



Robotic biomimicry demonstrates behavioral control of planktonic dispersal in the sea

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ABSTRACT: Plankton are widely considered to be at the mercy of ocean currents, even after decades of research revealing that plankton regulate dispersal by positioning themselves in surface and bottom currents flowing in different directions. The degree of effectiveness of these behaviors remains controversial, because tiny plankters cannot be tracked at sea. Here, we experimentally tested the effectiveness of 3 vertical positioning behaviors in nature by developing a biomimetic robot that emulates them. We conducted a challenging test by deploying them in complex circulation during strong upwelling winds and wind relaxation and reversal events. Behavior alone dramatically affected transport. Transport trajectories of robots with 3 different behaviors diverged markedly while those sharing the same behavior were very similar. Moreover, all 3 behaviors produced trajectories that matched previously modeled projections during both upwelling and relaxation conditions at the study site: shallow plankton disperse far, deep plankton move little, and plankton migrating from depth during the day to the surface at night travel an intermediate distance. The ability of weakly swimming plankton to control their fate and replenish populations in a dynamic ocean is of central importance to the ecology and evolution of marine life and to the management of resources in a changing climate.

KEY WORDS: Dispersal · Plankton · Larval transport · Vertical migration · Robotics

1. INTRODUCTION

Dispersal is fundamental to the ecology and evolution of marine life, with implications for spawning migrations, species range extensions due to climate change, the spread of invasive species, management of commercial species as one or more stocks, and the design, siting, and evaluation of networks of marine protected areas (Strathmann et al. 2002, Morgan 2014, Burgess et al. 2016). However, dispersal is challenging to determine in the sea, where most marine animals produce vast numbers of microscopic larvae that develop for weeks in the plankton. The sheer numbers of larvae produced, their poor swim-

ming capabilities, and episodic settlement events have led to the widespread belief that advection by strong currents and other sources of mortality often overwhelm larvae, carrying them far from natal populations, resulting in highly variable recruitment in time and space that is difficult to forecast (Hjort 1914, Thorson 1950, Scheltema 1975, Caley et al. 1996). The actual contribution of advection to mortality remains uncertain because the fate of tiny plankton cannot be tracked for weeks in ocean currents. Instead, estimates have been largely based on logical inference, small-scale empirical studies, and theoretical and numerical oceanographic models which often do not incorporate larval behavior, thereby

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overestimating the contribution of advection to mortality in the plankton (Morgan 1995, 2001, White et al. 2014, Shanks & Morgan 2018).

A long history of observations in the laboratory and field indicate that zooplankton may limit losses due to advection away from adult populations by moving vertically between currents that differ in speed or direction with depth (Young 1990, Queiroga & Blanton 2005, Naylor 2006, Morgan 2014, 2020, Epifanio & Cohen 2016). Zooplankton commonly change depth over the diel cycle (diel vertical migration; DVM), tidal cycle (tidal vertical migration; TVM) and during development (ontogenetic vertical migration; OVM). Early skeptics discounted the ability of zooplankton to effectively regulate depth in the field (e.g. DeWolf 1973, McCleave & Wippelhauser 1987). They argued that zooplankton drifting in open water do not have fixed visual or tactile references to judge speed and direction of water flow, and they remain in the same parcel of water over a tidal cycle, lacking changes in cues to stimulate TVMs. Moreover, responses of zooplankton to isolated variables in static laboratory conditions and complexes of variables in the field do not always match (Cronin & Forward 1986, Young 1986, James et al. 2019), and depth regulation may be more challenging for weakly swimming ciliated larvae, such as polychaetes and mollusks, than stronger swimming larvae, such as crabs and fishes (Young 1995).

Decades of surveys across estuaries and the continental shelf suggest that both larvae of benthic species (meroplankton) and permanent residents of the plankton (holoplankton) limit dispersal. Larvae of some species remain nearshore throughout development, while larvae of other species are initially transported offshore and later return onshore to adult habitats, consistent with a cross-shelf migration (Bousfield 1955, Peterson 1998, Queiroga & Blanton 2005, Morgan 2014, 2020). The evidence for the effectiveness of depth regulation is inferential and reveals little about alongshore dispersal given that larvae in sequential plankton samples may have originated from different alongshore locales. The advent of natural elemental marker and genetic relatedness techniques clearly indicate that larvae stay much closer to home than was widely believed (Swearer et al. 2002, Cowen & Sponaugle 2009, Jones et al. 2009, Burgess et al. 2014), but these studies typically lack mechanistic companion studies on larval behavior showing how this was accomplished. Despite growing evidence that larval behavior limits dispersal and facilitates recruitment by both vertical and onshore swimming (Kingsford et al. 2002, Quei-

roga & Blanton 2005, Arvedlund & Kavanagh 2009, Leis et al. 2011, Epifanio & Cohen 2016, Morgan 2020), models still often do not incorporate larval behavior, and larval advection from natal populations is still considered to be a key determinant in limiting recruitment to populations and communities (Roughgarden et al. 1988, Menge et al. 2003, Broitman et al. 2008, Woodson et al. 2012, Menge & Menge 2013).

Because individual zooplankters cannot be tracked at sea, the ability of zooplankton to regulate transport by vertical positioning could not be experimentally addressed until the advent of robotics and biomimicry (Vincent et al. 2006). We developed a novel instrumented robot, the Autonomous Behaving Lagrangian Explorer (ABLE; Fig. 1), that mimics verti-

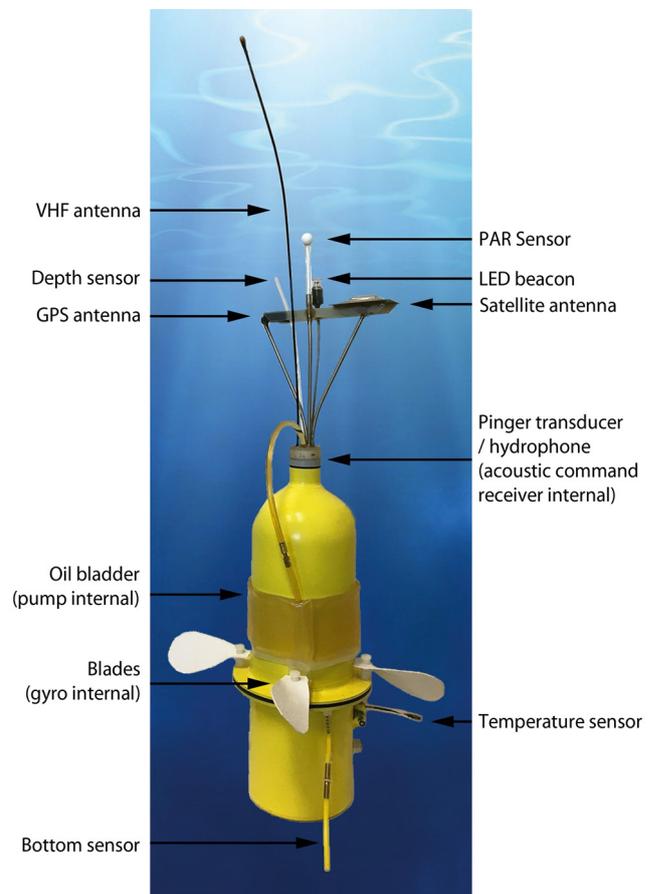


Fig. 1. The Autonomous Behaving Lagrangian Explorer (ABLE) weighs 3 kg and is 20 cm tall with a 15 cm antenna mast. It adjusts depth by pumping oil from an internal reserve into an external bladder to ascend, and the reverse to descend. A bottom sensor keeps it off the bottom. It logs vertical swimming speed by using a gyroscope to measure spinning induced by 'propeller' blades while profiling temperature and photosynthetically active radiation through the water column. We track it by GPS and home in on it by ultrasonic, VHF radio and LED beacons

cal swimming and dispersal of meroplankton and holoplankton in real-world settings. We deployed our biomimetic robot in the upwelling system at Bodega Bay, northern California, USA, where we conducted 13 previous studies on the complex circulation and its effects on larval transport, including mapping the horizontal and vertical structure of water column properties and currents of Bodega Bay (Roughan et al. 2005), larval surveys for many species of invertebrates relative to water column structure and currents in the bay and nearshore coastal waters (Mace & Morgan 2006a, Morgan & Fisher 2010, Morgan et al. 2011, 2012, Nickols et al. 2013) as well as across the shelf (Morgan et al. 2009a,b, 2018, Hameed et al. 2018), modeling the effect of documented interspecific differences of larval behavior on transport in the bay (Roughan et al. 2005) and the shelf (Drake et al. 2013), and interspecific differences in physical processes delivering recruiting postlarvae onshore (Mace & Morgan 2006b, Morgan et al. 2009a). If transport in the lee of Bodega Head is controlled by vertical swimming, we hypothesized that ABLEs simulating 3 common swimming behaviors of larvae would follow very different paths. In this region, strong, persistent alongshore winds from the north combine with the Coriolis effect to drive surface waters offshore and southward, while subsurface water flows onshore and upwells at the coast (Largier et al. 1993, Hickey 1998). In the bay, sheared flow occurs during northerly winds when near-surface waters flow southward with the wind, while near-bottom waters flow upwind and upwell at the north shore in a way that concentrates depth-seeking larvae (Roughan et al. 2005, Mace & Morgan 2006a, Morgan et al. 2011) (Fig. 2A). Winds peak during the afternoon and usually weaken at night (Dorman et al. 2006), reducing southward transport of near-surface water. When winds weaken or switch to a southerly direction, the surface flow reverses and flushes larvae from the bay (Morgan et al. 2012) (Fig. 2B).

During northerly wind, we hypothesized that ABLEs would be (1) retained in the bay if they remained

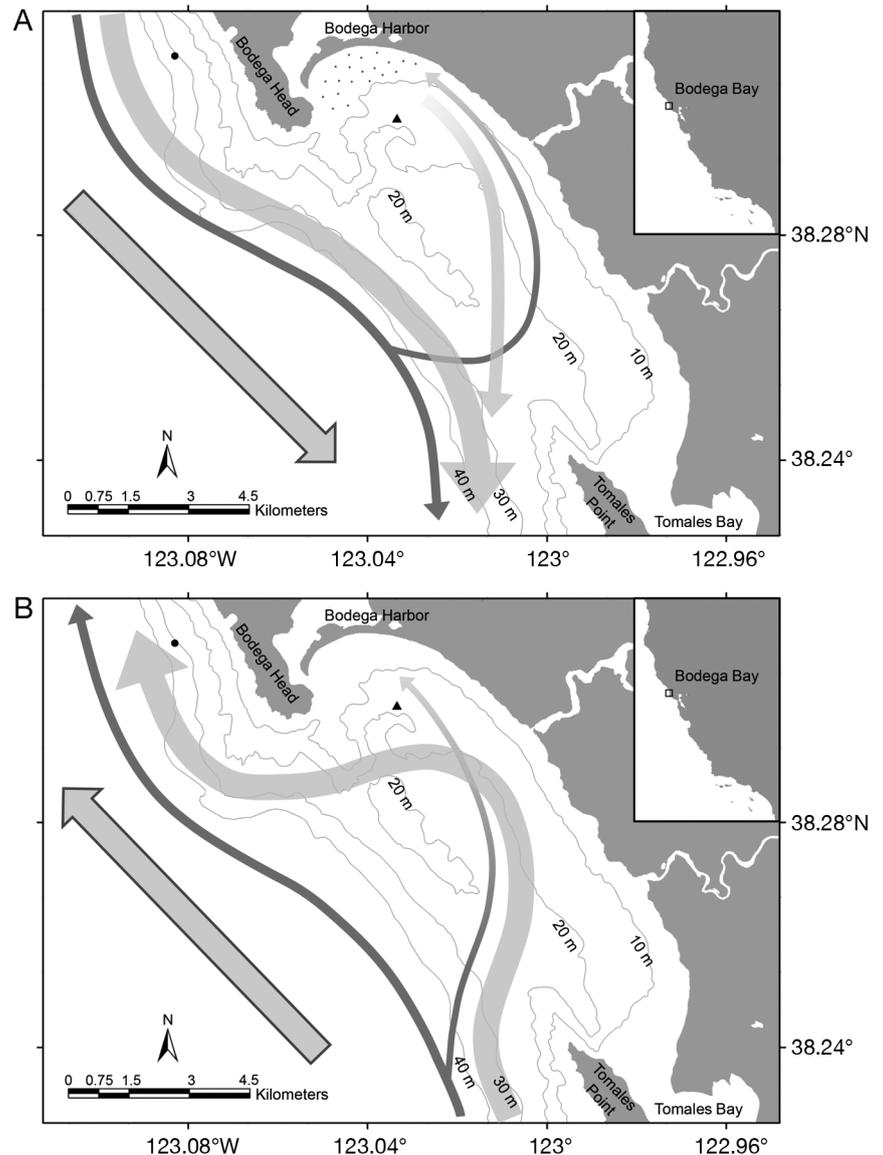


Fig. 2. Circulation in Bodega Bay, California, USA. (A) During strong northwesterly winds (large gray arrow), Bodega Head partially blocks the wind, slowing near-surface currents (light gray arrows) relative to the open coast while upwelling (stippling) occurs along the northern shore of the bay. Near-bottom (dark gray arrows) waters flow into the bay forming an eddy. (B) During weak northwesterly or southerly winds (large gray arrow), surface waters (light gray arrows) flow through the bay while near-bottom waters (dark gray arrows) flowing into the bay are partially obstructed from exiting by a shallow ridge crossing the northern mouth of the bay. The density of shading and width of arrows represent current speed. Solid circle: location of the mooring; solid triangle: location of deployments

near-bottom by maintaining a depth of 16 m, (2) retained if they performed a 2–16 m DVM on days when winds subsided at night, (3) transported southward and seaward out of the bay if they performed DVM on days when winds persisted at night, and (4) transported southward and seaward farthest if they

remained near-surface by maintaining 2 m depth. We also hypothesized that when winds weaken or become southerly, the flow reversal would transport ABLEs northward, with near-surface robots moving farthest, near-bottom ones moving least due to reduced flow from bottom drag, and those undertaking a DVM traveling an intermediate distance.

2. MATERIALS AND METHODS

We experimentally tested whether behavior controls transport by deploying ABLEs (Fig. 1) for about 24 h. The ABLE is a neutrally buoyant body moving with the surrounding water without inertial forces, like drogues long used by oceanographers to determine circulation and velocities of surface currents, but capable of adaptively changing the depth of the water parcel it is tracking as a function of time and its measurements of the physical microenvironment, such as depth, temperature, light, and displacements

by turbulence (Fig. 3). The ABLE has no structures like a float or pendant outside the parcel of water in which it is embedded and hence no extraneous drag to cause drift errors. However, ABLEs need to surface to obtain and report their position, which was done infrequently (every 4 h) to minimize error due to time spent away from target depth (Fig. 3).

Three replicate ABLEs simulating 3 vertical behaviors for a total of 9 ABLEs were deployed 12 times in the lee of Bodega Head between the 10 and 20 m isobaths (deployments at 38.30075° N, 123.03342° W) during a range of typical wind conditions (Table 1). We programmed ABLEs to remain 2 m below the surface, 16 m deep (otherwise 2 m above the bottom when in shallower water), or migrate from 16 m deep during the day to 2 m below the surface at night (DVM; Fig. 3). Based on a 14 h light and 10 h dark photoperiod, we programmed DVM ABLEs to start descending from the surface near dawn and ascend near dusk with transit taking approximately 12 min. ABLEs recalculated their target depth every 10 s and

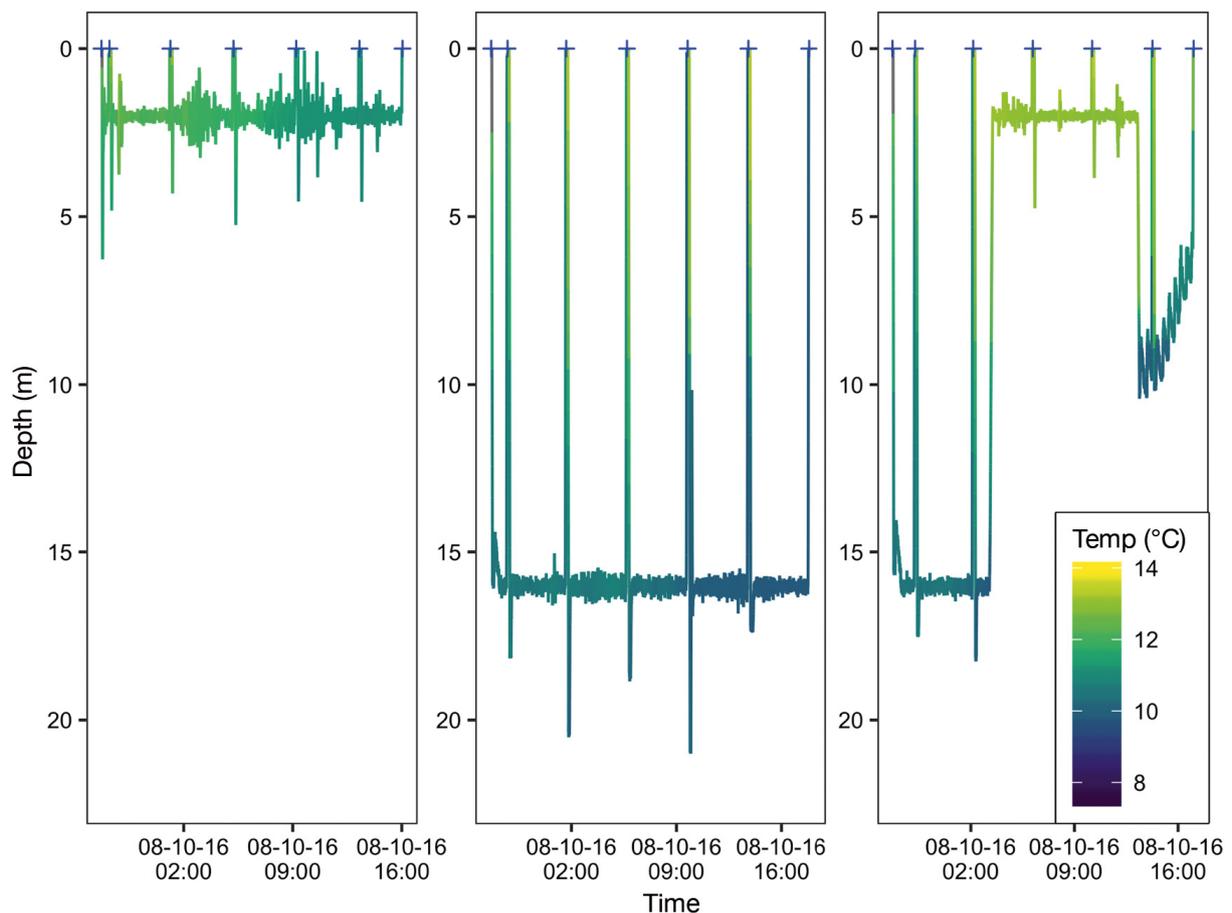


Fig. 3. Depth records from 10 August 2016 (time shown as GMT), of ABLEs targeting (A) a depth of 2 m, (B) a depth of 16 m, and (C) undertaking a diel vertical migration between 16 m during the day and 2 m at night. The rising trace in the right panel shows the ABLE sensing and remaining above a shoaling bottom. ABLEs made excursions to the surface for GPS fixes every 4 h

Table 1. Mean (\pm SE) wind conditions during 12 ABLE deployments. Representative trajectories of 6 of the deployments (indicated by asterisks) are illustrated in Fig. 4

Date	— Wind stress (N m^{-2}) —	
	Alongshore	Cross-shore
19–21 August 2015	-0.008 ± 0.001	0.003 ± 0.001
6–7 June 2016	0.001 ± 0.001	0.01 ± 0.001
16–17 June 2016	0.012 ± 0.002	0.003 ± 0.001
20–21 June 2016*	-0.049 ± 0.006	-0.002 ± 0.000
7–8 July 2016*	-0.051 ± 0.006	0.003 ± 0.001
9–10 August 2016*	0.009 ± 0.002	0.005 ± 0.001
10–11 May 2017*	0.002 ± 0.002	0.011 ± 0.003
21–22 June 2017*	0.012 ± 0.003	0.006 ± 0.001
27–29 June 2017	-0.053 ± 0.007	0.002 ± 0.001
26–27 March 2018	-0.058 ± 0.006	-0.004 ± 0.001
2–3 April 2018	-0.056 ± 0.011	0.000 ± 0.000
16–17 April 2018*	-0.031 ± 0.008	0.001 ± 0.001

moved toward the new target depth at speeds typical of many larvae (about 1 cm s^{-1} , limited to a maximum of 10 cm s^{-1}) (Young 1995). Whenever an ABLE encountered the bottom, it adjusted target depth dynamically to hover above it, avoiding dragging along it or getting lodged (Fig.). Every 10 s, ABLEs logged temperature and depth, photosynthetically active radiation, and rate of vertical movement through the water; from these data, the depth of the surface mixed layer (thermocline depth) can be observed, and vertical currents can be derived from the difference between measured movement through water and changes in depth from the pressure sensor. We programmed ABLEs to make brief excursions to the surface at 15 cm s^{-1} every 4 h to obtain a position fix from the GPS and transmit their coordinates via Globalstar satellites to our webserver before returning to their target depth (Fig. 3). The proportion of time spent off target depth to obtain fixes ranged from 5% for 2 m to 7% for 16 m, minimizing drift errors from surface currents.

We recovered ABLEs by taking a boat to the most recent position reported by satellite. If the ABLE had already surfaced for recovery, we proceeded to the latest satellite fix (updated every 20 min) and homed in using pulse-encoded coordinates from a VHF radio beacon (fix updated every 10 min, 5 km range). Final approach relied on searching for the ultrasonic beacon using a directional hydrophone (1 km range) and the LED beacon (helpful in daylight, essential at night when it could be seen for 1.5 km). If the ABLE was still submerged (had not reached its programmed recovery time), we extrapolated its probable location and searched for the ultrasonic beacon using the hydrophone. Once located, ABLEs could be re-

called to the surface with an ultrasonic command. ABLEs were captured with a large dip net. Logged data were uploaded via a Bluetooth link. Software, written in R v.3.5.1 (R Core Team 2017), expedited processing, visualizing, and analyzing data.

We obtained hourly wind velocity records from the Bodega Marine Laboratory, which is located on Bodega Head. Wind velocities were rotated and decomposed to alongshore and cross-shore components (assuming a coastline angle of 320° as in prior studies here; e.g. Roughan et al. 2005). We focused on the alongshore wind stress, which drives upwelling and currents. Weaker cross-shore winds do not significantly affect currents (Roughan et al. 2005), nor were they related to the observed transport of ABLEs. The trajectory of each ABLE was mapped and the mean (± 1 SE) displacement was determined for each of the 3 behaviors for each deployment.

ABLE displacements were analyzed in R for all 12 deployments using generalized linear mixed models (GLMMs) fit using maximum likelihood or restricted maximum likelihood, and post hoc hypothesis testing performed with ANOVA via the statistical packages ‘lme4,’ ‘lmerTest,’ ‘stats,’ and ‘car’. The GLMM response variable was either the overall speed of absolute transport (km h^{-1}) or the speed of north–south (latitudinal) transport (km h^{-1}), which were fitted to gamma and normal distributions with natural logarithm and identity link functions, respectively. In each GLMM analysis, we fixed effects of behavior, synoptic conditions (a categorical variable indicating upwelling if mean alongshore wind stress for the deployment was negative or reversal if it was positive), and elapsed time (to account for differences in the actual length of exposure among robots and deployments), up to third-order interaction terms and a random effect of deployment date (see Table 2). Data met the assumptions of normality and equal variances.

3. RESULTS

Transport trajectories of ABLEs with different behaviors dramatically diverged, while those of ABLEs sharing the same behavior were very similar (Fig. 4A–F). Trajectories of DVMs differed more among deployments than for the other 2 behaviors due to differences in wind velocities at night. During northerly upwelling winds, deep ABLEs remained near the point of release, whereas near-surface ones were transported far south (Fig. 4A–C). DVM ABLEs

traveled an intermediate distance because they were in slow bottom flow during the day while the wind was strong and reduced surface flow at night depending on how much the wind subsided (weakest in Fig. 4A). When flow reversed during wind relaxations and reversals, deep ABEs moved little, while near-surface ABEs moved quickly out of Bodega Bay and northward (Fig. 4D–F), like larvae displaying these behaviors evidently did in a previous study (Morgan et al. 2012). While most DVM ABEs remained in the bay during weak nocturnal winds (Fig. 4D,F), all DVM ABEs were flushed from the bay when strong southerly winds occurred at night (Fig. 4E).

The transport speed of ABEs and the distance displaced were quite different for different behaviors, whereas those of ABEs sharing the same behavior

were quite similar. Net speed in all deployments was strongly affected by behaviors (Table 2, Fig. 5A). Deep ABEs traveled slowest (mean \pm SE: 0.07 ± 0.01 km h⁻¹), near-surface ABEs were fastest (0.36 ± 0.04 km h⁻¹), and DVM ABEs were intermediate (0.17 ± 0.02 km h⁻¹). When wind relaxed, speed was similar among behaviors due to strong flow reversals, except that the speed of DVM ABEs was affected by variations in wind intensity at night (Table 2, Fig. 5A). Additionally, north–south directional rate of transport (latitudinal velocity) was affected by wind conditions (Table 2, Fig. 5B). ABEs moved faster latitudinally (positive = northward) during upwelling than reversal conditions when remaining near the surface (-0.33 ± 0.05 and $+0.25 \pm 0.07$ km h⁻¹, respectively) and when undertaking a DVM (-0.17 ± 0.03 and $+0.03 \pm 0.03$ km h⁻¹), but not when remaining

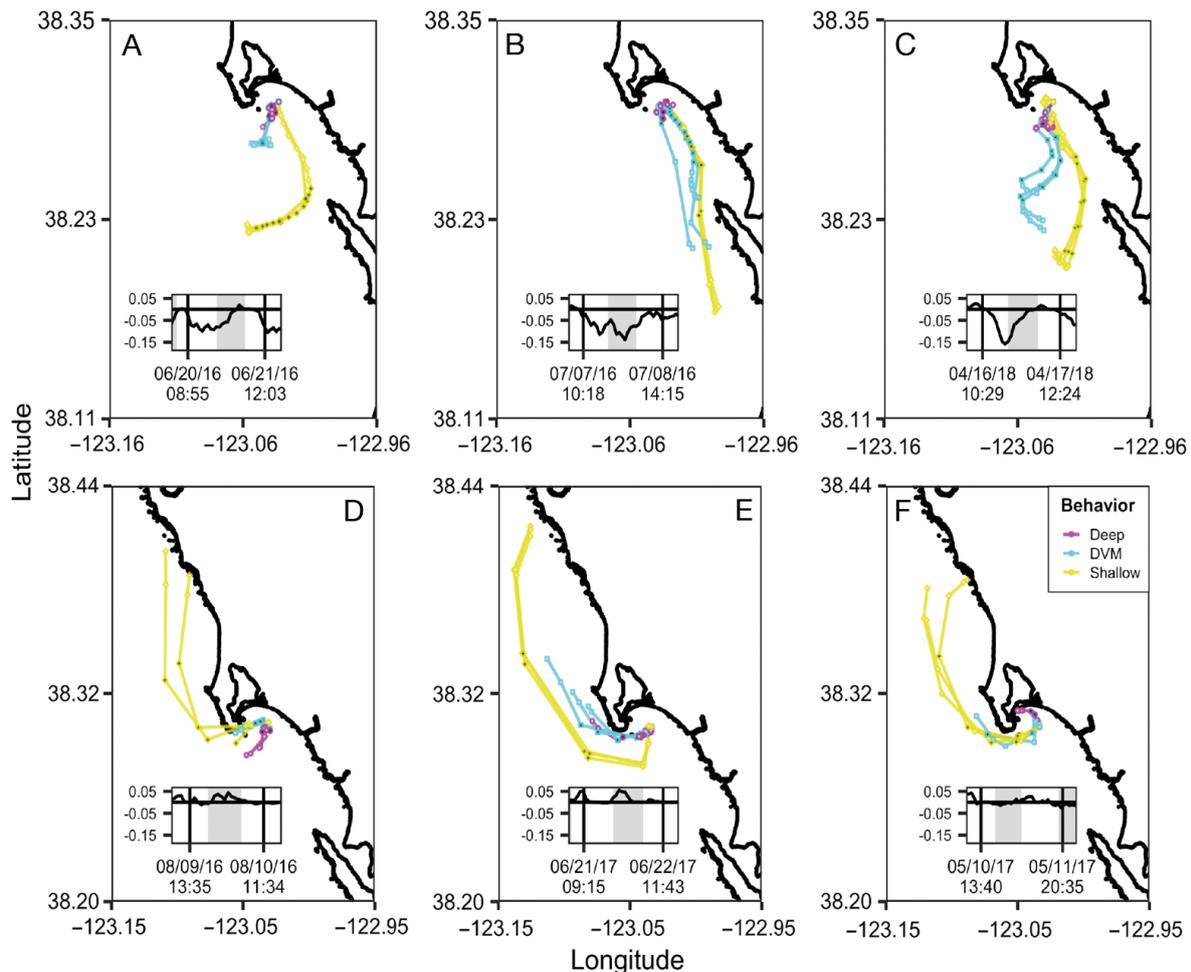


Fig. 4. Trajectories of ABEs simulating 3 larval behaviors in upwelling and reversal conditions: 'deep' remain 16 m deep (or 2 m above bottom in shallow water); 'shallow' remain 2 m below surface; 'DVM' migrate from 16 m deep during day to 2 m below surface at night. Three replicates of each behavior were deployed during (A–C) upwelling winds and (D–F) weak or reversed winds. Representative results for 6 of 12 deployments are shown. Insets show wind stress: poleward (positive) and equatorward (negative). Dates given as mo/d/yr

near bottom (-0.04 ± 0.02 and -0.04 ± 0.02 km h⁻¹). Near-surface ABLEs always moved fastest and farthest south during upwelling and fastest and farthest north during reversal conditions (Fig. 5B). DVM ABLEs also moved south during upwelling (Fig. 5B), slowing when northerly winds subsided overnight

(Fig. 4A–C). Deep ABLEs moved little and tended to move slightly southward (Fig. 5B), regardless of wind stress (Table 2, Fig. 5C). Accordingly, total 24 h displacements of ABLEs from the release site were greatest for shallow ones, least for deep ones, and intermediate for those undertaking a DVM (Fig. 5D).

Table 2. General linear mixed model (GLMM) and ANOVA results testing the effect of 3 simulated larval behaviors (see Fig. 4 for details). The GLMM was fit using maximum likelihood or restricted maximum likelihood, and post hoc hypothesis testing was conducted with ANOVA. Individual fixed effects and interactions of the GLMM (*t*-statistic) are reported as well as ANOVA of grouped effects (chi-squared test for overall velocity and *F*-test for latitudinal velocity)

Model response/predictor	Test statistic	p
Overall velocity GLMM (<i>t</i>-statistic)		
Deep behavior	15.825	<0.001
DVM behavior	6.863	<0.001
Shallow behavior	10.917	<0.001
Conditions (upwelling or reversal)	2.627	<0.01
Elapsed time	-3.29	0.001
DVM behavior × reversal	-3.669	<0.001
Shallow behavior × reversal	-2.998	0.002
Shallow behavior × elapsed time	2.059	0.04
DVM behavior × elapsed time	1.016	0.31
Conditions × elapsed time	0.168	0.87
DVM behavior × conditions × elapsed time	-0.74	0.46
Shallow behavior × conditions × elapsed time	-2.117	0.034
Overall velocity ANOVA (χ^2 statistic)		
Behavior	151.05	<0.001
Conditions (upwelling or reversal)	0.4824	0.49
Elapsed time	15.03	<0.001
Behavior × conditions	16.98	<0.001
Behavior × elapsed time	3.4782	0.18
Conditions × elapsed time	0.8753	0.35
Behavior × conditions × elapsed time	4.7297	0.094
Latitudinal velocity GLMM (<i>t</i>-statistic)		
Deep behavior	-0.329	0.75
DVM behavior	-2.797	<0.01
Shallow behavior	-6.605	<0.001
Conditions (upwelling or reversal)	-0.307	0.76
Elapsed time	1.276	0.21
DVM behavior × reversal	2.758	<0.01
Shallow behavior × reversal	9.029	<0.001
Shallow behavior × elapsed time	-1.213	0.23
DVM behavior × elapsed time	-0.362	0.72
Conditions × elapsed time	-0.594	0.55
DVM behavior × conditions × elapsed time	0.038	0.97
Shallow behavior × conditions × elapsed time	0.437	0.66
Latitudinal velocity ANOVA (<i>F</i>-statistic)		
Behavior	1.1505	0.32
Conditions (upwelling or reversal)	12.2559	<0.01
Elapsed time	0.0476	0.83
Behavior × conditions	42.1826	<0.001
Behavior × elapsed time	0.9651	0.39
Conditions × elapsed time	0.0509	0.82
Behavior × conditions × elapsed time	0.0964	0.91

4. DISCUSSION

Our ABLE experiments demonstrated that behavior alone is sufficient to dramatically affect transport at our study site. The experiments corroborated prior numerical simulations that embedded 'behaving particles' in the sheared flow measured around Bodega Head (Roughan et al. 2005). Each vertical swimming behavior emulated by ABLE produced trajectories consistent with the model's predictions during both upwelling and relaxation conditions: shallow plankton disperse far, deep plankton move little, and DVM plankton travel an intermediate distance (Roughan et al. 2005). The experiments were also consistent with field studies of larval distributions and recruitment to adult populations. Larvae are concentrated by vertical circulation in Bodega Bay during upwelling and increase the supply of larvae to adult populations, forming a recruitment hotspot (Roughan et al. 2005, Mace & Morgan 2006a, Morgan et al. 2011). When winds weaken or reverse, the flow reverses and these patches of larvae are flushed from the bay and travel northward, supplying larvae to populations that receive few recruits during upwelling conditions (Wing et al. 1998, Morgan et al. 2012).

How well can the movements of microscopic plankters be mimicked by mechanical surrogates that are orders of magnitude larger? The answer depends on the scale of the movements being investigated. Deployments of small robots (1 l displacement) recently provided the first empirical support for the hypothesis that plankton maintaining depth accumulate in patches over the troughs (flow convergences) of internal waves (Jaffe et al. 2017). Sixteen robots were programmed to maintain 10 m depth and were tracked by an array of acoustic transmitting floats for 5 h as internal waves passed through. Like ABLEs, those robots

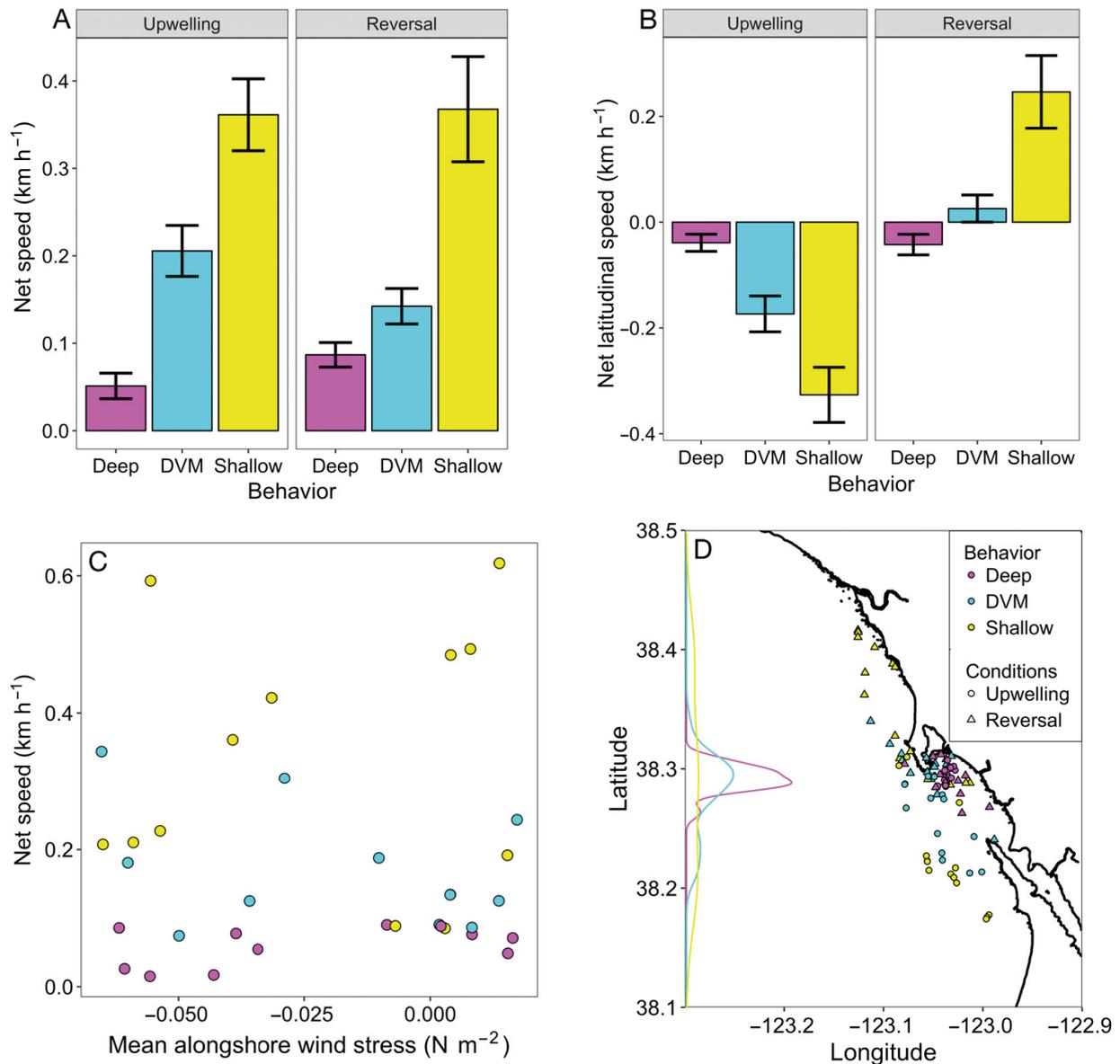


Fig. 5. Transport rates and displacement of ABLs simulating 3 larval behaviors relative to wind conditions. (A) Net (± 1 SE) speed traveled, (B) Net (± 1 SE) latitudinal speed, (C) Net speed relative to wind stress, and (D) final locations for all 12 deployments illustrating the diversity of outcomes (dispersion) and smoothed frequency distribution of final latitudinal positions (colored lines) for each behavior and wind scenario

capture the essential effects of transport in vertically sheared flow. They do not capture how small-scale turbulence drives separation (dispersion) of plankters at scales smaller than the body of the robot. While small-scale turbulence may be important in high shear between currents flowing in opposite directions, transport is dominated by advection within surface and lower layers (high Peclet number; Largier 2003).

ABLEs thus capture dispersion at scales greater than their size (Nyquist wavenumber of about 0.5 m

given a drag length scale of about 0.25 m). If spread, σ , is the maximum distance between any 2 ABLs in a behavioral group, then dispersion, D , is given by the relationship $\sigma(t) = \sqrt{2Dt}$ (Fischer et al. 1979). Spread varied from about 15 m h⁻¹ for deep ABLs during upwelling to 90 m h⁻¹ for shallow ABLs during relaxation so that dispersion estimates were on the order of 10² to 10⁴ m² h⁻¹. Dispersion due to motions at scales smaller than 0.25 m is typically on the order of only 10⁻³ to 10⁻¹ m² h⁻¹ (Rothschild & Osborn 1988), much smaller than observed, showing that

small-scale turbulence is not a significant factor in transport of ABLEs. ABLEs may also be influenced by vertical excursions caused by turbulence, but only by motions at scales greater than their size. Using the same scaling argument applied above to compare the effect of small-scale turbulent motion on the vertical position of microscopic plankton with that of vertical motions on scales sampled by ABLEs again revealed that the effects of small-scale turbulence are negligible compared to those of larger-scale water motions.

The ability of plankton to control transport fundamentally affects our understanding of the ecology and evolution of life in the sea. Species remaining deep move little during both upwelling and relaxation events (Peterson 1998, Morgan et al. 2009c, 2018, Morgan & Fisher 2010, Drake et al. 2013), resulting in retention near natal populations and increasing the potential for local adaptation, high recruitment, and dense, space-limited adult populations (Strathmann et al. 2002, Morgan 2001, 2014, 2020, Sanford & Kelly 2011). In contrast, species that primarily occur near-surface disperse much farther away (Peterson 1998, Morgan et al. 2009c, 2018, Morgan & Fisher 2010, Morgan 2014, Drake et al. 2013), potentially increasing population connectivity and gene flow (Strathmann et al. 2002, Morgan 2014, 2020, Burgess et al. 2014, 2016). Species undertaking a DVM (Peterson 1998, Morgan & Fisher 2010) are retained when winds subside at night and disperse when they persist, yielding diverse outcomes when aggregated over the reproductive season and across regions with varying diel wind cycles (Fig. 4D). Many species that change behavior ontogenetically facilitate seaward dispersal early in development by occurring near the surface and limit or reverse it later in planktonic life by occurring near the bottom (Peterson 1998, Morgan et al. 2009c, 2018, Morgan & Fisher 2010), thereby avoiding predation nearshore where fishes are abundant (Morgan 1990, Morgan & Anastasia 2008).

Field studies in estuaries and across the continental shelf throughout the world have shown that vertical and horizontal distributions of plankters are correlated, regardless of whether species permanently reside in the plankton or develop there temporarily as larvae (Peterson 1998, Epifanio & Garvine 2001, Shanks & Brink 2005, Kunze et al. 2013, Morgan 2020). In upwelling regimes, larvae of most nearshore invertebrates and copepods remain deep or perform DVMs throughout development, and all larval stages tend to occur within a few km of shore, suggesting that the surviving larvae avoided being swept offshore (Peterson 1998, Fisher et al. 2014,

Morgan 2014, Bonicelli et al. 2016, Hameed et al. 2018). Larvae of other nearshore species occur various distances from shore early and occur nearshore later in development, and these cross-shelf migrations are evidently mediated by species-specific differences in ontogenetic vertical positioning in sheared currents (Peterson 1998, Fisher et al. 2014, Morgan 2014, Bonicelli et al. 2016, Hameed et al. 2018). ABLE trajectories demonstrated that behavior has a primary and causal role in producing the observed distributions: by changing their vertical position, plankton can exert considerable control over their transport in nature. On rocky shores in upwelling regimes, such behaviors can modulate larval supply and recruitment dynamics (Drake et al. 2013, Morgan 2014, Shanks & Morgan 2018), so the probability of larvae being swept offshore and lost at sea can no longer be assumed to be simply a function of regional differences in the strength and persistence of upwelling, as has been argued for over 30 yr (Roughgarden et al. 1988, Menge & Menge 2013). Rather, larval supply fundamentally depends on the interaction between interspecific differences in vertical swimming behaviors of larvae and spatial and temporal variation in current flow. Larval mortality and other variables also affect the distribution, supply, and recruitment of larvae, but ABLE trajectories clearly demonstrate that behavior alone has profound effects on larval dispersal in the sea.

Acknowledgements. H. Killeen, S. McAfee and D. Dann assisted in the field. We thank the captain and crew of the R/V 'Mussel Point'. Comments by R. Grosberg, S. Bashevkin, and H. Killeen improved the manuscript. S. Small assisted with drafting Fig. 2. This is a contribution of the Bodega Marine Laboratory. This research was supported by the National Science Foundation (OCE-1334448) and California Sea Grant (NA18OAR4170073).

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Editorial responsibility: Alejandro Gallego,
Aberdeen, UK
Reviewed by: 3 anonymous referees

Submitted: May 23, 2020
Accepted: January 8, 2021
Proofs received from author(s): March 15, 2021