



Spatial and temporal variability of the Pacific saury (*Cololabis saira*) distribution in the northwestern Pacific Ocean

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Tseng, C.-T., Su, N.-J., Sun, C.-L., Punt, A. E., Yeh, S.-Z., Liu, D.-C., and Su, W.-C. 2013. Spatial and temporal variability of the Pacific saury (*Cololabis saira*) distribution in the northwestern Pacific Ocean. – ICES Journal of Marine Science, 70: 991–999.

Received 28 August 2012; accepted 20 December 2012; advance access publication 15 January 2013.

Logbook data for the Taiwanese Pacific saury fishery and multi-sensor satellite images for 2006–2010 were used to characterize the habitat of Pacific saury (*Cololabis saira*) in the northwestern Pacific (NWP). An empirical cumulative distribution function (ECDF) approach identified that high cpue (catch per unit of effort) of Pacific saury occurred when sea surface temperature (SST) ranged from 14 to 16°C, chlorophyll-*a* concentration (Chl *a*) ranged from 0.4 to 0.6 mg m⁻³, and net primary production (NPP) ranged from 600 to 800 mg C m⁻² d⁻¹. A generalized additive model (GAM) and spatial non-stationary geographically weighted regression (GWR) were applied to predict the habitats of Pacific saury in the NWP. The spatial distributions of Pacific saury in the NWP estimated using the two approaches were similar and matched the nominal cpue distributions and those inferred from preferred habitat ranges based on ECDF. The density of Pacific saury is higher in coastal waters close to the island of Hokkaido and near the southern Kuril Islands than in the open sea. SST, Chl *a*, and NPP were substantially higher in the fishing grounds for Pacific saury during the main fishing season (September and October), corresponding to a high cpue for Pacific saury (23.1 t fishing day⁻¹). The GAM explained more variability in spatial distribution (35.7%) than GWR (20.5%) VGPM (Vertically Generalized Production Model). Results derived from this study could improve our understanding of Pacific saury habitat distributions, which could be used to forecast fishing grounds and to develop fishery management advice based on oceanographic conditions that might be impacted by climate change.

Keywords: empirical cumulative distribution function, environmental factors, generalized additive model, geographical weighted regression, Pacific saury.

Introduction

Pacific saury is an epipelagic fish distributed from close to the sea surface down to around 230 m, with a preferred water temperature of 15–18°C in the North Pacific Subtropical Gyre (Eschmeyer *et al.*, 1983; Ito *et al.*, 2004). Pacific saury migrate seasonally from the subtropical Kuroshio Current in winter to the Subarctic Oyashio Current in summer, for feeding on zooplankton, such as copepods, euphausiids, amphipods, and the eggs and larvae of small pelagic fish, such as anchovies (Shimizu *et al.*, 2009; Taki, 2011).

The migratory pattern of Pacific saury has previously been associated with environmental factors, such as sea surface temperature (SST) and chlorophyll-*a* concentration (Chl *a*; Iwahashi

et al., 2006; Watanabe *et al.*, 2006; Mukai *et al.*, 2007). Oozeki *et al.* (2004) reported that SST and Chl *a* could impact the growth of Pacific saury. Furthermore, Chl *a* in the mixed layer from winter to early spring (January to April) has been shown to correlate with the success of Pacific saury recruitment (Yasuda and Watanabe, 2007).

Satellite-based remote sensing data have high spatial and temporal resolution and can be used to identify areas of fish aggregation and intense fishing activity based on relationships between fish abundance and environmental effects (Lehodey *et al.*, 1998; Zainuddin *et al.*, 2006). For example, SST and Chl *a* images have been used to identify fishing grounds for pelagic and demersal species in the northern Arabian Sea (Solanki *et al.*, 2005).

Previous studies have examined the relationship between the fishing grounds for Pacific saury and satellite-based SST (e.g. Yasuda and Watanabe, 1994; Huang *et al.*, 2007; Tseng *et al.*, 2011), whereas Teo *et al.* (2007) and Tseng *et al.* (2010) identified potential tuna habitats using a combination of satellite-based SST, Chl *a*, and sea surface height anomaly data.

Recently, generalized additive models (GAMs) have been applied to examine the relationships between environmental effects and the distribution and abundance of fish species (e.g. Venables and Dichmont, 2004; Damalas *et al.*, 2007; Su *et al.*, 2011). Tian *et al.* (2009) used GAMs and generalized linear models (GLMs) to standardize the catch per unit of effort (cpue) for neon flying squid (*Ommastrephes bartramii*) in the northwestern Pacific (NWP). They concluded that the GAMs tended to be more suitable than GLMs for the analysis of cpue and environmental data.

Spatial non-stationary geographically weighted regression (GWR) is a local modelling technique to detect spatially varying relationships between a response variable and covariates (Windle *et al.*, 2010). GWR involves fitting a model by estimating a set of local parameter coefficients for each datapoint using the data for all sampled locations. This approach consequently allows the use of local spatial statistics and highlights differences across space (Ciannelli *et al.*, 2008; Krivoruchko, 2011). For example, Windle *et al.* (2010) successfully applied GWR to examine the relationships between temperature and distance from shore and the distributions of snow crab (*Chionoecetes opilio*) and northern shrimp (*Pandalus borealis*).

Pacific saury is a species which is likely to be susceptible to environmental change. We therefore examine the spatial and temporal variability of the distribution of Pacific saury in the NWP using two models and identify the relationships between environmental factors and Pacific saury habitats. These relationships can be used to evaluate the likely change in spatial distribution due to environmental variation driven by climate change and to develop a scientific basis for sustainable management of the fishery for Pacific saury.

Material and methods

Data used

Logbook data for the Taiwanese Pacific saury stick-held dipnet fishery in the NWP were collected for 2006–2010. This dataset includes catches of Pacific saury (tonnes) and fishing effort (in fishing day). Nominal cpue is expressed as the catch of Pacific saury caught by 0.25° grid cell divided by the number of fishing days (Figure 1).

Monthly 4-km spatially-resolved SST and Chl *a* data, as well as net primary production (NPP, 9-km spatial resolution), defined as the net flux of aquatic carbon created through photosynthesis by phytoplankton, estimated using the VGPM (Behrenfeld and Falkowski, 1997; Behrenfeld *et al.*, 2006), were obtained from the ocean color website (<http://oceancolor.gsfc.nasa.gov/>) for 2006–2010. Satellite remote sensing oceanographic data were averaged to 0.25° grid to match the spatial resolution of the fishery data.

Empirical cumulative distribution function

The associations between Pacific saury cpue and satellite-based SST, Chl *a*, and NPP were explored using a cumulative distribution function approach (Perry and Smith, 1994; Andrade and Garcia,

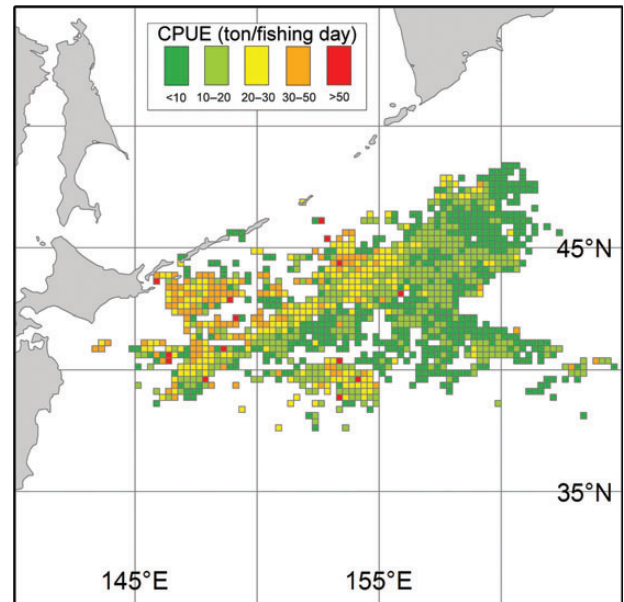


Figure 1. Distribution of nominal cpue averaged over 2006–2010 for Pacific saury in the Taiwanese Pacific saury fishery.

1999; Zainuddin *et al.*, 2008). This approach involves calculating the frequency distributions for the oceanographic variables using empirical cumulative distribution function (ECDF) curves:

$$f(t) = \frac{1}{n} \sum_{i=1}^n l(x_i|t)$$

and

$$l(x_i|t) = \begin{cases} 1 & \text{if } x_i \leq t \\ 0 & \text{otherwise,} \end{cases}$$

where n is the number of month \times 0.25° grid records, x_i represents the values for SST, Chl *a*, and NPP for each monthly 0.25° grid record, and t is an index of the ordered (lowest to highest) oceanographic observations. Pacific saury cpue is associated with the oceanographic variables using cpue-weighted cumulative distribution curves:

$$g(t) = \frac{1}{n} \sum_{i=1}^n \frac{y_i}{\bar{y}} l(x_i|t),$$

where y_i is the cpue for data point i , and \bar{y} is the overall mean cpue. The absolute value of the difference between the two curves at any point t is $D(t) = |f(t) - g(t)|$. The values of the variables at which $D(t)$ is maximized were used to predict the potential habitats of Pacific saury, because these values can represent the strongest association between the environment and the abundance of Pacific saury. A probability map of Pacific saury habitats in the NWP was determined from the preferred ranges of the environmental factors (SST, Chl *a*, and NPP).

Generalized additive model and GWR

The influences of the environmental factors (SST, Chl *a*, and NPP) on the spatial distribution of Pacific saury were examined using GAMs. GAMs can explore non-linear relationships between a dependent

variable such as cpue and multiple predictor variables (Hastie and Tibshirani, 1990). The GAM used in this study can be written as:

$$\ln(\text{cpue}) \sim s(\text{SST}) + s(\text{Chl } a) + s(\text{NPP}) + s(\text{latitude}) + s(\text{longitude}) \\ + s(\text{latitude:longitude}) + s(\text{year}) + s(\text{month}),$$

where cpue is log-transformed cpue of Pacific saury (all cpue data are positive) and $s(\cdot)$ is a spline smoothing function. Diagnostic plots, i.e. the distribution of residuals and quantile–quantile (Q–Q) plots, were used to evaluate whether the assumption of a lognormal distribution was suitable. The GAM

analysis was conducted using the *mgcv* package in R (R Development Core Team, 2012).

GWR is a local modelling approach that takes spatial non-stationarity into account and involves fitting the model locally using least squares to estimate the parameter values for each 0.25° square (Fotheringham *et al.*, 1998, 2002). The model for GWR can be written as:

$$\ln(\text{cpue}) \sim b_0 + b_1(\text{SST})_{(u,v)} + b_2(\text{Chl } a)_{(u,v)} + b_3(\text{NPP})_{(u,v)},$$

where b_0 , b_1 , b_2 , and b_3 are the parameters to be estimated and (u,v) is the location (0.25° grids) for each observation.

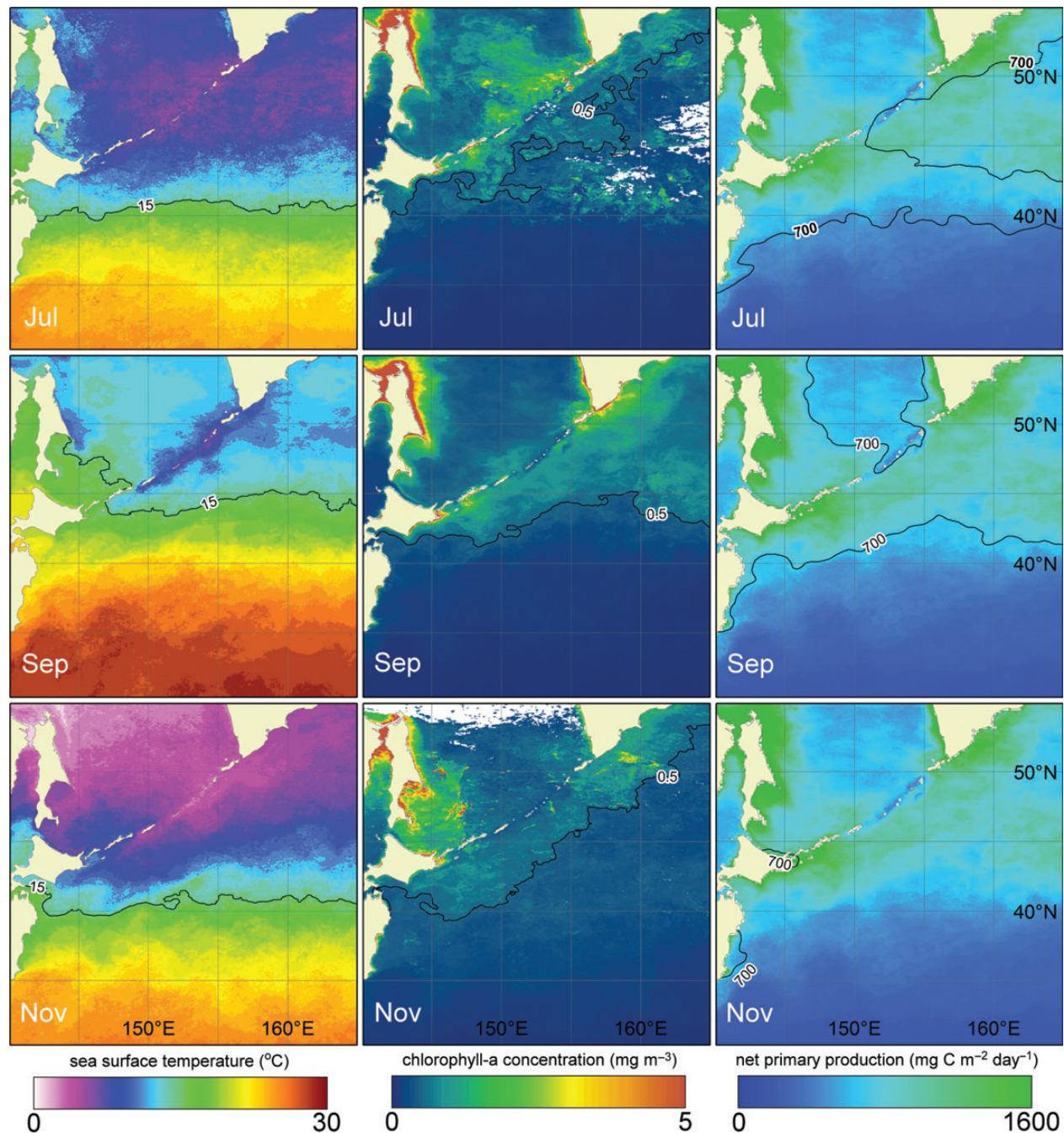


Figure 2. Monthly satellite-based SST (left column), Chl *a* (central column), and NPP (right column) images averaged over 2006–2010 in the NWP.

The GAM and GWR were then used to predict the distribution and potential habitats of Pacific saury in the NWP.

Results

There was seasonal variation in the oceanographic variables in the NWP during June to November (Figure 2). SST, Chl *a*, and NPP increased substantially from the early fishing season (June and July) to the main fishing season (September and October) in the fishing grounds of the Taiwanese fishery for Pacific saury (Figure 3), corresponding to a high cpue of Pacific saury (23.1 t fishing day⁻¹). However, Chl *a* and NPP in the fishing

grounds decreased from November and October, respectively (Figure 3).

The highest $D(t)$, and hence the inferred preferred ranges of Pacific saury in the NWP, corresponded to SST between 14 and 16°C, Chl *a* between 0.4 and 0.6 mg m⁻³, and NPP between 600 and 800 mg C m⁻² d⁻¹ (Figure 4). The preferred habitats inferred from these ranges occurred in the waters of the Oyashio Current, matching the major fishing grounds of the Taiwanese fishery for Pacific saury (Figure 5). Furthermore, the highest observed

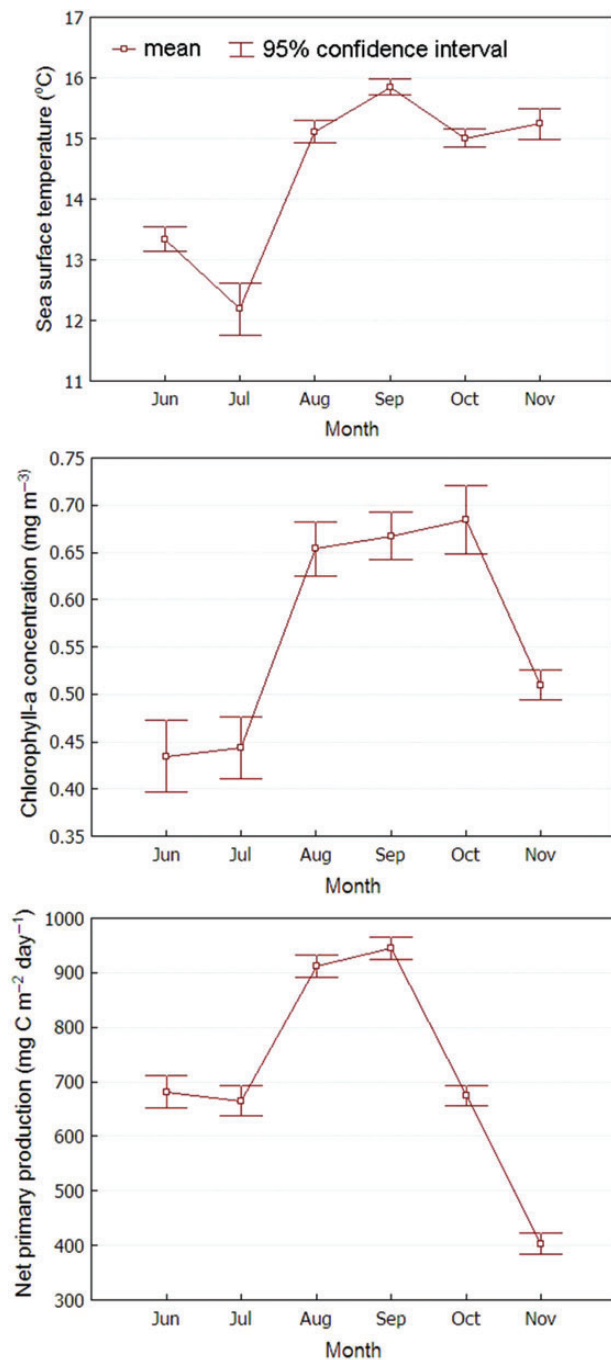


Figure 3. Monthly satellite-based SST, Chl *a*, and NPP values for the fishing grounds of the Taiwanese Pacific saury fishery for 2006–2010.

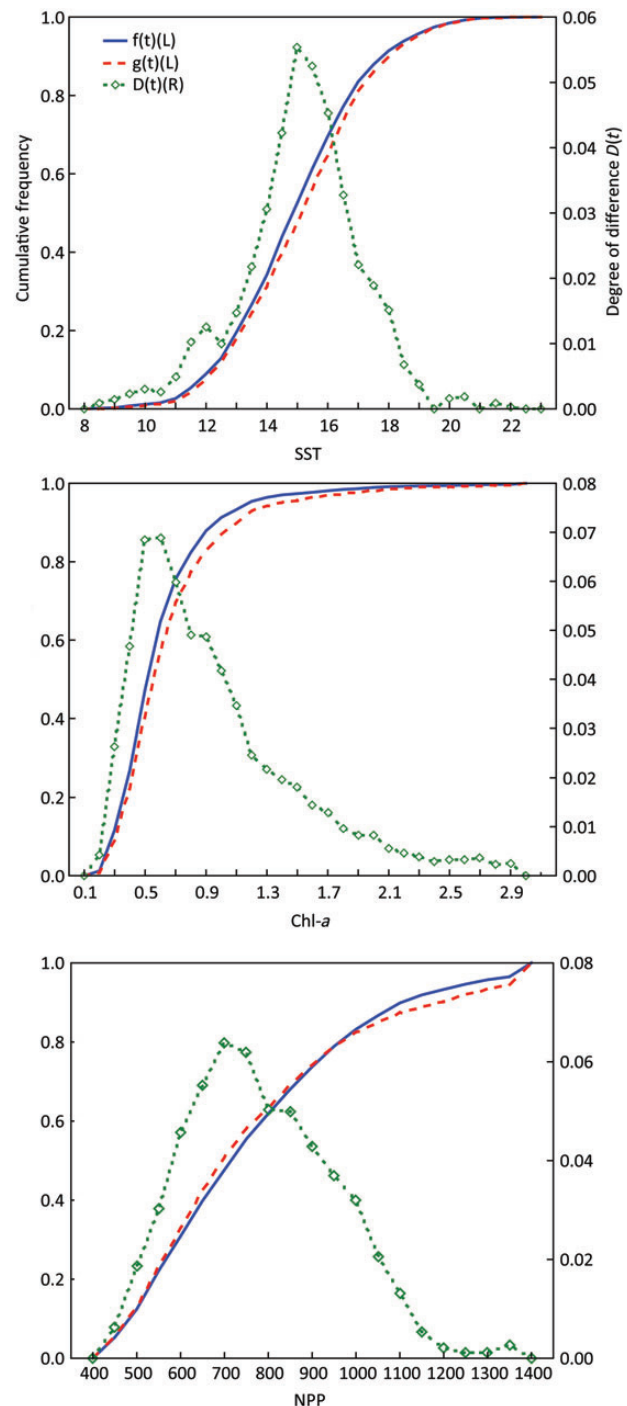


Figure 4. Relationships between Pacific saury cpue and satellite-based SST, Chl *a*, and NPP, based on the ECDF analysis.

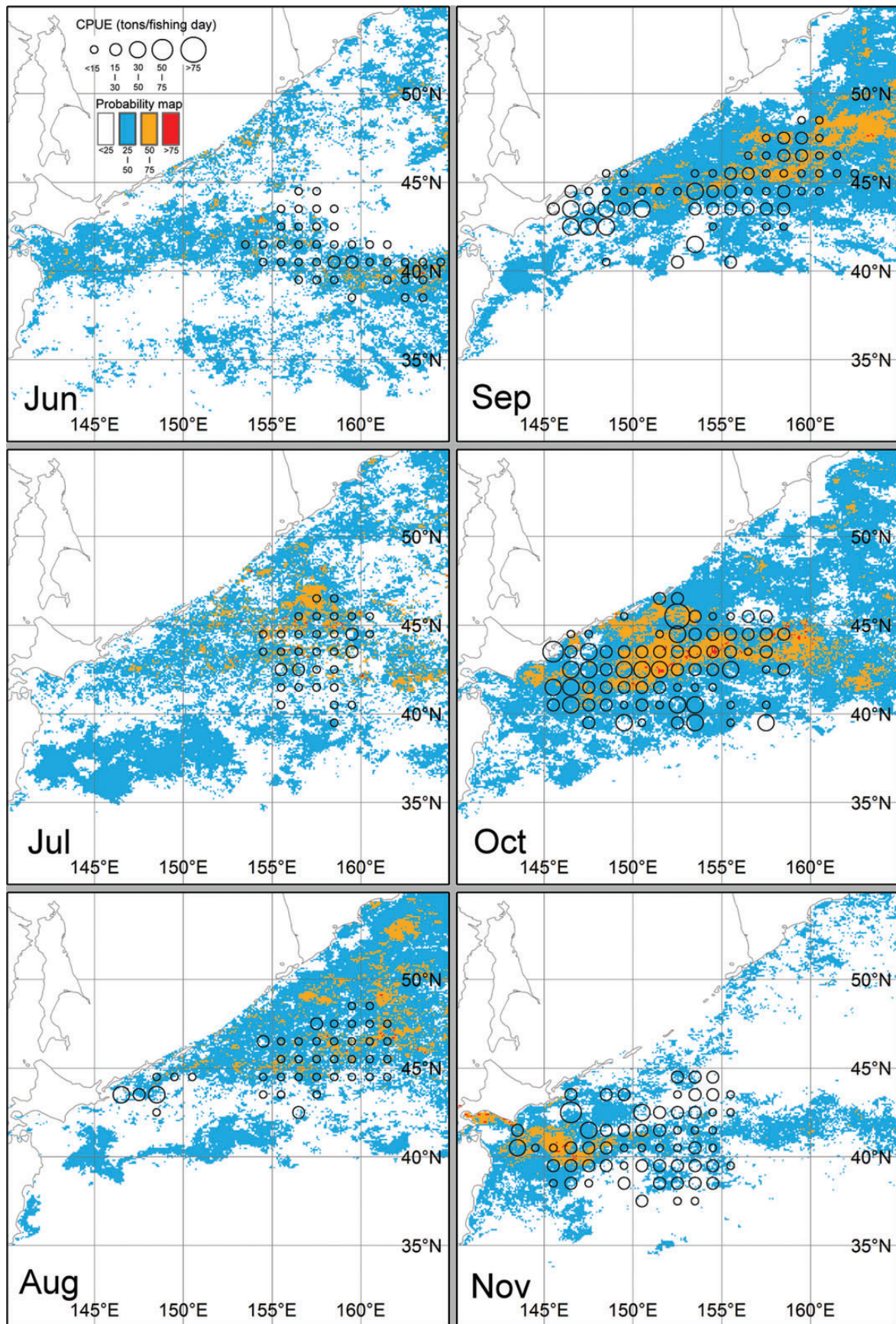


Figure 5. Distributions of nominal cpue (circles) and probability maps for the potential habitat of Pacific saury by month.

Table 1. The changes in residual deviance due to adding each of the factors in the GAM and the p -values derived from χ^2 tests between models that differ by one factor.

Predictor	Residual deviance	Deviance explained	Percentage of total deviance explained (%)	p -value
NULL	1 773.5			
+SST	1 751.5	22.1	3.5	<0.01
+Chl a	1 704.9	46.5	7.4	<0.01
+NPP	1 503.1	201.8	31.9	<0.01
+Latitude	1 402.0	101.0	16.0	<0.01
+Longitude	1 349.2	52.8	8.4	<0.01
+Latitude:Longitude	1 254.0	95.2	15.0	<0.01
+Year	1 153.0	101.0	16.0	<0.01
+Month	1 140.8	12.3	1.9	<0.01
Total deviance explained	35.7%			

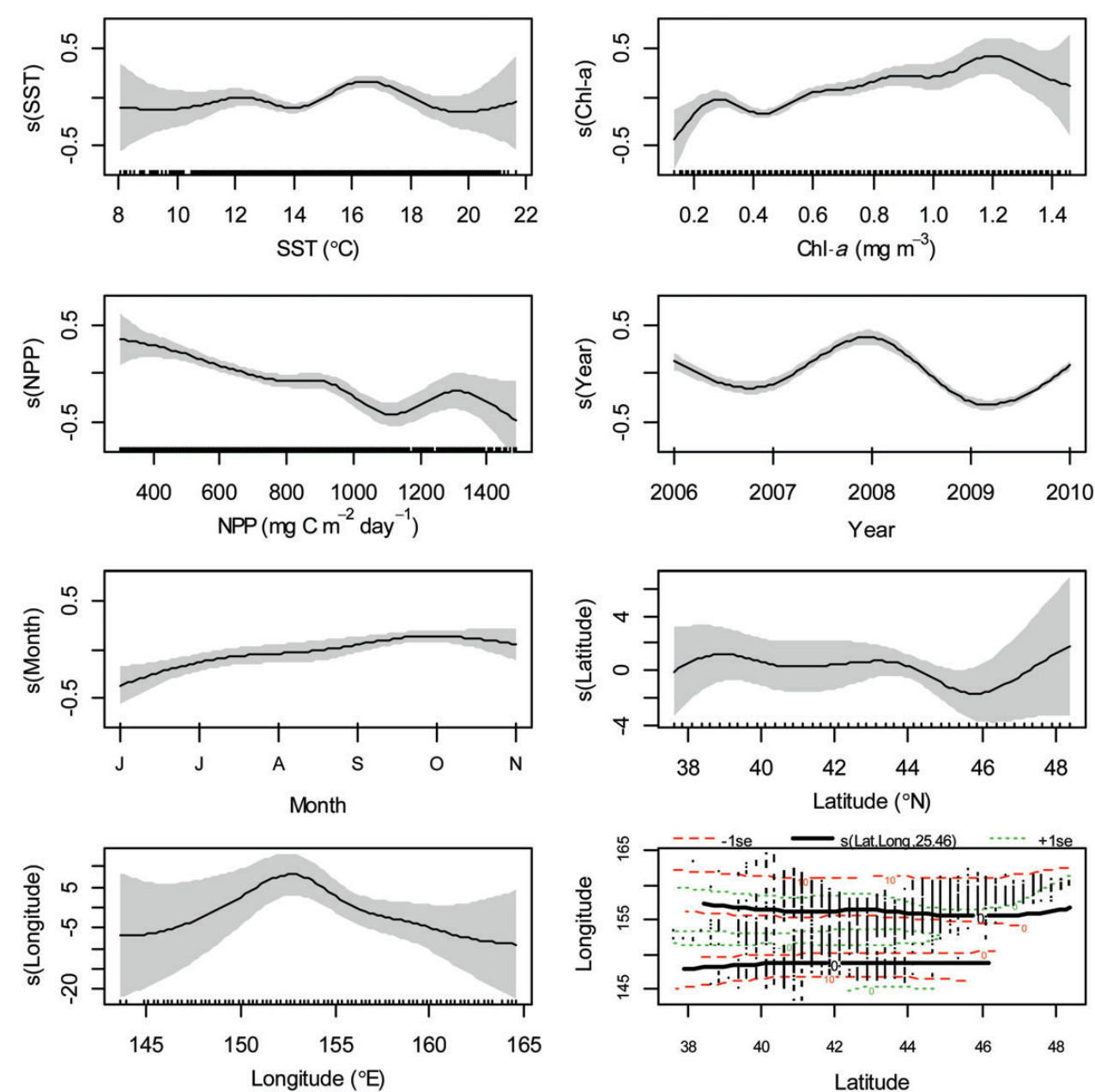


Figure 6. Relationships between Pacific saury cpue and predictor variables derived from the GAM. Shaded areas indicate 95% confidence intervals. The relative density of datapoints is shown in rug plots.

cues for Pacific saury by the Taiwanese Pacific saury fishery fall within the inferred potential habitats for each month (Figure 5).

The residuals from the lognormal distribution conform to the greatest extent with its assumptions according to a Q–Q plot for the GAM, and the residuals (in log-space) appear normal (results not shown). All the factors in the GAM were highly statistically significant ($p < 0.01$; Table 1). The variance explained by the final GAM was 35.7%. NPP explained the highest percentage (31.9%) of the total deviance, with Chl *a* explaining 7.4% and SST explaining 3.5% (Table 1).

The effects of the oceanographic variables on Pacific saury cpue inferred from the GAM indicated that high cpue occurs at $\sim 15.5^\circ\text{C}$ SST and correlates positively with Chl *a* and NPP, in areas of lower latitudes ($42\text{--}44^\circ\text{N}$) and lower longitudes (i.e. close to the coastal waters), as indicated by the effects of spatial variables (Figure 6). The spatial distributions of Pacific saury predicted using the GAM (upper panel in Figure 7) were similar to the patterns for observed nominal cpue averaged over 2006–2010 for each month (Figure 5). Specifically, high Pacific saury cpue was located in coastal waters close to the island of Hokkaido and near the southern Kuril Islands. In contrast, low Pacific saury cpue was predicted in the open ocean (upper panel in Figure 7).

There is considerable variation in the local parameter coefficients produced by GWR (Table 2), suggesting the presence of spatial non-stationarity in the relationships between Pacific saury distribution and the explanatory variables. The proportion of variance explained by the GWR (20.5%) for each location (u, v) was lower than that explained by the GAM with five predictor variables (SST, Chl *a*, NPP, latitude, and longitude; 23.9%), whereas the global proportion of the variance explained by the GAM was 35.7%. Nevertheless, the spatial distribution of Pacific saury predicted by GWR was similar to the output of the GAM. High cpue (>20 t fishing day $^{-1}$) of Pacific saury was predicted in coastal waters close to Hokkaido and the southern Kuril Islands, with low cpue of Pacific saury in the open ocean (lower panel in Figure 7).

Discussion

Environmental factors, such as SST and Chl *a*, influence not only the growth of Pacific saury (Oozeki *et al.*, 2004) but also their distribution and thus the migratory pattern (Ito *et al.*, 2004). However, as demonstrated in this study, NPP is another important factor that determines the distribution of Pacific saury in the NWP. These oceanographic variables can be obtained easily and reliably using satellite remote sensing techniques, combined with the conventional measurement of oceanographic variables. Satellite images are highly resolved in space and time and have been used to identify areas of intense fishing activity and fish aggregation, even for highly migratory species (Polovina and Howell, 2005; Palacios *et al.*, 2006; Zainuddin *et al.*, 2006).

The methods used to infer habitat preferences in this study showed their ability to identify preferred oceanographic characteristics of the Pacific saury habitats in the NWP. Based on the results, for example, from ECDF and GAMs, the preferred ranges of Pacific saury are $14\text{--}16^\circ\text{C}$ for SST, $0.4\text{--}0.6$ mg m $^{-3}$ for Chl *a*, and $600\text{--}800$ mg C m $^{-2}$ d $^{-1}$ for NPP. The range for SST is consistent with the results of previous studies (e.g. Eschmeyer *et al.*, 1983; Ito *et al.*, 2004). The oceanographic conditions in the fishing grounds of Pacific saury in the NWP vary seasonally (Figure 3), which could impact the distribution of this species.

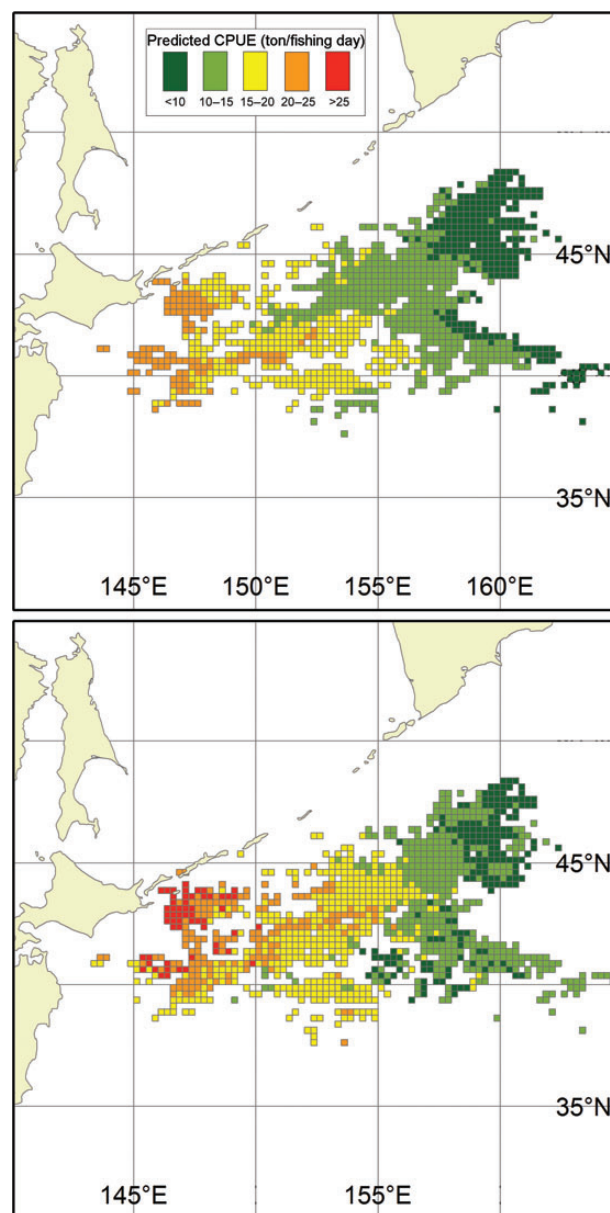


Figure 7. Distributions of predicted cpue for Pacific saury from the GAM (upper panel) and GWR (lower panel).

Table 2. Summary statistics for the GWR parameter estimates.

Variable	Minimum	Lower quartile	Median	Higher quartile	Maximum
Intercept	−7.013	−1.543	1.007	9.804	18.238
SST	−0.254	0.444	1.316	1.587	2.08
Chl <i>a</i>	−2.305	9.264	11.61	14.049	18.875
NPP	−0.026	−0.02	−0.016	−0.008	−0.002

AIC_C optimized bandwidth of 3.62° latitude and longitude.

The ECDF method has been successfully applied in the past to examine the relationships between environmental factors and the distribution of pelagic species, e.g. yellowfin tuna in longline fisheries in the northeastern Indian Ocean (Rajapaksha *et al.*, 2010). In this study, we showed that ECDF can identify the

preferred ranges for Pacific saury. In general, the preferred ranges for SST, Chl *a*, and NPP determined from the ECDF method were similar to those from the GAM. These results indicated that the Pacific saury distribution is positively related to SST and Chl *a*, with a peak at $\sim 15^{\circ}\text{C}$ SST and 0.5 mg m^{-3} Chl *a*, respectively, but, most importantly, is related negatively to NPP. High abundance of Pacific saury in coastal waters (Figure 5) is likely to be related to the southward extension of Oyashio fronts (Yasuda and Watanabe, 1994; Watanabe *et al.*, 2006; Tseng *et al.*, 2011), which corresponds to higher SST and Chl *a* and lower NPP in coastal areas.

As shown in several studies, the spatial distribution of catch and cpue can be related to satellite-based oceanographic conditions (e.g. Fiedler and Bernard, 1987; Forget *et al.*, 2009). We found that similar spatial patterns were obtained from the various approaches (GAM, GWR, and ECDF), partially validating them. As suggested by Polovina and Howell (2005), habitat modelling could be extended by including ecosystem indicators such as the Transition Zone Chlorophyll Front in the North Pacific to take regional ocean dynamics into account. Similarly, the study could be extended by using data for other fisheries, such as those of Japan and Russia.

The predicted distribution of Pacific saury in the NWP using GAMs showed that high cpue areas for Pacific saury in the NWP were located in the EEZ (exclusive economic zone) waters off Hokkaido and the Kuril Islands. This is probably related to the Oyashio Current when it moves southwestward along with the EEZ boundary off the Kuril Islands (Ito *et al.*, 2004), because this area has been shown to be important to Pacific saury recruitment, and the feeding migration of Pacific saury is associated with the Oyashio Current during summer (Olson, 2001; Kurita, 2003; Sugisaki and Kurita, 2004).

Results derived from this study could improve our understanding of how the spatial distribution of Pacific saury is likely to vary with climate and form the basis to forecast fishing grounds in the future (Su *et al.*, 2013). Fisheries management arrangements could be developed based on preferred habitat ranges to account for the variation in oceanographic conditions driven by climate change.

Acknowledgements

We thank two anonymous reviewers and the editor for their thoughtful comments and suggestions. This study was funded partially by the Fisheries Research Institute of Council of Agriculture, Taiwan, through the research grant 100AS-10.1.1-AI-A1 to C-T. Tseng.

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Handling Editor: Howard Browman