

Mesoscale flow variability and its impact on connectivity for the island of Hawai'i

A. C. Vaz,¹ K. J. Richards,² Y. Jia,³ and C. B. Paris¹

Received 9 November 2012; revised 12 December 2012; accepted 13 December 2012; published 28 January 2013.

[1] Understanding population connectivity is a contemporary challenge in marine ecology. Connectivity results from a combination of biological traits and physical mechanisms, at different life stages. We focus on the transport of particles around an oceanic island, simulating transport at early life stages of marine organisms. We aim to investigate through case studies how mesoscale features influence particle transport, recruitment, and connectivity. We determine particle dispersion by using an individual-based model and the flow fields derived from a regional implementation of an ocean circulation model. To understand the underlying physical processes of transport, we locate coherent structures in the flow field, identify recurrent physical features, and observe how particle transport is related to them. Our results show that the varying eddying flow increases connectivity among populations located on different sides of the island. Both the flow field and dispersal patterns are highly variable. In this scenario, eddy events influence transport in distinct ways, and the timing of release plays an important role in dispersal. Our results highlight the need for modeling studies to use hydrodynamical model flows that represent the scales of variability affecting transport and dispersion.
Citation: Vaz, A. C., K. J. Richards, Y. Jia, and C. B. Paris (2013), Mesoscale flow variability and its impact on connectivity for the island of Hawai'i, *Geophys. Res. Lett.*, 40, 332–337, doi:10.1029/2012GL054519.

1. Introduction

[2] One of the most important contemporary areas of investigation in marine ecology is the characterization of population connectivity, which has ecological, economical, and management implications [Botsford *et al.*, 2009; Mitarai *et al.*, 2008]. Marine organisms presenting a pelagic early life stage have their connectivity patterns shaped by a complex combination of biological traits and flow characteristics [Paris *et al.*, 2007]. This study focuses on the latter. Our study site is the island of Hawai'i, part of the

Hawaiian Ridge and located in the center of the North Pacific Subtropical Gyre (Figure 1a). The oceanic flow around the island is dominated by an energetic field of mesoscale eddies, both locally and remotely generated [Calil *et al.*, 2008; Jia *et al.*, 2011]. Connectivity in oceanic islands relies on mechanisms different from those typically acting in coastal environments [Paris and Cowen, 2004]. Since the 1970s, eddies have been regarded as the mechanism responsible for enhancing near-shore larval recruitment around oceanic islands, thereby increasing the chances of larval survival. It has been suggested that coral reef fish have developed spawning strategies that benefit from this transport mechanism: spawning in eddies close to the islands' coasts [Sale, 1970; Johannes, 1978]. Available evidence suggests that eddies influence larval transport and recruitment in the Hawaiian region [Walsh, 1987; Lobel and Robinson, 1986, 1988; Lobel, 2011; Christie *et al.*, 2010]. However, these studies were restricted to small temporal and spatial scales due to sampling methodologies limitations. As a result, the net effect of the eddying field on larval transport and connectivity is still unknown. Since larvae present a small size and relative scarcity in the environment, in situ studies accounting for their dispersal are rare [Paris and Cowen, 2004]. Individual-based models (IBMs) have been developed to evaluate population connectivity and generate dispersal characteristics not yet available from empirical data [Paris *et al.*, 2007; Botsford *et al.*, 2009]. Moreover, IBMs are useful in identifying the underlying physical mechanisms that provide transport pathways used by larvae [Paris and Cowen, 2004]. These pathways result from coherent structures in the time evolving turbulent flow that is typically characterized by Lagrangian methods [Haller and Yuan, 2000]. In an evolving two-dimensional flow, Lagrangian coherent structures (LCSs) can be characterized as material fluid lines. Of particular interest are those material lines that represent regions of rapid divergence and convergence of particles freely drifting in the flow: stable and unstable manifolds, respectively [Haller and Yuan, 2000; d'Ovidio *et al.*, 2004]. Attracting LCSs (unstable manifolds) act not only as attractors of particles, but also barriers to transport in the cross LCS direction [Calil and Richards, 2010; Rypina *et al.*, 2010]. The identification of LCSs therefore provides a powerful aid to the determination of processes affecting larval dispersal. The main objective of this study is twofold: (i) to investigate how the variability of the physical environment affects transport patterns and (ii) to understanding the role eddies play in the transport and recruitment of larvae in an oceanic island. Here we investigate case studies, where particle transport is determined using an IBM [Paris *et al.*, 2007], and the

¹Rosenstiel School of Marine and Atmospheric Science, Division of Applied Marine Physics, University of Miami, Miami, Florida, USA.

²Department of Oceanography, University of Hawai'i at Mānoa, Honolulu, Hawaii, USA.

³International Pacific Research Center, University of Hawai'i at Mānoa, Honolulu, Hawaii, USA.

Corresponding author: A. C. Vaz, Rosenstiel School of Marine and Atmospheric Science, Division of Applied Marine Physics, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, USA. (avaz@rsmas.miami.edu)

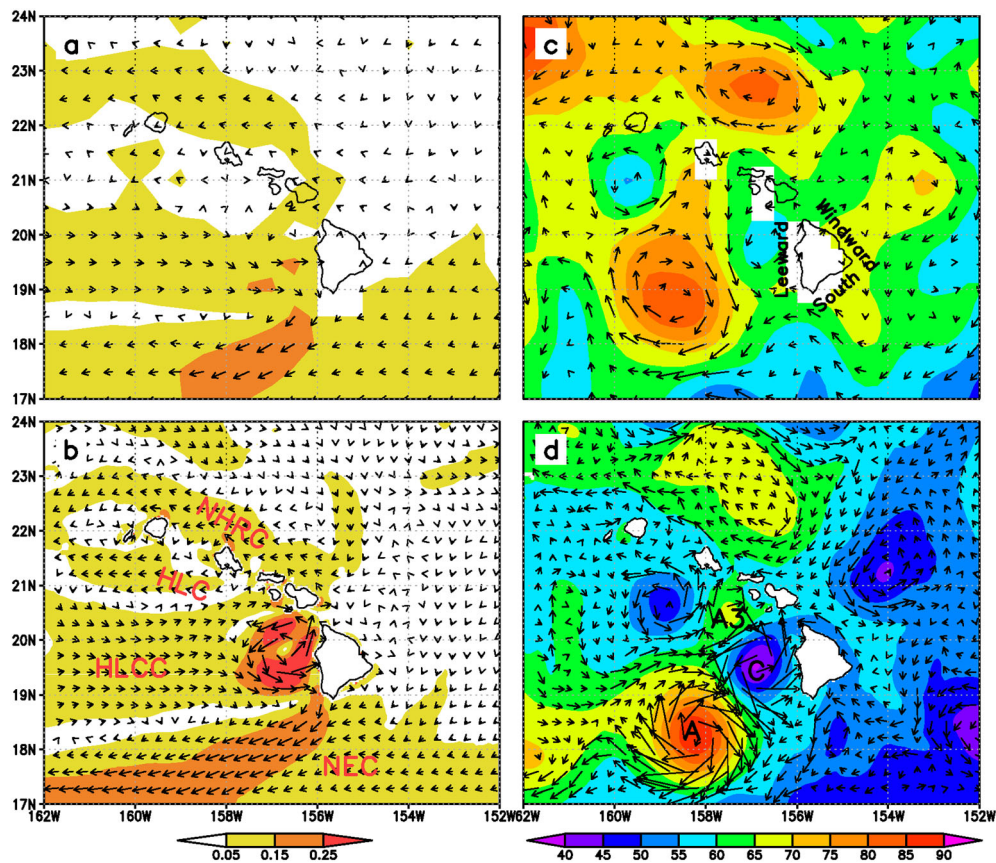


Figure 1. Mean surface geostrophic velocity derived from (a) weekly composites of altimeter observations for the period of 1992–2012 and (b) daily snapshots of sea surface height (SSH) as simulated by the regional HYCOM for the period of 2009–2012. SSH and surface geostrophic velocity from (c) altimetry for the week centered on 16 July 2009, and (d) the regional HYCOM on 18 July 2009.

flow fields derived from a regional implementation of the HYbrid Coordinate Ocean Model (HYCOM) [Jia *et al.*, 2011]. To understand the underlying physical processes of transport, we locate LCSs in the flow field, identify recurrent features, and observe their relation to particle transport.

2. Material and Methods

2.1. Hydrodynamic Model

[3] The regional HYCOM is configured in a nested subdomain (16° – 26° N, 150° – 166° W) within the Global HYCOM (<http://hycom.org/>). It has a horizontal resolution of 0.04° (~ 4 km) and 32 vertical layers. It is forced at the surface by wind stress, heat, and fresh water fluxes at a resolution of 6 km generated by a regional implementation [Tu and Chen, 2011] of the Weather Research and Forecasting (WRF) model. The bathymetry is given by the General Bathymetric Chart of the Oceans database (The GEBCO One Minute Grid, <http://www.gebco.net>). The region's major currents, including the North Equatorial Current (NEC), the Hawai'i Lee Counter Current (HLCC), the Hawai'i Lee Current (HLC), and the North Hawai'i Ridge Current (NHRC), are all reproduced in the regional HYCOM. Their strengths are comparable with that derived from altimetry estimates (Figures 1a and 1b) and field measurements [cf. Jia *et al.*, 2011]. A notable feature present

in the model solution, but not in altimetry, is the cyclonic circulation to the west (or in the lee) of the island of Hawai'i. This discrepancy likely results from: (i) an overestimate of cyclonic eddy generation by the model through the use of a high-resolution wind product and (ii) an underestimate of cyclonic circulation in the altimetry observations due to coarse spatio-temporal sampling resolution. This difference is also reflected in the eddy field at any given time (Figures 1c and 1d).

2.2. Individual-based Model

[4] We used an individual-based model (IBM) [cf. Paris *et al.*, 2007] to calculate particle displacement, which is given by both deterministic and turbulent velocities. The deterministic movement is simulated by a fourth-order Runge-Kutta integration scheme of the simulated velocity field. The turbulence is modeled by simple diffusion [Paris *et al.*, 2007] using a horizontal coefficient of diffusivity of $0.2 \text{ m}^2/\text{s}$ estimated from Okubo [1971]. The particle release and recruitment sites are the 10 km wide region around the island of Hawai'i, subdivided into 53 polygons (Figure S1).¹ The polygons are grouped according to their location: south, leeward (west side), and windward (east side, Figure 1c). From May 2009 to October 2010, 100 particles are released every 5 days in each of the polygons, and at each of the following depth levels: 0, 10, 30, 50, 100, and 200 m. The number of particles and interval of release were

determined after sensitivity analyses of the IBM [Paris *et al.*, 2007]. No vertical behavior is implemented, and particles are dispersed as 2D passive drifters. This allows the investigation of transport processes occurring at different layers, which can be used by fish larvae to enhance their recruitment. Particles are dispersed for 30 days and those older than 20 days found within the limits of recruitment sites are considered recruited, and thus are removed from the simulation. The depths of release, competency period (period during which a particle is able to recruit), dispersal time, and recruitment areas are chosen based on the biological characteristics of larvae from different families (e.g., Pomacentridae, Lutjanidae, Labridae, and Acanthuridae), which are a focus of management measures in the region. A mortality rate ($0.83 \times 10^{-3} \text{ day}^{-1}$) is implemented to account for differences in recruitment due to the decline in abundance over the competency period [Paris *et al.*, 2007], calculated so the e-folding time scale of the particles is equal to their dispersal time. We calculate particle connectivity, local retention, and export as defined by Botsford *et al.* [2009] and Paris *et al.* [2007]. Local retention [cf. Paris and Cowen, 2004] is the fraction of particles settling at the site where they are released. The connectivity patterns are represented by a matrix of probabilities, where the rows are the release sites (i), and the columns are the particles recruitment sites (j) [Paris *et al.*, 2007]. The content of each matrix cell element represents the probability of particles leaving the spawning site and arriving at a recruitment site. The probability at each cell (i,j) is given by the number of particles leaving release site i and arriving at recruitment site j , divided by the number of particles leaving release site i and arriving at all recruitment sites. Therefore, only the recruited particles are considered for the calculation of the probability matrices. For the period of the experiment, from 10% to 30% of the released particles are recruited.

2.3. Finite Size Lyapunov Exponents

[5] Locations of LCSs are estimated by computing Finite Size Lyapunov Exponents (FSLEs) [Haller and Yuan, 2000]. To calculate FSLEs, the drift of pairs of particles is simulated in a given 2D velocity field [d'Ovidio *et al.*, 2004]. FSLEs, $a(x,y,t)$, are given by $\lambda = \log(d_f/d_0)/\tau$, where τ is the time taken by two particles, initially separated by a distance d_0 , to reach a final distance d_f . High values of FSLEs, computed by integrating the particle trajectories forward (backward) in time, identify the repelling (attracting) LCSs. Therefore, strongly positive values of λ represent areas of high divergence for particle trajectories while negative values of λ represent areas to which particle trajectories converge. The methodology to compute the LCSs used a 2D flow field. Results are calculated taking $d_0 = 1 \text{ km}$ and $d_f = 60 \text{ km}$, which is approximately the Rossby radius of the first baroclinic mode in the region. Forward and backward FSLEs are calculated every day from June 2009 to March 2010, for 0, 10, 30, 50, 100, and 200 m, using output from the regional HYCOM. The period of integration is 30 days, which is the same period of particle dispersal. We analyze the FSLEs and track particle positions for all aforementioned depths and periods, from which we identify recurrent features, and how particle transport is related to them.

3. Results

3.1. Lagrangian Coherent Structures

[6] To exemplify the highly dynamic and complex nature of the flow, we consider particles released at 30 m depth on 18 July 2009 (Figure 2). Attracting LCS (unstable manifolds) are the ridges where λ reaches negative values, representing lines of compression on the flow [Joseph and Legras, 2002]. Repelling LCS (stable manifolds) are therefore regions with positive values of λ , representing lines of strong stretching and stirring in the flow [d'Ovidio *et al.*, 2004]. The attractive nature of the unstable manifolds is evident in Video S1, which shows the evolution of the LCS field and particle trajectories. At the time of release, the flow in the northern tip of the island is dominated by a vortex dipole (A3 and C) to the west of Hawai'i (Figure 1b). Seven days after particle release, LCSs are visible around the vortex dipole (Figure 2a), with a strong attracting LCS leading back to the northern tip of the island. Particles from the leeward coast (blue points) are transported and accumulated along this structure. Particles are subsequently advected around cyclonic vortex C (Figure 2b), while moving away from the island (Figure 2d). A strong attracting LCS is also present at the island's southern tip at the time of particle release, associated with anticyclonic vortex A (Figure 1b) shed days earlier. Particles from both the leeward and southern coasts are captured by this structure. As vortex A moves westward (Figure 2a), the strong stretching by two smaller anticyclonic eddies (A1 and A2) disrupts the original LCS, creating a new LCS (seen in Figure 2b oriented approximately north/south). Particles are now distributed along this feature. In addition, this unstable manifold is intersected by a stable manifold (at 18.4°N , 156.2°W to form a hyperbolic point, Figure 2a). The presence of the stable manifold splits the particles. Leeward particles predominantly head north (Figures 2a and 2b) and are entrained by vortex A1, which remains off the leeward shore for more than 2 weeks. By August 7, a number of particles from the southern and windward regions have also been entrained by the outer rings of vortex A1 (Figure 2c). On August 14, 28 days since particle release, the evolving eddy flow has created a colorful mosaic of particles in the lee of Hawai'i Island (Figure 2d). The transport and dispersion of particles are also affected by subtle changes in the LCSs. To illustrate, we compare the LCSs and distribution of particles released at the same time at different depths (Figure 3). Similar features of LCSs are discernible at all levels. The differences in the strength of the LCSs, however, affect particle distributions greatly. For instance, the attracting LCS located at the north of the island captures particles predominantly from the windward coast at 100 m, rather than leeward particles as is the case at 30 m. The less prominent feature at the surface fails to capture any particles. Similarly, the anticyclonic vortex centered at 19°N , 156.8°W , entrained windward particles only at 30 m. We observed that the pattern of particle transport (Figure 2) is controlled by the history of the time evolving LCSs. Initially we are able to follow the transport of particles by individual features, however, the evolution of the flow quickly produces a complex picture of stirring and stretching of particles and filament of particles (as seen in tracer fields produced by many simple time evolving flows; cf. Otinno [1989]). The eddy "events" described above are frequent

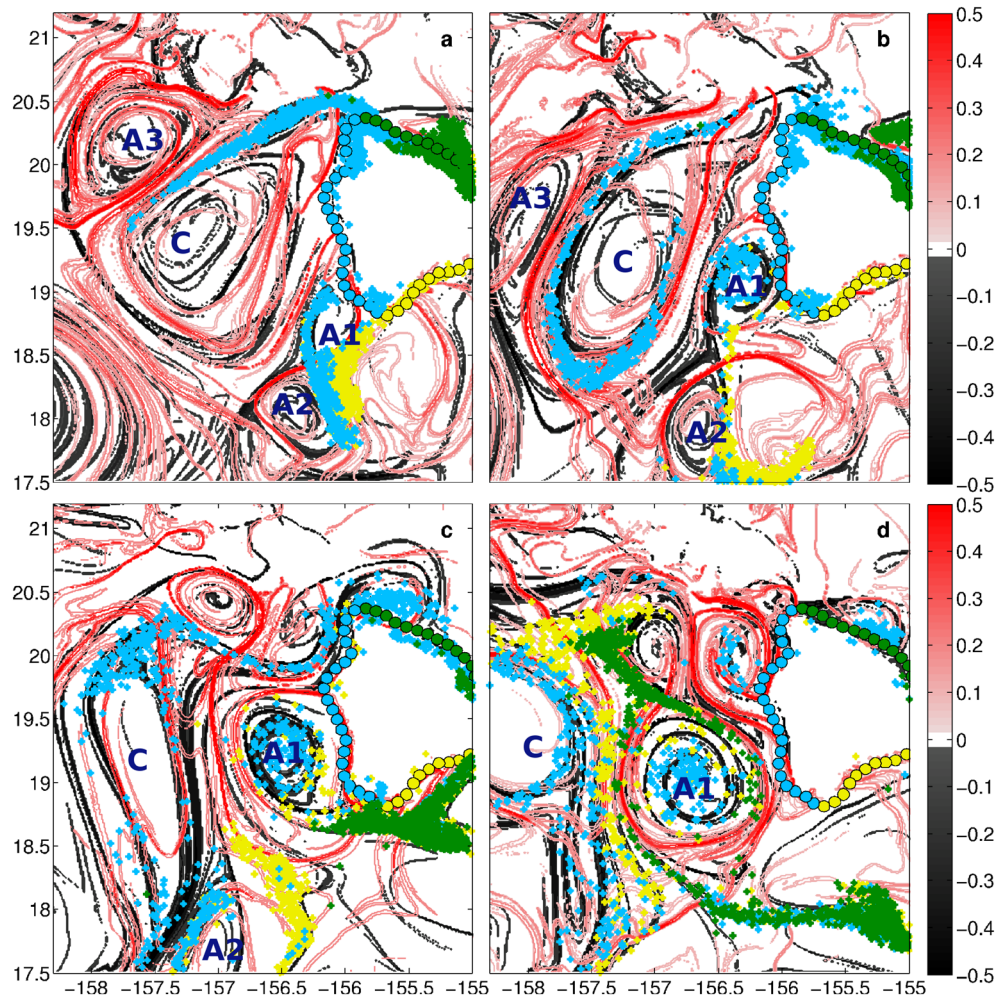


Figure 2. Distribution of particles, forward (red) and backward (black) FSLEs (d^{-1}) on (a) 25 of July, (b) 30 of July, (c) 7 of August, and (d) 15 of August 2009 for the regional HYCOM. In this figure, particles were released on 18 of July 2009 and tracked for 7, 12, 20, and 28 days (respectively) at 30 m. Particles are colored according to the face of the island where they were released.

occurrences in the lee of the islands and contribute to the elevated eddy kinetic energy observed in the region [Calil *et al.*, 2008]. The time average of the FSLEs is similarly elevated in the lee of Hawai'i. However, no individual structure is discernible in either the annual or seasonal mean, indicating there are no persistent transport barriers. To determine the net effect of the eddying flow for theoretical species living in the near-shore region, we next consider the connectivity of populations on different sides of the Hawai'i Island.

3.2. Connectivity Patterns

[7] Annual connectivity matrices (June 2009 to May 2010) obtained from different layers present distinct features, although main patterns of recruitment are consistent among depths (Figure 4). For instance, local retention on the leeward and windward coast is very high for all layers. However, at surface and at 30 m depth, particles released in the south region are both likely to be locally recruited and exported to the leeward coast, while at 100 m most particles are locally recruited. Connectivity patterns not only vary with depth but also present strong time variability. We calculated averages

of the proportion of retained particles for distinct periods, and the results indicate that recruitment levels vary with time. Moreover, the simulated connectivity matrices present daily, monthly, and interannual variability. Despite the variability, there are consistent connectivity patterns for the study period. The three regions around the island of Hawai'i show high local retention. The south shows the largest particle export with a strong flow directed to the leeward side, which is only interrupted in 2 months: June and December of 2009. In both cases, the formation of an anticyclonic eddy created a barrier to the transport. This transport pattern is corroborated by genetic parentage analysis [Christie *et al.*, 2010], which found that larvae of yellow tang (*Zebrasoma flavescens*) originating in the south of Hawai'i joined leeward populations. According to our results, such larval fluxes from south to leeward appear as a recurrent pattern. Local retention on the leeward coast found in our model was also detected by the genetic parentage study [Christie *et al.*, 2010], and it is suggested by drifters trajectories and larval sampling along an eddy in the leeward coast [Lobel and Robinson, 1986, 1988; Lobel, 2011]. To access the impact of the mean flow on the connectivity, we calculated connectivity matrices for particles dispersed by

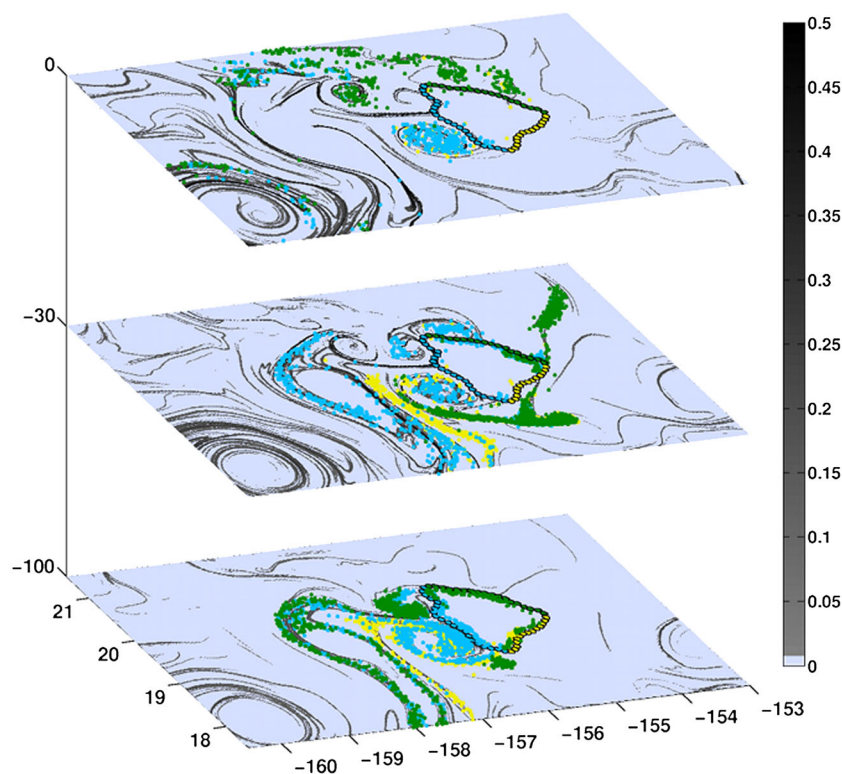


Figure 3. Distribution of particles and backward FSLEs (d^{-1}) for surface, 30, and 100 m on 10 of August 2009 for the regional HYCOM. In this figure, particles were released on 18 of July 2009 and tracked for 23 days. Particles are colored according to the face of the island where they were released.

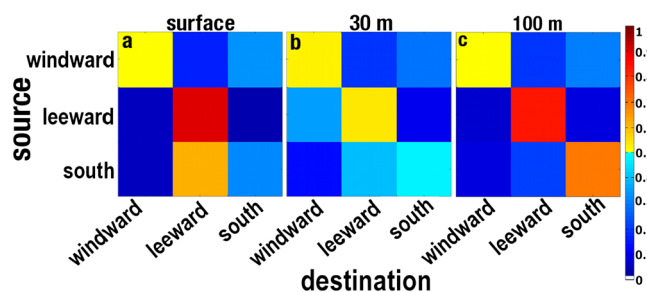


Figure 4. Connectivity matrices for the Hawai'i Island from June 2009 to May 2010. Particles were released at (a) surface, (b) 30, and (c) 100 m.

the mean flow field of the regional HYCOM (averages of daily velocities from June 2009 to May 2010 for the surface, 30 and 100 m, results not shown). Some transport patterns were observed for both the time evolving and the mean flow, such as local retention and transport from the south to the leeward. However, the time-evolving flow field increased the connectivity among all areas around the island. At 30 m, it also increased the probability of transport from south to leeward and local retention on the leeward coast. These results highlight the importance of the eddy field on particle dispersal.

4. Discussion

[8] The picture emerging from the analysis of LCSs for the modeled flow in Hawai'i is one of a highly dynamic and complex environment [Rypina *et al.*, 2010]. Despite

the complexity, it has been possible to identify features in the FSLEs fields such as dipoles, eddies, and hyperbolic points that have a strong influence on particle trajectories (Figure 2). Although the flow dynamic of attracting LCSs clearly leads to particle accumulation along these features, in a time-evolving flow, even subtle changes to the location and strength of the LCSs result in profound changes to the transport of particles and their connectivity. Thus, LCSs varying in both depth and time produce patterns of transport and connectivity that vary at time scales from days to years. Strong LCSs are seen in the observed flow as given by the gridded, satellite-derived SSH field [cf. Figure 10 from Calil and Richards, 2010]. As shown above, the LCSs shape the transport of particles in the regional HYCOM. During the study period, the eddying field was responsible for increasing connectivity and influencing recruitment. We observed that eddies can entrap and recirculate particles close to the coast, agreeing with larval sampling and drifter studies around the Hawai'i Island [Lobel and Robinson, 1986, 1988; Lobel, 2011]. However, eddies can also lower recruitment by transporting larvae offshore, as suggested by reef fish recruitment studies [Walsh, 1987]. Our results provide information about the role eddies play in recruitment and consolidate conflicting conclusions from previous empirical research. In short, both cyclonic and anticyclonic features were observed to influence the transport of particles in four distinct, and even opposing, ways: (i) by increasing the transport of particles from distinct regions, (ii) by enhancing local retention, (iii) by entrapping particles and transporting them away from the coast, decreasing recruitment, and (iv) by creating a transport barrier. Large

mesoscale eddies can dominate the flow from days to weeks and are the most studied features in the region. However, we observed that eddies with a smaller spatial scale were important for the transport and recruitment of particles, as suggested by *Leis* [1982]. Although eddies influence particle transport, the presence of an eddy and associated LCSs does not mean that enhanced or reduced recruitment will take place. Given such dynamical patterns, we did not find a simple correlation between eddy occurrence and recruitment over long periods of time. This indicates that the timing and location of spawning also play a role in the recruitment of larvae [Karnauskas et al., 2011]. Despite the high variability, there were recurrent connectivity patterns: (i) local retention for the three areas and (ii) a flow from south to leeward. Both patterns for the leeward coast agree with observational studies [Christie et al., 2010; Lobel, 2011]. Our results show that both local retention in the leeward and export from the south to leeward are recurrent and persistent throughout the year. The high variability observed for both the FSLEs fields and connectivity patterns highlights the need for modeling studies to use flow fields that represent such scales of variability.

[9] **Acknowledgments.** This project was funded by Cooperative Agreement NA09OAR4320075 between the Joint Institute for Marine and Atmospheric Research (JIMAR) and the National Oceanic and Atmospheric Administration (NOAA). The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its subdivisions. AC Vaz acknowledges support through a PhD scholarship from the Brazilian Ministry of Education (CAPES, Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, grant 2259/05-2) and the Fulbright Program (grant 15061655). Thanks are due to Francesco d'Ovidio for providing the original code for calculating the FSLEs. The authors also thank the two anonymous reviewers for their constructive comments.

References

- Botsford, L. W., J. W. White, M. A. Coffroth, C. B. Paris, S. Planes, T. L. Shearer, S. R. Thorrold, and G. P. Jones (2009), Connectivity and resilience of coral reef metapopulations in marine protected areas: Matching empirical efforts to predictive needs, *Coral Reefs*, doi:10.1007/s00338-009-0466-z.
- Calil, P. H. R., K. J. Richards, Y. Jia, and R. R. Bidigare (2008), Eddy activity in the lee of the Hawaiian Islands, *Deep-Sea Res. II*, doi:10.1016/j.dsr2.2008.01.008.
- Calil, P. H. R., and K. J. Richards (2010), Transient upwelling hot spots in the oligotrophic North Pacific, *J. Geophys. Res.*, *115*, C02003, doi:10.1029/2009JC005360.
- Christie, M. R., B. N. Tissot, M. A. Albins, J. P. Beets, and Y. Jia (2010), Larval connectivity in an effective network of marine protected areas, *PLoS One*, *5*(12), e15715, doi:10.1371/journal.pone.0015715.
- Haller, G., and G. Yuan (2000), Lagrangian coherent structures and mixing in two-dimensional turbulence, *Physica D*, *147*, 352–370.
- Johannes, R. E. (1978), Reproductive strategies of coastal marine fishes in the tropics, *Environ. Biol. Fishes*, *5*, 251–252.
- Jia, Y., P. H. R. Calil, E. P. Chassignet, E. J. Metzger, J. T. Potemra, K. J. Richards, and A. J. Wallcraft, (2011), Generation of mesoscale eddies in the lee of the Hawaiian Islands, *J. Geophys. Res.*, *116*, C11009, doi:10.1029/2011JC007305.
- Joseph, B., and B. Legras (2002), Relation between kinematic boundaries, stirring and barriers for the Antarctic Polar Vortex, *J. Atmos. Sci.*, *59*, 1198–1212, doi:http://dx.doi.org/10.1175/1520-0469(2002)059<1198:RBKBSA>2.0.CO;2.
- Karnauskas, M., L. M. Chérubin, and C. B. Paris (2011), Adaptive significance of the formation of multi species fish spawning aggregations near submerged capes, *PLoS One*, *6*(7), e22067, doi:10.1371/journal.pone.002206728.
- Leis, J. M. (1982), Nearshore distributional gradients of larval fish (15 taxa) and planktonic crustaceans (6 taxa) in Hawai'i, *Mar. Biol.*, *72*, 89–97.
- Lobel, P. S., and A. R. Robinson (1986), Transport and entrapment of fish larvae by ocean mesoscale eddies and currents in Hawaiian waters, *Deep-Sea Res.*, *33*, 483–500.
- Lobel, P. S., and A. R. Robinson (1988), Larval fishes and zooplankton in a cyclonic eddy in Hawaiian waters, *J. Plankton Res.*, *10*(6), 1209–1223.
- Lobel, P. S. (2011), Transport of reef lizardfish larvae by an ocean eddy in Hawaiian waters, *Dyn. Atmos. Oceans*, doi:10.1016/j.dynatmoce.2011.01.001.
- Mitarai, S., D. A. Siegel, and K. B. Winters (2008), A numerical study of stochastic larval settlement in the California Current system, *J. Mar. Syst.*, *69*, 295–309, doi:10.1016/j.jmarsys.2006.02.017.
- Okubo, A. (1971), Oceanic diffusion diagrams, *Deep-Sea Res.*, *18*, 789–802.
- Otinno, J. M. (1989), *The Kinematics of Mixing: Stretching, Chaos, and Transport*, Cambridge University Press, New York, NY.
- d'Ovidio, F., V. Fernandez, E. Hernandez-Garcia, and C. Lopez (2004), Mixing structures in the Mediterranean Sea from finite-size Lyapunov exponents, *Geophys. Res. Lett.*, *31*, L17203, doi:10.1029/2004GL020328.
- Paris, C. B., and R. K. Cowen (2004), Direct evidence of a biophysical retention mechanism for coral reef fish larvae, *Limnol. Oceanogr.*, *49*(6), 1944–1979.
- Paris, C. B., L. M. Cherubin, and R. K. Cowen (2007), Surfing, spinning, or diving from reef to reef: Effects on population connectivity, *Mar. Ecol. Prog. Ser.*, *347*, 285–300, doi:10.3354/meps06985.
- Rypina, I. I., L. J. Pratt, J. Pullen, J. Levin, and A. L. Gordon (2010), Chaotic advection in an archipelago, *J. Phys. Oceanogr.*, *40*, 1988–2006, doi:10.1175/2010JPO4336.1.
- Sale, P. F. (1970), Distribution of larval acanthuridae off Hawai'i, *Copeia*, *1970*, 765–766.
- Tu, C. C., and Y. L. Chen (2011), Favorable conditions for the development of a heavy rainfall event over Oahu during the 2006 wet period, *Weather Forecast.*, *26*, 280–300, doi:http://dx.doi.org/10.1175/2010WAF222449.1.
- Walsh, W. J. (1987), Patterns of recruitment and spawning in Hawaiian reef fishes, *Environ. Biol. Fishes*, *18*, 257–276.