Integrated diversification of locomotion and feeding in labrid fishes

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An organism’s performance on 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 1a; 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 1b) 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; Steenman & 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

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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 Steedman et al. (2001) and Westneat & Alfaro (2005). Details of our phylogenetic analysis are provided in the electronic supplementary material.

We used the computer program Mesquita (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).

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; Steelman & 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 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.

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