

Ecomorphology of the eyes and skull in zooplanktivorous labrid fishes

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Abstract Zooplanktivory is one of the most distinct trophic niches in coral reef fishes, and a number of skull traits are widely recognized as being adaptations for feeding in mid-water on small planktonic prey. Previous studies have concluded that zooplanktivores have larger eyes for sharper visual acuity, reduced mouth structures to match small prey sizes, and longer gill rakers to help retain captured prey. We tested these three traditional hypotheses plus two novel adaptive hypotheses in labrids, a clade of very diverse coral reef fishes that show multiple independent evolutionary origins of zooplanktivory. Using phylogenetic comparative methods with a data set from 21 species, we failed to find larger eyes in three independent transitions to zooplanktivory. Instead, an impression of large eyes may be caused by a size reduction of the anterior facial region. However, two zooplanktivores (*Clepticus parrae* and *Halichoeres pictus*) possess several features interpreted as adaptations to zooplankton feeding, namely large lens diameters relative to eye axial length, round pupil shape, and long gill rakers. The third zooplanktivore in our analysis, *Cirrhilabrus solorensis*, lacks all above features. It remains unclear whether *Cirrhilabrus* shows optical specializations for capturing planktonic prey. Our results support the prediction that increased visual acuity is adaptive for zooplanktivory, but in labrids increases in eye size are apparently not part of the evolutionary response.

Keywords Zooplanktivory · Labrids · Visual acuity · Eyeball morphology · Adaptation · Coral reef fish

Introduction

Zooplankton feeding is one of the most distinct and repeatedly evolved trophic niches observed in reef fishes. While virtually all reef fish species begin life feeding on zooplankton, evolutionary transitions to this diet in the adult have occurred in at least 10 families of reef fish making this a rich system for the study of convergent evolution (Wainwright and Bellwood 2002). The shift to midwater zooplanktivory is thought to generate specific requirements for swimming performance (higher sustained swimming speed), vision (detection of small, partly transparent, drifting prey), and feeding mode (capture of small, unattached prey) (Hobson 1991; Wainwright and Bellwood 2002). These requirements are thought to be met with a series of morphological adaptations (Davis and Birdsong 1973; Hobson 1991; Wainwright and Bellwood 2002). Both the morphology of the feeding apparatus (Barel 1982; Motta 1988; Wainwright and Richard 1995; Wainwright et al. 2004; Cooper and Westneat 2009) and locomotion (Hobson and Chess 1976, 1978; Hobson 1991; Langerhans et al. 2003; Wainwright et al. 2002) have received considerable attention. Studies of the visual system in zooplanktivores are mainly confined to comparisons of eye size (Davis and Birdsong 1973; McPhail 1984; Goatley and Bellwood 2009).

The extensive literature on zooplanktivory has produced a clear sense of the common features associated with transitions to this specialized diet. One of the classic findings is that zooplanktivores have larger eyes than other fish (Fryer and Iles 1972; Davis and Birdsong 1973; Dullemeijer and

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Barel 1977; McPhail 1984; Strauss 1984; Baumgartner et al. 1988; Pankhurst 1989; Hart and Gill 1994; Wainwright and Bellwood 2002; Kassam et al. 2003; Hulsey et al. 2007; Cooper and Westneat 2009; Goatley and Bellwood 2009). The functional reasoning for this is provided by predictions from physiological optics. A larger eye can house a larger lens with longer focal length, which improves visual acuity (Lythgoe 1979; Land 1981; Fernald 1990). Zooplanktivorous fish are highly visual foragers, which select and pick individual prey items in the water column above coral reefs. The detection of planktonic prey is a difficult visual task, because of the small size of zooplankton (<3 mm; Hobson 1991) and the low contrast between prey and visual background (Douglas and Hawryshyn 1990; Loew and McFarland 1990; Johnsen 2001). High visual acuity increases the probability of detecting prey and improves feeding rate and is therefore directly related to fitness. Since visual acuity scales with eye size (Hairston et al. 1982; Kiltie 2000), large eyes may represent an adaptation to zooplanktivory. This idea is deeply embedded in the literature on the ecology and morphology of fishes.

Previous studies have found that zooplanktivorous reef fish substantially modify their feeding apparatus, typically showing a reduction of feeding structures, especially mouth and adductor muscle size (Wainwright 1988; Wainwright and Bellwood 2002; Wainwright et al. 2004; Cooper and Westneat 2009). The length and density of gill rakers influences the retention of prey particles in the oral cavity (Magnuson and Heitz 1971; Drenner et al. 1984; Schluter 1993; Robinson and Parsons 2002; Ingram and Shurin 2009). Small prey such as zooplankton may escape after capture, and thus, long and closely spaced gill rakers that function like a sieve are considered an adaptation to zooplanktivory. As a cautionary note, some authors reported deviations from the general pattern (Motta 1988; Langeland and Nøst 1995), yet all in all, gill raker length and density are both considered to be frequently associated with zooplanktivory.

In this study, we analyze changes in eye, skull, and gill raker morphology associated with the evolution of zooplanktivory in Labridae (Teleostei, Perciformes). Labrid fishes are a morphologically, taxonomically, and ecologically very diverse clade of reef fish (Parenti and Randall 2000; Wainwright et al. 2004; Cowman et al. 2009). The phylogeny of labrid fishes is highly resolved (Westneat and Alfaro 2005; Alfaro et al. 2009; Cowman et al. 2009; Kazancıoğlu et al. 2009), which makes this an attractive system for testing ecomorphological hypotheses in a phylogenetic framework. We test for three classic ecomorphological correlates of zooplanktivory and introduce two novel predictions. We test whether zooplanktivorous fish show specializations of eye morphology: do they have relatively large eyes, large lenses, or other features of eye

shape that may enhance visual acuity? We also ask whether zooplanktivores have smaller oral structures, specifically compared to the size of their orbit. Finally, we ask whether zooplanktivorous labrids have longer and more densely packed gill rakers than non-planktivores.

Materials and methods

Morphological proxies of visual acuity

Visual acuity is an integrated result of the optics of the refractive apparatus, structure and composition of the retina, chemistry of visual pigments, and neural processing in the retina and brain (Hung and Ciuffreda 2002). A simplified proxy for acuity is resolving power, an index derived from retinal and optical features. The resolving power of a camera-type eye describes the ability to discriminate fine detail in the visual environment (Lythgoe 1979; Miller 1979; Land 1981; Land and Nilsson 2002; Schmitz 2009). Formally, the resolving power of the eye is defined as

$$v = f/2 \times s \times (180/\pi) \text{ [cycles/degree]} \text{ (Land 1981),}$$

where f is the first focal length, i.e., the distance from the nodal point to the image, and s is the photoreceptor separation.

Visual acuity can be improved by two mechanisms, assuming that neural processes in the retina and visual cortex remain the same. First, a longer focal length produces a larger retinal image (Hughes 1977; Land 1981; Schmitz and Motani 2010), which in turn improves discrimination of fine detail. Second, smaller photoreceptors and denser packing enhance resolving power. Thus, one mechanism to improve resolving power requires changes at the macroscopic level (focal length), while the other mechanism requires modifications at the microscopic level (photoreceptors). In this study, we focus on visual acuity at the macroscopic level.

The determinants of focal length, i.e., the components of the refractive apparatus, are the key to understanding macroscopic mechanisms for improved resolving power. The focal length of teleost eyes is determined by the radii of curvature of the front and back surface of the lens and its refractive index (Fernald 1990).

Larger radii of curvature equate to longer focal length, assuming the refractive index remains constant (Land and Nilsson 2002). Modifications of the radii of curvature to increase focal length include two possibilities. One is to make the lens bigger, maintaining its spherical shape. Either the entire eyeball, including lens, is scaled up isometrically, or the lens is enlarged independently, but the eyeball size is constant or increases at a slower rate. For

example, it is possible that the lens is scaled up while axial length remains the same, i.e., the size of the lens is maximized for a given axial length. In this scenario, the lens would have to be moved further toward the cornea in order to accommodate the longer focal length and maintain emmetropia. The other possibility is to flatten the front and back surfaces of the lens making it more elliptical, a feature rare in teleosts (Fernald 1990; Sivak 1990; Kröger et al. 2009).

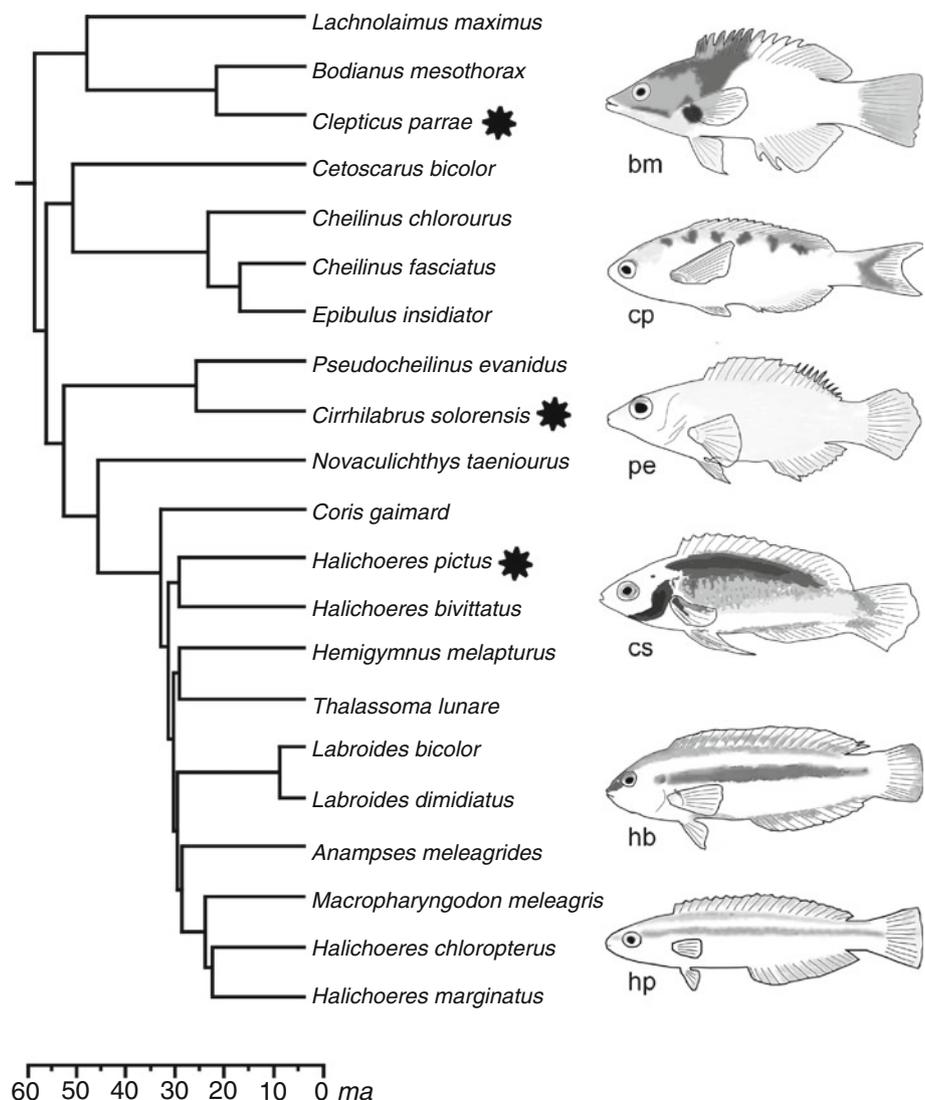
Species selection

The Labridae contain approximately 600 species with a high diversity of ecological and morphological specializations (Parenti and Randall 2000; Wainwright et al. 2004; Cowman et al. 2009). Labrids are a promising group for studying phenotypic adaptations and evolution of eye morphology with respect to zooplanktivory for two reasons. First, the

phylogenetic relationships among labrid species are reasonably well understood (Westneat and Alfaro 2005; Cowman et al. 2009; Kazancıoğlu et al. 2009) allowing examination of trait evolution in association with transitions to zooplanktivory to be made among very close relatives. Second, several independent origins of zooplanktivory have been identified in the Labridae (Wainwright and Bellwood 2002; Wainwright et al. 2004; Westneat et al. 2005; Cowman et al. 2009), and we sampled species that represent three of them: *Clepticus parrae*, *Cirrhilabrus solorensis*, and *Halichoeres pictus* (Fig. 1).

The other 18 labrid species in our dataset were chosen to capture a broad range of labrid diversity: most are benthic foragers that feed on invertebrates, but included are almost the entire diet spectrum found in the Labridae (Randall 1967; Westneat 1995; Wainwright et al. 2004; Westneat and Alfaro 2005; Cowman et al. 2009). Two of the species specialize on crustacean ectoparasites and fish mucus

Fig. 1 Phylogeny of the 21 labrid species included in this study (modified from Kazancıoğlu et al. 2009), with three independent origins of zooplanktivory. The schematic drawings illustrate the three zooplanktivores and their closest included relatives: *Clepticus parrae* (cp) and *Bodianus mesothorax* (bm), *Halichoeres pictus* (hp) and *Halichoeres bivittatus* (hb), *Cirrhilabrus solorensis* (cs), and *Pseudocheilinus evanidus* (pe). The star symbol signifies zooplanktivores



(*Labroides bicolor* and *L. dimidiatus*), and one species feeds on small fish and crustaceans (*Epibulus insidiator*). In order to achieve phylogenetically meaningful comparisons, we sampled species that are phylogenetically proximate to the zooplanktivores in our study, i.e., *Bodianus mesothorax* as sistertaxon to *C. parrae*, *Pseudocheilinus evanidus* as sistertaxon to *C. solorensis*, and *Halichoeres bivittatus* as sistertaxon to *H. pictus* (Fig. 1). Furthermore, representative species of most major subclades within Labridae are present (Hypsigenyines, Scarines, Cheilines, Pseudocheilines, Novaculines, and Julidines). The species sampling allows comparisons of zooplanktivores to close relatives and broader comparison within labrids.

Specimens, measurements, and procedures

We included 21 species of Labridae with a total number of 141 specimens (1–29 individuals per species) for eye morphometrics (Table 1). The size range across individuals is 44–255 mm standard length. The examinations of head proportions and gill raker morphology were largely based on the same specimens, with some minor deviations. For head size and proportions (Table 2), we included 57 specimens of the same 21 species (1–6 individuals per

species). For gill raker morphology (Table 3), we included the same 21 species, with a total number of 40 specimens, (1–4 individuals per species), with a similar size range. All specimens were large juveniles or adults.

We dissected all specimens shortly after euthanizing them with an overdose of MS-222. We measured body weight on a digital scale with 0.05-g accuracy. As additional proxies for body size, we measured standard length, body depth (at the level just anterior to the dorsal fin), and body width (at the level of the opercula) with dial calipers.

Next, we carefully excised the left eyeball, removed attached ocular muscles, and cut the optic nerve close to the sclera. We measured eyeball diameter, axial length, and the largest and smallest pupil diameter (Fig. 2) with a binocular stereomicroscope equipped with an optical micrometer. Then, we removed the iris and cornea, extracted the lens from the eye, and measured the equatorial diameter of the lens (Fig. 2). We repeated this procedure for the right eye.

Fish specimens were subsequently preserved in formalin and then cleared and stained. We quantified skull size and proportions with three different measures. Overall skull size is the area of the triangle defined by the tip of premaxilla, top of supraoccipital, and the posterior end of the

Table 1 Measurements of eye morphology

Species	n	BW	sd	SL	sd	ED	sd	AL	sd	PD1	sd	PD2	sd	LD	sd
<i>Anampses meleagriles</i>	1	7.55	–	77.00	–	5.07	–	3.62	–	2.29	–	2.05	–	1.93	–
<i>Bodianus mesothorax</i>	9	6.37	3.66	64.80	13.35	6.11	0.81	4.53	0.57	3.20	0.35	2.55	0.29	2.38	0.38
<i>Cetoscarus bicolor</i>	3	11.87	8.78	80.67	21.01	6.80	1.07	5.24	0.94	2.88	0.45	2.54	0.36	2.37	0.41
<i>Cheilinus chlorourus</i>	1	22.55	–	86.00	–	7.70	–	5.95	–	3.33	–	2.46	–	2.66	–
<i>Cheilinus fasciatus</i>	1	29.10	–	94.00	–	7.78	–	6.11	–	3.33	–	2.94	–	2.82	–
<i>Cirrhilabrus solorensis</i>	8	4.54	0.81	57.29	2.71	4.78	0.11	3.72	0.15	2.15	0.16	1.81	0.11	1.80	0.10
<i>Clepticus parrae</i>	25	42.99	46.17	102.30	53.02	7.20	2.58	4.95	1.79	3.37	1.14	3.09	1.06	2.91	1.03
<i>Coris gaimard</i>	5	18.72	7.36	105.66	7.46	6.19	0.31	4.58	0.26	2.74	0.12	2.42	0.15	2.29	0.14
<i>Epibulus insidiator</i>	1	15.05	–	81.00	–	6.19	–	4.52	–	2.72	–	2.24	–	2.17	–
<i>Halichoeres bivittatus</i>	29	17.00	12.57	90.35	26.42	5.54	0.93	3.74	0.84	2.36	0.41	2.03	0.36	2.04	0.37
<i>Halichoeres chloropterus</i>	3	2.42	1.09	51.33	8.22	4.18	0.36	3.17	0.36	1.72	0.24	1.37	0.16	1.48	0.24
<i>Halichoeres marginatus</i>	1	11.35	–	82.00	–	5.08	–	3.73	–	2.46	–	2.22	–	1.85	–
<i>Halichoeres pictus</i>	25	5.88	2.68	70.43	12.13	4.94	0.67	3.11	0.62	2.06	0.37	1.89	0.30	1.89	0.26
<i>Hemigymnus melapturus</i>	3	6.75	5.30	57.63	17.56	4.95	0.67	3.70	0.63	2.43	0.36	2.26	0.46	1.95	0.32
<i>Labroides bicolor</i>	3	1.67	0.38	44.79	2.54	3.23	0.10	2.37	0.04	1.66	0.08	1.54	0.06	1.27	0.04
<i>Labroides dimidiatus</i>	3	1.50	0.50	46.83	4.81	3.15	0.19	2.40	0.08	1.44	0.21	1.40	0.17	1.21	0.08
<i>Lachnolaimus maximus</i>	1	401.80	–	255.00	–	19.01	–	14.34	–	8.57	–	7.70	–	7.14	–
<i>Macropharyngodon meleagris</i>	3	8.32	2.02	72.73	5.37	4.87	0.07	3.64	0.17	2.24	0.06	2.01	0.03	1.89	0.02
<i>Novaculichthys taeniourus</i>	5	8.84	8.08	71.08	19.72	4.96	0.86	3.54	0.66	2.21	0.42	2.02	0.44	1.74	0.36
<i>Pseudocheilinus evanidus</i>	8	3.03	1.41	48.71	7.53	4.27	0.47	3.29	0.40	2.10	0.24	1.63	0.21	1.60	0.18
<i>Thalassoma lunare</i>	3	7.35	4.04	70.20	7.92	4.66	0.60	3.68	0.30	2.27	0.26	1.91	0.29	1.80	0.18

BW body weight, AL axial length, ED eye diameter, LD lens diameter, PD1 largest pupil diameter, PD2 smallest pupil diameter, sd standard deviation, SL standard length. Also see Fig. 2

BW in [g], all other measurements in [mm]

Table 2 Measurements of skull proportions

Species	n	BW	sd	SL	sd	Skull area	sd	Anterior facial area	sd	Orbit area	sd	Anterior facial length	sd
<i>Anampes meleagrises</i>	1	7.55	–	77.00	–	127.71	–	20.84	–	23.54	–	8.73	–
<i>Bodianus mesothorax</i>	3	5.82	1.08	67.90	6.41	116.57	15.73	21.43	4.13	30.75	5.19	6.98	0.95
<i>Cetoscarus bicolor</i>	3	11.87	8.78	80.67	21.01	179.84	76.91	37.77	18.09	45.42	14.42	10.84	2.79
<i>Cheilinus chlorourus</i>	1	22.55	–	86.00	–	248.55	–	45.44	–	44.59	–	7.94	–
<i>Cheilinus fasciatus</i>	1	29.10	–	94.00	–	148.92	–	52.58	–	52.81	–	10.60	–
<i>Cirrhitilabrus solorensis</i>	3	3.98	0.98	56.93	4.13	53.86	12.67	7.86	1.65	19.06	2.45	3.44	0.40
<i>Clepticus parrae</i>	6	2.00	0.40	45.92	3.57	39.39	3.76	5.76	0.50	14.19	0.84	3.07	0.16
<i>Coris gaimard</i>	3	21.72	8.57	111.07	7.86	179.89	28.88	37.43	8.93	34.02	10.21	8.73	0.69
<i>Epibulus insidiator</i>	1	15.05	–	81.00	–	210.93	–	62.94	–	40.06	–	9.30	–
<i>Halichoeres bivittatus</i>	3	10.33	1.57	84.33	4.16	95.15	8.12	21.96	0.77	25.41	1.77	7.72	0.09
<i>Halichoeres chloropterus</i>	4	2.94	1.37	55.48	10.66	63.93	18.21	11.92	4.17	17.09	3.87	5.16	1.01
<i>Halichoeres marginatus</i>	1	11.35	–	82.00	–	103.75	–	15.34	–	23.54	–	6.03	–
<i>Halichoeres pictus</i>	5	6.72	4.11	78.14	14.90	83.86	39.07	14.73	7.19	21.36	7.41	5.65	1.47
<i>Hemigymnus melapterus</i>	3	6.75	5.30	57.63	17.56	102.20	60.33	24.84	17.43	25.34	9.70	7.35	3.21
<i>Labroides bicolor</i>	3	1.67	0.38	44.79	2.54	29.44	4.16	5.80	0.24	8.18	0.91	4.71	0.09
<i>Labroides dimidiatus</i>	3	1.50	0.50	46.83	4.81	30.64	7.90	4.32	0.82	8.06	0.82	3.49	0.57
<i>Lachnolaimus maximus</i>	1	401.80	–	255.00	–	2070.71	–	826.63	–	322.01	–	43.00	–
<i>Macropharyngodon meleagris</i>	3	8.32	2.02	72.73	5.37	97.40	6.93	18.61	0.79	20.30	2.52	6.19	0.27
<i>Novaculichthys taenionurus</i>	2	16.33	8.59	90.10	18.24	170.87	70.19	38.55	15.76	32.03	10.04	8.17	1.91
<i>Pseudocheilinus evanidus</i>	4	2.35	1.79	44.78	9.41	51.25	20.52	10.50	5.60	13.11	4.57	4.32	1.47
<i>Thalassoma lunare</i>	3	7.35	4.04	72.73	15.82	85.82	28.73	16.70	6.82	22.56	6.62	6.08	1.15

BW body weight, sd standard deviation, SL standard length

BW in [g], all areas in [mm²]; anterior facial length and SL in [mm]

Table 3 Measurements of gill raker morphology

Species	n	BW	sd	SL	sd	Length	sd	Spacing	sd
<i>Anampses meleagrides</i>	1	7.55	–	77.00	–	0.72	–	0.35	–
<i>Bodianus mesothorax</i>	2	6.43	0.32	71.60	0.00	0.74	0.09	0.45	0.01
<i>Cetoscarus bicolor</i>	2	15.40	8.91	91.00	15.56	0.85	0.14	0.36	0.06
<i>Cheilinus chlorourus</i>	1	22.55	–	86.00	–	1.43	–	1.02	–
<i>Cheilinus fasciatus</i>	1	29.10	–	94.00	–	0.99	–	0.87	–
<i>Cirrhilabrus solorensis</i>	3	3.98	0.98	56.93	4.13	0.52	0.07	0.25	0.04
<i>Clepticus parrae</i>	2	2.33	0.11	48.40	0.71	1.11	0.06	0.22	0.01
<i>Coris gaimard</i>	2	26.60	1.91	113.40	2.55	1.35	0.06	0.73	0.07
<i>Epibulus insidiator</i>	1	15.05	–	81.00	–	1.47	–	0.64	–
<i>Halichoeres bivittatus</i>	3	10.33	1.57	84.33	4.16	0.83	0.07	0.45	0.02
<i>Halichoeres chloropterus</i>	2	3.90	0.85	62.70	7.35	0.63	0.05	0.31	0.00
<i>Halichoeres marginatus</i>	1	11.35	–	82.00	–	0.81	–	0.40	–
<i>Halichoeres pictus</i>	4	5.01	1.77	72.03	6.83	0.94	0.07	0.31	0.01
<i>Hemigymmus melapterus</i>	2	3.88	2.58	49.95	16.19	0.69	0.39	0.30	0.15
<i>Labroides bicolor</i>	2	1.68	0.53	45.39	3.27	0.15	0.01	0.19	0.01
<i>Labroides dimidiatus</i>	2	1.75	0.35	49.60	0.57	0.17	0.01	0.21	0.01
<i>Lachnolaimus maximus</i>	1	401.80	–	255.00	–	2.90	–	2.22	–
<i>Macropharyngodon meleagris</i>	2	8.95	2.40	73.70	7.21	0.53	0.07	0.32	0.00
<i>Novaculichthys taeniourus</i>	2	16.33	8.59	90.10	18.24	1.91	0.43	0.73	0.10
<i>Pseudocheilinus evanidus</i>	2	3.45	2.12	51.55	7.99	0.29	0.07	0.41	0.10
<i>Thalassoma lunare</i>	2	9.58	1.73	81.55	5.87	0.63	0.01	0.35	0.01

BW body weight, *sd* standard deviation, *SL* standard length

BW in [g]; SL, length, and spacing in [mm]

interopercle. Anterior facial region is the area of the triangle defined by tip of premaxilla, anterior orbit margin, and articular-quadrate lower jaw joint. Anterior facial length is the distance from the anterior orbit margin to the tip of the premaxilla. These measurements capture the overall size of jaw structures and mouth (Wainwright et al. 2004). We estimated orbit size, a proxy for eye size (Schmitz 2009), as the area of the ellipse defined by anteroposterior and dorsoventral orbit diameter in cleared and stained specimens.

We removed the first gill arch and assessed size and density of the gill rakers by measuring the length of the three longest rakers on the ceratohyal. Density was measured by counting the number of gill rakers for a given distance along the ceratohyal. We measured the distance from anterior edge of the first gill raker to the anterior edge of the last raker in the segment.

Data analysis

We calculated the mean of measurements from the left and right eye for each individual and calculated species means. We then log₁₀-transformed species averages. Our measure for body size was body mass. We analyzed data in a phylogenetically informed framework, because calculations of

Blomberg's K (Blomberg et al. 2003) indicated that the traits are phylogenetically patterned. We pruned the time-calibrated phylogeny of Kazancioğlu et al. (2009), so that the phylogeny contained only the species we included in this study (Fig. 1). Since *P. evanidus* and *C. solorensis* are not in the phylogenetic analysis of Kazancioğlu et al. (2009), we swapped these species for their close relatives *Pseudocheilinus octotaenia* and *Cirrhilabrus lubbocki*, respectively.

In order to describe the relationships between body size and eyeball dimensions, we followed two approaches. First, we described interspecific and ontogenetic scaling of eyeball diameter against body mass by calculating the regression slope with the standardized major axis (SMA) method. We chose SMA because both independent and dependent variable were measured with error, and SMA slope estimates are more efficient than major axis slope estimates (Warton et al. 2006). Calculations of SMA were implemented in the 'smatr' package (Warton and translated to R by Ormerod 2007) in R 2.11.1. Second, we calculated independent contrasts of the variables (Felsenstein 1985) with the 'ape' package (Paradis et al. 2004) in R 2.11.1 (R Development Core Team 2010). Then, we regressed the dependent variables using SMA and forced the y-intercept to be zero. Furthermore, we explored eye morphology with

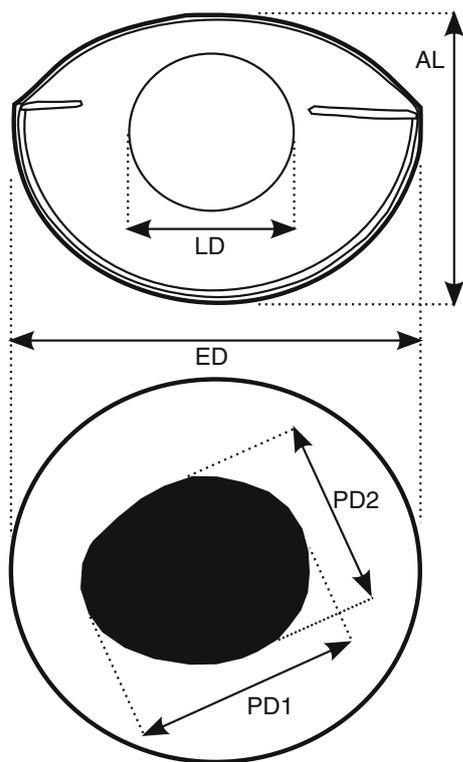


Fig. 2 Simplified drawings of a teleost eyeball illustrating morphological measurements in horizontal cross section (a) and lateral view (b). *AL* axial length, *ED* eyeball diameter, *LD* horizontal lens diameter, *PD1* largest pupil diameter, *PD2* smallest pupil diameter

a phylogenetically informed principal component analysis (Revell 2009) to facilitate the identification of other possible features associated with zooplanktivory. Calculations were implemented in R 2.11.1.

For most subsequent analyses, we were interested in the relative size of the traits. We used size-corrected trait dimensions that accounted for the phylogenetic correlation within our data (Revell 2009). We calculated least-square residuals of eye diameter, gill raker length, and gill raker density on body size in order to test whether zooplanktivorous labrid fishes have larger eyes, and longer and more densely packed gill rakers compared to body size. To test whether zooplanktivorous labrids have a larger lens for given axial length, we calculated residuals of lens diameter on axial length. Finally, we calculated residuals of skull area, anterior facial area, and anterior facial length on orbit area in order to test whether zooplanktivorous labrids have smaller skull features compared to their orbit size. This would make the eyes appear larger.

Residuals alone are insufficient to detect the adaptive significance of morphological features, since they are still phylogeny-dependent. As we were interested in evolutionary changes that happened along the last branch segment leading to a zooplanktivorous species, we approximated evolutionary changes along branch segments

by calculating point estimates of the rate of morphological evolution. For each trait (relative eyeball diameter, relative lens diameter, scores on principal components 2 and 3, relative skull proportions, and relative gill raker length and spacing), we first calculated maximum likelihood estimates for all ancestral states with the ‘geiger’ package (Harmon et al. 2008) in R 2.11.1. Then, we calculated standardized changes along each branch by subtracting ancestral from descendant state value and divided this value by branch length of the segment. Trait change divided by time (branch length) is equal to rate of change. This approach is similar to a method developed by McPeck (1995).

In order to test for differences between the means of phylogenetic residuals and standardized changes of zooplanktivores and non-zooplanktivores, we performed Welch Two Sample *t* tests and permutation tests (10,000 iterations). The permutation distribution results from repeated drawing of samples (with *n* equal to the number of zooplanktivores) from all observations (zooplanktivores and non-zooplanktivores). The difference of the means of the simulated zooplanktivores and non-zooplanktivores is calculated for all iterations. Then, the observed difference for the actual species is compared to the permutation distribution. We provide an approximate *P* value (rounded to second decimal) for the permutation tests, because the *P* values vary slightly for repeated tests. Both the *t* test and permutation test (‘DAAG’ package; Maindonald and Braun 2009) were implemented in R.2.11.1.

Results

Scaling of eye dimensions

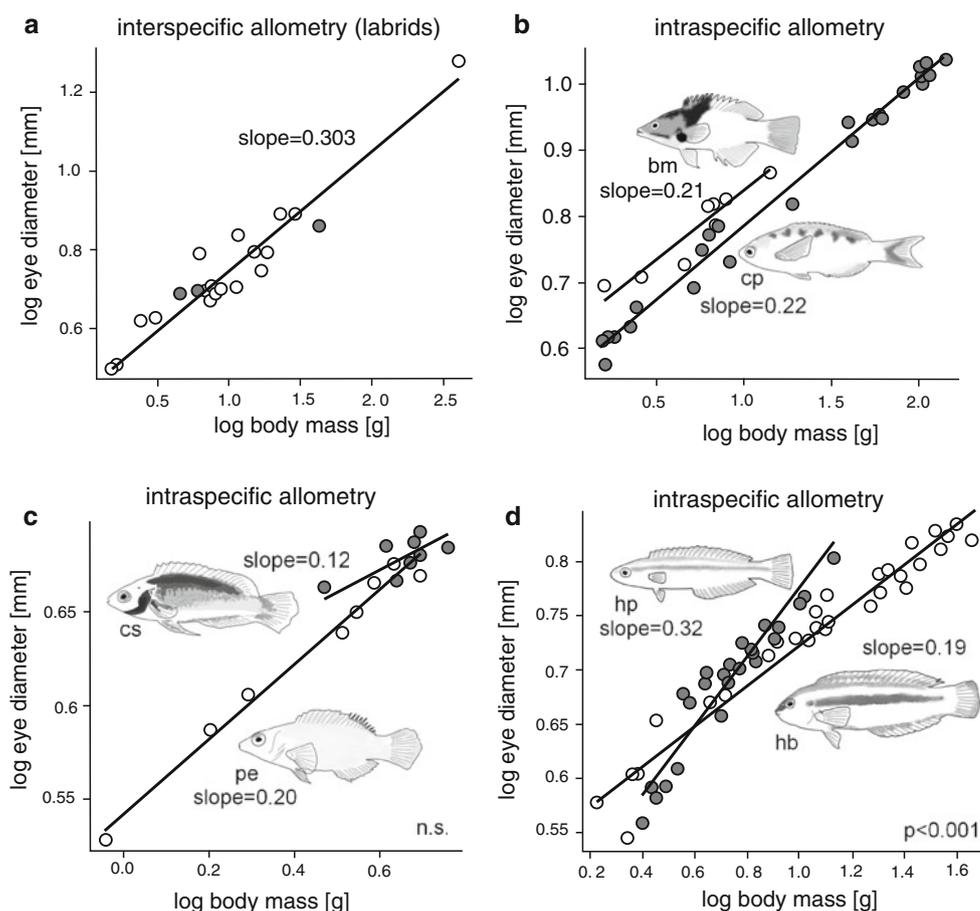
Eyeball diameter scales with negative allometry to body mass. The slope of the regression of the independent contrasts of eyeball diameter on contrasts of body mass is 0.26, which is different from 0.33 ($P = 0.021$), the expected slope for isometry. The slope of the phylogenetically uninformed regression of eye diameter on body mass is not different from 0.33 (slope = 0.303; Table 1; Fig. 3a).

We find similar patterns for ontogenetic scaling of eye diameter with body mass of zooplanktivores and their sister species (Fig. 3b–d). Regression slopes for *C. parrae* (slope = 0.22) vs. *B. mesothorax* (slope = 0.21) and *C. solorensis* (slope = 0.12) vs. *P. evanidus* (slope = 0.20) are not different. In contrast, eye diameter of *H. pictus* scales faster (slope = 0.32) with body mass than eye diameter of *H. bivittatus* (slope = 0.19, $P < 0.001$).

Shape of the eye and its components (Table 1) scale isometrically with an increase in body size. The independent contrasts of axial length (slope = 1.025), largest pupil diameter (slope = 0.994), smallest pupil diameter

Fig. 3 Scaling of eye diameter with body mass in labrids.

a Plot of log-transformed eye diameter against log-transformed body mass of 21 labrid species. The other panels illustrate ontogenetic scaling of eye diameter with body mass: **b** *Clepticus parrae* (cp) and *Bodianus mesothorax* (bm), **c** *Cirrhilabrus solorensis* (cs) and *Pseudocheilinus evanidus* (pe), **d** *Halichoeres pictus* (hp) and *Halichoeres bivittatus* (hb). Regression slopes for *C. parrae* vs. *B. mesothorax*, and *C. solorensis* vs. *P. evanidus* are not different. In contrast, eye diameter of *H. pictus* scales faster with body mass than eye diameter of *H. bivittatus*. Gray circles are zooplanktivores, open circles non-planktivores



(slope = 1.043), and lens diameter (slope = 0.999) scale isometrically and are tightly correlated with contrasts of eyeball diameter (P value for slope = 0 is smaller than 0.001 in all cases).

Eye size

Zooplanktivorous labrids do not have larger eyes than non-planktivores. The histogram of the phylogenetic residuals of eye diameter on body size reveals that all three zooplanktivores are in the middle of the overall distribution of Labridae (Fig. 4a). We did not find differences between the means of zooplanktivore and non-planktivore residuals. *Lachnolaimus maximus*, a benthic forager on invertebrates, has the largest relative eye diameter, whereas *H. bivittatus*, another benthic forager, has the smallest.

Branches leading to zooplanktivorous labrids are not associated with large increases of relative eye diameter (Fig. 4b). The mean of the three zooplanktivore lineages analyzed in this study is not different from the remaining species. The changes associated with zooplanktivore branches are widely scattered throughout the labrid distribution. In fact, some of the largest increases and decreases in relative eyeball diameter appear on branches leading to

zooplanktivorous species (*H. pictus* and *C. parrae*, respectively). Finally, the branch leading to *C. solorensis* has almost no change in relative eye diameter.

Lens size

Two of the three zooplanktivores (*C. parrae* and *H. pictus*) have the largest lenses relative to axial length among the labrids in this study. The residual of *C. solorensis* falls amidst the distribution of other labrids in the histogram of the phylogenetic residuals of lens diameter on axial length, and the mean of all zooplanktivore residuals is not different from the non-planktivores ($P = 0.266$). However, permutation tests yield a significant result ($P \sim 0.01$; we provide an approximate P value for the permutation tests, because the P values vary slightly for repeated tests).

Two of the three branches leading to zooplanktivores show large increases in relative lens size (Fig. 4c). The branches leading to *H. pictus* and *C. parrae* in fact have the largest and fourth largest changes of the entire labrid distribution. The second largest increase belongs to *L. bicolor*. The tip leading to *C. solorensis* features almost no change, and thus the mean of the changes associated with all three zooplanktivore branches is not different from all other

Fig. 4 Summary of the findings on relative eyeball size, lens size, and head proportions in labrids. **a** Residuals of eye diameter on body size. **b** Standardized changes (i.e., point estimates of the magnitude of morphological evolution) in relative eye diameter. **c** Standardized changes in lens diameter relative to axial length. **d** Standardized changes in anterior facial area relative to orbit area. *Gray bars* are zooplanktivores, *white bars* are non-zooplanktivores

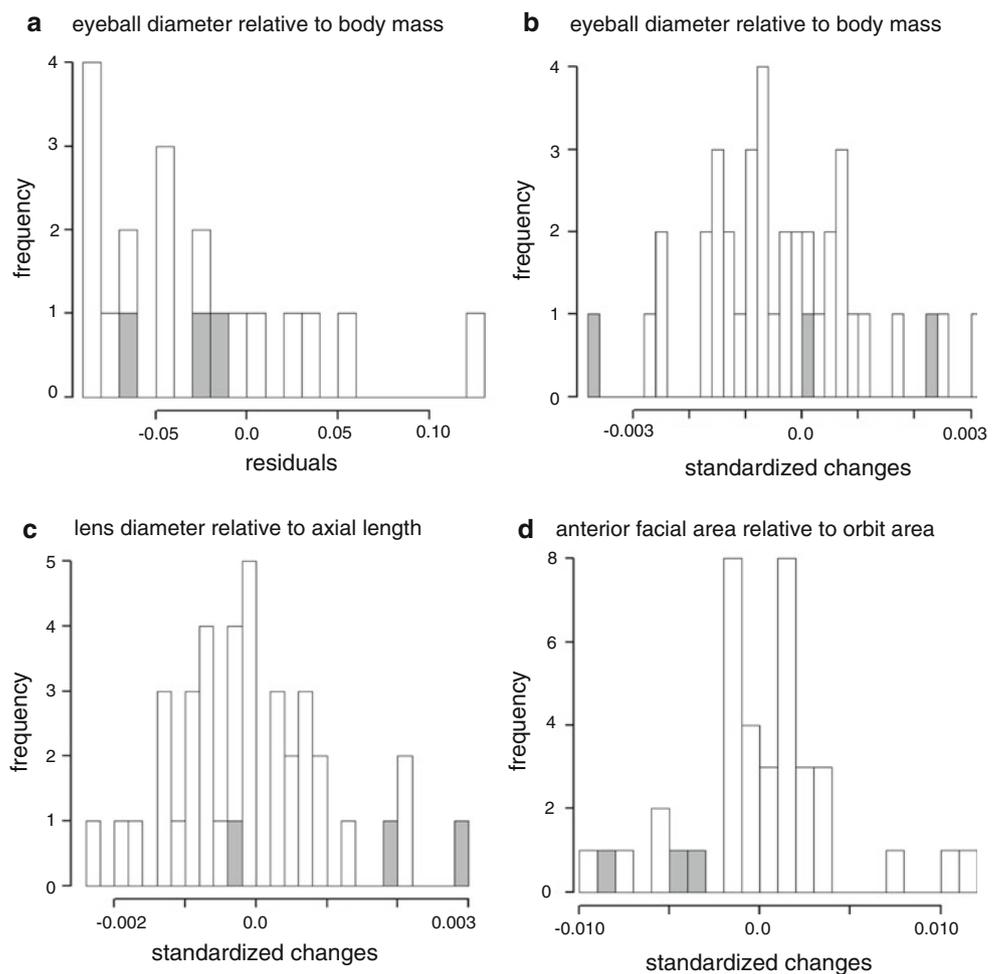


Table 4 Loadings on principal components (PC)

	PC1	PC2	PC3	PC4	PC5
Eye diameter (ED)	0.99	0.12	-0.05	0.05	0.05
Axial length (AL)	0.98	0.19	0.05	-0.09	-0.01
Largest pupil diameter (PD1)	0.98	-0.11	0.14	0.06	0.00
Smallest pupil diameter (PD2)	0.97	-0.22	-0.06	-0.07	0.01
Lens diameter (LD)	0.99	0.02	-0.09	0.06	-0.05
Explained variance [%]	96.47	2.23	0.73	0.44	0.12

branches ($P = 0.1958$). Again, permutation tests indicate overall significant differences of the means in planktivores and non-planktivores ($P \sim 0.01$).

Skull proportions

We analyzed the size of the head and parts of the head in comparison to orbit size, a proxy for eye diameter (Table 2). Zooplanktivores may have shorter anterior facial length (t test, $P = 0.099$) or a smaller anterior facial region (t test, $P = 0.074$) than non-planktivorous labrids. The

non-significance is potentially an effect of lack of power of the tests, as permutation tests indicate significant differences (anterior facial length: $P \sim 0.01$, anterior facial area: $P \sim 0.01$). A stronger pattern emerges when comparing standardized changes: zooplanktivores have a large decrease in anterior facial region (t test, $P = 0.051$, Fig. 4d) and anterior facial length (t test, $P = 0.001$). Permutation tests yielded similar support (anterior facial region: $P \sim 0.02$, anterior facial length: $P \sim 0.03$).

Phylogenetic principal component analysis of eyeball dimensions

We performed a phylogenetically informed principal component analysis on the log-transformed eyeball variables (eye diameter, axial length, largest and smallest pupil diameter, and lens diameter). Eye shape is not very variable: principal component (PC) 1, a size axis, explains 96.47% of the variation in the data set (Table 4); 3.53% of the variation can be ascribed to variation in shape alone (PC 2: 2.23%, PC 3: 0.73%, PC 4: 0.44%, PC 5: 0.12%). PC 2 has negative loading on largest and smallest pupil

diameter (-0.11 and -0.22 , respectively), and positive loading on eyeball diameter (0.12), axial length (0.19), and lens diameter (0.02), and thus we interpret PC 2 as a measure of relative pupil size. A small value for PC 2 translates into a relatively large pupil. PC 3 has positive loading on largest pupil diameter (0.14) and negative loading on smallest pupil diameter (-0.06) and lens diameter (-0.09). Therefore, we tentatively interpret this shape axis as a measure of pupil ellipticity. A large value for PC 3 relates to a large and strongly elliptical pupil, in combination with a small lens diameter.

The plot of PC 3 against PC 2 demonstrates that two zooplanktivores, namely *C. parrae* and *H. pictus*, may occupy a different region of morphospace than other labrids (Fig. 5). Both species have low scores on PC 2 and especially PC 3. All three zooplanktivores, including *C. solorensis*, have much lower scores on PC3 than their sister species (*B. mesothorax*, *P. evanidus*, and *H. bivittatus*, respectively). In fact, the mean of zooplanktivore scores on PC3 is lower than for non-planktivores, as indicated by permutation tests ($P \sim 0.03$), even though *C. solorensis* plots in the middle of the labrid distribution (Fig. 5). A similar result is found when standardized changes are

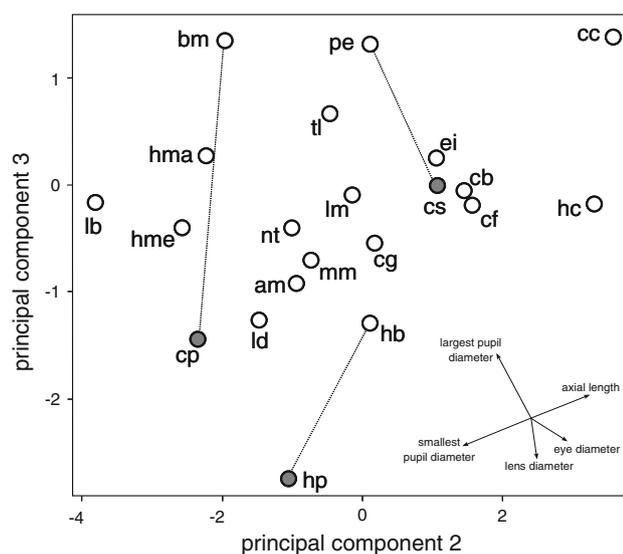


Fig. 5 Bivariate plot of principal components 2 and 3. Gray circles are zooplanktivores, open circles non-zooplanktivores. Zooplanktivores and their sister species are connected by dashed lines. The vector plot in the bottom right corner illustrates direction and magnitude of loadings of the variables on principal components 2 and 3. am *Anampses meleagrises*, bm *Bodianus mesothorax*, cb, *Cetoscarus bicolor*, cc *Cheilinus chlorourus*, cf *Cheilinus fasciatus*, cg *Coris gaimard*, cp *Clepticus parrae*, cs *Cirrhilabrus solorensis*, ei *Epibulus insidiator*, hb *Halichoeres bivittatus*, hc *Halichoeres chloroapterus*, hma *Halichoeres marginatus*, hme *Hemigymnus melapterus*, lb *Labroides bicolor*, ld *Labroides dimidiatus*, lm *Lachnolaimus maximus*, mm *Macropharyngodon meleagris*, nt *Novaculichthys taeniourus*, pe *Pseudocheilinus evanidus*, tl *Thalassoma lunare*

considered. Permutation tests point to differences between zooplanktivore transitions and others ($P \sim 0.01$).

Cheilinus chlorourus, *C. fasciatus*, *E. insidiator*, and *Cetoscarus bicolor* have large scores for PC 2 (i.e., relatively small pupil), which may indicate that the clade composed of cheilines and scarines (Fig. 1) occupies a distinct area in eyeball morphospace. However, note that the julidine *H. chloroapterus* also has a large score on PC 2.

Size and density of gill rakers

Zooplanktivorous labrids may have longer gill rakers than others, but they are not spaced closer together, i.e., their density is not higher (Table 3). *C. parrae* and *H. pictus* have the largest and fourth largest relative gill raker length of all sampled labrids, whereas *C. solorensis* plots near the middle of the distribution. The mean of the zooplanktivore residuals is not different from the mean of other labrids (t test, $P = 0.22$). Permutation tests yielded better support ($P \sim 0.01$).

However, we observe a stronger pattern when comparing the standardized changes in relative gill raker length. The branches leading to *C. parrae* and *H. pictus* display large increases in length, whereas the branch leading to *C. solorensis* features an intermediate increase (Fig. 6). The mean of all three changes associated with zooplanktivore lineages is different from that of all non-planktivores (t test, $P = 0.048$; permutation tests $P \sim 0.01$).

The density of gill rakers does not differ between zooplanktivores and non-planktivores, whether examining residuals or standardized changes.

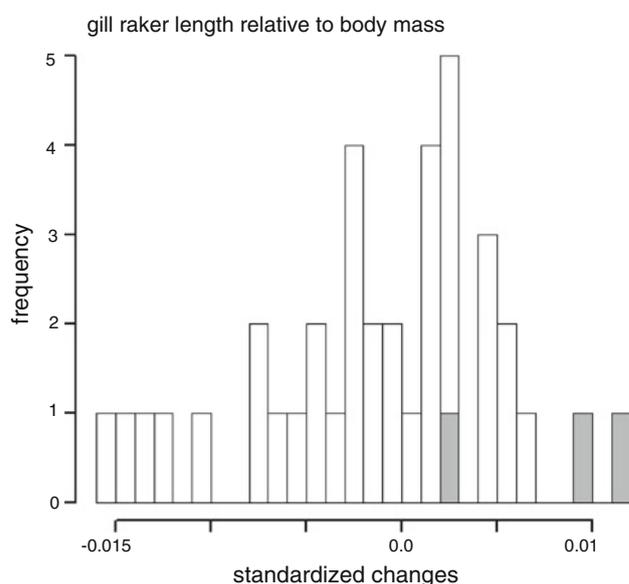


Fig. 6 Histogram of the standardized changes in gill raker length relative to body mass. Gray bars are zooplanktivores, white bars non-zooplanktivores

Discussion

Zooplanktivory evolved repeatedly during the latest phase of trophic innovations in labrid fishes (Cowman et al. 2009), and we tested whether transitions to this highly specialized feeding mode are linked with changes in morphology of the eye and skull. We found little support for the hypothesis that zooplanktivorous labrids have bigger eyes. However, two of the three zooplanktivores (*C. parrae* and *H. pictus*) show a suite of other morphological features that may reflect higher visual acuity (larger lens) and improved handling of zooplankton (longer gill rakers). The third zooplanktivore (*C. solorensis*) lacks all predicted adaptations for zooplanktivory.

The large-eye hypothesis was posed under the assumption that different feeding types require different visual abilities (Walls 1942). Highly selective visual foragers such as planktivores feeding on small prey may need better visual performance than visually non-selective foragers such as herbivores or detritivores. In fact, it is difficult to rank species according to their need for visual acuity. Zooplanktivores are expected to have excellent visual acuity because they feed on small, quickly drifting organisms with low contrast to their background (Johnsen 2001). The food items of other species are generally believed to be easier to detect than zooplankton. However, most labrids appear to use strong visual acuity in their feeding behavior, many to detect small animal prey, the ancestral feeding mode of labrids (Cowman et al. 2009). One potential explanation for the absence of larger eyes in zooplanktivorous labrids is that feeding in most labrids involves detecting small prey in a complex habitat, and thus, most labrids experience strong selection on visual acuity. The difficulty with this explanation is that the zooplanktivores in our study do show other predicted modifications of the eyes that are consistent with enhanced visual acuity.

Our inability to find evidence of larger eyes in zooplanktivores is slightly complicated by differences between species in the ontogenetic scaling of eye diameter. We compared regression slopes of the three zooplanktivores and their closest relatives in our analysis. The slopes of two species pairs (*C. parrae* and *B. mesothorax*; *C. solorensis* and *P. evanidus*) are the same, and thus comparisons of relative size are independent from body mass of the examined specimens. A more complex result is found in *H. pictus* and *H. bivittatus*. Eye diameter of *H. pictus* increases faster with body mass than in the non-planktivore *H. bivittatus*. Very small individuals of *H. pictus* have smaller eyes than *H. bivittatus*, whereas very large specimens of *H. pictus* have larger eyes. Thus, the difference in eye diameter between these species is body size specific. Our samples of *H. pictus* ranged from terminal phase males to small but reproductive initial phase fish.

We found evidence that transitions to zooplanktivory have influenced the evolution of eye shape. The size of the lens compared to the axial length of the eye was markedly enlarged in two of three sampled zooplanktivore lineages (*C. parrae* and *H. pictus*), confirming the prediction from physiological optics. In contrast, the relative size of the lens of *C. solorensis* was average for labrids. The lineage to *L. bicolor* is characterized by the second largest increase of relative lens size within labrids. *L. bicolor* feeds on small-sized parasites on other fish and thus could potentially benefit from high visual acuity as well. The lineage to *L. dimidiatus*, also an ectoparasite feeder, does not show a large increase, however, so the adaptive significance of an enlarged lens in *L. bicolor* is ambiguous.

Pupil shape also was associated with shifts to zooplanktivory, in combination with large lens size. In particular, *C. parrae* and *H. pictus* have lower scores on PC 3, indicating a round pupil combined with a large lens. *C. solorensis* has average scores on PC 3 although the pupil is rounder than its close relative, *P. evanidus*. Pupil shape is not directly related to visual acuity, yet is important for focusing on nearby objects. A strongly elliptical pupil correlates with the aphakic gap, in which the lens can be moved to focus on close objects in that direction (Sivak 1978; Fernald and Wright 1985). Zooplanktivores search the water column for prey, and their area of visual interest is not confined to a narrow frontal field. Thus, their particularly round pupil shape may represent an adaptation to search a three-dimensional body of water for food. To our knowledge, this is the first report of increases in lens size and pupil roundness in association with zooplanktivory.

Zooplanktivorous labrids had longer gill rakers than the other species, supporting the prediction from functional morphology, yet they did not have more closely packed gill rakers. It is interesting that the increase of relative gill raker length in *C. solorensis* is minimal, similar to the pattern we observed regarding relative lens size and PC 3. Species of *Cirrhilabrus* are considered to be typical zooplanktivores, feeding in the open water above coral reefs where they visually pick plankton. In addition, their gut contents were found to consist almost exclusively of zooplankton (Gerber and Marshall 1974). The *Cirrhilabrus* group has been shown to exhibit locomotor adaptations for the midwater habitat (Wainwright et al. 2002) and musculoskeletal modifications of the jaws consistent with feeding on zooplankton (Wainwright et al. 2004). However, *Cirrhilabrus* lacks long gill rakers and other potential zooplanktivore adaptations such as large lenses and round pupils. A possible visual adaptation of *Cirrhilabrus* is the presence of a divided pupil, which has been hypothesized to function as a ‘magnifier’ to detect small prey (Baensch and Debelius 1994). The optical significance of the divided pupil is unknown, and thus this

hypothesis cannot be tested at this point. The divided cornea is also present in the zooplanktivorous *Paracheilinus* but also in the benthic foragers *Pseudocheilinus*, *Pseudocheilinos*, and *Pteragogus* (Randall and Lubbock 1981). Hence, this feature may not be an adaptation to zooplanktivory in a strict sense. A final possibility is that *Cirrhilabrus* species are not the exclusive zooplanktivores that they are often portrayed to be. We have observed that *Cirrhilabrus* caught in the wild often have considerable amounts of amorphous organic matter in their guts, consistent with consumption of marine snow and other aggregations of detritus and microbes. Perhaps long gill rakers would hinder handling of detritus, tending to become entangled in it.

Comparative analyses of eye diameter in transitions to zooplanktivory can potentially be confounded with the influence of water depth and nocturnality, both of which expose the organism to low light levels (Lythgoe 1979). Nocturnal and mesopelagic fish tend to have relatively large eyes (Marshall 1979; Warrant 2004; Warrant and Lockett 2004), a pattern supported in recent quantitative analyses (Ingram and Shurin 2009; Goatley and Bellwood 2009). The visual environment of labrids is characterized by clear, well-illuminated ocean waters, since most species inhabit tropical reefs (Lythgoe 1979). Labrids are diurnal (Randall 1967) and occur in the photic zone (Randall 1983, 2005; Westneat and Alfaro 2005). Some species, for example *Bodianus* ssp. (Weitkamp and Sullivan 1939; Gomon 2001, 2006; Mundy 2005) and *Cirrhilabrus bathyphilus* (Randall and Nagareda 2002), may also migrate into deeper waters characterized by dim light, but do not seem to consistently inhabit this zone. None of the species that we investigated occur in deep-water. Light levels may also vary with microhabitat. For example, reef crevices, caves, and areas of dense coral rubble are less illuminated than other parts of the reef. It is possible that species specializing on these dark microhabitats have large eyes. Yet in all, light levels are unlikely to have a major influence on the evolution of eyeball morphology in labrids.

Although a number of previous studies have concluded that zooplanktivores have enlarged eyes (McPhail 1984; Strauss 1984; Baumgartner et al. 1988; Pankhurst 1989; Hulsey et al. 2007; Cooper and Westneat 2009; Goatley and Bellwood, 2009), at least one previous analysis of *Sebastes* rockfishes did not (Ingram and Shurin 2009). It appears then that enlarged eyes are not a universal adaptive visual specialization of zooplanktivores. Perhaps this should not be too surprising as convergent evolution virtually never produces identical phenotypes, both because the ancestral phenotype affects the response to selection and because in complex systems there can be multiple solutions to the same functional challenge. We did find modifications of labrid eye shape that are consistent with

an increase in visual performance during transitions to planktivory, but these measurements have not been reported yet in other groups, so their generality is unknown. It remains a goal of future research to determine the phylogenetic consistency of the evolutionary response of the visual system in coral reef zooplanktivores.

Our inability to find strong evidence of enlarged eyes in zooplanktivores coupled with the finding that these species have reduced facial structures suggests that the combination of these traits may give the impression of larger eyes. We feel that this result should raise a cautionary note about the patterns that have been reported in other groups. While some studies have shown that zooplanktivores have larger eyes relative to body size (e.g., McPhail 1984; Goatley and Bellwood 2009), other studies either report eye diameter changes relative to head length (Hulsey et al. 2007) or only include eye diameter as part of a larger multivariate construct (Strauss 1984; Cooper and Westneat 2009). Few studies account for phylogeny in their analyses.

Visual performance is a classically complex functional system, being an integrated result of multiple underlying components, including optics, retina, and neurology. In addition to the traits addressed in this study, visual performance of zooplanktivores may also be associated with ganglion cell densities (e.g., Collin and Pettigrew 1989) and sensitivity to ultraviolet light (Siebeck and Marshall 2007). Other examples of the potential for diversity in response to visual performance include work with larval reef fishes in which light sensitivity changes throughout early ontogeny independent of eye shape (Job and Bellwood 2000), indicating that other components of the visual system were modified. We predicted morphological changes to improve acuity based on physiological optics, assuming that the retina and neurological mechanism are the same. It seems clear that there is potential for diversity in the response of different lineages to the challenges of zooplanktivory. To conclude, it will be important to repeat this study on other groups of fishes, addressing multiple components of the visual system. Such analyses will provide us with a more integrative understanding of the evolution of the visual system in response to evolutionary transitions to zooplanktivory.

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References

- Alfaro M, Brock CD, Banbury B, Wainwright PC (2009) Does evolutionary innovation in pharyngeal jaws lead to rapid lineage diversification in labrid fishes? *BMC Evol Biol* 9:255
- Baensch HA, Debelius H (1994) Baensch marine atlas, volume 1. Microcosm, Shelburne
- Barel CDN (1982) Towards a constructional morphology of cichlid fishes. *Neth J Zool* 33:357–424
- Baumgartner HA, Bell MA, Weiberg PH (1988) Body form differences between the Enos Lake species pair of threespine sticklebacks (*Gasterosteus aculeatus* complex). *Can J Zool* 66:467–474
- Blomberg SP, Garland T Jr, Ives AR (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more liable. *Evolution* 57:717–745
- Collin SP, Pettigrew JD (1989) Quantitative comparison of the limits of visual spatial resolution set by the ganglion cell layer in twelve species of reef teleosts. *Brain Behav Evol* 34:184–192
- Cooper WJ, Westneat MW (2009) Form and function of damselfish skulls: rapid and repeated evolution into a limited number of trophic niches. *BMC Evol Biol* 9:24
- Cowman, Bellwood DR, van Herwerden L (2009) Dating the evolutionary origins of wrasse lineages (Labridae) and the rise of trophic novelty on coral reefs. *Mol Phylogenet Evol* 52:621–631
- Davis WP, Birdsong RS (1973) Coral reef fishes which forage in the water column. *Helgol Wiss Meeresunters* 24:292–306
- Douglas RH, Hawryshyn CW (1990) Behavioral studies of fish vision: an analysis of visual capabilities. In: Douglas RH, Djamgoz MBA (eds) *The visual system of fish*. Chapman and Hall, London, pp 373–418
- Drenner RW, Mummert JR, deNoyelles F Jr, Kettle D (1984) Selective particle ingestion by a filter-feeding fish and its impact on phytoplankton community structure. *Limnol Oceanogr* 29:941–948
- Dullemeijer P, Barel CDN (1977) Functional morphology and evolution. In: Hecht M, Goody P, Hecht B (eds) *Major patterns in vertebrate evolution*. NATO Adv Study Inst Ser A 14, pp 83–117
- Felsenstein J (1985) Phylogenies and the comparative method. *Am Nat* 125:1–15
- Fernald RD (1990) The optical system of fishes. In: Douglas RH, Djamgoz MBA (eds) *The visual system of fish*. Chapman and Hall, London, pp 45–62
- Fernald RD, Wright SE (1985) Growth of the visual system in the African cichlid fish, *Haplochromis burtoni*. *Vision Res* 25:163–170
- Fryer G, Iles TD (1972) The cichlid fishes of the Great Lakes of Africa: their biology and evolution. Oliver and Boyd, Edinburgh
- Gerber RP, Marshall N (1974) Ingestion of detritus by the lagoon pelagic community at Eniwetok Atoll. *Limnol Oceanogr* 19:815–824
- Goatley CHR, Bellwood D (2009) Morphological structure in a reef fish assemblage. *Coral Reefs* 28:449–457
- Gomon MF (2001) Descriptions of two new species of *Bodianus* (Perciformes: Labridae) from Australasian waters. *N Z J Zool* 28:407–416
- Gomon MF (2006) A revision of the labrid fish genus *Bodianus* with descriptions of eight new species. *Rec Aust Mus Suppl* 30:1–133
- Hairston NG, Li KT, Easter SS (1982) Fish vision and the detection of planktonic prey. *Science* 218:1240–1242
- Harmon LJ, Weir JT, Brock CD, Glor RE, Challenger W (2008) GEIGER: investigating evolutionary radiations. *Bioinformatics* 24:129–131
- Hart PJB, Gill AB (1994) Evolution of foraging behavior in the threespine stickleback. In: Bell MA, Foster SA (eds) *The evolutionary biology of the threespine stickleback*. Oxford University Press, Oxford
- Hobson ES (1991) Trophic relationships of fishes specialized to feed on zooplankters above coral reefs. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, San Diego, pp 69–95
- Hobson ES, Chess JR (1976) Trophic interactions among fishes and zooplankters nearshore at Santa Catalina Island, California. *Fish Bull* 74:567–598
- Hobson ES, Chess JR (1978) Trophic relationships among fishes and plankton in the lagoon at Enewetak Atoll, Marshall Islands. *Fish Bull* 76:133–153
- Hughes A (1977) The topography of vision in mammals of contrasting life style: comparative optics and retinal organisation. In: Crescitelli F (ed) *The visual system in vertebrates*. Springer-Verlag, Berlin, Heidelberg, New York, pp 613–756
- Hulsey CD, Mims MC, Streebman JT (2007) Do constructional constraints influence cichlid craniofacial diversification? *Proc R Soc B* 274:1867–1875
- Hung GK, Ciuffreda KJ (2002) *Models of the visual system*. Springer, Berlin, Heidelberg, New York
- Ingram T, Shurin JB (2009) Trait-based assembly and phylogenetic structure in northeast Pacific rockfish assemblage. *Ecology* 90:2444–2453
- Job SD, Bellwood DR (2000) Light sensitivity in larval fishes: implications for vertical zonation in the pelagic zone. *Limnol Oceanogr* 45:362–371
- Johnsen S (2001) Hidden in plain sight: the ecology and physiology of organismal transparency. *Biol Bull* 201:301–318
- Kassam DD, Adams DC, Ambali AJD, Yamaoka K (2003) Body shape variation in relation to resource partitioning within cichlid trophic guilds coexisting along the rocky shore of Lake Malawi. *Anim Biol* 53:59–70
- Kazancioğlu E, Near TJ, Hanel R, Wainwright PC (2009) Influence of sexual selection and feeding functional morphology on diversification rate of parrotfishes (Scaridae). *Proc R Soc, B* 276:3439–3446
- Kiltie RA (2000) Scaling of visual acuity with body size in mammals and birds. *Funct Ecol* 14:226–234
- Kröger RHH, Fritsches KA, Warrant EJ (2009) Lens optical properties in the eyes of large marine predatory teleosts. *J Comp Physiol A* 195:175–182
- Land MF (1981) Optics and vision in invertebrates. In: Land MF, Laughlin SB, Naessel DR, Strausfeld NJ, Waterman TH (eds) *Comparative physiology and evolution of vision in invertebrates B: invertebrate visual centers and behavior I*. Springer-Verlag, Berlin, Heidelberg, New York, pp 471–592
- Land MF, Nilsson D-E (2002) *Animal eyes*. Oxford University Press, Oxford
- Langeland A, Nøst T (1995) Gill raker structure and selective predation on zooplankton by particulate feeding fish. *J Fish Biol* 47:719–732
- Langerhans RB, Layman CA, Langerhans AK, Dewitt TJ (2003) Habitat-associated morphological divergence in two Neotropical fish species. *Biol J Linn Soc* 80:689–698
- Loew ER, McFarland WN (1990) The underwater visual environment. In: Douglas RH, Djamgoz MBA (eds) *The visual system of fish*. Chapman and Hall, London, pp 1–43
- Lythgoe JN (1979) *The ecology of vision*. Clarendon Press, Oxford
- Magnuson JJ, Heitz JG (1971) Gill raker apparatus and food selectivity among mackerels, tunas, and dolphins. *Fish Bull* 69:361–370
- Maindonald J, Braun WJ (2009) DAAG: data analysis and graphics data and functions. R package version 1.01. <http://CRAN.R-project.org/package=DAAG>

- Marshall NB (1979) Developments in deep-sea biology. Blandford Press, Poole, Dorset
- McPeck MA (1995) Testing hypotheses about evolutionary change on single branches of a phylogeny using evolutionary contrasts. *Am Nat* 145:686–703
- McPhail JD (1984) Ecology and evolution of sympatric sticklebacks (*Gasterosteus*): morphological and genetic evidence for a species pair in Enos Lake, British Columbia. *Can J Zool* 62:1402–1408
- Miller WH (1979) Intraocular filters. In: Autrum H (ed) Comparative physiology and evolution of vision in invertebrates A: invertebrate photoreceptors. Springer-Verlag, Berlin, Heidelberg, New York, pp 69–143
- Motta PJ (1988) Functional morphology of the feeding apparatus of ten species of Pacific butterflyfishes (Perciformes, Chaetodontidae): an ecomorphological approach. *Environ Biol Fish* 22: 39–67
- Mundy BC (2005) Checklist of the fishes of the Hawaiian Archipelago. *Bishop Mus Bull Zool* 6:1–704
- Pankhurst NW (1989) The relationship of ocular morphology to feeding modes and activity periods in shallow marine teleosts from New Zealand. *Environ Biol Fishes* 26:201–211
- Paradis E, Claude J, Strimmer K (2004) APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20:289–290
- Parenti P, Randall JE (2000) An annotated checklist of the species of the labroid fish families Labridae and Scaridae. *Ichthyol Bull JLB Smith Inst Ichthyol* 68:1–97
- R Development Core Team (2010) R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>
- Randall JE (1967) Food habits of reef fishes of the West Indies. *Stud Trop Oceanogr* 5:655–847
- Randall JE (1983) Caribbean reef fishes. TFH Publications, Neptune City, NJ
- Randall JE (2005) Reef and shore fishes of the South Pacific. University of Hawaii Press, Honolulu
- Randall JE, Lubbock R (1981) Labrid fishes of the genus *Paracheilinus*, with descriptions of three new species from the Philippines. *Jpn J Ichthyol* 28:19–30
- Randall JE, Nagareda BH (2002) *Cirrhilabrus bathyphilus*, a new deep-dwelling labrid fish from the Coral Sea. *Cybiurn* 26:123–127
- Revell LJ (2009) Size-correction and principal components for interspecific comparative studies. *Evolution* 63:3258–3268
- Robinson BW, Parsons KJ (2002) Changing times, spaces and faces: tests and implications of adaptive morphological plasticity in the fishes of northern postglacial lakes. *Can J Fish Aquat Sci* 59: 1819–1833
- Schluter D (1993) Adaptive radiation in sticklebacks: size, shape and habitat use efficiency. *Ecology* 74:699–709
- Schmitz L (2009) Quantitative estimates of visual performance features in fossil birds. *J Morph* 270:759–773
- Schmitz L, Motani R (2010) Morphological differences between the eyeballs of nocturnal and diurnal amniotes revisited from optical perspectives of visual environments. *Vision Res* 50:936–946
- Siebeck UE, Marshall NJ (2007) Potential ultraviolet vision in pre-settlement larvae and settled reef fish—a comparison across 23 families. *Vision Res* 47:2337–2352
- Sivak JG (1978) The functional significance of the aphakic space of the fish eye. *Can J Zool* 56:513–516
- Sivak JG (1990) Optical variability in the fish lens. In: Douglas RH, Djamgoz MBA (eds) The visual system of fish. Chapman and Hall, London, pp 63–108
- Strauss RE (1984) Allometry and functional feeding morphology in haplochromine cichlids. In: Echelle AA, Kornfield I (eds) Evolution of fish species flocks. Univ Maine Press, ME, pp 217–230
- Wainwright PC (1988) Morphology and ecology: the functional basis of feeding constraints in Caribbean labrid fishes. *Ecology* 69:635–645
- Wainwright PC, Bellwood DR (2002) Ecomorphology of feeding in coral reef fishes. In: Sale PF (ed) Coral reef fishes. Dynamics and diversity in a complex ecosystem. Academic Press, San Diego, pp 33–55
- Wainwright PC, Richard BA (1995) Predicting patterns of prey use from morphology of fishes. *Env Biol Fish* 44:97–113
- Wainwright PC, Bellwood DR, Westneat MW (2002) Ecomorphology of locomotion in labrid fishes. *Environ Biol Fish* 65:47–62
- Wainwright PC, Bellwood DR, Westneat MW, Grubich JR, Hoey AS (2004) A functional morphospace for the skull of labrid fishes: patterns of diversity in a complex biomechanical system. *Biol J Linn Soc* 82:1–25
- Walls GL (1942) The vertebrate eye and its adaptive radiation. Hafner Pub Co, New York
- Warrant EJ (2004) Vision in the dimmest habitats on earth. *J Comp Physiol A* 190:765–789
- Warrant EJ, Lockett NA (2004) Vision in the deep sea. *Biol Rev* 79: 671–712
- Warton D, and translated to R by Ormerod J (2007). smatr: (standardised) major axis estimation and testing routines. R package version 2.1. <http://web.maths.unsw.edu.au/~dwardon>
- Warton DI, Wright IJ, Falster DS, Westoby M (2006) Bivariate line-fitting methods for allometry. *Biol Rev* 81:259–291
- Weitkamp DE, Sullivan RD (1939) Fishes. The John Murray expedition 1933–1934. *Sci Rep John Murray Exped* 7:1–116
- Westneat MW (1995) Feeding, function, and phylogeny: analysis of historical biomechanics in labrid fishes using comparative methods. *Syst Biol* 44:361–383
- Westneat MW, Alfaro ME (2005) Phylogenetic relationships and evolutionary history of the reef fish family Labridae. *Mol Phylogenet Evol* 36:370–390
- Westneat MW, Alfaro ME, Wainwright PC, Bellwood DR, Grubich JR, Fessler J, Clements KD, Smith L (2005) Repeated convergence of skull biomechanics in coral reef fishes. *Proc R Soc B* 272:993–1000