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Title
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Permalink
https://escholarship.org/uc/item/96x1594c

Journal
San Francisco Estuary and Watershed Science, 14(3)

Authors
Kimmerer, Wim
Slaughter, Anne

Publication Date
2016

DOI
https://doi.org/10.15447/sfews.2016v14iss3art2

Peer reviewed

RESEARCH

Fine-Scale Distributions of Zooplankton in the Northern San Francisco Estuary

Wim Kimmerer*[1] and Anne Slaughter[1]

ABSTRACT

We studied zooplankton distributions in the upper San Francisco Estuary at nested scales of tens to thousands of meters. The purposes of the study were to assess how well the Interagency Ecological Program (IEP) zooplankton monitoring represents abundance, and to investigate the variability of plankton on scales similar to those of foraging by fish. Samples were taken at three sites in the western Sacramento–San Joaquin Delta. We took 18 sets of six samples each with a plankton net along transects from near shore to center channel, and six sets of ten samples in the vicinity of a drifter either in mid-channel or near shore. Sampling took place in June–July 2014 during neap and spring tides, ebb and flood, day and night (transects only). Analysis focused on three common copepod species. Transect samples showed little consistent variation along transects, except that *Pseudodiaptomus forbesi* was less abundant nearshore than offshore by day at Big Break, the most landward site. The ratio of adults to adults + copepodites was strongly and positively related to turbidity by day but not by night, indicating demersal behavior. Drifter samples showed a minimum standard deviation of $\log_{10}$ sample counts of about 0.1, indicating that about two-thirds of replicate abundance values were within 80% to 125% of the mean. A measure of difference between plankton samples at pairs of sample points was unrelated to distance between sample points for drifter samples, weakly related along transects for *Limnoithona spp.* stages, and strongly related for *P. forbesi* mainly because of the along-transect gradients at Big Break. The IEP sampling program is representative of plankton abundance except for demersal organisms, which can be ten-fold more abundant by night than by day. Small planktivorous fish could forage in patches of up to ~25% higher abundance than the mean.

KEY WORDS

Copepod, Sacramento–San Joaquin Delta, patchiness, planktivorous fish, demersal behavior, zooplankton monitoring, mixing, turbidity, salinity

INTRODUCTION

Spatial distributions of plankton have long been known to be patchy, or spatially heterogeneous (Steele 1978). There is a robust literature on the spatial and temporal scales, generation, dissipation, and consequences of plankton patchiness, and on analytical methods to reveal its characteristics (Steele 1978; Mackas et al. 1985; Powell and Okubo 1994). Patchiness can arise from propagation of large-scale

variability to smaller scales by water movement, interactions of vertical swimming behavior or sinking with water velocity, and propagation of spatial heterogeneity between trophic levels (Steele 1978; Koslow 1981; Genin et al. 2005). Spatial heterogeneity may be a key factor in providing an adequate concentration of food for larval fish when the mean concentration is too low to support growth (Lasker 1975; Vlymen 1977), and the ability of zooplankton to accommodate a spatially or temporally variable diet varies with species (Dagg 1977; Fancett and Kimmerer 1985). Therefore understanding the scale and extent of spatial and temporal variability in plankton is essential to understand feeding by their consumer organisms.

One of the reasons to monitor plankton in estuaries is to assess the availability of food for higher trophic levels such as fish. However, monitoring programs typically do not take into account spatial and temporal heterogeneity and its possible role in amplifying food availability for fish.

The San Francisco Estuary (estuary) has one of the most intensive and temporally consistent sets of monitoring data of any estuary in the world. The zooplankton monitoring program has used largely consistent sampling and laboratory methods (Orsi and Mecum 1986; Kimmerer 2004; Winder and Jassby 2011) with relatively few changes in key personnel since its inception in 1972. However, a question that plagues this and other monitoring programs is whether the sampling represents actual zooplankton distribution and abundance.

There are several aspects to this question. First, most of the sample points are in the centers of channels; do these adequately represent the entire channels and off-channel areas? This is obviously important for calculations of plankton biomass as consumers or as prey for higher trophic levels. Differences in abundance between channels and nearshore areas may result from interactions of hydrodynamics and behavior (e.g., Genin 2004; Kimmerer et al. 2014a) or from predation by consumer organisms whose feeding varies between channels and shoals, as commonly occurs in lakes (Cryer and Townsend 1988; Gliwicz and Rykowska 1992; Jeppesen et al. 1998).

Second, is consistent sampling by day adequate to represent zooplankton distributions? Obviously, sampling at night imposes some added risks and difficulties, but may be necessary to adequately describe zooplankton abundance. Many estuarine zooplankton taxa are known for demersal behavior, remaining on or near the bottom by day and dispersing throughout the water column at night (Alldredge and King 1977). In particular, the copepod genus *Pseudodiaptomus* is generally considered demersal (Walter 1989), which is apparently a mechanism by which larger, more visible individuals avoid visual predators (Fancett and Kimmerer 1985; Jerling and Wooldridge 1992).

Third, is it possible to infer the feeding environment of planktivorous fishes such as Delta Smelt (*Hypomesus transpacificus*) from historical monitoring data? In the estuary, organisms larger than 150 µm, which include most of the prey of post-larval planktivorous fish, are collected by a 10-minute tow with a 10-cm plankton net. This sample collects plankton over a distance of ~1000 m on a path from near bottom to the surface. However, the feeding ambit of small planktivorous fish may be much smaller than that, and zooplankton patchiness at the scale of feeding by fish may be obscured by long plankton tows (Baxter et al. 2010).

Pseudodiaptomus forbesi is the most common food of Delta Smelt and some other planktivorous fishes of the upper estuary during summer (Nobriga 2002; Hobbs et al. 2006; Bryant and Arnold 2007; Slater and Baxter 2014). If *P. forbesi* migrates demersally as others of its genus do, then we are currently underestimating food abundance for these fishes. *Pseudodiaptomus forbesi* and other copepods in the low-salinity zone of the estuary did not undergo demersal migration, although demersal behavior was apparent in data for amphipods and the bay shrimp *Crangon franciscorum* (Kimmerer et al. 2002), both of which are larger and therefore presumably more at risk from daytime visual predation than copepods. However, findings from that study cannot be extrapolated to the freshwater regions where *P. forbesi* is most abundant because differences in salinity, turbidity, abundance of planktivores, and water-column velocity profiles could all affect vertical distributions of zooplankton.

This paper reports on a study of fine-scale distributions of zooplankton in the upper estuary that is designed to answer these questions and to determine the approximate magnitude and scale of heterogeneity over distances from tens to hundreds of meters, nested within sample sites several km apart. Sampling took place in January, June, and July 2014; however, January data are not presented because plankton abundance was low, and examination of representative samples showed insufficient individuals for effective analysis.

METHODS

All sampling was conducted from San Francisco State University's research vessel R/V Questuary at three sites in the western Delta: Big Break, West Island, and Browns Island (Figure 1). We selected these sites to provide a gradient between nearshore shallow water and the offshore channel. At each sample point, we recorded the GPS position at an accuracy of ~10 m, and water depth from the

ship's echo sounder. Temperature and salinity were obtained from a Sea-Bird Model 19 CTD in the ship's onboard monitoring system and with a Hydrolab Quanta sonde. At the beginning and end of each set of samples, we took temperature and salinity profiles with a Sea-Bird Model 19 CTD, determined turbidity using a Hach 2100Q portable turbidimeter, and measured chlorophyll fluorescence with a Turner Designs Cyclops-7 submersible fluorometer.

At each of the three sites we took two types of samples (Figure 1). Samples were taken on transects designed to be approximately normal to the shoreline to detect gradients in abundance related to depth or proximity to shore. Because of differences in channel width and slope, the transects differed in length and depth profile among the three sites (Table 1). Each transect consisted of six samples taken in as rapid a succession as feasible, with a median time of 30 minutes to complete the sampling. The first sample point was as close to the shore as feasible, and the last was near center channel. We took 20-second
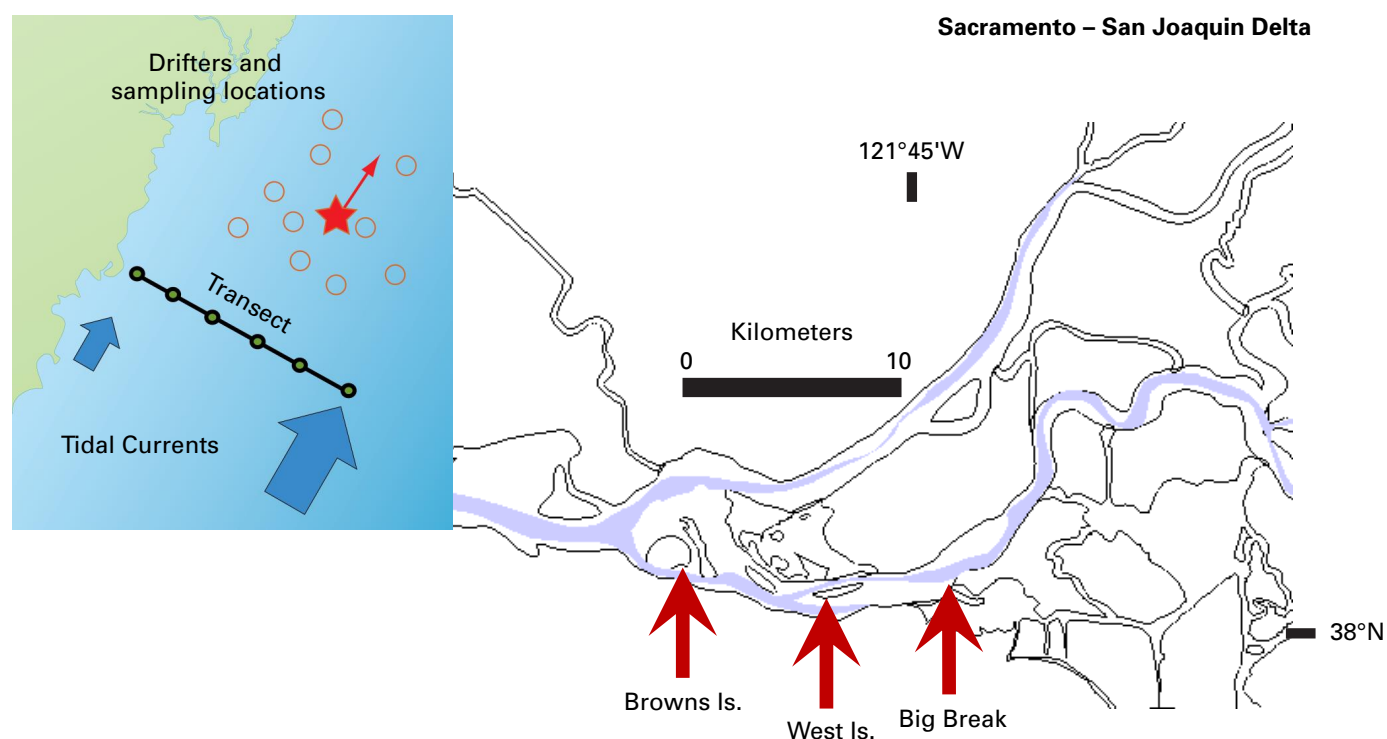
Figure 1 Map of the study area in the upper San Francisco Estuary. Arrows indicate sampling locations at Big Break, West Island, and Browns Island. Inset at upper left shows an idealized diagram of the sampling scheme including a typical onshore-offshore transect, the release location of a drifter (star), and typical locations for sampling in relation to the drifter's position. Actual positions of samples taken near drifter (red circles) varied from this ideal.

Table 1 Mean transect length and mean of maximum and minimum depth along transects

Site	Length, m	Mean depth	
		Minimum	**Maximum**
Browns Island	304	4.0	14
West Island	535	3.1	12
Big Break	722	2.2	11

subsurface horizontal tows of ~5 m^3 volume filtered with a 50-cm diameter, 53-µm mesh aperture plankton net equipped with a General Oceanics 2030R flowmeter. Samples were preserved with ~4% formaldehyde with rose bengal stain.

We took sets of ten samples in the vicinity of a drifter attached 0.5 to 1 m below a surface float. The purpose of the drifter samples was to examine the variability among samples taken within a short distance of each other. We used the drifter so that we could sample within the same water mass. Drifters were released near transect sites by day, either in center channel (four sets) or nearshore (two sets). We took initial and final samples at the drifter. The remaining samples were taken at sample points selected haphazardly by moving the vessel around the drifter and attempting to sample at variable distances and directions; estimated distances from the drifter had a median of 50 m and a range of 12 to 132 m. We took zooplankton samples in rapid succession with the same net we used in the transect samples towed vertically from 5 m to the surface. Sampling took ~20 to 32 minutes to complete for each set of drifter samples. We calculated the volume filtered as 0.98 m^3 based on the distance towed and a previously determined value of 70% for net efficiency.

In the laboratory we rinsed the samples with freshwater, then diluted to a known volume and subsampled with a piston pipet. We counted initial subsamples of 0.2% to 1% of the diluted volume for all taxa, and took additional subsamples if necessary to obtain sufficient counts of the target copepodite (juvenile) and adult stages of calanoid copepods. We recorded data as the number counted and number per cubic meter based on the volume filtered and the subsample fraction.

Additional data were obtained from the zooplankton monitoring program conducted by the Interagency Ecological Program (IEP) (Orsi and Mecum 1986). We compared IEP data from June and July 2014 to our data taken during the same period by examining plots of abundance vs. salinity between data sets for common copepod species and life stages. IEP data did not distinguish nauplii of the numerically dominant cyclopoid copepod *Limnoithona spp.* from other nauplii, so we compared abundance estimates for total copepod nauplii between the two data sets.

DATA ANALYSIS

All data analysis and graphing was done in R version 3.2.3 (R Development Core Team 2014). Latitude and longitude were converted to UTM coordinates with the R package "rgdal" using the WGS84 datum. Because actual transect paths were somewhat irregular, we calculated distances along transects as the projection of each data point onto the major axis of an ellipse fitted to all the positions on the transect. In a few cases, these indicated little movement between samples or even reversed movement on a transect. These were caused by the vessel drifting during the sampling process, particularly on windy days.

The purpose of the transect analysis was to examine differences in zooplankton composition and abundance across the transects, and how these differed by site, daylight, spring or neap tide, and ebb vs. flood. We selected a few abundant taxa for this analysis to obtain high counts in subsamples, thereby minimizing the influence of subsampling error (Lund et al. 1958). At least one life stage of the copepods *Pseudodiaptomus forbesi*, *Acartiella sinensis*, and *Limnoithona tetraspina* occurred in at least 100 of the 108 samples taken. Harpacticoid copepods were also abundant, but these are juvenile forms of species assumed to be benthic because adults are not generally found in the water column, so they were not included in analyses. Apart from these and unidentified gastropod larvae, no taxon occurred at all life stages in more than half of the samples. The analysis proceeded with nauplii, copepodites, and adults of the above three species, with males and females combined, although most analyses included only the more abundant *P. forbesi* and *L. tetraspina*.

The analysis was largely graphical. We were interested in changes along the transects but not so much in differences among transects or among dates and times, which were expected to be large because of known variability in abundance with salinity and potentially day vs. night. We examined trends along transects using linear models fitted to the log-transformed abundance data with distance from the shoreline along the transects. In most cases slopes differed among sites, dates, tidal stages, and day–night, and appeared sporadic, except for *P. forbesi* at Big Break by day.

We examined the relationship of geographic distance between pairs of sample points to dissimilarity of zooplankton abundance between the same pairs of samples. Dissimilarity was calculated as Euclidean distance in log-transformed abundance calculated separately for *P. forbesi* and *L. tetraspina*. For both species, we pooled data for copepodites and adults because their spatial patterns appeared similar, and reduced the data sets for each species to those transects with a minimum count of 18 for either nauplii or copepodites + adults. We selected this value to include as many samples as possible given that analysis of variability in the drifter samples, discussed below, indicated that a minimum count of ~20 would ensure that most of the variability was from sampling rather than subsampling.

We conducted this analysis using distance between pairs of sample points within individual transects as a covariate, and transect as a blocking variable. With six sample points there are 15 pairs of samples, so ordinary linear models can produce unrealistically small standard errors. We therefore estimated confidence limits of model parameters by randomly resampling the data 10,000 times with only six distance values per transect and recalculating slopes.

Data from the Big Break site (furthest landward) showed a strong day–night difference in abundance of *P. forbesi*, potentially indicating demersal behavior. Demersal behavior functions as a defensive mechanism against visual predators and is generally strongest in adult female copepods, which are the largest and most visible (Fancett and Kimmerer 1985; Vuorinen 1987). Selective or behavioral pressure to avoid the water column might be inversely related to turbidity (Utne–Palm 2002). Since this behavior

is strongest in the largest individuals, we used the ratio of adults to adults + copepodites (or adult : total ratio) from transect samples as an index of demersal migration, and determined how the relationship of this ratio to turbidity varied between day and night. We also examined this ratio as a function of the ratio of Secchi depth to water depth (day only), used as an index of the proportion of the water column that is well-lit (by whatever criteria visual planktivores use) and therefore avoided by the copepods.

We calculated distance measures for sets of drifter samples as for the transect samples after we had corrected sample positions for movement of the water mass. We determined the geographic position of the drifter at the beginning and end of each drifter run, and interpolated position at the time of each sample along a straight-line track of the drifter. Since the sampling took no more than 32 minutes and the drifter moved only 487 to 1065 m (median 800 m) during sampling, a linear track was probably reasonably close to the true drifter track. We then calculated sampling positions relative to the interpolated drifter position and calculated distances among these relative positions as for transects. Euclidean distances among samples included all three gross life stages of all three common copepod species.

We calculated sampling variability of each species and life stage for each drifter run. Variability among sample counts has two components: that resulting from sampling and that from subsampling. Since were randomly took small subsamples from the original sample (see earlier), we assumed that the number counted in the subsample had a Poisson distribution, in which the coefficient of variation is inversely proportional to the square root of the mean count (Lund et al. 1958).

We calculated the variance and standard deviation of log-transformed counts for each of the nine taxa (three species and three life stages) and each of the six drifter sample groups. We then related this to the minimum number counted in subsamples within each group. We used the minimum assuming that this value would best reflect the influence of subsampling variability on the sample statistics. We then estimated a model to fit these data assuming that sampling error and subsampling error were independent, and therefore their variances were additive. To estimate

the variance from subsampling, we took 10,000 random samples from Poisson distributions with the parameter λ set to the minimum counts for each of the 54 sets of samples (nine taxa × six drifter sets), and determined the variance of the log-transformed counts from each set of random samples. We subtracted this from the total variance of the log-transformed counts from the corresponding set of drifter samples. We then added the median of this difference to the subsampling error estimates for each set of samples and calculated the predicted standard deviation (SD_{Pred}). Thus the model was

$$\mathrm{SD}_{\mathrm{Pred}} \sim \sqrt{\sigma_{\mathrm{Sub}}^2 + \mathrm{Median}\left(\sigma_{\mathrm{Sample}}^2 - \sigma_{\mathrm{Sub}}^2\right)}, \qquad (1)$$

where subscripts indicate variances are (Pred)icted total, Sub(sample) from the simulation, and Sample.

RESULTS

Environmental conditions differed among sites and were generally similar along the transects with a few exceptions (Figure 2). Temperature decreased from east to west, but the differences were small. Salinity increased from east to west. At Browns Island, salinity varied with distance on transects during spring tides and slightly during neap tides. Turbidity increased with salinity; a linear model including salinity as a covariate and site as an additive blocking factor had a slope of 1.8 ± 0.9 (95% CI). Chlorophyll fluorescence was uniformly low and did not show strong patterns.

IEP and transect samples showed generally similar patterns of abundance of the two most common copepod species (Figure 3). All stages of *P. forbesi* (total *Pseudodiaptomus* of all species in the IEP data for copepodites and nauplii) were most abundant in freshwater and much less abundant at high salinity, and some day–night differences in adult abundance were evident in the transect data. *Limnoithona* adults and copepodites were most abundant at intermediate salinity. Total copepod nauplii were much less abundant in the transect samples than in the IEP data, but with a roughly similar pattern with respect to salinity.

Little consistent pattern in abundance was apparent along transects (Figures 4–6). Differences among the three transect sites were apparent and consistent with the known distributions of each species in salinity

space (Figure 3). Except for *P. forbesi*, there was little difference between transects conducted by day and by night.

Pseudodiaptomus forbesi was abundant in most samples, declining in abundance from Big Break to Brown's Island as salinity increased (Figure 4). Copepodites and adults had similar abundance patterns to each other, but both varied among sites. During the day at Big Break, abundance increased with distance from shore (slope of $\log_{10}$ abundance vs. distance = 0.70 ± 0.39, 95% CI with ebb/flood and spring/neap as factors). At night, we observed no patterns, nor was there a consistent pattern by day or night at the other sites. Nauplii differed in distribution from later stages, and were at least as abundant by day as by night. At both Big Break and West Island, daytime samples generally showed abundance declining from nauplii to copepodites to adults, but this pattern was absent at night. Abundance at Brown's Island was generally low and therefore variable.

Acartiella sinensis abundance (Figure 5) was less than that of *P. forbesi*, and increased with salinity. Nauplii greatly outnumbered copepodites and adults. Although some transects had apparent gradients in abundance for some stages, these were sporadic and probably attributable to random variability. *Limnoithona tetraspina* (Figure 6) had a similar pattern among sites to that of *A. sinensis*.

The Euclidean distance in log abundance between pairs of sample points within transects was related to the geographic distance between sample points, with a steeper slope for *P. forbesi* than for *L. tetraspina* (Figure 7, Table 2). That steeper slope was driven by daytime samples from transects at Big Break (Figure 1, black triangles in Figure 7). The non-zero intercepts (Figure 7, Table 2) indicate the approximate minimum Euclidean distance between pairs of samples taken at the same location. Confidence intervals of the slopes but not the intercepts were larger when the data were resampled to correct for the inflated degrees of freedom ($N = 6$ original samples resulting in 15 pairs).

The adult:total ratio of *P. forbesi* increased with increasing turbidity by day but not by night (Figure 8). The nighttime adult:total ratio was slightly higher than the daytime ratio at the highest
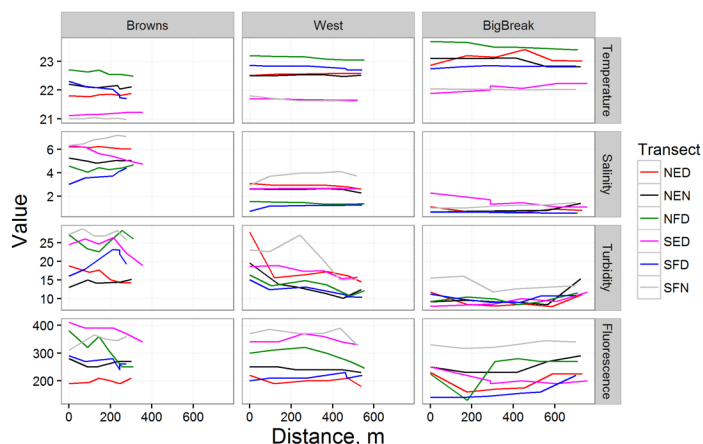
Figure 2 Environmental variables along transects. Key identifies transects by three letters indicating: (N)eap or (S)pring tide, (E) bb or (F)lood tide, and (D)ay or (N)ight. Temperature in °C, salinity (unitless) on the Practical Salinity Scale, turbidity in Nephelometric Turbidity Units (NTU), and chlorophyll fluorescence in arbitrary units.
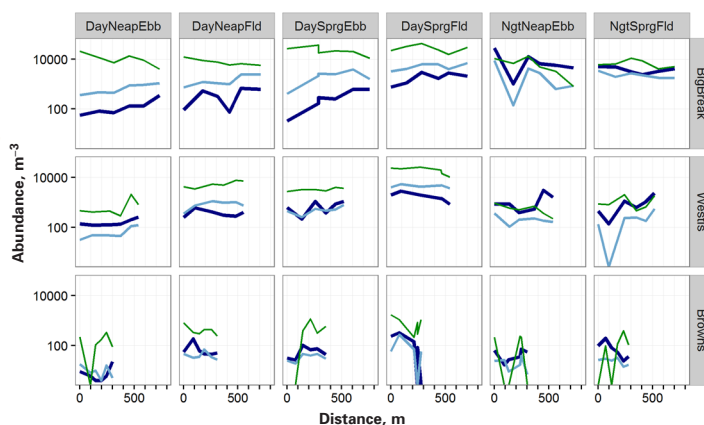
Figure 4 Abundance along all transects for *Pseudodiaptomus forbesi*. Thick (dark blue) lines, adults; thin (green) lines, nauplii; intermediate-thickness (light blue) lines, copepodites.
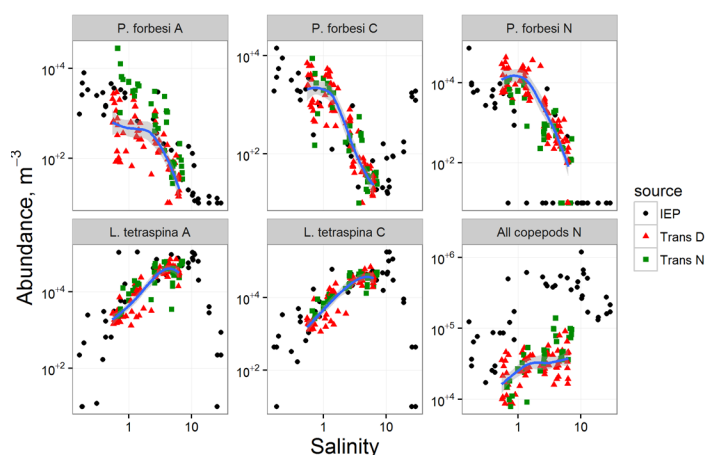

Figure 3 Abundance vs. salinity of *Pseudodiaptomus forbesi* (A) dults. (C)opepodites, and (N)auplii, *Limnoithona tetraspina* adults and copepodites, and total copepod nauplii, on transects and in Interagency Ecological Program (IEP) monitoring data. IEP data taken from June and July 2014 samples at all stations (*N* = 40). Transect data are shown by day (Trans D) and night (Trans N). Lines are loess-smoothed values for day transect data only.
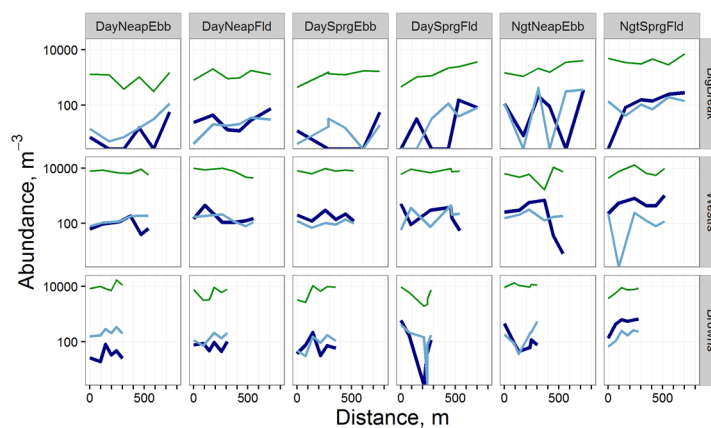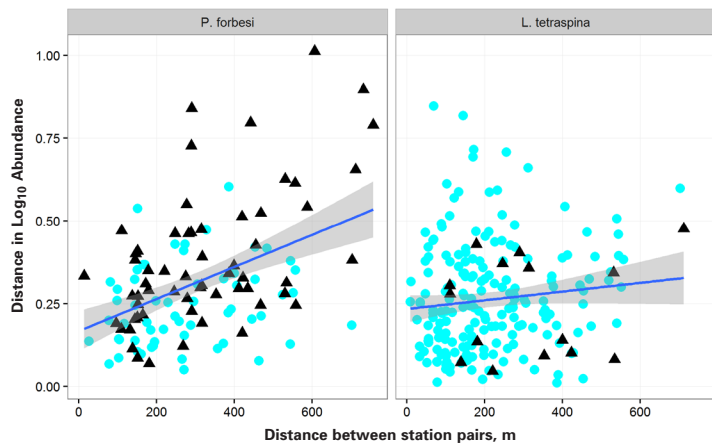

Figure 5 Abundance along all transects for *Acartiella sinensis*. Thick (dark blue) lines, adults; thin (green) lines, nauplii; intermediate-thickness (light blue) lines, copepodites.
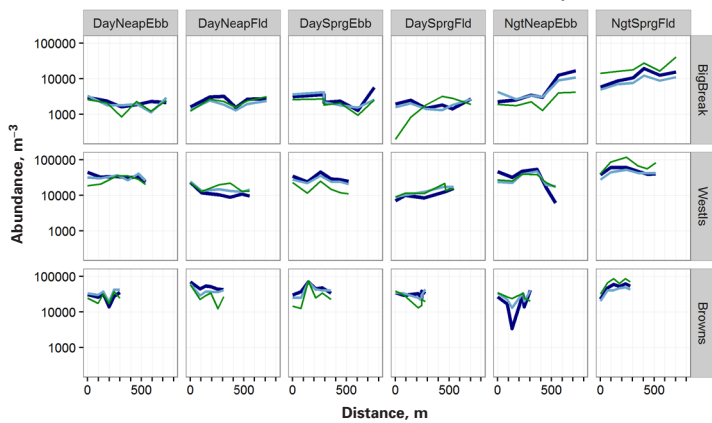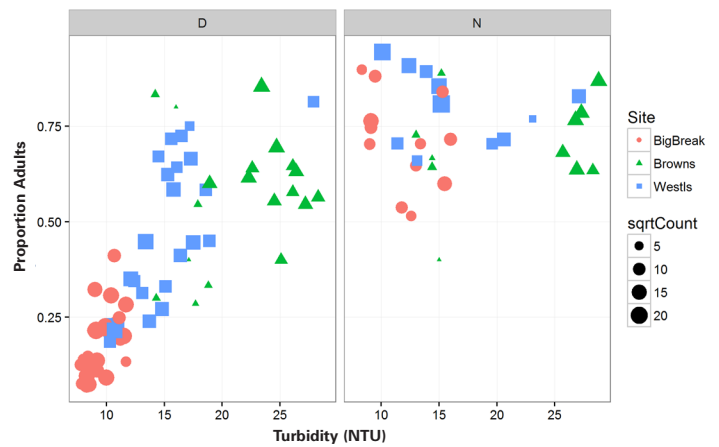
Figure 6 Abundance along all transects for *Limnoithona tetraspina.* Thick (dark blue) lines, adults; thin (green) lines, nauplii; intermediate-thickness (light blue) lines, copepodites.

Table 2 Statistics for relationships of geographic distance between pairs of sample points along transects to the Euclidean distance between pairs of sample points in log-transformed abundance of the two most common copepod species (Figure 7). True degrees of freedom are the number of original data points (6 per transect) less the number of parameters of the full model including individual transects as blocking factor and the geographic distance as a covariate.

	Pseudodiaptomus forbesi	*Limnoithona tetraspina*
Estimated intercept	0.27 ± 0.09	0.13 ± 0.09
Resampled intercept	0.27 ± 0.10	0.13 ± 0.07
Estimated slope (km^{-1})	0.44 ± 0.16	0.23 ± 0.17
Resampled slope (km^{-1})	0.44 ± 0.23	0.23 ± 0.21
Transects included (of 18)	8	14
True degrees of freedom	39	99

Figure 7 Euclidean distance in log$_{10}$ abundance between pairs of sample points within transects, plotted against geographic distance between the sample points in each pair, for *Pseudodiaptomus forbesi* and *Limnoithona tetraspina*. Black triangles, daytime transects at Big Break (Figures 1 and 4). Lines and shading give regression lines with 95% confidence intervals (Table 2).
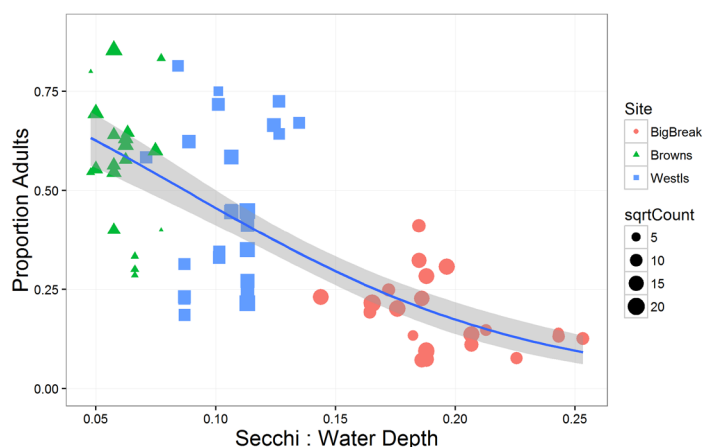

Figure 8 Proportion of *Pseudodiaptomus forbesi* adults to adults + copepodites plotted against turbidity for (D)ay and (N)ight transect samples. Colors indicate sites (see Figure 1) and diameters of symbols are proportional to the square root of the total count (sqrtCount) in each sample.
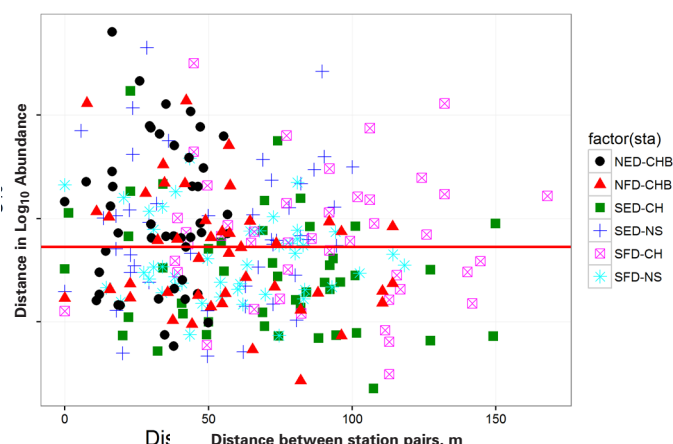
turbidity. Secchi depth scaled to water depth was a good predictor of the daytime adult : total ratio (Figure 9).

Drifter samples were all taken within 168 m of each other, and most were no more than 100 m apart (median distance 63 m). We calculated Euclidean distances alternatively using all three stages of either *P. forbesi* or *L. tetraspina*, or both species. Euclidean distance between log-transformed abundance values at pairs of samples was unrelated to the corresponding geographic distance for any of these cases (Figure 10).
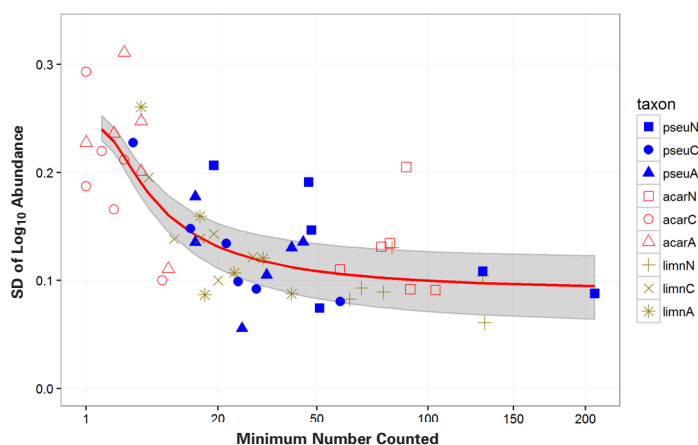
The standard deviation (*SD*) of log-transformed abundance within each set of 10 drifter samples varied as expected with the minimum number counted of each species and stage (Figure 11). The median estimated sampling error was 0.1. Adding this median sampling error to the subsampling error gave a curve that fit the data well ($SD_{Data} = 0.002 + (1.04 \pm 0.22)\ SD_{Predicted}$, $R^2 = 0.58$, $N = 54$). Residuals from this curve had no trend with number counted and did not appear to vary among taxa, because ranges of residuals included zero for

Figure 10 Euclidean distance in $\log_{10}$ abundance of *Pseudodiaptomus forbesi* between pairs of drifter sample points, plotted against geographic distance between the sample points in each pair. Key as in Figure 2 with the addition of (CH)annel and "NS" for nearshore. There was no relationship between Euclidean distance and geographic distance between pairs of sample points; the horizontal line indicates the mean.

Figure 9 Proportion of adults to adults + copepodites plotted against the ratio of Secchi depth to mean depth along each transect, daytime only. Symbols as in Figure 8. The line is the fit of a binomial regression weighted by the square root of the count, with 95% confidence bands (function *glm* in R version 3.2.3). The equation for the line with 95% confidence intervals of the slope is: $\text{logit}(P_{Adult}) = 1.2 - (13.8 \pm 1.6)(\text{Secchi} : \text{WaterDepth})$

Figure 11 Standard deviation of $\log_{10}$ abundance vs. the minimum number counted in each set of drifter samples, for all three gross life stages ((N)auplii, (C)opepodites, and (A)dults) of three copepod species: *Pseudodiaptomus forbesi*, *Acartiella sinensis*, and *Limnoithona tetraspina*. The line is the model calculated in Equation 1. The confidence band encloses values determined from upper and lower quartiles instead of median in Equation 1.

all taxa. Variance in counts of common taxa among samples within each set increased with the mean count. The slope of a log–log regression of variance on mean count was 1.56±0.08.

DISCUSSION

Patchiness in plankton populations is the outcome of competition between processes that generate spatial pattern and processes that mix, distort, and ultimately erase this pattern (Martin 2003). Although turbulent dispersion mixes scalar fields such as plankton and salinity, the mixing process is not a smooth diffusion but chaotic, increasing in strength with the length-scale of the mixing water mass (Okubo 1978). Mixing across the gradient of a scalar at the largest spatial scales therefore results in patchiness of the scalar at smaller scales. Results of this mixing can be seen in satellite imagery of chlorophyll concentration and in similarity of variance spectra of velocity and phytoplankton biomass over some intermediate range of length-scales (Mackas et al. 1985). In addition, deviations in variance spectra between temperature or salinity and biomass can indicate length-scales where pattern-generating processes are important, and these are generally where time-scales of biological and physical processes are similar (Lewis and Platt 1982). These findings probably apply to zooplankton, but many samples are required for spectral analysis, so reports of spectral or fractal distributions of zooplankton are rare (Seuront and Lagadeuc 2001).

Much of the modeling work on phytoplankton patchiness has focused on the roles of growth and mortality in generating spatial pattern in plankton biomass that is then mixed into smaller scales by turbulent flow (e.g., Levin and Segel 1976; Abraham 1998). Zooplankton have a ~10-fold longer biomass turnover time than phytoplankton, but can have very strong behavioral responses to physical cues such as light, salinity, tidal oscillations, turbulence, and shear flows generated by predatory attacks (Mackas et al. 1985; Genin 2004; Kimmerer and Lougee 2015). Spatially variable growth and mortality can generate spatial pattern in zooplankton at large scales (e.g., along the estuarine salinity gradient), which then cascades to smaller scales. However, in a tidal estuary, spatial variation in net growth is unlikely to generate spatial pattern in abundance at smaller

scales (meters to kilometers). For example, the time-scale for consumption of copepod nauplii by a patch of clams is at least half a tidal cycle, assuming the maximum observed clam biomass (Kimmerer and Thompson 2014) and typical consumption rates (Kimmerer and Lougee 2015); this effect would be diluted across the entire tidal excursion, with negligible effect on local spatial pattern. Thus, the interaction of behavior with the physical environment is the more important mechanism for generating spatial pattern in zooplankton at small scales (Mackas et al. 1985; Folt and Burns 1999; Genin 2004; Genin et al. 2005).

In estuaries, time-scales for physical processes can range from seconds to days depending on the particular process, whereas biological growth processes have time-scales of days. At the scale of the entire San Francisco estuary, residence time is usually on the order of weeks and turnover times of zooplankton populations are similar, implying the possibility of strong interactions between physical forcing and biological response (Kimmerer 2004). This can be seen, for example, in the large-scale differences in abundance of different species along the salinity gradient (Kimmerer 2004 and Figures 2–6). These patterns are maintained by a balance between net growth resulting from spatially variable reproductive rate and mortality, and net flow and tidal mixing. In addition, zooplankton behavior can cause their spatial patterns to diverge from those of passive particles, resulting in steeper spatial gradients in abundance than would be possible if the population were maintained only by an excess of reproduction over mortality (Genin 2004; Simons et al. 2006; Kimmerer et al. 2014a).

Abundance Patterns

Abundance of the two most common copepods had distributions in salinity space that were consistent with those from IEP monitoring during the same time frame (Figure 3). *Pseudodiaptomus* copepodites and nauplii were not identified to species in the IEP data, and the upturn in abundance of copepodites at high salinity probably reflects the contribution of the high-salinity congener *P. marinus*. The large difference in abundance of *P. forbesi* adults by day vs. night suggests demersal behavior, explored

further below. Otherwise, the decrease in abundance of *P. forbesi* from low to high salinity and the peaks in abundance of *L. tetraspina* copepodites and adults at intermediate salinity were similar between the two programs.

Most copepod nauplii including those of *Limnoithona* are not identified to species in the IEP samples. Comparing total nauplii between the two programs (Figure 3) shows a similar trend with salinity but a ~5- to 10-fold higher abundance in the IEP samples than in the transect samples. This is likely caused by undersampling of the small early stages of *Limnoithona* in our samples. Samples from the low-salinity zone taken by vertical tows with the same 53-μm plankton net in 2007 were used to calculate mortality of *Limnoithona*, but nauplius stages 1-3 were less abundant than expected for their stage durations (Kimmerer 2015). Correcting nauplius abundance using the calculated values based on mortality of stages N4-6 gave results that were about 5-fold higher than the actual observed value. The IEP sampling program uses a pump and filtration of preserved samples in the laboratory at 45 μm to concentrate samples. This is much more likely to capture early nauplii because of the smaller mesh size, and because plankton captured by a towed net typically contact the mesh numerous times and have more opportunities to be extruded than those collected on a mesh filter.

For the most part, copepod abundance was as we expected based on salinity (Figures 2–4 and Kimmerer 2004). The anomalous abundance pattern of *P. forbesi* adults and copepodites at Big Break (Figure 4) likely resulted from the demersal behavior of this copepod. Comparing data from Big Break with the other sites and day vs. night shows why this occurred only at this site, which had the lowest turbidity. The adult : total ratio was used as a proxy for demersal behavior which increases with size in *Pseudodiaptomus* species (Fancett and Kimmerer 1985; Jerling and Wooldridge 1992), probably because of increasing vulnerability to visual predation of copepods in the water column. The adult : total ratio was highest in turbid water by day but not by night (Figure 8). The daytime adult : total ratio was highly variable when the Secchi depth was a small fraction of water depth, but was uniformly

low when that fraction was larger than ~0.15 (Figure 9).

Demersal behavior was not observed in several hundred samples taken in the low-salinity zone during 1994–1996, but the copepods underwent tidal migration and therefore could overcome vertical turbulence (Kimmerer et al. 2002, 2014a). Therefore the absence of demersal behavior was likely resulted from the high turbidity in that region observed throughout that study. This difference illustrates the behavioral plasticity of zooplankton in responding to their physical environment.

Small-Scale Spatial Variability

Variability at scales larger than ~1 km is apparent in patterns in salinity space (Figure 3), which may arise from tidal vertical migration and from variation in physiological stress, predation rates, and food quantity and quality along the salinity gradient. As discussed above, smaller-scale variation arises from larger-scale variation cascading to smaller scales, as well as from interactions of behavior with the spatially varying flow field. Differences in abundance of *P. forbesi* expressed as Euclidean distance in log abundance for all three gross life stages showed a distinct trend with distance between pairs of transect sample points (Figure 7), but this relationship was much weaker for *L. tetraspina.* The difference was likely from the along-transect gradients in abundance of *P. forbesi* (Figure 4), which we have interpreted as a consequence of demersal behavior at the Big Break site. At the scale of the drifter samples no such pattern was evident, and pairs of samples were about equally similar (or different) irrespective of their distance (Figure 10). This contrasts sharply with results from lakes, where pairs of samples begin to differ at distances of ~10 m (Cryer and Townsend 1988). This difference in scale of patchiness probably arises from the strong tidal mixing in the estuary, which inhibits aggregation and also imposes patchiness that results from the transfer of variance in abundance from large scales to small.

The minimum difference between pairs of samples taken within a few hundred meters of each other can also be expressed as variance or standard deviation (Figure 11). Here the influence of subsampling error is evident: at least ~20 organisms must be counted to

limit the influence of subsampling error on standard deviation of log abundance. This is consistent with standard practices for analyzing plankton samples, but the number of organisms counted should be borne in mind as an additional source of variance when monitoring data are analyzed (Lund et al. 1958). The relationship of variance to mean of counts had an exponent (slope in the log-transformed regression) of 1.56, which fell within the range of similar slopes for a wide variety of planktonic organisms (Downing et al. 1987).

The median estimated sampling error of 0.1 (Figure 11) corresponds to an antilog value of 1.25. That implies that about two-thirds of replicated samples at these locations and times would have given values between 0.8 and 1.25 times the mean from all samples. This appears to be a minimum replication error for sampling zooplankton in this part of the estuary. It is fairly consistent among species, life stages, locations, and sampling events, yet swimming speeds and behaviors as well as trophic interactions differ among species and life stages. Therefore, the minimum replication error is unlikely to have arisen through behavior or propagation of variability between trophic levels. It is likely a consequence of turbulent mixing of large-scale spatial distributions. Although we detected no spatial structure in the relationships of Euclidean distance vs. geographic distance in the drifter samples (Figure 10), it was present in some of the transect samples (Figures 4–7). The method and scale of sampling in the drifter study was inadequate for discerning directional spatial structure, e.g., across-channel variation that might result from longitudinal mixing through tidal shear and trapping.

How Representative is the Monitoring Program?

The IEP zooplankton monitoring program and other programs that routinely collect zooplankton (e.g., 20-mm Survey, Dege and Brown 2004) take single samples at each station by day, almost exclusively in the centers of channels. Our results can be used to determine how representative these samples are of large-scale zooplankton abundance patterns. The transect samples were broadly consistent with the patterns of abundance in the IEP data where direct comparisons could be made (Figure 3). Previous

analyses have shown concordance between IEP sampling and other sampling despite rather large differences in sampling methods (Kimmerer et al. 1998, 2014b).

The lack of consistent gradients in abundance along the transects, other than that in Figure 4, contrasts with the situation in some lakes, where strong increases in zooplankton abundance from onshore to offshore can be set up by aggregations of planktivorous fish close to shore for protection from predators (Cryer and Townsend 1988). However, the lack of day–night differences in most of the along-transect patterns indicates that consumption by visually-feeding planktivores was not an important direct source of variability. If there are gradients in abundance of planktivores at these sites, it is likely that mixing between shallow and deep waters at the transect sites was strong enough to erase any gradient in plankton abundance that might have arisen through this mechanism.

The monitoring program is, therefore, representative of daytime abundance patterns for zooplankton species in the centers and margins of the channels where samples are taken. It is also representative of nighttime abundance for species that are not demersal (e.g., *L. tetraspina*, Figure 5, and *A. sinensis*, Figure 6) or in areas where high turbidity eliminates migratory behavior of demersal species such as *P. forbesi*. Our design did not include sampling in small backwaters and sloughs, where zooplankton abundance could vary considerably from that of the open waters. This is a topic that needs further investigation, especially given the current interest in marsh restoration and whether it could enhance the productivity of the pelagic foodweb (Herbold et al. 2014).

Feeding Environment of Fish

Routine swimming speeds of small fish are generally ~1 body length s^{-1}, or ~180 m hr^{-1} for a 50-mm fish such as a Delta Smelt in summer. The median distance between pairs of drifter samples was 63 m, so the drifter array was within 1 hour's swimming time of such a fish, and the tow distance was 5 m, which can be traversed by the fish in a few minutes. Thus, the drifter sample arrays can represent the feeding environment of Delta Smelt, to the extent that they

feed on plankton during the day. The mass of gut contents of juvenile Delta Smelt during 2005–2006 comprised mostly copepods, with *P. forbesi* adults making up 40% of the mass on average (Slater and Baxter 2014). Mysids made up ~1% of the mean prey mass and benthic amphipods another ~1%, and each was present in about half of the samples. No littoral prey were reported. Thus, Delta Smelt in summer appear to feed almost exclusively on zooplankton in the water column, and the monitoring data are representative of this environment on average.

The variability among samples in the drifter array was approximately log-normal, but feeding rates of individual fish are roughly linear in prey abundance when it is low, and constant at high abundance (Cosner et al. 1999). In the study area the abundance of food is generally low, as shown by evidence of low feeding rates of fish (Slater and Baxter 2014; Hammock et al. 2015). Assuming a linear functional response and given the variability among drifter samples a fish could increase its food intake by ~25% by foraging only when in an area of high relative abundance of prey instead of randomly. Whether Delta Smelt actually do that is unknown.

Late larval to juvenile Delta Smelt are more abundant in turbid than in clear water, which has been attributed to reduced predation risk and consequent increase in foraging ability (Feyrer et al. 2007; Nobriga et al. 2008). Stress responses at high and low turbidity reduced the feeding rate of larval Delta Smelt fed *Artemia* in the laboratory (Hasenbein et al. 2016). The variation in demersal behavior of *P. forbesi* with turbidity may also contribute to better feeding success of Delta Smelt in turbid than in clear water. Although it would be useful to determine the roles of these alternative mechanisms in the relationship of Delta Smelt abundance to turbidity, these fish are now at such low abundance that field evidence on their behavior would be difficult to obtain.

ACKNOWLEDGMENTS

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