Non-additive and non-stationary properties in the spatial distribution of a large marine fish population

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

Keywords: abundance–distribution; spatial dynamics; density-dependent habitat selection; Bering Sea

1. INTRODUCTION

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

Despite occurring in many systems, there is still controversy on the causality and anatomy of intraspecific abundance–distribution relationships [5,13]. These relationships are quantified by correlating population occupancy (typically, the spatial extent over which the species is present) with the population numerical abundance or total biomass. While this approach has been instrumental in revealing macroecological patterns over time and across species, it cannot simultaneously account for multiple sources of spatial variation on species distribution and does not reveal the spatial signature of a species change in distribution. This additional knowledge would enable us to address the genesis of a species abundance–distribution relationship. Gaston et al. [14] report that a species’ geographical distribution is more likely to significantly vary when the population abundance is steadily changing (i.e. when a trend in abundance or biomass is present), rather than when the abundance randomly fluctuates around a mean value. Indeed, Fisher & Frank’s [7] analysis of 34 intraspecific abundance–distribution relationships supports the link between time–trend and intraspecific abundance–distribution correlations. Turner [15] also points out that species distribution can undergo strong nonlinearities that
result in drastic changes in spatial configurations in relation to small changes in forcing variables. Within these contexts, it is crucial to investigate the underlying mechanisms that control species occupancy [11,16], and specifically, whether there are threshold values of population abundance that once crossed can cause drastic changes in the geographical distribution of species. In keeping with Gaston et al. [14], we expect that during periods in which population abundance is relatively constant species occupancy is mostly responsive to density-independent variables. By contrast, during periods in which population abundance experiences a trend, species occupancy becomes more tightly linked with its own abundance. Furthermore, in agreement with Turner [15], the passage between these two phases should be abrupt, once a threshold of population abundance is crossed. Collectively, the expectation of a threshold and temporally variable intraspecific abundance–distribution relationships leads to a prediction that we refer to as the non-stationary intraspecific abundance–distribution hypothesis.

In this study, we provide tests of both the non-additive species–environment and non-stationary abundance–distribution hypotheses by developing a spatial regression framework that incorporates localized, interactive and threshold effects of both environmental and demographic variables. The model is used to examine the spatial dynamics of a well-monitored large and piscivorous flatfish (arrowtooth flounder, *Atheresthes stomias*, hereafter referred as ‘flounder’) in the eastern Bering Sea (electronic supplementary material, figure S1).

### 2. MATERIAL AND METHODS

#### (a) Sampled region and data collections

We analysed the trawl data from the groundfish survey of the eastern Bering Sea conducted by the US National Marine Fisheries Service during 1982–2010. The sampling design is based on a fixed regular grid of $37 \times 37$ km, with sampling occurring over a period of six to eight weeks during late spring and summer [17,18]. The numerical catch was standardized by area swept (catch per unit effort, cpue, $n$ km$^{-2}$). Because of the ecological role played by adult flounder in the Bering Sea as predator of other fish species, we focused the analysis on individuals larger than 350 mm. In addition to flounder cpue from the groundfish survey, there were other variables included in the analysis. These were bottom temperature at each groundfish station was obtained from the groundfish database [18], and measured at the time of the sample collections with temperature profilers mounted on the net. Flounder population biomass was obtained from the latest National Marine Fisheries Service stock assessment [20], in turn estimated through a combination of catch at age analysis tuned to the survey data. The estimated biomass includes the entire Bering Sea (shelf, slope and Aleutian Islands areas). Our study focuses on the shelf portion of the Bering Sea, where according to the assessment report there is 76 per cent of the total flounder biomass. Sediment size, expressed as $-\log_2$ of grain size, was associated with each survey sample using information available from a high-resolution database of Bering Sea sediments [21].

#### (b) Data analysis

To test the non-additive and non-stationary species–environment and abundance–distribution hypotheses we implemented a model selection strategy to three competing formulations of generalized additive mixed models (GAMMs; [22]). Specifically, we formulated a (i) fully additive, (ii) variable coefficient and (iii) threshold model with variable coefficients formulation. The fully additive formulation assumes that all the variables included in the model are independently and therefore additively affecting flounder distribution. This is our null model, and it assumes additivity and stationarity of species–environment and abundance–occupancy relationships. The variable coefficients GAMM allow the coefficients of a function to smoothly change in relation to the geographical position (latitude and longitude; [23,24]). In this application, we tested the spatially variable effects of temperature ($T$), flounder population biomass ($B$) and their interaction on local flounder abundance ($s$, cpue), thus testing for the presence of non-additive and spatially variable effects between density-independent and density-dependent variables. The threshold formulation assumes that there is an abrupt change in flounder spatial dynamics in relation to a threshold of its own biomass, thus addressing the non-additive abundance–occupancy hypothesis. The error part of all models was separated into a random component described by within-years Gaussian spatially auto-correlated errors, and a normally distributed error term. A detailed description of the three competing formulations is presented in table 1 and electronic supplementary material, appendix S2.

The threshold value of the third model formulation was estimated by minimizing the model Akaike information criterion (AIC), searching over a range that included the middle 70th quantile of all the observed values [25,26]. Because smooth functions are fitted, the degrees of freedom associated with each term may vary with the threshold. In these circumstances, the AIC is an ideal criterion for estimating the threshold and other parameters [27]. Under very general conditions, minimizing the AIC results in an asymptotically efficient estimator. We also note that whether the degrees of freedom of the smooth functions do not vary with the threshold, minimizing the AIC is identical to maximum-likelihood estimation.

Prior to the analysis and for all model formulations, $B$ and $T$ were standardized and rescaled, so that their magnitudes are comparable and values are always greater than 0. Within each model formulation, variables were selected in a backward fashion, by removing one term at a time until the model AIC was minimized. Model selection was based on both the AIC and the genuine cross validation (gCV). The latter is the average of 500 average-squared prediction errors, each calculated by predicting flounder cpue in 200 randomly selected locations that were excluded from the parameter estimation of the target model [29]. All models were fitted using the restricted maximum-likelihood estimator method, except for models fitted during the threshold search routine, when to improve
Table 1. Final GAMM models selected for each of the three formulations implemented in the analysis of arrowtooth flounder spatial distribution in the eastern Bering Sea. Estimated Akaike information criteria (AIC) and genuine cross validation (gCV).

<table>
<thead>
<tr>
<th>Model</th>
<th>Degree of Freedom</th>
<th>AIC</th>
<th>gCV</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2</td>
<td>53.5</td>
<td>0.619</td>
</tr>
<tr>
<td>2</td>
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<tr>
<td>3</td>
<td>5</td>
<td>7176</td>
<td>0.510</td>
</tr>
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</table>

3. RESULTS

Flounder biomass has undergone a steady increase since the beginning of the 1980s (electronic supplementary material, figure S2). At the same time, the average water temperature in the middle shelf region of the Bering Sea has alternated over warm and cold regimes, with noteworthy increase in temperatures in the period of 2000–2005 and a subsequent decline in 2006–2010. Flounder occupancy appears to have sharply increased after 1999, in correspondence to the beginning of the warming period and to a continuous increase in flounder biomass. Before then, habitat occupancy fluctuated in synchrony with water temperatures, but the range of these fluctuations was reduced compared with the period after the late 1990s (electronic supplementary material, figure S2). A visual inspection of the distribution of flounder local abundance over 4 demographic and environmentally contrasting years reveals patterns that change in relation to bottom depth, summer bottom temperature and overall population biomass (electronic supplementary material, figure S1). However, the extent of habitat expansion appears curtailed during cold years, whereas it is accentuated during high population biomass years (electronic supplementary material, figure S1).

Results of the GAMM analysis confirmed the observed patterns of flounder time series and distribution described in the previous paragraph. Among the three formulations examined, model 3 (non-additive, spatially variable with threshold effects) was the most consistent with the data (table 1). The threshold abundance value was estimated to be about 630 000 metric tonnes (current flounder biomass is more than 1 000 000 metric tonnes), as indicated by the profile of AIC over standardized values of population biomass (electronic supplementary material, figure S3). Given that the flounder biomass has steadily increased throughout the examined time frame, such threshold effectively divides the time series in two temporal regimes: before and after 1995. This result implies that flounder spatial dynamics are non-stationary, and that the passage from one spatial configuration to the next occurred abruptly once the population biomass threshold was crossed. Further examination of this formulation indicated that the $T \times B$ interaction term from the before regime was not statistically significant, as the AIC further dropped from 7187 to 7176 once the term was removed (table 1). The removal of this interaction term implies that in the early portion of the time series, before 1995 density-dependent and density-independent variables had additive effects on the local flounder abundance, while in the later part (after 1995) they had a non-additive effect.

Results from model 3 are shown in figures 1 and 2, for the before and after regimes, respectively. We present the spatially variables effects of $B$ and $T$ as variations of flounder local abundance in relation to a unit increase in either standardized $B$ or $T$ or both if the final model includes an
interaction term\(^1\). Unit increase in the standardized and log-transformed \(B\) corresponds to a change of about 230 000 in the original units (metric tonnes). With respect to changes of \(B\), in the \textit{before} regime, when flounder population biomass increases, there is a corresponding increase in local cpue, but it is limited to the southeast portion of the grid, and occurs in greater intensity in the deeper areas, at the core of flounder cpue distribution (figure 1). This pattern promotes crowding, rather than habitat expansion because the increase in local flounder abundance occurs in areas that are already densely populated. It is also important to note that during this regime, because the interactive term \(T \times B\) dropped out from the formulation, the effect of a change in \(B\) is not influenced by the underlying water temperature (figure 1). In contrast, in the \textit{after} regime, when flounder population biomass increases, there is a corresponding increase in local abundance, but it is spread throughout the entire region, and occurs with a greater intensity in the shallower areas of the sampled grid, towards the boundary of the flounder distribution (figure 2). This pattern promotes habitat expansion, rather than crowding. Furthermore, in this regime, because the interactive term \(T \times B\) was retained in the formulation, the effect of a change in \(B\) depends also on the underlying thermal regime. Specifically, there is a greater increase in local cpue during warm years than during cold years (compare figures 1 and 2).

In model 3, a one-degree increase in water temperature caused an increase in flounder local abundance particularly in the middle shelf, in correspondence of the cold pool region. These patterns of variation promote...
changes of occupancy as they occur at the periphery of the flounder core habitat. However, the extent of the effects caused by a change in water $T$ was greater in the after than in the before regime (figures 1 and 2), indicating that water temperature has a stronger influence on flounder distribution in the later part of the time series (after 1995). Also, in the latter regime, because the interaction term $T \times B$ is retained in the model, there is a greater effect of a change in $T$ when $B$ is high as well. The inspection of the model 3 residuals for spatial ($\text{variog}$ function in the $\text{geoR}$ library) and temporal ($\text{pacf}$ function in R) autocorrelation did not reveal any residual spatial or temporal autocorrelation.

In addition to the GAMM, we fit two linear models to the time series of flounder occupancy, measured as the number of consistently sampled stations occupied by flounder in any given year (electronic supplementary material, appendix S5). Results of the linear analysis predicted that flounder occupancy is best and more parsimoniously modelled with a non-additive and non-stationary interaction between population biomass and temperature. Specifically, before 1995, water temperature was the only significant variable affecting flounder occupancy. By contrast, after 1995, flounder occupancy was significantly affected by water temperature and by its interaction with biomass (electronic supplementary material, table S1).

4. DISCUSSION

Our results indicate that (i) flounder local abundance and relative spatial dynamics have abruptly changed in relation to a threshold value of overall population biomass; (ii) flounder habitat occupancy was related to its overall biomass only in the later part of the time series, when the biomass in the Bering Sea was greater than about 630 000 metric tonnes. In contrast, in the former part of the time series, habitat occupancy was mostly related to water temperature; (iii) there can be non-additive effects of density-dependent and density-independent variables, but only during regimes characterized by high population biomass. Collectively, these results confirm the hypothesis of non-additive species–environment interactions and non-stationary abundance–occupancy relationships and offer an opportunity to mechanistically address the genesis and maintenance of intra-specific distribution–abundance relationships. Interestingly, the fact that the estimated threshold has occurred at a time when flounder population

Figure 2. As in figure 1, but during a high flounder abundance regime. Note the difference between (a) and (b), driven by the interaction term between water temperature and flounder population biomass.
biomass was still increasing but at a slower rate compared with before and after (electronic supplementary material, figure S1c) reinforces the view of Gaston et al. [14], which states that it is not much an increase in biomass from 1 year to the next, but rather the trend that matters. The fact that the trend is important may be due to a lagged response of species (similar to a delayed density-dependent effect under protracted conditions of high biomass) or to the very fact that a threshold of population biomass has to be crossed. Of the two possibilities, our results point to the latter as being more likely, because a lagged response to a protracted increase in population biomass would not have resulted in the estimated threshold dynamics.

There is still debate on the causality of abundance—distribution relationships [11,13], particularly with regard to intraspecific temporal dynamics [28]. Intraspecific relationships tend to be noisier than the interspecific counterparts, probably because of interacting nature of the factors that affect a single species distribution over time—a contention that underscores the importance of accounting for non-additive effects between density-dependent and density-independent variables. On the basis of results and previously acquired knowledge about flounder life history in the Bering Sea, we can formulate and discuss four hypotheses to explain the increase in habitat occupancy in recent years. First, it is possible that flounder has colonized new habitats and established new subpopulations in areas that were previously void of flounder. This would effectively establish a new deme in a metapopulation complex. An increase in demes number at high population biomass has been reported for several terrestrial [29] and marine species [30] and is in line with theoretical expectations [31]. In the context of flounder in the Bering Sea, the establishments of new demes would also imply the establishment of new spawning sites and larval drift trajectories. The genetic structure of the flounder in the Bering Sea is unknown. However, it is unlikely that flounder is present as a metapopulation complex, this species has very protracted pelagic larval duration and extensive larval drift that encompass most of the area examined in this study [32]; a set of traits that are typical of panmictic rather than metapopulation complexes [33]. Also, given that the processes that regulate flounder habitat expansion has changed abruptly, it is unlikely that the establishment of new subpopulations drove them. For that to occur, we would expect a more gradual change in spatial dynamics over time. Thus, the evidence from our analyses and previous information on flounder life history do not support the establishment of new flounder subpopulations in a metapopulation complex.

An alternative explanation to the recent increase in flounder occupancy is that habitat expansion was driven by a greater dispersal of adult individuals towards marginal habitats during periods of high population biomass. Here, we define marginal habitats as those areas where flounder was typically present at low abundance. This interpretation is in line with the density-dependent habitat selection of which, the ideal-free distribution is a possible theoretical manifestation [2]. In such circumstances, a positive abundance—distribution relationship is driven by an increase in intraspecific competition for space or resources within excessively crowded areas. This hypothesis is also in agreement with the basin model formulated by MacCall [6] for marine species. The basin model does not necessarily imply the establishment of new populations in a sympatric complex or demes in a metapopulation, and is more in line with what we know about the life history of flounder and spatial signature and chronology of its occupancy.

A third potential explanation is that flounder occupancy was driven by a co-occurring change in an external variable that was not accounted for in our analysis [11]. For example, in recent years, the centre of juvenile walleye pollock (Theragra chalcogramma) distribution, the main flounder prey, has also shifted from the southeast towards the northwest of the Bering Sea [34]. However, if prey distribution were the primary factors, it would be hard to explain why the bulk of flounder biomass is still found in the deeper and slope-edge habitats of the southeast. Finally, there is a possibility that the change in flounder abundance was driven by a misclassification of arrowtooth flounder and Kamchatka flounder (Atheresthes evermanni) during the 1980s. The separation between the two species in the survey data used for our analysis became very reliable after 1992 [20]. Prior to 1992, more Kamchatka flounder were classified as arrowtooth flounder, making it likely that the abundance and distribution of the latter was overestimated before 1992. Our analysis indicated that the threshold of the flounder abundance—distribution relationship occurred in 1995, 3 years after the alleged change in protocol to distinguish the two species of flounder. So it is likely that arrowtooth flounder abundance and occupancy were even lower than reported in our analysis for the pre-1992 years, which should only reinforce our conclusions. To rule out the possibility that the species misclassification drove the results, we rerun both the spatially explicit and the linear model analyses using only post-1992 data and got very similar spatial effects of B, T and their interaction of those obtained with the entire dataset.

Arrowtooth flounder in the Bering Sea is a typical example of subarctic species that shifted its distribution northward under warming conditions. Other species, both in the Bering Sea [24,35] and in other temperate and subarctic systems [36,37], have shown similar patterns. A less-understood process, however, is whether the expected northward increase in habitat occupancy of species that are at the northern end of their distribution will also result in an increase in their respective population biomass. If so, our study identifies a clear path through which a continuous increase in flounder biomass coupled with warming and loss of sea ice in the Bering Sea will result in even a greater increase in habitat occupancy. Interestingly, Mueter & Litizow [35] found that in the Bering Sea, while biomass of subarctic species have positive responses to water temperature, that of arctic species have negative responses to it. They speculated that this inverse relationship is driven by top-down trophic control of subarctic species that are in closer proximity to arctic species.

The groundfish species community of the Bering Sea shelf is separated by an incursion of cold water in the middle of the shelf [38]. In our analysis, flounder responded to changes of bottom temperature only in the middle shelf region, in correspondence of the Bering Sea cold pool. In addition to closer proximity and potential increase in trophic interactions with arctic species, the
flounder northwestern expansion will also cause a greater overlap with their main prey items, juvenile stages of walleye pollock. Currently, in the eastern Bering Sea, the overall numerical abundance of flounder is several orders of magnitude lower compared with that of pollock. So, it is likely that their impact on pollock biomass is still minimal. However, under continuous warming and increase in abundance, their effect may be more consequential on pollock survival, as observed in adjacent areas. In the Gulf of Alaska, for example, flounder is now the dominant groundfish species, and plays a key role in regulating walleye pollock recruitment through predation on the juvenile stages [39,40].

Other studies have looked at the effect of density-dependent and density-independent factors on flounder distribution in the Bering Sea [19,34,41–43], and found strong signals in the response of this species to both of these factors. With our analysis, we enrich previous results by characterizing the spatial signature of changes in habitat occupancy by clarifying the interactions between density-dependent and density-independent sources of variability. This in-depth view has in turn enabled us to address the causality of abundance–distribution and species–environment relationships, and to avoid potential spurious correlations associated with the analysis of central tendencies or macroecological patterns alone [13]. From a more applied perspective, understanding interannual variability of species spatial distribution may help us to reduce error estimates for survey-based indices. Moreover, spatial dynamics have implications for multispecies model assessment because of changes in overlap between prey and predators.

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ENDNOTE

1Because 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 in B in (1) low and (2) high T and for one unit increase in T in (3) low and (4) high B. This results in two pairs of four predictions.

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