

UC San Diego

UC San Diego Previously Published Works

Title

Decline and recovery of pelagic acoustic backscatter following El Niño events in the Gulf of California, Mexico

Permalink

<https://escholarship.org/uc/item/0md9q117>

Authors

Portner, Elan J
Benoit-Bird, Kelly J
Hazen, Elliott L
[et al.](#)

Publication Date

2022-08-01

DOI

10.1016/j.pocean.2022.102823

Copyright Information

This work is made available under the terms of a Creative Commons Attribution-NonCommercial-NoDerivatives License, available at <https://creativecommons.org/licenses/by-nc-nd/4.0/>

Peer reviewed

1 Decline and recovery of pelagic acoustic backscatter following El Niño
2 events in the Gulf of California, Mexico

3

4 Elan J. Portner^{a,*}, Kelly J. Benoit-Bird^b, Elliott L. Hazen^c, Chad M. Waluk^b, Carlos J. Robinson^d,
5 Jaime Gómez-Gutiérrez^e, William F. Gilly^a

6

7 ^a Hopkins Marine Station of Stanford University, Pacific Grove, CA, USA

8 ^b Monterey Bay Aquarium Research Institute, Moss Landing, CA, USA

9 ^c NOAA Southwest Fisheries Science Center, Monterey, CA, USA

10 ^d Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, D.F., Mexico

11 ^e Centro Interdisciplinario de Ciencias Marinas, Instituto Politécnico Nacional, La Paz, B.C.S., Mexico

12

13 *Corresponding author at current address:

14 Scripps Institution of Oceanography, UCSD

15 8622 Kennel Way, La Jolla, CA, USA 92037, E-mail: eportner@ucsd.edu (E.J. Portner)

16 A B S T R A C T

17 Climatic variability exerts enormous pressures on the structure and function of open ocean
18 ecosystems. Although the responses of primary producers and top predators to these pressures
19 are being increasingly well-documented, little is known about how midtrophic communities
20 respond to oceanographic and climatic variability. We address this knowledge gap through a
21 study of the effects of El Niño Southern Oscillation (ENSO) and local environmental conditions
22 on acoustic proxies of the midtrophic community in the Gulf of California, Mexico. We
23 quantified the intensity and distribution of nighttime acoustic backscatter (120 kHz) in the upper
24 200 m of the water column during 10 oceanographic cruises (2007–2017) and described its
25 response to environmental variability using generalized additive models. ENSO conditions were
26 the strongest drivers of variability in backscatter after accounting for seasonal increases in
27 backscatter with sea surface temperature and chlorophyll-*a* concentration. Acoustic backscatter
28 in the central Gulf of California decreased significantly during the positive phase of ENSO.
29 Following El Niño events in 2009-10 and 2015-16, mean backscatter declined by an order of
30 magnitude and remained depressed for more than two years before recovering to pre-El Niño
31 levels. Scattering layer density increased with total backscatter, likely an influential factor
32 determining prey availability for pelagic predators. Our findings demonstrate large and sustained
33 impacts of El Niño on the midtrophic community in the Gulf of California and further highlight
34 the need to better understand the responses of midtrophic communities to environmental
35 variability.

36 *Keywords:*

37 Hydroacoustic

38 Backscattering layers

39 Midtrophic communities

40 Generalized additive models

41 El Niño Southern Oscillation

42

43 **Highlights**

- 44 • Timeseries of acoustic backscatter as a proxy for midtrophic biomass in the Gulf of
45 California.
- 46 • ENSO explained more variability than regional temperature or chlorophyll concentration.
- 47 • Backscatter decreased significantly during the positive phase of ENSO (El Niño).
- 48 • Mean backscatter took more than two years to recover to pre-El Niño levels.

49 **1. Introduction**

50 Over the past century, marine capture fisheries production has quadrupled (FAO, 2016)
51 and human activities, particularly greenhouse gas emissions, have contributed to warming of the
52 global ocean by ~0.6 °C (Levitus et al., 2001; Gleckler et al., 2016). Our observations and
53 understanding of the ways pelagic organisms respond to these pressures are heavily skewed
54 toward primary producers and top predators. On average, the global biomass of primary
55 producers in the ocean is decreasing in response to ocean warming (Polovina et al., 2008; Boyce
56 et al., 2010; Rykaczewski and Dunne, 2011). Predatory fishes, birds, and mammals are also
57 rapidly changing in abundance and distribution, often in response to the combined pressures of
58 fishing and warming (Veit et al., 1997; Lewison et al., 2004; Polovina et al., 2009; Hazen et al.,
59 2013; Woodworth-Jefcoats et al., 2015).

60 Food-web models suggest anthropogenic pressures on pelagic ecosystems are not simply
61 additive, but that top-down and bottom-up effects of these pressures may be modulated by the
62 midtrophic organisms in pelagic food webs (Woodworth-Jefcoats et al., 2015; Choy et al., 2016).
63 Midtrophic biomass is composed of diverse fishes, crustaceans, gelatinous organisms, and
64 cephalopods, many of which aggregate into relatively dense communities that are observable as
65 acoustic scattering layers within the upper 1000 m of the water column (Kloser et al., 2009; Ritz
66 et al., 2011; Klevjer et al., 2016). In addition to linking production at the base of food webs
67 (phytoplankton) to top predators, midtrophic organisms help to link surface to deep pelagic
68 habitats through diel vertical migration (Ducklow et al., 2001; Ambriz-Arreola et al., 2017).
69 Daily movement between nighttime feeding grounds at the ocean surface and daytime refuge at
70 depth actively contributes to carbon sequestration as part of the pelagic biological pump. This
71 ‘mesopelagic-migrant pump’ component accounts up to 50% of the total downward carbon

72 transport (Zhang and Dam, 1997; Hidaka et al., 2001; Schukat et al., 2013), and is surpassed only
73 by the gravitational pump component with respect to carbon export rates (Boyd et al., 2019).

74 Changes in the abundance of midtrophic organisms are thus expected to impact both the
75 ecological and biogeochemical functions of pelagic ecosystems. Variability in the biomass of
76 midtrophic organisms has been observed at coarse spatial scales (e.g. across ocean basins, Kloser
77 et al., 2009; Irigoien et al., 2014) and fine temporal scales (e.g. days to weeks; McClatchie and
78 Dunford, 2003), but there are few time series that can demonstrate the responses of these
79 communities to large-scale environmental variability over a prolonged period (Godø et al., 2014;
80 Proud et al., 2017; Koslow et al., 2018). As such, the responses of midtrophic communities to
81 environmental variability represents a critical gap in our understanding of pelagic ecosystem
82 dynamics.

83 Climatic conditions define baseline ocean heat content and atmosphere interactions and
84 mitigate seasonal oceanographic variability in pelagic habitats. El Niño Southern Oscillation
85 (ENSO) is a recurring climate pattern that describes heat content distribution in the tropical
86 Pacific Ocean and is quantified by the multivariate ENSO Index (MEI.v2, NOAA Physical
87 Sciences Laboratory, <https://psl.noaa.gov/enso/mei/>). Over the past four decades (1980-2020),
88 there have been eight El Niño events (positive ENSO extremes defined as at least five
89 consecutive months of MEI.v2 > 0.5), characterized by a major redistribution of heat content
90 from west to east – in 1982-83, 1986-87, 1991-94, 1997-98, 2002-03, 2006-07, 2009-10, and
91 2015-16 (<https://psl.noaa.gov/enso/mei/>). Regional conditions in the Gulf of California, Mexico,
92 a marginal sea located in the northeastern subtropical Pacific, are greatly impacted by the water
93 masses available for exchange at the mouth of the gulf (Herrera-Cervantes et al., 2007; Staines-
94 Urías et al., 2009; Portela et al., 2016). During El Niño events, tropical water masses become

95 more available for exchange (Baumgartner et al., 1985; Frawley et al., 2019) and the Gulf of
96 California experiences increased sea surface temperature (SST) and subsurface warming (Lluch-
97 Cota et al., 2007, 2010), as well as overall diminution and redistribution of phytoplankton
98 biomass (Kahru et al., 2004; Robinson et al., 2016).

99 Strong El Niño events (MEI.v2 > 1) in 1982-83 and 1997-98 were associated with
100 changes in abundance of anchovy, sardines, and zooplankton in the Gulf of California
101 (Lavaniegos et al., 1989; Lavaniegos-Espejo and Lara-Lara, 1990; Sánchez-Velasco et al., 2004;
102 Velarde et al., 2013, 2015; Petatán-Ramírez et al., 2019; Arreguín-Sánchez et al., 2021) and a
103 range of responses was observed for predators at higher trophic levels in conjunction with events
104 in 1997-98 and 2009-10. Elegant terns (*Thalasseus elegans*) failed to nest on their specific site
105 on Isla Raza in the central Gulf of California and instead shifted north to nest well outside the
106 Gulf (Velarde et al., 2013, 2015). Humboldt squid (*Dosidicus gigas*) show a more complex
107 response: squid biomass redistributed from neritic to pelagic habitats; lifespan was severely
108 reduced (> 1.5 years to < 0.5 year); and size at maturity was reduced (> 60 cm mantle length
109 (ML) and 10 kg body mass to < 20 cm ML and 0.1 kg body mass) (Hoving et al., 2013;
110 Robinson et al., 2016). Although both predators recovered rapidly after the strong El Niño of
111 1997-98, recovery after the 2009-10 event was erratic and further hindered by the strong 2015-16
112 El Niño (Velarde, *pers. comm.*; Frawley et al., 2019). Prey biomass and density are both
113 important determinants of habitat selection and foraging success for marine predators (Benoit-
114 Bird, 2009; Hazen and Johnston, 2010; Benoit-Bird et al., 2013; Carroll et al., 2017), and prey
115 availability may mitigate predator responses to climatic events. However, the responses of
116 midtrophic prey in the Gulf of California to El Niño events are poorly described and represent a
117 critical gap in our understanding of the effects of environmental variability on pelagic food webs.

118 To estimate the response of midtrophic communities to environmental variability, we
119 quantified acoustic backscatter intensity and distribution in the central Gulf of California based
120 on ten oceanographic surveys carried out between January 2007 and June 2017. This period
121 included warm- and cool-season sampling as well as three El Niño events (2006-07, 2009-10,
122 and 2015-16). The goals of the present study were 1) to assess sensitivity of nighttime acoustic
123 backscatter in the upper 200 m of the water column to ENSO conditions, sea surface
124 temperature, and sea surface chlorophyll-*a* concentrations, and 2) to determine the time scales
125 over which El Niño events impacted the midtrophic assemblages that contribute to backscatter.
126 This work provides unique insight into the relative impacts of local environmental and ENSO
127 conditions on midtrophic biomass inferred from acoustic backscatter in the Gulf of California
128 and may help us understand how projected increases in the frequency and intensity of El Niño
129 events will affect midtrophic organisms in the eastern Pacific Ocean.

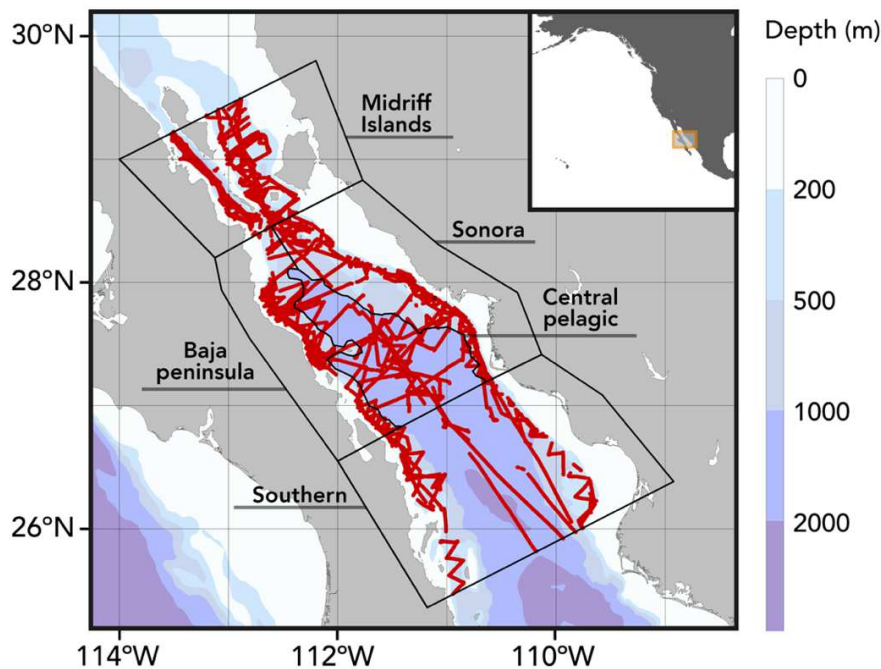
130

131 **2. Materials and methods**

132 *2.1. Acoustic sampling and data processing*

133 Acoustic data were recorded from the central Gulf of California (~26–29.5° N, [Fig. 1](#)) on
134 10 oceanographic cruises aboard the R/V El Puma (Universidad Nacional Autónoma de México)
135 during relatively “warm” (June – October) and “cool” seasons (November – May) between
136 January 2007 and June 2017 ([Table S1](#)). Each cruise lasted approximately three weeks (with
137 effective acoustic survey durations between 6 –18 days) and covered an average of ~3600 km of
138 transect at speeds of 7– 26 km h⁻¹ (4 –14 kts) ([Table S1](#)). Acoustic data were collected using a
139 120 kHz split-beam scientific echosounder (Simrad ES60 echosounder, Simrad ES120-7C, 7-
140 degree split-beam transducer). Pulse lengths (0.256 – 1.054 ms) and power settings of the

141 transducer (200-500 W) varied by cruise and are listed in [Table S1](#). The transducer was mounted
142 on the end of a steel pole that was extended into the water through a moon pool in the center of
143 the ship to a depth of 4 m below the sea surface. All reported depths are ranges (in meters) from
144 the transducer. Field calibrations of the transducer were performed periodically throughout the
145 study using a reference sphere as described in [Gómez-Gutiérrez and Robinson \(2006\)](#).
146 Calibrations indicated no change in system performance. Constant, nominal calibration values
147 were used for all data to allow relative changes in acoustic backscatter to be robustly assessed.



148 **Fig. 1.** Bathymetric map of the central Gulf of California, Mexico showing nighttime cruise
149 tracks over seafloor depths > 200 m from all ten cruises combined (red lines). Regions used for
150 monthly environmental covariate averages and NASC anomaly calculations are outlined in
151 black. Nighttime cruise tracks from each oceanographic cruise are given in [Fig. S1](#). The study
152 area is depicted as an orange box in the inset map of North America.
153

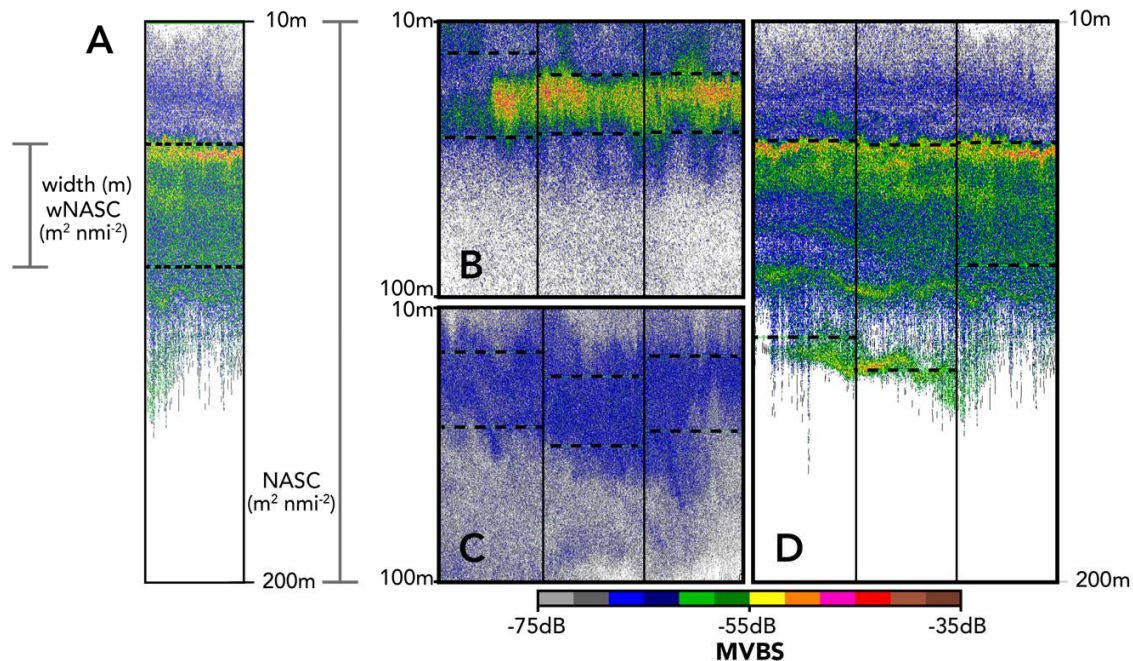
154 Acoustic data were processed in Echoview version 10 (Echoview, 2019) using built-in
155 background and transient noise removal procedures. ES60 data were corrected to remove the
156 triangle-wave error in Echoview following Keith et al. (2005). To account for variability in pulse
157 lengths among cruises, all data were resampled to 1000 samples per ping. To minimize
158 variability introduced by the inclusion of strictly shelf-associated species, we only included data
159 collected in waters with sea floor depths > 200 m as determined by automatic bottom detection
160 procedures in Echoview and verified by manual examination. Analyses were limited to data
161 collected between 10 and 200 m depth (hereafter, “upper 200 m”), representing data with a
162 signal-to-noise ratio that enabled robust ecological interpretation of echoes. This includes
163 organisms that are resident in the upper 200 m, as well as those that migrate into this depth range
164 at night from daytime habitats in the mesopelagic zone (200 – 1000 m) (Gómez-Gutiérrez and
165 Robinson, 2006; Benoit-Bird and Gilly, 2012). We therefore limited analyses to nighttime
166 samples as a proxy for prey available to predators that feed between the surface and mesopelagic
167 depths (Benoit-Bird and Au, 2003; Klevjer et al., 2016). “Nighttime” was defined based on
168 estimates of when vertically migrating animals end their diel ascent relative to local sunset times
169 (i.e. start of night) and begin their diel descent relative to local sunrise times (i.e. end of night)
170 (Table S1; Cade and Benoit-Bird, 2015). The cruise tracks of nighttime acoustic surveys in
171 waters with sea floor depths > 200 m for each cruise are given in Fig. S1. Acoustic data were
172 integrated per km of cruise track using a minimum Sv threshold of -125 dB.

173

174 2.2. Acoustic metrics of midtrophic community abundance and density

175 Metrics of acoustic backscatter were quantified to estimate variability in the total
176 abundance and density of midtrophic organisms in the water column, both of which affect their

177 availability to predators. The relative abundance of midtrophic organisms was estimated as the
178 nautical area backscattering coefficient (NASC, sA , $m^2 \text{ nmi}^{-1}$, [MacLennan et al., 2002](#)) per
179 kilometer of cruise track. To examine variability in the distribution of backscatter in the upper
180 200 m, features of scattering layers were defined as follows. First, data from each ping were
181 filtered for bins with mean volume backscattering strength (MVBS, S_v , dB re 1 m^{-1} , hereafter
182 dB, [MacLennan et al., 2002](#)) in the 90th percentile, allowing for identification of the shallowest
183 and deepest depths of these bins per ping. The averages of these depths were used to define the
184 vertical edges of a scattering layer's "width" (expressed in meters) over each kilometer of cruise
185 track ([Fig. 2](#)). NASC was integrated between these edges ("wNASC", $m^2 \text{ nmi}^{-1}$) and divided by
186 layer width to obtain an estimate of "density" within the scattering layer. When log-transformed,
187 these layer density values are proportional to MVBS. We examined the relationships between
188 layer width and wNASC, as well as layer density and total NASC to describe the vertical
189 distribution of backscatter within the upper 200 m.



190

191 **Fig. 2.** Visual representation of acoustic metric definitions and variability in acoustic backscatter

192 in the Gulf of California recorded during ten oceanographic surveys carried out from January

193 2007 to July 2017. (A) Schematic illustrating the definitions of scattering-layer width and

194 integrated wNASC that were used for estimating the abundance and distribution of midtrophic

195 organisms. Representative echograms in the upper water column from the cool season (B,

196 February 2014) and (C, March 2010) and the warm season (D, August 2014). Panels illustrate

197 differences in MVBS (dB) for cruises with relatively high (B, D) and low NASC (C). Panels B-D

198 each display 3 km of cruise track (km delimited by black vertical lines) collected at night in

199 waters with sea floor depths ≥ 200 m. Horizontal dashed lines indicate the average vertical edges

200 of acoustic scattering layers per kilometer of cruise track as defined in *Methods section 2.2*.

201 Increased vertical structure (e.g., multiple layers at different depths) of acoustic backscatter

202 decreases the measured density of a defined layer (Panels B and D have similar NASC, but

203 density in B is two- to four-fold higher than in D).

204 Although we were unable to directly sample and identify the scattering organisms with
205 trawls or other methods during the acoustic surveys, we contextualize backscatter measurements
206 by comparing them to observations of spatiotemporal trends in the size structure and
207 composition of midtrophic organisms in the Gulf of California ([Domínguez-Contreras et al.,](#)
208 [2012](#); [Robinson et al., 2014](#); [García-Fernández et al., this issue](#)). We did not explicitly filter out
209 signals from larger predators, and we assumed that most organisms scattering sound at 120 kHz
210 represented midtrophic organisms ~0.5 – 20cm in length, including both mesozooplankton and
211 micronekton ([Irigoién et al., 2014](#); [Proud et al., 2017](#)). Hereafter, organisms that contribute to
212 acoustic backscatter at 120 kHz are simply referred to as “midtrophic organisms”.

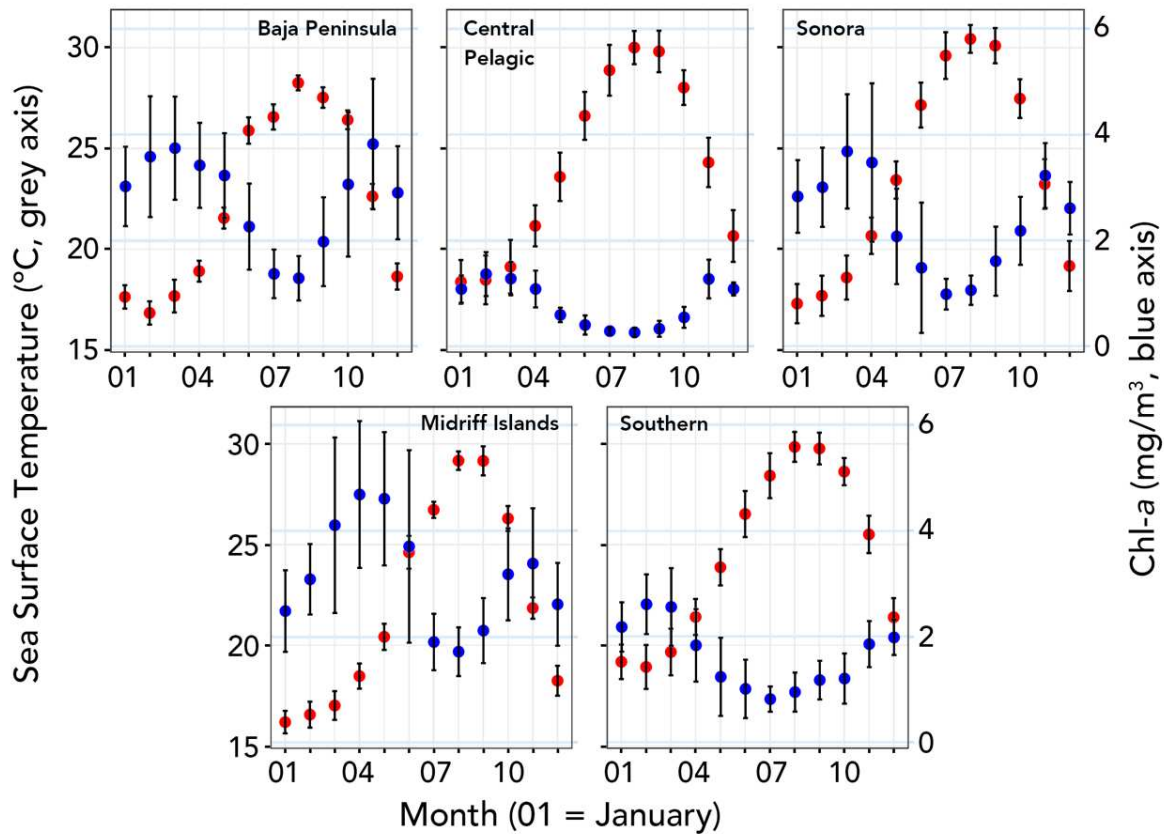
213 All analyses were performed using packages in the R statistical environment ([R Core](#)
214 [Team, 2020](#)). NASC and wNASC were log-transformed to better match the theoretical
215 assumptions of the statistical tests applied to these data. To examine variability in NASC among
216 cruises, NASC anomalies were quantified as deviations from the mean log-transformed NASC
217 per oceanographic region across our study period ([Fig. 1](#)). Regions were defined based on
218 oceanographic and biogeographic characteristics following [Portner et al. \(2020\)](#) to account for
219 diverse habitats within our study area that may be expected to support distinct midtrophic
220 communities. Briefly, the Midriff Islands region is separated from the rest of the gulf by a sill
221 and supports distinct taxa (e.g. [Brinton et al., 1986](#); [Alvarez-Borrego and Ruben Lara-Lara,](#)
222 [1991](#); [Robison, 1972](#)); the Southern region was distinguished from the central Gulf based on
223 biogeographic boundaries (e.g. [Round, 1967](#); [Brinton et al., 1986](#)); and the three central regions
224 (Baja Peninsula, Sonora, and Central Pelagic) were distinguished by the 1000 m isobath.

225 *2.3. Environmental covariates describing pelagic habitat conditions in the Gulf of California*

226 Sea surface temperature (SST) and chlorophyll-*a* concentration (Chl-*a*, as a proxy for
227 standing biomass of phytoplankton) were used to describe the environmental conditions of
228 pelagic habitats of the Gulf of California. Observation-based SST (monthly, 0.25° x 0.25°) and
229 Chl-*a* (monthly, 4 x 4 km) products were accessed from the E.U. Copernicus Marine Service
230 Information (<http://marine.copernicus.eu>). In addition, NOAA's Multivariate ENSO Index
231 (MEI.v2) ([Wolter and Timlin, 1993](#)) was used to provide a more global environmental correlate,
232 with bimonthly MEI values obtained from the NOAA Earth Systems Research Laboratory
233 (<https://www.esrl.noaa.gov/psd/enso/mei/table.html>).

234 Oceanographic conditions at the time of data collection do not necessarily capture the
235 environmental history that would influence recruitment, growth, movement, and reproduction
236 that ultimately determine the biomass and taxonomic composition of midtrophic communities.
237 To address the variable temporal scales of interest and spatiotemporal resolutions of our
238 environmental datasets we calculated monthly regional averages of SST and Chl-*a* ([Fig. 1](#), [Fig.](#)
239 [3](#)). Regional averages of SST over zero, three, and twelve-month periods prior to data collection
240 were thus considered to capture effects of intra-annual variability in SST, as well as inter-annual
241 temperature trends. Nine- and twelve-month averages of MEI.v2 were considered to examine the
242 effects of larger-scale climatic history at temporal scales that would describe the dominant water
243 masses entering the mouth of the gulf and their effects on water-column structure ([Baumgartner](#)
244 [et al., 1985](#); [Frawley et al., 2019](#)). Chl-*a* concentrations were assumed to be ecologically
245 important at shorter temporal scales than physical environmental conditions. [Croll et al. \(2005\)](#)
246 demonstrated a 4 – 6 month lag between peak Chl-*a* and peak krill biomass in an eastern Pacific

247 upwelling system off California, and we therefore considered three- and six-month averages of
248 Chl-*a* as an estimate of integrated food availability for midtrophic organisms.



249
250 **Fig. 3.** Monthly averages of sea surface temperatures (red) and chlorophyll-*a* concentrations
251 (Chl-*a*, blue) in the Gulf of California recorded during January 2006 – October 2017 from each
252 biogeographic region shown in Fig. 1 (black whiskers represent standard deviations).

253
254 The principal source of interannual climate variability in Gulf of California is the
255 changing intensity of equatorial circulation associated with ENSO (Baumgartner et al., 1985;
256 Lluich-Cota et al., 2007). El Niño events were defined as at least five consecutive months of
257 MEI.v2 > 0.5, following the National Weather Service Climate Prediction Center
258 (<https://origin.cpc.ncep.noaa.gov>). The end of an El Niño event was defined as the first

259 subsequent month with $MEI.v2 < 0.5$. Duration in months after the end of an El Niño event was
260 included as an environmental covariate to examine whether the effects of El Niño were sustained
261 beyond the duration of the climatic event itself. Data collected on cruises during El Niño events
262 (March 2010 and June 2016, [Table S1](#)), were assigned a value of zero months since the end of
263 the previous El Niño.

264

265 *2.4. Model fitting and selection protocols*

266 Generalized additive models (GAMs) were fit using restricted maximum likelihood
267 parameter estimation (REML) in the *mgcv* package in R ([Wood, 2011](#)) to explore the
268 relationship between NASC and environmental conditions. Time in months since the end of the
269 previous El Niño event was included as a covariate in all candidate GAMs. All possible models
270 with single SST (0, 3-, or 12-month average), MEI.v2 (9- or 12-month average) and Chl-*a* (3- or
271 6-month average) terms were explored ([Table 2](#)).

272 A spatial interaction term (thin plate spline of longitude and latitude) was included to
273 account for expected spatial variability in midtrophic community composition across the diverse
274 regions of our study area and to account for spatial autocorrelation between adjacent datapoints.
275 Residual spatial autocorrelation was examined using Moran's I ([Dormann et al., 2007](#)) in the
276 *spdep* package ([Bivand and Piras, 2015](#)), and adding a spatial interaction term reduced the spatial
277 autocorrelation of model residuals (Moran's I, decreased from 0.12 to 0.10 at 1 km lag, [Fig. S2](#)).

278 Covariates within each candidate model were examined for collinearity using Pearson's
279 correlation in the *corrplot* package ([Wei and Simko, 2017](#)). Residuals of all models of log-
280 transformed NASC were normally distributed, thus Gamma distributions with identity link
281 functions were used for smoothing parameter estimations. Automatic term selection was

282 performed in *mgcv* for all models using “double penalty” shrinkage as described in [Marra and](#)
283 [Wood \(2011\)](#). Model selection was performed by comparing second order Akaike Information
284 Criterion (AICc) among candidate models in the *AICcmodavg* package ([Mazerolle, 2020](#)).

285 GAMs with spatial interaction terms fit using REML were also used to describe
286 potentially non-linear relationships between metrics of acoustic backscatter and the vertical
287 distribution of backscatter in the upper 200 m of the water column. The effects of wNASC on
288 layer width and the effects of total NASC on the density of scattering layers were examined
289 using Gamma distributions for smoothing parameter estimation with log- and identity-link
290 functions respectively.

291

292 **Table 1.**

293 List of candidate GAM models and results of model selection by second order Akaike
 294 Information Criterion (AICc). All models include time in months since the end of the previous El
 295 Niño event (moEND) and a thin plate spline of the interaction between longitude and latitude
 296 (“s(lon, lat, bs = “tp”)”). A single term of NOAA’s Multivariate ENSO Index (MEI.v2), sea
 297 surface temperature (SST), and sea surface chlorophyll-*a* concentration (Chl-*a*) were included in
 298 each model. “s” denotes that the term was fit with a smooth spline. Subscripts after the
 299 environmental terms indicate the number of months prior to acoustic sampling over which the
 300 covariate was averaged.

301

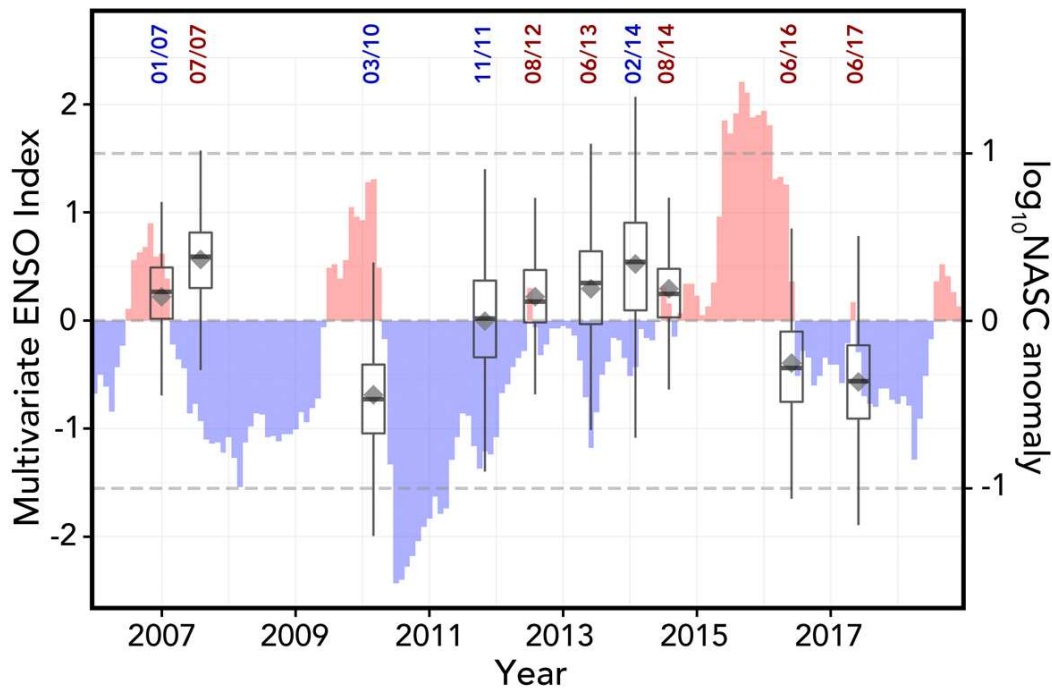
$\log_{10}\text{NASC} \sim s(\text{moEND}) + s(\text{lon, lat, bs} = \text{“tp”}) +$	ΔAIC_c	Weight
$s(\text{MEI}_{12}) + s(\text{SST}) + s(\text{Chl-}a_6)$	0	1
$s(\text{MEI}_{12}) + s(\text{SST}) + s(\text{Chl-}a_3)$	21.29	0
$s(\text{MEI}_9) + s(\text{SST}) + s(\text{Chl-}a_6)$	32.49	0
$s(\text{MEI}_9) + s(\text{SST}) + s(\text{Chl-}a_3)$	54.47	0
$s(\text{MEI}_{12}) + s(\text{SST}_3) + s(\text{Chl-}a_6)$	54.97	0
$s(\text{MEI}_9) + s(\text{SST}_3) + s(\text{Chl-}a_6)$	82.89	0
$s(\text{MEI}_{12}) + s(\text{SST}_3) + s(\text{Chl-}a_3)$	146.46	0
$s(\text{MEI}_{12}) + s(\text{SST}_{12}) + s(\text{Chl-}a_6)$	148.31	0
$s(\text{MEI}_{12}) + s(\text{SST}_{12}) + s(\text{Chl-}a_3)$	192.78	0
$s(\text{MEI}_9) + s(\text{SST}_3) + s(\text{Chl-}a_3)$	211.51	0
$s(\text{MEI}_9) + s(\text{SST}_{12}) + s(\text{Chl-}a_6)$	221.78	0
$s(\text{MEI}_9) + s(\text{SST}_{12}) + s(\text{Chl-}a_3)$	265.55	0

302

303 **3. Results**

304 NASC integrated between 10-200 m depth per km was quantified over 9,940 km of
305 cruise track covered at night in waters with sea floor depths ≥ 200 m. Layer width, wNASC, and
306 density were available for 9,931 km. NASC (computed over all of our defined Gulf of California
307 regions) was variable among cruises, with approximately an order of magnitude variability in
308 mean values and over two orders of magnitude of variability among the interquartile ranges (Fig.
309 4). Log-transformed NASC anomalies were highest (i.e., most positive) during July 2007 (mean
310 \pm sd = 0.38 ± 0.34), February 2014 (0.34 ± 0.40), and October 2014 (0.19 ± 0.28 , Fig. 4). The
311 most negative anomalies occurred during or shortly after strong El Niño events (March 2010: -
312 0.45 ± 0.38 ; June 2016: -0.25 ± 0.32 ; and June 2017: -0.48 ± 0.42 ; Fig. 4).

313 These qualitative patterns in NASC variability across our timeseries are relatively
314 consistent among the defined geographical regions (Fig. S3). However, variability in NASC
315 among regions was not more robustly compared due to spatio-temporally heterogenous data
316 among cruises and spatial autocorrelation within cruises. Thus, we focus on quantifying general
317 environmental mechanisms driving gulf-wide variability in NASC.



318

319 **Fig. 4.** Relationship between ENSO phase (NOAA’s Multivariate ENSO Index v2) and NASC
 320 during 2007-2017 represented as boxplots of log-transformed NASC anomalies (deviation from
 321 all regional means across our time series) from all ten oceanographic cruises, 2007-2017. Within
 322 each boxplot, the mean is represented by a grey diamond and the median as a horizontal black
 323 line. Dashed horizontal lines correspond to the \log_{10} NASC anomaly axis. Sampling start dates
 324 (MM/YY) for the cruises are indicated at the top of the figure and are color coded for warm (red)
 325 and cool (blue) sampling periods. Acoustic summaries per cruise are also presented with
 326 timeseries of mean monthly sea surface temperature and chlorophyll-*a* concentrations across the
 327 study area in [Fig. S4](#), for reference.

328 *3.1. Spatial and environmental effects on acoustic scattering*

329 Standardized model selection based on ΔAIC_c was used to determine which temporal
330 averages of MEI.v2, SST, and Chl-*a* best explained variability in NASC in the gulf (Table 1).
331 Most candidate models were comprised of covariates with |Pearson correlation coefficients| < 0.5
332 (Fig. S5). Our selected model included time in months since the end of the previous El Niño, a
333 spatial interaction term, average SST from the month of collection, average ENSO conditions
334 over the previous 12 months (MEI₁₂), and average Chl-*a* over the previous six months (Table 2,
335 $Adj-R^2 = 0.42$). All environmental covariates in our selected model were minimally correlated
336 (maximum |Pearson correlation coefficient| = 0.53, Fig. S5).

337 **Table 2.**

338 Summary of covariate contributions to the selected generalized additive model of acoustic
 339 backscatter in the Gulf of California, Mexico. Coefficient estimates (“estimate”), *t*-values and *p*-
 340 values are given for each parametric coefficient. Estimated degrees of freedom (*edf*), *F*-statistics
 341 and *p*-values are given for each smooth term (“*s*”). Covariates in the selected model included:
 342 time in months since the end of the previous El Niño (*moEND*); 12-month average MEI.v2
 343 (*MEI₁₂*); sea surface temperature during the month of collection (*SST*); average sea surface
 344 chlorophyll-*a* concentrations over the previous six months (*CHL₆*); and a spatial interaction term
 345 of longitude and latitude to account for spatial autocorrelation in the data (*lon, lat*). The
 346 maximum allowable number of knots (*k*) is given for each term.

$$\log_{10}NASC \sim s(MEI_{12}, k=6) + s(moEND, k=6) + s(SST, k=6) + s(Chl-a_6, k=6) + s(lon, lat, bs="tp", k=10)$$

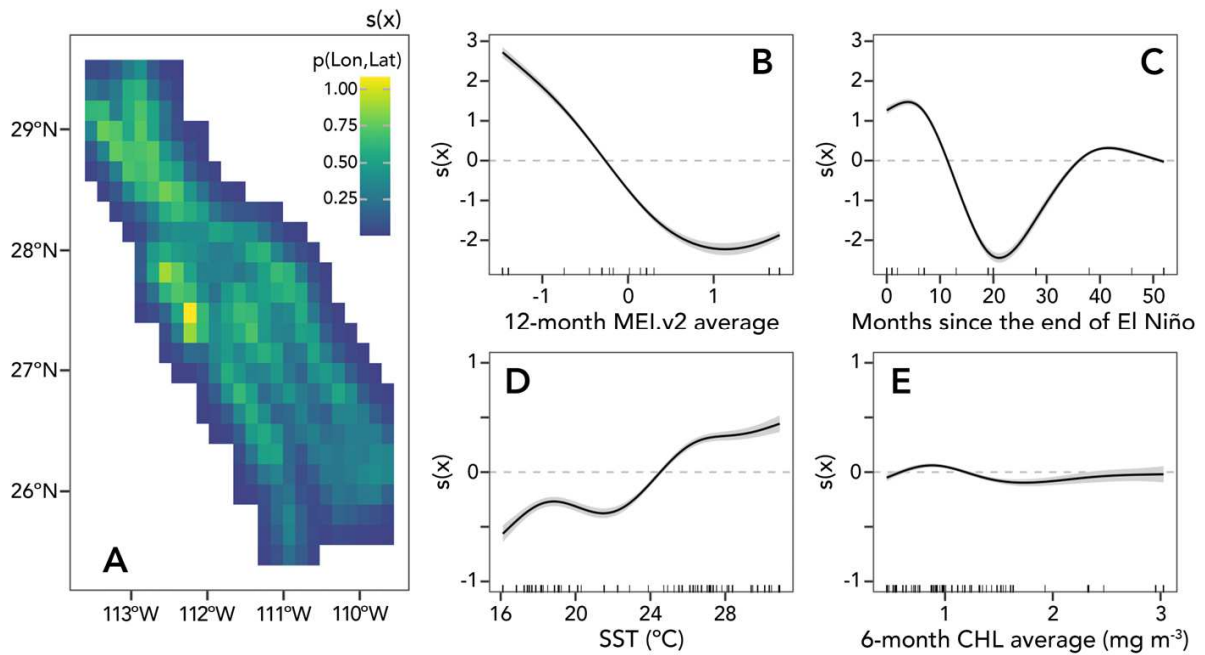
*Adj. R*² = 0.42

Parametric coefficients	estimate	<i>t</i>	<i>p</i>
<i>Intercept</i>	2.77	779.1	<< 0.01
Smooth terms	<i>edf</i>	<i>F</i>	<i>p</i>
<i>s(MEI₁₂)</i>	4.75	350.4	<< 0.01
<i>s(moEND)</i>	4.83	498.9	<< 0.01
<i>s(SST)</i>	4.95	64.2	<< 0.01
<i>s(Chl-<i>a</i>₆)</i>	4.68	19.6	<< 0.01
<i>s(lon, lat)</i>	8.57	33.0	<< 0.01

347

348 All environmental covariates included in the selected model explained significant
 349 variability in NASC. However, most of the explanatory power could be attributed to the time
 350 since the last El Niño (*F* = 498.9, *p* << 0.01), as well as the average MEI.v2 over the 12 months
 351 prior to sampling (*MEI₁₂*; *F* = 350.4, *p* << 0.01, [Table 2](#)). La Niña conditions (negative ENSO
 352 extremes defined as *MEI.v2* < -0.5) had a strong positive effect on backscatter, and increased

353 MEI₁₂ had a strong negative effect on NASC, driving approximately four orders of magnitude of
 354 variability across the range of observed MEI₁₂ values (Fig. 5B). The negative effect appeared to
 355 peak at MEI₁₂ > 1.0 and may suggest an upper limit on the possible impact of El Niño
 356 conditions, although we only had two observations of MEI₁₂ > 1.0 (Fig. 5B).



357
 358 **Fig. 5.** Partial-effects plots for the environmental covariates in the selected generalized additive
 359 model of $\log_{10}\text{NASC}$ showing the relationship between each covariate and the contribution of the
 360 smoother for that covariate to the model's fitted values (" $s(x)$ "). A) Thin plate spline of longitude
 361 and latitude; B) 12-month average MEI.v2 (MEI₁₂); C) Time in months since the end of the
 362 previous El Niño event (moEND); D) Regional monthly average of sea surface temperature at
 363 time of acoustic sampling (SST); E) 6-month average regional sea surface chlorophyll-*a*
 364 concentration (CHL₆). In panels B-E, grey shading indicates standard errors about the estimate
 365 for each covariate, and rug plots indicate covariate observations.

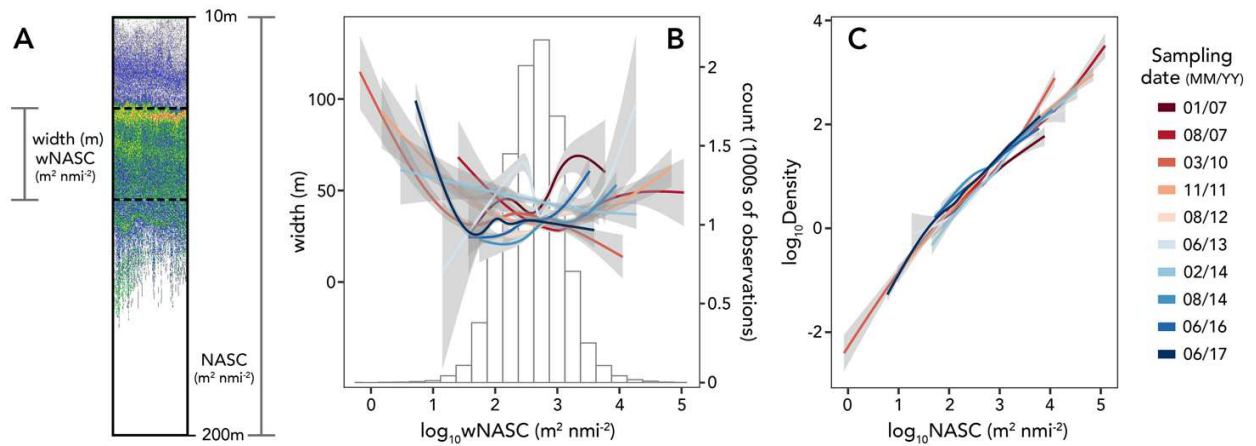
366 In the first ten months following an El Niño event, there is a decreasing positive effect of
367 time since the end of El Niño on NASC (Fig. 5C), but this turns into a strong negative after ten
368 months, peaking at 24 months, with NASC values being depressed more than 100-fold. The
369 negative effect of an El Niño event thus persists from ~10-36 months following the end of the
370 event, independent of local environmental conditions.

371 Increased SST had a significant positive effect on backscatter, but explained less than one
372 order of magnitude of variability across the entire range of values observed (Table 2, Fig. 5D).
373 The highest SST values are typically observed July-September (Fig. 3), suggesting the effect of
374 SST on acoustic backscatter may at least partially reflect a seasonal signal in local environmental
375 conditions. Although the relationship between CHL_6 and log-transformed NASC was significant,
376 it was largely uninformative and explained little variability across the range of observed values
377 (Table 2, Fig. 5E).

378

379 *3.2. Relationship between NASC, layer width, and density*

380 Integrated NASC within vertically-defined scattering layers (wNASC) was not a useful
381 predictor of the width of those scattering layers in the Gulf of California (GAM, $Adj-R^2 = 0.05$,
382 Table 3, Fig. S6). Width generally increased at the high and low extremes of observed wNASC,
383 but mean width (35.10 ± 19.47 m) remained relatively constant across the most frequently
384 observed values of wNASC (Fig. 6B). However, wNASC explained 75% of variability in layer
385 density (GAM, Table 3, Fig. S6). Scattering layer density increased linearly with NASC during
386 all ten oceanographic cruises, suggesting that as scattering increases, packing density within
387 scattering layers also increases (Fig. 6C).



388

389 **Fig. 6.** Relationships between backscatter and the vertical distribution of backscatter per km of
 390 cruise track. A) Definitions of width, wNASC, and NASC used for calculating layer density. B)
 391 Histogram of \log_{10} -transformed wNASC observations and its relationship with layer width for
 392 each cruise as identified in the inset on the right. C) Relationship between \log_{10} -transformed layer
 393 density (width /wNASC) and \log_{10} -transformed NASC. Locally estimated scatterplot smooths are
 394 given for each cruise and 95% confidence intervals are given as grey bands. Color legend applies
 395 to panels B and C.

396 **Table 3.**

397 Summary of covariate contributions models describing the relationship between nighttime
 398 backscatter and vertical density distribution in the upper 200 m of the water column in the Gulf
 399 of California. Coefficient estimates (“estimate”), *t*-values, and *p*-values are given for each
 400 parametric coefficient. Estimated degrees of freedom (*edf*), *F*-statistics, and *p*-values are given
 401 for each smooth term (“*s*”). Definitions of NASC, wNASC, width, and density are provided in
 402 the methods and Fig. 2. A spatial interaction term of longitude and latitude was included in each
 403 model to account for spatial autocorrelation in the data (lon, lat). The maximum allowable
 404 number of knots (*k*) is given for each term and the adjusted R^2 (*Adj. R^2*) is given for each model.

<i>width ~ s(log₁₀ wNASC, k = 6) + s(lon, lat, bs = “tp”, k = 10), Adj. R² = 0.05</i>			
Parametric coefficients	estimate	<i>t</i>	<i>p</i>
<i>Intercept</i>	3.55	678.7	<< 0.01
Smooth terms	<i>edf</i>	<i>F</i>	<i>p</i>
<i>s(log₁₀ wNASC)</i>	3.90	20.0	<< 0.01
<i>te(lon, lat)</i>	8.31	32.7	<< 0.01
<i>density ~ s(log₁₀ NASC, k = 6) + s(lon, lat, bs = “tp”, k = 10), Adj. R² = 0.75</i>			
Parametric coefficients	estimate	<i>t</i>	<i>p</i>
<i>Intercept</i>	2.64	688.2	<< 0.01
Smooth terms	<i>edf</i>	<i>F</i>	<i>p</i>
<i>s(log₁₀ NASC)</i>	4.52	14529.6	<< 0.01
<i>te(lon, lat)</i>	8.41	21.1	<< 0.01

405

406 **4. Discussion**

407 Midtrophic organisms play a central ecological role in open ocean ecosystems, but their
408 responses to seasonal and climatic variability remain poorly understood. We observed variability
409 of backscatter from midtrophic organisms in the central Gulf of California that spanned four
410 orders of magnitude and could largely be explained by ENSO conditions and a seasonal
411 temperature cycle. Although we were not able to directly sample the communities contributing to
412 backscatter during this study, numerous studies indicate that acoustic backscatter at 120 kHz can
413 be mostly attributed to mesozooplankton and micronekton (Domínguez-Contreras et al., 2012;
414 Díaz Santana-Iturríos et al., 2013; Gómez-Gutiérrez et al., 2006; Robinson et al., 2014; García-
415 Fernández et al., this issue). Our observations suggest that the biomass of midtrophic organisms
416 and their contribution to ecosystem function and biogeochemical cycling vary drastically in
417 response to environmental variability.

418

419 *4.1. Seasonal backscatter variability*

420 Intra-annual variability in NASC was characterized by a positive relationship with SST
421 (Fig. 5), suggesting that backscatter peaks in summer when sea surface temperatures are highest
422 (Hidalgo-González and Alvarez-Borrego, 2004; Kahru et al., 2004) (Fig. 3). Euphausiids,
423 myctophids, sardines, and anchovies often dominate the midtrophic biomass in upwelling
424 systems such as the Gulf of California (Lavaniegos-Espejo and Lara-Lara, 1990; Sánchez-
425 Velasco et al., 2004; Díaz Santana-Iturríos et al., 2013; Ambriz-Arreola et al., 2017; Contreras-
426 Domínguez et al., 2012; Petatán-Ramírez et al., 2019; Weber et al., 2021) and exhibit seasonal
427 breeding cycles that may help explain summer peaks in backscatter as growing individuals
428 become more acoustically visible with increasing size. Brinton and Townsend (1980) reported

429 April peaks in euphausiid abundance in the central gulf, driven by the neritic species
430 *Nyctiphanes simplex*. Summer peaks in the abundance of larvae and adults of the two most
431 abundant myctophids in our study region, *Benthosema panamense* and *Triphoturus mexicanus*,
432 have been observed during both warm and cool ENSO phases (Aceves-Medina et al., 2004; Díaz
433 Santana-Iturríos et al., 2013).

434 The sampling frequency and environmental history of our study period limited our ability
435 to robustly describe seasonal variability in backscatter in the Gulf of California (we only made
436 paired warm-cool season samplings in 2007 and 2014). For both paired seasonal sampling
437 events, each characterized by different oceanographic conditions and histories, the variability
438 observed between seasons was orders of magnitude smaller than interannual variability (Fig. 4).
439 The most notable contradictions to the observed summer peaks in backscatter are the abundances
440 of anchovy (*Engraulis mordax*) and sardine (*Sardinops sagax*), which typically peak in cooler
441 months (Contreras-Domínguez et al., 2012; Rubio-Rodríguez et al., 2018; Petatán-Ramírez et al.,
442 2019; Arreguín-Sánchez et al., 2021; Morales-Bojorquez et al., 2021). These fishes are generally
443 more coastal than the dominant euphausiid and myctophid species, which may have also
444 impacted their detectability and inclusion in our analyses. The contributions of anchovy and
445 sardine could be further complicated by commercial fishing pressure, which neither euphausiids
446 nor myctophids experience in the Gulf of California.

447 Regardless of the complex seasonal dynamics of midtrophic community composition and
448 biomass, impacts of climatic events such as El Niño appear to have a much stronger impact than
449 seasonal cycles on baseline productivity across trophic levels in the Gulf of California. Although
450 the average chlorophyll-*a* concentration over the six months prior to acoustic sampling was not a
451 useful predictor of backscatter, it is possible that we simply did not include this proxy of

452 phytoplankton biomass at appropriate spatial and temporal resolutions. It is also possible that the
453 spatial interaction term obscured potential effects of phytoplankton biomass on backscatter, as
454 sea surface chlorophyll-*a* concentration was positively correlated with latitude (Fig. S5).
455 Qualitatively, NASC was highest in the Baja Peninsula, Sonora, and Midriff Islands regions (Fig.
456 1, Fig. S3). These regions exhibit strong seasonal variability in wind- and tidally driven
457 upwelling (Roden, 1964) and experience some upwelling in early summer when the gulf-wide
458 coastal upwelling index is low (Lluch-Cota, 2000). Nutrient enrichment from upwelled waters in
459 these regions may thus support a relatively high biomass of scatterers compared to regions with
460 less upwelling such as the Central Pelagic and Southern regions (Lavaniegos-Espejo and Lara-
461 Lara, 1990; Lluch-Cota, 2000).

462

463 *4.2. Integrated ENSO conditions largely dictate pelagic acoustic backscatter*

464 Variability in backscatter could largely be explained by ENSO conditions over the twelve
465 months prior to sampling (MEI₁₂, Fig. 5, Table 2). Log-transformed NASC was lowest during or
466 immediately following El Niño events and corresponds to reductions of zooplankton biovolume,
467 as well as euphausiid and larval fish abundances observed in the Gulf of California following the
468 1982-83, 1997-98, and 2015-16 El Niño events (Lavaniegos et al., 1989; Sánchez-Velasco et al.,
469 2004, García-Fernández et al., this issue).

470 Changes in backscatter could also reflect variability in midtrophic community
471 composition with ENSO conditions. The relative biomass of gas-bearing organisms (e.g.
472 anchovy, some myctophids and siphonophores) and euphausiids would have the largest impact
473 on the relationship between backscatter at 120 kHz and midtrophic biomass (Lavery et al., 2007;
474 Benoit-Bird and Lawson, 2016). Timeseries describing variability in midtrophic community

475 composition are limited, but similar responses to ENSO events have been documented for
476 several midtrophic groups in the Gulf of California. Trawl-estimated biomass of fish larvae,
477 euphausiids, and gas-bearing siphonophores all decreased following the 1982-83 El Niño and
478 increased during the subsequent La Niña (Lavaniegos-Espejo and Lara-Lara, 1990; Sánchez-
479 Velasco et al., 2004). Landings of *S. sagax* decreased following the 2009-10 El Niño and
480 landings of *E. mordax* peaked during La Niña conditions in 2013-14 before decreasing during
481 the 2015-16 El Niño (Comisión Nacional de Acuacultura y Pesca,
482 <https://datos.gob.mx/busca/dataset/produccion-pesquera>). Additionally, Humboldt squid
483 collected from the central gulf following El Niño events consumed more crustaceans and fewer
484 fishes than those collected following ENSO-neutral or La Niña conditions, which could indicate
485 reduced availability of fish prey following El Niño events (Hoving et al., 2013; Portner et al.,
486 2020). Thus, although there have likely been changes in midtrophic community composition
487 during our study period, observed changes in NASC from the central Gulf of California are more
488 likely to reflect changes in total biomass of the midtrophic community.

489 Changes in the size structure of midtrophic organisms could also affect NASC. However,
490 limited variability in the size of myctophids (~3-4 cm standard length) and enoploteuthid squids
491 (~2 cm mantle length) with ENSO conditions in the diets of Humboldt squid (Portner et al.,
492 2020), suggests that there is limited variability in adult body size of these abundant prey. Thus,
493 we hypothesize that reduced backscatter is indicative of large-scale changes in the pelagic
494 ecosystem of the Gulf of California, likely driven by a combination of changes in the biomass
495 and possibly identity, of midtrophic community constituents in response to local and integrated
496 ENSO conditions.

497 *4.3. Acoustic backscatter is persistently low following El Niño events*

498 Nighttime NASC decreased significantly following El Niño events in 2009-10 and 2015-
499 16 and took two to three years after El Niño ended to recover to values observed prior to the
500 event (Fig. 5C). Our evidence for this pattern of recovery derives primarily from the 2009-10
501 event, because our dataset ends in June 2017, only one year after the 2015-16 El Niño (Fig. 4).
502 However, qualitative observations from surveys in June 2018 and 2019 suggest a continuation of
503 relatively low backscatter conditions (Robinson and Gómez-Gutiérrez, this issue, unpublished
504 data).

505 The time it takes to recover to pre-El Niño biomass is likely dependent on the generation
506 times of midtrophic organisms and the conditions experienced during the cool (La Niña) and
507 neutral phases of ENSO that follow El Niño events. Some common midtrophic constituents of
508 acoustic scattering layers in the upper 200 m of the Gulf of California, such as euphausiids and
509 small mesopelagic squids, have lifespans of less than one year (Lavaniegos, 1992; Harvey et al.,
510 2010; Ambriz-Arreola et al., 2012, 2017). Fishes such as myctophids and anchovies may mature
511 in as little as a year and reproduce for multiple years (Kawaguchi and Mauchline, 1982; Parrish
512 et al., 1986). If the observed reduction in NASC reflects a decreased abundance of midtrophic
513 organisms following El Niño events, these organisms would require multiple generations to
514 recover to large population sizes, even under favorable environmental conditions. García-
515 Fernández et al. (this issue) reported that euphausiid abundances in the central Gulf of California
516 during June 2013–2016 were relatively low and took approximately three years following the
517 2015-16 El Niño to recover to relatively high abundances that characterized historical
518 observations (Brinton and Townsend, 1980).

519 Strong La Niña conditions ($\text{MEI.v2} < -1$) following El Niño events coincided with the
520 recovery of midtrophic biomass, and thus the entire ecosystem including regional fisheries.
521 Following El Niño 2009-10, strong La Niña conditions persisted for ten months, and mean
522 NASC increased approximately three-fold by the end of 2011, fully recovering to levels
523 observed prior to El Niño by the beginning of 2014 (Fig. 4). Conversely, following El Niño
524 2015-16, La Niña was essentially non-existent, and NASC continued to decrease through mid-
525 2017. It is important to note that 2014 was an unusually warm year in the study region, both in
526 terms of SST and temperature at depth (Frawley et al., 2019; Martínez-Soler et al., 2021), and
527 this phenomenon may have influenced the midtrophic communities prior to El Niño 2015-16
528 and/or further enhanced its effects.

529

530 *4.4. Scattering layer density increases with backscatter*

531 Pelagic fishes and invertebrates engage in complex and dynamic social behaviors, called
532 aggregations, swarms, schools, and shoals (Ritz, 1994; Ritz et al., 2011) that likely modify
533 acoustic density. MVBS within acoustic layers, a proxy for animal density, increased with NASC
534 over a substantial range (Fig. 6C), suggesting that at intermediate spatial scales organisms pack
535 more tightly with their neighbors as the number of individuals increases (Benoit-Bird et al.,
536 2017). For most cruises, the slope of the relationship between density and NASC decreases at
537 relatively high NASC (Fig. 6C), which could indicate an ecologically relevant limiting effect.
538 This pattern, however, may also reflect how our metric of density characterized features with
539 multiple centers of acoustic biomass in the water column. Variability in layer density at higher
540 NASC could be due to more complex acoustic features or multiple acoustic features in the upper

541 200 m of the water column (Fig. 2C), perhaps composed of species assemblages with different
542 vertical migratory behaviors (Ambriz-Arreola et al., 2017).

543 A general increase in prey density with increasing backscatter suggests that the
544 accessibility of this midtrophic biomass to the predators it supports increases exponentially.
545 Conversely, reductions in prey biomass could be expected to have non-linear effects on predators
546 as prey density is often more important than overall biomass for a variety of foraging predators,
547 including seabirds (Weimerskirch et al., 2005; Benoit-Bird et al., 2013; Carroll et al., 2017) and
548 rorqual whales (Cade et al., 2021). Effects of environmental variability on predators are thus
549 compounded by changes in both the abundance and distribution of midtrophic prey. It is likely
550 that there were high-density patches of scatterers in our dataset when total NASC was relatively
551 low, but at scales smaller than the resolution of our analyses (Hazen et al., 2009; Benoit-Bird et
552 al., 2019). Examining effects of environmental variability on acoustic backscatter at finer spatial
553 scales than explored in this study would refine our understanding of the effects of climatic
554 variability on midtrophic communities.

555

556 *4.5. Potential consequences of reduced backscatter from midtrophic communities*

557 Anomalous warming events in the gulf have been more frequent and longer lasting, with
558 two strong El Niño events since 2010 and a pronounced sub-surface warming trend in the 50-150
559 m depth range between 2006 and 2017 (Frawley et al., 2019). If these patterns of more frequent
560 El Niño events and intervening warming trends continue, it is highly likely that conditions will
561 become increasingly unfavorable to support a large biomass of midtrophic organisms in the Gulf
562 of California (Petatán-Ramírez et al., 2019).

563 A declining trend in standing biomass of midtrophic forage species will negatively
564 impact pelagic predators, and this already appears to have happened in the case of Humboldt
565 squid, at least for individuals of the large phenotype. These squid supported a major fishery until
566 El Niño 2009-10 when squid hatchlings assumed a tropical phenotype characterized by reduced
567 size at maturity, and the fishery collapsed (Hoving et al., 2013; Robinson et al., 2016). A
568 subsequent warming trend flanked by El Niño 2009-10 and 2015-16 has accompanied the
569 persistence of the small phenotype to the present time, and the fishery has reported severely
570 reduced landings since 2010 (Frawley et al., 2019). Thus, the small phenotype replaced the large
571 in the gulf, and while biomass of the small-phenotype stock appeared to remain high until at least
572 2013 (Hoving et al. 2013; Benoit-Bird and Gilly, unpublished data), the current status is unclear.
573 Although subsurface temperature anomalies may directly affect development and maturation of
574 predators in the Gulf of California, our results suggest that temperature also affects the supply of
575 midtrophic organisms that form the diet of many predators in the region, exacerbating direct
576 thermal effects of warming events.

577

578 **5. Conclusions**

579 Perhaps the most ecologically relevant finding of the present study is the approximately
580 three years that may be necessary for midtrophic communities to recover from a strong El Niño
581 event. Increases in the frequency and intensity of El Niño events with global change (Cai et al.,
582 2014, 2015; Jin et al., 2015) could dramatically impact marine ecosystems by limiting the
583 recovery of midtrophic community biomass between El Niño events and result in a chronic,
584 sequential degradation of midtrophic forage, as well as the biomass of predators that depend on
585 this prey resource. Even if La Niña events are also strengthened, the decline in biomass, and

586 likely overall productivity, of midtrophic communities following El Niño still require multiple
587 generations to recover – a temporal scale that may be longer than the duration of a typical La
588 Niña event. Understanding the drivers and timescales of variability in midtrophic community
589 composition and biomass across diverse marine ecosystems would provide a more refined
590 perspective through which to understand how effects of ocean warming will propagate through
591 oceanic ecosystems.

592

593 **Declaration of Competing Interest**

594 The authors declare that they have no known competing financial interests or personal
595 relationships that could have appeared to influence the work reported in this paper.

596

597 **Acknowledgements**

598 We would like to thank the crew of the *R/V El Puma* and the technicians, graduate and
599 undergraduate students, and scientists from the Fisheries Ecology Laboratory, Instituto de
600 Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México (ICMyL-UNAM),
601 Universidad de Guadalajara, Centro de Investigaciones Biológicas del Noroeste (CIBNOR), and
602 Centro Interdisciplinario de Ciencias Marinas (CICIMAR-IPN) for their cooperation in
603 collecting hydroacoustic data. Stephanie Brodie, Gemma Carroll, and Barbara Muhling provided
604 thoughtful feedback on the environmental analyses and generalized additive models. Briony
605 Hutton provided invaluable assistance with the acoustic analyses. The use of the R/V El Puma
606 during the cruises was supported by UNAM, under grants PAPIIT-UNAM IN218106-3, IN2006-
607 10. This research project was funded by DGAPA-PAPIIT UNAM (No. IN200610), CONACYT
608 (Ciencia Básica 2012-152850, FOSEMARNAT-2004-01-C01-144, SAGARPA S007-2005-1-

609 11717, CB-2012-178615-01, CB-2016-01-284201) and El Centro Interdisciplinario de Ciencias
610 Marinas, Instituto Politécnico Nacional (SIP-IPN 2007–2017). C.J.R. and J.G.-G. are SNI
611 fellows. J.G.-G. is also an EDI-IPN and a COFAA-IPN fellow. W.F.G. was supported during the
612 course of this work by grants from the US National Science Foundation (IOS-1557754, OCE-
613 1338973 RAPID, IOS-1420693 EAGER, OCE 0850839, and OCE 0526640), the National
614 Geographic Committee for Research and Exploration (7578-04 and 9366-13), Lindblad
615 Expeditions-National Geographic Fund (LXII-15), and the David and Lucille Packard
616 Foundation (2005-2800 and 32708). K.B.B. was supported by NSF grant 0851239 with
617 additional support from the David and Lucille Packard Foundation through the Monterey Bay
618 Aquarium Research Institute. E.P. was supported in part by the National Science Foundation
619 Graduate Research Fellowship Program under Grant no. DGE-114747 as well as the Esther M.
620 Zimmer Lederberg Trust. The authors have no conflicts of interest to declare.
621

622 **References**

- 623 Aceves-Medina, G., Jiménez-Rosenberg, S.P.A., Hinojosa-Medina, A., Funes-Rodríguez, R.,
624 Saldierna-Martínez, R.J., Smith, P.E., 2004. Fish larvae assemblages in the Gulf of
625 California. *J. Fish Biol.*, 65(3), 832–847. [https://doi.org/10.1111/j.1095-](https://doi.org/10.1111/j.1095-8649.2004.00490.x)
626 [8649.2004.00490.x](https://doi.org/10.1111/j.1095-8649.2004.00490.x).
- 627 Alvarez-Borrego, S., Lara-Lara, J.R., 1991. The physical environment and primary productivity
628 of the Gulf of California: Chapter 26: Part V. Physical oceanography, primary
629 productivity, sedimentology. In *M 47: The Gulf and Peninsular Province of the*
630 *Californias* (pp. 555–567). American Association of Petroleum Geologists.
631 <http://archives.datapages.com/data/specpubs/history1/images/a114/a1140001/0550/05550>
632 [.pdf](http://archives.datapages.com/data/specpubs/history1/images/a114/a1140001/0550/05550)
- 633 Ambriz-Arreola, I., Gómez-Gutiérrez, J., Del Carmen Franco-Gordo, M., Lavaniegos, B.E.,
634 Godínez-Domínguez, E., 2012. Influence of coastal upwelling-downwelling variability
635 on tropical euphausiid abundance and community structure in the inshore Mexican
636 central Pacific. *Mar. Ecol. Prog. Ser.*, 451, 119–136. <https://doi.org/10.3354/meps09607>
- 637 Ambriz-Arreola, I., Gómez-Gutiérrez, J., Franco-Gordo, M.C., Palomares-García, R.J., Sánchez-
638 Velasco, L., Robinson, C.J., Seibel, B.A., 2017. Vertical pelagic habitat of euphausiid
639 species assemblages in the Gulf of California. *Deep-Sea Res. Part I* 123, 75–89.
640 <https://doi.org/10.1016/j.dsr.2017.03.008>.
- 641 Arreguín-Sánchez, F., Monte-Luna, P.D., Albañez-Lucero, M.O., Zetina-Rejón, M.J., Tripp-
642 Quezada, A., Ruiz-Barreiro, T.M., Hernández-Padilla, J.C., 2021. How much biomass
643 must remain in the sea after fishing to preserve ecosystem functioning? The case of the

644 sardine fishery in the Gulf of California, Mexico. In *Marine Coastal Ecosystems*
645 *Modelling and Conservation*, pp. 143–161. Springer, Cham.

646 Baumgartner, T., Ferreira-Bartrina, V., Schrader, H., Soutar, A., 1985. A 20-year varve record of
647 siliceous phytoplankton variability in the central Gulf of California. *Mar. Geol.*, 64(1–2),
648 113–129. [https://doi.org/10.1016/0025-3227\(85\)90163-X](https://doi.org/10.1016/0025-3227(85)90163-X).

649 Benoit-Bird, K.J., 2009. The effects of scattering-layer composition, animal size, and numerical
650 density on the frequency response of volume backscatter. *ICES J. Mar. Sci.*, 66(3), 582–
651 593. <https://doi.org/10.1093/icesjms/fsp013>.

652 Benoit-Bird, K.J., Au, W.W.L., 2003. Prey dynamics affect foraging by a pelagic predator
653 (*Stenella longirostris*) over a range of spatial and temporal scales. *Behav. Ecol.*
654 *Sociobiol.* 53(6), 364–373. <https://doi.org/10.1007/s00265-003-0585-4>.

655 Benoit-Bird, K.J., Gilly, W., 2012. Coordinated nocturnal behavior of foraging jumbo squid
656 *Dosidicus gigas*. *Mar. Ecol. Prog. Ser.*, 455, 211–228.
657 <https://doi.org/10.3354/meps09664>.

658 Benoit-Bird, K.J., Battaile, B.C., Heppell, S.A., Hoover, B., Irons, D., Jones, N., Kuletz, K.J.,
659 Nordstrom, C.A., Paredes, R., Suryan, R.M., Waluk, C.M., Trites, A.W., 2013. Prey
660 patch patterns predict habitat use by top marine predators with diverse foraging
661 strategies. *PLoS One*, 8(1), e53348. <https://doi.org/10.1371/journal.pone.0053348>.

662 Benoit-Bird, K.J., Lawson, G.L., 2016. Ecological insights from pelagic habitats acquired using
663 active acoustic techniques. *Ann. Rev. Ma. Sci.*, 8(1), 463–490.
664 <https://doi.org/10.1146/annurev-marine-122414-034001>.

665 Benoit-Bird, K.J., Moline, M.A., Southall, B.L., 2017. Prey in oceanic sound scattering layers
666 organize to get a little help from their friends. *Limnol. Oceanogr.*, 62(6), 2788–2798.
667 <https://doi.org/10.1002/lno.10606>.

668 Benoit-Bird, K.J., Waluk, C. M., Ryan, J.P., 2019. Forage species swarm in response to coastal
669 upwelling. *Geophys. Res. Lett.*, 46, 1537–1546. <https://doi.org/10.1029/2018GL081603>.

670 Bivand, R.S., Piras, G., 2015. Comparing implementations of estimation methods for spatial
671 econometrics. *J. Stat. Software*, 63(18), 1–36. <https://doi.org/10.18637/jss.v063.i18>.

672 Boyce, D.G., Lewis, M.R., Worm, B., 2010. Global phytoplankton decline over the past century.
673 *Nature*, 466(7306), 591–596. <https://doi.org/10.1038/nature09268>.

674 Boyd, P. W., Claustre, H., Levy, M., Siegel, D. A., Weber, T., 2019. Multi-faceted particle
675 pumps drive carbon sequestration in the ocean. *Nature*, 568(7752), 327–335.
676 <https://doi.org/10.1038/s41586-019-1098-2>.

677 Brinton, E., Townsend, A. W., 1980. Euphausiids in the Gulf of California—The 1957 cruises.
678 *Calif. Coop. Ocean. Fish. Invest. Rep.*, 21, 211–236.

679 Brinton, E., Fleminger, A., Siegel-Causey, D., 1986. The temperate and tropical planktonic
680 biotas of the Gulf of California. *Calif. Coop. Ocean. Fish. Invest. Rep.*, 27, 228–266.

681 Cade, D.E., Benoit-Bird, K.J., 2015. Depths, migration rates and environmental associations of
682 acoustic scattering layers in the Gulf of California. *Deep-Sea Res. Part I*, 102, 78–89.
683 <https://doi.org/10.1016/j.dsr.2015.05.001>.

684 Cade, D. E., Seakamela, S. M., Findlay, K. P., Fukunaga, J., Kahane-Rapport, S. R., Warren, J.
685 D., Calambokidis, J., Fahlbusch, J. A., Friedlaender, A. S., Hazen, E. L., Kotze, D.,
686 McCue, S., Meyer, M., Oestreich, W. K., Oudejans, M. G., Wilke, C., Goldbogen, J. A.
687 (2021). Predator-scale spatial analysis of intra-patch prey distribution reveals the

688 energetic drivers of rorqual whale super-group formation. *Funct. Ecol.*, 35(4), 894–908.
689 <https://doi.org/10.1111/1365-2435.13763>.

690 Cai, W., Borlace, S., Lengaigne, M., Van Rensch, P., Collins, M., Vecchi, G., Timmermann, A.,
691 Santoso, A., McPhaden, M. J., Wu, L., England, M. H., Wang, G., Guilyardi, E., Jin, F.F.,
692 2014. Increasing frequency of extreme El Niño events due to greenhouse warming. *Nat.*
693 *Clim. Change*, 4(2), 111–116. <https://doi.org/10.1038/nclimate2100>.

694 Cai, W., McPhaden, M.J., Santoso, A., Timmermann, A., Jin, F.F., Yeh, S.-W., Takahashi, K.,
695 Vecchi, G., Collins, M., Cobb, K.M., Watanabe, M., Wang, G., Lengaigne, M., Wu, L.,
696 An, S.-I., Guilyardi, E., Kug, J.-S., 2015. ENSO and greenhouse warming. *Nat. Clim.*
697 *Change*, 5(9), 849–859. <https://doi.org/10.1038/nclimate2743>.

698 Carroll, G., Cox, M., Harcourt, R., Pitcher, B. J., Slip, D., Jonsen, I., 2017. Hierarchical
699 influences of prey distribution on patterns of prey capture by a marine predator. *Funct.*
700 *Ecol.*, 31(9), 1750–1760. <https://doi.org/10.1111/1365-2435.12873>.

701 Chen, Z., Yan, X.-H., Jiang, Y., Jiang, L., 2013. Roles of shelf slope and wind on upwelling: A
702 case study off east and west coasts of the US. *Ocean Model.*, 69, 136–145.
703 <https://doi.org/10.1016/j.ocemod.2013.06.004>.

704 Choy, C., Wabnitz, C., Weijerman, M., Woodworth-Jefcoats, P., Polovina, J., 2016. Finding the
705 way to the top: How the composition of oceanic mid-trophic micronekton groups
706 determines apex predator biomass in the central North Pacific. *Mar. Ecol. Prog. Ser.*, 549,
707 9–25. <https://doi.org/10.3354/meps11680>.

708 Croll, D., Marinovic, B., Benson, S., Chavez, F., Black, N., Ternullo, R., Tershy, B., 2005. From
709 wind to whales: Trophic links in a coastal upwelling system. *Mar. Ecol. Prog. Ser.*, 289,
710 117–130. <https://doi.org/10.3354/meps289117>.

711 Díaz Santana-Iturríos, M., Palacios-Salgado, D.S., Salinas-Zavala, C.A., 2013. Abundance and
712 distribution of lantern fishes (Myctophiformes: Myctophidae) around San Pedro Martir
713 Island, Gulf of California, during 2008. *Lat Am. J. Aquat. Res.*, 41(3), 387–394.
714 <https://doi.org/10.3856/vol41-issue3-fulltext-2>.

715 Domínguez-Contreras, J.F., Robinson, C.J., Gómez-Gutiérrez, J., 2012. Hydroacoustical survey
716 of near-surface distribution, abundance and biomass of small pelagic fish in the Gulf of
717 California. *Pacif. Sci.*, 66(3), 311–326. <https://doi.org/10.2984/66.3.5>.

718 Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G.,
719 Hirzel, A., Jetz, W., Kissling, W.D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R.,
720 Reineking, B., Schröder, B., Schurr, F.M., Wilson, R., 2007. Methods to account for
721 spatial autocorrelation in the analysis of species distributional data: A review. *Ecography*,
722 30(5), 609–628. <https://doi.org/10.1111/j.2007.0906-7590.05171.x>.

723 [Ducklow, H.W., Steinberg, D.K., Buesseler, K.O., 2001. Upper ocean carbon export and the
724 biological pump. *Oceanography*, 14\(4\), 50–58.](#)

725 [Echoview Software Pty Ltd, 2019. Echoview® version 10. Echoview Software Pty Ltd, Hobart,
726 Australia.](#)

727 FAO, 2016. The State of World Fisheries and Aquaculture (SOFIA) | FAO | Food and
728 Agriculture Organization of the United Nations. <https://doi.org/92-5-105177-1>.

729 [Faria, J., Jelihovschi, E., Allaman, I., 2018. Conventional Tukey Test. Version 1.3–0. R package.](#)

730 Frawley, T.H., Briscoe, D. K., Daniel, P.C., Britten, G.L., Crowder, L.B., Robinson, C.J., Gilly,
731 W.F., 2019. Impacts of a shift to a warm-water regime in the Gulf of California on jumbo
732 squid (*Dosidicus gigas*). *ICES J. Mar. Sci.*, 76(7), 2413–2426.
733 <https://doi.org/10.1093/icesjms/fsz133>.

- 734 García-Fernández, F., Gómez-Gutiérrez, J., Haskpiel-Segura, C., Ambriz-Arreola, I., De Silva-
735 Dávila, R., Martínez-López, A., Sánchez-Uvera, A., Hernández-Rivas, M., Robinson,
736 C.J., this issue. Interannual spring-summer transition response of euphausiid community
737 abundance during a prolonged anomalous warming in the Gulf of California (2013–
738 2019). *Prog. Oceanogr.*
- 739 Gleckler, P.J., Durack, P.J., Stou, R.J., Johnson, G.C., Forest, C.E., 2016. Industrial-era global
740 ocean heat uptake doubles in recent decades. *Nature Clim. Change*, 6, 394–398.
741 <https://doi.org/10.1038/NCLIMATE2915>.
- 742 Godø, O.R., Handegard, N.O., Browman, H.I., Macaulay, G.J., Kaartvedt, S., Giske, J., Ona, E.,
743 Huse, G., Johnsen, E., 2014. Marine ecosystem acoustics (MEA): Quantifying processes
744 in the sea at the spatio-temporal scales on which they occur. *ICES J. Mar. Sci.*, 71(8),
745 2357–2369. <https://doi.org/10.1093/icesjms/fsu116>.
- 746 Gómez-Gutiérrez, J., Robinson, C.J., 2006. Tidal current transport of epibenthic swarms of the
747 euphausiid *Nyctiphanes simplex* in a shallow, subtropical bay on Baja California
748 peninsula, México. *Mar. Ecol. Prog. Ser.*, 320, 215–231.
749 <https://doi.org/10.3354/meps320215>.
- 750 Harvey, H. R., Ju, S. J., Son, S.K., Feinberg, L.R., Shaw, C.T., Peterson, W.T., 2010. The
751 biochemical estimation of age in Euphausiids: Laboratory calibration and field
752 comparisons. *Deep-Sea Res. Part II: Top. Studies Oceanog.*, 57(7–8), 663–671.
753 <https://doi.org/10.1016/j.dsr2.2009.10.015>.
- 754 Hazen, E.L., Craig, J.K., Good, C.P., Crowder, L.B., 2009. Vertical distribution of fish biomass
755 in hypoxic waters on the Gulf of Mexico shelf. *Mar. Ecol. Prog. Ser.*, 375, 195–207.
756 <https://doi.org/10.3354/meps07791>.

- 757 Hazen, E.L., Johnston, D.W., 2010. Meridional patterns in the deep scattering layers and top
758 predator distribution in the central equatorial Pacific. *Fish. Oceanogr.*, 19(6), 427–433.
759 <https://doi.org/10.1111/j.1365-2419.2010.00561.x>.
- 760 Hazen, E.L., Jorgensen, S., Rykaczewski, R.R., Bograd, S.J., Foley, D.G., Jonsen, I.D., Shaffer,
761 S.A., Dunne, J.P., Costa, D.P., Crowder, L.B., Block, B.A., 2013. Predicted habitat shifts
762 of Pacific top predators in a changing climate. *Nature Clim. Change*, 3(3), 234–238.
763 <https://doi.org/10.1038/nclimate1686>.
- 764 Herrera-Cervantes, H., Lluch-Cota, D.B., Lluch-Cota, S.E., Gutie, G., 2007. The ENSO
765 signature in sea-surface temperature in the Gulf of California. *J. Mar. Res.*, 65(5), 589–
766 605. <https://doi.org/10.1357/002224007783649529>.
- 767 Hidaka, K., Kawaguchi, K., Murakami, M., Takahashi, M., 2001. Downward transport of
768 organic carbon by diel migratory micronekton in the western equatorial Pacific: Its
769 quantitative and qualitative importance. *Deep Sea Res. Part I: Oceanog. Res. Papers*
770 48(8), 1923–1939. [https://doi.org/10.1016/S0967-0637\(01\)00003-6](https://doi.org/10.1016/S0967-0637(01)00003-6).
- 771 Hidalgo-González, R.M., Alvarez-Borrego, S., 2004. Total and new production in the Gulf of
772 California estimated from ocean color data from the satellite sensor SeaWiFS. *Deep Sea*
773 *Res. Part I: Oceanog. Res. Papers*, 51, 739–752.
774 <https://doi.org/10.1016/j.dsr2.2004.05.006>.
- 775 Hoving, H.-J.T., Gilly, W.F., Markaida, U., Benoit-Bird, K.J., Brown, Z.W., Daniel, P., Field, J.
776 C., Parassenti, L., Liu, B., Campos, B., 2013. Extreme plasticity in life-history strategy
777 allows a migratory predator (jumbo squid) to cope with a changing climate. *Global*
778 *Change Biol.*, 19(7), 2089–2103. <https://doi.org/10.1111/gcb.12198>.

779 Irigoien, X., Klevjer, T.A., Røstad, A., Martinez, U., Boyra, G., Acuña, J. L., Bode, A.,
780 Echevarria, F., Gonzalez-Gordillo, J. I., Hernandez-Leon, S., Agusti, S., Aksnes, D.L.,
781 Duarte, C.M., Kaartvedt, S., 2014. Large mesopelagic fishes biomass and trophic
782 efficiency in the open ocean. *Nature Comm.*, 5, 3271
783 <https://doi.org/10.1038/ncomms4271>.

784 Jin, F.-F., England, M.H., Takahashi, K., Cai, W., Collins, M., Guilyardi, E., Santoso, A.,
785 Timmermann, A., Lengaigne, M., Vecchi, G., Dommenges, D., Wang, G., Wu, L.,
786 McPhaden, M.J., 2015. Increased frequency of extreme La Niña events under greenhouse
787 warming. *Nature Clim. Change*, 5(2), 132–137. <https://doi.org/10.1038/nclimate2492>.

788 Kahru, M., Marinone, S. G., Lluch-Cota, S.E., Pares-Sierra, A., Mitchell, B.G., 2004. Ocean-
789 color variability in the Gulf of California: Scales from days to ENSO. *Deep-Sea Res. II*,
790 51, 139–146. <https://doi.org/10.1016/j.dsr2.2003.04.001>.

791 Kawaguchi, K., Mauchline, J., 1982. Biology of Myctophid fishes (Family Myctophidae) in the
792 Rockall Trough, Northeastern Atlantic Ocean. *Biol. Oceanogr.*, 1(4), 337–373.
793 <https://doi.org/10.1080/01965581.1982.10749447>.

794 Keith, G.J., Ryan, T.E., Kloser, R.J., 2005. ES60adjust. jar. Java software utility to remove a
795 systematic error in Simrad ES60 data. CSIRO Marine and Atmospheric Research,
796 Castray Esplanade, Hobart, Tasmania, Australia.

797 Klevjer, T.A., Irigoien, X., Røstad, A., Fraile-Nuez, E., Benítez-Barrios, V.M., Kaartvedt, S.,
798 2016. Large scale patterns in vertical distribution and behaviour of mesopelagic
799 scattering layers. *Sci. Rep.*, 6, 19873. <https://doi.org/10.1038/srep19873>.

800 Kloser, R.J., Ryan, T.E., Young, J.W., Lewis, M.E., 2009. Acoustic observations of micronekton
801 fish on the scale of an ocean basin: Potential and challenges. *ICES J. Mar. Sci.*, 66, 998–
802 1006. <https://doi.org/10.1093/icesjms/fsp077>.

803 Koslow, J.A., Davison, P., Ferrer, E., Jiménez-Rosenberg, S.P.A., Aceves-Medina, G., Watson,
804 W., 2018. The evolving response of mesopelagic fishes to declining midwater oxygen
805 concentrations in the southern and central California Current. *ICES J. Mar. Sci.* 76(3),
806 626–638. <https://doi.org/10.1093/icesjms/fsy154>.

807 Lavaniegos, B.E., Lara-Lara, J.R., Brinton, E., 1989. Effects of the 1982-83 El Niño event on the
808 Euphausiid populations of the Gulf of California. *Calif. Coop. Ocean. Fish. Invest. Rep.*,
809 30, pp. 73–87.

810 Lavaniegos-Espejo, B.E., Lara-Lara, J.R., 1990. Zooplankton of the Gulf of California Mexico
811 after the 1982 To 1983 El Niño event biomass distribution and abundance. *Pacif. Sci.*,
812 44(3), pp. 297–310.

813 Lavery A.C., Wiebe P.H., Stanton T.K., Lawson G.L., Benfield M.C., Copley N.C., 2007.
814 Determining dominant scatterers of sound in mixed zooplankton populations. *J. Acoust.*
815 *Soc. Am.*, 122, 3304–3326. <https://doi.org/10.1121/1.2793613>.

816 Levitus, S., Antonov, J.I., Wang, J., Delworth, T.L., Dixon, K.W., Broccoli, A.J., 2001.
817 Anthropogenic warming of Earth’s climate system. *Science*, 292, 267–271.
818 <https://doi.org/10.1126/science.1058154>.

819 Lewison, R.L., Crowder, L.B., Read, A.J., Freeman, S.A., 2004. Understanding impacts of
820 fisheries bycatch on marine megafauna. *TREE*, 19(11), 598–604.
821 <https://doi.org/10.1016/j.tree.2004.09.004>.

822 Lluch-Cota, S.E., 2000. Coastal upwelling in the eastern Gulf of California. *Oceanol. Acta*,
823 23(6), 731–740. [https://doi.org/10.1016/S0399-1784\(00\)00121-3](https://doi.org/10.1016/S0399-1784(00)00121-3).

824 Lluch-Cota, S.E., Aragón-Noriega, E.A., Arreguín-Sánchez, F., Aurióles-Gamboa, D., Jesús
825 Bautista-Romero, J., Brusca, R.C., Cervantes-Duarte, R., Cortés-Altamirano, R., Del-
826 Monte-Luna, P., Esquivel-Herrera, A., Fernández, G., Hendrickx, M.E., Hernández-
827 Vázquez, S., Herrera-Cervantes, H., Kahru, M., Lavín, M., Lluch-Belda, D., Lluch-Cota,
828 D.B., López-Martínez, J., Sierra-Beltrán, A.P., 2007. The Gulf of California: Review of
829 ecosystem status and sustainability challenges. *Prog. Oceanogr.*, 73(1), 1–26.
830 <https://doi.org/10.1016/j.pocean.2007.01.013>.

831 Lluch-Cota, S.E., Parés-Sierra, A., Magaña-Rueda, V.O., Arreguín-Sánchez, F., Bazzino, G.,
832 Herrera-Cervantes, H., Lluch-Belda, D., 2010. Changing climate in the Gulf of
833 California. *Prog. Oceanogr.*, 87(1–4), 114–126.
834 <https://doi.org/10.1016/j.pocean.2010.09.007>.

835 MacLennan, D.N., Fernandes, P.G., Dalen, J., 2002. A consistent approach to definitions and
836 symbols in fisheries acoustics. *ICES J. Mar. Sci.*, 59(2), 365–369.
837 <https://doi.org/10.1006/jmsc.2001.1158>

838 Marra, G., Wood, S.N., 2011. Practical variable selection for generalized additive models. *Comp.*
839 *Stat. Data Anal.*, 55(7), 2372–2387. <https://doi.org/10.1016/j.csda.2011.02.004>.

840 Martínez-Soler, E., Gómez-Gutiérrez, J., De Silva-Dávila, R., González-Rodríguez, E., Aburto-
841 Oropeza, O., 2021. Cephalopod paralarval species richness, abundance, and size structure
842 during the 2014–2017 anomalous warm period in the southern Gulf of California. *J.*
843 *Plankton Res.* 43, 224–243. <https://doi.org/10.1093/plankt/fbab010>.

844 Mazerolle, M.J., 2020. AICcmodavg: Model selection and multimodel inference based on
845 (Q)AIC(c). <https://cran.r-project.org/package=AICcmodavg>.

846 McClatchie, S., Dunford, A., 2003. Estimated biomass of vertically migrating mesopelagic fish
847 off New Zealand. Deep-Sea Res. Part I: Oceanogr. Res. Pap., 50(10–11), 1263–1281.
848 [https://doi.org/10.1016/S0967-0637\(03\)00128-6](https://doi.org/10.1016/S0967-0637(03)00128-6).

849 Morales-Bojórquez, E., Nevárez-Martínez, M. O., García-Alberto, G., Villalobos, H., Aguirre-
850 Villaseñor, H., Larios-Castro, E., González-Peláez, S.S., Arizmendiz-Rodríguez, D.I.,
851 Martínez-Zavala, M.Á., 2021. Interaction between marine fauna and the small pelagic
852 fishery in the coastal environment of the Gulf of California, Mexico. Front. Mar. Sci., 8,
853 685. <https://doi.org/10.3389/fmars.2021.669176>.

854 Parrish, R.H., Mallicoate, D.L., Klingbeil, R.A., 1986. Age dependent fecundity, number of
855 spawnings per year, sex ratio, and maturation stages in northern anchovy, *Engraulis*
856 *mordax*. Fish. Bull., 84(3), 503–517.

857 Petatán-Ramírez, D., Ojeda-Ruiz, M. Á., Sánchez-Velasco, L., Rivas, D., Reyes-Bonilla, H.,
858 Cruz-Piñón, G., Mozaira-Luna, H.N., Cisneros-Montemayor, A.M., Cheung, W.,
859 Salvadeo, C., 2019. Potential changes in the distribution of suitable habitat for Pacific
860 sardine (*Sardinops sagax*) under climate change scenarios. Deep Sea Res. Part II: Top.
861 Stud. Oceanogr., 169, 104632. <https://doi.org/10.1016/j.dsr2.2019.07.020>.

862 Polovina, J.J., Howell, E.A., Abecassis, M., 2008. Ocean's least productive waters are
863 expanding. Geophys. Res. Lett., 35, L03618. <https://doi.org/10.1029/2007GL031745>.

864 Polovina, J.J., Abecassis, M.A., Howell, E.A., Woodworth, P., 2009. Increases in the relative
865 abundance of mid-trophic levels fishes concurrent with declines in apex predators in the
866 subtropical North Pacific, 1996-2006. Fish. Bull., 107(4), 523–531.

867 Portela, E., Beier, E., Barton, E.D., Castro, R., Godínez, V., Palacios-Hernández, E., Trasviña,
868 A., 2016. Water masses and circulation in the tropical Pacific off central Mexico and
869 surrounding areas. *J. Physical Oceanogr.* 46, 3069–3081. [https://doi.org/10.1175/JPO-D-16-](https://doi.org/10.1175/JPO-D-16-0068.1)
870 [0068.1](https://doi.org/10.1175/JPO-D-16-0068.1).

871 Portner, E.J., Markaida, U., Robinson, C.J., Gilly, W.F., 2020. Trophic ecology of Humboldt
872 squid, *Dosidicus gigas*, in conjunction with body size and climatic variability in the Gulf
873 of California, Mexico. *Limnol. Oceanogr.*, 65, 732–748.
874 <https://doi.org/10.1002/lno.11343>.

875 Proud, R., Cox, M.J., Brierley, A.S., 2017. Biogeography of the Global Ocean’s mesopelagic
876 zone. *Current Biol.*, 27(1), 113–119. <https://doi.org/10.1016/j.cub.2016.11.003>.

877 R Core Team, 2020. *R: A language and environment for statistical computing*. R Foundation for
878 [Statistical Computing](https://www.R-project.org/). Vienna, Austria.

879 Ritz, D.A., 1994. Social aggregation in pelagic invertebrates. *Adv. Mar. Biol.*, 30, 155–216.
880 [https://doi.org/10.1016/S0065-2881\(08\)60063-2](https://doi.org/10.1016/S0065-2881(08)60063-2).

881 Ritz, D.A., Hobday, A.J., Montgomery, J.C., Ward, A.J., 2011. Social aggregation in the pelagic
882 zone with special reference to fish and invertebrates. *Adv. Mar. Biol.*, 60, 161227.
883 <https://doi.org/10.1016/B978-0-12-385529-9.00004-4>.

884 Robinson, C.J., Avilés-Díaz, L., Gómez-Gutiérrez, J., Salinas-Zavala, C., Camarillo-Coop, S.,
885 Mejía-Rebollo, A., 2014. Hydroacoustic survey of the jumbo squid *Dosidicus gigas* in the
886 [Gulf of California during March and September-October 2010](https://doi.org/10.1016/j.hydrobiologia.2014.03.011). *Hidrobiológica*, 24(1),
887 [39–49](https://doi.org/10.1016/j.hydrobiologia.2014.03.011).

888 Robinson, C.J., Gómez-Gutiérrez, J., Markaida, U., Gilly, W.F., 2016. Prolonged decline of
889 jumbo squid (*Dosidicus gigas*) landings in the Gulf of California is associated with

890 chronically low wind stress and decreased chlorophyll-*a* after El Niño 2009-2010. *Fish.*
891 *Res.* 173(2), 128–138. <https://doi.org/10.1016/j.fishres.2015.08.014>.

892 [Robison, B.H., 1972. Distribution of the midwater fishes of the Gulf of California. *Copeia*,](#)
893 [1972\(3\), 448–461.](#)

894 Roden, G.I., 1964. Oceanographic Aspects of Gulf of California1. In T. H. van Andeld Jr. Shor
895 George G. (Eds.), *Marine Geology of the Gulf of California: A symposium.* Amer. Ass.
896 *Petrol. Geol.* <https://doi.org/10.1306/M3359C2>.

897 Round, F.E., 1967. The phytoplankton of the Gulf of California. Part I. Its composition,
898 distribution and contribution to the sediments. *J. Exp. Mar. Biol. Ecol.*, 1(1), 76–97.
899 [https://doi.org/10.1016/0022-0981\(67\)90008-1](https://doi.org/10.1016/0022-0981(67)90008-1).

900 Rubio-Rodríguez, U., Villalobos, H., Nevárez-Martínez, M.O., 2018. Acoustic observations of
901 the vertical distribution and latitudinal range of small pelagic fish schools in the Midriff
902 Islands Region, Gulf of California, Mexico. *Lat. Amer. J. Aquat. Res.*, 46(5), 989–1000.
903 <http://dx.doi.org/10.3856/vol46-issue5-fulltext-12>.

904 Rykaczewski, R.R., Dunne, J.P., 2011. A measured look at ocean chlorophyll trends. *Nature*,
905 472, E5. <https://doi.org/10.1038/nature09952>.

906 Sánchez-Velasco, L., Avalos-García, C., Rentería-Cano, M., Shirasago, B., 2004. Fish larvae
907 abundance and distribution in the central Gulf of California during strong environmental
908 changes (1997–1998 El Niño and 1998–1999 La Niña). *Deep Sea Res. Part II: Top.*
909 *Studies Oceanogr.*, 51(6), 711–722. <https://doi.org/10.1016/j.dsr2.2004.05.021>.

910 Schukat, A., Bode, M., Auel, H., Carballo, R., Martin, B., Koppelman, R., Hagen, W., 2013.
911 Pelagic decapods in the northern Benguela upwelling system: Distribution,

912 ecophysiology and contribution to active carbon flux. *Deep Sea Res. Part I: Oceanogr.*
913 *Res. Pap.*, 75, 146–156. <https://doi.org/10.1016/j.dsr.2013.02.003>.

914 Staines-Urías, F., Douglas, R. G., Gorsline, D.S., 2009. Oceanographic variability in the southern
915 Gulf of California over the past 400 years: Evidence from faunal and isotopic records
916 from planktic foraminifera. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 284(3–4), 337–
917 354. <https://doi.org/10.1016/j.palaeo.2009.10.016>.

918 Veit, R.R., McGowan, J.A., Ainley, D.G., Wahl, T.R., Pyle, P., 1997. Apex marine predator
919 declines ninety percent in association with changing oceanic climate. *Global Change*
920 *Biol.*, 3(1), 23–28. <https://doi.org/10.1046/j.1365-2486.1997.d01-130.x>.

921 Velarde, E., Ezcurra, E. Anderson, D., 2013. Seabird diets provide early warning of sardine
922 fishery declines in the Gulf of California. *Sci. Rep.*, 3, 1332.
923 <https://doi.org/10.1038/srep01332>.

924 Velarde, E., Ezcurra, E., Horn, M.H., Patton, R.T., 2015. Warm oceanographic anomalies and
925 fishing pressure drive seabird nesting north. *Sci. Adv.*, 1(5), e1400210.
926 <https://doi.org/10.1126/sciadv.1400210>.

927 Weber, E.D., Auth, T.D., Baumann-Pickering, S., Baumgartner, T.R., Bjorkstedt, E.P., Bograd,
928 S.J., Burke, B.J., Cadena-Ramírez, J.L., Daly, E.A., de la Cruz, M., Dewar, H., Field, J.
929 C., Fisher, J.L., Giddings, A., Goericke, R., Gomez-Ocampo, E., Gomez-Valdes, J.,
930 Hazen, E.L., Hildebrand, J., Zeman, S.M., 2021. State of the California Current 2019–
931 2020: Back to the future with marine heatwaves? *Front. Mar. Sci.*, 8, 709454.
932 <https://doi.org/10.3389/fmars.2021.709454>.

933 Wei, T., Simko, V., 2017. R package "corrplot": Visualization of a Correlation Matrix (Version
934 0.84). Available from <https://github.com/taiyun/corrplot>.

935 Weimerskirch, H., Gault, A., Cherel, Y., 2005. Prey distribution and patchiness: Factors in
936 foraging. *Ecology*, 86(10), 2611–2622. <https://doi.org/10.1890/04-1866>.

937 Wolter, K., Timlin, M.S., 1993. Monitoring ENSO in COADS with a Seasonally Adjusted
938 Principal Component Index. *Proceedings of the 17th Climate Diagnostics Workshop*, 52–
939 57.

940 Wood, S., 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of
941 semiparametric generalized linear models. *J. Royal Stat. Soc. Ser. B*, 73(1), 3–36.
942 <https://doi.org/10.1111/j.1467-9868.2010.00749.x>.

943 Woodworth-Jefcoats, P., Polovina, J., Howell, E., Blanchard, J., 2015. Two takes on the
944 ecosystem impacts of climate change and fishing: Comparing a size-based and a species-
945 based ecosystem model in the central North Pacific. *Prog. Oceanogr.*
946 <https://doi.org/10.1016/j.pocean.2015.04.004>.

947 Young, J.W., Hunt, B.P.V, Cook, T.R., Llopiz, J.K., Hazen, E.L., Pethybridge, H.R., Ceccarelli,
948 D., Lorrain, A., Olson, R.J., Allain, V., Menkes, C., Patterson, T., Nicol, S., Lehodey, P.,
949 Kloser, R.J., Arrizabalaga, H., Anela Choy, C., 2015. The trophodynamics of marine top
950 predators: Current knowledge, recent advances and challenges. *Deep-Sea Res. Part II:*
951 *Top. Stud. Oceanogr.*, 113, 170–187. <https://doi.org/10.1016/j.dsr2.2014.05.015>.

952 Zhang, X., Dam, H.G., 1997. Downward export of carbon by diel migrant mesozooplankton in
953 the central equatorial Pacific. *Deep-Sea Res. II*, 44(9–10), 2191–2202.
954 [https://doi.org/10.1016/S0967-0645\(97\)00060-X](https://doi.org/10.1016/S0967-0645(97)00060-X).

955