Model sensitivity and robustness in the estimation of larval transport: A study of particle tracking parameters

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A B S T R A C T

Many marine organisms spend their early lives as planktonic larvae dispersed by ocean currents. Predictions of larval transport are important for a wide range of applications including the interpretation of population genetics, fisheries management, and the planning of no-take marine protected areas. A popular method for predicting larval transport is through the use of coupled ocean circulation and particle tracking models, termed “biophysical” models. Although much research has been done on the sensitivity and uncertainty of ocean circulation models, the sensitivity of particle tracking models for the assessment of larval transport has been largely overlooked. This study investigates the sensitivity of larval transport predictions to three input parameters universally required for particle tracking in biophysical models; namely the number of particles released, the particle release depth, and the particle tracking time. Using a three-dimensional biophysical model of the Southern California Bight, estimates of larval transport are quantified using a two-dimensional vertically-integrated particle density distribution (PDD) and the differences between PDDs are assessed using the fraction of unexplained variance (FUV). Overall, our study shows that larval transport predictions are sensitive to changes in all three input parameters and that the sensitivity is affected by the strength of mixing in the system. For the number of particles released, the FUV falls off rapidly as the number of particles increases. A minimum number of particles is identified that guarantees robustness of model predictions; this number increases as the complexity of the circulation patterns increases. For the particle release depth, the FUV between PDDs grew linearly as particles are released farther apart. The FUV is also inversely proportional to the strength of vertical mixing as the FUV is smaller in the winter when a deep mixed layer and weak stratification are present and larger in the summer when the system is strongly stratified. For the particle tracking time, the FUV between daily PDDs is much larger for short tracking times of 15 days or less than for longer tracking times of 20 days or more, showing a dependence on the length of time the particles take to be evenly mixed throughout the system. Our study quantifies the parameter sensitivity of larval transport predictions and presents a straightforward methodology to achieve robust predictions of larval transport from biophysical models.

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1. Introduction

Marine invertebrates and fish begin life in a planktonic larval stage that can range from days to months. Accurately predicting the transport of this early larval stage is critical for understanding marine population dynamics. A widely used method for predicting larval transport is through the use of biophysical models, which consist of coupled Eulerian ocean circulation and Lagrangian particle tracking models (Cowen and Sponaugle, 2009; Metaxas and Saunders, 2009; Miller, 2007; Werner et al., 2007). Biophysical models, which include individual-based models, are well suited to simulate larval transport because larval physiology and behavior can be easily imposed on individual particles (Hoffmann and Lascara, 1998) and predictions can be made over large geographical areas with many release sites (Metaxas and Saunders, 2009). For these reasons, biophysical models are being used globally to predict larval transport and connectivity for a wide range of applications including population genetics, spatial fisheries management, invasive species control, and the planning and design of marine protected areas (Botsford et al., 2009; Costello et al., 2010; Jones et al., 2009; Levin, 2006; Melbourne-Thomas et al., 2011). As the use of biophysical models continues to grow, rigorous methods for understanding model sensitivity and achieving model robustness are needed. Although much research has been devoted to the quantification of uncertainty in ocean circulation models, studies of uncertainty in biophysical models are limited (Miller, 2007). Most existing studies of uncertainty in biophysical models examine the sensitivity of larval transport predictions to larval mortality, growth, and behavior for a...
particular species or set of species (e.g., Huret et al., 2007, 2010; Paris et al., 2007; Peck and Hufnagl, 2012; Schmidt and Hinrichsen, 2008). This paper examines the sensitivity of larval transport predictions to particle tracking parameters that are required for all biophysical modeling studies of larval transport and connectivity, including studies that model species-specific characteristics such as mortality, growth, and behavior.

When a biophysical model is used to simulate larval transport, three parameters are universally required for particle tracking: the number of particles released, the particle release depth, and the particle tracking time. The first parameter, the number of particles released, should be selected such that a sufficient number of particles are used to generate robust larval transport predictions, but this is seldom tested. The second and third parameters, the particle release depth and particle tracking time, ideally should be based on the larval life history of the species being simulated, but these details are often uncertain, and thus the modeler is forced to select them with very little or no information. Once set, the number of particles released and the particle release depth are usually assumed to have no influence on the model results. Particle tracking time, which is based on the length of time a species spends in the larval stage, can more frequently be derived from literature than the other two parameters, but again, sensitivity to variation in these quoted values is not usually assessed. In this paper, we investigate the sensitivity of larval transport predictions produced from a biophysical model to these three input parameters and describe a general methodology for managing sensitivity and achieving model robustness.

Although our paper focuses on three critical particle tracking parameters, the methods presented could also be used to assess the sensitivity of larval transport predictions to many other parameters in biophysical models, such as time step, grid size, frequency of release, and online versus offline tracking.

A three-dimensional biophysical model of the Southern California Bight (SCB) is used for this study (Fig. 1). The SCB has a diverse ecology, an economically important fisheries industry, and a large network of marine protected areas, making larval recruitment and connectivity along its coastline of great interest (Dailey et al., 1993; McGinnis, 2006). In addition, the SCB is an ideal study area for testing model robustness because it contains complex physical oceanography including forcing by the California Current system, mesoscale eddies, wind-forced seasonal upwelling, coastal trapped waves, and strong thermal stratification (Dong et al., 2009; Hickey, 1993; Hickey et al., 2003). The biophysical model used for this study consists of off-line flow field solutions from a Regional Ocean Model System (ROMS) coupled with a Lagrangian particle tracking model. As particles are released and tracked in three-dimensions within the model domain, the vertically-integrated particle distribution at a particular point in time is quantified with a two-dimensional particle density distribution (PDD). To test the sensitivity of the biophysical model to the input parameters, a series of simulations are conducted where one of the input parameters is systematically perturbed while all the other model variables are held constant. The differences in the PDDs are quantified by calculating the fraction of unexplained variance (FUV) between PDDs, where a larger FUV represents a greater difference between PDD patterns. This process is repeated many times for different release locations and time periods.

We address the following questions for each input parameter using the process described above. Are predictions of larval transport, expressed in the form of PDDs, sensitive to parameter changes? If so, is there a consistent relationship in space and time between the perturbed parameter and the change in PDD expressed by the FUV? How does this relationship relate to the physical dynamics of the SCB? How can model robustness be achieved and thus sensitivity to the exact choices of input parameters be managed? Our paper begins with a description of the biophysical model and the methodology used to quantify model sensitivity. Next we describe the results of the sensitivity study for each input parameter and discuss those results with respect to the physical oceanography of the SCB. We close by offering some recommendations for achieving more robust larval transport estimates.

2. Methods

2.1. Biophysical model

Larval transport in the SCB was estimated using a three-dimensional biophysical model, which was comprised of an Eulerian ocean circulation model combined with a Lagrangian particle tracking model. The circulation model consisted of off-line flow field solutions from a high-resolution ROMS applied and calibrated to the SCB (Dong and McWilliams, 2007; Dong et al., 2009; Shchepetkin and McWilliams, 2005). The model domain, shown in Fig. 1, covered the SCB coastline from north of Point Conception to San Diego and included all eight Channel islands. The model grid was 258 km by 386 km with 1 km horizontal resolution and 40 vertical levels. Developed by Dong and McWilliams (2007), the model was driven by realistic boundary conditions extracted from a nested ROMS solution for the U.S. West Coast with high-resolution air–sea forcing. For detailed information on the lateral and surface boundary conditions and model validation, the reader is referred to Dong and McWilliams (2007), Dong et al. (2009), and Shchepetkin and McWilliams (2005). The Lagrangian particle tracking model was driven by 6-hour averaged off-line

![Fig. 1. Bathymetry of Southern California Bight and model domain. Particle release sites are identified with red circles.](image-url)
flow fields produced by the circulation model following the procedures in Mitarai et al. (2009). The study was conducted with averaged offline flow fields because it significantly reduced the simulation time. However, the methods presented in this paper are also applicable to biophysical models run online. When running a biophysical model with offline flow fields, the flow fields must be averaged over a time period smaller than the inertial period (North et al., 2009). The inertial period for the model domain was 21–22 h, which is significantly greater than the six hours over which the flow fields were averaged. Particles were advanced in time using a fourth-order accurate Adams–Bashforth–Moulton predictor-corrector scheme and a 900-s time step. The particle tracking model was validated against observational data from drifter experiments (Ohlmann and Mitarai, 2010).

2.2. PDD and FUV calculations

Particle distribution at a specified time after release was quantified using a two-dimensional particle density distribution (PDD). The PDD was similar to the probability density function (PDF) used in Mitarai et al. (2009), but does not always integrate to one, the definition of a PDF, due to the loss of particles from the domain over time. The PDD was produced from a three-dimensional distribution of individual particle locations within the following three steps (Mitarai et al., 2009): (1) vertically integrate the number of particles within a grid cell to create a two-dimensional distribution, (2) divide the distribution by the total number of particles released, and (3) spatially filter the distribution using a two-dimensional isotropic Gaussian filter with a 5 km standard deviation. Filtering was applied because it reduced the number of particles needed to achieve robust PDDs by an order of magnitude and therefore significantly decreased the computational load. Due to the 1 km grid size, the ocean circulation model accurately captures mesoscale processes of 10–100 km but not smaller (Dong et al., 2009); therefore no physical features were lost in applying the 5 km filter. Although the PDDs were constructed according to the three steps outlined above, the methods presented in this paper are applicable to any two-dimensional grid-based descriptor of particle distribution, which includes dispersal kernels (Ayata et al., 2010; Edwards et al., 2008; Huret et al., 2010), probability density functions (Mitarai et al., 2009; Roughan et al., 2011), and particle concentration (Simons et al., 2006). Another important descriptor of larval dispersal is the connectivity matrix, which represents the probability of larvae being transported from one location to another (C Owen et al., 2006; James et al., 2002; Siegel et al., 2008). The methods presented in this paper are also applicable to connectivity matrices, since connectivity matrices are often derived from two-dimensional descriptors of particle distribution, such as PDFs (e.g. Mitarai et al., 2009; Roughan et al., 2011; Watson et al., 2010) and dispersal kernels (e.g. Cowen et al., 2006; Huret et al., 2010).

To compare two PDDs, we define the fraction of unexplained variance (FUV) between them as:

\[ \text{FUV} = 1 - r^2 \]  

where \( r \) is the linear correlation coefficient between two different PDDs. To compute \( r \), the two-dimensional PDDs were vectorized for a grid cell to grid cell calculation. Although many statistical metrics were available for grid-wise image comparison (Kara et al., 2008; Stow et al., 2009), FUV was selected for the following four reasons. First, FUV was a conservative measure of difference since the grid cells are evaluated independently and would thus detect differences in the PDDs even if the same pattern was slightly shifted in space. Second, unlike other metrics such as root-mean-square error, FUV resulted in a value between 0 and 1, providing a consistent scale for comparing PDDs which may contain very different numbers. Third, FUV provided a single number that would quantify the difference between two PDDs. Fourth, the use of a squared correlation coefficient naturally induced a description of the magnitude of the difference in terms of residual variance; thus two PDDs with a very high FUV are virtually uncorrelated and represent two very different spatial distributions of particles.

2.3. Simulations

The following model set-up was used for all sensitivity studies. Particles were released from 12 nearshore sites located in different areas throughout the SCB (Fig. 1). Releases were made near the coastline because it is the location of spawning habitat for most species in the SCB. The configuration of the nearshore sites was based on a connectivity study of SCB (Mitarai et al., 2009). The nearshore sites were 10 km diameter circles and configured to release one particle at each grid point within their boundaries. Depending on how the circles were located relative to the model grid, they contained between 71 and 79 grid points. Since the grid has a horizontal spatial resolution of 1 km, the area that the particles cover per site only varies at most by 10%. We chose to use this site configuration because many studies are, and continue to be, based on larval connectivity matrices produced with this configuration (e.g. Alberto et al., 2011; Costello et al., 2010; Mitarai et al., 2009; Rassweiler et al., 2012; Selkoe et al., 2010; Watson et al., 2010, 2011, 2012). In addition, we evaluated the sites individually for each sensitivity study and found that this small variation in spatial coverage did not affect the results.

To test the model over periods of varying ocean dynamics, the particles were released from the 12 sites over five months, January, April, May, June and December, and three years, 1997, 1999, and 2000. These months were selected in order to allow comparisons between winter and spring, which can be dynamically very different in the SCB (Hickey, 1993). The years were selected to include an El Niño event in 1997, a La Niña event in 1999, and a normal year in 2000.

For each simulation, the particles were released from a single site at a constant frequency (e.g. every 3 h) over the month and passively tracked for 30–40 days. All the particles were released at 5 m below the surface, following Mitarai et al. (2009), with the exception of the particle release depth study. To study the number of particles released and the particle tracking time, simulations were conducted for all combinations of the 12 sites, 5 months and 3 years, producing a total of 180 simulations. For the particle release depth study, simulations were conducted for only two years, 1999 and 2000, due to the large number of simulations required. For each simulation, PDDs were then created at specified tracking times. The tracking time is defined as the length of time a particle is transported through the system. Each time an input parameter was changed, a new set of particle tracking simulations were run.

3. Results

In this section, we describe how the sensitivity study for each of the three input parameters was conducted and then present the results of the study. The sensitivity study for the first parameter, the number of particles released, addresses the question of how many particles are needed to accurately represent the underlying circulation patterns and avoid undersampling errors. For this parameter, a method is presented to identify a minimum number of particles that will achieve robust PDDs. The sensitivity studies for the second and third parameters, the particle release depth and particle tracking time, address the question of how does uncertainty in these parameters impact predictions of larval transport. For these two parameters, a method is presented where different, but equally valid, values for the parameters are selected and their impact on the resulting PDDs is evaluated. The set-up for each input parameter is summarized in Table 1.

3.1. Number of particles released

For this study, a two-step process was required to create PDDs with varying numbers of particles. First for each of the 180 site, month, and
year combinations, a reference simulation was conducted with particles released at a 1.5 h frequency and used to produce two reference PDDs with tracking times of 15 and 30 days. For the reference simulations, 34,000–39,000 particles were released for each site over one month. Second for each tracking time of 15 and 30 days, a series of 21 PDDs with the number of particles (N) ranging from N = 500 to N = 20,000 was created by randomly sampling the particle locations of the reference simulation. This second step was repeated 100 times for each of the 180 reference simulations, producing a total of 18,000 PDDs for each different N and tracking time. For each series of PDDs, the FUV was calculated between the reference PDD, which had the largest number of particles and hence yields the best PDD estimate, and the PDDs produced with fewer particles. For each N and tracking time, an FUV upper bound was calculated using the results from all site, month and year simulations. For our study, we defined the number of particles released as all the particles remaining in the domain at the time the PDD is constructed. Particles that have left the model domain were not included; this normalization is needed when a significant fraction of the input particles is advected out of the model domain.

Fig. 2 shows the FUV upper bound versus the number of particles released for tracking times of 15 days and 30 days for all site, month and year simulations. As the number of particles released increases, the FUV upper bound decreases, at first rapidly and then more slowly. By setting a cutoff of 0.05 for the FUV upper bound, the minimum number of particles required to achieve a robust PDD can be identified. This cutoff represents the maximum amount of dissimilarity that will be tolerated between the reference and sub-sampled PDDs. Since the FUV is proportional to the variance, a cutoff of 0.05 is chosen to be reminiscent of a 95% confidence level, represents a correlation between PDDs of 0.97. The FUV upper bound of 0.05 is identified by the gray line in Fig. 2. Using this cutoff, the minimum number of particles required for a robust PDD is 2800 for a tracking time of 15 days and 5900 for a tracking time of 30 days.

Fig. 3 shows six PDDs for particles released from site 10, located on the east side of Santa Catalina Island, for May of 1999 with a tracking time of 15 days. The PDDs in Fig. 3 are produced with 500, 1000, 2000, 4000, 6000 and 8000 particles and when compared to the reference PDD, correspond to FUVs of 0.219, 0.141, 0.078, 0.035, 0.019, and 0.016, respectively. Since the minimum number of particles required to achieve PDD robustness, defined as a FUV of 0.05 or less, was calculated at 2800 for a tracking time of 15 days, the PDDs shown in Fig. 3 (d), (e) and (f). As shown in Fig. 3, differences in PDDs became much smaller as larger and larger numbers of particles were used, clearly showing the stability of the PDDs as the number of particles increases. The low number PDDs in Fig. 3 (a), (b) and (c) appear very different because they were generated by randomly subsampling particles from a reference simulation with a large number of particles and consequently do not contain many of the same particles. Note in particular the patchiness induced by runs with small numbers of particles, which results from undersampling large, smooth density features.

### 3.2. Particle release depth

To study sensitivity to particle release depth, a series of 29 simulations was conducted for each of the 120 site, month, and year combinations. For each simulation, all of the particles were released at a 3 h frequency from the same depth, which ranged from 2 m to 30 m in 1 m intervals. A maximum release depth of 30 m was used because it is the maximum depth of the seasonal mixed layer in the SCB (Hickey, 1993). PDDs were produced for each of the 29 simulations at tracking times of 15 and 30 days. For each series of 29 simulations, the FUV was calculated between all the PDDs. Only the PDDs that had numbers of particles above the minimum value for model robustness, as determined in the previous section, were used in the analysis.

Fig. 4 shows FUV versus particle release depth for January simulations and a tracking time of 15 days. In Fig. 4, the FUV is calculated using reference PDDs from four release depths of 5 m, 10 m, 15 m and 20 m. Regardless of which release depth is used as a reference, the FUV increases steadily with increasing distance from the reference release depth. A similar pattern is observed for other months and a 30 day tracking time.

Fig. 5 shows the average FUV versus the distance between particle release depths for January simulations (Fig. 5 (a)) and May simulations (Fig. 5 (b)). The error bars in Fig. 5 represent an empirical 95% confidence interval. The average FUV and confidence interval are calculated using the FUVs from 348 different simulations, which include all release depths of 2 m to 30 m. The average FUV increases at a rate of 0.013/m for January and at a rate of 0.024/m for May.

Fig. 6 shows four PDDs for particles released from site 10, located on the east side of Santa Catalina Island, for May of 1999 with a tracking time of 15 days. The PDDs in Fig. 6 are produced using particle release depths of 5 m, 10 m, 15 m, and 20 m. If the PDD shown in Fig. 6 (a) with the 5 m release depth is used as a reference PDD, the FUVs for the PDDs shown in panels (b)–(d) are 0.18, 0.44, and 0.59, respectively. In general, a consistent and relatively rapid divergence in FUV is observed even for relatively small changes in the particle release depth.

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**Table 1**

Summary of model set-up for sensitivity studies.

<table>
<thead>
<tr>
<th>Input parameters</th>
<th>Range of values used</th>
<th>Simulation years</th>
<th>Simulation months</th>
<th>Release depth (m)</th>
<th>Release frequency (h)</th>
<th>Total number of particles released/month/site</th>
<th>Tracking times evaluated</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of particles released</td>
<td>500 particles and every 1000 particles up to 20,000 particles</td>
<td>1997, 1999, 2000</td>
<td>Jan, Apr, May, Jun, Dec</td>
<td>5</td>
<td>1.5</td>
<td>34,000–38,000</td>
<td>15 days</td>
</tr>
<tr>
<td>Particle release depth</td>
<td>Every meter from 2 to 30 m</td>
<td>1997, 1999, 2000</td>
<td>Jan, Apr, May, Jun, Dec</td>
<td>2–30</td>
<td>3</td>
<td>17,000–19,000</td>
<td>15 days</td>
</tr>
<tr>
<td>Particle tracking time</td>
<td>Every day from 1 to 40 days</td>
<td>1997, 1999, 2000</td>
<td>Jan, Apr, May, Jun, Dec</td>
<td>5</td>
<td>1.5</td>
<td>34,000–38,000</td>
<td>30 days</td>
</tr>
</tbody>
</table>

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![Fig. 2. FUV upper bound versus number of particles released for tracking times of 15 days (solid black line) and 30 days (dashed black line). The horizontal gray line is drawn at a FUV upper bound of 0.05.](image-url)
3.3. Particle tracking time

For all 180 site, month, and year combinations, simulations were conducted with particles released at a 1.5 h frequency and tracked for 40 days. For each simulation, 40 PDDs were produced for daily particle tracking times of 1–40 days. Four reference PDDs were selected with particle tracking times of 5, 15, 25, and 35 days. The FUV was then calculated between the 40 daily PDDs and each reference PDD. Sufficient numbers of particles were released to guarantee that the PDDs had numbers of particles above the minimum value for model robustness as discussed in Section 3.1.

Fig. 7 shows FUV versus the particle tracking time for all January simulations. In Fig. 7, the FUV is calculated using reference PDDs with particle tracking times of 5, 15, 25, and 35 days. Regardless of which reference PDD is used, the FUV increases rapidly with growing time from reference particle tracking time. Similar patterns are observed for the other months.

Fig. 8 shows the average FUV versus the particle tracking time for reference particle tracking times of 5 days, 15 days, 25 days, and 35 days. The error bars in Fig. 8 represent an empirical 95% confidence interval. The average FUV and confidence interval are calculated using the FUV from 180 different simulations. Similar patterns are observed for the other months.

Fig. 9 shows the average FUV versus the particle tracking time for reference particle tracking times of 5 days, 15 days, 25 days, and 35 days. The error bars in Fig. 8 represent an empirical 95% confidence interval. The average FUV and confidence interval are calculated using the FUV from 180 different simulations. Similar patterns are observed for the other months.

4. Discussion

In general, we find that larval transport predictions from the biophysical model are sensitive to perturbations in all three input parameters. For all parameters, consistent patterns are observed between the FUV and the perturbed parameter. Below we summarize the sensitivity studies and offer suggestions of how to manage model sensitivity to each parameter.

4.1. Number of particles released

Larval transport and connectivity estimates often span large geographic areas and numerous spawning sites. Thus the modeler’s challenge is to release enough particles to accurately capture the system dynamics, but not so many that the simulations become computationally cost prohibitive. Many studies state the total number of particles that are released (e.g. Cowen et al., 2006; James et al., 2002; Mitarai et al., 2009; Simons et al., 2006), but information on how this number is determined is not provided. One exception is Drake et al. (2011) where the sensitivity of the model results to the number of particle trajectories was tested. In the Manual of recommended practices for modeling physical–biological interactions during fish early life, North et al. (2009) strongly recommend testing biophysical models for sensitivity to the number of particles. Therefore
we have developed a straightforward method that identifies the minimum number of particles required to achieve robust model predictions using PDDs constructed with randomly drawn increasing numbers of particles and an FUV upper bound.

We observe that the FUV upper bound decreases roughly exponentially when the number of particles increases (Fig. 2). Large FUVs occur when there are not enough particles to accurately represent the statistics of the underlying distribution, a manifestation of undersampling (Brickman and Smith, 2002). Undersampling or underseeding occurs when too few particles give too coarse an estimate of the true or infinite particle PDD. This coarse estimate is especially inaccurate at the tails or edges of the distribution, which can result in poor estimates of larval connectivity at the shoreline. Using the relationship between the FUV upper bound and the number of particles released, we identify a minimum number of particles that guarantees a 0.05 FUV or less (Fig. 2). As long as the number of particles used to calculate the PDD is greater than this value, the PDDs are insensitive to the number of particles released.

We also find that as the particles are transported for longer time periods and dispersed over larger areas, the minimum number of particles required to achieve a robust PDD increases. For example, a PDD with a tracking time of 15 days requires a minimum of 2800 particles, while a PDD with a tracking time of 30 days requires a minimum of 5900 particles. Similarly, when particles are released simultaneously from four sites instead of one, the minimum number of particles increases from 2800 to 5800 particles for a tracking time of 15 days. As longer tracking times and more release sites drive the particles into increasingly complex circulation patterns, the complexity of the underlying distribution increases, requiring more particles to avoid undersampling and to achieve model robustness.

### 4.2. Particle release depth

Since species specific information on where spawning occurs in the water column is usually not available, the selection of particle release depth is often arbitrary and ranges from spanning the water column (e.g. Drake et al., 2011; Huret et al., 2010; Simons et al., 2006) to a single release depth (e.g. Mitarai et al., 2009; Watson et al., 2010). Our goal is to identify the sensitivity of the PDDs to particle release depth and make recommendations to manage this sensitivity. Overall, we observe that as the distance grows between particle release depths, the FUV between PDDs increases (Fig. 4). In addition, the FUVs are much greater in spring than in winter (Fig. 5). This seasonal pattern can be explained by thermal stratification in the SCB, which is accurately captured by the ocean circulation model (Dong et al., 2009). In general, the SCB displays strong year-round thermal stratification and a shallow mixed layer.

[Fig. 4. FUV versus particle release depth (m) for a tracking time of 15 days. The dashed vertical lines represent the reference particle release depth for the FUV calculations: (a) 5 m, (b) 10 m, (c) 15 m, and (d) 20 m. Simulations for January are shown.]

[Fig. 5. Average FUV versus distance between particle release depth (m) for a tracking time of 15 days (black circles). Error bars (black) denote an empirical 95% confidence interval. FUV calculations are based on (a) January simulations and (b) May simulations. Gray circles and error bars show results for January simulations with vertical sub-grid scale mixing included. Note that simply including vertical mixing does not remove differences caused by varying release depths.]
Although the mixed layer is shallow, it displays a distinct seasonal pattern with a depth of 10 m or less in April through October and a depth of about 30 m in November through March (Gelpi and Norris, 2008; Hickey, 1993). When particles are released in the winter months in the presence of a deeper mixed layer, the FUV will be small since most of the particles will be released into the mixed layer and therefore produce similar PDDs regardless of their release depth. On the other hand, when particles are released into stratified water during the summer months, very different PDDs will be produced depending on release depth, resulting in large FUVs.

Some biophysical models include parameterizations of sub-grid scale mixing to represent the turbulent mixing that occurs within a grid cell of the circulation model (Gallego et al., 2007; North et al., 2007).
To test the sensitivity of the relationship between FUV and distance between particle release depth to sub-grid scale mixing, a vertical sub-grid scale mixing scheme was added to the particle tracking model. Since Lagrangian length scales for horizontal dispersion in the SCB are determined to be much larger than a grid cell (Swenson and Niiler, 1996), it is not necessary to add horizontal sub-grid scale mixing to the model. Sub-grid scale vertical mixing is added to the particle tracking model using the following random walk formula for particle dispersion (Taylor, 1922):

$$\Delta z = Z(2K\Delta t)^{1/2}$$  \hspace{1cm} (2)

where $\Delta z$ is the vertical particle displacement, $K$ is the vertical eddy diffusivity, $\Delta t$ is the time step, and $Z$ is an independent random number.
with a normal distribution, a zero mean and a unit variance. The vertical particle displacement ($\Delta z$) is added after the particle is advected by the circulation model's flow fields. In general, vertical mixing in the SCB is small due to the year-round stratification and shallow mixed layer (Palacios et al., 2004), but several studies have predicted the vertical eddy diffusivity in the mixed layer to be around $10^{-4}$ m$^2$/s (Eppley et al., 1979; Gelpi and Norris, 2008), which is used in the random walk formula. Although the vertical eddy diffusivity is not in reality constant over depth, our choice of a vertically uniform diffusivity represents a worst case scenario in which we expect the difference between simulations with and without sub-grid scale mixing to be largest if the mixed layer spanned the entire water column.

Since the mixed layer is deepest and consistently present in winter, January simulations for all release depths were rerun with the random walk formula for sub-grid scale vertical mixing included in the model. May simulations were not rerun because the system is strongly stratified at this time of year and thus the effects of vertical mixing are significantly smaller. The results of the January simulations are displayed in Fig. 5(a). The addition of sub-grid scale vertical mixing did not significantly change the overall relationship between FUV and distance between particle release depths suggesting that the pattern of increasing FUV with distance between particle release depths is due to system dynamics rather than to the absence of vertical sub-grid scale mixing in the model. Hence, simply including sub-grid scale mixing does not alleviate the particle tracking model's sensitivity to particle release depth. Drake et al. (2011), using a biophysical model with a sub-grid scale mixing scheme, also found that larval transport patterns along the U.S. west coast differed when particles were released at different depths and attributed this difference to the presence of the surface mixed layer.

Overall, our study shows that biophysical model results are sensitive to the particle release depth and that the sensitivity is more pronounced in the presence of weak vertical mixing and strong stratification. To counteract the sensitivity of the PDDs to release depth, we recommend that particles be released evenly throughout the water column instead of from a single depth or a small range of depths, unless specific information about spawning depth is available. This procedure will allow the PDDs to represent an average of the varying vertical conditions. As a demonstration, all 120 site, month and year simulations were rerun, first, with particles released every meter from depths of 2–30 m and, second, with particles released every 5 m from depths of 5–30 m. PDDs were then constructed for tracking times of 15 and 30 days. Fig. 10 shows a PDD with particles released every meter from site 10, located on the east side of Santa Catalina Island, for May of 1999 and a tracking time of 15 days. When compared with Fig. 6, Fig. 10 shows an average of the features displayed in the PDDs released at individual depths.

FUVs were calculated between the PDDs with particles released at a single depth and the PDDs with particles released every meter over the water column. The average FUVs are displayed in Fig. 11 for a tracking time of 15 days. The error bars represent an empirical 95% confidence interval. Fig. 11 demonstrates that releasing particles from a single depth will not represent average water column conditions. However, the lowest FUVs are observed around the mid-depth range of 15–23 m implying that the releases from these depths are most similar to average conditions. Thus if it is impractical to release particles over the entire water column, releasing particles over a smaller depth range that most represents average conditions will help minimize model sensitivity. FUVs were also calculated between the PDDs with particles released every meter over the water column and the PDDs with particles released every 5 m over the water column. These FUVs are very low with an average of 0.01, suggesting that 5 m releases are sufficient for representing average water column conditions. Similar results are observed with a tracking time of 30 days (see Fig. 15, available in the Supplementary information).

4.3. Particle tracking time

Particle tracking time for biophysical modeling represents the length of time a marine species remains in the larval stage. This time period is called planktonic or pelagic larval duration (PLD). Unlike the two other parameters, an estimate of species' PLD can often be derived from field data or information about the species’ life history and used to set the particle tracking time in the model. Biophysical modeling studies usually use a single day (e.g. Watson et al., 2010) or a range of days (e.g. James et al., 2002; Siegel et al., 2008) for the particle tracking time. The sensitivity of larval transport predictions to variability in these derived values is rarely examined, and thus for this parameter, we investigate the sensitivity of the PDDs to shifts of 1–4 days in particle tracking time. We observe that when the particle tracking time is shifted farther and farther from a reference particle tracking time, the FUV increases rapidly (Fig. 7). In addition, we observe that PDDs are most sensitive to 1–4 day shifts in particle tracking times when the particle tracking times are about 15 days or less (Fig. 8). In the days immediately after particle release, large numbers of particles are concentrated in relatively small areas as shown in Fig. 9(a) and (b). Driven by the large horizontal eddy dispersion in the SCB (Swenson and Niiler, 1996), the shape of the PDDs initially changes quickly, producing large FUVs (Fig. 8). Once the particles are dispersed over a larger area and become more evenly mixed throughout the model domain as shown in Fig. 9(c) and (d), the change in the shape of the PDDs slows, leading to smaller FUVs. Mitarai et al. (2009) similarly observed that Lagrangian PDDs in the SCB become more homogenous as the particle tracking time lengthens.

For this parameter, we do not have a specific recommendation for model robustness as it is expected that marine fish and invertebrate species will have different PLDs and therefore different larval transport patterns. But since we did show that PDDs with short particle tracking times are more sensitive to 1–4 day shifts in particle tracking times than PDDs with long particle tracking times, we suggest that when predicting patterns of larval transport for species with short PLDs, PDDs be evaluated for a distribution of days around the target PLD.

PDDs for all 180 simulations were recalculated using a random number generator to select particle tracking times in a normal distribution.
around a particle tracking time of a single day (North et al., 2008). The normal distribution had a zero mean and a standard deviation of two days. Using the recalculated PDDs, the FUVs were recalculated between the daily PDDs and the PDDs with reference particle tracking times of 5 days and 15 days. The results are shown in Fig. 8 (a) and (b). This process substantially reduced the FUV between particle tracking times, mitigating the model sensitivity due to the selection of a single day particle tracking time. Additional results for a standard deviation of one day and tracking times of 25 and 35 days are shown in Fig. 25 of the Supplementary information.

5. Recommendations and conclusions

Here we provide a summary of our recommendations on testing and mitigating model sensitivity to the input parameters. It is important to note that although PDDs are used to evaluate model sensitivity, the methods presented are applicable to any two-dimensional grid-based representation of particle distribution. Before testing the parameters, typical release scenarios must be selected, which include the time period of particle release and the particle release locations. We selected a release time of one month and a release location of one nearshore site because previous studies, using the same biophysical model of the SCB, used this release scenario for estimating larval transport and connectivity (e.g. Alberto et al., 2011; Costello et al., 2010; Mitarai et al., 2009; Rassweiler et al., 2012; Selkoe et al., 2010; Watson et al., 2010, 2011, 2012). Once the release scenarios have been selected, sensitivity testing should be conducted over different ocean conditions, such as seasonal and inter-annual, to include possible variations in mixing strength. The modeler must also decide what level of similarity or percent FUV is acceptable for each input parameter. For example, a 5% upper bound was used for the number of particles released (see Fig. 2). However if the level of smoothness depicted in the PDDs in Fig. 3 for higher or lower numbers of particles is more appropriate for the purpose of the study, a different FUV upper bound can be used.

Using the methodology presented in this paper, the three input parameters should be tested with the following three steps.

Step 1. Conduct a sensitivity study for the number of particles released and determine the minimum number of particles required to avoid an undersampling error. If different tracking times will be used in the study, the minimum number of particles should be determined for each tracking time.

Step 2. Conduct a sensitivity study of particle release depth using the minimum number of particles determined in Step 1. If the goal is to avoid sensitivity to particle release depth and the particles are tracked passively with no behavior, particles should be released evenly over the depth of the water column. If the water column is too deep for this to be practical, particles can be released over different ranges of depths and the results compared to determine which range of depths best represents the average conditions in the water column. Some studies do not model larvae as passive particles as was done in this study, but instead impose species-specific behavior on the particles such as diel vertical migration or ontogenetic developmental migration, which keeps the larvae at a fixed depth (Carr et al., 2008; Xue et al., 2008). If this is the case, then sensitivity to release depth may not need to be tested. However, if there is any uncertainty in the biological data used to set the fixed depths, we recommend testing the sensitivity of the larval transport predictions to variations in the fixed depths. Both Vikebo et al. (2005) and Kim and Barth (2011) showed that particles set at fixed depths of 10 m or less apart can result in different larval transport predictions. Finally if the release depths selected for the study are significantly different than the ones used to test the number of particles, Step 1 may need to be repeated.

Step 3. Conduct a sensitivity study for shifts in particle tracking time based on PLD. We choose to evaluate shifts of 1–4 days in particle tracking time because the Lagrangian time scale for horizontal mixing in the Southern California Bight is on the order of days (Mitarai et al., 2009; Swenson and Niiler, 1996), but in systems that mix more slowly, longer shifts may need to be evaluated. If the PLD proposed for the study occurs during a time period that has a high sensitivity to shifts in particle tracking time and biological data is not available to support an exact day or window of days for the species specific PLD, we recommend using a distribution of particle tracking times around the literature-based value.

In summary, we have shown that biophysical models can be quite sensitive to three input parameters required for particle tracking, the number of particles released, the particle release depth, and the particle tracking time, and that the parameters should be carefully selected in order to obtain robust predictions of larval transport and connectivity. Model robustness is particularly important in light of the fact that larval connectivity estimates are being used around the world for the placement of marine protected areas (Botsford et al., 2009; Jones et al., 2009; Levin, 2006; Rassweiler et al., 2012). In addition, we find that model sensitivity is directly linked to the strength of mixing in the system, indicating the importance of sensitivity assessment in individual study areas. Although this paper presents a study of the larval transport in the SCB, the methodology for model robustness presented in this paper is applicable to any biophysical model used to predict larval transport in estuaries and oceans.

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Appendix A. Supplementary data

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References


