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# The visual pigments of crabs

## II. Environmental adaptations

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**Summary.** 1. Underwater downwelling quantal irradiance spectra were measured in estuarine and coastal areas under various tidal and rainfall conditions. At midday the available spectrum near the bottom has maximal irradiance in the region of about 570 to 700 nm in the estuary, whereas in offshore coastal areas greatest irradiance occurs between 500 and 570 nm. At twilight in an estuary, maximal underwater downwelling irradiance shifts to the 490–520 nm region.

2. The visual pigment absorption maxima of 27 species of benthic crustaceans from semi-terrestrial, estuarine and coastal areas have values ranging from 483 to 516 nm. There is no obvious shift in the $\lambda_{max}$ from long wavelengths in estuarine species to shorter wavelengths in coastal species. The only match between $\lambda_{max}$ and midday spectrum was for a continental shelf species, *Geryon quinquedens*.

3. The Sensitivity Hypothesis is predicted to account for the visual sensitivity of benthic crabs from estuarine and coastal areas. To assess the match between visual spectral sensitivity and environmental spectra, photon capture effectiveness was calculated for a range of idealized visual pigment absorption functions operating in the measured environmental spectra.

4. All crab species are poorly adapted for maximal photon capture at midday, since pigments having $\lambda_{max}$ longer than 540 nm function best under all daytime spectral conditions. Photon capture of visual pigments with $\lambda_{max}$ near 500 nm improves dramatically at twilight, particularly at lower visual pigment densities and shallow depths. However, pigments having $\lambda_{max}$ at wavelengths longer than those for the crabs are equally or more efficient at photon capture. Therefore the Sensitivity Hypothesis is not supported for crustaceans.

## Introduction

The relationship of the available light spectrum to visual pigment spectral absorption is especially well studied in fish (Munz and McFarland 1973; McFarland and Munz 1975b; Hobson et al. 1981; Crescitelli et al. 1985). Two hypotheses have emerged from these studies. The Sensitivity Hypothesis states that the spectral position of visual sensitivity is matched to the spectral distribution of light in an animal's environment (Munz 1958). In this situation, the photoreceptor is adapted for maximal light sensitivity (i.e. photon capture is maximized). Alternatively, the Contrast Hypothesis states that visual sensitivity is selected to maximize the contrast between a viewed object and its background (Lythgoe 1966, 1968). In this case the visual pigment maximum can be matched to or offset from the environmental spectrum depending upon the depth at which vision is used and the direction of the viewed object (McFarland and Munz 1975b).

Benthic crustaceans include species living in estuarine, coastal and continental shelf areas. Since these species are bottom dwellers, their direction of sight primarily consists of an overhead hemisphere. Near the surface, overhead objects are viewed against the downwelling quantal irradiance spectrum, which may differ from the background spectrum for objects viewed horizontally. With increasing depth the downwelling and horizontal quantal irradiance spectra become similar (McFarland and Munz 1975a). Thus for a benthic animal the spectral irradiance of downwelling light approximates the background against which objects are most often viewed.

Upon progression from estuarine through

coastal into oceanic areas, the wavelength region of greatest light transmission shifts from longer yellow (570–580 nm) wavelengths to shorter blue (470–475 nm) wavelengths (Jerlov 1968). Since the downwelling quantal irradiance spectrum shows a similar shift (Dartnall 1974), one may ask, 'what is the relationship between crustacean visual pigment absorption maxima and the spectra available in different photic environments?'

The present study attempts to answer this question by (1) measuring the available downwelling quantal irradiance spectra in coastal and estuarine areas under various conditions of rainwater runoff, tide, and time of day, (2) comparing these environmental spectra to the visual pigment absorption maxima ($\lambda_{max}$) of species inhabiting semi-terrestrial, estuarine, coastal and continental shelf areas and (3) calculating the relative performance of visual pigments with different $\lambda_{max}$ values in different environmental spectra.

## Materials and methods

The spectrum of downwelling irradiance from 410 to 694 nm was measured with a scanning spectroradiometer having a cosine collector (Biospherical Instruments, Inc. model MER-1000 modified for computer control). Downwelling spectral irradiance was monitored because it best approximates the available spectrum in the hemispherical field of view of a benthic crustacean. Thus in the following sections the term 'spectrum' refers to the downwelling quantal irradiance spectrum.

For measurements the instrument was calibrated in units of quanta/cm$^2$/s/nm. Dark currents were measured each time the machine was turned on and thereafter at about 30 min intervals and automatically subtracted from all measurements. Irradiance spectra at a series of depths in the water column were obtained by positioning the sensor in the vertical plane facing upward and then slowly lowering the instrument. Scans were made continuously during the descent. The averages of every 8 scans (total time for 8 scans was 0.391 s) were sequentially recorded by a computer (KAYPRO-4). Depth, as measured by a pressure sensor on the radiometer housing, was similarly averaged. Spectra were measured on clear days, and representative results are presented.

For data analysis, scans were averaged over 0.1 m intervals. To describe each spectrum, we used the technique of Munz and McFarland (1973) to calculate the wavelength which halves the total number of quanta from 410 to 694 nm ($\lambda P_{50}$). The half width of the spectrum was indicated by determining the wavelength interval enclosed by $\lambda P_{25}$ and $\lambda P_{75}$. The $\lambda P_{25}$ is the wavelength which halves the total number of quanta between 410 nm to the $\lambda P_{50}$ while the $\lambda P_{75}$ provides the value between the $\lambda P_{50}$ and 694 nm. This procedure is especially useful for describing unimodal spectra which occur during the day. At sunset, however, the spectra became bimodal. We acknowledge the potential problems with this calculation method at twilight (McFarland and Munz 1975a) but still used it because it provided a quantitative index of the direction of change in spectral composition over time.

For the horizontal transects, spectra were measured at 4 stations ranging from about 5.5 km into the Newport River estuary (North Carolina, USA), through the estuary mouth (Beaufort Inlet), to about 4.5 km offshore in coastal water. Stations were selected to represent the range of water conditions in local estuarine and coastal areas. Measurements were made between 1000 and 1330 h EDT on two days (August 26 and October 2, 1986). To test for an effect of tidal phase in the estuary upon midday spectra, measurements were made at the dock at the Duke University Marine Laboratory, which is located about 1.5 km from the entrance to the estuary. This location is normally occupied by nearshore coastal water at high tide and upper estuarine water at low tide. Water depth ranges from about 3 to 4 m. Spectra were determined between about 1200 and 1500 h within about 30 min of the time of high or low tide. Measurements of the spectra in the estuary near sunset were also determined at the Duke University Marine Laboratory dock.

The visual pigment absorption maxima of benthic Crustacea are taken from Cronin and Forward (1987). Four of these species were from the semi-terrestrial and continental shelf areas, 19 species were collected from the estuarine/coastal area where the light measurements were made, and the remaining 4 species came from other estuaries having similar photic conditions.

## Results

### *Environmental spectral measurements*

To present the quantal spectral irradiance change around midday upon progression from estuarine to coastal areas, spectra with approximately equal maximal irradiance levels are shown for each station (Fig. 1 A). The overall increase in water clarity upon moving seaward is indicated by the increase in the depth at which this spectrum was measured (Fig. 1 A) from the station highest in the estuary (S1 −1.4 m) to that furthest offshore (S4 −15 m). During conditions of normal rainfall (Fig. 1 A), the spectra also are typical of bottom conditions, since they are measurements just above the bottom at all stations except S3. (At S3 the water column was 12 m deep while the spectrum at 9 m depth is shown in Fig. 1 A.)

**Table 1.** Spectral distribution indices for spectra shown in Fig. 1. See Fig. 1 caption for locations of sampling stations

| | $\lambda P_{50}$ (nm) | $\lambda P_{75} - \lambda P_{25}$ (nm) |
|---|---|---|
| 10/2/86 Normal rain | | |
| Air | 549 | 115 |
| Station 1 | 592 | 99 |
| Station 2 | 553 | 59 |
| Station 3 | 538 | 49 |
| Station 4 | 530 | 47 |
| 8/26/86 Heavy rain | | |
| Air | 554 | 117 |
| Station 1 | 659 | 50 |
| Station 2 | 583 | 94 |
| Station 3 | 554 | 52 |
| Station 4 | 532 | 46 |

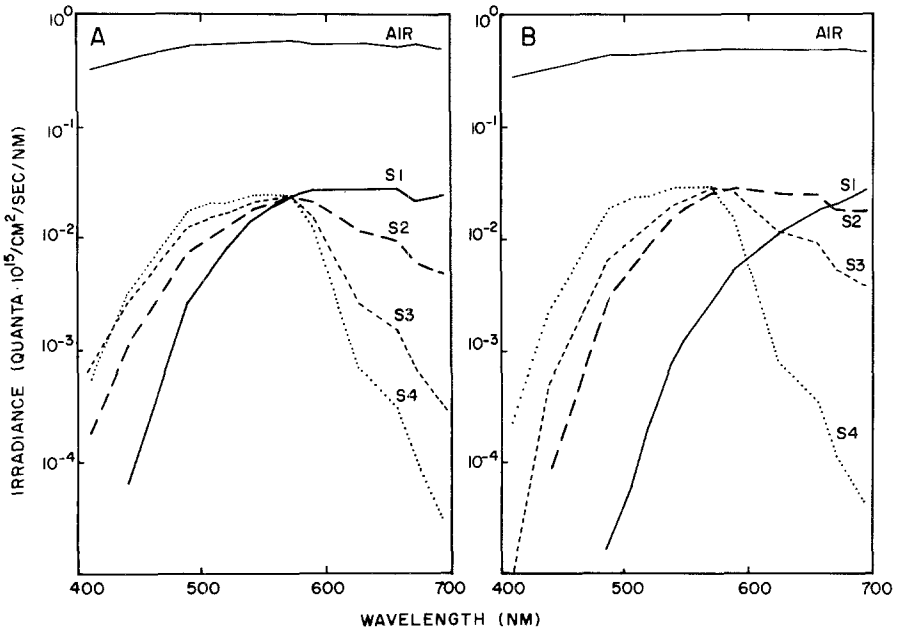



**Fig. 1 A, B.** Downwelling quantal irradiance spectra, measured after a period of normal rain (**A:** Oct. 2, 1986) and after heavy rains (**B:** Aug. 26, 1986). Measurements were made at 4 stations, S1 (5.5 km into the estuary), S2 (1.5 km into the estuary), S3 (2.5 km into coastal water) and S4 (4.5 km into coastal water). The depths at which the spectra were measured in **A** are S1 = 1.4 m, S2 = 3.7 m, S3 = 9.0 m, and S4 = 15 m and in **B** they are S1 = 0.9 m, S2 = 2.5 m, S3 = 5.2 m and S4 = 16 m. These depths were selected to have the maximal irradiances approximately equal. Typical spectra in air, just above the water surface as measured at about 1300 h, are also shown

The spectral distribution changes dramatically upon moving from estuarine to coastal waters. The $\lambda P_{50}$ occurred at 592 nm at station 1, which was furthest into the estuary (Table 1; S1) and progressively shifted to shorter wavelengths upon moving into coastal waters. The seaward-most station (S4) had a value of 530 nm. The spectral half width ($\lambda P_{75} - \lambda P_{25}$; Table 1) became narrower upon moving seaward. Thus the region of greatest number of quanta shifted from the yellow-red region in estuarine areas to the blue-green region in coastal waters.

After heavy rainfall the spectra in the estuary show increased attenuation of blue-green light (Fig. 1 B) due to runoff of water containing Gelbstoff (yellow-absorbing organic compounds) and suspended particulate matter from the land. At Station 1 furthest into the estuary, short wavelengths were removed rapidly and maximal irradiance probably occurred beyond the longest wavelength (694 nm) measured. The $\lambda P_{50}$ for the measured spectrum was 659 nm (Table 1). Near the estuary entrance (S2), the $\lambda P_{50}$ shifted to 583 nm (Table 1) and the overall spectrum (Fig. 1 B) resembled that at the most estuarine station (S1) under normal rain conditions (Fig. 1 A). A similar correspondence occurred between Station 3 after heavy rain (Fig. 1 B) and Station 2 after normal rain (Fig. 1 A). Finally the most seaward station (S4) appeared to be beyond the effects of runoff from heavy rain and had about the same $\lambda P_{50}$ (Fig. 1 B; Table 1) as under conditions of normal rain (Fig. 1 A).

To examine the possibility that tidal phases also modify the underwater spectrum, spectra were

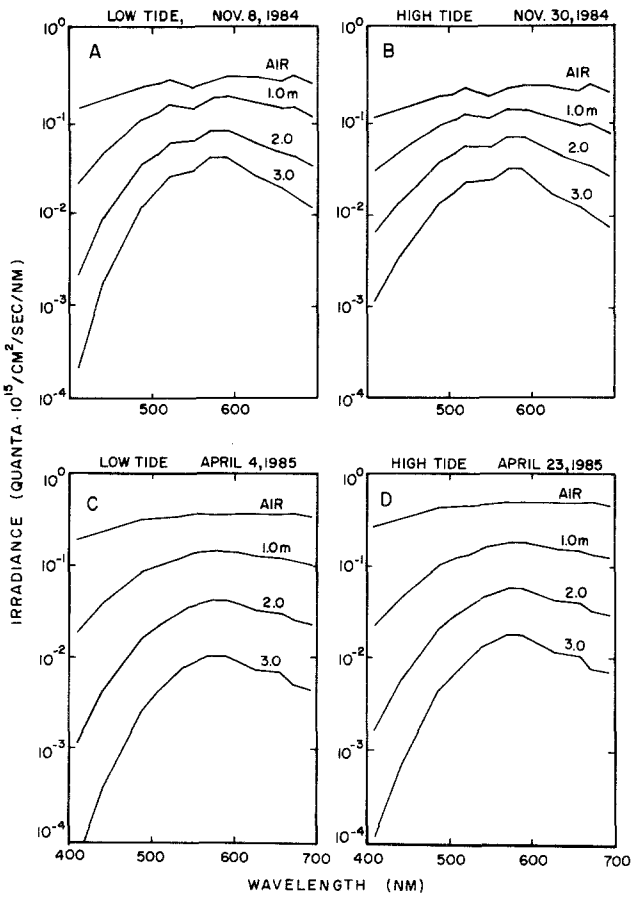



**Fig. 2.** Daytime quantal irradiance spectrum at Station 2 at low (**A, C**) and high (**B, D**) tide during November (**A, B**) and April (**C, D**). The measurement times for **A, B, C,** and **D** are 1357, 1412, 1445 and 1152 h EST, respectively. 'Air' indicates the quantal irradiance spectrum just above the water surface as determined within about 10 min of the water measurements. The maximum depth of the water column was 4 m and spectra are shown at 1 m intervals as measured from the surface

**Table 2.** Spectral distribution indices for spectra shown in Fig. 2

| | $\lambda P_{50}$ (nm) | $\lambda P_{75}-\lambda P_{25}$ (nm) | | $\lambda P_{50}$ (nm) | $\lambda P_{75}-\lambda P_{25}$ (nm) |
|---|---|---|---|---|---|
| 11/8/84 low tide | | | 11/30/84 high tide | | |
| air | 555 | 119 | air | 554 | 117 |
| 1.0 m | 558 | 101 | 1.0 m | 552 | 95 |
| 2.0 m | 559 | 84 | 2.0 m | 551 | 76 |
| 3.0 m | 560 | 69 | 3.0 m | 551 | 67 |
| 4/4/85 low tide | | | 4/23/85 high tide | | |
| air | 551 | 118 | air | 551 | 119 |
| 1.0 m | 559 | 103 | 1.0 m | 560 | 102 |
| 2.0 m | 563 | 90 | 2.0 m | 563 | 88 |
| 3.0 m | 565 | 89 | 3.0 m | 564 | 75 |

**Table 3.** Spectral distribution indices for spectra shown in Fig. 3

| | $\lambda P_{50}$ (nm) | $\lambda P_{25}-\lambda P_{75}$ (nm) |
|---|---|---|
| 4/4/85 high tide | | |
| Subsurface | 540 | 120 |
| 1.0 m | 544 | 105 |
| 2.0 m | 546 | 84 |
| 3.0 m | 547 | 73 |
| 4/23/85 low tide | | |
| Subsurface | 543 | 124 |
| 1.0 m | 547 | 107 |
| 2.0 m | 549 | 90 |
| 3.0 m | 551 | 75 |

measured at high and low tide at Station 2. Measurements were made at times of normal rainfall near midday during two different months (November and April). In both cases (Fig. 2) similar spectra were observed at high and low tides, and the maximum number of quanta always occurred in the region of 570 to 580 nm. In November, 1984 the $\lambda P_{50}$ was only an average of 8 nm lower at high tide as compared to low tide, whereas in April there was almost no difference with tide (Table 2). The $\lambda P_{50}$ increased slightly with depth (average between 1 to 3 m = 3 nm), and the width of the spectra decreased with depth (Table 2). Thus at this location in the estuary the spectrum of downwelling light remained relatively stable at different tidal phases.

It is known that the quantal irradiance spectrum in air changes radically at twilight as compared to that at midday (Rozenberg 1966). Underwater quantal irradiance spectra at sunset are presented at Station 2 for 2 representative days, one having high tide near the time of sunset and one having low tide at this time (Fig. 3). Conditions at the water's surface are approximated by the subsurface spectra. These spectra are bimodal with one maximum in the blue-green region and a second one in the red region. The bimodality is reduced with increasing depth as the red maximum becomes suppressed. The spectra are similar at both tidal phases. The maximum differences in $\lambda P_{50}$ and $\lambda P_{25}-\lambda P_{75}$ values at corresponding depths in the two studies are 4 and 6 nm, respectively (Table 3). At both tidal phases there is a slight shift in the $\lambda P_{50}$ to longer wavelengths with increasing depth.

The changes in spectra underwater at sunset are particularly evident if they are considered over time during twilight. Since the spectra at sunset

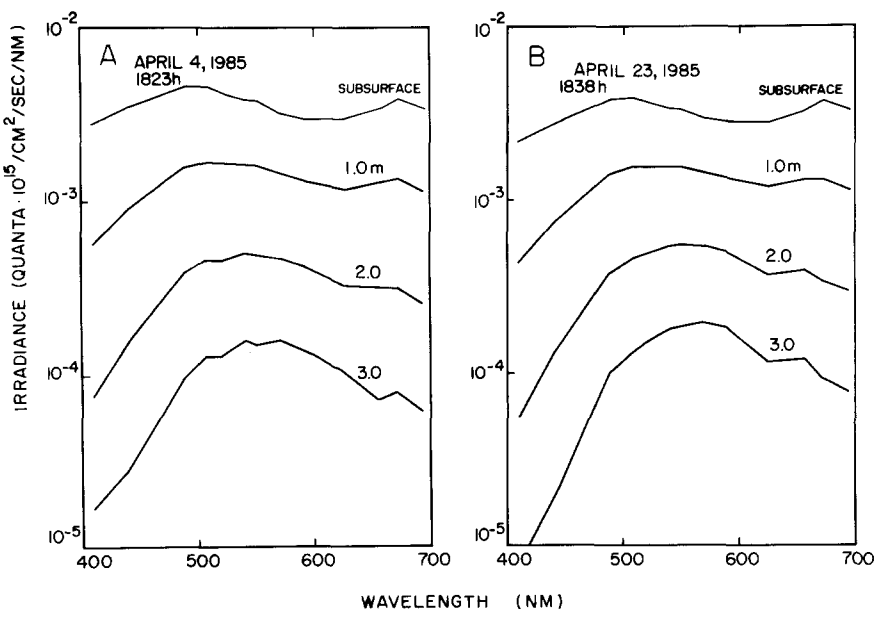
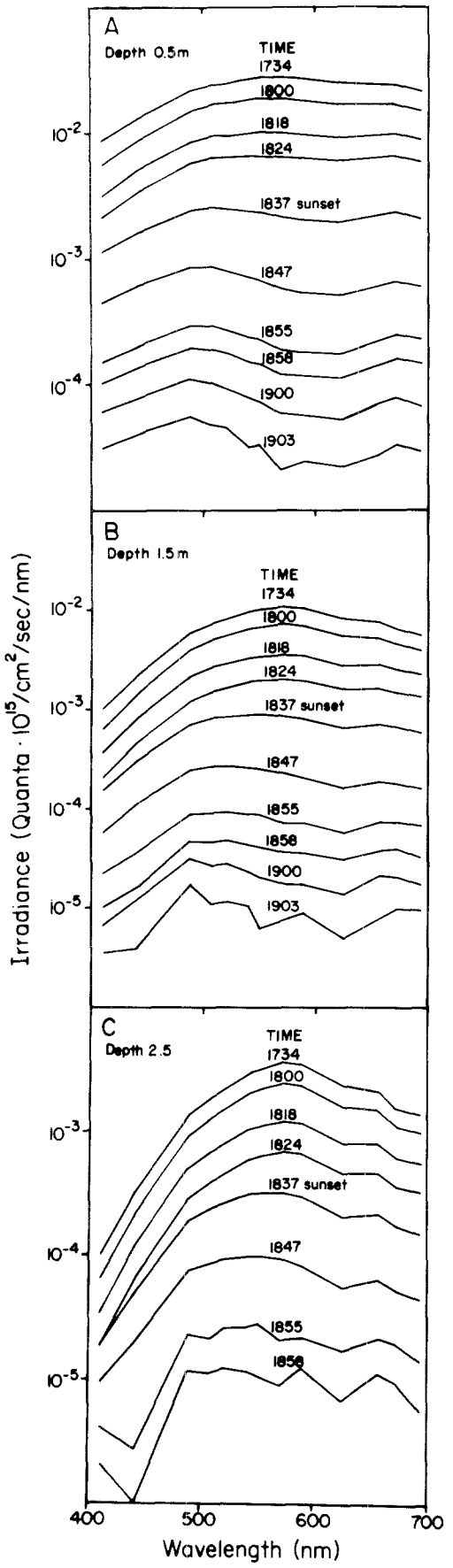



**Fig. 3A, B.** Downwelling quanta irradiance spectra measured at Station 2, at 1 min before sunset on two days having high (**A**) and low (**B**) tide occurring near this time. Sunset times in **A** and **B** were 1824 and 1838 h, respectively. Spectra are shown at 1 m depth intervals. Subsurface indicates the spectrum was measured within 10 cm of the surface



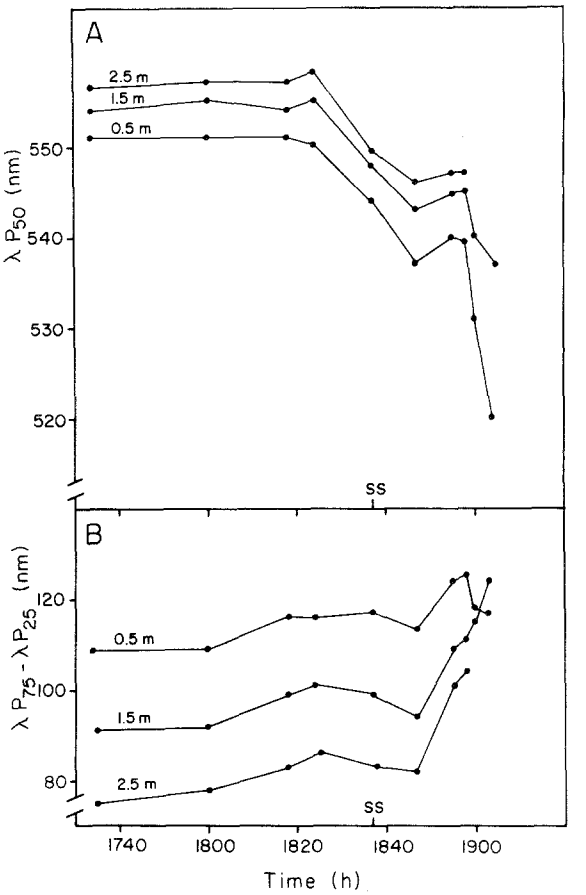




**Fig. 5.** The change in $\lambda P_{50}$ (**A**) and $\lambda P_{75} - \lambda P_{25}$ (**B**) over time for spectra shown in Fig. 4. SS is the time of sunset

are similar at different tidal phases (Fig. 3, Table 3), representative data are presented for one of the days shown in Fig. 3, April 23, 1985 (Fig. 4). One hour before sunset the spectrum underwater resembles that at midday (Fig. 2). At sunset the relative number of photons increased in the blue-green region, declined in the yellow region and increased around 670 nm (Fig. 4). This trend became increasingly pronounced at times after sunset. The relative increase in quanta in the blue-green region during twilight is evident if the $\lambda P_{50}$ at the 3 depths is plotted over time (Fig. 5A). The spectral shift to shorter wavelengths is greatest near the surface (0.5 m depth), where the underwater spectrum is least affected by the attenuation of estuarine water. The $\lambda P_{75} - \lambda P_{25}$ values increase at times after sunset (Fig. 5B) as the spectrum becomes bimodal.

**Fig. 4.** Quantal irradiance spectra at Station 2 at 0.5 m (**A**), 1.5 m (**B**) and 2.5 m (**C**) over time on 4/23/85. The times of measurement (EST) are shown

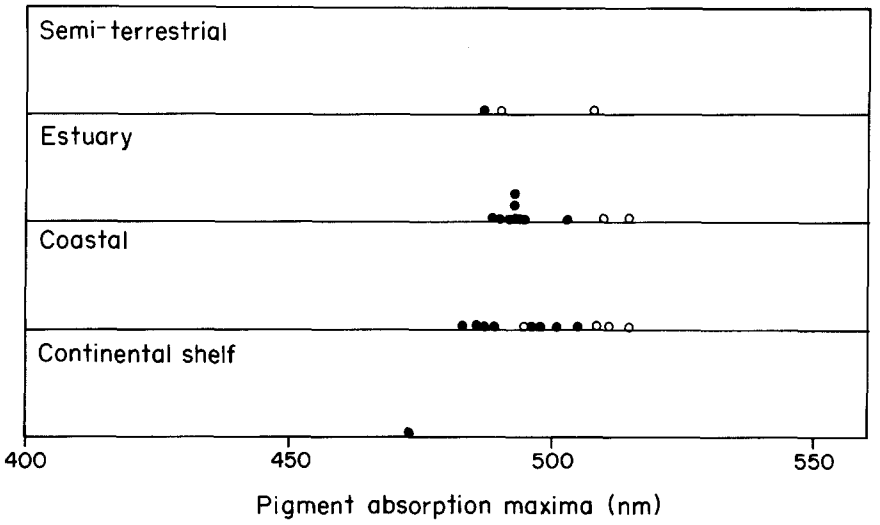



**Fig. 6.** Visual pigment absorption maxima for species living as adults in the various habitats. Filled circles show brachyurans; open circles are anomurans. The species are listed in Table 1

*Crustacean visual pigment absorption maxima*

The absorption maxima for rhodopsins of 27 species of crabs are shown in Table 4 and presented graphically by habitat in Fig. 6 (data from Cronin and Forward 1987). Species are assigned to a habitat on the basis of the adult distributions given in Williams (1984). The anomurans generally have slightly longer wavelength maxima (range 491–515 nm) than the brachyurans (range 473–505 nm). Overall, however, there are no obvious differences in maxima among species from semi-terrestrial (range 487–508 nm), estuarine (range 489–515 nm) and coastal (range 483–515 nm) environments. However the one species that lives in deep water (Table 4) on the continental shelf exhibits the shortest wavelength maximum of 473 nm.

*Performance of crab visual pigments in estuarine photic environments*

Using the spectral irradiance data of this study, it is possible to compute the relative photon catching effectiveness of visual pigments having a range of wavelengths of maximum absorption. The total number ($N$) of photons per unit time and area absorbed by a pigment irradiated by light of a particular distribution is:

$$N = \int A_p(\lambda)\, Q(\lambda)\, d\lambda, \qquad (1)$$

where $A_p(\lambda)$ is the absorptance (fraction of light absorbed) of the pigment at wavelength $\lambda$, and $Q(\lambda)$ is the quantum irradiance at that wavelength, in units of quanta per unit area per unit time per

**Table 4.** Crustacean visual pigment absorption maxima for species from different adult habitats (data from Cronin and Forward 1987)

| | Absorption maximum |
|---|---|
| Semi-terrestrial species | |
| *Coenobita clypeatus*[a] | 508 |
| *Coenobita rugosa*[a] | 491 |
| *Gecarcinus lateralis* | 487 |
| Estuarine species | |
| *Callinectes sapidus* | 503 |
| *Clibanarius vittatus*[a] | 510 |
| *Eurypanopeus depressus* | 490 |
| *Libinia dubia* | 489 |
| *Menippe mercenaria* | 494 |
| *Pagurus longicarpus*[a] | 515 |
| *Panopeus herbstii* | 493 |
| *Panopeus obesus* | 493 |
| *Rhithropanopeus harrisii* | 495 |
| *Sesarma cinereum* | 492 |
| *Sesarma reticulatum* | 493 |
| Coastal species | |
| *Arenaeus cribrarius* | 498 |
| *Calappa flammea* | 486 |
| *Callinectes ornatus* | 501 |
| *Cancer irroratus* | 496 |
| *Dardanus fucosus*[a] | 511 |
| *Hepatus epheliticus* | 487 |
| *Ovalipes stephensoni* | 505 |
| *Pagurus annulipes*[a] | 495 |
| *Pagurus pollicaris*[a] | 515 |
| *Petrochirus diogenes*[a] | 509 |
| *Pilumnus sayi* | 489 |
| *Portunus spinimanus* | 483 |
| Continental shelf species | |
| *Geryon quinquedens* | 473 |

[a] Indicated species is an anomuran. All other species are brachyurans

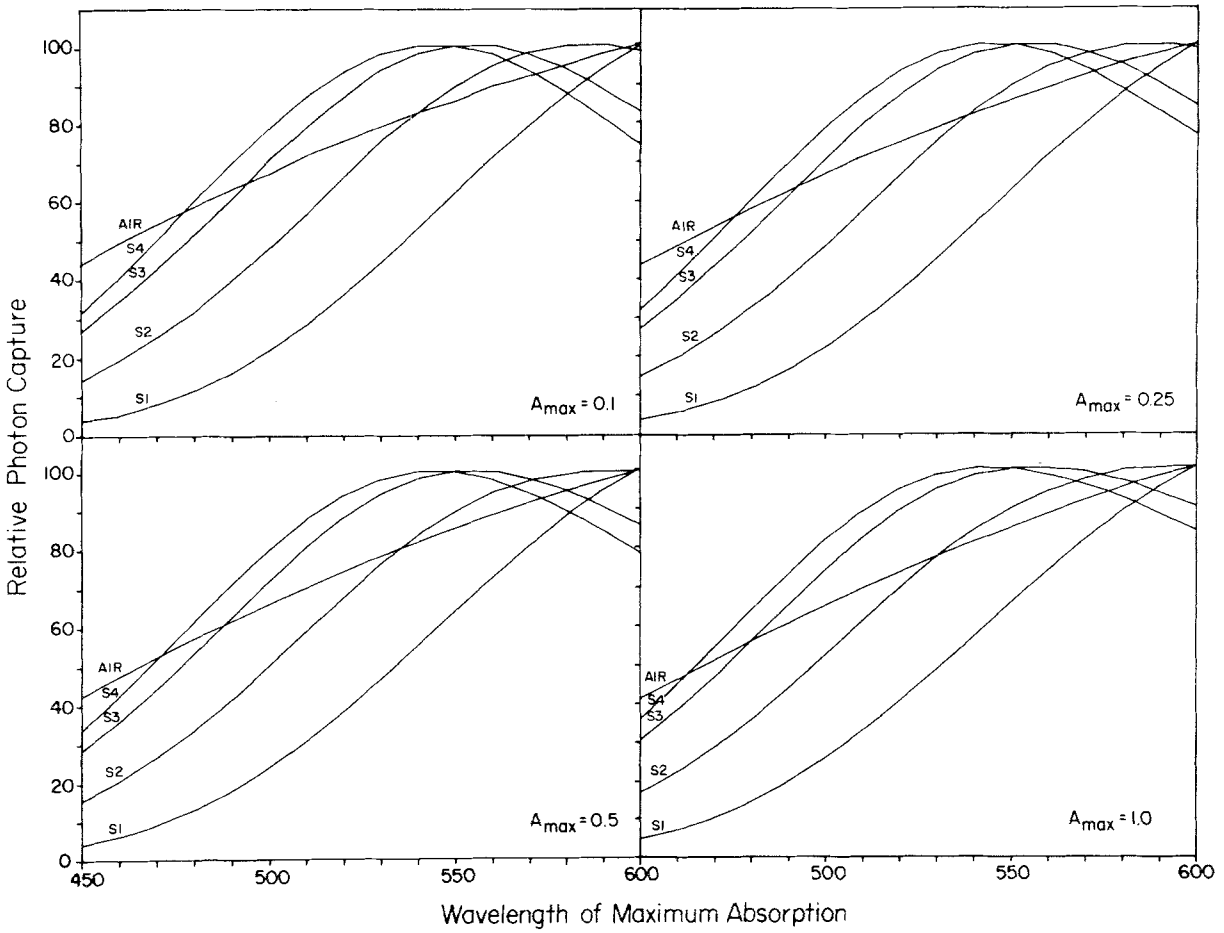



**Fig. 7.** Relative performances of visual pigments with $\lambda_{max}$ values from 450 to 600 nm in absorbing photons in the midday downwelling irradiance spectral conditions of Fig. 1A. Performances were computed using Eq. 1, and each curve is normalized to its maximum value in the range tested. Computations were performed at 4 maximum absorbance values ($A_{max}$), given in the lower right corner of each panel

nm. In practice, the integral may be computed for quantal irradiances in wavelength or wave number (frequency) intervals (see Govardovskii 1976); in this study it is convenient to use bins of quanta per wavelength interval since the spectroradiometer was calibrated in these units. The integral in the wavelength range between 410 and 690 nm was computed from values at 5-nm intervals. At wavelengths not directly measured by the spectroradiometer, quantum fluxes were estimated by linear interpolation between measured values. Each spectral irradiance spectrum was normalized to its peak value.

Idealized visual pigment absorptance spectra were obtained from 450 to 600 nm at 5-nm intervals using an 8th-order polynomial derived from data originally obtained from vertebrate cone photoreceptors, and kindly provided by G.D. Bernard. Isolated rhabdoms from the lobster have axial absorbances of 0.0029 absorbance units per μm for unpolarized light at the rhodopsin's $\lambda_{max}$ (Bruno et al. 1977). MSP data obtained from crabs are consistent with this value (Cronin and Forward 1987). Therefore absorptance spectra were computed for visual pigments having maximum absorbance values of 0.10, 0.25, 0.50, and 1.00. These would correspond to rhabdom lengths of roughly 30, 75, 150, and 300 μm, such as might be found in the larvae of crabs, juveniles, and small and large adult crabs, respectively. Results are summarized in Figs. 7–12.

The downwelling irradiance spectra of Fig. 1A were used to compute the relative performance of visual pigments in midday photic conditions (Fig. 7). At this time, performance monotonically increased with $\lambda_{max}$ up to at least 600 nm for stations S1 and S2. The shortest $\lambda_{max}$ for 100% photon capture is 540 nm under spectral conditions of S4. Thus performance declines in pigments having $\lambda_{max}$ shorter than 540 nm and is especially poor

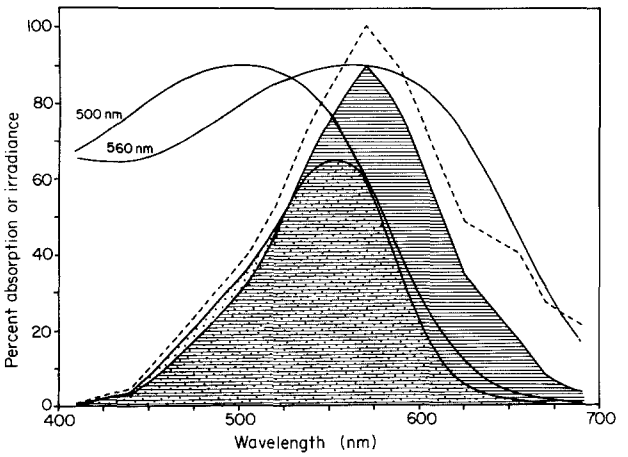



**Fig. 8.** Absorptance spectra for visual pigments having absorbances of 0.5 at $\lambda_{max}$ values of 500 and 560 nm, plotted together with midday downwelling irradiance spectrum from estuarine station 2 (see Fig. 1 A). The dashed curve is the irradiance spectrum normalized to its maximum value. The gray area represents the product of the absorptance spectrum for 500 nm and the irradiance spectrum, while the area for 560 nm is shown by the horizontal lines

for short-wavelength pigments in estuarine conditions (S1 and S2). The relatively poor performance of a 500-nm rhodopsin, such as that possessed by most of our study species, is graphically illustrated in Fig. 8, which shows midday spectral irradiance at Station 2 (Fig. 1 A), together with the absorptance spectra for visual pigments of maximum absorbance of 0.5 at $\lambda_{max}$ values at 500 and 560 nm. The hatched area under each visual pigment spectrum corresponds to the value of $N$ in Eq. 1. The longer-wavelength rhodopsin performs better both because its peak is better matched to the environmental maximum and because the short-wavelength limb of its absorption spectrum continues to absorb effectively down to 410 nm.

At sunset, the situation alters substantially. In Figs. 9, 10, and 11 are plotted the performance curves for visual pigments at depths of 0.5, 1.5, and 2.5 m respectively at Station 2, during the twilight spectral conditions shown in Fig. 4. Although long-wavelength rhodopsins continue to perform

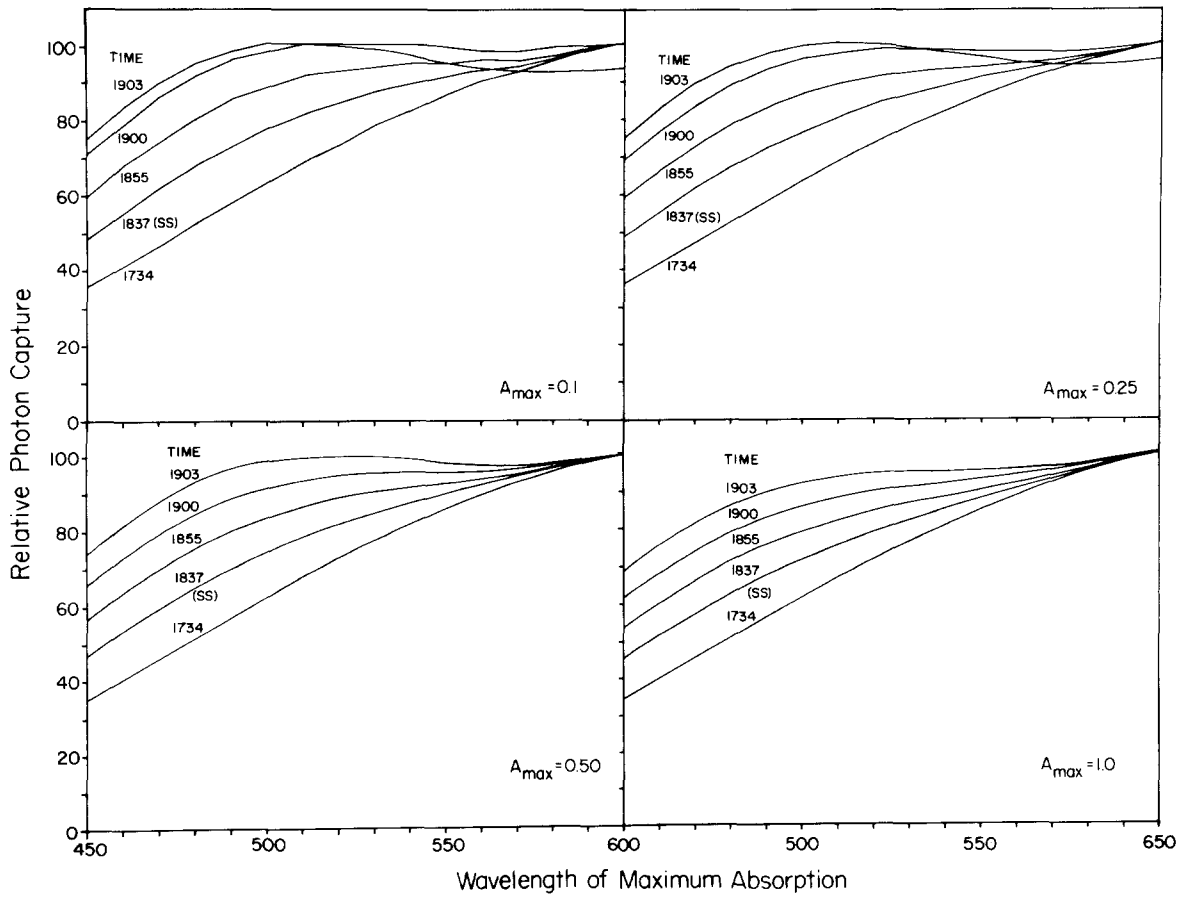



**Fig. 9.** Relative performances of visual pigments with $\lambda_{max}$ values from 450 to 600 nm in absorbing photons in the downwelling irradiance spectral conditions near sunset at estuarine station 2, at a depth of 0.5 m (see Fig. 4 A). Times for which each performance curve was computed are indicated on the graph. SS is sunset

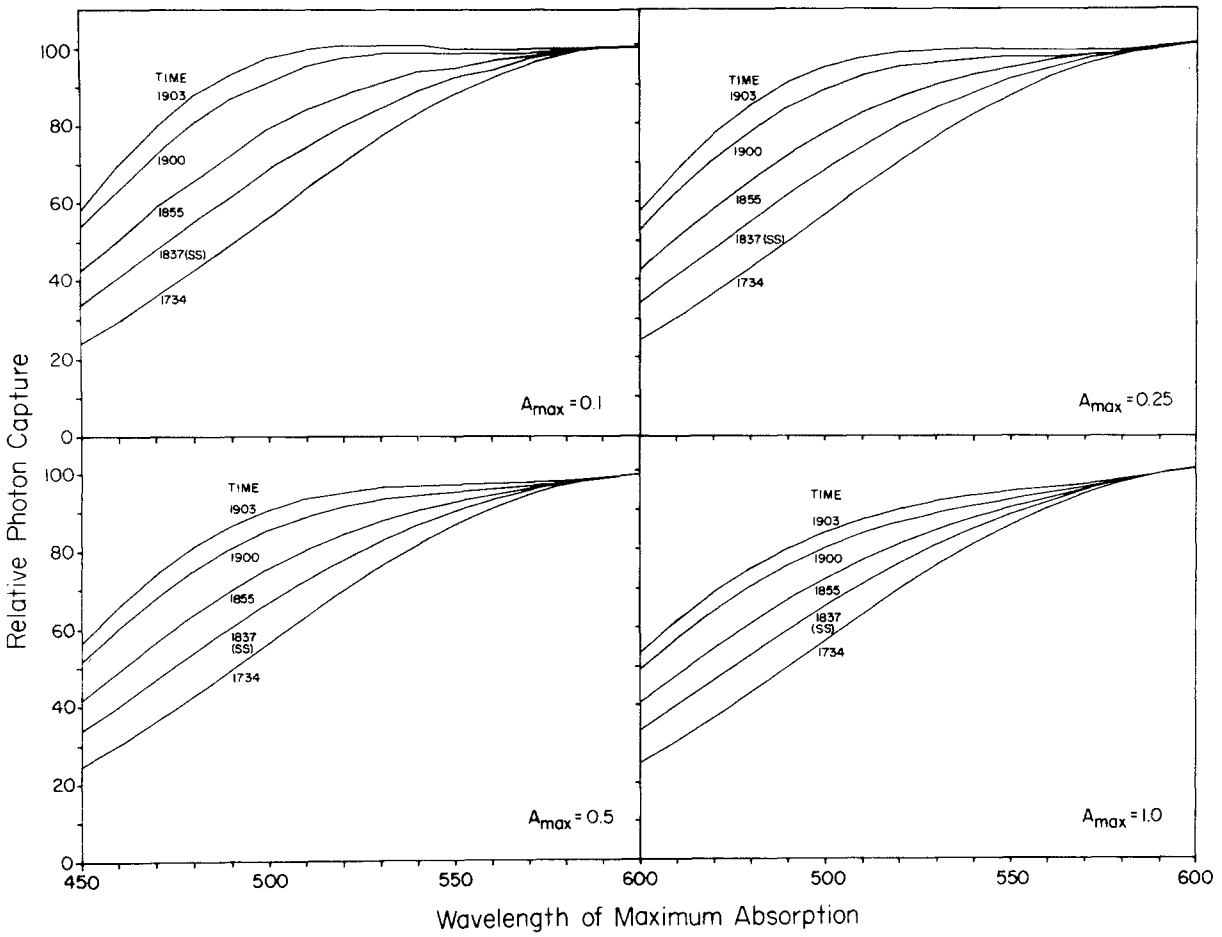



**Fig. 10.** Relative performances of visual pigments with $\lambda_{max}$ values from 450 to 600 nm in absorbing photons in the downwelling irradiance spectral conditions near sunset at estuarine station 2, at a depth of 1.5 m (see Fig. 4B). Otherwise as in Fig. 9

best before the sun sets, the blue-shifted irradiance spectra of twilight (Fig. 5) produce rapid improvements in the relative photon capture of visual pigments with $\lambda_{max}$ values in the range 490–520 nm at the 2 shallower depths. Most noteworthy is the rapid rise in their effectiveness about one-half hour after sunset, just as the spectral radiometer reached the limits of its sensitivity. Presumably, the trend would have continued for several minutes after our measurements ceased, until little or no light continued to penetrate even to shallow depths. Nevertheless, the long-wavelength pigments remained almost equally successful at absorbing photons during our twilight measurements, particularly at higher axial density (see Fig. 12).

## Discussion

Near the bottom of the water column the midday downwelling quantal irradiance spectrum changes upon moving from estuarine to coastal areas. Under normal rainfall conditions, this is well illustrated by the extreme stations of our measurements. In the upper areas of the estuary (Station 1; Fig. 1A) the $\lambda P_{50}$ occurs at 592 nm, while in the most seaward coastal station (S4) the value shifts to 538 nm. This shift is expected (Jerlov 1968; Dartnall 1974), but the present measurements document that the variability in underwater spectra may occur over a relatively short horizontal distance (10 km). The estuarine midday spectra shift to longer wavelengths after runoff from heavy rainfall (Fig. 1B), but under normal conditions they vary little with tidal phase (Fig. 2).

At twilight the underwater spectrum changes in the estuary, and maximal downwelling irradiance occurs in the blue-green region, from about 480 to 520 nm (Figs. 3, 4). Since estuarine water has the lowest attenuation at longer yellow-red wavelengths, this shift reflects the change in the atmospheric spectrum at twilight (Fig. 3) known as the Chappuis effect (Rozenberg 1966). Similar shifts have been observed in clear tropical water (Munz and McFarland 1973) and in the temperate region

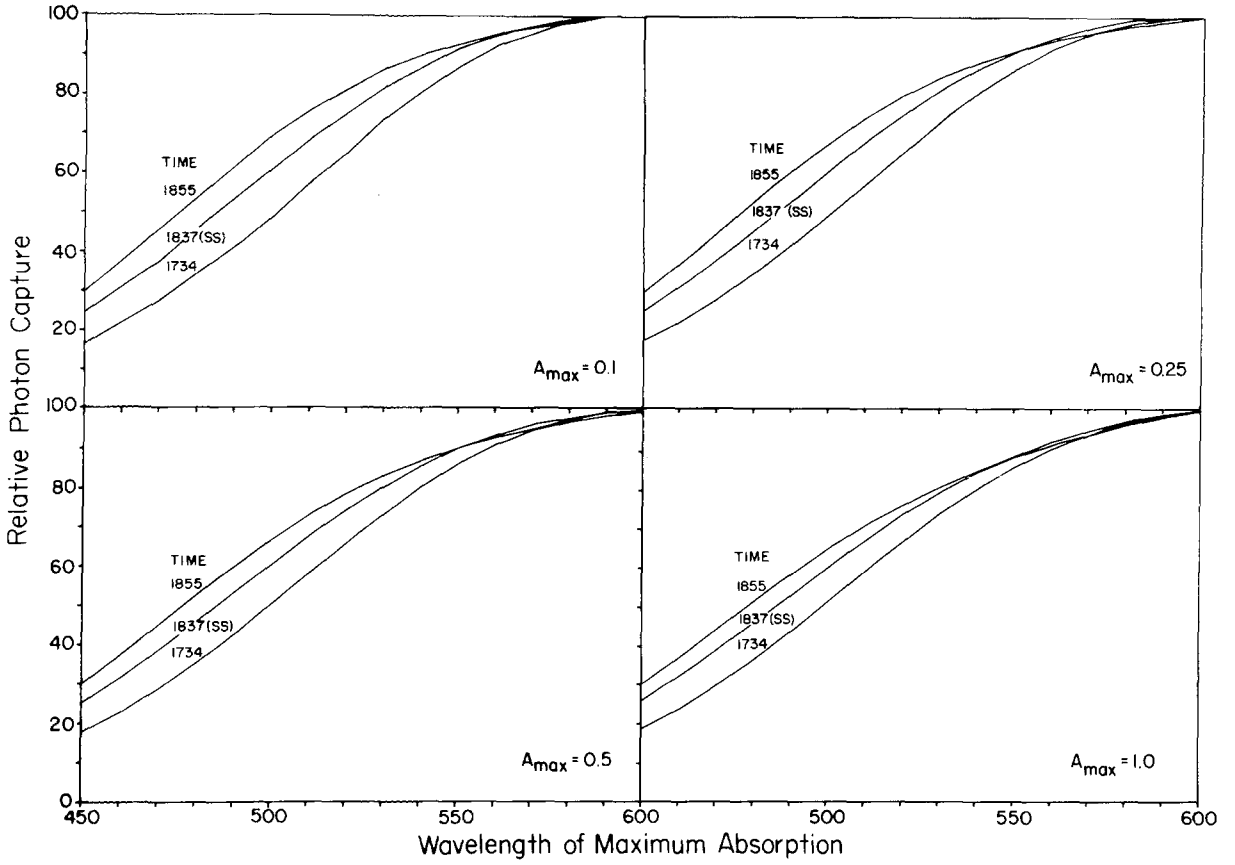



**Fig. 11.** Relative performances of visual pigments with $\lambda_{max}$ values from 450 to 600 nm in absorbing photons in the downwelling irradiance spectral conditions near sunset at estuarine station 2, at a depth of 2.5 m (see Fig. 4C). Otherwise as in Fig. 9

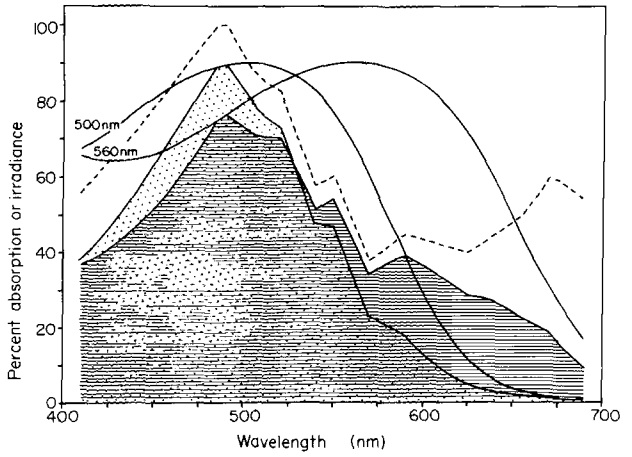



**Fig. 12.** Absorptance spectra for visual pigments having absorbances of 0.5 at $\lambda_{max}$ values of 500 and 560 nm, plotted together with the twilight downwelling irradiance spectrum at 1903 h at 0.5 m depth, from estuarine station 2 (see Fig. 4A). The dashed curve is the irradiance spectrum which is normalized to its maximum value. Gray areas represent the product of the absorptance spectrum and the irradiance spectrum for a 500 nm pigment while the horizontal lines show the area enclosed by a 560 nm pigment

at Catalina Island (Hobson et al. 1981), and no doubt also occur in the coastal regions we studied. Identical spectral changes reportedly take place at sunrise, and the change is evident under clear or overcast conditions (Munz and McFarland 1973; McFarland and Munz 1975a).

McFarland and Munz (1975b) present the predictions of the Sensitivity and Contrast Hypotheses for animals which occur near the surface or in deep water and which view objects in vertical or horizontal directions. A visual pigment that has an absorption maximum offset from the available background spectra is only advantageous for horizontal viewing of highly reflective objects near the surface in clear water. In this situation the downwelling quantal radiance spectrum, which is also reflected by the object, is broad while the background horizontal spectrum is compressed to those wavelengths attenuated the least. In the other cases of (1) all objects viewed from below in shallow and deep water, (2) dark objects viewed horizontally in shallow water and (3) all objects viewed

horizontally in deep water, contrast is maximized by a pigment which has its absorption spectrum matched to the available background spectrum (McFarland and Munz 1975b). Thus for benthic crabs (present study) which have a hemispheric field of view, a matched visual pigment would be best for discriminating (1) all overhead objects in water of any depth, (2) dark objects seen in a horizontal direction in shallow water and (3) all objects in deeper water.

In addition, having a matched pigment may not be disadvantageous for discriminating reflective objects in shallow temperate estuarine and coastal water. In these situations the downwelling quantal irradiance spectra are rapidly compressed to those wavelengths which are attenuated the least (Fig. 1). Downwelling and horizontal spectra then become similar in estuaries at shallow depths because of the high attenuation coefficients of estuarine/coastal water. This situation is analogous to that in deep clear water (McFarland and Munz 1975a), in which a matched pigment is optimal for perceiving all objects viewed in a horizontal direction. We predict that the Sensitivity Hypothesis should apply to benthic crabs from estuarine and coastal areas, and their spectral sensitivity should match the downwelling quantal irradiance spectra in their environment.

Two possible methods that can be used for assessing the match between spectral sensitivity and environmental spectra: First the pigment absorption maximum can be compared to environmental quantal irradiance maxima. This method has been used for fish (McFarland and Munz 1975b; Hobson et al. 1981) and crustaceans (Goldsmith 1972; Forward 1976; Menzel 1979). Alternatively, the photon capture effectiveness of a visual pigment can be determined by calculating the number of photons absorbed when irradiated by environmental spectra (Eq. 1).

Considering the first method, the present study predicts that if a crab's pigment absorption maximum is matched to the downwelling spectrum during the day, then species living in estuarine, shallow coastal and deep coastal areas should generally have a maximum in the regions of 570 to 700 nm (Stations 1, 2; Fig. 1A), 560–590 (Station 3) and 500 to 570 nm (Station 4), respectively. Actually, crabs' pigment absorption maxima occur at wavelengths shorter than 516 nm (Table 4) and thus are rarely in the predicted spectral regions. There is also no obvious shift in the pigment absorption maxima from long wavelengths in estuarine species to shorter wavelengths in coastal species (Fig. 6). The only clear case of a correspondence to daytime spectra is in the single continental shelf species studied (*Geryon quinquedens;* Table 4) which is adapted for lighting conditions in oceanic water (Dartnall 1974).

On the other hand, at twilight maximal irradiance in estuarine water occurs in the region of 480–520 nm. The pigment absorption maxima of estuarine crabs ($\lambda_{max}$ = 489–515 nm) are matched to this spectrum at twilight. A similar match no doubt exists for coastal species. In addition, the semi-terrestrial crabs show pigment absorption maxima in the blue-green region at 487 to 508 nm, which corresponds to the region of maximum subsurface irradiance at sunset (490–507 nm) (Fig. 3).

Even though the pigment absorption maxima appear to be matched to the spectral irradiance maxima at twilight, the effectiveness of a visual pigment is correctly judged by its overall photon capture efficiency. In estuarine and coastal areas, all species of crabs are poorly adapted for maximum photon capture at midday (Figs. 7, 8), because pigments with absorption maxima at wavelengths shorter than 540 nm are outperformed by pigments with longer absorption maxima. This may not be a penalty, however, since midday is the time of greatest photon flux and there is probably still sufficient environmental light available in the spectral region of greatest pigment absorption for visually directed activities.

At twilight in estuaries the environmental spectral shift to short wavelengths produces a better match between the available spectra and overall pigment absorption. At shallow depths the crab's pigments would have improved photon capture as compared to the situation at midday, especially at lower visual pigment density (Fig. 9). Nevertheless, pigment with absorption maxima at longer wavelengths still function as well or better (Figs. 9, 12). With increasing depth pigments having long wavelength absorption maxima always function better than the crabs' pigments (Figs. 10, 11).

Overall, then, the crab's visual pigments operate better at twilight than midday, but still at both times capture efficiency is equal or better for pigments having absorption maxima at wavelengths longer than found for the crabs. These conclusions agree with those of Govardovskii (1976) and do not support the Sensitivity Hypothesis. Thus we lack a satisfying explanation for the grouping of crustacean visual pigment absorption maxima in the blue-green region for animals living in coastal and estuarine areas.

It is worth noting that these conclusions may also be applied to dim light vision of fish (Munz and McFarland 1973; Hobson et al. 1981; Cresci-

telli et al. 1985) and terrestrial vertebrates (Dartnall and Lythgoe 1966; Lythgoe 1972; Dartnall 1974), all of which have maximum sensitivity in the blue-green region. The trend of improved visual performance at twilight may ultimately favor pigments with $\lambda_{max}$ in this region, if the irradiance spectrum continues to shift to shorter wavelengths as twilight proceeds. Nevertheless, nocturnal or moonlight spectra are once again red-shifted (reviewed by Lythgoe 1972; Dartnall 1974). Even at their best at twilight visual pigments with $\lambda_{max}$ near 500 nm capture photons only slightly better than pigments with $\lambda_{max}$ at longer wavelengths, particularly at densities like those in the photoreceptors of adult shallow-water fish, crabs or terrestrial vertebrates. The agents which have acted to select the visual pigments for dim light vision of these animals remain obscure.

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