Individual-based models of copepod populations in coastal upwelling regions: implications of physiologically and environmentally influenced diel vertical migration on demographic success and nearshore retention

Harold P. Batchelder a,*, Christopher A. Edwards b, Thomas M. Powell c

a College of Oceanic and Atmospheric Sciences, 104 Ocean Admin. Bldg., Oregon State University, Corvallis, OR 97331-5503, USA
b Department of Marine Sciences, University of Connecticut, 1084 Shennecossett Road, Groton, CT 06340, USA
c University of California, Department of Integrative Biology, 3060 Valley Life Sciences Building, Berkeley, CA 94720-3140, USA

Abstract

We link a two-dimension coastal upwelling circulation hydrodynamic-ecosystem (NPZ) model with an individual-based model (IBM) for an intermediate sized (ca. 2.5 mm) copepod capable of diel vertical migration (DVM) at larger sizes. The NPZ model is that of Franks, Wroblewski and Flierl (1986), with the zooplankton state variable parameterized for macrozooplankton. IBM simulations are done with different scenarios for behavioral responses; the interaction of the organisms with the circulation is evaluated by examining growth/development, reproduction, survival and distribution. Since ocean productivity in coastal upwelling systems is greatest nearshore, zooplankton production is favored by nearshore retention. Model results, using an idealized, intermittently wind-forced, upwelling circulation, indicate that non-migrating copepods are flushed from the nearshore system in offshore zonal surface flow; highest population abundances occur offshore, in a region of relatively low food resources. Conversely, migrating copepods interact with the stratified zonal flow within the upwelling system and are retained nearshore when the amplitude of the DVM is sufficient to place the individuals in near-bottom onshore flow during the day. Environmental features, like deep-extending food resources, and physiological controls, like satiation or body size, that permit copepods to remain deeper, or spend more time away from the surface, favor nearshore retention. Diel vertical migration is one mechanism, which may permit animals to exploit favorable habitats located nearshore in upwelling systems. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Modeling; Copepod; Zooplankton; Coastal upwelling; Circulation; Bioenergetics; North Pacific

* Corresponding author: Tel.: 541-737-4500; fax: 541-737-2064.
E-mail address: hbatchelder@oce.orst.edu (H.P. Batchelder).
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There is a widespread illusion among ecologists that mathematical models can always serve as the explanation of ecological mechanisms and processes. This may not be so: a mathematical model of population growth may be nothing more than a phenomenological description of the net result of many processes which are poorly understood or not understood at all. (Lomnicki (1992, p. 8))

It is individuals that survive to recruit; the unique characteristics of individuals, and not population averages, determine which individuals survive. Individual-based models are not only interesting, but are perhaps the only logical way to model these processes. (Crowder, Rice, Miller, & Marschall (1992, p. 245))

1. Introduction

The waters off the west coast of North America are biologically productive regions that support economically viable fisheries. Much of this productivity is directly related to wind-forced upwelling that occurs nearly continuously in some regions and intermittently or seasonally in others. Pelagic fish biomass in the coastal upwelling domain, defined by Ware and McFarlane (1989) as extending from Vancouver Island, BC to Baja, California, has averaged 11 million tons this century (Smith, 1978). During the first half of this century this biomass declined from ca. 25 million tons to ca. 4–5 million tons by 1950; since then it has fluctuated, but always remained at low levels. Ware and Thomson (1991), using a variety of environmental data indicative of upwelling intensity suggested that the intensity of alongshore winds and upwelling declined markedly between 1916 and 1942. This resulted in lower levels of primary productivity that cascaded through the food web, eventually resulting in lower biomass and fisheries yields of harvested pelagic fish resources.

Understanding the pathways of marine production from wind-forced upwelling of nutrients through the lower trophic levels to the harvested fish and shellfish resources, is crucial to understanding interannual, decadal and longer-term fluctuations and trends in coastal production, and in implementing improved management of those resources (Botsford, Castilla, & Peterson, 1997). Modeling studies provide a cost-effective means to evaluate some of these mechanisms and to explore potential consequences of management...
decisions. Examples include using simulations to track distributions of red seabream juveniles after experimental stocking in a coastal embayment of Japan (Yanagi, Okada, & Tsukamoto, 1992), and exploring the implications of the timing of transplants on growth, mortality and yield of oysters in Delaware Bay, USA (Powell, Klinck, Hofmann, & Ford, 1997). A model was also used to indicate that years of high Japanese sardine larval survival and recruitment may result from favorable interactions of spawning location and larval drift (Kasai, Kishi, & Sugimoto, 1992).

Traditionally, ecological models of lower trophic level pelagic processes in the ocean have represented functional groups. The simplest of these are nutrient–phytoplankton–zooplankton (NPZ) models, which include a single limiting nutrient (N), a single producer (P), and a single consumer (Z). An early model of this type was that of Franks et al. (1986). More complicated models, including detritus (a sinking component), bacteria and DOC (regenerative processes), or size structure of either P or Z (Moloney & Field, 1991; Moloney, 1992; Gin, Guo, & Cheong, 1998; Carr, 1998), have been developed when the simpler NPZ models have failed to replicate the patterns observed in nature. An early application of a slightly more complicated model to an upwelling ecosystem was that of Wroblewski (1977), which included state variables for two nutrients (nitrate and ammonia) and detritus as well as phytoplankton and zooplankton. Except where size is treated explicitly, these models assume that all individuals within a trophic compartment are identical. Conversely, at the upper trophic end of the pelagic ecosystem (esp. fish), there has been more emphasis on the individual organism, and recognition that not all individuals of the same age within a population are identical. Thus, it is not uncommon to find individual based models (IBMs) of fish populations (Cowan, Rose, Rutherford, & Houde, 1993; Peterman et al., 1994; Hinckley, Hermann, & Megrey, 1996; Wang, Cowan, Rose, & Houde, 1997). These models track a number of individual fish, each with their own physiological or behavioral traits through time, space, or both, and derive population abundances, distributions, and dynamics from ensembles of individual organisms. IBMs are of particular value for systems in which behaviors, such as diel vertical migration, vary as a function of size, age or condition of the individual fish. Because they represent individual properties and processes however, IBMs can be relatively complex, and the results can be difficult to interpret. However, they have a very important advantage over bulk models: because they include a detailed description of the mechanisms and processes that determine the vital rates in the population, they may increase understanding of the system. The dichotomy between population models (NPZ-like) and IBMs is aptly described by the two quotes above. NPZ and population models ignore many of the mechanistic details, whereas IBMs attempt explicitly to include all of the processes and properties thought to control vital rates.

One may then ask where mesozooplankton, such as copepods, lie within the continuum from phytoplankton to fish. On the one end, it may be appropriate to assume that all phytoplankton are identical (but see Woods & Onken, 1982; and Barber & Smith, 1981). On the other end, fish clearly have important individual properties and behaviors. If different species, perhaps of different size, or different life stages within a species have identical behaviors (feeding, migration, etc.) and properties (mortality rates), then it may not be necessary to model them as individuals. Alternatively, if behaviors or properties differ as the organisms grow, or between different species, and these are important in determining individual success, then models should include these properties and processes explicitly. Zooplankters do possess individual traits and behaviors, and operate independently of their neighbors or siblings (Paffenhöfer, Bundy, Lewis, & Metz, 1995). Batchelder and Miller (1989) and Batchelder and Williams (1995) have explored the implications of this in simple contexts. Recently, the IBM approach has been used to model zooplankton populations more extensively (Miller, Lynch, Carlotti, Gentleman, & Lewis, 1998; Carlotti & Wolf, 1998). IBMs of zooplankton have also been coupled to circulation models (or observations), and particle-tracking including behavior has been used to examine sources, sinks, and retention of plankton in dynamically changing flow fields (Bryant, Hainbuer, & Heath, 1998; Werner et al., 1993; Heath, Zenitani, Watanabe, Kimura, & Ishida, 1998; Davidson & DeYoung, 1995).

In this paper we examine the potential of diel vertical migration (DVM) and other individual properties
and processes, to interact with spatially-dependent transports and food resources in a coastal upwelling system to determine individual and population success. We couple a Lagrangian individual based model of the vital rates, physiology and behavior of an intermediate sized copepod with a two dimensional (x-z) Eulerian model of the circulation and other ecosystem components. This is an extension of earlier one-dimensional (1D) models with simplified physics (Batchelder & Williams, 1995) to more realistic, but still idealized, physics and food fields in 2D (Edwards, Batchelder, & Powell, 2000). We evaluate success using both demographic considerations (growth, survival and reproduction) and distributional considerations (nearshore retention).

2. Model structure and equations

The IBM requires several spatially dependent external forcing terms. These include transports (advection, diffusion), light, temperature, food resources, and predation intensity. Our approach is to use a coupled Eulerian ecosystem-circulation model to derive spatially dependent fields for advection, diffusion, temperature, and food resources. Other external forcing terms are calculated independently (light fields) or are assumed (predation intensity). Below we describe the physical framework and ecosystem model used to derive the spatially dependent forcing fields, and then describe how these are coupled to the individual based model of copepods.

2.1. Physical framework

The physical environment is two dimensional, represented by a water column (z) extending to the bottom (or to 200 m depth), and offshore (x) from the coast to 100 km (Fig. 1). The Eulerian grid of the model domain is stretched in both x and z, with δz of 1.5–3.7 m (smallest near surface) and δx of 500–1500 m (smallest nearshore). The bottom represents the topography offshore of Newport, Oregon. The physical

![Fig. 1. The model domain, bottom topography, and initial positions of 5000 individuals tracked in the biological simulations.](image-url)
model solves the time-dependent, hydrostatic Navier–Stokes Eqs. in finite difference form on a staggered grid. Fields in the westernmost 20 km of the domain are relaxed to initial conditions to mimic an open ocean boundary. The surface mixed layer was modeled using K profile parameterization (Large, McWilliams, & Doney, 1994) and the bottom boundary layer was modeled using a simple mixing-length model. Complete details of the physical circulation and mixing model can be found in Edwards, Batchelder and Powell (2000), who present results for 30 day simulations forced by spatially and temporally uniform winds. In the simulations presented here, wind forcing was spatially constant, but time dependent. Southward wind stress of 0.05 N m \(^{-2}\) was applied during upwelling favorable periods, while relaxation periods had no wind stress. Wind forcing was a repeating pattern of 10 days of upwelling favorable winds followed by 10 days of no wind. Temperature in the model was initialized with April climatological values, and the model was run for 120 d. Because the model does not include surface heat fluxes, temperatures are not realistic, being too low offshore, with a small onshore-offshore gradient at the surface. While adding heat fluxes to this model would alter the temperature structure, the vertical extent of the surface mixed layer, and the details of the along-shore flow in thermal wind balance, for this study we view these changes as secondary relative to the net cross-shelf transport determined by the along-shore wind stress alone. However, the departure of the temperature field from nature is sufficient, in our view, to prohibit using temperature dependent physiological functions in the IBMs (see below).

2.2. Ecosystem model

We use an Eulerian ecosystem model (Fig. 2) with three state variables: dissolved nutrient (N); phytoplankton (P); zooplankton (Z). The model is nitrogen-based, and we assume that phytoplankton and zooplankton have a fixed C/N ratio. This assumption oversimplifies nature (Cullen, 1982), but is required for later use of the resulting phytoplankton concentration as an external forcing in our carbon-based IBM of copepods. The ecosystem model is that of Franks, Wroblewski and Flierl (1986) and was explored in an idealized two-dimensional upwelling scenario by Edwards et al. (2000). Table 1 presents the Eqs. and parameter values of the ecosystem model. Phytoplankton growth is limited by light and nutrients. Diel variability in light is not considered in the ecosystem model; rather, an average constant surface value is used. Light declines exponentially with depth, but is not a function of phytoplankton concentration (e.g. self shading is not considered). Grazing and growth of zooplankton is a curvilinear function of food (phytoplankton) concentration, with saturation at high concentrations. A fraction of the phytoplankton con-

![Diagram of the NPZ ecosystem model](image)
Table 1

Equations and parameter values for the ecosystem model

\[
\begin{align*}
\frac{\partial P}{\partial t} & = \frac{V_m NP}{k_s + N} - R_m Z (1 - e^{\lambda P}) - mP - w_s \frac{\partial P}{\partial z} \\
\frac{\partial Z}{\partial t} & = \gamma R_m Z (1 - e^{\lambda P}) - gZ \\
\frac{\partial N}{\partial t} & = \frac{V_m NP}{k_s + N} e^{\kappa c} + (1 - \gamma) R_m Z (1 - e^{\lambda P}) + mP + gZ
\end{align*}
\]

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Value</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>(V_m)</td>
<td>2.0 day(^{-1})</td>
<td>maximum phytoplankton growth rate</td>
</tr>
<tr>
<td>(k_s)</td>
<td>0.1 (\mu)mole N (1^{-1})</td>
<td>half-saturation constant for nutrient uptake</td>
</tr>
<tr>
<td>(k_{ext})</td>
<td>0.06 m(^{-1})</td>
<td>light extinction coefficient</td>
</tr>
<tr>
<td>(R_m)</td>
<td>0.5 day(^{-1})</td>
<td>maximum zooplankton growth rate</td>
</tr>
<tr>
<td>(\lambda)</td>
<td>0.2 ((\mu)mole N (1^{-1}))(^{-1})</td>
<td>curvilinearity of the Ivlev function</td>
</tr>
<tr>
<td>(\gamma)</td>
<td>0.7</td>
<td>assimilation efficiency</td>
</tr>
<tr>
<td>(m)</td>
<td>0.1 day(^{-1})</td>
<td>non-grazing phytoplankton mortality rate</td>
</tr>
<tr>
<td>(g)</td>
<td>0.2 day(^{-1})</td>
<td>zooplankton mortality rate</td>
</tr>
<tr>
<td>(w_s)</td>
<td>0 m day(^{-1})</td>
<td>phytoplankton sinking rate</td>
</tr>
</tbody>
</table>

...umed is immediately regenerated to nutrients. Phytoplankton and zooplankton mortality contribute to the dissolved nutrient pool directly. For the runs presented here the ecosystem state-variables were initialized close to their stable steady-state values. This is a simple model with few state variables that produces spatially dependent distributions of nutrients, phytoplankton and zooplankton that mimics many features observed in coastal upwelling systems (Edwards et al., 2000). However, the limitation to three state variables does restrict the model’s ability to represent accurately some features observed in nature, such as the shift from a diatom dominated upwelling community nearshore to a flagellate-microzooplankton dominated community in more oligotrophic regions offshore, and the implications this has for both standing stocks and turnover times in the two regions.

2.3. Individual based model

The IBM is an elaboration of a model described earlier by Batchelder and Miller (1989) and Batchelder and Williams (1995) for intermediate-sized copepods of the genus Metridia. Eqs. describing growth, development, mortality and reproduction are presented in Table 2. In the present model, growth, development, reproduction, death, and DVM processes are tracked for individual organisms within the two dimensional spatial domain using a time step of \(\delta t=120\) s. Individual growth and egg production are based on bioenergetic relationships. Individuals were allowed to feed on only the \(P\) state variable or on both \(P\) and \(Z\) from the NPZ simulations in separate runs. In this paper, only results from the \(P\) as food only simulations are shown. Using both \(P\) and \(Z\) as food resulted in qualitatively similar results. Food concentrations from the coupled ecosystem-physical model were considered an external forcing; i.e. there was no dynamic negative feedback of ingestion by the individuals in the IBM causing depletion of phytoplankton. This is reasonable when the copepod populations being modeled are not the primary grazer in the system. Dynamical two-way coupling of a quasi-individual based model with an ecosystem model of lower trophic levels has been done in one dimension (see Carlotti & Wolf, 1998), but is more difficult for a true IBM in multiple...
Table 2
Equations describing growth bioenergetics, development, mortality and reproduction of an intermediate-sized copepod

**Bioenergetics.** Individual weight (\(W; \mu g\) C), for all but adult females, was described by:

\[
\frac{dW}{dt} = A - R_t
\]

where \(A\) is assimilated matter and \(R_t\) is total respiration which consists of a basal metabolic rate and a contribution related to ingestion.

\[
A = φI_{max}W^θ/k_{ing} + P - νF_h
\]

\[
R_t = βW^n + γA
\]

\[
F_h = \begin{cases} 
1.0 & \text{if } λ_i > k_{ing} \\
2.0 - \left(\frac{λ_i}{k_{ing}}\right) & \text{if } λ_i ≤ k_{ing}
\end{cases}
\]

\[
λ_i = λ_{i-1} + 2(P - λ_{i-1}Δ)/3
\]

where \(φ\) is the assimilation efficiency, assumed to be 0.7, the term \([I_{max}W^θ]\) specifies a weight dependent maximum ingestion rate (\(µg\) C time\(^{-1}\)) that scales with weight (\(µg\) C) allometrically by \(θ\), which is set to 0.7. \(P\) is food concentration (\(µg\) C l\(^{-1}\)) obtained from the NPZ model using an estimate of 77 \(µg\) C (µmole N). \(ν\) is a threshold concentration below which grazing does not occur (set to 0 \(µg\) C l\(^{-1}\)), and \(k_{ing}\) is the half saturation concentration for ingestion (set to 70 \(µg\) C l\(^{-1}\)). \(F_h\) is a multiplier correcting for an individual’s present hunger condition, and \(λ_i\) is a measure of an individual’s hunger factor, which is variable and dependent on its past hunger factor and present food level. \([βW^n]\) is a weight specific metabolic rate (units of \(µg\) C day\(^{-1}\)), which scales allometrically by \(θ\), and where \(β\) is set to 0.1; and, \(γ\) is the nondimensional fraction of assimilated food that is respired (0.4).

**Development.** Stage progression (molting) occurred when an individual’s weight achieved a stage-dependent critical weight (Batchelder & Miller, 1989). These weights (\(w_{crit,s}\)) were temporally and spatially independent.

**Mortality.** Mortality was implemented by generating a random uniform variate \(U(0, 1)\) for each individual at each time step; if \(U(0, 1)\) is greater than \(m_s/Δt\), where \(m_s\) is the stage-dependent per capita daily mortality rate and \(Δt\) is the time step, then the individual survives, otherwise the individual perishes. Starvation mortality occurs if the weight of an individual of stage \(s\) declines to less than \(w_{starv,s}\).

**Reproduction.** Reproductive material (\(W_r; \mu g\) C) by adult females was accumulated following,

\[
\frac{dW_r}{dt} = ε_1\frac{dW}{dt}\]

\[
\frac{dW_r}{dt} = -\min[(30-W),0.5W_r]\]

where \(ε\) is an efficiency of conversion of structural weight into reproductive weight (0.25) and \(ξ\) is a weight-dependent function relating the partitioning of assimilated matter into structural vs. reproductive weight,

\[
ξ = 0 \quad \text{for } W < 30
\]

\[
ξ = ξ_0 = 0.8 \quad \text{for } W = 30
\]

\[
ξ = ξ_1 + (W-30.0)20/ξ_2 \quad \text{for } 30 < W < 50; \ ξ_1 = 0.25
\]

\[
ξ = ξ_2 \quad \text{for } W = 50
\]
dimensions, requiring unrealistic averaging of grazing pressure from individuals extrapolated to discrete volumes of the Eulerian model.

Egg development was not modeled explicitly. The egg stage was lumped together with the first two naupliar stages (N₁, N₂) which in nature probably do not feed, and growth was modeled similarly to older stages, which do feed. Simulations (not shown) in which these three stages together did not feed, but were assumed to require a fixed 5 days for development (e.g. from egg laying to N₃) showed similar spatial patterns with slightly longer generation times and consequently marginally lower survival to adult. Individual body weight during the non-feeding stages declined as a result of metabolic losses. Growth in the feeding stages is calculated as assimilation less respiration. Maximum ingestion rate is a dynamic variable that is a property of the individual; when an individual experiences an extended period with little food, its maximum ingestion rate ramps up by a factor of two compared to a satiated individual. This is implemented as described in Batchelder and Williams (1995) and is based on observations for Metridia and other copepods (Batchelder, 1986; Mackas & Burns, 1986; Runge, 1980). In Batchelder and Williams, ingestion was also a function of temperature. Here, because we neglect the forcing resulting from surface heating, which would increase seasonal temperatures in the ecosystem-physical model, ingestion and all other metabolic rates are assumed to be independent of temperature. Stage-development is tracked in the model by assuming a constant transition weight for molting from one stage to the next. This is a reasonable assumption for relatively short-term (4 month) simulations, during which stage-dependent mean weights would vary little.

Mortality rates are difficult to estimate from observational data, and may vary according to lifestage, season, depth, ambient light and distance offshore, to name but a few factors. To simplify, the simulations presented here assume per capita mortality rates are independent of all these factors, except for lifestage. Mortality rates were set to 0.04 day⁻¹ for all naupliar stages (N₁-N₆) and copepodite stages C₁-C₄. The oldest immatures (C₅) and adults (C₆) were assumed to have higher mortality rates of 0.1 day⁻¹; higher mortality rates for the later stages prevented the accumulation of excessive numbers of adults and their consequent reproduction. This particular stage-dependent mortality pattern was chosen to provide reasonable balance between the production of new young and mortality losses, so that the number of individuals to be tracked in the model approached neither zero nor infinity. It was not intended to represent the real pattern of mortality for any particular copepod. In addition, individuals whose weight fell below a stage-dependent threshold (the midweight of the prior life stage) died of starvation.

In Batchelder and Miller (1989), egg production was a function of a mean and variable clutch size, with clutches produced at regular intervals, determined by field observations of egg-laying; egg production was independent of food concentration and individual assimilation. Here, fecundity was implemented differently, and was dynamically dependent on assimilation by the adult females. Transition from C₅ copepodites to adults was set at a body weight of 30 μg C and maximum adult female weight was assumed to be 60 μg C. Upon molting to the adult female, a fraction of the assimilated matter was directed toward the production of eggs, and the remaining fraction towards increasing structural (non-reproductive) weight. The fraction directed to reproduction increased linearly with body weight between the minimum and maximum female weights (see Table 2). An egg conversion efficiency of 0.25 was used to convert assimilated matter into reproductive tissue. If structural weight fell below 30 μg C, then reproductive weight, if available, is converted with 100% efficiency to structural weight. This makes the assumption that a minimum structural weight is maintained if possible, at the risk of reducing fecundity. When sufficient reproductive weight (at least 3.5 gC) had accumulated, a clutch of eggs, each of 0.1 μg C, would be released. Clutches of eggs were only released between the hours of 0100 and 0300 local, when the female (if undertaking DVM) is presumably in the upper mixed layer. Initial positions of newly produced eggs were identical to the position of the mother at the moment of laying. Nearshore retention of young stages is minimized by releasing eggs near the surface where flows are predominantly offshore. Retention nearshore would be enhanced by
releasing eggs at deeper depths or throughout the water column (not done). Within the IBM, a number of properties intrinsic to the individual were tracked and were represented by a state-vector (Table 3).

### 2.4. Diel vertical migration

In nature, vertical migration in copepods could be controlled by a number of factors, both in the environment and specific to the individual. Light is the primary cue for vertical migration. For the IBM simulations, diel variability in light intensity at the surface was modeled using the Eqs. given by Brock (1981), correcting for the fraction (0.38; Kirk, 1994) of total irradiance within 400–700 nm, and an assumed atmospheric attenuation of 0.5. This provided noon above-surface light levels of ca. 198 to 235 W m$^{-2}$ for April to July, at a latitude of 45°N. Light at depth was calculated by assuming an attenuation coefficient of 0.05 m$^{-1}$.

We explored a number of DVM scenarios that included biological processes. Our intent was not to model the causes of DVM, but rather to look at possible demographic and distributional effects. Consequently, our null model assumed no DVM with animal position determined by advection and diffusion only. Second, we considered a scenario in which vertical migration was determined by a maximum vertical swimming speed modified by: Ambient light intensity (LTSS); Individual size (SZSS; Huntley & Brooks, 1982); Ambient food concentration (FDSS; Harris, 1988); and An individual’s hunger condition (HFSS).

Food availability and an individual’s hunger are thought to influence both the occurrence of DVM and its amplitude (Dagg, 1985; Huntley & Brooks, 1982). We do not model depth-dependent predation, which may be a primary contributing cause to DVM (e.g. Ohman, Frost, & Cohen, 1983), because of insufficient data to parameterize predation intensity in time and space in upwelling systems. We include functions related to proximity to the bottom (NBSS) and surface (NBSS) to prevent individuals from exiting the water column. Finally, we calculate a size-dependent probability of migration (POM), with smaller organisms less likely to move vertically in response to intrinsic and extrinsic cues than larger individuals. Each of these functions is shown in Fig. 3. Thus, swimming speed (m day$^{-1}$) was calculated as:

$$SS = D \times MXSS \times POM \times HFSS \times LTSS \times FDSS \times NSSS \times NBSS \times SZSS \times DRSS$$

where direction, $D$, is 1 for upward migration and $-1$ for downward migration, DRSS is 1 for downward

---

**Table 3**

Components of state-vectors tracked on an individual-by-time or individual basis

<table>
<thead>
<tr>
<th>Individual-by-Time basis:</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>weight ($\mu$g C)</td>
<td></td>
</tr>
<tr>
<td>time of most recent reproduction (day)</td>
<td></td>
</tr>
<tr>
<td>time attained present stage (last molt)</td>
<td></td>
</tr>
<tr>
<td>position (depth (m), distance offshore (km), distance alongshore (km))</td>
<td></td>
</tr>
<tr>
<td>hunger condition (non-dimensional)</td>
<td></td>
</tr>
<tr>
<td>most recent food concentration ($\mu$g C liter$^{-1}$)</td>
<td></td>
</tr>
<tr>
<td>most recent temperature (°C)</td>
<td></td>
</tr>
<tr>
<td>present life stage</td>
<td></td>
</tr>
<tr>
<td>reproductive weight ($\mu$g C)</td>
<td></td>
</tr>
<tr>
<td>individual’s ID</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Individual basis:</th>
<th></th>
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<tbody>
<tr>
<td>birthdate (day)</td>
<td></td>
</tr>
<tr>
<td>deathdate (day)</td>
<td></td>
</tr>
<tr>
<td>cause of death (starvation, predation)</td>
<td></td>
</tr>
<tr>
<td>preferred daytime isolume (W m$^{-2}$)</td>
<td></td>
</tr>
<tr>
<td>sex</td>
<td></td>
</tr>
<tr>
<td>mother’s ID</td>
<td></td>
</tr>
</tbody>
</table>
Fig. 3. Seven factors that could potentially affect maximum vertical swimming speed. Maximum swimming speeds were defined for both upward and downward swimming. Actual swimming speed of an individual was affected by multipliers ranging from 0–1 for a) size (SZSS), b) light effects (LTSS), c) food concentration (FDSS), d) individual hunger (HFSS), e) proximity to the surface (NSSS; solid line) and bottom (NBSS; dashed line), and f) propensity to respond to migration cue.

migration and 2 for up-migration (a directional bias in maximum swimming speed), MXSS is the maximum sustained swimming speed (35 mm s\(^{-1}\)), and the other variables are as shown in Fig. 3. MXSS is only slightly higher than sustained swimming speeds reported for copepods and other large zooplankters (Enright, 1977), but is substantially greater than maximum speeds for *Metridia pacifica* in controlled laboratory conditions (Wong, 1988). However, because of the modifiers shown in Fig. 3, maximum swimming speed is rarely achieved in the model. The vertical swimming velocity was incorporated into the particle-tracking algorithm as an additional advective velocity (discussed below).

For simplicity, individual organisms were assumed to migrate by isolume tracking. At each time step, ambient light intensity at the organism’s depth was compared to its preferred isolume level, and the difference was used to provide a direction and speed of migration, relative to a weight-dependent maximum vertical swimming speed. This basic DVM pattern was modified in some simulations by including effects
of an individual’s hunger condition and ambient food concentration, which might inhibit either downward migration or upward migration, respectively. For all of the simulations presented, the preferred isolume for all individuals was identical and set to a value of 0.04 W m⁻². For the period of the year simulated, this provides a preferred daytime depth of ca. 160 m. During the night, this isolume is above the surface, so individuals were assumed to migrate only as shallow as 10 m, from which they were displaced by diffusion. As will be discussed shortly, we randomly seeded the modeled domain with organisms. Fig. 4 shows depth and growth trajectories for immatures, males and females from one-dimensional simulations for three starting depths and vertically uniform food concentrations of 1 and 4 µmole N l⁻¹. With the functions used here, substantial vertical migration does not occur until individual’s weights equal 8–10 µg C (C₄ copepodite), and even then the amplitude of migration is quite small. Displacements of smaller individuals occur through advection and diffusion only. At a body weight of 20 µg C, individuals undergo a DVM with an amplitude of ca. 50 m. At a weight of 40 µg C (adults), the individuals are able to migrate the full amplitude between their preferred daytime (160 m) and nighttime (10 m) depths. Individuals of ca. 20 µg C, which are incapable of their full migrational amplitude tended to move towards a mid-depth (60–70 m) compromise between their preferred daytime and nighttime depths. Adult females are larger than adult males, but have similar migration amplitudes.

2.5. Particle-tracking

Simulation of the movement of individual particles in a dynamic environment is an important tool for investigating ecological processes in the ocean (Miller, Lynch, Carlotti, Gentleman & Lewis, 1998; Werner et al., 1993; Bryant, Hainbucher & Heath, 1998; Heath, Zenitani, Watanabe, Kimura & Ishida, 1998; Hare et al., 1999). However, the motion of Lagrangian drifters driven by Eulerian fields is inherently inexact because of a loss of information when interpolating velocities from gridded physical fields. Careful attention must be directed towards conservation of local concentrations, e.g. local aggregations or depletions should not occur as a result of physical processes of advection and diffusion alone. Diffusion in individual particle models is often modeled as a random walk (Csanady, 1973). A random walk model for vertical position including advection is defined by:

\[ Z_n = Z_{n-1} + W\Delta t + \zeta_n\sqrt{2K_z\Delta t} \]

where \( Z_{n-1} \) and \( Z_n \) are the initial and final depths, respectively. \( W \) is the vertical velocity (advection), and the final term is a random walk where \( K_z \) is the vertical diffusivity, \( \zeta_n \) is a random normal variate with zero mean and unit variance, and \( \Delta t \) is the time step. An analogous Eq. is used for updating position in the offshore direction.

However, when turbulent diffusion varies spatially, as it does in nature and in the physical model, simple random walk models accumulate particles in regions of low diffusivity (Hunter, Craig, & Phillips, 1993; Visser, 1997). Hunter et al., 1993 derive a ‘corrected’ random walk model considering the probability and moment statistics for linearly-varying turbulent diffusion (Thomson, 1984; Okubo, 1986). Implementing this correction yields the following Eqs. for implementing a random walk in our model, where the time-step is split into an advective step and a diffusive step:

\[ Z^0 = Z_{n-1} + (W + W_s)\Delta t \quad \text{advection–migration step} \]

\[ Z^* = Z^0 + K_z(Z^0)\Delta t \]

\[ Z_n = Z^* + \zeta_n\sqrt{2K_z\left(\frac{1}{2}(Z^* + Z^0)\right)}\Delta t \quad \text{dispersion step} \]
where all quantities are defined as before, but $K'_z$ is the gradient in the vertical diffusivity at the initial location, and the vertical velocity also includes a biological component, $W_s$, which is the swimming vertical migration velocity. Visser (1997) presented several 1D examples illustrating the benefits of using the corrected random walk model in relation to the ‘naive’ random walk model, and provides a criterion for selecting a time-step for implementing the random walk. We followed their method for simulating turbulent
diffusion in a Lagrangian model, using stored snapshots of spatially dependent vertical diffusivity from the physical model. Horizontal diffusivity was uniform in the offshore direction. A fourth-order Runge–Kutta integration was used to update particle positions by advection and swimming migration, and a ‘diffusive’ random walk included after the advection step.

Using the coupled physical-NPZ model, phytoplankton concentration, temperature, velocities and diffusivities were estimated at a point corresponding to a particle’s location within the 2D domain by bilinear interpolation for each of the two snapshots that bracketed the current time. After interpolation in space, we interpolated linearly in time. Because variability of less than a day was neglected in the forcing of the coupled biophysical (circulation-NPZ) model (e.g. no diurnal light pattern, no high frequency variation in wind forcing), we were able to interpolate from daily snapshots of the physical and ecosystem fields averaged over an inertial period. For interpolation, we doubled the grid resolution, and extrapolated fields that were not specified on boundaries of the staggered grid of the physical-ecosystem model to the boundaries of the high-resolution grid. We evaluated the fidelity of the particle-tracking model by tracking passive particles randomly seeded in the domain. If the particle-tracking model for Lagrangian particles in Eulerian fields is unbiased, then randomly distributed particles, subject to diffusion and advection only, should remain randomly distributed; physical processes alone should not result in local particle accumulations or depletions.

3. Results

3.1. Physical fields and ecosystem conditions

Physical fields and ecosystem state variable concentrations for several times are shown in Fig. 5. The physical model captures many features that are documented in the nearshore circulation and structure of coastal upwelling systems (Huyer, 1976; Peterson, Miller, & Hutchinson, 1979; Small & Menzies, 1981). Day 10 of the simulation represents the end of a 10-day period of southward wind stress of 0.05 N m$^{-2}$, and the physics and ecosystem show clear upwelling related responses. The streamfunction shows offshore flow in the surface mixed layer and onshore flow along the bottom topography. Isotherms trend upward near the coast, surface nutrient concentrations are highest nearest shore in the cold upwelled water, and there is a substantial bloom of phytoplankton at 3–10 km from shore, with peak concentrations of ca. 15 $\mu$ mole N l$^{-1}$. This exceeds particulate N concentrations in the peak as reported by Small and Menzies (1981; ca. 5 $\mu$ mole N l$^{-1}$), but is similar to phytoplankton concentrations during active upwelling reported by Peterson et al., 1979. Moreover, the distance offshore of peak phytoplankton in the model is nearly coincident with observations (Peterson, Miller & Hutchinson, 1979; Small & Menzies, 1981). Peak zooplankton biomass (ca. 4 $\mu$ mole N l$^{-1}$) occurs just offshore (‘downstream’) of the surface phytoplankton maximum. In addition, there is a subsurface zooplankton maximum further offshore associated with the initial depth-dependent steady state conditions (Edwards et al., 2000). The 9°C isotherm intersects the surface approximately 9 km offshore, and the surface layer is well mixed. Following this snapshot, a wind relaxation event lasting 10 days begins. Day 20 shows the response of the system to the relaxation. Velocities are much reduced without wind forcing (note change in scale). There is no substantial onshore flow after wind cessation because the temperature field is in thermal wind balance with an alongshore current (not shown). However, there is a strong response by the phytoplankton. While there was little phytoplankton inshore of 3 km during active upwelling, at day 20, phytoplankton concentrations of ca. 15 $\mu$ mole N l$^{-1}$ extend through much of the region from the coast to ca. 7 km. The relaxation event affords the opportunity for the phytoplankton to respond to the high nutrient concentrations inshore, without being advected offshore. Concurrently, surface nutrients are depleted nearshore. By day 30, the end of a second 10 days of upwelling favorable winds, the phytoplankton bloom extends from the coast to 12 km offshore. Zooplankton
Fig. 5. Physical fields (streamfunction and temperature) and ecosystem state variables (dissolved nitrogen, phytoplankton biomass, and zooplankton biomass) for day 10, 20, 30, and 80 of the coupled biophysical ecosystem model. Days 10 and 30 are at the end of a 10 day period of upwelling. Days 20 and 80 are at the end of 10 days of no wind (relaxation period). Note the changes in the color scale bars for the different days of the simulation.
concentration is highest ca. 15 km from shore, and the maximum is quite broad, although peak concentrations remain relatively low (ca. 4–5 µmole N l\(^{-1}\)). Finally, day 80 documents conditions after four complete cycles of alternating upwelling favorable winds and periods of no forcing. The water inshore is cold, the 9°C isotherm at the surface is pushed off the shelf (>40 km from shore), and phytoplankton concentrations are high from the coast out to 15 km. Zooplankton from the NPZ model are much higher (~12 µmole N l\(^{-1}\)) at the offshore maximum than at day 30. It is significant that phytoplankton concentrations offshore (beyond 20 km from the coast) in these simulations are still high, ca. 4–5 µmole N l\(^{-1}\). This is substantially higher than observations offshore of the upwelling center off Oregon, where phytoplankton concentrations are more on the order of 1–2 µmole N l\(^{-1}\) (Hill & Wheeler, 2002, this issue).

### 3.2. Individual based simulations

First, we discuss particle-tracking simulations in which the only processes are advection and diffusion (NO BIOLOGY CASE). For most biological simulations we randomly seeded the initial domain, exclusive of the offshore relaxation region beyond 80 km from shore, with 5000 particles, each a female with identical properties (except location). However, to evaluate the fidelity of the particle-tracking routine, we seeded the region with 100,000 particles, and subjected them to advection and diffusion only. Fig. 6 shows particle density distributions for three snapshots of the ‘non-biological’ simulation. Particles were binned into 1 km by 1 m bins for contouring, and bins along the topography were corrected for the fraction in the bottom. Using the random walk model described above we observed that particle distributions for day 10 and 25 were nearly identical to those at the start. With a timestep of 120 s in the particle-tracking model the problem of non-uniform \(K_z\) was greatly minimized, but not eliminated entirely, as the few aggregations and depletions along the bottom topography indicate. However, the residual biases (aggregations) resulting from numerical inaccuracies in interpolating advection and implementing the random walk are completely overwhelmed by the robust biophysical interactions discussed later. We consider the particle-tracking algorithm adequate for subsequent simulations that include biological processes as well as advection and diffusion. Mean offshore displacement velocity of particles seeded into the region shallower than 10 m and within 20 km of shore was 1.85 km day\(^{-1}\) during the active upwelling of days 1–10. Subsequent upwelling events yielded lower offshore velocities, generally ca. 0.6–0.8 km day\(^{-1}\), but this was because of deepening of the mixed layer in successive upwelling events. Zonal offshore transport integrated over the depth of the mixed layer should be constant among upwelling events of identical duration and intensity. During wind relaxations, there was little zonal displacement of particles, with slight offshore displacements of 0.07–0.1 km day\(^{-1}\).

Our primary interest was to explore the interaction of diel vertical migration (DVM) by individuals with the vertically sheared nearshore flow fields typical of an idealized coastal upwelling system. Using the flow and ecosystem fields from the model described above, we simulated a population of zooplankton that did not migrate (BIOLOGY/NO DVM CASE) on a diel basis. We considered 5000 randomly located immature \(C_4\) females each with a weight of 10 µg C (Fig. 1). We assumed that growth and development were externally controlled by food resources only (i.e. phytoplankton from the NPZ model), that reproduction was also a function of food resources, and that mortality was stage dependent. Movement occurred through advection and diffusion only. Individuals responded to extended periods without food resources by ramping maximum ingestion rates upward (Batchelder & Williams, 1995; Runge, 1980). We tracked individuals for 118 days or until they died. Egg laying by adult females created new individuals, which were subsequently tracked individually. Fig. 7 shows snapshots of the distribution and sizes of individuals after 20, 40, and 80 days of simulation. After 20 days, individuals starting in the surface 60 m have experienced positive growth, reflecting the higher food concentrations there. Below 50–60 m, there has been no primary production, there is no phytoplankton, and the copepods are slowly diminishing in size because of metabolic losses (starvation). First reproduction occurs by several inshore individuals on day...
Fig. 6. NO-BIOLOGY Simulation. Contoured particle density after 0.1 days (essentially, the initial distribution; top panel), 10 days (middle panel), and 25 days (bottom panel) for non-biological passively advected and diffused particles. 100,000 particles were randomly seeded into the domain. Contouring was done by binning into 1 m vertical and 1 km horizontal bins. Forcing was upwelling favorable winds for days 0–10 and 20–30, and no wind for days 10–20.
Fig. 7. NO-DVM Simulation. Copepod distributions from the IBM at 20 days (top panel), 40 days (middle panel), and 80 days (bottom panel) for a simulation in which the copepods do not undergo diel vertical migration. Size of the bubble is related to the weight of the individual.

19 and is evident in day 20 as the clusters of small individuals at different depths at 5–15 km offshore. This is the region of highest food concentration and therefore the region most favorable for copepod growth and eventual reproduction. Individuals in adjacent surface waters are lagging in growth and development, but will produce young shortly. By day 25, most of the deepest offshore individuals have declined below their starvation threshold and have died. Reproduction occurs extensively in the surface layer, both nearshore and offshore. By day 40, the population consists of some of the original females and many small offspring. There are relatively few copepods within 7–8 km of the coast, in the center of the upwelling region. Nearshore, upwelling is bringing deeper water devoid of individuals (after the initial individuals have died through starvation) to the surface and displacing surface waters containing many copepods, offshore. By day 80, the nearshore surface region with few copepods extends further offshore, to about 12 km. Overall, copepod densities are quite high offshore. Inshore there are a few offspring from two clutches laid by females on day 75. The females later died. From this time until the end of the simulation (day 119), a few large adults were retained inshore of 10 km and were continuing to produce clutches of offspring. However, population densities inshore of 15–20 km remained substantially lower than further offshore. Comparing the plot of zooplankton abundance from the IBM with contours of zooplankton abundance from the Z component of the NPZ model (Fig. 5) is revealing. In both of these, the zooplankton are passive, but non-conservative tracers, and despite the large differences in the model formulations—concentration based NPZ versus the IBM—the patterns of the distributions through time are similar. This is convincing evidence that the IBM populations are responding appropriately to the spatially dependent transports and food resources.
A simulation with individuals capable of DVM (BIOLOGY/DVM CASE) is shown in Fig. 8. Conditions for this simulation were identical to those of the earlier simulation (Fig. 7), except that vertical movement of the individuals was also influenced by active migration, itself a function of environmental (food concentration) and intrinsic factors (body size, hunger) described earlier. By day 20, several notable changes have occurred. Firstly, the largest individuals, which are experiencing the greatest growth, occur over the shelf, and in particular inshore of about 12 km where food is most concentrated (Fig. 5). Further offshore, most of the individuals are actually not in the surface mixed layer, but rather layered along the lower border of the region of highest phytoplankton concentration. This results from having upward swimming speed that is a function of available food. If food is available at depth, the copepods do not migrate all the way to the surface for food, instead consuming the deeper food resources. Second, there are no individuals in the upper 40 m offshore, and a few small ones only deeper than ca. 60 m; in fact, all of the largest individuals offshore are clustered at depths of 50–60 m. Recall, that the size of the individuals at the start of the simulation was 10 µg C. As Fig. 4 shows, individuals of this weight have a limited ability to migrate vertically; those that grow a little initially, respond by moving toward a depth that balances their upward migrational tendencies at night and their daytime descents. Individuals below the mixed layer, where there is no food, decrease in weight, and lose any migrational ability they had, and eventually experience starvation mortality. By day 20 there has been no reproduction. The first production of eggs by an adult female occurs in the early morning hours of day 21, and substantial reproduction occurs during days 22–26, all of it by females located inshore in the region of the phytoplankton maximum. By day 40, most of the individuals present inshore are offspring from the original individuals. Some of the original females are

Fig. 8. DVM Simulation. Copepod distributions from the IBM at 20 days (top panel), 40 days (middle panel), and 80 days (bottom panel) for a simulation in which the copepods undergo diel vertical migration, where migration speed is dependent on light, food concentration, and individual’s weight and hunger. Size of the bubble is related to the weight of the individual.
still present but are obscured by the clouds of smaller individuals in the bubbleplot. The small offspring cannot DVM, so are advected offshore and dispersed from their mothers. There are many fewer individuals offshore of 30 km than in the no-DVM case and these are mostly aligned with the base of the high phytoplankton region. A few individuals are located between 10–30 km offshore, and these are migrating to near-surface depths in this region, where the food resources are relatively low. At day 80, most of the population is inshore of 15 km. Several days earlier, a female located ca. 30 km offshore produced a clutch of eggs, evident as the small copepods beyond 35 km from shore. All of the individuals that previously were clustered at 50–60 m depth offshore have disappeared. The contrast of these results with those of the earlier simulation in which the copepods do not migrate is marked. Here, after 80 days, the copepods are basically restricted to the region inshore of 15 km, whereas in the absence of migration, although some copepods are found nearshore, the bulk of the population is over 15–20 km from shore. Clearly, DVM capability has had a profound impact on the distributions of the organisms in a periodically varying upwelling regime. The mechanism is clear. When an individual is capable of DVM, its daytime descent takes it to depths, where during active upwelling there is onshore flow, or at least diminished offshore flow. This counteracts, or at least minimizes their residence in the relatively rapid offshore flow near the surface during upwelling, and provides a mechanism for nearshore retention. Our results depend on the assumption, modeled here, that the amplitude of vertical migration places individuals into the bottom boundary layer, in which there is onshore flow.

An unexpected result of our comparison of the no-DVM with the DVM case was that population abundances are higher overall in the non-migrating simulation than in the migrating simulation. We anticipated that the nearshore retention of individuals in the DVM scenario would provide copepods higher food concentrations, which would be reflected in larger population sizes than in the non-DVM scenario. The details of the specific model formulation and the forcing fields are responsible for this result. First, there was no predation penalty for remaining near-surface all the time, although there was substantial growth benefit in remaining shallow. Second, the coupled NPZ/physical model yields phytoplankton concentrations offshore that are substantially higher (ca. 4–6X) than those observed in nature. Thus, the model provides a smaller cross-shelf gradient in surface food concentrations than observations suggest. We examined the impact of the unrealistically high food concentrations offshore on a non-migrating copepod by repeating the non-migratory simulation, but with food concentrations reduced by a factor of 4 at all distances >20 km from shore. The decrease in food reduces the number of copepods offshore, but the general pattern of higher numbers offshore remains (Fig. 9).

We examined these spatial patterns further by identifying the individual females that produced young and their cumulative egg production during the course of the simulations. Because mortality and the random walk are stochastic (see Table 2), there is some patchiness in the initial distribution of the females that successfully matured and reproduced in these simulations (Fig. 10). However, there are still clearly interpretable patterns in the distributions of reproducing females from the various simulations. In the simulation in which the individuals undergo DVM, only a few of the females (1.1% = 55/5000) present initially produced offspring. Most of those producing offspring were initially located on the inner and middle shelf (Fig. 10a). The maximum number of eggs produced by a female was 356, which represents the cumulative eggs from 10 discretely laid clutches, but the majority of females producing eggs managed only a single clutch. Fig. 10b shows the initial position of the females (6.2%) that produced offspring in the non-migrating simulation. Most reproduction was by females in the surface mixed layer, but offshore, with highest egg production from females initially 15–35 km offshore. There was significantly higher egg production and a greater number of females producing eggs when DVM was absent. This resulted from non-migrating individuals located near-surface experiencing continuously high food resources, which promoted rapid growth and higher reproduction. Fig. 10c shows the effect of reduced offshore food concentrations on the number of females producing young. The patterns of the total population and initial distribution of reproducing females suggests that there is a region at midshelf (10–30 km from shore) where food concentration
is high enough to support growth and reproduction, but where offshore transport in the intermittent upwelling was slow enough to allow growth and reproduction to occur. Moreover, a few copepods further offshore successfully grow and reproduce as well. In the present model runs, mortality was not spatially-dependent, so there was no negative tradeoff of being near-surface all the time. If we had imposed higher mortality rates to individuals experiencing high light levels (shallow individuals during daylight periods), we expect that overall densities in the non-migrating populations would be lower than migrating populations. This is a subject of future modeling investigations.

4. Discussion

Coastal upwelling zones have seasonally and spatially variable and abundant food resources (phytoplankton), which should be advantageous to zooplankton living there. However, they are also highly advective environments (Peterson, 1998). A problem for copepods or other zooplankton to surmount in coastal upwelling environments is how to avoid being advected into nutrient and food depleted regions offshore or extensive distances alongshore, perhaps into less habitable regions. Peterson refers to this as the ‘life-cycle closure’ problem. Using a model, we have investigate one mechanism, diel vertical migration, that might enable copepods to maintain a position nearshore, within the region of active upwelling and high food resources. Our results indicate that diel vertical migration interacting with a typical upwelling
circulation of offshore surface flow and onshore subsurface flow can result in nearshore retention of copepods within a region that is favorable for growth and reproduction. The idealized two-dimensional (x-z) model we employ cannot address the issue of alongshore transport and retention, which is likely controlled by complex interactions between dynamical flows, and varying alongshore coastline geometry and bathymetry.

The physical model we used displaces surface water offshore and upwells water on the inner shelf yielding a one-cell zonal circulation (Halpern, 1976; Allen, Newberger, & Federiuk, 1995). In that sense our model is consistent with recent observations off Newport using high-resolution undulating nearshore profilers that show that isotherms during periods of active upwelling slope upwards as far inshore as the 10 m isobath (Jay Austin, personal communication). Peterson, Miller and Hutchinson (1979), using cross-shelf patterns of zooplankton and chlorophyll, inferred a two-cell zonal circulation during active upwelling, or at least a region in the innermost 5–10 km in which the offshore flow near the surface was not strong. Our physical model, with the Newport, Oregon, topography and an innermost bottom depth of 30 m, exhibits neither a two-celled structure nor a non-advective inner shelf region. Even between models, some variability in alongshore and offshore transports within the inner shelf domain during active upwelling is expected, because of local variations in topography and forcing. Using different (shallower) topography our model produces a quiescent region inshore with little offshore transport—a feature, which has been observed in other upwelling models as well (Austin, 1998). It is possible that width and slope of the shelf are important in determining whether the upwelling circulation is one- or two-celled, with narrow continental shelves favoring a single celled pattern.

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**Fig. 10.** Starting positions of the females present initially that produced offspring for the simulations with DVM (top panel; Fig. 8), without DVM (middle panel; Fig. 7), and without DVM and reduced offshore food (bottom panel; Fig. 9). Size of the bubble indicates the number of offspring produced by the individual; note that the scale for the bubble varies by panel.
Peterson et al. (1979) documented the cross-shelf and depth distributions of many of the more abundant copepods in the Oregon upwelling system. Of the copepods they examined, only the older copepodites (C4–C6) of *Calanus marshallae* showed evidence of diel depth differences. Wroblewski (1982) using a simulation model and the distributional data from Peterson et al. (1979), examined the interaction of ontogenetic and diel vertical migration with circulation during an active upwelling event. Diel vertical migration of the adults within the innermost region was required to simulate accurately the offshore distributions of eggs, nauplii and immature copepodites. Without DVM, females were swept too far offshore, so that egg laying and subsequent development occurred further offshore than the observations of Peterson et al. (1979). Wroblewski (1982) used a two-cell circulation model, which included offshore flow at depth within waters descending below the pycnocline 10–20 km from shore. Consequently, DVM of adults in those regions accelerated offshore transport. We do not see that acceleration in our one-celled simulation. In our model, DVM, which removes individuals from the surface waters during upwelling, always enhances nearshore retention, since it is determined by the balance between time spent in and magnitude of offshore surface flow and time spent in the onshore deep flow and its magnitude. Wroblewski (1982) noted that within the nearshore zone, alongshore transport to the south was retarded by ca. 50% for migrating versus surface dwelling copepods. For reasons discussed earlier, we refrained from estimating alongshore transport from our 2D model.

Our results indicate that changes in depth distribution or diel vertical migration behavior with ontogeny is important in retaining individuals in nearshore regions of relatively high productivity. This result is consistent with observations on euphausiids from eastern boundary upwelling ecosystems. Cross-shelf and vertical distributions of euphausiids in the Benguela upwelling ecosystem suggested that an ontogenetic increase in vertical migration amplitude is important in maintaining populations nearshore (Pillar, Armstrong, & Hutchings, 1989). Eggs and nauplii of *Euphausia lucens* are nonmigratory, being mostly found in surface waters, calyptopes are weakly migratory, and furcilia stages are strongly migratory. During active upwelling, *E. lucens* eggs and nauplii are found offshore, calyptopes are midshelf, and furcilia stages nearshore. Because the older larvae occupy the surface layers less and migrate to greater depths during the day, they are subject to less offshore transport, and have a higher probability of remaining nearshore (Pillar, Armstrong & Hutchings, 1989). Juvenile and adult *E. lucens* were found to migrate to within a few meters of the bottom in inshore regions during the day (Pillar, 1982, cited by Pillar, Armstrong & Hutchings, 1989), which during periods of active upwelling would result in onshore transport. In the northern Benguela upwelling system, similar cross-shelf patterns of stage abundance are reported for another euphausiid, *Euphausia hanseni*, which also has a marked ontogenetic increase in DVM (Barange & Pillar, 1992). In this case, though, *E. hanseni*, is rarely found inshore of 65 km. A two-cell circulation is hypothesized to explain its distribution, with an inshore coastal upwelling cell, and a second offshore upwelling front at the shelf break (ca. 90 km from shore); *E. hanseni* is found exclusively in the latter region.

A significant advance of the present model, compared to previous coupled biophysical ocean ecosystem models (Hofmann, 1988; McCreary, Kohler, Hood, & Olson, 1996; Sarmiento et al., 1993), is the inclusion of detailed individual properties and processes (e.g. hunger condition, DVM behavior) of the target species in responding to physical forcing and the biotic environment. Nutrient and phytoplankton distributions are simulated in a coupled physical–ecosystem model and the resulting biophysical fields are used as external forcing for an individual-based biological model that includes transient effects, resource acclimation, and dynamically variable vertical migration behavior. These are factors that are known to be important to individual success and by extension to population dynamics. We focus on the interaction of DVM with transports, because it is likely that DVM is controlled both by extrinsic (light, food concentration) and intrinsic (individual weight, hunger) factors, which are not adequately included in Eulerian models, but where IBMs have proven value (Batchelder & Williams, 1995; various papers in DeAngelis & Gross, 1992). Spatially explicit food and velocity fields have significant impacts on growth and reproduction, on DVM behavior, and on retention nearshore and perhaps population persistence. Had mortality also been
spatially explicit (e.g. a function of light or depth), then differential survival of migrants versus nonmigrators would likely have been important in determining overall population abundance and distribution.

Particle-tracking has become widely used for examining the interactions between biological processes and physical transports in ocean ecosystems. Behavior, when it is included, is commonly a function of size or age of the individual, which is often externally prescribed, or at best expressed as a function of temperature. For example, a temperature-dependent growth model of *Euphausia superba*, coupled with 3D circulation fields, indicated the importance of surface transports and specific geographic regions of spawning to krill distributions in the Bransfield Strait region of the Antarctic Peninsula (Capella, Quetin, Hofmann, & Ross, 1992). Similarly, an IBM of *Calanus finmarchicus* in the Gulf of Maine/Georges Bank region describes spatially and temporally explicit temperature-dependent growth and development, but does not include the spatio-temporal variability of food concentration on copepod growth (Miller, Lynch, Carlotti, Gentleman & Lewis, 1998). Another typical example is the interaction of prescribed size-dependent DVM with mean advection to explore the retention of cod larvae on Georges Bank, where fish size was a function of age only and independent of the environmental conditions experienced (Werner et al., 1993).

Moisan, Hofmann and Haidvogel (1996) coupled a 3D physical model with an Eulerian ecosystem model for the California Current coastal transition zone. Their ecosystem model included many more state variables than the one we used. Simulated drifters used to track water parcels indicated downstream evolution of the ecosystem from a nearshore food web to an offshore low-nutrient and low food system, but no biological drifters with vital rates or behavior were tracked (Moisan & Hofmann, 1996). Hood, Wang, Purcell, Houde and Harding (1999) used particle-tracking to examine how surface currents transport plankton, and by assuming positively buoyant particles, to identify regions of convergence and divergence within an estuarine system, but no significant biology was included in the model.

Perhaps the most comprehensive and sophisticated coupling of individual behavior and circulation modelling are the publications resulting from the South Atlantic Bight Recruitment Experiment (SABRE) investigations of recruitment dynamics of Atlantic menhaden. SABRE investigators made extensive use of coupled biological–physical models, supported by field observations, to predict spawning locations, time of spawning, and trajectories of larval menhaden to southeastern US estuaries (Werner, Blanton, Quinlan, & Luettich, 1999; Forward et al., 1999; Hare et al., 1999; Rice et al., 1999; Stegmann, Quinlan, Werner, Blanton, & Berrien, 1999; Quinlan, Blanton, Miller, & Werner, 1999). Hare et al. (1999), for example, compared seasonal larval transports for two fish species having different diel behaviors and ontogenetic depth distributions, and found that the interaction of the preferred depth ranges and physical processes had important effects on net transport and success in arriving near estuary inlets, but also that the response was very sensitive to the exact wind forcing of the nearshore circulation. The SABRE results indicate the usefulness of coupled IBM-circulation models in determining the potential spawning sites and times of recruits, and the environmental conditions, which would favor eventual recruitment from known spawning sites and times. However, few of these previous particle-tracking studies have included details of how individual physiology impacts behavior in the biological model.

To our knowledge the model presented here is the first that a coupled ecosystem–physical model has been used to provide multidimensional (2D space and time) environmental conditions coupled with an individual based model of a specific target species that includes detailed physiological and behavioral processes. The results of our 2D model investigations show that for species in which the amplitude of DVM increases with size, encounters of naupliar and early copepodite stages with favorable, high concentration food resources enhances nearshore retention. Since the early life-stages have limited swimming ability, their growth is enhanced by having adult females produce eggs in near-surface regions of high food. This is true even though surface waters tend to move individuals offshore. Deep egg-laying places young in regions with little food, and the individuals, despite onshore transport, do not survive. Individuals that grow slowly are advected offshore in the surface flow; copepods that grow rapidly increase their DVM amplitude and increase their opportunity for nearshore retention. In fish ecology, rapid larval growth (larger
age-dependent weight) is assumed to confer survival advantages through improved efficiency of feeding and reduced susceptibility to predation (see discussion in Rothschild, 1986). Ontogenetic (size-related) changes in diel vertical migration in coastal upwelling systems may have similar effects; it enhances retention nearshore where food is high, and growth is rapid. Positive-feedback interactions of this type are difficult to model, and are not generally decipherable from Eulerian concentration models, but can be examined in IBMs.

Coastal upwelling regions often have vertically stratified cross-shelf flow (Brink, 1998). It is well known that in regions of vertically stratified flow, slight displacements in vertical position can have dramatic effects upon horizontal transport (Cronin, 1982; Epifanio, Valenti, & Pembroke, 1984; Hill, 1998), and models have shown how important this may be to recruitment to nursery grounds and population success (Rothlisberg, Church, & Forbes, 1983). Model trajectories of a vertically migrating ciliate within an actively upwelling coastal regime maintained ciliates over the shelf (Barber & Smith, 1981). Our upwelling circulation results are similar to an effect hypothesized for oyster larvae in two-layered estuarine circulations, where larval growth is extended when salinity, temperature or food concentration is low (Dekshenieks, Hofmann, Klinck, & Powell, 1996). Under those conditions, slow growing larvae are more likely to be flushed to unfavorable environments outside of the estuary. Our studies indicate that diel vertical migration in an upwelling system is a potentially effective mechanism for maintaining individuals nearshore and for population persistence in a region having favorable conditions for growth and reproduction. Moreover, physiological or behavioral plasticity of individuals, such as hunger responses or limiting surface migrations when food is available at depth, may further reduce time spent in offshore near-surface flows and enhance retention in relatively productive nearshore regions.

Future simulations of the coupled IBM-ecosystem-physical system will include: Surface heat fluxes and the effects of including temperature dependent metabolic processes on the population dynamics of the target species, explorations of how varying mortality as a function of distance from shore, depth, and light intensity, as well as different ontogenetic patterns, affects individual success and population persistence, the use of realistic time- and space-varying wind forcing, and the extension of the present two-dimensional simulations to three-dimensions with realistic coastal geometry and bathymetry.

Three-dimensional models will permit the exploration of how planktonic individuals and populations may persist in these highly alongshore advective coastal upwelling regimes. Three dimensional models are particularly interesting because they relax the assumption of 2D mass balance (e.g. that along any transect onshore and offshore flows balance), and so allow for more exact representation of transport in eastern boundary current upwelling systems.

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