Predicting the local-scale spatial distribution of five megafaunal species associated with a deep-sea hydrothermal field in the Okinawa Trough, Japan

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Received 17 December 2018; Accepted 26 March 2019  Responsible Editor: Shigeaki Kojima

doi: 10.3800/pbr.14.150

Abstract: The optimal spatial resolution for analysis of the spatial distribution of organisms is determined by the scale of their ecological processes (e.g., mobility of target species). This study examined the spatial extent of habitats of five megafaunal species with different levels of mobility [(1) the shrimp, Nematocarcinus sp. (benthic, comparatively low mobility); (2) the galatheid crab, Shinkaia crosnieri (benthic, low mobility); (3) the lithodid crab, Paralomis sp. (benthic, high mobility); (4) the snailfish, Liparidae sp. (demersal, high mobility); and (5) the deep-sea spiny eel, Notacanthidae sp. (demersal, high mobility)], which are associated with a deep-sea hydrothermal field in the Okinawa Trough. We obtained species presence–absence and abiotic environmental data (water temperature, proportional coverage of soft-sediment area, water depth, and five bathymetric parameters) from observation records by deep-sea submersibles and conducted a spatial analysis using three types of statistical models and a multi-model ensemble forecasting method. We prepared 10 data sets of the environmental variables by changing the spatial resolution from finer 0.00005° (ca. 5.3 m) to coarser 0.0005° (ca. 52.5 m). Accuracy of the models for the benthic species with comparatively low mobility was higher than that for the benthic and demersal species with high mobility and enhanced with decreasing grid-cell size (finer resolutions) of environmental data. By contrast, the accuracy of the models for the latter group varied more gently with the changing spatial resolution. The results showed that the proposed method is potentially useful to map the local-scale spatial distribution of the target species, sedentary benthic animals in particular, and that considering an appropriate spatial resolution in predicting the species distributions is important. These findings will help to enable management and subsequent conservation of deep-sea ecosystems.

Key words: deep-sea hydrothermal field, megafauna, presence–absence model, mobility, spatial resolution

Introduction

For effective management planning of marine ecosystems which are faced with the impacts of human activities, mapping of the key species and/or ecosystems has been made at local to global scales (Harris & Baker 2012, Yamakita et al. 2015, 2017). In this context, species distribution modelling (SDM) techniques are a powerful tool (Franklin 2010) and have been broadly applied to coastal and some marine offshore ecosystems (Robinson et al. 2011, 2017), but not much to deep-sea ecosystems (Veron et al. 2014). Despite the limitation, the development of SDM techniques suitable for deep-sea organisms is increasingly required, since human impacts such as trawling and seabed mining disturbances in the deep sea are increasing and can cause substantial community shifts (Boschen et al. 2013, Collins et al. 2013, Van Dover 2014, Nakajima et al. 2015, Gollner et al. 2017).

In applying spatial analysis to a target species, appropriate spatial resolution of data is often critical, and such a resolution is determined by the scale of ecological processes, e.g., mobility of target species (Guisan & Thuiller 2005, Elith & Leathwick 2009). There are, however, a lim-
A limited number of studies on the effects of spatial resolution on the prediction performance for the spatial distribution pattern of deep-sea organisms (e.g., Basher et al. 2014, Miyamoto et al. 2017). This study examined the local-scale spatial distributions of the following five dominant megafaunal species associated with a deep-sea hydrothermal field in the Okinawa Trough, Japan (Fig. 1), focusing on differences in mobility of them: (1) the shrimp, *Nematocarcinus* sp. (benthic detritivore with comparatively low mobility, 3–5 cm in body length); (2) the galatheid crab, *Shinkaia crosnieri* (benthic bacterivore with low mobility, 5 cm in carapace length); (3) the lithodid crab, *Paralomis* sp. (benthic carnivore with high mobility, 10–12 cm in carapace width); (4) the snailfish, Liparidae sp. (demersal carnivore with high mobility, 20 cm in total length); and (5) the deep-sea spiny eel, *Notacanthidae* sp. (demersal carnivore with high mobility, 55 cm in total length) (Fujikura et al. 2012) (Fig. 2). For a variety of animals including fish and crustaceans, a positive relationship exists between home range and body sizes (Harestad & Bunnell 1979, Wada 1993, Minns 1995, Jetz et al. 2004). Assuming such a relationship for our target species, the order of their home range sizes could be estimated as follows: *Nematocarcinus* sp. ≈ *S. crosnieri* < *Paralomis* sp. < Liparidae sp. < *Notacanthidae* sp.

The objective of the present study is to predict the spatial extent of the habitats of the five megafaunal species and to assess appropriate spatial resolution for modelling.

**Fig. 1.** The study area, located in a deep-sea hydrothermal field of the Izena Cauldron in the mid Okinawa Trough, Japan. Dive site (27°14.5′ N, 127°4.0′ E) is indicated as a star mark.

**Fig. 2.** The five megafaunal species (target species) associated with the deep-sea hydrothermal field of the Izena Cauldron in the mid Okinawa Trough, Japan, used in this study. (A) The shrimp, *Nematocarcinus* sp.; (B) the galatheid crab, *Shinkaia crosnieri*; (C) the predatory lithodid crab, *Paralomis* sp.; (D) the snailfish, Liparidae sp.; and (E) the deep-sea spiny eel, *Notacanthidae* sp.
For these purposes, we obtained species presence—absence and abiotic environmental data from observation records by deep-sea submersibles and conducted spatial analyses using three types of statistical models and a multi-model ensemble forecasting method. To examine the appropriate spatial resolution for each species, we prepared 10 data sets of the environmental variables by changing the spatial resolution from finer 0.00005° (ca. 5.3 m) to coarser 0.0005° (ca. 52.5 m). Our results showed that the method presented here is potentially useful to map the local-scale spatial distribution of the target species and that it is important to consider the appropriate spatial resolution for predicting the species distributions. These findings will help to enable management and subsequent conservation of deep-sea ecosystems.

**Materials and Methods**

**Study area**

This study was carried out in a deep-sea hydrothermal field of the Izena Cauldron in the mid Okinawa Trough, Japan [27°14.5′N, 127°4.0′E; Fig. 1 (dive number: YK14-E03#1411)]. Water depth of the field is from 1,550 to 1,610 m. The seafloor is covered by soft sediment scattered with boulders and rocks.

**Presence/absence of the target species and abiotic environmental parameters**

The research cruise was carried out during 23 October to 4 November 2014, and data obtained on 27 October 2014 were used for the analysis. This data covered an ca. 0.13-km² area. To extract presence—absence data of the target species, we used video images recorded by use of a digital camcorder mounted frontward on the human occupied deep submersible vehicle **SHINKAI 6500** of JAMSTEC. The vehicle’s three-dimensional position [i.e., longitude—latitude coordinates (WGS84), water depth] and water temperature around the vehicle were monitored every second, during the seafloor survey. Presence/absence data for each species was visually determined from the video images which were captured as one frame per second by use of the software “GOM Player” [available at http://www.gomlab.com/ (accessed on 5 April 2019)]. Proportional coverage of soft-sediment area on the seafloor for each image was evaluated by use of the software “CPCe” (Kohler & Gill 2006). In this procedure, 20–100 spatially random points were generated over the seafloor of an image, and consequently, the proportion of the number of points on the soft-sediment area to the total was calculated as the proportional coverage of soft-sediment area. Data for water temperature and proportional coverage of soft-sediment area were spatially interpolated by use of the `variost` function of the “geoR” package (Ribeiro & Diggle 2018) of the software “R” (R Core Team 2018). The spatial interpolation was made for 0.00005°×0.00005° grid cells. The results were used as potential explanatory variables in species presence—absence modelling.

Bathymetric survey was conducted by use of the multi-beam echo sounder system of the research vessel **YOKOSUKA** (gross tonnage: 4,439 ton), which is the support ship for **SHINKAI 6500**. The bathymetric data were spatially interpolated by use of the `Triangulation` module of the software “SAGA GIS” (Conrad et al. 2015). The spatial interpolation was made for 0.00005°×0.00005° grid cells. From the interpolated water-depth data, five bathymetric parameters, i.e., slope, aspect, roughness, bathymetric position index (BPI), and bathymetric roughness index (BRI) were obtained by use of the `terrain` function (unit and neighbors arguments were set as “degrees” and “8”, respectively) of the “raster” package (Hijmans 2018). BPI and BRI are equivalent to TPI and TRI in the function, respectively. The value of slope indicates the degree of incline of the seafloor surface. The value of aspect indicates the orientation of the slope. The value of roughness indicates the difference between the maximum and minimum values of the focal cells (i.e., a central cell and its eight surrounding cells). BPI is the difference between the value of a central cell and the mean value of the surrounding cells. BRI is the mean of the absolute differences between the value of a central cell and each of the surrounding cells. Those five parameters and water depth were added to the potential explanatory variables for species presence—absence modelling.

**Presence—absence modelling**

Data sets that consisted of presence—absence data (i.e., 1 for presence and 0 for absence) for each species and environmental data were prepared. To select explanatory variables to be used in modelling from the eight potential parameters, (1) multicollinearity among the parameters was excluded; and (2) significance of the effect of each parameter on the presence—absence variation of each species was tested by the Wilcoxon rank sum test (`wilcox.test` function of “R”), by random resampling from the presence/absence-site data (sample function of “R”) to ensure homogenous sample sizes. From the whole data set, two subsets, i.e., training (70% of the 636 sampling points) and testing data sets (the other 30%), were randomly selected for model construction and validation, respectively. To examine the optimal spatial resolution for each species, we prepared 10 sets of environmental data by changing the spatial resolution [i.e., grid-cell size: 0.00005° (original), 0.0001°, 0.00015°, 0.0002°, 0.00025°, 0.0003°, 0.00035°, 0.0004°, 0.00045°, 0.0005°]. For this, we used the `aggregate` function of the “raster” package of “R”. In modelling, the following three models were used: i.e., (1) generalized linear model (GLM) with model selection based on Akaike’s information criterion (Akaike 1973), (2) generalized additive model (GAM), and (3) random forest (RF). These models are widely used in presence—absence modelling for marine organisms (e.g., MacLeod et al. 2008, Reiss et al. 2011, González-Irusta et al. 2015). For GLM and GAM, a binomial error distribution and a logit-link func-
tion were assumed. GLM, GAM, and RF were fit to the training data set, by use of the glm (nested by step function), gam ["mgcv" package (Wood 2011)], and randomForest ["randomForest" package (Liaw & Wiener 2002)] functions of "R", respectively. To keep randomness, the generation of random points, and model construction and validation were repeated 99 times.

**Model validation and multi-model ensemble forecasting**

To evaluate the prediction performance (accuracy) of [Figure 3](image). Spatial interpolation results for (A) water temperature, (B) proportional coverage of soft-sediment area, (C) water depth, (D) slope, (E) aspect, (F) roughness, (G) bathymetric position index (BPI), and (H) bathymetric roughness index (BRI).
Spatial interpolation for the environmental variables

The results of spatial interpolation for the eight environmental parameters are shown in Fig. 3. Water temperature ranged from 3.83 to 4.01°C (mean±SD=3.86±0.01°C, n: number of grid cells=4029). Proportional coverage of soft-sediment area ranged from 0 to 100% (mean±SD=75.8±29.5%, n=3475). Water depth ranged from 1581.1 to 1641.3 m (mean±SD=1619.2±10.0 m, n=5720). Values of slope ranged from 0.68° to 57.47° (mean±SD=14.52±9.57°, n=5720). Values of aspect ranged from 1.54° to 352.06° (mean±SD=152.37±77.94°, n=5720). Values of roughness ranged from 0.26 to 20.79 (mean±SD=4.00±2.81, n=5720). Values of BPI ranged from −5.66 to 3.96 (mean±SD=0.01±0.63, n=5720). Values of BRI ranged from 0.09 to 8.05 (mean±SD=1.25±0.90, n=5720).

Selection of environmental variables to be used in modelling

Correlation coefficients for each combination of the eight environmental parameters are summarized in Table 1. The results indicated that slope was highly correlated with roughness and BRI, and thus, the latter two variables were not used in modelling to avoid multicollinearity.

Relationships between the presence–absence variation of each species and each of the environmental variables are shown in Fig. 4. The results showed that (1) the presence–absence variation of Nematocarcinus sp. was associated with water temperature (p<0.001, Wilcoxon rank sum test), proportional coverage of soft-sediment area (p<0.001), water depth (p<0.001), slope (p<0.001), aspect (p<0.001), and BPI (0.01<p<0.05); (2) that of Shinkaia crosnieri was associated with water temperature (0.01<p<0.05), proportional coverage of soft-sediment area (p<0.001), water depth (p<0.001), and slope (p<0.001); (3) that of Paraliparidae sp. was associated with proportional coverage of soft-sediment area (0.001<p<0.01) and aspect (0.01<p<0.05); (4) that of Liparidae sp. was associated with water temperature (p<0.001), proportional coverage of soft-sediment area (p<0.001), water depth (p<0.001), and aspect (0.001<p<0.01); and (5) that of Notacanthidae sp. was associated with proportional coverage of soft-sediment area (p<0.001) and water depth (p<0.001). Therefore, these two to six environmental variables were used as explanatory variables for each modelling analysis.

Presence–absence modelling

Model accuracy (AUC values from the multi-model ensemble forecasting) for each set of species and grid-cell size are summarized in Table 2. The association between model accuracy and spatial resolution differed among the target species. The accuracy of the models for the benzene-related area under the receiver operating characteristic curve (AUC) was calculated using the roc function of the “pROC” package (Robin et al. 2011) of “R” and the testing data set. AUC takes a value from 0 to 1 and increases with model accuracy. The values of 0.5–0.7, 0.7–0.9, and >0.9 indicate low accuracy, potentially useful, and high accuracy, respectively (Swets 1988).

To obtain more robust predictions than single-model outcomes, the AUC-weighted multi-model ensemble forecasting method (Marmion et al. 2009) was adopted. Here, AUC-weighted presence probability (Pensemble) was calculated for each grid cell as follows: 

\[ P_{\text{ensemble}} = \frac{\sum_i P_{\text{GLM}}(i) \times n_{\text{GLM}}(i)}{\sum_i n_{\text{GLM}}(i)} \]

where PGLM(i) is the presence probability predicted by GLM, Pensemble is the presence probability calculated using the AUCROC package (Robin et al. 2011) of “R”, and nGLM(i) is the number of replicates for each model. The values of 0.5–0.7, 0.7–0.9, and >0.9 indicate low accuracy, potentially useful, and high accuracy, respectively (Swets 1988).

Table 1. Correlation coefficients for each combination of the abiotic environmental variables.

| Proportional coverage of soft-sediment area | Water depth | Slope | Aspect | Roughness | BPI | BRI |
|------------------------------------------|------------|------|-------|-----------|-----|-----|
| Water temperature (°C)                   | −0.39***   | −0.39*** | 0.22*** | 0.14*** | 0.23*** | −0.07*** | 0.23*** |
| Proportional coverage of soft-sediment area (%) | −   | 0.67*** | −0.37*** | −0.16*** | −0.36*** | 0.04* | −0.36*** |
| Water depth (m)                          | −   | −   | −0.39*** | −0.16*** | −0.43*** | 0.19*** | −0.43*** |
| Slope (°)                                | −   | −   | −   | 0.04** | 0.97*** | −0.01NS | 0.95*** |
| Aspect (°)                               | −   | −   | −   | −   | 0.02*** | −0.01NS | 0.06*** |
| Roughness                                | −   | −   | −   | −   | −   | −0.02NS | 0.98*** |
| BPI                                      | −   | −   | −   | −   | −   | −   | −0.03* |

Statistical significance of each correlation coefficient is indicated as follows: NS (non-significant); * (0.01<p<0.05); ** (0.001<p<0.01); *** (p<0.001).
thic species with comparatively low mobility (i.e., *Nematocarcinus* sp. and *Shinkaia crosetieri*) was higher than that for the benthic and demersal species with high mobility (i.e., *Paralomis* sp., *Liparidae* sp., and *Notacanthidae* sp.) and was enhanced with decreasing grid-cell size (finer resolutions) of environmental data. By contrast, the accuracy of the models for the latter group varied more gently with changing the spatial resolution. For instance,
Table 2. Model accuracy (area under the receiver operating characteristic curve from the multi-model ensemble forecasting) for each combination of species and grid-cell size.

| Species               | Grid-cell size (degree) | Number of trials | Mean ± SD (minimum–maximum) |
|-----------------------|-------------------------|------------------|-----------------------------|
| **Nematocarcinus sp.**| 0.00005                 | 99               | 0.90±0.02 (0.85–0.95)       |
|                       | 0.0001                  | 99               | 0.91±0.02 (0.86–0.94)       |
|                       | 0.00015                 | 99               | 0.92±0.02 (0.87–0.96)       |
|                       | 0.0002                  | 99               | 0.89±0.02 (0.84–0.94)       |
|                       | 0.00025                 | 99               | 0.91±0.02 (0.87–0.95)       |
|                       | 0.0003                  | 99               | 0.90±0.02 (0.83–0.94)       |
|                       | 0.00035                 | 99               | 0.85±0.02 (0.78–0.91)       |
|                       | 0.0004                  | 99               | 0.83±0.03 (0.77–0.89)       |
|                       | 0.00045                 | 99               | 0.86±0.02 (0.80–0.93)       |
|                       | 0.0005                  | 99               | 0.80±0.03 (0.75–0.88)       |
| **Shinkaia crosnieri**| 0.00005                 | 99               | 0.92±0.04 (0.78–0.98)       |
|                       | 0.0001                  | 99               | 0.93±0.04 (0.84–0.98)       |
|                       | 0.00015                 | 99               | 0.88±0.03 (0.78–0.98)       |
|                       | 0.0002                  | 99               | 0.88±0.04 (0.78–0.97)       |
|                       | 0.00025                 | 99               | 0.91±0.04 (0.81–0.98)       |
|                       | 0.0003                  | 99               | 0.89±0.03 (0.81–0.98)       |
|                       | 0.00035                 | 99               | 0.83±0.04 (0.71–0.94)       |
|                       | 0.0004                  | 99               | 0.83±0.04 (0.74–0.95)       |
|                       | 0.00045                 | 99               | 0.86±0.03 (0.75–0.93)       |
|                       | 0.0005                  | 99               | 0.81±0.04 (0.71–0.90)       |
| **Paralomis sp.**     | 0.00005                 | 99               | 0.78±0.08 (0.54–0.98)       |
|                       | 0.0001                  | 99               | 0.78±0.08 (0.59–0.97)       |
|                       | 0.00015                 | 99               | 0.78±0.08 (0.62–0.93)       |
|                       | 0.0002                  | 99               | 0.78±0.07 (0.57–0.98)       |
|                       | 0.00025                 | 99               | 0.78±0.08 (0.47–0.96)       |
|                       | 0.0003                  | 99               | 0.78±0.07 (0.52–0.98)       |
|                       | 0.00035                 | 99               | 0.71±0.08 (0.48–0.94)       |
|                       | 0.0004                  | 99               | 0.73±0.07 (0.53–0.91)       |
|                       | 0.00045                 | 99               | 0.74±0.08 (0.54–0.94)       |
|                       | 0.0005                  | 99               | 0.75±0.07 (0.42–0.90)       |
| **Liparidae sp.**     | 0.00005                 | 99               | 0.81±0.03 (0.68–0.89)       |
|                       | 0.0001                  | 99               | 0.81±0.04 (0.70–0.89)       |
|                       | 0.00015                 | 99               | 0.80±0.03 (0.68–0.87)       |
|                       | 0.0002                  | 99               | 0.78±0.04 (0.67–0.86)       |
|                       | 0.00025                 | 99               | 0.80±0.04 (0.69–0.89)       |
|                       | 0.0003                  | 99               | 0.79±0.04 (0.69–0.87)       |
|                       | 0.00035                 | 99               | 0.79±0.04 (0.64–0.89)       |
|                       | 0.0004                  | 99               | 0.77±0.04 (0.66–0.85)       |
|                       | 0.00045                 | 99               | 0.82±0.04 (0.69–0.89)       |
|                       | 0.0005                  | 99               | 0.75±0.04 (0.61–0.83)       |
| **Notacanthidae sp.** | 0.00005                 | 99               | 0.70±0.04 (0.58–0.81)       |
|                       | 0.0001                  | 99               | 0.68±0.04 (0.58–0.78)       |
|                       | 0.00015                 | 99               | 0.69±0.04 (0.57–0.84)       |
|                       | 0.0002                  | 99               | 0.69±0.04 (0.59–0.80)       |
|                       | 0.00025                 | 99               | 0.73±0.04 (0.64–0.83)       |
|                       | 0.0003                  | 99               | 0.68±0.05 (0.41–0.79)       |
|                       | 0.00035                 | 99               | 0.68±0.04 (0.55–0.79)       |
|                       | 0.0004                  | 99               | 0.70±0.04 (0.57–0.83)       |
|                       | 0.00045                 | 99               | 0.64±0.06 (0.42–0.76)       |
|                       | 0.0005                  | 99               | 0.69±0.04 (0.56–0.84)       |
Local distribution of deep-sea megafauna

The association between model accuracy and spatial resolution differed among the target species. Moreover, we found that interspecific differences in mobility should be taken into account when choosing the spatial resolution for an analysis. Spatial dependency of each species is briefly discussed below:

1. The shrimp, *Nematocarcinus* sp., is a benthic animal commonly found in deep-water benthic communities (Kuramochi et al. 2008, Komai 2011). These animals are detritivore, and thus sedimented planktonic materials are important resources in their diet (Cartes 1993). As a result, they could exhibit the high dependency on soft-sediment habitats (Fig. 4), which raises their spatial resolution dependency (Fig. 5A). A similar conclusion was obtained by Basher et al. (2014), who studied the spatial distribution pattern of deep-sea shrimps in the Ross Sea region of Antarctica.

2. The galatheid crab, *S. crosnieri*, is a benthic animal, and chemical compounds from hydrothermal vents are in-
dispensable for its specific nutrition depending on epibiotic chemosynthetic bacteria (Watsuji et al. 2015). In the present study, the presence sites of this species were distributed in higher water temperature, less soft-sediment coverage, and steeper slope environments than the absence sites (Fig. 4), which indicates the environments of a hydrothermal field. Therefore, it appears that S. crosnieri crabs have a spatial resolution dependency for such local environments (Fig. 5B).

(3) The predatory lophid crab, Paralomis sp., has a higher mobility than the above two crustacean species, and they are often attracted to dense assemblages of other animals, such as vent-associated communities, for foraging (Hashimoto et al. 1995, Ohta & Kim 2001, Thornton et al. 2016). In fact, the presence of Paralomis sp. crabs was observed around the S. crosnieri crabs’ habitat (i.e., less soft-sediment coverage and steeper slope; Fig. 4). Their higher mobility is consistent with a gentler spatial resolution dependency than that of the sedentary benthic animals (Fig. 5C).

(4) The snailfish, Liparidae sp., is a predatory demersal animal, and its diet is composed of small invertebrates, such as crustaceans, mollusks, and polychaetes (Glubokov 2010, Gerringer et al. 2017). Previous studies reported that Liparidae sp. is observed in a variety of habitats and often actively swimming with movements of the caudal part of their body (Chernova & Geistdoerfer 2003, Stein et al. 2006). In the present study, the model accuracy for this species varied more gently with changing spatial resolution. This suggests that their swimming ability results in their dispersed distribution over a comparatively larger spatial scale; and thus, their spatial resolution dependency is lower than that of the sedentary benthic animals (Fig. 5D).

(5) The deep-sea spiny eel, Notacanthidae sp., is a predatory demersal animal. Its mobility is the highest among the target species. The diet of some fishes of the family Notacanthidae is mainly composed of small invertebrates, such as crustaceans and polychaetes (Houston & Haedrich 1986, Gordon & Duncan 1987, Carrassón & Matallanas 2002). As with Liparidae sp., the Notacanthidae sp. eels were also generally actively swimming in the study area. Their highest mobility among the target species is consistent with their lower spatial resolution dependency than that of the sedentary benthic animals and with their lowest prediction performance among the target species (Fig. 5E).

In conclusion, our results of AUC values showed that the proposed method is potentially useful to map the local-scale spatial distribution of the target species, sedentary benthic animals in particular. Our results also showed that it is important to consider the spatial resolution dependency of the target species in predicting their distributions. Obtaining environmental data at a finer spatial resolution will contribute to improving the accuracy of spatial distribution modelling. Our findings will help to enable management and subsequent conservation of deep-sea ecosystems.

Acknowledgements

This work was supported by Council for Science, Technology and Innovation (CSTI), Cross-ministerial Strategic Innovation Promotion Program (SIP), “next-generation technology for ocean resources exploration” (lead agency: JAMSTEC). We have partially used the data set of projects commissioned by Agency for Natural Resources and Energy, Ministry of Economy, Trade and Industry. We also appreciate the constructive comments of two anonymous reviewers.

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