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Variation in eye abundance among scallops reveals ontogenetic and evolutionary convergence associated with life habits

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Eyes are remarkable systems to investigate the complex interaction between ecological drivers and phenotypic outcomes. Some animals, such as scallops, have many eyes for visual perception, but to date, the evolution of multiple-eye systems remains obscure. For instance, it is unclear whether eye number changes over a lifetime or varies among species. Scallops are a suitable model group to investigate these questions considering the interspecific variation of adult size and ecological diversity. We tested whether eye abundance scales with body size among individuals and species and whether it varies with life habits. We performed comparative analyses, including a phylogenetic ANCOVA and evolutionary model comparisons, based on eye count and shell height (as a proxy of body size) across 31 scallop species. Our analyses reveal that patterns of increasing relationship with body size are not concordant among taxa and suggest ontogenetic convergence caused by similar ecologies. Accordingly, selective optima in eye numbers are associated with shifts in life habits. For instance, species with increased mobility have significantly more eyes than less mobile species. The convergent evolution of greater eye abundance in more mobile scallops likely indicates a visual improvement based on increased levels of oversampling of the surrounding environment.

KEY WORDS: Adaptation, allometry, evolutionary association, evolutionary models, visual systems.

Environmental conditions and ecological interactions are key factors driving evolutionary radiations, often leading to diversification of phenotypic traits (Schluter 2000; Simões et al. 2016). Visual systems provide opportunities to investigate how different ecologies impact multiple levels of phenotypic diversity, from protein expression to light-focusing optics, within a single organ (Hauser and Chang 2017; Koenig and Gross 2020). Vertebrate and arthropods eyes, in particular, have long been used as model systems to elucidate visual adaptations and associations with an organism's photic environment (Carleton et al. 2020; Feller et al. 2021). However, not all visual systems are defined by a pair of cephalic eyes. Many invertebrate animals exhibit multiple eyes dispersed across the body or grouped in noncephalic regions, forming a distributed visual system. For example, repeated eyes are spread on the radiolar tentacles of fan worms (Bok et al. 2016), the tips of starfish arms (Garm and Nilsson 2014), the shell plates of chitons (Speiser et al. 2011), and the mantle margin of bivalve mollusks (Morton 2008).

Distributed visual systems have attracted recent attention in investigating the functional link between ecology and evolution (Birk et al. 2018; Audino et al. 2020; Sumner-Rooney et al. 2020; Sigwart and Sumner-Rooney 2021). Unlike paired, cephalic eyes, distributed visual systems prompt unique questions regarding network properties beyond those of individual photoreceptor organs (Bok et al. 2017). For instance, it is unclear how the addition of multiple eyes to a distributed visual system influences its performance. Thus, the organization of these systems, including number of eyes, arrangement over part or all of the body surface, and neural linkage, illustrates a variety of visual adaptations and visual ecologies that have yet to be fully elucidated (Birk et al. 2018; Kingston et al. 2018).

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Scallops (Pectinidae) comprise a diverse group of marine bivalves with a distributed visual system comprising of dozens to hundreds of mirror-based eyes (Land 1965; Palmer et al. 2017) along the mantle margins, that is, the membranous organ lining the shell edge. Eye abundance is a suitable trait to investigate key questions about distributed visual systems, such as why some species tend to have more eyes than others (Speiser and Wilkens 2016). To shed light on this problem, we have taken advantage of two important properties of our model system, variable adult size and ecological diversity, and evaluate the extent to which variation in these attributes associates with, and can explain, the evolutionary diversity of eye number in scallops.

First, in many distributed visual systems, new optical units are added at regular time intervals as the body grows (Sigwart and Sumner-Rooney 2021). This condition suggests an allometric relationship, generally defined by how a phenotypic trait scales with body size at different biological levels (Gould 1966; Cheverud 1982). To this end, ontogenetic evidence has been gathered for a few scallop species (Drew 1906; Dakin 1910; Butcher 1930; Whoriskey et al. 2014) and indicates that that new eyes form as the area of mantle margin increases (Speiser and Wilkens 2016), thus eye abundance increases during individual growth. Consequently, larger scallops should bear more eyes. However, whether the pattern of allometric scaling in eye number is concordant across species has yet to be investigated. Thus, macroevolutionary trends in eye number scaling remain unknown.

Second, scallops use a variety of distinct ecological niches, which are associated with the clade's adaptive diversity (Stanley 1972; Sherratt et al. 2016; Serb et al. 2017). Based on ecomorphological traits related to behavioral responses, locomotive ability, and relationship with the substratum, adult ecological niches (life habits) are organized into six general categories (Fig. 1a): gliding, free-living, byssal attaching, recessing, nestling, and cementing (Alejandrino et al. 2011). Furthermore, these life habits define different degrees of mobility and locomotive behaviors. For example, cementing species are sessile, while recessing and byssal-attaching species exhibit limited movement and long-standing use of the substratum (Brand 2016). In contrast, free-living and gliding species can swim among habitats (Cheng et al. 1996; Brand 2016). Further, in *Argopecten irradians*, experimental studies have demonstrated that visual cues are used to find preferred habitats (Hamilton and Koch 1996). This observation raises the question whether improved swimming skills require a better visual system.

One possible way to tackle this subject is to leverage from the assumption that eye number is a proxy for visual investment. Another way is to consider that eye distribution in scallops provides at least 270° of panoramic vision, and coarse spatial information is obtained by comparing visual input between individual eyes, each with a field of view of approximately 100 degrees

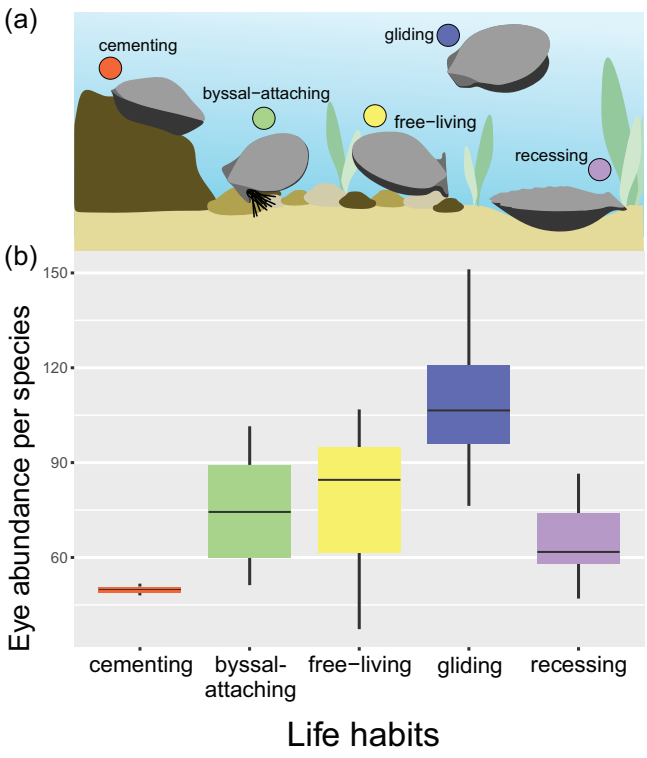


Figure 1. Schematic representation of five different life habits exhibited by scallop species (a) and boxplots of eye abundance per species according to life habits (b, color-coded). Each boxplot refers to eye abundance per species, grouped by life habit: cementing ($N = 2$), byssal-attaching ($N = 11$), free-living ($N = 10$), gliding ($N = 4$), and recessing ($N = 6$). Horizontal black lines indicate the medians, boxes are drawn from the first quartile to the third quartile, and vertical black lines run between maximums and minimums of eye abundance.

(Chappell et al. 2021). Since more eyes result in greater overlap of visual fields (Speiser and Wilkens 2016), oversampling the photic environment might add to visual performance. In addition, other anatomical factors are known for improving vision in swimming scallops, such as larger eyes, wider aperture, and longer focal length (Speiser and Johnsen 2008). As improved visual capabilities correspond to increased locomotion in many animals (Nilsson 2013; Nilsson and Bok 2017), we hypothesize that more mobile species have greater eye abundance to better sample their visual environment.

To elucidate the possible effects of different ecologies in distributed visual systems, we investigate evolutionary changes in the scallop visual system (eye abundance) as associated with life habits. First, we verify the widely held assumption that eye abundance differs among species. Next, we test the hypothesis that scallops display an allometric relationship, where larger animals bear more eyes on the mantle margin, and determine whether patterns of static allometry are concordant among species. We

then evaluate macroevolutionary trends in eye abundance by using a phylogenetic comparative approach to determine whether life habits and evolutionary allometry explain variation in eye abundance across the tree of life. Finally, we investigate the evolution of eye abundance across the scallop phylogeny in relation to shifts in life habits to determine whether there is evidence for selective optima in eye number.

Methods

We examined 324 scallop individuals preserved in ethanol from nine collections (Table S1). Eyes counts were obtained for 37 species, including left and right sides, and shell height (SH; mm) was measured for 31 species as a proxy of body size. Categorization of adult life habits follows Alejandrino et al. (2011), including cementing, recessing, byssal-attaching, free-living, and gliding (Fig. 1a). Cementing species are permanently attached to hard substratum as the adult shell grows, like oysters (Waller 1996). Species with dramatic left-right shell asymmetry excavate a cavity in soft sediment for concealment and are known as recessing species. These animals frequently reside a depression in the sediment, leaving the upper (left) valve nearly at the level of the sediment surface (Sakurai and Seto 2000; Brand 2016). Byssal-attaching scallops attach themselves to the substratum by temporary byssus threads, still being able to release, reorient, and reattach to a new place (Stanley 1972). Free-living species rest above the substratum, unattached, and can swim for short distances to escape predators or move toward preferred habitats (Hamilton and Koch 1996). Finally, gliding scallops are able to swim long distances (>5 m per effort). Unlike other mobile scallops, the gliding behavior includes a unique swimming phase with a glide component (Morton 1980; Joll 1989; Cheng et al. 1996; Ansell et al. 1998) and specific shell morphologies (Serb et al. 2017).

PHYLOGENETIC DATA

A phylogenetic tree for the 31 species of Pectinidae in our dataset was inferred from molecular data. Molecular data were curated from available sequences in GenBank (NCBI) for mitochondrial 12S rRNA and 16S rRNA regions and nuclear 18S rRNA, 28S rRNA, and histone H3 gene portions. Species and respective accession numbers are listed in Table S2. Sequences were aligned using MAFFT version 7.475 under the E-INS-i option (Katoh and Standley 2013). The best-fit model of nucleotide evolution (i.e., TVM) was selected in ModelFinder (Kalyaanamoorthy et al. 2017) based on the Bayesian information criterion. Bayesian inference of phylogeny was performed in RevBayes (Höhna et al. 2016), and posterior probabilities were sampled using the Markov chain Monte Carlo method from three independent chains with 100,000 iterations. Convergence of the posteriors was visually inspected in Tracer version 1.7 (Rambaut et al. 2018), then assessed based on effective sample size (threshold ESS = 625) for continuous parameters and split frequencies using *Convenience* package version 1.0 (Fabreti and Höhna 2022). After a burn-in of 25%, a Bayesian maximum clade credibility tree was summarized from 10,000 trees sampled from the stationary phase of the posterior distribution.

TESTING ASSOCIATION BETWEEN VARIABLES

Our main goal was to determine how ecological and morphological factors are associated with the phenotypic evolution of the scallop visual system. To accomplish this, we first evaluated allometric trends within species. We performed an analysis of variance (ANOVA) to test whether eye abundance significantly varied among scallop species, that is, log(EA) $\sim$ SP, using ordinary least squares. Next, we determined whether patterns of static allometry of eye abundance within species were concordant across taxa using an analysis of covariance (ANCOVA), using shell height as a proxy for body size, that is, log(EA) $\sim$log(SH) $\times$ SP. This analysis was restricted to those species for which we had sufficient sample sizes, that is, $n > 10$: *Aequipecten glyptus*, $n = 18$; *Amusium pleuronectes*, $n = 35$; *Chlamys behringiana*, $n = 19$; *Ylistrum balloti*, $n = 44$. In addition to our own observations ($n = 32$), we included published eye count and shell height data for another 48 individuals of *Placopecten magellanicus* (Whoriskey et al. 2014), resulting in 60 samples for the species. Three of the five species used in this analysis are gliding scallops (*A. pleuronectes*, *P. magellanicus*, and *Y. balloti*), whereas *C. behringiana* is a byssal-attaching species, and *A. glyptus* is free-living. Subsequent to the ANCOVA, we performed a series of pairwise comparisons to evaluate allometric slope differences between species, thereby testing whether the scaling relationship between eye abundance and body size varies.

Subsequent to within-species analyses, we performed a series of cross-species tests to investigate macroevolutionary trends in eye abundance across the scallop phylogeny. Specifically, we evaluated whether mean eye abundance among species associates with life habits and mean body size (i.e., evolutionary allometry), using a phylogenetic analysis of covariance, for example, log(EA) $\sim$ log(SH) $\times$ LH|phy. For this, we obtained a phylogenetic covariance matrix based on a Brownian motion model of evolution and estimated regression coefficients via phylogenetic generalized least squares (Martins and Hansen 1997). Because the interaction term was not significant (see Table S3), we proceeded with a common slope model, for example, log(EA) $\sim$ log(SH) + LH|phy, to determine whether eye abundance differed across life habit groups, while accounting for both allometry and phylogeny. Pairwise comparisons were also implemented to investigate differences in eye abundance between life habits.

For all analyses, we used randomized residuals in 10,000 permutation procedures to assess statistical significance and estimate effect sizes (Adams and Collyer 2018), using the *RRPP* package version 1.0 (Collyer and Adams 2018). The phylogenetic covariance matrix under Brownian motion was obtained using the *ape* package version 5.5 (Paradis and Schliep 2019). Diagnostic plots for each linear model, including histogram of residuals, Q-Q plots, and residuals versus fitted values, are available in Figures S1–S3.

TRAIT EVOLUTION

We used phylogenetic comparative methods in a maximum likelihood framework to estimate the evolutionary history of eye abundance across the phylogeny. First, we estimated ancestral states for this trait at internal nodes and then mapped these estimates onto the tree using *phytools* package version 0.7-80 (Revell 2012). Second, life habits were modeled as a categorical trait with five unordered states for 31 species. Here, we compared three evolutionary models (equal rates, ER; symmetrical rates, SYM; and all rates different, ARD) to determine the optimal model of transition rates under a maximum likelihood framework, using *geiger* package version 2.0.7 (Pennell et al. 2014). The equal rates (ER) model represented the optimal model for discrete trait evolution based on the Akaike information criterion (AIC). Based on this model, we then estimated the evolution of life habits across the phylogeny, performing Bayesian stochastic character mapping (Bollback 2006) in the *phytools* package. We sampled 100 trees from the posterior distribution and performed 10 simulations in each tree using the optimal ER model for transition rates. Finally, 1000 simmap trees were summarized to indicate the estimates of ancestral life habits for each node.

EVOLUTIONARY MODELS FOR TRAIT ASSOCIATION

To investigate possible evolutionary associations between eye abundance and life habits, we fit different evolutionary models to our data using the *OUwie* package version 2.6 (Beaulieu et al. 2012). The evolutionary dynamics of a continuous trait (eye abundance) were estimated based on its distribution across the phylogeny tips while accounting for ancestral estimates of a discrete trait (life habits). This approach provides a suitable framework to model evolutionary and phenotypic changes under selective regimes caused by ecological or morphological differences (Tung Ho and Ané 2014; Alencar et al. 2017; Brassey et al. 2020; Nascimento et al. 2020).

We compared the fit of four different evolutionary models (BM1, BMS, OU1, and OUM) for our dataset with 1000 simmap trees: (1) a single-rate Brownian motion (BM1) representing the simplest model; (2) a multi-rate Brownian motion model (BMS) allowing for differing evolutionary rates (σ^2) among life habit groups; (3) a single-peak Ornstein-Uhlenbeck (OU1) model with a single optimum θ; and (4) a multipeak Ornstein-Uhlenbeck model (OUM) with different optima for each discrete life habit regime. We discarded 126 reconstructions after checking the Hessian matrix for negative eigenvalues (Beaulieu et al. 2012) and unrealistic optimum for eye abundance ($\theta < 1$). Following model fitting, we used Akaike information criteria (AICc) to identify the model displaying the optimal fit.

Results

EYE ABUNDANCE VARIES AMONG SCALLOP SPECIES

We found that scallop species exhibit a remarkable variation in eye abundance (see boxplot in Fig. S4): for example, eye number ranges of 35–62 in *Crassadoma gigantea* (mean $\pm$ SD; 51.72 ± 9.48), 27–101 in *A. irradians* (59.44 ± 20.53), and 66–139 in *Y. balloti* (110.51 ± 16.44). The variance in eye abundance was explained by species grouping (Table 1; ANOVA, $P = 0.0001$). Therefore, our results provide evidence that eye abundance varies among scallop species.

EYE ABUNDANCE SCALES WITH BODY SIZE

Our regression analysis revealed that eye abundance has an increasing relationship with body size for the five species examined (Table 1; Fig. 2a; $P = 0.0001$), implying that larger individuals tended to have more eyes. Further, analysis of covariance found that patterns of static allometry differed across species (Table 1). Based on pairwise comparisons of slope vectors, we found that *A. pleuronectes* significantly differed from the other species (Table 2), displaying a steeper slope (Fig. 2a). Thus, more eyes are added per equivalent unit of body size in this species. In contrast, *P. magellanicus* seems to have the lower slope (Table 2; Fig. 2a), indicating a low rate of eye addition with body size. Interestingly, *A. pleuronectes* and *P. magellanicus* attain a similar number of eyes at large size by different allometric growth trajectories, that is, steep allometry in the former and early initial investment in the latter (Fig. 2). Thus, there is evidence of ontogenetic convergence among gliding taxa.

VARIATION IN EYE ABUNDANCE AMONG SPECIES

At the macroevolutionary level, a phylogenetic ANCOVA provided evidence for evolutionary allometry (Table 1), revealing an increasing relationship between eye abundance and body size among scallop species (Fig. 2b). Thus, larger species tend to have more eyes than smaller species, even when their phylogenetic relationships are taken into consideration. In addition, life habit represents an important ecomorphological factor for explaining eye abundance, as nearly 52% of the variation in eye abundance among scallop species can be attributed to this model effect (Fig. 1b; Table 1). Pairwise comparisons between life habits reveal significant eye abundance differences (Table 3), as expected

Table 1. Summary information for analyses using linear models to investigate whether variation in eye abundance is explained by independent variables, such as body size (shell height) and life habits. (a) ANOVA of eye abundance for 324 scallop individuals grouped by 37 species. (b) ANCOVA of eye abundance explained by shell height among adult individuals of five selected species. Pairwise comparisons are listed in Table 2. (c) Phylogenetic ANCOVA of mean eye abundance explained by mean shell height and life habits among 31 scallop species. Statistical significance and effect size were assessed via 10,000 residual random permutation procedures.

Eye Abundance	df	SS	MS	Rsq	*F*	*Z*	Pr(>*F*)
(a) *ANOVA*							
Scallop species	36	28.94	0.803	0.696	18.303	17.413	**0.0001**
Residuals	287	12.605	0.043	0.303			
(b) *ANCOVA*							
Shell height	1	4.805	4.805	0.235	216.860	7.295	**0.0001**
Scallop species	4	9.282	2.320	0.454	104.729	14.479	**0.0001**
Interaction term	4	2.605	0.651	0.127	29.391	7.974	**0.0001**
Residuals	157	3.744	0.022	0.183			
(c) *Phylogenetic ANCOVA*							
Shell height	1	0.314	0.314	0.21	19.464	3.233	**0.0002**
Life habits	4	0.778	0.194	0.52	12.05	4.243	**0.0001**
Residuals	25	0.403	0.016	0.269			

df = degrees of freedom; SS = sum of squares; MS = mean sum of squares; Rsq = coefficient of determination; *F* = *F*-statistic; β = regression coefficient; *Z* = *Z*-statistic; Pr(>*F*) = *P*-value. *P*-values <0.05 in bold.

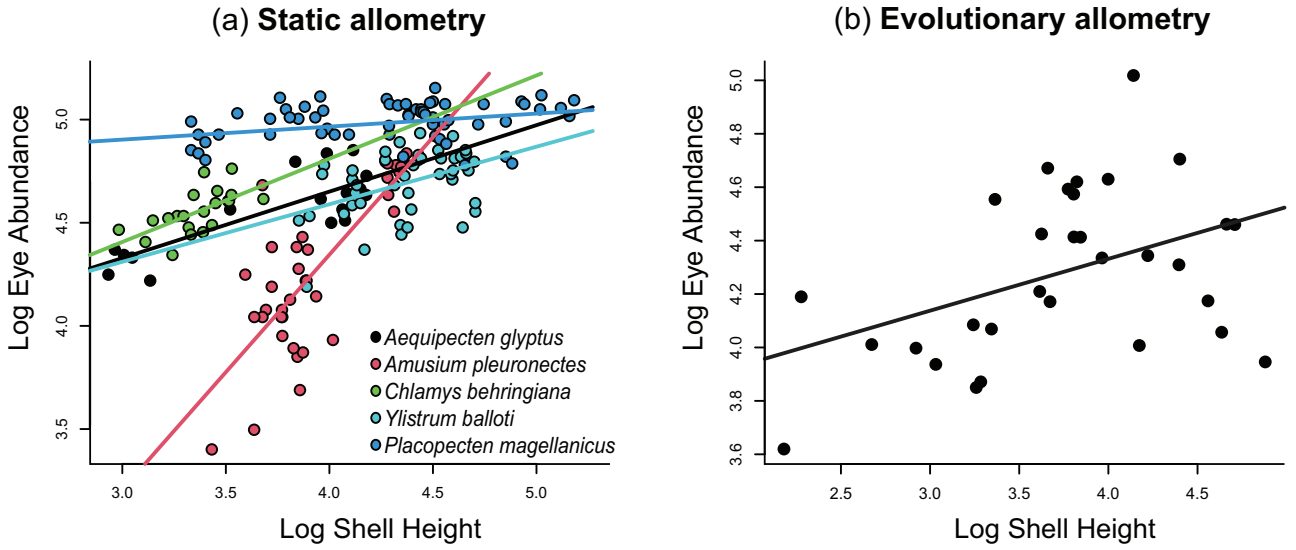


Figure 2. Scaling relationships between eye abundance and shell height (as a proxy of body size). (a) Intraspecific variation of eye abundance and shell height among adult individuals of five species (static allometry). (b) Interspecific variation of eye abundance and shell height among 31 scallop species (evolutionary allometry). Trends are significant, as indicated in Table 1.

by our initial hypothesis. In particular, cementing species have fewer eyes than species with byssal-attaching, gliding, and free-living habits, whereas recessing species have fewer eyes than gliding and byssal-attaching species. Overall, our results suggest that scallops with high mobility tend to have more eyes than those with reduced mobility living cemented (sessile) or concealed in the sediment (recessing).

EVOLUTION OF EYE ABUNDANCE

Estimates of ancestral states suggested multiple events of eye abundance increase and decrease across the scallop phylogeny (Fig. 3a). To investigate possible phylogenetic associations with life habits, we also estimated ancestral states for this categorical trait. We found that multiple shifts in life habits represent a widespread pattern among scallops (Fig. 3b), with 28.8 changes

Table 2. Pairwise absolute differences (*d*) between slope vector lengths by groups, according to the ANCOVA model described in Table 1. Variation in eye abundance is explained by the covariate body size (shell height), grouped by species. Statistical significance and effect size were assessed via 10,000 residual random permutation procedures.

Pairwise Comparisons	*d*	UCL (95%)	*Z*	Pr > *d*
Aequipecten glyptus : *Amusium pleuronectes*	0.816	0.288	3.969	**0.0001**
Aequipecten glyptus : *Chlamys behringiana*	0.081	0.47	−0.557	0.7089
Aequipecten glyptus : *Placopecten magellanicus*	0.273	0.208	2.111	**0.0079**
Aequipecten glyptus : *Ylistrum balloti*	0.043	0.285	−0.786	0.7668
Amusium pleuronectes : *Chlamys behringiana*	0.735	0.478	2.366	**0.0078**
Amusium pleuronectes : *Placopecten magellanicus*	1.09	0.239	5.525	**0.0001**
Amusium pleuronectes : *Ylistrum balloti*	0.859	0.309	3.887	**0.0001**
Chlamys behringiana : *Placopecten magellanicus*	0.355	0.441	1.29	0.0942
Chlamys behringiana : *Ylistrum balloti*	0.124	0.479	-0.178	0.5842
Placopecten magellanicus : *Ylistrum balloti*	0.23	0.232	1.554	0.0527

UCL = upper confidential level; *Z* = *Z*-statistic; Pr > *d* = *P*-value. *P*-values <0.05 in bold.

Table 3. Pairwise distances between means of eye abundance for each life habit, according to the phylogenetic ANCOVA model described in Table 1. Statistical significance and effect size were assessed via 10,000 residual random permutation procedures.

Pairwise Comparisons	*d*	UCL (95%)	*Z*	Pr > *d*
Byssal-attaching : cementing	0.874	0.487	2.802	**0.0003**
Byssal-attaching : free-living	0.187	0.38	0.439	0.3528
Byssal-attaching : gliding	0.05	0.487	−1.103	0.8448
Byssal-attaching : recessing	0.512	0.51	1.602	**0.0494**
Cementing : free-living	0.687	0.478	2.29	**0.0046**
Cementing :gliding	0.824	0.557	2.347	**0.0042**
Cementing : recessing	0.362	0.613	0.701	0.2621
Free-living : gliding	0.136	0.362	0.107	0.4737
Free-living : recessing	0.325	0.413	1.163	0.1304
Gliding : recessing	0.461	0.43	1.732	**0.0351**

UCL = upper confidential level; *Z* = *Z*-statistic; Pr > *d* = *P*-value. *P*-values <0.05 in bold.

between states on average based on 1000 simulations. The proportion of mean total time spent in each state is as follows: byssal-attaching = 0.3173, free-living = 0.2604, recessing = 0.1734, gliding = 0.1492, and cementing = 0.0994. Interestingly, shifts to gliding habits seem associated with increasing eye abundance in corresponding clades (Fig. 3a,b). In contrast, the adoption of cementing or recessing habits suggests a decrease in eye abundance (Fig. 3a,b).

Our comparison of evolutionary models revealed greater support for OUM and OU1 models (Fig. 4a; Table 4). By contrast, both BM1 and BMS models were poorly supported (Table 4; Fig. 4a,b). Higher evolutionary rates (σ^2) were estimated for OU1 and OUM as single rates for all selective regimes (Table 4; Fig. 4c). In the case of BMS, which allows σ^2 to vary, multiple rates represented a poor fit to the data (Table 4; Fig. 4c). The greatest support of OUM suggests the evolution of eye abundance is characterized by different selective trait optima (θ) for each life habit, highlighting differences among ecological groups (Table 4). In particular, the optimum for gliding species is consistently higher, whereas cementing and recessing species show lower estimates (Fig. 4d). In addition, the best fit of Ornstein-Uhlenbeck models over Brownian motion models indicate a significant improvement in modeling eye abundance when a parameter for the strength of selection (α) is included (Table 4; Fig. S5). Overall, our results support eye abundance as an adaptive trait characterized by the evolution of differing optima (θ) associated with shifts in life habits.

Discussion

A long-standing goal in evolutionary biology is understanding how ecological conditions impact the evolution of complex traits. In this study, we investigated variation in the distributed visual system of the scallops, a group with numerous eyes and

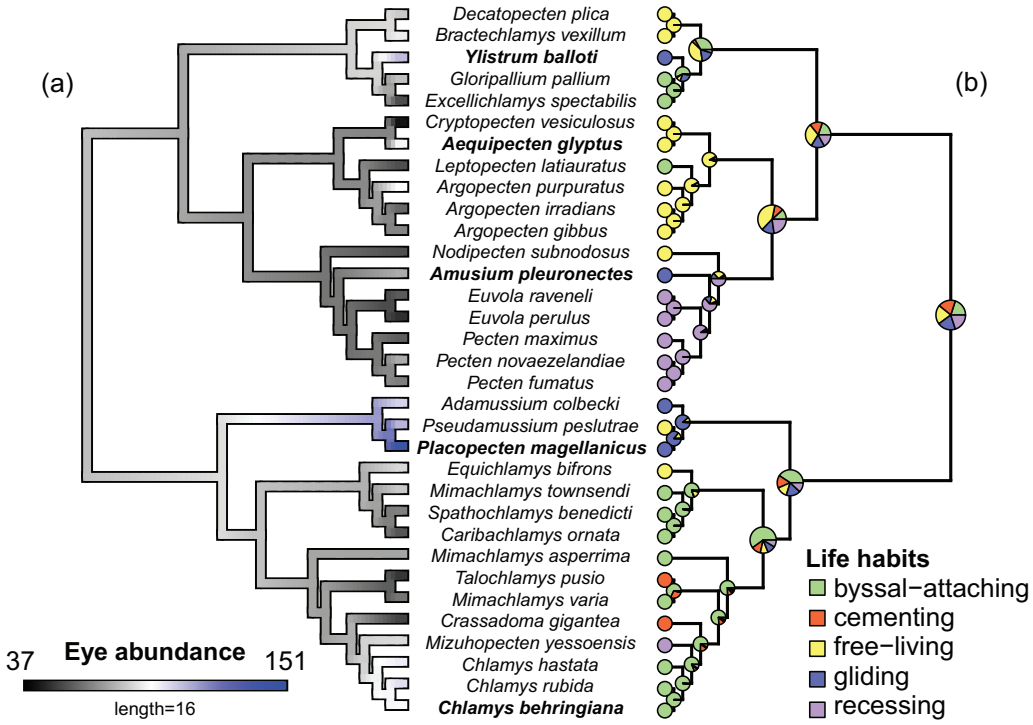


Figure 3. Ancestral state estimation of eye abundance (a) and Bayesian stochastic character mapping for life habits (b). Species used in static allometry analyses are indicated in bold.

remarkable ecological diversity. Based on comparative approaches and model analyses, we gathered evidence of adaptive differences in eye number across scallop species associated with ontogenetic and evolutionary convergence.

SCALING RELATIONSHIPS BETWEEN THE VISUAL SYSTEM AND BODY SIZE

Ontogenetic differences partially explain the number of eyes on the mantle margin of a scallop, that is, animals add more eyes as they grow (Butcher 1930). Ontogenetic allometry has been documented for individuals of *Argopecten gibbus* (Butcher 1930), *Pecten maximus* (Dakin 1910), and *P. magellanicus* (Drew 1906; Whoriskey et al. 2014). Consequently, it has been hypothesized that new eyes form as the area of mantle margin increases and eyes become more spaced out over the surface (Speiser and Wilkens 2016). Our results for eye abundance revealed an increasing relationship with body size; thus, larger individuals tend to have more eyes. These findings are consistent with previous results for the scallop *P. magellanicus*, with larger individuals having significantly more eyes than smaller conspecifics (Whoriskey et al. 2014).

Interestingly, the slope of the allometric relationship is not concordant across species. The rate of change in eye abundance as a function of body size differs across taxa, suggesting species-specific allometric trajectories. For example, a steep slope for *A. pleuronectes* compared to other species suggests that more eyes are added to the mantle margin per unit of body size. In this gliding species, long-distance swimming is likely associated with locomotive behaviors and possibly migration (Morton 1980), which might help to explain the observed investment in eye abundance. However, our data do not support the prediction that gliding species have higher rates of eye addition. In the gliding *P. magellanicus*, few eyes are added as body grows, implying that investment in eye number in this species is made early in development, not throughout. A great eye abundance in this species is present even in smaller individuals, which suggests that the number of eyes at newly metamorphosed individuals may vary by species. We hypothesize that the ontogenetic convergence of the upper-bound eye number in large individuals of both species may be due to similar life habits, that is, gliding (see discussion below). This evolutionary pattern illustrates how multiple developmental solutions may exist to the same selective pressures, as exemplified for climbing salamanders with ontogenetic convergence of foot morphology (Adams and Nistri 2010).

At macroevolutionary scales, our findings revealed a trend of positive evolutionary allometry across species, where larger species tended to have more eyes. This result is in accordance with predictions that more eyes are added when space is provided (Butcher 1930). Under a functional perspective, the acquisition of more eyes in larger species is consistent with the idea that the distributed visual system of scallops allows for a comprehensive sampling of spatial information from all directions of the

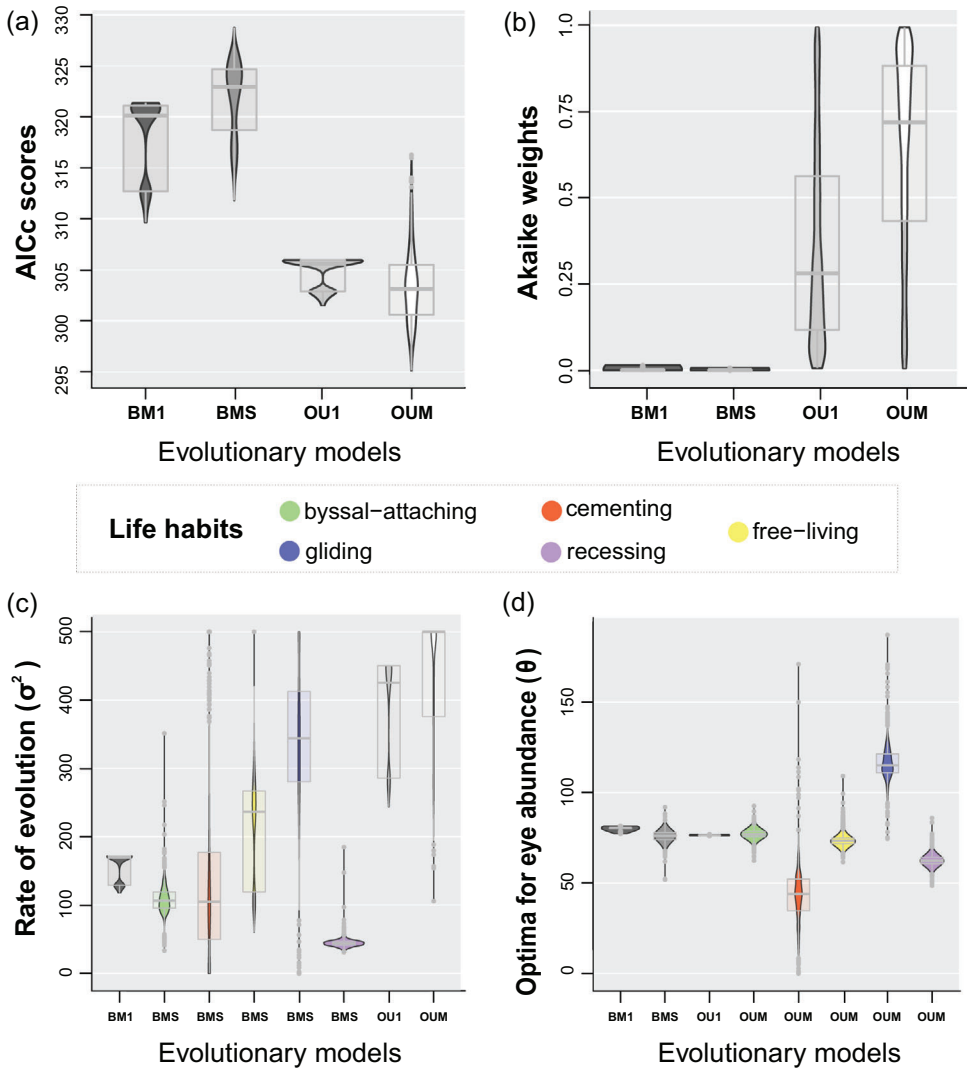


Figure 4. Violin plots comparing the evolutionary models fitted to our data to model eye abundance evolution under different life habits regimes, based on 874 phylogenetic reconstructions. (a) Akaike scores. (b) Akaike weights. (c) Rates of evolution (σ^2). The BMS model allows the rate to vary according to the regime. (d) Estimated optima (θ) for eye abundance. Only the OUM model allows different optima values for each life habit. BM1 = single-rate Brownian motion; BMS = Brownian motion with different rate parameters for each state; OU1 = Ornstein-Uhlenbeck model with a single optimum; OUM = Ornstein-Uhlenbeck model with different optima for each state.

surrounding environment (Nilsson 1994). Eye size and abundance of optical units are most likely key traits for comparative analysis of visual adaptations, as demonstrated for vertebrates (Thomas et al. 2020) and arthropods (Juarez et al. 2019). To our knowledge, few studies have investigated allometric predictors for distributed visual systems so far. For example, eyes are formed at regular time intervals during the life span of the chiton *Tonicia lebruni*, resulting in hundreds of eyes in large, adult animals (Sigwart and Sumner-Rooney 2021). However, the relationship between eye number and eye size is largely unexplored in distributed visual systems, leaving open questions regarding possible patterns and trade-offs. Differences in eye size have been reported for some scallops species with no further details (Dakin 1928; Speiser and Johnsen 2008; Malkowsky and Jochum 2014; pers. obs.), suggesting that eye size, in addition to abundance, is a valuable trait to investigate phenotypic changes associated with scallop visual ecology and evolution.

EVOLUTION OF VISUAL SYSTEM AND ASSOCIATED HABITATS

Our ancestral state estimations revealed that changes in eye abundance were common during scallop evolution and are concordant with shifts of life habits. In particular, our analyses revealed that gliding scallops—a life habit that has evolved multiple times (Serb et al. 2017)—also display higher levels of eye abundance as compared with other taxa. Thus, our analyses not only affirmed

Table 4. Summary information of evolutionary model comparisons for eye abundance under different regimes of life habits. Values are expressed as means obtained from 874 reconstructions.

	Evolutionary Models			
Parameters	BM1	BMS	OU1	OUM
AICc	318.294	321.865	304.915	303.313
Akaike weights	0.001	0.0001	0.361	0.637
Trait optimum (θ)	80.385	75.95	76.4	77.007 (BA) 43.977 (CE) 73.816 (FL) 116.852 (GL) 62.669 (RE)
Evolutionary rate (σ^2)	156.815	108.568 (BA) 129.032 (CE) 212.606 (FL) 344.542 (GL) 44.531 (RE)	390.328	434.279
Strength of selection (α)	–	–	0.357	0.671

BM1 = single-rate Brownian motion; BMS = Brownian motion with different evolutionary rates (σ^2) for each state; OU1 = Ornstein-Uhlenbeck model with a single optimum (θ) for all species; OUM = Ornstein-Uhlenbeck model with different optima for each state. Life habits: BA = byssal-attaching; CE = cementing; FL = free-living; GL = gliding; and RE = recessing. Parameters: AICc = Akaike Information Criterion corrected for small sample size, and Akaike weights, calculated as the relative likelihood of the model divided by the sum of likelihoods.

convergent evolution of life habit, but also convergence of phenotypic traits associated with those ecologies. Further, although byssal-attaching and free-living represent the most common life habits over the phylogenetic reconstructions, the estimated number of changes between states is relatively high, supporting multiple convergent shifts in these life habits as well.

Ecological conditions, including different life habits and photic niches, are mainly responsible for specific trajectories of eye evolution and visual adaptations (Hauser and Chang 2017; Sumner-Rooney 2018). In bivalved mollusks, life habits are intimately associated with adaptative patterns of photoreception (Audino et al. 2019, 2020). In support of our original hypothesis, phylogenetic ANCOVA and multipeak Ornstein-Uhlenbeck model (best-fit model) suggest that eye abundance varies among scallop life habits, particularly between cementing, recessing, and gliding species. Previous studies have investigated the complex evolutionary history of scallop phenotypes, including convergent and parallel evolution of life habits (Alejandrino et al. 2011). Ecomorphological associations are pervasive across the scallop phylogeny, as demonstrated for shell shape evolution in recessing (Sherratt et al. 2016) and gliding species (Serb et al. 2017). Consequently, our findings add to existing evidence that similar ecologies reflect similar morphologies (Wainwright and Reilly 1994; Schluter 2000) and that similar ecological conditions can correlate with convergent changes in the visual system (Lindgren et al. 2012; Härer et al. 2018; Thomas et al. 2020; Musilova et al. 2021). Interestingly, differences between eye components, such as photoreceptor spacing and focal length, provided anatomical evidence that swimming scallops may have more acute vision than nonswimmers (Speiser and Johnsen 2008). Therefore, our findings on eye abundance provide evidence of more comprehensive improvement to the visual system in swimming species in addition to the optical properties of individual eyes.

IMPLICATIONS FOR VISUAL ECOLOGY

At first sight, the increased number of units in the scallop visual system might seem an optical redundancy, just like the overlapping visual fields of the radiolar eyespots in fan worms (Bok et al. 2016). However, sampling points in the visual environment with greater numbers of eyes could represent an oversampling strategy used by these animals (Nilsson 1994), even though specific benefits are still unclear. In distributed visual systems, a larger number of overlapping optical units is supposed to provide better sensitivity, improve the signal-to-noise ratio of the visual signals, and/or provide complete visual coverage of the environment (Nilsson 1994). Consequently, the capacity to operate at lower light intensities and contrasts is not only advantageous to respond to predators without causing false alarms but also to obtain spatial information (Land 1968). For example, the regular organization of eyes on the shell plates of chitons is likely associated with an even and comprehensive sampling of the total field of view (Sigwart and Sumner-Rooney 2021).

In scallops, optical properties suggest that eyes are able to discriminate between spatial patterns, likely in association with different visual tasks (Land 1968; Speiser et al. 2016). Experiments with the bay scallop *A. irradians* suggest that the wide fields of view (at least 100 degrees) of each eye provide conditions to acquire coarse spatial information from the environment (Chappell et al. 2021). Moreover, it has been shown that scallops use spatial vision to select preferred habits (von Buddenbrock and Moller-Racke 1953; Hamilton and Koch 1996; Speiser and Johnsen 2008). Swimming scallops are predicted to have more acute vision, based on morphological proxies (Speiser and Johnsen 2008), and a larger number of eyes (present study), which follows expectations for organs capable of low-resolution and advanced light-guided behaviors, such as body orientation and navigation in relation to visual cues (Nilsson and Bok 2017). Consequently, the evolution of greater eye abundance in mobile scallops, as observed in this study, likely represents a visual improvement based on oversampling of the surrounding environment.

Given the limited knowledge of visual processing in scallops, the link between more numerous eyes and visual performance is intriguing. Increasing eye abundance seems to be a predictor of visual improvement, and oversampling may enhance the performance of distributed visual systems to discern shapes and details (e.g., acuity). For now, our results demonstrate that more mobile scallops have a greater investment in vision by developing more eyes. Future research should corroborate whether visual capabilities vary as a function of eye abundance and whether such acuity aids in visually guided behaviors. Other nonoptical reasons for greater eye number should also be investigated, such as redundancy in the case of eye damage or loss. In addition, as eyes are energetically expensive to use and maintain (Niven and Laughlin 2008), changes in eye abundance, as well as variation in eye size, naturally address questions regarding differences in energetic costs, a subject that remains largely unknown for scallop eyes.

Conclusions

Overall, the results revealed here support our original hypothesis that larger scallops with higher mobility tend to have more eyes. Our major conclusion is that eye number represents an adaptive trait of the scallop visual system and has evolved in association with ecological shifts. In addition, patterns of static allometry are not concordant among taxa and suggest ontogenetic convergence caused by similar life habits. Taken together, our findings suggest that the scallop visual system is not restricted to predator alarms because the larger number of eyes in swimming species likely contributes to improved visual capacities related to the selection of preferred habits. The findings presented here illustrate how different ontogenetic and evolutionary trajectories attain convergent outcomes shaping the visual system in the group.

AUTHOR CONTRIBUTIONS

JAA generated and analyzed data, assembled the figures and tables, and drafted the manuscript. DCA and JMS contributed to the acquisition, analysis, and interpretation of data, as well as to manuscript writing. All authors read and approved the final version of the manuscript.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA ARCHIVING

Summarized data and materials can be found in Supporting Information. The data underlying this study, including sequence alignments, phylogenetic trees, annotated scripts, and R codes used for analyses, are archived on the Dryad Digital Repository under the DOI: https://doi.org/10.5061/dryad.2547d7ws6.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Complete dataset with specimens investigated in this study and associated information: eye count, shell height, and location.

Table S2. Means of eye abundance and shell height per species, life habits, and respective accession numbers of the sequences used for the phylogenetic analysis.

Table S3. Testing whether variation in eye abundance among species is explained by life habits and evolutionary allometry via phylogenetic ANCOVA (full model: EA $\sim$ SH * LH). The interaction term is not significant ($P = 0.2335$).

Figure S1. Diagnostic plots for the ANOVA model: histogram of residuals, residual vs. fitted values, normal Q-Q, scale-location, and residual vs. leverage.

Figure S2. Diagnostic plots for the ANCOVA model: histogram of residuals, residual vs. fitted values, normal Q-Q, scale-location, and residual vs. leverage.

Figure S3. Diagnostic plots for the phylogenetic ANCOVA model: histogram of residuals, residual vs. fitted values, normal Q-Q, scale-location, and residual vs. leverage.

Figure S4. Boxplots of eye abundance for 37 scallop species (N = 324).

Figure S5. Strength of selection estimated for single-peak Ornstein–Uhlenbeck model (OU1) and multipeak Ornstein–Uhlenbeck model (OUM) in 874 reconstructions.