Larva
Deep-sea
Vertical migration
Larval nutrition
Echinoderm

Larve
Fond marin
Migration verticale
Nutrition larvaire
Echinoderme

The potential for ontogenetic vertical migration by larvae of bathyal echinoderms

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ABSTRACT

Planktotrophy is a relatively common developmental mode among bathyal and abyssal echinoderms, but the sources of food used by deep-sea planktotrophic larvae remain generally unknown. Very few deep-sea echinoderm larvae have been collected in plankton samples, so we do not know whether larvae migrate to the euphotic zone to feed or if they rely on bacteria or detritus at greater depths. We approached this question indirectly by investigating whether larvae of bathyal echinoids can tolerate the temperatures they would encounter in the euphotic zone and whether they possess sufficient energy stores to migrate to the euphotic zone without feeding. Twenty-four hour survival at 20 and 24 °C was always much lower than survival at colder temperatures, but there were species-specific and stage-specific differences in temperature tolerances. A numerical model of the energy consumed by migrating larvae predicted that larvae should be able to reach adequate phytoplankton concentrations before exhausting parental reserves, unless they swim very slowly and have very high metabolic rates. These results suggest that long vertical migrations are more likely to be limited by physiological tolerances than by energy stores.

RÉSUMÉ

Potentialités des larves d'échinodermes de la zone bathyale à effectuer des migrations ontogéniques verticales.

La planctotrophie est un mode de développement assez commun chez les échinodermes du milieu bathyal et abyssal, mais l'origine de la ressource alimentaire de ces larves planctotrophes de grande profondeur reste en général inconnue. La faible quantité de larves récoltées lors des pêches planctoniques ne nous permet pas de déterminer si elles se déplacent vers la zone euphotique pour se nourrir ou si elles subsistent aux dépens de bactéries ou de détritus présents en zone profonde. Cette question peut être posée de manière indirecte : les larves, provenant de la zone bathyale sinon abyssale, peuvent-elles tolérer les températures de la zone euphotique et arriver jusque-là sans se nourrir grâce à leurs réserves énergétiques ? Après 24 h, le taux de survie aux températures de 20-24 °C est toujours beaucoup plus faible qu'à des températures plus basses. De plus, ces différences sont propres à l'espèce et au stade de développement. Un modèle numérique, basé sur l'énergie consommée par ces larves en migration, indique qu'elles

peuvent atteindre des couches de phytoplancton avant l'épuisement de leurs réserves endogènes, à moins de nager très lentement et d'avoir un métabolisme très élevé. Ces résultats suggèrent qu'une migration verticale de cette ampleur serait limitée par la tolérance physiologique plutôt que par les réserves énergétiques des larves.

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INTRODUCTION

Ever since deep-sea animals were first studied carefully in the years following the Challenger expedition, there has been active discussion on the questions of how and where the young stages of deep-sea animals develop. Moseley (1880) was perhaps the first to suggest that larvae of abyssal species might reside in shallow water. His opinion, however, was ultimately overshadowed by the strongly articulated position of Gunnar Thorson (1950), who believed that migration of a planktonic larva to the surface would be impossible because of inadequate food along the way (reviewed by Young, 1994; Pearse, 1994). We now know that many deep-sea species produce pelagic feeding larvae, but whether these larvae actually move to the euphotic zone remains a topic of fervent discussion. Bouchet and Warén (1994) have recently reviewed the literature on ontogenetic migration of deep-sea gastropod larvae, the group for which the most direct evidence is available, and reported that larvae of abyssal gastropods have been found in shallow-water plankton samples in the North Atlantic, Mediterranean and Southwest Pacific. Isotope analyses of larval shells (Bouchet and Fontes, 1981; Killingley and Rex, 1985) and anatomical observations (*e.g.*, presence of eyes, shape of protoconch) support the idea that many species make substantial vertical migrations (Bouchet, 1994). Deep-sea brachiopod larvae have also been collected in the surface waters (Ashworth, 1914). For most other taxa, we do not have direct evidence either for or against ontogenetic vertical migration.

In those groups for which direct data on larval distributions (*i.e.* presence of larvae in collections made with opening and closing nets) are not available, we must presently depend on circumstantial evidence to infer whether migration to the euphotic zone is feasible or likely. In this paper, we consider two such kinds of indirect evidence: 1) tolerance of larvae to physical conditions (*e.g.*, temperature increases, pressure decreases) that would be encountered during migration and 2) energy requirements of deep-sea larvae.

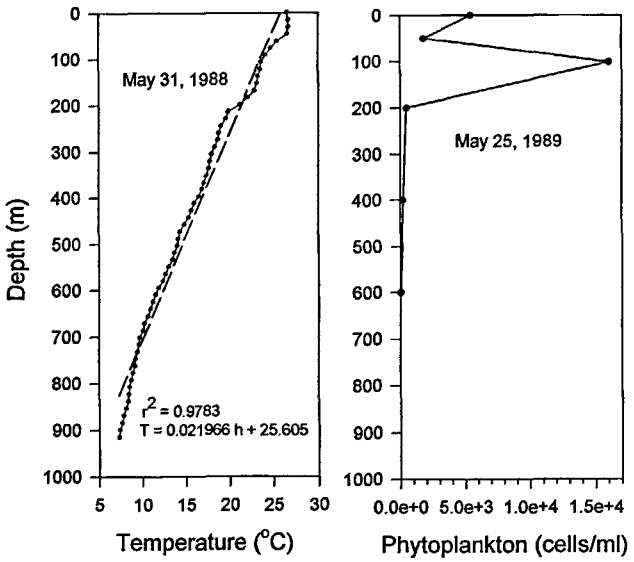

Figure 1

Left Graph: representative curve showing relationship between depth and temperature during the spring reproductive season. The dashed line is a least squares regression used for predicting temperatures at discrete depths. Right Graph: depth distribution of phytoplankton cells in the Bahamas during the spring of 1989. Water samples were collected in Niskin bottles, concentrated on black nucleopore filters, which were examined for autofluorescent cells under an epifluorescence microscope.

How far should planktotrophs migrate?

For the kinds of arguments we wish to make, we need an estimate of the metabolic compensation depth, which is defined as the depth at which phytoplanktonic food is sufficiently abundant to support the metabolic needs of deep-sea larvae. Estimation of this depth requires information on the vertical distribution of phytoplankton and on the particle clearance rates, assimilation efficiencies, and metabolic rates of larvae. Unfortunately, we know very little about these aspects of larval physiology for any deep-sea animal.

We have examined the distribution of phytoplankton and other potential food items for larvae in the water column overlying the Bahamian Slope (Young, Bosch and Cameron, unpublished data) and will report the complete results of this study elsewhere. In Bahamian waters, the chlorophyll maximum lies between 100 and 200 m and chlorophyll drops to very low levels below 200 m. A profile of algal cell counts taken in the Bahamas during the spring season (when most bathyal echinoids reproduce) is shown in Figure 1. In this particular hydrocast, algal density at 100 m depth exceeded 16,000 cells/ml, but there were only about 450 cells/ml at 200 m and 225 cells/ml at 400 m. This last point is probably an overestimate of the actual abundance, since it is extrapolated from nine subsamples containing no algal cells and a single subsample with only one cell.

One of us (WJ) has obtained preliminary respiration measurements for two developmental stages of a bathyal echinoid, *Lytechinus euerces*. These data were collected following procedures outlined in Jaeckle (1994) at a temperature of

15 ± 0.2 °C. The respiration rate of 4-arm-stage plutei of *L. euerces* averaged 3.11 pmol O_2/larva-h, a lower value than that expected for developmentally equivalent echinoplutei of shallow-water species. For example, Shilling and Manahan (1990) reported that the respiration rate of 4-arm plutei of *L. pictus* was *ca.* 20 pmol O_2/larva-h at 20 °C. If we assume a Q_{10} (a factor which represents the multiplicative increase in respiration rate for a temperature rise of 10_0) of 2, this would equal 14 pmol O_2/larva-h at 15 °C).

Fenaux *et al.* (1985) measured particle clearance of *Rhodomonas* sp. and *Pavlova lutheri* by 4-arm pluteus larvae of *Paracentrotus lividus*. We have borrowed these values, as no clearance rate data are available for any deep-sea species. The energy content per unit cell was calculated from the compositional data published by Wilfors *et al.* (1992) using the combustion enthalpies published in Gnaiger (1983). We estimate that a *Rhodomonas* cell and a *Pavlova* cell contain 2.78 µJ and 0.38 µJ of energy, respectively.

If we assume an unrealistically high assimilation efficiency of 100 %, an environmental temperature of 15 °C and a low larval respiration rate (3.11 pmol/larva-h), the number of algal cells that must be consumed to equal the energy requirements of a 4-arm pluteus can be calculated. Using an oxyenthalpic conversion of 480 kJ/mol O_2 [the average of the oxyenthalpic equivalents for protein, lipid and carbohydrate, all taken from Gnaiger (1983)], the larval respiration rate is equal to an energy utilization rate of 1.42 µJ/larva-h. Thus a larva must consume about 13 *Rhodomonas* cells or 95 *Pavlova* cells to equal the daily energy demand of metabolism. If the larva has a high metabolic rate of 20 pmol O_2/larva-h (= 9.6 µJ/larva-h), energy compensation would be accomplished after consumption of 83 cells of *Rhodomomas* or 606 cells of *Pavlova* per day. Pechenik and Fisher (1979) have estimated the assimilation efficiency of gastropod larvae to be about 30 %. To correct our model for more realistic assimilation efficiencies of, for example, 50 % and 25 %, larvae would have to clear more cells from suspension by factors of 2 and 4, respectively.

Representative temperature profiles for the spring and autumn seasons taken from sensors mounted on a manned submersible are shown in Figure 1. Assuming a realistic Q_{10} value of 2, we can predict the respiration rate of larvae for the temperature at any discrete depth by using the second order regression that describes the temperature/respiration curve. For example, a 4-arm pluteus with the high oxygen consumption rate measured by Shilling and Manahan and swimming at a depth of 200 m would experience an environmental temperature of 21.33 °C during May and would consume 22.05 pmol O_2/larva-h or 10.67 µJ/larva-h of energy. Algal density at 200 m during the month of May is 452 cells/ml (Fig. 1). Multiplying this density by the particle clearance rate of 6.25×10^{-3} ml/larva-h (Fenaux *et al.*, 1985), we may predict that a larva should obtain 2.82 algal cells per hour at this depth. If the algal cells are relatively large and have an energy value comparable to that of *Rhodomonas*, larvae would obtain about 7.83 µJ/h (2.82 cells/h × 2.78 µJ/cell). This is less than the 10.67 µJ/larva-h required for maintenance, so the metabolic compensation depth must lie at a shallower depth. Applying multiple iterations of the above procedure to the May temperature and particle concentration data, we estimate that larvae with 100 % assimilation efficiency should find their metabolic compensation depths at 195 m and 525 m for high and low metabolic rates, respectively. At a more realistic assimilation efficiency of 25 %, the metabolic compensation points converge: 190 m for high metabolic rate and 195 m for low metabolic rate. Three of the four estimates fall in the region just below the chlorophyll maximum, where particle concentrations drop by two orders of magnitude over a 200 m vertical distance.

Do physiological tolerances limit vertical movements?

Young and Cameron (1989) reported that the larvae of one bathyal Bahamian echinoid, *Linopneustes longispinus*, develops normally only at temperatures near those where the adult organisms live. Warmer temperatures resulted in mortality of embryos and cooler temperatures arrested development at the swimming gastrula stage indefinitely and reversibly. Although later larvae have not been tested, it appears that the range of temperatures tolerated by this species is relatively narrow. Pressure has also been implicated as a limiting factor on vertical movements. In *Echinus affinis*, a sea urchin that lives at about 2000 m depth in the Rockall Trough, the lower pressure threshold for embryonic development is at about 1500 m depth (Young and Tyler, 1992). This depth is very near the upper vertical limit of the species, suggesting that embryonic pressure tolerances may determine distribution. However, pressure tolerances of later larvae have not been examined, so we do not know if they migrate into shallower water during the feeding stages.

Both of the examples given above hint that physical factors may prevent ontogenetic migration to the euphotic zone. We may ask whether this is a general phenomenon for echinoderms or if some species are more tolerant of high temperatures and low pressures than others. Using larvae obtained from artificial spawnings (ripe adults collected in good condition by Johnson-Sea-Link submersibles) during April, 1994, we investigated this question in a series of laboratory experiments. Larvae were reared in mass culture to various pluteus stages, then 18 larvae were assigned to each of five temperatures at 5 °C increments. Each larva was held in an individual 2-ml tissue culture well placed in a dark table-top incubator at its assigned temperature. All larvae were examined under a dissecting microscope after 24 h to determine if they were alive (as indicated by ciliary activity and gut movements) or dead (indicated by lack of movement and often by necrosis of arm tissues).

Temperature tolerances of larvae at 33 decreased with increasing temperature in all species studied (Fig. 2). *Lytechinus euerces* and *Stylocidaris lineata* were more tolerant of 24 °C than the other two species, both of which did very poorly at surface temperatures. All four species reproduce during the springtime, when the 15 °C isotherm lies at about 400 m (Fig. 1) and the 20 °C isotherm lies at about the same depth (200 m) as the most likely metabolic compensation depth (190-195 m). From the data, it appears that *Lytechinus euerces* and *Stylocidaris lineata*

might be able to tolerate the temperatures at 200 m depth. *Aspidodiadema jacobyi* does not survive the temperature at 200 m in any larval stage. However, *Archaeopneustes hystrix* shows some ability to tolerate this temperature in the early stages and could be even more tolerant of high temperatures at later stages not examined in this study. These differences do not appear to be related to the bathymetric distributions of adults (Young, 1991), as all four species have substantially overlapping vertical distributions. In some instances, tolerances to warm temperatures increased as a function of larval age. For example, *Aspidodiadema jacobyi* larvae experienced 100 % mortality at 20 °C in the 2-arm and 4-arm stage but their tolerance increased in later larval stages.

Does available energy limit vertical migration ?

Thorson's classic argument for non-planktotrophic development in deep-sea animals rested on the assumption that larvae would have inadequate energy to migrate into the shallow waters where phytoplankton are sufficiently abundant to meet the needs of metabolism and growth. A test of this idea would require information on the parental investment of energy in the egg, the metabolic rate, swimming speed, and swimming direction of the migrating larva, and the ability of the larvae to use alternative sources of nutrition such as dissolved organic materials and bacteria.

We modelled the possibility of vertical migration to the euphotic zone by estimating the cumulative oxygen consumption during migration at specified speeds, beginning at specified depths (we used the ranges of bathymetric distribution for each species as starting points), assuming a Q_{10} value for respiration rate, and knowing the actual relationship between temperature and depth.

If the rate of energy consumption is known for a given temperature, the change in rate of consumption can be computed by,

$$Q_T = Q_0 e^{r \Delta T} \quad (1)$$

where Q_0 is the known rate of energy consumption, r is the rate of change and Δ T is the temperature difference in degrees Celsius, which can be expressed as,

$$\Delta T = T - T_0 \quad (2)$$

where T_0 is the initial temperature. Water temperature is related to depth in an approximately linear fashion (Fig. 2) except near the surface, so the temperature T may be predicted for any depth h (in meters) by the linear regression equation

$$T = mh + c \quad (3)$$

where m, the slope of the line, represents the temperature change per meter, h is the depth in meters and the constant c is the y intercept. The depth h is a function of time and is computed as

$$h = h_0 - vt \quad (4)$$

where h_0 is the depth in meters where the larva starts swimming towards the surface, v is the larva's swimming speed in meters/hour and t is time in hours. The term vt is negative because the larva is swimming into shallower depths. The initial temperature, T_0, can be computed from,

$$T_0 = mh_0 + c \quad (5)$$

Substituting (4) into (3) and distributing m,

$$T = mh_0 - mvt + c \quad (6)$$

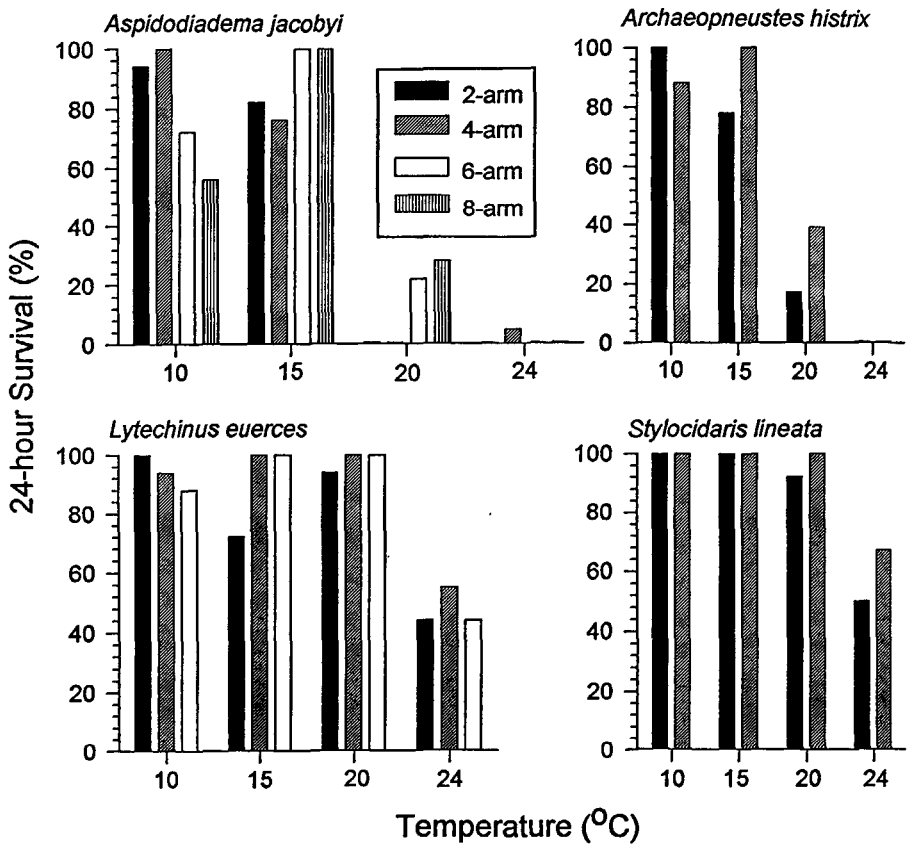

Figure 2

Twenty-four hour survival of echinopluteus larvae of four bathyal sea urchins from the Bahamas at four temperatures. Shading patterns indicate different larval stages (i.e. number of arms).

Substituting (5) and (6) into (2),

$$\Delta T = mh_0 - mvt + c - (mh_0 + c) \quad (7)$$

(7) reduces to

$$\Delta T = - mvt \quad (8)$$

Substituting (8) into (1):

$$Q_T = Q_0 e^{r(-mvt)} \quad (9)$$

Q_T is converted into units of energy by applying a conversion factor K,

$$E_t = KQ_T \quad (10)$$

By combining equations (9) and (10) we arrive at,

$$E_t = KQ_0 e^{-rmvt} \quad (11)$$

Now the total energy consumed by a swimming larva at time t can be estimated by setting up a definite integral from (11) and integrating with respect to t,

$$E_t = \int KQ_0 e^{-rmvt} dt \quad (12)$$

where E_t is the total energy consumed. Integrating (12) we obtain

$$E_t = - (KQ_0/rmv) e^{-rmvt} \Big|_0^t \quad (13)$$

a model that predicts the cumulative energy consumption for a larva that has been swimming upward for any specified time.

The parameters required for this model are respiration rate, swimming speed, and temperature change as a function of depth, Q_{10}, starting depths, and an oxyenthalpic equivalent to convert oxygen consumption to energy. Unfortunately, almost nothing is known about the physiology of deep-sea larvae, so the estimates we used were designed generally to illustrate the approach and to outline a range of possibilities. As actual parameter measurements become available in the future, the same equations may be used for obtaining a more realistic idea of what sort of ontogenetic migration planktotrophic larvae might be capable of achieving.

We used the same two extreme values for metabolic rate as in the calculation of metabolic compensation depth above. There are no published empirical values for swimming speeds of any bathyal larvae, so we used extremes of echinoid larval swimming speeds reported in the unpublished work of H. Lee of 1.44 m/h and 6.84 m/h. We assumed a Q_{10} value of 2, which appears to be realistic, based on other measurements for larvae and for bathyal and abyssal adult organisms. The temperature/depth regression (equation 3) was estimated by the least squares method from submersible data (Fig. 1). Starting values were determined from the upper and lower limits of the bathymetric range of each species in question, as determined from Johnson-Sea-Link submersible records accumulated over the past ten years and mostly published in Young (1991).

In order to determine if larvae would exhaust their supplies of available energy during migration, we must be able to estimate the amount of energy available in the egg. This parameter has not been measured directly for any bathyal echinoid species. However, Jaeckle (1995) has summarized published measurements of energy content and volume for echinoderm eggs. When plotted on a logarithmic scale, the points fall along a highly significant regression line, suggesting that energy can be predicted with some confidence from egg volume. We have measured diameters of eggs from a number of bathyal and abyssal echinoderm species (Young and Cameron, 1989; Young *et al.*, 1989; Young, unpublished data) and have used the regression equation from Jaeckle (1995) to estimate the energy content of eggs of selected species. Although total energy content is an instructive estimate of egg size, estimates of the time to total energy consumption during larval life (*i.e.* complete self-consumption) are ecologically and physiologically irrelevant. To our knowledge, there are no estimates available for the percentage of the initial energy content that can be consumed without deleterious developmental consequences for either shallow or deep-sea echinoid species. Lucas *et al.* (1979) reported that nonfeeding cypris larvae of the barnacle *Semibalanus balanoides* could consume up to 34 % of their energy stores (stores accumulated during the preceeding feeding naupliar stages) without negative consequences. We have used this percentage as a first approximation of the size of the metabolically labile energy stores in echinoderm eggs. We also make the following simplifying assumptions:

1. Swimming speed does not change as a function of temperature or viscosity.

2. Swimming is continuous and unidirectional (upward).

3. Metabolic rate does not change with larval age.

4. Larvae do not consume external food sources (including bacteria, dissolved organic matter) during migration.

5. Volume-specific energy content is similar in eggs of shallow and deep-sea echinoderms.

All of these assumptions are probably unrealistic, but they are necessary because of inadequate data on the physiology and behavior of deep-sea larvae.

The cumulative energy consumption curves predicted by the model for combinations of high and low respiration rates and swimming speeds are shown for four species of bathyal echinoids from the Bahamas in Figures 3-6. In each figure, the vertical line represents the estimated labile energy and the horizontal lines represent metabolic compensation depths at extreme values of 25 % and 100 % assimilation efficiencies. The distances migrated during each successive 24-h period are represented by points on the curves, and the two curves on each graph represent migrations that begin at the upper and lower limits of the species' bathymetric ranges.

In all four species, the model predicts that larvae should be capable of reaching the metabolic compensation point before expending all available energy in the egg, except under some circumstances of high metabolic rate combined with slow swimming speed. For example, larvae of *Aspidodiadema jacobyi* (Fig. 4) originating from the lower end of their range should be able to reach sufficient algal densities to support their metabolic needs in less than four days. Maternal provisions are sufficient to supply their needs for this period. At slow swimming speeds, larvae from the same depth would require 18 days to reach the surface, but there is still sufficient energy in the egg to support this migration at low metabolic rates. However, larvae with high metabolic rates and low swimming speeds are predicted to exhaust their available energy before arriving at the metabolic compensation point even when they must migrate only 150 m (a 5-d journey) from the top end of their range (Fig. 3). *Archaeopneustes hystrix* larvae

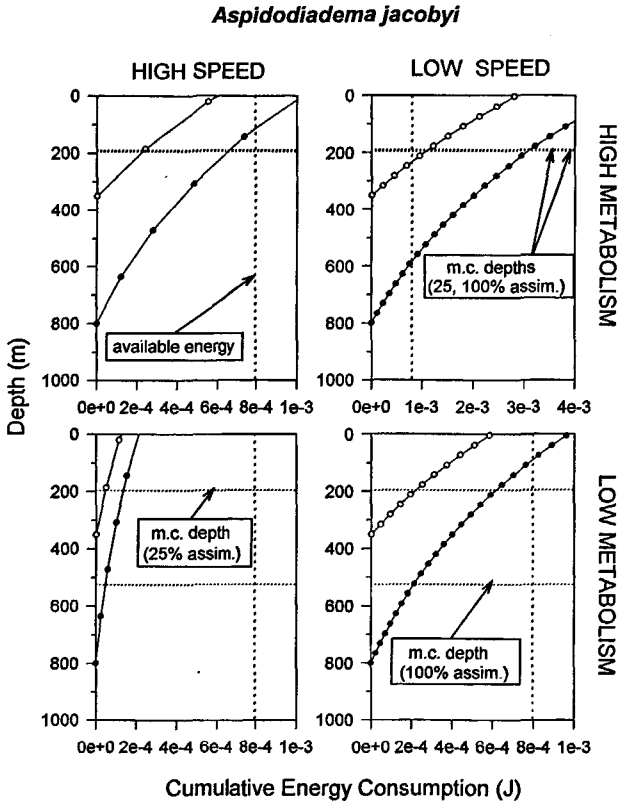

Figure 3

Predicted cumulative energy consumption as a function of depth for Aspidodiadema jacobyi *larvae at four combinations of high and low metabolism and high and low swimming speed (see text for values). Points on all curves are one-day apart. Solid points represent the migration of larvae beginning at the lower end of the adult bathymetric range and open points represent migration of larvae beginning at the upper end of the bathymetric range. All vertical dotted lines represent an estimate of the labile (available) energy in the egg. Horizontal dotted lines are the calculated metabolic compensation depths at 25 % and 100 % assimilation efficiency. Boxed labels and associated arrows on each graph also apply to the other graphs.*

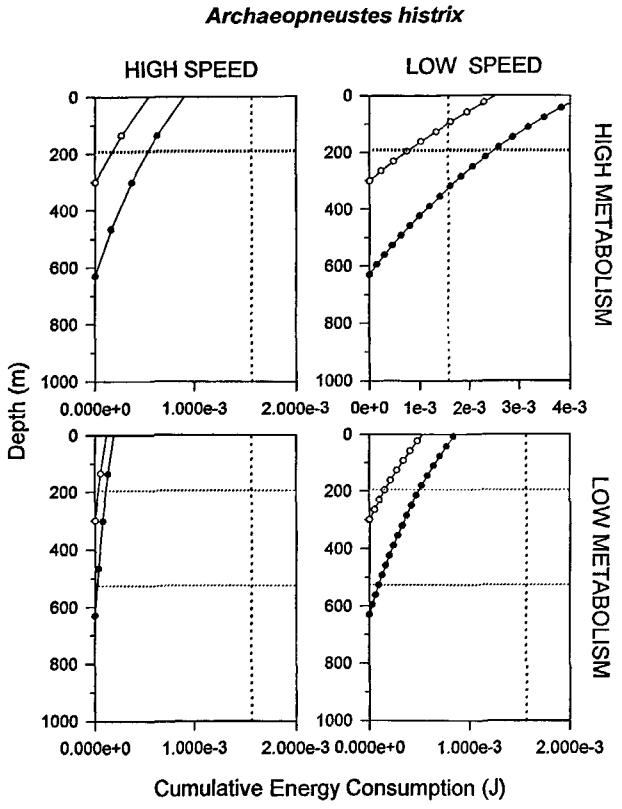

Figure 4

Predicted cumulative energy consumption for migrating larvae of Archaeopneustes hystrix. See *Figure 4 for complete explanation.*

show this same pattern except that larvae originating from the upper end of the adult range can attain the metabolic compensation point after only four days of migration, three days before they would run out of energy (Fig. 4). This species has a greater capacity to reach shallower depths than *A. jacobyi* because it lives slightly shallower and produces a substantially larger egg. It is also more tolerant than *A. jacobyi* of the temperature conditions at 190 m depth. Because of physiological tolerances, *Aspidodiadema jacobyi* larvae may not migrate to the euphotic zone despite their energetic capacity to do so.

The two species that can easily tolerate the 20 °C temperature conditions at 190 m depth, *Stylocidaris lineata* and *Lytechinus euerces*, should also be able to attain the metabolic compensation depth without running out of energy unless they have high metabolisms and low swimming speeds (Figs. 5, 6).

Figure 7 presents the results of the energy consumption model run for *Echinus affinis*, a common lower bathyal species living at a depth of 2000 m in the North Atlantic. During the late winter reproductive season of this animal off Scotland, the temperature at the surface is about 7 °C,

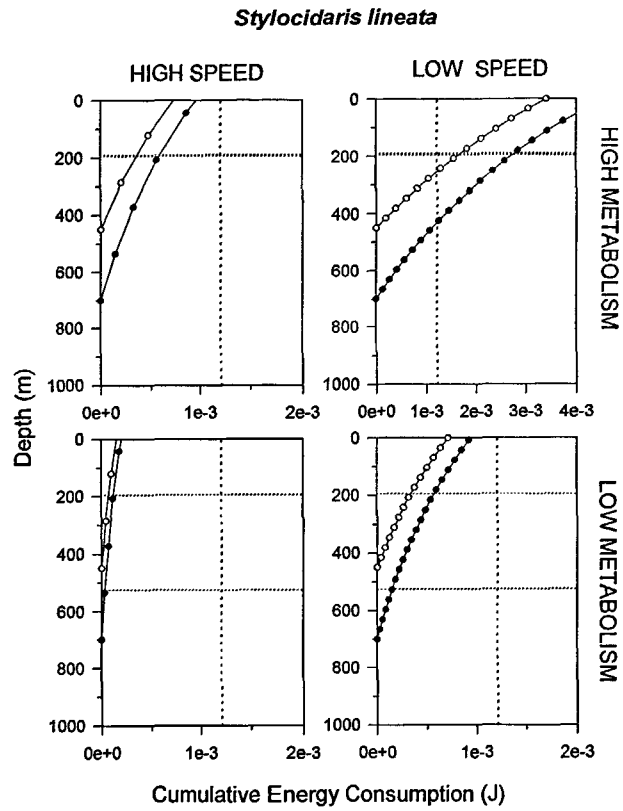

Figure 5

Predicted cumulative energy consumption for migrating larvae of Stylocidaris lineata. See *Figure 4 for complete explanation.*

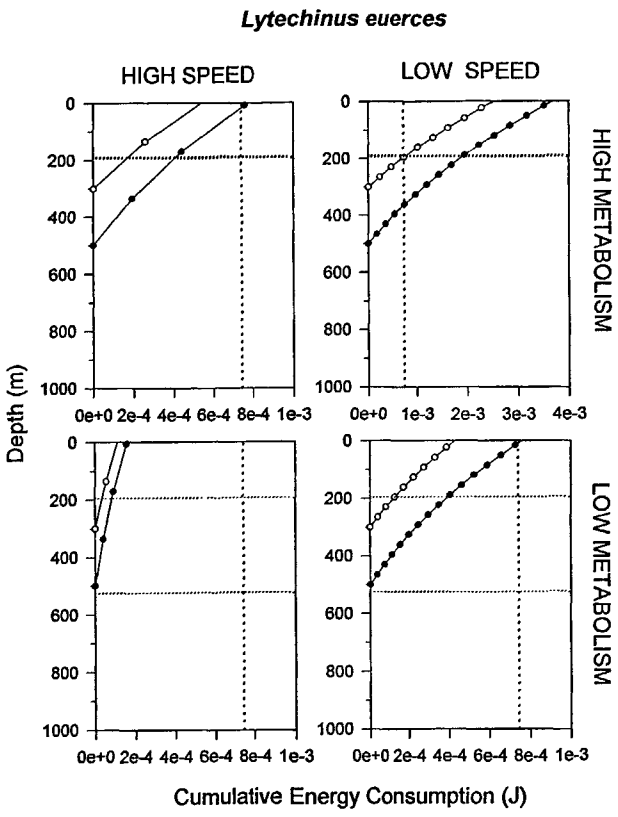

Figure 6

Predicted cumulative energy consumption for migrating larvae of Lytechinus euerces. See *Figure 4 for complete explanation.*

just five degrees higher than the 2 °C bottom temperature. Because of these low temperatures and slight differences, larvae should be able to migrate for relatively long periods of time before exhausting their available energy. At low metabolism, for example, larvae swimming at low speed should be able to migrate all the way to the surface (approximately seven weeks of continuous swimming) long before they consume their energy stores. However, the model predicts that slowly swimming larvae at high metabolic rates, should run out of energy after four weeks, having attained only 1000 m depth. Unfortunately, we do not have the data on phytoplankton abundances that would allow us to calculate the metabolic compensation point for this species. It has recently been shown that the benthos in this region experiences a regular annual pulse of phytodetritus following the spring plankton bloom (Lampitt *et al.*, 1985). As the larvae are not likely to migrate to the euphotic zone because of their narrow pressure tolerances (Young and Tyler, 1992), perhaps they feed on the phytodetritus before it reaches the sea floor.

DISCUSSION AND CONCLUSIONS

The models we have presented are designed to illustrate how one may approach the problem of vertical migration under circumstances where the larvae themselves are too rare to find in plankton samples. We have made several unrealistic assumptions because of the lack of physiological and behavioral data on deep-sea larvae. One such assumption that could have a major influence on the results of our metabolic model is that swimming speed remains constant with depth. Like other physiological rates, swimming speed of echinoid larvae is known to increase as a function of temperature. Moreover, water viscosity, which has a large influence on small moving organisms at low Reynolds numbers, covaries with temperature (Podolsky and Emlet, 1992). The combined effects of temperature and viscosity have been shown to have a Q_{10} value of 1.62 for larvae of the shallow-water sand dollar *Dendraster excentricus* (Podolsky and Emlet, 1992). When actual swimming rates are measured for larvae of deep-sea animals, the measurements should be done at multiple temperatures so depth-related rate changes can be incorporated into more realistic models of vertical movement.

A second unlikely assumption is that shallow- and deep-water eggs are qualitatively equivalent. Observations on some deep-sea planktotrophs hint that this may not be the case. For example, we have shown that the planktotrophic larvae of *Aspidodiadema jacobyi*, which develop from an opaque 90 µm egg, have large yolk reserves that fill the blastocoel during the blastula and gastrula stages and become concentrated around the gut of the develo-

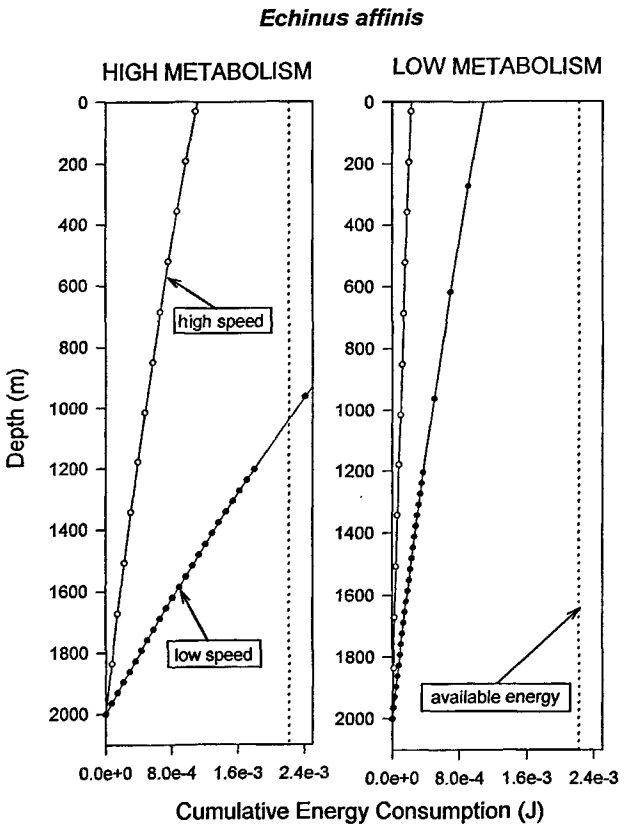

Figure 7

Predicted cumulative energy consumption for larvae of the lower bathyal echinoid Echinus affinis *migrating from a depth of 2000 m in the Rockall Trough, off Northern Scotland at two different speeds and with high and low metabolic rates. On the high speed curves (open points), points are 1-day apart. On the low speed curves (solid points), the first 24 points are 1-day apart and subsequent points represent 7-day intervals.*

ping echinopluteus (Young *et al.*, 1989). *A. jacobyi* larvae can subsist entirely on yolk for up to eight weeks, which is substantially longer than any shallow water planktotrophic species that has been studied. We suspect that eggs of this species have a much higher ratio of lipid to protein than shallow-water eggs of comparable diameter. Planktotrophic eggs of several other deep-sea echinoids, including *Echinus affinis* and *Archaeopneustes hystrix* also appear very dense and may have high lipid concentrations. If this is true, our estimates of available energy in the model may be completely wrong. Calorimetric or compositional studies of deep-sea eggs will be required to rectify this problem.

For simplicity, we have assumed that larvae would rely entirely on yolk reserves until they reached the metabolic compensation point where phytoplankton are sufficiently abundant to support metabolism. However, larvae of several antarctic and bathyal echinoderms are capable of ingesting bacterioplankton (Rivkin *et al.*, 1986; Young, Bosch and Cameron, unpublished data) and some bathyal echinoid larvae can transport dissolved fatty acids and amino acids (Jaeckle, unpublished data). Phytodetritus from surface plankton blooms is abundant in the deep north Atlantic during a portion of the developmental period of *Echinus affinis* (Lampitt, 1985). Thus, there are several potential food sources in the deep sea that may either provide the energy required for development or supplement maternal reserves during migrations to the euphotic zone. Our simplified model ignores the potential contributions of these energy sources.

In summary, we have demonstrated an approach but have not provided a final answer to the question of migration potential. Larvae may or may not migrate to the euphotic zone to feed. Given the best-guess parameters of metabolic rate and swimming speed it seems apparent that most species are probably energetically capable of reaching adequate algal concentrations (contrary to Thorson's 1950 prediction), but our data on physiological tolerances show that some species may not survive at the depths where algae are abundant. For these species, depth distribution of larvae and perhaps of adults is more likely to be controlled by physical extremes than by food limitation. Until we have empirical measurements of metabolic rate, swimming speed and orientation behavior of deep-sea larvae and the energy content of deep-sea eggs, we can still only guess at the depths where larvae might occur and the feeding strategies they employ. Obtaining values for the relevant physiological and behavioral parameters should take high priority in the study of deep-sea life history biology.

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