

1 **Combining seabird diet, acoustics and ecosystem surveys to assess temporal**
2 **variability and occurrence of forage fish**

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10

11 **ABSTRACT**

12 The abundance and distribution of Northern anchovy (*Engraulis mordax*) and young of the year
13 (YOY) rockfish (*Sebastes spp.*) are critical for the survival and reproduction of seabirds,
14 mammals, and predatory fish within the California Current Ecosystem. Traditional detection
15 and quantification of forage fish by trawling can be time consuming and expensive, and may
16 not provide the spatio-temporal resolution needed to examine ecological relationships in
17 quickly-changing marine environments. In an effort to accurately sample forage fish with less
18 expense and higher resolution, this study combined seabird diet and acoustic descriptors to
19 quantify anchovy schools and YOY rockfish in hydroacoustic surveys conducted between 2004
20 and 2015. Anchovy-like schools were selected from echograms assuming a volume
21 backscattering strength (S_v) range of -47.6 to -42.9 dB. YOY rockfish-like single targets were
22 selected considering a target strength (TS) range between -52.8 to -50.9 dB, calculated from a

23 lengths of fish consumed locally by three piscivorous seabirds. Acoustics indices of forage fish
24 were significantly correlated with abundance catches from trawl data collected from an
25 ecosystem assessment survey and relative abundance estimated from breeding seabird diet
26 data. Inter-annual and seasonal indices of forage fish indicated strong anchovy occurrence
27 during 2004-2008 and increased YOY rockfish from 2011-2015. These observations confirm
28 previously described changes in upwelling and forage fish variability off central California.
29 Importantly, these results provide new information on the spatio-temporal variability of the
30 vertical and cross-shelf distribution of anchovy schools and will benefit the design of habitat
31 preference models for anchovy and predators. To verify the acoustics, indices were compared
32 to trawl data from an ecosystem assessment survey and relative abundance estimated from
33 seabird diet data collected from locally-breeding piscivorous seabirds. Results add to the
34 existing knowledge of how these species distribute in the water column, and with regards to
35 anchovy provide insight on how they distribute across the shelf in opposing ocean phases. In
36 addition, acoustic indices derived for both forage fish species showed a significant coherence
37 with both the trawl surveys and seabird diets. Combining acoustic methodologies with trawl
38 data and predator diet can be used to monitor distribution and temporal variability of forage
39 fish species to benefit conservation of top marine predators.

40

41 Keywords: hydroacoustic, acoustic abundance, anchovy, rockfish, seabirds, target strength

42

43 **1. Introduction**

44 Forage fish are an important link between primary producers and higher trophic level
45 predators in pelagic ecosystems (Cury et al. 2000; Pikitch et al. 2014). In upwelling systems,
46 forage fish availability can determine reproductive success and survival of many upper trophic
47 level species (Cairns et al. 1987; Ainley et al. 1993). Forage fish abundance fluctuations often
48 display complex variability that is linked to inter-decadal variability of ocean-climate conditions
49 (e.g., ENSO), such as the well-documented sardine and anchovy regime shifts throughout the
50 world's eastern boundary current ecosystems (Chavez et al. 2003; Bertrand et al. 2008;
51 Schwartzlose et al. 1999). Moreover, the abundance and spatial distribution of these fish is
52 highly variable over shorter time scales, due to a tight coupling with time-varied physical
53 oceanographic processes driving zooplankton and phytoplankton abundance (Vlietstra 2005;
54 Ayón et al. 2008; Swartzman et al. 2008).

55 A key feature displayed by many forage fish species is their tendency to form dense
56 aggregations, or schools during the day and then disperse towards the surface at night to feed
57 (Pitcher and Parish 1993; Fréon et al. 1996; Fréon and Misund 1999; Kaltenberg and Benoit-Bird
58 2009). The spatio-temporal variability of forage fish aggregations are critical to the foraging of
59 dependent predators and important to fisheries and ecosystem management (Cairns 1987;
60 Sydeman et al. 2001; Hilborn 2011; McClatchie et al. 2016), but create challenges in assessing
61 their abundance and patchy distribution patterns with typical trawl surveys. Acoustic-trawl
62 surveys are frequently used to provide insight into forage fish abundance and distribution at
63 large spatial scales in support of population assessment and management (Mais 1974; Barange
64 et al. 1999; Simmonds et al. 2009; Zwolinski et al. 2012). However, such surveys typically

65 estimate abundance at the fish stock or ecosystem level, often with a single survey in any given
66 year, and rarely describe distributions at finer spatial scales (e.g. 10s of km) or across seasons,
67 which may be relevant to understanding interactions with central place (or other) foragers
68 (Churnside et al. 2009). Therefore, acoustic surveys implemented at finer spatial and greater
69 temporal resolution may provide more effective means of evaluating the spatial and temporal
70 variability in forage resources relative to dependent predators.

71 The California Current Ecosystem (CCE) is a highly productive upwelling system, where
72 seasonal winds stimulate upwelling of cold nutrient-rich water, resulting in a rich coastal food
73 web (Checkley and Barth 2009). In the marine food-web off central California, northern
74 anchovy (*Engraulis mordax*) and YOY rockfish (*Sebastes spp.*) play a pivotal role in the overall
75 success of upper trophic level predators (Miller and Sydeman 2004; Ainley et al. 2015;
76 Szoboszlai et al. 2015). Ocean-climate events strongly influence the regional abundance and
77 availability of northern anchovy and YOY rockfish species in the central California Current
78 (Chavez et al. 2003; Santora et al. 2014, 2017). Further, mid-water trawl surveys indicate that
79 northern anchovy tend to display higher relative abundances in years when upwelling is weak,
80 while YOY rockfish display higher abundances when ocean temperature is cool and upwelling is
81 strong (Santora et al. 2014; Ralston et al. 2015). However, this time series is limited in
82 seasonality, and does not survey the entire range (particularly the nearshore margin,
83 shoreward of approximately 50 m bottom depth) of the anchovy stock. Therefore, finer-scale
84 hydroacoustic surveys may provide an effective way of overcoming some of the difficulties
85 posed by the biological and external environmental factors that drive forage fish abundance
86 and variability (Barange et al. 2009).

87 While acoustic studies of krill, also a key forage species that display dense aggregations,
88 are developed in the CCE at high spatial resolutions (Santora et al. 2011; Manugian et al. 2015),
89 acoustic studies describing northern anchovy or YOY rockfish aggregations are not yet available
90 and would aid in better understanding the availability of forage fish to central place foragers.
91 Therefore, combining multiple sampling techniques, involving acoustics, trawl estimates and
92 predator diet, may provide a more complete picture of northern anchovy and YOY rockfish
93 populations, including consistencies or lack thereof among these very different sampling
94 methods (Churnside et al. 2009; Zwolinski et al., 2012).

95 Seabirds are conspicuous predators of marine environments and are sensitive to
96 changes in ocean-climate and availability of prey (Ainley et al. 1995; Furness and Camphuysen
97 1997; Sydeman et al. 2001; Vlietstra 2005; Santora et al. 2014). Seabird demographic
98 parameters are important indicators of forage fish availability (Piatt et al. 2007) and successful
99 reproduction is dependent on the abundance and availability of forage species near their
100 colony (Cairns 1987; Cury et al. 2000). Moreover, seabird diet provides information on the
101 timing and abundance of forage fish species occurrence, making them useful indicators of
102 forage fish availability. In the Gulf of the Farallones, northern anchovy and YOY rockfish
103 between 1.7 and 21 cm in length are the preferred prey items for many breeding seabirds
104 (Ainley et al. 1993; Elliott et al. 2016), and previous studies have demonstrated strong
105 correlations between fishery survey abundance estimates and the fraction of preferred prey in
106 diets (Mills et al. 2007).

107 Herein, we conduct an assessment using a combination of seabird diet, hydroacoustics,
108 and night-time mid-water trawl surveys, to evaluate the seasonal and inter-annual variability of

109 the occurrence of relative forage fish abundance and distribution off central California. We
110 quantify acoustic descriptors designed to classify forage fish schools and determine the
111 presence of anchovy-like schools and YOY rockfish-like single targets during 2004-2015. *TS*
112 methods rather than *S_v* methods were used to classify YOY rockfish, due to the lack of sufficient
113 details describing acoustic aggregations of YOY rockfish. Specifically, we test the hypothesis that
114 acoustic-derived estimates, as indicated by anchovy-like density measurements and population
115 counts of YOY rockfish-like single targets, will reflect known variability of anchovy and YOY
116 rockfish abundance as indicated by independent mid-water trawl surveys and the diet of three
117 seabird species. Our objectives were to: (1) assess the relative acoustic density of northern
118 anchovy and abundance of prey sized YOY rockfish; 2) examine seasonal and inter-annual
119 trends in the relative acoustic density of northern anchovy and prey sized YOY rockfish; and 3)
120 compare the relative acoustic fish estimates with independent metrics from night-time trawl
121 surveys and seabird diet studies. We discuss how our assessment benefits the monitoring
122 distribution of forage fish species off central California and how the results provide new
123 opportunities for studying the foraging ecology of seabirds breeding on the Farallon Islands
124 relative to their temporal and spatial distributions.

125

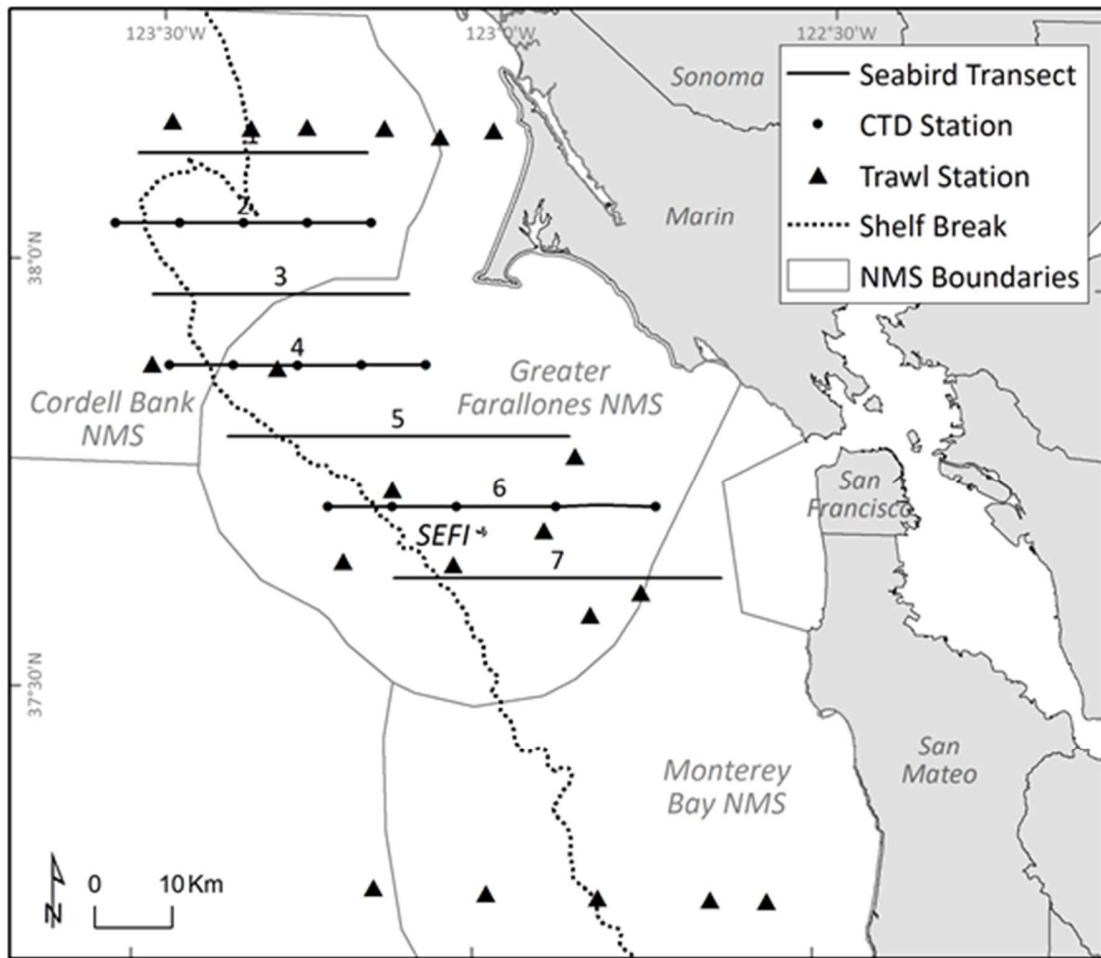
126 **2. Methods**

127 **2.1 Geographical setting and study area**

128 The Farallon Islands, located within the Gulf of the Farallones off central California, are
129 home to the largest seabird colony in the continental U.S. south of Alaska (Ainley and
130 Boekheilde 1990). Located on the continental shelf and adjacent to a steep shelf-break, the

131 archipelago comprises 50 hectares of critical breeding and resting habitat for seabirds and
132 pinnipeds. Other important geomorphic features include Cordell Bank, a seamount comprised
133 of rocky reef and other hard substrate habitat, and the Point Reyes headland, which together
134 influence ocean currents and biological activity in the region (Chin et al. 1997; Ryan et al. 2010;
135 Santora et al. 2012). The continental slope to the west of Farallon Islands is characterized as
136 highly irregular bathymetry and dissected by submarine canyons and gullies that begin at the
137 shelf break, providing a diverse complex of marine habitats (Chin et al. 1996; Santora et al.;
138 2012). During the upwelling season, cold nutrient rich waters are retained on the lee side of
139 prominent headlands resulting in upwelling shadows (Wing et al. 1998), and a high
140 concentration and retention of phytoplankton, zooplankton, forage fish, seabirds and marine
141 mammals (Largier et al. 2006; Ryan et al. 2010; Santora et al. 2012).

142 The Farallon Islands and Cordell Bank are key features of a highly unique ecosystem and
143 serve as the center points of the Greater Farallones (GFNMS) and Cordell Bank (CBNMS)
144 National Marine Sanctuaries. We analysed hydroacoustic data collected by the Applied
145 California Current Ecosystem Studies (ACCESS; www.accessoceans.org), a partnership between
146 Point Blue Conservation Science (Point Blue), GFNMS, and CBNMS. ACCESS implements an
147 annual sampling scheme designed to monitor marine birds and mammals, fish and zooplankton
148 abundance, and surface and water column properties within the sanctuaries during daylight
149 hours. Data included in this study were collected from April - October, 2004 - 2015. Fixed East-
150 west transect lines (n=7) were sampled, and spanned the continental shelf and slope region
151 (defined by the 20 m to the 1000 m isobaths, respectively), covering the offshore area between
152 Bodega Bay (38.3° N) and San Pedro Rock (37.6° N) (Figure 1).



153

154 Figure 1. Map showing the study area including seabird transect lines and oceanographic
 155 stations visited by the Applied California Current Ecosystem Studies (ACCESS), the location of
 156 Southeast Farallon Island (SEFI), and trawling stations visited by the Rockfish and Recruitment
 157 Ecosystem Studies cruises in their core study area in central California (NOAA-NMFS).
 158

159 **2.2 Fish sampling using seabird diets**

160 Seabird diet was collected on the Southeast Farallon Island, Farallon National Wildlife
161 Refuge, from three piscivorous seabirds: common murre (*Uria aalge*), rhinoceros auklet
162 (*Cerorhinca monocerata*), and Brandt's cormorant (*Phalacrocorax penicillatus*). Data collection
163 methods differed amongst species. Common murre diet were collected 4-5 times weekly during
164 the chick rearing period from 2000-2015 (Roth et al. 2008). The murre chick rearing period lasts
165 approximately 4 to 6 weeks beginning when chicks hatch in late May and ending when most
166 chicks have departed the colony in late June or early July (Roth et al. 2008). During two-hour
167 observation periods, feeding frequency and diet composition of chicks were recorded to the
168 lowest possible taxon based on morphological characteristics and location of the fins (Miller
169 and Lea 1972; Sydeman et al. 2001; Miller and Sydeman 2004; Roth et al. 2008). The size of
170 each prey item was visually estimated relative to the gape length and transformed to standard
171 length (see Roth et al. 2008 for details). Rhinoceros auklet diet was collected weekly using mist
172 nets to capture auklets returning to provision their young during June to July. Fish dropped
173 from their bill were collected, measured for standard length and identified to species (Thayer
174 and Sydeman 2007). Brandt's cormorant diet was determined from regurgitated pellets
175 collected from three main breeding sites on the island (Elliott et al. 2015, 2016). Pellets were
176 dissected for fish otoliths, and were measured and identified to the lowest taxonomic level
177 possible. Species-specific regression equations were applied to otolith measurements to
178 estimate prey lengths (Elliott et al. 2015, 2016).

179

180 **2.3 Hydroacoustic data collection and processing**

181 Hydroacoustic data were collected aboard three research vessels: R/V John H. Martin
182 (17 m), Ship McArthur II (60 m), and R/V Fulmar (20 m). Each vessel used in this study was
183 equipped with multi-frequency split-beam echo-sounders (Simrad EK-60) with an array of 38,
184 120, and 200 kHz transducers (calibrated each spring using a 38.1 mm tungsten carbide sphere)
185 (Demer et al. 2015). Acoustic absorbance (Francois and Garrison 1982) and sound speed
186 (Mackenzie 1981) used in acoustic processing were calculated for each monthly survey using
187 mean temperature and salinity in the top 25 m of the water column found from CTD casts.
188 Vessel speed was approximately 10 knots (5.2 ms) during surveys, and the echo-sounders
189 synchronously transmitted 1.024 ms pulses vertically through the water column. To sample
190 forage fish, data were collected every 2 seconds along transects, with raw data captured from
191 the minimum depth of the transducer face to at least 300 m. To avoid potential surface noise
192 (e.g. wave generated bubbles) and to account for near field effects, the upper 5 m of the water
193 column were excluded from analysis. In addition, we excluded processing in a zone of 2 - 5 m
194 from the bottom in a manual process that depended on degree bottom depth variability. This
195 method was designed to exclude strong bottom echoes from rocky substrate and pinnacles that
196 intermingled with biological signals and could not be separated. Acoustic data captured during
197 off transect periods, such as when oceanographic and zooplankton data were being collected,
198 were also removed from analysis. Acoustic data consisted of: volume backscattering strength
199 (S_v) (dB re 1 m⁻¹), which is a measure of the total amount of sound backscattered from 1 m³ of
200 water, and target strength (TS) (dB re 1 m²), representing the amount of sound backscattered
201 by a single target based on its material properties and orientation. Acoustic data collection time
202 and location were indexed using a GPS input into the echo-sounder.

203 Acoustic data for each cruise were independently uploaded and analysed using the
204 program Echoview Version 7 (Echoview Software Pty Ltd, Hobart, Tasmania, Australia), which
205 visualizes raw acoustic data into absolute measurements of backscatter for analysis. With all
206 acoustic data collected at sea, there is associated background noise which can't be attributed to
207 biological organisms or other water column sources. Background noise was reduced by
208 generating and subtracting time varied noise from all raw S_v and TS echograms (Hewitt et al.
209 2004). The level of noise reduction was adjusted by visually comparing echograms until the
210 signal to noise ratio (SNR) at depth appeared to be equal (Hewitt et al. 2004).

211

212 **2.4 Acoustic anchovy-like school detection**

213 To discriminate potential fish aggregations from zooplankton a dual frequency analysis
214 was conducted between $S_{v120kHz}$ and S_{v38kHz} . Fish with swim bladders tend to display as intense
215 scattering features at S_{v38kHz} , while zooplankton tend to display as intense scattering features at
216 $S_{v120kHz}$ (Fielding et al. 2012). By selecting a dB difference of S_v 8-23 dB between the two
217 frequencies, we were able to positively mask, bin, and remove a considerable number of
218 scattering features from the S_{v38kHz} data that could not be attributed to fish aggregations
219 (Manugian et al. 2015). The resulting echogram was then restricted with a S_v threshold range
220 between -60 and -38 dB, to remove low intensity targets such as plankton layers and to avoid
221 incorporating non-linear acoustic effects that results in multiple scatters from an individual
222 target within densely packed schools, respectively. The S_v maximum threshold level of -38 dB
223 was manually selected by examining densely packed schools for each cruise and year
224 independent from one another. We then detected acoustic schools by using the "school

225 detection module” to make measurements of acoustic descriptors. The module uses algorithms
226 derived from the Shoals Analysis and Patch Estimation System (SHAPES) (Barange 1994;
227 Coetzee 2000). The algorithms consider the echogram as a matrix of energy backscatter
228 measurements and acoustic samples. It then examines the data for contiguous acoustic
229 samples spatially based on user defined minima. We first set morphometric parameters based
230 on school length and height. A minimum school length was set at 10 m with a minimum
231 candidate length of 5 m. Minimum school height was set at 3 m with a minimum candidate
232 height of 2 m (Lawson et al. 2001; Kaltenberg and Benoit-Bird 2009). The module then draws an
233 ellipse around contiguous data points to identify schools meeting the length and height criteria
234 (Lawson et al. 2001; Vlietstra 2005). In order for schools in close proximity to each other to be
235 linked as one, they had to meet linking distance criteria, which was set at 20 m horizontally and
236 10 m vertically (Lawson et al. 2001; Kaltenberg and Benoit-Bird 2009). In some survey years, the
237 module detected large indeterminate aggregations, likely representing low intensity plankton
238 and fish scattering layers. These aggregations were considered not to be acoustic fish schools
239 and were removed from the analysis (Lawson et al. 2001). Schools that met these criteria were
240 classified as fish schools, and their acoustic descriptors were exported for further analysis.

241 Anchovy behaviour and schooling morphology have been found to vary enough from
242 other similar schooling species that it is possible to discriminate between them using a variety
243 of acoustic descriptors (Haralabous and Georgakarakos 1996; Lawson et al. 2001; Robotham et
244 al. 2010). Mean S_v is one acoustic descriptor that aids in the discrimination of anchovy, from
245 other schooling species such as sardine (*Sardinops sagax*), and round herring (*Etrumeus*
246 *whiteheadi*) (Lawson et al. 2001). S_v aids in discrimination due to the schooling characteristics of

247 the observed species and its' subsequent energetic response (i.e. mean S_v). Using discriminate
248 function analysis, Lawson et al. (2001) found that anchovy had a S_v mean of -42.8 dB (SE \pm 0.69)
249 within a region of the Benguela Current. However, we found that using an upper threshold of S_v
250 -38 dB excluded the densest regions of schools, and shifted the S_v properties of these schools
251 by an average of -2 dB. For this reason, we derived a 99% Confidence Interval (CI) around the S_v
252 mean of -44.8 dB (SE \pm 0.69), and used a S_v range of -47.6 to -42.02 dB to select a subset of
253 schools meeting these criteria. With the understanding that anchovy are not the only schooling
254 fish species in the CCE and the lack of collaborative net samples, we made an effort to visually
255 confirm anchovy schools in the raw echograms by using the following definition: acoustic
256 anchovy fish schools are described as strong scattering features that display discrete and
257 continuous edges and which are distinct from loosely aggregated fish layers (Kaltenberg and
258 Benoit-Bird 2009), and are pelagic (e.g. showing a clear distinction between the school and the
259 seafloor). If detected schools met both the S_v and physical characteristics, they were classified
260 as anchovy-like and were selected for further analysis. The acoustic school classification process
261 for anchovies was repeated separately for each cruise and enumerated all schools detected.
262 The following school descriptors were exported: nautical area scattering coefficient (s_A), height,
263 length, depth, bottom depth, survey effort, skewness, and kurtosis of each school in each
264 survey. s_A is a measure of density which provides an indication of relative abundance
265 (Kaltenberg and Benoit-Bird 2009) and is defined as square meters per square nautical mile (m^2
266 nmi^{-2}) (Maclennan et al. 2002). Furthermore, to provide spatial context anchovy-like school
267 distribution was mapped.
268

269 2.5 YOY rockfish-like target detection and classification

270 Following the methods for anchovy-like schools, we first conducted a dual frequency
271 analysis between $S_{v120kHz}$ and S_{v38kHz} to remove zooplankton. The resulting echogram was
272 converted into a single targets echogram, wherein single targets are represented as a peak in TS
273 (dB). In order to classify single targets as YOY rockfish, a length range based on the 95% CI of
274 YOY rockfish lengths observed in seabird species diet was used to calculate a TS range.
275 Estimation of YOY rockfish TS values were calculated using the following length dependent
276 model: $TS_{38kHz} = 20 \times \text{Log}_{10}(L) - b$; where L is the standard length of the fish and b (-67.7) is a
277 species-specific value for the intercept (Kang and Hwang 2003; Simmonds and MacLennan
278 2005). The coefficient b in the model, is determined by a least-squares fit of the mean TS
279 against the individual fish lengths (Kang and Hwang 2003). This equation provides a curved
280 distribution of the mean TS against the fish lengths of rockfish species that matches the TS of
281 rockfish in ex-situ experiments (Kang and Hwang 2003). The resulting target strength range of -
282 52.8 to -50.9 dB is fairly narrow compared to the range of TS that a single live fish may exhibit
283 at different orientations, however by restricting our TS range to this we are less likely to
284 mistakenly classify non-rockfish targets (see Method Caveats).

285 For a peak to be considered a single target, we first defined the pulse envelope with the
286 following criteria: 1) we set a peak TS threshold of -70 dB based on the values generated from
287 the length dependent model; 2) we used a 6 dB pulse length determination level, which is the
288 number of decibels below the peak that determines the pulse envelope; 3) the pulse length was
289 normalized by taking the received pulse length and dividing by the transmitted pulse length,
290 and then assigned a minimum of 0.6 and a maximum of 1.5; 4) we then corrected for

291 transducer directivity by selecting a maximum beam compensation of 6 dB; and 5) to ensure all
292 point scatters were within the measured pulse length contributing to a single target, all
293 measured samples had to be within 0.6 standard deviations of the major and minor axis angles.
294 If the target met these criteria, it was exported into a database for calculating total targets
295 detected for each survey. The process of single target detection for YOY rockfish-like targets
296 was repeated for each cruise and effort was recorded in the form of nautical miles (nmi)
297 surveyed. Detected single targets were then summed in the following depth layers: 5 to 15 m,
298 15 to 25 m, 25 to 35 m, 35 to 45 m and 45 to the maximum depth. Individual YOY rockfish-like
299 targets were not mapped because they were too numerous.

300

301 **2.6 Acoustic considerations and fish life-history**

302 The acoustic methods for anchovy-like school classification are restricted to densely-
303 packed schools observed during day light hours. Variability in school density is expected
304 however schools outside of our anchovy detection S_v range could bias our results low. False-
305 positive identification and the inclusion of mixed species fish schools are also possible, and
306 maybe biasing our indices (Lawson et al. 2001). Lawson et al. (2001) estimated that using S_v as a
307 primary descriptor for discriminating between species during day light hours had a success rate
308 of 80.8%. However, the life-history of other abundant fishes in the Gulf of the Farallones may
309 minimize false positive classification. The other two fish species with catch abundances in the
310 same order or magnitude as anchovy (and YOY rockfish) are YOY Pacific hake and YOY Pacific
311 sanddab (Sakuma 2017). The Pacific sanddab is benthic-oriented beyond the larval phase
312 (Sakuma and Larson 1995), when their size (and therefore potentially their target strength)

313 might overlap with YOY rockfish. Pacific hake may form dense daytime schools, but avoid light
314 during the day (Alverson and Larkins 1969; Bailey et al. 1982) making their distribution deeper
315 than typical daytime anchovy schools (ranging from the surface to less than 200m; Mais 1974),
316 and likely more pelagic than much of our shelf-habitat study area. The Pacific sardine may form
317 schools that acoustically resemble anchovy schools (Lawson 2001; Kaltenberg and Benoit-Bird
318 2009), and indeed may be the largest source of fish school misclassification error in our study,
319 however sardine schools are described by mean S_v values over an order of magnitude higher
320 (Lawson 2001). Typical adult and larger juvenile sardine schools should then be excluded by
321 our S_v range filter. Furthermore, sardine catch abundance was more than an order of
322 magnitude less than anchovy during the period of our study (Sakuma 2017).

323 Individual target strength data is highly susceptible to the angle of incidence of a fish in
324 an acoustic beam. The slightest tilt in angle can result in a drastically different TS when
325 compared to a mean range calculated from a length dependent model (Kang and Hwang 2003;
326 MacLennan & Simmonds 2013). Therefore, using the entire range of TS envelopes that our
327 target species are capable of producing is not practical in an environment with such high
328 diversity of fish species. The TS range selected was not meant to have a high classification rate,
329 but rather relied upon the broad spatial coverage of the acoustic data, and the relatively high
330 abundance of YOY rockfish compared to other similarly sized species (Sakuma 2017).
331 Furthermore, the TS range selected was meant to gather a representative sample of the
332 populations available to the seabirds as prey. Following this approach may have also resulted in
333 an underestimation of relative abundance, especially of smaller YOY rockfish earlier in the

334 season (as YOY rockfish grow rapidly following parturition in the winter of any given year). We
335 acknowledge this restrictive approach excludes many juvenile rockfish from our analysis.

336

337 **2.7 Ecosystem assessment surveys**

338 Catch data on YOY rockfish and anchovy were derived from the NOAA-NMFS Rockfish
339 Recruitment and Ecosystem Assessment trawl surveys conducted off central California (Ralston
340 et al. 2013; Sakuma et al. 2016). Surveys were conducted in May and June during the night
341 using a modified Cobb mid-water trawl. Trawl samples were taken 2-3 times per year and for 15
342 minute durations at each trawling station in each study region (Figure 1). The catch data from
343 the core region overlaps with our study area and were used for comparison with the relative
344 acoustic fish abundance estimates from this study. The number of trawling tows ranged
345 between 12 in 2008 to 42 in 2007, with an average of 28 tows being conducted per year. NOAA-
346 NMFS standardized abundance (catch-per-unit-effort; CPUE) indices for anchovy and YOY
347 rockfish were calculated relative to the average catch (log+1 transformed) for surveys
348 conducted from 2004 to 2015.

349

350 **2.8 Analysis**

351 Relative abundance estimates derived from the seabird diets served as an independent
352 set of data to test whether a Pearson correlation existed with estimates derived from the
353 acoustic analysis. Diet composition for each species was calculated and chi-squared tests were
354 performed to examine differences in anchovy and YOY rockfish consumption between years.
355 Length frequency distributions of fish consumed by each seabird species were calculated to

356 provide context on variability of fish size selected by seabirds. Analysis of Variance (ANOVA)
357 tests were conducted to examine differences in lengths of fish consumed by seabirds between
358 years and among species. Relative acoustic fish abundance estimates were scaled for anchovy-
359 like s_A and YOY rockfish-like single targets relative to sampling effort in nautical miles for each
360 cruise. The indices were calculated as the mean $s_A \text{ nmi}^{-1}$ of anchovy-like schools and mean
361 number of single targets nmi^{-1} of YOY rockfish-like targets during April to July. This time period
362 overlaps the time at which the NOAA-NMFS surveys occur (Figure 1), and the time when
363 breeding seabirds deliver fish to chicks at SEFI. Seasonal and inter-annual trends were
364 examined in anchovy-like s_A relative to effort and amongst the other exported school
365 descriptors. ANOVA tests were performed to test for significant differences in s_A , depth of the
366 schools and associated bottom depth between years and months. Regression analysis was used
367 to assess for linear and non-linear trends between s_A relative to year and month. We then
368 examined overall seasonal and inter-annual trends in the effort-corrected number of YOY
369 rockfish-like single targets. ANOVA tests were performed to assess significant differences in
370 total number of YOY rockfish-like targets (per nmi^{-1}) between years and months, and regression
371 analysis to assess for linear and non-linear trends in YOY rockfish-like targets nmi^{-1} across years
372 and months.

373 The independent observations of seabird diet, acoustics, and mid-water trawl surveys
374 allow for the evaluation of forage fish availability and specifically, the efficacy of using acoustics
375 to monitor forage fish. Standard anomalies of acoustics were calculated and compared with
376 indices from the mid-water trawl survey and seabird diets. Anomalies were calculated by
377 subtracting the long-term mean from each year's average and dividing it by the standard

378 deviation. Anomalies of anchovy and YOY rockfish from mid-water trawls surveys were derived
379 from Sakuma et al. (2016). Seabird diet data time series are represented by the proportion of
380 anchovy and YOY rockfish in the diets of common murre, rhinoceros auklet and Brandt's
381 cormorant for each year. Pearson correlation was used to compare the relative acoustic fish
382 abundance standardized anomalies with mid-water trawl and seabird diet anomalies. We used
383 regression and multi-regression analyses to determine what proportion of the variability
384 observed in the mid-water trawl surveys and seabird diet anomalies could be explained by the
385 relative acoustic fish abundance anomalies. Analyses were conducted separately for anchovy-
386 like acoustic densities and prey sized YOY rockfish-like relative abundance estimates.

387

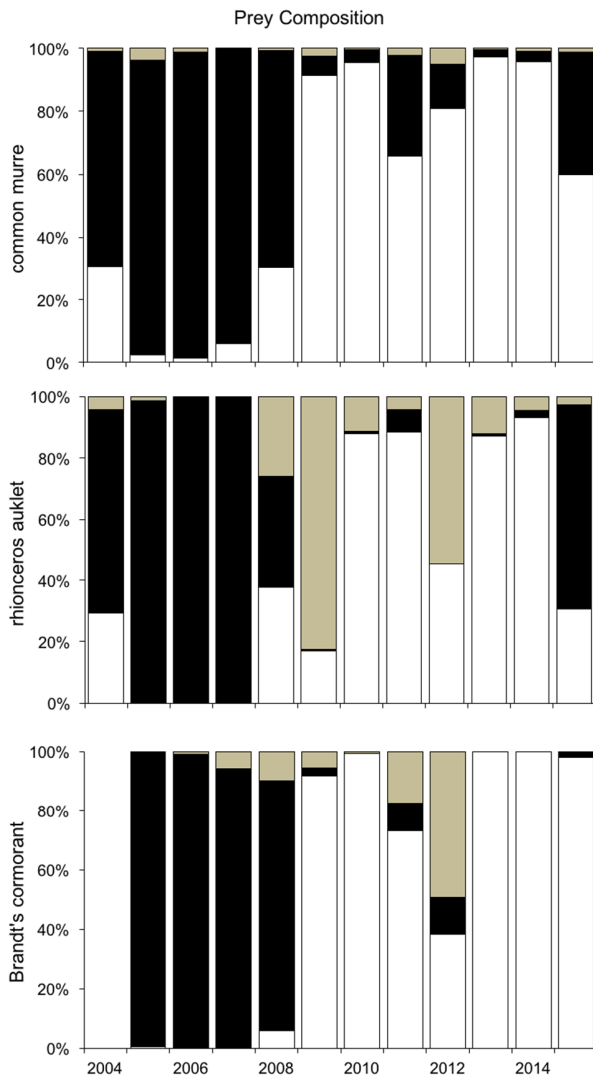
388 **3. Results**

389 **3.1 Fish sampling using seabird diets**

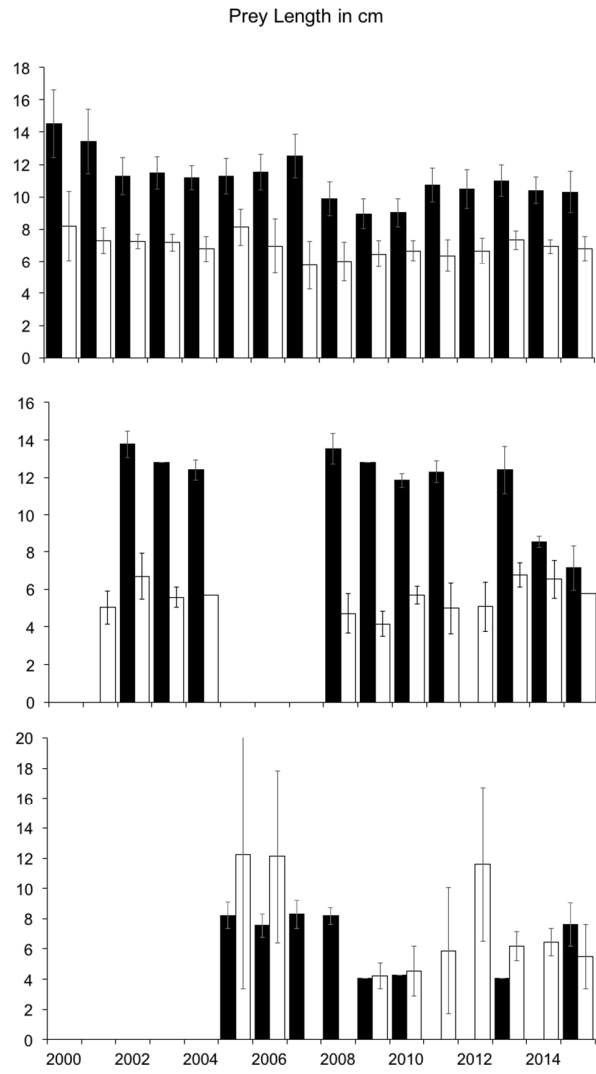
390 Anchovy and YOY rockfish were the predominant fish species observed in the seabird
391 diets, however we found significant annual differences in the proportions consumed by
392 common murre ($\chi^2 = 19,872$, $df = 11$, $p < 0.001$), Rhinoceros auklet ($\chi^2 = 1,549$, $df = 11$, $p <$
393 0.001), and Brandt's cormorant ($\chi^2 = 13,835$, $df = 9$, $p < 0.005$) (Figure 2). Anchovy was the
394 dominant prey from 2004 to 2008, and accounted for approximately 60% to 96% of the birds'
395 diets during this time period. YOY rockfish accounted for approximately 6% to 97% and was the
396 dominant prey from 2009 to 2015. Pacific Saury (*Cololabis Saira*) was a primary prey in the
397 rhinoceros auklet diet from 2009 to 2012, and sanddabs (*Citharichthys spp.*) in Brandt's
398 cormorant diet in 2011 and 2012.

399

400 a.



b.



401

402 Figure 2. Diet composition for common murre, rhinoceros auklet, and Brandt's cormorant by
403 year are depicted in the figures labeled (a). White bars represent juvenile rockfish, black
404 represents anchovy, and grey represents all other prey consumed. Figures labeled (b) represent
405 prey sizes (\pm SE) consumed by the seabirds by year. Years without bars represent years where
406 anchovy and juvenile rockfish were not present in the diet of the birds. No data was collected
407 for Brandt's cormorant in 2000 and 2001.

408

409

There were significant differences in the size of anchovy and YOY rockfish consumed

410

among years (ANOVA: $p < 0.001$) and YOY rockfish were significantly smaller in size than

411

anchovy for all seabirds (Table 1, ANOVA).

412

Prey Length								
Bird species	Length 95% CI YOY rockfish	N	Mean		Length 95% CI northern anchovy	N	Mean	
				±SE				±SE
Common murre	6.92 to 6.94	27,775	6.93	0.004	11.43 to 11.5	10,159	11.38	0.02
Rhinoceros auklet	5.57 to 5.75	996	5.89	0.03	12.59 to 12.79	614	12.69	0.05
Brandt's cormorant	5.74 to 6.01	1,172	5.88	0.06	7.86 to 8.24	146	8.06	0.09

ANOVA			
	df	F	P <
Common murre	39,925	86,080.8	0.001
Rhinoceros auklet	2,167	1,820.8	0.001
Brandt's cormorant	1,318	59.8	0.005

413

414 Table 1. Provides 95% CI's of YOY rockfish and northern anchovy sampled in the three seabirds' diets,
 415 number of samples collected, the mean length, and the standard error. The bottom left of the table
 416 shows the ANOVA results showing that YOY rockfish were significantly smaller in size than northern
 417 anchovy consumed by the birds.

418

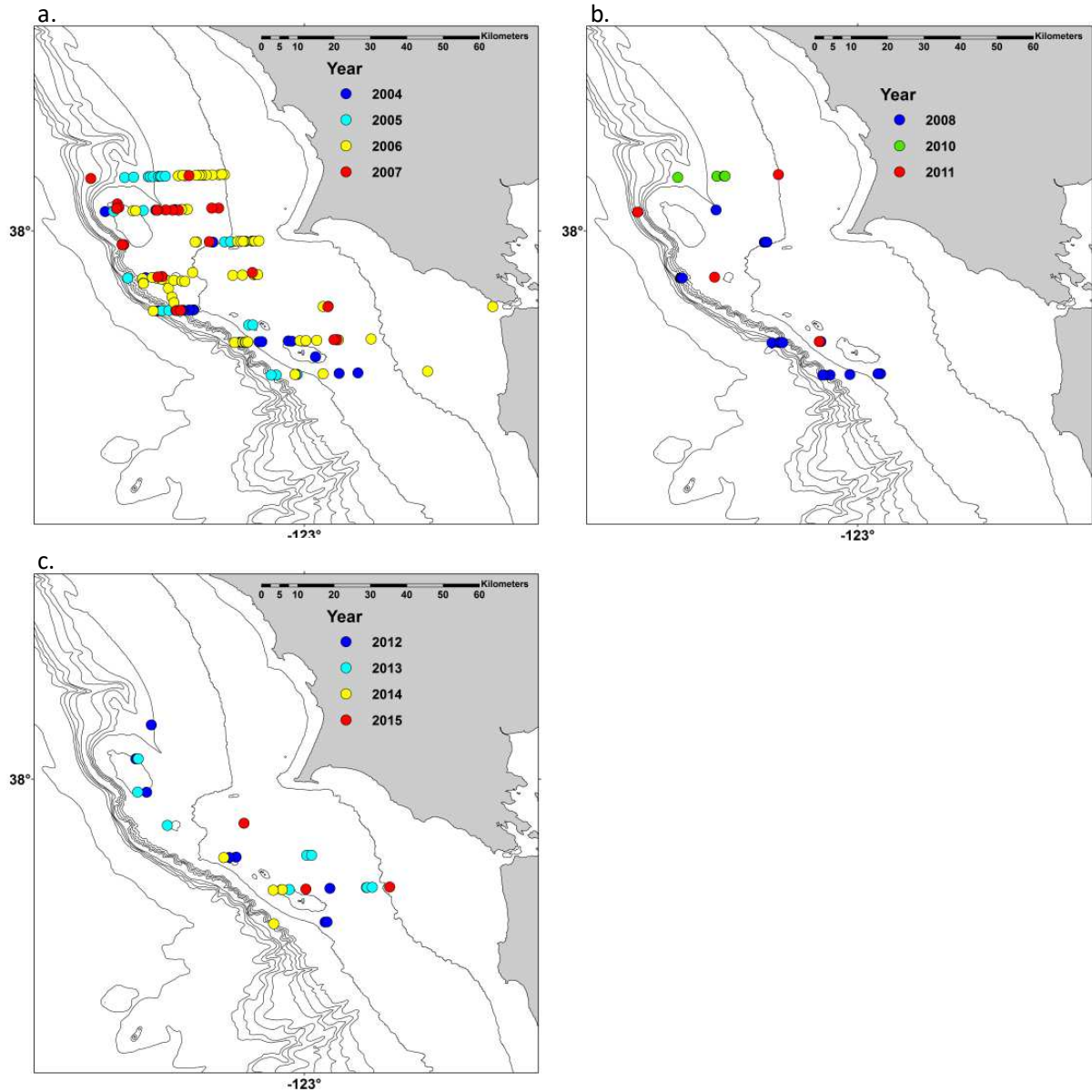
419 To estimate an appropriate *TS* value for YOY rockfish, a mean length range of 5.57 to
 420 6.94 was input into the length dependent model described in the methods, which output a *TS*
 421 range between -50.9 to -52.8 dB. While the fish length range used is tighter than would have
 422 been expected if using all observed intra and inter-annual variability in YOY rockfish length, it
 423 provides a narrow *TS* range for acoustic detection of prey-sized fish.

424

425 3.2 Acoustically observed anchovy schools

426 The school detection process resulted in 39,494 aggregations identified, 1,551 met the
 427 S_v requirement to be considered for visual inspection, and 208 schools passed the visual

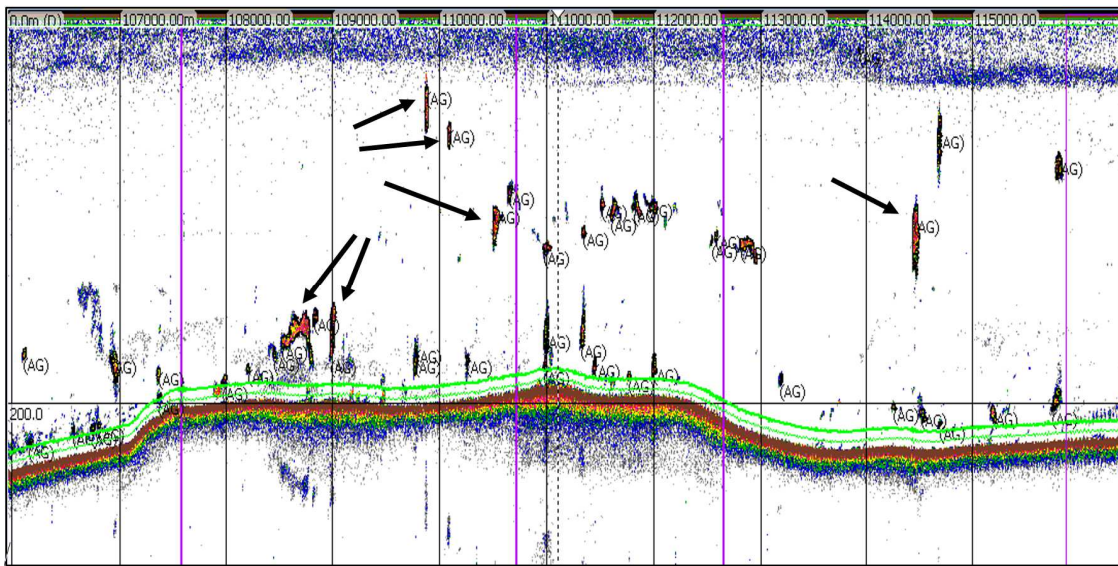
428 confirmation (Table S.1, Figures 3 and 4). Some schools, while still conforming to the visual
429 description, formed complex assemblages that covered large spatial areas (Figure 4).



430

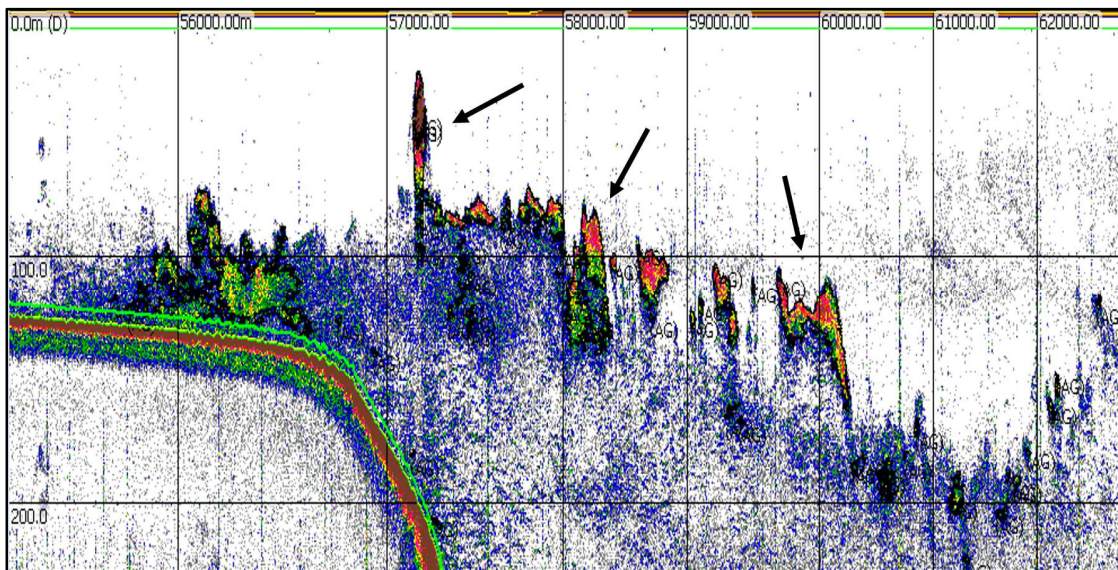
431 Figure 3. Spatial distribution of detected anchovy-like schools (n=208) partitioned into 3 time
432 periods for clear viewing, ranging from schools detected during (a) 2004-2007, (b) 2008-2011
433 (no schools were detected in 2009), and (c) 2012-2015.
434

435 a.



436

437 b.



438

439 Figure 4. Sections of an echogram in raw volume backscatter data showing acoustic fish schools
440 defined as strong scattering features that display discrete and continuous edges. The top
441 echogram shows several small anchovy-like schools included throughout the water column
442 from June 2008, and the bottom shows a large assemblage of schools near the shelf break from
443 July 2006. The top of the echogram represents the surface of the ocean. The sea floor is the
444 intense brown scattering feature at the bottom of the echogram and the upper green lines just
445 above represent the 2 and 5 meter integration stop lines. Black arrows indicate anchovy-like
446 schools as defined in the methods and that were included in the analysis.

447 Mean volume backscatter from the schools ranged from S_v -42.9 to -47.6 dB, with a S_v mean of -
 448 45.7 dB. Heights of schools varied between 1.2 and 36.2 m, with a mean of 9.3 m. The lengths
 449 of schools ranged from 4.2 to 2,074.1 m, with a mean of 125.2 m. Our acoustic descriptors of
 450 the 208 anchovy-like schools detected were larger, in deeper depths, and contained a slightly
 451 different S_v mean value than Lawson et al. (2001; Table S.2).

452

Anchovy-like Schools Detected During April and October											
Regression ANOVA											
Descriptor	N	Series	df	β	F	P <	Series	df	β	F	P <
School s_A nmi^{-1}	208	year	40	-64.0	5.61	0.023	month	40	-	0.12	0.74
School Depth	208	year	40	-	0.11	0.74	month	40	-	0.02	0.89
Bottom Depth	208	year	40	-	1.96	0.17	month	40	-	0.27	0.61

Anchovy-like Schools Detected During April and July											
Regression ANOVA											
Descriptor	N	Series	df	β	F	P <	Series	df	β	F	P <
School s_A nmi^{-1}	156	year	27	-65.1	4.20	0.051	month	27	-	0.08	0.78

453

454 Table 2. The top half of the table shows anchovy-like acoustic descriptors, number of schools detected
 455 between April and October, and regression ANOVA results showing a significant difference between
 456 years for s_A nmi^{-1} , but not for month. There were no significant differences between mean school depth,
 457 and bottom depth for both years and months. The bottom half of the table shows anchovy-like s_A nmi^{-1} ,
 458 number of schools detected between April and July, and regression ANOVA results showing significant
 459 differences in s_A nmi^{-1} between years, but not months.

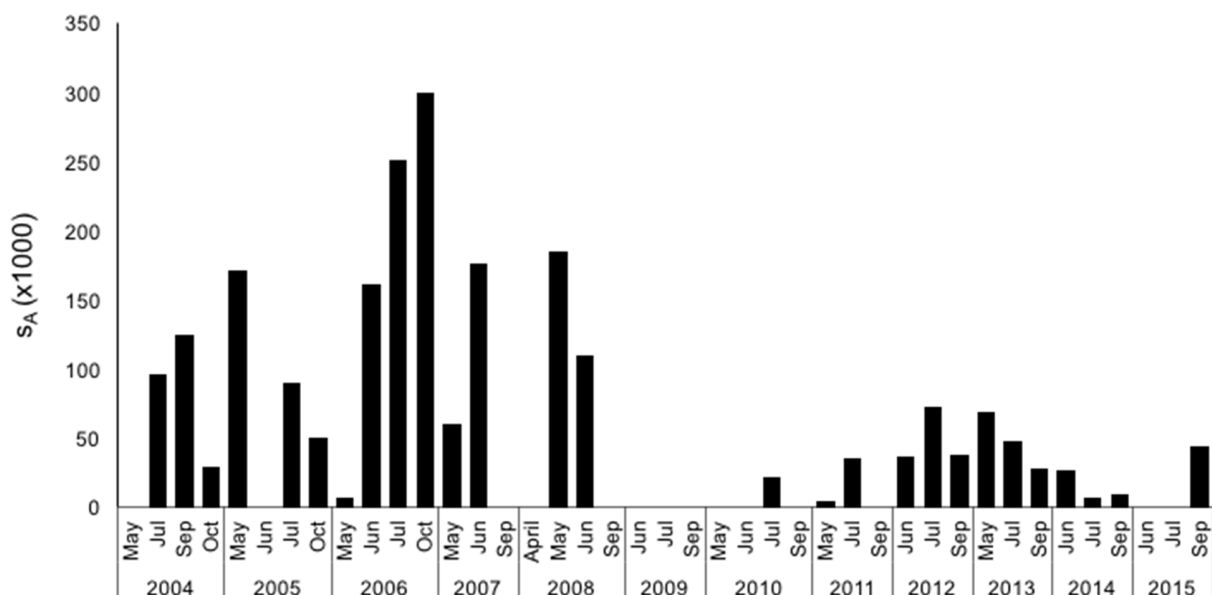
460

461 There were significant differences in s_A between years, but not months (Table 2).

462 Schools detected in 2006 covered a total area of 720,617 m^2 nmi^{-2} with an average of 1,163
 463 m^2 nmi^{-1} being detected along transects, while anchovy-like schools detected in 2010 and 2015
 464 represented the lowest total spatial coverage of the time series (Figure 5 and S.3). The number
 465 of schools detected nmi^{-1} in the months of May, June, July, September, and October was 0.04,
 466 0.07, 0.03, 0.02, and 0.12, respectively. On average, anchovy-like s_A was greatest during the
 467 month of October, with an average of 1,274 m^2 nmi^{-1} detected along transects. However,

468 October was only surveyed between 2004 and 2006. Surveys during September resulted the
 469 lowest average of anchovy-like coverage, with s_A 224 $\text{m}^2 \text{nmi}^{-1}$ detected along transects.

470 There were no significant differences in school depth between years and there was no
 471 difference in associated bottom depths between years (Table 2). Anchovy-like schools were
 472 detected between 8.1 to 183.9 m depth, with a mean of 67.3 m and had associated bottom
 473 depths ranging between 16.4 to 637.8 m depth, with a mean of 156 m (Figure 6). Of the 208
 474 anchovy-like schools detected, 37, or 17% were detected in offshore environments (mean
 475 bottom depth >200 m).



476

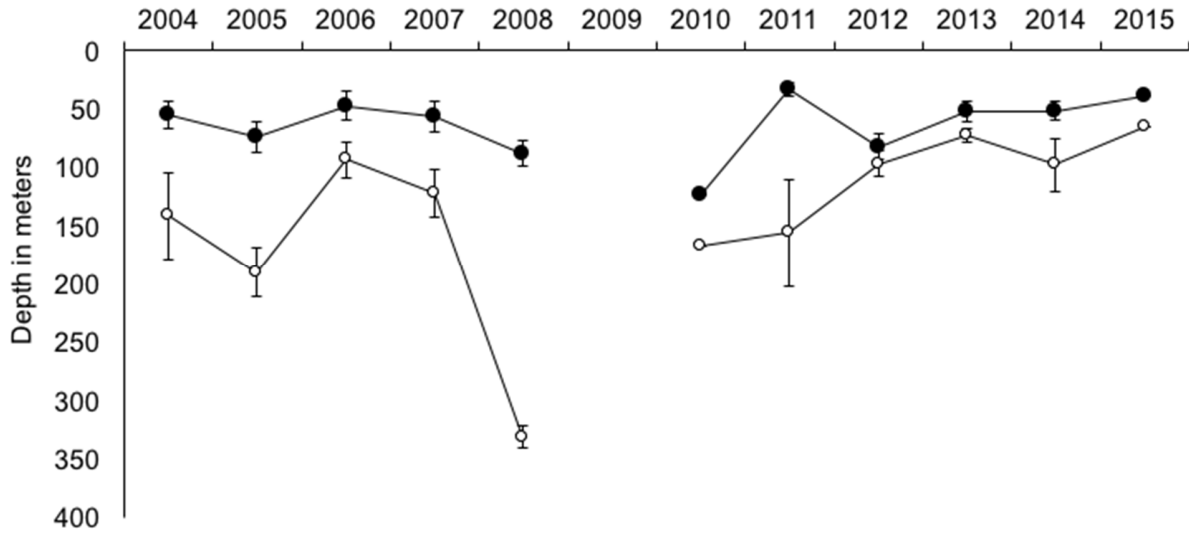
477 Figure 5. Represents total s_A of anchovy-like schools by year and month (n = 208).

478

479

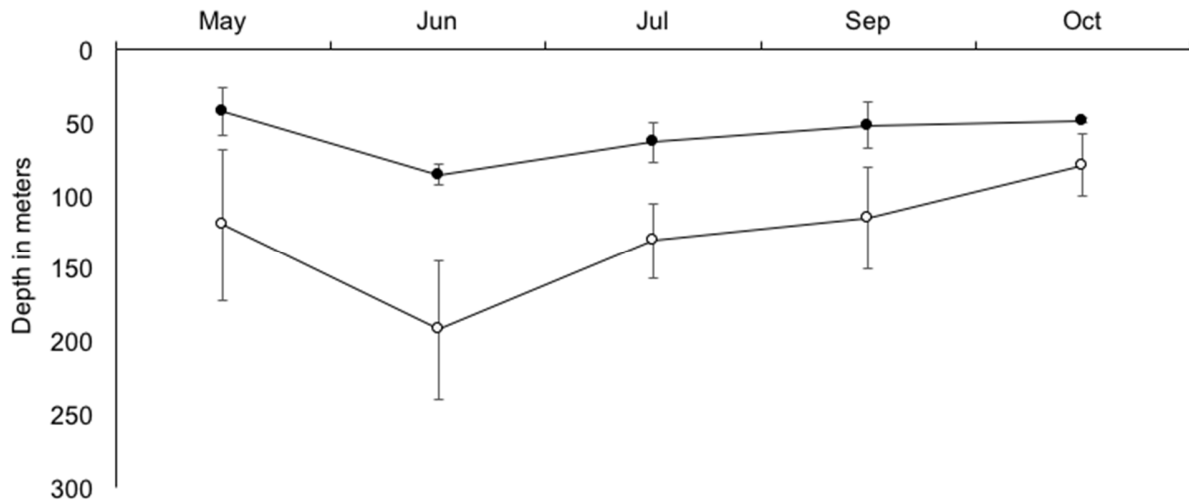
480

481 a.



482

483 b.



484

485 Figure 6. Mean depth (\pm SE) of acoustically identified anchovy-like schools (black circles) and
486 associated mean bottom depth (white circles) by year (a) and month (b).

487

488 A total of 156 anchovy-like schools were detected between April and July (April was only

489 sampled in 2008) (Figures 3 and 5). However, during 2009 and 2015, anchovy-like schools were

490 only detected in the months of October and September. There was a significant negative trend

491 in anchovy-like mean s_A from 2004 ($\bar{x} = 304 \text{ m}^2 \text{ nmi}^{-1}$) to 2015 ($\bar{x} = 0 \text{ m}^2 \text{ nmi}^{-1}$), but not between
 492 months (Table 2, Figure 5).

493

494 3.3 Acoustically observed YOY rockfish targets

495 The single target detection process resulted in 72,730 single targets with a TS equal to
 496 that of YOY rockfish consumed by seabirds (Table S.1). Acoustically-observed single targets do
 497 not display distinguishing characteristics like those of fish schools, therefore target strength was
 498 the sole feature used to classify YOY rockfish-like targets (Figure S.2). There were significant
 499 differences in total number of YOY rockfish-like targets nmi^{-1} between years, but no significant
 500 differences between months (Table 3). The total number of YOY rockfish-like targets detected
 501 was lowest between May 2004 and May 2011 ($\bar{x} = 3 \text{ nmi}^{-1}$), and highest between July 2011 and
 502 September 2015 ($\bar{x} = 76 \text{ nmi}^{-1}$) (Figure 7 and S.4).

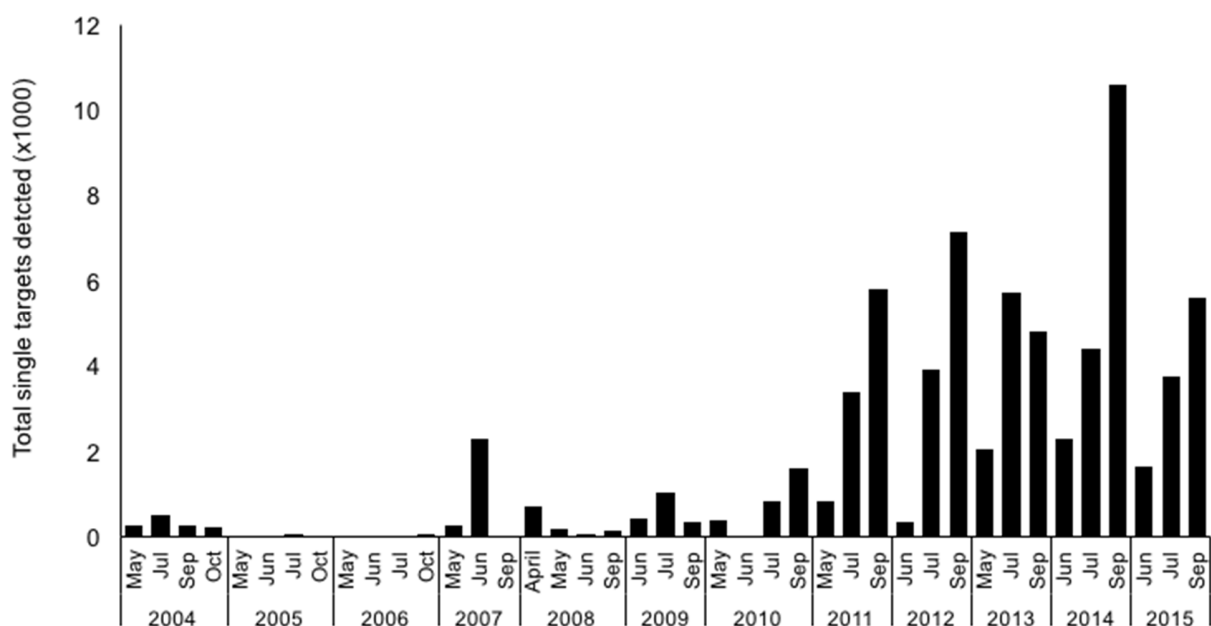
YOY Rockfish-like Targets Detected Between April and October						
Regression ANOVA						
Descriptor	Series	N	df	β	F	P <
YOY rockfish-like targets nmi^{-1}	year	72,730	40	4.39	31.59	0.00
	month	72,730	40	-	3.20	0.08
YOY Rockfish-like Targets Detected Between April and July						
Regression ANOVA						
Descriptor	Series	N	df	β	F	P <
YOY rockfish-like targets nmi^{-1}	year	35,887	27	2.68	38.2	0.00
	month	35,887	27	5.12	4.59	0.04

503

504 Table 3. The top half shows the number of YOY rockfish-like single targets detected between April and
 505 October, and regression ANOVA results showing that there were significant differences in the number of
 506 single targets detected between years, but not months. The bottom half shows the number of YOY
 507 rockfish-like single targets detected between April and July, and regression ANOVA results showing that
 508 there were significant differences in the number of single targets detected between years and months.

509

510 Approximately 77% of the YOY rockfish targets occurred in the 35 to 45m depth layer,
 511 with the remaining 23% dispersed down from 45 to 300 m depth (Figure S.1). For the purpose
 512 of the analysis between the seabird diets and acoustic YOY rockfish indices, we used the YOY
 513 rockfish-like targets detected between April and July and were detected in the 5 - 45 m depth
 514 layer which included 50% of the total targets identified. This approach was taken because of
 515 the seabirds diving capabilities and inability to sample deeper depths effectively.



516
 517 Figure 7. Represents total number of YOY rockfish-like single targets detected by year and
 518 month, not restricted by depth (n = 72,730).
 519

520 From the 72,730 single targets, 35,887 targets were detected between April and July.
 521 We found a significant positive trend in the total number of detected YOY rockfish-like targets
 522 from 2004 to 2015 and between years and months (Table 3). The years 2005 and 2006
 523 represented the lowest observed targets, with only 0.97 and 0.38 targets nmi⁻¹ being detected.
 524 Rockfish targets were observed most frequently during 2013 - 2015, with 36, 41, and 93 targets
 525 nmi⁻¹ detected on average, respectively (Figure 7 and S.4).

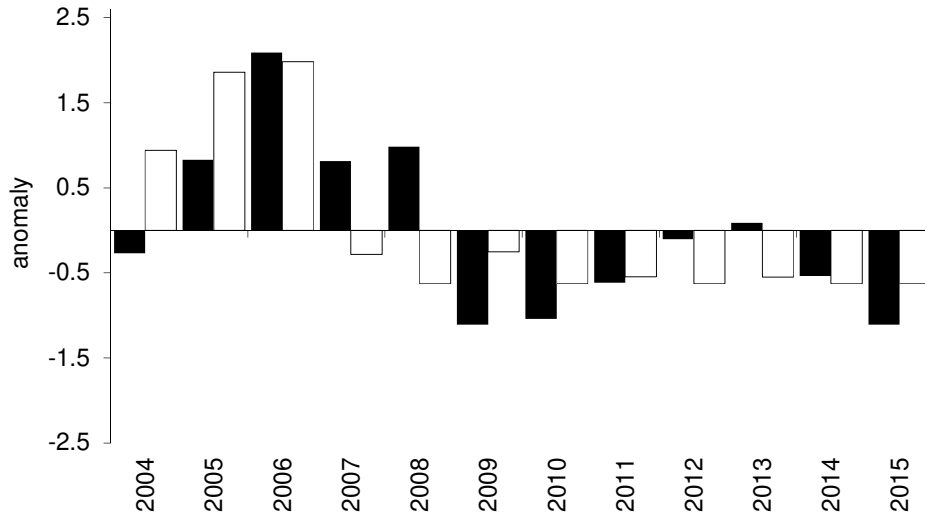
526

527 **3.4 Evaluation of acoustic fish estimates**

528 The standardized anomalies for anchovy-like s_A (hereafter, acoustic anchovy indices)
529 were significantly positively correlated with the standardized anchovy indices estimated by the
530 mid-water trawl survey (Table 4, Figure 8). Standardized anomalies representing the total
531 number of detected YOY rockfish-like targets (hereafter, acoustic YOY rockfish indices) were
532 significantly and positively correlated with the YOY rockfish indices estimated from the mid-
533 water trawl survey (Table 4, Figure 8). Regarding seabird diet, the acoustic anchovy indices
534 were significantly and positively correlated with the anomalies of anchovy consumed by all
535 three seabirds (Table 4, Figure 9). The acoustic YOY rockfish indices, based on targets detected
536 between 5 to 45 m depth, were significantly positively correlated with anomalies of YOY
537 rockfish consumed by common murre (Table 4, Figure 9). Although positively and strongly
538 correlated throughout the 5 to 45 m depth layer, YOY rockfish indices in the 5 to 15 m depth
539 layer were more strongly correlated to the anomalies of YOY rockfish consumed by rhinoceros
540 auklet, and by Brandt's cormorant (Table 4).

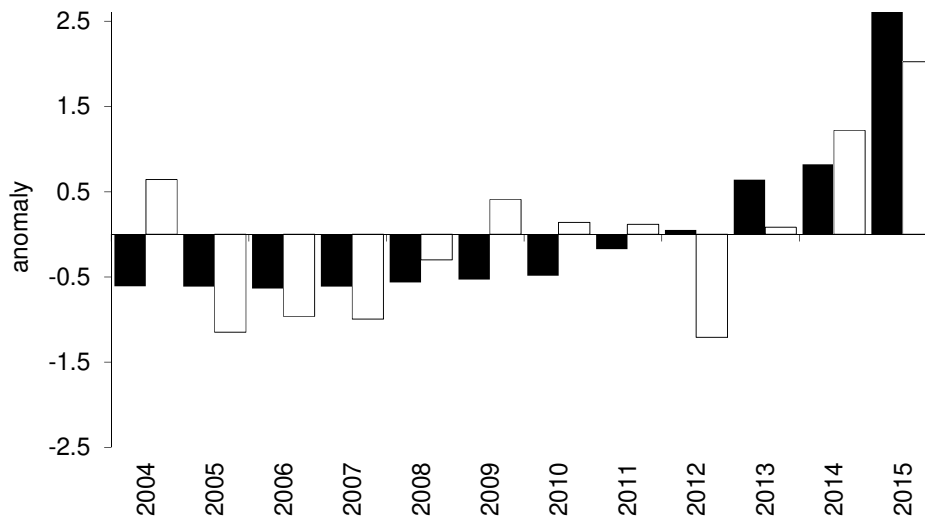
541

542 a.



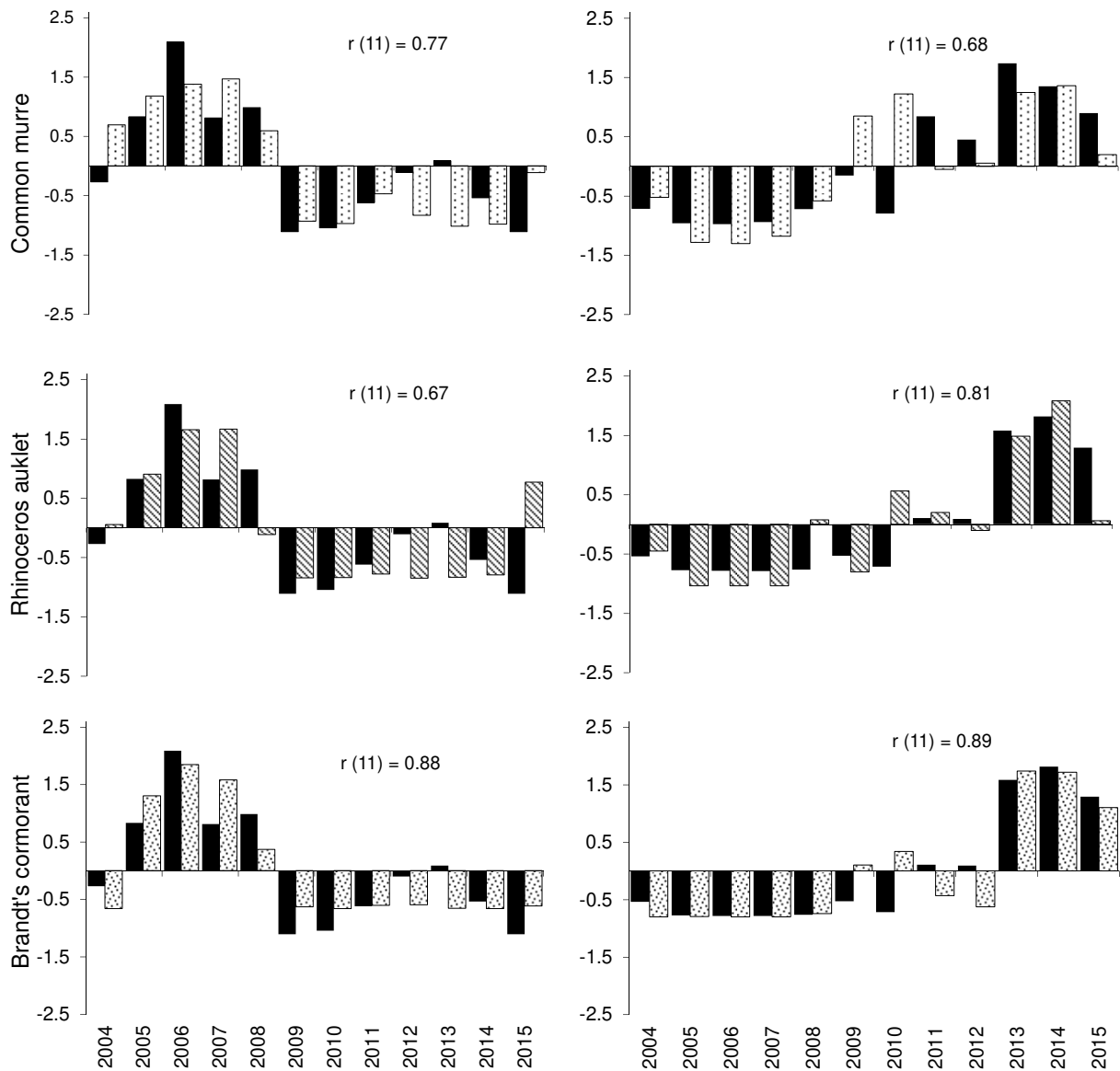
543

544 b.



545

546 Figure 8. Graph (a) represents the standardized anomalies of anchovy abundance metrics
547 indicated by $s_A \text{ nmi}^{-1}$ values calculated in this study (black bars) and NOAA-NMFS rockfish cruise
548 assessments in the core survey region (white bars). The two independent series were
549 correlated at $r = 0.63$ ($n = 12$). Graph (b) represents standardized anomalies of YOY rockfish
550 abundance metrics indicated by total single targets detected nmi^{-1} throughout the water
551 column (black bars) and NOAA-NMFS rockfish cruise assessments in the core survey region
552 (white bars). The two independent datasets were correlated at $r = 0.72$ ($n = 12$).
553



554

555 Figure 9. Standardized anomalies of anchovy-like s_A nmi^{-1} (left side, black bars) and
 556 YOY rockfish-like single targets nmi^{-1} (right side, black bars). YOY rockfish-like single targets for
 557 common murre were restricted to 5-45 m depth, for rhinoceros auklet and Brandt's cormorant
 558 targets were restricted to 5-15 m depth. Standardized anomalies of anchovy and YOY rockfish
 559 consumed by each bird species are represented by pattern filled bars.
 560

561

Indices Comparison	Pearson Correlation		Regression ANOVA			
	r	P	df	F	R ²	P <
Anchovy/NOAA-NMFS	0.63	0.05	11	6.51	0.39	0.03
YOY rockfish/NOAA-NMFS	0.72	0.01	11	10.95	0.52	0.03
Anchovy/Common murre	0.77	0.01	11	14.25	0.59	0.004
Anchovy/Rhinoceros auklet	0.67	0.05	11	7.92	0.44	0.02
Anchovy/Brandt's cormorant	0.87	0.01	11	31.54	0.76	0.000
YOY rockfish/Common murre	0.68	0.05	11	8.51	0.46	0.02
YOY rockfish/Rhinoceros auklet	0.81	0.01	11	18.57	0.65	0.002
YOY rockfish/Brandt's cormorant	0.89	0.001	10	37.72	0.79	0.000

562

563 Table 4. Pearson correlation results and the Regression ANOVA results showing that the acoustic
564 abundance indices for anchovy-like schools and YOY rockfish-like single targets are both significantly
565 correlated and able to explain the variability observed in the NOAA-NMFS trawling data and in the diet
566 of all three seabirds.

567

568 4. Discussion

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Acoustically-derived abundance estimates are frequently used to assess population trends, distribution, and classify habitat associations of zooplankton and forage fish in marine ecosystems. However, verification data is often difficult and expensive to acquire, and may result in large uncertainties of abundance estimates (MacLennan & Simmonds 2013). In our study, the availability of long-term seabird diet observations and mid-water trawl surveys, demonstrate that acoustics display a marked coherence with these independent estimates of relative forage fish abundance. There are three main points of our study: 1) acoustic classification methods resulted in forage fish indices that relate to variability of seabird diet, 2) although slightly weaker, the acoustic abundance indices for anchovy and YOY rockfish are correlated with mid-water trawl estimates, and 3) using prey size from the seabird diet to

579 calculate a *TS* range for YOY rockfish single targets is a viable method for developing population
580 indices and tracking the relative abundance of this critical life stage of rockfish.

581 Concurrent net sampling to aid in classification of fish in acoustic data is common
582 practice for fisheries management and science. The vessels used in ACCESS cruises lack the
583 capability to gather net samples of fish, leaving a large acoustic data set without a direct way to
584 classify or estimate forage fish abundance and distribution. To overcome this challenge, our
585 study combined seabird diet and independent trawl surveys to evaluate their use in estimating
586 temporal variability of forage fish occurrence. Acoustic classification of forage fish aggregations
587 is difficult and errors may arise due to fish orientation, misidentification, and shifts in behaviour
588 and distribution regionally (MacLennan 2013). Although our acoustic estimates are related to
589 indices derived from the mid-water trawl survey, due to technique and design, the trawl survey
590 may be missing patchily distributed forage fish aggregations, particularly at low population
591 sizes. Additionally, midwater trawl surveys that are conducted at night, to reduce net
592 avoidance, may miss an unknown percentage of the anchovy population that are dispersed at
593 the surface. For example, between 2010 and 2016 only two tows, out of over 200 conducted,
594 were positive for adult anchovies in this region, clearly indicating that the abundance was
595 below the range of meaningful detection by trawl surveys alone. Similarly, in coast wide
596 surveys to support stock assessments using the Acoustic Trawl Method, Zwolinski et al. (2012)
597 had only 6, 4 and 1 positive tows for anchovies in 2006, 2008 and 2010, respectively (years of
598 generally higher, albeit declining, anchovy abundance), further demonstrating the challenges of
599 developing indicators of abundance from trawl data alone.

600 The high correlations between seabird-and acoustically-derived forage fish indices is
601 likely attributable to sampling of the same forage fish populations due to overlap of the method
602 in time and space. As central-place foragers, seabirds in our study select particular length-
603 classes of forage fish surrounding their breeding colonies on the Farallon Islands, but can
604 effectively sample prey populations due to species' different diet preferences, varying habitat
605 preferences, and their ability to track patchy prey (Piatt et al. 2007). A primary caveat to using a
606 *TS* calculated from seabird diet is the inability to capture the entire inter-seasonal variability of
607 this life stage of rockfish. Although each sampling method is limited by spatial and temporal
608 bounds, their high level of correlation shows that each can provide remarkable utility for
609 describing the population trends of acoustically observed forage fish species.

610

611 **4.1 Implications for anchovy variability**

612 Anchovy tend to distribute in the water column forming densely packed schools during
613 the day, and then vertically migrating and dispersing near the surface at dusk (Fréon et al. 1996;
614 Kaltenberg and Benoit-Bird 2009). Acoustic-trawl surveys conducted between 1966 and 1973 in
615 the study region indicated that anchovy schools were most commonly found between 9.2 and
616 73.2 m water depth (Mais 1974). Large sized schools were detected in the autumn of 1966 and
617 1967 between 164.6 to 182.9 m depth (Mais 1974). Previous studies found depth distribution
618 to be critical for discriminating anchovy from other species, as their placement in the water
619 column in relation to the seafloor (e.g. altitude index) was the most important descriptor
620 (Lawson et al. 2001; Robotham et al. 2010). Of the 208 anchovy-like schools, 58% were
621 detected between 8 and 73 m depth. The deepest school we detected was during September

622 2012 at 183.9 m depth and similar to previous observations made by Mais 1974, was
623 considerably large with a height of 20.2 m and a length of 474.1 m. The depth distribution and
624 increase in detection during October of anchovy-like schools is consistent with previous
625 acoustic trawl surveys in the region (Mais 1974). However, in our study, discriminating based on
626 the altitude of schools was not sufficient for classifying anchovy-like schools. This study
627 required additional acoustic descriptors including schooling behavior and their associated
628 energy backscatter (e.g. S_v) and morphological characteristics (e.g. visual cues). In addition to
629 unique schooling behavior, anchovy display sensitivities to oceanographic conditions and tend
630 to be more abundant off central California during weaker upwelling years (Chavez et al. 2003;
631 Lindegren et al. 2013; Ralston et al. 2015; Elliott et al. 2016). In our study, the observed trends
632 in the acoustic anchovy indices is indicative of a population following warm to cool ocean
633 phases (e.g., 2004-2007) observed in the CCE (MacCall et al. 2016). Our findings on school
634 depth distribution, associated bottom depths, energy characteristics, and population trends
635 suggest that analysed schools fit the description of acoustically-observed anchovy schools (Mais
636 1974; Kaltenberg and Benoit-Bird 2009; Lawson et al. 2001; Robotham et al. 2010).

637

638 **4.2 Implications for YOY rockfish variability**

639 Adult rockfish in the CCE tend to form large aggregations in relation to high relief shelf
640 breaks and slope habitats between 150 to 250 m depth, and have been described using
641 acoustic methods (Chess et al. 1988; Demer et al. 2009; Keller et al. 2012). However, methods
642 describing acoustic aggregations of the pelagic life stage of YOY rockfish are not yet available.
643 YOY rockfish “habitat”, similar to anchovy, is best described in terms of depth distribution.

644 Using an earlier time series from the mid-water trawl survey, Lenarz et al. (1991) determined
645 that 18 species of juvenile rockfish inhabited the water column at a depth range of 30.4 to 80 m
646 with a mean depth of 56.7 m. However, Lenarz et al. (1991) found that catches of juvenile
647 rockfish were relatively low when trawls were conducted at depths below 37 m. Using a time
648 series from the mid-water trawl survey between 1987-1998, Ross and Larson (2003) found that
649 out of 173,238 juvenile rockfishes caught, 169,406 were caught during 10 m and 30 m tows,
650 with the remaining 3,832 being caught during 100 m tows. The acoustically-detected targets in
651 our study were between depths of 5 to 275.3 m with a mean depth of 34.6 m, with 50% of
652 targets being detected between 5-45 m (see results and Figure S.1). Depth distribution of the
653 acoustically observed YOY rockfish-like targets suggests that the sampled targets are within the
654 correct depth distribution range based on previous catch data, lending credence to the target
655 strength range used to detect prey sized YOY rockfish (Moser and Ahlstrom 1978; and Lenarz et
656 al. 1991; Ross and Larson, 2003). In addition to depth, peak abundances of acoustically
657 observed YOY rockfish-like targets coincides with documented peak abundances of wintertime
658 broods of YOY rockfish in the CCE (Ralston et al. 2013). In contrast to anchovy, YOY rockfish
659 peak abundances occur during cooler ocean phases (e.g., 2008-2014) and tend to peak between
660 April and July before settling into deeper habitats. Our findings on depth distribution and
661 population trends of observed rockfish-like targets in the acoustic indices for YOY rockfish are
662 reflective of findings observed in previous studies (Lenarz et al. 1991; Ross and Larson 2003;
663 Ralston et al. 2013).

664

665 **5. Conclusion**

666 The correlation between the acoustic surveys and the mid-water trawl survey for
667 Northern anchovy and YOY rockfish species is noteworthy, considering the incongruous spatial
668 extents of the different surveys. However, both surveys were conducted annually within the
669 central California Current and closely tracked a decade of marked ocean- climate variability,
670 upwelling conditions, and marked changes in the abundance and distribution of krill and forage
671 fish (Santora et al. 2014; Ralston et al. 2015). The coherence of local seabird diet with
672 acoustically-derived forage fish availability also adds to findings from previous studies off
673 central California, and confirms seabird diet as an exceptional indicator of food web structure
674 and ecosystem (Ainley et al. 1993; Mills et al. 2007; Elliott et al. 2015, 2016). Further, by
675 combining acoustics, seabird diets, and trawl surveys, our approach is likely useful for
676 conducting ecosystem assessments in other upwelling ecosystems to better understand the
677 spatial scales at which top marine predators and forage fish interact (Piatt et al. 2007; Bertrand
678 et al. 2008; Tremblay et al. 2009). Additional research into habitat associations of anchovy and
679 YOY rockfish acoustic indices could benefit the assessment of top predator foraging behavior
680 (e.g., habitat energy budgets) and may provide insight on species interactions within trophic
681 hotspots (Santora et al. 2017). For example, depths of forage fish species in particular play a
682 crucial role in the energetic demand placed on diving seabirds such as the common murre and
683 Brandt's cormorant (Warzybok et al. 2018). Vertical distribution patterns of fish schools may be
684 informative for designing forage fish habitat models specified with depth-specific ocean
685 conditions

686 The acoustic characterization of anchovy-like school depth distribution and morphometric
687 characteristics described in this study could benefit habitat forecasting models that aim to
688 further describe habitat associations (MaCall et al. 2016; Schroeder et al. 2014). Associated
689 bottom depths of anchovy-like schools described in this study provides some insight on
690 anchovy concentrations nearshore (< 50 m bottom depth) that are under-sampled during
691 current surveys (MaCall et al. 2016; Davison et al. 2017). Few anchovy-like schools were
692 identified nearshore (<50 m bottom depth) in 2006, and provided little contribution to the
693 estimated population size. This may suggest that if schools are missed, the relatively few
694 schools inhabiting the nearshore environment adds little to the total population size (Davison et
695 al. 2017). Research into how the two forage fish species distribute in relation to oceanographic
696 conditions may provide further information on what environmental mechanisms are involved in
697 the distribution of the two species. For example, exploring the effects of temperature, salinity,
698 strength of stratification, and depth of upwelling on the distribution of both anchovy and YOY
699 rockfish could provide a more complete overview of habitat requirements (Santora et al. 2014;
700 Schroeder et al. 2014). Lastly, improvement in fish identification in acoustic data may be
701 enhanced by incorporating numerical outputs into machine learning techniques (Robothom et
702 al. 2010). Continued work in the realm of acoustic classification of fish species, fish behaviour,
703 and predator prey relationships in the region will further our understanding of marine food
704 webs and help make informed management decisions concerning marine environments.
705

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727 **References**

- 728 Ahlstrom, E. H. (1961). Distribution and relative abundance of rockfish (*Sebastes* spp.) larvae off
729 California and Baja California. *Rapp. P.-V. Reun. Cons. Int. Explor. Mer*, 150, 169-176.
- 730 Ahlstrom, E. H., Moser, H. G., & Sandknap, E. M. (1978). Distributional atlas of fish larvae in the
731 California Current region: rockfishes, *Sebastes* spp., 1950 through 1975 (No. 26). *Marine*
732 *Life Research Program, Scripps Institution of Oceanography*.
- 733 Ainley, D.G., and R.J. Boekelheide. (1990). Seabirds of the Farallon Islands; structure and
734 dynamics of an upwelling system community. Stanford University Press, Stanford, CA.
- 735 Ainley, D. G., Sydeman, W. J., Parrish, R. H., & Lenarz, W. H. (1993). Oceanic factors influencing
736 distribution of young rockfish (*Sebastes*) in central California: a predator's perspective.
737 *California Cooperative Oceanic Fisheries Investigations Reports*, 34, 133–139.
738 http://www.calcofi.org/publications/calcofireports/v34/Vol_34_Ainley_etal.pdf
- 739 Ainley, D. G., Sydeman, W. J., & Norton, J. (1995). Upper trophic level predators indicate
740 interannual negative and positive anomalies in the California Current food web. *Marine*
741 *Ecology Progress Series*, 118(1-3), 69–80. <http://doi.org/10.3354/meps118069>
- 742 Ainley, D.G., Adams, P.B. and Jahncke, J., (2015). California current system-Predators and the
743 preyscape. *Journal of Marine Systems*, 146, pp.1-2.
- 744 Alverson, D.L., and H. A. Larkins. (1969). Status of the knowledge of the Pacific hake resource.
745 *Calif. Coop. Oceanic Fish. Invest. Report*. 13, pp.24-31.
- 746 Ayón, P., Criales-Hernandez, M. I., Schwamborn, R., & Hirche, H. J. (2008). Zooplankton
747 research off Peru: A review. *Progress in Oceanography*, 79(2-4), 238–255.
748 <http://doi.org/10.1016/j.pocean.2008.10.020>
- 749 Bailey, K. M., Francis, R. C., & Stevens, P. R. (1982). The life history and fishery of Pacific whiting,
750 *Merluccius productus*. *CalCOFI Reports*, XXIII(April), 81–98.
- 751 Barange, M. (1994). Acoustic identification, classification and structure of biological patchiness
752 on the edge of the Agulhas Bank and its relation to frontal features. *South African Journal*
753 *of Marine Science*, 14(1), 333–347. <https://doi.org/10.2989/025776194784286969>
- 754 Barange, M., Hampton, I., & Roel, B. a. (1999). Trends in the abundance and distribution of
755 anchovy and sardine on the South African continental shelf in the 1990s, deduced from
756 acoustic surveys. *South African Journal of Marine Science*, 21(1), 367–391.
757 <http://doi.org/10.2989/025776199784126088>

- 758 Barange, M., Coetzee, J., Takasuka, A., Hill, K., Gutierrez, M., Oozeki, Y., ... Agostini, V. (2009).
759 Habitat expansion and contraction in anchovy and sardine populations. *Progress in*
760 *Oceanography*, 83(1–4), 251–260. <http://doi.org/10.1016/j.pocean.2009.07.027>
- 761 Bertrand, A., Gerlotto, F., Bertrand, S., Gutiérrez, M., Alza, L., Chipollini, A., ... Chavez, F. (2008).
762 Schooling behaviour and environmental forcing in relation to anchoveta distribution: An
763 analysis across multiple spatial scales. *Progress in Oceanography*, 79(2–4), 264–277.
764 <https://doi.org/10.1016/j.pocean.2008.10.018>
- 765
- 766 Cairns, D. K. (1987). Seabirds as indicators of marine food supplies. *Biological Oceanography*,
767 5(August), 261–271. <https://doi.org/10.1080/01965581.1987.10749517>
- 768
- 769 Chavez, F. P., Ryan, J., Lluch-Cota, S. E., & Niquen, M. C. (2003). From Anchovies to Sardines and
770 back: Multidecadal Change in the Pacific Ocean. *Science*, 299(FEBRUARY), 217–221.
771 <https://doi.org/10.1126/science.1075880>
- 772
- 773 Chin, J. L., Karl, H. A., & Maher, N. M. (1997). Shallow subsurface geology of the continental
774 shelf, Gulf of the Farallones, California, and its relationship to surficial seafloor
775 characteristics. *Marine Geology*, 137(3–4), 251–269. [https://doi.org/10.1016/S0025-](https://doi.org/10.1016/S0025-3227(96)00091-6)
776 [3227\(96\)00091-6](https://doi.org/10.1016/S0025-3227(96)00091-6)
- 777 Checkley, D. M., & Barth, J. A. (2009). Patterns and processes in the California Current System.
778 *Progress in Oceanography*, 83(1–4), 49–64. <http://doi.org/10.1016/j.pocean.2009.07.028>
- 779 Chess, J.R., Smith, S.E. and Fischer, P.C., (1988). Trophic relationships of the shortbelly rockfish,
780 *Sebastes jordani*, off central California. *CalCOFI Rep*, 29, pp.129-136.
- 781 Churnside, J., Brodeur, R., Horne, J., Adam, P., Benoit-bird, K., Reese, D. C., ... Brown, E. (2008).
782 Combining Techniques for Remotely Assessing Pelagic Nekton : Getting the Whole Picture.
783 *Fisheries Science*, 345–356. https://doi.org/10.1007/978-1-4020-9210-7_19
- 784 Coetzee, J. (2000). Use of a shoal analysis and patch estimation system (SHAPES) to characterise
785 sardine schools. *Aquatic Living Resources*, 13(1), 1–10. [http://doi.org/10.1016/S0990-](http://doi.org/10.1016/S0990-7440(00)00139-X)
786 [7440\(00\)00139-X](http://doi.org/10.1016/S0990-7440(00)00139-X)
- 787 Cury, P., Bakun, A., Crawford, R. J. M., Jarre, A., Quiñones, R. A., Shannon, L. J., & Verheye, H. M.
788 (2000). Small pelagics in upwelling systems: Patterns of interaction and structural changes

- 789 in “wasp-waist” ecosystems. In *ICES Journal of Marine Science* (Vol. 57, pp. 603–618).
790 <https://doi.org/10.1006/jmsc.2000.0712>
- 791 Davison, P. C., Sydeman, W. J., & Thayer, J. A. (2017). Are there temporal or spatial gaps in
792 recent estimates of anchovy off California? California Cooperative Oceanic Fisheries
793 Investigations Reports.
- 794 Demer, D. A., Cutter, G. R., Renfree, J. S., & Butler, J. L. (2009). A statistical-spectral method for
795 echo classification. In *ICES Journal of Marine Science* (Vol. 66, pp. 1081–1090).
796 <http://doi.org/10.1093/icesjms/fsp054>
- 797 Demer, D. A., Berger, L., Bernasconi, M., Bethke, E., Boswell, K., Chu, D., ... & Hufnagle, L. T.
798 (2015). Calibration of acoustic instruments. *ICES Cooperative Research Report*, 133.
- 799 Elliott, M. L., Bradley, R. W., Robinette, D. P., & Jahncke, J. (2015). Changes in forage fish
800 community indicated by the diet of the Brandt’s cormorant (*Phalacrocorax penicillatus*) in
801 the central California Current. *Journal of Marine Systems*, 146, 50–58.
802 <http://doi.org/10.1016/j.jmarsys.2014.07.015>
- 803 Elliott, M. L., Schmidt, A. E., Acosta, S., Bradley, R., Warzybok, P., Sakuma, K. M., ... Jahncke, J.
804 (2016). Brandt’s cormorant diet (1994–2012) indicates the importance of fall ocean
805 conditions for northern anchovy in central California. *Fisheries Oceanography*, 25(5), 515–
806 528. <https://doi.org/10.1111/fog.12169>
- 807 Fielding, S., Watkins, J. L., Collins, M. A., Enderlein, P., & Venables, H. J. (2012). Acoustic
808 determination of the distribution of fish and krill across the Scotia Sea in spring 2006,
809 summer 2008 and autumn 2009. *Deep-Sea Research Part II: Topical Studies in*
810 *Oceanography*, 59–60, 173–188. <http://doi.org/10.1016/j.dsr2.2011.08.002>
- 811 Francois, R. E., & Garrison, G. R. (1982). Sound absorption based on ocean measurements: Part
812 I: Pure water and magnesium sulfate contributions. *The Journal of the Acoustical Society of*
813 *America*, 72(3), 896–907. <https://doi.org/10.1121/1.388170>
- 814 Fréon, P., Gerlotto, F., & Soria, M. (1996). Diel variability of school structure with special
815 reference to transition periods. *ICES Journal of Marine Science: Journal Du Conseil*, 53(2),
816 459–464. <http://doi.org/10.1006/jmsc.1996.0065>
- 817 Fréon, P., & Misund, O. A. (1998). *Dynamics of pelagic fish distribution and behaviour : effects*
818 *on fisheries and stock assessment. Reviews in Fish Biology and Fisheries* (Vol. 10).
819 <https://doi.org/10.1023/a:1008928315202>
- 820 Furness, R. W., & Camphuysen, C. J. (1997). Seabirds as monitors of the marine environment.
821 *ICES Journal of Marine Science*, 54, 726–737. <http://doi.org/10.1006/jmsc.1997.0243>

- 822 Haralabous, J., & Georgakarakos, S. (1996). Artificial neural networks as a tool for species
823 identification of fish schools. *ICES Journal of Marine Science: Journal Du Conseil*, 53(2),
824 173–180. <http://doi.org/10.1006/jmsc.1996.0019>
- 825 Hewitt, R. P., Watkins, J., Naganobu, M., Sushin, V., Brierley, A. S., Demer, D., ... Miller, D.
826 (2004). Biomass of Antarctic krill in the Scotia Sea in January/February 2000 and its use in
827 revising an estimate of precautionary yield. *Deep-Sea Research Part II: Topical Studies in*
828 *Oceanography*. <https://doi.org/10.1016/j.dsr2.2004.06.011>
- 829 Hilborn, R. (2011). Future directions in ecosystem based fisheries management: A personal
830 perspective. *Fisheries Research*. <http://doi.org/10.1016/j.fishres.2010.12.030>
- 831 Kaltenberg, A. M., & Benoit-Bird, K. J. (2009). Diel behavior of sardine and anchovy schools in
832 the California Current System. *Marine Ecology Progress Series*, 394, 247–262.
833 <http://doi.org/10.3354/meps08252>
- 834 Kang, D., & Hwang, D. (2003). Ex situ target strength of rockfish (*Sebastes schlegeli*) and red sea
835 bream (*Pagrus major*) in the Northwest Pacific. In *ICES Journal of Marine Science* (Vol. 60,
836 pp. 538–543). [http://doi.org/10.1016/S1054-3139\(03\)00040-7](http://doi.org/10.1016/S1054-3139(03)00040-7)
- 837 Keller, A.A., Wallace, J.R., Horness, B.H., Hamel, O.S. and Stewart, I.J., (2012). Variations in
838 eastern North Pacific demersal fish biomass based on the US west coast groundfish
839 bottom trawl survey (2003-2010). *Fishery Bulletin*, 110(2), pp.205-223.
- 840 Largier, J. L., Lawrence, C. A., Roughan, M., Kaplan, D. M., Dever, E. P., Dorman, C. E., ... &
841 Botsford, L. W. (2006). WEST: A northern California study of the role of wind-driven
842 transport in the productivity of coastal plankton communities. *Deep Sea Research Part II:*
843 *Topical Studies in Oceanography*, 53(25), 2833-2849.
- 844 Lawson, G. L., Barange, M., & Freon, P. (2001). Species identification of pelagic fish schools on
845 the South African continental shelf using acoustic descriptors and ancillary information.
846 *The Journal of the Acoustical Society of America*, 58, 275–287.
847 <http://doi.org/10.1121/1.4743189>
- 848 Lenarz, W. H., Larson, R. J., & Ralston, S. (1991). Depth Distributions of Late Larvae and Pelagic
849 Juveniles of Some Fishes of the California Current. *California Cooperative Oceanic Fisheries*
850 *Investigations Reports*, 32, 41–46.
- 851 Lindegren, M., Checkley, D. M., Rouyer, T., MacCall, A. D., & Stenseth, N. C. (2013). Climate,
852 fishing, and fluctuations of sardine and anchovy in the California Current. *Proceedings of*
853 *the National Academy of Sciences of the United States of America*, 110(33), 13672–7.
854 <http://doi.org/10.1073/pnas.1305733110>

- 855 MacCall, A. D., Sydeman, W. J., Davison, P. C., & Thayer, J. A. (2016). Recent collapse of
 856 northern anchovy biomass off California. *Fisheries Research*, 175, 87–94.
 857 <http://doi.org/10.1016/j.fishres.2015.11.013>
- 858 Mais, K. F. (1974). Pelagic fish surveys in the California Current. *California Department of Fish*
 859 *and Game Fish Bull.*, 162, 79.
- 860 MacLennan, D. N., Fernandes, P. G., & Dalen, J. (2002). A consistent approach to definitions
 861 and symbols in fisheries acoustics. *ICES Journal of Marine Science*, 59(2), 365–369.
 862 <http://doi.org/10.1006/jmsc.2001.1158>
- 863 MacLennan, D., & Simmonds, E. J. (2013). *Fisheries acoustics* (Vol. 5). Springer Science &
 864 Business Media.
- 865 Manugian, S., Elliott, M. L., Bradley, R., Howar, J., Karnovsky, N., Saenz, B., ... Jahncke, J. (2015).
 866 Spatial Distribution and Temporal Patterns of Cassin's Auklet Foraging and Their
 867 Euphausiid Prey in a Variable Ocean Environment. *PLoS ONE*, 10(12).
 868 <http://doi.org/10.1371/journal.pone.0144232>
- 869 McClatchie, S., Field, J., Thompson, A. R., Gerrodette, T., Lowry, M., Fiedler, P. C., ... Vetter, R. D.
 870 (2016). Food limitation of sea lion pups and the decline of forage off central and southern
 871 California. *Royal Society Open Science*, 3(3), 150628. <http://doi.org/10.1098/rsos.150628>
- 872 Mackenzie, K. V. (1981). Nine-term equation for sound speed in the oceans. *The Journal of the*
 873 *Acoustical Society of America*, 70(3), 807. <https://doi.org/10.1121/1.386920>
- 874 Miller, A. K., & Sydeman, W. J. (2004). Rockfish response to low-frequency ocean climate
 875 change as revealed by the diet of a marine bird over multiple time scales. *Marine Ecology*
 876 *Progress Series*, 281, 207–216. <http://doi.org/10.3354/meps281207>
- 877 Miller, D., & Lea, R. (1972). Guide to the coastal marine fishes of California. *Otro*, 235.
- 878 Mills, K. L., Laidig, T., Ralston, S., & Sydeman, W. J. (2007). Diets of top predators indicate
 879 pelagic juvenile rockfish (*Sebastes* spp.) abundance in the California Current System.
 880 *Fisheries Oceanography*, 16(3), 273–283. [http://doi.org/10.1111/j.1365-](http://doi.org/10.1111/j.1365-2419.2007.00429.x)
 881 [2419.2007.00429.x](http://doi.org/10.1111/j.1365-2419.2007.00429.x)
- 882 Moser, H. Geoffrey, and Elbert H. Ahlstrom (1978). Larvae and pelagic juveniles of blackgill
 883 rockfish, *Sebastes melanostomus*, taken in midwater trawls off southern California and
 884 Baja California. *Journal of the Fisheries Board of Canada*, 35.7, 981-996.
- 885 Moser, H. G., Charter, R. L., Watson, W., Ambrose, D. A., Butler, J. L., Charter, S. R., & Sandknop,
 886 E. M. (2000). Abundance and distribution of rockfish (*Sebastes*) larvae in the southern

- 887 California bight in relation to environmental conditions and fishery exploitation. *California*
888 *Cooperative Oceanic Fisheries Investigations Reports*, 41, 132–147.
- 889 Piatt, J. F., Sydeman, W. J., & Wiese, F. (2007). Introduction: a modern role for seabirds as
890 indicators. *Marine Ecology progress series*, 352, 199–204.
- 891 Pikitch, E. K., Rountos, K. J., Essington, T. E., Santora, C., Pauly, D., Watson, R., Munch, S. B.
892 (2014). The global contribution of forage fish to marine fisheries and ecosystems. *Fish and*
893 *Fisheries*, 15(1), 43–64. <http://doi.org/10.1111/faf.12004>
- 894 Pitcher, T. J., & Parrish, J. K. (1993). Functions of shoaling behavior in teleosts. *Behaviour of*
895 *Teleost Fishes*, 363–439. https://doi.org/10.1007/978-1-4684-8261-4_12
- 896 Ralston, S., Sakuma, K. M., & Field, J. C. (2013). Interannual variation in pelagic juvenile rockfish
897 (Sebastes spp.) abundance - going with the flow. *Fisheries Oceanography*, 22(4), 288–308.
898 <http://doi.org/10.1111/fog.12022>
- 899 Ralston, S., Field, J. C., & Sakuma, K. M. (2015). Long-term variation in a central California
900 pelagic forage assemblage. *Journal of Marine Systems*, 146, 26–37.
901 <http://doi.org/10.1016/j.jmarsys.2014.06.013>
- 902 Robotham, H., Bosch, P., Gutiérrez-Estrada, J. C., Castillo, J., & Pulido-Calvo, I. (2010). Acoustic
903 identification of small pelagic fish species in Chile using support vector machines and
904 neural networks. *Fisheries Research*, 102(1–2), 115–122.
905 <http://doi.org/10.1016/j.fishres.2009.10.015>
- 906 Roth, J. E., Nur, N., Warzybok, P., & Sydeman, W. J. (2008). Annual prey consumption of a
907 dominant seabird, the common murre, in the California Current system. *ICES Journal of*
908 *Marine Science*, 65(6), 1046–1056. <http://doi.org/10.1093/icesjms/fsn077>
- 909 Ross, J. R. M., & Larson, R. J. (2003). Influence of water column stratification on the depth
910 distributions of pelagic juvenile rockfishes off central California. *California Cooperative*
911 *Oceanic Fisheries Investigations Reports*, 44, 65–75.
- 912 Ryan, J. P., Fischer, A. M., Kudela, R. M., McManus, M. A., Myers, J. S., Paduan, J. D., ... Zhang,
913 Y. (2010). Recurrent frontal slicks of a coastal ocean upwelling shadow. *Journal of*
914 *Geophysical Research: Oceans*, 115(12). <http://doi.org/10.1029/2010JC006398>
- 915 Sakuma, K. M., & Larson, R. J. (1995). Distribution of pelagic metamorphic-stage sanddabs
916 *Citharichthys sordidus* and *C. stigmaeus* within areas of upwelling off central California.
917 *Fishery Bulletin*, 93(3), 516–529.

- 918 Sakuma, K. M., & Ralston, S. (1995). Distributional patterns of late larval groundfish off central
 919 California in relation to hydrographic features during 1992 and 1993. *California*
 920 *Cooperative Oceanic Fisheries Investigations Reports*, 36(Methot 1986), 179–192.
- 921 Sakuma, K. M., Field, J. C., Mantua, N. J., Ralston, S., Marinovic, B. B., & Carrion, C. N. (2016).
 922 Anomalous epipelagic micronekton assemblage patterns in the neritic waters of the
 923 California current in spring 2015 during a period of extreme ocean conditions. *California*
 924 *Cooperative Oceanic Fisheries Investigations Reports*, 57, 163–183.
- 925 Sakuma, K.M. (2017). Cruise report, NOAA Ship Reuben Lasker RL-17-03, April 26 - June 13,
 926 2017: Rockfish recruitment and ecosystem assessment. NOAA National Marine Fisheries
 927 Service, SWFSC Fisheries Ecology Division, Santa Cruz, California. 20 p
- 928 Santora, J. A., Ralston, S., & Sydeman, W. J. (2011). Spatial organization of krill and seabirds in
 929 the central California Current. *ICES Journal of Marine Science*, 68(7), 1391–1402.
 930 <https://doi.org/10.1093/icesjms/fsr046>
- 931 Santora, J. A., Field, J. C., Schroeder, I. D., Sakuma, K. M., Wells, B. K., & Sydeman, W. J. (2012).
 932 Spatial ecology of krill, micronekton and top predators in the central California Current:
 933 Implications for defining ecologically important areas. *Progress in Oceanography*, 106,
 934 154–174. <http://doi.org/10.1016/j.pocean.2012.08.005>
- 935 Santora, J. A., Schroeder, I. D., Field, J. C., Wells, B. K., & Sydeman, W. J. (2014). Spatio-temporal
 936 dynamics of ocean conditions and forage taxa reveal regional structuring of seabird-prey
 937 relationships. *Ecological Applications*, 24(7), 1730–1747. <http://doi.org/10.1890/13-1605.1>
- 938 Santora, J. A., Sydeman, W. J., Schroeder, I. D., Field, J. C., Miller, R. R., & Wells, B. K. (2017).
 939 Persistence of trophic hotspots and relation to human impacts within an upwelling marine
 940 ecosystem: *Ecological Applications*, 27(2), 560–574. <https://doi.org/10.1002/eap.1466>
- 941 Schroeder, I. D., Santora, J. A., Moore, A. M., Edwards, C. A., Fiechter, J., Hazen, E. L., ... Wells, B.
 942 K. (2014). Application of a data-assimilative regional ocean modeling system for assessing
 943 California Current System ocean conditions, krill, and juvenile rockfish interannual
 944 variability. *Geophysical Research Letters*, 41(16), 5942–5950.
 945 <https://doi.org/10.1002/2014GL061045>
- 946 Schwartzlose, R. A., Alheit, J., Bakun, A., Baumgartner, T. R., Cloete, R., Crawford, R. J. M., ...
 947 Zuzunaga, J. Z. (1999). Worldwide large-scale fluctuations of sardine and anchovy
 948 populations. *South African Journal of Marine Science*, 21(1), 289–347.
 949 <https://doi.org/10.2989/025776199784125962>
- 950 Simmonds, E.J., Gutiérrez, M., Chipollini, A., Gerlotto, F., Woillez, M. and Bertrand, A., (2009).
 951 Optimizing the design of acoustic surveys of Peruvian anchoveta. *ICES Journal of Marine*
 952 *Science: Journal du Conseil*, 66(6), pp.1341-1348

- 953 Swartzman, G., Bertrand, A., Gutiérrez, M., Bertrand, S., & Vasquez, L. (2008). The relationship
954 of anchovy and sardine to water masses in the Peruvian Humboldt Current System from
955 1983 to 2005. *Progress in Oceanography*, 79(2-4), 228–237.
956 <http://doi.org/10.1016/j.pocean.2008.10.021>
- 957 Sydeman, W. J., Hester, M. M., Thayer, J. a, Gress, F., Martin, P., & Buffa, J. (2001). Climate
958 change, reproductive performance and diet composition of marine birds in the southern
959 California Current system, 1969-1997. *Progress in Oceanography*, 49(1-4), 309–329.
960 [http://doi.org/http://dx.doi.org/10.1016/S0079-6611\(01\)00028-3](http://doi.org/http://dx.doi.org/10.1016/S0079-6611(01)00028-3)
- 961 Szoboszlai, A.I., J.A. Thayer, S.A. Wood, W.J. Sydeman, and L.E. Koehn. (2015). Forage species in
962 predator diets: Synthesis of data from the California Current. *Ecological Informatics* 29:45-
963 56.
- 964 Thayer, J. A., & Sydeman, W. J. (2007). Spatio-temporal variability in prey harvest and
965 reproductive ecology of a piscivorous seabird, *Cerorhinca monocerata*, in an upwelling
966 system. *Marine Ecology Progress Series*, 329, 253–265.
967 <http://doi.org/10.3354/meps329253>
- 968 Tremblay, Y. Bertrand, S., Henry, R. W., Kappes, M. A., Costa, D. P., & Shaffer, S. A. Analytical
969 approaches to investigating seabird–environment interactions: a review. *Marine Ecology*
970 *Progress Series* 391 (2009): 153-164.
- 971 Vlietstra, L. S. (2005). Spatial associations between seabirds and prey: Effects of large-scale prey
972 abundance on small-scale seabird distribution. *Marine Ecology Progress Series*, 291, 275–
973 287. <http://doi.org/10.3354/meps291275>
- 974 Warzybok, P., Santora, J. A., Ainley, D. G., Bradley, R. W., Field, J. C., Capitolo, P. J., ... Jahncke, J.
975 (2018). Prey switching and consumption by seabirds in the central California Current
976 upwelling ecosystem: Implications for forage fish management. *Journal of Marine Systems*.
977 <https://doi.org/10.1016/j.jmarsys.2018.04.009>
- 978 Wing, S. R., Botsford, L. W., Ralston, S. V., & Largier, J. L. (1998). Meroplanktonic distribution
979 and circulation in a coastal retention zone of the northern California upwelling system.
980 *Limnology and Oceanography*, 43(7), 1710–1721
981 <http://doi.org/10.4319/lo.1998.43.7.1710>
- 982 Zwolinski, J. P., Demer, D. A., Byers, K. A., Cutter, G. R., Renfree, J. S., Sessions, T. S., &
983 Macewicz, B. J. (2012). Distributions and abundances of Pacific sardine (*Sardinops sagax*)
984 and other pelagic fishes in the California Current Ecosystem during spring 2006, 2008, and
985 2010, estimated from acoustic–trawl surveys. *Fishery Bulletin*. Retrieved from
986 http://aquaticcommons.org/8694/1/zwolinski_Fish_Bull_2012.pdf
- 987

