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Spectral sensitivity of larval and juvenile coral reef fishes: implications for feeding in a variable light environment

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ABSTRACT: The spectral sensitivity of larval and juvenile stages of 3 species of coral reef fishes, *Apogon compressus* (Apogonidae), *Pomacentrus amboinensis* (Pomacentridae) and *Premnas biaculeatus* (Pomacentridae) has been investigated using feeding behaviour. Ontogenetic and taxonomic differences in spectral sensitivity were determined by establishing the minimum light intensity at which larvae and juveniles could strike prey at 12 restricted wavelength bands between 355 and 650 nm. Following construction of chromatic action spectra, the wavelength of maximum sensitivity (λ_{max}) and the median wavelength (λP_{50}) of the 3 species were found to be located close to 500 nm. All 3 species increased in sensitivity during growth, with *A. compressus* becoming the most sensitive prior to settlement. Ontogenetic shifts in spectral sensitivity towards longer wavelengths occurred in *P. amboinensis* and *P. biaculeatus*, but not in *A. compressus*. Spectral efficiency (wavelength-dependent efficiency of photon capture) was modelled for eutrophic and oligotrophic coral reef waters (Jerlov types Oceanic IA, Oceanic III and Coastal 1) at 2 different optical depths. Spectral efficiency was highest in the intermediate coral reef water type (JOIII) in all 3 larval fish taxa throughout early ontogeny, regardless of water depth. The results imply that the larvae would be able to feed across a broad spectrum of coral reef water types and depths.

KEY WORDS: Colour vision · Chromatic action spectrum · Feeding behaviour · Ontogeny · Pomacentridae · Apogonidae

INTRODUCTION

Light plays an influential role in the ecology and behaviour of most animals, and the structure and physiology of visual systems show adaptations to both the intensity and spectral quality of environmental light (Walls 1942, Lythgoe 1979, 1984). Because aquatic systems provide a natural diversity of spectral environments, our understanding of the significance of species-specific spectral sensitivity has been increased by a wealth of studies on adult teleost visual pigments (Partridge & Cummings 1999 for review). The spectral characteristics of marine waters can vary substantially both vertically and horizontally (Jerlov 1976). Inshore waters close to continental land masses tend to be eutrophic, with peak transmission in the green-yellow region of the spectrum, while offshore and oceanic waters tend to be relatively oligotrophic with peak transmission in the blue region of the spectrum (Jerlov 1976). Increasing depth further enhances the spectral differences between the different water types as the downwelling light becomes progressively monochromatic and centred around the wavelength of peak transmission (Partridge 1990, Nilsson 1996). A good match between the spectral absorption characteristics of the double cone photoreceptors of fishes and the spectral transmission characteristics of their habitat has been found (reviewed in Lythgoe 1984, Partridge 1990, Wehner 1997, Partridge & Cummings 1999). For example, fishes living in clear 'blue' oligotrophic waters possess double cones, which are more sensitive

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to short wavelengths than closely related species from 'greener' eutrophic waters (Lythgoe et al. 1994). Similarly, the spectral positioning of double cones and the increasingly monochromatic short wavelength-shifted light environment of deeper waters appear to be correlated (Bowmaker et al. 1994).

During the pelagic stage, larvae of coral reef fish may be transported by hydrographic processes across a range of water types (Williams et al. 1984, Doherty et al. 1995, Roberts 1997) and it is also known that there are depth-specific habitats for different larval taxa. For example, apogonids live at deeper depths than pomacentrids (Leis 1991a,b, 1993, Boehlert et al. 1992). Thus, both the spectral characteristics and light intensity of the ambient light environment the larvae of different taxa experience will differ from each other as well as from that of the reef-associated adults. However, nothing is known about inter-specific differences in the spectral sensitivity of coral reef fish during larval stages, and it is inappropriate to reconcile adaptations of adults to the variable conditions experienced by larvae (Warner 1997).

Many marine teleosts hatch with a rudimentary visual system, with only 1 type of photoreceptor, and during the subsequent pelagic larval stage the structure of the eye undergoes rapid changes as the adult complement of photoreceptors becomes differentiated (Shand et al. 1999a for review). It has recently been shown that the larvae of those taxa, such as Apogonidae, living in deeper water have greater sensitivity in low light conditions (Job & Bellwood 2000). However, it is not known whether interspecfic differences in spectral sensitivity of deeper-living larvae are tuned to increase sensitivity to the spectrally restricted downwelling light experienced by the deeper-living taxa. Nor is it known how spectral sensitivity changes as the full complement of photoreceptors develops.

In this study, we compare ontogenetic changes in spectral sensitivity in 3 species of coral reef fishes during the dispersive pelagic larval stage and early benthic juvenile stage. The wavelength-specific minimum light intensity at which a fish larva is able to detect and strike at live wild-caught zooplankton is used to construct action spectra and provide a measure of spectral sensitivity at different stages in larval and early juvenile development. The results are used to model wavelength-dependant spectral efficiency of each species in eutrophic and oligotrophic waters at different depths.

MATERIALS AND METHODS

Study species. Three species were examined: a cardinalfish (family Apogonidae: *Apogon compressus*); a damselfish (family Pomacentridae, subfamily Pomacentrinae: *Pomacentrus amboinensis*); and an anemonefish (family Pomacentridae, subfamily Amphiprioninae: *Premnas biaculeatus*). These species are widespread on Indo-Pacific coral reefs. Adult *A. compressus* are nocturnal planktivores, adult *P. amboinensis* are broadly omnivorous and adult *P. biaculeatus* are primarily diurnal planktivores. The larvae of all 3 species are diurnal planktivores. In clear oceanic coral reef waters, larval damselfishes are observed primarily in the upper levels of the water column (0 to 50 m) while larval cardinalfishes are more deeply distributed (50 to 200 m) (Boehlert et al. 1992). The distribution patterns of larval anemonefishes are unknown due to their rarity in field ichthyoplankton samples.

Newly hatched larvae of the 3 species were obtained from captive breeding adults and reared in 200 l glass aquaria at 27 to 29°C under a 14:10 h light:dark photoperiod. The rearing conditions were broadly similar to those on the Great Barrier Reef lagoon during the summer peak reproductive period. The larvae were reared according to standard protocols (Job et al. 1997) under broad spectrum lighting (combination of 1 Osram Biolux and 3 Daylight fluorescent tubes; 6500 and 5500 K respectively). Larvae were fed with wild-caught, size-sorted zooplankton (copepod nauplii and copepodites) throughout the larval stage to ensure that there was no conditioning to abnormal prey items (e.g. rotifers). Mean prey width was maintained at approximately 4% of larval standard length (SL).

Developmental schedules and the increase in eye size for the 3 study species are shown in Fig. 1. Experiments were carried out on the larvae of *Pomacentrus amboinensis* at 3 d intervals starting from 6 d post-hatch until Day 27. To obtain an estimate of spectral sensitivity just prior to settlement, individuals which had not completed metamorphosis were used on Day 21 (Fig. 1A). Because apogonid larvae do not display a distinct metamorphosis (Finn & Kingsford 1996), they were studied at 3 d intervals from 6 d post-hatch until 30 d post-hatch. The young apogonids were considered pre-settlement at Day 21 and post-settlement at Day 24 (Fig. 1A), based on the size at which they first appear on reefs (Finn & Kingsford 1996). Due to their markedly shorter larval duration, *Premnas biaculeatus* larvae were studied at two-day intervals beginning on Day 2 and ending on Day 14 post-hatch. As they metamorphosed on approximately Days 8 to 9 and settled on Days 10 to 11 (Fig. 1A), only individuals which had begun metamorphosis (dark body pigmentation with faint indication of middle white stripe) were used on Day 8 and only fully metamorphosed individuals were used on Day 10. It should be noted that despite the differences in the developmental schedules of the 3 species, the growth of the eye of all species follows the same trajectory (Fig. 1B cf. Job 2000).

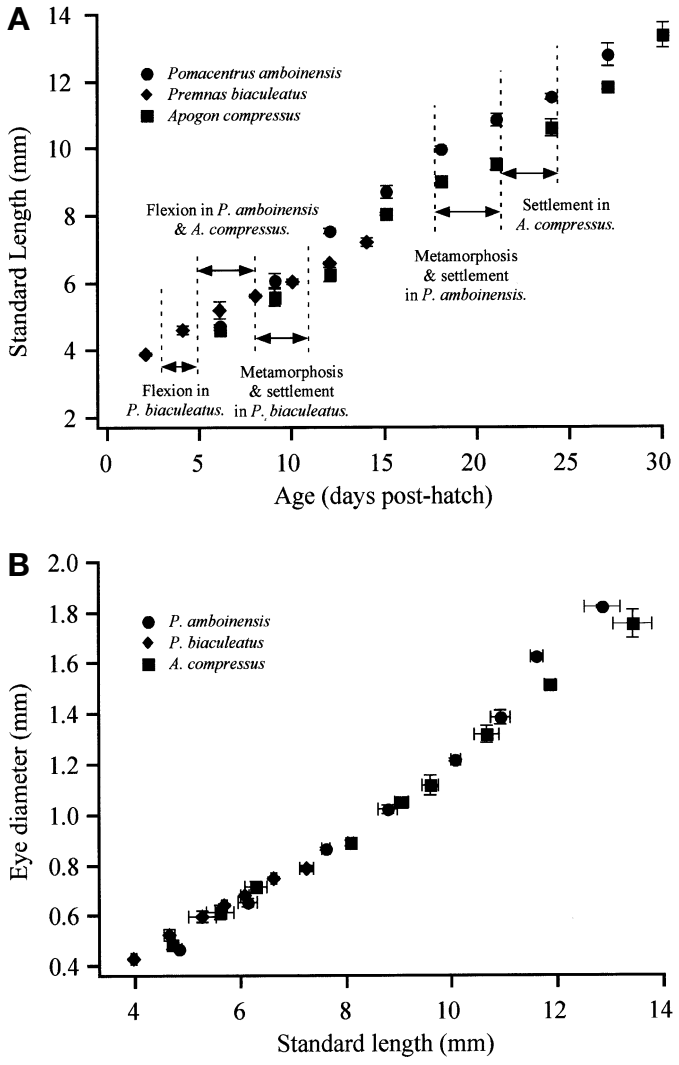

Fig. 1. Growth and developmental schedules of *Pomacentrus amboinensis*, *Premnas biaculeatus* and *Apogon compressus*. (A) Growth in standard length with post-hatch age. (B) Relationship between eye diameter and standard length. Note that *P. biaculeatus* hatches at a more advanced stage of development and undergoes flexion and settlement at an earlier age (post-hatch). Values for standard length and eye diameter are means ± SE. n = 60. After Job (2000)

Experimental procedure. The set-up and protocol for the experiments are based on Loew et al. (1993). Light was spectrally filtered using narrow-band interference filters [Andover Corp., New Hampshire, USA; approximately 10 nm half-bandwidth (FWHM), with out-of-band blocking to at least 1000 nm] before reaching an experimental tank. Larvae were tested at 12 wavelength bands with central wavelengths ranging from 365 to 650 nm (365, 400, 420, 450, 470, 500, 523, 550, 577, 600, 620 and 650 nm). The different wavelength bands were tested in a random sequence. UV photosensitivity was assessed within the approximate spectral range of 355 to 375 nm by using a UV light source (Osram HQV 125 W; spectrum similar to that given in Viitala et al. 1995) in conjunction with the 365 nm central wavelength interference filter (8.5 nm FWHM). Light sources for visible wavelengths were a metal halide lamp (Osram 150 W Daylight bulb) for wavelength bands centred at 400 nm and 420 nm, and a quartz-halogen dichroic lamp (Osram 100 W bulb) for the other wavelengths. The intensity of light reaching the tank was varied by using metallic-coated neutral density filters (Andover Corp., optical densities ranging from 0.2 to 2). Larval feeding behaviour was captured using an infra-red sensitive video camera located above the tank and imaged onto a monitor. An infra-red diode illuminator (880 ± 25 nm) was used to provide sufficient illumination for the video camera. Controls (n = 72) with no additional light source, recorded no feeding behaviour or directed movement in the larvae at any age.

Twelve sets of 5 larvae were sampled on each experimental day (1 set for each wavelength band) after being deprived of food for at least 10 h (i.e. overnight). Each set of larvae was placed in a 170 mm long × 120 mm wide × 120 mm high glass experimental tank containing filtered seawater (approximately 2.2 l volume). The outer surface and base of the experimental tanks were painted black, with the exception of a window where the infra-red diode illuminator was placed. Larvae were light adapted for approximately 30 min under low-intensity broad spectrum lighting (5500 K metal halide daylight bulb) prior to initiating a trial. Following acclimation, prey organisms (wild-caught zooplankton) were added gradually to the experimental tank in small aliquots until a density of 1 to 2 ml^{-1} was obtained. The use of natural prey ensured that larvae were presented with prey displaying movement patterns that closely replicated those of prey in the field. Prey sizes were scaled to larval size (approximately 4 % of larval length), being greater than the visual acuity threshold of the larvae in full spectrum lighting (cf. Job & Bellwood 1996).

During a trial, larval feeding behaviour was observed on the monitor. Initial pilot data had determined that there were no differences in the light intensity of the feeding threshold whether the experiment was conducted from high to low intensities, or low to high intensities. However, an increased time lag was involved in the low to high direction during light adaptation and the high to low regime was subsequently followed. To prevent selective adaptation of different cone mechanisms, the first observations were carried out using as dim a light as possible (no greater in intensity than 1 log unit above that needed to initiate a response). The light intensity was then decreased gradually by adding neutral density filters until feeding ceased. If no feeding events occurred within

10 min, the light intensity was then increased gradually, by altering the light intensity by 0.2 log units until feeding recommenced. This process was then repeated until a consistent light threshold was obtained by observing successful feeding at least 3 times. The threshold of light intensity for feeding was determined as the minimum light intensity at which at least 1 larva was able to strike consistently at live wild-caught zooplankton in 2 consecutive trials. Functional sensitivity at that wavelength band was then calculated as the reciprocal of the minimum light intensity for feeding. Larval feeding behaviour was clearly visible as the younger larvae formed a distinct S-shaped posture and tracked the prey before striking (Job & Bellwood 1996). Older larvae tracked the prey and displayed a prominent tail cocking prior to striking. Strikes preceded by larvae swimming directly into prey were ignored. The experiments were repeated on 3 separate batches of larvae for each species, resulting in 3 replicates for each wavelength band and age.

Given the shallow, clear water and that larvae generally fed close to the surface in the experimental tanks, it was assumed that the difference between the surface light intensity and that where the larvae fed would have been minimal. Light intensities at the surface for UV wavelengths (<400 nm) were measured with an International Light IL1702 UV-A sensor (315 to 390 nm range). For wavelengths greater than 410 nm, surface light intensities down to 0.005 µE m^{-2} s^{-1} (1 Einstein = 1 mole quanta = 6.022E+23 photons) were measured with a Li-Cor LI-192SA quantum sensor (Photosynthetically Active Radiation [PAR] sensor, 400 to 700 nm range). Light intensities below 0.005 µE m^{-2} s^{-1} were outside the accurate range of the sensor and were calculated based on the measured transmission characteristics of the neutral density filters. Wavelength-specific correction factors based on the sensor's spectral characteristics (Li-Cor Corp.) were used to adjust for spectral unevenness in the performance of the sensor over narrow band-widths (Tarrant 1989). Intensities at 400 nm (approximately 395 to 405 nm FWHM) were outside the accurate spectral range of both the PAR and UV-A sensors and were measured using a silicon photodiode (RS Components, USA). A cosine correction factor was empirically derived by comparing the response of the photodiode to that of the Li-Cor and International Light sensors at the other 11 wavelength bands. This factor was then used to correct the response of the photodiode at 400 nm. It should be noted that this method of obtaining the cosine correction factor may introduce a possible error as the cosine response of the Li-Cor and International Light sensors may themselves be limited to a narrow waveband.

Data analysis. The reciprocal of the minimum light intensity for feeding was calculated to obtain a linear sensitivity scale (*sensu* Loew et al. 1993) and the mean linear sensitivity for each larval age at each experimental wavelength band was calculated. Because threshold light intensities for feeding involve physiologically supra-threshold stimuli and supra-threshold wavelength discrimination operates on a log scale (McMahon & MacLeod 1998), the linear sensitivity results are displayed on a log (base 10) scale (log sensitivity). To compare the chromatic sensitivity differences both within and between taxa at selected stages of development across the region of the spectrum investigated, the linear sensitivity values for each batch were normalised (i.e. expressed as a percentage of the maximum sensitivity value for that batch) at selected ages within each species. The mean normalised sensitivity was then calculated from the 3 batches for each species at each of the selected ages.

Because the spectral distributions were skewed, the median wavelength (that which divides the total number of photons under the linear sensitivity curve into 2 halves) (λP_{50}) (sensu McFarland 1991a) was calculated for each species, for each batch, at each age, from the linear sensitivity data. The mean λP_{50} values for each age were then calculated. Similarly, the mean wavelength of peak sensitivity (mean λ_{max}) for each species was calculated from the nominal peak sensitivity values (λ_{max}) of each batch at each age from the linear sensitivity data. Analysis of variance was used to compare the mean λP_{50} values at different ages within a species. As the spectral range over which sensitivity was measurable was narrower in the young larvae, the λP_{50} values for the analysis were calculated over the spectral range of 400 to 620 nm at all ages in all the 3 species. Data for 400 and 620 nm in the youngest *Pomacentrus amboinensis* larvae were estimated from the linear sensitivity graphs. Non-parametric ANOVA (Kruskal-Wallis Test) was used to compare the mean λ_{max} values at different ages within species.

Modelling effective spectral sensitivity. We lack direct measurements of spectral absorption coefficients of Great Barrier Reef waters, however it is possible to make approximate calculations of spectral distribution at different depths, based on the surface irradiance data for tropical coral reef waters (Lesser 1995), and the wavelength-specific attenuation in different water-types (Jerlov 1976). Three Jerlov water types were selected: Oceanic Type IA (JOIA); Oceanic Type III (JOIII); and Coastal Type 1 (JC1). JOIA and JC1 were chosen as they lie at either end of the range of coral reef water types, and JOIII because it shares common features with both oceanic and coastal waters and, in many ways, is intermediate between the two (Jerlov 1976). Within each water type, 2 depths were selected: 12 and 70 m for JOIA; 4 and 15 m for JOIII; and 3 and 12 m for JC1. The shallow depths represent those at

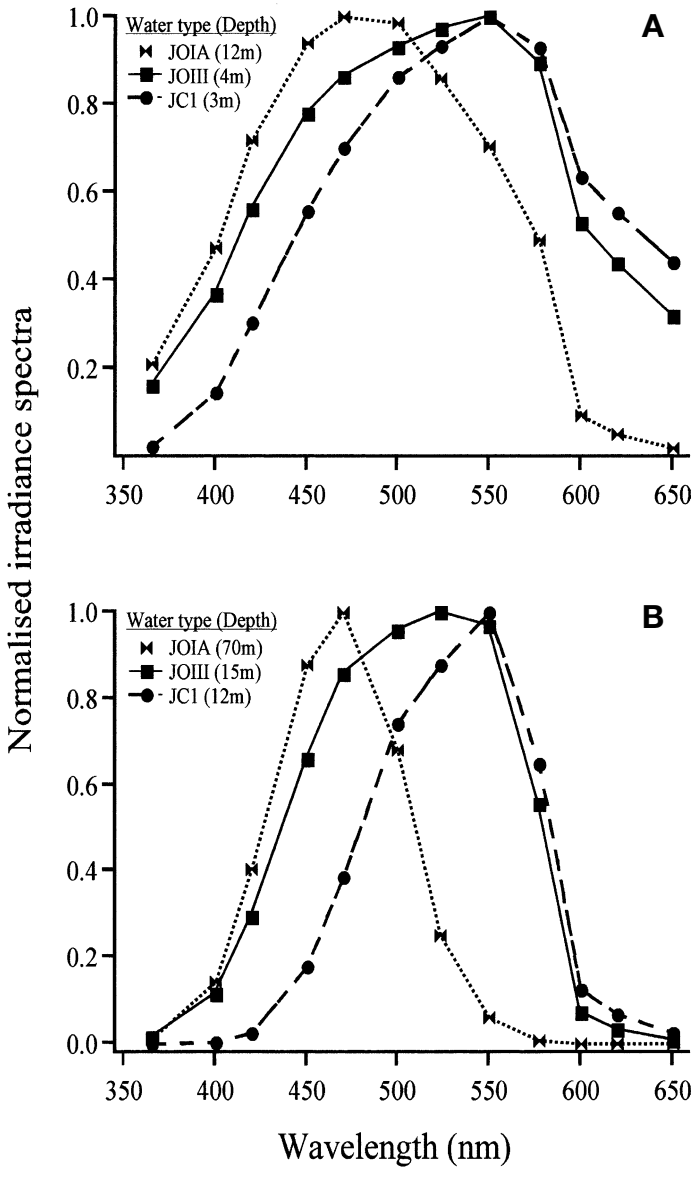

Fig. 2. Normalised irradiance spectra (%) in 3 water types at 2 different depths. (A) Normalised irradiance spectra at shallow depths. (B) Normalised irradiance spectra at moderate depths. Data points calculated for the same wavelengths as used in the experiments. All values were converted to μE m^{-2} s^{-1} before normalisation. After Job (2000)

which the pomacentrine pomacentrid larvae would be expected to occur, but at which apogonid larvae would not be expected. The deeper depths are those at which the apogonid larvae would be relatively abundant, but at which the damselfish larvae would be absent (Leis 1991a,b). The field normalised down-welling spectral irradiance curves for each of the water types/depths are shown in Fig. 2. All 3 shallow depths represent similar optical depths in terms of light intensity (in quanta), as do the 3 deeper depths (Jerlov 1976).

The effective spectral sensitivity of each batch of larvae at specified ages was calculated as the product of the normalised linear sensitivity of the larvae and the normalised down-welling spectral irradiance in the field (cf. Endler 1986, Lythgoe et al. 1994). The relative spectral efficiency of photon capture by the young fishes at different depths in different water types was used for comparison across the taxa and ages using analysis of variance (for further details see Job 2000).

Modelling the spectral distribution of downwelling light. The effective depth to which different wavelengths penetrate and are detected is a function of both the wavelength-dependent attenuation characteristics of the different water types and the functional spectral sensitivity of the larvae. Using the diffuse attenuation coefficients for marine waters (Jerlov 1976) and the surface irradiance values for tropical reef waters (Lesser 1995), the approximate depths to which light of a specified wavelength length could penetrate and be used for feeding can be estimated by rearranging the equation:

$$I_f = I_0 e^{-KD} \quad (1)$$

Where I_f is the minimum light intensity for feeding in W m^{-2} s^{-1}, I_0 is the surface irradiance in W m^{-2} s^{-1}, K is the diffuse attenuation coefficient and D is the depth in metres (Lythgoe et al. 1994). D was estimated, in the 3 Jerlov water types used above, for early- and mid-stage larvae.

RESULTS

Ontogenetic and inter-taxon differences

The spectral range over which feeding was measurable was restricted to approximately 400 to 620 nm in the early stage larvae. With growth, the larvae were able to feed using both shorter and longer wavelengths and the chromatic action spectra were extended to cover 365 to 650 nm. The sensitivity of the larvae of all 3 species increased during ontogeny (Fig. 3, Table 1). For example, an approximately 3.5-fold increase in sensitivity was recorded at 500 nm in *Apogon compressus*. The increase in sensitivity appeared to be most rapid during the pelagic larval stage with post-settlement increases in the juveniles being of smaller magnitude (Fig. 3). In all 3 species the λP_{50} values were distributed over similar wavelengths, ranging from a mean of approximately 493 nm in pre-flexion *Premnas biaculeatus* to 513 nm in juvenile *Pomacentrus amboinensis* (Table 2). During ontogeny the λP_{50} estimates of each species tended towards longer wavelengths, although the shift in sensitivity was only significant in the two pomacentrid species (Table 3). The λ_{max} values covered a similar range to the λP_{50} esti-

mates, however the tendency for a shift towards longer wavelength sensitivity during ontogeny was only significant in *P. biaculeatus*, in which values increased from 490 to 523 nm (Tables 2 & 3).

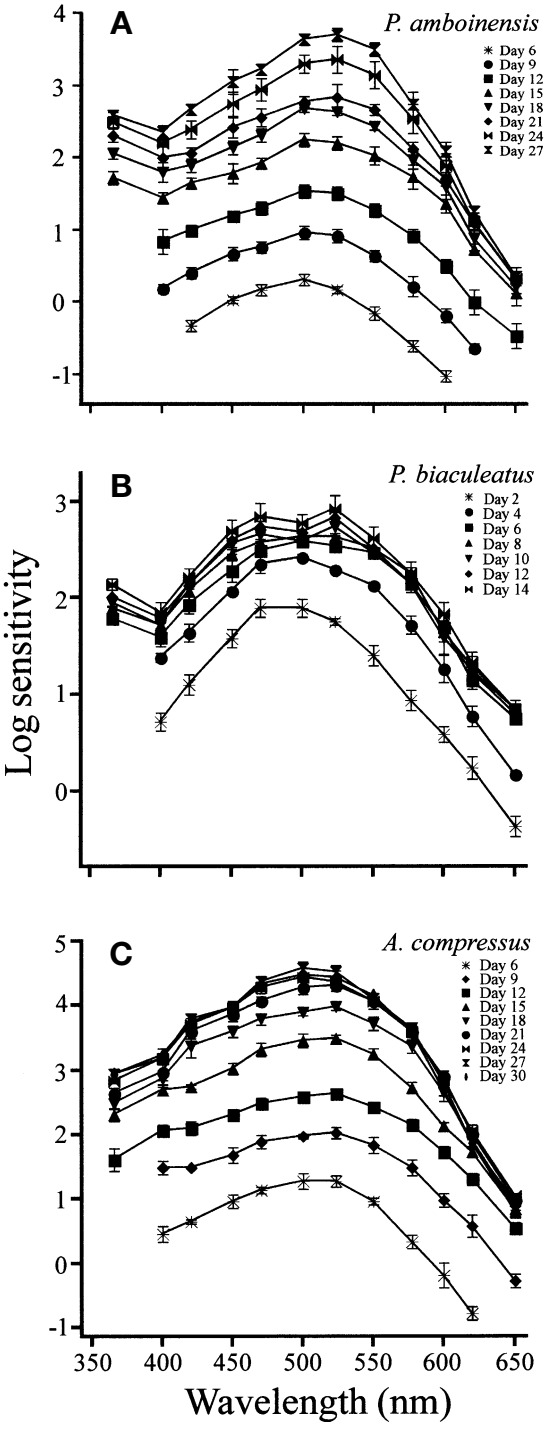

Fig. 3. Ontogenetic changes in $\log_{10}$ spectral sensitivity in (A) *Pomacentrus amboinensis*, (B) *Premnas biaculeatus*, (C) *Apogon compressus*. See Table 1 for raw sensitivity data

The normalised linear sensitivity values for the 3 species were compared at 3 different larval stages (Fig. 4). In the early-stage (pre-flexion and flexion) larvae (ages 2, 6 and 6 for *Premnas biaculeatus*, *Pomacentrus am-*

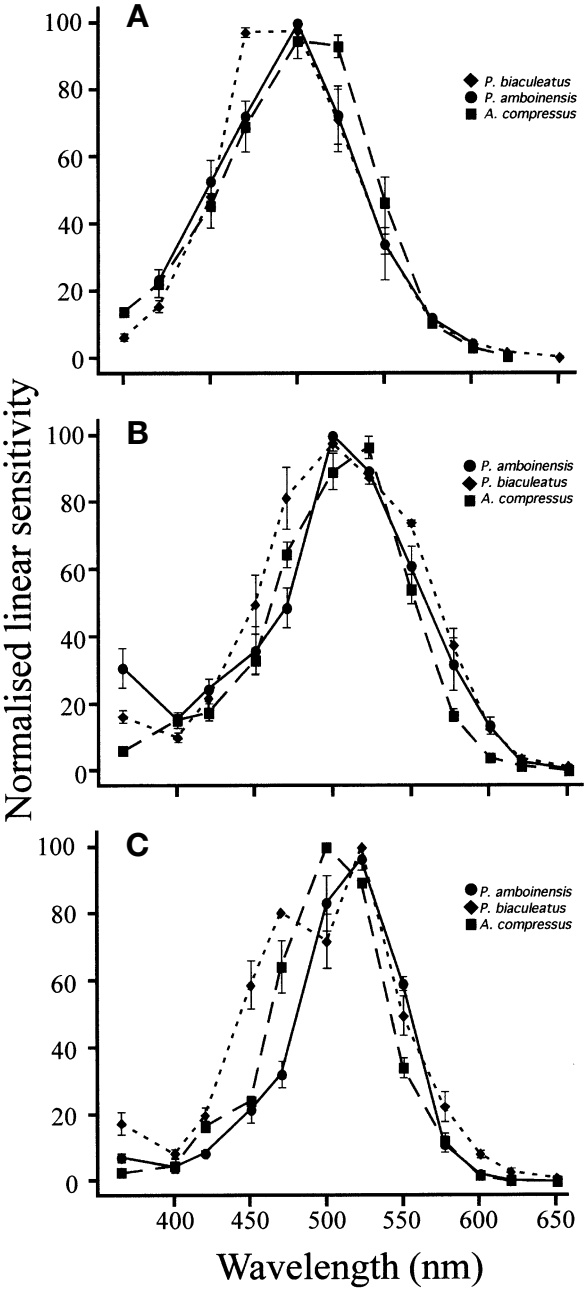

Fig. 4. Normalised spectral sensitivity in (A) the early stage larvae of *Pomacentrus amboinensis* (Day 6), *Premnas biaculeatus* (Day 2) and *Apogon compressus* (Day 6). (B) Mid-stage post-flexion larvae of *P. amboinensis* (Day 15), *P. biaculeatus* (Day 6) and *A. compressus* (Day 15). (C) Post-settlement juveniles of *P. amboinensis* (Day 27), *P. biaculeatus* (Day 14) and *A. compressus* (Day 27)

Table 1. Reciprocal of mean minimum light intensity for feeding, in the 3 species at 3 ages, at the most sensitive wave length (μE m^{-2} s^{-1})

	Mean sensitivity	SE	Wavelength (nm)
Apogon compressus			
Day 6	21.04	5.29	500
Day 15	3218.07	446.64	523
Day 27	39902.73	7820.20	500
Pomacentrus amboinensis			
Day 6	2.13	0.42	500
Day 15	187.31	36.53	500
Day 27	5436.51	1325.16	523
Premnas biaculeatus			
Day 2	82.79	16.43	500
Day 6	392.44	47.83	500
Day 14	942.72	301.54	523

boinensis and *Apogon compressus* respectively), the normalised spectral sensitivity of the *P. biaculeatus* larvae are slightly short wavelength-shifted, while that of the *A. compressus* larvae is slightly long wavelength-shifted compared to *P. amboinensis* larvae (Fig. 4A). In the mid-stage post-flexion larvae (ages 6, 15 and 15 for *P. biaculeatus*, *P. amboinensis* and *A. compressus* respectively), *P. biaculeatus* larvae have a broader spectral sensitivity distribution than the other 2 species (Fig. 4B). In the post-settlement juveniles (ages 14, 27 and 27 for *P. biaculeatus*, *P. amboinensis* and *A. compressus* respectively), the spectral distributions of the *P. amboinensis* and *A. compressus* larvae were similar in shape, but with the λ_{max} of *P. amboinensis* located at longer wavelengths (Fig. 4C). In contrast, the λ_{max} of *P. biaculeatus* larvae was similar to *P. amboinensis.* The appearance of a secondary peak, at approximately 470 nm, in the post-settlement *P. biaculeatus* juveniles was not found to be significant (single factor ANOVA showed no difference in the minimum light intensity for feeding at 470, 500 and 523 nm ($F = 0.336$; df = 2.6; $p = 0.727$)).

Effective spectral sensitivity

The relative spectral efficiency of the young fishes differed significantly between species, developmental stages (age categories), water types and depths (Table 4). Of the first order interactions, 3 were significant, suggesting that some of the main effects need to be interpreted with caution (Zar 1999). Nevertheless, some general patterns are clear. All the 3 species display greater relative spectral efficiency in shallow reef waters than in deeper water of the same type. However, relative spectral efficiency in JOIII waters remained high even at greater depths (Fig. 5). Patterns between species were less consistent and varied depending on developmental stage with differences being minimal in the early stage larvae, but becoming more pronounced during development (Fig. 5). The *Premnas biaculeatus* larvae displayed markedly higher spectral efficiency than the other 2 species after flexion. In contrast, the spectral efficiency of the *Pomacentrus amboinensis* and *Apogon compressus* larvae remained broadly similar until after settlement.

Estimates of feeding at depth

The possible effect of different water types on the depth at which the different species may be able to feed, at 2 different stages of development, is shown in Fig. 6. In eutrophic coastal reef waters, the effective depth range for feeding may be less than 100 m and the wavelengths of maximum sensitivity for feeding in all 3 species shifted towards longer wavelengths (Fig. 6A,B) compared with JOIII waters (Fig. 6 C,D). In the clearest coral reef waters (JOIA, Jerlov 1976), shorter wavelengths penetrate deepest and long wavelengths are at-

Table 2. Ontogenetic changes in the λP_{50} and λ_{max} values of the 3 species. Mean values ± SE (n = 3)

Species/ Age (d)	λP_{50} (355 to 650 nm)	λP_{50} (400 to 620 nm)	λ_{max}
Pomacentrus amboinensis			
6	496.2 ± 0.59	495.0 ± 0.61	500.0 ± 0.00
9	500.1 ± 1.59	500.1 ± 1.59	500.0 ± 0.00
12	503.3 ± 2.90	503.0 ± 2.92	500.0 ± 0.00
15	505.2 ± 2.10	509.1 ± 1.52	500.0 ± 0.00
18	505.7 ± 1.43	508.9 ± 1.24	500.0 ± 0.00
21	506.2 ± 1.30	510.1 ± 1.27	507.7 ± 7.67
24	511.2 ± 2.29	513.0 ± 1.88	515.3 ± 7.67
27	513.0 ± 2.07	514.1 ± 1.94	515.3 ± 7.67
Premnas biaculeatus			
2	493.3 ± 2.87	493.1 ± 2.87	490.0 ± 10.00
4	499.3 ± 1.61	499.1 ± 1.63	490.0 ± 10.00
6	504.0 ± 0.59	506.0 ± 0.41	490.0 ± 10.00
8	502.5 ± 1.79	504.7 ± 2.10	507.7 ± 7.67
10	497.8 ± 1.41	500.5 ± 1.57	523.0 ± 0.00
12	499.1 ± 1.07	501.8 ± 0.98	523.0 ± 0.00
14	499.3 ± 0.19	502.0 ± 0.26	523.0 ± 0.00
Apogon compressus			
6	500.1 ± 0.38	500.1 ± 0.38	507.7 ± 7.67
9	505.7 ± 2.27	505.3 ± 2.19	515.3 ± 7.67
12	502.5 ± 3.49	505.6 ± 3.13	515.3 ± 7.67
15	504.0 ± 0.85	505.9 ± 1.10	515.3 ± 7.67
18	504.8 ± 2.53	505.9 ± 2.36	523.0 ± 0.00
21	507.1 ± 0.59	507.7 ± 0.64	515.3 ± 7.67
24	500.9 ± 1.80	501.6 ± 2.05	507.7 ± 7.67
27	501.8 ± 0.70	502.4 ± 0.55	500.0 ± 0.00
30	501.5 ± 1.73	502.2 ± 1.57	500.0 ± 0.00

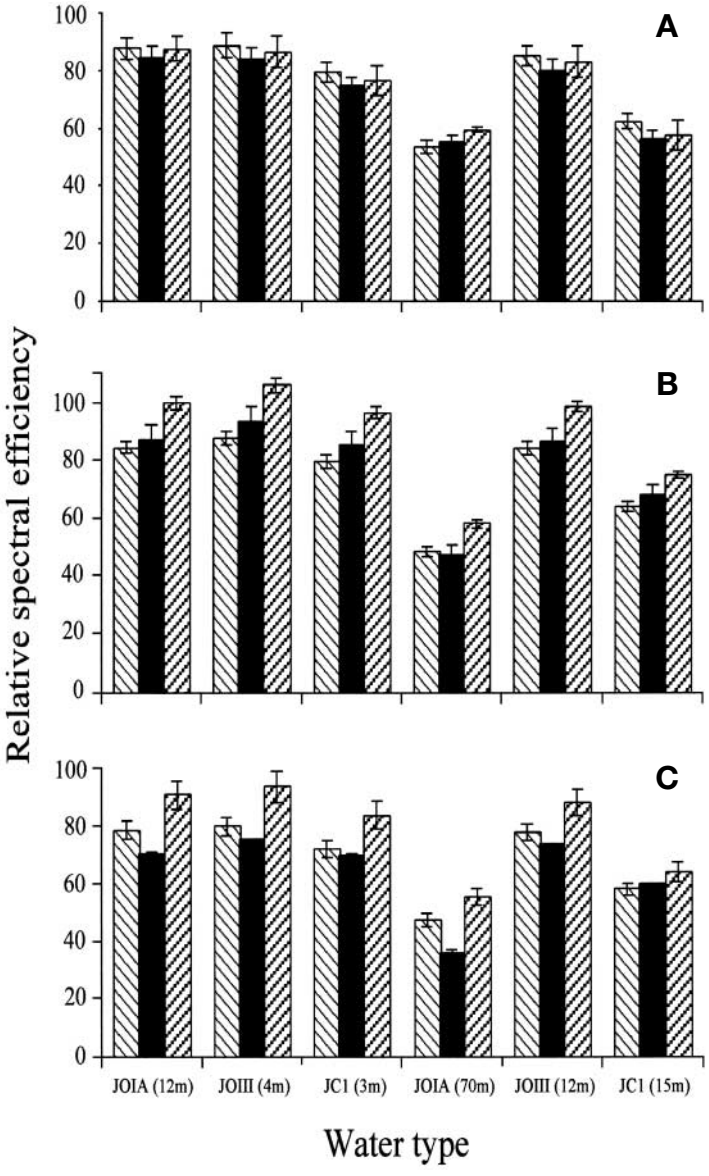

Fig. 5. Relative spectral efficiency of (■) *Pomacentrus amboinensis*, (▨) *Premnas biaculeatus*, and (▧) *Apogon compressus*, in the different water types and depths. (A) Early stage larvae (Days 2, 6 and 6 for *Premnas biaculeatus*, *Pomacentrus amboinensis* and *Apogon compressus* respectively). (B) Mid-stage post-flexion larvae (Days 6, 15 and 15 for *P. biaculeatus*, *P. amboinensis* and *A. compressus* respectively). (C) Post-settlement juveniles (Days 14, 27 and 27 for *P. biaculeatus*, *P. amboinensis* and *A. compressus* respectively)

tenuated relatively rapidly (Fig. 2) so that although feeding may be possible at greater depths, maximum sensitivity would be at even shorter wavelengths (Fig. 6E,F). In all water types, sensitivity of larvae increases during development but the potential feeding depth of the *Apogon compressus* larvae increases relative to that of the *Premnas biaculeatus* larvae (Fig. 6).

Table 3. Statistical comparison of the ontogenetic change in λP_{50} (400 to 620 nm) and λ_{max} values in the 3 species

λP_{50} (1-way ANOVA)			
Pomacentrus amboinensis	$F = 14.77$	df = 7, 16	$p < 0.001$*
Premnas biaculeatus	$F = 6.60$	df = 6, 14	$p = 0.002$*
Apogon compressus	$F = 2.01$	df = 8, 18	$p = 0.104$
λ_{max} (Kruskal-Wallis test)			
Pomacentrus amboinensis	$\chi^2 = 11.38$	df = 7	$p = 0.123$
Premnas biaculeatus	$\chi^2 = 16.44$	df = 6	$p = 0.012$*
Apogon compressus	$\chi^2 = 10.56$	df = 8	$p = 0.227$

DISCUSSION

Spectral sensitivity and ambient light: coastal versus oceanic water

Pomacentrids and apogonids, like most coral reef fishes, have a bipartite life history, undergoing their early development in the pelagic environment (Leis 1991a,b, 1993). During this time they can occupy a range of light environments, depending upon depth within the water column and proximity to land. The λP_{50} (irradiance) values of light in shallow coral reef waters range from approximately 490 nm in oligotrophic reef waters to approximately 530 nm in more eutrophic reef waters (McFarland 1991a,b, Lesser 1995, Maritorena & Guillocheau 1996). The spectral sensitivity of the larvae of *Apogon compressus*, *Pomacentrus amboinensis* and *Premnus biaculeatus*, assessed in this study by feeding behaviour, is located in similar regions of the spectrum, with their λP_{50} values ranging between 493 and 507 nm. Therefore, the relative spectral efficiency of the 3 species remains high across a range of water types at shallow depths and these species appear to be well adapted to the range of possible photic conditions in shallow coral reef waters.

Modelling the relative sensitivity of the 3 experimental species, using irradiance data for 3 water types at 2 different depths, shows how the nature of the photic environment could affect the functional sensitivity of larvae. In coastal waters, the greater attenuation of short wavelength radiation relative to oceanic waters means larvae transported into eutrophic reef waters will be in a light environment with relatively fewer short wavelength photons. In contrast, oligotrophic waters reduce spectral efficiency by preferentially reducing the effectiveness of long wavelength sensitivity. The coral reef species studied here all display the highest spectral efficiency in JOIII waters, which tend to be intermediate between oceanic and coastal waters in terms of spectral composition. Locating the spectral

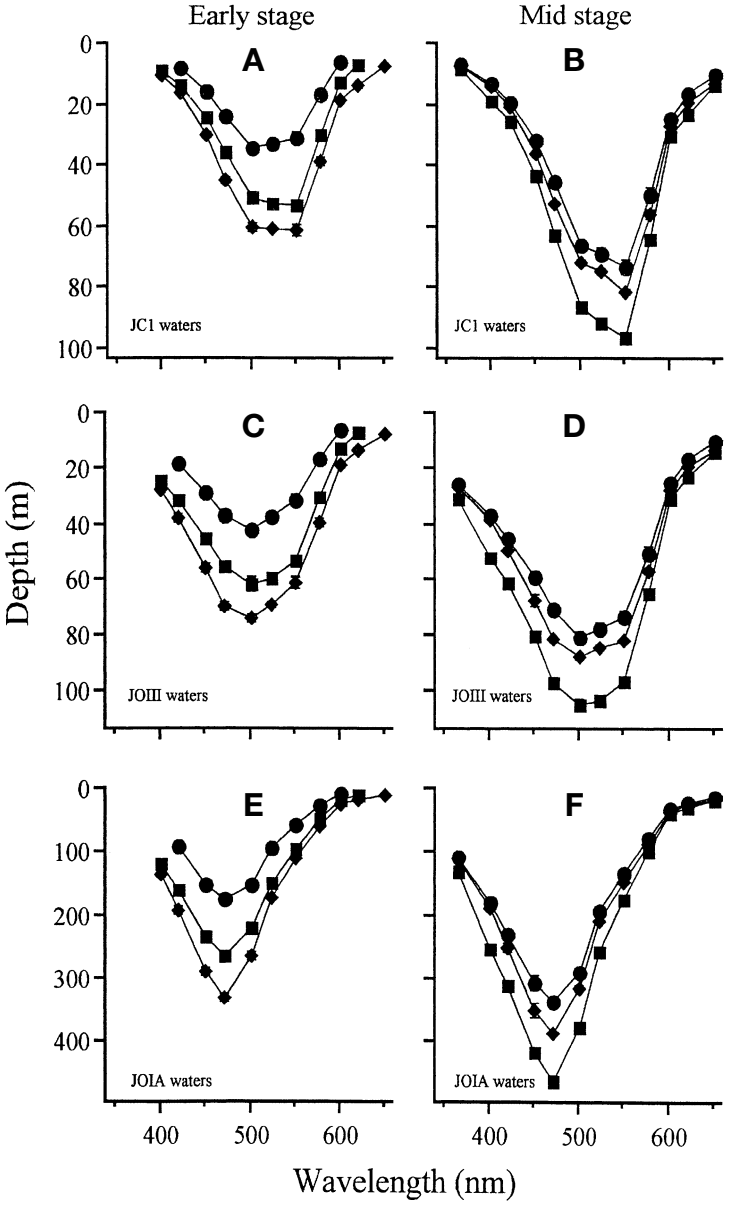

Fig. 6. Model of depths to which sufficient light of different wavelength bands may penetrate, in 3 water types, to enable feeding at 2 stages of development: early stage larvae (A, C, E) and mid-stage postflexion larvae (B, D, F). (●) *Pomacentrus amboinensis* (Days 6 and 15 respectively); (◆) *Premnas biaculeatus* (Days 2 and 6 respectively); and (■) *Apogon compressus* (Days 6 and 15 respectively). Values are means ± SE (n = 3)

sensitivity at longer wavelengths would reduce exploitation of oligotrophic waters, whereas sensitivity shifted to shorter wavelengths would further disadvantage larvae carried into eutrophic waters. With spectral sensitivity tuned to intermediate reef waters, the larvae are still able to detect enough light for feeding at a range of depths in both coastal and oceanic waters, despite the reduction in spectral efficiency. Thus, although reef fish larvae may be vulnerable to transportation by water currents (Roberts 1997), it would appear that their spectral sensitivity allows exploitation of a range of spectral environments.

Spectral sensitivity and ambient light: shallow versus deep water

Field evidence from a range of coral reef water types suggest that the larvae from the family Apogonidae are generally distributed at moderate depths, down to at least 200 m in clear oceanic waters (Boehlert et al. 1992). In comparison, larvae from the pomacentrid subfamily Pomacentrinae are generally distributed at shallow depths, less than 50 m in clear oceanic waters. It is at greater depths that the importance of matching spectral sensitivity to the available light spectrum is likely to become visually significant, because increasing depth results in a marked reduction in both the intensity and spectral bandwidth of the available light (Jerlov 1976, Nilsson 1996). One mechanism whereby fishes can increase their photon capture rates is through matching their spectral sensitivity to the ambient light. Such spectral tuning has been observed in the cottoid fishes of Lake Baikal, in which species living in deeper water have double cones absorbing shorter wavelengths than shallow living species (Bowmaker et al. 1994). However, in the present study, we have not found the spectral efficiency of *Apogon compressus* larvae to be tuned to the narrow bandwidth light of deeper water.

Vertebrates possess a number of other mechanisms for increasing the photon capture, independent of spectral matching (Land 1981, Warrant 1999 for reviews). The apogonids may therefore be able to increase their sensitivity in other ways. These could include: increasing photoreceptor size (van der Meer 1994, Shand 1997, Pankhurst & Hilder 1998); increasing convergence ratios of photoreceptors to higher order neurones (van der Meer et al. 1995, Fuiman and Delbos 1998); or changes in relative eye dimensions resulting in a reduction in Matthiessen's ratio (McFarland 1991a, Shand et al. 1999b, Job & Bellwood 2000).

When modelling the potential depths to which the larvae of the 3 species may be able to feed, it is clear that the apogonids do indeed have greater overall sensitivity than the pomacentrine pomacentrids, despite similarities in both somatic and eye development (see also Job & Bellwood 2000). Our depth estimates predict that in JOIA waters, early stage *Apogon compressus* larvae may be able to feed down to depths of at least 280 m,

Table 4. Comparison of the mean areas under the effective sensitivity curves (mean spectral efficiency) between species, developmental stages (age categories), water types and depths. Analysis done using ANOVA (residual df = 108)

Factor	*F*	df	p
Species	44.64	2	<0.001*
Developmental stage	41.43	2	<0.001*
Water type	183.38	2	<0.001*
Depth	518.18	1	<0.001*
Species by Developmental stage	11.74	4	<0.001*
Species by Water type	2.23	4	0.071
Species by Depth	0.24	2	0.789
Developmental stage by Water type	7.27	4	<0.001*
Developmental stage by Depth	0.83	2	0.439
Water type by Depth	134.44	2	<0.001*
Species by Developmental stage by Water type	1.55	8	0.148
Species by Developmental stage by Depth	0.15	4	0.962
Species by Water type by Depth	1.07	4	0.375
Developmental stage by Water type by Depth	2.04	4	0.093
Species by Developmental stage by Water type by Depth	0.57	8	0.803

while early stage *Pomacentrus amboinensis* larvae may be restricted to depths of approximately 180 m. Thus, the greater depth distribution of the apogonids may simply be a result of their greater overall sensitivity, allowing them greater flexibility for inhabiting spectrally sub-optimal depths across a range of water types (Job & Bellwood 2000). It should be noted that selective adaptation of different cone mechanisms could have occurred during our experimental procedure. Furthermore, a broader chromatic environment in the natural environment compared with the experimental regime may facilitate interactions between different types of photoreceptors, when developed. However, our models provide estimates of the minimum depths to which the larvae can feed and it is possible that a combination of the use of colour contrast and variation in the dynamic range of different cone mechanisms could further extend the depth ranges of all 3 species.

Ontogenetic changes in spectral sensitivity

An increase in sensitivity, throughout the spectrum, was recorded for all 3 species during ontogeny. In addition, a change in either λP_{50}, λ_{max}, or both, occurred in the pomacentrid species, with a shift in spectral sensitivity towards longer wavelengths. The spectral changes were moderate with a maximum range of about 20 nm in the λP_{50} values and about 35 nm in the λ_{max} values for *Premnas biaculeatus*. It is possible that our experimental design is not detecting the full extent of chromatic changes and the mechanisms driving the observed spectral shifts in the species investigated are unclear. Single cones develop first during the early stages of larval life in many marine teleosts, followed at a later stage by double cones, and rod photoreceptors (reviewed by Shand et al. 1999a). Thus, initially at least, it is likely that only 1 class of visual pigment will be present, such as found in larval winter flounder (Evans et al. 1993), and feeding will therefore be photopic. The subsequent shift in spectral sensitivity could be a result of longer-wavelength sensitive double cones being incorporated into the photoreceptor mosaic. However, the exact stage at which the use of wavelength discrimination begins is not detectable using our experimental design.

The functional significance of the spectral shifts in the species investigated is uncertain. Ontogenetic shifts in the spectral sensitivity of cone photoreceptors have been observed in juvenile teleosts, associated with changes in either habitat or diet (Shand et al. 1988, Shand 1993). Marked changes in light environment and feeding behaviour are likely to occur during settlement in reef fishes as the juveniles take up their reef-associated mode of life. The upwelling spectral distribution, in particular, will vary between the pelagic larval and benthic juvenile habitats, becoming more prevalent in long wavelength light (McFarland & Munz 1975, McFarland 1991b). However, further information is required about the exact nature of the visual tasks confronting the larvae and juveniles, at specific times during their development, to fully assess the significance of ontogenetic changes in spectral sensitivity.

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