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# Thin layer formation during runaway stratification in the tidally dynamic San Francisco Estuary

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*During the course of a year, we repeatedly collected high-resolution vertical fluorometer data timed to coincide with a specific state during the tidal cycle. The time (end of the ebb during neap tide) and the location (a deep channel half-way between the Golden Gate and the point of tidally averaged bottom salinity of 2 psu) were chosen with the goal to observe runaway stratification. We consistently found at least one pronounced chlorophyll peak in the water column; however, the vertical location of these peaks varied within three types including surface, bottom and subsurface maxima. Our results showed that heterogeneity of chlorophyll in the water column and thin layer formation do occur in systems that are characterized by high tidal flow speeds thus resulting in patchy prey fields for zooplankton that migrate in tidal cycles through the water column. Using these chlorophyll profiles, approximate calculations suggested that only during the spring phytoplankton bloom did all layers of the water column provide sufficient food for maximum egg production of the San Francisco Estuary copepod *Acartia* sp.*

## INTRODUCTION

In order to better understand the prey environment of migrating zooplankton, it is necessary to determine the spatial distribution of food (e.g. Napp *et al.*, 1988; Sutor and Dagg, 2008). Thin layers have become an increasing focus of research and their presence has been described for a wide range of environments, from stable protected embayments to many coastal sites (Tiselius, 1994; Cowles, 1998; Deksheniaks *et al.*, 2001; Alldredge *et al.*, 2002; Herren *et al.*, 2004; McManus *et al.*, 2005; Sutor *et al.*, 2005; Cheriton *et al.*, 2007; Gillibrand *et al.*, 2007; McManus *et al.*, 2008; Menden-Deuer, 2008; Ryan *et al.*, 2008). Thin layers are likely to occur in water that is stratified with well-developed pycnoclines and where current velocities are relatively low (resulting in high Richardson numbers, McManus *et al.*, 2005). One would not necessarily anticipate thin layer

formation in estuaries that are characterized by large tidal excursions and high flow speeds, such as the San Francisco Estuary. However, the water column is not always well mixed in these systems. It is well known that stratification takes place as a result of sheared tidal currents that carry freshwater over a gravitationally driven saltwater wedge moving upstream during ebb tide. When the density gradient becomes large enough to remain stable over several tidal cycles, this persistent stratification is strong enough to resist mixing during flood tides and is called “runaway stratification” (Monismith *et al.*, 1996; Lucas *et al.*, 1998). We hypothesized that during runaway stratification, the physical conditions may exist that consistently lead to heterogeneity in the distribution of phytoplankton (measured as chlorophyll fluorescence). Here, we report the occurrence of chlorophyll layers in the San Francisco Estuary

in observations spread over the period of  $\sim 1$  year, and speculate on their effect on the availability of food for zooplankton.

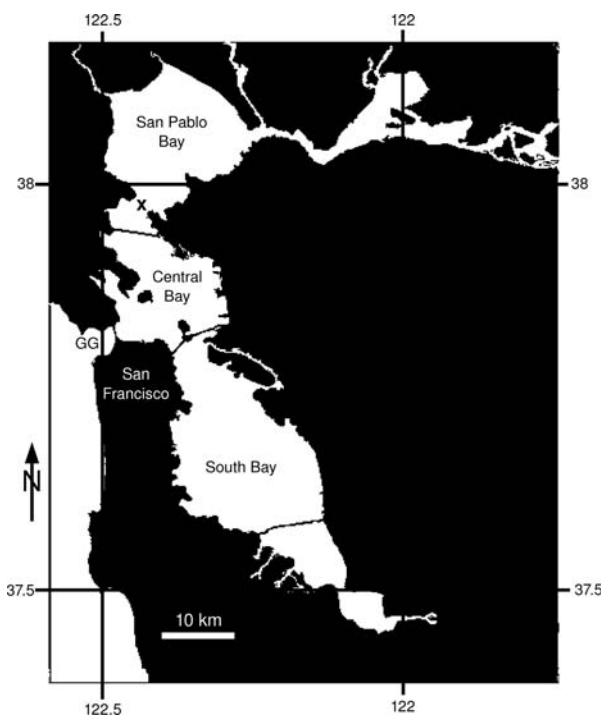
## METHOD

The distance from the Golden Gate to where the tidally averaged bottom salinity is 2 psu was termed  $X2$  (Kimmerer, 2004). It effectively represents freshwater outflow and is a useful metric for a range of biologically relevant metrics such as the location of the entrainment zone, habitat range of fish larvae, fish recruitment and stock abundances (Kimmerer, 2004). Stratification was previously determined to be maximal approximately half of  $X2$  (Monismith *et al.*, 1996; Lucas *et al.*, 1998). We thus chose a deep-water station (USGS station 15, ca. 20 m depth) located at approximately half of  $X2$  (Fig. 1). We timed our sampling to coincide with the end of the ebb tide during the neap tidal cycle in order to increase the likelihood of encountering runaway stratification (Monismith *et al.*, 1996; Lucas *et al.*, 1998). A Seabird CTD equipped with a Wetlabs DFL fluorometer was deployed by hand from a drifting 16 ft fiberglass boat. The instruments were lowered and retrieved at a rate of

$\sim 20$  cm/s. At a sampling frequency of 2 Hz (for the CTD) and 1 Hz (for the fluorometer), this resulted in  $\sim 10$  and 5 measurements per 1 m depth interval, respectively. We aimed to obtain six vertical profiles within one Lagrangian deployment (Table I). Locations were determined before and after each CTD deployment using a handheld GPS. Drifting speeds, which primarily reflected surface currents, and to a smaller extent wind drift, were calculated as the linear distance between these coordinates divided by elapsed time.

## RESULTS AND DISCUSSION

In all our casts, the water column at station 15 was characterized by strong stratification with at least one pycnocline (Fig. 2). Chlorophyll was never distributed homogeneously in the water column. *In situ* fluorescence changed over short depth increments, and our observations did not include sub-meter thin layers observed in more stable systems such as East Sound, WA (Deksheniaks *et al.*, 2001; McManus *et al.*, 2003). The broader peaks we observed may either be the result of the high current speeds or the fact that we used tethered as opposed to free-falling instruments, thereby translating some of the ship's motion to the sensors. The figures show representative examples of one surface peak (Fig. 2a), subsurface and bottom peaks (Fig. 2b), and a combination of surface and subsurface peaks (Fig. 2c). For comparison with other studies, we invoked four criteria for distinguishing thin layers specified by Deksheniaks *et al.* (Deksheniaks *et al.*, 2001). Although these criteria were chosen arbitrarily by Deksheniaks *et al.* (Deksheniaks *et al.*, 2001) and reflected the situation in East Sound, they have proved to be useful in subsequent studies (e.g. Ryan *et al.*, 2008). The first criterion was that the feature had to be present in at least two consecutive profiles. Each of the features we observed was present in all six consecutive profiles. Second, a thin layer should have a thickness of  $< 5$  m at half of peak maximum. The features we observed in the San Francisco Estuary were broader than the thin layers observed in East Sound. In our case, all surface peaks and 80% of the subsurface peaks were  $< 5$  m thick at half maximum. Third, the optical signal should contain at least six data points to avoid ephemeral features. In our case, each peak consisted of more than 30 data points. And finally, the signal should be three times the background value. In our case, 57% of the features were three times above the lowest recorded value in the water column (after accounting for instrument blanks) with an average of 3.7 (SD  $\pm 1.6$ ) times above background.



**Fig. 1.** Map of the San Francisco Estuary with the study location (X), which is water quality monitoring station 15 of the United States Geological Survey ( $37^{\circ}58.5'N$ ,  $122^{\circ}26.2'W$ , water depth = 22.9 m). GG, Golden Gate.

Table I: Examples of one cast for each deployment taken at USGS station 15 in San Pablo Bay in 2002 and 2003 as shown in Fig. 4

Deployment number	Date (Month/Day/Year)	Time of first cast (h:m)	Drift velocity (m s <sup>-1</sup> )	Surface density ( $\sigma_t$ )	Bottom density ( $\sigma_t$ )	Stratification index ( $\Delta\sigma_t/m$ )	Chl <i>a</i> max (RFU)	Chl <i>a</i> min (RFU)	$\Delta$ Chl <i>a</i> (RFU)	$r^2$	Water column peaks ( <i>n</i> peaks)
1	6/21/2002	16:36	0.6	19	19	0.015	220	105	115	0.82	1
2 <sup>a</sup>	6/21/2002	17:10	0.4	18	19	0.065	230	75	155	0.96	1
3	7/1/2002	10:18	1.2	15	21	0.290	110	20	90	0.93	2
4	7/1/2002	10:39	1.2	13	n.d.	n.d.	130	50	80	0.96	1
5	3/24/2003	10:00	1.3	13	18	0.265	550	275	275	0.59	1
6	3/24/2003	11:42	1.2	11	18	0.335	450	240	210	0.90	1
7	4/8/2003	10:29	1.4	12	20	0.400	280	100	180	0.95	2
8	4/8/2003	13:21	0.7	12	20	0.385	280	80	200	0.99	4
9	5/23/2003	11:47	1.2	7	18	0.550	230	40	190	0.93	2
10	5/23/2003	13:34	1.2	8	17	0.465	160	30	130	0.94	2
11	6/3/2003	11:05	1.4	13	18	0.250	94	40	54	0.63	2
12	6/6/2003	12:45	0.9	12	16	0.210	150	35	115	0.86	2
13	8/21/2003	12:37	0.9	18	21	0.125	275	75	200	0.98	2
14 <sup>a</sup>	8/21/2003	14:16	0.1	18	21	0.150	400	60	340	0.98	2

<sup>a</sup>Deployments 2 and 14 were made out of phase of the tidal cycle (not at the end of the ebb tide). Drift velocity over ground of the boat was calculated based on GPS coordinates at the beginning and the end of the casts and elapsed time assuming a straight line of drift. Times are given in Pacific Standard Time.

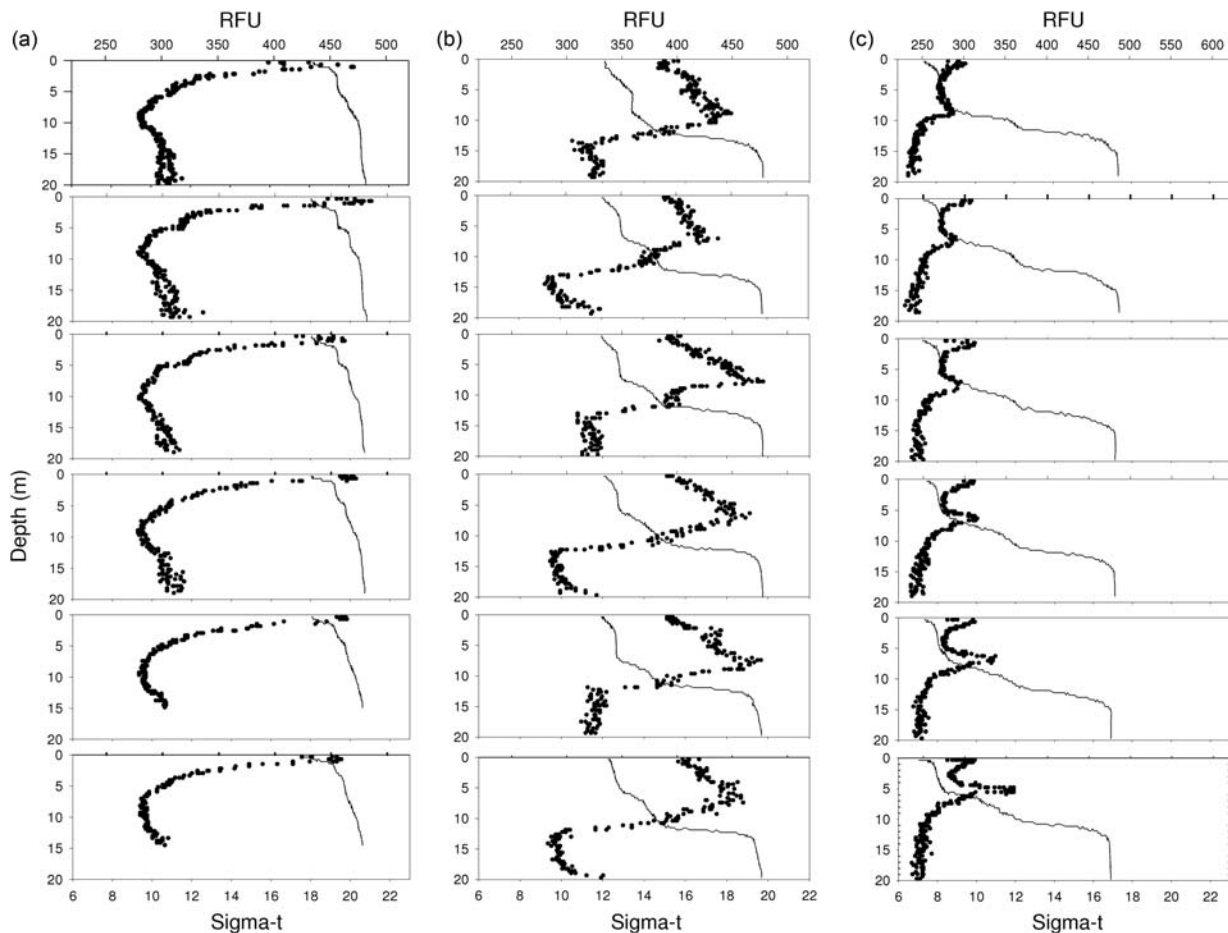
In order to visually compare the shapes of the fluorescence profiles with each other, we fit Lorentz curves using least-square Newton approximations (Fig. 3) and the equation:

$$F = I + \frac{2A}{\pi} \frac{w}{4(z - z_c)^2 + w^2} \quad (1)$$

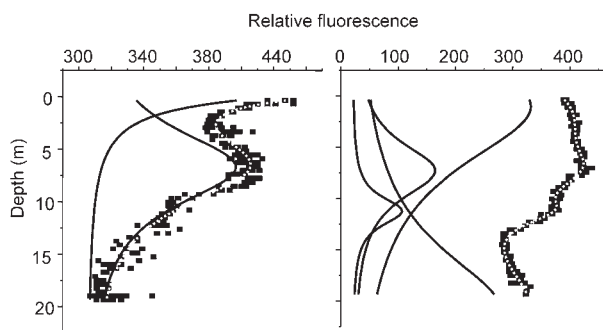
where  $F$  is the relative fluorescence,  $I$  the baseline after instrument blank correction,  $A$  the peak area,  $w$  the peak width at half maximum,  $z$  the water depth and  $z_c$  the depth of the peak center. Although other algorithms are conceivable such as linear and non-linear interpolations, Gauss curves or higher-order polynomials, the Lorentz algorithm has a slight advantage in that it contains useful descriptive parameters that have been used in other studies such as the mean depth of the thin layer (i.e.  $z_c$ ) and the width at half maximum ( $w$ ) (Dekshenieks *et al.*, 2001). The number of Lorentz peaks needed to adequately fit the data ( $r^2 > 0.8$ ) corresponded to the number of peaks by visual inspection. In one extreme case, four smaller peaks were necessary to reconstruct the broad peak shown in Fig. 3. This, however, was the only exception. All the other peak combinations were readily deconvoluted into 1–2 peaks, making an accurate representation of water column chlorophyll values surprisingly simple (Fig. 3, white dotted lines). The peaks closest to the surface had an average depth of  $1.38 \text{ m} \pm 1.28 \text{ (SD)}$ . It is not useful to state the width ( $w$ ) of the surface peaks because they are truncated by the water surface (Fig. 3). The average

depth of the subsurface peaks was  $9.85 \pm 4.82 \text{ m (SD)}$  and was usually above the center of the pycnocline, with an average width of  $4.57 \pm 1.5 \text{ m (SD)}$ .

Although the exact causes for the observed heterogeneity of chlorophyll at station 15 are unknown, there are a number of plausible explanations. Persistent stratification over several tidal cycles enhances phytoplankton peaks due to the accumulation of sinking cells above pycnoclines (Cloern, 1984). An alternative mechanism is lateral transport and the stacking of water masses of different origin and with variable chlorophyll content on top of each other. In the San Francisco Estuary, net primary production is restricted to the upper 0.5–1 m in the North Bay and 2–3.5 m in the South Bay (Alpine and Cloern, 1988; Cloern, 1991) and is therefore highest in the tidal flats surrounding the shipping channel because water does not mix below the critical depth (Lucas *et al.*, 1998). Owing to evaporation and mixing, this water is also saltier than the water coming from the San Joaquin–Sacramento rivers delta, but less salty than the gravitationally driven, upward-moving salt wedge. During ebb tide, the water drawn from adjacent tidal flats may then be forced above the salt wedge and below the estuarine freshwater in the channel due to its density. The role of lateral transport and vertical shear in the creation of thin layers has been described for other systems such as in Monterey Bay (Ryan *et al.*, 2008) and in model simulations (Birch *et al.*, 2008). In these cases, most thin layers were associated with the depths of maximum shear due to strong gradients in the direction of flows.

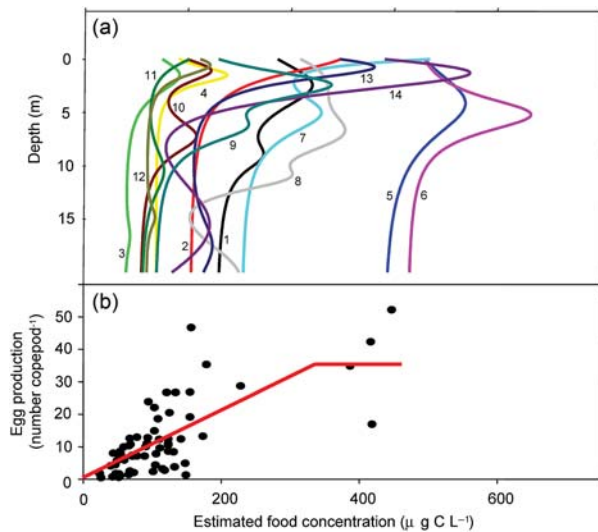


**Fig. 2.** Examples of chlorophyll distributions at station 15 in the San Francisco Estuary at three different times of the year using six replicate casts (alternating downward and upward). **(a)** Surface peak (deployment 14), **(b)** bottom and subsurface peak (deployment 6), **(c)** surface and subsurface peak (deployment 7). Sigma-t (solid line) and relative fluorescence units are superimposed.



**Fig. 3.** Example of deconvolution of chlorophyll peaks at station 15 using simple Lorentz curves [equation (1)]. Left: a typical 2-peak example encountered most of the time (Table I, deployment 7). Right: the most complicated scenario we encountered (Table I, deployment 8) that required the use of four distinct peaks to deconvolute the vertical profile for a sufficient fit ( $r^2 > 0.8$ ). The white dotted lines show the final model (i.e. the sum of the peaks) superimposed over the raw data. These composite lines were then used for comparison of all fluorescence distributions in Fig. 4.

Many zooplankton species migrate according to a tidal signal in order to maintain position in the estuary (Kimmerer *et al.*, 1998) and thus move through patches of chlorophyll. Not all chlorophyll-containing organisms are suitable food and, conversely, many valuable food items such as microzooplankton do not contain chlorophyll. In order to understand the extent to which the observed heterogeneity in the water column may be biologically relevant, we examined our field data in the context of food availability and egg production of the abundant copepod genus *Acartia* which usually dominates the mesozooplankton of Central and San Pablo Bays (Hooff and Bollens, 2004; Rollwagen-Bollens *et al.*, 2006; Gifford *et al.*, 2007). *Acartia* sp., like most zooplankton, is an omnivore but nevertheless a definite relationship between egg production and chlorophyll *a* was demonstrated in the laboratory and in the field (Bochdansky and Bollens, 2004; Kimmerer *et al.*, 2005).



**Fig. 4.** (a) Vertical profiles of prey carbon at station 15 for all casts shown in Table I. (b) Egg production rates of incubations using natural water in San Francisco Estuary with *Acartia* sp. as shown in Fig. 5 in Kimmerer *et al.* (Kimmerer *et al.*, 2005). The total chlorophyll values for the field incubations of *Acartia* sp. were converted into carbon using an average chlorophyll:carbon value of 0.036 for the North Bay (Cloern *et al.*, 1995). The piece-wise regression model fit is also taken directly from Kimmerer *et al.* (Kimmerer *et al.*, 2005).

The potential prey carbon values were plotted using prey carbon instead of relative fluorescence units (RFU) and using the Lorentz models of each deployment (Fig. 4a). Figure 4b shows the empirical relationships of egg production for *Acartia* sp., with estimated prey carbon (Kimmerer *et al.*, 2005). For this comparison, chlorophyll values in Kimmerer *et al.* (Kimmerer *et al.*, 2005) were converted using a chlorophyll:carbon ratio for the North San Francisco Bay of 0.036 (Cloern *et al.*, 1995). It is remarkable how the relative carbon distributions between our profiles and those observed by Kimmerer *et al.* (Kimmerer *et al.*, 2005) converged (Fig. 4). Zooplankton in the San Francisco Estuary encounter a wide-ranging prey field, with calculated carbon values which were below those needed for maximum egg production in many parts of the water column (Fig. 4). The only time when maximum egg production was supported was during spring diatom blooms (deployments 5 and 6 in Fig. 4a), consistent with the conclusions in Kimmerer *et al.* (Kimmerer *et al.*, 2005), who showed that for most of the year, *Acartia* sp. is food limited in the San Francisco Estuary.

An interesting question is whether values in prey patches (i.e. water column maxima), rather than water column averages, should be used to determine feeding success in copepods. This concept of zooplankton being able to exploit prey patches was most famously portrayed in the stable ocean hypothesis for fish larvae

(Lasker, 1981; Peterman and Bradford, 1987). Copepods also adjust well to patchy prey distributions and do not necessarily starve under circumstances of prey heterogeneity: in laboratory experiments, Bochdansky and Bollens (Bochdansky and Bollens, 2004) showed that *A. hudsonica* (collected in the San Francisco Estuary) can take advantage of thin layers of diatoms as a food source even when these copepods spend only short periods of time in the layers. Whereas the presence of food alone did not cause the copepods to aggregate, density discontinuities, on the other hand, did (Lougee *et al.*, 2002; Woodson *et al.*, 2005). Any co-location of chlorophyll and copepods is consequently driven by physical gradients of salinity, and to a lesser degree by behavioral modifications such as area-restricted search (Woodson *et al.*, 2005), making the physical structure of the water column the primary forcing function for the distribution of copepods. The relationship between egg production in the San Francisco Estuary (Kimmerer *et al.*, 2005) and our profiles suggests that even when prey occurs in patches, prey concentrations were never sufficiently high to support maximum egg production in *Acartia* sp. except for brief periods during the spring phytoplankton bloom fueled by freshwater run-off.

In conclusion, we provide an example of vertical heterogeneity of phytoplankton biomass over small vertical scales in a tidally highly dynamic environment. The San Francisco Estuary differs from other locations in which thin layers have been reported such as East Sound and the coastal ocean in Monterey Bay. Freshwater outflow and tidally driven gravitational circulation, as well as extreme light limitation due to suspended sediment, are the major drivers of the physical and planktonic heterogeneity in this system. As a result, vertically migrating zooplankton negotiate a highly patchy prey environment with prey concentrations that may fall below saturating feeding levels for most of the non-bloom periods.

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## REFERENCES

- Allredge, A. L., Cowles, T. J., MacIntyre, S. *et al.* (2002) Occurrence and mechanisms of formation of a dramatic thin layer of marine snow in a shallow Pacific fjord. *Mar. Ecol.-Prog. Ser.*, **233**, 1–12.
- Alpine, A. E. and Cloern, J. E. (1988) Phytoplankton growth rate in a light-limited environment, San Francisco Bay. *Mar. Ecol.-Prog. Ser.*, **44**, 167–173.
- Birch, D. A., Young, W. R. and Franks, P. J. S. (2008) Thin layers of plankton: formation by shear and death by diffusion. *Deep-Sea Res. Part I*, **55**, 277–295.
- Bochdansky, A. B. and Bollens, S. M. (2004) Relevant scales in zooplankton: distribution, feeding and reproduction of the copepod *Acartia hudsonica* in response to thin layers of the diatom *Skeletonema costatum*. *Limnol. Oceanogr.*, **49**, 625–636.
- Cheriton, O. M., McManus, M. A., Holliday, D. V. *et al.* (2007) Effects of mesoscale physical processes on thin zooplankton layers at four sites along the west coast of the US. *Estuaries and Coasts*, **30**, 575–590.
- Cloern, J. E. (1984) Temporal dynamics and ecological significance of salinity stratification in an estuary (South San Francisco Bay, USA). *Oceanol. Acta*, **7**, 137–141.
- Cloern, J. E. (1991) Tidal stirring and phytoplankton bloom dynamics in an estuary. *J. Mar. Res.*, **49**, 203–221.
- Cloern, J. E. C., Grenz, C. and Lucas, L. V. (1995) An empirical model of the phytoplankton chlorophyll:carbon ratio—The conversion factor between productivity and growth rate. *Limnol. Oceanogr.*, **40**, 1313–1321.
- Cowles, T. J., Desiderio, R. A. and Carr, M.-E. (1998) Small-scale planktonic structure: Persistence and trophic consequences. *Oceanography*, **11**, 4–9.
- Deksheniaks, M. M., Donaghay, P. L., Sullivan, J. M. *et al.* (2001) Temporal and spatial occurrence of thin phytoplankton layers in relation to physical processes. *Mar. Ecol.-Prog. Ser.*, **223**, 61–71.
- Gifford, S. M., Rollwagen-Bollens, G. and Bollens, S. M. (2007) Mesozooplankton omnivory in the upper San Francisco Estuary. *Mar. Ecol.-Prog. Ser.*, **348**, 33–46.
- Gillibrand, E. J. V., Jamieson, A. J., Bagley, P. M. *et al.* (2007) Seasonal development of a deep pelagic bioluminescent layer in the temperate NE Atlantic Ocean. *Mar. Ecol.-Prog. Ser.*, **341**, 37–44.
- Herren, C. M., Allredge, A. L. and Case, J. E. (2004) Coastal bioluminescent marine snow: fine structure of bioluminescence distribution. *Cont. Shelf Res.*, **24**, 413–429.
- Hooff, R. C. and Bollens, S. M. (2004) Functional response and potential predatory impact of *Tortanus dextrilobatus*, a recently introduced carnivorous copepod in the San Francisco Estuary. *Mar. Ecol.-Prog. Ser.*, **277**, 167–179.
- Kimmerer, W. J. (2004) Open water processes of the San Francisco Estuary: from physical forcing to biological responses. San Francisco Estuary and Watershed Science [online serial], Vol. 2, Article 1.
- Kimmerer, W. J., Burau, J. R. and Bennett, W. A. (1998) Tidally oriented vertical migration and position maintenance of zooplankton in a temperate estuary. *Limnol. Oceanogr.*, **43**, 1697–1709.
- Kimmerer, W. J., Ferm, N., Nicolini, M. H. *et al.* (2005) Chronic food limitation of egg production in populations of copepods of the genus *Acartia* in the San Francisco Estuary. *Estuaries*, **28**, 541–550.
- Lasker, R. (1981) The role of a stable ocean in larval fish survival and subsequent recruitment. In Lasker, R. (ed.), *Marine Fish Larvae: Morphology, Ecology and Relation to Fisheries*. University of Washington Press, Seattle, pp. 80–87.
- Lougee, L. A., Bollens, S. M. and Avent, S. R. (2002) The effects of haloclines on the vertical distribution and migration of zooplankton. *J. Exp. Mar. Biol. Ecol.*, **278**, 111–134.
- Lucas, L. V., Cloern, J. E., Koseff, J. R. *et al.* (1998) Does Sverdrup critical depth model explain bloom dynamics in estuaries? *J. Mar. Res.*, **56**, 375–415.
- McManus, M. A., Allredge, A. L., Barnard, A. H. *et al.* (2003) Characteristics, distribution and persistence of thin layers over a 48 hour period. *Mar. Ecol.-Prog. Ser.*, **261**, 1–9.
- McManus, M. A., Cheriton, O. M., Drake, P. J. *et al.* (2005) Effects of physical processes on structure and transport of thin zooplankton layers in the coastal ocean. *Mar. Ecol.-Prog. Ser.*, **301**, 199–215.
- McManus, M. A., Kudela, R. M., Silver, M. W. *et al.* (2008) Cryptic blooms: are thin layers the missing connection? *Estuaries and Coasts*, **31**, 396–401.
- Menden-Deuer, S. (2008) Spatial and temporal characteristics of plankton-rich layers in a shallow, temperate fjord. *Mar. Ecol.-Prog. Ser.*, **355**, 21–30.
- Monismith, S. G., Burau, J. R. and Stacey, M. T. (1996) Stratification dynamics and gravitational circulation in Northern San Francisco Bay. In Hollibaugh, J. T. (ed.), *San Francisco Bay: The Ecosystem*. California Academy of Sciences: San Francisco, pp. 123–153.
- Napp, J. M., Brooks, E. R., Matrai, P. *et al.* (1988) Vertical distribution of marine particles and grazers. 2. Relation of grazer distribution to food quality and quantity. *Mar. Ecol.-Prog. Ser.*, **50**, 59–72.
- Peterman, R. M. and Bradford, M. J. (1987) Wind speed and mortality rate of a marine fish, the Northern Anchovy (*Engraulis mordax*). *Science*, **235**, 354–356.
- Rollwagen-Bollens, G. C., Bollens, S. M. and Penry, D. L. (2006) Vertical distribution of micro- and nanoplankton in the San Francisco Estuary, in relation to hydrography and predators. *Aquat. Microb. Ecol.*, **44**, 143–163.
- Ryan, J. P., McManus, M. A., Paduan, J. D. *et al.* (2008) Phytoplankton thin layers caused by shear in frontal zones of a coastal upwelling system. *Mar. Ecol.-Prog. Ser.*, **3584**, 21–34.
- Sutor, M. M. and Dagg, M. J. (2008) The effects of vertical sampling resolution on estimates of plankton biomass and rate calculations in stratified water columns. *Estuar. Coast. Shelf. Sci.*, **78**, 107–121.
- Sutor, M. M., Cowles, T. J., Peterson, W. T. *et al.* (2005) Acoustic observations of finescale zooplankton distributions in the Oregon upwelling region. *Deep-Sea Res. Part II*, **52**, 109–121.
- Tiselius, P. (1994) Microscale patchiness of plankton within a sharp pycnocline. *J. Plankton Res.*, **16**, 543–554.
- Woodson, C. B., Webster, D. R., Weissburg, M. J. *et al.* (2005) Response of copepods to physical gradients associated with structure in the ocean. *Limnol. Oceanogr.*, **50**, 1552–1564.