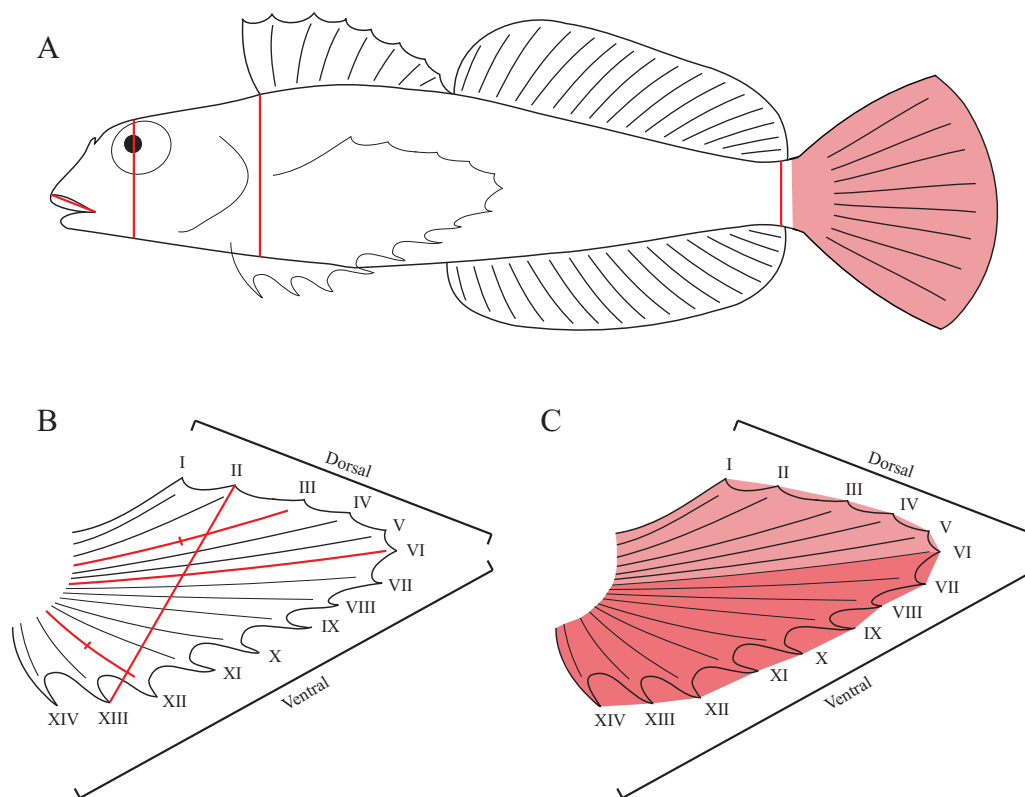


Fig. 3. Representative diagrams of (A) linear, angular, and area measurements taken from intact bodies; (B) linear measurements and (C) area measurements taken from mounted fins of sculpins. Red lines indicate linear measurements whereas filled shapes represent measures of area. Fin rays are labeled with roman numerals. See text for additional description.

Prior to euthanasia, specimens were housed in flow-through sea tables and were starved for 3–5 days to ensure cleared gut contents for unbiased mass measurements. Euthanized specimens were photographed (Nikon D3000 or D90; Nikon Inc., Melville, NY, USA), and body and pectoral fin morphometrics were quantified using Image J (version 1.43r; NIH, Bethesda, MD, USA). Body measurements (Fig. 3A) included mouth size (premaxilla length; a measure of feeding mode following Norton, 1991a), head depth (vertical height through the middle of the pupil), body depth (vertical height at the first dorsal fin ray), peduncle depth (vertical height at the narrowest portion of the peduncle), and caudal fin area.

Although collection methods could introduce bias in body size of species collected due to differences in mesh size, a comparison of maximum size and maximum depth across 56 sculpin species indicates that larger species are generally found in deeper habitats and vice versa (Eschmeyer et al., 1983). For example, for 6 species that are only found in the intertidal, mean body size was 8.9 cm, compared to 36 species that are not found in the intertidal where mean body size was 20.1 cm. The remaining 21 species can be found in habitats ranging from the intertidal to a mean depth of 67.8 m, and a similar trend was apparent. Additionally, no collection method was available that could be used in all habitats. Therefore, sampling was considered representative.

Pectoral fins were removed, mounted, and photographed as in Higham (2007a). Linear measurements (Fig. 3B) included dorsal fin ray diameter (at 50% of the length of the third ray), dorsal fin ray length (of the third ray), ventral fin ray diameter (at 50% of the length of the third from the last ray), ventral fin ray length (at the third to the last ray), length of the longest fin ray, and fin height (from the tip of the second ray to the tip of the second to last ray).

Area measurements (Fig. 3C) included area of the dorsal region of the fin (across terminal ends of the rays, independent of webbing), area of the ventral region of the fin (across terminal ends of the rays, independent of webbing), total pectoral fin area (sum of dorsal and ventral areas), and webbed area of the fin (tracing the webbing, including dorsal and ventral regions). Additionally, total number of fin rays and number of rays with reduced webbing (RW rays; rays with webbing that does not fully extend to the tip) were determined. Measurements and counts were used to calculate dorsal ray thickness ratio (ratio of dorsal ray width to length), ventral ray thickness ratio (ratio of ventral ray width to length), pectoral fin aspect ratio (square of longest ray length to total pectoral fin area), long ray position (long ray number to total number of rays), proportion of RW rays (number RW rays to total number of rays), regionalization ratio (ventral area to dorsal area), and webbing ratio (webbed area to total area, an indicator of the magnitude of webbing reduction).

Prior to statistical analyses, measurements of mass were cube root transformed and measurements of area were square root transformed. Linear and area measurements (excluding counts and ratios) were size corrected by dividing values by mass^{1/3}. Corrected values were only used for statistical purposes, and all values presented here are uncorrected. Specimens were collected and analyzed opportunistically, resulting in low sample sizes of individuals within species. Although this can inherently lead to false statistical interpretations, small sample sizes can retain statistical power when variation across species is greater than variation within species (Harmon and Losos, 2005). When mean standard deviation within species was compared to standard deviation across species for all variables in this study, this was the case (intraspecific variation ranged from 23.6% to 79.7% of the variation across species),

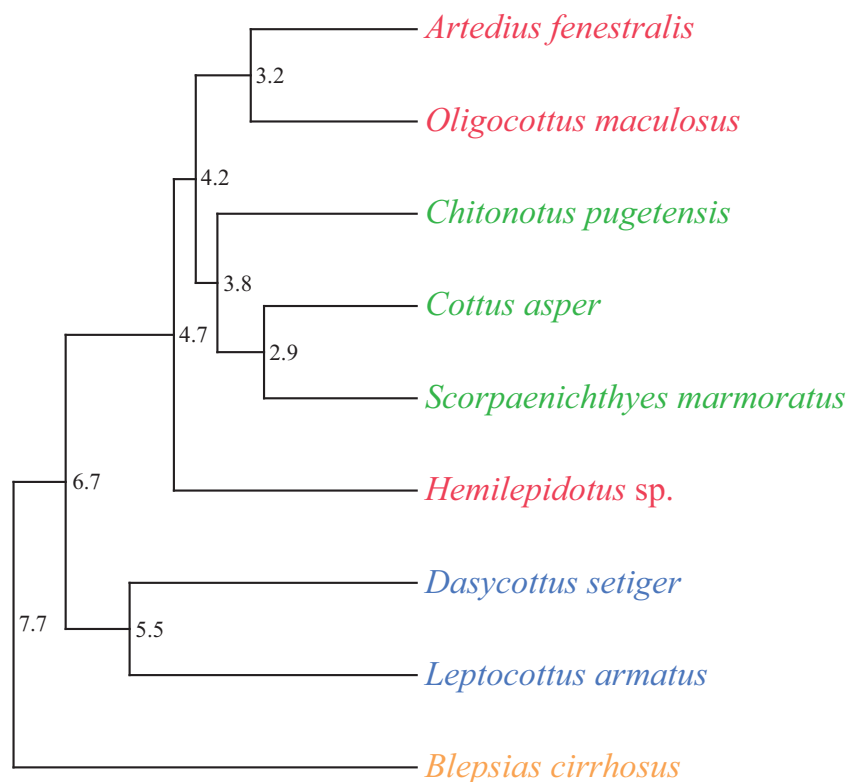


Fig. 4. Cluster analysis results from species means displaying similarities and differences among sculpin species in this study. Values at nodes are the Euclidean distances represented at each joining. Species are coded by suggested groups (orange: group 1, blue: group 2, green: group 3, red: group 4). See text for justification of including *Hemilepidotus* sp. in group 3.

indicating that larger sample sizes would not have significantly altered the results.

Data analysis was performed in two parts: (i) a univariate analysis of body morphology (excluding pectoral fin morphology) across species, for comparison with prior studies, and (ii) a multivariate analysis of species (including body and pectoral fin morphology) to determine the relationship among body and pectoral fin morphology across species. All statistical tests were performed in JMP 9.0.0 (SAS Institute, Inc., Cary, NC, USA).

First, to determine changes in body morphology for comparison to prior studies, one-way ANOVAs were performed on species (independent variable) for total length, mass, head depth, body depth, and peduncle depth (dependent variables). Residuals were saved and assumptions of normality were checked with a Shapiro–Wilks test for normality. Equality of variance was determined using Levene’s test, and where this assumption was not met, Welch’s test was performed. Where normality was not met, a non-parametric Kruskal–Wallis test was used to test for differences among species. Tukey–Kramer HSD post hoc tests were used to determine differences between species when significant differences among species were found.

Second, species means of all variables were entered into a cluster analysis to determine the presence of groups. Ward’s linkage, which is a space-conserving method, was used to join groups. Groups were then tested using a stepwise discriminant function analysis (DFA) to determine the variables driving the divergence among sculpins. Variables were included when the *p*-value indicated a significant contribution. The reduced dataset was then used to model the relationship among groups. Variables were correlated to each DFA axis to determine which were responsible for group separation. Scores for individuals on the first two DFA axes were saved and used to determine which groups were significantly different along each DF axis. Univariate tests were performed as above for DFA axis scores

(dependent variable) and group (independent variable). All values presented are uncorrected mean \pm SEM.

3. Results

The species in our study exhibited changes in body morphology that suggest species are exposed to variation in flow regime. Species were significantly different in total length (Kruskal–Wallis, $\chi^2_8 = 33.4$, $p < 0.001$), mass (Kruskal–Wallis, $\chi^2_8 = 34.1$, $p < 0.001$), head depth (ANOVA, $F_{8,32} = 9.6$, $p < 0.001$), body depth (ANOVA, $F_{8,32} = 7.4$, $p < 0.001$), and peduncle depth (ANOVA, $F_{8,32} = 41.7$, $p < 0.001$). General similarities among species across variables were apparent. For example, *Oligocottus maculosus* and *Artedius fenestralis* had the smallest total length and mass (with the exception of *B. cirrhosus*), and also had a decreased head and body depth and increased peduncle depth. Alternatively, *Leptocottus armatus*, *Dasycottus setiger*, and *Hemilepidotus* sp. had the greatest total length, mass, head height, and body height. However, *Scorpaenichthyes marmoratus* was a smaller species but had among the greatest head and body heights, and *L. armatus* was one of the largest but had the smallest head height, indicating that not all species followed the general trend.

Pectoral fin functional regionalization was present to varying degrees in all species of cottoids in this study (Fig. 3). Although some species exhibited distinct differences from one another, a general grouping was apparent (Fig. 4). These groups included (1) epi-benthic *B. cirrhosus*, (2) *Leptocottus armatus* and *Dasycottus setiger*, (3) *Cottus asper*, *Scorpaenichthyes marmoratus*, and *Chitonotus pugetensis*, and (4) *Hemilepidotus* sp., *Artedius fenestralis*, and *Oligocottus maculosus*. The cluster analysis resulted in the placement of *Hemilepidotus* sp. as similar to both groups 3 and 4. To prevent forming a monotypic group (with the exception of the monotypic group formed by *B. cirrhosus*, which is highly divergent

Table 2
Variable selection and correlations to discriminant function axes.

Variable	F ratio	p	DF1	DF2
Total length	6.78	0.0021*	0.15	0.68*
Mass	8.65	0.0006*	0.14	0.71*
Mouth size	7.36	0.0014*	−0.05	0.34*
Head depth	5.43	0.0060*	−0.20	0.45*
Body depth	1.36	0.2831	–	–
Peduncle depth	8.51	0.0006*	0.73*	−0.45*
Caudal fin area	1.13	0.3583	–	–
Fin height	3.66	0.0280*	0.71*	0.45*
Longest ray length	6.77	0.0021*	−0.12	−0.81*
Position of the longest ray	2.06	0.1362	–	–
Aspect ratio	12.16	0.0001*	−0.71*	−0.38*
Total fin area	5.20	0.0072*	0.66*	−0.38*
Area of webbing	5.30	0.0066*	0.59*	−0.31
Webbing ratio	5.25	0.0070*	−0.60*	0.48*
Dorsal area	1.41	0.2681	–	–
Ventral area	2.44	0.0926	–	–
Regionalization ratio	0.85	0.4825	–	–
Dorsal ray length	1.37	0.2789	–	–
Dorsal ray diameter	11.12	0.0001*	−0.34*	−0.16
Dorsal ray thickness ratio	9.52	0.0003*	−0.05	−0.03
Ventral ray length	1.12	0.3637	–	–
Ventral ray diameter	1.73	0.1908	–	–
Ventral ray thickness ratio	1.18	0.3426	–	–
Total # rays	3.71	0.0268*	0.22	0.92*
# RW rays	4.66	0.0114*	0.36*	0.78*
Proportion of RW rays	5.74	0.0047*	0.58*	0.46*

F ratio and associated p refer to the final step of the stepwise DFA and significant values represent the inclusion of the variable in the DFA. DF1 and DF2 correspond to discriminant function axes 1 and 2 in Fig. 3.

* Significant correlation at $p < 0.05$.

from the remaining species and deserves to be distinguished in this way), *Hemilepidotus* sp. were qualitatively assigned to group 4 based on the distance matrix used to join groups. Specifically, *Hemilepidotus* sp. were more similar to *Artedius* and *Oligocottus* (Euclidean distance of 5.79 and 5.97, respectively, mean distance of 5.88) than they were to *Chitonotus*, *Cottus*, and *Scorpaenichthys* (Euclidean distance of 5.73, 6.31, and 6.25, respectively, mean distance of 6.10). Additionally, the habitat in which *Hemilepidotus* sp. occur is more similar to that of group 4 (Eschmeyer et al., 1983; Lamb and Edgell, 1986).

Groups were significantly different along two DFA axes (Fig. 5A; DFA, Wilk's lambda $F_{48,66} = 27.3$, $p < 0.0001$), which together explained 92.6% of variance. Excluded variables were body depth, caudal fin area, position of the longest ray, dorsal and ventral areas, regionalization ratio, dorsal ray length, and ventral ray length, diameter, and thickness ratio (Table 2). All variables entered were significantly correlated to either DFA axis 1 or 2 with the exception of dorsal ray thickness ratio (Table 2 and Fig. 5B). All groups were significantly different from each other along DFA axes 1 (ANOVA, $F_{3,37} = 763.0$, $p < 0.0001$) and 2 (ANOVA, $F_{3,37} = 210.9$, $p < 0.2398$) with the exception of groups 2 and 3 along DFA axis 1 (Tukey–Kramer HSD, $p = 0.999$). Assumptions of normality and equality of variances of the residuals were met (Shapiro–Wilks, $p > 0.32$; Levene's test, $p > 0.52$).

The positions of the four groups along each DFA axis suggest that these groups represent variation in functional demand for gripping and lift generation, so that each group likely experiences (1) no demand, (2) low demand, (3) intermediate demand, or (4) high demand for station-holding (Fig. 5A). Epi-benthic *B. cirrhosus* represented the negative extremes of both DFA axes (Fig. 5A), and was distinct from all other groups in having a decrease in size and specialization of the ventral fin region (increased webbing ratio, and reduced number and proportion of rays with reduced webbing), as well as the greatest pectoral fin aspect ratio (increased aspect ratio, decreased fin height, and increased long ray length) (Fig. 5B). Although this species may be capable of some

station-holding behaviors, the demand for station-holding in this species is likely minimal (or non-existent) in comparison to more typical species, and for simplification they have been categorized as having “no demand”.

All remaining groups likely experience a demand for station-holding. Variables that were positively correlated with DFA axis 1 describe morphological characteristics that would be expected in species exposed to high station-holding demand, including decreased head depth, increased peduncle depth, larger pectoral fins (total pectoral fin area), and less webbed (webbing ratio) ventral rays (Table 2 and Fig. 5B). DFA axis 1 indicates a gradient in specialization for a locomotor mode with high acceleration and pectoral fins used for mechanical gripping. Similarly, negative correlations to DFA axis 2 also describe characteristics expected of high-demand morphology. These include reduced body size (total length and mass) and changes in pectoral fin shape (aspect ratio) to shorter (reduced fin height) or longer (increased longest ray length) pectoral fins. Additionally, the number of fin rays (total number of fin rays) are consolidated (Table 2 and Fig. 5B). DFA axis 2 indicates a gradient in specialization for lift generation. Therefore, the level of station-holding demand experienced by benthic species is hypothesized based on the level of specialization for gripping and lift generation exhibited by their pectoral fins.

4. Discussion

Our study is the first to reveal functionally relevant differences in pectoral fin morphology among sculpins. Although many fish species and/or populations occupying different habitats exhibit morphological differences in relation to overall body form (Robinson and Wilson, 1994; Langerhans et al., 2003; Kerfoot and Schaefer, 2006), differences in pectoral fins, which can contribute to station-holding ability in high-flow habitats (Webb, 1989), had not been quantified so far. Here, we show that the functional differences in pectoral fin morphology present among sculpins suggest transitions in functional demand for station-holding across species. Benthic species that are likely exposed to high flows exhibited decreased body drag (reduction in head and body depth), specialization for friction with the substrate (increased pectoral fin size and decreased webbing) (Taft et al., 2008), and increased thrust generation and acceleration capabilities (increased peduncle height) (Webb, 1978; Walker, 1997; Imre et al., 2002) compared to species likely exposed to low demand (Table 2 and Fig. 5). Our results suggest that these morphological changes contribute to the success of some species in high-demand habitats.

4.1. Functional implications of changes in body morphology

We found significant differences in body morphology among sculpin species, which coincides with results from prior studies (Kerfoot and Schaefer, 2006; Bogdanov, 2007). In marine sculpins studied here, larger species (greater mass and total length) generally had greater head and body depth, and decreased peduncle depth. This trend is similar to that observed between populations of *Cottus carolinae*, where individuals from fast-flowing Ozark streams had a reduced body profile and smaller body size, compared to those from slow-flowing prairie streams (Kerfoot and Schaefer, 2006). A reduction in head or body depth (body profile) is also apparent in populations of the Baikal sculpin *Paracottus knerii* (Bogdanov, 2007) and of benthic station-holding darters (Matthews, 1985) that are exposed to increased flow regimes. Additionally, small body size allows darters to exploit the area of reduced water velocity present in the boundary layer with the substrate, effectively increasing their station-holding ability (Carlson and Lauder, 2011). Morphological adaptations such as these have

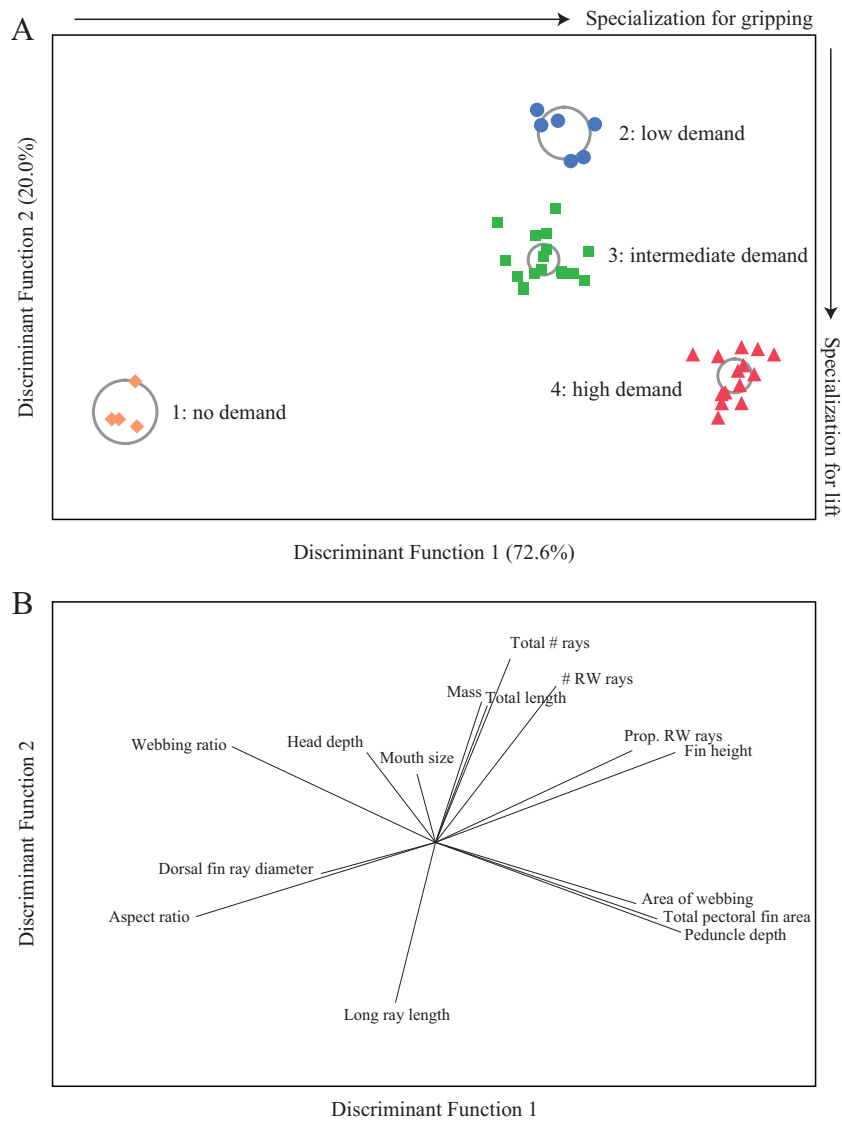


Fig. 5. (A) Discriminant function plot of scores for each individual that demonstrates the separation of sculpin body and pectoral fin morphology. Color scheme follows Fig. 4 and is indicated by the text in the figure (orange diamonds: group 1, blue circles: group 2, green squares: group 3, red triangles: group 4). Hypotheses of functional demand are also indicated for each group. A 95% confidence interval (gray circle) is given around the multivariate mean for each group. (B) Biplot of variable correlations to each discriminant function axis (cf. Table 2).

led to the hypothesis that, for benthic species exposed to high flow regimes, water flow is likely the primary selective pressure on morphology (Kerfoot and Schaefer, 2006). Therefore, differences in body profile and size as observed in the current study indicate that marine sculpins are also likely exposed to a range of flow regimes. Work quantifying habitat characteristics in association with morphology across marine sculpins would further support this hypothesis.

Although a general pattern of body morphology was observed in the present study, some species deviated from this pattern, indicating that body morphology might be influenced by a number of developmental or physiological factors, in addition to abiotic demands of flow. For example, *Leptocottus armatus* was one of the largest specimens collected, but its head depth was the smallest. Alternatively, *Scorpaenichthys marmoratus* individuals were among the smallest (specimens were juveniles), but this species had the greatest head depth (as suggested by the common name “cabezón”, meaning “big-headed”). Since head and body depth reflect the composite of several functional systems (i.e., feeding mode, locomotor strategy, sensory physiology, etc.), adaptation

of body morphology may be less flexible to changes in flow demand. Therefore, the differences found in body morphology among sculpins in this study may reflect both functional responses to flow as well as responses to other demands that are non-functional for flow, and body morphology may not be the best predictor of flow demand in sculpins.

The pectoral fins of sculpins in this study exhibit changes in morphology that suggest differences in demand across species, and sculpin pectoral fins appear flexible to these demands. The exclusion of body depth from the DFA (Figs. 4 and 5) indicates that the pectoral fins may be more flexible to, or more important for adapting to, changes in flow regime than the body. Further work could test this hypothesis by relating body and fin morphology to measured habitat characteristics.

4.2. Functional implications of changes in pectoral fin morphology

Pectoral fin regionalization was present in all species of cottoids studied here. Species represented a gradient in regionalization

of the pectoral fin from *B. cirrhosus* with little specialization of the ventral fin rays to *Oligocottus maculosus* with significantly thicker ventral fin rays and significantly reduced fin ray webbing (Figs. 4 and 5). *B. cirrhosus* is an epi-benthic swimmer (Marliave, 1975), and minimal regionalization in this species supports the conclusion that benthic station-holding is the primary function of regionalized pectoral fins. Among the remaining cottoids studied, regionalization was prominent, and the significance of morphological changes in the ventral region indicates that this region may be the key to success for species occupying habitats that vary in demand. Future work should address the functional significance of this adaptation across teleost fishes to determine how pectoral fin regionalization compares to other benthic station-holding strategies.

Pectoral fin function likely changes from primarily gripping in low-demand species, to a more equal dependence on gripping and lift generation in high-demand species (Fig. 5). Low- and intermediate-demand species do not differ along DFA axis 1 (reliance on gripping) but high-demand species do. Along DFA axis 2 (specialization for lift generation) all groups are significantly different, and reliance on lift increases from low-, to intermediate-, to high-demand species. Since lift increases with the square of fluid speed across a hydrofoil, significant negative lift could be generated in high-demand environments that have greater demands on station-holding. This additional hydrodynamic strategy could provide an advantage over more mechanical strategies (gripping) in these habitats. Alternatively, in low-demand habitats, gripping may be sufficient or fluid flow may not be fast enough for a substantial reliance on negative lift generation. Performance tests of sculpin species exposed to variation in flow regime would help support these hypotheses.

The greatest morphological specialization was observed in *O. maculosus*, *A. fenestralis*, and *Hemilepidotus* sp., where large, symmetrical pectoral fins with thicker, less webbed ventral rays likely function to increase friction with the substrate. In bamboo sharks (*Chiloscyllium plagiosum*), pectoral fins are held at a negative angle relative to water flow, which generates a lift force into the substrate to increase friction for station-holding (Wilga and Lauder, 2001). Additionally, the pectoral fin rays of darters are increasingly spread as water flow increases (Carlson and Lauder, 2010), increasing negative lift. These behaviors have also been observed in sculpins (Webb, 1989; Webb et al., 1996; Coombs et al., 2007; Taft et al., 2008). Since greater aspect ratios increase the amount of lift produced for a given amount of drag, large symmetrical pectoral fins would result in a greater negative lift force to increase friction with the substrate.

Sculpins also utilize the ventral fin rays for gripping the substrate. European plaice (*Pleuronectes platessa*) are capable of maintaining position on the substrate in flows of up to 35 cm s^{-1} , due in part to an ability to grip the substrate with the tips of the dorsal and anal fin rays (Webb, 1989). In comparison, the ability of lashers (*Myoxocephalus scorpius*) to maintain their position in flows of up to 55 cm s^{-1} is likely due to an increased ability of this species to grip the substrate (Webb, 1989). This behavior is likely facilitated by stiff ventral fin rays that can provide structural support (Summers and Long, 2006), and a decrease in fin webbing so that fin rays are flexible distally (Taft, 2011). Together, specializations for negative lift and gripping in *O. maculosus*, *A. fenestralis*, and *Hemilepidotus* sp. in this study indicate performance in high flow habitats where station-holding is necessary.

Interestingly, *B. cirrhosus* is likely specialized for lift generation only (Fig. 5), and its pectoral fins are often not in contact with the substrate when exposed to flow in a flume (unpublished data). Like other sculpins, *B. cirrhosus* does not have a swim bladder, and likely relies on positive lift generation to overcome the force of negative buoyancy and to maintain a steady swimming position in the water

column. *M. octodecimspinosus* holds the dorsal pectoral fin region in a rigid lateral posture during steady swimming, which likely generates positive lift (Taft et al., 2008). This is similar to the rigid lateral posture of the entire fin in *B. cirrhosus* during steady swimming (E.A.K., personal observation). This alternative pectoral fin function in *B. cirrhosus* indicates that in this species, demands placed on the pectoral fins for steady swimming may outweigh demands for station-holding, and further work is needed to more fully assess pectoral fin functional tradeoffs among sculpins.

4.3. Constraints and diversification in sculpins

Sculpins are a large radiation where large variation is present among species. They occupy a wide range in habitats, including freshwater systems, deep marine canyons, kelp canopies, exposed rocky shores, and protected subtidal sand flats. Within these habitats, sculpins can be found on sand, silt, mud, rock or shell substrate, and even in vegetation. Although larger species are generally found in deeper habitats (Eschmeyer et al., 1983), the two largest species can be found in the intertidal (*S. marmoratus* and *Myoxocephalus polyacanthocephalus*), and one of the deepest species is only 6.4 cm long (*Zesticelus profundorum*) (Eschmeyer et al., 1983). The present study suggests that the latent factor explaining the diversity among sculpins is not habitat (Ramon and Knope, 2008), substrate type, or maximum depth (Mandic et al., 2009), but rather functional capability.

In this study, pectoral fins of 9 sculpin species displayed considerable variation in shape, size, and morphology that was more important in describing differences among species than general measures of overall body size (Table 2 and Fig. 5). This not only indicates that pectoral fin morphology might be a more ecologically relevant descriptor of diversity in marine sculpins than traditional body morphometrics, but also that demand from flow regime may be the most significant factor shaping pectoral fin morphology in these species (with the exception of *B. cirrhosus* as noted above), despite other potential behavioral demands on pectoral fins (Gosline, 1994).

In sculpins, the body and caudal fin are used predominantly over paired fins for swimming, which permits specialization of the pectoral fins for other functions (station-holding in high-flow habitats). In many species, such as centrarchids and cichlids, pectoral fins are utilized for steering and braking behaviors during prey capture (Higham, 2007a,b). We previously hypothesized that a tradeoff exists between generating trimming forces during swimming and generating increased friction forces during station-holding so that species specialized for station-holding display decreased integration of the locomotor and feeding systems during prey capture (Kane and Higham, 2011). In the present analysis, mouth size tended to decrease as species transition to high-demand habitats (Table 2). However, this correlation was weak and may have been biased by the small number of species included in each group. For this reason, we cannot determine constraints imposed by station-holding morphology on feeding mode in sculpins. Alternatively, constraints could be more prominent on overall feeding strategy, as this includes the locomotor behavior as a predator approaches the prey (Kane and Higham, 2011), which is the most variable portion of the feeding event among cichlid fishes (Wainwright et al., 2001).

Given the considerable morphological disparity between the 9 species in this study, the ability of the pectoral fins to adapt to functional demand across species does not appear constrained. This is not surprising since prior studies have noted flexibility in pectoral fin morphology among Scorpaeniform fishes (Gosline, 1994). However, constraints on pectoral fin morphology may become more apparent with analyses of plasticity within species. For example, the ventral-most pectoral fin rays of *Rhamphocottus richardsoni* are completely separated from each other (no webbing) and are used

for walking and jumping behaviors (Lamb and Edgell, 1986; Norton, 1991a). This extreme pectoral fin modification might constrain the ability of this species to adapt to varying flow regimes. Additionally, species exposed to greater demand, such as *O. maculosus*, might be expected to exhibit the greatest range in plasticity of pectoral fin morphology. Plasticity of morphology and function represent a rich area for future studies exploring diversity among sculpins.

Divergence among sculpin species (Fig. 4) likely represents convergence within groups due to demands of flow regime. Species likely exposed to high demand (*A. fenestralis*, *O. maculosus*, and *Hemilepidotus* sp.) inhabit tidepools and shallow waters with rocks or rocky ledges (Eschmeyer et al., 1983; Lamb and Edgell, 1986), and these habitats likely require a similar station-holding ability. Species exposed to intermediate demand (*S. marmoratus*, *C. pugetensis*, and *C. asper*) have more generalized pectoral fin morphology that results from their wide occurrence in both shallow and deep habitats, either within individuals or across the species. Specifically, *C. pugetensis* is encountered on soft substrates (Norton, 1991b) where it buries in the sediment. Although soft sediment would imply low demand, this species occurs from the intertidal to a depth of 140 m (Eschmeyer et al., 1983; Lamb and Edgell, 1986). It is possible that with such a wide distribution, this species might encounter various demands, and that its success across this range might be due to more generalized pectoral fins. This is also likely for *C. asper*, which is commonly found in deep, slow-moving bodies of freshwater (White and Harvey, 1999). However, this species migrates to and from brackish estuaries at various stages of its life cycle (Eschmeyer et al., 1983; Lamb and Edgell, 1986), where it might experience multiple demands. *C. asper* is also a more ancestral lineage in the radiation of *Cottus* sp. into freshwater habitats (Kinziger et al., 2005), where a range of flow demands are possible. An ancestor with more generalized pectoral fin morphology could have given rise not only to the freshwater clade, but could also have contributed to the adaptive radiation of the Lake Baikal species flock (Sherbakov, 1999) which is nested within this clade (Kontula et al., 2003; Kinziger et al., 2005).

Morphological divergence (Figs. 4 and 5) of closely related taxa (i.e., *L. armatus* and *C. asper*, *B. cirrhosus* and *S. marmoratus*) (Mandic et al., 2009) indicates that demands from the habitat can overcome constraints of evolutionary history. Alternatively, the true cottids *A. fenestralis* and *O. maculosus* have diverged more recently (Ramon and Knope, 2008; Mandic et al., 2009) and likely share a high functional demand (Fig. 4). This supports the recent and current divergence into high-demand habitats, such as the intertidal. Changes in pectoral fin morphology, particularly the ventral portion, in relation to flow regime in true cottids (Cottidae) may help to explain why this family has more successfully radiated into shallow and intertidal high-demand habitats (Ramon and Knope, 2008). Phylogenetic analyses across scorpaeniform fishes could more directly indicate whether diversification in pectoral fin morphology has resulted in diversification of benthic station-holding cottoid fishes.

Acknowledgements

The staff at BMSC facilitated this work, especially the crew of M.V. Alta, B. Rogers, and the biomechanics class. B. Brown assisted with multivariate statistics. Funding was provided by the R.C. Edwards Fellowship from Clemson University to E.A.K. and start-up funds to T.E.H.

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