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RESPONSE OF SETTLING OYSTER LARVAE, CRASSOSTREA VIRGINICA, TO SPECIFIC PORTIONS OF THE VISIBLE LIGHT SPECTRUM

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ABSTRACT Settlement site choice was used to test the ability of competent-to-settle oyster (Crassostrea virginica) larvae to detect specific portions of the visible light spectrum. Larvae were permitted to settle on illuminated or shaded sides of vertically oriented settlement substrates. Five light treatments were used, including white light (400–700 nm), three fractions of white light: red light (600–700 nm), green light (450–575 nm, peak at 525 nm), blue light (400–500 nm, peak at 425 nm), and total darkness. In total darkness, no settlement preference for either side of the substrates was detected. In all light treatments, larvae settled in significantly higher numbers onto shaded surfaces than illuminated surfaces. Crassostrea virginica larvae respond to most portions of the visible light spectrum, unlike many previously studied marine invertebrate larvae. This ability may reflect the diverse light conditions in the largely estuarine habitat of this species.

KEY WORDS: Crassostrea virginica, larvae, settlement, light

INTRODUCTION

Phototactic behavior in marine larvae can contribute to site selection during the settlement process even though the presence or absence of light is not required for settlement (Baker 1997). Pediveliger (competent-to-settle) larvae of the American oyster, Crassostrea virginica (Gmelin), settled primarily on shaded surfaces of substrates in laboratory trials (Ritchie and Menzel 1969). The pediveliger larvae of some bivalve mollusks, including oysters (Ostreidae), has a distinct pigmented region termed the eyespot, and believed to be photosensitive. Cole (1938) initially described the eyespot and its presumed function for the larvae of the oyster Ostrea edulis, although Thompson et al. (1996) point out that research clarifying "eyespot" function is still needed.

Coastal planktonic invertebrates are usually unresponsive, or only weakly responsive, to long visible light wavelengths (orange and red). Serpulid polychaete larvae, which are negatively phototactic when swimming, are responsive to blue and green light (400–550 nm), but indifferent or respond weakly to orange and red light (>600 nm) (Young and Chia 1982, Marsden 1986, 1988, 1990). Barnacle (Balanus improvisus Darwin) nauplii, which are positively phototactic, respond strongly to blue and green light, and also to long-wave ultraviolet (350 nm), but show a marked decrease in response to wavelengths above 600 nm (Lang et al. 1979). The larvae of some estuarine brachyuran crabs, including Sesarma reticulatum and Uca minax, appear to be most sensitive to light wavelengths of 500–600 nm (green to orange), but sensitivity of most species declines sharply above 600 nm (Forw@ard and Cronin 1979). This phenomenon is not limited to larvae; coastal planktonic adult arrow worms, Sagitta hyspida Conant, are most sensitive to blue and green light (400–540 nm) but much less sensitive to wavelengths above 520 nm (Sweat and Forward 1985). The above phototactic responses correlate with spectral attenuation pattern in coastal oceanic waters in which red light (>600 nm) is strongly attenuated, whereas violet to yellow light (400–600 nm) is attenuated the least (Austin and Petzold 1984).

Crassostrea virginica is not primarily an oceanic species, like most of the above examples, but occurs in greatest abundance in estuaries. The adult and larval life history of C. virginica has been reviewed by Stanley and Sellers (1986). In the estuarine environment of the Chesapeake Bay, Virginia, the attenuation of visible light is greatest for short wavelengths (<500 nm), and greatest during the summer when C. virginica larvae are most abundant. Yellow and orange light (550–650 nm) generally have the greatest irradiance (transmission) through the water column (Champ et al. 1980, van Tine 1987). The attenuation coefficient (a natural log scale of light reduction with depth) in the Chesapeake Bay during summer is about 3.1 at 400 nm, 1.6 at 500 nm, 1.1 at 600 nm, and 1.4 at 700 nm (van Tine 1987). At a depth of 1 meter, less than 5% of the surface violet light (400 nm) penetrates, but about 30% of the yellow and orange light (550–650 nm) is still present. Water quality, including inorganic and organic particulate matter, strongly affects light quality in estuarine waters (Pierce et al. 1986). It is probable, therefore, that C. virginica larvae experience a wide range of light quality within a single estuary.

If oysters are unresponsive to certain portions of the visible light spectrum, as are the larval species discussed above, then water quality parameters that affect light quality (Pierce et al. 1986) could affect the ability of oyster larvae to use light as a settlement cue. If oyster larvae do not respond to red and orange light wavelengths, then much of the Chesapeake Bay would be a light-poor environment to larval oysters (van Tine 1987). This study addresses the question: Do larvae of oysters (C. virginica) respond to different portions of the visible light spectrum, as observed by settlement site choice?

MATERIALS AND METHODS

Oyster larval settlement chambers were constructed from 1/8 inch (3 mm) thick black acrylic Plexiglas. One side was made of clear acrylic to permit light entry. Each chamber had internal dimensions of 7.5 cm in height, 7.5 cm in width, and 2.5 cm in depth, and a volume of about 60 ml. A clear acrylic bracket was placed in the bottom of each chamber, at least 2 cm from the sides of the chamber (Fig. 1), to hold a settlement substrate plate in a vertical position. The vertical orientation of the settlement plate was used to eliminate geotaxis (Pireta and Woollacott 1983, Baker 1997) and barokinesis (Crisp and Ghobashy 1971, Mann and Wolf 1983) as confounding settlement cues.

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competent-to-settle pediveliger larva of *Crassostrea virginica* were reared at 20 ppt salinity in the Virginia Institute of Marine Science oyster hatchery. Approximately 500 larvae, in 55 ml of 20 micron-filtered seawater (20 ppt), were pipetted into each settlement chamber. A fan was used to circulate air past the settlement chambers, and temperature within the chambers remained at 25–28°C throughout the trial.

All settlement trials ran simultaneously for 24 h at constant light conditions. There were six settlement chambers for each color treatment, and each series of trials (five treatments) was run twice, for a total of 12 replicates per treatment. At the end of each trial, settled juveniles (spat) on the illuminated (“front”) and shaded (“back”) surfaces of each substrate plate were recorded. Settlement on each side (illuminated and shaded, or front and back in the case of the no-light treatment), was expressed as a proportion of total settlement for each substrate plate. The difference between proportional settlement onto shaded and illuminated surfaces was calculated for each replicate substrate.

Paired-sample t-tests were used to test the null hypothesis that the mean proportional difference between illuminated and shaded (front and back) for each light treatment was equal to zero (Zar 1996). Prior to analysis, the absolute of each difference was transformed using the arcsine-square root transformation (Zar 1996), and then converted back to its original sign.

**RESULTS**

In total darkness, no significant settlement difference between front and back surfaces of the settlement substrate plates was detected. In all other treatments, proportional settlement of *Crassostrea virginica* was significantly higher onto shaded sides of settlement plates. Results are summarized in Table 1.

Larval mortality was less than 1% in any treatment, and larvae that had not settled were still swimming. About 10–12% of the larvae in each trial settled, which was typical for hatchery-reared *C. virginica* larvae at that time (Baker 1994).

**DISCUSSION**

Competent-to-settle larvae of *Crassostrea virginica* respond to red, green, and blue portions of the visible light spectrum in the same manner as they do to white light. In this regard, they are unlike many previously studied coastal larvae, which appear to be unable to use orange or red light (Lang et al. 1979, Young and

### TABLE 1.

Summary of differences of settled *Crassostrea virginica* between back (shaded) and front (illuminated) surfaces. Values are given for mean proportion of larvae settled on shaded (Back) surfaces; the means (Δ Mean) and standard deviations (Δ STDS) of the differences between proportions on shaded and illuminated surfaces, and type 1 error probabilities (p) from one-sample t-tests (based on arcsine-square root data transformations).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Total Darkness</th>
<th>Blue Light</th>
<th>Green Light</th>
<th>Red Light</th>
<th>White Light</th>
</tr>
</thead>
<tbody>
<tr>
<td>Back</td>
<td>0.483</td>
<td>0.783</td>
<td>0.792</td>
<td>0.711</td>
<td>0.743</td>
</tr>
<tr>
<td>Δ Mean</td>
<td>−0.035</td>
<td>0.565</td>
<td>0.583</td>
<td>0.422</td>
<td>0.485</td>
</tr>
<tr>
<td>Δ STDS</td>
<td>0.513</td>
<td>0.265</td>
<td>0.346</td>
<td>0.267</td>
<td>0.309</td>
</tr>
<tr>
<td>p</td>
<td>0.9467</td>
<td>&lt;0.0001</td>
<td>0.0001</td>
<td>&lt;0.0001</td>
<td>0.0001</td>
</tr>
</tbody>
</table>

The breadth of the spectral responsivity of C. virginica larvae reflects the range of water column conditions this species encounters. The spectral transmittance of sea water is strongly modified by dissolved and particulate terrigenous matter, and thus varies between and within estuaries (Pierce et al. 1986). The adult habitat of C. virginica, and thus the habitat of competent-to-settle larvae, ranges from estuarine to seasonal salinities as low as 5%e (Wells and Gray 1960, Stanley and Sellers 1986). A broad spectral responsivity would be a beneficial adaptation for a species occupying this range of habitats. The brine shrimp, Artemia salina, also has a broad spectral sensitivity, and also occupies highly variable water column conditions (temporary ponds), although peak sensitivity appears to be below 600 nm (Aiken and Hallman 1978).

On the other hand, light is not a required settlement cue for C. virginica. In both this study and others (Richie and Menzel 1969, Baker 1997), C. virginica larvae settled in the total absence of light. Gravity appears to be a strong settlement cue by itself. Either light avoidance or geotaxis could permit larvae to settle on lower surfaces of adult oyster shells in the field, but the settlement patterns that result are equally marked in darkness (Baker 1997), indicating gravity as a sufficient cue. Gravity is a constant, light is not. Furthermore, other cues are also available: C. virginica has been shown to settle in response to water-borne chemicals from conspecifics (Hidu et al. 1978), and C. gigas, a similar species, settles in response to chemicals produced by certain bacterial conditions on the substrate (Fitt et al. 1990).

The question then arises: Why has C. virginica evolved a phototactic response during settlement? Assuming that the eyespot is, in fact, a photosensory organ (Thompson et al. 1996), why does it develop only in the competent-to-settle larvae?

One possibility is that phototaxis permits a “fine-tuning” of the settlement response. Oysters, unlike most bivalve mollusks, cement permanently to the substrate immediately upon settlement, and cannot subsequently adjust their habitat choice (Kennedy 1996). Laboratory studies deliberately reduce variables and provide larvae with clear choices (up-down, light-dark), but natural ecosystems are likely to be more complex. It is, therefore, probably of selective advantage to gain in additional sensory systems to gain as much information as possible about a potential permanent home.

LITERATURE CITED


