biology
letters

Biol. Lett. (2008) **4**, 84–86
doi:10.1098/rsbl.2007.0509

Evolutionary biology

Integrated diversification of locomotion and feeding in labrid fishes

David C. Collar[1,*], **Peter C. Wainwright**[1] **and Michael E. Alfaro**[2]

[1] *Section of Evolution and Ecology, University of California, Davis, CA 95616, USA*
[2] *School of Biological Sciences, Washington State University, Pullman, WA 99164, USA*
**Author and address for correspondence: Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA* (*dcollar@oeb.harvard.edu*).

An organism's performance of any ecological task involves coordination of multiple functional systems. Feeding performance is influenced by locomotor abilities which are used during search and capture of prey, as well as cranial mechanics, which affect prey capture and processing. But, does this integration of functional systems manifest itself during evolution? We asked whether the locomotor and feeding systems evolved in association in one of the most prominent and diverse reef fish radiations, the Labridae. We examined features of the pectoral fins that affect swimming performance and aspects of the skull that describe force and motion of the jaws. We applied a recent phylogeny, calculated independent contrasts for 60 nodes and performed principal components analyses separately on contrasts for fin and skull traits. The major axes of fin and skull diversification are highly correlated; modifications of the skull to amplify the speed of jaw movements are correlated with changes in the pectoral fins that increase swimming speed, and increases in force capacity of the skull are associated with changes towards fins that produce high thrust at slow speeds. These results indicate that the labrid radiation involved a strong connection between locomotion and feeding abilities.

Keywords: ecomorphology; independent contrasts; labriform swimming; performance

1. INTRODUCTION

Multiple functional systems work together to determine an organism's ability to perform any ecological task. In many predators, locomotor and feeding abilities are coordinated during prey capture (Rice & Westneat 2006; Higham 2007), and locomotor performance influences the search for prey (Irschick & Losos 1998; Fulton & Bellwood 2002). Although an organism's fitness will depend on the combined abilities of functional systems (Arnold 1983; Lande & Arnold 1983), it is unclear whether this integration translates into correlated evolution during diversification. We asked whether locomotor and feeding morphologies have evolved in association in one of the most successful and diverse radiations of modern reef fishes, the Labridae (wrasses and parrotfishes).

Labrid fishes are found in a wide range of reef habitats (Bellwood & Wainwright 2001; Fulton *et al.* 2005) and exhibit an array of feeding ecologies, including species that feed primarily on molluscs, corals, fish parasites, zooplankton and other fishes (Bellwood *et al.* 2006). This ecological variation is reflected in morphological diversity of the pectoral fins—the primary propulsive structures—and the skull (figure 1; Wainwright *et al.* 2002, 2004). Labrid pectoral fins vary between high aspect ratio (AR), wing-like shapes that use a flapping (up–down) stroke and low AR, paddle-like shapes that oscillate with a rowing (fore–aft) stroke (figure 1*a*; Walker & Westneat 2000, 2002). These axes of morphological and functional variation correlate with swimming speed differences, where species with wing-like, flapping fins achieve higher critical swimming speeds in the laboratory (Walker & Westneat 2002; Fulton *et al.* 2005) and higher routine swimming speeds in the field (Wainwright *et al.* 2002). Species with high swimming speed performance tend to occupy open water habitats that experience higher-energy water flow (Bellwood & Wainwright 2001; Fulton *et al.* 2005). In addition, labrid species display skull forms ranging from gracile, speed-modified morphologies to robust, force-modified forms (figure 1*b*) and species with similar cranial mechanics feed on similar prey items (Wainwright *et al.* 2004), though the strength of this association depends on prey type (Bellwood *et al.* 2006). Additionally, evolutionary changes in jaw speed and force correlate with changes in the amount of hard or evasive prey in labrid diets (Wainwright 1988; Westneat 1995).

We ask whether pectoral fin morphology evolved in concert with cranial features that describe the production and transmission of force and motion during feeding as a test of the 'radiation in stages model'. This model posits that habitat differences arise early during a clade's evolution and trophic diversification follows (Diamond 1986; Streelman & Danley 2003) and implies that habitat use and diet are orthogonal axes of diversification. If labrid evolution has progressed in this stepwise manner, then we expect changes in locomotor and feeding morphology to be uncorrelated. Alternatively, if integration of locomotor and feeding performance has constrained diversification, then we expect correlated evolution of pectoral fin and skull morphology.

To test these competing models of functional evolution, we calculated independent contrasts for labrid pectoral fin and cranial variables using recently constructed molecular phylogenies. We performed principal component analyses (PCA) separately on the sets of fin and skull variables to identify the major axes of locomotor and feeding diversification, and tested for correlations between these axes.

2. MATERIAL AND METHODS

We used species' values for pectoral fin AR and attachment angle that are reported in Wainwright *et al.* (2002). Species' cranial morphology data were taken from Wainwright *et al.* (2004), and we included gape width, upper jaw protrusion distance, lower jaw opening and closing lever ratios, kinematic transmission coefficient (KT) of the oral jaws four-bar linkage, and masses of three cranial

Electronic supplementary material is available at http://dx.doi.org/10.1098/rsbl.2007.0509 or via http://journals.royalsociety.org.

Received 10 October 2007
Accepted 20 November 2007

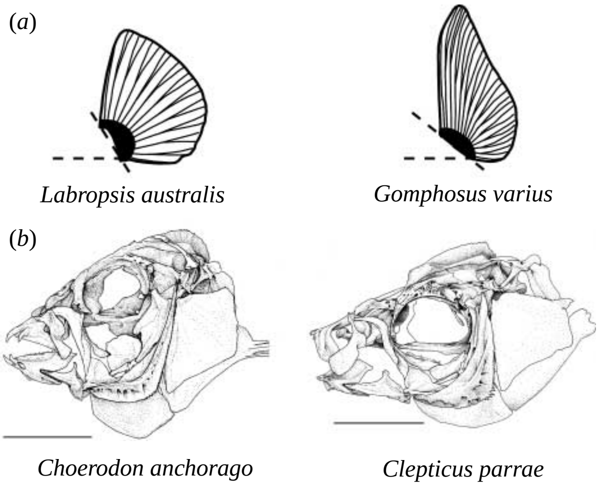

Figure 1. (*a*) Labrid pectoral fins vary in AR, including low AR forms, as in *Labropsis australis* (southern tubelip) and high AR forms, as in *Gomphosus varius* (bird wrasse). Species with high AR fins typically employ a flapping stroke during swimming, which is reflected in the shallow angle of attachment between the fin (oblique, dashed line) and the long axis of the body (horizontal, dashed line). Species with low AR fins use a rowing fin stroke, associated with a deep angle of attachment. (*b*) Labrid skull morphology varies between forceful jaws, as in *Choerodon anchorago* (orange-dotted tuskfish), and jaws that amplify velocity, as seen in *Clepticus parrae* (creole wrasse). The morphological differences between species depicted in (*a*,*b*) reflect the principal axes of pectoral fin and skull evolution, respectively.

muscles: the primary mouth-closing muscle, the adductor mandibulae (AM); the primary hyoid depressor, the sternohyoideus (SH); and the primary pharyngeal jaw adductor, the levator posterior (LP). Details regarding specimen collection and measurement methods are provided in Wainwright *et al.* (2002, 2004). Variation in species' values was corrected for differences in body size using a regression procedure that accounts for phylogeny, described in Blomberg *et al.* (2003).

To achieve maximum overlap between species in the Wainwright *et al.* (2002, 2004) morphological data and species used in recent phylogenetic analyses, we combined molecular datasets from Streelman *et al.* (2001) and Westneat & Alfaro (2005). Details of our phylogenetic analysis are provided in the electronic supplementary material.

We used the computer program MESQUITE (Maddison & Maddison 2006) and the PDAP module (Midford *et al.* 2005) to calculate standardized independent contrasts for each size-corrected morphological variable for 60 internal nodes on the labrid phylogeny. To account for correlations among skull traits and to reduce dimensionality, we performed PCA on the correlation matrix of cranial morphology contrasts (Ackerly & Donoghue 1998). We also performed a separate PCA on the correlation matrix of fin morphology contrasts to account for correlation between fin AR and attachment angle ($r=-0.61$, $p<0.001$). We retained the first principal component (PC) from each PCA as the primary axis of skull or fin evolution and tested the correlation between skull PC 1 and fin PC 1. Analysis of individual trait correlations produced similar results (electronic supplementary material, table S1). All correlations were through the origin (Garland *et al.* 1992).

3. RESULTS

The first PC of skull contrasts is significantly correlated with the first PC of pectoral fin contrasts (figure 2; $r=-0.53$, $p<0.001$). Skull PC 1 accounts for 30% of the total variation in skull character contrasts and loads strongly with four out of eight characters and moderately with three; PC loadings on original variables are reported in table 1. Pectoral fin PC 1 explains 80% of the total variation in fin contrasts and loads positively with AR (0.71) and negatively with attachment angle (−0.71). These results are robust to the influence of outliers and uncertainty in the model of character evolution (see electronic supplementary material).

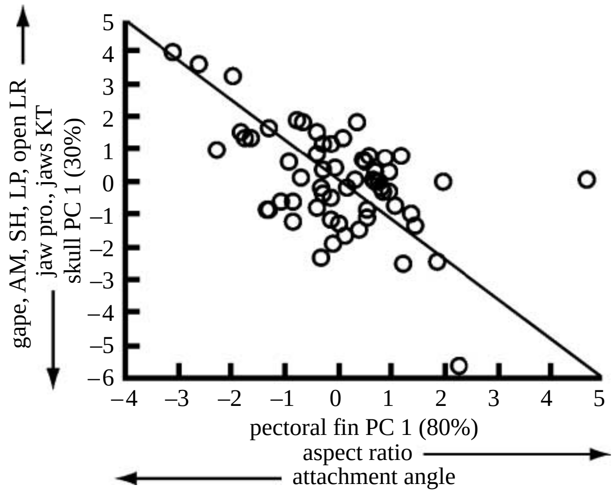

Figure 2. Plot of pectoral fin PC 1 and skull PC 1. Points are PC scores for 60 internal nodes of the labrid phylogeny and were derived from PCA on independent contrasts for pectoral fin and cranial traits. Fin PC 1 explains 80% of the total variation in fin contrasts and skull PC 1 accounts for 30% of the total variation in skull contrasts. Variables with significant PC loadings are shown on each axis, and arrows indicate their directions. These two primary axes of locomotor and cranial diversification are significantly correlated ($r=-0.53$; $p<0.001$).

Table 1. Loadings of cranial variables on skull PC 1.

variable	skull PC 1
gape	0.24
jaw protrusion	−0.21
AM mass	0.53
SH mass	0.45
LP mass	0.42
close LR	0.12
open LR	0.23
jaws KT	−0.42
eigenvalue	2.38
percentage of total var.	29.69

4. DISCUSSION

Locomotor and feeding morphologies have diversified in concert in labrid fishes; the primary axes of pectoral fin and skull evolution are significantly and strongly correlated (figure 2). The major axis of pectoral fin evolution involves correlated changes in AR and attachment angle, and the primary axis of skull evolution involves a suite of changes in mouth size, jaw protrusion, cranial muscle mass, and the force and velocity transmission properties of the oral jaws. Correlation between these axes indicates a history of integrated locomotor and feeding performance evolution; changes in the skull to increase jaw speed are associated with pectoral fin shape changes that increase swimming speed performance; and increases in the skull's force output are associated with changes in the pectoral fin to produce greater thrust at slow speeds.

Our results extend the conclusions of Westneat *et al.* (2005), who find repeated transitions between fast and forceful jaws within the Labridae. The emerging picture of morphological and functional diversification in this clade is one of frequent, integrated changes in locomotor and feeding performance. This pattern does not reflect the radiation in stages model in which early changes in habitat use are followed by trophic diversification (Diamond 1986; Streelman & Danley 2003).

Correlated feeding and locomotor evolution may result from associations between prey and habitat, which would limit opportunities for independent skull and fin diversification. For example, zooplankton occur in open water, away from the protection of reef refuges, and origin of zooplanktivory probably involves changes in the skull to increase strike speed as well as changes in pectoral fins to increase swimming speed and enhance foraging efficiency or predator evasion in this habitat. Similarly, molluscivores and corallivores feed on prey that attach to substrates associated with the reef, and force enhancements of feeding structures are likely to be correlated with changes in the pectoral fins that confer manoeuvrability. In addition, genes that influence both cranial and appendicular skeletal morphology (Piotrowski *et al.* 1996) may also contribute to correlated fin and skull diversification.

Ian Hart prepared the skull drawings in figure 1*b*. This work was supported by NSF grants DEB0717009 to P.C.W. and DEB0445453 to M.E.A.

Ackerly, D. D. & Donoghue, M. J. 1998 Leaf size, sapling allometry, and Corner's rules: phylogeny and correlated evolution in maples (*Acer*). *Am. Nat.* **152**, 767–791. (doi:10.1086/286208)

Arnold, S. J. 1983 Morphology, performance, and fitness. *Am. Zool.* **23**, 347–361.

Bellwood, D. R. & Wainwright, P. C. 2001 Locomotion in labrid fishes: implications for habitat use and cross-shelf biogeography on the Great Barrier Reef. *Coral Reefs* **20**, 139–150. (doi:10.1007/s003380100156)

Bellwood, D. R., Wainwright, P. C., Fulton, C. J. & Hoey, A. S. 2006 Functional versatility supports coral reef biodiversity. *Proc. R. Soc. B* **273**, 101–107. (doi:10.1098/rspb.2005.3276)

Blomberg, S. P., Garland Jr, T. & Ives, A. R. 2003 Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**, 714–745.

Diamond, J. 1986 Evolution of ecological segregation in the New Guinea montane avifauna. In *Community ecology* (eds J. Diamond & T. J. Case), pp. 98–125. New York, NY: Harper and Rowe.

Fulton, C. J. & Bellwood, D. R. 2002 Patterns of foraging in labrid fishes. *Mar. Ecol. Prog. Ser.* **226**, 135–142. (doi:10.3354/meps226135)

Fulton, C. J., Bellwood, D. R. & Wainwright, P. C. 2005 Wave energy and swimming performance shape coral reef fish assemblages. *Proc. R. Soc. B* **272**, 827–832. (doi:10.1098/rspb.2004.3029)

Garland Jr, T., Harvey, P. H. & Ives, A. R. 1992 Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.* **41**, 18–32. (doi:10.2307/2992503)

Higham, T. E. 2007 Feeding, fins and braking maneuvers: locomotion during prey capture in centrarchid fishes. *J. Exp. Biol.* **210**, 107–117. (doi:10.1242/jeb.02634)

Irschick, D. J. & Losos, J. B. 1998 A comparative analysis of the ecological significance of maximal locomotor performance in Caribbean *Anolis* lizards. *Evolution* **52**, 219–226. (doi:10.2307/2410937)

Lande, R. & Arnold, S. J. 1983 The measurement of selection on correlated characters. *Evolution* **37**, 1210–1226. (doi:10.2307/2408842)

Maddison, W. P. & Maddison, D. R. 2006 *MESQUITE: a modular system for evolutionary analysis*, version 1.1. See http://mesquiteproject.org.

Midford, P. E., Garland Jr, T. & Maddison, W. P. 2005 *PDAP package of MESQUITE*, version 1.07.

Piotrowski, T. *et al.* 1996 Jaw and branchial arch mutants in zebrafish II: anterior arches and cartilage differentiation. *Development* **123**, 345–356.

Rice, A. N. & Westneat, M. W. 2006 Coordination of feeding, locomotor and visual systems in parrotfishes (Teleostei: Labridae). *J. Exp. Biol.* **208**, 3503–3518. (doi:10.1242/jeb.01779)

Streelman, J. T. & Danley, P. D. 2003 The stages of vertebrate evolutionary radiation. *Trends Ecol. Evol.* **18**, 126–133. (doi:10.1016/S0169-5347(02)00036-8)

Streelman, J. T., Alfaro, M. E., Westneat, M. W., Bellwood, D. R. & Karl, S. A. 2001 Evolutionary history of the parrotfishes: biogeography, ecomorphology, and comparative diversity. *Evolution* **56**, 961–971.

Wainwright, P. C. 1988 Morphology and ecology: the functional basis of feeding constraints in Caribbean labrid fishes. *Ecology* **69**, 635–645. (doi:10.2307/1941012)

Wainwright, P. C., Bellwood, D. R. & Westneat, M. W. 2002 Ecomorphology of locomotion in labrid fishes. *Environ. Biol. Fish.* **65**, 47–62. (doi:10.1023/A:1019671131001)

Wainwright, P. C., Bellwood, D. R., Westneat, M. W., Grubich, J. R. & Hoey, A. S. 2004 A functional morphospace for the skull of labrid fishes: patterns of diversity in a complex biomechanical system. *Biol. J. Linn. Soc. Lond.* **82**, 1–25. (doi:10.1111/j.1095-8312.2004.00313.x)

Walker, J. A. & Westneat, M. W. 2000 Mechanical performance of aquatic rowing and flying. *Proc. R. Soc. B* **267**, 1875–1881. (doi:10.1098/rspb.2000.1224)

Walker, J. A. & Westneat, M. W. 2002 Performance limits of labriform propulsion and correlates with fin shape and motion. *J. Exp. Biol.* **205**, 177–187.

Westneat, M. W. 1995 Feeding, function, and phylogeny: analysis of historical biomechanics in labrid fishes using comparative methods. *Syst. Biol.* **44**, 361–383. (doi:10.2307/2413598)

Westneat, M. W. & Alfaro, M. E. 2005 Phylogenetic relationships and evolutionary history of the reef fish family Labridae. *Mol. Phylogenet. Evol.* **36**, 370–390. (doi:10.1016/j.ympev.2005.02.001)

Westneat, M. W., Alfaro, M. E., Wainwright, P. C., Bellwood, D. R., Grubich, J. R., Fessler, J. L., Clements, K. D. & Smith, L. L. 2005 Local phylogenetic divergence and global evolutionary convergence of skull function in reef fishes of the family Labridae. *Proc. R. Soc. B* **272**, 993–1000. (doi:10.1098/rspb.2004.3013)