

1 *Dynamic spatial heterogeneity reveals interdependence of marine faunal density and fishery*  
2 *removals*

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19 **Abstract**

20           The spatial structure and dynamics of populations, their environment, interacting species,  
21 and anthropogenic stressors influences community stability and ecological resilience. Despite the  
22 importance of spatial processes in ecological outcomes and increasing desire to implement  
23 ecosystem-based management, fine-scale spatial dynamics have been rarely incorporated in  
24 marine fisheries management. However, advances in population modeling and data availability  
25 provide the necessary ingredients to address this disconnect between the fields of ecology and  
26 fisheries. We used random forests and spatial indices to quantify spatial heterogeneity and  
27 dynamics of US west coast demersal marine faunal density (biomass of a community or  
28 assemblage per unit area) and the total removals (catches plus discards) from the system by the  
29 groundfish bottom trawl fishery from 2002 to 2017. We expected spatial heterogeneity of  
30 removals and density to increase following implementation of depth and habitat closures--due to  
31 proximally increasing density gradients and fishing-the-line--and following catch shares because  
32 of fleet consolidation and behavioral consequences of eliminating the race to fish. However, we  
33 found mixed responses, where at the broadest community levels spatial variation in removals and  
34 density declined with habitat closures, while spatial autocorrelation of removals increased with  
35 habitat closures and declined with catch shares. Our results reveal a complex interdependence  
36 between spatial distributions of faunal density and fishery removals that has been absent in  
37 previous studies focusing on catch only, and shows how these patterns are shaped by marine  
38 policy. The spatial variation of density and removals were positively correlated within year (i.e.,  
39 each responded with the same sign and timescale), while there was also evidence that interannual  
40 changes in the spatial variation of removals among years led those of density by one year (i.e.,  
41 increases in patchiness of removals were followed by increased patchiness of density). These

42 results hint at the presence of a stronger than expected top-down effect of fishing, given that this  
43 system is considered to be dominated by strong bottom-up effects of environmental variation on  
44 primary and secondary productivity.

45

46 *Keywords:* spatial heterogeneity, ecological stability, discards, species distributions, spatial  
47 dynamics

## 48 **Introduction**

49           Incorporating spatial heterogeneity--or variability--of biotic and abiotic processes can be  
50 critical for the effectiveness of natural resource management (Noss, 1983; Turner, 1989; Turner  
51 et al., 1995). Many population processes – births, deaths, strength of density dependence, and  
52 immigration vary across space (Bjørnstad et al., 1999), and these patterns can be related to static  
53 habitat features or more ephemeral environmental conditions. Not accounting for these spatial  
54 processes when they are present can lead to biased predictions of population dynamics (Cadrin et  
55 al., 2018; Punt, 2019) and suboptimal management outcomes (Sanchirico and Wilen, 2005). The  
56 distribution of pressures affecting wild populations – including human disturbances – also often  
57 has a spatial component. Spatially heterogenous (i.e., unevenly distributed) human impacts  
58 include, for example, oil spills (Rooker et al., 2013), chemical contamination and eutrophication  
59 from sewage or runoff, habitat loss and fragmentation from logging, urbanization, and  
60 agriculture, and direct removals from hunting or fishing (Dulvy et al., 2004). Spatially  
61 heterogenous human impacts may also have positive effects, particularly for conservation –  
62 examples include parks or reserves which can preserve habitat, increase population densities, and  
63 increase biodiversity (Baskett and Barnett, 2015; Bruner et al., 2001; Halpern and Warner, 2002;  
64 Lester et al., 2009). Regardless of the direction of human impacts or other pressures, ignoring  
65 spatial variability in impacts can result in sub-optimal management strategies and outcomes  
66 (Sanchirico and Wilen, 2005; Ying et al., 2011). How best to incorporate spatial structure in the  
67 design and assessment of natural resource use policy is an outstanding question.

68           Together, the spatial and temporal heterogeneity in habitat, anthropogenic pressures, and  
69 environmental drivers significantly influence community stability (Hassell, 2000; Huffaker,  
70 1958; Tilman and Kareiva, 1997) and ecological resilience (Barnett and Baskett, 2015; Baskett et

71 al., 2006; Holling, 1973; Takashina and Mougi, 2014). The relative importance of habitat, human  
72 disturbance, or environmental variability depends on the life histories of the species in question  
73 and the spatial scale being analyzed (Rouyer et al., 2008). In addition, these drivers could have  
74 complex interactions such that species affected by higher rates of harvest, for example, may  
75 experience larger population fluctuations as a result of environmental variability (Essington et  
76 al., 2015; Hsieh et al., 2006). Even effects of a single driver can be complex. Although fishing is  
77 thought to typically diminish spatial population structure and homogenize density (reviewed by  
78 Ciannelli et al., 2013), spatial variation in recruitment may increase with harvesting in some  
79 cases (Hsieh et al., 2008; Hsieh et al., 2010), and more nuanced patterns may arise depending on  
80 the spatial distribution of harvest and the presence and form of density dependent growth or  
81 movement.

82         Predicting the spatial variability of fishery take is complicated, because in addition to  
83 biological factors, such as availability of fish, a suite of economic drivers can also influence the  
84 choice of where to fish. Effort is typically concentrated in coastal areas (Stewart et al., 2010), but  
85 other factors that could affect the spatial distribution of effort include prices offered by  
86 producers, fuel prices, and distances to port or protected areas (Girardin et al., 2017; Sanchirico  
87 and Wilen, 1999; Stelzenmüller et al., 2008). Under the ideal free distribution (IFD; Fretwell and  
88 Lucas, 1970), effort is expected to positively correlate with available biomass. There are multiple  
89 examples of fishing effort approximating the ideal free distribution (Gillis, 2003), but there are  
90 also situations where the spatial distribution of effort departs from the ideal free distribution  
91 (Abernethy et al., 2007) as fishers often choose fishing locations based on expected revenue  
92 among other factors (Abbott et al., 2011; Girardin et al., 2017; Haynie et al., 2009; Holland and  
93 Sutinen, 2000; Kuriyama et al., In review). These factors that could cause departures from ideal

94 free distribution include the costs of steaming (fuel and time), gear limitations or restrictions,  
95 conflict avoidance, variability in vessel size, habits, and experience of individual fishers, or for  
96 multi-species fisheries, fluctuations in the relative abundance and biomass distribution of target  
97 and nontarget or protected species.

98         Despite the known consequences of spatial heterogeneity on population and community  
99 dynamics (Hassell, 2000; Huffaker, 1958; Tilman and Kareiva, 1997), spatial processes have  
100 rarely been incorporated into systematic management of marine fisheries at scales fine enough to  
101 match that of the underlying biological process (but see, e.g., salmon harvest allocation by the  
102 Pacific Salmon Commission: <http://www.psc.org/>). However, there is increasing recognition that  
103 quantifying the effects of spatial heterogeneity on the amount and distribution of fishery catches  
104 and discards is important for implementing ecosystem-based fishery management (EBFM;  
105 Katsanevakis et al., 2011; Link, 2005). Spatial processes are likely particularly important for  
106 management of marine systems because fishing is a dominant driver of marine community  
107 change. The spatial distribution of fishing effort likely affects spatial population and community  
108 dynamics through catch of target and nontarget species and physical damage to habitat from  
109 fishing gear, particularly dredges and trawls (Amoroso et al., 2018; Kaiser et al., 2002; Watling  
110 and Norse, 1998). Furthermore, the local effects of fishing have the potential to influence  
111 ecological dynamics at larger spatial scales in marine systems because the physical features of  
112 oceans create the potential for long-distance dispersal (Kinlan and Gaines, 2003; Strathmann,  
113 1990). This combination of physical connectivity and influence of harvesting on marine  
114 ecosystems has led to increasing desire for marine spatial planning, from implementation of no-  
115 take areas to spatial gear restrictions and area-specific catch limits (Crowder and Norse, 2008;  
116 Wood et al., 2008).

117           Despite the recognition that spatial processes are important to consider in marine fisheries  
118 management, there is still debate regarding how spatial management policies affect catches and  
119 abundance beyond closure boundaries (Hastings and Botsford, 1999; Hilborn et al., 2004; White  
120 and Kendall, 2007). While spatial closures typically cause biomass of harvested species to  
121 increase within the closure (Lester et al., 2009), biomasses outside can potentially decrease due  
122 to concentration of displaced fishing effort (which often occurs particularly close to closure  
123 edges) unless there is adequate “spillover” of fish moving outside (Karnauskas et al., 2011;  
124 Kellner et al., 2008; Kellner et al., 2007; Moffitt et al., 2009; Rassweiler et al., 2012; White et  
125 al., 2010). Thus, the effect of spatial closures on the amount and distribution of biomass  
126 available to fishers depends on the form and timing of density-dependent population growth and  
127 dispersal, the scale of animal movement relative to closure dimensions, the intensity and spatial  
128 distribution of fishing, and the general effect of fishing on abundance distributions (Baskett and  
129 Barnett, 2015; Ciannelli et al., 2013; Hilborn et al., 2004; Kellner et al., 2008; Moffitt et al.,  
130 2009; White and Kendall, 2007; White et al., 2011; White et al., 2010). In this study, we use an  
131 empirical example to integrate over responses of fish and fisher behavior to advance the  
132 understanding of how spatial closures and other marine policies affect the spatial dynamics of  
133 marine faunal density (biomass of a community or assemblage per unit area) and fishery take  
134 throughout a region.

135           To determine how the spatial dynamics of marine communities and fisheries are  
136 interconnected, we focus on groundfish and their associated bottom trawl fishery on the US west  
137 coast. This system provides an ideal case study because it is a rare instance where fine-scale  
138 spatial information on both catch and discards is available, allowing what—to our knowledge—  
139 is the first comprehensive contrast between the spatial heterogeneity of marine faunal density

140 and fishing mortality. Furthermore, the existence of discrete, sequential management changes in  
141 the US west coast groundfish trawl fishery during the study period provides a set of natural  
142 experiments that we use to determine the spatial consequences of marine policy changes. We  
143 leverage the presence of persistent geographical contrast in fishing effort within the study region  
144 to identify the relationship between fishing and the distribution of abundance of marine  
145 assemblages. Specifically, we tested whether interannual changes in spatial heterogeneity of  
146 demersal faunal densities were correlated with those of fishery removals across a range of  
147 timescales, and whether the policy changes during our study period altered the spatial  
148 heterogeneity of densities and removals. We expected that spatial heterogeneity of faunal  
149 densities and fishery removals would increase as fishing effort would become more concentrated  
150 in discrete areas because spatial closures would reduce the trawlable area and catch shares would  
151 cause geographical fleet consolidation.

152

## 153 **Methods**

### 154 *System*

155 US west coast demersal communities and groundfish have a prominent role in the  
156 California Current food web and support large commercial fisheries. Groundfishes are strongly  
157 connected to the larger ecosystem through pelagic larval and juvenile stages that constitute a  
158 major source of forage for other fishes, seabirds, and marine mammals (Field et al., 2007; Mills  
159 et al., 2007; Sydeman et al., 2001), and their ontogenetic movements connect benthic and pelagic  
160 productivity. The US west coast groundfish bottom trawl fleet includes approximately 60 catcher  
161 vessels, and is part of a broader catch share fishery with combined annual net revenue of \$59  
162 million USD (catcher vessels alone net \$11 million; Errend et al., 2018; PFMC and NMFS,



163 2017). This fishery lands many species (~80 total, ~50 commonly) and also discards many at sea.  
164 While some of these species have seasonal migrations, there are apparently few coastwide  
165 interannual trends in spatial community structure (Tolimieri et al., 2015) and individual species  
166 distributions (Thorson et al., 2016), making this system ideal for disentangling the causes of  
167 change in the distribution of catches and local faunal densities.

168

### 169 *Approach*

170 To quantify spatial and temporal changes in the demersal community in response to  
171 fishing, we combined information for fishery-dependent and -independent datasets from 2002 to  
172 2017. We created annual spatial predictions of groundfish biomass and fishery removals (see  
173 Fig. 1 for the spatial prediction domain) and then summarized these outputs with spatial  
174 statistics. To estimate spatial and temporal variation in fishery removals, we fit random forest  
175 models to the total removals (catch and discards) recorded by at-sea observers in the bottom-  
176 trawl sector of the US west coast groundfish fishery. As some fishing trips were not attended by  
177 fisheries observers, we predicted the removals from hauls that were not monitored by observers  
178 to describe the spatiotemporal distribution of removals by the entire fleet. We applied similar  
179 models to fishery-independent surveys of biomass density to assess the extent to which  
180 interannual changes in the spatial distribution of removals might have been caused by changes in  
181 animal movement and productivity as compared to fleet dynamics. Following previous studies,  
182 which demonstrated that the influence of fishing on ecosystems is best identified at the guild and  
183 community level (Fay et al., 2013; Fulton et al., 2005; Samhuri et al., 2009; Tam et al., 2017),  
184 we summed catches into assemblages: all animals, fishes, predatory fishes, forage fishes,  
185 flatfishes, rockfishes and protected fishes (see Tables S1-7 for details of the taxonomic

186 composition of each group). When testing for an effect of policy changes on the distribution of  
187 density and removals, we compared our outputs for each assemblage among sets of years defined  
188 by their prevailing management type or “regime.” Finally, we describe how we computed spatial  
189 heterogeneity indices for each group and time period to develop spatial ecosystem indicators and  
190 assess whether and how changes in the spatial heterogeneity of removals is related to that of  
191 biomass density. We elaborate on each of these processes below.

192

### 193 *Modeling observed catch*

194 To estimate the spatial and temporal pattern of fishery removals, we analyzed data  
195 reported by at-sea observations of catch provided by the West Coast Groundfish Observer  
196 Program (WCGOP) at the Northwest Fisheries Science Center. The WCGOP records catch  
197 discarded at-sea, which is not recorded in landings data. Observers were present on 100% of trips  
198 since 2011 but only approximately 20% of trips between 2002 and 2010. We performed several  
199 filtering steps to ensure data quality. We confirmed that each haul was unique after merging the  
200 observer and logbook databases based on the fish ticket numbers from recorded landings. We  
201 removed hauls missing fundamental covariate data (e.g., location) and erroneous location or  
202 depth. Fishery logbook data provides basic information for the unobserved hauls during the  
203 2000’s, but the total catches are uncertain given lack of incentives for reporting discards.  
204 Exploratory analyses showed that observed trips were representative of fisher behavior for trips  
205 without observers; there were no substantial differences in the spatial (location and depth) or  
206 temporal (day of year and time of day) distribution of fishing effort between trips with and  
207 without observers. Therefore, we used random forest models fit to the observed hauls from 2002  
208 to 2010 to predict removals from the remaining unobserved hauls in the logbook data (R package

209 'randomForest'; R v3.5.1, (R Core Team, 2018)). We chose to make predictions with random  
210 forests because they had the best predictive skill compared to other spatial models (also see  
211 Stock et al., 2018).

212 The full fitted models included the following predictor variables: location (haul midpoint  
213 northing and easting, as linear and quadratic terms); depth (natural log-transformed average  
214 depth of haul in meters); date (day of year); time of day (in decimal hours); fishing effort (haul  
215 duration in hours); and year (the only categorical variable). We did not include the retained catch  
216 recorded in the landings data as a predictor because exploratory analyses indicated that discarded  
217 catch quantities were independent of the retained catch within hauls. We assessed predictive  
218 performance for all model fits based on the root-mean-square error and variation explained, as  
219 derived from the feature-bagging technique of the random forest algorithm (which is analogous  
220 to cross-validation (Breiman, 2001)).

221

### 222 *Predicting unobserved catch*

223 To estimate total removals from all hauls performed by the fishery, we summed the  
224 known removals from the observed hauls and the predicted removals from hauls not monitored  
225 by the WCGOP. To estimate removals from unobserved hauls, we performed predictions from  
226 the random forest models fit to the WCGOP data to the haul information recorded in fishery  
227 logbook data provided by the Pacific Fisheries Information Network (representing self-reported  
228 data for each haul from all groundfish bottom-trawl vessels operating off the US west coast  
229 between 2002 and 2010; 133,716 total hauls, 25,701 of which had an observer present). Adding  
230 in 48,578 observed hauls from 2011-2016 yielded removal biomass for each assemblage from a  
231 total of 182,294 hauls from 2002 to 2016. To summarize spatial patterns of removals, we

232 computed the sum of known and predicted catches of each group for each cell in each year, with  
233 resolution and extent matching that for density (described in the section *Modeling biomass*  
234 *density* below). We mapped these predictions to visualize the location of anomalous cumulative  
235 removals across all years.

236

### 237 *Modeling biomass density*

238 To assess spatial and temporal variation in faunal density of the demersal community (see  
239 Tables S1-7), we analyzed data from the NOAA Fisheries, Northwest Fisheries Science Center,  
240 US West Coast Groundfish Bottom Trawl Survey (Bradburn et al., 2011). This annual survey  
241 occurs from May to October at depths from 55 to 1280 m, from Cape Flattery, Washington (US-  
242 Canada border) to the US-Mexico border. We analyzed the 2003–2017 surveys, which consisted  
243 of 9,671 hauls, where locations were selected randomly on trawlable seafloor habitat (i.e., areas  
244 without extensive rocks or boulders) stratified by depth and latitude. The survey included hauls  
245 from within an area closed to trawling, defined by a narrow depth band (termed the trawl  
246 Rockfish Conservation Area), but not from another large block of area near the southern  
247 boundary of the region (the Cowcod Conservation Area) that was closed to all fishing. We  
248 expected that inclusion of the trawl depth closure would increase spatial heterogeneity biomass  
249 as we discuss in the section below, but that the exclusion of the southern closure would have  
250 little effect on our estimated spatial heterogeneity of biomass unless fish movement rates were  
251 quite high. We fit random forest models with similar structure to that fit to the WCGOP data,  
252 where the response variable was catch-per-area-swept (kg/ha) and predictors included location  
253 (linear and quadratic terms), log depth, day of year, and year (note that time of day was not  
254 included as the survey is constrained to daylight hours). To obtain a smooth surface of predicted

255 density across the footprint of the survey area, we predicted biomass density from the random  
256 forest models using depth defined by NOAA bathymetry data  
257 (<https://www.ngdc.noaa.gov/mgg/coastal/crm.html>), averaged over space to match the resolution  
258 of the survey sampling grid (~2.8 x 3.7 km), which is the spatial resolution we used for all  
259 analyses.

260 To distinguish the effects of fishing on the spatial distribution of faunal densities, we  
261 separately modeled survey data from trawled (northern) and untrawled (southern) regions (Fig.  
262 1). We defined this boundary to be just north of the Channel Islands National Park, California.  
263 We selected this as the boundary because it represented the latitude at the southernmost location  
264 of the logbook and observer data of commercial trawl activity over all years.

265

#### 266 *Evaluating the effect of management changes on spatial distributions of density and removals*

267 We used sequential management policy changes that occurred during our study period as  
268 natural experiments to determine how shifts in the distribution of fishing effort influence the  
269 distribution of fishery removals and faunal densities. A spatial gear closure called the trawl  
270 Rockfish Conservation Area (RCA) was implemented beginning in 2002, which prohibited  
271 trawling at temporally varying depths (generally between 175 and 450 m) along the continental  
272 shelf. To protect Essential Fish Habitat, roughly 25% of the area historically fished was closed to  
273 bottom trawling in 2006 (PFMC, 2008). Catch shares were implemented in 2011. For species  
274 regularly captured in the fishery, we expected that spatial heterogeneity of fishing effort--and  
275 therefore fishery removals--would increase due to the closure policies reducing the trawlable  
276 area and thereby concentrating effort spatially (e.g., fishing-the-line, or the tendency of fishing  
277 effort to concentrate near the boundary of fishery closures; see Table S8 for all hypothesized

278 responses to changes in the fishery). Furthermore, we expected catch shares to cause fleet  
279 consolidation toward major ports (PFMC and NMFS, 2017) and to eliminate the race to fish  
280 (perhaps incentivizing shorter steam distances to reduce costs, e.g., Watson et al., 2018).  
281 However, the effect of catch shares on the spatial distribution of effort is difficult to predict,  
282 because of tradeoffs between bycatch risk avoidance and the opportunity for exploratory fishing  
283 (Branch, 2009). It is possible that the presence of fewer vessels—if spread over more area and  
284 time within the year—could reduce the spatial concentration of effort, yet there appears to be no  
285 change in effort concentration resulting from catch shares in this case (Kuriyama et al., In  
286 review).

287         We expected similar responses of faunal density to management shifts. We hypothesized  
288 that density distributions would become patchier as populations, and potentially productivity-  
289 enhancing habitats, recover within spatial closures while relative fishing mortality increases  
290 outside closed areas due to displacement of effort and the catch-maximizing behavior of fishing-  
291 the-line (Kellner et al., 2007). Furthermore, if the prevailing assumption that fishing reduces  
292 spatial population structure holds, faunal densities should be becoming more spatially variable in  
293 response to the massive fleetwide effort reduction over the last 30 years (Hilborn et al., 2012)  
294 and subsequent rebuilding of groundfish biomass (PFMC and NMFS, 2017). Alternatively, these  
295 predicted responses may be disrupted by time lags in population responses, animal movement,  
296 density-dependence, unexpected responses of fisher behavior, or short-term fluctuations in  
297 fleetwide effort before and during the study period.

298         To test our hypotheses regarding the influence of management actions on spatial  
299 heterogeneity of density and removals we summarized temporal changes in patchiness  
300 corresponding to the timing of major policy changes. Within each assemblage and output

301 category, we pooled annual measures of spatial heterogeneity among three discrete time periods  
302 representing the phase of each new management regime described above: 1) 2002-2005, when  
303 depth closures (RCA) were implemented and fleetwide effort generally declined (Fig. S1); 2)  
304 2006-2010, when habitat closures (EFH) were implemented and fleetwide effort increased until  
305 2010; 3) 2011-2017, when catch shares were implemented and effort declined slightly (following  
306 a larger effort decline from 2009 to 2011). Hereafter, we will refer to these time periods by their  
307 management regime: depth closures, habitat closures, and catch shares. We tested for differences  
308 in spatial heterogeneity metrics (described in the following section) among management regimes  
309 (where the sampling unit was years) within each assemblage and output type using one-way  
310 analysis of variance (ANOVA) and Tukey's honestly significant difference (HSD) test, after  
311 confirming that there was no evidence for unequal variances.

312

### 313 *Contrasting change in spatial heterogeneity of density and removals using spatial indices*

314 To quantify how spatial heterogeneity of density and removals changes with time and  
315 management policies, we computed indices of spatial autocorrelation and spatial variance for  
316 each combination of outputs in each year. We chose these metrics because they describe the two  
317 main axes of easily interpretable patterns in spatial data and researchers have demonstrated that  
318 they can be leading indicators of ecological regime shifts in other systems (Kéfi et al., 2014). To  
319 visually demonstrate what these measures represent, we simulated data with varying spatial  
320 autocorrelation while keeping spatial variance constant and data with changing spatial variance  
321 while keeping spatial autocorrelation constant (Fig. S2). Figure S2 shows that spatial  
322 autocorrelation can be interpreted as a measure of clustering of similar values among nearby  
323 locations (which can be correlated with relative patch size) and spatial variation as a measure of

324 the strength of spatial gradients or simply the magnitude of variation across space regardless of  
325 spatial arrangement. To increase comparability among assemblages and between our study and  
326 others, we applied indices of the above metrics to the output for each assemblage as follows:  
327 from each annual set of predictions of removals, northern density, and southern density, we  
328 expressed the spatial variation in the form of the spatial coefficient of variation (CV) and  
329 Moran's I as an index of spatial autocorrelation. Annual values were standardized by subtracting  
330 each value by their group mean and dividing by their standard deviation.

331 To determine whether there was a relationship between the spatial pattern of fishery  
332 removals and density, we performed cross-correlation analyses for each assemblage on the time  
333 series of spatial autocorrelation and CV between removals and density in the northern portion of  
334 study region (the only area where trawl fishing occurs). This test allowed us to determine  
335 whether changes in spatial patterns of removals and density are correlated, and with what lag and  
336 sign. For example, high correlation at negative lags indicate that changes in removals lead  
337 changes in density, whereas positive lags indicate that changes in density occur prior to that of  
338 removals. Prior to performing cross-correlation tests, we pre-whitened each series (removed the  
339 autocorrelation structure) with the best fit autoregressive integrated moving average model  
340 (Johnson, 2018).

341

## 342 **Results**

343 The final models displayed a broad range of predictive ability across assemblages and  
344 response type and area (Table S9). In general, removals were more predictable than density.  
345 Density was better predicted in the southern part of the study region than the northern region for  
346 all fauna, fishes, predators, and flatfishes, while the opposite was true for rockfishes, forage, and



347 protected species. Variation explained was highest for rockfish, flatfish, and predator removals.  
348 Due to poor performance of the models predicting southern density of forage and protected  
349 species (pseudo- $R^2 < 6\%$ ; Table S9), we did not include these results in map predictions or post-  
350 hoc testing.

351 Mean predicted densities of all groups were typically highest within a band of  
352 intermediate depth on the outer shelf and near the shelf break, whereas densities of forage and  
353 protected species were sparse and patchier due to lower detection rates (Fig. 2). High densities of  
354 flatfishes also extended to shallower shelf waters north of central Oregon. Predators and  
355 rockfishes were in greatest densities at slightly deeper depths. All groups except forage species  
356 had high density areas in the far northern end of the study region, west-southwest of Cape  
357 Flattery, Washington. Another high density area common to all groups (but much less prominent  
358 for predators and protected species) was located within a small area of the outer shelf off Half  
359 Moon Bay in central California.

360 Across all years of the study period, cumulative removals were distributed similarly to  
361 the density distributions for most groups, with particular exceptions of forage and protected  
362 species (Fig. 3); however, the highest densities of all species combined were typically nearer to  
363 shore than removals, particularly off northern California and Oregon. Rockfish removals were  
364 somewhat more diffuse and less patchy than predicted densities, and protected species removals  
365 were much more broadly distributed than predicted densities. All removals occurred north of the  
366 Channel Islands National Park and predominantly north of Point Conception, with the majority  
367 of large removals taken north of Monterey, California. The largest concentrations of high  
368 removals were found off Washington for all groups except rockfishes and forage species.

369

370 *Change in spatial heterogeneity among management regimes*

371           The spatial CV of removals was typically highest during the beginning of the study  
372 period when managers implemented depth closures and declined in the middle years after  
373 implementation of habitat closures (Fig. 4a-g). This pattern was statistically significant for the  
374 broadest assemblages (all species, fishes, predators) and protected species (Fig. 4a-c,g; Table  
375 S10). Rockfish and forage removal spatial CVs increased significantly from the periods with  
376 depth and habitat closures to the end of the study period, when catch shares were in effect.  
377 Spatial autocorrelation of removals was typically highest during the habitat closure period (Fig.  
378 4h-n). Furthermore, values were significantly lower in the catch share period than the depth  
379 closure period for all species, fishes, flatfishes, and protected species (Fig 4h,i,k,n). Values for  
380 rockfish and forage species were also lowest in the catch share period, yet had no significant  
381 differences between the depth closure and habitat closure periods (Fig. 4l,m).

382           Trends in spatial heterogeneity were less consistent for density than removals. No  
383 statistically significant changes were apparent in the spatial CV or autocorrelation of density in  
384 the untrawled (southern) region (Fig 5). In the trawled (northern) region the CV of density for all  
385 species and fishes were lowest during the habitat closure period, but values in the depth closure  
386 and catch share periods were statistically indistinguishable (Fig. 6a,b). In contrast, protected  
387 species CV was highest during the habitat closure period (Fig. 6g). Spatial autocorrelation of  
388 flatfish and forage species densities in the trawled region was lowest in the habitat closure period  
389 (Fig 6k,m); although the difference between the habitat closure and catch share period was not  
390 statistically significant for forage species. Spatial autocorrelation in density of the trawled region  
391 appeared to generally increase for some groups, particularly fishes and all species combined  
392 (Fig. 6h,i); however, the differences were not statistically significant.

393

394 *Leading and lagging indicators in fished areas*

395         The cross-correlation of spatial CV indicated that for all species combined and all fishes,  
396 there were significant positive correlations between density and removals at lags of -1 or 0 years  
397 (Fig. 7a,b), meaning that changes in removals lead changes in density by one year and they  
398 respond with a similar sign within year. Similarly, correlations were strong at lag -1 for predators  
399 and protected species (Fig. 7c,g), although neither were statistically significant and the latter  
400 correlation was negative and accompanied by a statistically significant correlation at lag 3.  
401 Flatfishes had a statistically negative correlation at lag -3 (Fig. 7d). Forage species had the best  
402 support for changes in density leading removals, with a statistically significant negative  
403 correlation at lag 1. Relationships were weaker and not statistically significant for rockfishes  
404 (Fig. 7e).

405         Patterns of cross-correlation of spatial autocorrelation were less clear than that of spatial  
406 CV, but the most prominent pattern was that changes in density led those of removals by 3 years  
407 (Fig. 8). Lag 3 correlations were high for all groups except protected species, and were positive  
408 for all species combined, fishes, predators, and forage species, while negative for flatfishes and  
409 rockfishes, yet the correlation was statistically significant only for the two broadest groups and  
410 forage species. Predators had greater correlation at lag 0 (negative) and rockfishes had greater  
411 correlation at lag 2 (positive). Correlations for protected species were greatest at lag 0 (positive)  
412 and lag -4 (negative), but the correlations were not statistically significant.

413

414 **Discussion**

415           Our results demonstrate that the spatial heterogeneity of demersal marine communities  
416 and associated fisheries is variable in time and responsive to changes in management regimes.  
417 We show that there is a strong relationship between spatial heterogeneity in fishery removals and  
418 spatial heterogeneity in a wide range of marine animal assemblages. Our result is particularly  
419 notable because fishing intensity was low compared to past levels within our system and relative  
420 to other demersal systems (Hilborn and Ovando, 2014; Hilborn et al., 2012); furthermore, choice  
421 of fishing location is driven substantially by fishers habits (Girardin et al., 2017; Holland and  
422 Sutinen, 2000; Kuriyama et al., In review) and distance from port or previous location, rather  
423 than expected revenue alone (Abbott et al., 2011; Haynie et al., 2009). Our finding that changes  
424 in spatial CV of removals lead those of density provides evidence of a direct top-down influence  
425 of fishing in a system considered to be driven largely by bottom-up dynamics (Field et al., 2006;  
426 Ware and Thomson, 2005). For the broadest assemblages, fishes and all fauna, trends in spatial  
427 CV among management regimes were fairly similar for removals and density in the trawled  
428 region, whereas patterns of spatial autocorrelation were less consistent. Changes in spatial  
429 heterogeneity of density in the untrawled region rarely bore any relationship to either density in  
430 the trawled region or removals, providing some additional support for fishing as a driver of  
431 change in density distributions.

432           Previous research identified fishery catch as an inconsistent ecological indicator of  
433 pressure, yet most of these analyses use only the magnitude of the landed catch (Shin et al.,  
434 2010), missing much of the consequences of fishing by not accounting for discarded bycatch and  
435 the spatial distribution of fishery removals. Here, we find that spatial heterogeneity of catch and  
436 discards combined appears to be an effective indicator of change in spatial distribution of marine  
437 faunal density, as reflected by the high leading correlation and within-year correlation of the

438 spatial CV of removals and fish density. However, the relationship varied among assemblages  
439 and in some cases it appeared that changes in the spatial field of removals—particularly the  
440 spatial autocorrelation of removals—lagged that of density, perhaps reflecting fishers moving to  
441 find fish. One interpretation is that changes in the scale of patchiness of density drives that of  
442 removals, in other words, bottom-up influences may be more noticeable at larger spatial scales.  
443 While we used the footprint of trawling effort to delineate our spatial strata (i.e.,  
444 northern/trawled, southern/untrawled), management applications of spatial ecological indicators  
445 would likely require tailoring the selection of the number and position of strata based on the  
446 specific populations or fisheries of interest.

447         The notion that fishery removals at regional scales influence the distribution of fish  
448 biomass within fished areas is intuitive, yet many studies have not found such a relationship—or  
449 have found that the effects of fishing are small relative to environmental drivers. If removals are  
450 large enough relative to local biomass, surveys performed immediately before and after catch  
451 should detect the influence of fishing on faunal density, yet longer durations between sampling  
452 and removals allow for these direct effects to be obscured by animal movement, reproduction,  
453 growth and to a lesser extent natural mortality. Ono et al. (2016) used the same fishery-  
454 independent survey data as that used in this study to evaluate causes of change in Dover sole  
455 (*Microstomus pacificus*) distribution and found no evidence of fishery influence between  
456 sampling periods of approximately 1-7 months, citing low exploitation rates for the lack of  
457 relationship. If low exploitation rates were the sole reason for this result, we should have also  
458 found no relationship between density and removals, as Dover sole are among the primary target  
459 species within our assemblages. That said, our results may not be as different as they appear on  
460 the surface, as we also found no correlation between flatfish removals and density at timescales

461 shorter than three years. There did appear to be some negative relationship at longer timescales,  
462 reflected in both the cross-correlation of spatial CV and opposing trends in spatial  
463 autocorrelation among management regimes. Some of this discrepancy could be due to the fact  
464 that Ono et al. (2016) relied on logbook data, which suffers from reporting error and inconsistent  
465 reporting of discards, issues addressed by our use of observer data. Furthermore, most flatfishes  
466 have greater rates of movement and faster life histories than reef-associated groundfishes such as  
467 rockfishes, so their population responses may generally make it more difficult to detect spatial  
468 influences of fishing.

469         While there were many similarities between spatial distributions of density and fishery  
470 removals, some notable differences highlight how policy drivers can cause removal patterns to  
471 deviate from what is expected under the ideal free distribution. The largest removals often came  
472 from somewhat deeper waters further off shore than the highest densities, particularly off  
473 northern California and Oregon, likely due in part to the closure of waters between 90 and 275m  
474 depths to trawling coastwide (Fig. S3). Greater prevalence of rock outcrops in shallower shelf  
475 waters than deeper slope waters is also likely a factor, as footrope gear restrictions made it  
476 difficult and risky to trawl over rocky substrates, preventing the majority of trawling in such  
477 habitats (Bellman et al., 2005). As many of the later closures of essential fish habitat encompass  
478 rocky substrates, submarine canyons, or extend deeper than our study domain, it is difficult to  
479 say to what extent they contribute to discrepancies between distributions of removals and  
480 densities, but we found some evidence of large removals near the boundary of habitat and depth  
481 closures northward from the greater Monterey, California region (Fig. S3). While the adjacency  
482 of large removals and high density near closures is somewhat consistent with fishing-the-line and  
483 associated spillover effects (Halpern et al., 2009; Kellner et al., 2007; Murawski et al., 2004;

484 Stelzenmüller et al., 2008), such inference is beyond the scope of our study; furthermore, this  
485 pattern could be a reflection of trawlable habitat and fleet distribution rather than explicit effort  
486 or catch redistribution toward boundaries of fishery closures.

487         Spatial heterogeneity in fishery removals typically declined during the study period,  
488 which is counter to our expectation that policy changes would increase spatial heterogeneity of  
489 removals (particularly for groups with species targeted by the fishery). Perhaps habitat closures  
490 did not lead to increased spatial CV because fishers were already effectively prevented from  
491 trawling in these areas due to footrope restrictions implemented in 2000 (Bellman et al., 2005),  
492 or that closures did not lead to fishing-the-line behavior and instead spread effort over remaining  
493 habitat features in soft sediments (Barnett et al., 2017). This "filling-in" of fishing effort might  
494 explain the countertrend in spatial autocorrelation of removals, which did increase during the  
495 time period when habitat closures were implemented. The subsequent decline in spatial  
496 autocorrelation of removals coinciding with catch share implementation was not well explained  
497 by the distribution of trawl effort, which actually became more positively autocorrelated across  
498 this period (Kuriyama et al., In review). Decreasing patchiness of removals could have been the  
499 result of increasing fine-scale contrast in density (as observed in this study for all fishes), or  
500 increased targeting efficiency (Kuriyama et al., In review) likely related to nuanced changes in  
501 fisher behavior such as tow duration and time of day that coincided with catch shares  
502 implementation (Miller and Deacon, 2017).

503         Similar to patterns of removals, trends in spatial heterogeneity of density in the trawled  
504 region did not increase as we expected. Trends in spatial heterogeneity of density were either not  
505 statistically significant or inconsistent across assemblages. Spatial heterogeneity of some groups  
506 declined during the period when habitat closures began. This period also contained the only

507 years with a substantial increase in the number of hauls fleetwide, as effort generally declined  
508 over the study period (Fig. S1). Because fishing is thought to decrease spatial variation in  
509 density, declines in spatial CV of overall fish density during the habitat closure period could  
510 have been driven by increasing effort concentrated on a smaller amount of fishable habitat.  
511 Likewise, increased spatial heterogeneity of density in the following period of catch share  
512 management might have been caused by decreasing fleetwide effort. However, the changes in  
513 effort occurring over the study period are likely small relative to those over the history of the  
514 fishery (Hilborn et al., 2012). Decreases in density CV (of fishes) and autocorrelation (of  
515 flatfishes and forage species) could have also resulted from high rates of fish movement, density-  
516 dependent movement out of closures, or density-dependent population or individual growth, but  
517 this does not explain the subsequent increase in these metrics for fishes and flatfishes observed  
518 after catch shares. Other potential causes of the deviation between our expectations and results  
519 could be due to time lags in density responses or unknown factors regulating the effect of fishing  
520 on faunal distributions (e.g., fisher foraging behavior or harvest control rules). Further, there  
521 could be a complex interaction between changes in spatial heterogeneity of the system and the  
522 pressure that we have yet to understand. Thus, the direct inference that spatial closures have  
523 mixed results and catch shares increase spatial heterogeneity of faunal density distributions  
524 and—by association—ecological stability, should be evaluated with caution.

525         Like many observational studies in fisheries science, the results of our study must be  
526 interpreted with some caveats. First, although we ascribe differences in density responses in the  
527 Southern California Bight and the rest of the study region to the presence of trawling, there are  
528 also differences in oceanography, coastal and seafloor topography, and species composition  
529 between the two subregions. Second, predictability of density and removals was low for the



530 forage and protected species groups as they are inherently patchily distributed and not well  
531 sampled by trawl gear. However, we contend that there is still value in including these groups to  
532 determine responses for species not targeted—or actively avoided—by the fishery. Third, we  
533 note that our use of multiple comparisons means it is likely that at least one test resulted in  
534 falsely rejecting the null hypothesis; however, one inappropriate inference would not change the  
535 broader conclusions of this study. Finally, we do not explicitly account for movement and  
536 density-dependent population responses, yet these factors might reduce our ability to explain  
537 relationships between patterns of removals and density.

538         Beyond the local direct effects of fishing, faunal distributions may be affected indirectly  
539 by reductions in population size, as evidenced by hyperstability or hyperdepletion in some  
540 fisheries (Rose and Kulka, 1999). However, such effects require high levels of contrast in  
541 population size that is rarely observed over the same period as extensive spatially-referenced  
542 sampling, and thus abundance-distribution relationships are not yet well understood for fishes  
543 (Shepherd and Litvak, 2004). Future work on how fishing affects species distributions would  
544 benefit from continuing and extending large-scale spatial monitoring efforts and experimental  
545 manipulations of at least moderate scale relative to the body size and dispersal ability of a given  
546 species.

547         We show how spatial indicators of fishery activity and faunal densities can be analyzed to  
548 monitor communities and assess ecosystem effects of fishing even in lightly exploited systems.  
549 Although our analytical framework revealed the relationship between distributions of fish and  
550 fishing that have proven elusive in other studies, the system did not always respond as expected  
551 to management changes. Understanding of how management and conservation actions modify  
552 the influence of fishing on metacommunities could be advanced by differentiating the general

553 effect of changing intensity of fishing from changing the spatial distribution of fishing. Defining  
554 how these dimensions of fishing influence distributions and how they scale with changes in  
555 faunal density and community composition will make spatial indicators of fishing a useful  
556 measure of ecosystem pressure to combine with spatial indicators of environmental drivers in  
557 advancing ecosystem-based fishery management. To apply spatial ecological indicators to  
558 management, further research would be required to evaluate appropriate scales of analysis based  
559 on factors specific to a system, such as the distribution, movement and demographic connectivity  
560 of species and the spatial distribution of their associated fisheries and oceanographic drivers of  
561 productivity. If one could find consistent relationships between fishing and spatial heterogeneity  
562 of density, they could quantify how fishing may be modify population and community stability  
563 beyond its potential influence on temporal variation of abundance (Ciannelli et al., 2013; Hsieh  
564 et al., 2008; Hsieh et al., 2006; Hsieh et al., 2010).

565

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1 Title: **How do ecological resilience metrics relate to community stability and collapse?**

2

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13

14 **ABSTRACT**

15           The concept of ecological resilience (the amount of disturbance a system can absorb  
16 before collapsing and reorganizing) holds potential for predicting community change and  
17 collapse—increasingly common issues in the Anthropocene. Yet neither the predictions nor  
18 metrics of resilience have received rigorous testing. The cross-scale resilience model, a leading  
19 operationalization of resilience, proposes resilience can be quantified by the combination of  
20 diversity and redundancy of functions performed by species operating at different scales. Here,  
21 we use 48 years of sub-continental avian community data aggregated at multiple spatial scales to  
22 calculate resilience metrics derived from the cross-scale resilience model (i.e., cross-scale  
23 diversity, cross-scale redundancy, within-scale redundancy, and number of body mass  
24 aggregations) and test core predictions inherent to community persistence and change.  
25 Specifically, we ask how cross-scale resilience metrics relate community stability and collapse.  
26 We found low mean cross-correlation between species richness and cross-scale resilience  
27 metrics. Resilience metrics constrained the magnitude of community fluctuations over time  
28 (mean species turnover), but resilience metrics but did not influence variability of community  
29 fluctuations (variance in turnover). We show shifts in resilience metrics closely predict  
30 community collapse: shifts in cross-scale redundancy preceded abrupt changes in community  
31 composition, and shifts in cross-scale diversity synchronized with abrupt changes in community  
32 composition. However, we found resilience metrics only weakly relate to maintenance of  
33 particular species assemblages over time. Our results distinguish ecological resilience from  
34 ecological stability and allied concepts such as elasticity and resistance: we show communities  
35 may fluctuate widely yet still be resilient. Our findings also differentiate the roles of functional  
36 redundancy and diversity as metrics of resilience and reemphasize the importance of considering



37 resilience metrics from a multivariate perspective. Finally, we support the contention that  
38 ecological stability is nested within ecological resilience: stability predicts the behavior of  
39 systems within an ecological regime, and resilience predicts the maintenance of regimes and  
40 behavior of systems collapsing into alternative regimes.

41

42 ***Key Words***

43 Resilience, cross-scale resilience model, elasticity, functional diversity, functional redundancy,  
44 regime shift, species richness, stability, turnover

45

46 **INTRODUCTION**

47 “If there is a worthwhile distinction between resilience and stability it is important that both be  
48 measurable.” – C. S. Holling, 1973

49

50 As the Anthropocene progresses, community change and collapse are increasingly  
51 common (Folke et al., 2004; Steffen et al., 2015). The concept of ecological resilience, defined  
52 by C. S. Holling (1973) as the amount of disturbance a system can absorb before collapsing into  
53 an alternative regime, holds potential for predicting community change and collapse (Angeler &  
54 Allen, 2016). Quantifying ecological resilience has been a long-term pursuit in ecology  
55 (Carpenter, Westley, & Turner, 2005; Cumming et al., 2005; Standish et al., 2014), ecological  
56 resilience has been applied internationally in management frameworks (Briske et al., 2008;  
57 Bestlemeyer et al., 2017; Seidl et al., 2016), and multiple ecological resilience metrics have been  
58 proposed (Allen et al., 2005; Baho et al., 2017). Yet neither the core predictions nor metrics of  
59 ecological resilience theory have received rigorous testing (Angeler and Allen, 2016; Sundstrom  
60 et al., 2018).

61 Ecological resilience theory makes key predictions concerning complex, nonlinear, and  
62 abruptly shifting system behavior, making it uniquely applicable to Anthropocene issues (L. H.  
63 Gunderson, 2000). Ecological resilience is related to, but distinct from, ecological stability (the  
64 ability of a system to return to an equilibrium state post-disturbance—also known as  
65 “engineering resilience,” “bounce-back time,” “resistance,” and “elasticity”; C. S. Holling,  
66 1973; Hillebrand et al., 2018; Pimm, 1984). This is a crucial distinction because while ecological  
67 resilience makes predictions concerning abrupt regime shifts into alternative states, ecological  
68 stability only makes predictions concerning a single regime (Angeler and Allen, 2016).

69 Ecological resilience theory predicts that a system may fluctuate greatly (have low stability and  
70 exhibit non-equilibrium behavior) and yet have high ecological resilience or conversely fluctuate  
71 little and have low ecological resilience (Angeler & Allen, 2016; C. S. Holling, 1973). That is, a  
72 resilient system will constrain the magnitude of fluctuations so that the system stays within a  
73 given regime, but the same resilient system may exhibit high instability within the regime (L. H.  
74 Gunderson, Allen, & Holling, 2012). By definition, loss of ecological resilience increases the  
75 likelihood of system collapse and regime shifts due to loss of structures, functions, and feedbacks  
76 that maintain the current regime (Allen, Gunderson, & Johnson, 2005). Thus, ecological  
77 resilience should be both quantifiably distinct from stability and clearly correspond with  
78 community change and collapse (C. S. Holling, 1973; Standish et al., 2014).

79         The cross-scale resilience model, a leading model for operationalizing and quantifying  
80 ecological resilience (hereafter referred to simply as “resilience”), provides the opportunity to  
81 test these core predictions of resilience theory (G. Peterson et al., 1998; S. M. Sundstrom et al.,  
82 2018). The cross-scale resilience model establishes that redundancy and diversity of organism  
83 functions across discontinuous scale domains of resource use in a system confer resilience (C. S.  
84 Holling, 1992; G. Peterson et al., 1998; Figure 1). Quantifying redundancy and diversity of  
85 functions across these discontinuous scale domains can produce metrics to estimate the relative  
86 resilience of systems (Bouska, 2018, Sundstrom et al., 2018; Angeler et al., 2019a). For example,  
87 Allen et al. (2005) proposed several cross-scale resilience metrics such as within-scale  
88 redundancy, cross-scale redundancy, cross-scale diversity, and number of scale domains.

89         Here, we use a half-century of sub-continental avian community data to calculate cross-  
90 scale resilience metrics and test how resilience relates to community stability and collapse. We  
91 do this by testing two core resilience theory predictions concerning its relationship with stability

92 and two concerning its relationship with community change and collapse. The first resilience-  
93 stability relationship prediction is that resilience is distinct from stability: we test this by  
94 quantifying the degree of correlation between species richness and cross-scale resilience metrics.  
95 Although species richness is not a direct metric of stability, it is correlated with stability and  
96 influences the ability of a system to “bounce back” from disturbances (Hautier et al., 2015; Ives  
97 & Carpenter, 2007; McCann, 2000; Mougi & Kondoh, 2012; Tilman & Downing, 1994). The  
98 second resilience-stability relationship prediction is that resilience will constrain the magnitude  
99 of system fluctuations but not their variability: we test this by determining the relationship  
100 between cross-scale resilience metrics and the mean and variance of annual species turnover. In  
101 this case, cross-scale diversity is expected to reduce mean turnover the most, and all resilience  
102 metrics should have little influence on turnover variance (Allen et al., 2005; Angeler et al.,  
103 2019a). The first resilience-collapse relationship prediction is that changes in cross-scale  
104 resilience metrics will predict community collapse: we test this by determining if changes in  
105 cross-scale resilience metrics synchronize with abrupt shifts in community composition. Within-  
106 scale redundancy, cross-scale redundancy, and number of scale domains are expected to most  
107 strongly predict community collapse (Nash et al., 2016; Roberts et al., 2019; Spanbauer et al.,  
108 2016). Finally, the second resilience-collapse prediction is cross-scale resilience metrics will  
109 only weakly predict maintenance of specific species assemblages: we test this by determining  
110 how cross-scale resilience metrics relate to changes in community similarity over time (L. H.  
111 Gunderson, 2000; Angeler et al., 2019b).

112

113 **METHODS**

114 *Calculating cross-scale resilience metrics*

115 Cross-scale resilience metrics are calculated by first identifying a biotic community  
116 within a system (e.g., an avian forest community) and acquiring census presence/absence data  
117 from the biotic community (Allen et al., 2005), identifying the discontinuous scale domains at  
118 which functions are performed by each species in the biotic community (Nash et al., 2014a, b),  
119 and finally using functional traits of species across scale domains to estimate functional  
120 redundancy and diversity within and across scale domains (Fischer et al., 2007).

121

122 *Identifying biotic communities*

123 For biotic community data, we used the North American Breeding Bird Survey (BBS)  
124 which estimates bird community composition via yearly roadside avian point-count surveys  
125 (Sauer et al., 2013). Begun in 1966, the BBS is conducted along a series of > 2500 permanent,  
126 randomly-distributed routes during the breeding season (Sauer et al., 2013). We analyzed BBS  
127 route data from 1967 - 2014.

128 We defined avian communities by spatially binning BBS routes according to US  
129 Environmental Protection Agency (EPA) ecoregions (Omernik & Griffith, 2014; Figure 2).  
130 These ecoregions are spatially hierarchical, meaning that finer-scaled ecoregions are bounded by  
131 and nested within larger-scaled ecoregions. Because smaller-scale EPA ecoregion boundaries are  
132 bounded by US political boundaries, we only consider BBS routes within the continental United  
133 States. We considered avian communities at the three progressively smaller spatial scales (EPA  
134 ecoregion levels II, III, IV; Figure 2). If binned BBS data within an ecoregion did not extend for

135  $\geq 24$  years (i.e.,  $\geq 50\%$  of the study period), we excluded that ecoregion from analysis (Table S1;  
136 see supplementary computer code for further details).

137

### 138 *Identifying discontinuous scale domains*

139 We performed discontinuity analysis on binned BBS data for each ecoregion at each  
140 scale using the “discontinuity detector” method (Barichievy et al., 2018) based on the Gap Rarity  
141 Index which identifies scale domains by detecting discontinuities in log-ranked organism body  
142 masses (Restrepo et al., 1997). For taxa with determinant growth, mean body mass reliably  
143 differentiates size aggregations and is strongly allometric to the scale domains at which functions  
144 are carried out by organisms (Allen et al., 2006; C. S. Holling, 1992; Nash et al., 2014b).

145 Because of known negative observation biases for waterfowl and allied families and because

146 water-dwelling avian families’ follow different body masses patterns than terrestrial avian

147 families, we removed all species from the Anseriformes, Gaviiformes, Gruiformes,

148 Pelecaniformes, Phaethontiformes, Phoenicopteriformes, Podicipediformes, Procellariiformes,

149 and Suliformes families from the analysis (C. S. Holling, 1992; S. M. Sundstrom, Allen, &

150 Barichievy, 2012). We obtained mean body mass estimates for all remaining species from the

151 CRC Handbook of Avian Body Masses (Dunning Jr, 2007). Because Gap Rarity Index tends to

152 overestimate discontinuities in species-poor samples, we removed any route with  $< 40$  species

153 observed (Barichievy et al., 2018; Stow, Allen, & Garmestani, 2007). We simply counted the

154 number of body mass aggregations to obtain that metric.

155

156 *Estimating within- and cross-scale functional redundancy, cross-scale diversity*

157 We assigned functional types to each species according to diet and foraging strategies  
158 (Ehrlich, Dobkin, & Wheye, 1988). We broke diets into carnivore, herbivore, and omnivore  
159 groups, where omnivores are defined as species with approximately even proportions of plant  
160 and animal intake (Bouska, 2018). We divided foraging strategies into five groups: water,  
161 ground, foliage, bark, and air (S. M. Sundstrom et al., 2012). Thus, functional groups represented  
162 combinations of diet and foraging strategies (e.g., water carnivore, ground herbivore, etc.).

163 We then used functional groups along with body mass aggregations to calculate cross-  
164 scale redundancy (average number of aggregations for which each functional group has at least  
165 one representative), within-scale redundancy (the average number of representatives from each  
166 functional group within each aggregation), and cross-scale diversity (the average diversity of  
167 functional groups across aggregations) metrics for each ecoregion within each of the three spatial  
168 scales (Figure 2). The equations for these are as follows:

169 
$$\text{Cross - scale Redundancy} = \frac{1}{a} \sum_{i=1}^a (\varphi)_i$$

170

171 
$$\text{Within - scale Redundancy} = \frac{1}{a} \sum_{i=1}^a \left( \frac{1}{f} \sum_{j=1}^f f_j \right)_i$$

172

173 
$$\text{Cross - scale Diversity} = \frac{1}{a} \sum_{i=1}^a \left( - \sum_{j=1}^f p_j \ln p_j \right)_i$$

174 Where  $a$  is the number of body mass aggregations,  $\varphi$  is the number of functional groups with at  
175 least one representative in an aggregation,  $f$  is the  $j^{\text{th}}$  functional group, and  $p$  is the  $j^{\text{th}}$  species in  
176 each aggregation.

177

### 178 ***Resilience-Stability Test 1: Relationship between cross-scale resilience and richness***

179 We used cross-correlation to compare species richness with each cross-scale resilience  
180 metric (number of body mass aggregations, cross-scale redundancy, within-scale redundancy,  
181 cross-scale diversity) for each ecoregion across -5 to 5 lags. That is, we used cross-correlation to  
182 quantify temporal covariance of richness and resilience metrics, determining if patterns of  
183 resilience metrics preceded (back to 5 time steps before) or followed (forward to 5 time steps  
184 after) patterns of richness. For each lag, we calculated the mean and 85% confidence intervals of  
185 the absolute values of correlation coefficients across ecoregions.

186

### 187 ***Resilience-Stability Test 2: Relationship between cross-scale resilience and turnover***

188 Second, we determined the relationship between cross-scale resilience metrics and  
189 species turnover. We calculated relative species turnover (the proportion of the species pool that  
190 turns over annually) using the following equation (Diamond, 1969; Wonkka, West, Twidwell, &  
191 Rogers, 2017):

192

$$193 \text{Turnover}_{t+1} = (U_t + U_{t+1}) / (S_t + S_{t+1})$$

194

195 where  $U_t$  is the number of species present in the ecoregion at year  $t$  that were not present in year  $t$   
196  $+ 1$ ;  $U_{t+1}$  is the number of species present in the ecoregion at year  $t+1$  that were not present in



197 year  $t$ ;  $S_t$  is the total number of species present in the ecoregion at year  $t$ ; and  $S_{t+1}$  is the total  
198 number of species present in the ecoregion at year  $t + 1$ .

199 We then developed two linear mixed models: 1) to determine if resilience metrics  
200 influenced the magnitude of species turnover, we used the mean of the absolute value of species  
201 turnover over time as the response variable, and 2) to determine if resilience metrics influenced  
202 the variability of species turnover, we used the standard deviation of species turnover over time  
203 as the response variable. For both models, we set mean resilience metrics over time as the  
204 predictor variables. We allowed intercepts to vary by hierarchically nested EPA ecoregions (e.g.,  
205 for level III ecoregions, random effect in R package “lme4” syntax was “( 1 | Level I / Level II )”  
206 ). To minimize collinearity, we calculated variance inflation factors and sequentially removed  
207 predictor variables (resilience metrics) with the highest variance inflation factor until variance  
208 inflation factor values for all variables were  $\leq 3$ .

209

### 210 ***Resilience-Collapse Test 1: Relationship between cross-scale resilience and abrupt shifts***

211 We determined whether significant temporal shifts in cross-scale resilience metrics  
212 synchronized with abrupt shifts in community composition. To identify abrupt shifts in  
213 community composition, we 1) performed detrended correspondence analysis (DCA; “decorana”  
214 function from the vegan package in R) on Hellinger-transformed relative abundances of species  
215 in each ecoregion over time, 2) extracted values of the first DCA axis (DCA1) for each year, 3)  
216 used generalized additive models (GAMs) to model changes in DCA1 over time (with year as  
217 the smoothed predictor) for each ecoregion, 4) extracted predicted DCA1 response values from  
218 GAMs for each ecoregion (Figure 3a), and 5) determined where community structure  
219 significantly changed by first calculating derivatives and 85% confidence limits around the

220 derivatives from the GAM predictions and then locating ranges in the time series where  
221 derivative confidence limits did not encompass zero (Simpson, 2018; Figure 3b). We located  
222 shifts in cross-scale resilience metrics in a similar fashion—by extracting GAM predictions,  
223 calculating derivatives and confidence intervals, and locating ranges where confidence limits did  
224 not encompass zero (Figure 3b). To test for synchrony between cross-scale resilience metrics and  
225 structural community change, we encoded DCA1 and resilience metric time series as binary  
226 variables, where either a significant shift (85% confidence limit of derivative did not encompass  
227 zero) occurred or did not for each time step (i.e., each year of BBS data; Figure 3c). We  
228 aggregated significant increases and decreases into an absolute value because both significant  
229 increases and decreases in ordinated values (e.g., DCA) or resilience metrics, regardless of  
230 directionality, could signal regime shifts. We set the binary DCA1 variable as the response and  
231 binary resilience metrics predictors in a binomial generalized linear mixed model. We checked  
232 for collinearity with variance inflation factors.

233

### 234 ***Resilience-Collapse Test 2: Relationship between cross-scale resilience and community*** 235 ***similarity***

236 We determined the relationship between cross-scale resilience metrics and patterns of  
237 community similarity over time. We estimated community similarity over time via the Jaccard  
238 index. That is, we calculated Jaccard similarity between each year of BBS data for each  
239 ecoregion and then used linear regression to estimate change in community identity over time  
240 (i.e., slope; *sensu* Dornelas et al., 2014). Because the Jaccard index ranges from 0 (complete  
241 dissimilarity in species) to 1 (complete similarity in species), a slope of zero indicates no change  
242 in community composition over time, and a slope of -1 indicates a complete change in species

243 pool. We then developed linear mixed models, setting the slope of the Jaccard index as the  
244 response variable. For predictor variables, we used initial resilience metric values (the  
245 chronologically first value for each resilience metric for each ecoregion) and mean resilience  
246 metric values (the average of each resilience metric value across the time series for each  
247 ecoregion). To account for variance in certainty of Jaccard slope fits, we used  $1 / \text{standard error}$   
248 of each Jaccard slope fit as prior weights for linear mixed models. We used the methods from  
249 Test 2 for minimizing collinearity as above (i.e., sequential removal of predictor variables via  
250 variance inflation factors).

251

## 252 **RESULTS**

### 253 ***Resilience-Stability Test 1: Relationship between cross-scale resilience and richness***

254 Mean cross-correlation between richness and resilience metrics was low across scales and  
255 individual metrics, ranging from  $r = 0.16 \pm 0.01$  (cross-scale redundancy at lag -5 at the finest  
256 scale) to  $r = 0.63 \pm 0.02$  (cross-scale diversity at lag 0 at the finest scale; Figure 4). Patterns were  
257 consistent across scales: the strongest correlation between richness and all metrics at all scales  
258 occurred at lag zero (annually) after which correlations decreased sharply (Figure 4). At the  
259 broadest scale (level II), confidence limits show little difference between individual metrics'  
260 correlations with richness (Figure 4). At the finer scales (levels III, IV), cross-scale diversity  
261 correlated most strongly with richness (Figure 4). Within-scale redundancy showed the second  
262 greatest correlation with richness (max  $r = 0.50 \pm 0.02$  at level IV, lag 0; Figure 4). Cross-scale  
263 redundancy ( $r = 0.34 \pm 0.02$  at lag 0) and number of aggregations ( $0.29 \pm 0.02$  at lag 0) displayed  
264 the weakest correlation with richness at finer scales (Figure 4).

265

266 ***Resilience-Stability Test 2: Relationship between cross-scale resilience and turnover***

267 Resilience metrics had significantly negative relationships with mean annual species  
268 turnover at all scales, but resilience metrics showed little or no association with standard  
269 deviation of annual species turnover (Figure 5; Table S1). Cross-scale diversity was a significant  
270 predictor of mean species turnover at the broadest scale and the strongest predictor at the finest  
271 scale ( $-0.027 \pm 0.001$  and  $-0.034 \pm 0.002$  at levels II and IV respectively), and cross-scale  
272 diversity was a significant negative predictor of standard deviation in species turnover at the  
273 finest scale ( $-0.004 \pm 0.002$ ). Cross-scale redundancy was a significant predictor at all scales,  
274 although its strength decreased at finer scales until it was the weakest predictor at the finest scale  
275 ( $-0.018 \pm 0.011$ ,  $-0.015 \pm 0.001$ , and  $-0.0059 \pm 0.004$  at ecoregion levels II, III, and IV  
276 respectively). Cross-scale redundancy also significantly negatively predicted standard deviation  
277 in species turnover at the finest scale ( $-0.005 \pm 0.003$ ). Within-scale redundancy was a  
278 significant predictor at the middle scale ( $-0.017 \pm 0.006$ ), and number of aggregations was a  
279 significant predictor of middling strength at the finest scale ( $-0.018 \pm 0.004$ ).

280

281 ***Resilience-Collapse Test 1: Relationship between cross-scale resilience and abrupt shifts***

282 At all scales, resilience metrics synchronized significantly with abrupt community shifts  
283 (Figures 3, 4; Table S3). At the broadest scale (level II), cross-scale diversity ( $1.0 \pm 0.53$ ) and  
284 cross-scale redundancy ( $0.67 \pm 0.55$ ) synchronized with community change (Figure 4). At the  
285 middle scale (level III), number of aggregations ( $0.21 \pm 0.20$ ) and within-scale redundancy ( $0.62$   
286  $\pm 0.20$ ) exhibited synchrony with community change (Figure 3), but cross-scale redundancy  
287 exhibited asynchrony (i.e., a negative model coefficient;  $-0.3 \pm 0.19$ ) with community change  
288 (Figures 3, 4). And at the finest scale (level IV), all resilience metrics synchronized with abrupt

289 community shifts: cross-scale diversity showed the strongest synchrony ( $0.58 \pm 0.08$ ; Figure 3),  
290 and number of aggregations showed the weakest synchrony ( $0.11 \pm 0.09$ ).

291

292 ***Resilience-Collapse Test 2: Relationship between cross-scale resilience and community***  
293 ***similarity***

294 At the broadest and middle scales (levels II, III), neither initial nor mean resilience metric  
295 values significantly predicted changes in community similarity over time (Table S2). But at the  
296 finest scale (level IV), initial values of cross-scale diversity ( $0.0002 \pm 0.0001$ ) and number of  
297 aggregations ( $0.0002 \pm 0.0001$ ) significantly, albeit weakly, predicted reduced community  
298 change (i.e., pushed Jaccard slopes closer to zero—no net community change; Table S2).

299

300 ***DISCUSSION***

301 Using a half-century of subcontinental community data, we provide quantitative support  
302 for core predictions of ecological resilience theory regarding how ecological resilience relates to  
303 ecological stability and collapse. Per Holling's call in his seminal manuscript on resilience theory  
304 (C. S. Holling, 1973), we found resilience is related to but distinct from stability. Importantly,  
305 our results distinguish ecological resilience from concepts allied with stability such as  
306 engineering resilience, “bounce-back” time to equilibrium, resistance, and elasticity (L. H.  
307 Gunderson, 2000; Pimm, 1984; Standish et al., 2014). We also show that shifts in cross-scale  
308 resilience metrics clearly predict and coincide with abrupt community shifts, but at the same  
309 time, resilience is weakly related to community change in terms of maintenance of a particular  
310 species assemblages over time. We also provide interpretability for cross-scale resilience  
311 metrics: we distinguish the roles of functional redundancy and diversity metrics of community

312 collapse and community similarity, respectively (G. Peterson et al., 1998; Walker, Kinzig, &  
313 Langridge, 1999), and we show number of aggregations (i.e., scale domains) may be an  
314 unresponsive metric if systems reorganize around similar numbers of scale domains during and  
315 post-collapse, meaning this metric may only detect extreme collapse events (Angeler et al.,  
316 2019b; Roberts et al., 2019).

317         Our results reaffirm the importance of avoiding the conflation of ecological resilience and  
318 ecological stability. Stability theory predicts a particular community composition (e.g., higher  
319 species richness) will reduce variance in system functionality but makes no assertions concerning  
320 alternative states (Allan et al., 2011; Cardinale et al., 2013; Tilman, 1996; Wagg et al., 2018).  
321 Additionally, stability typically does not consider ecological complexity features, such as spatial  
322 and temporal scaling structures or thresholds (Baho et al., 2017; Hillebrand et al., 2018). In  
323 contrast, resilience theory predicts resilient systems may exhibit wide ranges of variance,  
324 community composition will be dynamic and adaptive, and scaling patterns of functional  
325 redundancy and diversity within communities (instead of particular community compositions)  
326 will determine the ability of a system to remain within one of multiple alternative regimes  
327 (Allen, Angeler, Garmestani, Gunderson, & Holling, 2014; Angeler et al., 2019a; Chillo, Anand,  
328 & Ojeda, 2011; S. M. Sundstrom et al., 2018). Our results support these differences between  
329 stability and resilience: resilience metrics had low degrees of correlation with species richness, a  
330 metric that is closely correlated to stability and the ability of a system to “bounce back” from  
331 disturbances (Hautier et al., 2015; Ives & Carpenter, 2007; McCann, 2000; Mougi & Kondoh,  
332 2012; Tilman & Downing, 1994). That is, greater richness did not necessarily beget greater  
333 resilience. This finding contrasts with a pervasive conflation of richness and resilience  
334 (Bellwood & Hughes, 2001; J. Fischer et al., 2007; Oliver et al., 2015; Standish et al., 2014). As

335 expected, cross-scale diversity exhibited the highest correlation with richness, although its  
336 correlation was much less than typical cutoffs for collinearity. Cross-scale resilience metrics also  
337 did not predict variability in community composition (standard deviation in species turnover)  
338 except weakly at the finest scale. This supports the resilience theory prediction that systems may  
339 have low stability (high variance in species turnover) but high resilience (Holling, 1973). Our  
340 results also support the contention that the concept of ecological stability is nested within  
341 ecological resilience: resilience metrics constrained the magnitude of temporal community  
342 fluctuations (mean species turnover) but only weakly predicted variability in community  
343 fluctuations—which is the purview of stability theory (Angeler and Allen, 2016; Hautier et al.,  
344 2015; Mougi & Kondoh, 2012).

345         Similarly, resilience theory predicts systems with higher resilience will be more likely to  
346 retain similar structures and functions over time, but unlike stability, resilience theory makes few  
347 predictions on the maintenance of a particular species assemblage (Allen & Holling, 2010;  
348 Bellwood & Hughes, 2001; L. H. Gunderson, 2000). Our results support this premise. Cross-  
349 scale resilience metrics were not strongly associated with maintenance of a particular group of  
350 species. Instead, resilience metrics predicted maintenance of overall community structure per  
351 their synchrony with abrupt community shifts across scales. That is, resilience metrics predict  
352 significant abrupt community shifts but not community similarity over time (Angeler et al.,  
353 2019b). However, higher resilience metrics did weakly predict maintenance of community  
354 composition over time as well as constraining mean species turnover which still supports a  
355 connection between species composition and resilience.

356         The cross-scale resilience model differentiates the roles of functional redundancy and  
357 functional diversity, and we corroborate this (Bellwood & Hughes, 2001; Elmqvist et al., 2003;