Models of the early life history of *Euphausia superba*—Part I. Time and temperature dependence during the descent–ascent cycle

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Abstract—A time- and temperature-dependent model was developed to simulate the descent–ascent behavior of the embryos and early larval stages of the Antarctic krill, *Euphausia superba*. This model combines laboratory measurements of temperature effects on developmental times, density and physiology of krill embryos and larvae and the observed water temperature structure in the Bransfield Strait—South Shetland Islands region. Simulations with observed vertical temperature profiles from this region show that embryos that develop at temperatures less than 0°C hatch relatively deep (~1000 m) or hit the bottom before hatching. The presence of warm (1–2°C) Circumpolar Deep Water (CDW), between 200 and 700 m, results in hatching depths of about 700 m. The sinking rate pattern characteristic of the embryos of *Euphausia superba* retains the embryos in the CDW, where development is accelerated. Larval ascent rate through the CDW is rapid, so larvae reach the surface before metamorphosing into the first feeding stage, and have sufficient carbon reserves to drift at the surface for several weeks before needing to find food. These results suggest that the sinking rate pattern characteristic of embryos of Antarctic krill may be part of a reproductive strategy that evolved in response to the thermal structure of its environment. The complementary component of this reproductive strategy is the observed correlation between the distribution of krill schools containing reproducing individuals and the presence of CDW. With this reproductive strategy, the spawning regions of Antarctic krill are in areas where oceanic conditions enhance the probability of survival of its embryos and non-feeding larvae.

INTRODUCTION

The majority of the 85 known species of euphausiids live in oceanic epipelagic and mesopelagic environments. Embryos of some of these euphausiid species are heavier than water and sink from the moment of release. After hatching, larvae ascend through the water column in order to reach the surface waters where they feed. For embryos and early non-feeding larval stages of Antarctic krill, *Euphausia superba*, this descent–ascent behavior spans a wide depth range.

The descent–ascent cycle of embryos and larvae of *E. superba* was first suggested by MARR (1962) on the basis of net tows taken during the H M S *Discovery* cruises (1925–
Table 1  Initial krill embryo sinking rates obtained from laboratory measurements

<table>
<thead>
<tr>
<th>Time (h)</th>
<th>Sinking rate (m day$^{-1}$)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt;24</td>
<td>130-160</td>
<td>GEORGE and STROMBERG (1985)</td>
</tr>
<tr>
<td>&gt;12</td>
<td>140-320</td>
<td>MARSCHALL (1983)</td>
</tr>
<tr>
<td>12</td>
<td>175</td>
<td>QUETIN and Ross (1984a)</td>
</tr>
<tr>
<td>12</td>
<td>201</td>
<td>ROSS and QUETIN (1985)</td>
</tr>
</tbody>
</table>

1939 and 1950–1951) in the Antarctic, and later confirmed by other investigators (HEMPEL and HEMPEL, 1986) As the krill embryo sinks, it passes through six distinct developmental stages: multiple cell, blastula, gastrula, limb bud, pulsating heart or twitching, and hatching (QUETIN and Ross, 1984a) As the larva ascends, it passes through two non-feeding (Nauplius, Metanauplius) and several feeding (Calyptopls 1–3) developmental stages.

The descent–ascent cycle described by MARR (1962) was refined by QUETIN and Ross (1984a) who showed that embryos of *E. superba* do not sink at the initial high rates (Table 1) throughout development. The sinking rate pattern described by QUETIN and Ross (1984a) is characterized by a decrease in sinking speed to a minimum during the gastrula stage, between 48 and 72 h after release, that ranges from 51–73 m day$^{-1}$ (QUETIN and Ross, 1984a; ROSS and QUETIN, 1985) to 80–90 m day$^{-1}$ (GEORGE and STROMBERG, 1985) Sinking rates then accelerate before hatching to about the initial sinking rate. This pattern is independent of temperatures and salinity (QUETIN and Ross, 1984a). Whether the sinking rate pattern of the embryos of *E. superba* confers advantages to these early stages is unknown.

Another pattern relevant to reproduction of *E. superba* is the observed spatial segregation between sexually mature krill and subadult krill during the spawning season. This spatial segregation has been observed in several regions: the Scotia and northern Weddell Seas (MAKAROV, 1970), the waters west of the Antarctic Peninsula (KOCK and STEIN, 1978, JAZDZEWSKI et al., 1978, MAKAROV, 1979, WITK et al., 1981; QUETIN and ROSS, 1984b; SIEGEL, 1988, and refs cited within), the Bransfield Strait region (QUETIN and ROSS, 1984b; KALINOWSKI, 1982; KITELL and JAZDZEWSKI, 1982, WOLNOMIEJSKI et al., 1982) West of the Antarctic Peninsula in the Bransfield Strait region (Fig 1) schools of reproducing krill are generally found to the north of the South Shetland Islands, with schools composed of juvenile or non-reproducing krill inside the Strait (QUETIN and ROSS, 1984b) The spatial separation of schools of reproducing and non-reproducing krill can be the result of either physical or behavioral processes.

The first objective of this research was to investigate what processes underlie the pattern of sinking rate during embryonic development. The second objective was to simulate the effects of actual temperature regimes on the rate and timing of this pattern. To achieve these two research objectives a model was developed to simulate the effect of ambient water temperature on developmental and physiological processes during the descent and ascent of embryos and early larval stages of krill.

The region of interest for this modeling study is the Bransfield Strait–South Shetland Islands (cf Fig 1). Circulation in this region can be complex (CAPELLA, 1989) and has an
important effect on the distribution of early life stages of krill. Therefore, understanding developmental (i.e., biological) effects independent of circulation effects is necessary to accurately interpret the space and time-dependent embryo–larva particle trajectories calculated with the Lagrangian model, which combines the developmental and circulation effects (Capella et al., 1992a).

The time- and temperature-dependent model is described in the following section. This is followed by a discussion of simulated descent–ascent profiles of krill embryos and larvae. Finally, these modeling results are discussed in relation to the more general understanding of whether factors such as the pattern of sinking rate of the embryo and the observed spatial distribution of schools or reproducing Antarctic krill *E. superba* contribute to recruitment success in this species.
METHODS

*Time- and temperature-dependent model*

Simulated descent and ascent patterns from the time- and temperature-dependent model are influenced greatly by temperature effects on developmental time of the krill embryo and larva. Because early development in krill is equiproportional (Ross et al., 1988) the biological processes in the model are formulated in terms of fraction of total development time. Equiproportional development means that the duration of any developmental stage is the same proportion of total development at all temperatures. The proportion is not the same for all stages, however. In the descent portion of the model, sinking rate of an embryo stage is calculated from the difference between embryo and water density. In the model, embryo wet weight (mass) and diameter are dependent on the fraction of total embryo developmental time (from release to hatching), which is controlled by temperature. Stated mathematically

$$\frac{d(\text{diameter})}{dt} = \text{diameter change(development)}$$

(1)

and

$$\frac{d(\text{wet weight})}{dt} = \text{wet weight change(development)}$$

(2)

From the embryo diameter and wet weight, embryo density can be calculated as

$$\rho_{\text{embryo}} = \frac{6 \text{ embryo wet weight}}{\pi (\text{embryo diameter})^3}$$

(3)

From embryo density, sinking rate can then be calculated from Stokes' Law as

$$\text{sinking rate} = \frac{2 r^2}{9 \nu} g \left( \frac{\rho_{\text{embryo}}}{\rho_w} - 1 \right)$$

(4)

where \( r \) is the embryo radius, \( \nu \) is the kinematic viscosity of water, \( g \) is the gravitational acceleration, \( \rho_{\text{embryo}} \) is the embryo density and \( \rho_w \) is the ambient water density. For the calculations presented in the following sections the value of \( \nu \) was \( 1.787 \times 10^{-6} \text{ m}^2 \text{ s}^{-1} \), which is the kinematic viscosity for seawater at 0°C. With a known sinking rate, a time-dependent depth profile for the embryo can be determined. Ambient pressure does not have a direct effect on embryo sinking rates (Ross and QUETIN, 1985).

The ascent portion of the model simulates the behavior and physiology of the non-feeding larval stages. Larval ascent rate is dependent on ambient water temperature:

$$\frac{d(\text{ascent})}{dt} = \text{ascent change(temperature)}. \quad (5)$$

Larval ascent rate can be used to construct a depth profile, as for the embryo.

Additionally, carbon loss from respiration in the embryo and the larva is estimated as

$$\frac{d(\text{carbon})}{dt} = -\text{respiration(development)}$$

(6)
where carbon use at any time is dependent on the fraction of the total developmental time. Descriptions of the krill embryo and larva measurements used to formulate the terms on the right side of equations (1)—(6) follow.

**Embryo and larva developmental time**

Embryo developmental times were measured at temperatures of \(-1\), 0, 1 and 2°C, which encompass the range of temperatures experienced by Antarctic krill (Ross et al., 1988). Total developmental time of embryos is faster at temperatures greater than 0°C and ranges from 5–8 days (Marschall, 1984; Ikeda, 1984, Ross et al., 1988). As part of the experiments reported in Ross et al. (1988), developmental times of five embryo stages—single cell to early gastrula (SC–eG), early gastrula to gastrula (eG–G), gastrula to early limb bud (G–eLB), early limb bud to late limb bud (eLB–ILB) and late limb bud to hatch (ILB–N1)—were also measured. Developmental time for a given embryo stage follows the same pattern as found for total developmental time. Relationships between developmental time and temperature for the first, third and fifth embryo stages were best described by exponentially decreasing functions (Table 2). Development of the second and fourth stages was best described by linear functions (Table 2). These developmental relationships are used in the descent portion of the model.

Larval developmental time is sensitive to temperature, despite the relatively narrow temperature range in regions where krill are found (Ross et al., 1988). The relationships between larval developmental time and temperature for the first three larval stages—Nauplius (N1) to Metanauplius (MN), N1 to Calyptopis 1 (C1), and N1 to Calyptopis 2 (C2)—used in the ascent portion of the model are exponentially decreasing functions (Ross et al., 1988, Table 2). One additional finding of importance is that larvae reared at

<table>
<thead>
<tr>
<th>Variable</th>
<th>Temperature</th>
<th>Equation</th>
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<tr>
<td>Developmental times</td>
<td></td>
<td></td>
</tr>
<tr>
<td>SC–eG</td>
<td>(-1)°C–2°C</td>
<td>(y = 1 \times 225e^{-2.351T} + 24.147)</td>
</tr>
<tr>
<td>eG–G</td>
<td>(T &lt; 0°C)</td>
<td>(y = 33.3 - 10T)</td>
</tr>
<tr>
<td></td>
<td>(T \geq 0°C)</td>
<td>(y = 33.3)</td>
</tr>
<tr>
<td>G–eLB</td>
<td>(-1)°C–2°C</td>
<td>(y = 11.85e^{-1.123T} + 62.404)</td>
</tr>
<tr>
<td>eLB–ILB</td>
<td>(-1)°C–2°C</td>
<td>(y = 110.15 + 14.8T)</td>
</tr>
<tr>
<td>ILB–N1</td>
<td>(-1)°C–2°C</td>
<td>(y = 37.258e^{-0.907T} + 108.644)</td>
</tr>
<tr>
<td>N1–MN</td>
<td>(-1)°C–2°C</td>
<td>(y = 38.36e^{-1.417} + 225.29)</td>
</tr>
<tr>
<td>N1–C1</td>
<td>(-1)°C–2°C</td>
<td>(y = 78.26e^{-1.537} + 417.93)</td>
</tr>
<tr>
<td>N1–C2</td>
<td>0°C–2°C</td>
<td>(y = 320.58e^{-1.107} + 752.22)</td>
</tr>
<tr>
<td>Embryo diameter</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(-1)°C</td>
<td>(y = 626.605 + 104.936e - 247.258x^2 + 192.003x^3)</td>
</tr>
<tr>
<td></td>
<td>0°C</td>
<td>(y = 621.557 + 153.305x - 355.408x^2 + 260.204x^3)</td>
</tr>
<tr>
<td></td>
<td>1°C</td>
<td>(y = 620.460 + 150.220x - 334.003x^2 + 238.811x^3)</td>
</tr>
<tr>
<td></td>
<td>2°C</td>
<td>(y = 621.505 + 138.389x - 325.546x^2 + 260.204x^3)</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td>(y = 621.557 + 153.305x - 355.408x^2 + 260.204x^3)</td>
</tr>
<tr>
<td>Larval ascent rate</td>
<td></td>
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<tr>
<td></td>
<td>(-1)°C (\leq T \leq 0°C)</td>
<td>(y = (-0.208 - 0.0117T)P),</td>
</tr>
<tr>
<td></td>
<td>0°C (\leq T \leq 1°C)</td>
<td>(y = (-0.208 - 0.043T)P),</td>
</tr>
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$-1{^\circ}$C generally fail to develop beyond the C1 stage, suggesting that the larvae undergo a period of strong cold sensitivity (Ross et al., 1988)

**Embryo diameter and wet weight**

Throughout experiments on developmental times of embryos and larvae, diameter and wet weight of embryos from each of four broods reared at four temperatures ($-1, 0, 1$ and $2{^\circ}$C) were monitored (see Ross et al., 1988, for rearing techniques). Diameters of five embryos from each of the 16 brood–temperature combinations were measured under a dissecting microscope at about 12 h intervals. At 36 h intervals, 10 individual embryos from each brood–temperature combination were weighed with a Cahn electrobalance, diameters of five of these same embryos were measured prior to weighing. Embryos were discarded after any handling. Diameter measurements have an individual precision of $\pm 10 \mu m$, and are within the brood standard deviation of 9–15 $\mu m$ (1–2%) for any one measurement period (methodology in Quetin and Ross, 1984a).

Evidence suggests embryos are fragile and deform easily during the first 3–6 h, and measurements during this time period may be overestimates. Estimates of initial diameter (<12 h after release) were greater than those for embryos from previous experiments. Mean initial diameters were 626.4 $\mu m$ (three broods, Quetin and Ross, 1984a) and 619.8 $\mu m$ (three other broods, 619, 625 and 615 $\mu m$) during this experimental period. Since estimates for later stages were similar (Quetin and Ross, 1984a), we presume that initial diameters in this experiment were overestimates. An initial embryo diameter of 620 $\mu m$ was used for the model.

Variability among broods at any one time was greater than within brood variability, with a range among broods in mean diameter of about 20 $\mu m$. Embryos that are larger initially do not necessarily remain larger throughout development. However, the patterns of increase and decrease in diameter during development were the same for all broods. Trends in average diameter for all four broods as a function of developmental time were similar at all temperatures (Fig. 2). After the first 18–24 h (~0.15 of developmental time), diameters were relatively constant until about 0.33 of the way through development before increasing to a maximum prior to hatching.

The average diameter of embryos from broods at the four temperatures can be described by third order polynomials (Table 2), that reproduce the pattern of two maxima and one minimum seen in the embryo diameter measurements. The embryo diameter curves at all four temperatures were similar, therefore, the average of the four (Table 2) was used to calculate the krill embryo diameter at a given developmental time.

The simultaneous observations of wet weight and diameter were grouped by developmental stage of the embryo. Additional estimates of wet weight for a given developmental stage were obtained by matching sinking rate curves (Quetin and Ross, 1984a) with the average embryo diameter relationship (Table 2) and calculating the wet weight of the embryo for a specific sinking rate and diameter. Given the patterns in embryo sinking rate and diameter change, wet weight might be expected to also exhibit nonlinear changes during development. However, wet weight measurements at 36 h intervals are not adequate to fully resolve trends in wet weight change. Therefore, embryo wet weight and diameters were grouped into subsets according to developmental stage, and linear relationships were fit to these subsetted data (Fig. 3). These linear relationships should be regarded as approximations to a nonlinear response.
Fig 2 Relationship between krill embryo diameter and development (a) Average diameter of krill embryos as a function of fraction of embryo development time, for four temperatures. Each point is the mean (n = 20) for embryos from all four broods combined at any one temperature. (b) Curve fits for the relationships between embryo diameter and fraction of development time for the four temperatures, coefficients in Table 2. Data from Ross and Quetin.

**Larval ascent rate**

The krill embryo hatches at depth into the first of several non-feeding larval stages, N1. Once hatched, the larva must swim back to the lighted surface to begin feeding because it is a herbivore (Marschall, 1985). Newly hatched larvae are either neutrally buoyant or have a slight negative buoyancy (Marschall, 1984; Ross et al., 1985) and sink unless swimming actively. This negative buoyancy and records of early larvae in very deep tows (>2000 m) have led to suggestions that the Nauplius I and II are weak swimmers that continue to sink for several days (Marschall, 1984; Hempel and Hempel, 1986). However, because the larva is capable of swimming upward at the time of hatching, it is assumed in this model that the larva starts its upward ascent immediately after hatching.

Ross et al. (1985) observed that larvae swim in a spiral and measured upward vertical displacement rates of nauplii of the order of 170 m day\(^{-1}\). In general, the average rate of vertical displacement increases with increasing temperature. For the model, larval ascent rate was parameterized on the basis of data in Ross et al. (1985) as two linear functions (Table 2).

The value used for \(P_s\), the fraction of time the larva spends swimming, was chosen by comparing the depth of the various larval stages in the model with observed depths from
trawl data. For example, in simulations with a $P_s$ of 10%, larvae did not reach the surface before running out of carbon. With a $P_s$ of 50%, metanauplii occurred at the surface, contrary to observations. A $P_s$ of 30% gave larval depth distributions that match observations (HEMPEL and HEMPEL, 1986) and is the value used in the reported simulations.

**Embryo and larva respiration**

Carbon budgets for embryos and larvae also are calculated, which allows estimation of the carbon reserves available to larvae as they ascend through the water column. Respiration rates of known-age krill embryos at 0°C and larvae at three temperatures, -1, 0 and 2°C, increase with increasing age, even within a stage, and are affected by temperature (QUETIN and Ross, 1989).

The relationships between embryo and larva oxygen consumption rates and the fraction of total developmental time (Fig 4) were used in the model to estimate carbon used by the embryo or larva with a standard conversion constant of 0.385 μg carbon used per μl of oxygen consumed (QUETIN and Ross, 1989). Embryo or larva carbon use gives the respiration loss on the right side of equation (6).

Initial carbon content of the embryo is 15 μg (IKEDA, 1984; Ross and QUETIN, 1989). This carbon content must sustain the embryo throughout its descent and the larva throughout its ascent until it is able to begin feeding. Ross and QUETIN (1989) found that the point-of-no-return (PNR) for the C1 was 10–14 days or 7.5 μg carbon. At the PNR, the animal will not survive even if food becomes available. Thus, 7.5 μg carbon was taken to be
the threshold value in the model, once the carbon content decreased below this value the simulation was ended because the larva was past the PNR and would not survive.

RESULTS

In the Bransfield Strait–South Shetland Islands region, the krill embryos and larvae are typically exposed to temperatures that range between -1 and 2°C. In the following section, we present simulated depth profiles for krill embryos and larvae exposed to constant temperatures of -1 and 2°C, which bracket the range of temperatures of interest for this study. Next we describe simulations in which the krill embryos and larvae descend and ascend through the vertical temperature structure observed at various locations around the South Shetland Islands and in the Bransfield Strait.

Constant temperature simulations

The model at -1°C (Fig 5a) correctly simulates the sinking rate pattern of krill embryos (Fig 5b) measured by QUETIN and Ross (1984a) and Ross and QUETIN (1985). Sinking rates are high (~180 m day⁻¹) initially, then decrease to about 70 m day⁻¹ during the gastrula to early limb bud stage. As the embryo develops into the limb bud stages, sinking rates again increase, reaching a second maximum just prior to embryo hatching. However, initial sinking rates from the model tend to underestimate observed sinking rates. This discrepancy is related to the difficulty in accurately estimating initial embryo diameter. Small differences in embryo diameter have a large effect on the calculation of embryo density [cf equation (3)] and hence sinking rate. As previously mentioned, initial embryo

![Diagram](image_url)
Fig 5  (a) Temperature distributions used for the constant temperature simulations  (b) Simulated embryo sinking rate profile at a constant temperature of −1°C The vertical lines along the bottom correspond to the embryo developmental stages SC-eG (I), eG-G (II), G-eLB (III), eLB-eLB (IV), and eLB-N1 (V) Embryo sinking rates from laboratory measurements are also shown ○, embryos that developed at 0°C (QUETIN and Ross, 1984a), △, embryos that developed at 1°C (Ross and QUETIN, 1985) The developmental time recorded for these sinking rate experiments was scaled to −1°C using the relationships for each embryo developmental stage given in Table 2  (c) Simulated larval ascent rate at a constant temperature of −1°C The vertical lines along the bottom axis correspond to the larval developmental stages N1 and C1

diameter measurements tend to be overestimates and result in lower sinking rates in the model. However, the range of sinking velocities can be quite large (cf Figs 2 and 3 in QUETIN and Ross, 1984a) and those obtained from the model are well within measured values

Embryos at −1°C sink to approximately 1100 m before hatching (Fig 6a) whereas at 2°C embryos hatch at about 600 m (Fig 6b). At the time of hatching, the carbon content of the embryo at −1°C is 14.8 μg C, only a 1% loss from the low respiration rate The carbon content of embryos at 2°C is similar

After hatching larvae at −1°C require approximately 25 days to complete the ascent to the surface (Fig. 6a) Larval ascent rate at −1°C is low, only about 40 m day⁻¹ (Fig 5c). During the ascent the larvae pass through two developmental stages, the MN, at about 10
The early life history of *Euphausia superba*—Part I

![Simulated depth profile](image)

Fig 6 Simulated depth profile (solid line) of a krill embryo–larva particle exposed to constant temperatures of (a) −1°C and (b) 2°C. Dashed lines are carbon use by the embryo–larva particle.

Days, and C1, the first feeding stage, prior to reaching the surface. When the larva reaches the surface its carbon content has decreased to approximately 11 μg C (Fig 6a).

The ascent time for the larvae at 2°C (Fig. 6b) is much shorter than that at −1°C. The shallower hatching depth of approximately 600 m and the increased ascent rate at 2°C mean that the larva only takes about 10 days to reach the surface. About half way through its ascent, at a depth of about 300 m, the larva develops into the C1 stage. Upon reaching the surface the carbon content of the larva is about 13.5 μg C (Fig 6b).

**Observed temperature simulations**

The vertical temperature profiles used for the following simulations are from an XBT and CTD data set from the region of Bransfield Strait and the South Shetland Islands obtained during the past several years (Capella et al., 1992b). The temperature profiles selected for the simulations were chosen to illustrate the effects of the different water masses found in the model region. These temperature profiles correspond to areas where krill schools have been observed and are consistent with the regions where krill embryos...
Southern Gerlache Strait near Anvers Island. At the southern end of the Gerlache Strait near Anvers Island temperatures in the upper 100 m are cold, reaching $-2^\circ$C (Fig 7a). Below 100 m temperatures increase to almost 0°C near the bottom at 400 m. The cold water in the upper water column is winter water formed by cooling during the previous winter. The warmer water at depth is CDW, which is found throughout the eastern part of the Bellingshausen Sea (GORDON and BAKER, 1982).

The cold water in the upper 100 m extends the developmental time, and hence the period of initially high sinking rates, so the embryo hits the bottom at 400 m in about 3.5 days (Fig. 7b). The embryo has passed through only two of its five developmental stages and must complete the remainder of its development on the bottom. Carbon loss (Fig. 7b) results in about a 1% depletion of the initial carbon content of the embryo.

After hatching, the larva ascends (Fig. 7b) reaching the surface in approximately 8 days. The initial larval ascent rate is high (50 m day$^{-1}$), decreases to approximately 20 m day$^{-1}$ as the larva encounters the cold winter water, and again increases just prior to reaching the surface. During ascent the larva develops into the MN and C1 stages and remains as a C1.
The early life history of *Euphausia superba*—Part I

Fig 8  (a) Temperature profile from the western Bransfield Strait, between Deception and Low Islands (63°S, 61.5°W)  (b) Simulated depth profile (solid line) and carbon usage (dashed line) for a krill embryo–larva particle exposed to the temperature profile shown in (a)

until reaching the surface. Carbon content of the larva on reaching the surface is 13.7 μg C (Fig 7b), about a 9% depletion of the initial carbon content of the embryo.

**Inside Bransfield Strait.** In the western Bransfield Strait at a location approximately half way between Deception and Low Islands, temperature in the upper 200 m is nearly isothermal at -1°C (Fig. 8a). The warmer water below 200 m coincides with a band of CDW that extends into the western portion of the Bransfield Strait from Drake Passage through the gap between Smith and Snow Islands (CAPELLA et al., 1992b). This temperature profile is from the edge of the CDW and therefore the warmest temperatures observed are only 0°C.

The cold temperatures at this location extend embryonic developmental time to about 7 days. Consequently, the embryo hits the bottom about 1 day prior to hatching (Fig. 8b) and the carbon usage is small. After hatching the larva reaches the surface in about 13 days, passing through two developmental stages (MN and C1) as it ascends (Fig 8b). About 13% of the initial carbon (Fig 8b) content of the embryo is used throughout the descent–ascent cycle.
North of the South Shetland Islands Temperature profiles from north of the South Shetland Islands (Figs 9a, 10a and 11a) all show increasing temperature with depth, which results from the presence of CDW. Below 200 m, temperature increases to about 1°C and remains constant at this temperature to the bottom.

The simulated depth profiles at the three locations show essentially the same behavior. High initial sinking rates place the embryo near the top of the 1°C water in about 1.5–2 days (Figs 9b, 10b and 11b). The sinking rate then decreases and the embryo hatches in about 5–6 days at depths of 680–790 m. Carbon usage by the embryo is small at all locations. After hatching the larva swims upwards and reaches the surface in about 12–15 days (Figs 9b, 10b and 11b).

Western Bransfield Strait near the Antarctic Peninsula. Waters in the region around the Antarctic Peninsula are cold, less than –1°C at all depths (Fig. 12a), which increases embryo hatching time to almost 10 days. However, before hatching the embryo hits the bottom at 1000 m, about 2 days prior to hatching. Because high initial sinking rates persist for almost 3 days, the embryo reaches depths of about 500 m early in development and early in the descent cycle. Carbon use by the embryo (Fig. 12b) is about 1 μg C, which is a 6% decrease in the initial carbon value. This is the largest depletion due to embryo respiration in all the scenarios tested.
Krill embryos and larvae reared at $-1^\circ$C do not continue to develop past C1 (Ross et al., 1988). Whether the embryos or larvae are critically sensitive to low temperatures during a specific period sometime during development is not known. For the comparative purposes of this study, consideration of the larval ascent profile and vertical ascent rate when exposed to cold temperatures (Fig. 12a) is appropriate because larvae exposed to $-1^\circ$C temperatures early in development survive until late C1. At the cold temperatures found near the Antarctic Peninsula, the larva required about 25 days to complete its ascent to the surface. At approximately 750 m the larva developed into a C1. Larva ascent rate was low due to the low temperatures and, consequently, the carbon use (Fig. 12b) was high. Carbon use throughout the descent–ascent cycle represents a 26% depletion of the initial carbon content of the embryo.

**DISCUSSION**

*Temperature effects and implications for the descent–ascent pattern*

The constant and observed temperature simulations illustrate the importance of temperature in determining the hatching depth of krill embryos, the total descent–ascent
Fig 11 (a) Temperature profile from north of King George Island (60°S, 58°W), (b) Simulated depth profile (solid line) and carbon usage (dashed line) for a krill embryo–larva particle exposed to the temperature profile shown in (a)

time, and the carbon reserves of the larvae on reaching the surface (Table 3). In regions where depths are shallow (<500 m), or the water temperatures are cold, the embryos can hit the bottom prior to hatching and, therefore, spend a portion of their developmental time on the bottom. In regions with deeper depths and cold water, the larvae have a longer ascent and a shorter time to find food once reaching the surface. The time to reach the PNR for the C1 larvae, both calculated and experimental, increases from 9 to 15 days between −1 and 2°C (Ross and QUETIN, 1989). For all temperature simulations, the amount of carbon consumed by the krill embryo through respiration is small, generally less than 0.25 µg C. Therefore, as suggested by QUETIN and Ross (1989), the carbon content of the larva upon reaching the first feeding stage is 12–13 µg C, regardless of the temperature at which it developed. Even at the coldest temperatures, the total carbon use during the descent–ascent cycle was only 20–25%, far less than the 50% of the PNR (Ross and QUETIN, 1989).

In the regions characterized by CDW at depth, such as north of the South Shetland Islands, the krill embryos sank to only about 700 m prior to hatching (Table 3). This depth is shallower than the bottom. High initial sinking rates of krill embryos transport the embryos to the top of the warm water (200 m) in about 1.5–2 days. At this point in development, the sinking rate decreases, retaining the krill embryos in the layer of warm CDW between 200 and 700 m, allowing the embryo to complete development at
temperatures greater than 0°C. Thus, development is accelerated, and the embryo hatches in 5–6 days. The high sinking rate prior to hatching coincides with the embryo shedding its outer gelatinous sheath in preparation for hatching. The increased sinking rate does not persist for very long and as a result does not cause the embryo to sink much deeper in this brief time. Thus, these simulations lead to the suggestion that the sinking rate pattern characteristic of krill embryos may be the result of an evolutionary adaptation by this animal to the thermal structure of its environment.

Larval ascent rate in warm water is high so the larva usually reaches the surface before developing into the first feeding stage. The larva then has sufficient carbon reserves to drift at the surface for several weeks before food must be available.

**Krill school distributions and relation to water mass distributions**

During six austral summers, schools of Antarctic krill in the Bransfield Strait–South Shetland Islands region have been identified and sampled as described in Quetin and Ross (1984b). These schools can be categorized as reproducing or non-reproducing and by being located over CDW or not. Reproducing schools have greater than 20% gravid females, i.e., with red thelyca, swollen carapaces and fully developed ovaries. The
Table 3  Summary of results from the embryo-larva simulations

<table>
<thead>
<tr>
<th>Depth of hatch (m)</th>
<th>Time to hatch (days)</th>
<th>Percentage development on bottom</th>
<th>Time for ascent (days)</th>
<th>Total time (days)</th>
<th>Percentage remaining</th>
</tr>
</thead>
<tbody>
<tr>
<td>-1°C</td>
<td>1090</td>
<td>8.4</td>
<td>—</td>
<td>24.6</td>
<td>33</td>
</tr>
<tr>
<td>2°C</td>
<td>600</td>
<td>4.8</td>
<td>—</td>
<td>10.2</td>
<td>15</td>
</tr>
<tr>
<td>Gerlache Strait</td>
<td>425</td>
<td>7.5</td>
<td>56</td>
<td>10.5</td>
<td>18</td>
</tr>
<tr>
<td>Western Bransfield Strait</td>
<td>660</td>
<td>6.9</td>
<td>0</td>
<td>14.1</td>
<td>21</td>
</tr>
<tr>
<td>North Smith Island</td>
<td>700</td>
<td>5.5</td>
<td>19</td>
<td>13.5</td>
<td>19</td>
</tr>
<tr>
<td>Snow Island</td>
<td>790</td>
<td>6.1</td>
<td>0</td>
<td>15.4</td>
<td>21.5</td>
</tr>
<tr>
<td>North King George Island</td>
<td>680</td>
<td>5.2</td>
<td>0</td>
<td>13.8</td>
<td>19</td>
</tr>
<tr>
<td>Antarctic Peninsula-Western Bransfield Strait</td>
<td>1025</td>
<td>9.8</td>
<td>17</td>
<td>25.3</td>
<td>35.1</td>
</tr>
</tbody>
</table>
The early life history of *Euphausia superba*—Part I

**Fig. 13** Distribution of schools of *Euphausia superba* in the Bransfield Strait—South Shetland Islands region with gravid females greater than 20% of the population (n = 56). Observations are from seven austral seasons (1981–1982 through 1987–1988). The solid circle (●) represents all years except 1983–1984, which are represented by ○. For five of these years seasonal coverage was good, from early December through February, with some observations in March. For 2 years, observations were limited to December–early January. Schools were identified with a Simrad echo-sounder as the RV *Polar Duke* transected areas where krill are historically found, and a 1-m Isaacs Kidd Midwater Trawl was used to collect animals. Details of the materials and methods used to collect the krill are given in Ross and Quetin (1983). The solid line is the 0°C isotherm at 500 m, indicating the approximate southern boundary of CDW obtained from the temperature data presented in Capella et al. (1992b). Geographic names are abbreviated as Eastern Bellingshausen Sea (EBS), Brabant Island (BI) and Snow Island (SI).

In all years except 1983–1984 the majority of the krill schools were usually found to the north of the South Shetland Islands, outside Smith Island, in the eastern Bellingshausen Sea, and in the southern Bransfield Strait. Siegel's (1988) analysis of the distribution of the different life stages of krill in this region from several years confirms that gravid and spawning adults occur along the continental slope, although a small number of adults spawn in the deep basin of Bransfield Strait. Gravid females were rarely found in the central or eastern Bransfield Strait or in Gerlache Strait, except in austral summer 1983–1984. Croxall et al. (1988) show that predators on krill did poorly in the seasons 1977–1978 and 1983–1984, both seasons followed years when strong El Niño/Southern Oscillation events occurred. The 1983–1984 season is considered unusual by several other investigators as well because of poor spawning success (Witek and Kittel, 1985) or a reverse in the usual seasonal trends in mean monthly abundance (Siegel, 1988).

When only categorical information such as the above is available, a nonparametric
Table 4  Observed frequency of reproducing and non-reproducing schools of Euphausia superba found over CDW (>0°C at 500 m) or over colder water in the Bransfield Strait, Gerlache Strait and outside the South Shetland Islands. Data are for schools sampled during five summer seasons (early December through early March), 1981–1982 to 1982–1983, and 1984–1985 to 1986–1987. The season following the strong El Niño (1983–1984) was omitted from the analysis. \( \chi^2 = 5.048 \), contingency coefficient = 0.21, significant \( (P < 0.05) \) Numbers in parentheses are expected values

<table>
<thead>
<tr>
<th></th>
<th>CDW</th>
<th>Cold deep</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reproducing</td>
<td>23</td>
<td>15</td>
<td>38</td>
</tr>
<tr>
<td>(17.4)</td>
<td>(20.6)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Non-reproducing</td>
<td>27</td>
<td>44</td>
<td>71</td>
</tr>
<tr>
<td>(32.6)</td>
<td>(38.4)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>50</td>
<td>59</td>
<td>109</td>
</tr>
</tbody>
</table>

Contingency coefficient is a useful statistic for determining whether the two sets of attributes are not related or if the observed association represents a genuine relationship in the population (Siegel, 1956). The contingency coefficient calculated for data combined for all years except for 1983–1984 (Table 4) was statistically significant \( (P < 0.05) \). This evidence that the observed association between schools of reproducing krill and CDW is not a result of chance alone provides support for the hypothesis that the distribution of reproducing schools may be part of a reproductive strategy that locates spawning populations in water masses where development and survival of the embryos and larvae is enhanced.

Schools of reproducing krill also have been observed in the area around the tip of the Antarctic Peninsula where warm water is not present at depth. At colder temperatures, the krill embryos sink deeper, and often these embryos hit the bottom (cf. Table 3), especially when released in water that is less than 500 m deep. Once on the bottom the fragile embryos may be destroyed mechanically or lost by predation. The occurrence of juvenile krill forms in the Antarctic Peninsula region suggests either that some portion of the embryos survive or that the krill larvae observed in this region are advected there by the prevailing circulation. This point is addressed with the Lagrangian calculations presented in the following paper (Capella et al., 1992a). The final answer, however, remains to be determined by additional observations, experiments and modeling studies.

It has been suggested that the descent-ascent behavior of the embryos and larvae of *E superba* is a mechanism that serves to rapidly transport the embryos away from predation by adults. While this may be a benefit of the descent portion of the cycle, it does not explain the strong correlation between krill spawning regions and water mass distributions. Voronina (1974) attempted to explain the distribution of *E superba* in the Southern Ocean by considering the factors that affect the survival of the larvae. Her hypothesis was that the krill are restricted to the regions of the Weddell Sea and East Wind Drift circulations because the presence of dense water at depth would prevent the krill embryos from sinking to depths greater than the larvae would be able to swim back to the surface.
and survive. This hypothesis has since been rejected on the basis of laboratory measurements that show that krill embryos are always denser than sea water and would continue to sink through dense water at depth, even under pressure (Marschall, 1983; Quetin and Ross, 1984a; Ross and Quetin, 1985). Additionally, for all scenarios tested with the model, the krill embryos sank through all parts of the water column.

Throughout the southern ocean, warm water is found between 300 and 600 m (Gordon and Baker, 1982) in response to the northward transport of surface water induced by the zonal circumpolar wind stress. The limited number of observations of krill embryos outside the Antarctic Peninsula region suggest that the correlation between reproducing krill schools and CDW may be circumpolar in nature (Fig 14). However, quantifying the extent of this relationship must await additional observations.

**Evolutionary implications**

The circumpolar circulation in the Southern Ocean developed when Drake Passage opened approximately 20 million years ago (Kennett, 1982) in the early Miocene. The circulation and water mass structure similar to that of the present day developed in the late
Miocene (Kennett and Barker, 1990), about 10 million years ago. The stem form of the Euphausiacea may have developed approximately 300 million years ago (Burkenroad, 1963), predating development of the Antarctic Circumpolar Current. Even if *E. superba* did not appear until present day circulation patterns developed, 10 million years would be sufficient for the reproductive strategy proposed here to evolve, especially given the strong nature of the trait.

An effective evolutionary selection strategy is one that is applied to the reproductive behavior of an organism. There are many examples of marine species with spawning strategies that take advantage of features in the environment (e.g. Parrish et al., 1981; Sherman et al., 1984). For these species the various reproductive strategies are designed to enhance the survival of the young. The reproductive strategy of *E. superba*, which includes both the pattern of sinking rates during embryonic development and where and when spawning occurs, may have evolved in response to the effect of the thermal structure of its environment on the probability of survival of its young. If such suggestions are true, then an intriguing area for further research is that of the paleocirculation of the Southern Ocean and the concurrent evolutionary adaptation of the krill.

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