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ABSTRACT

Spatial estimation of prey consumption by sei whales in the JARPNII survey area was preliminary attempted using data from 2002 to 2013. Two levels of models are constructed to achieve the goal. Firstly, relative abundance of sei whales in relation with oceanographic conditions is estimated by using a generalized additive model (GAM). Secondary, amount of prey consumed by a sei whale in relation with oceanographic conditions is also estimated by using GAM. Finally, prey consumption of sei whales in the JARPNII survey area is calculated as the product of these two models. Data obtained from 2002 to 2013 are used in the analysis. Spatial distribution of prey consumption shifted toward north as the season progress. Estimated amount of prey consumption by sei whales using the spatial model was comparable to estimates based on traditional methods (Tamura *et al.*, 2016: SC/F16/JR15). SST was selected as environmental covariates in the first and second models. However, the shape of functional form for the first level model (prey consumption) was relatively flat in comparison with the second level model (abundance). The results indicated that spatial distribution of sei whales at meso scale were largely determined by oceanographic conditions such as SST. Sei whales could then search for their prey with the optimal oceanographic conditions as indicated by feeding behaviour study (Ishii *et al*., 2016: SC/F16/JR25). Future study on feeding ecology of baleen whales should pursuit such an integrated approach further.

INTRODUCTION

Prey consumption of sei whales in the JARPNII survey area has been estimated based on traditional methods (Konishi *et al,* 2009; Tamura *et al.*, 2016: SC/F16/JR15). These estimations have their values as the estimation methods are relatively simple. However, these methods cannot estimate spatio-temporal changes of prey consumption by whales. The Panel of the JARPNII expert workshop held in 2009 recommended pursuing such an attempt as medium to long term project (IWC, 2010).

In this paper, a preliminary result of spatial estimation of prey consumption by sei whales in the JARPNII survey area is presented to see whether the consumption is heterogeneous in both spatially and temporally. Two levels of models are constructed to achieve the goal. Firstly, relative abundance of sei whales in relation with oceanographic conditions is estimated by using a generalized additive model (GAM). Secondary, amount of prey consumed by a sei whale in relation with oceanographic conditions is also estimated by using GAM. Finally, prey consumption of sei whales in the JARPNII survey area is calculated as the product of these two models. Data obtained in JARPNII (the second phase of the Japanese Whale Research Program under Special Permit in the western North Pacific) from 2002 to 2013 are used in the analysis.

There are three spatiotemporal scale to link feeding ecology of cetaceans with distribution pattern of them and the definitions are follows; at the macro scale, cetaceans migrate seasonally between feeding and breeding grounds; at the meso scale, cetaceans move over days and weeks in search of preferred local abundance of food; and at the micro scale, whales dive and search for food within localised areas (IWC, 2003). This study corresponds to the meso scale.

MATERIALS AND METHODS

Sighting survey

A brief summary of sighting survey related to this s provided hear. The details can be found in Matsuoka *et al,* (2016: SC/F16/JR2) and Bando *et al.* (2016: SC/F16/JR4). The cetacean sighting surveys were conducted in the western North Pacific in July from 2002 to 2013 as part of JARPNII (Fig. 1). The boundaries of the survey area were 35°N, the boundary of the economic exclusive zone (EEZ) claimed by countries other than Japan and 170°E and the eastern coast line of Japan. Sighting data obtained outside but adjacent to the area during the period were also used as supplemental data. Several survey vessels were engaged in the cetacean sighting surveys but their specifications were similar. Their gross tonnages were approximately 1000 GT with two main observation platforms: top barrels were set at 20 m above the sea surface and upper bridges were set at 10 m above the sea surface. Data obtained by sighting vessels (SVs) and sighting and sampling vessels (SSVs) were used in the analysis as the relative abundance of sei whales was estimated using a model based method instead of a design based method. Three observers at each observation platform using 7 × 50 binoculars were engaged in the sighting surveys. Sightings within 3 n.miles from the survey tracklines were counted. The survey vessels steamed around 10.5 knots along the survey tracklines during the survey hours. The survey was conducted during the daytime from 1 hour after sunrise to 1 hour before sunset. Surveying was stopped when the visibility was <3.7 km (≈ 2 nm) and/or sea state >4 on the Beaufort wind force scale.

Activities aboard the ship were basically classified into two categories: on-effort and off-effort. On-effort activities were times when a full search effort was executed within the acceptable conditions. Off-effort activities were all times other than on-efforts. On-effort data used in the analysis. All sightings of sei whales recorded during on-effort activities were classified as primary-sightings. All other sightings were considered secondary sightings and not used in this analysis. On-effort surveys were conducted in the closing and passing mode; the survey vessels approached all sightings during the closing-mode to confirm the species and number of individuals in a school, and all sightings during the passing-mode were not approached although the species and estimated number of individuals in a school were recorded.

Sampling survey

The research area of the JARPNII was a part of sub-areas 7, 8 and 9, which were established by the International Whaling Commission/Scientific committee (IWC/SC) (IWC, 1994). All sei whales of primary and secondary sighting were targeted for sampling. The order of individuals to be sampled in a school were chosen by a researcher on board using a series of tables of random sampling numbers (TRS), which were prepared according the size of the schools. When the sighting of the sei whales was occurred, the SSV approached to the school of whales within 0.2 n.miles. Observers on the top barrel counted a number of whales and estimated body length of each animal. If a sighting was solitary whale, it was sampled immediately after the body length estimation. If a school was consisted of two or more animals, the researcher assigned a serial number to each individual, ranging from left to right. The first target whale was chosen using the TRS specific to the school size. When two whales should be sampled from a school, the second target was selected by the same manner after the first animal was sampled. In this case, the remaining individuals were renumbered according to the latest position in the school and TRS was used for the original school size minus one. After sampling, whales were brought to the research base vessel where the animals were examined by a biologist onboard. The whale sampling procedure is described by Bando *et al* (2016: SC/F16/JR4) in detail. In the JARPNII surveys, the stomach contents were removed from each compartments and weighed to the nearest 0.1kg on the ship’s flensing deck after capture. The analysis of prey consumption in this study was based on data collected from the first compartment (forestomach) and second compartment (fundus). The sampling and treatment procedure of stomach contents from whales is described by Tamura *et al* (2016: SC/F16/JR15) in detail.

Daily prey consumption by sei whales

Prey consumption by sei whales are being made using a same methodology described in Tamura *et al*. (2016: SC/F16/JR15). In Tamura *et al* (2016: SC/F16/JR15), it applied three equations for estimating daily and seasonal prey consumption. In this document, it applied for each sampled sei whale following equation:

$SMR = 803.71M^{0.75}$ (Perez *et al,* 1990)

SMR is the daily prey consumption (expressed by KJ day^{-1}) and M is body mass of sei whales sampled in kg.

The value from this equation was intermediate one among equations. It was considered appropriate value for this analysis at this stage. Daily prey consumption for dominant prey in each sampled sei whale was calculated by using the equation.

Reproductive status of sei whales

Spatial distribution of reproductive status of sampled sei whales was plotted in maps to see whether the distribution was segregated by reproductive status. Males were defined as sexually matured by testis weight (larger side) of more than 1,090 g. Female were defined as sexually mature by the occurrence of at least one corpus luteum or albicans in their ovaries.

Spatial modelling

A hierarchical structure with three levels of spatial distribution models is considered in this paper: (1) daily prey consumption by sei whales and (2) relative abundance of sei whales. Prey consumption by sei whales was as the product of the results from the two levels. Generalized additive models (GAMs) having a Tweedie error distribution with logarithmic link function were used for both levels. A Tweedie random variable with $1<p<2$ is a sum of N gamma random variables in which N has a Poisson distribution (Wood, 2015). If p equals 1, then it is a generalization of a Poisson distribution and a discrete distribution supported on integer multiples of the scale parameter. If p is larger than 1 and smaller than 2 ($1<p<2$), then the distribution is supported on the positive reals with a point mass at zero. If p equals 2, then it is a gamma distribution. Initially, we experimentally changed the value of p in each GAM and set it as 1.1. The models with the lowest GCV scores were selected. For this analysis, the mgcv package (Wood, 2006) version 1.8-7 of the R software version 3.2.2 (R Development Core Team, 2015) was used. The shapes of the functional forms for the all covariates were also plotted with that package.

Sea surface temperature (SST), sea surface height anomaly (SSHa) and sea surface chlorophyll-a concentration (Chl-*a*) recorded by satellites and a digital seafloor depth data were used as environmental covariates in the models. SST and Chl-*a* data (4x4 km grid) obtained by Moderate Resolution Imaging Spectroradiometer aboard the Aqua satellite (Aqua MODIS) were used. Monthly mean from July 2002 to September 2013 in Level 3 Standard Mapped Image products downloaded from Ocean Color Web (http://oceancolor.gsfc.nasa.gov/, NASA Goddard Space Flight Center "Last accessed on 10 January 2014") were used. It should be noted that recording of MODIS data was started in July 2002. Missing data in these data were estimated by ordinary kriging with the aid of the geographic information system (GIS), ArcGIS 10.1 (ESRI, California, USA). Daily data of Sea Level Anomalies (MSLA) were also downloaded and used as SSHa. The altimeter products were produced by Ssalto/Duacs and distributed by Aviso, with support from Cnes (http://www.aviso.oceanobs.com/duacs/ "Last Last accessed on 18 September 2014"). ETOPO1 Global Relief Model for bottom topography" (Amante and Eakins, 2009) was used as seafloor depth data. "A Global Self-consistent, Hierarchical, High-resolution Geography Database" (Wessel and Smith, 1996) was used in figures to depict coastline. Mean values in 1x1 longitude and latitudinal grid cell in each month in each year were calculated using these data. Year and month were used as categorical covariates in both levels. Spatial resolution considered in the models was 1x1 longitude and latitudinal grid cell. Data recoded from May to September in each (2002-2013) were used in the modelling.

At the first level model, daily prey consumption of a sei whale (t/day by an individual) in a grid cell was modelled using a GAM. Five major prey species, namely, copepods, euphausiids, Japanese anchovy, Pacific saury and mackerels were considered in the modelling and these were used as categorical covariates as well. Number of individuals in a grid cell was treated as weight in the model so that prey consumption by an individual in a grid cell could be estimated.

At the second level abundance in a grid cell was modelled using a GAM. The following procedures were conducted to estimate abundance. Original sighting effort data were divided first into 1 km segments, and then these segments were pooled in each grid cell (d). Because sighting effort was discontinuous in closing mode, especially in high density area of baleen whales, a relatively short segment length (1 km) was chosen for the analysis. The number of schools of sei whales was also pooled in each grid cell (n). Effective strip width (esw) and mean school size (E(s)) were estimated by a program, DISTANCE version 6.2 release 1 (Thomas *et al.*, 2010). All sighting data from 2002 to 2013 recorded by SVs and SSVs were pooled for the estimation. Probability of detection on the trackline (g(0)) was assumed as 1. Abundance in a grid cell was first calculated by unit density, i.e. $(n \times E(s))/(d \times 2 \times esw \times g(0))$, and then multiplied by the area of the grid cell. Some grid cells had unusually high abundance. Abundance falling more than 95 percentiles were treated as outliers and not considered in the GAM to avoid unrealistic over estimation. Details of methods are also shown in Murase *et al.* (2016: SC/F16/JR7).

RESULTS AND DISCUSSION

Maps of mean SST, SSHa and Chl-*a* in each month from 2002 to 2013 are shown in Figs. 2-4. These maps showed seasonal changes of these environmental covariates. Spatial segregation by maturity stage and prey species of sei whales was not considered in this analysis as maps of maturity status and prey species of sampled sei whales indicated there was no obvious concertation by these categories (Figs. 5-6). Selected GAM based on GCV score for daily prey consumption of a sei whale is summarized in Table 1. The shapes of the functional forms for selected covariates (SST and Chl-*a*) are shown in Fig. 7. Selected GAM based on GCV score for abundance of sei whales is summarized in Table 2. The shapes of the functional forms for selected covariates (SST and Chl-*a*) are shown in Fig. 8. Estimated spatial distribution and abundance of sei whales are shown in

Fig. 9 and Table 3. Spatial distribution of prey consumption shifted toward north as the season progress. Estimated spatial distribution of prey consumption and the amount are shown in Figs. 10-14 and Table 4-8. Estimated amount of prey consumption by sei whales using the spatial model was comparable to estimates based on traditional methods (Tamura *et al*., 2016: SC/F16/JR15). Uncertainty associated with estimated amount of prey consumption was not considered as this is a preliminary attempt. The Sub-Committee on the RMP of the IWC/SC is currently trying to develop a guideline for model-based abundance estimation methods, mainly focusing on GAMs (Hedley and Bravington, 2014). The Working Group on Ecosystem Modelling (EM) of the IWC/SC recognized the necessity for the development of a guideline on the techniques and underlying assumptions of SDMs based on up-to-date and comprehensive knowledge (IWC, 2015). Consideration of uncertainty of prey consumption in spatial context should be investigated in the future along with development of associated techniques in the IWC/SC. SST was selected as environmental covariates in the first and second models. However, the shape of functional form for the first level model (prey consumption) was relatively flat in comparison with the second level model (abundance). The results indicated that spatial distribution of sei whales at meso scale were largely determined by oceanographic conditions such as SST. Sei whales could then search for their prey with the optimal oceanographic conditions as indicated by feeding behaviour study (Ishii *et al*., 2016: SC/F16/JR25). Future study on feeding ecology of baleen whales should pursuit such an integrated approach further.

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Table 1. Selected generalized additive model (GAM) for daily prey consumption of a sei whale. Approximate significance levels (*p*-value) and degrees-of-freedom (edf) are shown for each covariate.

Family	Tweedie	
Link function	log	
Power (p)	1.1	
Adjusted R^2	0.73	
Deviance explained (%)	76.7	
GCV score	124.50	
Parametric coefficients	Estimate	*p*-value
Intercept	6.69	<0.05
Year		
2003	-0.07	0.12
2004	-0.05	0.25
2005	0.00	0.96
2006	-0.07	0.10
2007	-0.05	0.27
2008	-0.02	0.56
2009	-0.05	0.28
2010	0.04	0.28
2011	-0.03	0.53
2012	0.01	0.75
2013	0.03	0.60
Month		
6	0.00	0.90
7	0.04	0.28
8	0.03	0.44
9	-0.02	0.68
Prey		
Euphausiids	0.20	<0.05
Anchovy	-0.57	<0.05
Saury	-0.93	<0.05
Mackerels	-0.57	<0.05
Approximate significance of smooth terms	edf	p-value
SST	7.40	<0.05
log(Chl-*a*)	7.22	<0.05

Table 2. Selected generalized additive model (GAM) for abundance of a sei whale. Approximate significance levels (*p*-value) and degrees-of-freedom (edf) are shown for each covariate.

Family	Tweedie	
Link function	log	
Power (p)	1.1	
Adjusted R^2	0.08	
Deviance explained (%)	21.1	
GCV score	33.60	
Parametric coefficients	Estimate	*p*-value
Intercept	-7.93	<0.05
Year		
2003	-0.48	0.07
2004	-0.20	0.42
2005	-0.02	0.94
2006	0.04	0.87
2007	0.21	0.37
2008	-0.30	0.26
2009	-0.13	0.65
2010	-0.01	0.98
2011	-0.32	0.28
2012	-1.11	<0.05
2013	-0.01	0.96
Month		
6	0.56	<0.05
7	0.59	<0.05
8	0.43	<0.05
9	0.53	0.07
Approximate significance of smooth terms	edf	*p*-value
SST	4.39	<0.05
SSHa	-	-
log(Chl-*a*)	-	-
Depth	6.99	<0.05

Table 3. Estimated number of sei whale individuals from May to September in each year (2002-2013).

Year	May	June	July	August	September
2002	-	-	3,622	3,134	3,525
2003	1,368	2,719	2,322	1,744	1,997
2004	1,842	3,305	2,659	2,403	2,943
2005	2,443	4,364	4,026	2,809	2,801
2006	2,556	5,116	4,281	3,382	3,443
2007	2,871	5,798	5,734	3,325	3,540
2008	1,866	3,490	3,257	2,253	2,005
2009	2,206	3,809	3,239	2,150	2,547
2010	2,312	4,600	3,163	2,152	2,508
2011	1,721	3,413	3,228	2,166	2,134
2012	870	1,637	1,281	798	793
2013	2,529	4,417	3,186	2,788	2,969

Table 4. Estimated amount of copepods consumed by sei whales (t) from May to September in each year (2002-2013).

Year	May	June	July	August	September	Total
2002	-	-	92,762	80,002	83,049	255,814
2003	32,038	60,365	54,905	41,247	43,891	140,042
2004	43,473	74,700	64,620	59,252	65,749	189,622
2005	61,232	104,888	103,183	72,054	66,554	241,791
2006	59,618	114,790	101,257	80,712	75,307	257,276
2007	67,881	131,517	138,645	80,357	79,186	298,189
2008	45,359	82,040	80,874	56,311	45,764	182,949
2009	52,363	86,790	79,337	52,177	57,390	188,903
2010	60,033	114,430	83,620	57,782	61,453	202,855
2011	41,753	79,721	80,040	53,651	48,652	182,343
2012	21,789	39,591	32,911	20,773	18,940	72,624
2013	64,678	107,983	82,859	73,454	71,902	228,215

Table 5. Estimated amount of euphausiids consumed by sei whales (t) from May to September in each year (2002-2013).

Year	May	June	July	August	September	Total
2002	-	-	113,160	97,594	101,311	312,065
2003	39,083	73,639	66,978	50,317	53,542	170,837
2004	53,033	91,126	78,830	72,281	80,207	231,318
2005	74,697	127,952	125,872	87,898	81,189	294,959
2006	72,728	140,031	123,523	98,460	91,866	313,850
2007	82,808	160,437	169,133	98,027	96,598	363,758
2008	55,334	100,080	98,658	68,694	55,827	223,179
2009	63,877	105,874	96,783	63,650	70,009	230,442
2010	73,234	139,592	102,008	70,488	74,966	247,462
2011	50,934	97,251	97,640	65,449	59,350	222,439
2012	26,580	48,296	40,148	25,341	23,105	88,594
2013	78,900	131,728	101,079	89,606	87,713	278,398

Table 6. Estimated amount of Japanese anchovy consumed by sei whales (t) from May to September in each year (2002-2013).

Year	May	June	July	August	September	Total
2002	-	-	52,359	45,156	46,876	144,392
2003	18,084	34,072	30,990	23,281	24,774	79,046
2004	24,538	42,164	36,474	33,444	37,112	107,030
2005	34,562	59,203	58,241	40,670	37,566	136,476
2006	33,651	64,792	57,154	45,557	42,506	145,217
2007	38,315	74,234	78,257	45,357	44,696	168,310
2008	25,603	46,307	45,649	31,784	25,831	103,264
2009	29,556	48,988	44,781	29,451	32,393	106,625
2010	33,885	64,589	47,199	32,615	34,686	114,500
2011	23,567	44,998	45,178	30,283	27,461	102,922
2012	12,298	22,347	18,576	11,725	10,690	40,992
2013	36,507	60,950	46,769	41,460	40,584	128,814

Table 7. Estimated amount of Pacific saury consumed by sei whales (t) from May to September in each year (2002-2013).

Year	May	June	July	August	September	Total
2002	-	-	36,598	31,564	32,766	100,927
2003	12,640	23,816	21,662	16,273	17,316	55,252
2004	17,152	29,472	25,495	23,377	25,940	74,812
2005	24,158	41,382	40,709	28,428	26,258	95,395
2006	23,522	45,289	39,949	31,844	29,711	101,504
2007	26,782	51,888	54,700	31,704	31,242	117,646
2008	17,896	32,368	31,908	22,217	18,055	72,180
2009	20,659	34,242	31,301	20,585	22,642	74,529
2010	23,685	45,147	32,991	22,797	24,245	80,033
2011	16,473	31,453	31,578	21,167	19,195	71,941
2012	8,596	15,620	12,985	8,196	7,472	28,653
2013	25,518	42,603	32,691	28,980	28,368	90,039

Table 8. Estimated amount of mackerels consumed by sei whales (t) from May to September in each year (2003-2013).

Year	May	June	July	August	September	Total
2002	-	-	52,491	45,271	46,995	144,757
2003	18,129	34,159	31,069	23,340	24,836	79,246
2004	24,600	42,270	36,567	33,529	37,206	107,301
2005	34,650	59,353	58,388	40,773	37,661	136,822
2006	33,736	64,956	57,298	45,673	42,614	145,585
2007	38,412	74,421	78,455	45,472	44,809	168,736
2008	25,668	46,424	45,764	31,865	25,896	103,525
2009	29,630	49,112	44,894	29,525	32,475	106,894
2010	33,971	64,752	47,318	32,697	34,774	114,790
2011	23,627	45,112	45,292	30,360	27,531	103,182
2012	12,330	22,403	18,623	11,755	10,718	41,096
2013	36,599	61,104	46,887	41,565	40,687	129,140

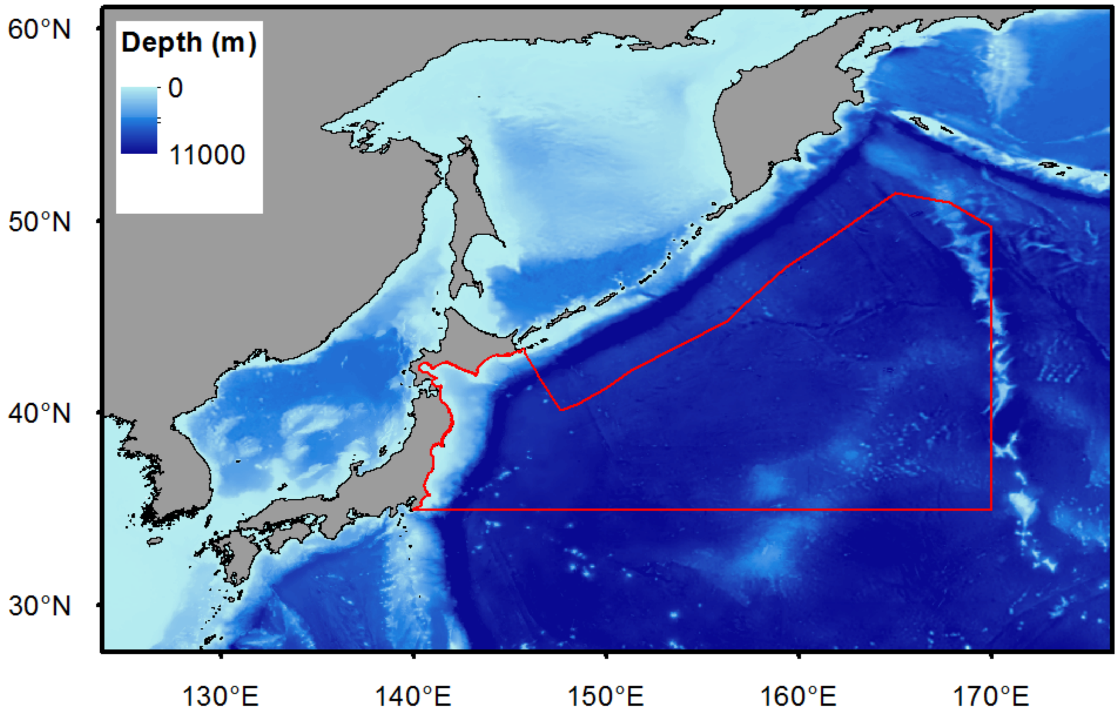

Figure 1. The survey area of JARPNII (red line). Seafloor depth is also shown.

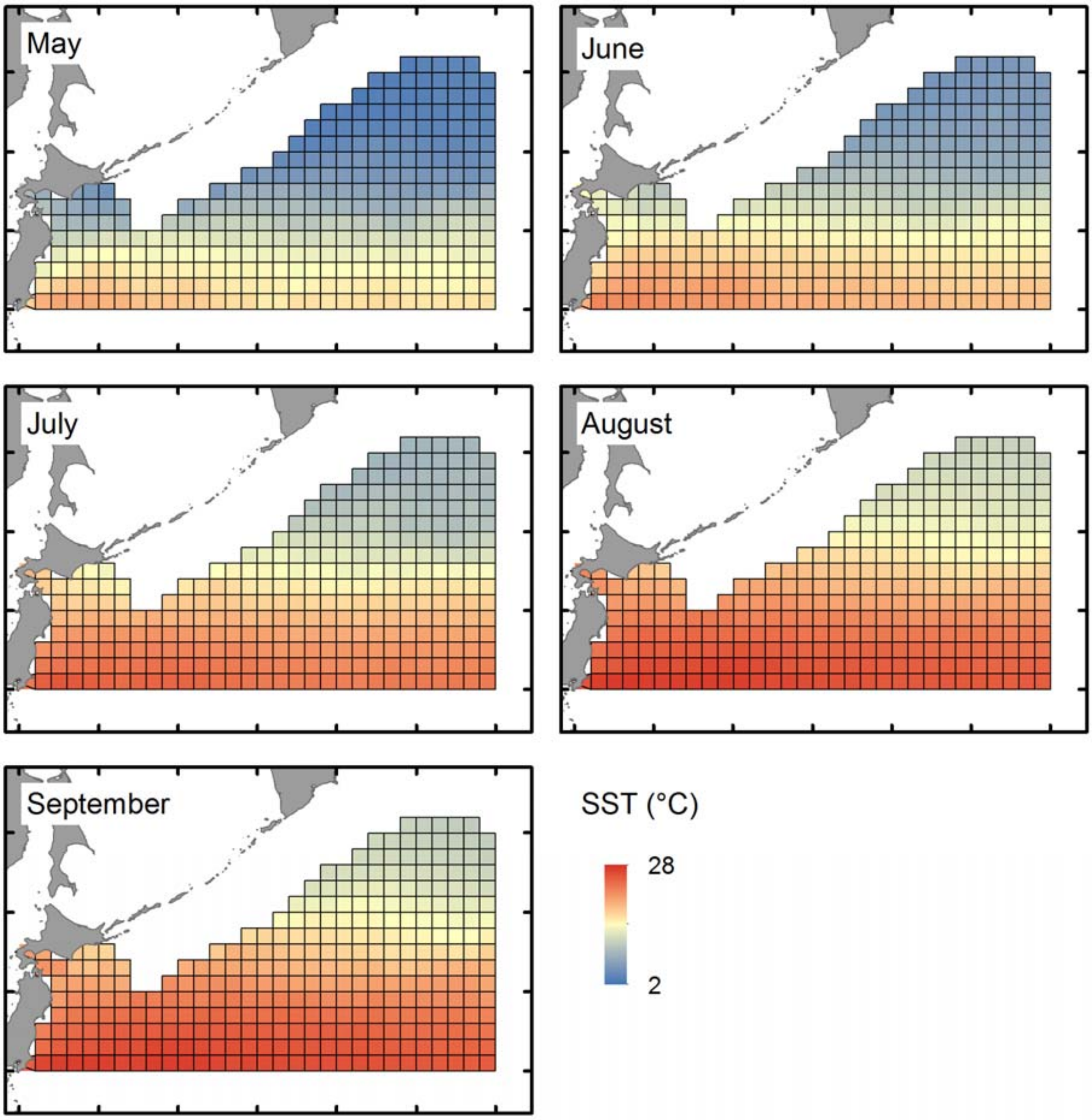

Figure 2. Sea surface temperate (SST) from May to September. Means of values in 1×1 longitude and latitude grids from 2002 to 2013 are shown.

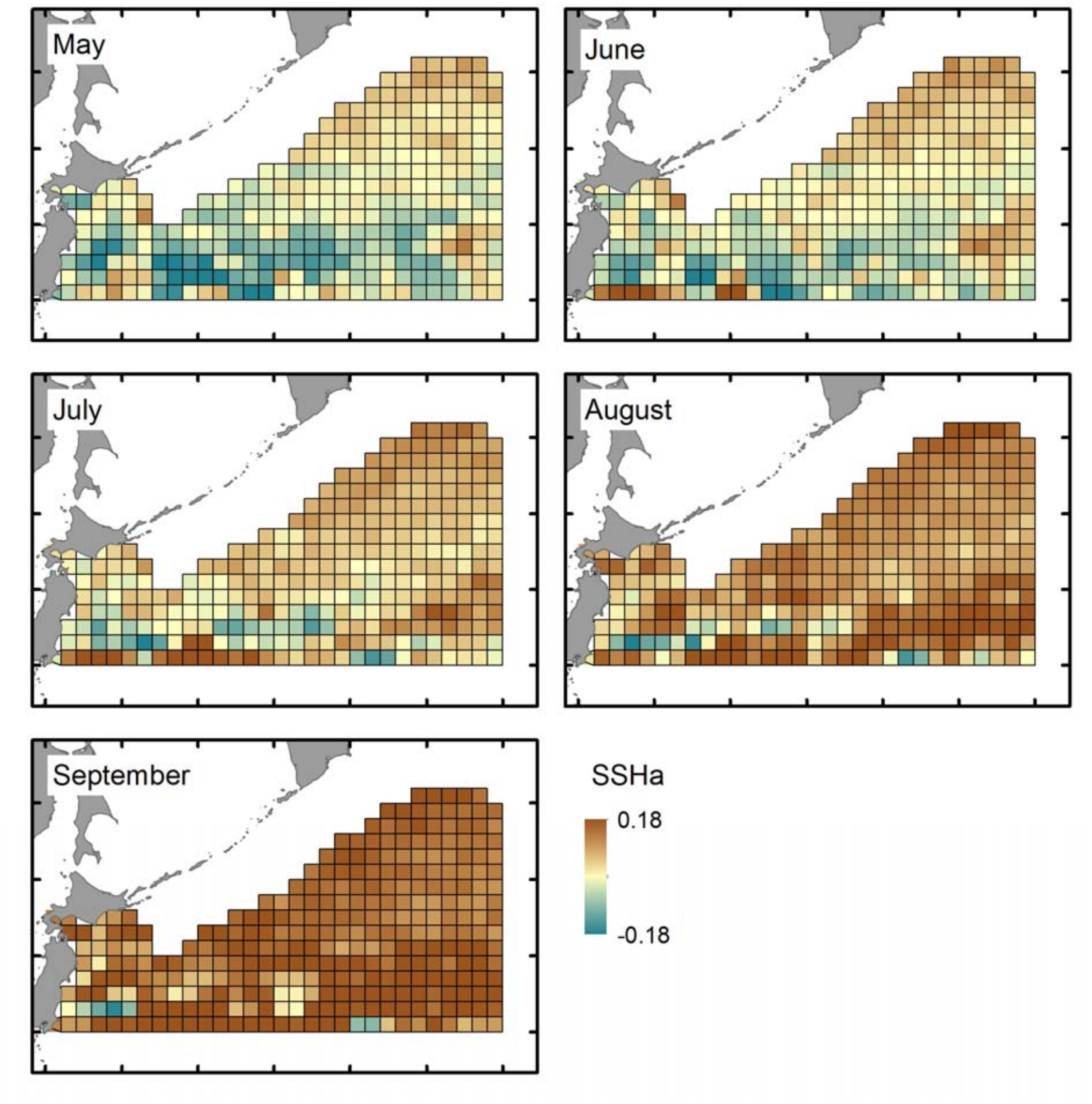

Figure 3. Sea surface height anomaly (SSHa) from May to September. Means of values in 1×1 longitude and latitude grids from 2002 to 2013 are shown.

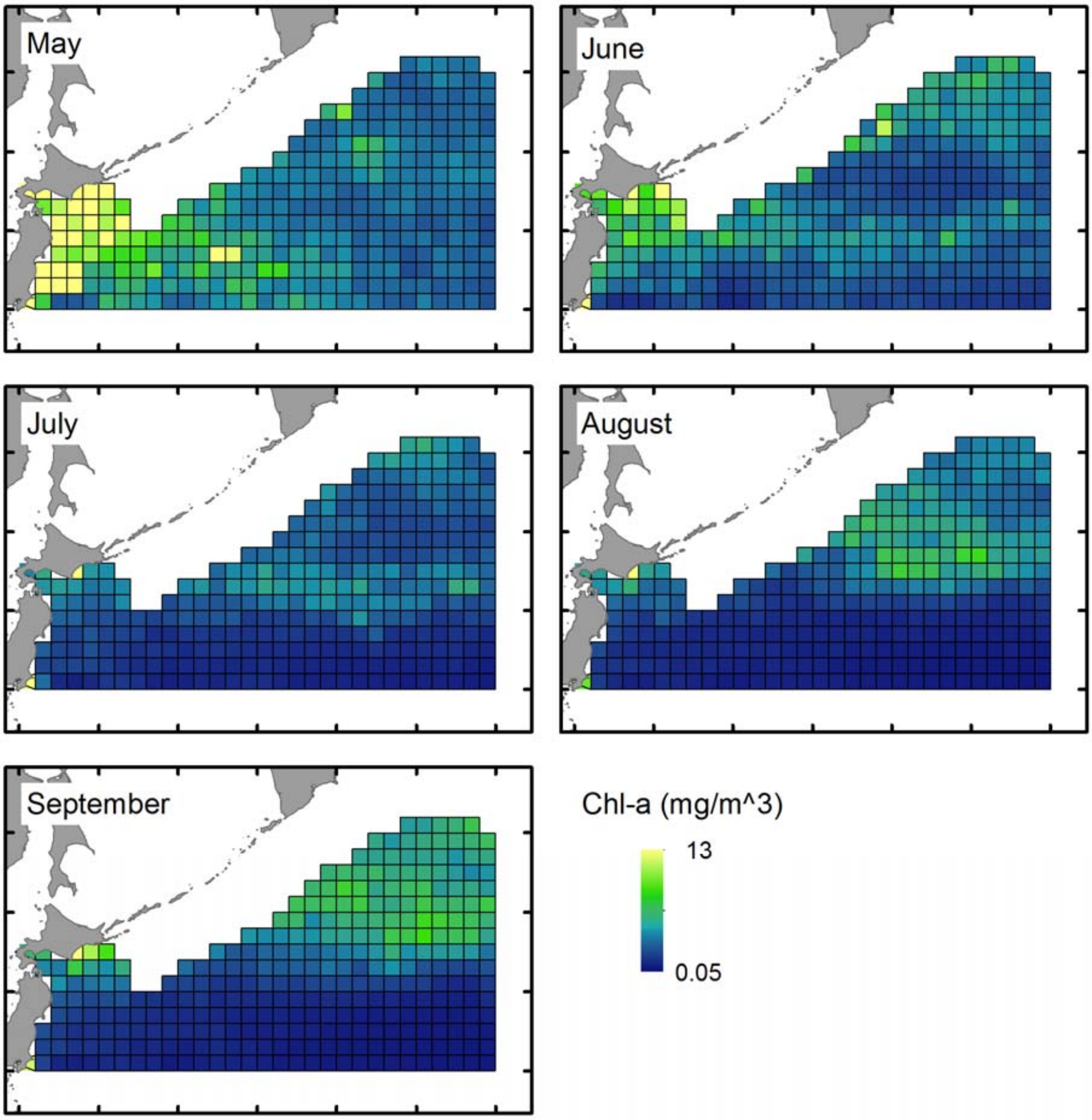

Figure 4. Chlorophyll-*a* concentrations (Chl-*a*) from May to September. Means of values in 1×1 longitude and latitude grids from 2002 to 2013 are shown.

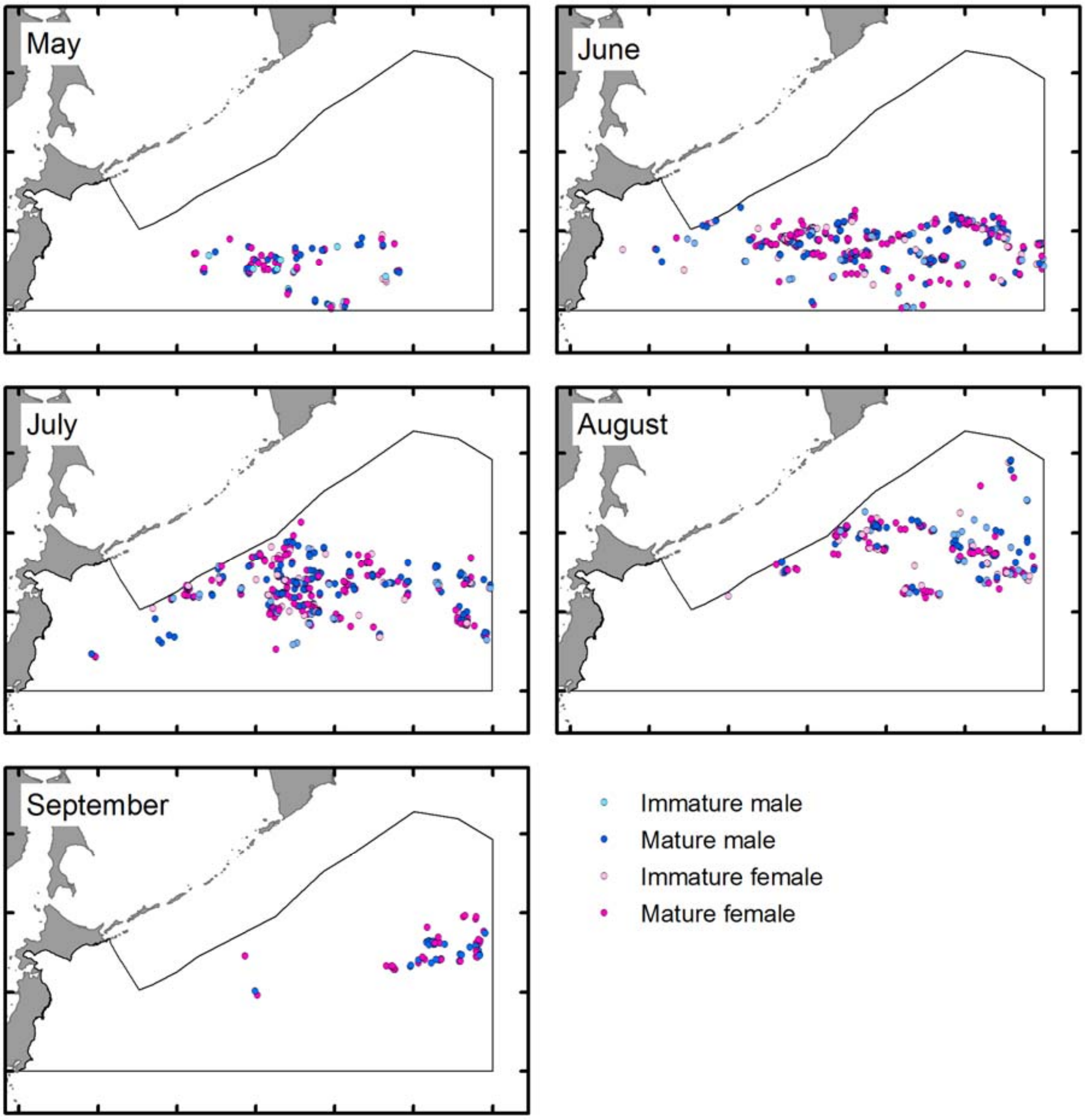

Figure 5. Maturity of sei whales from May to September. Data from 2002 to 2013 are pooled.

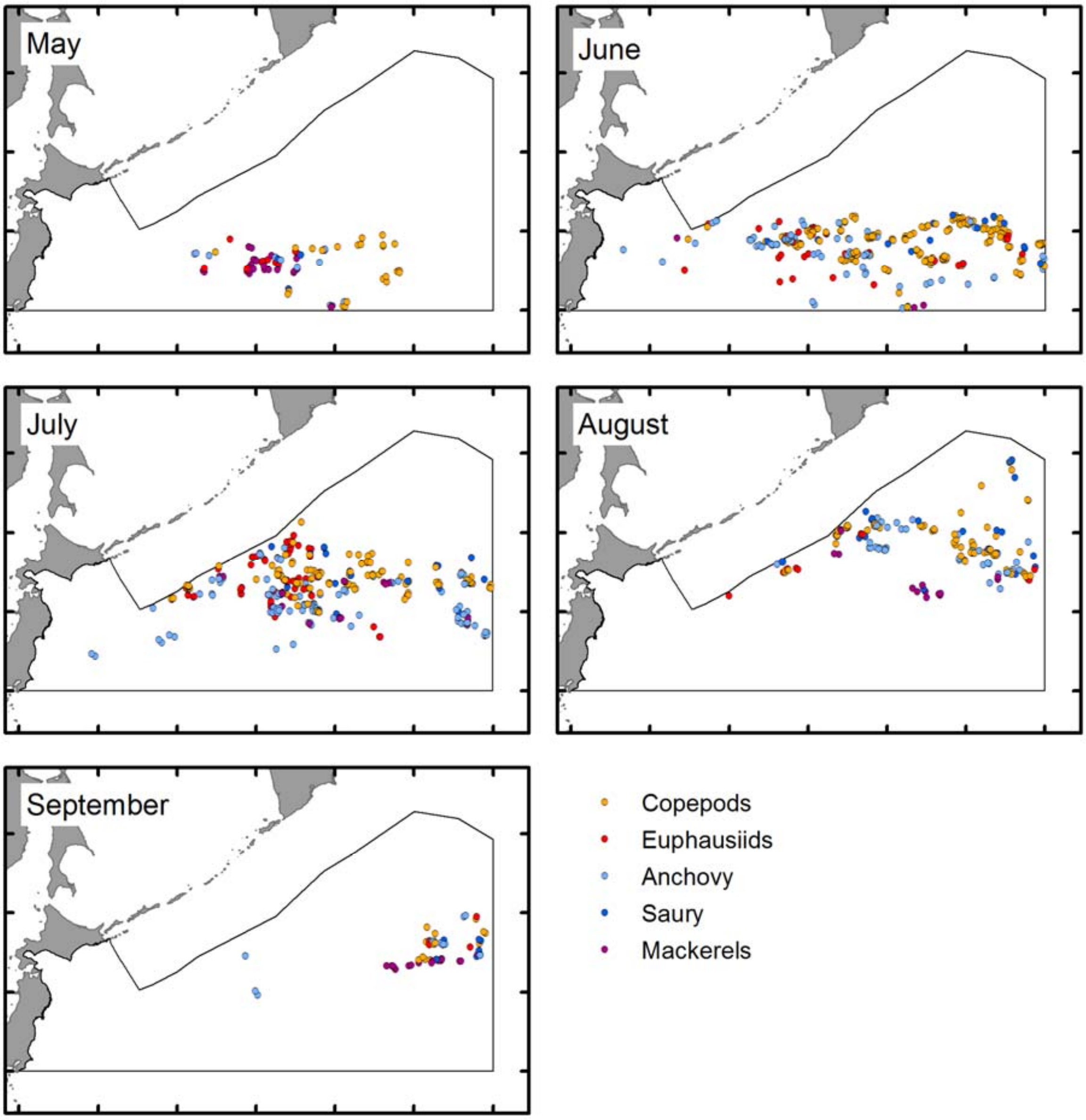

Figure 6. Prey of sei whales from May to September. Data from 2002 to 2013 are pooled

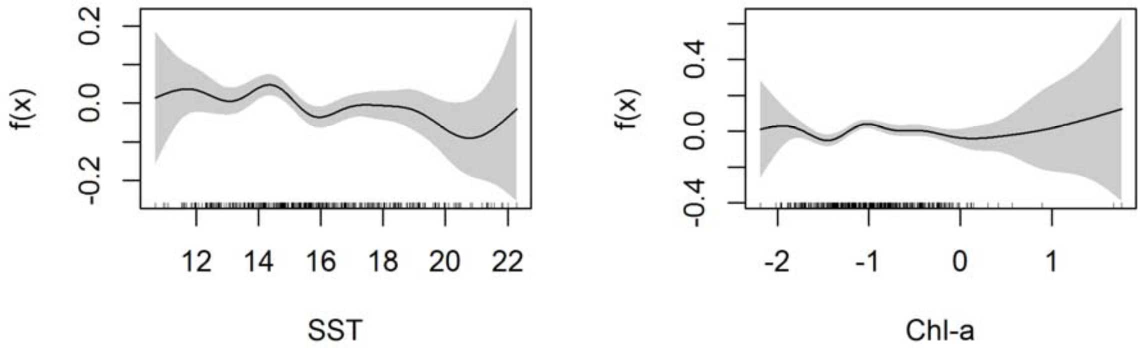

Figure 7. Smoothed fits of selected covariate modelling prey consumption of sei whales. Ticks on the x-axis are observed data points. The y-axis represents the spline function. Shaded areas indicate 95% confidence intervals

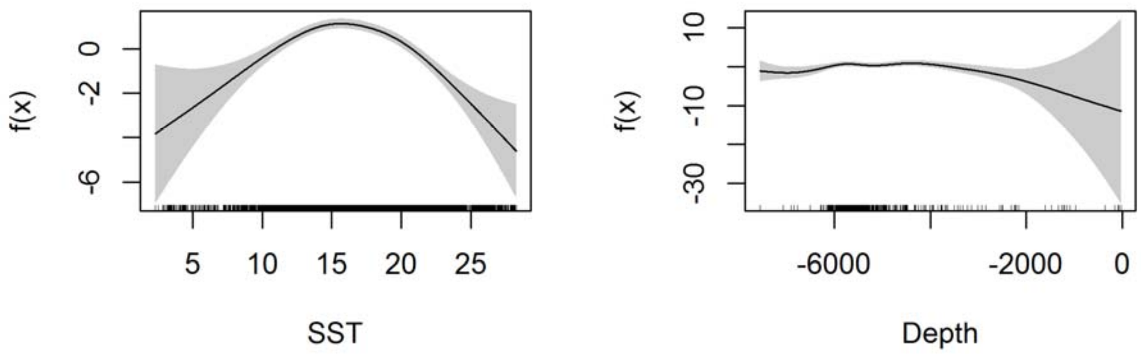

Figure 8. Smoothed fits of selected covariate modelling number of sei whale individuals. Ticks on the x-axis are observed data points. The y-axis represents the spline function. Shaded areas indicate 95% confidence intervals

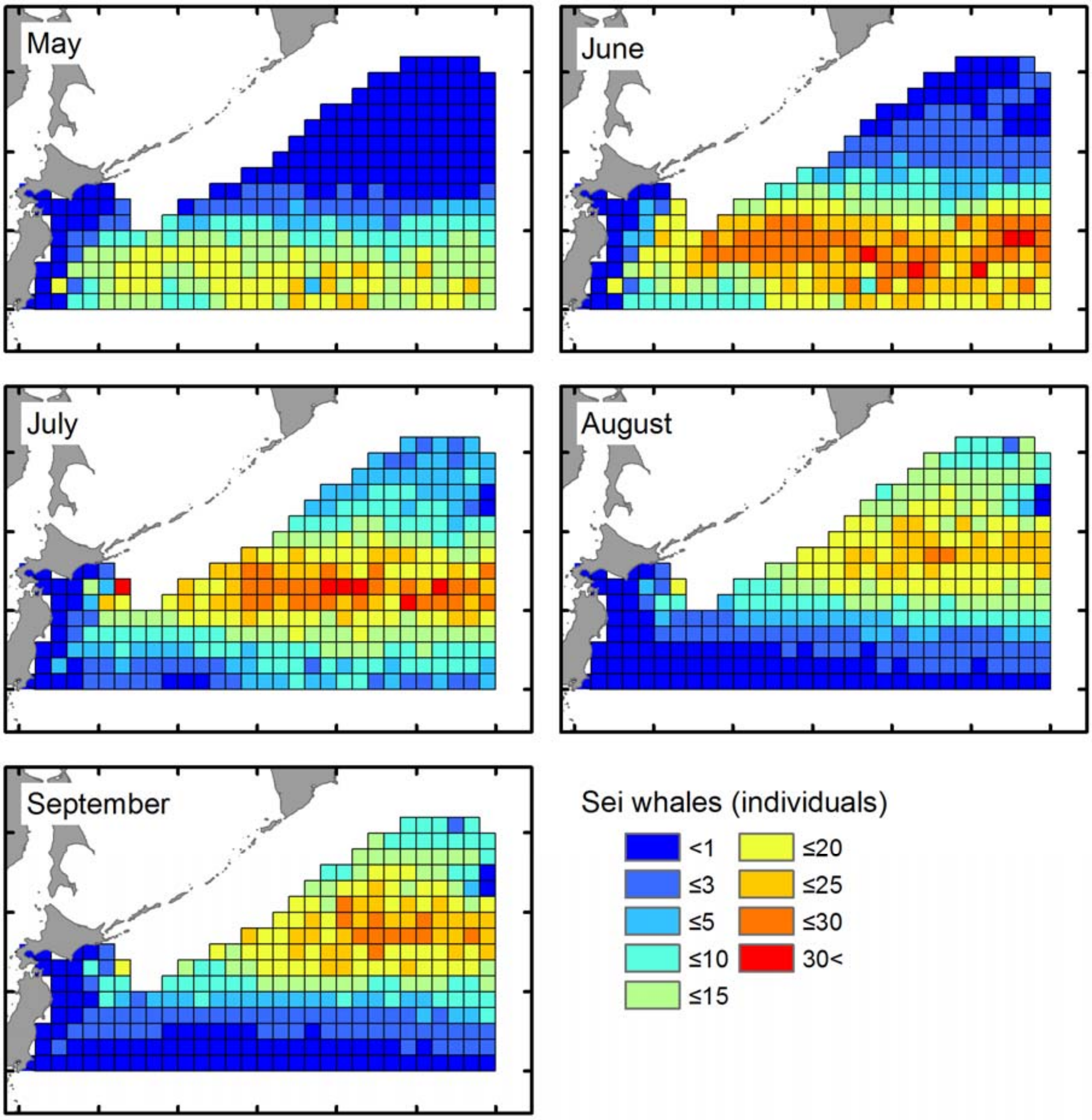

Figure 9. Estimated spatial distribution of sei whales from May to September. Means of estimated number of individuals in 1×1 longitude and latitude grids from 2002 to 2013 are shown.

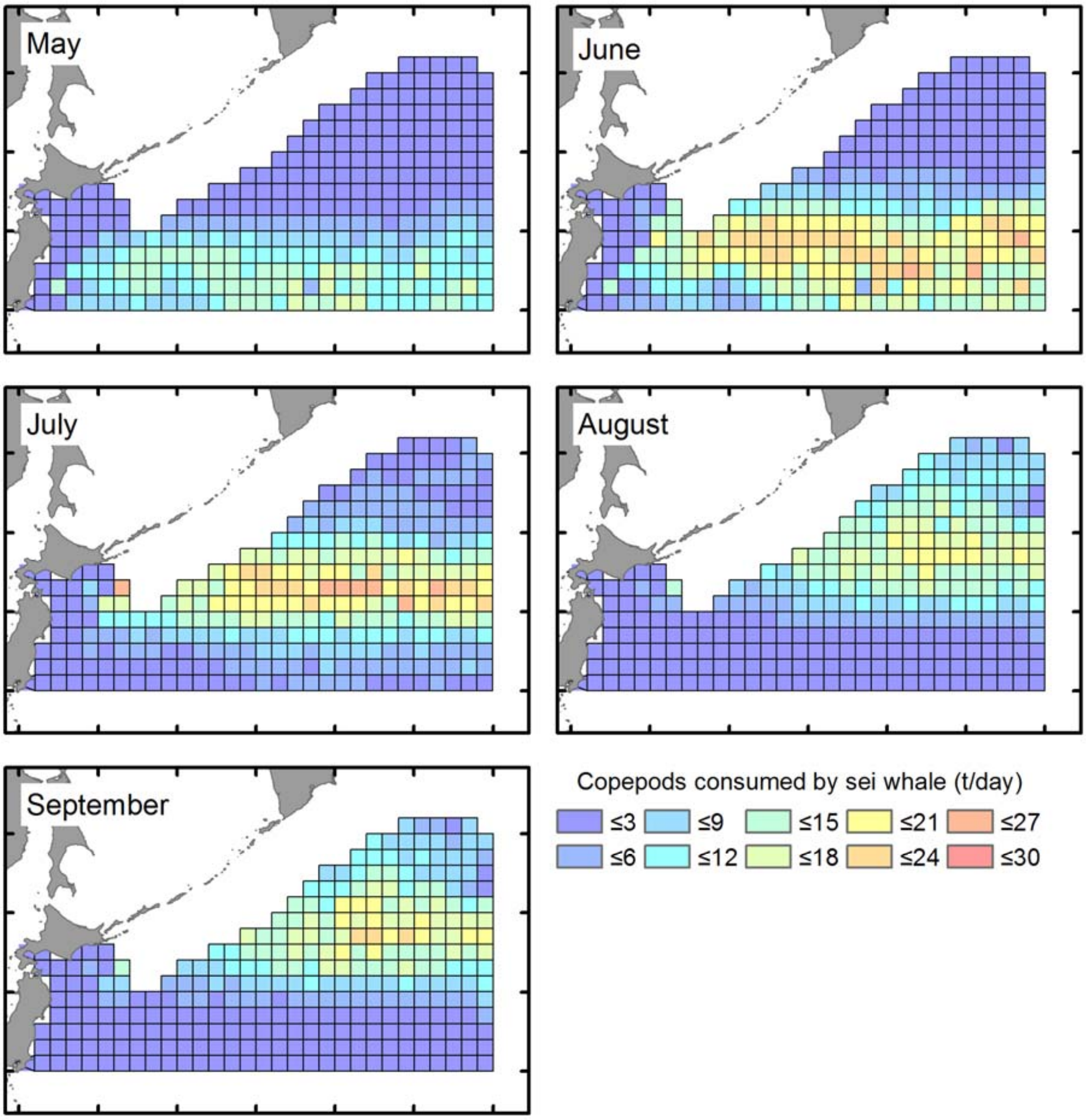

Figure 10. Spatial distribution of estimated amount of copepods consumed by sei whales (t/day) in 1×1 longitude and latitude grids from May to September. Means from 2002 to 2013 are shown.

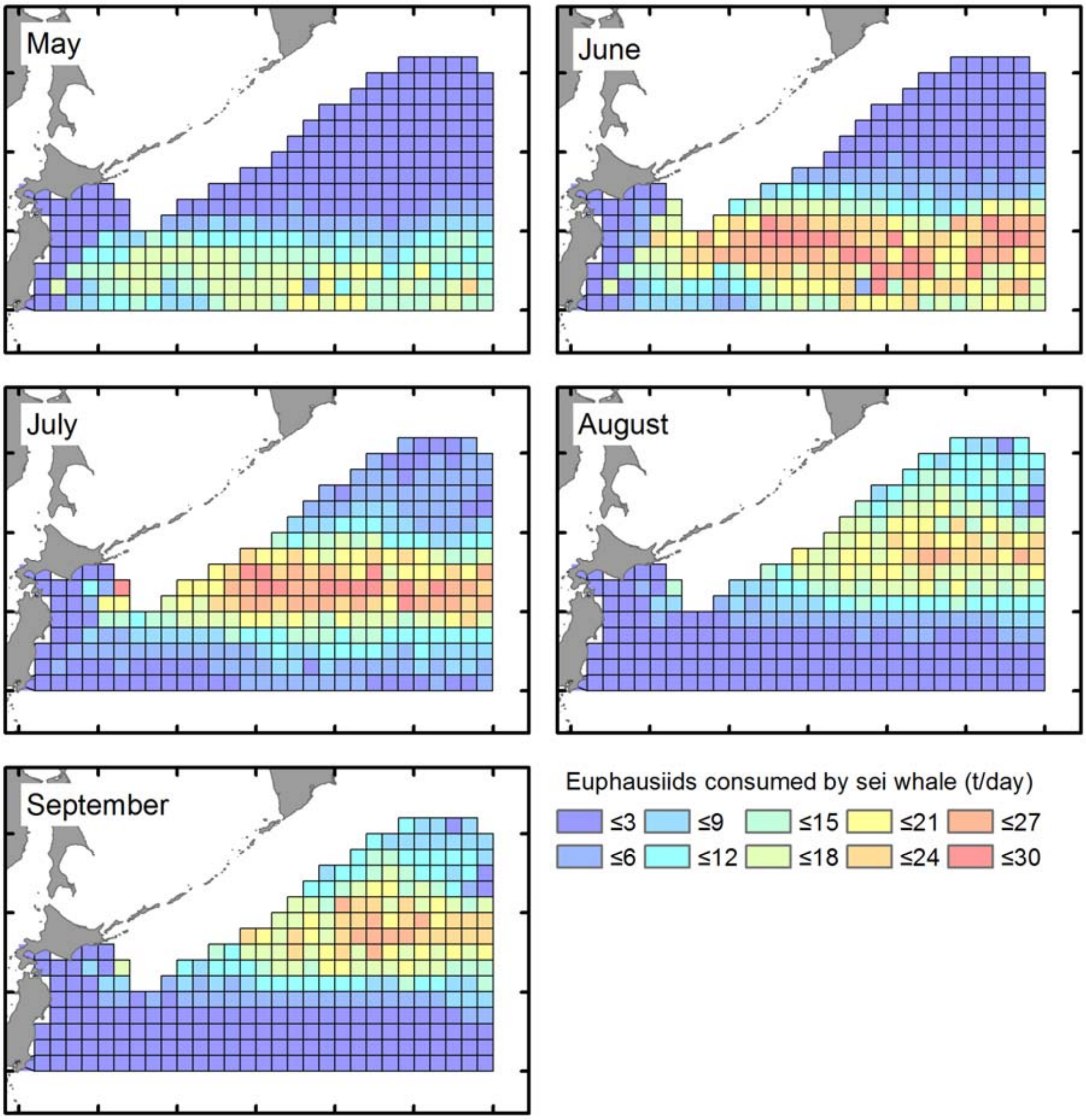

Figure 11. Spatial distribution of estimated amount of euphausiids consumed by sei whales (t/day) in 1×1 longitude and latitude grids from May to September. Means from 2002 to 2013 are shown.

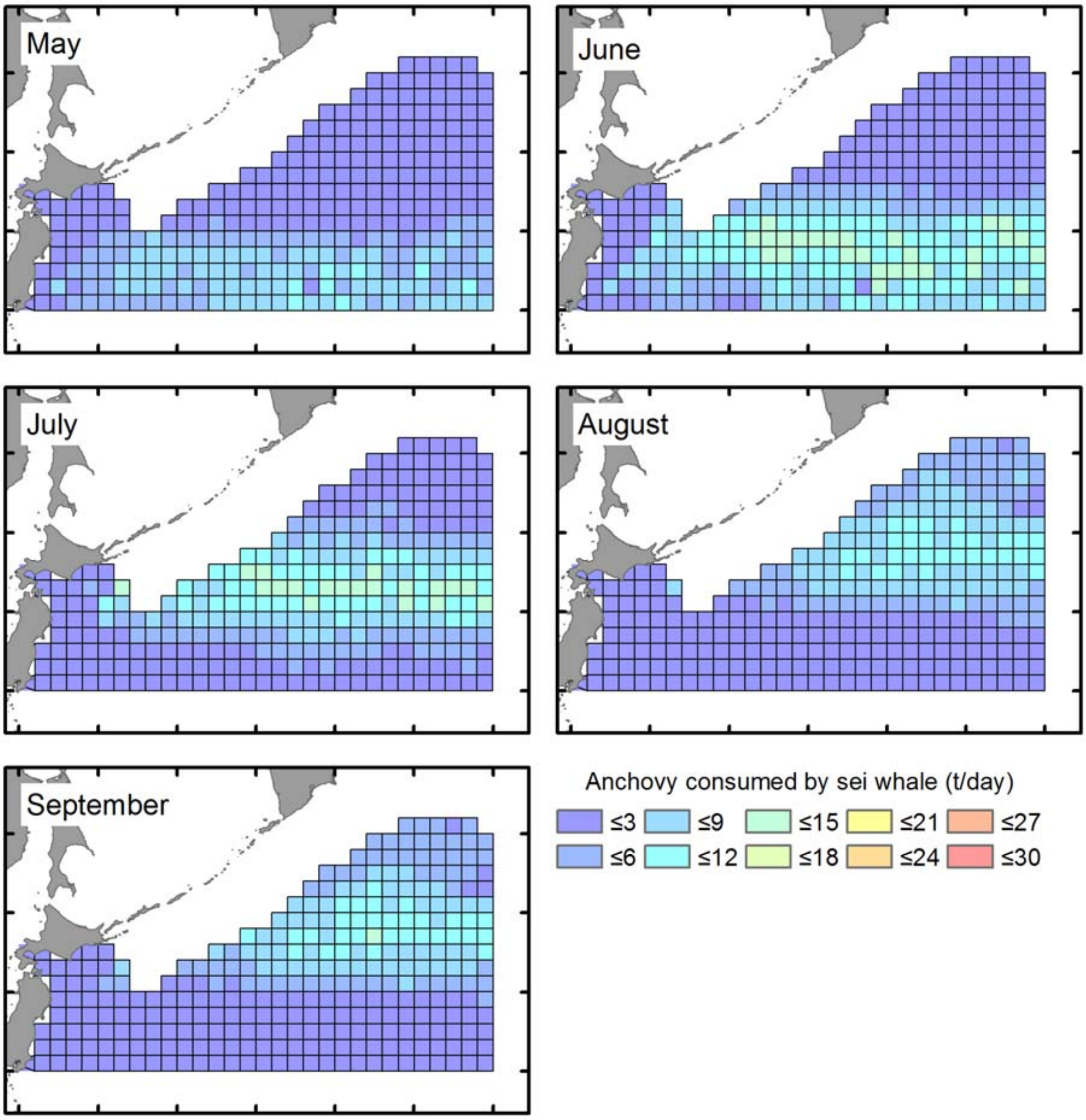

Figure 12. Spatial distribution of estimated amount of Japanese anchovy consumed by sei whales (t/day) in 1×1 longitude and latitude grids from May to September. Means from 2002 to 2013 are shown.

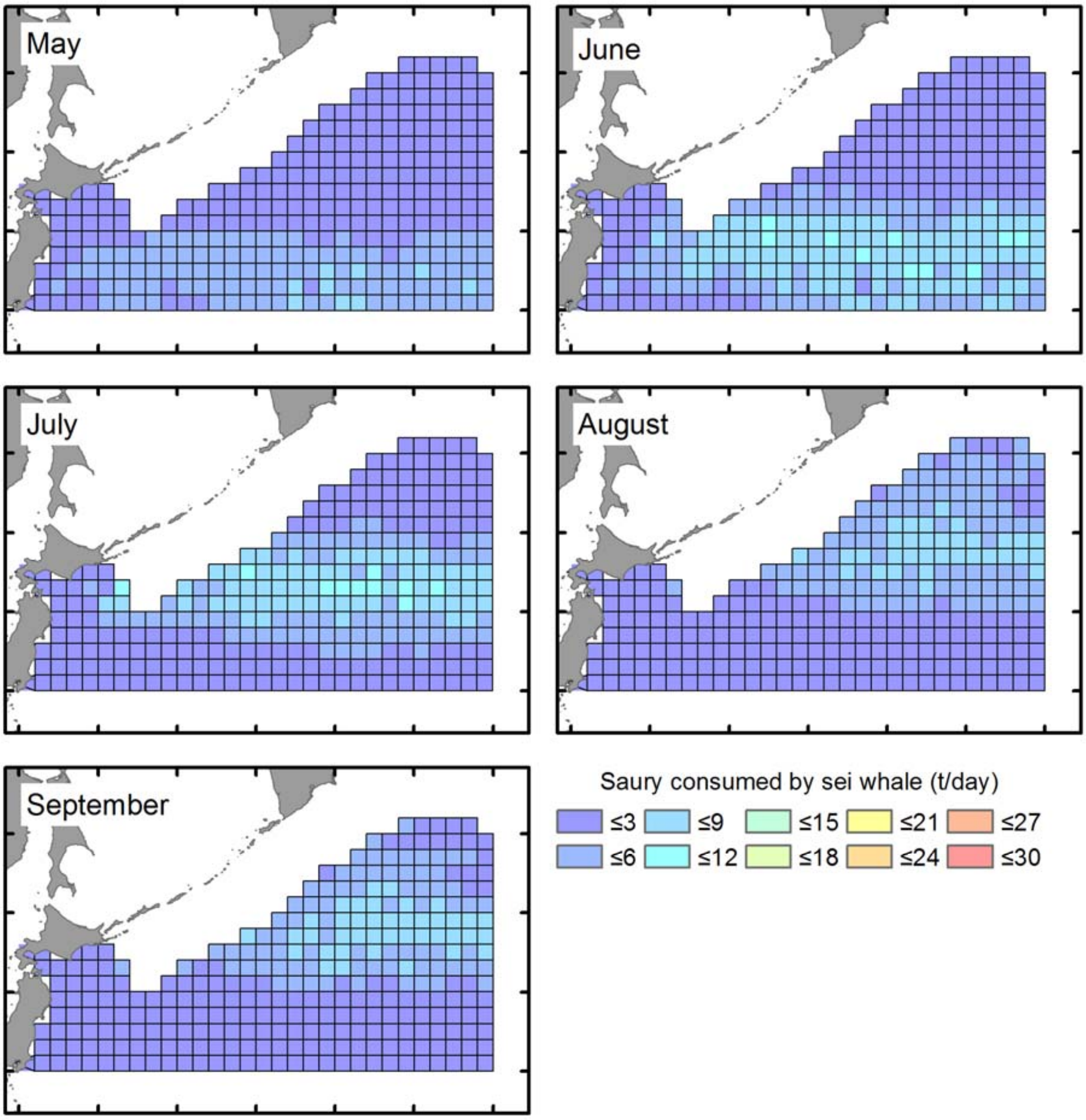

Figure 13. Spatial distribution of estimated amount of Pacific saury consumed by sei whales (t/day) in 1×1 longitude and latitude grids from May to September. Means from 2002 to 2013 are shown.

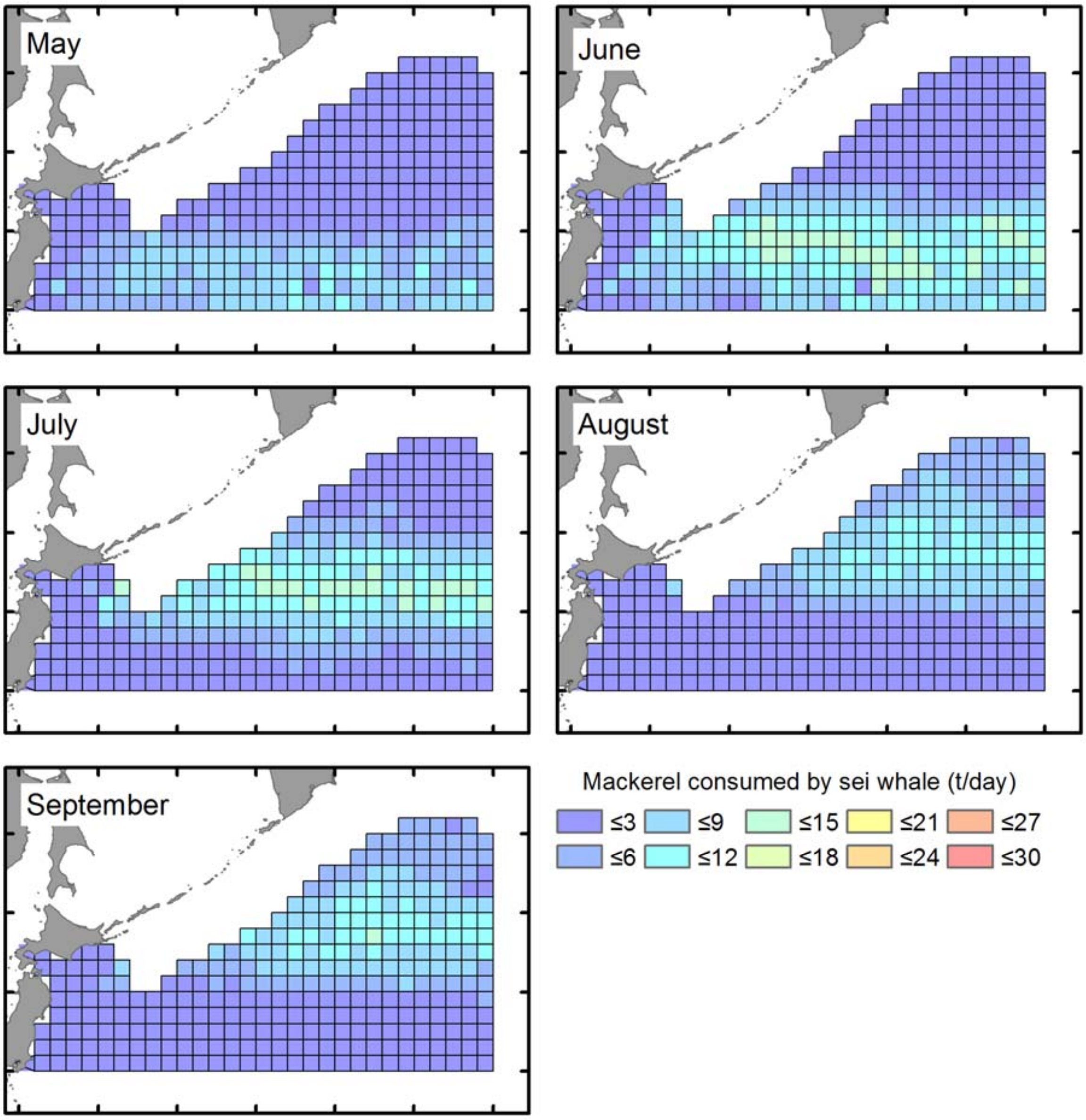

Figure 14. Spatial distribution of estimated amount of mackerels consumed by sei whales (t/day) in 1×1 longitude and latitude grids from May to September. Means from 2002 to 2013 are shown.