Forward-in-Time-/Backward-in-Time-Trajectory (FITT/BITT) Modeling of Particles and Organisms in the Coastal Ocean*

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ABSTRACT

Lagrangian particle-tracking models (LPTMs) were used to identify sources, destinations, and transport pathways of particles (plankton). The LPTM simulations were forced using stored fields from the Spectral Element Ocean Model simulation for a coastal upwelling system having idealized geometry, bathymetry, and simple wind forcing. Forward-in-time-trajectory (FITT) simulations are common in ocean science, although they often do not include diffusion. Results from LPTM comparisons with and without diffusion suggest that ignoring diffusion can lead to incorrect identification of source or destination regions. FITT is efficient for identifying destinations from known sources, but inefficient for identifying sources from known destinations (or receptors). Backward-in-time-trajectory (BITT) modeling from known destinations efficiently identifies sources, or particle positions, at earlier times. Although advection and some biological processes (e.g., growth) are reversible and amenable to BITT simulations, other processes, such as physical diffusion, reproduction, and mortality, are not time reversible. The reliability of BITT-derived estimates of prior particle positions was evaluated using a BITT followed by a FITT coupled approach. The results suggest that BITT approaches are valuable in identifying probability densities of prior positions. Such information is particularly useful in the ocean sciences where many of the interesting questions concern where particles (e.g., plankton, meroplankton) have been (or came from) rather than where they are headed (identifying the destination). BITT simulations provide a computationally efficient technique to examine these questions.

1. Introduction

Lagrangian particle-tracking models (LPTMs) and individual-based models (IBMs) have been used within the oceanographic community during the past two decades to explore processes that influence the transport of eggs and developing larval stages of invertebrates and fish prior to settlement or attainment of sizes capable of countering strictly passive transport. Often these "model experiments" include only advection or advection combined with simple age- or size-dependent directed movement processes; dispersal processes are rarely considered (although for exceptions see Ådlandsvik and Sundby 1994; Heath et al. 1998; Miller et al. 1998; Ådlandsvik et al. 2004). A major reason is that

including diffusive processes, because of their stochasticity, requires an order of magnitude (or more) increase in the number of particles tracked. For advection alone, all particles from a specified starting location in space and time have identical trajectories, governed by the u, v, and w velocities from the model. Conversely, replicate particles from a given starting location whose motions are controlled both by advection and diffusion may have distinctly different trajectories and locations in the model (or real world) at a subsequent time.

In ocean science, LPTMs have proven most useful (and may be essential) when the particles are not strictly passive, especially when the particles have behavior like diel vertical migration (DVM) or ontogenetic vertical migration (OVM), which may be influenced by both extrinsic (light, food concentration) and intrinsic (such as an individual's size, condition, or nutritional status) factors (Batchelder et al. 2002). Concentration-based (Eulerian) models cannot usually handle the complexity introduced when particles at a given site in time are not identical in all respects.

Almost all LPTMs in ocean sciences to date have assumed that the spatial and temporal patterns of the

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particle sources are known (Proctor et al. 1998; Murphy et al. 1998; Miller et al. 1998). An example is where the spawning sites of eggs are known and it is desired to know their transport pathways under different atmospheric forcing scenarios, and to evaluate retention in suitable areas, transport to nursery grounds, or loss to unfavorable habitats. Such simulations have been valuable in providing guidance for marine protected area site evaluation and management of fisheries (Cowen et al. 2000, 2003). These simulations are referred to as forward-in-time-trajectory (FITT) simulations. They may include advection alone, advection and diffusion acting in concert, or more complex simulations, such as advection, diffusion, and reactions (ADR), where reactions refers to any nonpassive changes resulting from behavior, mortality, and reproduction. In the atmospheric sciences, models that include both advection and diffusion are commonly referred to as Lagrangian stochastic dispersion models (Flesch et al. 1995). An example of an ocean ADR FITT simulation is that of Batchelder et al. (2002) for copepods in an idealized upwelling system off the west coast of the United States. In those simulations mortality (a linear process) and reproduction (a nonlinear process), remove and introduce individuals from the model domain, respectively. FITT simulations work well and efficiently when the sources of particles are known.

However, FITT models are inefficient and computationally expensive for identifying the source of particles arriving to a particular known destination, such as a plankton net sample, a fishery region, a section of coastal habitat, or a single settlement plate. To identify the source location, you must seed everywhere (or at least on a finely resolved grid) "upstream" of the destination and identify the few particles that arrive at or near, or pass by the destination within the window of time of interest (Pepin et al. 2003). This inefficiency is illustrated with two published examples. Pedersen et al. (2001) used particle tracking and a hydrodynamic model to investigate the sources of *Calanus finmarchicus* that arrived to the Ocean Marine Exchange (OMEX) site off northern Norway during the first 2 weeks of July 1994 (Halvorsen and Tande 1999). They observed that only ~0.1% of the particles released 6 months earlier from presumed source sites contributed to the individuals that arrived at the destination during the specified time interval. Similarly, Hare et al. (1999) coupled a model of vertical migration to a hydrodynamic circulation model to explore the fate of larval menhaden and spot on the southeast coast of the United States. They considered only advection. Moreover, the imposed age-dependent migration model was time reversible. Growth was not environmentally con-
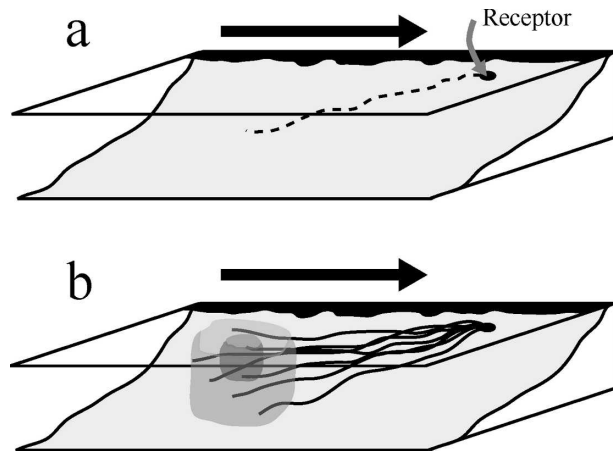

FIG. 1. Schematic of source region identification using BITT with (a) advection only and (b) with advection and vertical diffusion. Large arrow shows predominant direction of alongshore flow. At a given instant in time, a receptor in (a) has a single history (trajectory). With diffusive processes considered in (b), at a given instant in time, particles or water arriving at a single receptor have a suite of trajectories. Multiple replicate particles in BITT simulations can be used to derive probability densities of prior positions [shaded source regions in (b)].

trolled and there was no nonadvective mortality considered. Particles could have been tracked backward in time from the destination estuarine nurseries using stored velocities from the 3D model to identify sites and times of adult spawning that provided successful recruitment.

An alternative to FITT that may be useful in some, but not all, instances is to track particles backward in time from their destination to their source. This backward-in-time-trajectory (BITT) modeling can be seen in Fig. 1.

Backward-in-time Lagrangian modeling, including diffusion, has been less widely used in ocean science than in atmospheric fields, such as boundary layer meteorology (e.g., Flesch et al. 1995) and air quality monitoring (Lin et al. 2003; Seibert and Frank 2004), where the goal is to identify the source of a pollutant or to estimate substance emissions from multiple potential emission sites, when measurements are available from a relatively few receptors. The benefits of backward-mode modeling become most apparent when the number of receptors (destinations) is significantly fewer than the number of potential sources. The paper by Seibert and Frank (2004), where potential sources are determined from nearly continuous measurements at a fixed, finite number of receptors, is an especially nice review of the situations when backward-in-time simulations are desirable in atmospheric sciences, including for the potential application for monitoring violations of the Comprehensive Nuclear Test Ban Treaty. BITT

modeling could have provided significant computational advantages for Pedersen et al.'s (2001) investigation of the source sites of *Calanus finmarchicus* that passed through the OMEX study site off Norway. Because the Pedersen et al. (2001) model did not include diffusion, and because it had a time-reversible stage-structured population model, it could have been run as a BITT simulation starting with individuals at the destination, thus ensuring that 100% (rather than the 0.1% from the FITT simulation) of the computational effort provided locations of sources.

Physical oceanographer colleagues agree that advection-only FITT simulations are reversible (Da Costa and Blanke 2004). Strangely, this fact has been little used within ocean sciences, even in cases where the sources of recruits to a limited geographic region (e.g., Georges Bank) are desired. However, these colleagues argue that diffusion is an irreversible process that cannot be incorporated into backward-in-time simulations, and thus, BITT simulations that include both advection and diffusion are meaningless. This concern is expressed because diffusion in backward time is nonphysical, being negative diffusion, or "aggregation." I argue that even though advection–diffusion BITT simulations trace particles backward in time, they provide valuable information in the form of probability or likelihood maps of particular locations being sources. Note that "source" need not refer to the ultimate source, but may refer to spatial distributions of organisms at an earlier time. FITT simulations may be of particular value in ocean sciences where many of the questions asked about particles or organisms concern knowing where they came from, rather than where they are headed. Specific examples that will be asked in this paper are 1) where are the benthic adults that produced the meroplanktonic larvae that settled on a nearshore-moored collector, and 2) where were the plankton previously and what ocean conditions did they experience prior to their capture in a plankton net. This paper has two goals—first, to demonstrate the impact of neglecting diffusive processes in particle-tracking simulations, and how this can lead to incorrect conclusions; and second, to demonstrate the value of backward-in-time simulations in ocean science trajectory modeling, to describe the appropriate interpretation of BITT simulations, and to describe the situations when BITT may be advantageous over FITT simulations.

2. Methods

a. Physical circulation model

The use of BITT and FITT simulations is illustrated using a simple, idealized physical realization of a 3D upwelling ecosystem. The physical circulation model is the Spectral Element Ocean Model (SEOM), developed by Iskandarani et al. (2003), in which the primitive equations are solved in spectral form across quadrilateral elements of variable scales. The model is configured in a periodic meridional channel, 600 km × 900 km in scale. No flow boundary conditions are applied at the meridional walls. Horizontal resolution is roughly 1 km in the region where trajectories are examined, and vertical structure is resolved by 31 terrain-following levels. Simulations have been conducted for the following two simple geometries: 1) a Gaussian-shaped cape protruding 25 km from the eastern boundary with a 50-km meridional *e*-folding scale, and 2) a channel with straight coastlines but with a shallow (20 m) bank of the same horizontal scale as the cape in 1. For brevity, and to illustrate the main results, only the idealized bank geometry is presented. To facilitate spatial interpolation, the SEOM fields for this subregion were regridded to a rectangular coordinate system (500 grid points north–south, 70 grid points east–west, and 31 vertical levels). The presence of the bank changes the bottom slope quite far offshore, but most strongly in the region extending 30–50-km offshore (Fig. 2).

Density is considered a function of temperature only (salinity is not varied). The model is initialized at rest and with horizontally uniform stratification. Mixing is represented by the *K*-profile parameterization of Large et al. (1994). There was no bottom boundary layer in the model. The model is forced by an idealized upwelling-favorable surface stress of $\tau = -0.5$ dyne cm^{-2} on average and is sinusoidal in time with a 0.3 dyne cm^{-2} amplitude and 5-day period. Physical simulations were run for 30 days, with snapshots of the horizontal (u, v) and vertical (w) velocity, vertical diffusivity (K_v), and density fields stored at 12-h intervals for all 31 vertical levels.

b. Particle tracking—Advection, diffusion, and DVM

Simulating the movement of individual particles is an important tool for investigating ecological processes coupled with ocean transports (Hare et al. 1999; Hermann et al. 1996; Miller et al. 1998). The basic framework for tracking particles used here follows that described by Batchelder et al. (2002). Briefly, stored velocities (u, v, w) and vertical diffusivity (K_v) provided by the SEOM model were used to estimate the velocities and vertical diffusivity at a point corresponding to a particle's location within the 3D domain using trilinear interpolation for each of the two snapshots that bracketed the current time and linear interpolation in
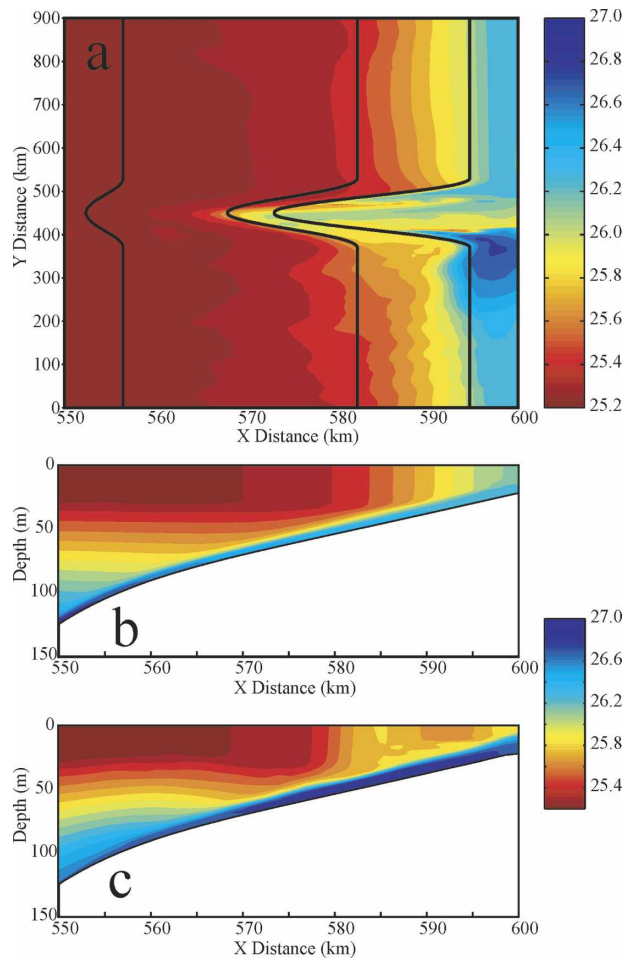
FIG. 2. (a) Sigma-*t* at 20-m depth on day 20 of the SEOM simulation. Note that the densest water (dark blue) has upwelled just south of the shelf bank. Vertical structure of sigma-*t* from two cross-shelf transects, (b) one located just north of the shelf bank and (c) one located just south of the bank. Dark blues are densest water, and reds are lightest water.

time. Horizontal diffusion was not considered in these simulations. Dispersion in the model was provided solely by vertical diffusion, modeled using a random walk with a 120-s time step. The random vertical displacement of a particle placed it at a different vertical level, and in regions of vertical current shear to different advection, resulting in "horizontal" dispersion.

BITT simulations are compared, which include only advection, advection plus vertical diffusion, advection plus DVM, and advection plus both vertical diffusion and DVM. For these simulations the robustness of the BITT simulation were not evaluated by coupling it to a FITT simulation as described later. The scenario of interest is one in which settling pelagic meroplankton (the dispersal stage of benthic adults) are sampled using settlement substrates suspended from a mooring lo-

cated close to shore (4 km) south of the bank, in water of ~22 m water depth Fig. 3). BITT simulations for varying periods (up to 14 days) were done, but only results from several simulations that assumed a 7-day pelagic duration are discussed. It is assumed for these simulations that a single collector (at 5-m depth) was in place for 48 h and then retrieved. Because there is no way of knowing when an individual organism settled on the collector during the 48 h, it is also assumed that settlement was uniform in time through the 2 days. Thus, replicate particles (number depending on simulation conditions) were released at 40 equally spaced times spanning the 2-day sampling interval. The BITT simulations could have included temperature-dependent pelagic durations of the meroplankton, but this complication is ignored here (although the method can accommodate such issues). The source adult populations must be nearshore (within 10 km of the coast), so the analysis focused on potential nearshore source populations.

c. Particle tracking—BITT and FITT comparisons

Coupled BITT–FITT simulations are used to evaluate the reliability of the BITT simulations that include vertical diffusion (Table 1). In each case the BITT simulation was implemented with both advection and vertical diffusion. DVM or other directed movements were not considered in these simulations. For most cases, 100 replicates of each initial particle condition were used to provide reasonable statistics. At the conclusion of the BITT simulation, the final location of each of the simulated particles (depending on simulation, the number of particles BITT simulated varied from 100 to 14 400) was used to initiate a FITT simulation with 100 particles for each location (simulations tracked from 10 000 to 1 440 000 particles). It is important to note that both the BITT and FITT simulations were subjected to vertical diffusion. The location of each particle following the roundtrip (R/T; BITT, then FITT) was compared with its known "destination" to evaluate whether the BITT simulation provided a reasonable estimate of the previous particle location. For all four cases described below backward trajectories provided estimates of positions 6 days prior to their arrival at the receptor (destination). Although the simulations were of a relatively short duration, they are illustrative of results that might be expected from longer, larger domain simulations. Evaluating longer-duration trajectory models was not possible because of the short duration (30 days) of the physical simulation, by the rather limited domain size, and by a desire to avoid the boundaries of the domain.
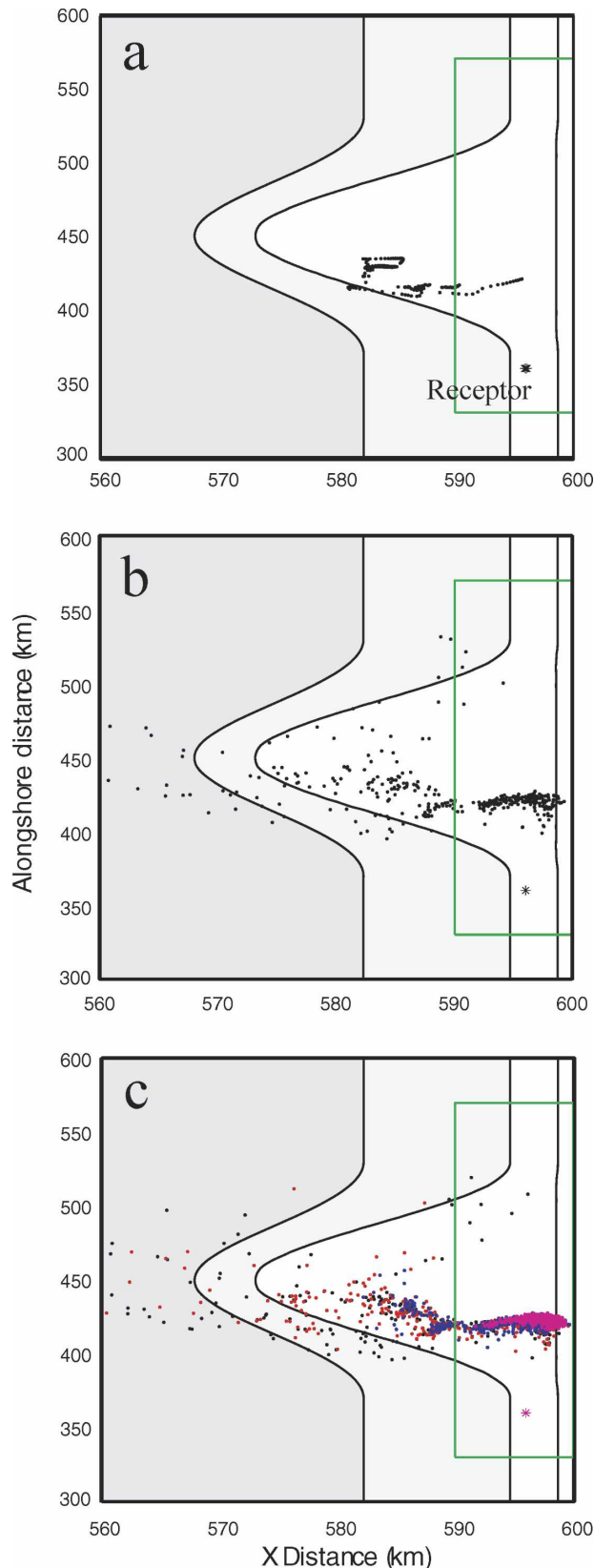
1) CASE 1

Case 1 simulated a scenario where a single collector was located 30 km off the coast. Ten replicate particles were initiated at each of 151 depths between the surface and 15 m (every 0.1 m) from a single release time. Results from this scenario revealed that multiple depth releases at a single x–y site were likely not needed, because the vertical random walk rapidly mixed (within ~3 h) the replicates vertically within the upper mixed layer (ML).

2) CASE 2

Case 2 was similar to case 1, except that the single collector was located only 4 km from shore and slightly south of the submarine bank (x_o = 596; y_o = 360]. The question for this scenario is "Where are the adult populations that produced the larvae that are collected at the destination (receptor) site?" It was assumed that the adult populations must be nearshore, with nearshore defined as being <10 km from the coast.

3) CASE 3

Case 3 was similar to case 2, except that 100 replicates from a cluster of nine nearshore stations arranged as a "+" sign were tracked in BITT mode. The goal of this simulation was to evaluate whether small changes in the "destination" release site impacted the interpretation of "source" regions. Because earlier (cases 1 and 2) simulations revealed that initial depth mattered little to the results, provided the particles were within the upper mixed layer, for case 3 all particles were released at a depth of 7.5 m.

4) CASE 4

Case 4 simulates a scenario where a gridded collection of samples has been made over a broad ocean region, such as might be done in a plankton sampling survey [e.g., California Cooperative Oceanic Fisheries

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FIG. 3. Results of BITT for transport scenarios that consider different processes: (a) advection only, (b) advection and vertical diffusion, (c) advection + vertical diffusion + DVM. Different colors in (c) indicate different-sized organisms, with purple being largest (capable of ~8 m vertical DVM) and black being smallest (totally passive). Asterisk is receptor location; dots are projected positions 7 days before arrival at receptor. Curved lines and shading offshore are bathymetric contours (coast is on the right). Green box indicates region within 10 km of the coast, considered "nearshore."

TABLE 1. BITT and FITT model scenarios to evaluate the robustness of BITT models for identifying prior particle or water locations.

| Case | BITT simulation | | | | FITT simulation | |
	Days simulated	No. of receptors	Replicates per location	Notes	No. of initial locations	Replicates per location
1	6	151 depths at 1 x, y locations	10	Offshore location	1510	100
2	6	151 depths at 1 x, y locations	10	Nearshore location	1510	100
3	6	1 depth at 9 x, y locations	100	Nearshore; fine spacing	900	100
4	6	1 depth at 144 x, y locations	100	Nearshore and offshore	14400	100

Investigations (CalCOFI)-like survey; e.g., Venrick et al. 2003]. Receptors were organized as a grid of 144 destinations (nine sampling transects equally spaced along 160 km of coastline, e.g., every 20 km; 16 sampling stations per 90-km transect, with finer station spacing nearshore). One hundred replicate particles were tracked backward-in-time from each "destination" sample location. The 14 400 particle locations after 6 days of BITT simulation were used to initialize a FITT run, with 100 replicates each (over 1.4 million individual particles tracked). The question is where was the plankton prior to collection in the survey.

3. Results

a. Physical circulation fields

Figure 2a shows water density at 20-m depth for day 20 of the simulation. The variable upwelling-favorable winds created prototypical coastal upwelling, as evidenced by the significantly more dense water nearshore throughout the full domain. Velocity fields (not shown) indicate the presence of a southward-flowing upwelling jet, and slight northward inshore flows downstream of the shelf bank. Highest density water occurs in a region inshore just south of the bank, where upwelling is most pronounced. Figures 2b,c shows cross sections of density for transects north and south of the bank, showing significantly more dense water on the shelf and isopycnals pushed farther offshore in the southern transect.

b. Particle tracking—Advection, diffusion, and DVM

The assumed observations from this system are the number of settling meroplankton larvae arriving at a fixed collector location over a 2-day period, obtained from suspended settlement substrates at several depths on a mooring. Because only individuals that arrive at the collector (receptor) are of interest, this is a problem with a single receptor and a nearly infinite number of potential sources. The "data" do not provide the actual arrival times, but provides the total number of larvae that settled during a prescribed window of time. Water and larvae that pass by the collector at different times during the sampling interval may have different histories and origins. The goal is to identify where the larvae were in the past, or, more specifically, the locations of the adult populations that produced the settlers. This is a situation where BITT simulations are much more efficient than FITT simulations, provided that the assumptions needed for BITT simulations are satisfied. The principal assumptions required are that the particles are passive tracers, or that any nonpassive movements (usually because of behavior, like DVM) are time reversible. In the first series of simulations an in situ sampler has "collected" continuously for 2 days. "Collect" here is when a device absorbs all larvae that are competent to settle when they occur within a short range of the device. If it is further assumed that the pelagic duration of the meroplankton is fixed, for example, for 7 days, then it can be asked, "Where are the adult populations that released the young that settled on the collectors?" BITT simulations were done for this case, and others (results not shown) that have more extended pelagic durations, or a window of competent settlement times, for example, varying pelagic duration. A first goal was to determine what fraction of the arriving meroplankton could have come (been spawned) from nearshore adult populations. The BITT simulation that transported larvae by advection alone (Fig. 3a) indicated that most of the larvae 7 days earlier were further offshore than the collection site, with only 9% of them from waters within 10 km of the coastline (Table 2). This indicates that with advection alone, most of the water that passes by the collector is from offshore—regions where there are no adult source populations. There was a substantial influence of the timing of larval release from the "destination" (results not shown) on the fraction of larval trajectories indicating nearshore sources. Presumably this temporal variability is related to interactions between the phasing of the 5-day wind cycle and the 7-day larval duration. Figure 3b shows the predicted 7-day-prior particle

TABLE 2. Percentage of individuals arriving at receptor location ($x = 596$; $y = 360$) that had sources within 10 km of shore 7 days prior for simulations where transport was solely by advection, by advection and vertical diffusion, by advection and weight-dependent DVM, and by advection, diffusion, and DVM combined (see Fig. 3).

Individual weight (μg)	Advection only	Advection and vertical diffusion	Advection and DVM	Advection, diffusion, and DVM
1.3	9.0	53.0	7.5	54
5.0	—	—	20	56
10	—	—	67	80
25	—	—	100	100

positions when the particles experience vertical diffusion as well as advection. There is greater horizontal dispersion than that from advection alone; significantly, the results indicate that a greater fraction, exceeding 50%, of the source sites may have been nearshore, and ~80 km north of the receptor. Results for simulations with advection and diel vertical migration, but without vertical diffusion, are summarized in Table 2. As the capacity to DVM increases with body size (from none for 1.3-μg individuals to 8 m from day to night for 25-μg individuals), there is a higher probability that the adult

source site is nearshore. Figure 3c shows results for four different-sized organisms that have different amplitude diel vertical migrations (plus advection and vertical diffusion). As Table 2 indicates, the results are consistent with expectations from the earlier simulations.

c. Particle tracking—BITT and FITT comparisons

1) CASE 1

Figure 4a shows particle locations for several earlier times from a BITT simulation that began at the asterisked location 30 km off the coast. Far from shore the flow patterns are reasonably coherent, with east–west (x coordinate) dispersal after 6 days of ~10 km, and most of this occurring between days 1 and 2 of the backward simulation (cf. distributions at days 26 and 25) as the flow interacts with the bathymetry of the submarine bank. Dispersal in the north–south (y coordinate) direction is ~32 km (range) or roughly 3 times larger than that of the east–west dispersal. This is expected because the horizontal shear of alongshore transports are significantly greater than cross-shore transports. Total alongshore transport in 6 days is ~300 km, or about 10 times the alongshore dispersal, and ~4 times the alongshore transport from the nearshore re-
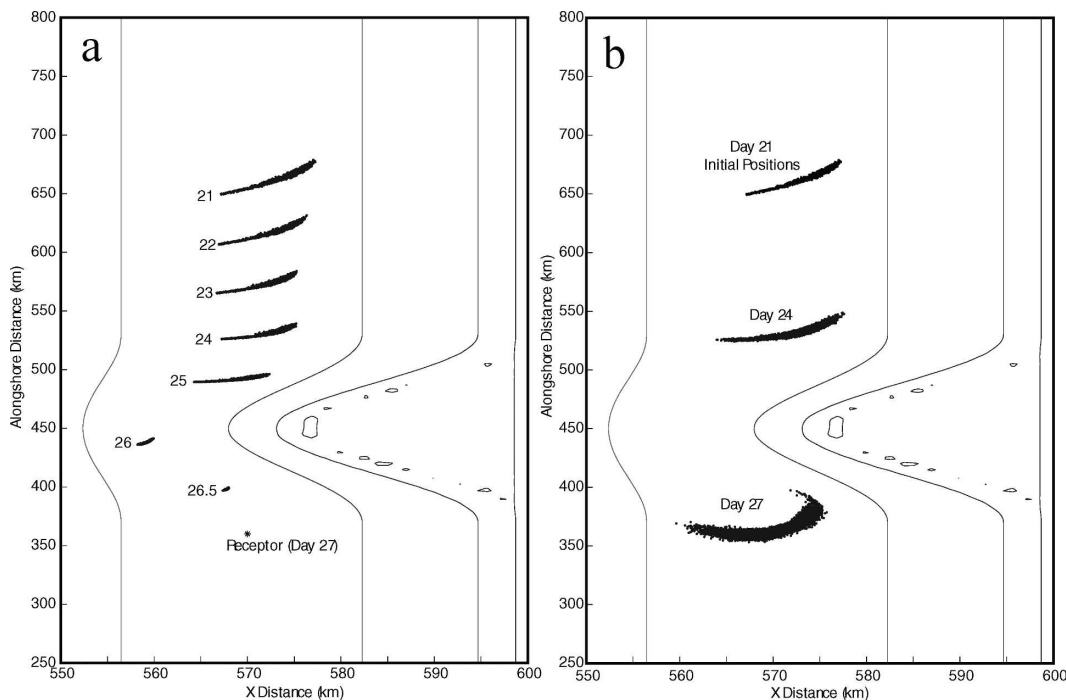

FIG. 4. (a) Case 1 BITT simulation: Predicted prior positions of particles that arrived on day 27 at receptor site (570, 360; asterisk) for times of 21, 22, 23, 24, 25, 26, and 26.5 days (north-to-south clusters, respectively). Thin lines are bathymetry contours. (b) Case 1 FITT simulation showing initial position of particles on day 21 and locations of particles on days 24 and 27 (southernmost). Thin lines are bathymetry contours.
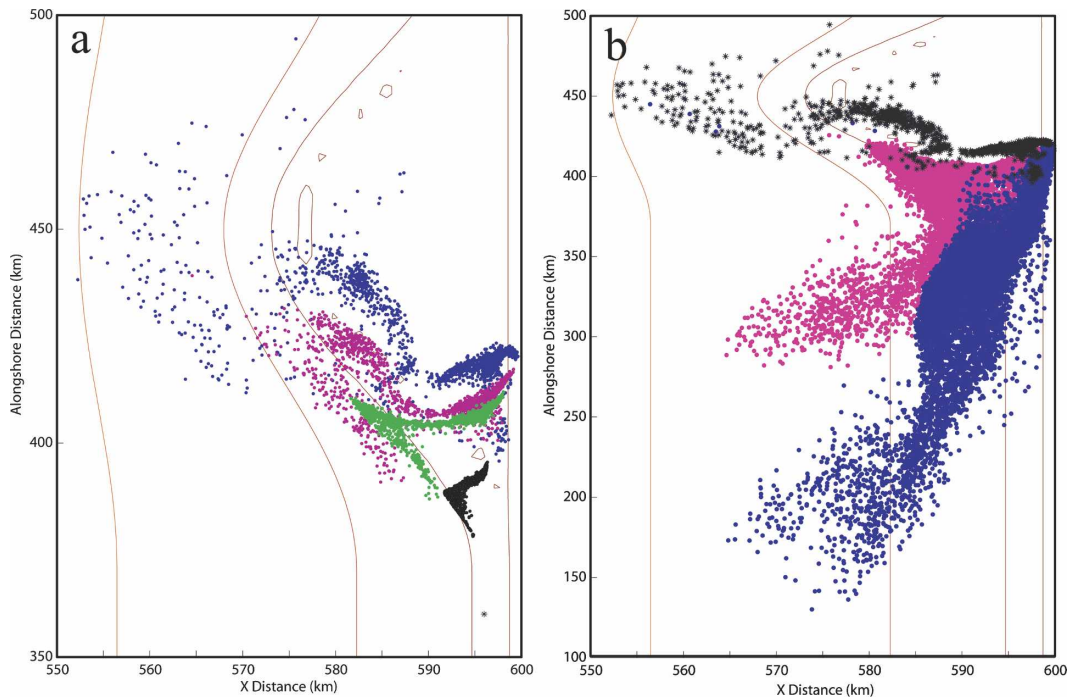
FIG. 5. (a) Case 2 BITT simulation: predicted prior particle positions for day 21 (blue), day 22.5 (magenta), day 24 (green), day 25.5 (black), and receptor location on day 27 (asterisk). Red lines are bathymetry contours. (b) Case 2 FITT simulation using final BITT locations [day 21, from (a)] as starting locations (asterisks). Shown are positions on day 24 (magenta) and day 27 (blue). Red lines are bathymetry contours. Note different scaling of y axis.

ceptor site (Fig. 3). Most of the particle locations on day 21 (after 6 days of BITT) are slightly inshore (<4 km) of the eventual destination (receptor), but a few particles, mostly those that went deeper, are offshore (by <5 km) of the eventual destination. Plots (not shown) of particle depths at times of 0.2 and 0.5 days indicate that the "memory" of the initial starting depth of the particles are lost through vertical diffusion within 0.2 days of the simulation start. The forward simulation results, with particles started at the positions of the particles after 6 days of BITT, are shown in Fig. 4b. After the roundtrip, which includes vertical diffusion in both directions, the mean particle position was (569.92, 363.02) compared to the expected receptor (and initial) position of (570, 360). The mean particle depth after the roundtrip was 16.5 m. The median (mean) vector displacement from the expected perfect return position after the roundtrip was 3.02 (4.49) km, mostly in the alongshore position. Only 25% of the particles were further than 5.3 km from the expected receptor after the full roundtrip transport of nearly 600 km. Thus, for this offshore case with rather coherent flow, the BITT and FITT comparisons suggest that backward trajectory tracking has significant value for projecting the likely positions of particles (or probability density functions) to earlier times.

2) CASE 2

Figure 5a shows the predicted particle locations for several earlier times from a BITT simulation that began nearshore (4 km off the coast). The results from this inshore simulation show less coherent flow than that in case 1. Most of the particles after 6 days of BITT are shallower than 12 m deep, but the remainder might be as deep as 120 m. The interaction of the generally southward (and upwelling) flow with the bank bathymetry has resulted in a more dispersed pattern of particles from the BITT simulation, especially because the receptor region was selected because it was within the region of maximum upwelling south of the bank (Fig. 2). This region experiences greater horizontal shear in alongshore flow and a greater possibility of cross-shelf flow because waters from further offshore and much deeper are advected into the nearshore zone. This should be the region where the BITT simulation might be expected to perform most poorly, and it does. To evaluate how poorly, the positions of the particles after a paired BITT–FITT roundtrip were compared to the known original destination. Figure 5b shows the locations of the particles after the roundtrip. The particles are widely dispersed in a southwest-to-northeast cluster that spans 300 km north–south and ~33 km east–west.

The mean R/T location is (593.1, 343.3), compared to the expected destination location of (596, 360), with a mean depth of 10.1 m. The modal R/T vector distance offset was 5.8 km (Fig. 6); 50% of the particles were within 20.2 km of their original release site, but the remainder were widely dispersed. To evaluate patterns and identify processes responsible for the discrepancies, the return fidelity (to known receptor) for each group of 100 replicates for each release site in the FITT simulation was compared to the median vector distance offset of 20.2 km (Fig. 7). The highest return fidelity (red dots in Fig. 7) occurred for particles that were shallow (<22 m) and nearshore (within 20 km of the coast), that is on the shelf, after BITT. The lowest return fidelity occurred for particles that during BITT escaped from the nearshore shelf waters to deeper, offshore waters, that is, particles that tracked the furthest offshore, deep upwelling water (only in reverse). The probability of those particles returning through the FITT simulation to the receptor location was very low; most of them during FITT were advected far to the south of their receptor. For identifying nearshore adult source populations, these deep, offshore locations should be neglected as potential source sites.

3) CASE 3

This case was done to evaluate the sensitivity of the BITT results to the initial starting (receptor) location. A destination region spanning 20 km alongshore and 4 km cross-shore around a central station ($x = 596$; $x = 360$) corresponding to the destination explored in case 2 was explored. Figure 8 shows the nine initial locations and the 900 particle locations after 6 days of BITT.
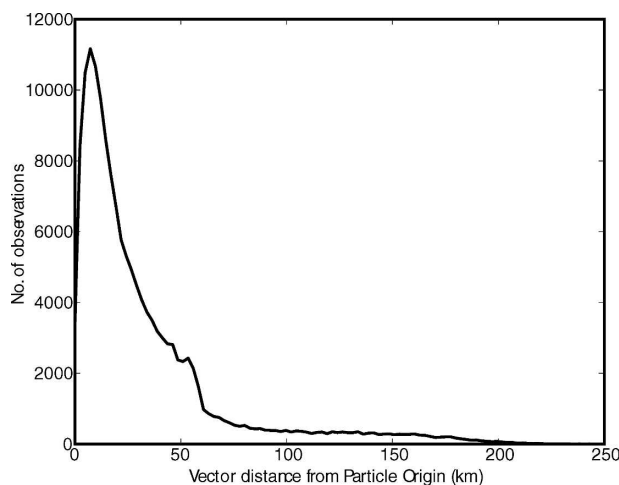

FIG. 6. Vector offset distance from expected particle receptor location after the 6-day BITT and 6-day FITT simulations of case 2.
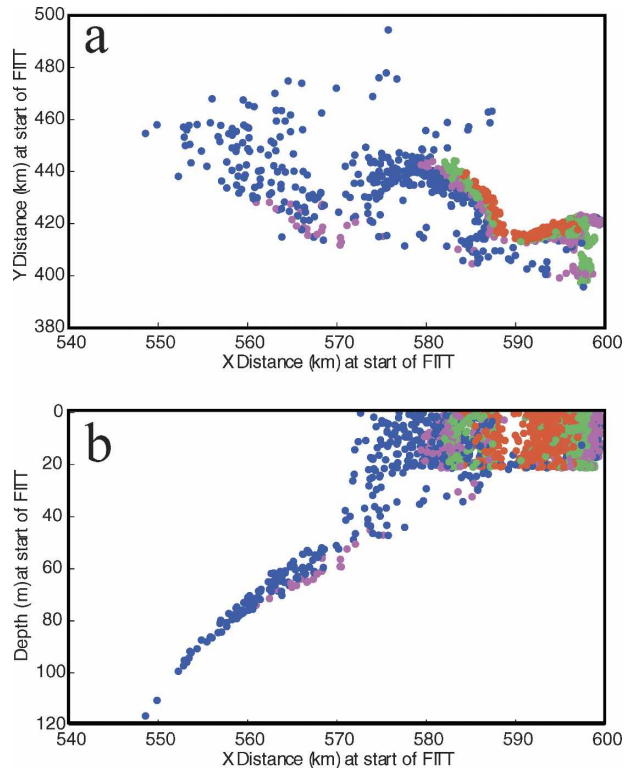

FIG. 7. Case 2 day 21 locations after 6-day BITT simulation in (a) x–y space and (b) x–z space. Positions are color coded by their probability of returning to near their expected receptor location. Red had highest return fidelity, followed by green, then magenta and blue.

Median positions after 6 days of BITT varied only a little among receptors, spanning x_{med} = 588–596 km and y_{med} = 400–423 km. The two northernmost release sites and the two inshore sites had similar mean and median x and y positions. The offshore stations had different mean and median alongshore transports, while the central and two southernmost stations had different mean and median cross-shore transports. For some receptor locations the mean centroid was not near any of the replicate points because there was strong curvilinearity in the transports, presumably reflecting the strong horizontal shear in this inshore region. The median was more often near particle positions than the mean, so it was used as the more reliable measure of central tendency. The vector distance for each particle to the median for the 100 replicate particles for a given receptor location was calculated. Of the 900 particles total, 96% were within 30 km of the median for the receptor. Examination of the 36 particles that were greater than 30 km from the group median revealed that all of those particles were below the surface mixed layer between days 4 and 6 of the simulation (Fig. 9). Many particles that were within 30 km of the median
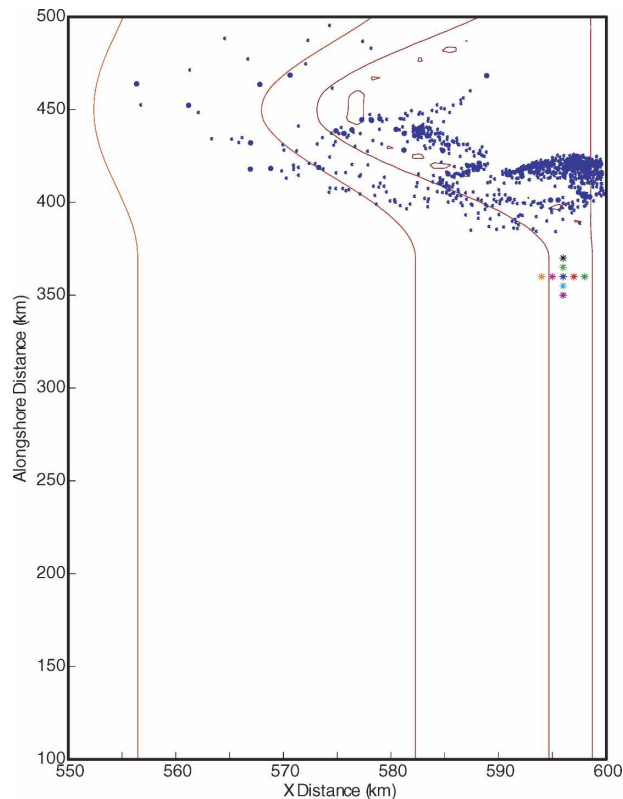
FIG. 8. Case 3 BITT simulation showing the nine initial nearshore receptor locations (asterisks), and the predicted prior particle positions (dots) on day 21 (6 days prior to arrival at the asterisks). Different colors indicate different receptor locations. Red lines are bathymetry contours. Figure scaled for comparison with Fig. 10b.

after 6 days of BITT were deeper than the ML during days 4–6, but none of the particles that were far from the median were within the ML during those 2 days. Because of their deeper depths and the upwelling conditions of the forward simulation (downwelling in the BITT), these particles were transported farther off-
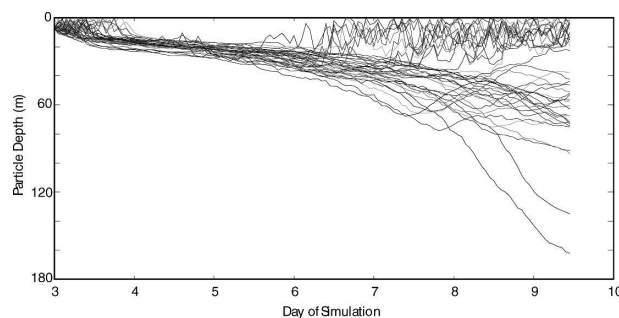

FIG. 9. Depth trajectories of the 36 particles (of 900 total) from case 3 that were more distant than 30 km from the group median for the receptor location after 6 days of BITT.

shore (Fig. 10a), and often, but not always, remained deep (Fig. 9). Particles from the two nearest shore stations remained in a tight cluster nearshore after 6 days of BITT. This BITT simulation indicates that 1) there are differences in "source location" because of initial receptor location, but the differences at the scales of 1–4 km cross-shelf and 10–40 km along shelf are relatively minor; 2) particles nearest the shore (within 3 km of the coast) are less likely to be entrained in cross-shelf flows, and consequently are most likely to have sources nearshore (upstream); 3) some of the particles from the offshore release sites get trapped below the level of surface mixing, which because of the downwelling flows (upwelling in the forward time sense) are transported more rapidly off the shelf; 4) this last effect is most marked in the region where the cross-shelf flow and upwelling is most intense. Revisiting the hypothesis that source locations must be nearshore (within 10 km of the coast), the probability of nearshore sources has a monotonically decreasing trend from north to south, but a more complicated trend east–west with the lowest probabilities of a nearshore source for the furthest west station (~40%) and the second nearest shore station (~50%) (Table 3). The return FITT simulation for 100 replicates from each of the 900 particles from the BITT simulation is shown in Fig. 10b, and the results are summarized in Table 3. The results for this BITT–FITT simulation differ only slightly from those for case 2 (cf. Fig. 5b), and so detailed discussion is omitted.

4) CASE 4

This case provided a more geographically comprehensive evaluation of the sensitivity of the BITT modeling estimation of source regions to a range of flow–topography interactions. The scenario is modeled to estimate prior locations of plankton given the results of a gridded survey of plankton over a limited region. Figure 11 shows the receptor locations (asterisks), the predicted particle locations 6 days prior to arriving at the receptors (dots), and the fidelity of the BITT simulations as a function of the receptor locations (color contours). Overall, alongshore transports were greatest for receptors located 550–580 km in the x direction (e.g., 20–50 km from the coast). Particles released from receptors at those stations had alongshore displacements of ~270–300 km in 6 days, which is roughly a 50 km day^{-1} alongshore transport. Alongshore flow decreased at greater distances offshore to a minimum of ~15 km day^{-1} for receptors located 90 km from the coast. Alongshore transports were markedly reduced for particles released at receptor locations on the continental shelf, and there was a strong gradient in alongshore displacement as the slope was crossed. Nearest shore
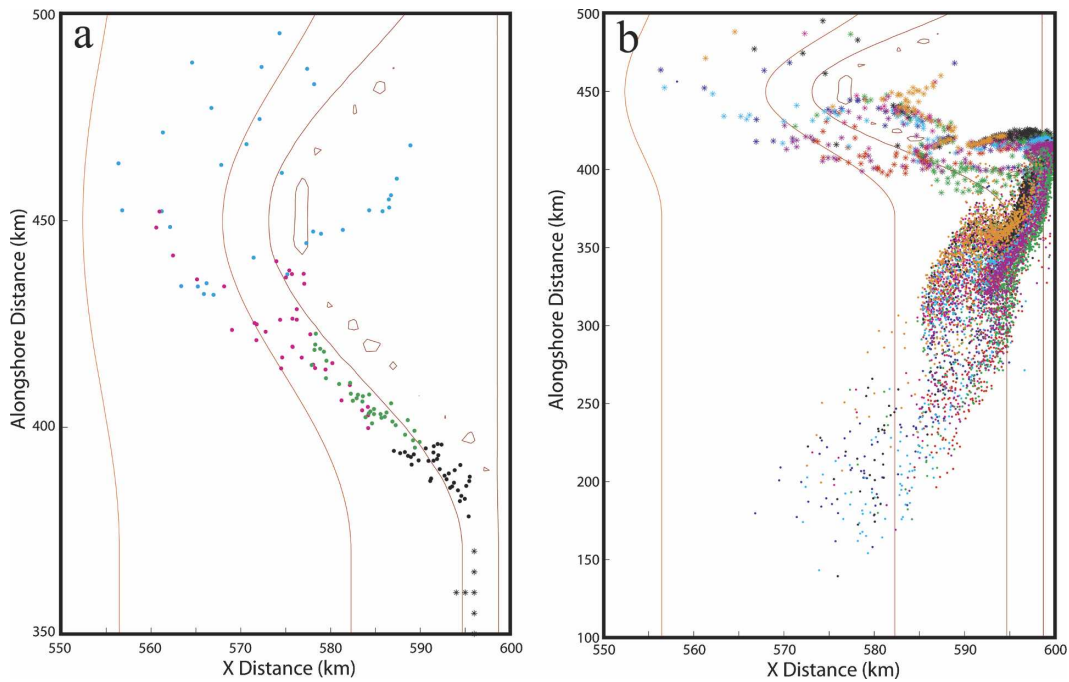
FIG. 10. (a) Case 3 BITT simulation indicating locations of particles at days 1.5 (black), 3 (green), 4.5 (magenta), and 6 days (blue) into simulation. Asterisks indicate receptor locations. Only particles that ended up greater than 30 km from the group median after 6 days of simulation are shown; no particles from the innermost two stations were beyond 30 km from the group median after 6 days, so those receptor locations are not shown. Red lines are bathymetry contours. (b) FITT simulation for case 3 using final positions from Fig. 8 (asterisks) as initial locations. Positions of particles after 6 days of FITT are shown as dots (color coded by initial receptor locations from BITT simulation shown in Fig. 8). For clarity, only 10 of the 100 replicates per origin are plotted. Red lines are bathymetry contours.

stations had the least alongshore displacement, generally <50 km. Beyond the continental slope, there was some dispersion cross shelf, but it was small (of the order of 10 km or so in the 6 days). Cross-shelf mixing (dispersion) was more pronounced for initial receptor locations that were on the shelf. This is because of their being more influenced by the vertical shear of upwelling during their 6-day journey, with some particles (those at depth) entrained into the strong cross-

bathymetry downwelling flows (upwelling flows in forward time), which transported some nearshore particles 50 km or more offshore during the 6-day BITT simulation.

As in the other cases, the robustness of the predicted prior positions was evaluated by seeding each of the BITT final positions with 100 replicate particles and conducting a FITT simulation. The color shading of Fig. 11 shows the mean vector offset displacements from the

TABLE 3. BITT–FITT case 3 summary. Bold values indicate starting locations that did not have high fidelity return rate to expected receptor location following R/T. Major discrepancy in return was in alongshore position.

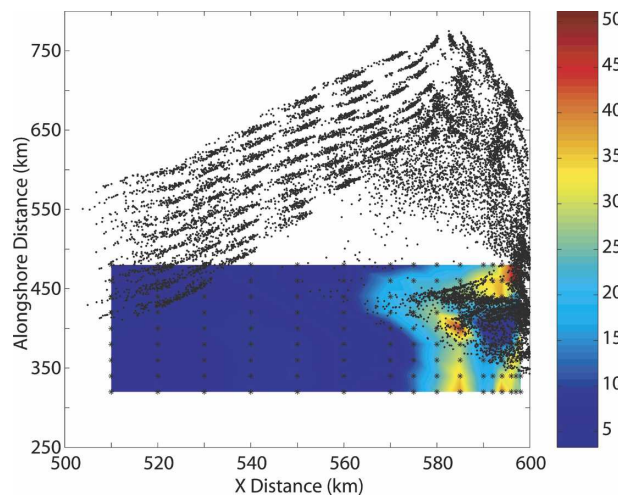| Receptor location (km)		Distance from center site	Median positions after R/T		
x	y	km–direction	x	y	Percent of replicates "nearshore"
596	360	0	595.1	355.9	64
596	365	5–north	595.3	361.5	69
597	360	1–east	594.7	**336.6**	50
596	355	5–south	594.1	**343.2**	59
595	360	1–west	594.3	359.0	62
596	370	10–north	595.9	370.0	79
598	360	2–east	597.6	357.7	76
596	350	10–south	595.0	**340.5**	59
594	360	2–west	592.9	359.2	40

FIG. 11. Case 4 coupled BITT–FITT simulation results. Asterisks within color-contoured region indicate receptor locations. Black dots indicate projected positions of 14 400 particles (100 replicates for each of 144 receptors) 6 days prior to their arrivals at their receptors. Color contours of receptor locations provide a measure of fidelity of return of particles to their receptor after a roundtrip of BITT followed by FITT. Color contours indicate the mean vector distance offset (km) from the initial receptor location after the roundtrip.

expected return site for each of the receptor locations. Consistent with the results from case 1, offshore (off shelf) receptor locations had high return fidelity with most receptor locations having <10 km mean vector offsets. There was also a region near the center of the bank where alongshore displacements were small, which had high return fidelity. There were a couple of hotspots (nearshore, just upstream of the bank; and along the continental slope downstream of the bank) that had the poorest return fidelity (>35 km vector offset). These are regions where flow–topography interactions are most nonlinear, where vertical and horizontal shears are greatest, and where small vertical displacements in particle position can dramatically alter trajectories.

4. Discussion

The prior history of environmental conditions experienced by individual organisms may be critical for understanding the dynamics of marine ecosystems (Pepin 2004). Variations in growth and mortality rates are highly dependent on the temperature and prey density and types experienced by individuals, and these are in large part determined by the organism's spatial trajectories through time-varying marine environments. Gridded broad-scale sampling of marine habitats rarely describes conditions at spatial scales smaller than a few

kilometers (Skjoldal et al. 2000); instead, one is forced to rely on subgrid-scale parameterizations. One approach to obtaining the finescale spatial structure needed for this parameterization is to nest finescale sampling within a coarser survey of a larger region (Barth et al. 2005). Provided a sufficient number of smaller regions are sampled at finescales, the results may be up-scaled to larger domains. Another approach is to sample space continuously (along a ship track) using optical or acoustic devices (Foote 2000; Foote and Stanton 2000) to describe the aggregations of organisms and their relation to other biotic components and the physical environment at scales finer than that provided by separated point sampling.

A third approach is to use physical and coupled physical–biological models to examine abiotic–biotic interactions at multiple scales, and down to the limitations of the model grid. This approach, Lagrangian particle tracking using output from a circulation model, was used here to estimate the diversity of potential "individual histories" that organisms might have experienced over a previous short interval (of the order of a week). The reliability of particle trajectories is dependent on the quality of the underlying physical circulation model. Qualitatively, the SEOM coastal physical circulation model forced by sinusoidally varying winds produced coastal upwelling, southward alongshore flow, and a region of intensified flow on the outer shelf (an upwelling jet). Upwelling of cold, subsurface water was greatest in a region just downstream of a shelf bank. These features are consistent with expectations from prior modeling and field observations (Gan and Allen 2002; Castelao and Barth 2005; Song and Chao 2004).

In estimating potential source regions, Lagrangian tracking with and without vertical diffusivity provided very different results, confirming the importance of including diffusive processes in transport modeling, especially at the relatively short spatial and temporal scales considered here. A previous sensitivity analysis of several factors, including particle depth and the magnitude of horizontal diffusion in estimating the distribution and dispersal of cod larvae off Norway (Ådlandsvik and Sundby 1994), illustrated the importance of order of magnitude changes in the level of diffusion. Moreover, shallower depths (which were fixed to a constant depth in a single run) led to different dispersion than that of deeper fixed depths. They conclude that their modeled particle distributions are robust to minor fluctuations in particle depth, level of diffusion, and release time and location. In the work reported here, vertical diffusion, implemented as a random walk, displaced individuals vertically, which when coupled with vertical shear in

flow, resulted in dispersion. Ådlandsvik and Sundby's (1994) physical simulations and particle tracking spanned 90 days, whereas the simulations shown here are for much shorter intervals (<10 days). They suggest that the "integrated wind history" is more important than the detailed timing of smaller-scale wind-forced events. The robustness of that conclusion may be directly due to the fairly coarse-resolution (20 km horizontally, nine sigma levels vertically) long-term simulations of their simulations. The simulations reported here clearly document at smaller spatial and temporal modeling scales the important influence of vertical diffusion and small-scale (2–10 km) spatial heterogeneity in coastal systems—even for the very simplified (idealized) geometry and bathymetry used here. Backward-in-time-trajectory simulations with vertical diffusion suggested potential upstream "nearshore" adult population sites that were not predicted by simulations lacking vertical diffusion. The latter simulations indicated a low probability (<10%) of the adult sources being nearshore.

The overall pattern of probability densities of "source" regions was strongly impacted by including vertical diffusion, through a random walk process, in the transport process. These results argue that ignoring diffusive processes in particle tracking can lead to incorrect source or destination identifications. This result suggests that both dispersion and advection must be included in forward- (and backward)-in-time simulations of particle trajectories, especially for short-duration simulations, such as those conducted in this study.

These results document the value of backward-in-time-trajectory modeling for identifying probable source regions, or, more generally, prior positions of planktonic organisms. The robustness of the BITT simulations is evaluated by using the resulting prior positions as "starting positions" for FITT simulations, and evaluating the fidelity of the particles to return to their known receptor locations. For destinations (receptors) offshore (case 1), the results suggest that the BITT simulations reliably predict prior positions for the short-duration simulations. In nearshore regions, where flow–bathymetry interactions are stronger, the BITT simulations did less well. Some of the particles in the nearshore receptor BITT simulations (case 2) escaped to substantially deeper depths while nearshore and were subsequently advected offshore and deeper. Few of those deep, offshore particles after BITT simulations were able to return to their known nearshore destination in the subsequent FITT simulation. Simulations that evaluated small-scale differences in alongshore and cross-shore receptor locations (case 3) showed mostly

similar source regions. Median positions after 6 days of BITT spanned from 588 to 596 km in x (4–12 km offshore), with alongshore displacements spanning 40–63 km. When examined in detail, there was some dependence on the initial destination location. For instance, the two nearest shore destinations had significantly less dispersion of replicate particles than did the other seven locations, and are less likely to be entrained in deeper cross-shelf flows and are more likely to have nearshore upstream sources than nearby destinations 2-km further offshore. BITT simulations from a grid of receptors spanning from very nearshore to far offshore and a range of alongshore transects (case 4) showed the greatest dispersion from shelf receptors, but also regions of both very high and very poor return fidelity (from paired BITT–FITT simulations). High return fidelity occurred for offshore receptors and for shelf receptors that had small alongshore displacements, whereas the poorest return fidelity occurred at receptors just upstream of the bank and along the continental slope downstream of the bank, where strong, probably nonlinear, flow–topography interactions were greatest. These were also the regions with the strongest alongshore jet shear gradients (both horizontally and vertically), and where dispersions could place a particle in a very different flow regime.

Overall, the comparison of the paired BITT–FITT simulations suggests that BITT approaches are valuable in identifying prior positions of plankton. Information on prior position is valuable for specifying the environmental history of the organisms and interpreting the environments effects on growth and population dynamics of zooplankton and ichthyoplankton. Pepin et al. (2003) created "backward drift reconstructions" using forward-in-time simulations from an earlier time, with a uniform seeding (500-m grid of particles) of the environment. Only the small subset of particles that passed within a predetermined distance of a known receptor site at a known time were considered as possible trajectories of prior positions. In their simulation they constructed an average drift trajectory to specify the mean environmental conditions experienced by the fish larvae during the prior 7 days. BITT simulations can directly consider the reversible processes of advection, growth, and size-dependent behaviors (which in turn may modify trajectories and environmental histories), and indirectly, a nonreversible process of vertical diffusion. Several scenarios are described for which BITT simulations of advection and diffusion provide reasonable prior positions (based on evaluation using subsequent FITT simulation). The biological processes that can be dealt with appropriately in BITT simulations are those that conserve numbers, for example, growth and

size-dependent DVM are feasible. What are not feasible in BITT simulations are biological processes that create or eliminate individuals from the population, for example, birth and death (mortality). Mortality in forward time would be the creation of new individuals of some unknown age and history in reverse time. That is not feasible. Technically, birth in forward time could be simulated in backward time by tracking negative growth of individuals until they "shrink" to the size of a newborn, at which point they are considered "born" and deleted from the BITT simulation. However, it would be highly unlikely that the BITT positions of all of the eggs from a single reproductive event (in forward time) would co-occur in space and time during a BITT simulation. More research on the reversibility of biological processes could be examined with future size- and condition-dependent BITT simulations.

BITT simulations are feasible when the processes are exactly reversible (e.g., with advection, and constrained size- or condition-dependent biological processes), when backward diffusion is evaluated with paired FITT simulations, and BITT simulations offer significant computational advantages when the number of receptors is small compared to the number of prior positions or sources. All trajectories provide meaningful information to the question—not just those few from FITT that pass within some short distance of a known destination. BITT simulations could significantly decrease computation requirements in many cases where uniformly gridded FITT simulations have been used instead (Allain et al. 2003; Pedersen et al. 2001; Hare et al. 1999) to identify potential past trajectories of individuals. The Allain et al. (2003) study is somewhat similar to the study of Pepin et al. (2003) where multiple collection surveys were done with a desire to reconstruct environmental histories during the intervening time periods using mean trajectories between the source and destination. In such studies, the relative area of source and destinations should be the determinant of whether to use BITT or FITT approaches, especially in a case like that of Allain et al. (2003) where diffusion was not considered. Particle tracking of ocean ecosystem processes should include diffusion, or risk coming to incorrect conclusions on sources, destinations, and pathways. Diffusion, especially in the vertical dimension, is an important process in the real ocean, and hence should be important in models of the ocean.

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