# VISUAL PIGMENTS IN THE EARLY LIFE STAGES OF PACIFIC NORTHWEST MARINE FISHES

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## Summary

Microspectrophotometry was used to measure the visual pigments in the rods and cones of 22 species of marine fish larvae netted from the surface waters off Friday Harbor Laboratories, Washington, USA. 13 species had rods, 12 of which contained visual pigments with a wavelength of maximum absorbance near 500 nm, while one, the sand lance (*Ammodytes hexapterus*), had its absorbance maximum at 482 nm. The 22 species of fish larvae possessed varied combinations of single, double and twin cones, ranging in peak absorbance from 353 nm to 584 nm. Of these, green-sensitive single cones were present in 20 of the 22 species, and were the dominant cone type. Double and twin cones were present in 13 of the species. Most common were identical green-sensitive (twin) cones (in 11 species). Green/yellow-sensitive double cones occurred in four species. In a single instance (*Hemilepidotus hemilepidotus*) twin blue-sensitive, twin green-sensitive and double blue/yellow-sensitive cones were recorded. Of particular interest was the finding that 18 of the species had ultraviolet- and/or violet-absorbing single cones.

It has been suggested that short-wavelength photosensitivity may be beneficial for planktivory by extending the spectral range over which vision can occur. The high percentage (82 %) of ultraviolet and violet visual pigments in Pacific northwest fish larvae supports the prediction that short-wavelength sensitivity may be common in marine fish larvae.

Key words: visual pigment, microspectrophotometry, ultraviolet vision, fish larvae, planktivory.

## Introduction

The stages from the egg through the larval period are considered most crucial in the life history of marine fishes (Hjort, 1926). Mortality in these stages is high, because starvation and/or predation are considered to be major impediments to successful recruitment into juvenile/adult populations (see Gerking, 1994). Successful passage through the early larval stages is dependent on the detection of plankton, which usually are distributed in patches. Given the unpredictability of encountering these patches, any adaptations that enhance awareness of their presence and increase the likelihood of encountering food particles should be favored by selection. Since the vast majority of fish larvae are planktonic diurnal particulate visual planktivores (Arthur, 1976; Hunter, 1981; Gerking, 1994), adaptations that enhance visual particle detection are probably present. The visual range over which zooplankton can be detected by most fish larvae is at best one or two bodylengths (Wahl et al., 1993). Furthermore, because they are small, low-contrast targets (McFall-Ngai, 1990; Hamner, 1996; Johnsen and Widder, 1998), zooplankton present planktivorous fish, especially fish larvae, with a difficult visual task.

Over the last decade, attention has been directed towards the spectral photosensitivity of planktivorous fishes. Several behavioural investigations have shown that fish larvae are capable of using near-ultraviolet light to detect zooplankton (Loew et al., 1993; Browman et al., 1994; Loew et al., 1996). This capacity appears to reside in a class of cone photoreceptors containing a visual pigment absorbing maximally in the ultraviolet and/or violet regions of the spectrum. The idea that the presence of ultraviolet-sensitive visual pigments could be a general adaptation for animals foraging on zooplankton (see Bowmaker, 1991) is supported by studies showing that several adult planktivorous fishes possess ultraviolet-sensitive cones (McFarland and Loew, 1994). Ultraviolet-sensitive vision in fishes may be useful for other behaviours, i.e. orientation, navigation, species recognition, etc. (see review in Losey et al., 1999). The only current conclusive experimental demonstrations, however, are in planktivory (Browman et al., 1994; Loew et al., 1996) and in orientation (Hawryshyn and Bolger, 1991; Hawryshyn, 1992).

In this paper, evidence is presented that short-wavelength-sensitive visual pigments are common in marine fish larvae, at

least, as demonstrated in fishes from a variety of families common to the Pacific Northwest coast of North America.

## Materials and methods
### Collection and identification of species

All of the specimens collected were identified to species and life history stage based on the work of Matarese et al. (Matarese et al., 1989). 21 of the 22 species examined were collected using an underwater nightlight from the Friday Harbor Laboratory dock. Using a fine-mesh net, larvae were dipped from the surface, transferred to buckets, and then maintained in large shallow aquaria (120 cm×60 cm×22 cm) supplied with 9 °C running sea water. Specimens were also collected by towing a 61 cm diameter plankton net (333 μm mesh) within the immediate vicinity (<0.5 km) of the Friday Harbor Laboratories. The net was deployed just beneath the surface and towed at approximately 3 km h$^{-1}$ for 15 min. Larvae were maintained in the laboratory on a diet of *Artemia franciscana* (Argent Chemical Laboratories) supplemented with freshly caught zooplankton.

Additionally, newly hatched walleye pollock larvae (*Theragra chalcogramma*) were provided by Dr Janet Duffy-Anderson, from the NOAA/National Marine Fisheries Service/Alaska Fisheries Science Center, in Seattle, WA, USA. Some of the lingcod larvae used were provided by Dr Mike Rust, from the NOAA/National Marine Fisheries Service/Northwest Fisheries Science Centers' marine fish enhancement program located at the Manchester Field Station in Manchester, WA, USA.

### Visual pigments

Spectral absorbance curves from rod and cone cells isolated from the retinae were obtained using a single-beam, computer-controlled microspectrophotometer fitted with quartz optics. Individual larvae were dark-adapted for at least 2 h, anesthetized with tricaine methanesulfonate (MS 222), killed by severing the spinal cord at the base of the head and enucleated under infrared or dim red illumination. The entire retina was removed into buffered saline (Sigma, modified MEM, pH 7.6) onto a 22 mm×30 mm coverslip and teased apart using scalpel blades and needles. The preparation was covered with a second 18 mm×18 mm coverslip edged with silicone grease. The preparation was placed on the stage of the microspectrophotometer and a spectral measurement taken through the medium adjacent to a photoreceptor. Wavelengths were scanned in both directions from 750 nm to 350 nm, and the resulting absorbance spectrum was stored in the computer as a baseline. A photoreceptor cell outer segment was then moved over the measuring beam and another absorbance spectrum obtained. Absorbance was calculated as the logarithm of the ratio of the baseline over the sample data. Two criteria were used to confirm that the measured absorbance was due to a visual pigment: (i) that the outer segment was dichroic and (ii) that the pigment was photolabile.

To establish the wavelength of peak absorbance, the $\lambda_{max}$, each curve was analyzed by first digitally filtering the data ('smooft'; Press et al., 1987) and then fitting them to accepted templates. For each class of photoreceptor cell in a preparation, the $\lambda_{max}$ values were averaged from the number of spectral scans recorded to yield a final estimate of $\lambda_{max}\pm1$ S.D. Further details of microspectrophotometry procedures can be found in Loew et al. (Loew et al., 1996).

Photoreceptor cell types were identified by their morphological appearance on the microscope stage. Rod outer segments were isolated from their inner segments and possessed a bulbous swelling at their proximal end (site of attachment to the inner segment). The morphology of single cones varied in appearance from small cells to much larger elongated cells. The outer segments of double cones appeared as unequal pairs, each of which contained a different visual pigment. Twin cones were identifiable as morphologically equal pairs, the outer segments of which contained the same visual pigment. In any instance where we were uncertain about a photoreceptor cell type the results have been omitted.

## Results

21 of the 22 species examined fell within the definition of a larva, specific to each species, as described in Matarese et al., 1989 (Table 1). The first observation of rods and/or double cones was also noted. The only exception, the wolf-eel, *Anarrichthys oculofasciatus*, hatches as a juvenile with fins fully developed, but with yolk reserves still present. During this intermediate stage of development, the wolf-eel is unpigmented and does not exhibit behavioural characteristics typical of its later juvenile and adult stages (i.e. early juveniles are pelagic, as opposed to the benthic habits of late juveniles and adults). It was therefore included in this study.

### Visual pigments

For the 22 species examined, the visual pigments ranged from the UV-A to the longer-wave yellow regions of the spectrum (Table 2). Absorbance spectra for the cones of the dwarf wrymouth and the best-fitting photopigment template curves illustrate the estimation of $\lambda_{max}$ (Fig. 1).

#### Rods

13 species possessed rods. They were present in the pre-flexion larvae of three species and in the post-flexion larvae of 10 species (Table 1). 12 species had visual pigments with $\lambda_{max}$ values centered around 500 nm. The sand lance, in contrast, possessed a rod pigment located in the blue region of the spectrum (482 nm).

#### Single cones

We have grouped these photoreceptors into five spectrally sensitive classes by wavelength: ultraviolet (353–378 nm), violet (398–432 nm), blue (435–480 nm), blue-green to green (497–529 nm) and yellow (541–584 nm). The ultraviolet, blue-green and yellow classes clearly fall in distinct classes (Fig. 2). The separation between the violet and blue classes is arbitrary,

Table 1. *Species of larval fish surveyed*

| Family | Species | Common name | Larval length (mm) | | | | Rod | Double cones |
|---|---|---|---|---|---|---|---|---|
| | | | Post-hatch | Pre-flexion | Post-flexion | Transformation* | | |
| Clupeidae | *Clupea pallasi* | Pacific herring | | | 26,27 | 35 | 26 | 26 |
| Engraulidae | *Engraulis mordax* | Northern anchovy | | | 25,30,33 | >31 | ND | 25 |
| Gadidae | *Theragra chalcogramma* | walleye pollock | 4,4 | | | 30–40 | ND | ND |
| Scorpaenidae | *Sebastes auriculatus* | brown rockfish | | | 23,29 | >31 | 23 | 23 |
| Hexagrammidae | *Hexagrammos decagrammus* | kelp greenling | | 12 | 20 | >50 | 12 | 12 |
| | *H. stelleri* | white-spotted greenling | 10 | 12.5 | 16.5 | >33 | ND | 10 |
| | *Ophiodon elongatus* | lingcod | 9,9,9,10 | 13,13,15 | 28,33 | 30–52 | 13 | ND |
| Cottidae | *Artedius meanyi* | Puget Sound sculpin | | | 12 | 13–19 | ND | 12 |
| | *Blepsias cirrhosus* | silver-spotted sculpin | | | 27‡ | UNK | 27 | 27 |
| | *Hemilepidotus hemilepidotus* | red Irish lord | | | 15 | 19–23 | 15 | 15 |
| | *Myoxocephalus polyacanthocephalus* | great sculpin | | 8 | | >12 | ND | ND |
| | *Nautichthys oculofasciatus* | sailfin sculpin | 6 | | | 26 | ND | ND |
| | *Rhamphocottus richardsoni* | grunt sculpin | | 8 | | 14–15 | ND | ND |
| | *Scorpaenichthys marmoratus* | cabezon | | 8 | | 14–35 | 8 | ND |
| Stichaeidae | *Xiphister mucosus* | rock prickleback | | | 28,31§ | 18 | 28 | ND |
| Cryptacanthodidae | *Lyconectes aleutensis* | dwarf wrymouth | | 12,15 | 17,25‡ | U | ND | 17 |
| Anarhichadidae | *Anarrhichthys ocellatus* | wolf-eel | | | 67,79,100 | PTH | 67 | 67 |
| Ptilichthyidae | *Ptilichthys goodei* | quillfish | | | 115 | >114 | 115 | 115 |
| Trichodontidae | *Trichodon trichodon* | Pacific sandfish | | | 29,34 | >32 | 29 | 29 |
| Ammodytidae | *Ammodytes hexapterus* | Pacific sand lance | | | 25(H) | 16–31 | 25 | 25 |
| Pleuronectidae | *Parophrys vetulus* | English sole | | | 12 | 17.5(EM) | ND | ND |
| | *Psettichthys melanostictus* | sand sole | | | 16,17 | >23(EM) | ND | ND |

U, unknown; ND, none detected; PTH, prior to hatch; EM, eye migration.
*Taken from Matarese et al., 1989.
‡Size at transformation for this species is not reported in the literature; determined to be Pre-transformation by authors.
§Over reported size at transformation, but confirmed by FOCI Ichthyoplankton Laboratory (National Marine Fisheries Service, Alaska Fisheries Service Center RACE Division, Seattle, WA, USA) as Pre-transformation.
H, courtesy of Tribble, 2000.

All larvae were measured for standard length (mm) and categorized as Post-hatch, Pre-flexion, Post-flexion or Post-flexion. Post-hatch was defined as those larvae sampled directly after hatch and post-flexion was defined as those larvae sampled prior to transformation but after flexion. Size at Transformation data (taken from Matarese et al., 1989) is provided for reference. The sizes of the smallest larvae (mm) in which rods and/or double cones were observed are also given (Rod, Double cones).
Where more than one length is given, values are from more than one specimen.
Each value in the table is for an individual fish.

Table 2. *Visual pigment $\lambda_{max}$ data for the 22 species surveyed*

| Species (common name) | Single cones | | | | | | Double cones | | |
|---|---|---|---|---|---|---|---|---|---|
| | Rod | UV | Violet | Blue | Green | Yellow | Principal | Secondary | Twin |
| Pacific herring | 500±3.69 (18) | ND | ND | 480 | 500±2.34 (16) 521±7.78 (20) | 584,584 | ND | ND | 522±0.7 (4) |
| Northern anchovy | ND | 358, 365 | ND | 472 | 529±8.26 (56) | ND | ND | ND | 530±2.54 (3) |
| walleye pollock | ND | ND | ND | ND | 520±3.11 (17) | ND | ND | ND | ND |
| brown rockfish | 498±1.21 (4) | ND | 417±19.73 (5) | 439±5.87 (13) | 521±3.24 (15) | ND | ND | ND | 520±3.59 (21) |
| kelp greenling | 497 | 350, 358 | ND | ND | 524±5.03 (17) | 541 | 516±7.74 (4) | Y (4) | ND |
| white-spotted greenling | ND | 364±5.39 (5) | ND | ND | 519±4.47 (18) | ND | 519, 520 | 554, 558 | 522±3.75 (14) |
| lingcod | 500±3.24 (10) | 359±8.71 (3) | 403±11.36 (30) | ND | 513±4.76 (208) | 562±8.07 (30) | ND | ND | ND |
| Puget Sound sculpin | ND | 363, 375 | ND | ND | 516±7.11 (13) | ND | ND | ND | 519±2.00 (18) |
| silver-spotted sculpin | 502±3.24 (10) | ND | 420±9.23 (5) | 436, 434 | ND | ND | 521±6.42 (6) | 569±3.37 (6) | ND |
| red Irish lord | 499±4.99 (7) | ND | 408±6.04 (4) | 482±4.00 (24) | 498±4.03 (5) | 568±1.82 (12) | 482 | 568 | 498, 500 477, 485 |
| great sculpin | ND | 353 | 407 | ND | 513±0.78 (8) 519±2.60 (32) | ND | ND | ND | ND |
| sailfin sculpin | ND | ND | 404±2.90 (11) | ND | 502±1.30 (4) 511±2.10 (33) | ND | ND | ND | 509±1.10 (8) |
| grunt sculpin | ND | ND | ND | 450±8.19 (4) | 513±9.17 (35) | ND | ND | ND | ND |
| cabezon | 502±2.94 (12) | 364±18.02 (4) | ND | 479±6.16 (13) | ND | 569±4.56 (11) | ND | ND | ND |
| rock prickleback | 495±3.50 (16) | 364±16.42 (4) | 411±2.32 (4) | ND | 513±2.64 (37) | ND | ND | ND | ND |
| dwarf wrymouth | ND | 355±4.35 (14) | 409±5.09 (17) | ND | 513±3.79 (73) | 574±5.03 (4) | ND | ND | 511, 519 |
| wolf-eel | 501±3.23 (25) | 378±3.66 (6) | ND | 442±7.42 (5) | 512±9.76 (42) | ND | ND | ND | 520±3.47 (18) |
| quillfish | 497±5.91 (4) | ND | 432 | ND | 517±3.19 (19) | ND | ND | ND | 516± 3.08 (4) |
| Pacific sandfish | 504±1.36 (20) | 359±3.10 (3) | ND | ND | 501±3.12 (3) | ND | 514±5.00 (7) | 567±4.34 (7) | 502±3.45 (8) 514±1.68 (20) |
| Pacific sand lance | 482±7.10 (7) | ND | 398±3.10 (3) | 480±7.10 (5) | ND | ND | 527±3.00 (6) | 493 | ND |
| English sole | ND | ND | ND | 436 | 513±2.07 (12) | ND | ND | ND | ND |
| sand sole | 497± 3.22 (10) | ND | 421, 421 | 446±1.05 (6) | 497±1.94 (7) | ND | ND | ND | ND |

Values are means ± 1 S.D. The numbers of spectra included in the average are given in parentheses. If fewer than three cells were measured in a given class, the $\lambda_{max}$ for each cell is given.

ND, no cell in a given class was found.

Y, a cell with a $\lambda_{max}$ in the yellow part of the spectrum was found, but fell outside the criteria needed to estimate the $\lambda_{max}$ using template fitting.
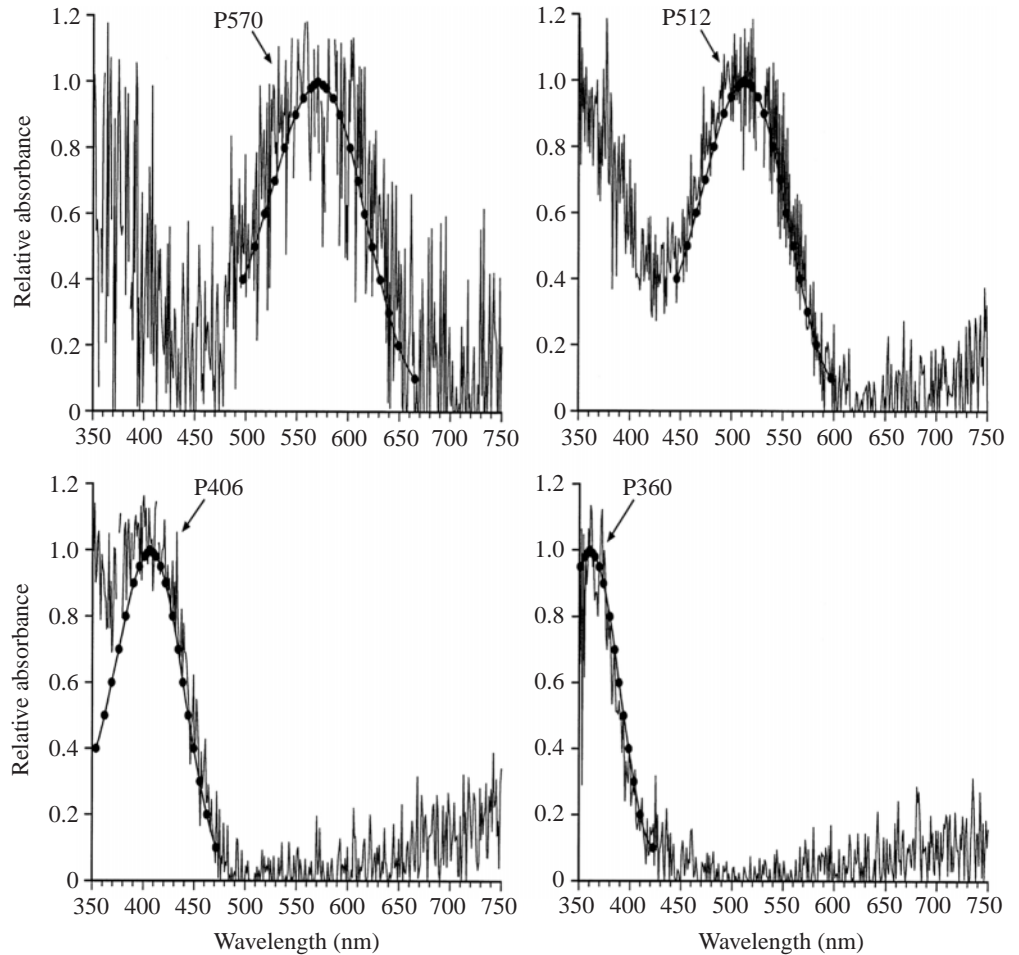
Fig. 1. Spectral absorbance curves from the four single-cone photoreceptor cell types found in the dwarf wrymouth, *Lyconectes aleutensis*. Each absorbance curve was normalized to the $\lambda_{max}$ of the best-fitting template curve (filled circles connected by a solid line). $\lambda_{max}$ of visual pigments of cones sensitive in the yellow (P570), green (P512), violet (P406) and ultraviolet (P360) regions of the spectrum are indicated (arrows). The noise in each recording is typical of that obtained for all the other species examined.

but defined to emphasize visual pigments that are sensitive at short wavelengths. Visual pigments in these five classes, however, were not present in a single species. The presence of three pigments was most common (13 species). In lingcod, dwarf wrymouth, red Irish lord and the silver-spotted sculpin, four visual pigments were present, ranging from the ultraviolet/violet to the yellow regions of the spectrum. Ultraviolet- and violet-absorbing single cones were found in 18 of the 22 species, and in most of the species the outer segments, when viewed on the microscope stage, appeared square to rectangular and large (e.g. in the red Irish lord; length 15 μm, base and distal tip 4.7 μm).

Blue–green- and green-sensitive classes of single cones were present in all but two species. In several instances, closely apposed single cones each containing the same green visual pigment were recorded from the same preparation indicating the likely initial formation of twin cones.

*Double and twin cones*

These cones were present in 13 of the species. Most common were morphologically identical green-sensitive (twin) cones (10 species). In the red Irish lord, in addition to twin green-absorbing cones, twin blue-absorbing cones were also present. Green/yellow-absorbing double cones occurred in four species.
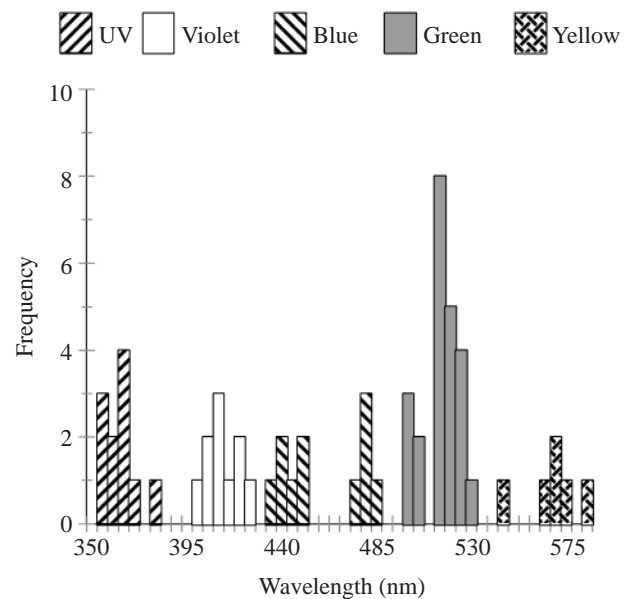


Fig. 2. Frequency distribution for all of the single-cone photoreceptor $\lambda_{max}$ values sampled from all 22 species. Five classes of single-cone photoreceptors were categorized based upon the observed frequency distribution.

## Discussion

The $\lambda_{max}$ values of the visual pigments of the 22 species examined spanned a wavelength range from the ultraviolet to the yellow region of the spectrum. However, only six species had a compliment of visual pigments spanning this entire range. Although our sampling technique included photoreceptor cells from the entire retina, it was difficult to obtain more than 40–50 recordings from a single larva. It is likely that in some species the number of photoreceptor cell classes present was underestimated. However, with the exception of the cabezon, all species possessed green-absorbing cones. Their dominance over other cone types must optimize each larva's photosensitivity to the middle wavebands of the spectrum and correlates with the chromatic characteristics of many inshore waters of the Pacific northwest, where greenish light predominates (Novales Flamarique and Hawryshyn, 1993).

### Rods

It has been assumed that early stage fish larvae possess only cone photoreceptor cells, rods being excluded from the retina until later stages (Powers and Raymond, 1990; Blaxter, 1991; Fernald, 1993; Shand, 1993; Higgs and Fuiman, 1996; Poling and Fuiman, 1997). In the red drum, *Sciaenops ocellata*, Fuiman and Delbos (Fuiman and Delbos, 1998) demonstrated that the scotopic sensitivity increased 5000-fold as the rods proliferated in the late post-flexion stage. However, rods in three of the species we examined (kelp greenling, lingcod and cabezon), although few in number, were present in pre-flexion larvae. 10 of the 13 species in which we identified rods were only analyzed at a post-flexion stage, but this does not preclude the possibility that rods are present at earlier stages in these species. Given the presence of rods in some preflexion larvae, the function they serve, if any, remains to be demonstrated.

The rod $\lambda_{max}$ values were centered around 500 nm except in sand lance larvae, which possessed a more blue-sensitive pigment. The functional explanation for this lower $\lambda_{max}$ (if any) is not obvious, but this species is often active during the dusk-twilight periods until it burrows into the substrate before emerging again during the dawn-twilight periods (Hobson, 1986). The reduction in yellow-orange light during these periods of the day tends to shift the underwater spectrum toward the blue, which might improve scotopic photosensitivity during twilight (Munz and McFarland, 1973).

### Cones

In two of the 22 species examined (kelp greenling and white-spotted greenling), double cones were observed in preflexion larvae. In the white-spotted greenling, twin cones were also observed. However, at hatch the hexagrammid family, which includes the greenlings and lingcod, possess several precocious characteristics (e.g. large pigmented eye, established pigment pattern, large open mouth, limited yolk reserves, etc.) compared to many of the other species examined. The relevance of this early development of double and/or twin cones is, however, obscure. In 13 of the 22 species, including the two greenlings, double and/or twin cones were present in post-flexion larvae. In most of the 22 species examined, photopic vision in the pre-flexion stages appears to depend on the presence of single cones.

The high percentage of ultraviolet and/or violet visual pigment-containing cones emphasizes that 'seeing' in the short-wavelength regions of the spectrum must, in some manner, benefit larval survival. Most of the larvae we examined are distributed during the day near the surface of the water column where they forage on zooplankton. The dominance of green-sensitive cones must benefit visual behaviours in these larvae, including foraging, particularly since blue-green to green are the most abundant photons in the surface waters where they occur (Novales Flamarique and Hawryshyn, 1993). Short-wavelength single cones are also prevalent in the retinae and some fish larvae can orient to plankton and feed in ultraviolet-light alone (Loew et al., 1993; Loew et al., 1996), which implies that these cones extend the spectral range over which foraging can occur.

Due to the increased scatter of short-wavelength light by water molecules, a short-wavelength visual system, especially an ultraviolet-sensitive visual system, is limited to short optical distances (Loew and McFarland, 1990; Losey et al., 1999). However, because fish larvae can only detect targets over short optical paths (1–2 body lengths), the effect of short-wavelength scatter on the visibility of targets is decreased. Because most zooplankton, in spite of their transparency, are as or more reflective to short-wavelength light than to longer-wavelength light, short-wavelength photosensitivity may be adaptive to planktivory (E. R. Loew and W. N. McFarland, personal observations). We do not imply that short-wavelength-sensitive vision is necessarily critical to larval survival, but that it may serve to extend vision into a spectral range where zooplankton are still reflective.

Observations that short-wavelength light can contribute enough photons in near-surface waters to excite an ultraviolet visual system (see Novales Flamarique and Hawryshyn, 1993) bolster the prediction that short-wavelength-photosensitivity is widespread in larval fishes (Loew et al., 1996). The number of marine species is estimated to be near 14,000 (Bond, 1996). The larvae of virtually all of these marine fish species pass through a diurnal planktivorous stage suggesting, in our view, that short-wavelength photosensitivity due to violet- and/or ultraviolet-sensitive visual pigments should be the norm. It remains to be determined by expanded sampling of a variety of fish larvae precisely how ubiquitous short-wavelength photosensitivity is in fishes.

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