

Context-dependent evolution of ostracod morphology along the ecogeographical gradient of ocean depth

Bryan H. Juarez,¹  Daniel I. Speiser,²  and Todd H. Oakley^{3,4} 

¹Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, Iowa 50011

²Department of Biological Sciences, University of South Carolina, Columbia, South Carolina 29208

³Santa Barbara, Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California 93106

⁴E-mail: oakley@lifesci.ucsb.edu

Received December 13, 2018

Accepted April 7, 2019

Ecogeographical rules inform our understanding of biodiversity by seeking reliable associations between organismal phenotypes and environmental factors. Reminiscent of classic ecogeographical rules, environmental factors vary in predictable ways with ocean depth, leading to predictions about organismal phenotypes. A valuable group for studying associations between habitat depth and phenotype is cylindroleberidid ostracods (*Crustacea*) because of previous phylogenetic analyses and their enormous depth range. Using phylogenetic comparative methods, we asked how habitat depth relates to body size and eye morphology in 232 cylindroleberidid species measured from museum specimens and literature descriptions. For each species, we recorded maximum habitat depth, body size, absolute eye size, number of ommatidia (facets) per eye, and diameter of the largest ommatidium. We find that the relationship between morphology and habitat depth in cylindroleberidids depends on pelagic zone: as depth increases in the photic zone, body size increases and eyes have fewer ommatidia; as depth increases in the disphotic zone, body size does not change and eyes have more ommatidia. We did not find a relationship between absolute eye size and depth in either pelagic zone. Overall, we find that associations between phenotypes and ecogeographical gradients depend on interactions between contexts such as pelagic zone, character state, and evolutionary history.

KEY WORDS: Deep sea, ecogeographic gradient, macroevolution, phylogenetic comparative methods, visual ecology.

Patterns of association between organismal form and habitat can help us understand the evolutionary mechanisms that generate biodiversity. In particular, associations that relate geographical variables to morphological variation are often called “ecogeographical rules” (Mayr 1956; Gaston et al. 2008; Sigwart 2018). For example, Bergmann’s Rule and Allen’s Rule posit an association between latitude and body size or limb length, respectively (e.g., De Queiroz and Ashton 2004; Symonds and Tattersall 2010). Gloger’s Rule hypothesizes that organisms with more pigment live in more humid environments (Koski and Ashman 2015). Thorson’s Rule predicts low latitude marine invertebrates produce many pelagic larvae, while those at higher latitudes produce fewer benthic larvae (Gallardo and

Penchaszadeh 2001). These and other ecogeographical patterns occur within species, but may also influence patterns of morphological variation between species (De Queiroz and Ashton 2004; Gaston et al. 2008). Mechanistically, the association between morphology and geography might be caused by natural selection, phenotypic plasticity, and/or phylogenetic history. For example, animals living at high latitudes have shorter limbs that help reduce heat loss, a plausible adaptation to surviving cold temperatures. At the same time, phenotypic plasticity could cause ecogeographic associations. For Allen’s Rule, plasticity in limb length results from slower growth of cartilage of mammals in colder temperatures (Serrat et al. 2008). Even though ecogeographic rules often have exceptions, they have stimulated much

research integrating biogeography, evolution, physiology, and morphology.

Analogous to the abiotic factors that vary with latitude (or altitude) in the ecogeographical rules named above, abiotic factors also vary across ocean depths in predictable ways that are important to the organisms that live there (Jerlov 1976; Kirk 1994). Oceanic environments are often divided into three different pelagic zones (Pickard and Emery 2016). First, the photic zone (< 200 m) is relatively well-lit, nutrient-rich, and warm compared to the deeper zones. It is characterized by high quantities of downwelling light and plankton biomass, both of which decrease exponentially with depth (Childress 1995; Wishner et al. 1995). The entire photic zone typically has enough light for both photosynthesis and vision. Second, the disphotic zone (200–1000 m) is relatively dim, nutrient-poor, and colder in comparison to the photic zone. Although the depth of the disphotic zone may vary with factors such as water clarity, 100–200 m is the depth at which light levels tend to fall below that needed for photosynthesis. Vision based on downwelling light in the disphotic zone requires increasingly sensitive visual systems (Warrant and Locket 2004). The third zone, the aphotic zone (>1000 m), is the darkest, most nutrient-poor, and coldest. A minute amount of downwelling light reaches this zone, but not enough for photosynthesis or vision. Despite this, eyes can be useful in the aphotic zone if used to detect bioluminescence, which is common to at least 2000 m (Haddock et al. 2010; Nilsson et al. 2014).

Changes in food availability and downwelling light with depth in the ocean create ecogeographic gradients. Knowledge of these gradients, coupled with our understanding of metabolism and visual ecology, leads to predictions about associations between animal phenotypes and depth. For example, lower food availability suggests that lower energetic requirements and lower metabolic rates might be adaptive at depth (Childress 1995). Absolute metabolic demands tend to be lower in smaller animals, leading to a prediction that smaller animals tend to live in deeper waters. In fact, in a meta-analysis including many species, this “food availability” hypothesis is clearly supported at a global scale, with smaller animals living at greater depths; however, at regional scales, there is considerable variation in the relationships between body size and depth (van der Grient and Rogers 2015). In addition to predictions about body size, less downwelling light suggests eye morphology might change predictably with depth. On one hand, eyes might get smaller with depth because eyes are energetically demanding and there is less food at greater depths. In fact, in freshwater systems, eye size varies with light levels and food availability, mediated by natural selection (Brandon et al. 2015) and phenotypic plasticity (Brandon and Dudycha 2014). On the other hand, increased sensitivity to light in deeper oceans could come directly at the expense of spatial resolution; for example, compound eyes from deeper dwelling species may tend to

have fewer, larger ommatidia (facets) than those of their shallow-dwelling relatives; this will tend to enhance light capture, although at the cost of sampling the visual environment more coarsely (Warrant and Locket 2004). To avoid a trade-off, having larger eyes may allow animals to enhance light capture without sacrificing resolution. But because eyes are metabolically expensive (e.g., Laughlin 2001) and food decreases with depth, larger eyes may become relatively more expensive with depth. In the deepest seas, organisms often lack eyes altogether, and they may be lost via different evolutionary pathways (Sumner-Rooney et al. 2016).

Defining ecogeographical rules that accurately predict relationships between phenotypes and depth for crustaceans has proved challenging. This difficulty in finding general ecogeographical rules might imply that the evolution of phenotypic diversity along gradients of ocean depth is context dependent, a general result sometimes noted in other taxa (e.g., Schmitz and Higham 2018). In crustaceans, there are often exceptions to ecogeographical rules relating the morphology and physiology of species to the depths at which they live. For example, the “food availability” hypothesis is challenged by reports that body size correlates positively with depth in crustaceans, including ostracods, that dwell in the photic and disphotic zones (Van Morkhoven 1972; Belyaev 1974; Kornicker 1975, pp. 52–53). Furthermore, Sardà and Cartes (1993) found that relationships between body size and depth in decapod crustaceans depend on the species surveyed: some species increased in size with depth, whereas others decreased in size. Like body size, eye morphology shows complex relationships with habitat depth in crustaceans. Hiller-Adams and Case (1984, 1985, 1988) found that absolute eye size decreases with habitat depth in pelagic mysids, while Brinton (1987) reported the age class of individuals influences the relationship between absolute eye size and habitat depth in a species of euphausiid. Consistent with the hypothesis that compound eyes tend to have fewer, larger ommatidia with depth, Land (1989) found that the eyes of deeper dwelling species of hyperiid amphipods have larger ommatidia than those of shallower-living species; additionally, Kornicker (1992, figs. 3 and 4) reported that the average number of ommatidia per eye decreases with depth for members of four families of ostracods (including *Cylindroleberididae*).

Benthic cylindroleberidid ostracods (*Crustacea*) are a valuable group for comparing how habitat depth relates to body size and eye morphology in a phylogenetic context. First, cylindroleberidids are distributed in marine environments all around the world and can be found from about 0–5000 m depth. Second, cylindroleberidids also have diverse eye morphologies. Like many other myodocopid ostracods, cylindroleberidids typically possess one median eye and two lateral eyes (Oakley and Cunningham 2002). Except when highly reduced, each lateral compound eye typically has 1–70 ommatidia, with each ommatidium acting as a single sampling unit of the visual

environment. Myodocopid species that lack lateral eyes altogether are sometimes called “eyeless,” but typically still possess a median eye. Third, we do not have a detailed understanding of the ecology of each cylindroleberidid species, but we know that all cylindroleberidids possess structures that allow them to filter-feed (Kornicker 1986). Fourth, even though many species of ostracods are bioluminescent, no cylindroleberidid produces light so it is unlikely that sexual selection related to bioluminescence influences the evolution of their eyes. Finally, *Cylindroleberididae* is the only myodocopid family with a detailed and relatively complete species list (Syme and Poore 2006) and a nearly comprehensive phylogeny (Syme and Oakley 2012). These attributes make cylindroleberidid ostracods a good target for understanding how habitat depth is related to eye morphology and body size.

The vast majority of comparative studies on crustaceans have used nonphylogenetic methods, which are known to have notable statistical limitations (Felsenstein 1985). Here we use phylogenetic comparative methods to ask how habitat depth relates to body size and eye morphology in cylindroleberidid ostracods. We collected and analyzed data for 232 species, including 46 without eyes, from museum specimens and literature descriptions. For each species, we recorded maximum habitat depth, carapace length (as a proxy for body size), absolute eye length (as a proxy for eye size), number of ommatidia per eye, and diameter of the largest ommatidium in the eye. Our results indicate that morphological changes along ecogeographical gradients do not necessarily follow simple linear relationships. Instead, we find that simple predictions of morphological changes along ecogeographical gradients are context dependent: morphological evolution in cylindroleberidid ostracods is influenced by interactions between pelagic zones, character states (such as the presence or absence of eyes), and evolutionary history.

Methods

DATA COLLECTION

To ask how maximum habitat depth is related to eye morphology and body size in cylindroleberidid ostracods, we collected morphological data on all 232 described species, including the 222 species listed in Syme and Poore (2006), and 10 additional species. We obtained data from multiple sources: measurements and photographs taken of the physical collections at the Smithsonian National Museum of Natural History (NMNH) during Summer 2012, a literature search, a checklist of the species in the ostracod family *Cylindroleberididae* (Syme and Poore 2006), and an online database available through the Invertebrate Zoology Department of the Smithsonian Institution (<http://invertebrates.si.edu/>).

We collected data for the following traits for both male and female cylindroleberidids: (1) maximum habitat depth (HD), (2)

carapace length (CL) as an estimate of body size, (3) ommatidium diameter (OD), (4) absolute eye length (EL) as an estimate of eye size, and (5) ommatidia count (OC). Relative EL was estimated as EL/CL. Due to reporting bias and to prioritize broad phylogenetic sampling, we opted to collect maximum values for HD, CL, and OC from the sources listed above. We measured CL, OD, EL, and OC from only the largest individual in the NMNH collections and primarily measured nontypes to minimize destructive sampling, an important consideration because many of these species are rare. We prioritized large brooding females over large nonbrooding females to guarantee accurate identification of sex. We collected data from juveniles only when there was no adult available or when the only specimen available was a juvenile holotype (e.g., *Asteropterygion hirsutum*). Furthermore, we did not record data on ommatidia count from species with eyes described in the literature as having “numerous ommatidia.” The data (including catalog numbers, type status, and juvenile status) used for analyses in this study are in the Supporting Information and can be found at <https://doi.org/10.5061/dryad.qh46k18.2>. Scripts used for analyses and to generate figures can be found at <https://github.com/bhjuarez/context-dependent-evolution>.

We acquired maximum habitat depth for each species from both published and unpublished sources. We recorded habitat depth in meters (m) and any depth of <1 m as 1 m. To collect morphological measurements from samples in the Smithsonian’s Invertebrate Zoology Collection, we used a Meiji RZ scope with a mount, an ocular micrometer, a Canon Powershot G9 camera, and ImageJ (Schneider et al. 2012). We collected data on OC, OD, and EL from photographs of each ostracod’s left or right lateral eye; we did not collect data from the same (left or right) lateral eye every time because the amount of pigment concentration in one eye was often too high to take accurate measurements. We measured OD for each species as the width of the largest unobscured ommatidium in the lateral eye, EL as the largest possible distance between two points on the perimeter of the eye when seen from a dorsal or lateral view, and CL (mm) using an ocular micrometer as the longest distance from the tip of the rostrum to the posterior edge or point of the carapace. We measured OD (μm) and EL (μm) by converting pixel counts from photographs (with a total magnification of $420\times$, $\pm 0.4 \mu\text{m}$; $600\times$, $\pm 0.3 \mu\text{m}$; $2400\times$, $\pm 0.08 \mu\text{m}$; or $3720\times$, $\pm 0.05 \mu\text{m}$) into distance units.

TESTS OF CORRELATED EVOLUTION BETWEEN PHENOTYPES AND MAXIMUM HABITAT DEPTH

To implement our tests of correlated evolution, we used the phylogeny of Syme and Oakley (2012) that was estimated from nuclear and mitochondrial genetic data (16S, 18S, 28S vx, 28S eemm) as well as 69 morphological characters using maximum likelihood estimates of topology and divergence times. We applied phylogenetic comparative methods to our analysis because

all species share a common ancestor, so any nonphylogenetic comparisons between them lack statistical independence. Among other issues, nonphylogenetic methods may suffer from high Type I error rates (as high as 16%), relatively low power, and relatively poor estimates of correlation coefficients (Martins and Garland 1991; Rohlf 2006). Specifically, we use phylogenetic linear models to test for correlated evolution between maximum habitat depth and morphology (CL, OD, EL, relative EL, OC) of cylindroleberidid ostracods. We also tested whether eyeless species in the photic zone have longer carapaces than eyed species in the photic zone. We chose to analyze this pattern for only photic zone species because we know that the greatest rate of change in nutrients happens in the photic zone, therefore increasing our ability to observe potential trade-offs resulting from changes in species' energy budgets. We matched our trait data to the phylogeny using the *treedata* function in the *geiger* package version 2.0.6 (Harmon et al. 2008). Due to low sample sizes, we did not analyze data on species from the aphotic zone (MHD > 1000 m) or data from males. Finally, we log-transformed our data on morphology and maximum habitat depth to normalize linear model residuals.

We used phylogenetic ANCOVA to test whether the relationship between each morphological trait and habitat depth differed between the photic and disphotic zones. In our full model, we included the interaction between habitat depth and a factor representing the pelagic zone inhabited by each species. A significant interaction term prompted us to determine the relationship between a morphological trait and habitat depth separately for each zone using phylogenetic regression. If we found a nonsignificant interaction term, we reduced the model in two different ways. First, we reduced the model by removing only the interaction term, and second, we switched the order in which we added terms into our model. This allowed us to determine whether our analyses were affected by the order of the terms in our model. We used this same approach to determine the relationship between carapace length and habitat depth among the eyed and eyeless species that inhabit the photic zone. We implemented these models using *procD.pgls* function (Blomberg et al. 2012; Adams 2014) in the *geomorph* package version 3.0.7 (Adams and Otárola-Castillo 2013) using 100,000 permutations. We chose this number of permutations because preliminary analyses suggested that the variance in *P*-values across many runs approached zero at ~100,000 permutations. Finally, we used a *Z*-test to determine whether our effect size was large enough to show statistical significance of the relationship between carapace length and habitat depth among eyeless species living in the photic zone, because there were only eight species that we were able to include in our analysis.

ANCESTRAL STATE ESTIMATION

To further investigate an unexpected finding that OC increases with depth in the disphotic zone, we performed a series of analyses

to determine if this pattern might be explained by phylogenetic history. First, to determine the evolutionary history of ommatidia count and maximum habitat depth, we computed ancestral state estimates using maximum likelihood and then mapped these estimates onto our phylogeny using *phytools* package version 0.6-60 (Revell 2012). Second, to examine whether the presence of large-eyed ostracods in the disphotic zone was the result of many macroevolutionary-level dispersal events of large-eyed ostracods from the photic zone, we plotted a phylomorphospace using code from the *phylomorphospace* function in *phytools*. Species from the aphotic zone were included in ancestral state estimates.

PERMUTATION TESTS FOR RATIO OF EYELESS SPECIES

To test whether eyeless species evolve more commonly in the deepest parts of the ocean, we conducted a permutation test that we implemented using a custom script. First, we randomly permuted individual species in between zones 100,000 times while keeping the original number of species within zones constant. For each of these permutations, we then calculated the proportion of eyeless to eyed species in each pelagic zone (including the aphotic zone for this analysis). With these data, we obtained a null distribution under the null hypothesis that the ratio of eyeless species to eyed species is the same for all three pelagic zones. To obtain *P*-values, we compared the observed proportions in each pelagic zone to the distributions of values generated from the permutation procedure. The *P*-value is given by determining the number of times that the observed ratio is larger or smaller than the ratios given by the permutation procedure, and then dividing this value by the number of permutations.

Results

CYLINDROLEBERIDID OSTRACODS ARE MORPHOLOGICALLY DIVERSE

We found that cylindroleberidid ostracods live at maximum habitat depths ranging from 1 to 4715 m (mean \pm SD = 465 \pm 929 m), have maximum carapace lengths in each species of 0.71–8.80 mm (2.20 \pm 1.25 mm), and have eyes that range in length from 23 to 592 μ m (162 \pm 143 μ m). When present, these compound eyes contain 3–70 (19 \pm 14) ommatidia, the largest of which in each species have diameters ranging from 8 to 74 μ m (30 \pm 15 μ m).

CONTEXT-DEPENDENT RELATIONSHIPS BETWEEN CARAPACE LENGTH AND MAXIMUM HABITAT DEPTH

We found that relationships between carapace length and maximum habitat depth in cylindroleberidids are context dependent: separate patterns reveal themselves for species from different pelagic zones and for species with or without eyes (Fig. 1).

Table 1. Phylogenetic linear model results for carapace length (CL), absolute eye length (EL), and relative eye length (EL/CL) variables regressed onto maximum habitat depth. CL (Eye) = carapace length (we restricted this analysis to only include species from the photic zone).

	CL	df	SS	MS	Rsq	<i>F</i>	β	<i>Z</i>	Pr(> <i>F</i>)
1	D	1	0.001	0.010	0.077	8.605	0.067	1.535	0.005
2	P	1	0.001	0.001	0.009	1.043	1.107	0.623	0.292
3	Intx	1	0.003	0.003	0.022	2.487	-0.201	1.027	0.104
4	Resid	99	0.113	0.001	0.891		0.329		
5	Photic	1	0.012	0.012	0.102	8.105	0.071	1.508	0.008
6	Resid	71	0.104	0.001	0.898		0.332		
7	Disphotic	1	0.001	0.001	0.106	3.311	-0.131	1.088	0.080
8	Resid	28	0.010	0.000	0.894		1.454		
CL (Eye)									
9	D	1	0.012	0.012	0.102	8.033	0.349	1.504	0.008
10	Eye	1	0.000	0.000	0.004	0.283	1.079	0.096	0.542
11	Intx	1	0.002	0.002	0.014	1.084	-0.281	0.692	0.249
12	Resid	69	0.102	0.001	0.880		-0.727		
13	Eyed	1	0.011	0.011	0.099	6.914	0.068	1.429	0.013
14	Resid	63	0.099	0.002	0.901		0.354		
15	Eyeless	1	0.002	0.002	0.352	3.263	0.357	0.986	0.113
16	Resid	6	0.003	0.001	0.648		-0.754		
EL									
17	D	1	0.000	0.000	0.000	0.003	0.076	-1.978	0.952
18	P	1	0.004	0.004	0.050	1.586	-3.666	0.760	0.219
19	Intx	1	0.002	0.002	0.029	0.923	0.559	0.537	0.332
20	Resid	29	0.073	0.003	0.920		4.586		
21	Photic	1	0.003	0.003	0.046	1.101	0.092	0.588	0.306
22	Resid	23	0.055	0.002	0.954		4.548		
23	Disphotic	1	0.003	0.003	0.398	3.974	0.682	1.077	0.101
24	Resid	6	0.005	0.001	0.602		0.559		
EL/CL									
25	D	1	0.009	0.009	0.103	3.562	-0.155	1.120	0.069
26	P	1	0.001	0.001	0.011	0.390	-5.313	0.174	0.518
27	Intx	1	0.007	0.007	0.079	2.730	0.942	1.061	0.097
28	Resid	28	0.068	0.002	0.807		-2.342		
29	Photic	1	0.009	0.009	0.171	4.535	-0.168	1.220	0.043
30	Resid	22	0.042	0.002	0.829		-2.299		
31	disphotic	1	0.004	0.004	0.360	3.381	0.707	0.989	0.109
32	Resid	6	0.007	0.001	0.640		-7.321		

Note. D = maximum habitat depth, P = pelagic zone factor, Intx = interaction term, Resid = residual error, photic = depth for species in the photic zone (<200 m), disphotic = depth for species in the disphotic zone (200–1000 m), Eye = factor for eyeless/eyed species in the photic zone, Eyed = depth for eyed species in the photic zone, Eyeless = depth for eyeless species in the photic zone. 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, and Pr(>*F*) = *P*-value. β values in the residual error row indicate intercepts for each model. *P*-values <0.05 in bold.

Contrary to our prediction that species living at greater depths will tend to have smaller body sizes due to lower food availability, we found that carapace length increases with habitat depth in the photic zone (Table 1, row 5, *P* = 0.008). However, in the disphotic zone, we fail to find a relationship between carapace length and depth (Table 1, row 7, *P* = 0.080). Phylogenetic

ANCOVA suggested that the relationship between carapace length and habitat depth does not differ between the photic and disphotic zones (Table 1, row 3, *P* = 0.104), and this failure to reject the null model was due to the lack of a significant relationship between carapace length and habitat depth in the disphotic.

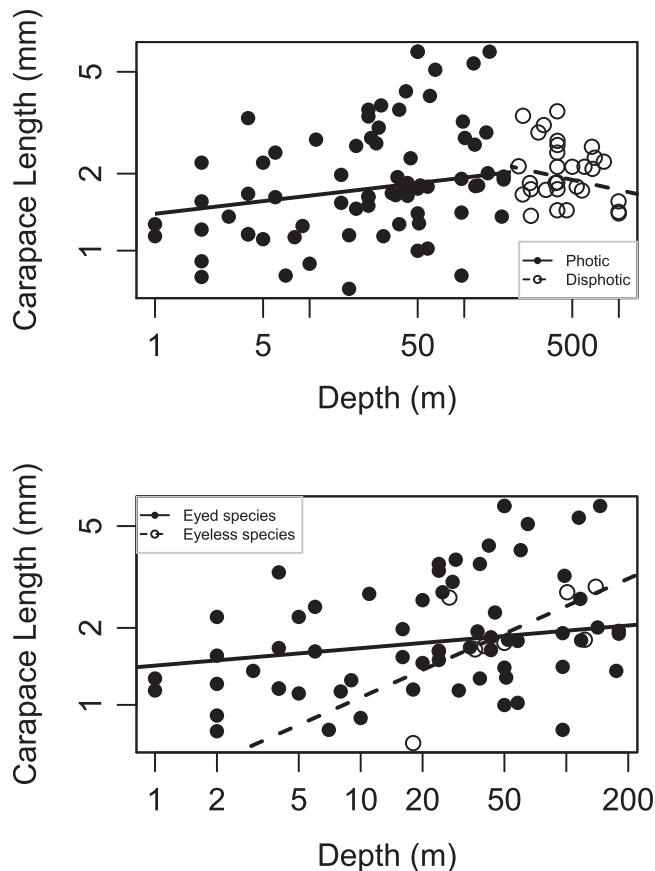


Figure 1. The relationship between maximum habitat depth and carapace length for (top) cylindroleberidids in the photic and disphotic zone and (bottom) eyed and eyeless species in the photic zone. Only the (top) photic zone and (bottom) eyed species trends are significant (Table 1, rows 5 and 7, $P = 0.008$, $P = 0.013$, respectively).

Along with pelagic zone, character state—namely the presence or absence of eyes—also influenced the relationship between carapace length and maximum habitat depth in cylindroleberidids. Due to the metabolic cost of eyes and decreases in food abundance with depth, we predicted that at any given depth in the photic zone, eyeless species would tend to have larger bodies than species with eyes. These predictions were not met: we found that species with eyes living in the photic zone have larger carapaces at greater depths (Table 1, row 13, $P = 0.013$) and that carapace length does not change with depth in eyeless species (Table 1, row 15, $P = 0.113$). Our test to detect an association between carapace length and habitat depth in eyeless species did not suffer from low statistical power, as indicated by the lack of a significantly large effect size (Z -test, $z = 0.986$, $P = 0.162$). Although phylogenetic ANCOVA suggested that the relationship between carapace length and habitat depth does not differ between eyeless and eyed species, (Table 1, row 11, $P = 0.249$), this failure to reject the null model was due to the lack of a significant relationship between carapace length and depth among eyeless species.

CONTEXT-DEPENDENT RELATIONSHIPS BETWEEN EYE MORPHOLOGY AND MAXIMUM HABITAT DEPTH

We found that the relationship between eye morphology and habitat depth in cylindroleberidids depends on pelagic zone. The relationship between absolute eye length and maximum habitat depth did not differ between the photic and disphotic zones (Table 1, row 19, $P = 0.332$). Deeper dwelling species have eyes that are just as large as those of shallower-dwelling species within both the photic zone (Table 1, row 21, $P = 0.306$), and the disphotic zone (Table 1, row 23, $P = 0.101$). Although absolute eye length does not change with depth within the photic or disphotic zones, we found that the relationship between relative eye length and maximum habitat depth does depend on the context of pelagic zone. In the photic zone, deeper dwelling species have eyes that are smaller relative to their bodies when compared to shallower dwelling species (Table 1, row 29, $P = 0.043$). However, in the disphotic zone, we found no indication that relative eye length is associated with habitat depth among species (Table 1, row 31, $P = 0.109$). Phylogenetic ANCOVA suggested that the relationship between relative eye length and depth does not differ between pelagic zones (Table 1, row 27, $P = 0.097$), and we found that this failure to reject the null model was due to the lack of a significant relationship between relative eye length and depth in the disphotic zone.

Although we did not find a relationship between absolute eye size and depth in cylindroleberidids, visual function may still vary with depth in these ostracods because apposition compound eyes of similar sizes can have ommatidia that vary in size or number. For example, we predicted that deeper dwelling species sacrifice spatial resolution for sensitivity by having eyes with fewer, larger ommatidia. This prediction was not met: we did not find that the association between ommatidium diameter and habitat depth differed between zones (Table 2, row 3, $P = 0.215$), or that ommatidium diameter changed with habitat depth in either zone (Table 2, rows 5 and 7). Next, we removed the interaction term and habitat depth from our model to test for a difference in ommatidia diameter between the photic and disphotic zones. Contrary to our prediction that deeper dwelling species would have wider ommatidia, we found that species from the photic zone have eyes in which the largest ommatidium tends to be wider than the largest ommatidium in the eyes of species from the disphotic zone (Fig. 2; Table 2, row 1, $P = 0.044$). Although we found that the factors representing pelagic zone and habitat depth in our model displayed multicollinearity for our data for ommatidium diameter, the qualitative results of this analysis do not change upon using only pelagic zone as a predictor of ommatidium diameter; therefore, we present the full model in Table 2.

Finally, we found that the relationship between ommatidia count and maximum habitat depth depends on the context of

Table 2. Phylogenetic linear model results for eye morphology regressed onto maximum habitat depth.

	OD	df	SS	MS	Rsqr	F	β	Z	Pr(>F)
1	P	1	0.008	0.008	0.126	4.411	-3.672	1.215	0.044
2	D	1	0.000	0.000	0.005	0.162	-0.046	-0.200	0.670
3	Intx	1	0.003	0.003	0.041	1.431	0.592	0.764	0.215
4	Resid	29	0.053	0.002	0.828		3.341		
5	Photic	1	0.001	0.001	0.017	0.400	-0.044	0.14	0.532
6	Resid	23	0.034	0.001	0.983		3.312		
7	Disphotic	1	0.002	0.002	0.212	1.610	0.553	0.672	0.248
8	Resid	6	0.008	0.001	0.788		-0.147		
OC									
9	D	1	0.031	0.031	0.103	10.642	-0.108	1.621	0.002
10	P	1	0.000	0.000	0.001	0.058	-4.521	-0.658	0.798
11	Intx	1	0.025	0.025	0.083	8.599	0.773	1.584	0.006
12	Resid	84	0.246	0.003	0.813		2.939		
13	Photic	1	0.028	0.028	0.127	9.622	-0.109	1.583	0.005
14	Resid	66	0.193	0.003	0.873		2.939		
15	Disphotic	1	0.016	0.016	0.285	7.175	0.642	1.407	0.015
16	Resid	18	0.041	0.002	0.715		-1.538		

Notes: OD = ommatidium diameter, OC = ommatidia count, P = pelagic zone factor, D = maximum habitat depth, Intx = interaction term, Resid = residual error, Photic = depth for species in the photic zone (<200 m), and disphotic = depth for species in the disphotic zone (200 – 1000 m). df = degrees of freedom, SS = sum of squares, MS = mean sum of squares, Rsqr = coefficient of determination, F = F-statistic, β = regression coefficient, Z = Z-statistic, and Pr(>F) = P-value. β values in the residual error row indicate intercepts for each model. P-values < 0.05 in bold.

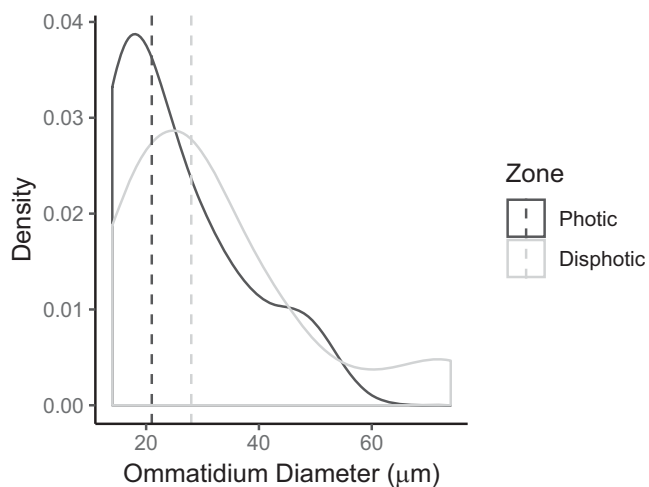


Figure 2. The relationship between the diameter of the largest ommatidium in the eye and pelagic zone. Graphs plotted are kernel density estimates of ommatidium diameter. Vertical lines indicate the median ommatidium diameter for each pelagic zone. Ommatidium diameter is significantly larger in the photic zone (Table 2, row 1, $P = 0.044$).

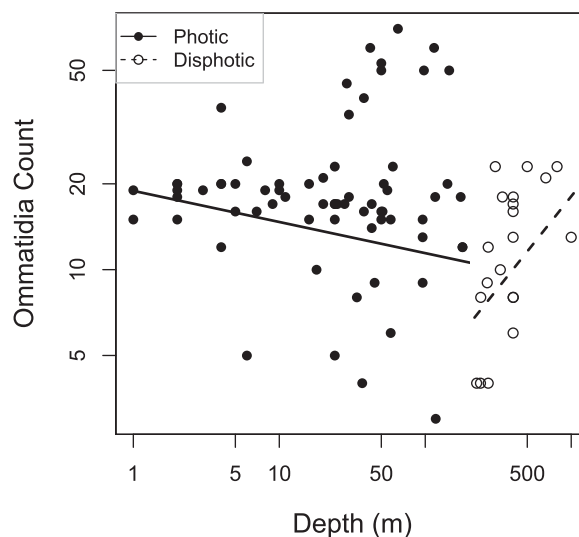


Figure 3. The relationship between maximum habitat depth and ommatidia count for cylindroleberidids in the photic and disphotic zone. Trends are significant within both the photic (Table 2, row 13, $P = 0.005$) and disphotic zones (Table 2, row 15, $P = 0.015$).

pelagic zone (Fig. 3; Table 2, row 11, $P = 0.006$). Consistent with our prediction that deeper dwelling species have eyes with fewer, larger ommatidia, we found that deeper dwelling species in the photic zone have fewer ommatidia than shallower-dwelling species (Table 2, row 13, $P = 0.005$). Surprisingly, we found the

opposite pattern in the disphotic zone: here, shallower dwelling species have eyes with fewer ommatidia than deeper dwelling species (Table 2, row 15, $P = 0.015$).

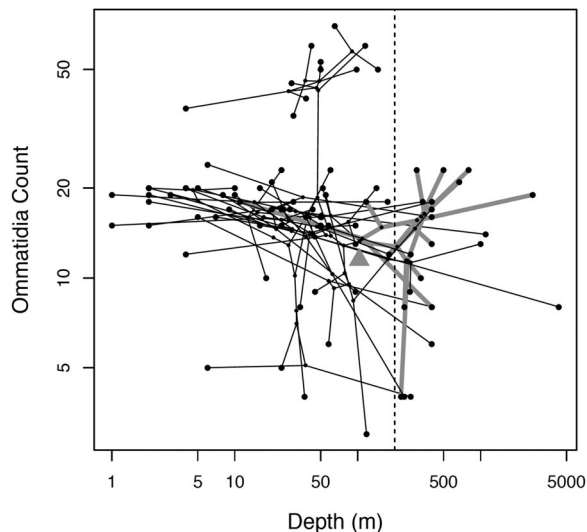


Figure 4. Phylomorphospace showing the relationship between maximum habitat depth and ommatidia count. The gray triangle is pointing up at the common ancestor of the clade in gray whose descendants generally possess numerous ommatidia despite living in the disphotic zone. Vertical dashed line represents the transition between the photic and disphotic zone at 200 m. Large black circles represent species; smaller black circles represent ancestral node estimates.

PHYLOGENETIC HISTORY DOES NOT EXPLAIN WHY SPECIES IN THE DEEP DISPHOTIC HAVE MORE OMMATIDIA

Next, we asked if evolutionary history might explain our unexpected discovery that within the disphotic zone, deeper dwelling species have eyes with more ommatidia than those of shallower dwelling species. One cause of this pattern could be that species with many ommatidia from shallower habitats dispersed deep into the disphotic zone, a prediction that is consistent with the onshore–offshore hypothesis of biodiversity (Jablonski 2005). However, we did not see evidence of such a history. Although the phylogenetic history of maximum habitat depth (Fig. 4) shows several evolutionary transitions between the photic and disphotic zones, ancestral state estimation suggests that most ostracods in the disphotic zone that have eyes with many (18–23) ommatidia are descendants of a lineage that lived in the photic zone and had eyes with relatively few (13) ommatidia (Fig. 5).

EYELESS SPECIES ARE MORE COMMON IN THE DEEP

Although we did not find a correlation between absolute eye size and maximum habitat depth in cylindroleberidid ostracods, we find more species with eyes in the photic zone and more species without eyes in the aphotic zone, relative to chance. These results are consistent with previous, nonphylogenetic studies that find that eyeless species are common at great depths (Kornicker 1992). Relative to the null expectation from our permutation test,

we found a lower proportion of eyeless species in the photic zone ($P < 0.001$) and a greater proportion of eyeless species in the aphotic zone ($P < 0.001$) than expected (Fig. 6). However, the proportion of eyeless species in the disphotic zone did not differ from the expectations of our null model ($P = 0.199$).

Discussion

Although some studies suggest simple, predictable ecogeographic rules (Gallardo and Penchaszadeh 2001; e.g., De Queiroz and Ashton 2004; Symonds and Tattersall 2010; Koski and Ashman 2015), correlations between organismal traits and environments may often belie simple relationships. In addition to being driven by adaptation to different environments, traits are often strongly influenced by phylogenetic history and structural or developmental constraints (Briggs 2017) that could make relationships between environments and morphology complicated and context dependent. Here, we show the macroevolution of body size and eye morphology in cylindroleberidid ostracods along the gradient of ocean depth to be context dependent. First, carapace length is not clearly predicted by maximum habitat depth. Instead, it depends on the photic zone where species live, and whether those species have eyes. Second, eye morphology is not always clearly predicted by maximum habitat depth. Instead, species living in different pelagic zones show different relationships between eye morphology and depth. Taken together, our results indicate that even when there exist intuitively understandable causal relationships between morphology and environment, complex relationships can still result, calling into question the generality of ecogeographical rules.

CONTEXT-DEPENDENT RELATIONSHIPS BETWEEN CARAPACE LENGTH AND MAXIMUM HABITAT DEPTH

The relationship between carapace length and maximum habitat depth in cylindroleberidids depends on the context of pelagic zone. In the photic zone, we see a positive relationship between carapace length and depth, similar to previous nonphylogenetic studies (Kornicker 1975 pp. 52–53). In contrast, we see no relationship between carapace length and habitat depth in the disphotic zone. These two results run counter to the food availability hypothesis that predicts an association between smaller bodied animals and the increasing scarcity of food at greater depths (van der Grint and Rogers 2015). Previous researchers also found evidence inconsistent with the food availability hypothesis. For example, Van Morkhoven (1972), Belyaev (1974), and Kornicker (1975) found positive correlations between body size and depth in crustaceans both in the photic and disphotic zones, but not in the aphotic zone. Given the limited information about deep sea ecology at a global scale, the reasons for these exceptions are difficult to define with certainty, but taxonomic affiliation may be important. For

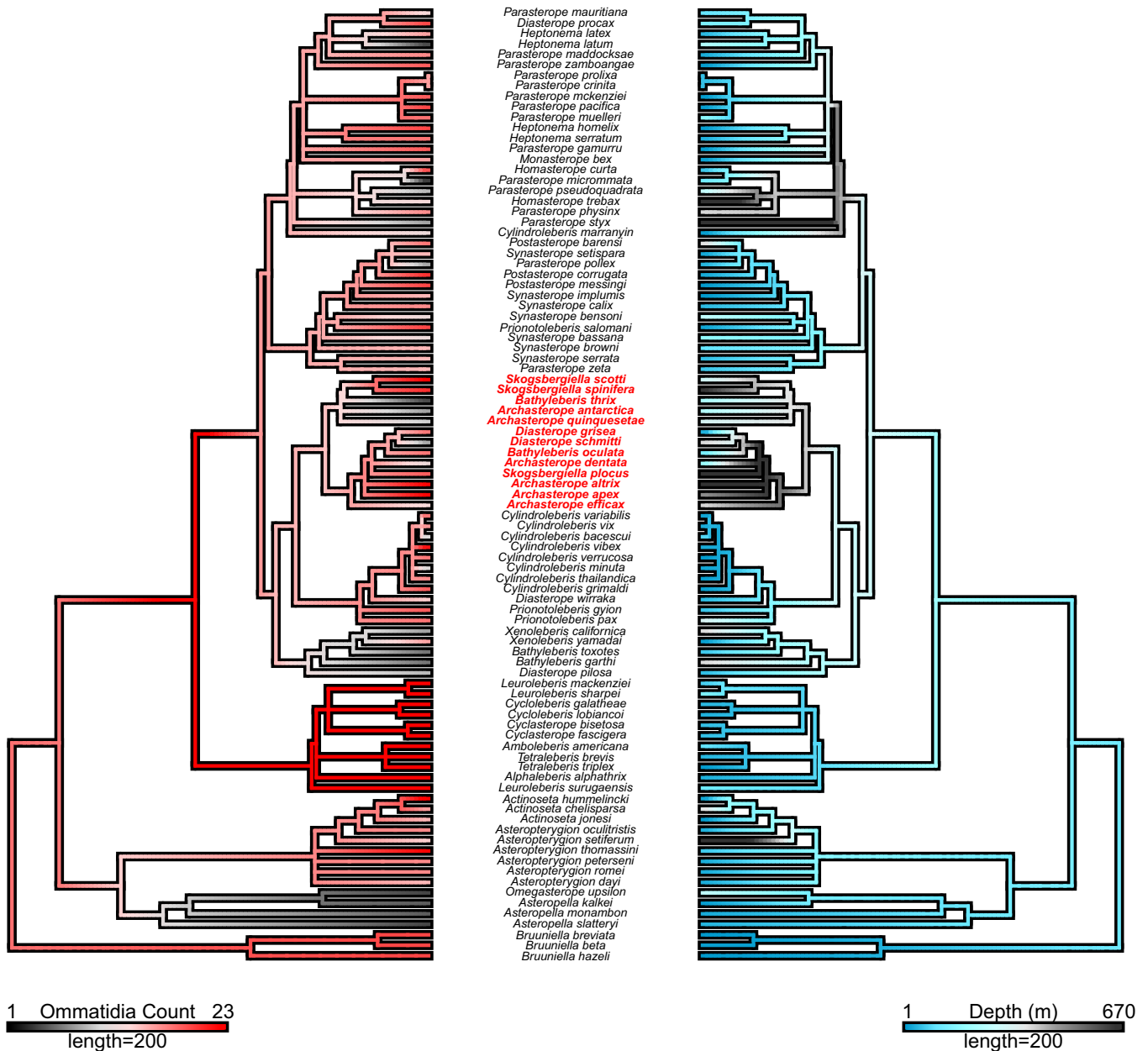


Figure 5. Ancestral state estimation of ommatidia count and maximum habitat depth. Species appearing in bold generally possess many ommatidia despite living in the disphotic zone. Branch lengths and length of scale bar are in millions of years. We mapped the same color to species with >23 ommatidia as we did to species with 23 ommatidia to emphasize the trait changes of species in bold. We did the same for the phylogeny on the right that uses the same color to represent species living at, or deeper than 670 m.

example, van der Grient and Rogers (2015) found that relationships between body size and depth in crustaceans were different than those of other types of animals living in the same communities, a result echoed by Childress (1995).

In addition to taxonomic affiliation, van der Grient and Rogers (2015) hypothesized that trophic position affects the relationship between body size and depth, with body size increasing with depth for scavengers because the availability of food is unpredictable in the deep sea and larger organisms may

capture more food per unit biomass. For example, scavenging fish increase and nonscavenging fish decrease in size with depth (Collins et al. 2005). Further support for this hypothesis may come from cylindroleberidids, which are mainly comb feeders, meaning that individuals actively capture small food particles, although some species may be scavengers (Cannon 1932; Kornicker and Harrison-Nelson 1999). Alternatively, from an adaptive perspective, cylindroleberidids could be forming larger carapaces at greater depths because this would increase their reproductive

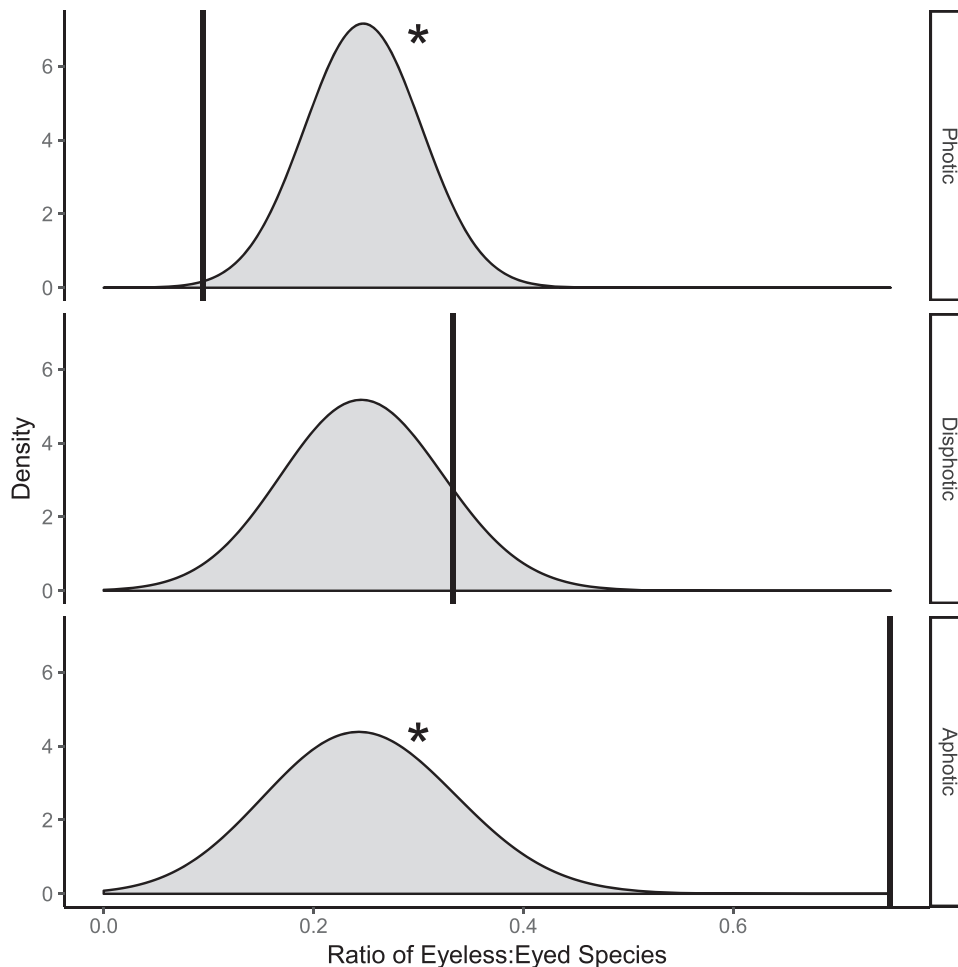


Figure 6. The relationship between the ratio of eyeless to eyed species and pelagic zone. Densities represent null distribution of ratios calculated from permuting species across pelagic zones while keeping the original number of species in each zone constant. Black vertical lines show observed ratio of eyeless to eyes species in each zone. Asterisks next to null distributions indicate statistical significance of observed ratios; photic zone: $P < 0.001$, disphotic zone: $P = 0.199$, aphotic zone: $P < 0.001$.

output by allowing them to brood more young within their shells (Kornicker 1975, pp. 50–51). In sum, depth may not be a reliable predictor of body size due to interactions between food availability, trophic position, evolutionary history (taxonomic group), and metabolism. To this list of interactions, we also add character state (presence or absence of eyes), which we discuss next.

We did not find support for our prediction that species in the photic zone without eyes have larger bodies than species with eyes. Instead, we found the opposite for species with eyes: deeper dwelling species actually have larger carapaces than shallower dwelling species. Furthermore, for eyeless species in the photic zone, we found no relationship at all between carapace length and habitat depth. Taken together, we see an overall positive relationship between carapace length and depth in the photic zone that is likely driven by the species with eyes. This finding that the relationship between carapace length and depth differs between species with and without eyes bolsters our conclusion

that habitat depth is not always a reliable predictor of body size, but rather depends on context.

CONTEXT-DEPENDENT RELATIONSHIPS BETWEEN EYE MORPHOLOGY AND MAXIMUM HABITAT DEPTH

Similar to body size, we find in cylindroleberidid ostracods that relationships between eye morphology and maximum habitat depth also depend on context. In the photic zone, we find that deeper dwelling species tend to have eyes with fewer ommatidia. In the disphotic zone, we find the opposite pattern: deeper dwelling species tend to have eyes with more numerous ommatidia. Given that we fail to find associations between absolute eye size and depth for species in either pelagic zone, we suggest that the average size of ommatidia may increase with depth in the photic zone and decrease with depth in the disphotic zone. We fail to find relationships between maximum ommatidium diameter and depth in either zone, but average ommatidia size and maximum ommatidium size may show separate relationships with depth

in cylindroleberidids because the size and spacing of ommatidia often vary across a single apposition eye (Cronin et al. 2014).

The eyes of species from the photic and disphotic zones may show different relationships between morphology and depth because of the types of visual scenes that they are adapted to viewing (Warrant and Locket 2004; Nilsson et al. 2014). Highly sensitive eyes are required to detect low-contrast extended scenes, such as objects lit dimly by down-welling light or bioluminescence. Eyes that are less sensitive to light may be sufficient for detecting high-contrast point sources, such as flashes of bioluminescence viewed against the dark background of the deep sea. Evidence that the eyes of cylindroleberidids may have fewer, larger ommatidia with depth in the photic zone is consistent with the hypothesis that animals in dim environments tend to sacrifice spatial resolution for sensitivity. Cylindroleberidids having more numerous, smaller ommatidia at greater depths in the disphotic zone suggests that these ostracods may be sacrificing sensitivity for resolution, perhaps to localize points of bioluminescence. One complication to our hypothesis is that cylindroleberidids—unlike some other groups of ostracods—are not themselves bioluminescent (Cohen and Morin 2003). Instead, we hypothesize cylindroleberidids may be detecting bioluminescence associated with the activities of would-be predators. A second complication is that deep sea crustaceans may improve the sensitivities of their eyes by summing input across neighboring ommatidia, a process termed spatial summation (Warrant and Locket 2004; Baldwin Fergus et al. 2015). If the eyes of cylindroleberidids employ spatial summation, then the sizes of their ommatidia may not be a good predictor of sensitivity.

Nonadaptive reasons, such as evolutionary history, may also explain why we observe cylindroleberidids with eyes with numerous ommatidia living in the disphotic zone. For example, the onshore–offshore hypothesis of biodiversity (Jablonski 2005) posits the common dispersal of species from shallow to deeper water. Although ancestral state estimates support dispersal between pelagic zones in cylindroleberidids, they do not support a history whereby numerous separate dispersal events brought species with many ommatidia into the disphotic zone. Instead, our results indicate species with numerous (18–23) ommatidia living in the disphotic zone are mainly descendants of a single lineage with fewer (13) ommatidia that lived in the photic zone, which migrated to the disphotic zone and gave rise to multiple species with more numerous ommatidia *in situ*. Therefore, evolutionary history is consistent with cylindroleberidid eyes sacrificing sensitivity for resolution after species dispersed to the disphotic zone.

Finally, the pelagic zone where a species lives also influences the relationship we observe between habitat depth and relative eye size. In the photic zone, deeper dwelling species have eyes that are smaller relative to their body size. Thus, compared to shallow-dwelling species, deeper dwelling species in the photic

zone may be contributing a smaller portion of their metabolic budget to building and maintaining eyes. The pattern that we observe here appears to be driven by differences in body size and not differences in absolute eye length: as described earlier, deeper dwelling species in the photic zone have larger carapaces than shallower dwelling species, but we fail to find a relationship between habitat depth and absolute eye size for species living in the photic zone. Given that eyes are metabolically expensive and food becomes increasingly scarce with depth, we are puzzled by our failure to see smaller eyes at greater depths or trade-offs between eye and body size.

CONTEXT-DEPENDENT RELATIONSHIPS BETWEEN NUMBER OF EYELESS SPECIES AND PELAGIC ZONE

The number of eyeless species relative to the number of species with eyes depends on the context of pelagic zone. Compared to the predictions of our null model, we found a lower proportion of eyeless species in the photic zone and a higher proportion of eyeless species in the aphotic zone. The proportion of eyeless species in the disphotic zone did not differ from the predictions of our null model. The pattern that we observe here may be explained by the relative metabolic cost of eyes increasing with depth. In dim environments like the deep sea, eyes will not provide reliable information about light unless they are highly sensitive and larger eyes will tend to be more sensitive than smaller eyes. However, a challenge to developing larger eyes with greater depth is that there is less food available. Therefore, our results are consistent with our expectation that we should find fewer eyeless species in the photic zone, where both food and light are relatively abundant. Despite the relative scarcity of both light and food in the disphotic zone, we did not find that the proportion of eyeless species in the disphotic was higher than expected from our null model. Finally, as expected in the aphotic zone, an environment where the lack of both food and light is extreme relative to the photic and disphotic zones, we found a significantly higher proportion of eyeless species. Overall, our findings support our expectation that the relationship between the proportion of eyeless species and pelagic zone is dependent on differences in both food and light between zones, as well as phylogeographic history.

Conclusion

The evolution of phenotypic traits along the ecogeographical gradient of ocean depth does not indicate simple relationships between morphology and habitat in ostracods. Instead, we present evidence that the relationship between morphology and maximum habitat depth can depend on different contexts including pelagic zone, character state, and phylogeographic history. We found that expectations drawn from ecogeographical rules, such as the food availability hypothesis, are supported in certain contexts but not in

others, demonstrating that these ecogeographical rules are not necessarily universal. It is unlikely that context-dependent trait evolution is unique to the depth gradient in the marine ecosystem; similar situations of context-dependent evolution undoubtedly exist in other aquatic ecosystems, such as in salinity or thermal gradients.

AUTHOR CONTRIBUTIONS

B.H.J., D.I.S., and T.H.O. conceived of the study, B.H.J. collected the data and conducted all analyses, B.H.J., D.I.S., and T.H.O. contributed equally to the writing of the manuscript.

ACKNOWLEDGMENTS

We thank the Smithsonian National Museum of Natural History for giving us access to specimens, Dr. Anna Syme for access to data, and the VASH lab group at Iowa State University for comments on previous versions of the manuscript. This work was sponsored in part by the University of California, Santa Barbara Undergraduate Research and Creative Activities (URCA) grant to B.H.J. D.I.S. was supported in part by IOS-1457148, T.H.O. in part by DEB-1146337, and B.H.J. in part by a GRFP award from the National Science Foundation.

DATA ARCHIVING

Data used for analyses in this study are in the Supporting Information and can be found at <https://doi.org/10.5061/dryad.qh46k18.2>

LITERATURE CITED

- Adams, D. C. 2014. A method for assessing phylogenetic least squares models for shape and other high-dimensional multivariate data. *Evolution* 68:2675–2688.
- Adams, D. C., and E. Otárola-Castillo. 2013. geomorph: an R package for the collection and analysis of geometric morphometric shape data. *Methods Ecol. Evol.* 4:393–399.
- Baldwin Fergus, J. L., S. Johnsen, and K. J. Osborn. 2015. A unique apposition compound eye in the mesopelagic hyperiid amphipod *Paraphronima gracilis*. *Curr. Biol.* 25:473–478.
- Belyaev, G. M. 1974. Hadal Bottom Fauna of the World Ocean. Israel Program for Scientific Translations, Jerusalem, Israel.
- Blomberg, S. P., J. G. Lefevre, J. A. Wells, and M. Waterhouse. 2012. Independent contrasts and PGLS regression estimators are equivalent. *Syst. Biol.* 61:382–391.
- Brandon, C. S., and J. L. Dudycha. 2014. Ecological constraints on sensory systems: compound eye size in *Daphnia* is reduced by resource limitation. *J. Comp. Physiol. A* 200:749–758.
- Brandon, C. S., T. James, and J. L. Dudycha. 2015. Selection on incremental variation of eye size in a wild population of *Daphnia*. *J. Evol. Biol.* 28:2112–2118.
- Briggs, D. E. G. 2017. Seilacher, konstruktions-morphologie, morphodynamics, and the evolution of form. *J. Exp. Zool. Part B* 328:197–206.
- Brinton, E. 1987. A new abyssal euphausiid, *Thysanopoda minyops*, with comparisons of eye size, photophores, and associated structures among deep-living species. *J. Crustacean Biol.* 7:636–666.
- Cannon, H. G. 1932. On the feeding mechanism of the Branchiopoda. *Philos. Trans. R. Soc. Lond. B* 222:267–339.
- Childress, J. J. 1995. Are there physiological and biochemical adaptations of metabolism in deep-sea animals? *Trends Ecol. Evol.* 10:30–36.
- Cohen, A. C., and J. G. Morin. 2003. Sexual morphology, reproduction and the evolution of bioluminescence in Ostracoda. *Paleontological Soc.* 9:37–70.
- Collins, M. A., D. M. Bailey, G. D. Ruxton, and I. G. Priede. 2005. Trends in body size across an environmental gradient: a differential response in scavenging and non-scavenging demersal deep-sea fish. *Proc. Biol. Sci.* 272:2051–2057.
- Cronin, T. W., S. Johnsen, N. Justin Marshall, and E. J. Warrant. 2014. Visual ecology. Princeton Univ. Press, Princeton, NJ.
- De Queiroz, A., and K. G. Ashton. 2004. The phylogeny of a species-level tendency: species heritability and possible deep origins of Bergmann's rule in tetrapods. *Evolution* 58:1674–1684.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *Am. Nat.* 125:1–15.
- Gallardo, C. S., and P. E. Penchaszadeh. 2001. Hatching mode and latitude in marine gastropods: revisiting Thorson's paradigm in the southern hemisphere. *Mar. Biol.* 138:547–552.
- Gaston, K. J., S. L. Chown, and K. L. Evans. 2008. Ecogeographical rules: elements of a synthesis. *J. Biogeogr.* 35:483–500.
- Haddock, S. H. D., M. A. Moline, and J. F. Case. 2010. Bioluminescence in the sea. *Ann. Rev. Mar. Sci.* 2:443–493.
- Harmon, L. J., J. T. Weir, C. D. Brock, R. E. Glor, and W. Challenger. 2008. GEIGER: investigating evolutionary radiations. *Bioinformatics* 24:129–131.
- Hiller-Adams, P., and J. F. Case. 1984. Optical parameters of euphausiid eyes as a function of habitat depth. *J. Comp. Physiol.* 154:307–318.
- Hiller-Adams, P., and J. F. Case. 1985. Optical parameters of the eyes of some benthic decapods as a function of habitat depth (Crustacea, Decapoda). *Zoomorphology* 105:108–113.
- Hiller-Adams, P., and J. F. Case. 1988. Eye size of pelagic crustaceans as a function of habitat depth and possession of photophores. *Vision Res.* 28:667–680.
- Jablonski, D. 2005. Evolutionary innovations in the fossil record: the intersection of ecology, development, and macroevolution. *J. Exp. Zool. B Mol. Dev. Evol.* 304:504–519.
- Jerlov, N. G. 1976. Marine optics. Elsevier, Amsterdam, The Netherlands.
- Kirk, J. T. O. 1994. Light and photosynthesis in aquatic ecosystems. Cambridge Univ. Press, Cambridge, U. K.
- Kornicker, L. S. 1975. Antarctic Ostracoda (Myodocopina) parts 1 and 2. *Smithson. Contrib. Zool.* 163:1–720.
- . 1986. Cylindroleberididae of the western North Atlantic and the northern Gulf of Mexico, and zoogeography of the Myodocopina (Ostracoda). *Smithson. Contrib. Zool.* 425:1–139.
- . 1992. Myodocopid ostracoda of the benthedi expedition, 1977, to the NE mozambique channel, Indian Ocean. *Smithson. Contrib. Zool.* 531:1–243.
- Kornicker, L. S., and E. Harrison-Nelson. 1999. Eumeli expeditions, Part 1: *Tetragonodon rex*, new species, and general reproductive biology of the myodocopina. *Smithson. Contrib. Zool.* 602:1–55.
- Koski, M. H., and T.-L. Ashman. 2015. Floral pigmentation patterns provide an example of Gloger's rule in plants. *Nat Plants* 1:1–5.
- Land, M. F. 1989. The eyes of hyperiid amphipods: relations of optical structure to depth. *J. Comp. Physiol.* 164:751–762.
- Laughlin, S. B. 2001. The metabolic cost of information- a fundamental factor in visual ecology. Pp. 169–185 in F. G. Barth and A. Schmid, eds. *Ecology of sensing*. Springer, Berlin, Germany.
- Martins, E. P., and T. Garland Jr. 1991. Phylogenetic analyses of the correlated evolution of continuous characters: a simulation study. *Evolution* 45:534–557.
- Mayr, E. 1956. Geographical character gradients and climatic adaptation. *Evolution* 10:105–108.
- Nilsson, D. E., E. Warrant, and S. Johnsen. 2014. Computational visual ecology in the pelagic realm. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 369:20130038.

- Oakley, T. H., and C. W. Cunningham. 2002. Molecular phylogenetic evidence for the independent evolutionary origin of an arthropod compound eye. *Proc. Natl. Acad. Sci. U. S. A.* 99:1426–1430.
- Pickard, G. L., and W. J. Emery. 2016. *Descriptive physical oceanography: an introduction*. Pergamon Press, Oxford, U. K.
- Revell, L. J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* 3:217–223.
- Rohlf, F. J. 2006. A comment on phylogenetic correction. *Evolution* 60:1509–1515.
- Sardà, F., and J. E. Cartes. 1993. Relationship between size and depth in decapod crustacean populations on the deep slope in the Western Mediterranean. *Deep Sea Res. Part I* 40:2389–2400.
- Schmitz, L., and T. E. Higham. 2018. Non-uniform evolutionary response of gecko eye size to changes in diel activity patterns. *Biol. Lett.* 14:20180064.
- Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* 9:671–675.
- Serrat, M. A., D. King, and C. O. Lovejoy. 2008. Temperature regulates limb length in homeotherms by directly modulating cartilage growth. *Proc. Natl. Acad. Sci. U. S. A.* 105:19348–19353.
- Sigwart, J. D. 2018. *What species mean: a user's guide to the units of biodiversity*. CRC Press, Boca Raton, FL.
- Sumner-Rooney, L., J. D. Sigwart, J. McAfee, L. Smith, and S. T. Williams. 2016. Repeated eye reduction events reveal multiple pathways to degeneration in a family of marine snails. *Evolution* 70:2268–2295.
- Syme, A. E., and G. C. B. Poore. 2006. A checklist of species of Cyndroleberididae (Crustacea: Ostracoda). *Mus. Vic. Sci. Rep.* 9:1–20.
- Syme, A. E., and T. H. Oakley. 2012. Dispersal between shallow and abyssal seas and evolutionary loss and regain of compound eyes in cyndroleberidid ostracods: conflicting conclusions from different comparative methods. *Syst. Biol.* 61:314–336.
- Symonds, M. R. E., and G. J. Tattersall. 2010. Geographical variation in bill size across bird species provides evidence for Allen's rule. *Am. Nat.* 176:188–197.
- van der Grient, J. M. A., and A. D. Rogers. 2015. Body size versus depth: regional and taxonomical variation in deep-sea meio- and macrofaunal organisms. *Adv. Mar. Biol.* 71:71–108.
- Van Morkhoven, F. 1972. Bathymetry of recent marine Ostracoda in north-west Gulf of Mexico. *Gulf Coast Assoc. Geol. Soc. Trans.* 22:241–252.
- Warrant, E. J., and N. A. Lockett. 2004. Vision in the deep sea. *Biol. Rev. Camb. Philos. Soc.* 79:671–712.
- Wishner, K. F., C. J. Ashjian, C. Gelfman, M. M. Gowing, L. Kann, L. A. Levin, L. S. Mullineaux, and J. Saltzman. 1995. Pelagic and benthic ecology of the lower interface of the Eastern Tropical Pacific oxygen minimum zone. *Deep Sea Res. Part I* 42:93–115.

Associate Editor: J. W. McGlothlin
 Handling Editor: M. Servedio