

1 **NONADDITIVE AND NONSTATIONARY PROPERTIES IN THE SPATIAL DISTRIBUTION OF A**  
2 **LARGE MARINE FISH POPULATION**

3 Lorenzo Ciannelli\*, College of Earth, Ocean and Atmospheric Sciences, Oregon State  
4 University, Corvallis, Oregon 97331, USA. Email: lciannel@coas.oregonstate.edu

5 Valerio Bartolino, Department of Aquatic Resources, Swedish University of Agricultural  
6 Sciences, Lysekil 45330, Sweden & Department of Earth Sciences, Gothenburg  
7 University, Gothenburg 40530, Sweden, email: valerio.bartolino@slu.se

8 Kung-Sik Chan, Department of Statistics and Actuarial Science, University of Iowa, Iowa  
9 City, Iowa 52242, USA, email: kung-sik-chan@uiowa.edu

10 (\*) Corresponding author: Tel: + 1 – 541 – 737-3142; Fax: + 1 – 541-737-2064

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17 *Summary*

18 Density-independent and density-dependent variables both affect the spatial distributions  
19 of species. However, their effects often are separately addressed using different analytical  
20 techniques. We apply a spatially-explicit regression framework that incorporates  
21 localized, interactive and threshold effects of both density-independent (water  
22 temperature) and density-dependent (population abundance) variables, to study the spatial  
23 distribution of a well-monitored flatfish population in the eastern Bering Sea. Results  
24 indicate that when population biomass was beyond a threshold a further increase in  
25 biomass promoted habitat expansion in a nonadditive fashion with water temperature. In  
26 contrast, during years of low population size, habitat occupancy was only affected  
27 positively by water temperature. These results reveal the spatial signature of intraspecific  
28 abundance distribution relationships and the nonadditive and nonstationary responses of  
29 species spatial dynamics. Furthermore these results underscore the importance of  
30 implementing analytical techniques that can simultaneously account for density-  
31 dependent and density-independent sources of variability when studying geographic  
32 distribution patterns.

33

34 **Key words:** abundance-distribution, spatial dynamics, density-dependent habitat  
35 selection, Bering Sea

36

37 INTRODUCTION

38           Density-independent (i.e., environmental) and density-dependent (i.e.,  
39 demographic) variables are both known to affect species spatial distribution. For  
40 example, species are often distributed over space following environmental preferences to  
41 optimize the use of spatially heterogeneous resources [1], or in relation to their own  
42 abundance, to reduce intraspecific competition [2]. Geographic distribution patterns  
43 resulting from density-dependent and density-independent variables have often been  
44 studied in isolation and with different analytical techniques, despite these variables being  
45 very likely to interact both in space [3] and time [4]. Density-dependent spatial dynamics  
46 can promote geographic expansion when the population reaches a high level of  
47 abundance, so that the habitat suitability or the individuals' fitness is equalized over the  
48 species spatial domain [2]. When a species expands its geographic distribution (also  
49 referred to as occupancy) in relation to its own abundance a positive intraspecific  
50 abundance-distribution relationship occurs (for a review see 5). In marine contexts, many  
51 studies have shown that species occupancy changes with species abundance [6, 7, 8, 9].  
52 Often however, changes in population abundance (and occupancy) can co-occur with  
53 large-scale changes in environmental variables, such as water temperature [10]. In such  
54 circumstances it becomes harder to disentangle the multiple influences on species  
55 occupancy, or the degree to which a change of temperature may facilitate or curtail a  
56 change of occupancy [11, 12]. We contend that density-dependent and density-  
57 independent sources of variability affect population spatial distribution in a nonadditive  
58 fashion, a prediction that we refer to as the *nonadditive species-environment hypothesis*.

59           Despite occurring in many systems, there is still controversy on the causality and  
60 anatomy of intraspecific abundance-distribution relationships [5, 13]. These relationships  
61 are quantified by correlating population occupancy (typically the spatial extent over  
62 which the species is present) with the population numerical abundance or total biomass.  
63 While this approach has been instrumental in revealing macroecological patterns over  
64 time and across species, it cannot simultaneously account for multiple sources of spatial  
65 variation on species distribution and does not reveal the spatial signature of a species  
66 change in distribution. This additional knowledge would enable us to address the genesis  
67 of a species abundance-distribution relationship. Gaston et al. [14] report that a species'  
68 geographic distribution is more likely to significantly vary when the population  
69 abundance is steadily changing (i.e., when a trend in abundance or biomass is present),  
70 rather than when the abundance randomly fluctuates around a mean value. Indeed, Fisher  
71 & Frank's [7] analysis of 34 intraspecific abundance-distribution relationships supports  
72 the link between time-trend and intraspecific abundance-distribution correlations. Turner  
73 [15] also points out that species distribution can undergo strong nonlinearities, which  
74 result in drastic changes in spatial configurations in relation to small changes in forcing  
75 variables. Within these contexts, it is crucial to investigate the underlying mechanisms  
76 that control the species occupancy [11, 16], and specifically, whether there are threshold  
77 values of population abundance that once crossed can cause drastic changes in the species  
78 geographic distribution. In keeping with Gaston *et al.* [14], we expect that during periods  
79 in which population abundance is relatively constant the species occupancy is mostly  
80 responsive to density-independent variables. In contrast, during periods in which  
81 population abundance experiences a trend, the species occupancy becomes more tightly

82 linked with its own abundance. Furthermore, in agreement with Turner [15], the passage  
83 between these two phases should be abrupt, once a threshold of population abundance is  
84 crossed. Collectively, the expectation of a threshold and temporally variable intraspecific  
85 abundance-distribution relationships leads to a prediction which we refer to as the  
86 *nonstationary intraspecific abundance-distribution hypothesis*.

87 In this study we provide tests of both the nonadditive species-environment and  
88 nonstationary abundance-distribution hypotheses by developing a spatial regression  
89 framework that incorporates localized, interactive and threshold effects of both  
90 environmental and demographic variables. The model is used to examine the spatial  
91 dynamics of a well-monitored large and piscivorous flatfish (arrowtooth flounder,  
92 *Atherestes stomias*, hereafter referred as ‘flounder’) in the eastern Bering Sea (Fig. A1).

93

#### 94 MATERIAL AND METHODS

##### 95 *Sampled region and data collections*

96 We analyzed the trawl data from the groundfish survey of the eastern Bering Sea  
97 conducted by the U.S. National Marine Fisheries Service (NMFS) during 1982-2010. The  
98 sampling design is based on a fixed regular grid of 37 km x 37 km, with sampling  
99 occurring over a period of six to eight weeks during late spring and summer [17, 18]. The  
100 numerical catch was standardized by area swept (cpue,  $n \cdot \text{km}^{-2}$ ). Because of the ecological  
101 role played by adult flounder in the Bering Sea as predator of other fish species, we  
102 focused the analysis on individuals larger than 350 mm. In addition to flounder cpue  
103 from the groundfish survey, there were other variables included in the analysis. These

104 were bottom temperature at each sampling location (T), flounder population biomass (B)  
105 and sediment size (K), all known to influence flounder distribution [19].

106 Henceforth, we refer to the ‘population biomass’ to indicate the total population  
107 size (in weight units) of flounder in the Bering Sea. We refer to ‘local abundance’ to  
108 indicate the flounder cpue (in numbers) at any sampled location included in the analysis.  
109 Bottom temperature at each groundfish station was obtained from the groundfish  
110 database (18), and measured at the time of the sample collections with temperature  
111 profilers mounted on the net. Flounder population biomass was obtained from the latest  
112 National Marine Fisheries Service stock assessment (20), in turn estimated through a  
113 combination of catch at age analysis tuned to the survey data. The estimated biomass  
114 includes the entire Bering Sea (shelf, slope and Aleutian Islands areas). Our study focuses  
115 on the shelf portion of the Bering Sea, where according to the assessment report there is  
116 74% of the total flounder biomass. Sediment size, expressed as  $-\log_2$  of grain size, was  
117 associated with each survey sample using information available from a high-resolution  
118 database of Bering Sea sediments (21).

119

## 120 *Data analysis*

121 To test the nonadditive and nonstationary species-environment and abundance-  
122 distribution hypotheses we implemented a model selection strategy to three competing  
123 formulations of Generalized Additive Mixed Models (GAMM, 22). Specifically, we  
124 formulated a 1) *fully additive*, 2) *variable coefficient*, and 3) *threshold model* with  
125 variable coefficients formulation. The *fully additive* formulation assumes that all the  
126 variables included in the model are independently and therefore additively affecting

127 flounder distribution. This is our null model, and it assumes additivity and stationarity of  
128 species-environment and abundance-occupancy relationships. The *variable coefficients*  
129 GAMM allow the coefficients of a function to smoothly change in relation to the  
130 geographical position (latitude and longitude; 23, 24). In this application we tested the  
131 spatially variable effects of temperature (T), flounder population biomass (B), and their  
132 interaction on local flounder abundance ( $x$ , cpue), thus testing for the presence of  
133 nonadditive and spatially variable effects between density-independent and density-  
134 dependent variables. The *threshold formulation* assumes that there is an abrupt change of  
135 flounder spatial dynamics in relation to a threshold of its own biomass, thus addressing  
136 the nonadditive abundance-occupancy hypothesis. The error part of all models was  
137 separated into a random component described by within-years Gaussian spatially-  
138 autocorrelated errors, and a normally distributed error term. A detailed description of the  
139 three competing formulations is presented in Table 1 and Appendix B.

140         The threshold value of the third model formulation was estimated by minimizing  
141 the model Akaike Information Criterion (AIC), searching over a range which included the  
142 middle 70<sup>th</sup> quantile of all the observed values (25,26). Since smooth functions are fitted,  
143 the degrees of freedom associated to each term may vary with the threshold. In these  
144 circumstances, the AIC is an ideal criterion for estimating the threshold and other  
145 parameters (27). Under very general conditions, minimizing the AIC results in an  
146 asymptotically efficient estimator. We also note that if the degrees of freedom of the  
147 smooth functions do not vary with the threshold, minimizing the AIC is identical to  
148 maximum likelihood estimation.

149 Prior to the analysis and for all model formulations, B and T were standardized  
150 and rescaled, so that their magnitudes are comparable and values are always  $> 0$ . Within  
151 each model formulation, variables were selected in a backward fashion, by removing one  
152 term at-a-time until the model AIC was minimized. Model selection was based on both  
153 the AIC and the genuine cross validation (gCV). The latter is the average of 500 average  
154 squared prediction errors, each calculated by predicting flounder cpue in 200 randomly  
155 selected locations that were excluded from the parameter estimation of the target model  
156 (25). All models were fitted using the restricted maximum likelihood estimator method,  
157 except for models fitted during the threshold search routine, when to improve speed and  
158 convergence we used a simpler maximum likelihood estimator. All analyses were  
159 performed in R (2.10.1, <http://www.r-project.org/>) using the `gamm` function of the `mgcv`  
160 library (22), version 1.6-1.

161

## 162 RESULTS

163 Flounder biomass has undergone a steady increase since the beginning of the 1980s (Fig.  
164 C1). At the same time the average water temperature in the middle shelf region of the  
165 Bering Sea has alternated over warm and cold regimes, with a noteworthy increase of  
166 temperatures in the period 2000-2005 and a subsequent decline in 2006-2010. Flounder  
167 occupancy appears to sharply increase after 1999, in correspondence to the beginning of  
168 the warming period and to a continuous increase of flounder biomass. Before then,  
169 habitat occupancy fluctuated in synchrony with water temperatures but the range of these  
170 fluctuations was reduced compared to the period after the late 1990s (Fig. C1). A visual  
171 inspection of the distribution of flounder local abundance over four demographic and



172 environmentally contrasting years reveals patterns that change in relation to bottom  
173 depth, summer bottom temperature, and overall population biomass (Fig. A1). However,  
174 the extent of habitat expansion appears curtailed during cold years while it is accentuated  
175 during high population biomass years (Fig. A1).

176 Results of the GAMM analysis confirmed the observed patterns of flounder time  
177 series and distribution described in the previous paragraph. Among the three formulations  
178 examined, model 3 (nonadditive, spatially variable with threshold effects) was the most  
179 consistent with the data (Table 1). The threshold abundance value was estimated to be  
180 about 630,000 metric tons (current flounder biomass is > 1,000,000 metric tons), as  
181 indicated by the profile of AIC over standardized values of population biomass (Fig. D1).  
182 Given that the flounder biomass has steadily increased throughout the examined time  
183 frame, such threshold effectively divides the time series in two temporal regimes, *before*  
184 and *after* 1995. This result implies that flounder spatial dynamics are nonstationary, and  
185 that the passage from one spatial configuration to the next occurred abruptly once the  
186 population biomass threshold was crossed. Further examination of this formulation  
187 indicated that the T•B interaction term from the *before* regime was not statistically  
188 significant, as the AIC further dropped from 7187 to 7176 once the term was removed  
189 (Table 1). The removal of this interaction term implies that in the early portion of the time  
190 series, (before 1997) density-dependent and density-independent variables had additive  
191 effects on the local flounder abundance, while in the later part (after 1995) they had a  
192 nonadditive effect.

193 Results from Model 3 are shown in Figs. 1 and 2, for the before and after regimes,  
194 respectively. We present the spatially variables effects of B and T as variations of

195 flounder local abundance in relation to a unit increase of either standardized B or T or  
196 both if the final model includes an interaction term<sup>1</sup>. Unit increase of the standardized  
197 and log-transformed B corresponds to a change of about 230,000 in the original units  
198 (metric tons). With respect to changes of B, in the *before* regime, when flounder  
199 population biomass increases, there is a corresponding increase of local cpue, but it is  
200 limited to the southeast portion of the grid, and occurs in greater intensity in the deeper  
201 areas, at the core of flounder cpue distribution (Fig. 1). This pattern promotes crowding,  
202 rather than habitat expansion because the increase of local flounder abundance occurs in  
203 areas that are already densely populated. It is also important to note that during this  
204 regime, because the interactive term T•B dropped out from the formulation, the effect of a  
205 change of B is not influenced by the underlying water temperature (Fig. 1). In contrast,  
206 in the *after* regime, when flounder population biomass increases, there is a corresponding  
207 increase of local abundance, but it is spread throughout the entire region, and occurs with  
208 greater intensity in the shallower areas of the sampled grid, toward the boundary of the  
209 flounder distribution. This pattern promotes habitat expansion, rather than crowding.  
210 Furthermore in this regime, because the interactive term T•B was retained in the  
211 formulation, the effect of a change of B depends also on the underlying thermal regime.  
212 Specifically, there is a greater increase of local cpue during warm years than during cold  
213 years (compare Figs 1 and 2).

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<sup>1</sup> Because of the two regimes (above and below B\* or before and after 1995) and the interaction between B and T of formulation 3, for each regime the differences in flounder local abundance are predicted for one unit increase of B in 1) low and 2) high T, and for one unit increase of T in 3) low and 4) high B. This results in two pairs of four predictions.

214 In model 3, a one-degree increase of water temperature caused an increase of  
215 flounder local abundance particularly in the middle shelf, in correspondence of the cold  
216 pool region. These patterns of variation promote changes of occupancy as they occur at  
217 the periphery of the flounder core habitat. However, the extent of the effects caused by a  
218 change of water T was greater in the *after* than in the *before* regime (Figs. 1 and 2),  
219 indicating that water temperature has a much stronger influence on flounder distribution  
220 in the later part of the time series (after 1997). Also, in the latter regime, because the  
221 interaction term T·B is retained in the model, there is a greater effect of a change of T  
222 when B is high as well. The inspection of the model 3 residuals for spatial (`variog`  
223 function in the `geoR` library) and temporal (`pacf` function in R) autocorrelation did not  
224 reveal any residual spatial or temporal autocorrelation.

225 In addition to the GAMM, we fit two linear models to the time series of flounder  
226 occupancy, measured as the number of consistently sampled stations occupied by  
227 flounder in any given year (Appendix E). Results of the linear analysis predicted that  
228 flounder occupancy is best and more parsimoniously modeled with a nonadditive and  
229 nonstationary interaction between population biomass and temperature. Specifically,  
230 before 1995, water temperature was the only significant variable affecting flounder  
231 occupancy. In contrast, after 1995, flounder occupancy was significantly affected by  
232 water temperature and by its interaction with biomass (Table E1).

233

## 234 DISCUSSION

235 Our results indicate that: i) flounder local abundance and relative spatial dynamics  
236 have abruptly changed in relation to a threshold value of overall population biomass; ii)

237 flounder habitat occupancy was related to its overall biomass only in the later part of the  
238 time series, when the biomass in the Bering Sea was greater than about 630,000 metric  
239 tones. In contrast, in the former part of the time series, habitat occupancy was mostly  
240 related to water temperature; iii) there can be nonadditive effects of density-dependent  
241 and density-independent variables, but only during regimes characterized by high  
242 population biomass. Collectively these results confirm the hypothesis of nonadditive  
243 species-environment interactions and nonstationary abundance-occupancy relationships  
244 and offer an opportunity to mechanistically address the genesis and maintenance of intra-  
245 specific distribution-abundance relationships. Interestingly, the fact that the estimated  
246 threshold has occurred at a time when flounder population biomass was still increasing  
247 but at a relatively slower rate compared to before and after (Fig C1) reinforces the view  
248 of Gaston et al. [14] that it is not much an increase of biomass from one year to the next,  
249 but rather the trend that matters. The fact that the trend is important may be due to a  
250 lagged response of species (similar to a delayed density-dependent effect under protracted  
251 conditions of high biomass) or to the very fact that a threshold of population biomass has  
252 to be crossed. Of the two possibilities, our results point to the latter as being more likely,  
253 since a lagged response to a protracted increase of population biomass would not have  
254 resulted in the estimated threshold dynamics.

255         There is still debate on the causality of abundance-distribution relationships [11,  
256 13], particularly with regard to intraspecific temporal dynamics [28]. Intraspecific  
257 relationships tend to be noisier than the interspecific counterparts, probably because of  
258 interacting nature of the factors that affect a single species distribution over time – a  
259 contention that underscores the importance of accounting for nonadditive effects between

260 density-dependent and density-independent variables. Based on the results and previously  
261 acquired knowledge about flounder life history in the Bering Sea, we can formulate and  
262 discuss four hypotheses to explain the increase of habitat occupancy in recent years. First,  
263 it is possible that flounder has colonized new habitats and established new subpopulations  
264 in areas that were previously void of flounder. This would effectively establish a new  
265 deme in a metapopulation complex. An increase in demes number at high population  
266 biomass has been reported for several terrestrial [29] and marine species [30] and is in  
267 line with theoretical expectations [31]. In the context of flounder in the Bering Sea, the  
268 establishments of new demes would also imply the establishment of new spawning sites  
269 and larval drift trajectories. The genetic structure of the flounder in the Bering Sea is  
270 unknown. However, it is unlikely that flounder is present as a metapopulation complex,  
271 this species has very protracted pelagic larval duration and extensive larval drift that  
272 encompass most of the area examined in this study [32]; a set of traits that are typical of  
273 panmictic rather than metapopulation complexes [33]. Also, given that the processes that  
274 regulate flounder habitat expansion has changed abruptly, it is unlikely that the  
275 establishment of new subpopulations drove them. For that to occur we would expect a  
276 more gradual change of spatial dynamics over time. Thus, the evidence from our analyses  
277 and previous information on the flounder life history do not support the establishment of  
278 new flounder subpopulations in a metapopulation complex.

279         An alternative explanation to the recent increase of flounder occupancy is that  
280 habitat expansion was driven by a greater dispersal of adult individuals toward marginal  
281 habitats during periods of high population biomass. Here we define marginal habitats as  
282 those areas where flounder was typically present at low abundance. This interpretation is

283 in line with the density-dependent habitat selection of which, the Ideal Free Distribution  
284 (IFD) is a possible theoretical manifestation [2]. In such circumstances, a positive  
285 abundance-distribution relationship is driven by an increase of intraspecific competition  
286 for space or resources within excessively crowded areas. This hypothesis is also in  
287 agreement with the basin model formulated by MacCall [6] for marine species. The basin  
288 model does not necessarily imply the establishment of new populations in a sympatric  
289 complex or demes in a metapopulation, and is more in line with what we know about the  
290 life history of flounder and spatial signature and chronology of its occupancy.

291 A third potential explanation is that flounder occupancy was driven by a co-  
292 occurring change of an external variable that was not accounted for in our analysis [11].  
293 For example, in recent years the center of juvenile walleye pollock (*Theragra*  
294 *chalcogramma*) distribution, the main flounder prey, has also shifted from the southeast  
295 toward the northwest of the Bering Sea [34]. However, if prey distribution were the  
296 primary factors, it would be hard to explain why the bulk of flounder biomass is still  
297 found in the deeper and slope-edge habitats of the southeast. Finally, there is a possibility  
298 that the change of flounder abundance was driven by a misclassification of arrowtooth  
299 flounder and Kamchatka flounder (*Atheresthes evermanni*) during the 1980s. The  
300 separation between the two species in the survey data utilized for our analysis became  
301 very reliable after 1992 (20). Prior to 1992, more Kamchatka flounder were classified as  
302 arrowtooth flounder, making it likely that the abundance and distribution of the latter was  
303 overestimated before 1992. Our analysis indicated that the threshold of flounder  
304 abundance-distribution relationship occurred in 1995, three years after the alleged change  
305 of protocol to distinguish the two species of flounder. So it is likely that arrowtooth

306 flounder abundance and occupancy were even lower than reported in our analysis for the  
307 pre-1992 years, which should only reinforce our conclusions. To rule out the possibility  
308 that the species misclassification drove the results, we re-run both the spatially-explicit  
309 and the linear model analyses using only post-1992 data and got very similar spatial  
310 effects of B, T and their interaction of those obtained with the entire data set.

311         Arrowtooth flounder in the Bering Sea is a typical example of sub-arctic species  
312 that shifted its distribution northward under warming conditions. Other species, both in  
313 the Bering Sea (35, 36) and in other temperate and subarctic systems (37, 38) have shown  
314 similar patterns. A less understood process however, is whether the expected northward  
315 increase of habitat occupancy of species that are at the northern end of their distribution  
316 will also result in an increase of their respective population biomass. If so, our study  
317 identifies a clear path through which a continuous increase of flounder biomass coupled  
318 with warming and loss of sea ice in the Bering Sea will result in even greater increase of  
319 habitat occupancy. Interestingly, Mueter and Litzow (35) found that in the Bering Sea,  
320 while biomass of subarctic species have positive responses to water temperature, that of  
321 arctic species have negative responses to it. They speculated that this inverse relationship  
322 is driven by top-down trophic control of subarctic species that are in closer proximity to  
323 arctic species.

324         The groundfish species community of the Bering Sea shelf is separated by an  
325 incursion of cold water in the middle of the shelf (39). In our analysis flounder responded  
326 to changes of bottom temperature only in the middle shelf region, in correspondence of  
327 the Bering Sea cold pool. In addition to closer proximity and potential increase of trophic  
328 interactions with arctic species, the flounder northwestward expansion will also cause

329 greater overlap with their main prey items, juvenile stages of walleye pollock. Currently,  
330 in the eastern Bering Sea the overall numerical abundance of flounder is several orders of  
331 magnitude lower compared to that of pollock. So it is likely that their impact on pollock  
332 biomass is still minimal. However, under continuous warming and increase of abundance,  
333 their effect may be more consequential on pollock survival, as observed in adjacent areas.  
334 In the Gulf of Alaska, for example, flounder is now the dominant groundfish species, and  
335 plays a key role in regulating walleye pollock recruitment through predation on the  
336 juvenile stages (40,41).

337 Other studies have looked at the effect of density-dependent and density-  
338 independent factors on flounder distribution in the Bering Sea [19, 34, 42, 43, 44], and  
339 found strong signals in the response of this species to both of these factors. With our  
340 analysis, we enrich previous results by characterizing the spatial signature of changes in  
341 habitat occupancy by clarifying the interactions between density-dependent and density-  
342 independent sources of variability. This in-depth view has in turn enabled us to address  
343 the causality of abundance-distribution and species-environment relationships, and to  
344 avoid potential spurious correlations associated with the analysis of central tendencies or  
345 macroecological patterns alone [13]. From a more applied perspective, understanding  
346 interannual variability of species spatial distribution may help to reduce error estimates  
347 for survey-based indices. Moreover, spatial dynamics have implications for multispecies  
348 model assessment because of changes in overlap between preys and predators.

349

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357

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484

485 Table 1. Final GAMM models selected for each of the three formulations implemented in  
 486 the analysis of arrowtooth flounder spatial distribution in the Eastern Bering Sea.  
 487 Estimated degrees of freedom (or linear coefficient in the case of parametric terms) and  
 488 statistical significance are shown for each term (\*\*  $p \leq 0.01$ , \*  $p \leq 0.05$ ), as well as the  
 489 adjusted  $R^2$ , Akaike Information Criteria (AIC) and genuine cross validation (gCV). For  
 490 further explanations of model terms and formulation see Appendix 1.

<b>Model 1</b>							<b>R<sup>2</sup>(%)</b>	<b>AIC</b>	<b>gCV</b>
$a_1 B_y$	$a_2 T_{(\varphi, \lambda, y)}$	$g_1[K_{(\varphi, \lambda)}]$	$g_2[D_{(\varphi, \lambda)}]$	$s_1(\varphi, \lambda)$					
0.32**	0.38**	5.92**	7.07**	25.28**			53.5	7514	0.619
<b>Model 2</b>									
$g_1[K_{(\varphi, \lambda)}]$	$g_2[D_{(\varphi, \lambda)}]$	$s_1(\varphi, \lambda)$	$s_2(\varphi, \lambda) \cdot$	$s_3(\varphi, \lambda) \cdot$	$s_4(\varphi, \lambda) \cdot$				
			$T_{(\varphi, \lambda)}$	$B_{(y)}$	$T_{(\varphi, \lambda)} \cdot B_{(y)}$				
5.83**	6.93**	13.43**	18.36**	3.00**	14.072		56.1	7457	0.589
<b>Model 3</b>									
$g_1[K_{(\varphi, \lambda)}]$	$g_2[D_{(\varphi, \lambda)}]$	$s_1(\varphi, \lambda)$	$s_2(\varphi, \lambda) \cdot$	$s_3(\varphi, \lambda) \cdot$	$s_5(\varphi, \lambda) \cdot$	$s_6(\varphi, \lambda) \cdot$	$s_7(\varphi, \lambda) \cdot$		
			$T_{(\varphi, \lambda)}$	$B_{(y)}$	$T_{(\varphi, \lambda)}$	$B_{(y)}$	$T_{(\varphi, \lambda)} \cdot B_{(y)}$		
5.96**	6.81**	15.65**	16.12**	3.00**	10.55**	4.46**	20.73**		62.5

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500 FIGURE LEGENDS

501 **Figure 1.** Spatial variation in predictions of flounder change of local abundance (natural  
502 log of catch per unit effort, cpue) obtained from the nonadditive and nonstationary  
503 GAMM model (Model 3, Table 1) during the low biomass (*before*) regime. Four different  
504 scenarios are depicted; namely, as a result of a unit change of flounder biomass (High  
505 Biomass – Low biomass), during (A) low and (B) high temperature years; as a result of a  
506 unit change of bottom temperature throughout the entire study region (High temperature  
507 – Low temperature), during (C) low and (D) high biomass years. Red and blue bubbles  
508 indicate increase and decrease in local abundance, respectively. The statistical  
509 significance of each predicted difference is illustrated as a shade of the bubble fill color,  
510 with the faint shade indicating nonsignificant differences, and it is based on the estimates  
511 of the 95% confidence interval ( $95\% \text{ CI} = 1.96 \cdot \text{standard error} \pm \text{prediction}$ ). Dark line is  
512 200 m isobath. Plots A and C also show the background average distribution of flounder,  
513 as determined by the spatial term in Model 3 (Table 1). Note that in high temperature  
514 years (panel B), a change of flounder biomass results in less significant differences  
515 compared to low temperature years (panel C), due to greater uncertainty in the prediction  
516 of local flounder abundance.

517  
518 **Figure 2.** As in Figure 1, but during a high flounder abundance regime. Note the  
519 difference between panels A and B, driven by the interaction term between water  
520 temperature and flounder population biomass.