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Variation in rod spectral sensitivity of fishes is best predicted by habitat and depth

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Rod spectral sensitivity data (λ_{\max}), measured by microspectrophotometry, were compiled for 403 species of ray-finned fishes in order to examine four hypothesized predictors of rod spectral sensitivity (depth, habitat, diet and temperature). From this database, a subset of species that were known to be adults and available on a published phylogeny ($n = 210$) were included in analysis, indicating rod λ_{\max} values averaging 503 nm and ranging from 477 to 541 nm. Linear models that corrected for phylogenetic relatedness showed that variation in rod sensitivity was best predicted by habitat and depth, with shorter wavelength λ_{\max} values occurring in fishes found offshore or in the deep sea. Neither diet, nor the interaction of diet and habitat, had significant explanatory power. Although temperature significantly correlated with rod sensitivity, in that fishes in temperate latitudes had longer wavelength rod λ_{\max} values than those in tropical latitudes, sampling inequity and other confounds require the role of the temperature to be studied further. Together, these findings indicate that fish rod λ_{\max} is influenced by several ecological factors, suggesting that selection can act on even small differences in fish spectral sensitivity.

KEYWORDS

absorbance, light, photoreceptor, scotopic, vision, visual ecology

1 | INTRODUCTION

Understanding the relationship between the visual environment and visual ability is a central question in sensory ecology. While some aspects of vertebrate vision are conserved, others vary significantly, resulting in the diverse capacities of animals to detect contrast, motion, detail and colour (Cronin *et al.*, 2014). The key factors used to explain this diversity include visually-mediated behaviours and differences in environmental light (Lythgoe, 1979), both of which have been intensely studied in ray-finned fishes due to their phylogenetic diversity, occupation of diverse optical habitats and variation in retinal function (Lythgoe, 1972; Munz & McFarland, 1977).

Among vertebrates, fishes have the greatest diversity of spectral sensitivities, the ability of the retina to discriminate light of different spectral compositions (Cronin *et al.*, 2014). Membrane-bound molecules called visual pigments confer light sensitivity to rod and cone photoreceptor cells over a c. 200 nm range that surrounds a wavelength of peak sensitivity known as λ_{\max} (MacNichol, 1986). Rod

photoreceptors are typically more light sensitive than cone photoreceptors (Rodieck, 1973) and thus able to support vision in scotopic (*i.e.*, dim-light) conditions that occur at night or at depth. Also, all rods in a given eye typically contain the same visual pigment, facilitating multiple methods for the characterization of rod sensitivity. Over time, a wealth of data has been produced on rod λ_{\max} variation, which as early as 1936 (Bayliss *et al.*, 1936; Clarke, 1936), was hypothesized as an adaptation to variable light environments, particularly within fishes.

Several ecological hypotheses have been proposed to explain the diversity of both rod and cone spectral sensitivities in fishes. First, the sensitivity hypothesis states that variation in visual pigment λ_{\max} should correlate with dominant wavelengths of environmental light (Lythgoe, 1968), since shifting photoreceptor sensitivity toward the available light spectrum improves photon capture by the retina. The broad illumination spectra typical of shallow waters permit more variable spectral sensitivity than in deeper waters, where the distribution of λ_{\max} as well as the available light spectrum both narrow toward 480 nm with increasing depth (Bowmaker *et al.*, 1994; Denton &

Warren, 1957, Levine & MacNichol, 1982). As for habitat, the photic environments of offshore, inshore and many freshwater systems are typically dominated by short, medium and long-wavelength light respectively, producing distinct underwater spectra that have been shown in some species to correlate with photoreceptor λ_{\max} (Bowmaker, 1990; Lythgoe *et al.*, 1994; Munz, 1958a; Munz & McFarland, 1973).

Another major hypothesis regarding spectral sensitivity variation in fishes is the contrast hypothesis (Munz & McFarland, 1973), which states that, relative to the spectrum of background light, photoreceptor λ_{\max} values vary with the appearance of visual targets such as prey (Munz & McFarland, 1973). The degree to which photoreceptor sensitivity correlates with the environmental light spectrum determines the detectability of different prey types (Munz & McFarland, 1973), a situation that is affected by viewing angle, distance and the appearance of prey (Lythgoe, 1979). Finally, a third hypothesis is that rod λ_{\max} may be shorter in wavelength than predicted by the spectrum of the underwater light to reduce the probability of incidental thermal activation of rod photoreceptors (Cronin *et al.*, 2014). The high sensitivity of rod visual pigments makes them vulnerable to spontaneous activation by thermal radiation (Luo *et al.*, 2011), a situation that worsens as λ_{\max} increases, but which may be lessened by reduced environmental temperature (Aho *et al.*, 1988).

These hypotheses have existed for several decades, though the literature currently lacks a systematic and comprehensive analysis of rod spectral sensitivity across fishes. Several clade-specific case studies of rod spectral sensitivity have been performed, providing variable levels of support for the existing hypotheses (Dartnall & Lythgoe, 1965). Here, we compiled published rod λ_{\max} values in ray-finned fishes to examine the relationships between rod spectral sensitivity and four ecological factors (depth, habitat, diet and temperature), while accounting for phylogenetic relatedness.

2 | MATERIALS AND METHODS

2.1 | Compilation of rod spectral sensitivity database

Rod λ_{\max} values in ray-finned fishes ($n = 403$) were compiled from the literature (Supporting Information Appendix S1) as analysed by microspectrophotometry (MSP), a method that yields single-cell measurements of photoreceptor absorption spectra (Bowmaker, 1984). Several other methods exist for estimating spectral sensitivity, including the measurement of extracted visual pigments and electrophysiological recordings of whole-retinal responses to light (*i.e.*, electroretinography). However, rod spectra from retinal extracts can be affected by preparation method (Collins *et al.*, 1952) and those from electroretinography can be obscured by the response of cones and thus can be difficult to compare with those obtained from MSP.

2.2 | Estimating phylogenetic signal

Only rod λ_{\max} values measured from adult individuals were included in analysis, as both fish ecology and spectral sensitivity can vary over ontogeny (Cronin *et al.*, 2014). To control for the effects of

phylogenetic relatedness, the analysis was restricted to species included in a recently published phylogeny of 7,822 ray-finned fishes (Rabosky *et al.*, 2013). Of the total 269 species known to be adults in the compiled rod spectral-sensitivity database, 210 were present in the phylogeny. These species, along with branch length information from the original phylogeny, were extracted to create a sub-tree for analysis. The degree of phylogenetic signal among fish rod λ_{\max} values was estimated by calculating Pagel's λ (Freckleton *et al.*, 2002; Pagel, 1999), using the phytools package (Revell, 2012) in R version (www.r-project.org). The value of Pagel's λ represents a branch length transformation that maximizes the likelihood of the observed data assuming a Brownian model of evolution. This parameter is expressed as a value ranging from 0 to 1, which denotes the independence or covariance of trait variation to phylogenetic structure, respectively. A likelihood ratio test was used to determine significance against the null hypothesis that $\lambda = 0$.

2.3 | Assignment of ecological variables to fish species

Four ecological variables (depth, habitat, diet and temperature) were selected to help examine the existing sensitivity, contrast and thermal activation hypotheses of rod λ_{\max} variation in fishes. Each variable was segmented into three categories (based on criteria established *a priori*) to facilitate ecological assignments for each species using information available on FishBase (Froese & Pauly, 2000). Ecological variables were assigned according to the life history of adults. For the depth variable, bins were classified broadly to address spectral narrowing over short wavelengths that occurs over depth, across shallow (0–49 m), moderate (50–199 m) and deep (200 m+) water ranges. Habitats were binned to serve as a proxy of water colour, with fishes occupying freshwater (lakes and rivers; brown water), inshore (estuaries and coasts; green water), or offshore (pelagic and coral reef; blue water) habitats. The diet variable was organized into two categories relative to visual foraging scenarios, with fishes consuming mostly benthic or pelagic prey. Additionally, diet analyses were conducted to address differences in prey appearance found across trophic levels (Supporting Information: Appendix S2). Lastly, for temperature, fishes were classified according to geographic distribution, either as polar (latitude 90°–66.5°), temperate (latitude 66.5°–23.5°) or tropical (latitude 23.5°–0°). All fishes in the > 200 m depth bin were excluded from temperature analyses, as the uniformly cold water at this depth confounds the potential effects of latitude on rod λ_{\max} .

2.4 | Phylogenetic generalized least-squares models and statistical analyses

The relationship between rod spectral sensitivity and fish ecology was assessed using phylogenetically-corrected linear models using the R package phylolm (Ho *et al.*, 2015) with rod λ_{\max} as the response variable and all possible linear combinations of depth, habitat, diet and habitat \times diet interaction as co-predictors. The interaction of habitat and diet was selected because the contrast hypothesis of fish spectral sensitivity is based generally on both water colour and the appearance of prey. The fit of each model was evaluated and ranked using

Akaike's information criterion (AIC; Akaike, 1974; Burnham & Anderson, 2002), in which the lowest AIC value indicates the best-fit model. ΔAIC values were obtained by calculating the difference between the AIC value of a given model and the lowest AIC value. Models with $\Delta\text{AIC} < 4$ relative to the best fit model were also considered to have some support (Burnham *et al.*, 2011). In addition to ΔAIC , model weights (w_i), the probability of each model i being the best model of the set, were calculated using the formula following (Burnham *et al.*, 2011): $w_i = (e^{-0.5\Delta\text{AIC}_i} / \sum_j e^{-0.5\Delta\text{AIC}_j})^{-1}$.

In order to examine relationships between the ecological predictor variables, contingency table analyses were performed for all pairwise combinations of ecological factors considered in the phylogenetic generalized least-squares (PGLS). As the data did not meet equal variance assumptions, one-way Welch's ANOVA was used to compare mean rod λ_{max} between the categories of each ecological variable, except for the bins of diet variable, which were compared using a Welch's t -test. Because of unequal sample size, the data subset for the temperature variable was excluded from the PGLS models analysis and examined separately by a one-way Welch's ANOVA. Where appropriate, *post hoc* Games-Howell tests, (which also do not assume equal variances) were used to examine pairwise differences: $n = 3$ for all variables except diet where $n = 2$. Critical α -level was adjusted for multiple testing using the Bonferroni correction (Dunn, 1961).

3 | RESULTS

3.1 | Rod spectral sensitivity in ray-finned fishes

Across the 210 species included in the analyses, rod λ_{max} ranged from 477 to 541 nm. The mean, median and mode of this dataset were 503, 501 and 500 nm respectively, all in the blue-green portion of the spectrum. A histogram of the rod λ_{max} values indicated a primarily unimodal dataset, with a secondary peak at c. 520 nm (Figure 1). Significant phylogenetic signal was detected among rod λ_{max} values (Pagel's $\lambda = 0.829$, $P < 0.001$), indicating that rod spectral sensitivity significantly covaries with phylogenetic structure in ray-finned fishes

(Figure 2) and that phylogeny should be accounted for in further analyses.

3.2 | The relationship between rod spectral sensitivity and ecology

Phylogenetically corrected linear models showed that the best-fit model contained both depth and habitat as co-predictors ($w_i = 0.67$; Table 1). The addition of diet as a co-predictor produced the second-best model, which had the only ΔAIC value < 4 relative to the best-fit model. However, the second-best model had an Akaike weight of only 0.23, indicating that the probability of the relationship represented by this model is roughly one third of the probability of the relationship represented by the best-fit model.

To further investigate the relationships underlying the best-fit model, we examined the degree of independence between each ecological variable, as well as the variation in the rod λ_{max} values of fishes assigned to each ecological category. Contingency table analyses of ecological variables detected significant associations between habitat and diet ($P < 0.01$; Table 2) and between habitat and depth ($P < 0.001$), but not between diet and depth ($P > 0.05$).

Comparing rod λ_{max} across the categories of each ecological variable indicated that spectral sensitivity varies significantly across depth ($P < 0.001$), habitat ($P < 0.001$) and temperature ($P < 0.001$) categories, but not between diet categories ($P > 0.05$); Figure 3; Table 2; Appendix S2). Species in shallow waters had the longest-wavelength rod λ_{max} values (mean \pm SD = 509 ± 13.65 nm, $P < 0.01$), while species in deep waters had the shortest (mean \pm SD = 494 ± 8.67 nm, $P < 0.01$). Across habitats, fish species found offshore had shorter wavelength rod λ_{max} values (mean \pm SD = 496 ± 6.18 nm) than fishes found either inshore (mean = 504 nm, S.D. = 10.83, $P < 0.01$) or in freshwater habitats (mean \pm SD = 510 ± 17.38 nm, $P < 0.01$). No significant difference in rod λ_{max} was found between inshore and freshwater species ($P > 0.05$).

Lastly, a subset of data comprising 177 species that excluded those found at depths > 200 m was tested for rod λ_{max} variation across temperature regimes assigned by geographic location. Rod λ_{max}

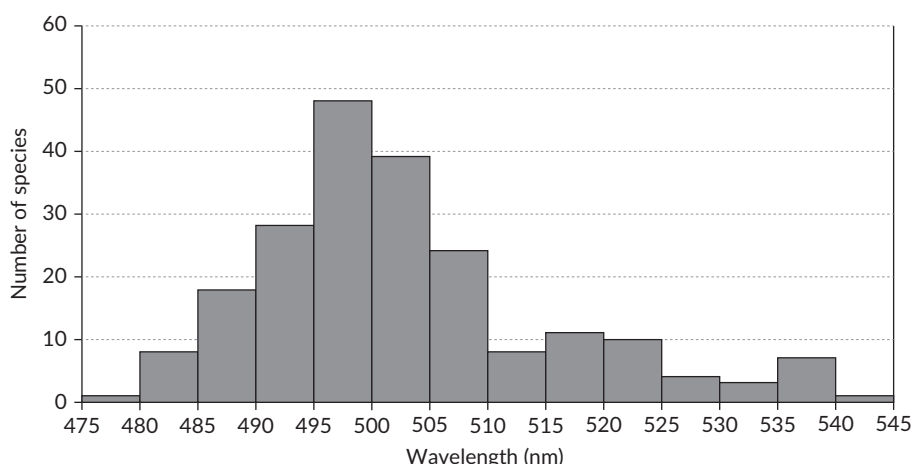


FIGURE 1 The frequency distribution of rod λ_{max} among ray-finned fishes (Actinopterygii). The distribution comprises data that were collected from adult fish, with suitable phylogenetic information and by microspectrophotometry ($n = 210$)

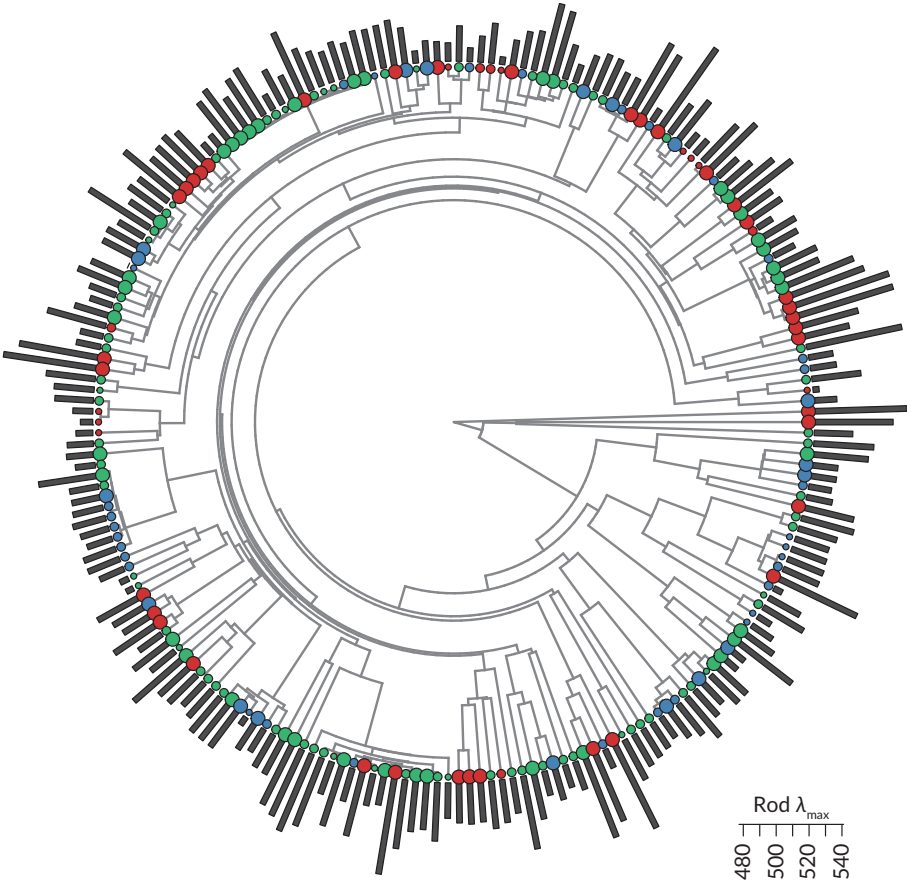


FIGURE 2 The relationship of habitat and depth to rod sensitivity across a subset of Actinopterygii. Habitat is indicated by color: ●, fresh water; ●, marine inshore; ●, marine offshore, and depth is indicated by dot size: ●, deep; ●, medium; ●, shallow. Rod λ_{\max} is indicated by the gray bars. The minimum length shown is 477 nm and maximum length shown is 541 nm. Original phylogeny from Rabosky *et al.* (2013)

was only found to differ between fish that occupy tropical (mean \pm SD = 498 \pm 7.48 nm) and temperate waters (mean \pm SD = 508 \pm 18.83 nm, $P < 0.01$). The λ_{\max} values of fish that occupy polar waters (mean \pm SD = 508 \pm 7.41 nm) did not significantly differ from those in temperate or tropical waters ($P > 0.05$); power was reduced for these comparisons as the sample size of polar species was quite low ($n = 4$).

TABLE 1 Summary of phylogenetic generalized least-squares multivariate models of rod spectral sensitivity in Actinopterygii; ΔAIC values were calculated relative to the best fit model and w_i is model probability

Model	ΔAIC	w_i
H + DE	0	0.67
DI + H + DE	2.13	0.23
DI + H + DE + DI \times H	4.20	0.08
DE	8.43	0.01
DI + DE	10.3	0
H	32.6	0
DI + H	34.0	0
DI + H + DI \times H	34.1	0
Null	42.9	0
DI	44.7	0

Note. H, Habitat; DE, depth; DI, diet; \times , denotes parameter interaction.

4 | DISCUSSION

4.1 | Rod spectral sensitivity in ray-finned fishes

Over the past several decades, studies of fish spectral sensitivity have contributed to our understanding of how evolution and ecology influence variation in sensory function. Here, spectral sensitivity data for hundreds of species were compiled and analysed to explore how phylogenetic heritage, environment and diet correlate with rod λ_{\max} variation among ray-finned fishes. Our analyses, after controlling for phylogenetic relatedness, provide support for the sensitivity hypothesis, as rod λ_{\max} variation is best predicted by habitat and depth.

TABLE 2 Summary of *post hoc* analysis of rod spectral sensitivity and ecological relationships across Actinopterygii

Contingency table analysis	χ^2	df	P
Diet \times Depth	2.9	2	> 0.05
Diet \times Habitat	10.9	2	< 0.01
Depth \times Habitat	29.5	4	< 0.001
Welch's one-way ANOVA	F		
Depth	25.6	2, 103	< 0.001
Habitat	28.5	2, 107	< 0.001
Temperature	19.2	2, 9	< 0.001
Welch's t-test	t		
Diet	0.18	208	> 0.05

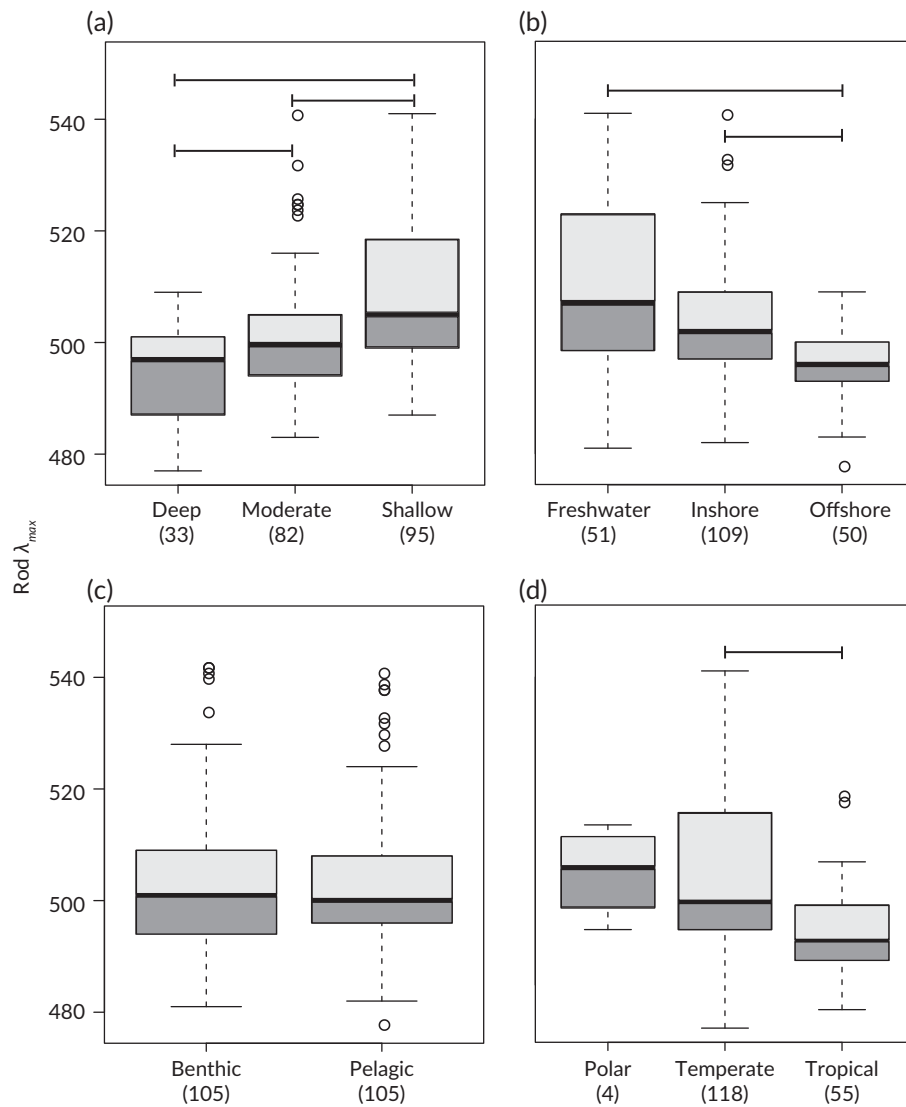


FIGURE 3 Rod λ_{\max} in Actinopterygii across (a) depth, (b) habitat, (c) diet, and (d) temperature categories. For the boxplots shown, the line represents the median, the box outlines the 25th and 75th quantiles, the whiskers extend to the minimum and maximum, and circles are outliers. Thirty-three deep-water species were excluded from temperature analyses, as the uniformly cold water at this depth confounds the potential effects of latitude on rod λ_{\max} . Bars span boxes that are significantly different (Games-Howell pairwise test, $P < 0.01$). Critical α -level was adjusted for multiple testing ($n = 3$ pairwise comparisons) using the Bonferroni correction. Values on the x-axis in parentheses give the sample size for that category

Consistent with the trend observed among vertebrates (Cronin *et al.*, 2014), the rod λ_{\max} distribution of fishes centred on c. 500 nm. A secondary peak in this distribution occurred at c. 520 nm, which may have resulted from differences in vitamin-A type chromophores used by the retinas of different fish species. Visual pigment sensitivity is determined by its constitutive parts, an opsin protein bound to either retinal A₁ or A₂-based chromophore types (Dartnall, 1976). Interestingly, the two peaks in the distribution of fish rod λ_{\max} values are spaced at a distance on the light spectrum that could be explained by the fact that some species use retinal A₁ while others use retinal A₂ (Whitmore & Bowmaker, 1989), with the latter making the rods sensitive to longer wavelengths of light.

Over the 210 species studied, rod λ_{\max} values ranged from 477 to 541 nm, indicating relatively low variability in rod sensitivity across fishes. In general, rod and cone photoreceptors are sensitive to a c. 200 nm range of wavelengths that surround λ_{\max} and the distribution of values observed here indicates that the rods of all sampled fishes

overlap in their wavelength sensitivity. This limited variation in the distribution of λ_{\max} suggests that rod spectral sensitivity is constrained by use of a single opsin class (*i.e.*, RH1) and that limited change has occurred either due to evolutionary drift or narrowed ecological and physiological requirements of rod vision in fishes, both of which were addressed by the current study.

4.2 | Rod λ_{\max} versus depth, habitat and diet

Overall, our results indicated that depth and habitat are greater predictors of rod λ_{\max} than the interaction of diet and habitat, or diet alone. For depth, the results are consistent with previously reported trends of negative correlation between depth and rod λ_{\max} , which has been repeatedly observed in deep-sea fishes (Hunt *et al.*, 2001; Munz, 1958b). Unlike most vertebrates, deep-sea fish typically contain a rod-only retina (Wagner *et al.*, 1998), with λ_{\max} values that

fall between 474 and 490 nm (Douglas & Partridge, 1997). These approximate both the dominant wavelength of downwelling light and the wavelength of maximal emission of most deep-sea bioluminescence (Douglas & Partridge, 1997).

Aside from the attenuation of light by water, light is also absorbed and scattered by phytoplankton, suspended sediment and dissolved organic matter (Johnsen, 2012), all of which may represent selective pressures on the spectral sensitivity of fishes. In addition to depth, habitat type was shown to be a significant predictor of rod λ_{\max} variation. Offshore fishes had shorter wavelength rod λ_{\max} values than both inshore and freshwater fishes, corresponding to trends in light spectrum typically observed among these environments (Jerlov, 1976).

Together, these data lend support to the sensitivity hypothesis suggesting that photoreceptor λ_{\max} values in fishes vary with respect to the spectral qualities of environmental light. These findings, however, provide less support for the contrast hypothesis suggesting that fish rod λ_{\max} may correlate with prey contrast (Lythgoe, 1966; Munz & McFarland, 1973), depending on prey appearance and the spectrum of environmental light. To address this hypothesis, the relationship of fish rod λ_{\max} values to diet were examined three ways, relative to benthic or pelagic foraging scenarios, according to prey appearance over trophic levels (Supporting Information: Appendix S2) and in conjunction with habitat light as an interaction term, with the results indicating that these variables do not predict rod spectral sensitivity in fishes. These findings suggest that the selective pressures of light environment across habitat and depth have superseded the role of diet in tuning fish rod λ_{\max} values.

Alternatively, of course, the parameters selected here may have been ineffective in addressing the contrast hypothesis, which describes a complex visual scenario dependent on both predator and prey. In addition, as rod photoreceptors are primarily active in dim-light conditions (twilight and night), fish rod λ_{\max} values are likely affected by visual requirements relative to time of day. It is difficult to identify the circadian activity of fish species, although many fishes are considered cathemeral (active at day and night; Helfman, 1986). As rods can be active at twilight, our ecological assignments may be relevant to rod sensitivity regardless of circadian activity. Yet, other sources of variation existed in the ecological classification of the study species. For example, freshwater fishes are primarily found in shallow water habitats, yet nine freshwater species in this study are endemic to the deepest lake in the world (Lake Baikal) and found at depths > 200 m (Bowmaker *et al.*, 1994), thus inhabiting shorter-wavelength light environments than are typical of freshwater systems (rod λ_{\max} mean = 489 nm). However, much of this variation was unavoidable, as the intensity and spectrum of underwater light is dynamic over both space and time and many fish species are migratory both across depth and geographic distance. Thus to contend with this variability, broad ecological categories were selected for this study, allowing patterns of rod sensitivity to be detected despite the ecological complexities of fishes.

4.3 | Rod λ_{\max} and temperature

Consistent with what has been observed in other studies (Cronin *et al.*, 2014; Loew & Lythgoe, 1978), rod λ_{\max} values did not surpass c.

540 nm. This threshold is predicted to minimize the incidental activation of rod visual pigments by thermal energy (Barlow, 1964), which is more likely in rods with longer-wavelength λ_{\max} values. As some ectothermic vertebrates have better rod performance (*i.e.*, lower noise) in colder water (Aho *et al.*, 1988), species located in colder water were predicted to permit longer wavelength rod sensitivity. In line with this theory, fish rod λ_{\max} values were higher in fishes that occupied cooler waters. Although no significant differences were detected against the coldest water condition (polar $n = 4$), the results are consistent with the temperature hypothesis. However, given the low sample size of polar species and the fact that cooler water is typically more productive and thus greener, further investigation is required. Looking ahead, greater effort should be made to examine the spectral sensitivity in fishes that occupy deep-sea, offshore and polar environments.

In conclusion, studying spectral sensitivity among fish has proved to be a challenging yet useful way to explore the evolutionary ecology of sensory-trait variation in nature. The present study represents the largest ever examination of rod spectral sensitivity in ray-finned fishes, yet the spectral sensitivity of thousands of fishes remain to be characterized, with little to no data on some large fish orders, such as Characiformes, Lophiiformes, Siluriformes. Further studies will help to fill in parts of the phylogeny for which no data was available for this study. The data gathered here revealed a narrow spread of rod λ_{\max} values among fishes across just 64 nm. Because of this, all rod photoreceptors examined here overlap in their c. 200 nm sensitivity range that surrounds λ_{\max} . Despite this shared functional range, phylogenetic history and at least two ecological variables (depth and habitat) appear to influence this variation. Current theory in visual ecology suggests that similar spectral sensitivities may perform equally well in visual tasks, allowing considerable flexibility in photoreceptor λ_{\max} (Cronin *et al.*, 2014; Marshall *et al.*, 2015). However, in this study, after correcting for phylogenetic relatedness, ecological predictors of fish-rod spectral sensitivity were revealed, suggesting that selection can act on even small differences in visual capability.

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Author contributions

L.E.S and S.J. conceived of the study, L.E.S., E.M.C and S.J. analysed the data and drafted the manuscript, S.E.S and T.T.S. compiled data and all authors contributed to the final version of the manuscript.

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SUPPORTING INFORMATION

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

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