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Abstract: We analyzed several records of mean volume backscattering strength (Sv) derived from 150 kHz Acoustic Doppler Current Profilers (ADCPs) moored along the equator in upwelling mesotrophic conditions and in the warm pool oligotrophic ecosystem of the Pacific Ocean. The ADCPs allow for gathering long time-series of non-intrusive information about zooplankton and micronekton at the same spatial and temporal scales as physical observations. High Sv are found from the surface to the middle of the thermocline between dusk and dawn in the mesotrophic regime. Biological and physical influences modified this classical diel cycle. In oligotrophic conditions observed at 170°W and 140°W during El Niño years, a subsurface Sv maximum characterized nighttime Sv profiles. Variations of the thermocline depth correlated with variations of the base of the high Sv layer and the subsurface maximum closely tracked the thermocline depth from intraseasonal to interannual time-scales. A recurring deepening (20 to 60 m) of the high Sv layer was observed at a frequency close to the lunar cycle frequency. At 165°E, high day-to-day variations prevailed and our results suggest the influence of moderately mesotrophic waters that would be advected from the western warm pool during westerly wind events. A review of the literature suggests that Sv variations may result from changes in biomass and species assemblages among which myctophids and euphausiids would be the most likely scatterers.

1 **Impact of environmental forcing on the acoustic backscattering strength in the**
2 **equatorial Pacific: diurnal, lunar, intraseasonal, and interannual variability**

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14

15 **Abstract**

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17 150 kHz Acoustic Doppler Current Profilers (ADCPs) moored along the equator in upwelling
18 mesotrophic conditions and in the warm pool oligotrophic ecosystem of the Pacific Ocean.
19 The ADCPs allow for gathering long time-series of non-intrusive information about
20 zooplankton and micronekton at the same spatial and temporal scales as physical
21 observations. High S_v are found from the surface to the middle of the thermocline between
22 dusk and dawn in the mesotrophic regime. Biological and physical influences modified this
23 classical diel cycle. In oligotrophic conditions observed at 170°W and 140°W during El Niño
24 years, a subsurface S_v maximum characterized nighttime S_v profiles. Variations of the
25 thermocline depth correlated with variations of the base of the high S_v layer and the

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27 time-scales. A recurring deepening (20 to 60 m) of the high S_v layer was observed at a
28 frequency close to the lunar cycle frequency. At 165°E, high day-to-day variations prevailed
29 and our results suggest the influence of moderately mesotrophic waters that would be
30 advected from the western warm pool during westerly wind events. A review of the literature
31 suggests that S_v variations may result from changes in biomass and species assemblages
32 among which myctophids and euphausiids would be the most likely scatterers.

34 **Keywords:** biological-physical interactions; equatorial Pacific; sound scattering;
35 micronekton; ADCP moorings

37 **1. Introduction**

38 The range of influences of zooplankton and micronekton (crustaceans, molluscs, fish of 1 to
39 10 cm length) on biogeochemistry is wide. These include the impact on nutrient cycling
40 through the relative magnitude of ingestion and excretion, export of inorganic and organic
41 matter by migrating organisms (Longhurst et al., 1989; Dam et al., 1995; Steinberg et al.,
42 2002), and influence on the distribution of top predators because they largely feed on
43 micronekton (Lehodey et al., 2010).

45 In the open ocean, distributions of zooplankton and micronekton vary over a broad range of
46 spatial and temporal scales in response to biological and environmental controls (Folt and
47 Burns, 1999). Diel vertical migration is commonly observed in many mesozooplankton (200-
48 2000 μm) or micronekton species. Organisms rise toward the surface at dusk and swim to
49 deeper waters at dawn. A “reverse migration” pattern is also observed (ascent at dawn and
50 descent at dusk) for some species as well as many intermediate migrating behaviors. These

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general upward or downward movements of mixed species populations are influenced by environmental (light, temperature) and/or biological (endogenous cycle, food availability, predator avoidance, population composition) factors (Haney, 1988; Folt and Burns, 1999). Discriminating the impact of different mechanisms is difficult because they often interact. In particular, the light level and predation pressure are linked as mortality due to visual predation is reduced when the light level is low in the surface layer where food is available (Gliwicz, 1986). In general, diel vertical migration can be seen as a strategy for organisms to escape visual predators at depth during the day and feed in the surface layer during the night.

Light is considered as the major factor that triggers diel vertical migration. In the classical migration pattern, the timing of upward (downward) movement is modulated by the length of day (Fisher and Visbeck, 1993; Asjian et al., 2002; Jiang et al., 2007). Reduced amplitude of downward migrations have been observed on cloudy days (Pinot and Jansá, 2001; Ashjian et al., 2002). Moonlight also modulates the vertical migration patterns. Some micronekton organisms stop their upward migration and do not reach the surface layer or dive slowly after dusk when moonlight is bright; abundance of some species may also increase because of the decrease of predation pressure (Legand et al., 1972; Roger, 1974; Gliwicz, 1986; Hernández-León, 1998; Tarling et al., 1999, Pinot and Jansá, 2001). Interestingly, during the night of an eclipse, animals did not descend until the end of the umbra (the time that the moon is in the Earth's shadow) (Tarling et al. 1999). Possible interactions of external factors with endogenous rhythm have been mentioned by Velsch and Champalbert (1994) and Tarling et al. (1999). Physical structures such as fronts, eddies, stratification variations may also alter the characteristics of the diel migration patterns at different spatial and temporal scales (Marchal et al., 1993; Fielding et al., 2001; Wade and Heywood, 2001; Vélez-Belchi et al., 2002).

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2 77 Diel migration behavior has been observed using net sampling (for example: Roger, 1974;
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4 78 Longhurst et al., 1989; Le Borgne and Rodier, 1997) by contrasting day and night
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7 79 measurements, and time-series derived from repeated cruises allowed for studying seasonal
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10 80 and interannual variability (Madin et al., 2001). Generally, episodic events and fine vertical
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12 81 distribution cannot be resolved over long periods of time because of sampling constraints.
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14 82 Acoustic devices have allowed for monitoring animals' behavior at fine vertical and temporal
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17 83 resolution as they detect targets mainly composed of zooplankton and micronekton organisms
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19 84 at frequencies on the order of 100 kHz (Ressler, 2002). Following Plueddemann and Pinkel
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22 85 (1989), acoustic studies (for example, Fisher and Visbeck, 1993; Heywood, 1996; Kaneko et
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24 86 al., 1996; Tarling et al., 1999; Pinot and Jansá, 2001; Asjian et al., 2002; Jiang et al., 2007)
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27 87 have described the characteristic alternate pattern of low and high backscattering during the
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29 88 day and night, and their modulations. Since Schott and Johns (1987), many studies used
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32 89 moored Acoustic Doppler Current Profilers (ADCPs) to describe seasonal variations of diel
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34 90 migration, including periods of rough conditions, and how they are affected by variations in
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37 91 light intensity or other physical forcing (Fisher and Visbeck, 1993; Flagg et al., 1994; Asjian
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39 92 et al., 1998; Pinot and Jansá, 2001).

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41 93
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43 94 Equatorial Pacific ecosystems reflect different physical forcing and characteristics. The
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46 95 western basin is occupied by warm, fresh, and oligotrophic nitrate depleted surface waters
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49 96 (Fig. 1a). In this region, sea surface temperature (SST) is higher than 29°C, sea surface
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51 97 salinity lower than 35, and surface chlorophyll lower than 0.1 mg m⁻³. The nitracline and the
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54 98 subsurface chlorophyll maximum are closely associated with the thermocline depth (Radenac
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56 99 and Rodier, 1996; Mackey et al., 1997; Navarette, 1998). The ocean variability is
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58 100 characterized by intraseasonal scales related to westerly wind variability and by interannual
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101 scales related to the El Niño Southern Oscillation (ENSO) (McPhaden, 1999; 2004). East of
102 the warm pool, equatorial upwelling brings cooler and saltier waters toward the surface in a
103 huge region spreading westward from the South American coast. Although the surface nitrate
104 concentration is high, the chlorophyll content remains moderate (less than 0.25 mg m^{-3} on
105 average between 1999 and 2004) because of an iron-limited and grazing-balanced ecosystem
106 (Landry et al., 1997). Variability occurs at intraseasonal (tropical instability waves, equatorial
107 Kelvin waves), seasonal, and ENSO time-scales. The sharp salinity front at the limit between
108 the warm pool and the cold tongue (Kuroda and McPhaden, 1993) also marks the
109 discontinuity of chemical and biological properties (Rodier et al., 2000) between the
110 oligotrophic and mesotrophic ecosystems. Small zooplankton ($35\text{-}200\mu\text{m}$) biomass is not
111 significantly different in the oligotrophic and mesotrophic regions whereas the
112 mesozooplankton biomass is higher (e.g., 2.5-fold increase in September-October 1994) in the
113 mesotrophic system (Le Borgne and Rodier, 1997). Little is known about micronekton
114 biomass and behavior along the equator. Population dynamics model results show that the
115 zonal distribution of the micronekton biomass in the 0-100 m layer increases from the warm
116 pool to the cold tongue (Lehodey et al., 2010) and intriguingly, highest tuna catch in the
117 Pacific occur on the oligotrophic warm pool side of the front (Lehodey et al., 1997).

118
119 Subsurface ADCP moorings are typically deployed within 5-15 kms of several equatorial
120 Autonomous Temperature Line Acquisition System (ATLAS) moorings of the Tropical
121 Atmosphere Ocean/Triangle Trans Ocean Buoy Network (TAO/TRITON) (McPhaden et al.,
122 1998). They are used to monitor the variability of the equatorial Pacific current system, but
123 they also provide long time-series of mean volume backscattering strength (S_v). Although
124 temperature, salinity, current, and meteorological data are widely used in the oceanography
125 community, S_v has not yet been used for biological purposes. Such long records are a unique

126 opportunity to monitor perturbations of the diel migration at the same vertical and temporal
127 scales as physical variables. In this study, we describe the variability of the acoustic
128 backscattering signal at three equatorial sites (165°E, 170°W, 140°W) located in both
129 equatorial ecosystems (Fig. 1a). Our objective is to investigate whether the response of the
130 ADCP signal in terms of magnitude and diel vertical migration pattern is specific to each
131 ecosystem. We also discuss the impact of environmental factors (moonlight and stratification)
132 in both ecosystems at the lunar, intraseasonal, and interannual timescales.

133

134 **2. Data and processing**

135 *2.1. The ADCP data*

136 We have selected a subset of data in order to describe the biomass signals in the oligotrophic
137 warm pool and in the mesotrophic upwelling region under the influence of different physical
138 conditions. Processing of the data for the purposes of this study is very labor intensive.
139 Therefore, we have focused on recent records at three equatorial sites of the TAO/TRITON
140 array: November 2001-November 2003 at 165°E, July 2002-July 2004 at 170°W and
141 September 1996-September 1999 at 140°W during the strong 1997-1998 El Niño and
142 subsequent La Niña. Instruments are 153.6 kHz RDI narrowband ADCPs mounted in an
143 upward-looking configuration at nominal depths of 250 to 300 m on subsurface moorings
144 (Plimpton et al., 2004). Data in the upper 40 m “deadzone” are excluded because of
145 contamination from reflections off the sea surface. Moorings are recovered and replaced with
146 new instruments approximately once per year (Table 1).

147

148 The equation of the mean volume backscattering strength (RDI, 1990), S_v in decibels, can be
149 rearranged into four components:

$$S_v = 10 \log_{10} \left[\frac{4.47 \times 10^{-20} K_2 K_s (T_x + 273.18)}{c P K_1} \right] + 20 \log_{10} R + 2 \alpha R + 10 \log_{10} \left[10^{K_c (E_a - E_r) / 10} - 1 \right]$$

150
151 The first component combines system dependant variables: K_2 is the system noise factor, K_s is
152 a constant that depends on ADCP frequency, K_1 is the power transmitted into the water
153 (watts), c is the speed of sound (m s^{-1}) at the scattering layer being measured, T_x is the
154 temperature of the transducer ($^{\circ}\text{C}$) recorded by the ADCP, and P is the transmit pulse length
155 (m). The second and third components account for beam spreading and absorption,
156 respectively. R is the range along the beam to the scatterers (m) and α is the absorption
157 coefficient in seawater (dB m^{-1}). We used the Francois and Garrison (1982) equation to
158 calculate α which is a function of temperature, salinity, sound frequency, depth, and pH.
159 Since temperature and salinity profiles are not continuously available from the moorings, we
160 calculated mean α profiles for each deployment and assumed a constant pH value of 8.1
161 which is sufficient in the buffered seawater. The last component represents the volume
162 scattering strength of the water mass. E_a is the echo intensity (counts) measured by the ADCP,
163 E_r is the background reference noise value (counts) taken as the minimum value measured for
164 each beam during each deployment, and K_c is a conversion factor (dB counts^{-1}).

165
166 In the following study, we present the mean S_v of the four beams (the antilog value of S_v was
167 taken before averaging). For most deployments, S_v offset of each beam (relative to the mean
168 S_v profile of the four beams) was less than 1 dB. However, at 165°E , offsets of about 1.5 dB
169 and -2 dB were detected for beams 1 and 4 during deployment wa3, and 1.16 dB for beam 2
170 during deployment wa4. In such cases, the offset was removed from S_v before averaging. In
171 order to study variations in the diel vertical migration associated with environmental forcing
172 at different time scales, we constructed nighttime (daytime) S_v profiles by averaging S_v

173 profiles within 2 hours of midnight (noon). Note that ADCPs are not calibrated and
174 uncertainty remains in comparing S_v between moorings.

175

176 2.2. Other data

177 We use additional *in situ* and satellite data to set up the environmental context. Although the
178 conversion ratio between the carbon biomass and chlorophyll (C:Chl) varies (Wang et al.,
179 2009), surface chlorophyll can be used as a realistic index of the trophic conditions. Surface
180 chlorophyll concentrations are SeaWiFS version 4, 9 km, 8-day composites computed by the
181 NASA Goddard Space Flight Center (GSFC) Distributed Active Archive Center (DAAC)
182 (McClain et al., 2004). Weekly SST are retrieved from the Tropical Rainfall Measuring
183 Mission (TRMM) Microwave Imager (TMI) starting in December 1997 and from the
184 Reynolds et al. (2002) *in situ* and satellite analysis before that date. Depths of the 29°C ($Z_{29^\circ\text{C}}$)
185 and 20°C ($Z_{20^\circ\text{C}}$) isotherms are derived from daily temperature profiles recorded at the
186 TAO/TRITON equatorial moorings. We also use daily SST, ADCP currents, wind speed, and
187 short-wave solar radiation from the moorings. When TAO/TRITON winds are missing, we
188 use the weekly QuickSCAT wind speed retrieved from the SeaWind scatterometer and
189 delivered by CERSAT, IFREMER. Phases of the moon and times of sunrise and sunset
190 originate from the web site of the US Naval Observatory (<http://aa.usno.navy.mil/>).

191

192 3. Results: the backscattering strength at the three sites

193 The TAO/TRITON mooring time-series that we use are from the central (140°W) and the
194 western part (170°W) of the mesotrophic ecosystem, and the eastern part of the oligotrophic
195 warm pool (165°E) (Fig. 1a). In this chapter, we first set the context by describing the large
196 scale physical dynamics and ecosystem variability. Then, we report S_v time-series

197 representative of conditions encountered at each mooring and describe the main types of
198 diurnal migration and perturbations under the influence of the physical environment.

199

200 *3.1. The large scale context*

201 The frontal zone between the oligotrophic and mesotrophic ecosystems closely follows the
202 0.1 mg m^{-3} surface chlorophyll isoline (Murtugudde et al., 1999; Stoens et al., 1999; Fig. 1a).

203 Its longitudinal location varies mainly at the El Niño Southern Oscillation (ENSO) time-scale
204 (Murtugudde et al., 1999; Radenac et al., 2001; Le Borgne et al., 2002; Ryan et al., 2002;

205 Radenac et al., 2005) as can be seen from the evolution of satellite-derived chlorophyll in the
206 equatorial Pacific (Fig. 1b). During El Niño years, oligotrophic waters of the warm pool

207 spread eastward. The front reached 160°W during the moderate 2002 El Niño event and

208 130°W during the peak period of the major 1997 event. Very low chlorophyll values

209 ($< 0.07 \text{ mg m}^{-3}$), such as those found in the subtropical gyres (McClain et al., 2004), were

210 confined in the eastern part of the warm pool. Further west, surface chlorophyll and biological

211 production were higher than during non-El Niño years (Dandonneau, 1986; Mackey et al.,

212 1997; Turk et al., 2001) and episodic increases of surface chlorophyll were associated with

213 westerly wind events (Siegel et al., 1995; Radenac et al., unpublished results). The

214 thermocline, represented here by the depth of the 20°C isotherm (Kessler, 1990), was uplifted

215 in the western Pacific warm pool and depressed in the cold tongue (Fig. 1c) in 1997 and 2002.

216 During the period of the study, equatorial downwelling Kelvin waves were forced in the

217 western basin by intraseasonal westerlies and propagated eastward. They depressed the

218 thermocline and initiated eastward displacements of the front, particularly in December 1996,

219 March 1997, December 2001, the second half of 2002, December 2003, and the second half

220 of 2004 (Fig. 1c).

221

222 During La Niña events, the equatorial cold tongue extends westward as observed during the
1
2 223 long-lasting La Niña period between mid 1998 and 2001 when chlorophyll-rich waters
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4 224 expanded west of 170°E (Fig. 1b). In mid-1998, the chlorophyll bloom was the strongest and
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7 225 largest observed by SeaWiFS in the central and eastern equatorial Pacific. This unusually
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10 226 strong manifestation of interannual variability following the major 1997-1998 El Niño event
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12 227 resulted from strong vertical macro- and micro-nutrient fluxes associated with the surfacing of
13
14 228 the Equatorial Undercurrent (EUC) and thermocline outcropping (Chavez et al., 1999; Ryan
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17 229 et al., 2002). The thermocline depth remained shallower than climatological values until early
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19 230 2000 (Fig. 1c).

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232 3.2. 170°W

233 The 0°, 170°W mooring was situated at the western end of the cold mesotrophic tongue (SST
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27 233 < 29°C, surface chlorophyll $\approx 0.2 \text{ mg m}^{-3}$) except from September to December 2002 when
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29 234 the eastern edge of the oligotrophic warm pool migrated past 170°W during the mild El Niño
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32 235 event (Fig. 1b; Fig. 2a). At this mooring as well as at the two other sites, the dominant S_v
33
34 236 variability occurs at the diurnal frequency. The two records we present (Table 1) allow
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36
37 237 contrasting observations of the diurnal migration in two ecosystems at this site.
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239

240 3.2.1. Diel cycles

241 Diel cycles in early June 2003 (Fig. 3a) are representative of those encountered in
242 mesotrophic cold tongue conditions that lasted from February 2003 to June 2004 (Fig. 2). The
243 mean nighttime S_v profile was fairly homogeneous above $Z_{20^\circ\text{C}}$ and decreased below (Fig. 3b).
244 Daytime S_v was more homogeneously distributed over the observed layer. As a consequence,
245 the averaged difference between the nighttime and daytime S_v was about 10 dB above $Z_{20^\circ\text{C}}$
246 (Table 2) while it was slightly negative below. The characteristic alternate pattern of low

247 daytime S_v and high nighttime S_v in the upper layer reflects the migratory behavior of
248 zooplankton and micronekton organisms that rise from below the transducer depth at dusk
249 and descend at dawn.

250
251 Between September and December 2002, the 170°W mooring was in the oligotrophic warm
252 pool. Vertical S_v distribution exhibited several distinctive features compared to S_v profiles in
253 mesotrophic conditions. The first one was a S_v decrease (5 to 10 dB) above $Z_{20^\circ\text{C}}$ nighttime or
254 daytime. The difference between night and day S_v above $Z_{20^\circ\text{C}}$ tended to be lower in the
255 oligotrophic system than in the mesotrophic one (Fig. 3b, d; Table 2). The second remarkable
256 feature was an alteration of nighttime profiles (Fig. 2b) characterized by a subsurface
257 maximum located in the upper part of the thermocline (Fig. 3d) that did not persist during
258 daytime. The depth of the subsurface S_v maximum deepened concurrently with $Z_{20^\circ\text{C}}$ and
259 $Z_{29^\circ\text{C}}$ in early September, mid-October, and mid-December (Fig. 2b) when three downwelling
260 Kelvin waves passed the 170°W mooring while oligotrophic conditions prevailed (Fig. 1c).
261 The correlation coefficient between the depth of the subsurface S_v maximum and $Z_{20^\circ\text{C}}$
262 between 10 September and 31 December 2002 is 0.77 ($p < 0.01$), suggesting a significant
263 influence of changes in stratification on S_v . The correlation relative to $Z_{29^\circ\text{C}}$ yields $r = 0.87$ (p
264 < 0.01). Moon light is also a significant influence on S_v as discussed below.

265 266 3.2.2. *The lunar cycle*

267 The influence of the lunar cycle is clearly seen in the time-series of nocturnal S_v between
268 February 2003 and June 2004 (Fig. 2b) during mesotrophic conditions. During full moon
269 periods, S_v decreased in the surface layer and high S_v values extended deeper into the
270 thermocline by 20 to 30 m. As expected from these observations, a strong peak at the
271 frequency closest to the frequency of the lunar cycle (frequency of 0.034 cpd) dominates S_v

272 power spectra (not shown). Little energy was found between 70 and 120 m while maximum
273 energy was observed between 150 and 200 m. Unfortunately, data above 40 m depth were
274 unavailable and only the lower part of a high energy surface layer was captured above 60 m.
275 During full moon periods, S_v decreased sharply by 5 to 10 dB at the bottom of the surface
276 layer (40 m; Fig. 4a) while the range of increases in the middle of the thermocline was larger
(Fig. 4b).

278
279 Such variations can be assessed by examining S_v diel cycles during a representative lunar
280 cycle (Fig. 5). We chose September 2003 because short wave radiation measured at the
281 TAO/TRITON mooring during the day was high (not shown). Therefore, although it tends to
282 be cloudier and rainier over the tropical oceans at night compared to during the day (Serra and
283 McPhaden, 2004), we might expect nighttime cloudiness at this time and location to be
284 relatively low. Sunset is around 1800 local time (LT) and sunrise is around 0600 LT. At new
285 moon, the moon and sun rise together (27 August and 26 September) while at full moon, the
286 moon rises when the sun sets (9 September).

287
288 Diel cycles surrounding new moon (26-27 August, 25-26 September) exhibited a “classical”
289 pattern with a rapid vertical ascent at sunset. High S_v levels extended from 40 m depth to the
290 middle of the thermocline until sunrise. Between new moon (26-27 August) and full moon (9-
291 10 September), duration of period between moonset and sunrise decreased. S_v in the surface
292 layer was lower at the beginning of the night when moonlight was bright than when
293 moonlight became dimmer. On the full moon night (9 September), surface S_v decreased after
294 the swift vertical upward migration at dusk. During the following days, the nighttime descent
295 happened later in the night. As a consequence, duration of observation of high S_v in the
296 surface layer was longer around new moon than around full moon. At depth, the high S_v layer

297 tended to go deeper during the early hours of the night preceding full moon while it deepened
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2 298 at the end of the night after full moon, leading to asymmetrical patterns over the night.

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7 300 Although it is not as clear as in the mesotrophic regime, examination of individual daily S_v in
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9 301 the oligotrophic regime cycles suggests that the lunar cycle influenced the vertical distribution
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11 302 in the upper layer and the depth of the subsurface maximum layer (not shown). Following full
12
13 303 moon, a surface decrease and a deepening of the subsurface S_v maximum was often observed
14
15 304 after moonrise. Before full moon, surface S_v increased during darkness following moonset.
16
17 305 Yet, time-series in oligotrophic ecosystems encompassed only three lunar cycles (see Fig. 2b)
18
19 306 and no definitive conclusion can be drawn from this data set.
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26 308 *3.3. 140°W*

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29 309 Situated in the central equatorial Pacific, the mooring at 140°W experienced very unusual
30
31 310 ecosystem and stratification conditions during the major 1997 El Niño and 1998 La Niña
32
33 311 events (McPhaden, 1999; Strutton and Chavez, 2000; Radenac et al., 2001). During the pre-El
34
35 312 Niño period (September 1996 - September 1997), the ecosystem was mesotrophic with
36
37 313 surface chlorophyll measured by the Ocean Color and Temperature Scanner (OCTS) and
38
39 314 Polarization and Directionality of the Earth Reflectances (POLDER) mission between
40
41 315 November 1996 and June 1997 around 0.15 mg m^{-3} (Radenac et al., 2001; Ryan et al., 2002).
42
43 316 SST was close to climatology in 1996 and increased in 1997 as the El Niño event proceeded
44
45 317 (Fig. 6a). S_v patterns were close to those encountered in the mesotrophic regime at 170°W
46
47 318 with high nighttime S_v above $Z_{20^\circ\text{C}}$. The thermocline depth was close to climatology in late
48
49 319 1996 after which two downwelling Kelvin waves depressed the thermocline by more than
50
51 320 20 m in January and March 1997 (Fig. 1c; Fig. 6b). The depth of the high nighttime S_v layer
52
53 321 followed $Z_{20^\circ\text{C}}$ variations (Fig. 6b) during the pre-El Niño period and during the passage of
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322 the downwelling Kelvin waves. Correlation coefficient between the depth of the high
323 nighttime S_v layer (represented by the -58 dB isoline) and $Z_{20^\circ\text{C}}$ (removing short time scale
324 variations with a 15-day-Hanning filter) is 0.84 ($p < 0.01$). During this period, variations at
325 the lunar frequency (Fig. 6b) were comparable to observations in the 170°W mesotrophic
326 ecosystem. The power spectrum peaked in the surface layer and at the base of the high
327 nighttime S_v layer (not shown).

328
329 During the peak of the El Niño event (October 1997 - January 1998), waters of the
330 oligotrophic warm pool reached 140°W (Fig. 6a; Chavez et al., 1999; Strutton and Chavez,
331 2000; Radenac et al., 2001). Accordingly, the lowest S_v were observed in November-
332 December (Fig. 6a, b). The vertical structure changed. Adjustment from a uniform nighttime
333 high S_v layer to oligotrophic type profiles with a nighttime S_v maximum squeezed between
334 $Z_{29^\circ\text{C}}$ and $Z_{20^\circ\text{C}}$ was swift. Narrowing of the low nighttime S_v layer above $Z_{29^\circ\text{C}}$ and shoaling
335 of the underlying layer of maximum S_v were significant features of the period. They closely
336 followed the shoaling of the thermocline (Fig. 1c). As for the 170°W time-series, surface
337 decreases were observed during full moon and there were hints of deepening of the subsurface
338 S_v maximum in November and December 1997 (not shown).

339
340 Following the strong El Niño event, the sudden recovery of trade winds triggered an abrupt
341 onset of La Niña conditions. Unusually shallow thermocline ($Z_{20^\circ\text{C}}$ was only 30 m deep; Fig.
342 6b) and high surface chlorophyll (almost fourfold the average value of 0.21 mg m^{-3}) prevailed
343 between June and August 1998 (Fig. 6a). During this “shallow mesotrophic” period, the
344 highest nighttime S_v were trapped above $Z_{20^\circ\text{C}}$ in the upper 40 m layer where the ADCP signal
345 is missing (Fig. 6b; Fig. 7). During the mid-1998 bloom period, a high S_v layer was located
346 below $Z_{20^\circ\text{C}}$ during the day (Fig. 6c). It sank gradually from sunrise to noon then rose toward

347 the surface until sunset (Fig. 7). Above 200 m, it merged with rapid vertical migrating layer
348 from below the transducer. The nighttime surface decrease associated with full moon period
349 was not observed, but some increases were observed from $Z_{20^{\circ}\text{C}}$ to the bottom of the sampled
350 layer (Fig. 6b) for a few cycles (September 1998-April 1999).

352 3.4. 165°E

353 S_v data at 165°E exhibits high frequency variability (Fig. 8) that possibly reflects the special
354 location of the mooring close to the frontal zone between the oligotrophic and mesotrophic
355 ecosystems (Fig. 1b). Although, the mooring was situated in surface chlorophyll poor waters
356 in January-June 2002, January-March 2003, and July-November 2003 (Fig. 8a), oligotrophic
357 type profiles with a subsurface nighttime S_v maximum were observed only in January-
358 February 2003; during the other periods of time, the day to day variability was high, with
359 vertical distribution suggesting oligotrophic or mesotrophic type profiles, or numerous
360 intermediate vertical patterns.

361
362 During the second half of 2002, El Niño conditions developed with repeated westerly wind
363 events (WWE; Fig. 8a), eastward equatorial surface currents (Fig. 8d), shoaling of the
364 thermocline (Fig. 1c), and modest increases of surface chlorophyll to about 0.1 mg m^{-3} (Fig.
365 8a). S_v profiles showed relatively high nighttime values in the warm isothermal layer (above
366 $Z_{29^{\circ}\text{C}}$). Variability was high and transient intermediate patterns between oligotrophic and
367 mesotrophic configurations were also observed. The successive WWE gave rise to easterly
368 equatorial surface currents (Fig. 8). Interestingly, nighttime S_v above $Z_{29^{\circ}\text{C}}$ increased to
369 around -54 dB when the zonal current was eastward while it was around -58 dB at the
370 beginning of the year (Fig. 9a) suggesting that a water mass with different chlorophyll content
371 and micronekton properties was advected from the west during El Niño. The relative minima

372 in June 2002 and February 2003 corresponded to the occurrence of very oligotrophic waters
373 around the mooring. The increase in S_v after March 2003 (Fig. 9) was related to the westward
374 extent of the mesotrophic ecosystem that reached the mooring site (Fig. 1b).

375
376 Some S_v decreases during full moon nights were observed in the surface layer after July 2002
377 (Fig. 8b). They were simultaneous with deepening of the base of the nighttime high S_v layer.

378 Although this pattern is not always clear by visual examination, power spectral analysis
379 captures it with the highest energy in the vicinity of $Z_{20^\circ\text{C}}$ and a moderate energy layer above
380 100 m (not shown).

381

382 4. Discussion

383 4.1. ADCP detection range

384 ADCPs in an upward-looking configuration involve a “deadzone” near the air/sea boundary
385 where separating between targets and surface signal is not possible (Ona and Mitson, 1996)
386 because of contamination from sidelobe reflections. We set the deadzone for the moored
387 TAO/TRITON ADCPs at about 40 m. Also, the depths of the transducers are between 250
388 and 300 m (Plimpton et al., 2004). So, overall, the detection range is limited to a 40-250 m
389 layer. Micronekton organisms may be divided into epipelagic (above 150 m) and mesopelagic
390 (150-1000 m) groups (Roger, 1971; Legand et al., 1972; Legendre and Rivkin, 2005). Migrant
391 species move at night from deep layers toward more superficial layers. Therefore, equatorial
392 ADCPs sample a great part of the epipelagic layer. Nighttime biomass derived from net
393 samples is high above depths of 100 to 200 m and high S_v have been observed above 50 m in
394 the warm pool (Kaneko et al., 1996) and in different sites of the world ocean (Tarling et al.,
395 1999; Wade and Heywood, 2001; Pinot and Jansá, 2001). So, the deadzone limitation
396 prevents us from monitoring 20 to 40% of the high biomass layer. In particular, we are not

397 able to describe thoroughly the vertical distribution in oligotrophic conditions (some
398 situations suggest a high S_v layer above 40 m) and we miss the high S_v layer during the 1998
399 bloom at 140°W. Nonetheless, for that part of the water column we do observe, the sampling
400 is continuous and highly resolved in the vertical.

401

402 *4.2. Sources of scattering*

403 Zooplankton and micronekton targets are responsible for a great part of the backscattering
404 signal at frequencies of the order of 10^2 kHz (Wiebe et al., 1990). Typically, this
405 backscattering is determined by the product of the wave number for the sound ($k = 2\pi/\lambda$)
406 times the scatterer size (a) expressed as an equivalent radius. In the Rayleigh domain ($ka \ll$
407 1), the signal increases strongly with the frequency (or the size) until a transition zone around
408 $ka = 1$, and then the scattering enters in the geometric domain ($ka \gg 1$), where the signal is
409 non-monotonic (Holliday and Pieper, 1995). For a 150 kHz ADCP, the transition zone
410 corresponds to organisms of size around 1 cm at the smallest. Nevertheless, the backscattering
411 is related to the sound frequency used and to the size, shape, orientation, and physical
412 properties of the targets (Stanton et al., 1994; McGehee et al., 1998). Because it is not
413 possible to discriminate between variations in size and in abundance with single-frequency
414 techniques, Holliday and Pieper (1995) reviewed optimal conditions to estimate abundance.
415 In particular, they pointed out that a single organism should dominate the acoustic scattering
416 and predicting the animal target strength with an appropriate acoustic scattering model would
417 help interpreting the single-frequency signal. Yet, zooplankton and micronekton populations
418 are usually composed of a complex assemblage of species that complicates the interpretation
419 of S_v in terms of biologically relevant quantities. For instance, efficient sound scatterers
420 (pteropods, siphonophores, fish) may strongly contribute to S_v although their abundance or
421 biomass is low at specific depths and locations (Wiebe et al., 1996; Fielding et al., 2004; Mair

422 et al., 2005; Lavery et al., 2007; Lawson et al., 2008). In particular, gas-bearing
423 siphonophores were responsible for the strong scattering layer observed at 120 kHz in the
424 seasonal thermocline in the Gulf of Maine (Lavery et al., 2007). Pelagic fish that can
425 dominate the acoustic scattering at 150 kHz, probably do not strongly alter the signal because
426 of their patchiness and scarcity (Plimpton et al., 1997; Lawson et al., 2008). Changes in the
427 taxonomic composition (relative contribution of euphausiids, amphipods, myctophids, and
428 copepods) explained most of changes in S_v over three zones in the northeast Atlantic (Wade
429 and Heywood, 2001). Similarly, Ashjian et al. (1998) associated the occurrence or absence of
430 diel vertical migrations to various species advected with water masses. Other factors such as
431 size or orientation that vary between species and within species can further confound the
432 interpretation of S_v . Different vertical migration patterns related to sizes of animals at larval
433 or post-larval stages (Munk et al., 1988; León et al., 2008) and the size increase along the year
434 may impact S_v variability at seasonal or longer time scales. Different species assemblages
435 during day and night also affect S_v diel cycle. For example, Ballón Soto (2010) observed a
436 mean size increase of about 5% during the night in the epipelagic layer of the Humboldt
437 Current System, indicative of the migration of larger animals from deeper layers. In addition,
438 animal orientation probably influences nighttime and daytime S_v as this orientation changes
439 among species and seems to differ according to behaviors such as migration or feeding
440 (Warren et al., 2002; Fielding et al., 2004).

441
442 No concurrent echo-sounder measurements or net samples were available for this study to
443 constrain the complex interpretation of single-frequency S_v . Therefore, we relied on a review
444 of the literature to identify likely scatterers in the equatorial Pacific. Several zooplankton and
445 micronekton species have been identified as possible migrating scatterers in the 10s to 100s
446 kHz range. Copepods and pteropods contributed most to the 420 kHz S_v on Georges Bank

447 (Wiebe et al., 1996). Migrating layers at 150 kHz were composed of euphausiids, amphipods,
448 myctophids, and copepods in the northeast Atlantic (Wade and Heywood, 2001); myctophids
449 and euphausiids in the Mediterranean Sea (Tarling et al., 1999; Pinot and Jansá, 2001;
450 Fielding et al., 2001) and in the Gulf of Mexico (Ressler, 2002); and fish in the Arabian Sea
451 (Ashjian et al., 2002). To our knowledge, only net samples were used to evaluate variations of
452 biomass and taxonomic composition in the equatorial Pacific. The nighttime micronekton
453 biomass in the 0-100 m layer was about 4 times higher than the daytime biomass in the
454 central equatorial Pacific (Legand et al., 1972) while in the western part of the warm pool,
455 micronekton nighttime biomass in the 0-200 m layer was almost 8 times higher than daytime
456 biomass and peaked in the 80-120 m layer (Hidaka et al., 2003). Flagg and Smith (1989)
457 proposed a linear relationship between $\log(DW/4\pi)$ and S_v with a slope around 0.1 (DW is the
458 dry-weight biomass in mg m^{-3}). Following this assumption, a four-fold biomass increase
459 corresponds to a 6 dB S_v increase which is the order of magnitude of the 5 to 10 dB difference
460 between observed nighttime and daytime S_v . Actually, the range of slopes derived for
461 different sites and scatterers populations (0.115, Flagg and Smith, 1989; 0.055, Batchelder et
462 al., 1995; 0.085 and 0.055, Wade and Heywood, 2001) shows that such a relationship is not
463 universal and should be used with caution. The night/day variation of the mesozooplankton
464 biomass was much lower than that of micronekton biomass: about 25% (15%) higher
465 nighttime in the mesotrophic (oligotrophic) ecosystem (Le Borgne and Rodier, 1997). In the
466 central Pacific, migrant organisms were mainly fish among which myctophids were the most
467 numerous, large (> 2 mm) euphausiids, cephalopods, and shrimp (about 30%, 17%, 11%, and
468 8%, respectively, of the biomass; Legand et al., 1972). Copepods and chaetognaths dominated
469 the mesozooplankton biomass (Le Borgne and Rodier, 1997). In the western warm pool,
470 myctophids dominated the nighttime biomass and, to a lesser extent, squids, euphausiids and
471 shrimp (77%, 6.5%, 2.9%, and 2.8% of the biomass; Hidaka et al., 2003). Pteropods

472 represented a few percent of the micronekton (Legand et al., 1972) and of the
473 mesozooplankton (Le Borgne and Rodier, 1997) biomass in both equatorial ecosystems.
474 Comparable observations are reported for siphonophores (Legand et al., 1972; Le Borgne and
475 Rodier, 1997), unfortunately, no information was given about possible gas inclusion.

476

477 *4.3. Scattering variability in the equatorial Pacific*

478 *4.3.1. Oligotrophic and mesotrophic conditions*

479 S_v records at the 170°W and 140°W sites show clear differences associated with the
480 occurrence of oligotrophic or mesotrophic conditions. In mesotrophic conditions, nighttime
481 (daytime) S_v was about 6 dB (4 dB) higher than in oligotrophic conditions (Table 2) which
482 represent 4-fold (2.5-fold) biomass increases. S_v variations are highly consistent with
483 mesozooplankton net measurements along the equator showing that the biomass tripled
484 abruptly at the oligotrophic/mesotrophic limit (Le Borgne and Rodier, 1997). Comparison
485 with micronekton biomass is less obvious. In the upper 200 m, nighttime biomass in the
486 central equatorial Pacific (770 mg wet weight (WW) m⁻²; Legand et al., 1972) was lower than
487 in the North Equatorial Counter Current (NECC) region of the western warm pool
488 (1350 mg WW m⁻²; Hidaka et al., 2003). The ratio of daytime biomass between the warm
489 pool and the central Pacific was about the same. Reasons for the discrepancy in variations
490 between net samples and acoustic measurements are unclear. The S_v drop between
491 mesotrophic and oligotrophic regimes does not necessarily reflect a biomass decrease but
492 could result from different species assemblage seen in the preceding section. Another point
493 could be that Hidaka et al. (2003) micronekton biomass in the nascent NECC is not
494 representative of the very oligotrophic ecosystem of the eastern warm pool as chlorophyll
495 concentrations slightly higher than 0.1 mg m⁻³ are recurrently observed in the NECC
496 meanders (Christian et al., 2004; Messié and Radenac, 2006). However, nighttime biomass in

497 the very oligotrophic water of the North Equatorial Current would be 730 mg WW m^{-2}
498 (Hidaka et al., 2003) which is the order of magnitude of the central Pacific biomass. These
499 very few net samples suggest that micronekton biomass in the upper layer is higher (or of the
500 same order of magnitude) in the oligotrophic than in mesotrophic conditions and does not
501 explain S_v variations between the two ecosystems. The abrupt increase of the zooplankton
502 biomass along the equator from oligotrophic to mesotrophic regimes evokes its possible
503 influence on S_v , bearing in mind that zooplankton biomass represents more than 90% of the
504 upper layer biomass (Legand et al., 1972). To be more conclusive, the influence of the
505 taxonomic compositions on S_v in each ecosystem needs to be investigated.

506
507 Vertical S_v distributions within each ecosystem may reflect different species assemblages and
508 migrating behavior. High nighttime S_v above the middle of the thermocline in mesotrophic
509 conditions is consistent with the migration behavior of fish and large crustaceans that
510 constitute most of the nighttime biomass in the 0-200 m layer (Legand et al., 1972). In the
511 oligotrophic ecosystem, the S_v maximum in the upper part of the thermocline corresponds to
512 the peak biomass situated between 80 and 120 m in net observations where myctophids
513 represented more than 70% of the biomass (Hidaka et al., 2003). As well, distribution of
514 euphausiids in French Polynesia oligotrophic waters showed an abundance maximum
515 between 100 and 200 m depth (Legand et al., 1972). The agreement between vertical
516 distribution patterns of S_v and those of myctophids and euphausiids indicates that these
517 organisms possibly contribute to the nighttime S_v measured in the upper thermocline. Yet,
518 gas-bearing siphonophores have not been sampled and could influence the scattering at such
519 depth.

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521 *4.3.2. Influence of westerly wind events at 165°E*

522 WWE dominate the intraseasonal variability in the western equatorial Pacific. They occur
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2 523 mostly between November and April and are stronger and more frequent during El Niño
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4 524 events. Local responses of the upper ocean are eastward equatorial surface jets, SST
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7 525 decreases, and deepening of the isothermal layer. The local biological response of the ocean is
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10 526 less well known and increases of surface chlorophyll have been observed during cruises or
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12 527 with satellite data. Siegel et al. (1995) proposed that such blooms were the result of vertical
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14 528 nutrient inputs because of enhanced vertical mixing. An alternative explanation is that
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17 529 nutrient- and chlorophyll-rich waters from the western warm pool, in particular from the
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19 530 upwelling north of New Guinea Island that develops when wind is westerly, may be advected
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21
22 531 eastward (Messié, 2006; Radenac et al., unpublished results). During the second half of 2002,
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24 532 very oligotrophic conditions prevailed east of 165°E, in particular at 170°W (Fig. 1b, Fig. 2).
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26 533 At 165°E, the ecosystem was moderately mesotrophic (surface chlorophyll around 0.1 mg m⁻³
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28
29 534 or slightly higher) and the surface current was eastward (Fig. 8). Between July and December,
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31 535 nighttime S_v was about 4 dB higher than at the beginning of the year. The relative S_v
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34 536 minimum that flanked that period were concurrent with the passage of very oligotrophic
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36 537 waters of the eastern edge of the warm pool at 165°E, eastward in June 2002 and westward in
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39 538 February 2003. This pattern suggests that a water mass with distinct properties (nutrients,
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41 539 phytoplankton, and zooplankton and micronekton communities) occupied the western part of
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44 540 the equatorial warm pool during the 2002 El Niño while very oligotrophic waters persisted on
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46 541 its eastern edge. We can only speculate about mechanisms that maintain moderately
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48
49 542 mesotrophic conditions. SeaWiFS chlorophyll features indicate that advection of chlorophyll-
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51 543 rich (and nutrient-rich) water may significantly contribute (Radenac et al., unpublished
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53 544 results). Also, pulsating increases of nighttime S_v, simultaneous with or lagging WWE by a
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55
56 545 few days (Fig. 9b) suggest local influence of intense vertical mixing.
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547 4.3.3. *Influence of moonlight*

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2 548 We observed at 170°W that the delay between the dusk upward migration and downward
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5 549 movement progressively increased as the period between sunset and moonrise increased. This
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7 550 sequence is similar (except for the eclipse night) to the one described by Tarling et al. (1999)
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10 551 during 7 days around full moon in the Liguria Sea. Our time-series provide the opportunity to
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12 552 examine more precisely the evolution of the S_v signal during the entire lunar cycle and we
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14 553 found that patterns during the nights before full moon roughly mirrored those after full moon.
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17 554 Tarling et al. (1999) observed this behavior whatever the depth of food and concluded that it
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19 555 probably aimed at avoiding visual predators. They excluded a possible influence of
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21
22 556 endogenous rhythm because no sinking happened during darkness of an eclipse night. Among
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24 557 the main migrators (euphausiids and pteropods), only euphausiids responded to moonlight.
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26
27 558 Also, Roger (1974) observed that the time of euphausiid sinking in the southwest tropical
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29 559 Pacific was closely related to the time of moonrise during full moon periods. In the central
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31 560 equatorial Pacific, myctophids did not ascend during full moon periods (Legand et al., 1972).
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34 561 Based on this published literature, it appears that euphausiids and myctophids can be
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36 562 responsible for a part of the S_v modulations we observed in both equatorial ecosystems.
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41 564 4.3.4. *Influence of stratification and food availability*

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43 565 Our results suggest that thermocline depth strongly influences the vertical distribution of
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46 566 organisms, especially during the night. In oligotrophic conditions, downwelling Kelvin waves
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49 567 that depressed the thermocline in late 2002 at 170°W also deepened the subsurface high S_v
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51 568 layer. In the same way, the depth of the subsurface S_v maximum at 140°W strikingly followed
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53 569 the shoaling of the thermocline during the peak period of the 1997 El Niño. In mesotrophic
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56 570 conditions, the lower limit of the high S_v layer was lowered by downwelling Kelvin waves
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58 571 and matched variations of the thermocline depth at interannual scale as evidenced during the
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572 pre- and post-El Niño periods in 1996-1999 at 140°W. This result is reminiscent of the
573 deepening of the deep scattering layer west of 155°W associated with the deepening of the
574 EUC and the zonal tilt of the thermocline during the Alizé trans-equatorial cruise
(Grandperrin, 1969). The shallow thermal vertical structure following the 1997 El Niño
576 conditions is unusual in the TAO/TRITON data. A similar event, marked with a shallow
577 thermocline, occurred during the strong 1988-1989 La Niña when $Z_{20^{\circ}\text{C}}$ was around 50 m. The
578 shallowest $Z_{20^{\circ}\text{C}}$ occurred in June-August 1998 during the bloom period. The migration
579 pattern was uncommon as part of the organisms consistently found their daytime residence
580 layer around 200 m during these months leading to anomalous high daytime S_v below $Z_{20^{\circ}\text{C}}$.
581 Reasons for this are unclear. Organisms, whose daytime residence layer was below the
582 transducer when the thermal structure was deeper, could adapt to a new environment and
583 found better temperature and feeding conditions around 200 m. Also, species with reduced
584 vertical migration may have developed because of favorable conditions during the bloom.
585
586 The vertical structure of chlorophyll is closely related to the vertical thermal structure in the
587 equatorial Pacific and, therefore, we cannot fully separate the influence of stratification on S_v
588 from that of food availability. The nitracline and the subsurface chlorophyll maximum
589 coincide with the thermocline depth in the oligotrophic ecosystem while in the upwelling
590 region, nitrate and phytoplankton are observed up to the surface. In both situations, nighttime
591 vertical S_v distribution evokes the vertical distribution of phytoplankton. Phytoplankton are
592 grazed by microzooplankton, which are ingested by mesozooplankton, which feed
593 micronekton via the phytoplankton food chain (Legendre and Rivkin, 2005). Thus,
594 chlorophyll-rich layers should sustain high microzooplankton and mesozooplankton and, in
595 turn, higher micronekton biomass. Nighttime vertical S_v profiles may reflect the tendency for
596 organisms to stop their migration at a preferred depth where they can feed easily: from the

597 middle of the thermocline to the surface in the upwelling zone and in the upper thermocline in
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2 598 the oligotrophic warm pool.

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6 700 **5. Concluding remarks**

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9 601 This study is an example of the use of single-frequency ADCPs to retrieve qualitative

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11 602 biological information at the same spatial and temporal scale as physical observations. In

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13 603 particular, we showed that different migrating patterns occur in oligotrophic and mesotrophic

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15 604 ecosystems and therefore, the limit between the warm pool and the upwelling region is also a

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17 605 transition in biomass and composition of zooplankton and micronekton species. We described

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19 606 the evolution of the migratory patterns during a lunar cycle and the response of the vertical S_v

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21 607 distribution to variations of the thermocline depth and, possibly, to food availability, at intra-

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23 608 seasonal and interannual scales. Finally, the complexity of the variations of the acoustic

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25 609 scattering in the eastern edge of the warm pool illustrates the great quantity of information the

26
27 610 moored ADCP provided in vertical and temporal scales, information that cannot be resolved

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29 611 by conventional net hauls. However, we show that although some cues exist to explain

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31 612 observed S_v variations in the equatorial Pacific, many questions remain. More in situ data

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33 613 coupled to S_v estimates from acoustic scattering models are needed for obtaining quantitative

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35 614 biologically relevant variables and better understanding the behavior of zooplankton and

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37 615 micronekton along the equator, especially in the warm pool which does not appear as a very

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39 616 uniform oligotrophic region. Despite their limitations, long time-series of ADCP

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41 617 backscattering signal in the tropical Pacific offer a potentially valuable complement to more

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43 618 traditional approaches of studying mid-trophic levels and population dynamics.

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46 620 **Acknowledgements**

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4
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9 625

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position	deployment	time period
0°, 140°W	ca2	4 Sept. 1996 – 21 Oct. 1997
	ca3	21 Oct. 1997 – 27 Sept. 1998
	ca4	28 Sept. 1998 – 19 Sept. 1999
0°, 170°W	ka7	20 Jun. 2002 – 29 Jun. 2003
	ka8	30 Jun. 2003 – 9 Jul. 2004
0°, 165°E	wa3	4 Nov. 2001 – 5 Nov. 2002
	wa4	6 Nov. 2002 – 21 Nov. 2003

Table 1. ADCP deployments along the equator.

Table[Click here to download Table: Table_2.doc](#)

	mesotr.	oligo<tr>.</tr>
170°W	Feb. 2003 – Jun. 2004	Sep. – Dec. 2002
night	-49.4	-56.1
day	-58.2	-61.8
140°W	Sep. 1996 – Sep. 1997	Nov. – Dec. 1997
night	-49.5	-55.9
day	-59.0	-63.5

Table 2. Mean nighttime and daytime S_v (dB) averaged above $Z_{20^\circ\text{C}}$ in oligotrophic and mesotrophic conditions at 170°W and 140°W.

1 Figure captions

2

3 Fig.1. (a) SeaWiFS chlorophyll in May 2002. The dark line is the 0.1 mg m^{-3} isoline, black
4 squares indicate the 3 ADCP mooring sites. Longitude–time diagrams of (b) eight-day
5 SeaWiFS chlorophyll averaged between 1°S and 1°N and (c) five-day average anomalies of
6 the 20°C isotherm depth from the TAO/TRITON equatorial moorings. The dark line is the
7 29°C surface isotherm derived from Reynolds (2002) and TMI. Vertical black lines mark the
8 duration of the ADCP time-series at 165°E , 170°W , and 140°W .

9

10 Fig.2. Time evolution at 0° , 170°W of the SeaWiFS chlorophyll (a), the vertical structure of
11 nighttime (b) and daytime (c) S_v . The dashed line in (a) marks the 0.1 mg m^{-3} chlorophyll
12 concentration. The upper (lower) black lines superimposed on S_v distribution in (b) and (c)
13 are the 29°C (20°C) isotherm depths. Vertical dashed lines in (b) indicate full moon nights.

14

15 Fig. 3. Top panels: example of mesotrophic conditions at the 0° , 170°W mooring in June
16 2003. (a) Two successive S_v diel cycles. (b) Vertical profiles of the nighttime S_v (thick line),
17 daytime S_v (thin line), and temperature (dashed line). Bottom panels: the same for
18 oligotrophic conditions in October 2002. In (a) and (c), contour interval is every 2 dB; thick
19 contours are the -70, -60, and -50 dB. Time is local time.

20

21 Fig.4. Evolution of the nighttime S_v (dB) at 40 m (a) and at 170 m (b). Dashed lines indicate
22 full moon nights.

23

24 Fig. 5. Influence of the moon on the S_v diel cycles of September 2003 (local time) at 0° ,
25 170°W in the mesotrophic regime. New moon (NM), first quarter (FQ), full moon (FM), and

26 last quarter (LQ) are indicated. Heavy black lines indicate hours of darkness between sunrise
27 (06:00LT) and moonset before full moon, and between sunset (18:00 LT) and moonrise after
28 full moon. Contour interval is 2 dB; dark lines are the -70, -60, and -50 dB levels.

29

30 Fig.6. Time evolution at 0° , 140°W of the SeaWiFS chlorophyll and TAO/TRITON SST (a),
31 the vertical structure of nighttime (b) and daytime (c) S_v . The dashed line in (a) marks the
32 0.1 mg m^{-3} chlorophyll concentration. The upper (lower) black line superimposed on S_v
33 distribution in (b) and (c) is the 29°C (20°C) isotherm depth. Vertical dashed lines in (b)
34 indicate full moon nights.

35

36 Fig. 7. S_v diel cycles (dB) during the bloom period at 0° , 140°W in July 1998. Time is local
37 time. Contour interval is 2 dB; dark contours are the -70, -60, and -50 dB isolines.

38

39 Fig.8. Time evolution at 0° , 165°E of SeaWiFS chlorophyll (black line) and zonal wind speed
40 (TAO: red line; QuickScat: dashed red line) (a), the vertical structure of nighttime (b) and
41 daytime (c) S_v , and the zonal current component (d). The dashed line in (a) marks the
42 0.1 mg m^{-3} chlorophyll concentration and the 0.0 m s^{-1} zonal wind speed. The upper (lower)
43 black line in (b), (c), and (d) is the 29°C (20°C) isotherm depth. Vertical dashed lines in (b)
44 indicate full moon nights.

45

46 Fig. 9. Temporal evolution at 0° , 165°E during the mild 2002 El Niño of nighttime S_v
47 averaged above $Z_{29^\circ\text{C}}$ (black line) and of (a) the zonal current at 50 m (red line); (b) the same
48 zonal wind speed as in Fig. 8 (red lines).

49

50

Figure
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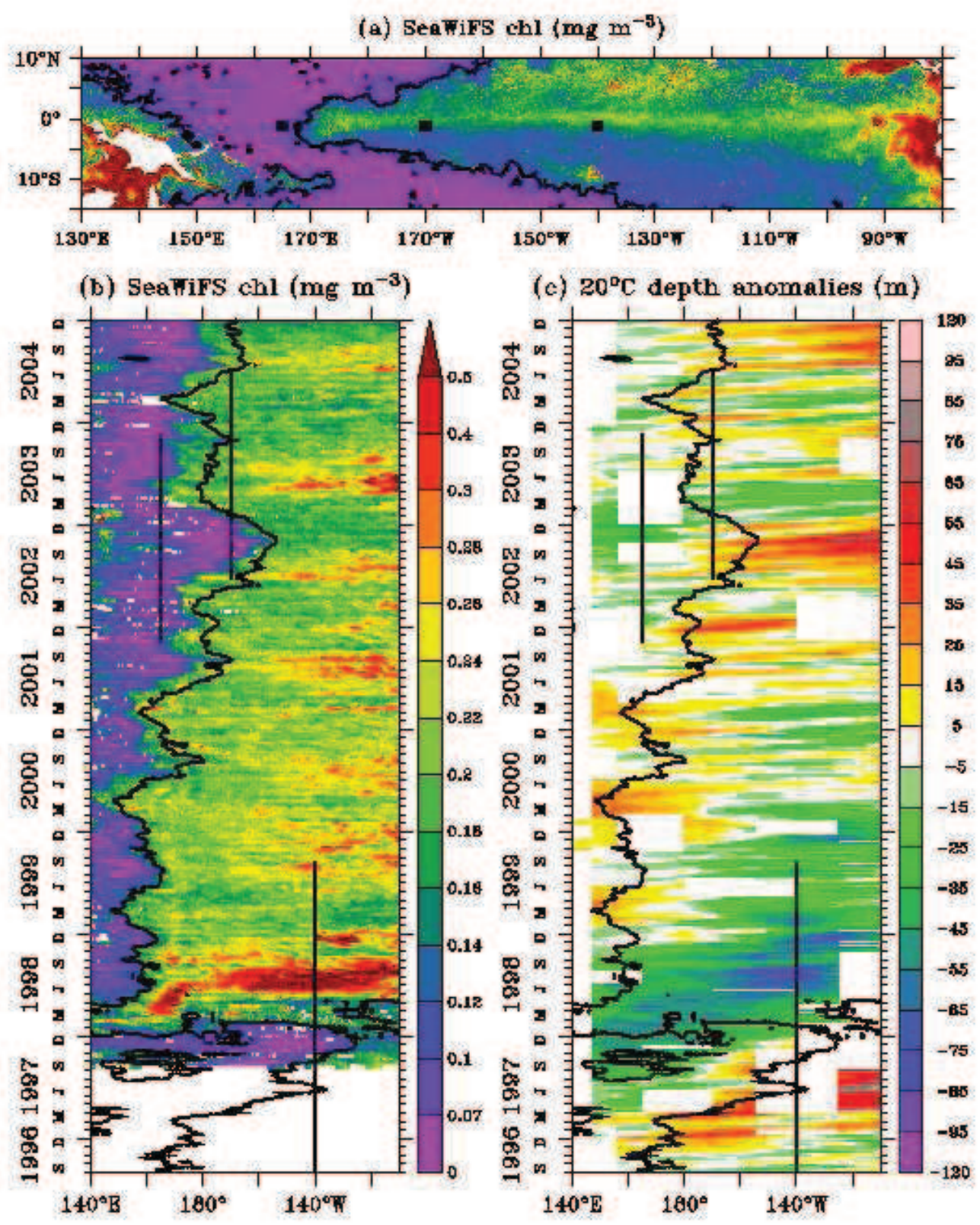


Figure
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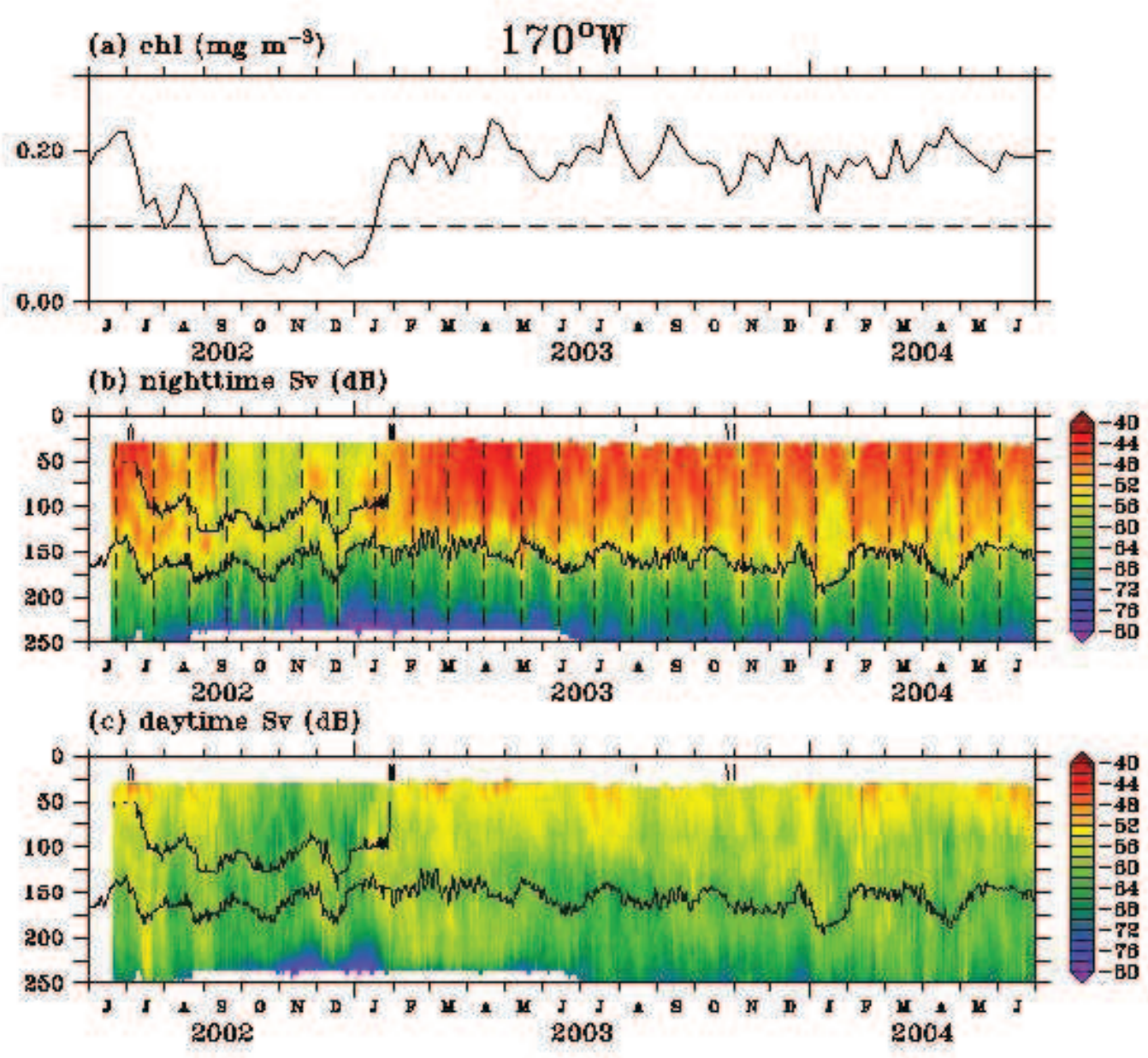


Figure
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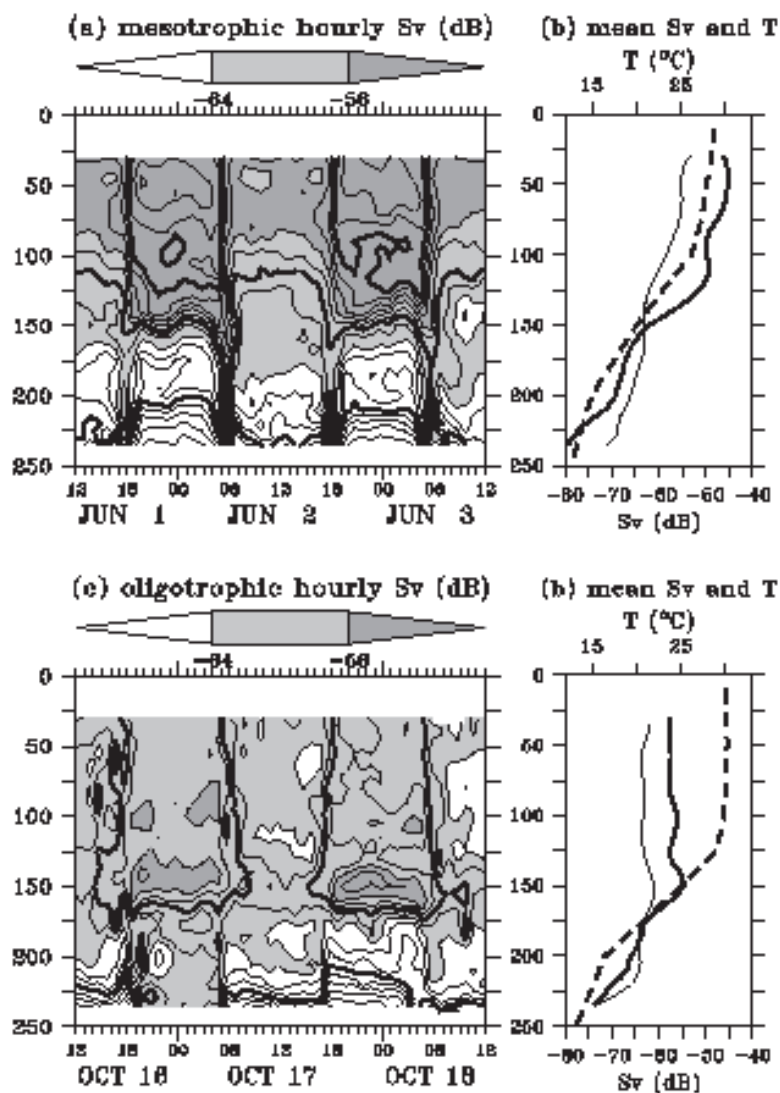


Figure
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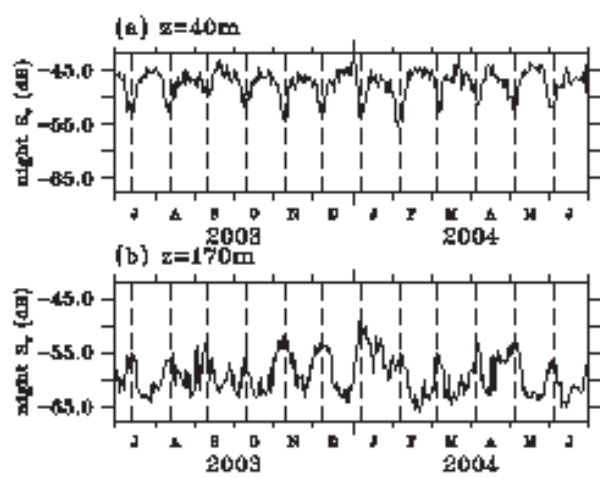


Figure
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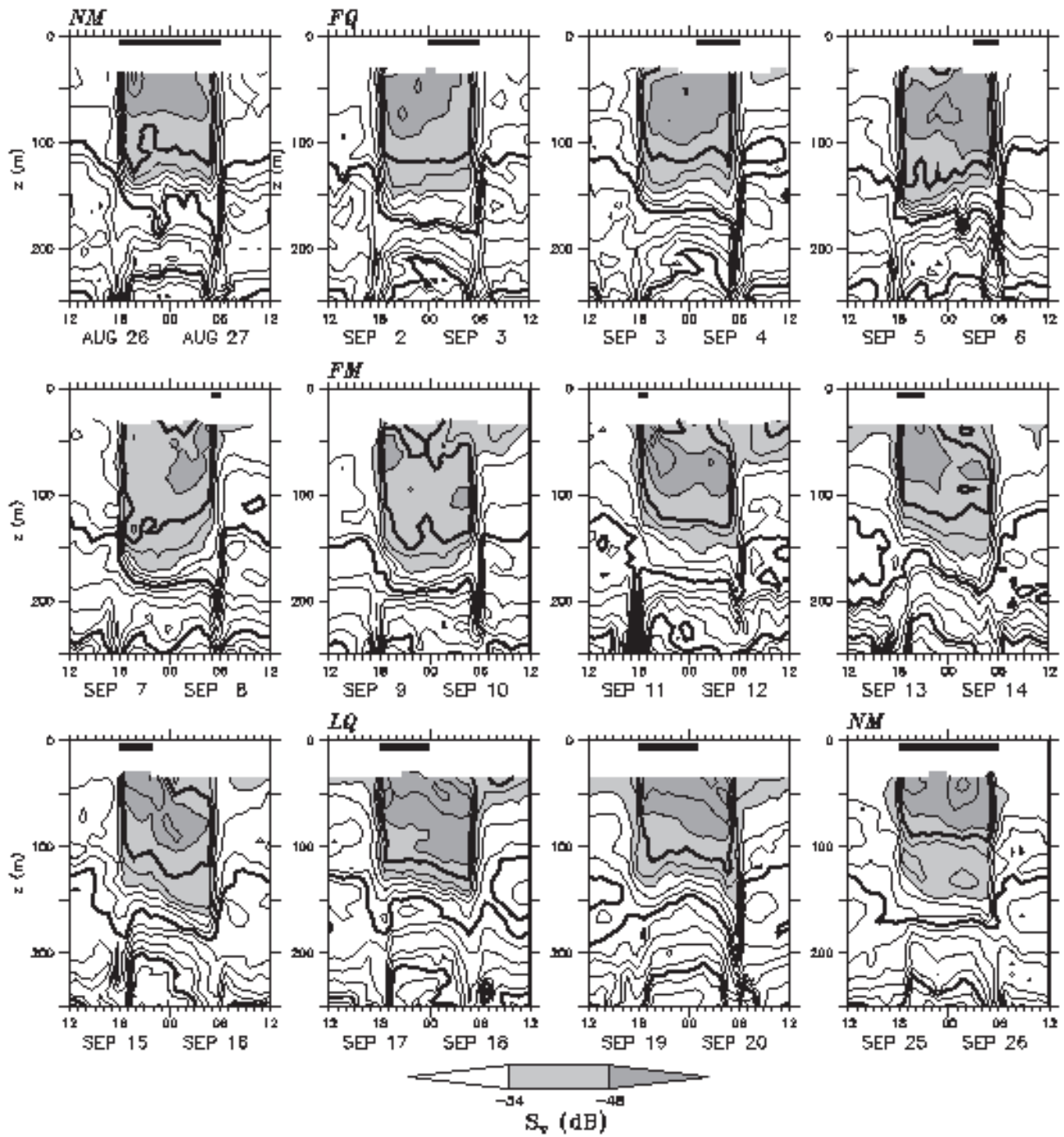


Figure
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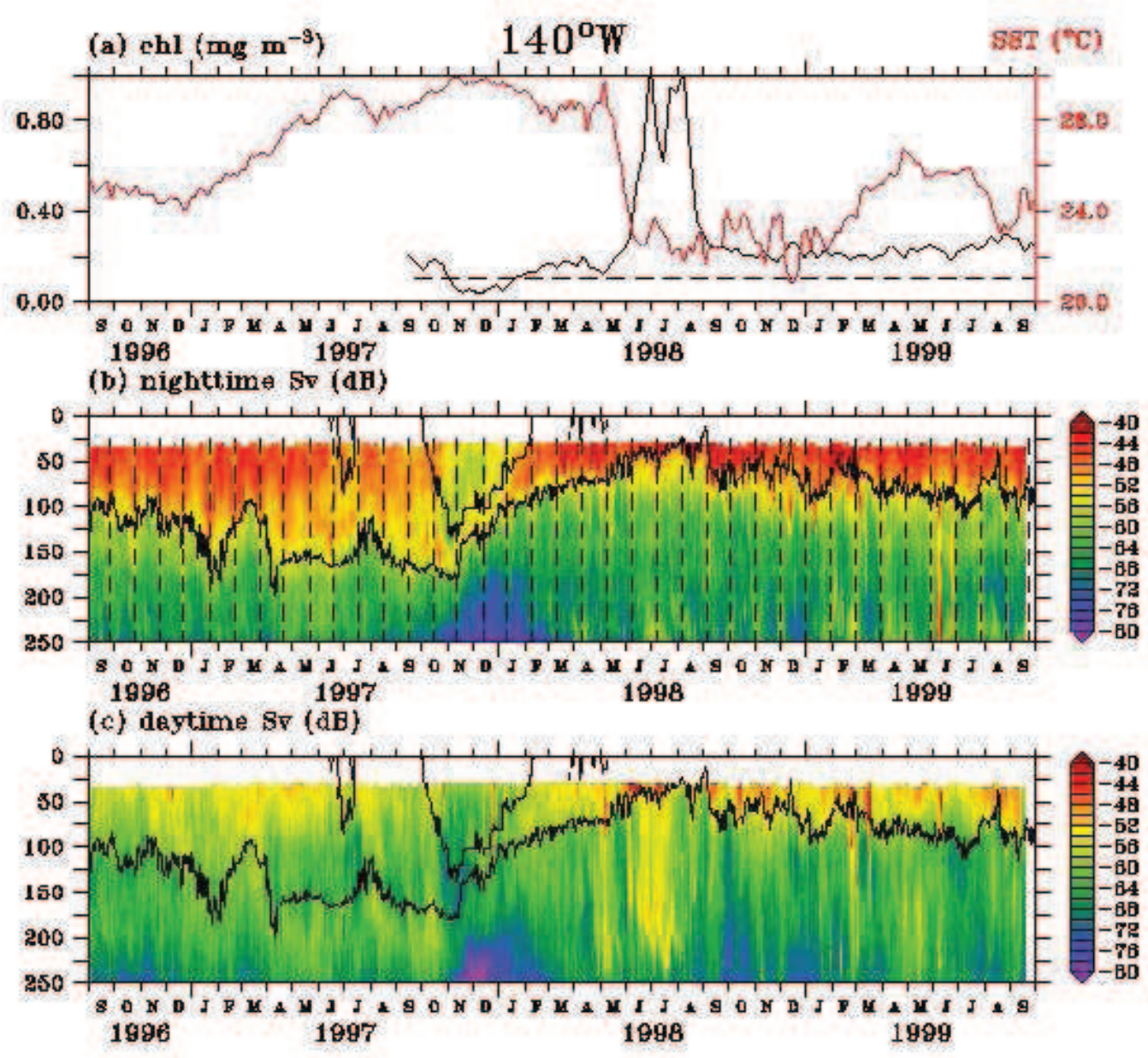


Figure
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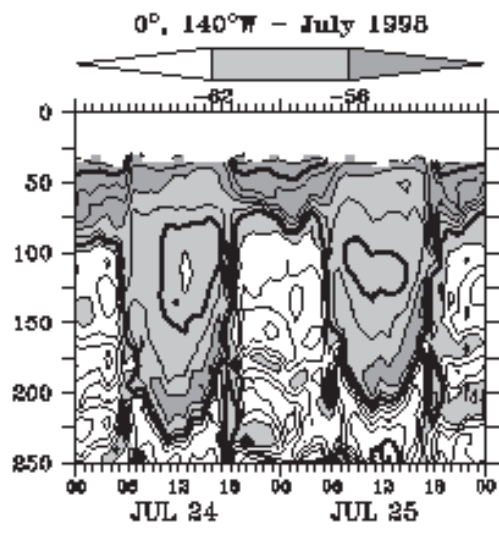


Figure
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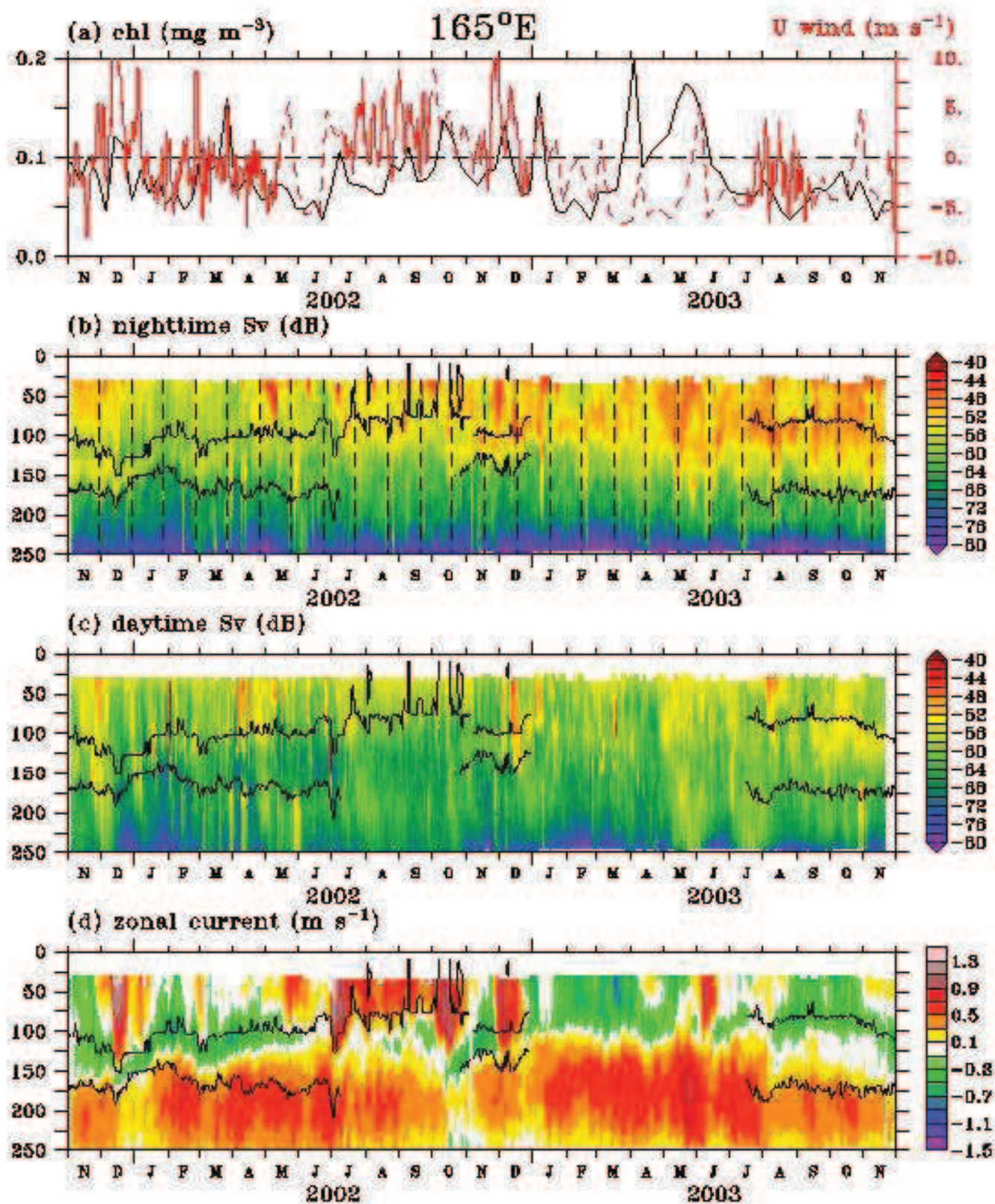


Figure
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