Theoretical analyses show that positively buoyant copepods are able to generate feeding currents by adopting upside-down body positions and pushing water upward. Thus, the excess buoyancy acting on the copepods will be balanced and cone-shaped feeding currents generated to transport water to the capture areas. The intensities of the feeding currents, which can be measured in the present modeling study by calculating the volumetric flux going through the capture areas, are proportional to the mass density contrasts between the copepods and the ambient seawater. The mass density contrasts may vary spatially and temporally depending on copepod body contents and on the properties of the seawater immediately surrounding them. We focus on the case where the mass density contrast between a wax ester-rich copepod and its ambient seawater can vary strongly with depth because wax esters are more compressible and 6–10 times more thermally expansible than seawater. These theoretical analyses show that the intensities of the feeding currents generated by wax ester-rich copepods vary strongly with depth. Our conclusions from these theoretical analyses need to be tested by direct observations.

INTRODUCTION

Archimedes' principle of buoyancy states that an object immersed in water sinks or floats depending on the weight of water it displaces. If the weight of water displaced is less than the object's weight, it sinks (i.e. it is negatively buoyant); if the displaced water weighs more, the object floats (i.e. it is positively buoyant) and only if the two weights are the same the object is neutrally buoyant. Archimedes' principle certainly applies to microorganisms living in water, such as copepods. That is, a copepod's in situ mass density contrast with respect to its ambient water determines its overall buoyancy state (negatively, neutrally or positively buoyant).

Calanus species, especially those living at high latitudes, can accumulate large amounts of lipids consisting predominantly of wax esters (Lee et al., 1970a,b, 1971a,b, 1972, 1974; Lee and Hirota, 1973; Lee, 1974, 1975; Lee and Barnes, 1975). Excellent reviews of the biochemistry and biophysics of lipids of marine organisms are available in the literature (Sargent, 1976; Sargent and Henderson, 1986; Sargent and Falk-Petersen, 1988). One of the implications of having lipids in the body is their effect on the overall buoyancy state of copepods.

Lewis reported that pure wax esters have a mass density of 0.86 × 10³ kg m⁻³ (Lewis, 1970), which is considerably less than the mass density of seawater (≈1026.95 kg m⁻³ at S ≈ 35°C at 1°C and at one normal atmosphere) and even freshwater (≈1099.73 kg m⁻³ at 1°C and at one normal atmosphere). Since calanoid copepods, such as Calanus finmarchicus and Calanus hyperboreus, can contain up to 70% of their dry weight as total lipids—largely as wax esters—they can experience a considerable buoyancy force in seawater (Sargent and Henderson, 1986). Yayanos et al. (Yayanos et al., 1978) measured the variation of mass density of a lipid sample (85% wax esters) isolated from the calanoid copepod Calanus plumchrus (Neocalanus plumchrus) as a function of both temperature and pressure. From the measurements, they calculated coefficients of thermal expansion and compressibility of lipids. Their results show that the lipids are more compressible and much more thermally expansible (6–10 times) than seawater. Because of these...
properties and because of the fact that the immediate environment of the copepods at depth is at higher pressure and colder temperature than at the surface, the buoyancy force acting on a wax ester-rich copepod will increase when the copepod ascends starting from deep water or will decrease when the copepod descends starting from the surface. Thus, the authors pointed out that when *C. finmarchicus* makes a vertical migration to depth after accumulating a large amount of lipids at the surface, they have to exert energy in locomotion against the buoyancy force. Therefore, the buoyancy force due to the lipids of these organisms hinders rather than assists the onset of their downward vertical migration.

Visser and Jonasdottir (Visser and Jonasdottir, 1999) fitted a two-dimensional polynomial to the wax ester mass density data reported by Yayanos et al. (Yayanos et al., 1978). The polynomial gives the mass density of lipids as a function of *in situ* temperature and pressure. Using this function, they constructed a simple analytical model for the overall mass density of the copepod *C. finmarchicus*. It was shown that copepods with a high wax ester content and neutrally buoyant at depth are likely to be positively buoyant in surface waters. This conclusion is contrary to the common view that copepods are negatively buoyant at depth during diapause with the aid of lipids, which have much greater thermal expansibility and greater compressibility than seawater. In doing so, energy has to be expended in locomotion during the downward migration. Those copepods, rich in lipids, are more likely to be positively buoyant in surface waters. On the other hand, they can achieve neutral buoyancy at depth during diapause with the aid of lipids, which have much greater thermal expansibility and greater compressibility than seawater. In doing so, energy has to be expended in locomotion during the downward migration. However, above the depth of neutral buoyancy, the copepods are positively buoyant, which then assists their subsequent upward migration.

Campbell and Dower pointed out that the greater compressibility of lipids compared to seawater makes any depth of neutral buoyancy unstable (Campbell and Dower, 2003). The instability means that with a small displacement of a copepod above the depth of neutral buoyancy, as pressure decreases the lipids will become lighter, which further displaces the copepod upward away from the depth of neutral buoyancy. Vice versa, a small displacement downwards results in becoming heavier; again destabilizing neutrality. Their modeling study shows that the ascent rates due to this instability are small at depth where temperature changes are small, so that the copepods could remain at their depth during overwintering or diapause.

Not included in the aforementioned studies is the fact that many calanoid copepods create feeding currents. A review of hydrodynamics of copepod feeding currents is recently available (Jiang and Osborn, 2004). Mass density contrast between a copepod and its ambient water has been previously related to the feeding current generated by the copepod, mostly in the context of a copepod being negatively buoyant (Strickler, 1982; Childress et al., 1987; Tiselius and Jonsson, 1990; Yen et al., 1991; Bundy and Paffenhofer, 1996; Jiang et al., 2002a,b; Jiang, 2004). Strickler first pointed out that a negatively buoyant copepod’s excess weight, determined from the copepod’s excess density and body volume, is important for the copepod to create a strong feeding current (Strickler, 1982). His hypothesis has received support from a theoretical study by Jiang et al. (Jiang et al., 2002a), in which a flow field model is developed for a self-propelled, negatively buoyant copepod swimming steadily to create a feeding current. The inclusion of feeding currents into the debate about buoyancy explained the paradox that copepods are negatively buoyant in nutritionally dilute waters (Strickler, 1982).

In this study, we explore the interaction between the generation of feeding currents and the buoyancy of copepods. For wax ester-rich copepods, which can be either positively or negatively buoyant depending on their body content and on their position in the water column, we will show that the feeding currents generated can vary strongly with depth.

**MODELING METHODS AND RESULTS**

Because the present work is a theoretical modeling study, we feel it is more appropriate to present modeling methods and results together. This approach follows in general the studies previously published in this journal (Jiang et al., 2002a,b).

**Feeding current generated by a positively buoyant, hovering copepod**

The Stokes flow model for the flow field created by a negatively buoyant, self-propelled spherical model copepod (Jiang et al., 2002a) has been modified and applied in this study to model the flow field created by a positively buoyant, self-propelled spherical model copepod which swims steadily. We only present the case that a copepod hovers, i.e. its global swimming velocity is zero. When it hovers, a positively buoyant copepod has to apply a suitable propulsive force, $f$, in the upward direction to the ambient water, by beating its cephalic appendages in a suitable way. In this way, the reaction force of $f$ from the ambient water, which acts on the copepod, can counterbalance the drag force acting on the copepod’s main body and the excess buoyancy acting on the copepod as well (Fig. 1). In this modeling study, the propulsive force, $f$, is associated with the creation of a feeding current.
current. For an analytical treatment, three assumptions have to be made. (i) Stokes flow is employed; (ii) a spherical body shape is used and (iii) the propulsive force, \( f \), is simplified to be a point force with its pole located outside the sphere. For convenience, the center of the sphere is chosen to be the origin of the coordinate system, the positive \( z \)-direction is opposite to the direction of gravity. The propulsive force, \( f \), is upward. The curved arrow indicates the torque acting on the model copepod due to the reaction force of \( f \). Note that for simplicity the balance of the torques on the model copepod is not considered here. We assume that choosing a suitable center of mass relative to the center of volume enforces the torque balance. (ii) Spherical body and a point force, \( f \), is the point force exerted on the water by the copepod; \( F \) stands for the force by the copepod on the surrounding water flow over the surface of the body; \( f' \) is the reaction force by the water acting on the copepod’s cephalic appendages; \( F' + B' \) stands for the force for the by the copepod on the surrounding water through the body–fluid interface. Note that \( f' = -f \), \( F' = -F \), \( B' = -B \) (Newton’s third law) and \( |B| > |W| \) (positively buoyant).

In the present specific case, only the \( z \)-direction component is nonzero. That is,

\[
f = \frac{|B_{\text{excess}}|}{1 - \frac{1}{4} \left( \frac{a}{a} + \frac{4}{3} \right)} k
\]  

where \( \beta = (a + a/2)/a = 1.5 \) (a parameter determined from the model copepod’s body dimension), \( k \) is the unit vector in the \( z \)-direction, and the excess buoyancy, \( B_{\text{excess}} \), is calculated as

\[
B_{\text{excess}} = \Delta \rho \cdot g \cdot \frac{4}{3} \pi a^3
\]

where \( \Delta \rho \) is the mass density contrast between the copepod and its ambient seawater, which is defined as

\[
\Delta \rho = \rho_c - \rho_w
\]

where \( \rho_c \) is the mass density of the copepod and \( \rho_w \) is the mass density of the ambient seawater. For a positively buoyant copepod, \( \Delta \rho < 0 \). By examining the properties of Green’s function \( G^{\text{SPH}} \), a feeding current as formulated by equation (1) falls off as \( 1/r \) where \( r \) is the distance from the center of the model copepod.

A calculation example of the feeding current generated by a positively buoyant, downward pointing, hovering copepod is shown in Fig. 2. The main features are (i) a strong water current is generated ventrally to the copepod; (ii) the velocity magnitudes in the space surrounding the capture area are a few times larger than the terminal ascending velocity of the model copepod and (iii) the main direction of the current is against the direction of gravity (Fig. 2a and b). The streamtube going through the capture area is plotted in Fig. 2c, which visualizes a large capture volume by the copepod within a time interval of 10 s. Interestingly, the streamtube transports water from below the copepod to the capture area. For this specific example, the resulting volumetric flux through the capture area is 1.67 \( \times \) 10\(^{-9} \) m\(^3\) s\(^{-1}\) (144 mL day\(^{-1}\)). Because of the constraint imposed by the movement pattern and direction of the cephalic appendages (e.g. Strickler, 1984), a positively buoyant copepod has to adopt an upside-down body position in order to generate such a feeding current (Fig. 2).
be upside down in order to generate the feeding current. The parameters copepod to show that in the real world a plots, a realistic copepod body is overlapped with the spherical model through the model copepod’s capture area. In each of these three model copepod. (c) which is ventral to the model copepod.

–2.0 kg m–3. The capture area is defined for the spherical model –4 0.5

Fig. 2. Feeding current generated by a positively buoyant, hovering copepod. (a) Velocity vector plot along the model copepod’s median plane (i.e. the plane of y = 0). (b) Velocity vector plot along the plane of x = a, which is ventral to the model copepod. a is the radius of the spherical model copepod. (c) Three-dimensional view of the streamtube going through the model copepod’s capture area. In each of these three plots, a realistic copepod body is overlapped with the spherical model copepod to show that in the real world a positively buoyant copepod should be upside down in order to generate the feeding current. The parameters for the calculation: \( \mu = 1.5 \times 10^{-3} \text{ kg m}^{-1} \text{ s}^{-1} \), \( a = 0.65 \text{ mm} \) and \( \Delta \rho = -2.0 \text{ kg m}^{-3} \). The capture area is defined for the spherical model copepod as the area enclosed by a small horizontal circle of radius of 0.5a centered at the point (1.7a, 0, 0.4a); the circle is in a yz-plane.

As done by Jiang et al. (Jiang et al., 2002a), more swimming behaviors of copepods can be considered, such as steadily swimming horizontally or downward, or ascending at a velocity less than the copepod’s terminal ascending velocity ‘partial ascending’. Depending on the swimming velocity, the resulting flow geometry can be a cone-shaped, or elongated cylindrical streamtube tilting towards the swimming direction. For partial ascending, as for partial descending by a negatively buoyant copepod, a circulatory flow pattern can be generated (Malkiel et al., 2003; Jiang and Strickler, submitted for publication).

Three case studies
From equations (1)–(3), one can see that the intensity of the feeding current generated by a hovering copepod is proportional to the copepod’s mass density contrast with respect to the ambient water which is defined in equation (4). Since the mass density of both the copepod and the ambient water may vary spatially and temporally, the intensity of the feeding current may also vary spatially and temporally. In our modeling study, the intensity of the feeding current can be conveniently measured by calculating the volumetric flux going through the capture area of the copepod. As a modeling example, we will show how the intensity of the feeding current created by a wax ester-rich copepod varies strongly with depth, based on the data of vertical profiles of salinity and temperature used by Visser and Jónasdóttir (Visser and Jónasdóttir, 1999).

From the salinity and temperature data (Fig. 3a and b), we have calculated pressure distribution with depth (Fig. 3c), the vertical profile of dynamic viscosity of seawater (Fig. 3d) and vertical profiles of mass density of both lipids (mostly wax esters) and seawater (Fig. 4). The calculation methods are detailed in Table I. Next, a simple model for the mass density of a copepod is applied. This model was first proposed by Visser and Jónasdóttir (Visser and Jónasdóttir, 1999) and later modified by Campbell and Dower (Campbell and Dower, 2003). The mass density of the model copepod is written as

\[
\rho_c = \left(\frac{\delta_w + \delta_l + \delta_o}{\rho_o} + \rho_l + \rho_p\right)^{-1}
\]

where \( \delta_w, \delta_l \) and \( \delta_o \) are, respectively, the mass proportion of water, lipid and other ‘structural mass’ components of the model copepod. Therefore, \( \delta_w + \delta_l + \delta_o = 1 \) needs to be satisfied. \( \rho_o \) represents the density of the structural mass of the copepod (e.g. protein, exoskeleton) and is held constant (Campbell and Dower, 2003). By assuming osmotic equilibrium between the copepod and the seawater immediately surrounding it, \( \rho_o \) is taken to be the same as the in situ mass density of seawater. To test our calculation procedure, we have successfully reproduced Fig. 2 of Campbell and Dower (Campbell and Dower, 2003) by using the same parameters (i.e. \( \delta_w = 0.82, \delta_l = 0.11, \delta_o = 0.07 \) and \( \rho_o = 1260 \text{ kg m}^{-3} \)). In this study, more conservative ranges of the parameters, i.e. \( 0.79 \leq \delta_w \leq 0.83 \) and \( 1080 \leq \rho_o \leq 1240 \text{ kg m}^{-3} \), are chosen by combining the discussions on parameter ranges by others (Visser and Jónasdóttir, 1999; Campbell and Dower, 2003).
The results of three case studies are presented in the following. In these three case studies, explicit reference is made to the depth of neutral buoyancy, and $\Delta \rho = 0$ is verified for equation (4). In case study 1, the parameters for the model copepod are $\delta_\omega = 0.791$, $\delta_r = 0.124$, $\delta_\rho = 0.085$ and $\rho_\omega = 1239.52 \text{ kg m}^{-3}$. The model copepod is neutrally buoyant at depth. Right above the depth of neutral buoyancy, the model copepod becomes positively buoyant and reaches the largest positive buoyancy at the surface (Fig. 3a and b). In calculating the vertical variations of the volumetric flux through the model copepod's capture area, the vertical variations of both mass density contrast (Fig. 3b) and seawater dynamic viscosity (Fig. 3d) are taken into account. The model
results show that the volumetric flux varies from 0.15 \times 10^{-9} to 1.89 \times 10^{-9} m^3 s^{-1} as depth changes from 400 to 11 m (Fig. 5c). In terms of the units of the clearance rate which are more familiar to biological oceanographers, the calculated volumetric flux varies from 13 to 163 mL day^{-1} as the depth changes from 400 to 11 m. Information about the clearance rate can be found in the book by Miller (Miller, 2004). For case study 1, the strongest feeding current would be generated at the surface water.

In case study 2, the parameters for the model copepod are \( \delta_c = 0.791, \delta_l = 0.118, \delta_s = 0.091 \) and \( \rho_s = 1236.19 \text{ kg m}^{-3} \). The model copepod is neutrally buoyant at a middle water depth of \( \sim 150 \text{ m} \). Right below the depth of neutral buoyancy, the model copepod becomes negatively buoyant and reaches the greatest negative buoyancy at depth; right above the depth of neutral buoyancy, the model copepod becomes positively buoyant and reaches the largest positive buoyancy at the surface (Fig. 6a and b). The model results show that the volumetric flux varies from \(-1.00 \times 10^{-9} \) to \( 0 \text{ m}^3 \text{ s}^{-1} \) (i.e. \(-86 \) to \( 0 \text{ mL day}^{-1} \)) in terms of the units of the clearance rate) when depth changes from 400 to 150 m, and from \( 0 \) to \( +0.37 \times 10^{-9} \text{ m}^3 \text{ s}^{-1} \) (i.e. from \( 0 \) to \( +32 \text{ mL day}^{-1} \)) when depth changes from 150 to 11 m (Fig. 6c). (The ‘\(-\)’ sign indicates the downward volumetric flux, and the ‘\(+\)’ sign indicates the upward volumetric flux.) To create the feeding currents, the copepod needs to maintain an anterior-pointing-upward body position at depths below the

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Table I: Calculation methods for vertical profiles of density of lipids, density of seawater, pressure and dynamic viscosity of seawater

<table>
<thead>
<tr>
<th>Calculation Method</th>
<th>Formula</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density of lipids, ( \rho_l(T, \phi) )</td>
<td>( \rho_l(T, \phi) = 0.9198 - 8.2418 \times 10^{-4} T - 1.2086 \times 10^{-4} T^2 - 8.9357 \times 10^{-7} T^3 + 7.1703 \times 10^{-9} )</td>
</tr>
<tr>
<td>(Visser and Jónasdóttir, 1999)</td>
<td></td>
</tr>
<tr>
<td>Density of seawater, ( \rho_w )</td>
<td>( \rho_w = 1.0100 - 2.5853 \times 10^{-8} p^2, ) where ( 0 \leq T \leq 10 \text{°C} ) and ( 0 \leq p \leq 100 \text{ bar}. \rho_w(T, \phi) ) is in g cm^{-3}</td>
</tr>
<tr>
<td>(S, T, ( \rho )) (UNESCO, 1981)</td>
<td></td>
</tr>
<tr>
<td>Conversion of depth ( Z ) into pressure ( \rho )</td>
<td>( \rho(Z, \phi) = h(Z, 45) \times k(Z, \phi) - \rho h(Z, \phi) ), where ( h(Z, 45) = 1.00818 \times 10^{-2} Z + 2.465 \times 10^{-8} Z^2 - 1.25 \times 10^{-13} Z^3 + 2.8 \times 10^{-19} Z^4 )</td>
</tr>
<tr>
<td>(Leroy and Parthiot, 1998)</td>
<td></td>
</tr>
<tr>
<td>Seawater dynamic viscosity, ( \mu(S, T, \phi) )</td>
<td>( \mu(S, T, \phi) = 1.7900 \times 10^{-3} - 6.1299 \times 10^{-6} T + 1.4487 \times 10^{-6} T^2 - 1.6826 \times 10^{-9} T^3 - 1.7913 \times 10^{-7} p + 9.5182 \times 10^{-11} p^2 + 2.4727 \times 10^{-6} S + 5(4.8429 \times 10^{-6} T - 4.7172 \times 10^{-9} T^2 + 7.5986 \times 10^{-11} T^3) + 3(5.3500 \times 10^{-8} T - 2.5853 \times 10^{-12} T^2 - 1.1652 \times 10^{-13} T^3), )</td>
</tr>
<tr>
<td>(Matthäus, 1972)</td>
<td></td>
</tr>
</tbody>
</table>

For the site in the Faroe–Shetland Channel, the latitude \( \phi \) is chosen to be 60.5° N. \( h(Z, \phi) \) is in meters and \( p \) in megaPascal.
depth of neutral buoyancy and an upside-down body position above the depth of neutral buoyancy.

In case study 3, the parameters for the model copepod are $\delta_w = 0.7905$, $\delta_l = 0.117$, $\delta_o = 0.0925$ and $\rho_o = 1239.32 \text{ kg m}^{-3}$. The model copepod is neutrally buoyant at the surface. Right below the depth of neutral buoyancy, the model copepod becomes negatively buoyant and reaches the largest negative buoyancy at depth (Fig. 7a and b). The model results show that the volumetric flux varies from 0 to $-1.35 \times 10^{-9} \text{ m}^3 \text{ s}^{-1}$ (i.e. from 0 to $-117 \text{ mL day}^{-1}$ in terms of the units of the clearance rate), when depth changes from 11 to 400 m (Fig. 7c). For case study 3, the strongest feeding current would be generated in deep water.

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**Fig. 5.** Model results for case study 1 in which the model copepod would be neutrally buoyant at depth (of depth of 855.4 m). The parameters for the model copepod: $\delta_w = 0.791$, $\delta_l = 0.124$, $\delta_o = 0.085$ and $\rho_o = 1239.32 \text{ kg m}^{-3}$. (a) Vertical profiles of density of copepod and density of seawater; (b) density contrast between copepod and seawater as a function of depth and (c) feeding current induced volumetric flux, going through the model copepod’s capture area, as a function of depth. A ‘+’ sign (in Figs 5 and 6) indicates the upward volumetric flux, and a ‘–’ sign (in Figs 6 and 7) indicates the downward volumetric flux.

**Fig. 6.** Model results for case study 2 in which the model copepod would be neutrally buoyant at depth of 150.2 m. $\delta_w = 0.791$, $\delta_l = 0.118$, $\delta_o = 0.091$ and $\rho_o = 1238.19 \text{ kg m}^{-3}$. See Fig. 5 legend for additional explanations.
DISCUSSION

Both laboratory observational studies and theoretical modeling studies have previously revealed that the excess weight of a negatively buoyant copepod is important for the copepod to create a strong feeding current. However, wax ester-rich copepods may become largely positively buoyant at the surface because their body consists of a large amount of wax esters, which is much lighter than seawater and even freshwater. Our hydrodynamic modeling study shows that a positively buoyant copepod is able to generate a strong feeding current by pushing water upward to retard its ascending motion and by hovering in the water column. In order to create such a feeding current the copepod would have to adopt an upside-down body position. The cone-shaped feeding current transports water from below the copepod to its capture area and decays spatially as $1/r$. The theoretical clearance rates calculated for the feeding currents generated by positively buoyant copepods are quite large at the surface and within the range of the ‘volume swept clear’ (VSC) values measured for some adult copepod species (e.g. Paffenho¨fer and Harris, 1976).

Citing a personal communication, Strickler briefly mentioned that Arctic calanoids which are most likely positively buoyant, due to the large amounts of wax esters stored in their body, behave in an upside-down fashion (Strickler, 1982). To our knowledge, no other contributions have considered the feeding currents generated by positively buoyant copepods. In view of this, we must point out that our theoretical results await confirmation from observational evidence in the field. Furthermore, when we ascribe the body position of a positively buoyant copepod creating a strong feeding current as ‘upside down’, we make use of our global coordinate system. However, copepods orient within their own local coordinate system; they orient themselves according to the information obtained by their sensory system. Strickler and Bal (Strickler and Bal, 1973) suggested that the mechanoreceptors located on a copepod’s first antennae serve to measure the direction of sinking (gravity). However, if the copepods are positively buoyant, they ascend when they stop moving their appendages. In this situation, mechanoreception would point in the direction of ascending (buoyancy). Since, especially at night, no other environmental cues could tell the animal whether it is ascending or descending it seems logical to assume that the animal will orient in such a way to optimize feeding success. Additionally, Woltereck (Woltereck, 1913) argued that the spines and setae, including the antennae, serve to slow down the sinking speed and that because these structures are longer at one end of the body, animals of the same species are always oriented the same way with respect to the direction of ‘sinking’. This means that the orientation of positively buoyant animals will be a mirror picture of the orientation of negatively buoyant animals. When both start to create their feeding currents, the flow directions should also be mirror images as well.

It is also noted that the intensity of the feeding current is proportional to a copepod’s mass density contrast with respect to its ambient water. This indicates that the

Fig. 7. Model results for case study 3 in which the model copepod would be neutrally buoyant at surface (of depth of 11.8 m). $\delta_w = 0.7905$, $\delta_l = 0.117$, $\delta_o = 0.0925$ and $\rho_0 = 1238.63$ kg m$^{-3}$. See Fig. 5 legend for additional explanations.
intensity of the feeding current may vary spatially and temporally, corresponding to the variations in the mass density of both the copepod and the seawater. The variation in the intensity of the feeding current may also be due to the variation in the dynamic viscosity of seawater, but to a lesser extent. For wax-ester-rich copepods, because of the strong variation of the mass density of wax esters with temperature and pressure, the intensities of feeding currents created by negatively or positively buoyant copepods vary strongly with depth. The difference between the negatively buoyant case and the positively buoyant one is that a positively buoyant copepod would create the strongest feeding current at the surface. In contrast, a negatively buoyant copepod would create the strongest feeding current at depth. Thus, our modeling results for the positively buoyant cases could be relevant to copepod feeding currents in the real world.

We can think of two scenarios where the interactions of mass density contrast and feeding currents may be of importance. In the first train of thinking we would start with a positively buoyant copepod at night in the surface waters. The animal creates a feeding current and captures food, resulting in even more positive buoyancy. However, in early morning, the animal swims actively down to greater depth, bypassing the depth where it would be neutrally buoyant. Due to greater pressure and lower temperature it is now negatively buoyant and, therefore, can still generate a large feeding current. The second train of thinking takes into account the fact that the vertical distribution of nutritionally important food items is also depth dependent. While a copepod may not generate such a large feeding current at the surface due to a low mass density contrast, the food concentration is high and the encounter rate may be sufficient. At greater depth, where the food concentration is low, it may happen that due to a much higher mass density contrast the feeding current is strong enough to counterbalance the low concentration, and therefore the encounter rate is still sufficient.

Finally, we try to relate our modeling results to the feeding strategies of calanoid copepods in oceans. To maintain a finite mass density contrast against their ambient seawater, either negatively or positively, is of great benefit to those feeding current-creating copepods in creating a strong feeding current. Although cruising may be a way of solving the problem of being neutrally buoyant, it is less energetically efficient than creating a feeding current by being negatively or positively buoyant but not neutrally buoyant (Jiang et al., 2002b; Jiang, 2004). In order to maintain their negative or positive buoyancy, copepods can either adjust their body content or actively select their habitat (e.g. vertical migration to suitable depth). A recent field study showed that zooplankton (50–85% as copepods) effectively maintained their depth by swimming against upwelling and downwelling currents moving at rates of up to tens of body lengths per second (Genin et al., 2005). These animals formed patches with vertical extent of a few meters in a water column of ~30 m. Individual zooplankters (copepods) had their own preferred depth ranging from 8.1 through 15-m depth in the water column, and they swam actively against upwelling and downwelling in order to maintain their preferred depth (A. Genin, Eilat, Israel, personal communication). We speculate that the reason for these copepods to exhibit such a persistent depth retention behavior is to maintain a finite mass density contrast against their ambient seawater.

Our modeling results suggest that the mass density contrast between copepods and their ambient water may be important and related to their feeding behaviors and biomechanics, their seasonal and diel vertical migrations and even their spatial distributions in lakes and oceans. Our theoretical consideration reveals a problem that zooplankton may have to face while storing lots of lipid for survival during adverse times. It highlights that the depth of the animal’s position in the water column may influence its behavior. However, we fully recognize that our conclusions are obtained from theoretical analyses only. One of the purposes of this article is to bring these research questions to the attention of other interested researchers. We envisage that the orientations of positively buoyant copepods may be observed in the Northern Atlantic, Arctic and Antarctic waters either by diving or by using cameras on ROVs. It will not be surprising if such observations show clearly that upside-down feeding currents are created by positively buoyant copepods, as the theoretical analyses have shown that such a behavior is allowed by physics. It would be interesting if convincing evidence shows the opposite. Then some new behaviors would be found for those copepods which might have already solved the problem of being positively buoyant in other ways. Such behaviors would encompass some interesting factors which were not considered in our theoretical predictions.

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REFERENCES


