

REVIEW

Behavioral basis of depth regulation in the larvae of brachyuran crabs*

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ABSTRACT: A model for behavioral regulation of depth of negatively buoyant zooplankters is used as the basis for discussion of research on depth regulation by brachyuran larvae. Behavioral responses to conservative environmental stimuli modify the effects of negative buoyancy. Basic distribution patterns which result may be further modified by responses to increasingly more variable stimuli. Techniques and experimental results for orientation responses to gravity and light are reviewed, as are kinesis responses to light, temperature, salinity, and hydrostatic pressure. Other modifying regulators such as endogenous rhythms in locomotor activity, starvation, and pollutants are discussed. A summary of results by stimulus is provided. Negative geotaxis and high barokinesis promote upward migration in first stage larvae of most species. Ontogenetic changes in sign of geotaxis and presence of barokinesis result in less precise depth regulation and thus vertical scattering in later zoeal stages. Megalopae regain behavioral traits which yield precision in depth regulation. The tactic contributes to dispersal by early stages and recruitment to favorable adult habitats by later instars. Implementation of the model in experimental systems is discussed and its utility in the study of dispersal and recruitment tactics in brachyurans is described, using examples from the literature.

INTRODUCTION

In the estuarine and coastal marine environment, water currents may move in different directions and at different rates at different depths. Because of the role of early life history stages in species dispersal, vertical distribution can be of particular significance to meroplanktonic larvae of benthic marine invertebrates (Thorson, 1950; Mileikovsky, 1972).

A substantial literature exists on studies of vertical distribution of meroplankters and its significance to dispersal. The most direct approach has involved *in situ* measurements of vertical distribution of specific meroplankters (e.g. Carriker, 1951; Bousfield, 1955; Wood and Hargis, 1971; Smyth, 1980; Dittel and Epifanio, 1982). Such studies, however, often are limited in time and space by logistical and financial constraints. A useful complement to such field studies

has been investigation of species-specific behavioral and morphological adaptations that contribute to vertical migration in meroplankters.

This review summarizes and evaluates research on such adaptations in one group of meroplankters: the larvae of brachyuran crabs. There has been increased interest in using brachyuran species as model systems for the study of dispersal and recruitment strategy (e.g. Cronin, 1982; Christy and Stancyk, 1982; Kelly et al., 1982; Sulkin et al., 1982). Brachyurans are amenable to such studies because of their relatively large size, the growing collection of detailed descriptions of specific larval stages of a large number of species, and their ecological and often commercial significance. Furthermore, brachyuran larvae long have been the subject of experimental research on larval behavior (Spooner, 1933; Foxon, 1934; Hardy and Bainbridge, 1951). Recent advances in culture technique for brachyurans (Costlow and Bookhout, 1959; Rice and Williamson, 1970; Sulkin and Epifanio, 1975) have led to greatly improved capacity to rear large numbers of larvae

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under controlled conditions, a phenomenon which has permitted an expansion of such research.

It is therefore timely to review the published research on behavioral and morphological adaptations which influence vertical migration in brachyuran larvae in order to summarize the present state of knowledge and to evaluate critically the value of such research to an understanding of the dispersal process. This review is limited to research which deals directly with larval behavioral traits or other phenomena which may be considered as manifestations of the genome and hence the product of natural selection.

A theoretical model for the study of depth regulation by brachyuran larvae is proposed, followed by a discussion of the specific components of the model. Finally the value of such research to study of larval dispersal and recruitment in brachyurans is assessed.

THEORETICAL MODEL FOR VERTICAL DISTRIBUTION

A simplified model for depth regulation has been described in 'Marine Ecology' by Schöne (1975) for zooplankters in general, and by Sulkin (1973) and Sulkin et al. (1983) for brachyuran larvae specifically. Vertical position of a zooplankter is the net result of complex interactions among morphological and behavioral traits.

An inanimate particle suspended in a column of seawater will exhibit buoyancy, the direction of its vertical movement dependent upon its density relative to that of the surrounding medium. A living particle suspended in seawater will also exhibit buoyancy, the direction and rate of passive vertical movement depending upon morphological (e.g. size, shape) and biochemical (e.g. protein/lipid ratio) adaptations. Control of vertical movement by living aquatic organisms results from modification of the effects of buoyancy by

active means. An understanding of the processes which regulate vertical distribution must, therefore, begin with a consideration of buoyancy.

If brachyuran larvae are anesthetized (0.1 M ethyl carbamate; Sulkin, 1973) and dropped gently into a column of seawater, they immediately will sink with their head positioned downward and their prominent dorsal and rostral spines in a nearly horizontal position (Foxon, 1934; Sulkin, 1973). Brachyuran larvae thus exhibit the negative buoyancy typical of marine invertebrates (Spaargaren, 1979).

Rates of passive descent have been measured for various ontogenetic stages of the species shown in Table 1. Interspecific variation can be substantial, but sinking rates appear to increase during the course of zoeal development by 2 to 3 fold in each species. Upon molt to the megalopa, however, the pattern varies among species.

It is apparent that the effects of negative buoyancy must be overcome if larvae are to maintain vertical position above the bottom or move upward. There is no evidence that brachyuran larvae can regulate buoyancy directly by morphological or physiological mechanisms. Gas-filled bladders, such as employed by teleosts to adjust body density, are not present. Ability to alter body shape is limited. Furthermore, in spite of general increases in percent lipid content through ontogeny, a phenomenon which should decrease density (Mootz and Epifanio, 1974; Frank et al., 1975), sinking rates increase through the course of zoeal development. Effects of negative buoyancy, therefore, can be modified only by locomotor responses mediated by the behavioral repertoire of the species.

Downward movement accordingly may be effected either by cessation of locomotor activity or by complementary action of locomotion on negative buoyancy; upward movement, however, can be effected only by active locomotion, oriented such that it compensates for negative buoyancy.

Table 1. Mean passive sinking rates (cm s^{-1}) for the ontogenetic stages and species indicated

Species	First zoeal stage	Terminal zoeal stage	Megalopa	Source
<i>Panopeus herbstii</i>	0.30	0.90	0.70	Sulkin (1973)
<i>Leptodius floridanus</i>	0.40	0.75	0.60	Sulkin (1973)
<i>Callinectes sapidus</i>	0.35	1.05	1.80	Sulkin et al. (1980); Sulkin and Van Heukelem (1982)
<i>Geryon quinquedens</i>	1.10	—	—	Kelly et al. (1982)
<i>Porcellana</i> sp.*	0.30	—	—	Foxon (1934)
<i>Portunus</i> sp.*	1.20	—	—	Foxon (1934)
<i>Rhithropanopeus harrisi</i>	0.30	0.80	—	Latz and Forward (1977)
<i>Ebalia tuberosa</i>	0.60	—	—	Schembri (1982)
<i>Cancer magister</i>	0.64	2.06	—	Jacoby (1982)

* Zoeal instar not identified by author

The principal orienting stimuli in nature which can elicit directional response in the vertical plane are light (phototaxis) and gravity (geotaxis) (Fraenkel and Gunn, 1961). Gravity is a conservative environmental parameter, being ubiquitous and essentially constant with depth. By definition, negative geotaxis produces orientation resulting in upward movement; positive geotaxis, downward movement. Light is a more highly variable parameter in the marine environment, its intensity, wavelength, and angular distribution varying with depth as well as with many other factors. Nevertheless, at a given depth, the downward ambient flux will be 100 times the upward flux (Clarke and Denton, 1962). In general, therefore, positive phototaxis produces orientation resulting in upward movement; negative phototaxis, downward movement. The sign of response to light and gravity can be altered by external factors such as light intensity, temperature, and salinity. Furthermore, there may be endogenous factors which impose changes in sign of response on various temporal scales (e.g. rhythmic or ontogenetic).

While these orientation responses will determine whether locomotion will complement the influence of negative buoyancy, or compensate for it, net vertical movement will depend upon the relationship between rate of sinking on one hand and rate and frequency of locomotion on the other. Level of locomotor activity also is subject to control by internal and external factors. Internal control of base locomotor activity is presumably a manifestation of metabolic processes and may vary temporally. Changes in level of locomotor activity in response to external stimuli are termed 'kinesis' responses (Fraenkel and Gunn, 1961). High kinesis results from increased locomotor activity with an increase in stimulus intensity; low kinesis, from an increase in activity in response to a decrease in stimulus intensity. Kinesis reactions occur without regard to stimulus direction. The kinesis stimuli most important in the present discussion are light, temperature, salinity, and hydrostatic pressure. In the marine environment hydrostatic pressure is the most conservative of these stimuli being ubiquitous and varying predictably with depth.

The depth regulation model thus has 3 major components: buoyancy, which results in downward movement at a characteristic rate; orientation, which determines whether locomotion will complement or compensate for buoyancy; and level of locomotor activity, which determines the degree to which buoyancy will be modified.

Because external stimuli which elicit taxis and kinesis responses vary with depth, the components of the model may interact to create negative or positive feedback. In general, those interactions which produce negative feedback result in depth regulation in mid-

water while those that produce positive feedback result in movement to the surface or bottom. For example, when larvae are inactive they sink to deeper water and are exposed to higher pressure. If they show high barokinesis, locomotor activity will increase. If they are also negatively geotactic, locomotion will result in upward movement, thus reducing the pressure to which they are exposed and ultimately reducing the level of locomotor activity. This negative feedback results in depth regulation. If, on the other hand, the larvae are positively geotactic, they will swim downward, thus being exposed to ever increasing pressure. Positive feedback, in this case, would result in rapid movement to the bottom.

Vertical distribution of a brachyuran larva is thus the result of a dynamic balance among the various components of the model, such that as one or more of the components changes, there may be predictable changes in vertical position. The time frame over which such changes may occur can vary from seconds to months and may be manifest as changes in vertical distribution which are rhythmic (e.g. diel, tidal) or ontogenetic.

There are relatively few comprehensive studies of the components of the vertical distribution model in larvae of any one brachyuran species; however, there does exist a substantial literature on selected traits. In the following sections the relevant literature for orientation and locomotor components of the generalized model is reviewed. Interactions among the model components which produce negative and positive feedback are illustrated.

ORIENTATION RESPONSES

Geotaxis

Definition and experimental approach

Ubiquitous and virtually constant in direction and intensity, gravity is a conservative orientation stimulus for movement in the vertical plane. Fraenkel and Gunn (1961) define geotaxis as active movement along lines of gravitational force; positive response directed towards the center of the earth, negative away from it. Evidence for true geotaxis in brachyuran larvae is somewhat circumstantial. Early instars do not possess statocysts, the gravity receptor typical of aquatic animals (Gurney, 1902). Foxon (1934) reported that amputation of certain (unidentified) thoracic spines resulted in loss of orientation capacity in darkness, but not in directed light, implicating such spines in gravity reception. The mechanism involved has not been explained further, however. In spite of the absence of

direct evidence for a gravity receptor, there is substantial evidence that brachyuran larvae undergo oriented (non-random) movement in the vertical plane in the absence of light. Such behavior traditionally has been assigned to geotaxis, although the reference may be more descriptive than functional (Foxon, 1934; Sulkin, 1973; Pires and Woollacott, 1983).

In brachyuran larvae swimming almost always occurs in the direction of the dorsal spine (Weldon, 1889; Foxon, 1934; Sulkin, 1973, 1975). Spooner (1933) and Sulkin (1975) reported occasional backwards movements towards a light source, but Sulkin (1975) attributed this response to the experimental conditions employed in which gravity and light stimuli were directed perpendicular to one another. It would thus appear that direction of movement is determined by the power stroke of the maxillipeds and the central orientation of the whole body.

Sulkin (1973) defines the position of the dorsal spine during negative geotaxis as pointing upward 30° from the vertical plane (Fig. 1-A). This orientation must be actively maintained, for cessation of locomotor activity (Foxon, 1934) or application of anesthesia (Foxon, 1934; Sulkin, 1973) will cause larvae to sink after rolling forward to the position shown in Fig. 1B. The orientation producing positive geotaxis also must be maintained actively, since orientation characteristic of passive sinking differs from that of active downward locomotion. Passive sinking occurs with the head down and the dorsal spine in a nearly horizontal position (Fig. 1B). Active downward swimming on the other hand, occurs, as before, in the direction of the dorsal spine, which in this case is pointed downward (Fig. 1C). Thus, in the absence of light, three orientations may be present, two actively maintained and one the result of purely physical forces.



Fig. 1. Diagrammatic two-dimensional representation of orientations of brachyuran zoeae: (A) negative geotaxis; (B) passive sinking; (C) positive geotaxis

Experimental methods used to quantify orientation response usually involve measuring shifts in distribution of a sample of larvae which have been stimulated by the environmental cue in question. Orientation is thus inferred and it is essential to manipulate the experimental system in a way which can produce unequivocal results. This can be particularly difficult

when testing the sign of gravity response, since changes in distribution in the vertical plane can be confounded by buoyancy effects. For example, if net shift in distribution is downward, the result could be attributed solely to negative buoyancy, to a combination of negative buoyancy and positive geotaxis, or to the dominance of passive sinking over locomotor response in negatively geotactic larvae.

Because of these complexities, results from experiments which measure only shifts in distribution in vertically oriented observation tanks (Sulkin, 1973; Bigford, 1977, 1979; Jacoby, 1982; Schembri, 1982) should be interpreted with caution. Such experiments should be supplemented with additional data. Sulkin (1973) provided direct observation of orientation of individual larvae. Ott and Forward (1976) and Latz and Forward (1977) compared passive sinking rates with downward movement of unanesthetized larvae. If the rate of downward movement exceeded that of passive sinking, positive geotaxis was inferred.

Sulkin et al. (1980) have supplemented the vertically-oriented chamber with an identical chamber positioned horizontally. The experimental design employs groups of sibling larvae initially placed at the bottom of the vertically-oriented chamber and at one end of the horizontal chamber. Movement in darkness along the axis of the horizontal chamber provides a measure of random (non-oriented) activity, while movement in darkness along the axis of the vertical chamber reflects both random and oriented response. Distribution in the 2 chambers can be compared statistically after a given period of time. If movement along the axis of the vertical chamber (up from the bottom) exceeds that in the horizontal chamber, negative geotaxis is indicated; if, on the other hand, movement in the vertical chamber is less than that which can be attributed to random activity alone (horizontal chamber), positive geotaxis can be inferred. The use of the horizontal chamber yields the additional advantage of providing a measure of locomotor activity level that can be compared among replicates and among experiments that test the effects of such variables as temperature and salinity upon sign of geotaxis. In this way, differences in vertical distribution can be assigned unequivocally to taxis or locomotor activity differences.

Ontogeny of geotaxis

In general, Stage I larvae tested in the condition of salinity and temperature acclimation are negatively geotactic (Foxon, 1934; Sulkin, 1973; Ott and Forward, 1976; Bigford, 1977, 1979; Latz and Forward, 1977; Sulkin et al., 1980, 1983; Jacoby, 1982; Kelly et al., 1982; Schembri, 1982). This ubiquitous response seems

to cut across a significant range of taxa and habitat types. Recently, Sulkin et al. (1983) have described negative geotaxis in Stage I larvae of *Eurypanopeus depressus*, a shallow-water estuarine form, while Kelly et al. (1982) have reported virtually identical results for *Geryon quinquedens*, a species occupying depths in excess of 200 m. *Cancer magister* larvae exhibit the characteristic negative response to gravity during both the day and night (Jacoby, 1982). Even Stage I larvae of *Ebalia tuberosa*, widely reported as benthic rather than planktonic, exhibit negative geotaxis and initially move upward in an experimental tank (Schembri, 1982). Toward the end of the first zoeal stage, *E. tuberosa* larvae descend to the bottom, although the experimental design cannot distinguish between cessation of locomotion and reversal in sign of geotaxis. In contrast to uniformity in response among Stage I larvae, geotaxis of older zoeal stages and megalopae varies widely among species.

Sulkin et al. (1980) demonstrated the predominance of negative geotaxis in Stage I larvae of *Callinectes sapidus* in salinities of 25, 30, and 35 ‰ (25 °C). The sign of geotaxis shifted however, as zoeal development proceeded. In the intermediate fourth zoeal stage, negative geotaxis prevailed at high salinity, while positive geotaxis prevailed at low salinity. By the terminal seventh zoeal stage, all larvae showed positive geotaxis, independent of salinity. However, Sulkin and Van Heukelem (1982) reported a reversal of this ontogenetic trend when larvae molted to the megalopa. In individuals tested within several days after the megalopa molt, locomotion invariably caused upward movement (negative geotaxis) while downward movement resulted only from passive sinking.

Sulkin (1973) described the gravity responses of the crabs *Panopeus herbstii* and *Leptodius floridanus* (renamed *Cataleptodius floridanus*, Guinot, 1968). In a vertical tank in darkness, early stage larvae were near

the surface while later stages were progressively deeper. Direct observation of individuals confirmed, however, that all zoeal stages retained negative geotaxis, while the observed shifts in distribution were due to a change in the relationship during ontogeny between swimming and sinking rates. Megalopae of both species spent considerable time passively sinking, but when swimming occurred, it resulted in downward movement (positive geotaxis).

Sign of geotaxis and the effects of hydrocarbon contamination on such responses have been described for larvae of the rock crab *Cancer irroratus* (Bigford, 1977, 1979). Using a vertically-oriented column, Bigford (1977, 1979) demonstrated that larvae of Stages I and III showed a higher net position than did those of Stages II, IV, and V. Furthermore as Stage V larvae approached the megalopa molt, they moved closer to the bottom. Megalopae were found on the bottom of the tank. These changes in distribution were attributed by Bigford to 'geokinesis', indicating correctly that the observed shifts in distribution did not indicate a reversal of taxis response, but rather a variation in the relationship between rates of swimming and passive sinking. Stage I and III larvae were described as more 'geonegative' and Stages II, IV, and V as more 'geopositive'. Put into the context of the proposed depth regulation model it seems likely that all *C. irroratus* zoeal instars are negatively geotactic, the differences in vertical distribution among instars being attributed to changes in the relationships between swimming and sinking. Bigford (1979) described megalopae as both sinking and swimming downward, an indication of positive geotaxis. Note that these results are identical to those described for *Panopeus herbstii* and *Leptodius floridanus* (Sulkin, 1973). The application of hydrocarbons at levels of 0.1 and 1.0 ppm (water-accommodated fraction) caused net downward movement in Stages I to III, with variable

Table 2. Typical geotactic response for specified instars of species indicated. (+) positive geotaxis; (-) negative geotaxis; * no data; SI: first zoeal stage; INT: intermediate instars; TERM: terminal zoeal stage; MEG: megalopa

Species	Geotactic response				Source
	SI	INT	TERM	MEG	
<i>Rhithropanopeus harrisi</i>	(-)	*	(-)(+)	*	Ott and Forward (1976); Latz and Forward (1977)
<i>Eurypanopeus depressus</i>	(-)	*	*	*	Sulkin et al. (1983)
<i>Panopeus herbstii</i>	(-)	*	(-)	(+)	Sulkin (1973)
<i>Leptodius floridanus</i>	(-)	*	(-)	(+)	Sulkin (1973)
<i>Cancer irroratus</i>	(-)	(-)	(-)	(+)	Bigford (1977, 1979)
<i>Cancer magister</i>	(-)	(-)	(-)	*	Jacoby (1982)
<i>Ebalia tuberosa</i>	(-)	*	*	*	Schembri (1982)
<i>Geryon quinquedens</i>	(-)	*	(+) ¹	*	Kelly et al. (1982)
<i>Callinectes sapidus</i>	(-)	(-)(+)	(+)	(-)	Sulkin et al. (1980); Sulkin and Van Heukelem (1982)

¹ Sulkin and Van Heukelem, unpubl.

results thereafter. Bigford (1977) stated that larvae were noticeably sluggish in oil treatments, an observation consistent with the conclusion that the oil treatment affected swimming activity. There is the suggestion in his data, however, that swimming activity of later instars may be stimulated rather than depressed in response to hydrocarbon contamination.

Although interpretation of results are often complicated by the difficulty of isolating true taxis responses from the effects of buoyancy, 2 patterns emerge: those species which retain negative geotaxis throughout zoeal development (*Panopeus herbstii*, *Leptodius floridanus*, *Cancer irroratus*) and those in which at least some larvae show reversal to positive geotaxis later in development (*Callinectes sapidus*, *Rhithropanopeus harrisii*). There seems to be no relationship between these trends and geotactic behavior of the megalopa. Geotactic responses of brachyuran larvae are summarized in Table 2.

Effects of temperature and salinity on sign of geotaxis

Studies described previously have been conducted in moderate temperatures and salinities and with larvae acclimated to the experimental conditions. However, larvae moving vertically can rapidly encounter changes in both temperature and salinity, with consequence to taxis response.

The influence of temperature and salinity on sign of geotaxis has been most thoroughly studied in *Rhithropanopeus harrisii* (Ott and Forward, 1976; Latz and Forward, 1977). When tested in darkness at the salinity (20 ‰) and temperature (25 °C) of acclimation, Stage I larvae exhibited negative geotaxis. When placed in higher salinities (up to 40 ‰), virtually all larvae remained in the top portion of the observation chamber, indicating maintenance of negative geotaxis. When placed in salinities below 15 ‰, however, larvae moved to the bottom of the chamber, a response attributed by Latz and Forward (1977) to reversal in sign of geotaxis. At temperatures above 25 °C there was a moderate shift downward in vertical distribution and a more substantial one at 5 and 10 °C. In both cases, rate of descent did not exceed that attributable to passive sinking, leading to the conclusion that temperature extremes promote cessation of locomotor activity to varying degrees rather than stimulating a reversal in sign of geotaxis.

Results for the terminal fourth zoeal stage of *Rhithropanopeus harrisii* are less clear cut. Ott and Forward (1976) reported negative geotaxis at 20 ‰, 20 to 25 °C, while Latz and Forward (1977) indicated that virtually all Stage IV larvae were on the bottom of the experimental chamber under these same conditions.

These apparently conflicting results may be reconciled if one assumes that either the culture or experimental conditions employed by Latz and Forward (1977) produced a lower level of locomotor activity on the part of the late stage larvae. At temperatures below and above the 20 to 25 °C range, most Stage IV larvae were near the bottom of the tank (Ott and Forward, 1976). In contrast to Stage I, the descent to the bottom is due to reversal in sign of geotaxis, except at 10 °C where sinking is the cause. Latz and Forward (1977) reported that most Stage IV larvae were near the bottom of the vertical tank in darkness at all salinities from 5 to 40 ‰. Appropriate experiments confirmed positive geotaxis at the lower salinities (as in Stage I), but sinking and swimming rate measurements of anesthetized and normal larvae were not made at higher salinities.

These results indicate that reversal of negative geotaxis occurs at reduced salinity for both instars and at increased temperatures for Stage IV. Decrease in temperature results in reduction in locomotor activity in both instars.

Phototaxis

Experimental approach

Light is a highly variable parameter in the marine environment, its intensity and spectral composition varying predictably as a function of season and time of day and less predictably as a function of water quality and local weather conditions. The diagram in Fig. 2 (after Clarke, 1970) provides a useful frame of reference for understanding light penetration as a function of depth. Note, for example, that at a depth of 200 m, intensity may vary as much as 10 orders of magnitude depending upon water quality. The more turbid conditions found in near-shore coastal and estuarine regions reduce further the penetration of light into the water column. Clarke (1954) provides a thorough treatment of the physical properties of light in the sea and its biological consequences.

The study of light as an orientation stimulus is complicated by its variability in nature. The problems extend both to experimental procedures employed and to interpretation of results and their application to field conditions. Mechanisms of phototaxis are discussed by Fraenkel and Gunn (1961). The animal adjusts its whole body orientation in response to the light stimulus so that when locomotion occurs, the larva moves toward or away from the light. Among the external variables which may influence sign of response are light intensity, previous light adaptation, temperature, and salinity.

Experimental approaches have varied considerably

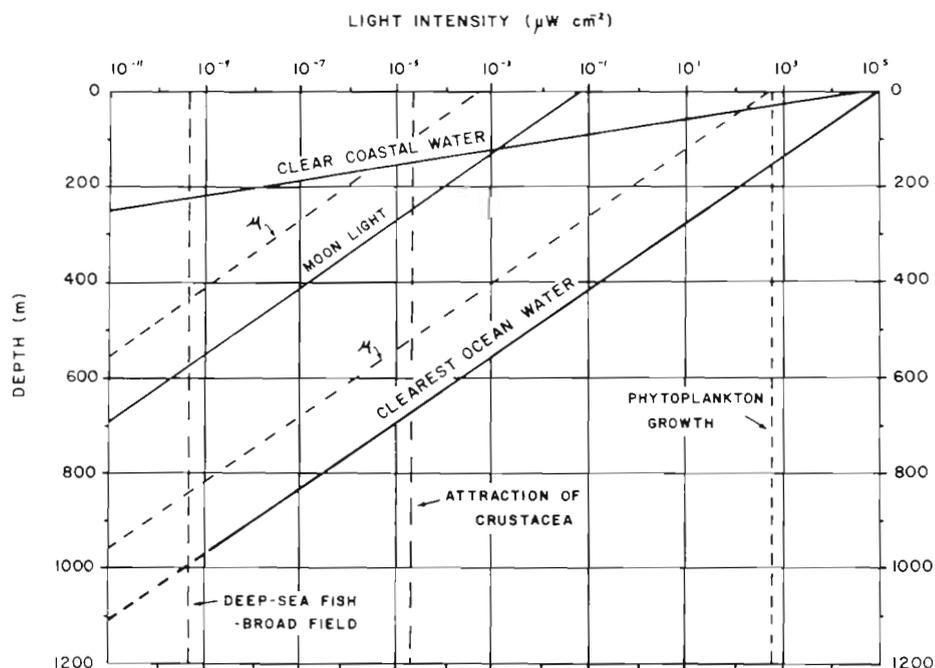


Fig. 2. Schematic diagram showing penetration of sunlight into seawater of various qualities. Penetration of moonlight and approximate intensities of upward scattered (μ) sunlight and moonlight in clearest ocean water are also shown. Minimum intensity values for a variety of biological functions requiring light are indicated. (After Clarke, 1970)

among such studies, but most employ a horizontally-oriented chamber, with light shining along the axis from one side. Although an unnatural optical arrangement, this does eliminate the confounding effects of gravity (e.g. Forward and Costlow, 1974; Sulkin, 1975). Neutral density and band pass or interference filters are employed to control light intensity and wavelength, respectively. Unfortunately, because the spectral sensitivity of irradiance meters often used to measure the intensity of white light seldom have been provided with the data, it is not possible to transform lux or foot-candle measurements to a consistent W/m^2 system. Intensity measurements reported here, therefore, are those used in each primary source.

The basic measurement of phototaxis has been the movement of an individual larva toward or away from a defined light stimulus. Variability among individuals in the sign and threshold of response is common. Sign of response has been assigned to a sample based on an arbitrarily chosen proportional response level. For example, when a response is described as being more positively (or negatively) phototactic, a larger percent of a sample is responding accordingly. In functional terms, this means that the response threshold of a larger proportion of the sample has been reached by experimental manipulation. For the purpose of the present discussion, we shall assume that results obtained from different techniques are comparable; however, it is recommended that the original refer-

ences be examined before results reviewed here are extrapolated to other species.

Phototaxis in *Rhithropanopeus harrisi*

Larvae of the mud crab *Rhithropanopeus harrisi* have been the subject of comprehensive studies on phototaxis, including ontogenetic changes in photic response as a function of wavelength and intensity of light; the influence of light adaptation, temperature, salinity, starvation, and pollutants on photic response; and the presence of rhythms in sign of phototaxis. A review of this research provides a useful basis for general discussion of phototaxis in brachyuran larvae.

An organism's spectral sensitivity may be measured either as an action spectrum or a response spectrum (Forward and Cronin, 1979). The former measures variation in response to a range of intensities at each test wavelength. A specific response level is chosen and the increase in the quantal level producing that response is plotted against wavelength. Response spectra measure per cent response to various wavelengths at approximately equal quantal intensities. Both methods were used to test spectral sensitivity of Stage I *Rhithropanopeus harrisi* larvae (Forward and Costlow, 1974; Forward and Cronin, 1979). The results were similar, indicating a primary maximum of positive response at approximately 500 nm, with a sec-

ondary maximum in the 400 to 440 nm range. Response spectra were virtually the same for dark and light-adapted larvae. Forward and Costlow (1974) reported no ontogenetic change in response spectra of light-adapted zoeae.

Sign of phototaxis in stimulus intensities of from 10^{-5} $W m^{-2}$ to 10^2 $W m^{-2}$ was measured at 500 nm (Forward, 1974; Forward and Costlow, 1974). Response was measured as positive or negative for individuals and was considered characteristic if greater than 30 % of larvae tested responded in a given way.

Basic responses differed between dark and light-adapted larvae, as shown in Fig. 3 (adapted from Forward, 1974). Dark-adapted Stage I larvae showed

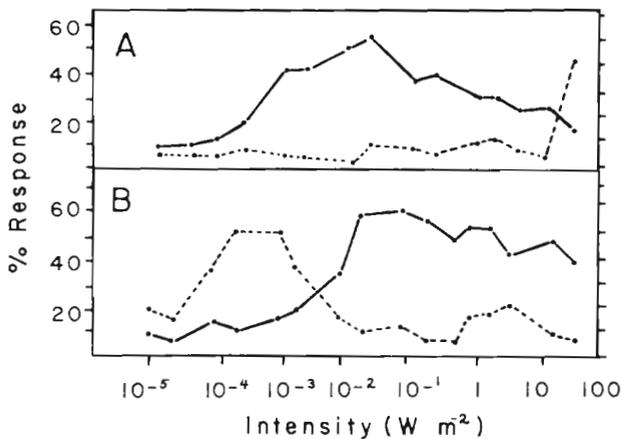


Fig. 3. *Rhithropanopeus harrisi*. Percentage response for dark-adapted (A) and light-adapted (B) Stage I larvae upon stimulation with 500 nm light in a range of intensities. Solid line: positive response; dashed line: negative response. (Adapted from Forward, 1974)

strong positive response to short stimulus times (2 s) at intensities between 1 and 10^{-3} $W m^{-2}$. Below and above this range most larvae did not respond to directional light in a clear fashion. Substantial negative response was measured only at the highest stimulation intensity (33 $W m^{-2}$) in zoeal Stage I (Forward, 1974). Response of subsequent zoeal stages was identical, except that negative response to 33 $W m^{-2}$ light was not present (Forward and Costlow, 1974). By contrast, light-adapted larvae showed negative response at intensities below 2×10^{-3} $W m^{-2}$. In general, light-adapted larvae were more sensitive to high intensities than were dark-adapted larvae (Forward, 1974). No change in this general pattern for light-adapted larvae was seen during zoeal development. Megalopae, however, were indifferent to light (Forward and Costlow, 1974).

The above experiments were conducted at $25^{\circ}C$ and at 25 ‰ S. The effect of temperature on sign of phototaxis was studied in light-adapted Stage I and Stage IV

Rhithropanopeus harrisi larvae acclimated to $20^{\circ}C$ (Ott and Forward, 1976). There was no evidence of phototactic response to any intensity at $5^{\circ}C$, probably a manifestation of a general lack of locomotory activity at this low temperature. At $10^{\circ}C$, only Stage IV larvae responded (positive) and only at the highest intensity tested. At temperatures above $15^{\circ}C$, the characteristic pattern of positive response at high intensities and negative response at low intensities occurred in both stages. However, while the profile of positive response shifted very little as a function of temperature, percent negative phototaxis to low intensity increased with increasing temperature. As a result, the light intensity at which negative phototaxis predominated over positive response in Stage I increased by an order of magnitude as temperature increased from 15 to $35^{\circ}C$. Stage I larvae retained positive response up to $35^{\circ}C$, while Stage IV was active only up to $30^{\circ}C$. Furthermore, Stage IV larvae showed substantial negative response to low intensities only between 20 and $30^{\circ}C$. Thus the temperature range of maximum response seemed to shift downward as zoeal development proceeded.

Latz and Forward (1977) determined the effect of salinity change on phototactic response in light-adapted *Rhithropanopeus harrisi* larvae. Larvae acclimated to 20 ‰ S were exposed to salinities of from 5 ‰ to 40 ‰. Exposure to 40 ‰ S had little effect upon response, although positive response to higher intensities was enhanced slightly and negative response to lower intensities suppressed. This pattern was more pronounced in Stage IV than in Stage I. However, when Stage I larvae were exposed to 5 ‰ S, the typical positive response at high intensity reversed to negative, while typical negative response to lower intensities was maintained. In Stage IV, exposure to 5 ‰ S resulted in reduced negative response at low intensities and increased negative response at high intensities. However, in contrast to Stage I, a significant percent of the Stage IV larvae retained positive phototaxis at higher intensities.

Latz and Forward (1977) determined that the threshold level of salinity decrease required to elicit reversal of phototaxis was 1.1 ‰ S for Stage I larvae acclimated to 20 ‰ S and 1.3 ‰ S for Stage I larvae acclimated to 10 ‰ S (2.0 ‰ and 1.3 ‰ respectively for Stage IV larvae). Reversal of positive phototaxis is a short-term phenomenon that is independent of acclimation salinity or magnitude of the decrease. Total recovery occurred within 5.5 min, with 50 % recovery within 1.5 to 3.2 min.

Changes in sodium and chloride ion concentration seem to be the primary factors in stimulating perception of salinity changes (Harges and Forward, 1982). However, other salt-water ion species can mimic these

2 and the characteristics of the environmental cues which can stimulate the appropriate receptors differ depending upon whether salinity increases or decreases from that of acclimation. Such factors as size of the ion, osmolality, and pH may be involved.

Cronin and Forward (1980) have determined the effect of starvation on phototaxis in *Rhithropanopeus harrisi* larvae. In Stage I, starvation generally increased the percent of sample showing positive phototaxis in a wide range of light intensities and slightly decreased the level of negative phototaxis (light-adapted larvae). In Stage II, a higher level of positive phototaxis was measured in starved larvae, although their negative phototaxis was unchanged. In Stages III and IV, no statistically significant differences were found attributable to starvation. Moreover, length of starvation had no impact in older zoeal stages.

Phototaxis is affected by application of insecticide. Forward and Costlow (1976, 1978) have applied various concentrations of 4 insect growth regulators to light-adapted larvae of all 4 zoeal instars. The general effect was to reduce the percentage of larvae which characteristically respond positively or negatively to given light intensities. Positive phototaxis to higher intensities seemed more sensitive than did negative response, especially at low insecticide concentrations. The reduced level of sample response to a given intensity can be attributed to an increase in response threshold among individuals, since swimming activity was not diminished at the dosages which affected phototaxis. Dosage effects and specific instar affected varied considerably among the four insecticides tested.

An apparent rhythm in phototactic response has been reported for field-captured Stage III *Rhithropanopeus harrisi* larvae (Forward and Cronin, 1980). The data suggested a circatidal rhythm in which the proportion of a sample of light-adapted larvae responding negatively at low intensities increased during a rising tide and decreased during a falling tide. Positive response to higher intensities generally exhibited the opposite pattern. Possible functional significance of this pattern will be discussed later.

In summary, *Rhithropanopeus harrisi* larvae exhibit peak response to wavelengths around 500 nm, with generally positive response to intensities greater than 10^{-2} W m⁻² and negative response to lower intensities in light-adapted larvae. Dark-adapted larvae retain positive phototaxis at intensities as low as 10^{-7} W m⁻² at long stimulus duration (Forward, pers. comm.). At intensities lower than 10^{-7} W m⁻², larvae generally were non-responsive to light. No significant changes in these basic responses occur through the course of zoeal development, although megalopae appear to be indifferent to light. Although activity level varies with temperature and salinity, a significant reversal of sign

occurs only at reduced salinity with larvae becoming negatively phototactic to high intensities. The effect is much less pronounced in Stage IV than in Stage I and is reversible in both instars. Starvation enhances positive response and suppresses negative response slightly in early zoeal stages, but not in later instars. Insecticides can influence the level of phototactic response, especially positive response to high light intensity; however, the pattern of effect is not consistent through zoeal development and varies among products tested. There is evidence of a circatidal rhythm in phototaxis in Stage III, with the level of positive response increasing on falling tides and negative response increasing on rising tides. A complete evaluation of the consequences of phototactic response in *R. harrisi* to vertical migration requires consideration of other components of the model and will be presented later.

Shadow response

The difference in photic response to low intensities between light and dark-adapted larvae has been the subject of speculation. Forward (1974) initially suggested that these differences could contribute to diurnal vertical migration, with dark-adapted larvae rising in the water column at sunrise in response to low intensities, remaining there during daylight hours in response to relatively high intensities, and moving downward at dusk as the now light-adapted larvae responded negatively to low intensities. However, for descent at sunset to occur, either the low light intensity which induces negative phototaxis must be sufficient to produce the light-adapted condition (negative response to low intensities) or after light adaptation to higher intensities occurs, the light-adapted condition must persist long enough for natural light to decrease to an intensity which will evoke negative phototaxis. Using characteristic negative response to low intensities as the criterion for the presence of light-adaptation, Forward and Cronin (1978) demonstrated that intensities which stimulate negative response are too low to produce the light-adapted condition. Forward and Cronin (1978) further determined that the time required in nature for light intensity to drop from the lowest value capable of inducing light adaptation to the highest capable of evoking negative phototaxis will always exceed the length of time the response will persist. In other words, the rate of intensity decrease at sunset produces dark adaptation before an intensity is reached which would have produced a characteristic negative response. It therefore seems unlikely that negative phototaxis in light-adapted larvae can promote descent at sunset.

Forward (1976a) has suggested an alternate function for negative response to low intensity; namely, a 'shadow response' promoting predator avoidance. Forward (1974) indicated that the reversal from positive to negative phototaxis in light-adapted larvae at low intensities required a decrease to an absolute stimulus intensity and was independent of the magnitude of the decrease, a phenomenon which clearly would limit the value of the response in predator avoidance. Forward (1976a) tested the effects of 3 kinds of light change which might be caused by a shadow passing overhead: (1) from high intensity to darkness, (2) from high intensity to an intensity low enough to produce negative phototaxis, and (3) from high intensity to a lower intensity, but one still high enough to produce positive phototaxis.

When light was extinguished, larvae suspended in a water column began to sink passively within 20 to 30 ms. The percent of larvae descending was related directly to length of original stimulus duration and its intensity. When light intensity was decreased from a level sufficient to induce positive response to one low enough to promote negative phototaxis, larvae responded first by passively sinking, then by active negative phototaxis. There was a direct relationship between duration of the initial stimulus and the time initially spent sinking. When stimulus intensity was lowered to a level still high enough to promote positive phototaxis, an initial period of passive sinking resulted. This response appeared to be largely independent of initial stimulus condition. Forward (1976a) suggested that this type of response is an avoidance reaction which would be effective when larvae encounter passive predators, such as ctenophores. The initial response may be passive sinking only, but if the predator comes close enough to reduce intensity substantially, negative phototaxis will augment the response. However, the response would be unlikely to promote avoidance of rapidly swimming predators.

Forward (1977) demonstrated a similar pattern of phototaxis response to high intensity in 6 other species of brachyurans. In *Panopeus herbstii*, *Menippe mercenaria*, *Uca pugilator*, *Callinectes sapidus*, *Sesarma cinereum*, and *Libinia emarginata*, moderate intensities of 500 nm light produced a substantial level of positive phototaxis, while decrease in intensity resulted in the characteristic decline in positive response and increase in negative response. The same pattern has also been described for larvae of *Uca pugilator* by Herrnkind (1968). In *Pinnotheres maculatas*, the pattern of positive phototaxis was similar to that described for the other species, except that there was no evidence of increase in negative response with reduced light intensity. However, the widespread occurrence of negative phototaxis at low intensities

among these brachyurans suggests the presence of the shadow response described by Forward (1976a) for *Rhithropanopeus harrisi*. Forward (1977) confirmed that indeed the components of such a response are present. If light intensity high enough to promote positive phototaxis was extinguished, Stage I larvae of *P. herbstii*, *M. mercenaria*, *S. cinereum*, *U. pugilator*, and *C. sapidus* immediately began to sink, a response also reported for larvae of *Ebalia tuberosa* (Schembri, 1982). Only larvae of *L. emarginata* did not respond in this fashion. If light intensity was reduced from that sufficient to promote positive response to that sufficient to promote negative response, larvae of *U. pugilator* and *C. sapidus* responded by sinking, while the other 4 species tested responded with negative phototaxis. If initial light intensity was reduced to a level which still evoked positive response, the result was a sinking response in all 6 species. Thus with the noted exceptions of *Pinnotheres maculatas* and *L. emarginata*, the responses among these species were very similar to those described as a shadow response in *R. harrisi* (Forward, 1976a). As with *R. harrisi*, the shadow response is presumably related to predator avoidance and is probably not directly related to diurnal vertical migration (Forward, 1977).

Comparison of photic responses among brachyuran species

Spectral sensitivity has been compared among larvae of several coastal brachyuran species (Forward and Cronin, 1979). *Uca pugilator* and *U. minax* exhibit a broad, relatively uniform sensitivity to a wide spectral range of from 380 to 500 nm and from 420 to 540 nm respectively. *Panopeus herbstii* exhibits greatest sensitivity at 460 to 500 nm, but lacks UV sensitivity. *Sesarma reticulatum* and *S. cinereum* show maxima at 360 nm and 500 to 520 nm, while *Pinnotheres ostreum* shows maximum response at 360 and 460 nm. Since larvae of all species inhabit similar estuarine waters where spectral distribution of light should be similar, it is of interest that their response spectra differ and that the maximum sensitivity is not consistently in the 550 to 625 nm range, the wavelengths likely to be transmitted maximally in coastal water. It would seem that these larvae are not well-adapted to perceive the greatest amount of underwater light in estuaries (Forward and Cronin, 1979).

Moderate intensities of broad spectrum (white) light have been reported to elicit positive phototaxis in Stage I larvae of many brachyuran species. These species are presented by Family in Table 3. Comparatively few studies have been conducted on ontogenetic change in phototaxis. Welsh (1932) reported that later

Table 3. Species which respond to the indicated intensities of white light with positive phototaxis in the first zoeal stage

Family	Species	Light intensity	Source
Cancridae	<i>Atelecyclus rotundatus</i>	1000 lux	Rice (1964)
	<i>Cancer irroratus</i>	110 $\mu\text{W cm}^{-2}$	Bigford (1979)
	<i>Cancer pagurus</i>	1000 lux	Rice (1964)
Corystidae	<i>Corystes cassivelaunas</i>	1000 lux	Rice (1964)
Geryonidae	<i>Geryon quinquedens</i>	75 W m^{-2}	Kelly et al. (1982)
Leucosiidae	<i>Ebalia tuberosa</i>	1000 lux	Rice (1964)
		140, 1400 lux	Schembri (1982)
Majidae	<i>Eurynome aspera</i>	1000 lux	Rice (1964)
	<i>Hyas coarctatus</i>	1000 lux	Rice (1964)
	<i>Inachus dorsettensis</i>	1000 lux	Rice (1964)
	<i>Macropodia rostrata</i>	1000 lux	Rice (1964)
Ocypodidae	<i>Uca pugilator</i>	10^{-3} – 10^{-5} mW cm^{-2}	Hyman (1920), Herrnkind (1968)
	<i>Uca pugnax</i>	1.8×10^{-3} W cm^{-2}	O'Connor (1982)
Pinnotheridae	<i>Pinnotheres maculatas</i>	10^{-2} – 10^2 m-c	Welsh (1932)
	<i>Pinnotheres ostreum</i>	–	Christiansen and McDermott (1958)
	<i>Pinnotheres pisum</i>	1000 lux	Rice (1964)
Portunidae	<i>Callinectes sapidus</i>	75 W m^{-2}	Sulkin et al. (1980)
	<i>Carcinus maenas</i>	1000 lux	Rice (1964)
	<i>Macropipus depurator</i>	1000 lux	Rice (1964)
	<i>Macropipus puber</i>	1000 lux	Rice (1964)
	<i>Macropipus pusillus</i>	1000 lux	Rice (1964)
Xanthidae	<i>Eurypanopeus depressus</i>	75 W m^{-2}	Sulkin et al. (1983)
	<i>Leptodius floridanus</i>	10 foot candles	Sulkin (1975)
	<i>Panopeus herbstii</i>	10 foot candles	Sulkin (1975)
	<i>Xantho couchii</i>	1000 lux	Rice (1964)

zoeal stages of *Pinnotheres maculatas* became 'photo-negative'. Sulkin (1975), however, reported that late zoeal instars of the xanthid crabs *Leptodius floridanus* and *Panopeus herbstii* retained positive phototaxis, as did *Uca pugilator* (Herrnkind, 1968) and *Rhithropanopeus harrisi* (Forward and Costlow, 1974). However, in contrast to *R. harrisi* megalopae, which were indifferent to light, *L. floridanus* and *P. herbstii* megalopae showed positive phototaxis (Sulkin, 1975). Maintenance of positive phototaxis throughout larval development also has been shown for *Cancer magister*, although responsiveness to intensity varied among ontogenetic stages (Jacoby, 1982). In general, later zoeal stages were increasingly responsive to higher intensities.

More comprehensive studies of light response through larval development have been conducted on *Cancer irroratus* (Bigford, 1977, 1979) and *Callinectes sapidus* (Sulkin and Van Heukelem, 1982).

Bigford (1979) determined distributions of larvae of each stage in horizontally-oriented chambers in both

darkness and light ($110 \mu\text{W cm}^{-2}$). Although distributions in darkness were not random, the results nevertheless support the conclusion that positive phototaxis persists throughout zoeal development. Results for the megalopae are equivocal. Bigford (1977) reported that the addition of 0.1 ppm and 1.0 ppm water-accommodated fraction of oil generally reduced the level of phototactic response in all stages. This result is consistent with the conclusion that these concentrations of hydrocarbons reduce general activity level.

Using moderate intensities of diffuse white light to test for presence of barokinesis in zoeal Stages I, IV, and VII of *Callinectes sapidus*, Sulkin et al. (1980) demonstrated persistent positive phototaxis through zoeal development. Sulkin and Van Heukelem (1982) reported the effect on phototaxis of temperature and salinity change in *C. sapidus*. Larvae of Stages I, IV, and VII were light-adapted and tested at 0.25 W m^{-2} in light filtered to 500 nm. In the temperature tests, groups of larvae were adapted for 24 h to 15, 20, or

25 °C and tested in 15, 20, and 25 °C, so that all possible combinations of adaptation and test temperatures were employed. When larvae of all 3 stages were tested at the temperature of adaptation, positive phototaxis predominated. No change in response occurred when larvae adapted to any of the 3 temperatures were tested at higher or lower temperatures, a result consistent with that of Ott and Forward (1976) for *Rhithropanopeus harrisii*. In the salinity tests, groups of *C. sapidus* larvae were adapted for 24 h to 25, 30, and 25‰ S and tested at all 3 salinities in all possible combinations of adaptation and test salinity. Responses for larvae tested at or above the salinity of adaptation were uniformly positive in all three zoeal stages. The same result was obtained for zoeal Stages IV and VII when tested at salinities below that of adaptation. In zoeal Stage I, however, reduction of salinity by 5 ‰ produced neutral response, the result of temporary cessation of locomotor activity. Megalopae appeared far less responsive to light than did the zoeae; however, pronounced positive response to 75 W m^{-2} white light occasionally occurred.

The significance of phototaxis in orienting movement in the vertical plane in brachyuran larvae is difficult to assess. While it clearly is a stimulus to which virtually all larvae respond, the sign of response will vary according to the specific characteristics of light-penetration (wavelength and intensity) in the habitat of interest. Indeed, it is reasonable to suggest that a parameter as variable as light in the marine environment would not be an effective stimulus upon which to base an adaptive behavioral tactic to regulate vertical migration. This point will be analysed further in the 'Discussion'.

Polarotaxis

The scattering effect due to suspension of small particles in the water column produces linear polarization of light. The plane of maximum polarization is perpendicular to refracted solar rays underwater. Thus when the sun is at its zenith, the angle of polarization will be 0 (horizontal). Near the surface, the plane of polarization will shift as does the position of the sun (Jerlov, 1968). With increasing depth and/or turbidity, net flux of light becomes vertical and the plane of polarization shifts toward the horizontal (Ivanoff and Waterman, 1958). The plane of linear polarization has been shown to influence animal orientation (Waterman, 1973) and is a discrete stimulus.

In *Rhithropanopeus harrisii*, light-adapted larvae of zoeal Stages II and III oriented with respect to polarized light, with maximal response at 10^{-2} W m^{-2} and at 500 nm (Via and Forward, 1975). The second

stage preferentially oriented perpendicular to the plane of polarization, while the third stage oriented parallel to it. Upon dark adaptation, polarotaxis disappeared. Neither Stages I nor IV showed evidence of polarotaxis in this species. While phototactic spectral and intensity sensitivity were unchanged throughout zoeal development (Forward and Costlow, 1974), polarotaxis varied considerably. Furthermore, phototaxis and polarotaxis exhibited maximum sensitivity at different intensities. Thus while the presence of light obviously is required for both polarotaxis and phototaxis, the two responses are actually quite distinct.

Bardolph and Stavn (1978) determined that Stage I larvae of *Panopeus herbstii* also exhibit polarotaxis, with maximum response perpendicular to the plane of polarization. Thus, when the plane of polarization was horizontal, larvae responded by orienting such that upward movement would occur. When this orientation was compared with that seen in non-polarized light adjusted also to produce upward movement, there was less angular dispersion of body orientation among larvae in the polarized light. Thus, although the plane of orientation was not affected, body orientation was more precise in response to polarized light. If the plane of polarization was tilted up from the horizontal by 20°, body orientation shifted in the same direction, but only by 1 to 5°.

The actual role played by polarized light in orienting vertical movement in brachyuran larvae is unclear. However, in addition to serving as a potential orientation modifier, polarized light can also serve to increase contrast in light intensity perception. The presence of behavioral adaptations which increase contrast perception suggests that polarotaxis may be a trait keyed primarily to predator avoidance or prey capture.

LOCOMOTOR ACTIVITY

Definitions and experimental approaches

Two alternative approaches have been used to investigate endogenous and exogenous regulation of locomotor activity in brachyuran larvae. Each has its advantages and disadvantages.

General activity level has been determined by measuring shifts in net distribution of a sample of larvae over time. As the larvae are subjected to a specific treatment, a characteristic proportion of the sample may respond by altering its locomotor activity. If as the treatment level increases, response thresholds of an increasing proportion of the sample are surpassed, an apparent increase in sample response level will occur. A net shift in distribution of a sample thus may reflect both frequency of locomotion among individu-

als and change in rate of locomotion by already active larvae. These 2 response alternatives are difficult to evaluate independently and compare among different treatments (e.g. temperature vs pressure).

The alternative is to measure directly swimming speed of individual larvae in a range of treatment levels. This method has the advantage of ease of quantification and comparison among treatments, but eliminates the frequency component. Furthermore, swimming speed usually is measured during oriented movement toward light. This not only introduces light as a complicating factor, but also measures only orthokinesis, eliminating klinokinesis (modification of turning frequency) which can also affect dispersion rates (Fraenkel and Gunn, 1961).

The principal variables affecting locomotor activity that have been investigated experimentally include light intensity, endogenous rhythmicity, hydrostatic pressure, temperature, and salinity. Effects of starvation and pollutants have received limited attention.

In order to eliminate the confounding effects of passive sinking on measurements of locomotor activity, a horizontal chamber with light as an orientation stimulus has been used widely as an experimental tool. The effects of light on locomotor activity are thus paramount and results of experiments testing other variables should be evaluated in the context of the experimental design, which often includes light.

Base activity level may be defined as movement which occurs in the absence of apparent external stimuli. However, because taxis response is such an integral part of the behavioral repertoire of brachyuran larvae, base activity level by this definition is difficult to investigate experimentally and, indeed, may be a moot point in nature.

Base locomotor activity

Undirected swimming speeds have been measured for larvae of *Rhithropanopeus harrisi* (Forward, 1974; Forward and Costlow, 1974) and for Stage I larvae of 7 other species of brachyurans (Forward, 1977). Measurements were made on the distance larvae swim in 0.5 s in a cuvette placed upon a microscope stage. Forward (1977) states that because the measurements are rigorous only in 2 dimensions (limited by plane of focus), the speeds may be biased toward lower values although the error is presumably constant among species and instars. The following generalities pertain. Within each zoeal stage of *R. harrisi*, undirected swimming speeds of light and dark-adapted larvae are the same. Mean undirected swimming speed increases with succeeding zoeal stage, from approximately 0.2 cm s^{-1} at Stage I to approximately 0.4 cm s^{-1} at

Stage IV. Cronin and Forward (1980) showed that starved larvae of all stages swam more slowly than did fed larvae. Table 4 lists the mean undirected swimming speeds for Stage I larvae of all 8 species. The fastest species (*M. mercenaria*) exceeds the slowest (*U. pugilator*) by a factor of 2.5.

The effect of light on locomotor activity

In contrast to the results obtained for random swimming, condition of light adaptation does affect speed of swimming oriented by light in *Rhithropanopeus harrisi* (Forward, 1974; Forward and Costlow, 1974). In dark-adapted larvae, for example, swimming speeds of positive animals exceeded those of randomly swimming larvae only in Stages I and II, while in light-adapted larvae, swimming speeds during positive response exceeded those during random activity in all 4 zoeal stages. In dark-adapted larvae, mean swimming speed during positive response did not differ with stimulus intensity. Furthermore, speed of positive response equaled that of negative response when the latter occurred in Stage I. In light-adapted larvae, speed of positive response was independent of stimulus intensity except in Stage IV; however, speed of movement during negative response varied directly with light intensity. As a consequence, swimming speed during negative response exceeded that during positive response at the highest light intensity which elicited negative phototaxis in *R. harrisi*. Bentley and Sulkin (1977) have reported that swimming speeds of negatively phototactic Stage II *R. harrisi* larvae exceeded those of positively phototactic larvae at a light intensity of 5 foot-candles.

Table 4 compares mean swimming speeds of light-adapted Stage I larvae of 8 brachyuran species for undirected, positive, and negative response. Swimming speeds during positive response exceeded those of random swimming in 7 of the 8 cases. Speeds during negative response consistently exceeded those of random responses, and exceeded those of positive response in 4 of the 7 species. The value of direct comparisons of swimming speeds among species is questionable because light intensities were not identical, but were chosen for each species in order to provide appropriate stimuli to promote positive and negative response.

The absence of photokinesis in positively phototactic *Rhithropanopeus harrisi* larvae differs from reports that show an increase in swimming speed with an increase in intensity in other species. Welsh (1932) showed that swimming speed in *Pinnotheres maculatas* was inversely related to the intensity of light to which larvae had been adapted, although dark-

Table 4. Mean swimming speeds (cm s^{-1}) of Stage I larvae which are positively or negatively phototactic or which are undirected. (Adapted from Forward, 1977)

Species	Undirected	+ Phototaxis	- Phototaxis
<i>Panopeus herbstii</i>	0.18	0.31	0.88
<i>Menippe mercenaria</i>	0.28	0.60	1.23
<i>Uca pugilator</i>	0.11	0.25	0.35**
<i>Callinectes sapidus</i>	0.25	2.02	2.46**
<i>Sesarma cinereum</i>	0.19	0.22*	0.39
<i>Libinia emarginata</i>	0.22	0.71	0.95**
<i>Pinnotheres maculatas</i>	0.14	0.48	-
<i>Rhithropanopeus harrisi</i> ***	0.18	0.32	0.85

* Not significantly different from undirected swimming speed
 ** Not significantly different from positive phototaxis swimming speed
 *** Estimated from plots in Fig. 1 of Forward (1974), using maximum values for positive and negative response

adapted larvae were generally slower. Swimming speeds of larvae adapted to 0.093 m-candles (m-c) was 2.17 cm s^{-1} , while larvae adapted to 93.0 m-c swam at a mean speed of only 1.97 cm s^{-1} . However, for larvae initially adapted to a common light intensity, swimming speed varied directly with stimulus intensity (0.86 cm s^{-1} at 0.47 m-c to 1.75 cm s^{-1} at 93 m-c). Welsh (1932) also reported that the relationship between swimming speed and stimulus intensity varied with temperature (13.4 to 27.1 °C), with larvae showing greater sensitivity to light intensity change at lower temperature. Temperature *per se* had a direct effect upon swimming speed at each light intensity tested.

Sulkin (1975) measured swimming speeds of Stages I and IV *Leptodius floridanus* and Stage I *Panopeus herbstii* in light intensities ranging from 10 to 70 foot-candles. Larvae of *L. floridanus* showed no change in swimming speed with change in light intensity; however, Stage I larvae of *P. herbstii* showed high photokinesis (increase in swimming speed in response to increases in light intensity). Sulkin (1975) attributed the difference between the two species to the higher 'base' level of swimming speed in *L. floridanus* and suggested that increase in stimulus intensity did not affect this species because it already was swimming at or near its maximum capacity at low light intensity.

The presence of photokinesis suggests that in some species locomotor activity can vary predictably as the quality and quantity of light changes with season and time of day. Furthermore, high photokinesis could produce positive feedback in upward swimming positively phototactic larvae by exposing them to ever increasing intensities, thus further increasing locomotor activity. On the other hand, negative feedback could occur in downward moving, negatively phototactic individuals as they become exposed to ever decreasing intensities, a circumstance which would

reduce locomotor activity. Clearly, there is considerable variation in locomotor activity among species in response to light condition. While experiments which employ light as an orienting stimulus to test the effects of other variables on swimming speed may be internally consistent and therefore valid, comparisons among experiments should be made with caution.

Rhythmicity in locomotor activity

Sulkin et al. (1979) demonstrated a locomotor rhythm in the first zoeal stage of *Callinectes sapidus*. An increase in swimming speed during the dark hours (peak at 0200) was followed by a decrease at 0800, prior to the onset of light. The diel rhythm persisted only if a 12:12 light:dark cycle was maintained.

Larvae of *Rhithropanopeus harrisi* showed a clear tidal rhythm in vertical migration in the field, with larvae ascending to minimum depth several hours after low tide and rapidly descending prior to high tide (Cronin and Forward, 1982). In laboratory-reared larvae cultured in 12:12 light:dark cycle and tested in constant darkness, a weak circadian rhythm in vertical migration occurred. However, larvae captured in the field and tested in the laboratory under constant conditions exhibited a clear tidal rhythm of vertical migration. Larvae reached the greatest depth coincident with the time of low tide at the collection site (Cronin and Forward, 1979). Because alternative cycles had slightly different forms, with greater amplitude changes occurring at night, the possibility of a circadian rhythm superimposed upon the dominant tidal one exists (Cronin and Forward, 1979, 1982). An endogenous rhythm in swimming speed reported for *R. harrisi* by Forward and Cronin (1980) is the likely mechanism responsible for this pattern of vertical mig-

ration. Larvae exhibited maximum swimming speed 3 h after low tide and minimum swimming speed 2 h after high tide, a pattern sufficient to produce the observed vertical migrations, given appropriate orienting stimuli.

Brachyuran larvae are readily susceptible to circadian entrainment in the laboratory as both Sulkin et al. (1979) and Cronin and Forward (1982) have demonstrated. The evidence from *Rhithropanopeus harrisi* suggests, however, that tidal rhythms are dominant in an estuary having semi-diurnal tides. Possession of a tidal rhythm synchronizer poses a particularly interesting problem for a meroplankter suspended in the water column. The synchronizer remains to be described. The presence of rhythmic vertical migration in larvae of *Uca* sp. (DeCoursey, 1976) suggests that the phenomenon may be widespread among estuarine species. Endogenous rhythms of locomotor activity are sufficient to explain periodic vertical migration, assuming a body orientation that will produce upward movement when swimming occurs. Experimental designs which employ locomotion must control for or account for the possibility of activity rhythms which may exist.

Effects of temperature on locomotor activity

In most cases temperature has been shown to have a direct effect upon swimming speed (high thermokinesis). For example swimming speed of *Pinnotheres maculatas* larvae, oriented to light (0.93 m-c), increased from 0.33 cm s^{-1} at 13.4°C to 1.70 cm s^{-1} at 27.1°C (Welsh, 1932). When larvae swam toward a light of 23.3 m-c, the increase was from 0.73 cm s^{-1} to 2.19 cm s^{-1} in the same temperature range.

Sulkin et al. (1980) showed that reduction in temperature from 25 to 15°C resulted in a significant reduction in swimming speed in *Callinectes sapidus* zoeal Stages IV and VII, but not in Stage I. As a consequence, if Stage I larvae sink to the colder water that is present near the bottom of the estuarine hatching zone, subsequent upward migration will not be disrupted due to reduced swimming activity. Sulkin et al. (1980) suggested that maintenance of swimming speed in Stage I in the face of such temperature decrease may be one of several behavioral adaptations promoting distribution of this stage near the surface of the water column. Indeed, laboratory and field data both strongly indicate that Stage I *C. sapidus* are found in surface waters (Sulkin et al., 1982).

In contrast, Stage I larvae of the estuarine mud crab *Eurypanopeus depressus* show higher swimming speed at 25°C than at 15°C in a wide range of hydro-

static pressure, indicating high thermokinesis in this species (Sulkin et al., 1983).

Stage I larvae of a deeper sea species, *Geryon quinquedens*, respond to temperature in similar fashion (Kelly et al., 1982). Swimming speeds at 25°C consistently exceeded those measured at 11°C in hydrostatic pressures up to 20 atm above ambient. Furthermore, swimming speed at 15°C exceeded that measured at 11°C in larvae adapted prior to the experiment either to 11 or to 15°C . In addition, swimming speed at 15°C did not differ between larvae adapted to 11 or to 15°C . Thus there appears to be a direct relationship between temperature and swimming speed with no apparent acclimation effect.

Brachyuran larvae migrating vertically in the estuarine or coastal marine environments are likely to encounter substantial thermal gradients. Change in temperature has been shown to influence swimming speed as well as sign of orientation (Ott and Forward, 1976). The net effect of sharp thermal gradients upon vertical movement has been investigated experimentally. The general technique was described by Kelly et al. (1982). A vertical observation chamber is surrounded by water baths in a way that produces a sharp temperature gradient (thermocline) in the middle section of the chamber. Larvae are introduced at the bottom of both the experimental chamber and a control chamber in which the water column is vertically homogenous with respect to temperature and equal to the temperature at the bottom of the experimental chamber. Larvae are stimulated to swim upward in both chambers by both geotaxis and phototaxis. The influence of the thermocline can be evaluated by comparing the percentage of the sample in the top of both chambers after a specified time interval.

Stage I larvae of *Geryon quinquedens* were tested in a 10°C thermocline (12 to 22°C) in which temperature increased at a rate of 2°C cm^{-1} (Kelly et al., 1982). No significant difference between control and experimental chambers was present after 30 min. Indeed, direct observation revealed that larvae traversed the thermocline with no apparent change in behavior. Stage I larvae of *Eurypanopeus depressus* also traversed a 10°C thermocline (15 to 25°C), although temporary disruption of swimming activity in the region of the sharp thermal gradient was observed (Sulkin et al., 1983).

McConnaughey (1983) has determined the effect of temperature gradients of various magnitudes on vertical movement of Stage I *Callinectes sapidus* larvae. Larvae were tested in 2 series of thermoclines with the lowest temperature (LT) set at 15°C in one series and 17.5°C in the other. In the 15°C series, 8 thermoclines from 2.5 to 20°C (upper temperature, 17.5 to 35°C) were tested; in the 17.5°C series, 4 thermoclines from

10 to 17.5 °C (upper temperature, 27.5 to 35 °C) were tested. Results indicated that larvae could penetrate very sharp thermoclines, but avoided an upper temperature of 27.5 °C or above, independent of the magnitude of the thermocline. In spite of their ability to penetrate very sharp thermoclines, even moderate gradients in the $T = 5$ °C range caused temporary disruption of upward migration. The result was a protracted period during which sinking and upward swimming alternated, creating a characteristic 'hop and sink' behavior. However, if the upper temperature was less than 27.5 °C, larvae eventually penetrated the thermocline and rapidly swam to the top of the experimental chamber.

The effect of salinity on locomotor activity

Sulkin et al. (1980) have determined swimming speeds of zoeal Stages I, IV, and VII of *Callinectes sapidus* adapted to 25, 30, or 35 ‰ S. When larvae adapted to 25 ‰ S were tested at 35 ‰ S, swimming rate decreased in Stage I, but remained unchanged in Stages IV and VII. However, when Stage I larvae were tested at the salinity of adaptation, they showed no significant change in swimming speed as a function of salinity, while swimming speeds in Stages IV and VII decreased as salinity increased. These results imply that if Stage I larvae descend in the estuary to areas of higher salinity, reduction in swimming speed which occurs will be only temporary. In later zoeal stages, however, permanent reduction in swimming speed eventually will occur under the same circumstances. This phenomenon is consistent with the contention of Sulkin et al. (1980) that the first zoeal stage in *C. sapidus* possesses adaptations to promote upward migration and maintenance of position high in the water column that are lacking in later zoeal stages.

The responses of *Callinectes sapidus* zoeae to laboratory-constructed haloclines are generally consistent with this conclusion. Sulkin and Van Heukelem (1982) determined the responses of Stages I, IV, and VII *C. sapidus* larvae to a series of vertically oriented haloclines ranging in magnitude from 2.5 to 10 ‰ S (the salinity below the halocline being a constant 30 ‰ S). The experimental design was similar to that described above for thermoclines. In all 3 zoeal stages the percentage of samples penetrating the halocline and moving up into the top third of the experimental chamber decreased with increase in the salinity gradient, while the percentage in the middle section of the chamber (halocline) increased. A significant reduction in numbers of larvae passing completely through the halocline was defined as 'inhibition' of vertical migration, whereas a significant increase in larvae in the

region of the haloclines was defined as 'disruption' of vertical migration. In Stage I, disruption occurred at a Δ salinity as low as 2.5 ‰; however, inhibition was apparent only at a halocline as large as 10 ‰. In general, as zoeal development proceeded, the effective halocline which caused inhibition declined (2.5 ‰ in Stage VII). These results suggest that although a halocline may have a temporary effect upon upward migration in *C. sapidus*, salinity stratification in the range seen in nature is unlikely to alter the vertical migration pattern that is under regulation of other behavioral and environmental factors.

O'Connor (1982) determined the effects of haloclines on both upward and downward movement of *Uca pugnax* larvae. As Δ salinity increased (from 2.5 ‰), increasing numbers of upward moving Stage I larvae collected near the halocline, a pattern similar to that described for *Callinectes sapidus*. Inhibition was not apparent until a Δ salinity of 6 ‰ had been reached. Stage V larvae, on the other hand, did not collect near the halocline and inhibition was not obtained until Δ salinity of 10 ‰ had been reached. An evaluation of the controls suggests that the results for Stage V may be attributed to comparatively inactive late stage larvae in these experiments. Downward moving larvae were not influenced by the presence of the haloclines in either stage tested, although O'Connor (1982) reported abdominal flexing when larvae encountered Δ salinity greater than 4 ‰.

Effects of hydrostatic pressure on locomotor activity

Since Hardy and Bainbridge (1951) first reported that brachyuran larvae swam faster as hydrostatic pressure increased (high barokinesis), the significance of pressure sensitivity to depth regulation of zooplankters has been a popular topic of study. Knight-Jones and Morgan (1966) provide a review of the phenomenon. Rice (1964) and Knight-Jones and Morgan (1966) have suggested a useful classification of pressure responses based upon the principal orienting mechanisms that have been employed to investigate the phenomenon. Brachyuran larvae fall into 1 of 2 general categories: those that orient principally to gravity and move upward in response to pressure increase (primarily megalopae) and those, including most zoeae, that orient primarily to light, with enhanced positive response measured when pressure increases. Significantly, in both cases, reduction of pressure results in passive sinking as a consequence of reduced locomotor activity. The general response, therefore, fits the definition of high barokinesis; that is, an increase in hydrostatic pressure produces increased locomotor activity which, in a sample of larvae, is manifest in

enhanced response to whatever orientation stimulus is dominant.

Experimental approaches have included both measurements of shift in vertical distribution of a sample in response to pressure variation and direct measurement of swimming speed as a function of pressure change (orthokinesis). It may be instructive to compare results on 2 species in which both approaches have been employed: *Rhithropanopeus harrisi* and *Leptodius floridanus*.

Bentley and Sulkin (1977) measured swimming speeds of *Rhithropanopeus harrisi* larvae subjected to pressure increments of 0 to 0.8 atm. In all 4 zoeal stages, a significant increase in swimming speed occurred with an increase in pressure. Swimming speed also increased progressively through zoeal development. Wheeler and Epifanio (1978) determined the influence of pressure increase on vertical movement of a sample of *R. harrisi* larvae. When pressure was increased at a rate of $0.1 \text{ atm (2 min)}^{-1}$, all 4 zoeal stages showed net upward movement with an increase in pressure at a minimum threshold increment of 0.2 atm. Stage III larvae actually responded at an increment of 0.1 atm. In general, when pressure was decreased, the mean position of larvae in the observation chamber descended. When pressure was raised at a slower rate, $0.025 \text{ atm (2 min)}^{-1}$, larvae of all 4 zoeal stages again responded by rising in the chamber. Ascent was more gradual, however, and the threshold of significant response lower than at the more rapid rate of pressure increase. The results of the 2 experimental approaches are qualitatively the same and fit the general response pattern suggested for brachyuran zoeae by Rice (1964) and Knight-Jones and Morgan (1966). An increase in pressure produced an increase in swimming speed in individuals (with considerable variation in response threshold). This resulted in upward movement of negatively geotactic larvae when those larvae began to swim. Subsequent decrease in pressure resulted in reduced locomotor activity, with net descent produced by the dominance of passive sinking.

The 2 approaches produce consistent results in *Leptodius floridanus* as well. Sulkin (1973) demonstrated an increase in swimming speed of Stage I larvae with an increase in pressure up to 1 atm above ambient. Moreover, the response was reversible, with no evidence of accommodation to 10 h sustained pressure increment of 0.6 atm. However, Stage IV larvae showed no such response. Wheeler and Epifanio (1978) measured net vertical movement of samples of larvae in response to pressure increase for all 4 zoeal stages of *L. floridanus*. Stages I and II responded to an increase in pressure, $0.1 \text{ atm (2 min)}^{-1}$, by a net ascent in the column, but Stages III and IV did not change their

vertical position. The response threshold of Stage I larvae was 0.1 atm, while Stage II larvae responded at 0.2 atm. As with *Rhithropanopeus harrisi*, pressure decrease resulted in gradual descent of *L. floridanus* larvae.

Results for *Rhithropanopeus harrisi* and *Leptodius floridanus* indicate that the response threshold to increasing pressure is a function of rate of change, a phenomenon which has received little additional attention. Change in response of larvae to pressure increment through ontogeny has been the subject of more extensive investigation, however.

Rice (1964) reported increased locomotor activity in response to pressure increase in Stage I larvae of the following brachyuran species: *Macropipus puber*, *M. pusillus*, *M. depurator*, *Carcinus maenas*, *Cancer pagurus*, *Atelecyclus rotundatus*, *Corystes casivelaunas*, *Xantho couchii*, *Pinnotheres pisum*, *Eurynome aspera*, *Hyas coactatus*, *Inachus dorsettensis*, *Macropodia rostrata*, and *Ebalia tuberosa* (confirmed by Schembri, 1982). Light was the dominant orienting stimulus in these species.

A direct relationship between pressure and swimming speed has been reported for light-oriented Stage I larvae of the shallow water crab *Eurypanopeus depressus* (Sulkin et al., 1983) and the deeper sea species *Geryon quinquedens* (Kelly et al., 1982), although a much higher response threshold is indicated for the latter species.

The late zoeal stages of *Macropipus* sp., *Ebalia tuberosa*, and *Carcinus maenas* also exhibited high barokinesis, except that gravity seemed to have a greater influence as an orienting stimulus than was the case for the earlier instars (Rice, 1966).

With gravity acting as the dominant orienting stimulus, megalopae of *Carcinus* sp. moved up when pressure was increased (Rice, 1964, 1966). Megalopae of *Macropipus* sp. responded in a similar fashion (Rice, 1966). Naylor and Isaac (1973) reported a response threshold for *Macropipus* sp. megalopae of 0.8 atm. The megalopa of *Eurypanopeus depressus* was responsive to pressure increments as low as 0.17 atm and an increasing proportion of the sample responded as pressure was increased in stepwise fashion to 1.4 atm. If pressure was raised instantaneously to 1.4 atm, the distribution was the same as that obtained when the pressure was raised in 0.17 atm increments. Subsequent reduction of pressure resulted in net descent in both cases.

The blue crab *Callinectes sapidus* has been the subject of comprehensive study of the ontogeny of barokinesis. Preliminary experiments showed an increase in swimming speed at ambient pressure through the course of zoeal development, but no response to pressure increments up to 0.8 atm. Baylor

and Smith (1957) had reported that *C. sapidus* zoeae responded to comparatively low pressure increments (0.6 atm). When larvae of zoeal Stages I, IV, and VII were tested by Sulkin et al. (1980) in pressure increments of 1, 2, and 3 atm at 25, 30 and 35 ‰ S, pressure response proved to be stage dependent, although there was no interaction between pressure and salinity. In zoeal Stage I, larvae showed the high barokinesis typical of brachyurans. In both Stages IV and VII, however, the reverse response was observed: swimming speed significantly decreased with pressure increase (low barokinesis). Pressure response in the megalopa was quite different. Using vertical movement of a sample of megalopae as the criterion of response, Naylor and Isaac (1973) had reported a response threshold for high barokinesis of 0.4 atm. Using a similar technique, Sulkin and Van Heukelem (1982) reported an even lower threshold (0.17 atm). Furthermore, an increasing proportion of the sample moved up in the column as pressure was raised to 1 atm in 0.17 atm increments. If pressure was raised instantaneously to 1 atm, the result was identical to that obtained by incremental steps. Direct measurement of horizontal swimming speed in megalopae orienting to light indicated a significant increase with pressure increments of from 0.2 to 1 atm. Substantial changes in pressure response occurred during ontogeny in *C. sapidus*: the first zoeal stage showed high barokinesis at a comparatively high minimum response threshold; later zoeal stages actually showed low barokinesis; the megalopa reversed once again to high barokinesis, with comparatively low response threshold.

Pressure response through the course of zoeal development also has been investigated in *Cancer irroratus* (Bigford, 1977). Measurements of change in vertical distribution were made for each of the 5 zoeal stages and the megalopa when pressure was raised to approximately 0.5 atm above ambient. In darkness, zoeal Stage II showed upward movement associated with high barokinesis (in negatively geotactic larvae), while Stage V showed descent which is consistent with the low barokinesis seen also in later stage *Callinectes sapidus* larvae. Positions of other larval stages remained unchanged. However, when light augmented gravity as an orientation stimulus, both Stages I and II moved upward as pressure increased while Stage IV moved downward and positions of the other stages remained unchanged. These results suggest that pressure response changes during ontogeny in a manner much like that described for *C. sapidus*.

In contrast, larvae of *Cancer magister* appear to maintain high barokinesis throughout larval development (Jacoby, 1982). Mean swimming speed increased through the course of larval development. As pressure increased, more larvae swam more often for all instars,

although the orientation of the response seemed to differ according to instar.

Results reported to this point have been based on larvae which are positively phototactic. Bentley and Sulkin (1977) showed a reverse response to pressure increment in larvae that were negatively phototactic at the time of the experiment (low barokinesis). A group of negatively phototactic Stage II *Rhithropanopeus harrisi* larvae showed a 27 % reduction in swimming speed when pressure was increased to 0.8 atm.

Evaluation of the role played by pressure response in vertical migration frequently has been complicated by reference to its effect on orientation response. Literature reports are almost universally consistent, however, if the clear distinction between kinesis and taxis responses is maintained. In Stage I larvae, increased pressure invariably results in increased locomotor activity (high barokinesis). In a sample of negatively geotactic larvae placed in a vertical column in darkness, for example, high barokinesis will be manifest by net upward movement. If light is used as an orienting stimulus in the experimental design, increased pressure will result in faster swimming toward the light or an increased proportion of a sample stimulated to swim toward the light. When light and gravity are apposed experimentally, enhanced movement due to pressure increase will occur, its direction dependent upon the relative dominance of the competing taxis stimuli. The minimum thresholds of response do vary among species and ontogenetic changes do occur. In general, later zoeal stages are less sensitive to pressure change, although late zoeal instars of both *Callinectes sapidus* and *Cancer irroratus* seem to exhibit low barokinesis.

Because pressure is a ubiquitous stimulus and one that varies predictably with depth, it can play an important role in depth regulation. It is only one component of the overall mechanism, however, and its significance to depth regulation is dependent upon interaction with orientation response. For example, as previously described, high barokinesis coupled with negative geotaxis (and/or positive phototaxis) forms the basis of negative feedback in depth regulation in a negatively buoyant animal. Thus the mechanism for depth regulation results from appropriate combinations of taxis and kinesis responses. The precision of the mechanism is controlled by pressure sensitivity. Moreover, available evidence suggests that while barokinesis will promote negative feedback, pressure responses do not contribute to positive feedback in directional movement. For example, in late stage *Callinectes sapidus* larvae which are positively geotactic and in *Rhithropanopeus harrisi* larvae which are negatively phototactic, low rather than high barokinesis is the rule. Therefore, as larvae move

deeper in response to these taxis stimuli, high barokinesis is not present to stimulate faster swimming. Responses of megalopae differ considerably from those of zoeal stages of the same species, a phenomenon whose significance will be discussed below.

Other factors influencing locomotor activity

Starvation has a direct effect upon locomotor activity. Cronin and Forward (1980) reported that swimming speeds of starved *Rhithropanopeus harrisi* larvae invariably were lower than those for fed larvae of the same stage. Prolongation of starvation, however, seemed to have little additive effect.

The effect of pollutants on locomotor activity has varied according to pollutant type. Forward and Costlow (1976, 1978) using various sublethal doses of 4 insecticides reported that swimming speed in *Rhithropanopeus harrisi* larvae was elevated at the lowest dosage to cause an effect, with a decline in swimming speed as the lethal level was approached. Effective dosages varied among insecticides and zoeal instars tested. Bigford (1977) reported that the water-accommodated fraction of No. 2 fuel oil in general depressed the effects of pressure increment on vertical movement in *Cancer irroratus* larvae. Bigford (1977) noted that larvae exposed to the oil pollutant were sluggish. The results imply a reduced level of locomotor activity in the presence of the oil pollutant. Decoursey and Vernberg (1972) obtained a similar result for mercury on larvae of *Uca pugilator* at a concentration of 0.18 ppm Hg (6 to 24 h). Older stages seemed more sensitive at this dosage and all stages showed evidence of swimming abnormality. Larvae exposed to lower concentrations of mercury ($1.8 \times 10^{-3-4}$), however, showed no effect. Application of the pesticide Sevin produced a reversible cessation of swimming in Stage I larvae of *Cancer magister*, with 50 % of the sample affected by a concentration of 6.5×10^{-3} mg l⁻¹ after 24 h (Buchanan et al., 1970).

SUMMARY OF EFFECTS BY STIMULUS

Presented below is a summary of effects on behavior of the major environmental stimuli discussed in this review.

(1) *Gravity* is a constant and ubiquitous orientation stimulus. Most Stage I larvae are negatively geotactic, although subsequent instars vary among species. Table 2 summarizes ontogenetic changes.

(2) *Light* is a complex, highly variable parameter which serves as both a taxis and kinesis stimulus. History of light adaptation is important in determining

behavioral response. Brachyuran larvae generally respond to a fairly broad range of wavelengths, although response peaks which vary among species do occur. The response spectrum for a given species is generally the same for light- and dark-adapted larvae. Dark-adapted larvae are generally positively phototactic over a wide range of intensities. Light-adapted larvae retain positive phototaxis to high intensity, but become negatively phototactic at lower intensities. The pattern of phototactic response remains unchanged through zoeal development, although responses of megalopae vary among species. Polarized light has been shown to influence orientation of larvae, although the relationship between plane of polarization and consequent orientation varies with stage and species. History of light adaptation influences swimming speed in response to light, although not in a consistent manner. Swimming speed oriented by light is generally faster than that during random swimming. Some species swim faster with change in light intensity; some do not. Swimming speeds towards or away from light or randomly vary according to condition of light adaptation, stage of development, and species. There is evidence to suggest that response to light is not an adaptation primarily related to vertical migration.

(3) *Hydrostatic Pressure* is an ubiquitous kinesis stimulus that varies in intensity predictably with depth. In Stage I larvae, swimming speed invariably increases with increasing pressure, although the minimum response thresholds vary among species. Later zoeal stages are either insensitive to pressure change or exhibit low barokinesis. Megalopae, however, show high barokinesis at comparatively low response thresholds.

(4) *Salinity* is a parameter which can vary in time and space in both a conservative and non-conservative manner. In estuarine and coastal marine systems, surface water is usually of lower salinity than is deeper water. Salinity has minor modifying effects on taxis stimuli, if larvae are tested at or above the adaptation salinity. Increased salinity may enhance locomotor activity slightly and in so doing, increase the proportion of a sample of larvae actively swimming at any given time. This may produce an apparently higher level of sample response to a given taxis stimulus. If larvae are rested at salinities below that of adaptation there can occur an actual reversal in sign of geotaxis and phototaxis. The influence of salinity on swimming speed may be stage dependent and may depend further upon whether or not larvae are adapted to the different salinities being tested. Sharp vertical haloclines can disrupt upward vertical movement, but do not seem to inhibit it.

(5) *Temperature* is a parameter whose patterns of

variability are similar to those described for salinity. Indeed, the 2 parameters often vary inversely with depth in the estuarine and coastal marine environment. Larvae tested in temperatures either above or below that of adaptation often respond by cessation of locomotory activity and consequently sink. There is evidence, however, that later stage *Rhithropanopeus harrisi* larvae reverse sign of geotaxis when exposed to high temperatures. Sign of phototaxis is largely independent of temperature, although percent response of negative phototaxis increases at low light intensities as temperature increases. Decrease in temperature causes decrease in swimming speed, with a few notable exceptions (e.g. Stage I *Callinectes sapidus*). Sharp vertically oriented thermal gradients have little effect on upward vertical migration, although avoidance to high temperatures can occur.

(6) *Food*. Compared to fed controls, a sample of starved larvae shows a higher proportion of individuals responding positively to light and a reduced proportion showing negative phototaxis in early stage larvae, but not in later zoeal instars. Length of starvation has no effect on later instars. Swimming speeds of starved larvae are invariably lower than those of fed larvae.

(7) *Pollutants*. Although a sizeable literature exists on the effects of pollutants on larval development in brachyurans (see review by Epifanio, 1979), relatively few studies have included effects on behavior. Larvae exposed to sublethal dosages of insecticides show elevated swimming speed, although swimming speed drops as the lethal dosage is approached. Hydrocarbon and heavy metal stresses seem to reduce locomotor activity. Sign of phototaxis can be affected by insecticides although the pattern of response is not consistent among instars or products tested.

DISCUSSION

Behavioral basis of depth regulation

Results of research reviewed here for brachyuran larvae can be applied to the generalized model of depth regulation described earlier. Although there exists considerable variation among species, responses to the more conservative environmental parameters are remarkably consistent, particularly considering the wide variety of experimental designs used. Maintenance of vertical position above the bottom, a phenomenon essential to maintenance of the planktonic habit, requires compensation for the effects of negative buoyancy.

Geotaxis is a response to a very conservative stimulus. The pervasive negative geotaxis which is characteristic of the first zoeal stage provides a strong

orientation basis for upward movement. This orientation component may or may not be complemented by light, which is a more highly variable stimulus and which evokes a less predictable response. The degree of upward movement which actually occurs will depend upon locomotor activity, which is subject to a variety of endogenous and exogenous stimuli. Endogenous activity rhythms, however, are probably keyed to exogenous factors and are undoubtedly species specific. Hydrostatic pressure provides the most conservative kinesis stimulus. Virtually all first stage larvae exhibit high barokinesis, with shallow water forms showing relatively low response thresholds. A behavioral basis thus exists to promote movement toward surface waters and maintenance of position high in the water column soon after larvae hatch, a phenomenon widely reported among larvae of benthic invertebrate taxa (Thorson, 1950; Mileikovsky, 1971; Longhurst, 1976).

Although behavioral responses of later zoeal stages are more variable, even to the most conservative stimuli, the same principles used for Stage I may be applied to understanding the role of behavior in vertical distribution of later instars. For a given instar of a particular species, an assessment can be made of the dynamic balance between negative buoyancy on one hand and relevant taxis and kinesis responses on the other. Because later instars tend to be less sensitive to pressure change, precision in depth regulation is not likely to be pronounced (Knight-Jones and Qasim, 1966). As a consequence, later stage larvae are likely to be exposed to a greater range of environmental parameters which vary with depth, such as temperature and salinity. Although such parameters can modify behavior to produce feedback, the results reviewed here for brachyuran larvae suggest a lower sensitivity to temperature and salinity change than has been reported for other zooplankters (e.g. Ewald, 1912; Fraenkel, 1931; Lance, 1962; Thorson, 1964; Harder, 1968; Roberts, 1971). Furthermore, examples have been provided in which change in taxis response during ontogeny is complemented by change in kinesis response in a way that reduces the probability of positive feedback leading to excessive downward displacement (e.g. the shift from negative to positive geotaxis accompanied by a shift from high to low barokinesis in *Callinectes sapidus*). The absence of positive feedback that would accentuate downward displacement may be an adaptation to sustain the planktonic habit of even late zoeal instars. A similar limitation on positive feedback is not present in larvae oriented such that they will swim upward. For example, both high photokinesis and high thermokinesis are often coupled with negative geotaxis and/or positive phototaxis.

Behavioral responses of brachyuran megalopae often differ considerably from those of the zoeal stages. Taxis responses vary widely among species, although high barokinesis at comparatively low thresholds seems a widespread phenomenon. This suggests high precision in depth regulation by megalopae. The megalopa stage is one of transition between the primarily planktonic zoeal stage and the adult, whose habits vary widely among species. It seems reasonable to predict strong selection for behavioral traits which can promote successful recruitment to and settlement in habitats favorable to adult life. Unlike the zoeal stage which is suspended in the water column, megalopae may be benthic at times. Because they can use the substrate as a reference point, they can perceive changes in environmental variables, including pressure, which are related to the passing of the tidal wave. Preferential movement on flood or ebb tides has been proposed for megalopae of *Carcinus* sp. (Knight-Jones and Qasim, 1966) and *Callinectes sapidus* (Epifanio, pers. comm.). In addition, there are reports that megalopae swim at discrete depths (Williams, 1971; Lough, 1976; Chace and Barnish, 1976; Rice and Kristensen, 1982). Precision in depth regulation, whether manifest in preferential use of tidal flow or swarming at discrete depths, may be important to the recruitment and settlement process. If so, the operative mechanism for this phenomenon may be high sensitivity to pressure change.

Application of the proposed experimental depth regulation model provides a useful framework for study of the behavioral and morphological adaptations that contribute to vertical migration in specific cases. It follows that the most productive approach is to identify the principal components of the model, isolate and measure them rigorously, and reconstruct the model using the resultant data base. The advantage to this approach is that it provides a mechanistic basis for depth regulation and thus has predictive value. By stressing rigorous measurement of individual behavior traits, it avoids a principal, and justified, criticism of many laboratory-based behavioral experiments; namely, that no experimental design can pretend to simulate the natural water column. Although the questions pursued by this approach are limited in scope, they can be combined to formulate a working hypothesis for vertical distribution which can be tested in the field.

In pursuing this approach, it may be profitable to develop a 'base model' which is dependent upon the modifying effects on negative buoyancy of responses to the more conservative environmental parameters, such as gravity as the taxis stimulus and hydrostatic pressure as the kinesis stimulus. This base model then can be modified as appropriate by determining

behavioral responses to progressively less conservative stimuli. This concept may be justified on theoretical as well as logistical grounds. If there is selective advantage to the evolution of a combination of behavioral traits (a 'tactic', *sensu* Stearns, 1976) which regulates vertical movement of the dispersal stage of benthic marine invertebrates, it is reasonable to suggest that selection has acted preferentially on responses to conservative stimuli. The most controversial implication of this assertion is the relegation of light to secondary significance in regulation of vertical distribution in brachyuran larvae.

There exists evidence to support this contention (Forward, 1976b). Forward and Cronin (1978) argue convincingly that differential response to low light intensity as a function of light adaptation will not produce diurnal vertical migration, but rather is keyed to predator avoidance. Furthermore, tidal rhythms in sign of phototaxis (positive on falling tides; negative on rising tides) in *Rhithropanopeus harrisii* predicts the opposite pattern from that actually measured in the field (Forward and Cronin, 1980). The authors conclude that phototaxis does not contribute to vertical migration in this species.

The pattern of spectral sensitivity exhibited by brachyuran larvae is not consistent with use of light as a primary orientation stimulus in vertical migration (Forward and Cronin, 1979). If larval photoreceptors are used primarily for vertical migration, it is reasonable to assume that they will be adapted for maximum light sensitivity. The spectral response of the animals consequently should match the spectral distribution of light in the animal's habitat (Munz, 1958). Forward and Cronin (1979) indicated that this is not the case for many species tested. Furthermore, in *Rhithropanopeus harrisii* spectral sensitivity remains constant throughout zoeal development (Forward and Costlow, 1974) and in some species, larvae and adults show similar response spectra. These arguments are consistent with the conclusion that photic responses may be adapted to the requirements of adult life and are not, therefore, primarily adapted for pelagic larval life.

Nevertheless, it is obvious that larvae respond to specific light conditions in predictable ways. Because of the angular distribution of light in the sea, it can influence vertical movement. When light is aimed down the axis of a vertically oriented chamber, a larger proportion of the sample moves into the upper portion of the chamber as compared to the distribution seen in darkness (Sulkin, 1975; Bigford, 1977, 1979). This is probably a reflection of the fact that the percentage of the sample responding positively to light exceeds that responding negatively to gravity. On the other hand, Forward (pers. comm.) suggests that in some cases the effect of negative geotaxis can be modified by photo-

kinesis response in which larvae become inactive when they ascend to regions of high intensity light. It may be useful, therefore, to consider geotaxis as fundamental in the orientation of vertical movement, with light as a potential modifier depending upon extant conditions.

As adaptive radiation occurred and as brachyurans exploited new habitats, a number of more highly variable stimuli were encountered (e.g. estuarine salinity gradients). Successful exploitation of these new environments required behavioral accommodation of the additional stimuli and the behavioral tactic regulating vertical distribution was modified accordingly. Differences in recruitment strategy among species may be the result of specialized modifications to the base model of depth regulation. Behavioral adaptations which promote estuarine retention of larvae in *Rhithropanopeus harrisii* and exportation of larvae from the parent estuary in *Callinectes sapidus* are examples.

Application of depth regulation models

Behavioral studies such as those reviewed here can contribute to better understanding of meroplankton ecology in at least two ways, as illustrated by the cases considered below.

Such studies significantly aid in the interpretation of distribution data from field studies when both are part of a comprehensive effort. Such an effort has been conducted on *Rhithropanopeus harrisii*. Cronin (1982) and Cronin and Forward (1982) reported that larvae of *R. harrisii* are retained within a restricted region of a shallow estuary. Field data suggest that their mean vertical distribution places larvae near the depth of no net motion when averaged over the duration of zoeal development. The data also suggest, however, that larvae do not exhibit precise depth regulation, but rather engage in substantial vertical excursions throughout zoeal development. Results of behavioral studies revealed potential mechanisms for this phenomenon. Tidal rhythms in both sign of phototaxis and locomotor activity occur which could contribute to the observed distribution (Cronin and Forward, 1979; Forward and Cronin, 1980; Cronin and Forward, 1982). Vertical distribution is also influenced in the field by the degree of water stratification (Cronin, 1982). Latz and Forward (1977) showed that signs of phototaxis and geotaxis are sensitive to salinity change in the order of 1 to 2 ‰. Salinity changes associated with the breakdown of a previously stratified water column to one that is vertically homogeneous with respect to salinity may be sufficient to alter larval behavior. Significantly, despite strong phototactic behavior (Forward, 1974; Forward and Costlow, 1974), the natural

light-dark cycle has little effect upon vertical migration (Cronin, 1982). Indeed in nature larvae rarely moved above the depth of an isolume that was strong enough to evoke phototaxis. Larval responses to a variety of environmental stimuli thus produce substantial vertical migration, but in a pattern which keeps the larvae, on average, near the depth of no net motion. Larvae thus achieve the advantage of exploration of the water column, while exhibiting a depth regulatory pattern required to assure retention near the parent population (Cronin, 1982). The complexities and subtlety of this tactic are revealed because of the comprehensive approach which employed both field distribution and experimental behavioral studies.

Study of the behavioral basis of depth regulation is also valuable in focusing field effort, as in the case of the deep sea red crab *Geryon quinquedens* (Kelly et al., 1982). Larvae of *G. quinquedens* hatch at depths of from 200 to 400 m on the continental slope off the east coast of North America. Because of complex current and temperature patterns in the slope and shelf waters that overlie the hatching zone, dispersal distances of the larvae will be affected greatly by their vertical distribution. Migration of the first zoeal stage from the bottom to the surface, for example, could expose larvae to temperatures ranging from 3 to 24 °C depending upon the date of hatching. Transport distance thus will be determined by length of planktonic duration, which is a function of temperature, and the velocities of the currents that larvae encounter. Kelly et al. (1982) demonstrated that, indeed, the first zoeal stage possesses the behavioral traits typical of other first stage brachyuran larvae, traits which should promote movement up into the water column. Because of their relatively long pelagic duration at the low temperatures typical of the water column during much of the hatching season, transport distances in excess of 500 km will be common.

Based on this analysis, Kelly et al. (1982) presented the following recruitment hypothesis. Larvae hatching on the continental slope north of Cape Hatteras, North Carolina, will be transported toward the southwest in both slope and shelf currents. As a consequence, prior to their metamorphosis great numbers of them are likely to be entrained in the northeastward flowing Gulf Stream, which is located close to shore at Cape Hatteras. Larvae hatched progressively to the southwest will be transported in the Gulf Stream farther to the northeast prior to settlement. The model thus predicts recruitment to the slope from offshore, a mechanism consistent with reports that small juveniles are present only at the base of the slope at the northern end of the species range (Wigley et al., 1975).

This model has a number of consequences which lend themselves to field testing. For example, there

should be large numbers of *Geryon quinquedens* larvae in the Gulf Stream, with all stages represented at the entry point north of Cape Hatteras and the larval population characterized by increasingly older individuals towards the northeast. Because the southwest end of the range should receive recruits directly from larvae hatched at the northeast end, while populations at the northeast end are dependent upon a more variable source of recruitment from the Gulf Stream, annual recruitment may be more stable in the southern population. This may be apparent in a comparison of size-frequency distributions between the two sub-populations. Furthermore, the southwestern sub-population should receive new recruits throughout the depth range rather than at the base of the slope only.

Behavioral studies thus have contributed to a specific hypothesis for distribution of larvae and for recruitment strategy in *Geryon quinquedens*. A well-defined field study now can be designed to focus on specific consequences of the hypothesis.

Studies of the behavioral basis of vertical migration of larvae thus have value in contributing to the understanding of dispersal and recruitment in brachyurans. Such research will be most effective if the results are interpreted within the context of a generalized model for depth regulation and that model is used to interpret or focus field studies.

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