

1 **Inshore Acoustic Surveys in the Eastern and Central Gulf of Alaska**

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18 ABSTRACT

19 A series of daytime replicate (spring/summer/fall) acoustic surveys were conducted at 11 inshore  
20 sites along the Kodiak Island/Kenai Peninsula area and the outer coast of Southeast Alaska as  
21 part of the Gulf of Alaska Integrated Ecosystem Research Program in 2010, 2011, and 2013. A  
22 two-frequency technique was used to classify backscatter as 'fish' or 'macrozooplankton' based  
23 on the observed relative frequency response, which are used as proxies for the abundance of fish  
24 with swimbladders and large-bodied zooplankton. There was a strong 'site effect'; that is,  
25 consistent differences among sites. However, acoustic backscatter classified as fish and  
26 macrozooplankton was highly variable among repeat visits. The effects of site (i.e. sampling  
27 location) were larger than those of season or year. There were no consistent differences in  
28 backscatter between sites in the Kodiak Island/Kenai Peninsula area and Southeast Alaska. The  
29 acoustic proxies for the abundance of fish and large-bodied zooplankton increased substantially  
30 with increasing bottom depth over a depth range of 5-250 m, both within and across inshore  
31 sites. Backscatter from both fish and macrozooplankton was low at water depths < 80 m. In the  
32 inshore Gulf of Alaska, water depth appears to be a key characteristic structuring pelagic  
33 communities during daytime with sound-scattering fishes and large-bodied zooplankton being  
34 scarce in relatively shallow inshore habitats compared to adjacent deeper habitats.

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36 Key words: Gulf of Alaska, acoustic surveys, echo surveys, fish, macrozooplankton, nearshore  
37 pelagic environment, depth.

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## 42 **1. Introduction**

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44           The Gulf of Alaska (GOA) is a complex and productive environment supporting diverse  
45 fish communities and sizeable fisheries (reviewed in Hood and Zimmerman, 1987; Mundy,  
46 2005). Compared to the eastern GOA, the western GOA exhibits a wider continental shelf (Fig.  
47 1, Weingartner, 2005), a later spring bloom and a higher mean chlorophyll-*a* concentrations  
48 (Waite and Mueter, 2013), and a more abundant but less diverse demersal fish community  
49 (Mueter and Norcross, 2002). A primary aim of the Gulf of Alaska Integrated Ecosystem  
50 Research Program (GOAIERP) described in this volume was to provide a synoptic view of the  
51 distribution and abundance of key species of fishes and their habitat associations from the  
52 shoreline out to beyond the shelf-break across the region (NRC, 2002; Dickson and Baker,  
53 2016). Field sampling of fishes during this program consisted of a series of seasonal surveys  
54 from the nearshore to the offshore GOA basin. This was accomplished by sampling the offshore  
55 areas with a large survey vessel (McGowan et al., 2016) while a series of inshore sites (i.e.  
56 coastal bays and areas adjacent to islands) were sampled with a smaller survey vessel (Ormseth  
57 et al., 2017). The goals of this field sampling were to assess spatial and temporal variability of  
58 the ecosystem by comparing the east and west GOA regions across spring, summer, and fall and  
59 to determine habitat associations of key fish species. Here, we broadly characterize the relative  
60 abundance and distribution of pelagic fishes and large-bodied zooplankton at a series of inshore  
61 study sites within bays and around islands in the eastern and central GOA by means of repeated  
62 seasonal acoustic surveys.

63           The mountainous and glaciated coastline of the GOA is a diverse and complex coastal  
64 landscape which includes many fjords, embayments and islands, which are the result of

65 interacting tectonic and glacial processes (Hampton et al., 1987; Weingartner, 2005). Many  
66 fishes inhabit inshore areas in the GOA, often as juveniles (Rogers et al., 1986; Johnson et al.,  
67 2012). These areas are considered important nursery grounds for juvenile fishes (Rogers et al.,  
68 1986; Manson et al., 2005; Johnson et al., 2012; Sheaves et al., 2015), exhibiting environmental  
69 and biological conditions that differ from those in more offshore areas. For example, inshore  
70 habitats in the GOA are heavily influenced by freshwater input from watersheds and glacial  
71 runoff (Royer, 1982; Weingartner, 2005). Inshore habitats are subject to substantial summer  
72 heating and winter cooling and experience higher seasonal environmental variability than deeper  
73 and more offshore habitats (Weingartner, 2005; Johnson et al., 2012). Fishes may exploit this  
74 environmental variability by occupying inshore habitats when conditions favor survival and  
75 growth (Rogers et al., 1986, Johnson et al, 2009). The dynamics of habitat choice at different life  
76 history stages thus has the potential to influence the survival and growth of fish populations.  
77 This underscores the importance of a comprehensive understanding of how inshore habitats are  
78 used by fishes in the GOA. Although there has been substantial sampling of fishes in intertidal  
79 and shallow (< 10 m) subtidal areas; e.g. Rogers et al., 1986; Johnson et al., 2012), less  
80 information is available regarding pelagic fishes and zooplankton in the adjacent inshore pelagic  
81 habitats. Surveys in these areas have generally been limited in their geographic and temporal  
82 scope, and have used different methods in shallow and deep water (e.g. Rogers et al., 1986;  
83 Sigler et al., 2004; Arimitsu et al., 2008; Witteveen et al., 2008). Thus, it remains unclear to  
84 what extent fishes use shallow inshore pelagic habitats in the GOA.

85           In this study, we examine the broad-scale abundance and distribution of acoustically  
86 detected fishes and macrozooplankton over a wide depth range (5-250 m) in poorly sampled  
87 inshore sites in the GOA. The primary goals of this work were to conduct a series of acoustic

88 surveys in representative inshore study sites (Zimmermann et al., 2016 ; Ormseth et al., 2017,  
89 Zimmermann, in press) to quantify the abundance and distribution of fishes and  
90 macrozooplankton in these habitats, and to quantify seasonal, regional, and interannual patterns  
91 in abundance. We used acoustic methods to quantify the abundance of sound-scattering fish and  
92 zooplankton in coastal bays and island systems as these methods allow a large range of water  
93 depths to be sampled with consistent methods at high sampling density. In addition, acoustic  
94 methods allow for future comparison of inshore and offshore habitats (NRC, 2002), as offshore  
95 surveys have been conducted as part of this program (McGowan et al., 2016; Ormseth et al.,  
96 2017) and previous studies in the GOA have also used comparable methods (e.g. Logerwell et  
97 al., 2007; Jones et. al., 2014; Witteveen et al., 2015; Simonsen et al., 2016).

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## 99 **2. Methods**

100

### 101 *2.1 Inshore acoustic surveys*

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103 A series of seasonal acoustic surveys (spring, summer, fall) were conducted in 11 inshore  
104 areas of the GOA (Table 1, Fig. 1) as part of GOAIERP in 2011 and 2013. These coastal areas  
105 (bays, and waters immediately surrounding islands) were chosen as study sites representative of  
106 the diverse inshore habitats in the east and west GOA that may be important nursery areas for  
107 fishes. The study sites were selected to represent the diversity of habitats of the inshore GOA  
108 region (e.g. small bays, large bays, and island systems). The sites were selected such that to the  
109 degree possible, sites with similar characteristics were identified in the east and west study  
110 regions to allow for regional comparisons (Ormseth et al., 2017).

111 Surveys were conducted at five sites (Fig. 1) in the Kodiak Island/Kenai Peninsula area  
112 (hereafter referred to as the “west study region”): (1) Kiliuda Bay, (2) Izhut Bay, (3) the Barren  
113 Islands, (4) Port Dick, and (5) Aialik Bay. An additional six sites on the outer coast of Southeast  
114 Alaska (hereafter referred to as the “east study region”) were also surveyed (Fig. 1): (1) Whale  
115 Bay, (2) St. Lazaria Island, (3) Salisbury Sound, (4) Islas Bay, (5) Torch Bay, and (6) Graves  
116 Harbor. These study sites, which are described in detail elsewhere (Ormseth et al., 2017;  
117 Zimmermann et al.; 2016, and Zimmermann, in press), are summarized in Table 1.

118 To explore how physical differences among sites influenced fish and macrozooplankton  
119 distributions, we assigned each site to a group following Zimmermann (in press), who classified  
120 the sites into groups on the basis of 56 metrics characterizing the shoreline, bathymetry,  
121 sediments, depths and watersheds. This resulted in the following groups: east small bays (ES;  
122 Islas Bay, Torch Bay, Graves Harbor), east large bays (EL; Salisbury Sound and Whale Bay),  
123 west medium bays (WM; Port Dick, Izhut Bay, Kiliuda Bay), islands (IS; Barren Islands), and  
124 Aialik Bay (AB). Aialik Bay had a unique set of physical features and formed its own distinct  
125 group (Zimmermann, 2016). St. Lazaria, which was not considered by Zimmermann (in press),  
126 was included in the IS site group as it is also an island system.

127 We conducted surveys of acoustic backscatter in these sites in spring, summer, and fall of  
128 2011 and 2013 (Table 1). In addition, surveys of 4 sites in the east study region were conducted  
129 during a summer 2010 pilot study using the same methods. Each site was sampled 4-7 times  
130 during 13 cruises of ~15 days duration. During each season, the east study region was sampled  
131 first followed by the west study region. All sites could not be sampled during the fall cruises  
132 (Table 1) due to inclement weather and a U.S. government shutdown which prematurely

133 terminated the fall 2013 cruise. A total of 61 site-surveys covering 4100 km of acoustic transects  
134 were completed.

135         The surveys were conducted aboard two chartered vessels: work in the west study region  
136 was conducted on the R/V *Island C*, a 22.5 m research vessel, and surveys in the west study  
137 region were conducted aboard the F/V *Seaview*, a 16.5 m crabber/longliner. Surveys covered the  
138 inshore area, which in the case of the coastal bays was defined as the area within the mouth of  
139 the bay, and in the case of islands all transects were within 4.6 km of land (see Ormseth et al.,  
140 2017 for maps of the survey tracks). A systematic parallel transect design was used except in  
141 narrow bays where a parallel design would result in a substantial portion of effort expended on  
142 cross-transect transits (Simmonds and MacLennan, 2005). In the narrow bays of Whale Bay, the  
143 northwestern arm of Kiliuda Bay, and near the entrance to Taylor Bay in Port Dick, a zigzag  
144 transect pattern was used, with each leg of the zig-zag pattern defining a transect. The spacing of  
145 parallel transects ranged from 0.25 km apart in smaller bays such as Torch Bay and Graves  
146 Harbor to 3.7 km apart in the Barren Islands. Transects were conducted during daylight hours  
147 and extended as close to shore as safe navigation allowed and typically terminated when depths  
148 of ~15-20 m were encountered.

149         Acoustic backscattering was measured using calibrated Simrad EK60 38 and 120 kHz  
150 echo sounders equipped with model 38-12 and 120-7C transducers in a YSI tow body towed at  
151 speeds of 3-4 m s<sup>-1</sup> from the side of the survey vessel at a depth of ~1.5 m. The echosounder,  
152 which produced conical beams of 12° at 38 kHz and 7° at 120 kHz, was operated continuously at  
153 a pulse rate of 2 s<sup>-1</sup> and a pulse duration of 0.512 ms. The echosounder was calibrated 2-3 times  
154 per survey using the standard sphere method (Foote et al., 1987; Demer et al., 2015) with a 38.1  
155 mm tungsten carbide sphere.



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157 *2.2 Skiff acoustic surveys in shallow water*

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159           Shallow areas adjacent to the shoreline (water depths of 5-30 m) were not accessible to  
160 the survey vessel (e.g. in many fjords the walls are steep and 30 m depth is very close to  
161 shore). To investigate whether high densities of fish were present in these areas, we made  
162 additional acoustic observations adjacent to the shoreline at the study sites from a 5 m inflatable  
163 boat (hereafter referred to as the ‘skiff’) powered by a 20-hp 4-stroke outboard motor. A total of  
164 20 skiff surveys covering 381 km of trackline were conducted at 7 of the study sites starting in  
165 summer 2011 (Table 1). The skiff was equipped with a battery-powered EK60 echosounder and  
166 a 38/200 kHz combi-D single-beam transducer mounted to the transom on a 1 m pole, which was  
167 operated at a pulse rate of 2 s<sup>-1</sup> and a pulse duration of 0.512 ms. The transducer used on the  
168 skiff had a 13° by 21° elliptical beam at 38 kHz, and a 7° conical beam at 200 kHz. The skiff  
169 echosounder was calibrated once per cruise using the single-beam method described in Demer et  
170 al. (2015) with a 38.1 mm tungsten carbide sphere.

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172 *2.3 Fish sampling*

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174           In acoustic surveys of fish, trawls are typically used to determine the size and species  
175 composition of acoustic scatterers (e.g. McClatchie et al., 2000; Simmonds and MacLennan,  
176 2005). However, the vessels used for the inshore surveys were not equipped to deploy standard  
177 trawl gear. An otter trawl was modified into a small single-warp midwater trawl (3 m vertical

178 and 6 m horizontal opening; additional detail in Ormseth et al., 2017), and deployments from the  
179 survey vessels were attempted, but due to limitations in vessel horsepower and the equipment  
180 available, we were not able to tow this net adequately in midwater. We thus attempted alternate  
181 methods to capture fishes to determine the identity of the acoustic scatters, including a gill net,  
182 cast nets, an underwater video camera, dip nets, and jigging lures with rod and reel (Ormseth et  
183 al., 2017).

184 Jigging lures was the only method to consistently capture fishes and was thus adopted as  
185 the primary method to sample fish during the acoustic surveys. As time allowed, the acoustic  
186 survey was interrupted to deploy lures at the depths of scattering layers, which in some instances  
187 resulted in fish catches. We used small multi-hook herring lures (Sabiki rigs) which were more  
188 successful for capturing smaller species such as Pacific herring (*Clupea pallasii*), as well as dart  
189 lures resembling forage fishes which were more successful for capturing larger fishes such as  
190 rockfishes (*Sebastes* spp) and walleye pollock (*Gadus chalcogrammus*). Typically, both lure  
191 types were used at a location until it was determined which was most effective.

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#### 193 *2.4 Post-processing methods*

194

195 The spring and summer 2011 38 kHz data from the tow body were compromised due to  
196 undiscovered damage caused by flexing of the conductors in the transducer cable, which  
197 intermittently impacted the observations. These data were corrected for this bias by using both  
198 the transmit pulse and the bottom echo as a reference (see Ormseth et al., 2017, appendix D),  
199 which are useful measures of instrument performance (e.g. Ryan and Kloser, 2004; Hjellvik and  
200 De Robertis, 2007; Shabangu et al., 2014). After correction, residual uncertainty for 38 kHz

201 backscatter was estimated as  $\sim 0.5$  dB ( $\sim 12$  % in linear terms), while the fish/macrozooplankton  
202 classification used in this study is robust to errors of  $\pm 3$  dB (Ormseth et al.,  
203 2017). Consequently, the unaffected 120 kHz data are used as an index of abundance, and the 38  
204 kHz data, which are subject to more uncertainty due to the correction, are used only for  
205 classification of backscatter, which is robust to residual errors remaining after correction. Data  
206 from the 2010 pilot study and after summer 2011 were not subject to biases introduced by the  
207 damaged cable. After the damage was discovered, more robust armored data cables were used  
208 with the tow body and the instrumentation was carefully monitored during surveys for any signs  
209 of cable damage by 1) continuously monitoring the strength of the transmit pulse, 2) monitoring  
210 the resistance across transducer quadrants, and 3) conducting more frequent sphere calibrations.

211 Acoustic backscatter was processed in Echoview 5.4 (Myriax Pty Ltd, Hobart, Tasmania,  
212 Australia). Backscatter from the survey vessel was partitioned into signals consistent with either  
213 fish or macrozooplankton (Fig. 2) based on their relative frequency response, using a two-  
214 frequency variant of the method described in De Robertis et al. (2010). The water column data  
215 from the acoustic records (i.e. samples  $> 1$  m from the transducer and 1 m above the first bottom  
216 echo) were smoothed with a 5 ping by 0.5 m sample sliding window (using a ‘top hat’  
217 convolution algorithm, i.e. with equal weights of 1), and the frequency response ( $S_{V,120\text{kHz}} -$   
218  $S_{V,38\text{kHz}}$ ) in each cell was computed. This spatial averaging increased the spatial overlap of the  
219 backscatter measurements (i.e. as 38 and 120 kHz had different beam widths), and reduced the  
220 variability in frequency response. Analysis cells with a frequency response in the range of -16 to  
221 8 dB were assigned to the “fish” category and those in the range of 8 to 30 dB were assigned to  
222 the “macrozooplankton” category (cf. De Robertis et al., 2010, their Fig. 2). In some instances  
223 (6.2% of observations), a continuous, diffuse, and low-backscatter near-surface scattering layer

224 with a frequency response partially overlapping with that of the fish category was evident.  
225 Although the scatterers constituting this layer are unknown (e.g. Wolliez et al., 2012), the  
226 backscatter is not consistent with juvenile or adult fishes in terms of aggregation behavior,  
227 scattering strength, and frequency response. This backscatter (3.5% of total 120 kHz  
228 backscatter) was manually excluded.

229 The 120 kHz backscatter data from 6 m below the surface to 0.5 m above the sounder-  
230 detected bottom were echo-integrated as the nautical area scattering coefficient ( $s_A$ ,  $m^2 \text{ nmi}^{-2}$ ) or  
231 the volume backscattering coefficient ( $s_v$ ,  $m^{-1}$ ), which are linear measures of total water column  
232 (i.e. integrated over the water column) or backscatter per unit volume, respectively (MacLennan  
233 et al., 2002). The data were averaged in 100 m along-track units and 5 m depth bins. A  $-67 \text{ dB}$   
234 re  $1 \text{ m}^{-1}$  minimum  $S_v$  integration threshold was used for the fish category, and  $-75 \text{ dB}$  re  $1 \text{ m}^{-1}$  for  
235 the macrozooplankton category. Data were summarized by transect by first excluding  
236 observations while the vessel transited between transects and then computing the mean  
237 backscatter for each transect by averaging all 100 m along-track samples on that transect. The  
238 mean backscatter per unit area for each site sampled on a given cruise was computed by  
239 averaging the observations over all transects consistently visited on all cruises (Table 1).

240 The backscatter measurements from the skiff's 38/200 kHz system were processed in an  
241 analogous manner to those from the survey vessel except that 200 kHz was used in place of 120  
242 kHz. Analysis cells from skiff acoustic data with a  $S_{V,200\text{kHz}} - S_{V,38\text{kHz}}$  frequency response in the  
243 range of  $-16$  to  $8 \text{ dB}$  were assigned to the "fish" category and those in the range of  $8$  to  $30 \text{ dB}$   
244 were assigned to the "macrozooplankton" category (De Robertis et al., 2010). The skiff  
245 transducer is subject to ringing of the transmit pulse which masks echoes from organisms at short

246 ranges (Knudsen and Larsson, 2009). Therefore, backscatter with the skiff system could be  
247 measured from a depth of 5 m below the surface to 0.5 m above the sounder-detected bottom.

248

## 249 *2.5 Statistical analysis*

250

251 To identify spatial and temporal differences in backscatter at the scale of repeated visits  
252 to each study site, we conducted a series of paired t-tests that tested for differences in the mean  
253 log-transformed backscatter observed at each site (i.e.  $\log_{10}[s_A]$ ). We limited these comparisons  
254 to the years and seasons where all study sites were sampled (spring/summer and 2011/2013).

255 To examine the relative importance of various descriptors of broad spatial scale (region  
256 [east/west], group [site grouping, see Table 1], site [sampling location, see Table 1]) and time  
257 (year, season) on fish and macrozooplankton backscatter, we conducted a series of 2-factor  
258 analyses of variance (ANOVAs) on the log-transformed site-visit average backscatter ( $\log_{10}[s_A]$ ).  
259 Tests for homogeneity of variance (Levene's test; Levene, 1960) revealed that for both fish and  
260 macrozooplankton backscatter, variances were unequal among site groups ( $p < 0.05$ ) but that all  
261 other factors met the assumption of equal variance ( $p > 0.05$ ). Therefore, ANOVA was  
262 conducted using generalized least squares and models that included site group as a factor were  
263 weighted by the site-group variances (Pinheiro et al., 2017). We sequentially tested a single  
264 combination of spatial and temporal variables in each analysis (i.e. 6 combinations of spatial and  
265 temporal predictors were tested separately, see Table 2). Explanatory factors and their  
266 interactions were considered significant at  $p < 0.05$ . Pairwise comparisons were performed to  
267 identify differences among site groups when significant differences were observed.

268 Acoustic data aggregated at the scale of a transect were used to explore potential factors  
269 influencing fish and macrozooplankton backscatter at a finer scale. We used generalized additive  
270 models (GAMs; Hastie and Tibshiriani, 1990) to evaluate the relative importance of site, season,  
271 year, and bottom depth on the acoustic backscatter categorized as fish and macrozooplankton. In  
272 this method, the functional relationship between each covariate and the response variable is  
273 estimated by simultaneously fitting multiple covariates to the data as categorical variables or  
274 nonlinear functions under the assumption that the covariates have an additive effect on the  
275 response variable. An advantage of the GAM method is that it does not require *a priori*  
276 designation of the functional form of the relationship among variables, and the model considers  
277 multiple variables simultaneously. A GAM was fit to the ‘fish’ and ‘macrozooplankton’  
278 backscatter as a means to interpret how backscatter changes with the covariates. In contrast to  
279 the statistical tests described above, this analysis used all available data as it does not require a  
280 balanced design.

281 The following model was fit to the transect-averaged acoustic measurements:

$$282 \quad b = s(\text{depth}) + f(\text{season}) + f(\text{site}) + f(\text{year}) + \text{error}, \quad (1)$$

283 where  $b$  is the  $\log_{10}$ -transformed transect-average acoustic backscatter ( $S_{A,\text{fish}}$  or  $S_{A,\text{zooplankton}}$ ),  
284  $\text{depth}$  is the mean seafloor depth observed on all echosounder observations on a given transect,  
285  $\text{season}$  (i.e. spring, summer, fall),  $\text{site}$  (see Fig. 1),  $\text{year}$  (i.e. 2010, 2011, 2013), and  $\text{error}$  is a  
286 normally distributed error term. The function  $s$  represents a nonlinear regression spline, and  $f$   
287 represents a factor accounting for categorical differences. Models were fit using the MGCV  
288 library (1.8-10, Wood, 2006) for R (R Core Team, 2015), using the Gaussian family model and  
289 identity link function. The depth effect was fit with a penalized regression spline with the shape  
290 of the spline constrained to 3 knots (Wood and Augustin, 2002). Generalized cross-validation

291 (GCV) was used to select the covariates included in the final models. The model variables were  
292 reduced by sequentially eliminating covariates whose partial effect had the lowest significance  
293 level. This process was repeated until all non-significant terms were removed and further  
294 elimination of a covariate increased the model GCV. To achieve approximately normally  
295 distributed residuals as assumed by the model, transformations were applied to transect-level fish  
296 and macrozooplankton backscatter [ $b = \log_{10}(s_A + 0.1)$ ]. We excluded 68 of 1772 transects from  
297 the analysis as the maximum depth on these transects exceeded the 250 m maximum data  
298 collection range (i.e. areas with unobserved portions of the water column were excluded).

299

### 300 **3. Results**

301

#### 302 *3.1 Fish and macrozooplankton backscatter*

303

304 Water column backscatter classified as either fish or macrozooplankton varied  
305 substantially among sites and seasons (Fig. 3). Backscatter varied with season and year although  
306 temporal trends were generally not consistent among sites. The observed backscatter was highly  
307 variable, with changes of more than an order of magnitude among repeat visits to a single site  
308 (Fig. 3). However, some patterns are evident in the data. Fish backscatter was greater than  
309 macrozooplankton backscatter during most of the surveys. Fish and macrozooplankton  
310 backscatter was low at the Islas Bay and Barren Islands sites (i.e. the IS group) during all  
311 surveys. The paired t-tests indicated that year and season had a limited effect on site-visit mean  
312 backscatter. Fish backscatter did not vary significantly with year or season ( $p > 0.05$  in both

313 cases). Macrozooplankton backscatter was significantly lower in 2013 relative to 2011 ( $p < 0.05$ )  
314 but spring and summer were not significantly different ( $p > 0.05$ ).

315 The two-way ANOVA revealed significant differences in site-mean water column  
316 backscatter among sites and site groups. In all combinations tested, fish backscatter differed  
317 among study sites and groups (Table 2, models 2a-f, Fig. 4a). Year and season did not  
318 significantly affect fish backscatter but the interaction terms were significant for all models  
319 where season was included (models 1d-f in Table 2), indicating that while seasonal differences  
320 exist, they are not consistent at the study sites. Pairwise comparisons revealed that fish  
321 backscatter in east large bays (EL) was higher than in east small bays (ES;  $p < 0.05$ ). Similarly,  
322 west medium bays (WM) exhibited higher fish backscatter than ES ( $p < 0.05$ ). The EL-WM and  
323 ES-IS pairwise comparisons were not significantly different and Aialik Bay (AB) was not  
324 different from other groups.

325 Macrozooplankton backscatter was also significantly different for all tests considering  
326 site and site groups, but not for comparisons of the east and west regions (Table 2, models 2a-2f;  
327 Fig. 4 b). Macrozooplankton water column backscatter was higher in 2011 than in 2013 when  
328 group and site were tested, but not when region was included (Table 2, model 2a). When season  
329 and group were included in a model, both were significant (Table 2, model 2e). No interaction  
330 terms were significant for the macrozooplankton analysis. Pairwise comparisons indicated that  
331 macrozooplankton backscatter was higher at WM bays relative to IS ( $p < 0.05$ ), and that the sites  
332 in the EL group exhibited higher zooplankton backscatter than the ES ( $p < 0.05$ ) and IS ( $p <$   
333  $0.01$ ) sites.

334 The acoustic observations exhibited a strong and consistent relationship between water  
335 column backscatter and seafloor depth. Backscatter from both fish and macrozooplankton was



336 substantially higher in deeper areas, with low water column backscatter in areas with bottom  
337 depths < 80 m and increasing with depth until bottom depths of ~175 m (Fig. 5a-b). The skiff  
338 surveys indicated that water column backscatter from both fish and macrozooplankton was low  
339 in the shallow areas adjacent to shore which were inaccessible to the survey vessel (Fig. 5c-d).  
340 Site-mean water column backscatter was also correlated with mean site depth for both fish and  
341 macrozooplankton (Fig. 6), indicating that despite the variability among sites (Fig. 4), on  
342 average, water column backscatter from fish and macrozooplankton was higher at the deeper  
343 study sites.

344 One potential explanation for the increase in water column backscatter with depth is the  
345 larger observation volume as site depth increases (as this is a measure of backscatter per unit area  
346 and the volume sampled increases in proportion to depth). However, measures of backscatter per  
347 unit volume were low in the upper 80 m and increased substantially at greater depth for both fish  
348 and macrozooplankton, with the highest values in the depth range of 110-150 m (Fig. 7). Thus,  
349 the observed increase in water column backscatter with seafloor depth (Figs 5-6) is primarily  
350 attributable to higher abundances of organisms at depths >80 m.

351 The GAM models fitted to the transect-average data sets supports the relationship  
352 between water column backscatter and depth. In the best-fitting fish backscatter model (Table 3,  
353 model 1a) fish backscatter was strongly associated with mean transect depth, increasing by more  
354 than an order of magnitude (i.e. 1 log<sub>10</sub> unit) between 10 and 100 m (Fig. 8a). Fish backscatter  
355 was lower in 2011 compared to other years (Fig. 8b), and there was a strong site effect (Fig. 8c)  
356 with higher backscatter at St. Lazaria, Torch Bay, and Kiliuda Bay, and lower backscatter at  
357 Graves Harbor and the Barren Islands. In addition, there was a seasonal effect with higher  
358 average backscatter in summer and fall than in spring (Fig. 8d). Analysis of macrozooplankton

359 backscatter (Table 3, model 2a) revealed increased backscatter with mean transect depth (Fig.  
360 9a), with a ~300-fold (i.e.  $2.5 \log_{10}$  units) predicted change in total water column backscatter as  
361 depth increases from 10-200 m, lower abundance in 2013 compared to other years (Fig. 9b),  
362 differences among sites (Fig. 8c), and higher macrozooplankton backscatter in summer than  
363 spring, and lower backscatter in fall (Fig. 9d).

364         Of the factors considered, depth had the largest effect on transect-mean fish and  
365 macrozooplankton water column backscatter (i.e. compare the magnitudes of the partial effects  
366 in Figs. 8 and 9). To gauge the importance of the depth effect, we fit alternative models. When  
367 depth is excluded from consideration in the transect-level GAM, performance drops substantially  
368 for both fish and macrozooplankton backscatter (i.e. compare models 1a-b and 2a-b in Table  
369 3). When only depth is used to predict backscatter, the resulting models explain more of the  
370 deviance with many fewer degrees of freedom and lower GCV scores than when season or year  
371 are considered (i.e. compare models 1b-c and 2b-c in Table 3). Thus, depth was a better  
372 predictor of fish and zooplankton backscatter than season or year at the transect level.

373

### 374 *3.2 Fish catches*

375

376         A total of 302 fishes were captured when targeting fish aggregations observed  
377 acoustically by jigging lures on survey transects (Table 4). The primary species captured were  
378 rockfishes, Pacific herring, walleye pollock, and Pacific cod (*Gadus macrocephalus*). Walleye  
379 pollock, and Pacific cod were more abundant in the west study region sites, and rockfishes  
380 tended to be more abundant in the catches in the east study region (e.g. rockfishes were the most

381 common species at 5 of 6 sites). In some cases, the jig catches likely reflected the primary  
382 sources of the acoustic backscatter observed with the echosounder. For example, rockfishes were  
383 readily captured when targeting demersal schools at the Saint Lazaria Island site, and it is likely  
384 that the fish in this area are dominated by demersal rockfish. In addition, jigging on high-  
385 backscatter schools in Kiliuda and Aialik bays suspected to be Pacific herring based on their  
386 aggregation behavior confirmed that these were schools of herring. However, it was clear that  
387 jigging was highly selective and often inefficient as it was not always effective in identifying  
388 sound-scattering aggregations (e.g. sampling of near-bottom aggregations in rocky areas often  
389 confirmed the presence of rockfishes, but jigging on midwater scattering layers often yielded no  
390 catch).

391

392

#### 393 **4. Discussion**

394

395 Acoustic backscatter from fish and macrozooplankton at the 11 inshore study sites  
396 sampled in the GOA was highly variable but exhibited consistent differences among sites, both  
397 when study sites were considered individually and when the sites were grouped based on  
398 physical similarities (Zimmermann et al., 2016; Zimmermann, in press). These site effects were  
399 stronger than the temporal changes attributable to season or year across the habitats. Backscatter  
400 did not differ consistently between sites in the west (Kodiak Island/Kenai Peninsula) and east  
401 (Southeast Alaska) study regions. This contrasts with observations of groundfish distribution on  
402 the GOA shelf where biomass was higher in the western GOA (Mueter and Norcross, 2002). It is  
403 possible that the difference in the habitats sampled in the two regions increases variability and

404 masks (the smaller) differences in abundance between the two regions. The east large (Salisbury  
405 Sound, Whale Bay) and west medium (Port Dick, Izhut Bay, Kiliuda Bay) sites tended to exhibit  
406 higher fish and macrozooplankton backscatter than the smaller, shallower bays. These larger  
407 bays tend to be similar: they cluster together in an analysis of the physical characteristics of the  
408 bays (Zimmermann, in press). Thus, although fish and zooplankton backscatter was highly  
409 variable, on average, there were consistent differences in backscatter across sites.

410 We relied on a two-frequency acoustic discrimination method to classify acoustic  
411 backscatter as consistent with either 'fish' or 'macrozooplankton'. The method allows for fishes  
412 to be discriminated from smaller fluid-like scatters (i.e. zooplankton) as there is a sizeable and  
413 consistent difference in frequency-dependent scattering for many zooplankton-like targets but  
414 not for fishes with swimbladders (e.g. Kang et al., 2002; Lavery et al., 2007; De Robertis et al.,  
415 2010; Lezama-Ochoa et al., 2011). Although this technique allows for large areas to be surveyed  
416 using acoustic-based proxies of abundance in a consistent fashion, it does not produce species-  
417 level or size information. Small fishes with swimbladders are strong acoustic scatters and cannot  
418 be distinguished from larger individuals with any confidence based on differences in frequency  
419 or amplitude at the frequencies used in this study (Horne et al., 2000; Gauthier and Horne, 2004;  
420 De Robertis et al., 2010). Thus, the fish backscatter cannot be attributed to a given species or  
421 size class of fish based on the acoustic signal. In contrast, at the frequencies used in this study,  
422 scattering from zooplankton is highly dependent on material properties and size (Kang et al.,  
423 2002; Lavery et al., 2007). At these frequencies, the backscatter from many zooplankton taxa  
424 (e.g. crustaceans) scales roughly as the fourth power of length (Greenlaw, 1979). Thus, the  
425 index of macrozooplankton backscatter is likely dominated by the contributions from the largest

426 organisms such as amphipods and euphausiids as is the case in other areas (e.g. Ballón et al.,  
427 2011; Ressler et al. 2012) including the offshore GOA (Simonsen et al., 2016).

428         There was a strong depth gradient in acoustically determined fish and macrozooplankton  
429 abundance in inshore bays in the GOA, with much higher abundance in deeper habitats. Water  
430 depth was an important factor at all three scales considered (100 m along-track interval, transect,  
431 study site), and depth likely explains some of the differences in fish and zooplankton abundance  
432 across sites and site groups. A similar increase in fish abundance with depth has been noted by  
433 Mueter and Norcross (2002) and Rooper and Martin (2012), who demonstrated that bottom trawl  
434 catches of adult fishes on the GOA shelf increased substantially with water depth over the ~20-  
435 200 m depth range. Our observations are also consistent with the distribution of age 1+ walleye  
436 pollock, which are the dominant sound scatterers in daytime acoustic surveys of the offshore  
437 GOA shelf: pollock are abundant at depths > 75 m (Jones et al., 2014). The largest zooplankton  
438 in the GOA tend to vertically migrate, avoiding surface waters during daytime (Mauchline, 1980;  
439 Coyle and Pinchuk, 2005). This is consistent with our observations of low macrozooplankton  
440 backscatter in near-surface waters during daytime. However, an acoustic index of total water-  
441 column euphausiid abundance derived from these offshore GOA surveys was not significantly  
442 related to bottom depth (Simonsen et al., 2016). This discrepancy may be because this offshore  
443 study did not sample the shallow areas (< 80 m) where backscatter from large zooplankton was  
444 lowest in our inshore measurements.

445         Backscatter observed in shallow water sampled with the skiff was low compared to that  
446 observed in deeper water farther from shore with the larger survey vessel. It should be noted that  
447 the skiff and survey vessels used different high frequencies (120 vs 200 kHz). The difference in  
448 frequency combined with frequency-dependent scattering of biological scattering means that the

449 results from the skiff and the survey vessel are not directly comparable. The macrozooplankton  
450 index from the 200 kHz skiff observations will be higher 120 kHz index from larger survey  
451 vessel when small zooplankton are dominant as small zooplankton will contribute more to the  
452 higher-frequency observations (Lavery et al., 2007). For fishes and large-bodied zooplankton  
453 such as adult euphausiids, the difference in frequencies used is expected to account for  
454 backscatter differences of approximately a factor of 2 (Gauthier and Horne, 2004, De Robertis et  
455 al., 2010). Given that very low backscatter was observed by the skiff, biases of this magnitude  
456 would not invalidate the conclusion that during daytime, acoustically detectable juvenile and  
457 adult fish and large-bodied zooplankton are scarce in shallow inshore pelagic habitats (i.e. areas  
458 with water depths of 5-80 m) including those adjacent to the shoreline.

459 Acoustic backscatter with a frequency response consistent with macrozooplankton (i.e.  
460  $S_{V,120\text{ kHz}} \gg S_{V,38\text{ kHz}}$ ) varied spatially and temporally, and was highly depth-dependent. On  
461 average, macrozooplankton backscatter was lower in 2013 relative to 2011, and tended to be  
462 higher in summer than in the fall. It is possible that the reduced macrozooplankton backscatter  
463 in fall results from mortality or transport during summer months: for example, the transect-mean  
464 GAM indicated that on average, fish abundance was higher in the summer and fall than in spring.  
465 This seasonal pattern is consistent with previous sampling in the nearshore GOA (Rogers et al.,  
466 1986; Johnson et al., 2009), and the reduction in zooplankton biomass may result from predation  
467 by fishes during the summer. We did not sample acoustically-detected zooplankton aggregations  
468 and thus cannot determine the identity of the species in these sound-scattering layers. Despite  
469 the uncertainties in the species causing the ‘macrozooplankton’ backscatter, it is clear that  
470 backscatter with a frequency response consistent with large-bodied zooplankton is strongly  
471 depth-dependent. Very little zooplankton backscatter was observed in shallow water (< 80 m

472 deep) during daytime. Large zooplankton in shallow water can be associated with the seafloor  
473 (e.g. Kringel et al., 2003), where they would be less detectable with acoustic methods (Ona and  
474 Mitson, 1996). However, the most likely explanation is that macrozooplankton in these inshore  
475 areas adjacent to deep water are avoiding surface waters during the day. Planktivorous fishes are  
476 highly effective predators in well-lit environments even at low density (e.g. Brooks and Dodson,  
477 1965; Gliwicz, 1986; Aksnes et al, 2004), and large zooplankton likely avoid near-surface  
478 pelagic habitats to minimize predation risk. Many optically conspicuous (i.e. large-bodied and  
479 pigmented) species of zooplankton engage in diel vertical migration behavior to deep, poorly  
480 illuminated midwater habitats during the day (e.g. Mauchline, 1980; Ohman and Romagnan,  
481 2015), including the largest large zooplankters in the GOA (euphausiids and amphipods, Coyle  
482 and Pinchuk, 2005)

483           Acoustic methods offer only indirect measures of abundance and acoustic surveys  
484 typically rely on trawl sampling to attribute acoustic backscattering to organisms of a given  
485 species and size (e.g. McClatchie et al., 2000; De Robertis et al., 2017). A limitation of this study  
486 is that trawl-capable vessels were not available for this study: these vessels tend to be larger,  
487 costlier, and less able to access shallow areas than those used in this study. The lack of trawl  
488 fisheries in the east study region made the availability of such vessels extremely limited. We  
489 were not successful in initial attempts with a single-warp trawl (e.g. Sarda et al., 2002) and  
490 prioritized other aspects of the multidisciplinary GOA IERP project over developing this method  
491 during this study. Development of midwater trawls that can be reliably used to target a broad  
492 size range of pelagic fishes from small, non-specialized vessels will greatly improve acoustic  
493 surveys of this type.

494           Although we attempted several methods to identify the size and species composition of  
495 fish aggregations observed acoustically, these attempts were met with limited success. Jigging  
496 proved to be the most effective method of capturing fishes. However, jigging is selective in  
497 terms of which species and size/age classes are captured (Ralston, 1990; Millar and Fryer, 1999).  
498 In addition, a large fraction of the backscatter could not be identified with confidence (i.e. in  
499 many instances no fish were captured, particularly in midwater, and the probability of capture as  
500 a function of species and size remains unknown). Despite these limitations, some general trends  
501 are evident from the jig catches: walleye pollock and Pacific cod were more abundant in the west  
502 study region, particularly at the deeper sites, and rockfishes were consistently captured in the east  
503 study region. This is consistent with previous sampling of nearshore fishes (Rogers et al., 1986)  
504 and acoustic-trawl surveys of the GOA shelf, which include Kiliuda Bay and Kenai Peninsula  
505 bays (including Port Dick, and Aailik Bay) where adult pollock were the primary sound-  
506 scattering organisms detected (Wilson et al., 2003, Guttormsen and Jones, 2010). In some  
507 situations, jigging confirmed suspected species aggregations inferred from the shapes of schools  
508 observed on the echosounder (Horne, 2000; Reid et al., 2000). For example, at the St. Lazaria  
509 Island site, backscatter was observed as near-bottom schools where rockfishes were readily  
510 captured, and very dense midwater schools in Kiliuda Bay yielded Pacific herring. Because we  
511 were often unable to identify the scatterers in our surveys, we focused on drawing broad-scale  
512 inferences based on abundance proxies (i.e. backscatter with a frequency response consistent  
513 with fish and macrozooplankton, Lezama-Ochoa et al., 2011; De Robertis and Cokelet, 2012) as  
514 this allows for the data to be considered in a consistent manner.

515           Juvenile fishes are often abundant close to shore in complex structured habitats (e.g.  
516 vegetation such as eelgrass and kelp beds) which may serve as nursery grounds (Johnson et al.,



517 2009; Laurel et al., 2007; Johnson et al., 2012). Fishes likely use these habitats as a refuge from  
518 predation (Gregory and Levings, 1996; Laurel et al., 2007; Anderson et al., 2007). Although  
519 sampling with a purse seine during these cruises indicated that fish were abundant in vegetated  
520 nearshore habitats at these study sites (Ormseth et al., 2017), our acoustic surveys of inshore  
521 bays and island systems in the GOA indicate that fish backscatter was low in the shallow pelagic  
522 habitats adjacent to the shoreline. These exposed shallow pelagic habitats are likely to be risky,  
523 and fishes likely either distribute themselves in habitats with cover (e.g. near bottom or very  
524 close to shore) or in deeper poorly-lit waters where visual predators will be less efficient  
525 (Brodeur and Wilson, 1996, Lewin et al., 2004). Patterns of habitat use are linked to the trade-  
526 off between feeding and predation risk (Lima and Dill, 1990), and fishes are likely avoiding  
527 well-lit pelagic waters where predation risk is high, and/or following their vertically migrating  
528 zooplankton prey to depth or occupying vegetated habitats during daytime. Fishes and  
529 zooplankton often exhibit diel patterns in habitat use and aggregation behavior, (e.g., Kaltenberg  
530 and Benoit-Bird, 2009), and likely make use of these shallow inshore pelagic habitats more  
531 extensively at night (Keats, 1990).

532

## 533 5. Summary

534

535 The primary finding of this study is that the abundance of fishes and large-bodied  
536 zooplankton in inshore habitats during daytime is highly depth-dependent: these organisms are  
537 scarce in shallow habitats in (< 80 m) in GOA bays and around islands compared to adjacent  
538 deeper habitats. Water depth appears to be a key characteristic structuring inshore pelagic

539 habitats in the GOA, as backscatter per unit volume was low at depths < 80 m, and water column  
540 backscatter (a proxy for abundance per unit area) increased dramatically from the shallowest  
541 depths sampled to ~ 150-200 m. Acoustic methods are well-suited for detecting aggregations of  
542 fishes with swimbladders, which are strong sound scatterers (e.g. Gauthier and Horne, 2004;  
543 Parker-Stetter et al., 2013; De Robertis et al., 2017), and allow for efficient sampling of large  
544 areas. If fish aggregations had been abundant in the shallow pelagic habitats in these daytime  
545 surveys, they would have been detected using acoustic methods. For example, we did not  
546 observe the shallow sound-scattering layers dominated by age-0 pollock that were observed  
547 throughout the offshore GOA in 2013 (McGowan et al., 2016). Similarly, we did not detect fish  
548 aggregations in pelagic habitats adjacent to the vegetated shoreline. The distributions of  
549 macrozooplankton backscatter were similar to those of fish: there was little evidence for sound-  
550 scattering aggregations of macrozooplankton in pelagic habitats at depths of < 80 m. Although  
551 in most instances, we were unable to distinguish among backscatter from different species and  
552 size classes in this study, it is clear from backscatter measurements that overall, at the inshore  
553 sites sampled in the GOA, fishes and large-bodied zooplankton are relatively scarce in shallow  
554 inshore pelagic habitats compared to the adjacent deeper habitats.

555

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557

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569

570 **References**

571

- 572 Aksnes, D.L., Nejstgaard, J., Soedberg, E., Sornes, T., 2004. Optical control of fish and  
573 zooplankton populations. *Limnol. Oceanogr.* 49, 233–238.
- 574 Anderson, J. L., Laurel, B. J., and Brown, J. A. 2007. Diel changes in behaviour and habitat use  
575 by age-0 Atlantic cod (*Gadus morhua* L.) in the laboratory and field. *J. Exp. Mar. Biol.*  
576 *Ecol.*, 351: 267-275.
- 577 Arimitsu, M.L., Piatt, J.F., Litzow, M.A., Abookire, A.A., Romano, M.D., Robards, M.D., 2008.  
578 Distribution and spawning dynamics of capelin (*Mallotus villosus*) in Glacier Bay,  
579 Alaska: a cold water refugium. *Fish. Oceanogr.* 17 (2), 137-146.
- 580 Ballon, M., Bertrand, A., Lebourges-Dhaussy, A., Gutierrez, M., Ayon, P., Grados, D., and  
581 Gerlotto, F. 2011. Is there enough zooplankton to feed forage fish populations off Peru?  
582 An acoustic (positive) answer. *Prog. Oceanogr.* 91, 360-381.
- 583 Brodeur, R. D., and Wilson, M. T. 1996. Mesoscale acoustic patterns of juvenile walleye pollock  
584 (*Theragra chalcogramma*) in the Western Gulf of Alaska. *Can. J. Fish. Aquat. Sci.*, 53:  
585 1951-1963.
- 586 Brooks, J.L., Dodson, S.I., 1965. Predation, body size, and composition of plankton. *Science*  
587 150, 28-35.
- 588 Coyle, K. O., and Pinchuk, A. I. 2005. Seasonal cross-shelf distribution of major zooplankton  
589 taxa on the northern Gulf of Alaska shelf relative to water mass properties, species depth  
590 preferences and vertical migration behavior. *Deep-Sea Res. II*, 52: 217-245.
- 591 De Robertis, A., McKelvey, D., Ressler, P.H., 2010. Development and application of empirical  
592 multi-frequency methods for backscatter classification. *Can. J. Fish. Aquat. Sci.* 67,  
593 1459–1474.
- 594 De Robertis, A., Cokelet, E.D., 2012. Distribution of fish and macrozooplankton in ice-covered  
595 and open-water areas of the eastern Bering Sea. *Deep-Sea Res. II* (65-70), 217-229.
- 596 De Robertis, A., Taylor, K., Wilson, C., Farley, E., 2017. Abundance and distribution of Arctic  
597 cod (*Boreogadus saida*) and other pelagic fishes over the U.S. continental shelf of the  
598 northern Bering and Chukchi seas *Deep-Sea Res. II* 135: 51-65
- 599 Demer, D.A., Berger, L., Bernasconi, M., Bethke, E., Boswell, K., Chu, D., Domokos, R. et al.,  
600 2015. Calibration of acoustic instruments. ICES Cooperative Research Report No. 326,  
601 130 pp.
- 602 Dickson, D. M. S., and Baker, M. R. 2016. Introduction to the North Pacific Research Board  
603 Gulf of Alaska Integrated Ecosystem Research Program (GOAIERP): Volume I  
604 Introduction. *Deep-Sea Res. II*, 132: 1-5.
- 605 Foote, K.G., Knudsen, H.P., Vestnes, G., MacLennan, D.N., Simmonds, E.J., 1987. Calibration  
606 of acoustic instruments for fish density estimation. ICES Cooperative Research Report  
607 No. 144, 81 pp.
- 608 Gauthier, S., Horne, J.K., 2004. Acoustic characteristics of forage fish species in the Gulf of  
609 Alaska and Bering Sea based on Kirchhoff-approximation models. *Can. Journal of*  
610 *Fisheries and Aquatic Sciences* 61 (10), 1839-1850.
- 611 Gliwicz, M.Z., 1986. A lunar cycle in zooplankton. *Ecology* 67 (4), 883-897.
- 612 Guttormsen, M.A., Jones, D., 2010. Results of the acoustic-trawl surveys of walleye pollock  
613 (*Theragra chalcogramma*) in the Gulf of Alaska, February-March 2010 (DY2010-01 and

614 DY2010-02). AFSC Processed Rep. 2010-05, 85 p. Alaska Fish. Sci. Cent., NOAA, Natl.  
615 Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.

616 Greenlaw, C.F., 1979. Acoustical estimation of zooplankton populations. *Limnol. Oceanogr.* 24  
617 (2), 226-242.

618 Gregory, R. S., and Levings, C. D. 1996. The effects of turbidity and vegetation on the risk of  
619 juvenile salmonids, *Oncorhynchus* spp to predation by adult cutthroat trout, *O. clarkii*.  
620 *Envir. Biol. Fish.*, 47: 279-288.

621 Hampton, M.A., Carlson, P.R., Lee, H.J., Feely, R.A., 1987. Geomorphology, sediment, and  
622 sedimentary processes. P 93-133 in Hood, D. W. and Zimmerman, S. T. , *The Gulf of  
623 Alaska: Physical Environment and Biological Resources*. United States. Ocean  
624 Assessments Division. Alaska Office; United States Minerals Management Service.  
625 Alaska OCS Region. 653 pp.

626 Hastie, T.J., Tibshirani, R.J., 1990. *Generalized Additive Models*. Chapman and Hall, London.  
627 335 pp.

628 Hjellvik, V., De Robertis, A., 2007. Vessel comparison on the seabed echo: Influence of vessel  
629 attitude. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-  
630 171, 34 p.

631 Hood, D.W., Zimmerman, S.T., 1987. *The Gulf of Alaska: Physical environment and biological  
632 resources*. United States. Ocean Assessments Division. Alaska Office; United States  
633 Minerals Management Service. Alaska OCS Region. 653 pp.

634 Horne, J.K., 2000. Acoustic approaches to remote species identification: a review. *Fish.  
635 Oceanogr.* 9 (4), 356-371.

636 Johnson, S.W., Neff, A.D., Thedinga, J.F., Lindeberg, M.R., Maseko, J.M., 2012. Atlas of  
637 nearshore fishes of Alaska: A synthesis of marine surveys from 1998 to 2011. U.S.  
638 Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-239, 261 pp.

639 Johnson, S.W., Thedinga, J.F., Neff, A.D., 2009. Invasion by saffron cod *Eleginus gracilis* into  
640 nearshore habitats of Prince William Sound, Alaska, USA. *Mar. Ecol. Prog. Ser.* 389,  
641 203-212.

642 Jones, D.T., Ressler, S.C., Steinessen, S.C., McCarthy, A., Simonsen, K.A., 2014. Results of the  
643 acoustic-trawl survey of walleye pollock (*Gadus chalcogrammus*) in the Gulf of Alaska,  
644 June-August 2013 (DY2013-07). AFSC Processed Report. 2014-06, 95 p. Alaska Fish.  
645 Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.

646 Kaltenberg, A. M., and Benoit-Bird, K. J. 2009. Diel behavior of sardine and anchovy schools in  
647 the California Current System. *Mar. Ecol. Prog. Ser.*, 394: 247-262.

648 Kang, M., Furusawa, M., Miyashita, K., 2002. Effective and accurate use of difference in mean  
649 volume backscattering strength to identify fish and plankton. *ICES J. Mar. Sci.* 59, 794-  
650 804.

651 Keats, D. 1990. A nocturnal inshore movement of juvenile cod *Gadus morhua* L. in eastern  
652 Newfoundland. *J. Exp. Mar. Biol. Ecol.*, 139: 167-173.

653 Knudsen, F. R., and Larsson, P. 2009. Discriminating the diel vertical migration of fish and  
654 *Chaoborus flavicans* larvae in a lake using a dual-frequency echo sounder. *Aquat. Living  
655 Resour.*, 22: 1-8.

656 Kringel, K., Jumars, P. A., and Holliday, D. V. 2003. A shallow scattering layer: High-resolution  
657 acoustic analysis of nocturnal vertical migration from the seabed. *Limnol. Oceanogr.*, 48:  
658 1223-1234.

- 659 Laurel, J., Stoner, A. W., Ryer, C. H., Hurst, T. P., and Abookire, A. A. 2007. Comparative  
660 habitat associations in juvenile Pacific cod and other gadids using seines, baited cameras  
661 and laboratory techniques. *J. of Exp. Mar. Biol. Ecol.*, 351: 42-55.
- 662 Lavery, A.C., Wiebe, P.H., Stanton, T.K., Lawson, G.L., Benfield, M.C., Copely, N., 2007.  
663 Determining dominant scatterers of sound in mixed zooplankton populations. *J. Acoust.*  
664 *Soc. Am.* 122, 3304-3326.
- 665 Levene, H., 1960. Robust tests for equality of variances, in: Olkin, I., Ghurye, S.G., Hoeffding,  
666 W., Madow, W.G., Mann, H.B. (Eds.) *Contributions to Probability and Statistics: Essays*  
667 *in Honor of Harold Hotelling*. Stanford University Press, Redwood City, CA, pp. 278–  
668 292.
- 669 Lewin, W. C., Okun, N., and Mehner, T. 2004. Determinants of the distribution of juvenile fish  
670 in the littoral area of a shallow lake. *Freshwater Biol.*, 49: 410-424.
- 671 Lezama-Ochoa, A., Ballon, M., Woillez, M., Grados, D., Irigoien, X., Bertrand, A., 2011. Spatial  
672 patterns and scale-dependent relationships between macrozooplankton and fish in the Bay  
673 of Biscay: an acoustic study. *Mar. Ecol. Prog. Ser.* 439, 151-168.
- 674 Lima, S. L., and Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a  
675 review and prospectus. *Can. J. Zool.*, 68: 619-640.
- 676 Logerwell, E.A., Stabeno, P.J., Wilson, C.D., Hollowed, A.B., 2007. The effect of oceanographic  
677 variability and interspecific competition on juvenile pollock (*Theragra chalcogramma*)  
678 and capelin (*Mallotus villosus*) distributions on the Gulf of Alaska shelf. *Deep-Sea Res.*  
679 *II*, 54 (23-26), 2849-2868.
- 680 MacLennan, D.N., Fernandes, P.G., Dalen, J., 2002. A consistent approach to definitions and  
681 symbols in fisheries acoustics. *ICES J. Mar. Sci.*, 59, 365-369.
- 682 Manson, F.J., Loneragan, N.R., Harch, B.D., Skilleter, G.A., Williams, L., 2005. A broad-scale  
683 analysis of links between coastal fisheries production and mangrove extent: A case-study  
684 for northeastern Australia. *Fish. Res.*, 74 (1-3), 69-85.
- 685 Mauchline, J., 1980. The biology of mysids and euphausiids *Adv. Mar. Biol.*, 18, 1-677.
- 686 McClatchie, S., Thorne, R.E., Grimes, P., Hanchet, S., 2000. Ground truth and target  
687 identification for fisheries acoustics. *Fish. Res.*, 47 (2-3), 173-191.
- 688 McGowan, D. W., Horne, J. K., and Parker-Stetter, S. L. 2016. Variability in species  
689 composition and distribution of forage fish in the Gulf of Alaska. *Deep-Sea Res. II*,  
690 doi.org/10.1016/j.dsr2.2016.11.019.
- 691 Millar, R.B., Fryer, R.J., 1999. Estimating the size-selection curves of towed gears, traps, nets  
692 and hooks. *Rev. Fish. Biol. Fisher.* , 9 (1), 89-116.
- 693 Mueter, F.J., Norcross, B.L., 2002. Spatial and temporal patterns in the demersal fish  
694 community on the shelf and upper slope regions of the Gulf of Alaska. *Fish. Bull.*, 100  
695 (3), 559-581.
- 696 Mundy, P.R., Ed., 2005. *The Gulf of Alaska: biology and oceanography*. Alaska Sea Grant  
697 College Program report AK-SG-05-01, University of Alaska Fairbanks. 214 pp.
- 698 NRC, 2002. *A century of ecosystem science: Planning long-term research in the Gulf of Alaska*.  
699 National Research Council, National Academy Press, Washington, D.C. 108 pp.  
700 Available at <http://www.nap.edu/catalog/10469.html>.
- 701 Ohman, M.D., Romagnan, J.-B., 2015. Nonlinear effects of body size and optical attenuation on  
702 diel vertical migration by zooplankton. *Limnol. Oceanogr.* 61, p 765-770. doi:  
703 10.1002/lno.10251.

- 704 Ona, E., and Mitson, R. B., 1996. Acoustic sampling and signal processing near the seabed: the  
705 deadzone revisited. *ICES J. Mar. Sci.*, 53: 677-690.  
706
- 707 Ormseth, O. A., Rand, K., and De Robertis, A. 2017. Fishes and invertebrates in Gulf of Alaska  
708 bays and islands: Results from inshore ecosystem surveys in 2011 and 2013. U.S. Dep.  
709 Commer., NOAA Tech. Memo. NMFS-AFSC-344, 140 p.  
710 [www.afsc.noaa.gov/Publications/AFSC-TM/NOAA-TM-AFSC-344.pdf](http://www.afsc.noaa.gov/Publications/AFSC-TM/NOAA-TM-AFSC-344.pdf)
- 711 Parker-Stetter, S., Horne, J.K., Farley, E., Barbee, D.H., Andrews, A.G., Eisner, L.B., Nomura,  
712 J.M., 2013. Summer distributions of forage fish in the eastern Bering Sea. *Deep-Sea*  
713 *Research II* 94, 211-230.
- 714 Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. and R Core Team (2017). nlme: Linear and  
715 Nonlinear Mixed Effects Models. R package version 3.1-131, [https://CRAN.R-](https://CRAN.R-project.org/package=nlme)  
716 [project.org/package=nlme](https://CRAN.R-project.org/package=nlme).
- 717 R Core Team, 2015. R: A language and environment for statistical computing. R Foundation for  
718 Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL [http://www.R-](http://www.R-project.org/)  
719 [project.org/](http://www.R-project.org/)
- 720 Ralston, S., 1990. Size selection of snappers (*Lutjanidae*) by hook and line gear. *Can. J.Fish.*  
721 *Aquat. Sci.*, 47 (4), 696-700.
- 722 Reid, D., Scalabrin, C., Petigas, P., Masse, J., Aukland, R., Carrera, P., Gregorakarakos, S.,  
723 2000. Standard protocols for the analysis of school based data from echo sounder  
724 surveys. *Fish. Res.*, 47, 125-136.
- 725 Ressler, P.H., De Robertis, A., Warren, J.D., Smith, J.D., Kotwicki, S., 2012. Developing an  
726 acoustic index of euphausiid abundance to understand trophic interactions in the Bering  
727 Sea ecosystem. *Deep-Sea Research II*, 65-70, 184-195.
- 728 Rogers, D.E., Rogers, B.J., Rosenthal, R.J., 1986. The nearshore fishes. P 399-415 in Hood, D.  
729 W. and Zimmerman, S. T. *The Gulf of Alaska Physical Environment and Biological*  
730 *Resources*. United States. Ocean Assessments Division. Alaska Office; United States  
731 Minerals Management Service. Alaska OCS Region. 653 pp.
- 732 Rooper, C. N., and Martin, M. H. 2012. Comparison of habitat-based indices of abundance with  
733 fishery-independent biomass estimates from bottom trawl surveys. *Fish. Bull.*, 110: 21-  
734 35.
- 735 Royer, T.C., 1982. Coastal fresh-water discharge in the northeast Pacific. *J. Geophys. Res. –*  
736 *Oceans*, 87 (Nc3), 2017-2021.
- 737 Ryan, T. E., and Kloser, R. J. 2004. Quantification and correction of a systematic error in Simrad  
738 ES60 echosounders. ICES FAST white paper, Gdansk. Copy available from CSIRO  
739 Marine and Atmospheric Research, GPO Box 1538, Hobart, Australia.
- 740 Sarda, F., Recasens, L., Abello, P., Rotllant, G., Moli, B., 2002. Commercial feasibility trial for a  
741 single-warp deep-water "Maireta" (OTMS) trawl gear. *Fish. Res.*, 55 (1-3), 121-130.
- 742 Shabangu, F.W., Ona, E., Yemane, D., 2014. Measurements of acoustic attenuation at 38 kHz by  
743 wind-induced air bubbles with suggested correction factors for hull-mounted transducers.  
744 *Fish. Res.*, 151, 47-56.
- 745 Sheaves, M., Baker, R., Nagelkerken, I., Connolly, R.M., 2015. True Value of Estuarine and  
746 Coastal Nurseries for Fish: Incorporating Complexity and Dynamics. *Estuaries and*  
747 *Coasts*, 38 (2), 401-414.
- 748 Simmonds, E.J., MacLennan, D.N., 2005. *Fisheries Acoustics* 2nd. Ed. Blackwell Science LTD,  
749 Oxford, UK 437 p.

750 Simonsen, K.A., Ressler, P.H., Rooper, C., Zandor, S.G., 2016. Spatio-temporal distribution of  
751 euphausiids: an important component to understanding ecosystem processes in the Gulf  
752 of Alaska and eastern Bering Sea. ICES J. Mar. Sci., doi:10.1093/icesjms/fsv1272.

753 Sigler, M.F., Womble, J.N., Vollenweider, J.J., 2004. Availability to Steller sea lions  
754 (*Eumetopias jubatus*) of a seasonal prey resource: a prespawning aggregation of eulachon  
755 (*Thaleichthys pacificus*). Can. J. Fish. Aquat. Sci., 61 (8), 1475-1484.

756 Waite, J. N., and Mueter, F. J. 2013. Spatial and temporal variability of chlorophyll-a  
757 concentrations in the coastal Gulf of Alaska, 1998–2011, using cloud-free reconstructions  
758 of SeaWiFS and MODIS-Aqua data. Prog. Oceanogr., 116: 179-192.

759 Weingartner, T.C., 2005. Physical and Geological Oceanography: Coastal Boundaries and  
760 Coastal and Ocean Circulation. P 35 -48 in Mundy, P. R, ed. The Gulf of Alaska:  
761 Biology and Oceanography. Alaska Sea Grant College Program report AK-SG-05-01,  
762 University of Alaska Fairbanks. 219 pp.

763 Wilson, C.D., Hollwed, A.B., Shima, M., Walline, P., Stienessen, S., 2003. Interactions  
764 between commercial fishing and walleye pollock. Alaska Fishery Research Bulletin 10,  
765 61-77.

766 Witteveen, B.H., Foy, R.J., Wynne, K.M., Tremblay, Y., 2008. Investigation of foraging habits  
767 and prey selection by humpback whales (*Megaptera novaeangliae*) using acoustic tags  
768 and concurrent fish surveys. Mar. Mammal Sci. 24, 516-534.

769 Witteveen, B.H., De Robertis, A., Guo, L., Wynne, K.M., 2015. Using dive behavior and active  
770 acoustics to assess prey use and partitioning by fin and humpback whales near Kodiak  
771 Island, Alaska. Mar. Mammal Sci. 31 (1), 255-278.

772 Woillez, M., Ressler, P.H., Wilson, C.D., 2012. Multifrequency species classification of  
773 acoustic-trawl survey data using semi-supervised learning with class discovery. J.  
774 Acoust. Soc. Am. 131, EL184-EL190.

775 Wood, S.N., 2006. Generalized additive models: An introduction with R. Chapman and Hall,  
776 Boca Raton, Florida, 392 pp.

777 Wood, S.N., Augustin, N.H., 2002. GAMs with integrated model selection using penalized  
778 regression splines and applications to environmental modelling. Ecol. Model., 157, 157-  
779 177.

780 Zimmermann, M., in press, this issue. Comparison of central and eastern Gulf of Alaska study  
781 sites. Deep-Sea Research II.

782 Zimmermann, M., Reid, J.A., Golden, N., 2016. Using smooth sheets to describe groundfish  
783 habitat in Alaskan waters, with specific application to two flatfishes. Deep-Sea Research  
784 II, <http://dx.doi.org/10.1016/j.dsr2.2015.02.020i>.

785



Table 1. Inshore surveys and sampling effort at each site listed from west to east. The study region and group each site was assigned to (see text), the area of the bay, the number of survey transects that were consistently visited, the total distance surveyed in a single survey, and the mean depth observed along the survey trackline is given. The date each survey started (duration was 1-3 days) is given. The ‘\*’ indicates that skiff sampling of shallow (< 30 m) nearshore areas occurred at the site, the ‘x’ indicates that a site was not sampled, and *n/a* indicates that the area is not reported for islands as there is no clear demarcation of surface area in this case.

Study site	Region	Site group	Latitude (°N)	Longitude (°W)	Area (km <sup>2</sup> )	# transects per survey	Survey length (km)	Mean depth (m)	2010 summer	2011 spring	2011 summer	2011 fall	2013 spring	2013 summer	2013 fall
Kiliuda Bay	West	WM	57.308	153.048	93.5	28	86.9	66.3	x	5/7	8/7*	10/16*	5/11*	8/15	11/3*
Izhut Bay	West	WM	58.205	152.266	89.5	30	69.1	71.9	x	5/10	8/3	10/21*	5/21	8/18*	x
Barren Islands	West	IS	58.948	152.159	n/a	5	29.4	79.21	x	5/14	8/11	10/23	5/15	8/21	x
Port Dick	West	WM	59.279	151.133	64.4	21	50.1	116.2	x	5/14	8/12	10/25*	5/17*	8/22*	11/7
Aialik Bay	West	AB	59.775	149.657	239.1	16	50.2	119.4	x	5/17	8/15	x	5/19	8/25	x
Graves Harbor	East	ES	58.284	136.736	12.6	16	23.9	74.8	x	4/29	7/18	x	4/27*	8/4*	x
Torch Bay	East	ES	58.322	136.808	7.5	24	23.1	52.8	7/16	4/27	7/17	x	4/27	8/3	x
Islas Bay	East	ES	57.808	136.384	7.3	27	31.7	41.3	7/14	4/25	7/14	9/30	4/25*	8/1	x
Salisbury Sound	East	EL	57.332	135.696	70.2	22	53.8	106.2	x	4/22	7/11	9/21*	4/22*	7/30*	9/22*
Saint Lazaria Island	East	IS	56.980	135.702	n/a	11	51.4	38.6	7/20	4/21	7/10	9/24	4/21	7/28	9/25
Whale Bay	East	EL	56.655	134.951	71.5	76	57.1	100.2	7/22	4/17	7/7	9/25*	4/18*	7/24*	9/26*

Table 2. Results of a series of 2-factor ANOVAs with interactions exploring the effects of time and space on site-mean fish and macrozooplankton backscatter. For each model the table indicates the response variable and the predictor variables used. The time predictors considered are year (2011/2013), season (spring/summer), and the space predictors are region (east GOA/west GOA), group (see Table 1), and study site (see Table 1). P-values and predictors in bold indicate significance at the  $p < 0.05$  level. df = denominator degrees of freedom.

Model	Response	Predictors		df	F			p-value		
		time	space		time	space	int.	time	space	int.
1a	$\log_{10}(S_{A, \text{fish}})$	year	region	40	0.50	1.04	0.97	0.482	0.313	0.330
1b	$\log_{10}(S_{A, \text{fish}})$	year	<b>group</b>	34	0.44	8.14	1.03	0.512	<b>0.000</b>	0.407
1c	$\log_{10}(S_{A, \text{fish}})$	year	<b>site</b>	22	0.89	4.93	0.28	0.356	<b>0.001</b>	0.978
1d	$\log_{10}(S_{A, \text{fish}})$	season	region	40	0.08	1.13	4.63	0.782	0.295	<b>0.038</b>
1e	$\log_{10}(S_{A, \text{fish}})$	season	<b>group</b>	34	3.84	8.75	3.52	0.058	<b>0.001</b>	<b>0.017</b>
1f	$\log_{10}(S_{A, \text{fish}})$	season	<b>site</b>	22	0.23	8.74	2.34	0.638	<b>0.000</b>	<b>0.047</b>
2a	$\log_{10}(S_{A, \text{zp}})$	year	region	40	2.976	0.018	0.077	0.092	0.894	0.782
2b	$\log_{10}(S_{A, \text{zp}})$	<b>year</b>	<b>group</b>	34	4.630	10.150	0.619	<b>0.039</b>	<b>0.000</b>	0.652
2c	$\log_{10}(S_{A, \text{zp}})$	<b>year</b>	<b>site</b>	22	6.399	5.992	0.431	<b>0.019</b>	<b>0.000</b>	0.916
2d	$\log_{10}(S_{A, \text{zp}})$	season	region	40	0.171	0.017	0.402	0.681	0.897	0.530
2e	$\log_{10}(S_{A, \text{zp}})$	<b>season</b>	<b>group</b>	34	4.335	12.252	0.423	<b>0.045</b>	<b>0.000</b>	0.791
2f	$\log_{10}(S_{A, \text{zp}})$	season	<b>site</b>	22	0.323	4.965	0.478	0.575	<b>0.001</b>	0.887

Table 3. Results of generalized additive model selection for the transect-averaged data. The ‘full model’ refers to the model considering all variables, the ‘depth excluded’ model considers all variables but transect mean depth, and the ‘depth only’ model considers only transect depth. The generalized cross-validation (GCV) score, effective degrees of freedom of the model (Total DF), and the p value from approximate F or t tests (Wood and Augustin, 2002) for each covariate remaining in the models are listed. The notation *ex* denotes covariates excluded from the model during model selection, and *n/a* denotes covariates that were not considered in the model.

Model	n	GCV score	Total DF	Deviance explained	Site	Depth	Season	Year
1a: $S_{A, \text{fish}}$ full model	1704	0.67	16.99	25.1 %	< 0.001	< 0.001	< 0.001	< 0.05
1b: $S_{A, \text{fish}}$ depth excluded	1704	0.79	13	10.9 %	< 0.001	<i>n/a</i>	< 0.001	<i>ex</i>
1c: $S_{A, \text{fish}}$ depth only	1704	0.73	2.98	17.1 %	<i>n/a</i>	< 0.001	<i>n/a</i>	<i>n/a</i>
2a: $S_{A, \text{zp}}$ full model	1704	0.49	16.96	49.9 %	< 0.001	< 0.001	< 0.001	< 0.001
2b: $S_{A, \text{zp}}$ depth excluded	1704	0.79	15	17.8 %	< 0.001	<i>n/a</i>	< 0.001	< 0.001
2c: $S_{A, \text{zp}}$ depth only	1704	0.62	2.97	34.2 %	<i>n/a</i>	< 0.001	<i>n/a</i>	<i>n/a</i>

Table 4. Catches from jig fishing summarized by study site. The species captured (where at least two individuals of a given species were captured) are listed from most to least common. Sites are listed from west to east. The term ‘rockfishes’ is used to describe members of the genus *Sebastes*.

Study Region	Site	# cruises with catch	# individuals captured	Species captured
West	Kiliuda Bay	3	53	walleye pollock, Pacific cod, Pacific herring, sandfish, Pacific halibut
West	Izhut Bay	2	29	rockfishes, Pacific cod , Atka mackerel
West	Barren Islands	1	6	rockfishes
West	Port Dick	3	41	walleye pollock, rockfishes
West	Aialik Bay	2	14	Pacific herring, walleye pollock, Pacific cod, rockfishes
East	Graves Harbor	1	4	rockfishes
East	Torch Bay	2	24	Pacific herring, rockfishes
East	Islas Bay	0	0	n/a
East	Salisbury Sound	5	32	rockfishes, sablefish
East	Saint Lazaria	5	31	rockfishes
East	Whale Bay	5	68	rockfishes, Pacific herring, walleye pollock

## Figure legends

Fig. 1. Map of study area with boxes indicating the nearshore sampling sites in the Gulf of Alaska. Acoustic surveys were conducted in bays and in the immediate vicinity of islands. As can be seen from the 200 m depth contour (light grey line) the continental shelf is wider in the west study region.

Fig. 2. Example of the dual-frequency classification method used to classify volume backscatter into 'fish' and 'macrozooplankton' categories. a) Raw 38 kHz echogram showing backscatter from fishes. b) Raw 120 kHz echogram showing backscatter from fish similar to the 38 kHz in addition to a dense band of macrozooplankton backscatter between 70-120 m which is not evident at 38 kHz. c) Post-processed 120 kHz backscatter with a frequency response consistent with fish (i.e. 38 kHz is similar to 120 kHz). d) Post-processed 120 kHz backscatter with a frequency response consistent with zooplankton (i.e. 120 kHz  $\gg$  38 kHz).

Fig. 3. Mean site-visit water column backscatter at 120 kHz classified as fish (left side, panels a, c, e) and zooplankton (right side, panels b, d, f) for inshore sites sampled in 2010, 2011, and 2013 by season. Black bars represent spring, white bars represent summer, gray bars represent fall. Sites (see Table 1 and Figure 1) are listed from west to east. Some locations were not sampled in the summer of 2010, and fall of 2011 and 2013 (see Table 1).

Fig. 4. Box plots of a)  $\log_{10}$  transformed fish and b) macrozooplankton water column backscatter by study site groups (see text and Table 1 for explanation). Filled circle indicates median; lower and upper box bounds indicate 25th and 75th percentiles, and bar ends indicate 1.5 times the inter-quartile range.

Fig. 5. Fish and zooplankton total water column backscatter is low and less variable in shallow water and increases substantially with water depth. Top panels show a) 38 kHz fish backscatter and b) 120 kHz macrozooplankton from the larger vessel used to survey inshore areas. Bottom panels show shallow-water backscatter recorded in areas adjacent to the shoreline with the skiff c) 38 kHz fish backscatter and d) 200 kHz macrozooplankton backscatter. Box plots summarize the distribution of vertically integrated backscatter for all 100 m along-track observations in a given depth range where > 25 observations were made. The box plots depict the 10th, 25th, 50th, 75th and 90th percentiles of the observations. Note that the y-axis scales for the survey vessel (a-b) are 50 times greater than those of the skiff (c-d).

Fig. 6. Site-mean water column acoustic backscatter classified as a) fish and b) macrozooplankton plotted against to the average depth from all observations each time a given site was surveyed. A least-squares line is fit to the data points, and the correlation coefficient and the p-value for the hypothesis test of no correlation is given.

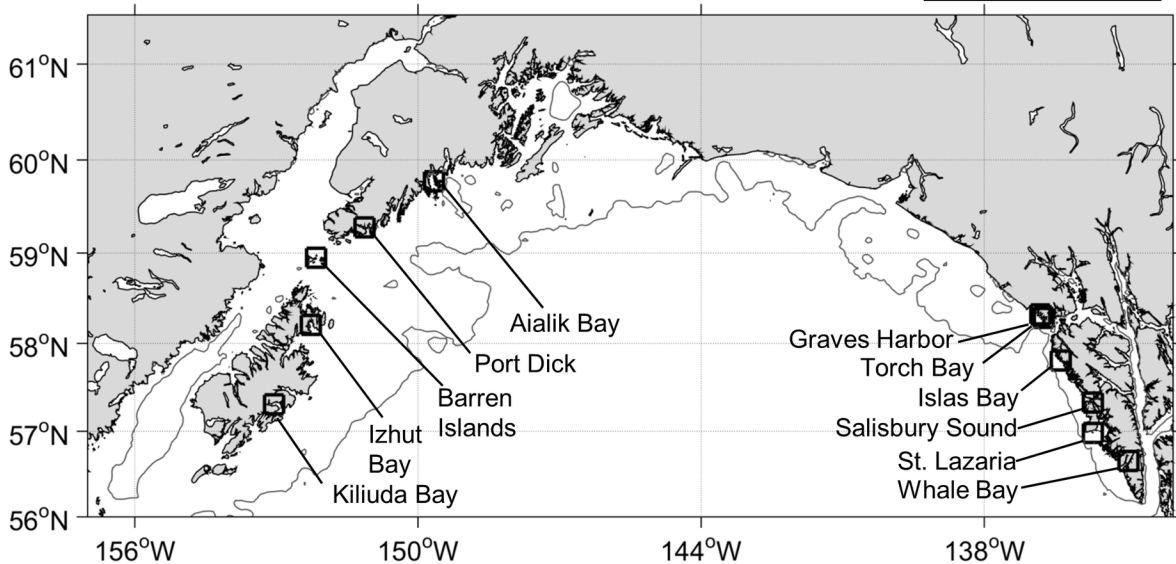
Fig. 7. Volume backscatter increases substantially with depth, indicating that acoustic backscatter from both a) fish and b) macrozooplankton is low in shallow water, and increases at greater depths (all survey vessel observations pooled). In both cases, backscatter is low and less variable at depths < 80 m. The box plots depict the 10th, 25th, 50th, 75th and 90th percentiles of all 120 kHz observations.

Fig. 8. Effects of explanatory variables on transect-mean water column fish acoustic backscatter resulting from the best-fitting generalized additive model. The significant effects in the best-fitting model were a) depth, b) year, c) site, and d) season (see Table 4). The symbols are the partial residuals (i.e. the residuals after removing the mean effects of the other covariates) for each data point. The units of the y-axis are the additive effect on  $\log_{10}(S_A+0.1)$ ; that is, a 1 unit change reflects a 10-fold change in acoustic backscatter. Factor coefficients determined to be significant ( $p < 0.05$ ) are indicated with an asterisk.

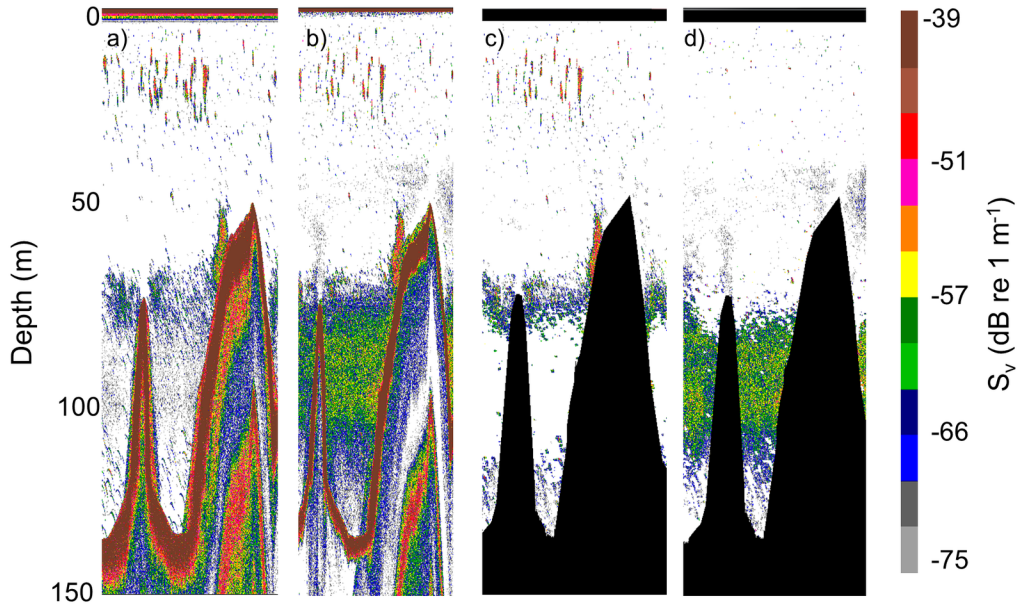
Fig. 9. Effects of explanatory variables on transect-mean water column macrozooplankton acoustic backscatter resulting from the best-fitting generalized additive model. The significant effects in the best-fitting model were a) depth, b) year, c) site, and d) season (see Table 4). The symbols are the partial residuals (i.e. the residuals after removing the mean effects of the other covariates) for each data point. The units of the y-axis are the additive effect on  $\log_{10}(S_A+0.1)$ ; that is, a 1 unit change reflects a 10-fold change in acoustic backscatter. Factor coefficients determined to be significant ( $p < 0.05$ ) are indicated with an asterisk.

West study region

East study region

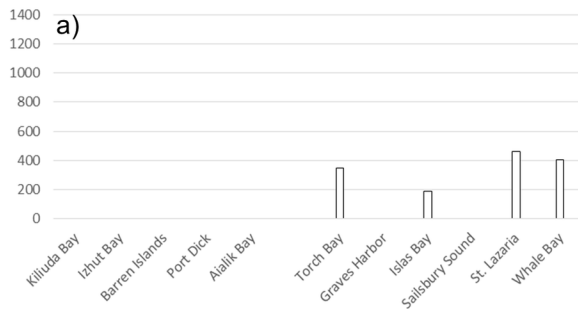






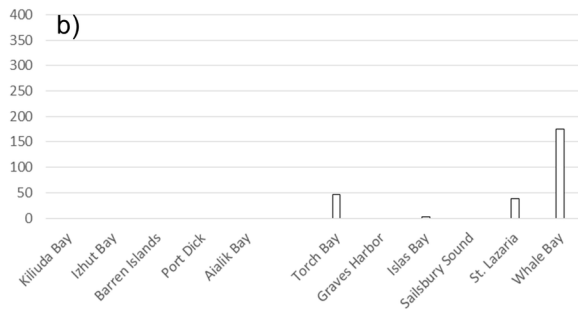
## Fish

2010

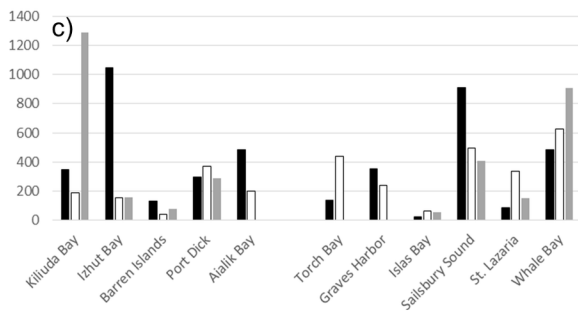


## Zooplankton

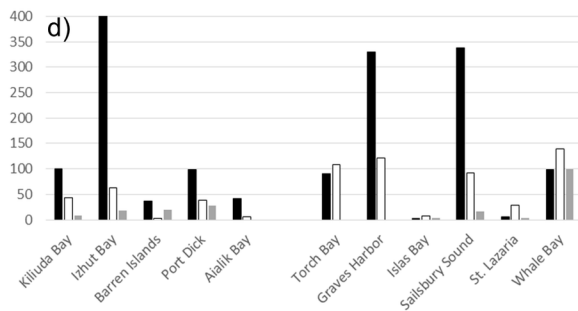
2010



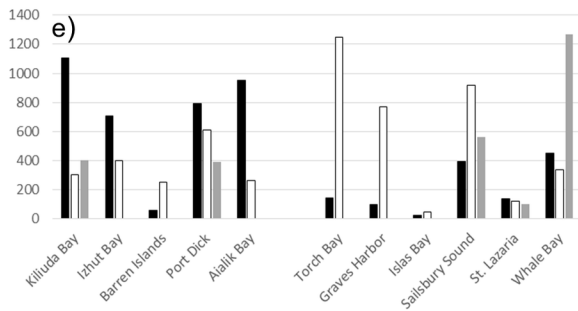
2011



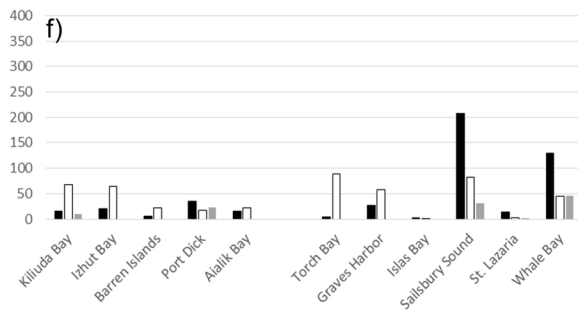
2011



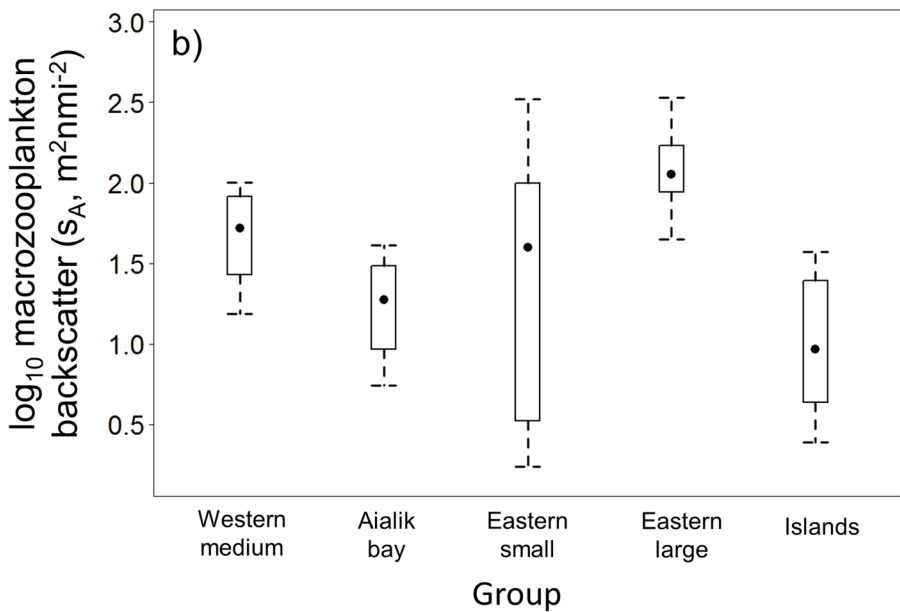
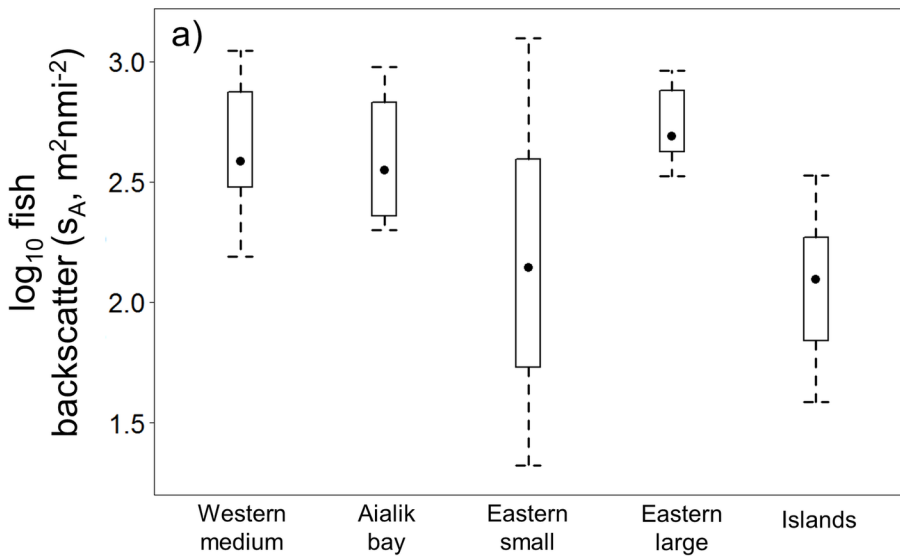
2013

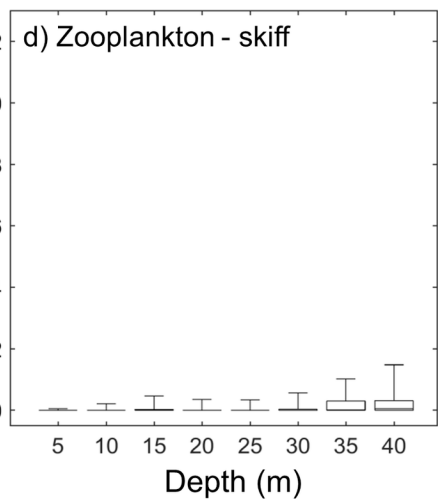
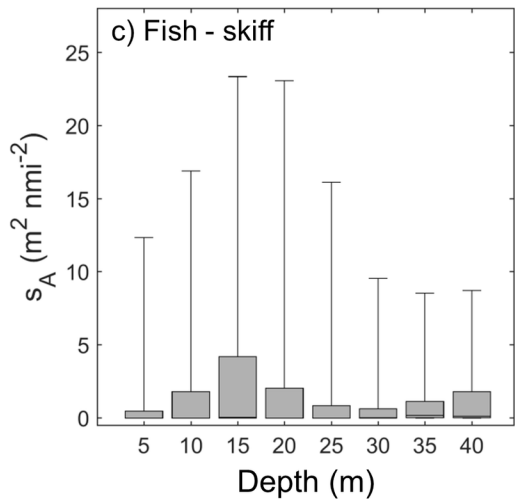
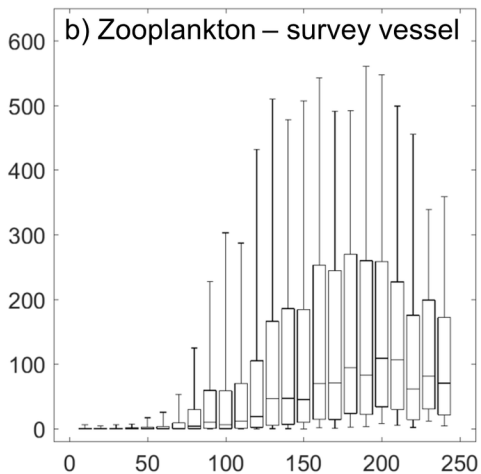
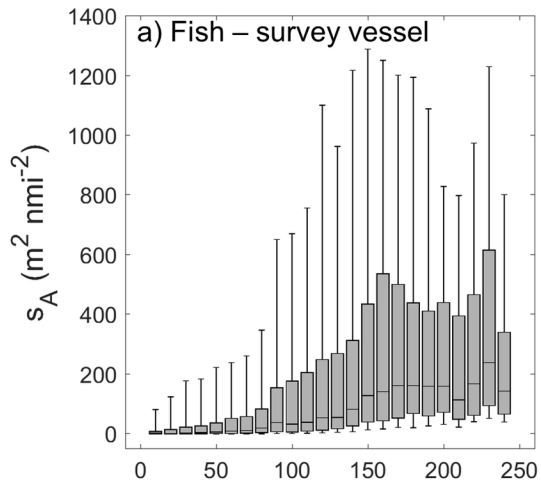


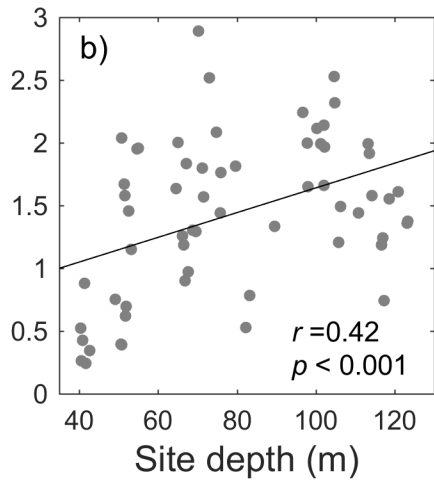
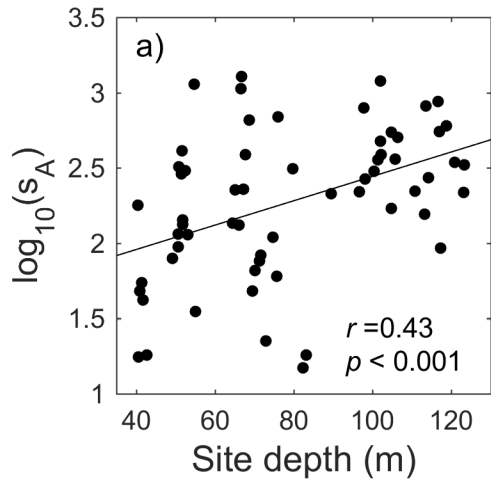
2013



120 kHz backscatter ( $s_A, m^2 nmi^{-2}$ )







# Volume backscatter ( $s_v$ , $m^{-1}$ )

