

Multi-scale responses of scattering layers to environmental variability in Monterey Bay, California

Samuel S. Urmy^{a,**}, John K. Horne^a

^a*University of Washington School of Aquatic and Fishery Sciences, Box 355020, Seattle, WA 98195, USA*

Abstract

A 38 kHz upward-facing echosounder was deployed on the seafloor at a depth of 875 m in Monterey Bay, CA, USA (36° 42.748' N, 122° 11.214' W) from 27 February 2009 to 18 August 2010. This 18-month record of acoustic backscatter was compared to oceanographic time series from a nearby data buoy to investigate the responses of animals in sound-scattering layers to oceanic variability at seasonal and sub-seasonal time scales. Pelagic animals, as measured by acoustic backscatter, moved higher in the water column and decreased in abundance during spring upwelling, attributed to avoidance of a shoaling oxycline and advection offshore. Seasonal changes were most evident in a non-migrating scattering layer near 500 m depth that disappeared in spring and reappeared in summer, building to a seasonal maximum in fall. At sub-seasonal time scales, similar responses were observed after individual upwelling events, though they were much weaker than the seasonal relationship. Correlations of acoustic backscatter with oceanographic vari-

*Corresponding author

**Current address: Stony Brook University School of Marine and Atmospheric Sciences, 239 Montauk Hwy, Southampton, NY 11968, USA

Email address: samuel.urmy@stonybrook.edu (Samuel S. Urmy)

ability also differed with depth. Backscatter in the upper water column decreased immediately following upwelling, then increased approximately 20 days later. Similar correlations existed deeper in the water column, but at increasing lags, suggesting that near-surface productivity propagated down the water column at $10\text{-}15\text{ m d}^{-1}$, consistent with sinking speeds of marine snow measured in Monterey Bay. Sub-seasonal variability in backscatter was best correlated with sea-surface height, suggesting that passive physical transport was most important at these time scales.

Keywords:

acoustics, California Current, ocean observatories, physical-biological coupling, time series, upwelling

1 **1. Introduction**

2 Physical variability is a fundamental feature of the ocean’s pelagic habi-
3 tat, and the responses of pelagic organisms to this variability play a large role
4 in determining their distribution, abundance, and survival. As such, under-
5 standing the effects of physical change and variability on ocean life has long
6 been recognized as a central challenge in oceanography and marine ecology.
7 Physical variability can influence organisms at the individual or population
8 level, and its effects can be direct (e.g. advection) or indirect (e.g. production
9 fertilized by upwelled nutrients).

10 “Physical-biological coupling” has most often been studied in the plank-
11 ton, whose abundance and distribution are closely tied to physical variability
12 (Platt and Denman, 1975). However, because ocean currents are variable
13 across a wide range of spatial and temporal scales, the division between

14 plankton and nekton (Haeckel, 1890) is somewhat arbitrary. Coupling to
15 physical processes is thus expected to extend from zooplankton to micronek-
16 ton: animals roughly 2-10 cm in length with swimming abilities in between
17 those of drifting plankton and freely swimming nekton (Brodeur and Yama-
18 mura, 2005). These include krill, pelagic shrimps, small squids, and fishes
19 such as myctophids.

20 Assemblages of micronekton are important constituents of deep scatter-
21 ing layers (DSLs, Dietz 1948; Barham 1956). DSLs are layers of elevated
22 animal biomass, and consequently acoustic backscattering, which are found
23 worldwide in the ocean's mesopelagic zone, ≈ 200 to 1,000 m below the sur-
24 face. Many undergo diel vertical migration (DVM) of several hundred meters
25 to feed near the surface each night (Dietz, 1948; Hays, 2003). Micronekton,
26 from both the meso- and epipelagic (0-200 m depth), are important food
27 resources for a variety of larger fish, birds, and marine mammals and are
28 important carriers of energy, both up the food chain and down the water
29 column. Recent research suggests that the global biomass of small fishes in
30 the DSL is on the order of 10^{10} metric tons, and that they could respire as
31 much as 10% of primary productivity in the deep ocean (Kaartvedt et al.,
32 2012; Irigoien et al., 2014). They are probably also influenced by physical
33 variability, especially in dynamic environments.

34 The California Current is one such dynamic environment. As in other
35 eastern-boundary systems, Ekman pumping driven by seasonal equatorward-
36 flowing winds brings nutrient-rich water to the surface near the coast, fueling
37 a highly productive ecosystem. Though limited in area, upwelling systems
38 support a disproportionate amount of global fish landings (Pauly and Chris-

39 tensen, 1995), and attract large predators from great distances (Block et al.,
40 2011). The seasonal cycle of upwelling and productivity in the California
41 Current is generally consistent (Pennington and Chavez, 2000), but within
42 any given year upwelling is irregular, supplying nutrients to the food web in
43 episodic pulses. Upwelling is also spatially variable. Mesoscale (10s to 100s
44 of km) squirts, jets, eddies, and coastal waves all introduce variability into
45 the movement of water (Keister and Strub, 2008).

46 The effects of oceanic variability on micronekton are only now beginning
47 to be understood. Responses of phytoplankton to environmental variabil-
48 ity have been well studied at interannual (McGowan et al., 2003), seasonal
49 (Bolin and Abbot, 1963; Service et al., 1998), and sub-seasonal time scales
50 (Service et al., 1998; Legaard and Thomas, 2007). Environmental effects on
51 zooplankton and micronekton have also been studied, though mostly at sea-
52 sonal and longer time scales (e.g. Roesler and Chelton 1987; McGowan et al.
53 1996; Brinton and Townsend 2003; Rebstock 2003). Several recent studies
54 have examined spatial relationships between physical features and micronek-
55 ton distribution. These have regularly found changes in DSL structure and
56 density associated with mesoscale eddies (Kloser et al., 2009; Godø et al.,
57 2012; Fennell and Rose, 2015) and across frontal zones (Opdal et al., 2008;
58 Irigoien et al., 2014; Boersch-Supan et al., 2015). Fewer studies have exam-
59 ined the temporal evolution of DSLs in relation to physical oceanography
60 (Wang et al., 2014), and at sub-seasonal temporal scales, these effects are
61 largely unknown.

62 This study used a bottom-mounted echosounder in outer Monterey Bay,
63 CA to monitor changes in acoustic backscatter over 18 months. This sam-

64 pling allowed us to characterize macrozooplankton and micronekton biomass
65 through the entire water column at high temporal and spatial resolutions.
66 We compared these acoustic backscatter measurements to coincident mea-
67 surements of wind, temperature, and fluorescence as proxies of upwelling,
68 and sea levels, to investigate possible links between sea-surface topography
69 and animal biomass (e.g. Clarke and Dottori 2008). We also examined how
70 these responses varied as a function of depth. We expected a lagged increase
71 in backscatter following upwelling events, due to a combination of animal
72 aggregation, somatic growth, and population increase. A similar response to
73 increased productivity at the surface was expected from animals at depth,
74 but delayed and damped when compared to the response of surface animals.
75 Finally, we estimate the relative importance of different processes in gener-
76 ating the observed physical-biological relationships.

77 **2. Methods**

78 *2.1. Study location*

79 Monterey Bay is a large, open embayment in the central California coast.
80 The Bay’s oceanographic seasons follow those of the California Current, with
81 wind-driven upwelling in spring and early summer, a warm water “oceanic
82 period” in the late summer and fall, and a winter downwelling or “Davidson
83 current” period (Skogsberg et al., 1946; Pennington and Chavez, 2000). Point
84 Año Nuevo, to the north of the Bay, is the source of a persistent upwelling
85 plume that typically trails south across the mouth of the Bay (Rosenfeld
86 et al. 1994, Figure 1). Mean circulation within the bay is counterclockwise,
87 with enhanced productivity in the “upwelling shadows” near shore (Graham

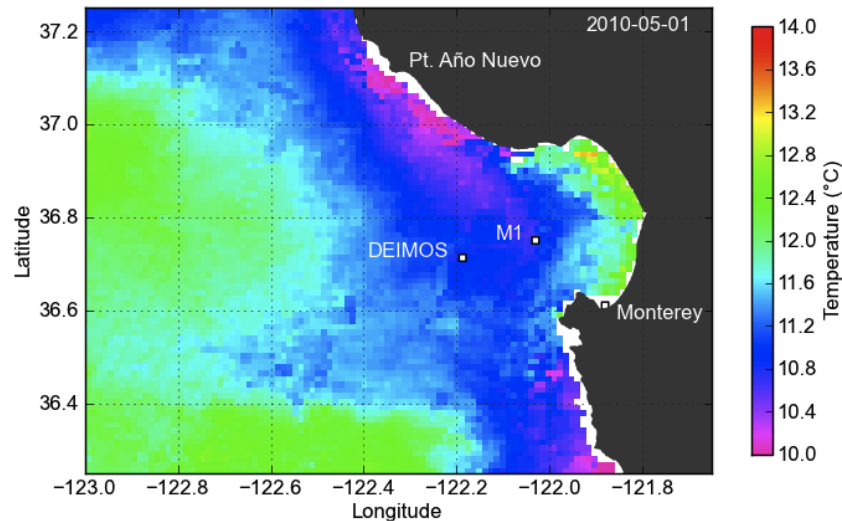


Figure 1: Monterey Bay, showing location of the upward-facing echosounder (DEIMOS) and oceanographic data buoy (M1) used in this study, as well as a typical pattern of sea-surface temperature during the upwelling season (AVHRR 3-day composite, 1 May, 2010). A band of cold, upwelled water is located along the coast, with warmer water offshore and inside the Bay. The coldest waters are near Point Año Nuevo and Point Sur.

88 et al., 1992).

89 *2.2. Acoustic Data*

90 Animal density through the water column was estimated using a bottom-
91 mounted echosounder. The Deep Echo Integrating Marine Observatory Sys-
92 tem (DEIMOS) is an acoustic package built around a 38 kHz scientific echosounder
93 (Horne et al., 2010). It was deployed at 875 m depth from February 27, 2009
94 to August 18, 2010 at the Monterey Accelerated Research System (MARS), a
95 cabled observatory node, located at 36°42.748' N, 122°11.214' W on Smooth
96 Ridge, to the north of the Monterey Submarine Canyon. MARS is main-
97 tained and operated by the Monterey Bay Aquarium Research Institute

98 (MBARI), and provides continuous power and communications for scientific
99 instruments. Several multi-day gaps in the data were caused by electrical
100 interference, software crashes, and burrowing rodents (Urmy et al., 2012).
101 DEIMOS sampled continuously at 0.2 Hz with a 0.5 m vertical resolution
102 through the water column. DEIMOS was calibrated *in situ* using a standard
103 target (Foote et al., 1987) hung from a float above the transducer during the
104 final 7 weeks of the deployment.

105 We were not able to take direct samples to identify scattering organisms,
106 so acoustic volume and area backscattering coefficients (s_v and s_a , and their
107 logarithmic forms S_v and S_a , MacLennan et al. 2002) were used as proxies
108 of animal biomass. This is a reasonable assumption for both single species
109 (Foote, 1983) and mixed communities (Benoit-Bird and Au, 2002).

110 Acoustic data were processed using Echoview software (version 4.8, Myr-
111 iax Pty. Ltd. 2010). Background noise was estimated and subtracted using
112 methods described in De Robertis and Higginbottom (2007). A backscatter
113 threshold was applied to eliminate acoustic returns with volume-scattering
114 strengths below -90 dB, the approximate backscattering intensity generated
115 by one krill m^{-3} at 38 kHz (Demer and Conti, 2003). All echograms were
116 visually inspected, and regions with external noise (e.g. ship or ROV noise)
117 were excluded from further analysis. Also excluded were regions within 7
118 m of the bottom, to eliminate targets in the acoustic near field, and within
119 10 m of the surface, to avoid integrating bubbles from breaking waves. The
120 mean depth of backscatter was measured using the acoustic center of mass
121 (CM, Urmy et al. 2012).

122 2.3. Oceanographic Data

123 Time series of wind velocity, sea-surface temperature (SST), and fluo-
124 rescence, a proxy for chlorophyll (Kirk, 1994), were measured at MBARI's
125 M1 data buoy, located 15 km ENE of DEIMOS at 36°45' N, 122°1.8' W
126 (Chavez et al. 1997, Figure 1). Service et al. (1998) found that wind velocity
127 at M1 was highly correlated ($R^2 = 0.78$) with wind velocity at MBARI's M2
128 mooring, 18 km WSW of DEIMOS. This correlation held during our study
129 period ($R^2 = 0.73$), indicating that winds at M1 were representative of those
130 at DEIMOS, located approximately midway between the M1 and M2 moor-
131 ings. Daily satellite measurements of SST and log chlorophyll-a at DEIMOS
132 and M1, from Level-3 AVHRR and MODIS-Aqua imagery, were also corre-
133 lated ($R^2 = 0.86$ and 0.37), giving us confidence that SST and fluorescence
134 measurements at M1 were representative of these values at the DEIMOS site.

135 Ekman transport of water offshore, an estimate of wind-driven upwelling,
136 was calculated from wind measurements at M1 following Bakun (1973). Off-
137 shore Ekman transport was estimated as $M_E = \tau_a / f$, where τ_a is the along-
138 shore component of the wind stress and f is the Coriolis acceleration, equal
139 to $8.326 \times 10^{-5} \text{ s}^{-1}$ at latitude 36°45' N. Wind stress was calculated as
140 $\boldsymbol{\tau} = \rho C_d |\mathbf{u}| \mathbf{u}$, where \mathbf{u} is wind velocity, ρ is the density of air (assumed
141 constant at 1.22 kg m^{-3}), and C_d is a non-dimensional drag coefficient, taken
142 to be 0.0013 (Bakun, 1973; Schwing et al., 1996). Alongshore wind stress was
143 defined as the component parallel to 150°, with positive stresses towards the
144 southeast. Sea-surface height (SSH) was measured by the National Oceanog-
145 raphic and Atmospheric Administration (NOAA) tide gauge in Monterey
146 (<http://tidesandcurrents.noaa.gov/geo.shtml?location=monterey>). SSH was

147 corrected for the reverse-barometer effect (Chelton and Enfield, 1986) and
148 low-pass filtered with a 25-hour moving average to remove the effects of di-
149 urnal and semidiurnal tides.

150 *2.4. Analysis*

151 Prior to analysis, values in all time series were averaged into one-day bins.
152 For the acoustic data, these averages used only values within four hours of
153 local noon (i.e. 08:00-16:00) to avoid “blurring” by diel vertical migration.
154 Oceanographic series were averaged over the full 24 hour period.

155 Correlations between environmental and acoustic variables at the seasonal
156 scale were quantified by calculating Pearson product-moment correlation co-
157 efficients between the respective time series. We also quantified the seasonal
158 cycles by fitting composite sinusoids with periods of 12 and 6 months to
159 the data by least squares. This allowed us to estimate the amplitudes and
160 timings of these cycles, even though only 18 months of acoustic data were
161 available. All further analyses used the residuals from these model fits.

162 We calculated the correlation between oceanographic and acoustic series
163 at time lags from 0 to 90 days—i.e., the cross-correlation function (CCF).
164 We used only the half of the CCF where the oceanographic variable led
165 the acoustic variable, since we were interested in the influence of oceanog-
166 raphy on micronekton. This is consistent with “bottom-up” forcing, from
167 physics to primary production and consumption, usually assumed to operate
168 through lower trophic levels (cf. Micheli et al. 1999). Assuming an uncorre-
169 lated white-noise null hypothesis, CCFs were considered significant if their
170 absolute value was greater than $z_{0.975}/\sqrt{n}$, where $z_{0.975}$ is the 0.975 quan-
171 tile of the standard normal distribution and n is the number of observations

172 in each time series (Brockwell and Davis, 2002). We calculated CCFs of
173 temperature and fluorescence with wind stress to check the time lag of phy-
174toplankton blooms behind upwelling events. We then calculated the lagged
175 correlation of upwelling wind stress, temperature, fluorescence, and sea level
176 with depth-integrated backscatter (S_a) and the CM. We also calculated the
177 lagged correlation of backscatter, at each depth in the water column, with
178 the oceanographic series.

179 To test the predictive power of the bio-physical relationships, we built
180 a statistical model for backscatter in the top 300 m of the water column,
181 representing prey available to surface-diving and epipelagic predators. We
182 regressed S_a , integrated from 0-300 m, on the values of the four environmen-
183tal variables at their best-correlated lag below 30 days, selecting significant
184 covariates using a backwards-deletion procedure. An autoregressive (AR)
185 model accounted for autocorrelation in the residuals. We computed the cor-
186rected Akaike information criterion (AICc, Hurvich and Tsai 1989) for AR
187 models using 0 to 15 AR terms, selecting the model with the lowest score.
188 This procedure optimizes the tradeoff between a model's goodness-of-fit and
189 the number of parameters estimated (Akaike, 1974). Parameters were fit by
190 maximizing the likelihood, using a state-space representation of the AR pro-
191cess to handle the missing values (Jones, 1980). Residuals were tested for
192 difference from white noise at the 0.05 level using the Ljung-Box test (Ljung
193 and Box, 1978). All analyses were run in R (R Development Core Team,
194 2014).

195 **3. Results**

196 *3.1. Seasonal cycles*

197 Weather and oceanography followed a clear annual cycle (Figure 2, Ta-
198 ble 1). Northwesterly winds and offshore Ekman transport were strongest
199 in early spring, co-occurring with low SSH and high fluorescence. The SSH
200 anomaly was lowest in April and May. SST and SSH had the strongest sea-
201 sonal patterns, with the seasonal models accounting for 39% and 50% of their
202 overall variabilities (Table 1). Upwelling and fluorescence were more episodic,
203 with only 13% and 14% of their variabilities explained by the seasonal models
204 (Table 1).

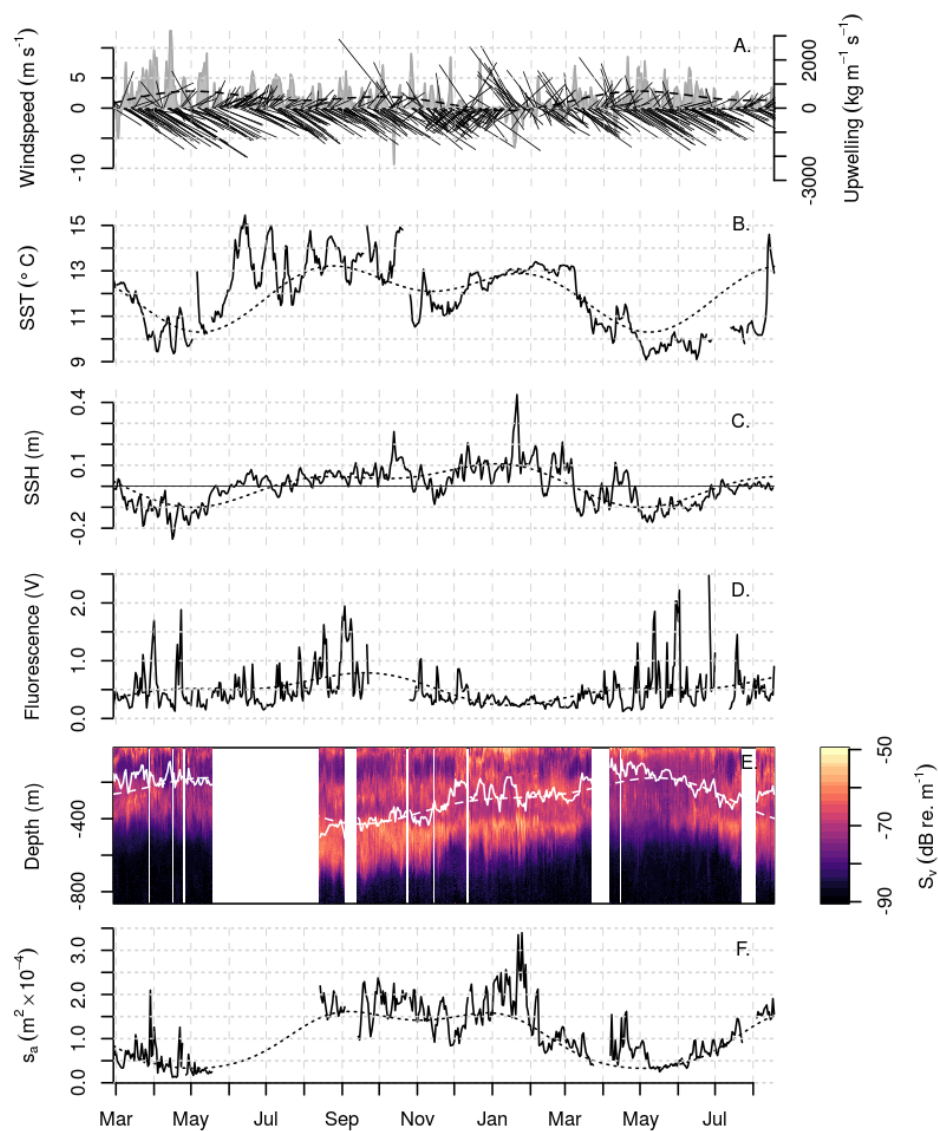


Figure 2: Oceanographic and acoustic time series from 27 February, 2009, to 18 August, 2010, with seasonal sinusoidal models (dotted lines). A) Wind vectors (magnitudes on left axis) and calculated upwelling (gray area, right axis). B) Sea-surface temperatures. C) Fluorescence. D) Sea-surface height. E) Daytime acoustic backscatter. White line shows vertical center of mass (CM). F) Depth-integrated area backscattering coefficient (s_a).

Table 1: Summary of sinusoidal models fit to environmental and acoustic time series.

Variable	Units	Mean	High	(date)	Low	(date)	R^2
Upwelling	kg (m s)^{-1}	341.27	703.3	Apr 30	-97.5	Jan 11	0.13
SST	$^{\circ}\text{C}$	12.07	13.2	Aug 24	10.3	May 7	0.39
Fluorescence	V	0.51	0.8	Sep 18	0.2	Jan 16	0.14
SSH	m	0.02	0.1	Jan 5	-0.1	May 2	0.50
CM	m	-296.99	-175.8	May 12	-428.7	Sep 15	0.70
Sa	dB	-40.26	-37.9	Sep 6	-44.8	May 3	0.72

205 The acoustic variables also had distinct seasonal cycles. Depth-integrated
206 backscatter was lowest in May, coinciding with the coolest temperatures and
207 highest fluorescence. It was highest in the fall and winter, with the seasonal
208 model peaking in September at -37.5 dB, while the highest overall S_a values
209 came during a short spike to -34.7 dB over several days in January 2010.
210 During its spring minima, backscatter moved up in the water column, with
211 its CM near 155 m depth. Backscatter was deepest in the water column in
212 September, centered near 420 m. This change in the CM was due to the
213 formation of a deep, thick, mostly non-migratory scattering layer between
214 400 and 700 m depth (Figure 2). The seasonal model for S_a accounted for
215 71% of its variability, and the seasonal model for the CM accounted for 74%
216 (Table 1).

217 The seasonal cycle of backscatter was out of phase with that of upwelling
218 and primary production (Table 1). The correlation coefficient of S_a with SST
219 was -0.64; with SSH it was 0.73 (Figure 3). The CM was negatively correlated
220 with SST ($r = -0.6$) and SSH ($r = -0.48$). All other correlation coefficients
221 were less than 0.3 (Figure 3).

222 3.2. Sub-seasonal dynamics

223 At sub-seasonal time scales, fluorescence was negatively correlated with
224 SST, with the highest correlation found at a lag of 3 days (Figure 4). Flu-
225 orescence displayed a characteristic scale of variability between 10 and 20
226 days, representing the average time between upwelling events and correspond-
227 ing phytoplankton blooms. Sea level also showed semi-periodic fluctuations
228 with a period of approximately 20 days. These fluctuations were correlated
229 ($\rho = -0.45$) with alongshore wind stress at lags of 1 day (Figure 4).

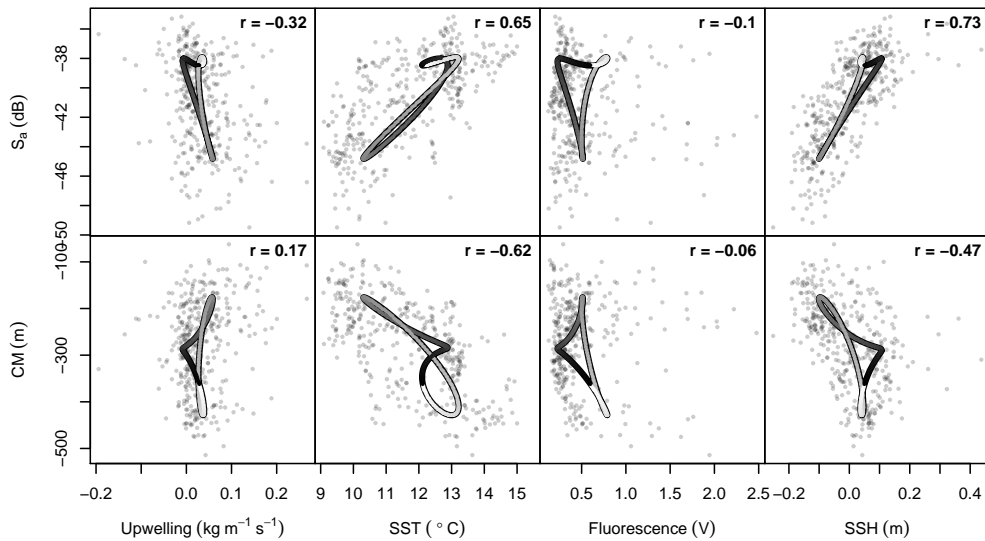


Figure 3: Pairwise relationships between oceanographic and acoustic time series at the seasonal time scale. Oceanographic variables, in columns from left to right, are upwelling Ekman transport, sea surface temperature (SST), chlorophyll fluorescence, and sea-surface height (SSH). Acoustic variables, in rows, are total depth-integrated backscatter (S_a) and the acoustic center of mass (CM). Points show daily values of the raw time series, with Pearson's product-moment correlation coefficient (r) displayed in upper-right corner. Curves show the modeled seasonal cycles for each pair of variables. The curves' color indicates day of the year, starting with black on 1 January and ending with white on 31 December. Because these models are sinusoidal, they must form loops, ending where they started. The closer a loop is to a straight line, the closer the cycles are to being perfectly in phase.

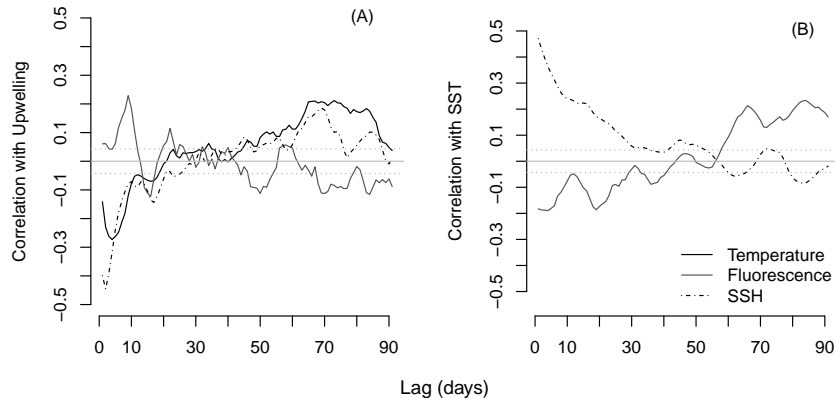


Figure 4: Cross-correlations between environmental series. A) Lagged correlations of sea-surface temperature, sea level, and fluorescence with alongshore wind stress. B) Lagged correlations of sea level and fluorescence with sea-surface temperature. Dotted grey lines show significance at the 0.05 level for a white-noise null hypothesis.

230 The density of pelagic animals was also related to oceanographic variability
231 at sub-seasonal time scales. Total backscatter had weak but significant
232 negative correlations with indicators of upwelling (alongshore wind stress,
233 below-average SST and above-average fluorescence) at lags less than 20 days
234 (Figure 5). The strongest relationship between upwelling variables and ani-
235 mal distribution was found in the CM, which was negatively correlated with
236 SST at all lags, with its minimum ($\rho = -0.23$) at 14-15-day lags. The CM
237 was also negatively correlated with fluorescence at lags between 0 and 18
238 days, though not as strongly as with temperature. Taken together, these
239 correlations indicate that the total animal abundance decreased slightly over
240 one to three weeks following upwelling events, while moving up in the water
241 column.

242 Of the environmental series examined, backscatter was best correlated

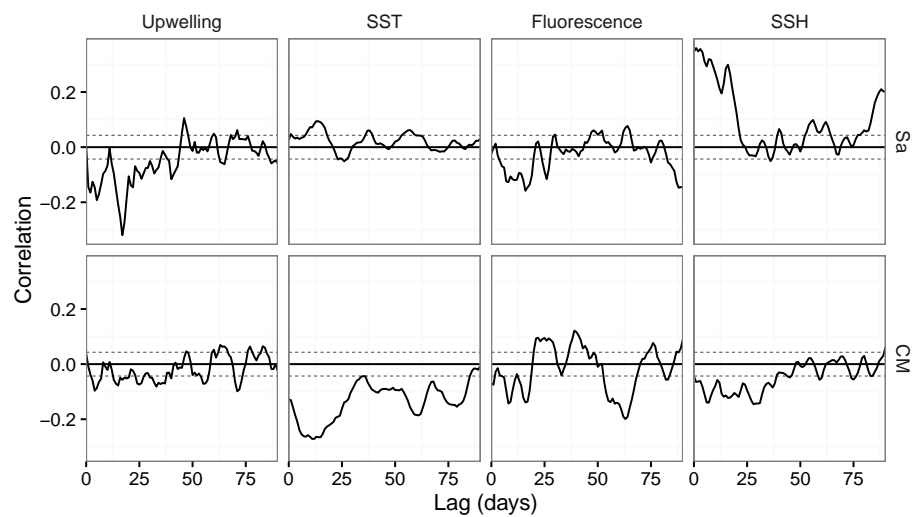


Figure 5: Cross-correlations between acoustic and environmental series. Plots show lagged correlation of total backscatter (S_a , top row) and its mean location in the water column (the center of mass CM, bottom row) with alongshore wind stress, sea-surface temperature (SST), Fluorescence, and sea-surface height (SSH). Dotted lines show significance at the 0.05 level for a white-noise null hypothesis.

243 with sea level. Cross-correlation of total backscatter with sea level was high-
244 est ($\rho = 0.31$) at a 0-day lag. The center of mass was significantly negatively
245 correlated with sea level at lags from 0 to 38 days. Together, these corre-
246 lations indicate that above-average sea levels were associated with increased
247 backscatter deeper in the water column.

248 The correlation of backscatter to environmental variability also varied as
249 a function of depth (Figure 6). Backscatter through the water column was
250 negatively correlated with alongshore wind stress, indicating decreases in
251 animal density immediately following upwelling winds (Figure 6A). At 40-75
252 day lags, the CCF became positive around 300 and 600 m, indicating that
253 backscatter increased at these depths.

254 The effects of temperature on backscatter depended more on depth than
255 on time lag. Backscatter above 200 m was negatively correlated with surface
256 temperature at lags from two to almost 90 days. Conversely, backscatter at
257 all depths below about 500 m was negatively correlated with temperature at
258 all lags (Figure 6B). These results agreed with those for the CM, and indicate
259 that decreases in surface temperature were associated with a long-lasting
260 increase in animal density in the upper water column, and a corresponding
261 decrease in density in the mesopelagic zone.

262 Backscatter was negatively correlated with fluorescence at lags from 0-20
263 days through most of the water column above 600 m, indicating a decrease
264 in animal density following phytoplankton blooms (Figure 6C). The corre-
265 lation became positive at 20-25 day lags near the surface. Below 600 m,
266 this relationship appeared to be reversed. At increasing lags, positive cor-
267 relations appeared at deeper depths, in an apparent propagation down the

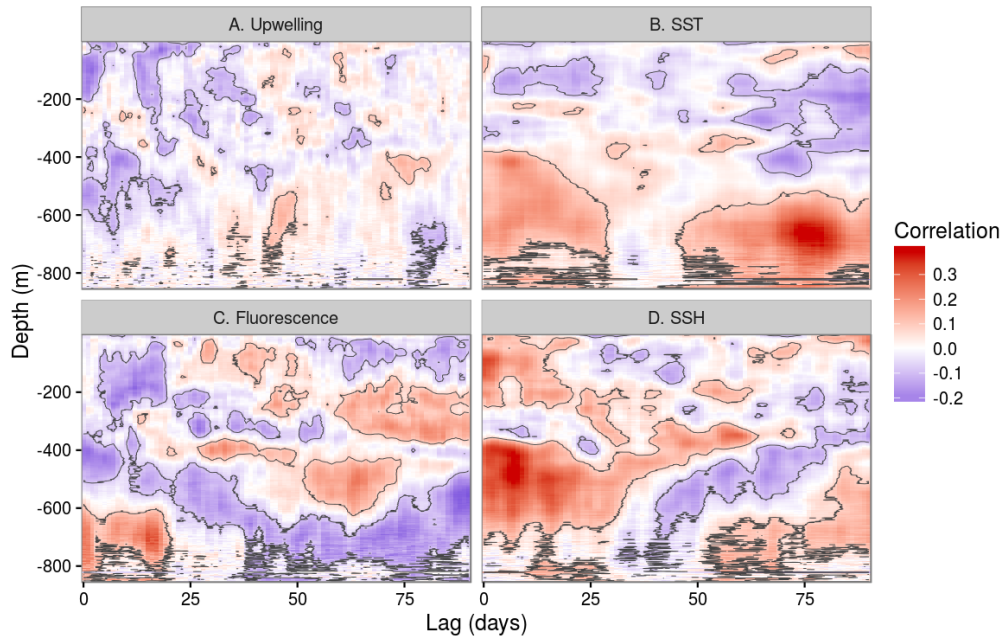


Figure 6: Correlations between environmental series and acoustic backscatter, as a function of lag (x-axis) and depth (y-axis). Red represents positive correlation, while blue represents negative correlation. Black contours enclose areas significantly different from zero at the 0.05 level, assuming a white-noise null hypothesis. Sub-figures show correlations between backscatter and A) alongshore (i.e., upwelling) wind stress, B) sea-surface temperature, C) surface fluorescence, and D) sea-surface height.

268 water column to about 300 m at a 60 day lag behind fluorescence. A similar
269 downward movement of the fluorescence signal was apparent over approxi-
270 mately the same range of temporal lags, but deeper, beginning near 350 m
271 and descending to about 550 m depth (Figure 6C).

272 For the regression model of micronekton in the upper 300 m of the water
273 column, wind stress at a 5-day lag and sea level at a 0-day lag were significant
274 ($p < 0.05$) predictors of backscatter above 300 m. The AICc procedure se-
275 lected a model including these covariates and seven past values of backscatter

Table 2: Parameter estimates, standard errors, and units for model of backscatter (dB re. 1 m² m⁻²) in the upper 300 m of the water column: $\alpha_{wind}^{(5)}$ is the regression coefficient for wind stress at a 5-day lag, $\alpha_{SSH}^{(0)}$ is the regression coefficient for sea-surface height at a 0-day lag, and $\phi^{(h)}$ is the autoregressive coefficient at lag h (in days).

Parameter	$\alpha_{wind}^{(5)}$	$\alpha_{SSH}^{(0)}$	$\phi^{(1)}$	$\phi^{(2)}$	$\phi^{(3)}$	$\phi^{(4)}$	$\phi^{(5)}$	$\phi^{(6)}$	$\phi^{(7)}$
Estimate	7.336	-8.170	0.657	-0.055	0.120	0.025	-0.018	-0.200	0.252
St. Error	2.036	1.447	0.050	0.062	0.062	0.066	0.064	0.062	0.051
Units	dB m ⁻¹	dB m ⁻¹	-	-	-	-	-	-	-

276 (Table 2). The model’s one-step-ahead prediction errors were uncorrelated
 277 (all Ljung-Box p-values > 0.8), with an error variance of 1.57 (dB re. 1 m²
 278 m⁻¹)². In the simple linear regression with no autoregressive component,
 279 wind and sea level explained 8% of the variability. The addition of seven
 280 autoregressive terms improved the R^2 value to 0.53.

281 4. Discussion

282 4.1. Identity and biology of scattering species

283 Though it is not possible to determine species composition from single-
 284 frequency acoustic data without direct sampling, we can use knowledge of
 285 the backscattering properties of common zooplankton and fish (Stanton et al.,
 286 1996; Horne and Clay, 1998) and literature on the California Current (Barham,
 287 1956; Kalish et al., 1986) to attribute most of the observed backscatter to
 288 mesopelagic micronekton.

289 Micronekton in the California Current are dominated by a relatively
 290 small number of species, including krill (*Euphausia pacifica* and *Thysanoessa*

291 *spinifera*), *Sergestes similis*, a panaeid shrimp, and myctophid fishes (*Dia-*
292 *phus theta*, *Stenobranchius leucopsarus*, and *Tarletonbeania crenularis*) (Phillips
293 et al., 2009). All of these animals have been associated with sound-scattering
294 layers (Barham, 1956; Kalish et al., 1986). Larger nekton are present as
295 well, including macrourids (Yeh and Drazen, 2011), Pacific hake (*Merluc-*
296 *cius productus*) and, in recent years, Humboldt squid (*Dosidicus gigas*, see
297 Field et al. 2007), though the relative contribution of these species to overall
298 biomass and backscatter is likely to be small compared to the smaller but
299 much more abundant micronekton species. When the acoustic threshold on
300 30 randomly-selected echograms was raised from -90 dB (the level used in
301 our analysis) to -58.5 dB (the level used for fisheries surveys of Pacific hake
302 *Mallotus villosus*, Wilson and Guttormsen 1997), an average of 77% of the
303 backscatter was eliminated. This difference suggests that the majority of
304 backscatter is attributable to smaller animals.

305 Dense surface aggregations were sometimes present, especially from Febru-
306 ary through April, probably representing surface-schooling krill (*Euphausia*
307 *pacifica* or *Thysanoessa spinifera*, Smith and Adams 1988), sardine (*Sardinops*
308 *sagax*), or anchovy (*Engraulis mordax*, Cailliet et al. 1979). These aggrega-
309 tions make substantial contributions to water column biomass on the tem-
310 poral scale of minutes as they pass through the acoustic beam, but do not
311 affect trends at scales of days or longer.

312 Visual surveys from ROVs have shown that a substantial portion of Mon-
313 terey Bay's mesopelagic fauna is gelatinous (Robison, 2004; Robison et al.,
314 2010). Though often considered weak acoustic targets relative to swimblad-
315 dered fish, gelatinous animals may in fact make substantial contributions to

316 backscatter (Colombo et al., 2003). The physonect siphonophore *Nanomia*
317 *bijuga* may be particularly important, since it is both abundant in Monterey
318 Bay and possesses a gas-filled pneumatophore (Stanton et al., 1998; Warren,
319 2001). *Nanomia's* seasonal cycle matches that of backscatter quite well,
320 peaking in summer between 200 and 600 m depth (Robison et al., 1998).
321 Siphonophores have long been recognized as potential contributors to DSLs
322 (Barham, 1963), but they are probably even worse-represented in net catches
323 than mesopelagic fish (Hamner et al., 1975; Kaartvedt et al., 2012).

324 4.2. Seasonal cycles

325 The environmental time series showed typical seasonal cycles for Mon-
326 terey Bay and the California Current. Northwesterly winds were highest
327 in spring, along with the surface expression of cooler water and spikes in
328 fluorescence, indicating upwelling and blooms of phytoplankton. Sea surface
329 height at the coast was also lowest in spring, likely associated with upwelling-
330 favorable winds pushing the surface layer offshore and lower the sea level near
331 the coast.

332 At the same time, the acoustic center of mass moved up in the water
333 column and overall backscatter decreased. This cycle agrees with previous
334 measurements from an ADCP on the M1 mooring (Croll et al., 2005), and
335 appears similar to recent measurements from the monsoon-driven upwelling
336 system in the Arabian Sea (Wang et al., 2014). The upward movement of
337 the CM may be explained by avoidance of a shoaling oxygen minimum zone
338 (OMZ). An oxygen minimum zone is found between approximately 500 and
339 1000 m depth in Monterey Bay, and is associated with a decrease in animal
340 density and changes in species assemblages (Lynn et al., 1982; Robison et al.,

341 2010). Globally, DSLs are found higher in the water column where dissolved
342 oxygen is lower (Klevjer et al., 2016). The OMZ in eastern boundary currents
343 rises during upwelling, changing the distribution of micronekton and fish
344 (Escribano et al., 2000; Chan et al., 2008; Bertrand et al., 2011). The decrease
345 in overall backscatter may be attributed to offshore transport of animals in
346 the upper water column.

347 Alternatively, these changes in the distribution of animals could be due
348 to seasonal cycles of reproduction and population dynamics. The winter
349 backscatter peak also appeared to agree with annual cycles of common mi-
350 cronekton in the California Current. *Euphausia pacifica*, the dominant krill
351 species, spawn mostly in the spring, with adult abundance peaking in fall
352 (Marinovic et al., 2002). Market squid (*Loligo opalescens*) are most abun-
353 dant in Monterey Bay from April through July (Fields, 1965). *Sergestes*
354 *similis* reproduce year-round with a springtime peak, and are most abundant
355 over the continental slope during winter (Pearcy and Forss, 1969; Omori and
356 Gluck, 1979). Myctophids in southern California were most abundant in win-
357 ter (Paxton, 1967). With the exception of squid, these animals' life-histories
358 are consistent with the observed seasonal changes in backscatter, supporting
359 our attribution of most of this acoustic energy to micronekton.

360 4.3. Sub-seasonal dynamics

361 4.3.1. Backscatter and sea level

362 At sub-seasonal time scales, sea surface height had the strongest and
363 most immediate correlation with acoustic backscatter. This correlation was
364 present through the water column, and suggests that advection is the most
365 important physical processes affecting the density of micronekton on time

366 scales of days to weeks.

367 Variation in coastal sea level is caused by several different processes, in-
368 cluding atmospheric pressure, wind-driven upwelling, and coastally-trapped
369 waves (Chelton and Enfield, 1986). Changes in atmospheric pressure force
370 a static response in sea-surface height, which rises approximately 1 cm per
371 1 mbar drop in air pressure (the “inverted barometer” effect, Chelton and
372 Enfield 1986). As described above, wind also affects sea level by pulling the
373 surface layer away or pushing it towards the coast. Together, these two fac-
374 tors (measured at M1) explain 63% of the variability in our de-seasonalized
375 sea level data.

376 Nearshore sea levels also vary with the passage of coastally trapped Kelvin
377 waves, which propagate northward along the California coast (Enfield and
378 Allen, 1980; Lyman and Johnson, 2008). Marinovic et al. (2002) found evi-
379 dence that Kelvin waves moved southern zooplankton species into Monterey
380 Bay during the 1997-1998 El Niño. Clarke and Dottori (2008) also found
381 that aggregate zooplankton biomass in the southern California Current was
382 correlated with sea level at San Diego with a two-month lag. They attributed
383 this correlation to enhanced upwelling, primary production, and zooplank-
384 ton population growth behind the waves, where sea level is lowest and the
385 thermocline is shallowest.

386 In contrast to Clarke and Dottori’s (2008) results, the correlations ob-
387 served in this study occurred at a scale of days to weeks, with no lag. The
388 near-immediate response of micronekton to sea level change, the consistency
389 of this response through the water column, and the days-to-weeks-scale corre-
390 lation all suggest passive aggregation by fluid motion. This result aligns with

391 the analysis in Urmy et al. (2012), which showed that the power spectrum of
392 the backscatter time series from DEIMOS was similar to that expected for
393 the velocity of a turbulent fluid.

394 A dramatic example of an immediate response occurred from 16-31 Jan-
395 uary 2010, when SSH and backscatter both spiked to their 18-month highs
396 within the same 3-day period (Figure 2, Figure 7). On January 18, 19, and
397 20, strong southeasterly winds caused onshore Ekman transport (Figure 7B).
398 Combined with low atmospheric pressure (986.6 mbar, measured at M1)
399 this transport led to the highest sea level of the 18-month series, increasing
400 from 0.1 to 0.5 m above normal (Figure 7C). Shortly before the peak SSH on
401 21 January, depth-integrated backscatter began to rise, increasing four-fold
402 from its minimum on 20 January (Figure 7D). This increase was driven by an
403 abrupt thickening of the deep scattering layer centered around 400 m depth
404 (Figure 7A). SSH declined over the next two days, rising slightly again on
405 25-26 January with another, weaker, southeasterly wind event. Backscatter
406 fell on 24 January, then spiked again to its 18-month high ($0.46 \times 10^{-4} \text{ m}^2$)
407 on 25 January before declining back to its previous level ($1.2 \times 10^{-4} \text{ m}^2$) over
408 the next five days.

409 Several mechanisms could be proposed to explain the correlation be-
410 tween SSH and backscatter. Onshore Ekman transport could collect zoo-
411 plankton and micronekton in the surface layers against the coast, but would
412 not extend to the mesopelagic zone, where sea level and micronekton were
413 also correlated. Downwelling resulting from onshore Ekman transport could
414 perhaps carry animals from the surface to deeper water, but Ekman up-
415 welling/downwelling velocities in the California Current are on the order of

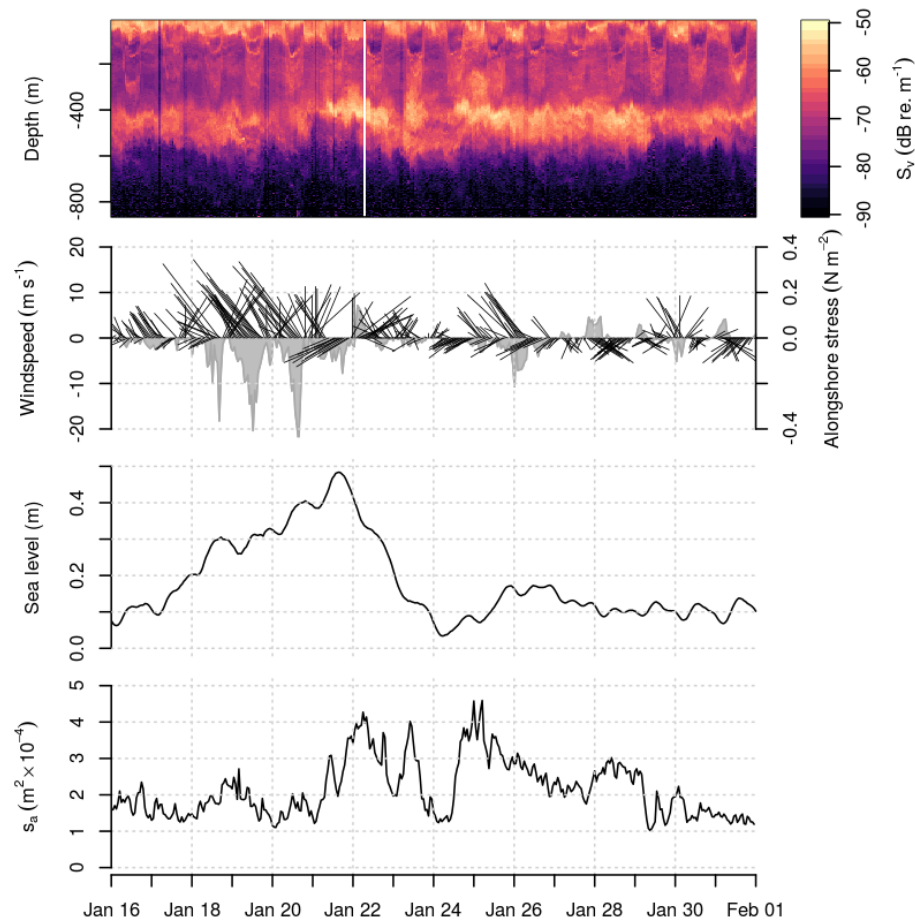


Figure 7: Hourly wind, sea level, and backscatter from 16-30 January, 2010. A) Echogram, showing volume backscattering strength (color) as a function of depth (y-axis) and time (x-axis). B) Wind direction and alongshore wind stress, as in Figure 2. C) Low-pass filtered Monterey sea level. D) Depth-integrated backscatter, approximately proportional to water column biomass. Strong southeasterly winds from 18-20 January precede a rise in sea level and total backscatter the next day.

416 10 m d^{-1} (Huyer, 1983; Münchow, 2000), and do not explain the sudden
417 thickening of a biological layer centered at 400 m depth. Alongshore advec-
418 tion of a pre-existing aggregation is another possibility. Flagg et al. (1994), in
419 a long-term acoustic Doppler current profiler deployment in the Mid-Atlantic
420 Bight, observed similar abrupt (i.e. day-scale) increases in backscatter asso-
421 ciated with reversals in alongshore currents.

422 Offshore, mesoscale eddies and jets can aggregate zooplankton (Huntley
423 et al., 2000) and alter deep scattering layers (Kloser et al., 2009; Godø et al.,
424 2012; Fennell and Rose, 2015). Both Godø et al. (2012) and Fennell and Rose
425 (2015) found the DSL thickened under anticyclonic eddies, where the SSH is
426 anomalously high and the isopycnals are deflected downwards. Anticyclonic
427 eddies are associated with downwelling and low primary production, suggest-
428 ing the thickened DSL is due to physical aggregation. Indeed, boundaries of
429 the DSL appear to closely track the isopycnals, further suggesting passive
430 transport (Godø et al., 2012).

431 Echograms of thickened DSLs under anticyclonic eddies (Godø et al.,
432 2012; Fennell and Rose, 2015) appear qualitatively similar to Figure 7. While
433 we did not measure hydrographic profiles to accompany our SSH data, iso-
434 static balance requires a downward deflection in the isopycnals accompanying
435 an upward deflection of the sea surface. If an anticyclonic eddy were to im-
436 pinge on the shelf, it could potentially bring zooplankton and micronekton
437 with it. A coastally-trapped Kelvin wave would have similar effects, since
438 it it is, in a sense, a geostrophic eddy with a coastline running through its
439 center (Gill and Clarke, 1974; Wang and Mooers, 1976).

440 *4.3.2. Backscatter and upwelling*

441 The response of micronekton to upwelling events was less pronounced
442 than the response to sea level, but still measurable. At time lags less than
443 one month following low SST, backscatter decreased in the mesopelagic and
444 increased in the epipelagic, while decreasing slightly overall. This is con-
445 sistent with upward animal movement, to avoid the shoaling of the OMZ,
446 followed by transport offshore with the surface layer. An alternate possibil-
447 ity is that increased primary production near the surface shaded the water
448 column below. Similar changes in downwelling irradiance can induce dra-
449 matic changes in the distribution of zooplankton (Frank and Widder, 2002).

450 The negative correlation between backscatter and fluorescence at lags
451 less than 20 days is related to correlations of backscatter with sea level and
452 temperature, since upwelling events that precede phytoplankton blooms are
453 also associated with decreases in sea level and temperature. Decreased mi-
454 cronekton abundances following phytoplankton blooms are interpreted as a
455 product of these physical processes, rather than a biological response to phy-
456 toplankton production. We cannot explain the positive correlation between
457 backscatter and fluorescence below 600 m (Figure 6C) from 0-20 day lags.
458 However, S_v at these depths was 20-40 dB (i.e., 2-4 orders of magnitude)
459 lower than in the main scattering layers, so the biological significance of
460 these correlations is expected to be minor.

461 At time lags greater than 20 days, there appeared to be a depth-dependent
462 response of micronekton to increased productivity at the surface. Positive
463 correlations of backscatter with fluorescence peaked at the surface at ap-
464 proximately 20-day lags, and propagated downward to 300 m within another

465 20-30 days, translating to a speed of 10-15 m d⁻¹. This rate is faster than
466 sinking phytoplankton (up to 1.69 m d⁻¹, Bienfang 1980), and slower than
467 the fecal pellets of krill (126-862 m d⁻¹, Fowler and Small 1972), midwater
468 fish (1028 m d⁻¹, Robison and Bailey 1981), or larvacean houses (800 m d⁻¹,
469 Robison et al. 2005). It is slower than sinking aggregates at the end of the
470 North Atlantic spring bloom (75 m d⁻¹, Briggs et al. 2011), but agrees fairly
471 well with sinking rates of marine snow measured in Monterey Bay (16.29 to
472 25.46 m d⁻¹ depending on particle size, PilskaIn et al. 1998).

473 The timing of these depth-dependent cross-correlations is suggestive of
474 a near-surface pulse of secondary production in zooplankton following up-
475 welling events, which then propagates down the water column as marine
476 aggregates. Detritus and marine snow are weak scatterers, but not acous-
477 tically invisible. Sinking pulses of krill fecal pellets can be resolved at 200
478 kHz (Røstad and Kaartvedt, 2013), and it is possible that some aggregates
479 contain gas bubbles, which would make them “visible” at 38 kHz (Opdal
480 et al., 2008). Sinking aggregates can also support dense communities of zoo-
481 plankton with benthic-like morphology and feeding behavior (Steinberg et al.,
482 1994), which would also increase their acoustic cross-section. Alternatively,
483 free-swimming animals could track pulses of sinking detritus down the water
484 column, since these particles represent a valuable food resource in the deep
485 ocean (McClain, 2010).

486 *4.3.3. Strength of sub-seasonal coupling*

487 While statistically significant relationships were detected between en-
488 vironmental and acoustic time series at sub-seasonal time scales, none of
489 these relationships were particularly strong. The maximum correlation coef-

490 ficient (between sea level and backscatter) was only 0.31, and in the lagged-
491 regression model, far more variance was explained by autocorrelation than
492 by any of the explanatory variables. Several aspects of the study's design
493 may have masked physical-biological relationships. DEIMOS and M1 were
494 separated by approximately 15 km, and even though physical measurements
495 were correlated across this distance, the separation between the two sen-
496 sors could have obscured relationships. Similarly, DEIMOS's acoustic beam
497 spanned only 115 m horizontally at its widest point, which might not be an
498 appropriate scale to observe the biological-physical coupling (cf. Schneider
499 and Piatt 1986).

500 The response of micronekton to upwelling and other environmental vari-
501 ability could simply be weak at sub-seasonal time scales. Population dy-
502 namics, somatic growth, and kinematics (i.e., passive or active aggregation
503 of animals in productive areas) could all link environmental variability to
504 changes in biomass and backscatter. While there is evidence that some
505 micronekton cue reproduction on upwelling events (Dorman et al., 2005),
506 the productivity-population relationship is not expected to be strong. Mid-
507 trophic-level micronekton must wait for smaller zooplankton to increase their
508 populations first. In effect, each successive trophic level acts as a low-pass
509 filter, smoothing out variability at scales shorter than its generation time.

510 Somatic growth could also account for increases in backscatter. As an ex-
511 ample, Moku et al. (2001) estimated growth rates for juvenile *Diaphus theta*,
512 the most common myctophid in DSLs in the California Current (Barham,
513 1956; Kalish et al., 1986). Combined with a target-strength/length relation-
514 ship from Yasuma et al. (2003), we can predict target strength (dB re. 1 m²)

515 as a function of age in days (t) as $TS = 11.83 \log_{10}(0.354 + 0.0129t) - 63.53$.
516 This equation implies that cohort of juveniles could increase its scattering
517 cross-section 36% in one month. On the other hand, some mesopelagic fishes
518 have swim bladders that deflate or fill with wax esters as they reach adult-
519 hood, leading to *decreases* in target strength (Yasuma et al., 2010). In any
520 case, somatic growth is not expected to respond quickly to individual pulses
521 of food.

522 Aggregation through active swimming also seems unlikely. Though myc-
523 topheids can swim up to 8 cm s^{-1} , translating to 6.9 km d^{-1} (Kaartvedt
524 et al., 2009), they have little reason to travel horizontally. Consider an aver-
525 age *Diaphus theta* weighing 0.4 g (Sassa et al., 2002), which must eat 1-6%
526 of its weight in food each day (Kosenok et al., 2006; Moku et al., 2000). If,
527 during several hours of nighttime foraging at the surface, it captures a single
528 medium-sized krill (10-40 mg for *Euphausia pacifica*, Wilson et al. 2009), its
529 energy needs will be met. Directed horizontal swimming is therefore proba-
530 bly not energetically favorable for vertically migrating micronekton. Indeed,
531 most myctophids tracked in a deep fjord drifted passively at depth (Kaartvedt
532 et al., 2009).

533 **5. Conclusion**

534 Our results illustrate a complex relationship between the variability of
535 animal biomass density and variability in their environment. Biomass density
536 at any location varies as animals swim, drift with currents, grow, interact
537 with other species, and increase or decline in population. Quantifying the
538 relative importance of these processes depends on the spatial and temporal

539 scales over which they occur, as well as measurement resolution (Horne and
540 Schneider, 1994).

541 The seasonal cycle of backscatter was negatively correlated and almost
542 exactly out of phase with that of upwelling. These changes were mostly
543 due to a deep, non-migrating scattering layer centered near 500 m depth,
544 which disappeared during the spring upwelling season and thickened to its
545 maximum during the fall and winter oceanic period.

546 Correlations between oceanography and the distribution of animals were
547 present at sub-seasonal time scales, though they were weaker than those ob-
548 served at seasonal scales. During upwelling events, the overall abundance of
549 animals decreased and moved upwards, consistent with vertical swimming to
550 avoid the shoaling OMZ and movement offshore with the Ekman layer. Ap-
551 proximately three weeks after upwelling events, backscatter increased in the
552 surface layer, suggesting reproduction of small or medium-sized zooplankton.
553 The upwelling signal then appeared to propagate down the water column at
554 rates similar to those measured for sinking marine aggregates. The strongest
555 physical-biological correlations at short time scales appeared to be driven by
556 passive aggregation of micronekton by fluid motion.

557 Variability in animal density influenced by physical processes is distributed
558 across a wide range of temporal scales. High-resolution, temporally-indexed
559 observations of animal density allow variability in animal densities to be mea-
560 sured and compared to other biological and physical processes at temporal
561 scales not possible when sampled using mobile platforms. Ultimately, station-
562 ary acoustic instruments could be used to augment fisheries and ecosystem
563 assessments by adding independent, temporal indices of population abun-

564 dance, flux, and variance.

565 Analyses used here were correlative and linear simplifications of a com-
566 plex, dynamic pelagic ecosystem. More realistic dynamic models for the
567 changing distribution of animals, explicitly based on physics and biology,
568 would ultimately be more appropriate and informative. While we currently
569 lack the detailed knowledge necessary to build such models, acoustic observ-
570 ing systems like DEIMOS can identify patterns in the underwater “land-
571 scape” and highlight complementary measurements necessary to interpret
572 the acoustic records. In the present work, we have attempted to start this
573 process.

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582 **7. References**

- 583 Akaike, H., 1974. A new look at the statistical model identification. IEEE
584 Transactions on Automatic Control 19 (6), 716–723.
- 585 Bakun, A., 1973. Coastal upwelling indices: West Coast of North America
586 1946-95. Tech. Rep. NMFS SSRF-693, U.S. Department of Commerce.

- 587 Barham, E. G., 1956. The ecology of sound scattering layers in the Monterey
588 Bay area, California. Ph.D. thesis, Stanford University.
- 589 Barham, E. G., 1963. Siphonophores and the deep scattering layer. *Science*
590 140 (3568), 826–828.
- 591 Benoit-Bird, K. J., Au, W. W. L., 2002. Energy: Converting from acoustic to
592 biological resource units. *The Journal of the Acoustical Society of America*
593 111, 2070–2075.
- 594 Bertrand, A., Chaigneau, A., Peraltilla, S., Ledesma, J., Graco, M., Monetti,
595 F., Chavez, F. P., 2011. Oxygen: a fundamental property regulating pelagic
596 ecosystem structure in the coastal southeastern tropical Pacific. *PloS one*
597 6 (12), e29558.
- 598 Bienfang, P. K., 1980. Phytoplankton sinking rates in oligotrophic waters off
599 Hawaii, USA. *Marine Biology* 61 (1), 69–77.
- 600 Block, B. A., Jonsen, I. D., Jorgensen, S. J., Winship, A. J., Shaffer, S. A.,
601 Bograd, S. J., Hazen, E. L., Foley, D. G., Breed, G. A., Harrison, A. L.,
602 Ganong, J. E., Swithenbank, A., Castleton, M., Dewar, H., Mate, B. R.,
603 Shillinger, G. L., Schaefer, K. M., Benson, S. R., Weise, M. J., Henry,
604 R. W., Costa, D. P., 2011. Tracking apex marine predator movements in
605 a dynamic ocean. *Nature* 475, 86–90.
- 606 Boersch-Supan, P. H., Rogers, A. D., Brierley, A. S., 2015. The distribution
607 of pelagic sound scattering layers across the southwest Indian Ocean. *Deep*
608 *Sea Research Part II: Topical Studies in Oceanography*.

- 609 Bolin, R. L., Abbot, D. P., 1963. Studies on the marine climate and phy-
610 toplankton of the central coastal area of California, 1954-1960. CalCOFI
611 Reports 9, 23–45.
- 612 Briggs, N., Perry, M. J., Cetinic, I., Lee, C., D’Asaro, E., Gray, A. M., Rehm,
613 E., 2011. High-resolution observations of aggregate flux during a sub-polar
614 North Atlantic spring bloom. Deep-Sea Research Part I: Oceanographic
615 Research Papers 58 (10), 1031–1039.
- 616 Brinton, E., Townsend, A., 2003. Decadal variability in abundances of the
617 dominant euphausiid species in southern sectors of the California Current.
618 Deep-Sea Research II 50 (14-16), 2449–2472.
- 619 Brockwell, P. J., Davis, R. A., 2002. Introduction to Time Series and Fore-
620 casting, 2nd Edition. Springer-Verlag.
- 621 Brodeur, R., Yamamura, O., 2005. Micronekton of the North Pacific. PICES
622 Scientific Report (30).
- 623 Cailliet, G. M., Karpov, K. A., Ambrose, D. A., 1979. Pelagic assemblages as
624 determined from purse seine and large midwater trawl catches in Monterey
625 Bay and their affinities with the market squid, *Loligo opalescens*. CalCOFI
626 Reports 20, 21–30.
- 627 Chan, F., Barth, J. A., Lubchenco, J., Kirincich, A., Weeks, H., Peterson,
628 W. T., Menge, B. A., 2008. Emergence of anoxia in the California Current
629 Large Marine Ecosystem. Science 319, 920.
- 630 Chavez, F. P., Pennington, J. T., Herlien, R., Jannasch, H., Thurmond, G.,
631 Friederich, G. E., 1997. Moorings and drifters for real-time interdisciplinary

- 632 oceanography. *Journal of Atmospheric and Oceanic Technology* 14 (1991),
633 1199–1211.
- 634 Chelton, D. B., Enfield, D. B., 1986. Ocean signals in tide gauge records.
635 *Journal of Geophysical Research* 91 (B9), 9081–9098.
- 636 Clarke, A. J., Dottori, M., 2008. Planetary wave propagation off California
637 and its effect on zooplankton. *Journal of Physical Oceanography* 38 (3),
638 702–714.
- 639 Colombo, G. A., Mianzan, H., Madirolas, A., 2003. Acoustic characterization
640 of gelatinous-plankton aggregations: four case studies from the Argentine
641 continental shelf. *ICES Journal of Marine Science* 3139 (3), 1352–1360.
- 642 Croll, D. A., Marinovic, B. B., Benson, S. R., Chavez, F. P., 2005. From wind
643 to whales: trophic links in a coastal upwelling system. *Marine Ecology*
644 *Progress Series* 289, 117–130.
- 645 De Robertis, A., Higginbottom, I., 2007. A post-processing technique to esti-
646 mate the signal-to-noise ratio and remove echosounder background noise.
647 *ICES Journal of Marine Science* 64 (6), 1282–1291.
- 648 Demer, D. A., Conti, S. G., 2003. Validation of the stochastic distorted-wave
649 Born approximation model with broad bandwidth total target strength
650 measurements of Antarctic krill. *ICES Journal of Marine Science* 60 (3),
651 625–635.
- 652 Dietz, R. S., 1948. Deep scattering layer in the Pacific and Antarctic Oceans.
653 *Journal of Marine Research* 7 (3), 430–442.

- 654 Dorman, J. G., Bollens, S. M., Slaughter, A. M., 2005. Population biology
655 of euphausiids off northern California and effects of short time-scale wind
656 events on *Euphausia pacifica*. Marine Ecology Progress Series 288, 183–
657 198.
- 658 Enfield, D. B., Allen, J. S., 1980. On the structure and dynamics of monthly
659 mean sea level anomalies along the Pacific coast of North and South Amer-
660 ica. Journal of Physical Oceanography 10, 557–578.
- 661 Escribano, R., Marin, V. H., Irribarren, C., 2000. Distribution of *Euphausia*
662 *mucronata* at the upwelling area of Peninsula Mejillones, northern Chile:
663 the influence of the oxygen minimum layer. Scientia Marina 64 (1), 69–77.
- 664 Fennell, S., Rose, G., 2015. Oceanographic influences on Deep Scattering
665 Layers across the North Atlantic. Deep Sea Research Part I: Oceanographic
666 Research Papers 105, 132–141.
- 667 Field, J. C., Baltz, K., Phillips, A. J., Walker, W. A., 2007. Range expan-
668 sion and trophic interactions of the jumbo squid, *Dosidicus gigas*, in the
669 California Current. CalCOFI Reports 48, 131–146.
- 670 Fields, W. G., 1965. The Structure, Development, Food Relations, Repro-
671 duction, and Life History of the Squid *Loligo opalescens* Berry. Fishery
672 Bulletin 131, 108 pp.
- 673 Flagg, C., Wirick, C., Smith, S., 1994. The interaction of phytoplankton,
674 zooplankton and currents from 15 months of continuous data in the Mid-
675 Atlantic Bight. Deep-Sea Research II 41 (2-3), 411–435.

- 676 Foote, K. G., 1983. Linearity of fisheries acoustics, with addition theorems.
677 The Journal of the Acoustical Society of America 73 (6), 1932–1940.
- 678 Foote, K. G., Knudsen, H. P., Vestnes, G., 1987. Calibration of acoustic
679 instruments for fish density estimation: a practical guide. Tech. Rep. 144,
680 International Council for the Exploration of the Sea, Copenhagen.
- 681 Fowler, S. W., Small, L. F., 1972. Sinking rates of euphausiid fecal pellets.
682 Limnology and Oceanography 17 (2), 293–296.
- 683 Frank, T., Widder, E., 2002. Effects of a decrease in downwelling irradiance
684 on the daytime vertical distribution patterns of zooplankton and micronek-
685 ton. Marine Biology 140 (6), 1181–1193.
- 686 Gill, A. E., Clarke, A. J., 1974. Wind-induced upwelling, coastal currents and
687 sea-level changes. Deep-Sea Research and Oceanographic Abstracts 21 (5),
688 325–345.
- 689 Godø, O.-R., Samuelsen, A., Macaulay, G. J., Patel, R., Hjøllø, S. S., Horne,
690 J. K., Kaartvedt, S., Johannessen, J. A., 2012. Mesoscale Eddies Are Oases
691 for Higher Trophic Marine Life. PLoS ONE 7 (1), e30161.
- 692 Graham, W. M., Field, J., Potts, D., 1992. Persistent “upwelling shadows”
693 and their influence on zooplankton distributions. Marine Biology 114, 561–
694 570.
- 695 Haeckel, E. H. P. A., 1890. Plankton-studien: Vergleichende untersuchungen
696 über die bedeutung und zusammensetzung der pelagischen fauna und flora.
697 Verlag von Gustav Fischer, Jena.

- 698 Hamner, W. M., Madin, L. P., Alldredge, a. L., Gilmer, R. W., Hamner,
699 P. P., 1975. Underwater observations of gelatinous zooplankton: Sampling
700 problems, feeding biology, and behavior. *Limnology and Oceanography*
701 20 (6), 907–917.
- 702 Hays, G. C., 2003. A review of the adaptive significance and ecosystem con-
703 sequences of zooplankton diel vertical migrations. *Hydrobiologia* 503, 163–
704 170.
- 705 Horne, J. K., Clay, C. S., 1998. Sonar systems and aquatic organisms: match-
706 ing equipment and model parameters. *Canadian Journal of Fisheries and*
707 *Aquatic Sciences* 55 (5), 1296–1306.
- 708 Horne, J. K., Schneider, D. C., 1994. Analysis of scale-dependent processes
709 with dimensionless ratios. *Oikos* 70 (2), 201–211.
- 710 Horne, J. K., Urmy, S. S., Barbee, D. H., 2010. Using sonar to describe tem-
711 poral patterns of oceanic organisms from the MARS Observatory. *Oceans*
712 2010 MTS/IEEE Seattle, 1–7.
- 713 Huntley, M. E., Gonzalez, A., Zhu, Y., Zhou, M., Irigoien, X., 2000. Zoo-
714 plankton dynamics in a mesoscale eddy-jet system off California. *Marine*
715 *Ecology Progress Series* 201, 165–178.
- 716 Hurvich, C. M., Tsai, C.-L., 1989. Regression and time series model selection
717 in small samples. *Biometrika* 76 (2), 297–307.
- 718 Huyer, A., 1983. Coastal upwelling in the California Current System.
719 *Progress in Oceanography* 12 (3), 259–284.

- 720 Irigoien, X., Klevjer, T. A., Røstad, A., Martinez, U., Boyra, G., Acuña,
721 J. L., Bode, A., Echevarria, F., Gonzalez-Gordillo, J. I., Hernandez-Leon,
722 S., Agusti, S., Aksnes, D. L., Duarte, C. M., Kaartvedt, S., 2014. Large
723 mesopelagic fishes biomass and trophic efficiency in the open ocean. *Nature*
724 *Communications* 5 (May 2013), 3271.
- 725 Jones, R. H., 1980. Maximum likelihood fitting of ARMA models to time
726 series with missing observations. *Technometrics* 22 (3), 389–395.
- 727 Kaartvedt, S., Røstad, A., Klevjer, T. A., Staby, A., 2009. Use of bottom-
728 mounted echo sounders in exploring behavior of mesopelagic fishes. *Marine*
729 *Ecology Progress Series* 395, 109–118.
- 730 Kaartvedt, S., Staby, A., Aksnes, D. L., 2012. Efficient trawl avoidance by
731 mesopelagic fishes causes large underestimation of their biomass. *Marine*
732 *Ecology Progress Series* 456, 1–6.
- 733 Kalish, J. M., Greenlaw, C. F., Percy, W. G., Holliday, D. V., 1986. The
734 biological and acoustical structure of sound scattering layers off Oregon.
735 *Deep-Sea Research I* 33 (5), 631–653.
- 736 Keister, J. E., Strub, P. T., 2008. Spatial and interannual variability in
737 mesoscale circulation in the northern California Current System. *Journal*
738 *of Geophysical Research* 113 (C4), C04015.
- 739 Kirk, J. T. O., 1994. *Light and Photosynthesis in Aquatic Ecosystems*. Cam-
740 bridge University Press.
- 741 Klevjer, T. A., Irigoien, X., Røstad, A., Fraile-Nuez, E., Benítez-Barrios,
742 V. M., Kaartvedt, S., 2016. Large scale patterns in vertical distribution and

- 743 behaviour of mesopelagic scattering layers. *Scientific Reports* 6 (19873), 1–
744 11.
- 745 Kloser, R., Ryan, T., Young, J., Lewis, M., 2009. Acoustic observations of
746 micronekton fish on the scale of an ocean basin: potential and challenges.
747 *ICES Journal of Marine Science* 66 (6), 998–1006.
- 748 Kosenok, N. S., Chuchukalo, V. I., Savinykh, V. F., 2006. The characteristics
749 of feeding of *Diaphus theta* (Myctophidae) in the northwestern part of the
750 Pacific Ocean in the Summer-Autumn period. *J. Ichthyol.* 46 (8), 606–612.
- 751 Legaard, K. R., Thomas, A. C., 2007. Spatial patterns of intraseasonal vari-
752 ability of chlorophyll and sea surface temperature in the California Current.
753 *Journal of Geophysical Research* 112 (C9), C09006.
- 754 Ljung, G. M., Box, G. E. P., 1978. On a measure of lack of fit in time series
755 models. *Biometrika* 65 (2), 297–303.
- 756 Lyman, J. M., Johnson, G. C., 2008. Equatorial Kelvin wave influences may
757 reach the Bering Sea during 2002 to 2005. *Geophysical Research Letters*
758 35 (14), L14607.
- 759 Lynn, R. J., Bliss, K. A., Eber, L. E., 1982. Distributions of seasonal mean
760 temperature, salinity, sigma-t, stability, dynamic height, oxygen, and oxy-
761 gen saturation in the California Current, 1950-1978. *CalCOFI Atlas* 30,
762 432.
- 763 MacLennan, D. N., Fernandes, P. G., Dalen, J., 2002. A consistent approach
764 to definitions and symbols in fisheries acoustics. *ICES Journal of Marine*
765 *Science* 59 (2), 365–369.

- 766 Marinovic, B. B., Croll, D. A., Gong, N., Benson, S. R., Chavez, F. P.,
767 2002. Effects of the 1997-1999 El Niño and La Niña events on zooplankton
768 abundance and euphausiid community composition within the Monterey
769 Bay coastal upwelling system. *Progress in Oceanography* 54, 265–277.
- 770 McClain, C., 2010. An empire lacking food. *American Scientist* 98 (6), 470.
- 771 McGowan, J. A., Bograd, S. J., Lynn, R. J., Miller, A. J., 2003. The biolog-
772 ical response to the 1977 regime shift in the California Current. *Deep-Sea*
773 *Research II* 50 (14-16), 2567–2582.
- 774 McGowan, J. A., Chelton, D. B., Conversi, A., 1996. Plankton patterns,
775 climate, and change in the California Current. *CalCOFI Reports* 37, 45–
776 68.
- 777 Micheli, F., Cottingham, K. L., Bascompte, J., Eckert, G. L., Fischer, J. M.,
778 Keitt, T. H., Kendall, B. E., Klug, J. L., Rusak, J. A., 1999. The dual
779 nature of community variability. *Oikos* 85 (1), 161–169.
- 780 Moku, M., Ishimaru, K., Kawaguchi, K., 2001. Growth of larval and juve-
781 nile (October 1998), 1–6.
- 782 Moku, M., Kawaguchi, K., Watanabe, H., Ohno, A., 2000. Feeding habits of
783 three dominant myctophid fishes, *Diaphus theta*, *Stenobrachius leucopsarus*
784 and *S. nannochir*, in the subarctic and transitional waters of the western
785 North Pacific. *Marine Ecology Progress Series* 207, 129–140.
- 786 Münchow, A., 2000. Wind Stress Curl Forcing of the Coastal Ocean near
787 Point Conception, California. *Journal of Physical Oceanography* 30 (6),
788 1265–1280.

- 789 Omori, M., Gluck, D., 1979. Life history and vertical migration of the pelagic
790 shrimp *Sergestes similis* off the Southern California coast. Fishery Bulletin
791 77 (1), 183–198.
- 792 Opdal, A. F., Godo, O.-R., Bergstad, O. A., Fiksen, O., Fiksen, b. U., 2008.
793 Distribution, identity, and possible processes sustaining meso-and bathy-
794 pelagic scattering layers on the northern Mid-Atlantic Ridge. Deep-Sea
795 Research II 55 (1-2), 45–58.
- 796 Pauly, D., Christensen, V., 1995. Primary production required to sustain
797 global fisheries. Nature 374 (6519), 255–257.
- 798 Paxton, J. R., 1967. A distributional analysis for the lanternfishes (family
799 Myctophidae) of the San Pedro Basin, California. Copeia 1967 (2), 422–
800 440.
- 801 Percy, W. G., Forss, C. A., 1969. The oceanic shrimp *Sergestes similis* off
802 the Oregon coast. Limnology and Oceanography 14, 755–765.
- 803 Pennington, J. T., Chavez, F. P., 2000. Seasonal fluctuations of temperature,
804 salinity, nitrate, chlorophyll and primary production at station H3/M1
805 over 1989-1996 in Monterey Bay, California. Deep-Sea Research II 47 (5-
806 6), 947–973.
- 807 Phillips, A. J., Brodeur, R. D., Suntsov, A. V., 2009. Micronekton commu-
808 nity structure in the epipelagic zone of the northern California Current
809 upwelling system. Progress in Oceanography 80 (1-2), 74–92.
- 810 Pilskaln, C. H., Lehmann, C., Paduan, J. B., Silver, M. W., 1998. Spatial
811 and temporal dynamics in marine aggregate abundance, sinking rate and

- 812 flux: Monterey Bay, central California. *Deep-Sea Research II* 45 (8-9),
813 1803–1837.
- 814 Platt, T., Denman, K. L., 1975. Spectral analysis in ecology. *Annual Review*
815 *of Ecology and Systematics* 6 (1975), 189–210.
- 816 R Development Core Team, 2014. R: A language and environment for statis-
817 tical computing.
- 818 Rebstock, G. A., 2003. Long-term change and stability in the California
819 Current System: lessons from CalCOFI and other long-term data sets.
820 *Deep-Sea Research II* 50 (14-16), 2583–2594.
- 821 Robison, B. H., 2004. Deep pelagic biology. *Journal of Experimental Marine*
822 *Biology and Ecology* 300, 253–272.
- 823 Robison, B. H., Bailey, T. G., 1981. Sinking rates and dissolution of midwater
824 fish fecal matter. *Marine Biology* 65 (2), 135–142.
- 825 Robison, B. H., Reisenbichler, K. R., Sherlock, R. E., 2005. Giant Lar-
826 vacean Houses: Rapid Carbon Transport to the Deep Sea Floor. *Science*
827 308 (5728), 1609–1611.
- 828 Robison, B. H., Reisenbichler, K. R., Sherlock, R. E., Silguero, J. M. B.,
829 Chavez, F. P., 1998. Seasonal abundance of the siphonophore, *Nanomia*
830 *bijuga*, in Monterey Bay. *Deep-Sea Research II* 45 (8-9), 1741–1751.
- 831 Robison, B. H., Sherlock, R. E., Reisenbichler, K. R., 2010. The bathypelagic
832 community of Monterey Canyon. *Deep-Sea Research II* 57 (16), 1551–1556.

- 833 Roesler, C. S., Chelton, D. B., 1987. Zooplankton variability in the California
834 Current, 1951-1982. *CalCOFI Reports* 28, 59–96.
- 835 Rosenfeld, L. K., Schwing, F. B., Garfield, N., Tracy, D. E., 1994. Bifurcated
836 flow from an upwelling center: a cold water source for Monterey Bay.
837 *Continental Shelf Research* 14 (9), 931–964.
- 838 Røstad, A., Kaartvedt, S., 2013. Seasonal and diel patterns in sedimentary
839 flux of krill fecal pellets recorded by an echo sounder. *Limnology and*
840 *Oceanography* 58 (6), 1985–1997.
- 841 Sassa, C., Kawaguchi, K., Kinoshita, T., Watanabe, C., 2002. Assemblages of
842 vertical migratory mesopelagic fish in the transitional region of the western
843 North Pacific. *Fisheries Oceanography* 11 (4), 193–204.
- 844 Schneider, D. C., Piatt, J. F., 1986. Scale-dependent correlation of seabirds
845 with schooling fish in a coastal ecosystem. *Marine Ecology Progress Series*
846 32, 237–246.
- 847 Schwing, F. B., O’Farrell, M., Steger, J. M., Baltz, K., 1996. Coastal up-
848 welling indices: West Coast of North America 1946-95. NOAA Technical
849 Memorandum NOAA-TM-NMFS-SWFSC-231, U.S. Department of Com-
850 merce.
- 851 Service, S. K., Rice, J. A., Chavez, F. P., 1998. Relationship between physical
852 and biological variables during the upwelling period in Monterey Bay, CA.
853 *Deep-Sea Research II* 45 (8-9), 1669–1685.
- 854 Skogsberg, T., Phelps, A., Society, A. P., 1946. *Hydrography of Monterey*

- 855 Bay, California. Thermal Conditions, Part II (1934-1937). Proceedings of
856 the American Philosophical Society 90 (5), 350–386.
- 857 Smith, S. E., Adams, P. B., 1988. Daytime surface swarms of *Thysanoessa*
858 *spinifera* (Euphausiacea) in the Gulf of the Farallones, California. Bulletin
859 of Marine Science 42 (1), 76–84.
- 860 Stanton, T. K., Chu, D., Wiebe, P. H., 1996. Acoustic scattering character-
861 istics of several zooplankton groups. ICES Journal of Marine Science 53,
862 289–295.
- 863 Stanton, T. K., Chu, D., Wiebe, P. H., 1998. Sound scattering by several
864 zooplankton groups. II. Scattering models. The Journal of the Acoustical
865 Society of America 103 (1), 236–253.
- 866 Steinberg, D. K., Silver, M. W., Pilskaln, C. H., Coale, S. L., Paduan, J. B.,
867 1994. Midwater zooplankton communities on pelagic detritus (giant lar-
868 vacean houses) in Monterey Bay, California. Limnology and Oceanography
869 39 (7), 1606–1620.
- 870 Urmey, S. S., Horne, J. K., Barbee, D. H., 2012. Measuring the vertical dis-
871 tributional variability of pelagic fauna in Monterey Bay. ICES Journal of
872 Marine Science 69 (2), 184–196.
- 873 Wang, D.-P., Mooers, C. N. K., 1976. Coastal-Trapped Waves in a Continu-
874 ously Stratified Ocean.
- 875 Wang, Z., DiMarco, S. F., Ingle, S., Belabbassi, L., Al-Kharusi, L. H., 2014.
876 Seasonal and annual variability of vertically migrating scattering layers

- 877 in the northern Arabian Sea. Deep-Sea Research Part I: Oceanographic
878 Research Papers 90, 152–165.
- 879 Warren, J., 2001. In situ measurements of acoustic target strengths of gas-
880 bearing siphonophores. ICES Journal of Marine Science 58 (4), 740–749.
- 881 Wilson, C. D., Guttormsen, M. A., 1997. Echo Integration-Trawl Survey of
882 Pacific Whiting, *Merluccius productus*, off the West Coasts of the United
883 States and Canada During July-September 1995. NOAA Technical Mem-
884 orandum NMFS-AFSC-74, U.S. Department of Commerce.
- 885 Wilson, M. T., Jump, C. M., Buchheister, A., 2009. Ecology of small neritic
886 fishes in the western Gulf of Alaska. II. Consumption of krill in relation to
887 krill standing stock and the physical environment. Marine Ecology Progress
888 Series 392, 239–251.
- 889 Yasuma, H., Sawada, K., Ohshima, T., Miyashita, K., Aoki, I., 2003. Tar-
890 get strength of mesopelagic lanternfishes (family Myctophidae) based on
891 swimbladder morphology. ICES Journal of Marine Science: Journal du
892 Conseil 60 (3), 584–591.
- 893 Yasuma, H., Sawada, K., Takao, Y., Miyashita, K., Aoki, I., 2010. Swim-
894 bladder condition and target strength of myctophid fish in the temperate
895 zone of the Northwest Pacific. ICES Journal of Marine Science: Journal
896 du Conseil 67 (1), 135–144.
- 897 Yeh, J., Drazen, J. C., 2011. Baited-camera observations of deep-sea megafau-
898 nal scavenger ecology on the California slope. Marine Ecology Progress
899 Series 424, 145–156.