

SPECIAL FEATURE

Marine Ecology – learn about a tough but wonderful world

Predictions of kelp distribution shifts along the northern coast of Japan

Kenji Sudo^{1,2}  | Kentaro Watanabe¹ | Norishige Yotsukura³ | Masahiro Nakaoka¹ ¹Akkeshi Marine Station, Field Science Center for Northern Biosphere, Hokkaido University, Akkeshi, Japan²Graduate School of Environmental Science, Hokkaido University, Akkeshi, Japan³Field Science Center for Northern Biosphere, Hokkaido University, Sapporo, Japan**Correspondence**Kenji Sudo, Akkeshi Marine Station, Field Science Center for Northern Biosphere, Hokkaido University, Akkeshi, Hokkaido 088-1113, Japan.
Email: ksudo.hokudai@gmail.com**Present address**

Kentaro Watanabe, Okinawa Office, Waterfront Vitalization and Environment Research Foundation, Naha, Okinawa 902-0067, Japan

Funding information

Japan Science and Technology Agency, Grant/Award Number: Belmont Forum Collaborative Research; Ministry of the Environment, Japan, Grant/Award Numbers: S-15 Predicting and assessing natural capital and ecosystem services, S-9 Integrative observations and assessments of Asian biodiversity

Abstract

Japanese kelps are important because they perform a valuable ecosystem function of coastal kelp forest formation, and they are important food resources. The present study aimed to predict future shifts in major kelp species in northern Japan under different climate change scenarios. From a database of cold temperate kelp species in Japan, we extracted 1,958 data points to estimate the distribution of 11 kelp species that inhabit the waters around northern Japan. Distributions of the past (1980s) and the future (2040s and 2090s) were estimated using a species distribution model (MaxEnt). Variation in summer and winter sea surface temperatures was the factor most responsible for the estimated distribution patterns for most species; the length of natural rocky coasts and wave height were also important for some species. A forecast of shifts in distributions based on different Intergovernmental Panel on Climate Change scenarios showed that kelp species diversity in Japan would significantly decrease. By the 2090s, their habitat range overall was estimated to decline to 30–51% of that of the 1980s with moderate warming (Representative concentration pathways [RCP] 4.5) and to 0–25% with severe warming (RCP 8.5). The model predicted that 6 of 11 cold temperate kelp species may become extinct around Japan by the 2090s (RCP 8.5). Commercially important species, such as *Saccharina japonica*, are also expected to decline greatly, which may affect kelp fisheries and aquaculture in northern Japan.

KEYWORDS

biodiversity, Intergovernmental Panel on Climate Change (IPCC), marine macroalgae, Northwest Pacific, species distribution model

1 | INTRODUCTION

Ongoing climate change will affect the global demographics, abundance, distribution and phenology of many marine species through environmental changes, such as water temperature increases and ocean acidification (Harley et al. 2006; Orr et al. 2005; Poloczanska et al. 2016; Yara et al. 2012). Future projections suggest that changes in community composition and local species loss would occur worldwide (e.g., Beaugrand et al. 2015; García Molinos et al. 2016),

which can further affect the use of marine resources by human, such as by fisheries and aquacultures. However, our knowledge of the patterns of marine biodiversity and their future response to climate change is limited in the northwest Pacific Ocean region (Fishery agency Japan 2017; Poloczanska et al. 2016).

Kelp forests are one of the most important coastal habitats from temperate to near polar regions. They are highly productive, performing valuable ecosystem functions, such as habitat provision and acting as a food source to many marine

organisms (Bennett et al. 2016; Bertocci et al. 2015; Smale et al. 2013; Vásquez et al. 2014). Japanese kelps are also important food resources. In 2015, around 15,000 tons of kelp were harvested in Hokkaido, northern Japan, with a total yield of 22.7 billion Japanese yen (Sasaki 2017). However, kelp forests are decreasing globally at a rate of 1.5 to 18% per year due to anthropogenic-related factors, such as water temperature increases, water quality deterioration, sedimentation and land reclamation (Araújo et al. 2016; Connell et al. 2008; Krumhansl et al. 2016; Steneck et al. 2002). In Japan, the area of seaweed beds decreased greatly in the late 20th century (Environmental Agency Japan 1994, 1999; Kumagai et al. 2018). The decline of kelp species can cause community-wide impacts because it can also lead to the decline of kelp-associated animals such as fish and crustaceans (Bertocci et al. 2015; Teagle & Smale 2018). It can also cause decrease in ecosystem functions such as nutrient cycling, energy flow and coastal defense (Smale et al. 2013). Thus, understanding current status and predicting future changes in major kelp species are essential to protect marine biodiversity of kelp forest and plan sustainable use of its ecosystem services.

Water temperature increases because of climate change has been considered one of the most critical drivers of kelp forest decline. Kelps are sensitive to increases in water temperature because this phyletic group originally occurs from temperate to cold water regions (Assis et al. 2016). Decreases in kelp forests have been reported as a result of water temperature increases from various parts of the world (Filbee-Dexter et al. 2016; Johnson et al. 2011; Moy and Christie 2012), including temperate waters around Japan (Tanaka et al. 2012; Kumagai et al. 2018). Future shifts in distribution and abundance have been predicted for some kelp species in the Atlantic Ocean (Assis et al. 2016; Assis et al. 2017; Assis et al. 2018; Franco et al. 2018; Gorman et al. 2013; Raybaud et al. 2013) and offshore Japan (Kuwahara et al. 2006, Takao et al. 2015). However, information on kelp forecasts is still insufficient in northern Japan, especially for species living in cold temperate regions (i.e., 40°N and higher), where kelp harvesting is important for the fisheries industry.

Recently, studies on broad-scale marine biodiversity have been facilitated by the development of open-access global databases, such as Global Biodiversity Information Facility (GBIF; <http://www.gbif.org/>), Ocean Biogeographic Information System (OBIS; <http://www.iobis.org/>), FishBase (<http://www.fishbase.org/>) and AlgaeBase (<http://www.algaebase.org/>). Information on the distribution of marine life in Japanese waters has been collated in BISMAL (<http://www.godac.jamstec.go.jp/bismal/e/index.html>).

Using these databases, global patterns of marine biodiversity have been estimated for a variety of taxa (Tittensor et al. 2010; Kaschner et al. 2016) and future changes in species distribution have been predicted by modeling under different

climate change scenarios (Beaugrand et al. 2015, García Molinos et al. 2016). Nevertheless, data on marine species remain insufficient and still contain large geographic gaps around the northwest Pacific Ocean. Filling these information gaps is necessary to understand the current distribution patterns and to forecast changes in regional marine biodiversity.

In this study, we estimated the past distribution of cold temperate kelp species in northern Japan and predicted changes in their distribution based on different Intergovernmental Panel on Climate Change (IPCC) scenarios for future ocean climates. We first developed species distribution models (SDMs) for 11 cold temperate kelp species belonging to the order Laminariales. The models reconstructed species distribution for the 1980s because at this time water temperatures had not been increasing around northern Japan (Meteorological Agency Japan, 2017). We then examined which combination of environmental factors explained the species distribution patterns. Based on the relationships between occurrence and environmental data, we projected changes in the distribution of each species and species diversity using models of the future ocean environment (Coupled Model Intercomparison Project Phase 5 [CMIP5]; Taylor et al. 2012) based on different emission scenarios from representative concentration pathways (RCPs 4.5 and 8.5; Moss et al. 2010). We particularly addressed the question of whether the use of summer and winter temperatures affects distribution predictions differently because temperature sensitivity varies seasonally in different kelp life stages (Kamiya et al. 2006).

2 | METHODS

2.1 | Scope and species

In this study, the research area was along the coast of northern Japan between 35.7 and 45.5°N and 139.4 and 145.8°E

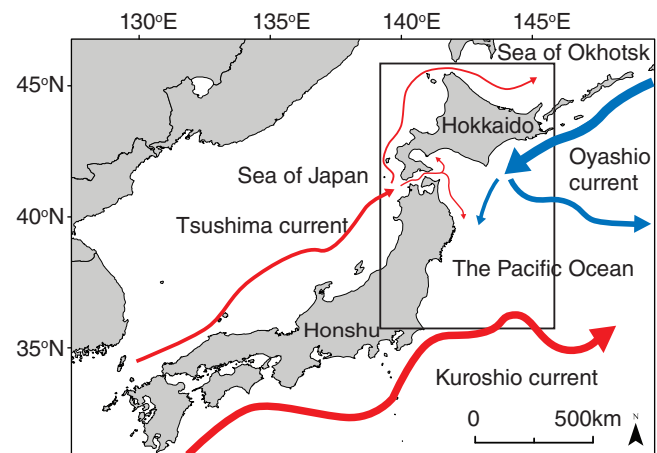


FIGURE 1 Study area (outlined in bold) and major ocean currents around Japan. The warm currents are in red and the cold currents in blue. Current data are based on Nishimura (1981)

(Figure 1). Forty-five species of Laminariales occur along the coast of Japan (Yoshida et al. 2015). We targeted 11 cold temperate species belonging to the three families that are dominant in northern Japan (Table 1). Other species that also occur in the study area were excluded from the analyses because of insufficient occurrence data to retain model accuracy (<20 data points). Among the 11 species, *Saccharina japonica* had the widest distribution, ranging from 39°N (Sea of Japan) and 37°N (Pacific coast of Honshu) to the northernmost point of Hokkaido (45°N). In contrast, *Arthrothamnus bifidus*, *Saccharina angustata*, *Saccharina cichorioides*, *Saccharina coriacea*, *Saccharina gyrata* and *Saccharina longissima* were recorded only from Hokkaido.

2.2 | Data collection

The distribution data of Laminariales in Japan contained a total of 27,189 recorded occurrences from literature, government reports and museum herbarium in the BISMAL (Nakaoka et al. 2017). In addition, national museum of nature and science specimens (<http://db.kahaku.go.jp/webmuseum/>) and data paper of seaweed in Japan (Kumagai et al. 2016) are also containing occurrences data of Laminariales. We extracted 1,958 of these data of the 11 targeted kelp species recorded between the 1950s and 1980s from these databases and the data paper (Table S1). The data were most abundant and covered the widest areas of Japan in the 1980s when a nationwide census of algal bed distribution was conducted by the Ministry of the Environment (Environment Agency Japan, 1994). Fewer data were collected in and after the 1990s because additional nationwide monitoring programs were not conducted. Water temperatures around northern Japan did not significantly

increase from 1950 to 1990 (Meteorological Agency Japan, 2017). We thus set the baseline period to examine the effect of temperature increases on kelp distribution as the 1980s and used all of the occurrence data collected between the 1950s and 1980s to retain sufficient data for species distribution ranges.

2.3 | Species distribution models

The SDMs identify the relationships between presence of a species and environmental variables. Many algorithms exist for SDMs, among which maximum entropy modeling (MaxEnt) has been most used commonly because it is robust against georeferencing errors using presence-only records (Elith et al. 2011, Graham et al. 2008, Phillips et al. 2006). It outperforms most other algorithms, such as generalized linear models, generalized additive models and random forests, and is particularly appropriate for marine species (Aguirre-Gutiérrez et al. 2013; Elith et al. 2006; Ready et al. 2010). MaxEnt also performs well in estimating potential range shifts for a species due to climate change (Hijmans and Graham 2006). Therefore, we chose to use MaxEnt in this study. All MaxEnt models were run using the default settings (version 3.3.3k; Phillips et al. 2006) and replicated 10-fold cross validation. Random test percentage for the cross validation used 20% of the data. The model accuracy was examined by the area under the curve (AUC) (Fielding and Bell 1997) for which values >0.7 are commonly accepted (Raes and ter Steege 2007; Swets 1988). Predicted logistic values of each grid were converted to presence/absence values using a threshold of 0.5; a probability lower than this threshold was classified as absence and higher probabilities classified as

TABLE 1 Kelp species analyzed in this study

Family	Scientific name	Number of data				
		1950s	1960s	1970s	1980s	Total
Alariaceae	<i>Alaria crassifolia</i>	14	143	64	77	298
Costariaceae	<i>Agarum clathratum</i>	8	40	53	24	125
	<i>Costaria costata</i>	0	24	79	131	234
Laminariaceae	<i>Arthrothamnus bifidus</i>	7	3	11	43	64
	<i>Saccharina angustata</i>	24	29	76	35	164
	<i>Saccharina cichorioides</i>	0	0	8	28	36
	<i>Saccharina coriacea</i>	5	6	6	53	70
	<i>Saccharina gyrata</i>	8	9	21	23	61
	<i>Saccharina japonica</i>	57	227	129	366	779
	<i>Saccharina longissima</i>	0	9	6	56	71
	<i>Saccharina sculpera</i>	5	4	2	45	56
Total		128	494	455	881	1958

presence. The converted model results of 11 species were summed to estimate variation in kelp species diversity.

2.4 | Environmental dataset for estimating species distribution

We created a database of five environmental variables based on large-scale modeling in the northern Atlantic Ocean (Franco et al. 2018; Gorman et al. 2013; Raybaud et al. 2013) at 5 km resolution. The variables were (a) coldest month sea surface temperature (SST), (b) warmest month SST, (c) annual mean SST, (d) mean significant wind wave height and (e) the length of natural and semi-natural rocky coasts. From these variables, we excluded the annual mean SST because of collinearity with the coldest and warmest month SST because collinearity can decrease accuracy of prediction in ecological models including SDM (Dormann et al. 2013). As a result, four environmental variables were used in the SDMs (Table 2). Data collected during the 1990s were used for the wind wave height due to difficulty of acquiring long-term measured data sets. We set the resolution of all variables to a 5 km grid by interpolation with the inverse distance weighting method (Bartier and Keller 1996).

Summer and winter SSTs correlated over the entire study area, and thus it was difficult to include both in one SDM for each species. Therefore, we constructed two SDMs for each species, (a) a combination of warmest month SST, wind wave height and rocky coast length and (b) coldest month SST, wind wave height and rocky coast length, and these are called the “summer model” and “winter model,” respectively.

2.5 | Environmental dataset for future projections

Monthly mean SSTs were obtained from a climate model, Model for Interdisciplinary Research on Climate - Earth System Model (MIROC-ESM; Watanabe et al. 2011). This model is one of the most recent climate models developed in the CMIP5 (Taylor et al. 2012) with a future emission scenario based on the RCPs (Moss et al. 2010); it was also used in the Fifth Assessment Report of the IPCC (Stocker et al.

2013). The biases between the observed and the model values were corrected by adding the anomaly of the model to the observed climatology using the method of Yara et al. (2011). We used climate change projections from the 2040s to 2090s under RCP 4.5 and 8.5 simulations (Fig. S1) to examine the effects of ocean warming on potential habitats. Sea surface temperatures during the 1980s were substituted with RCP climate scenario water temperature data for both the summer and winter models and suitability was recalculated by MaxEnt for each species.

The shift in latitudinal distribution of each kelp species was compared between the Pacific coast and Sea of Japan. The percent occurrence within each degree of latitude (e.g., 39.00 to 39.99°N) was calculated by dividing the number of grids with a species' presence probability >0.5 by the total number of grids. Even though it is influenced by a warm current, the coastal area of the Sea of Okhotsk was classified to the Pacific coast in this study for graphical presentation.

3 | RESULTS

3.1 | Species distribution and biodiversity of Laminariaceae

The predicted distribution of 11 kelp species in the 1980s varied from 30 to 320 grids in the winter model and 27 to 313 in the summer model (Table 3). *Saccharina japonica* had the widest distribution, ranging from 39 to 45°N along the Pacific Ocean coast and 42 to 45°N along the Sea of Japan (Figure 2a, S2a). *Costaria costata*, the second most abundant species, was suggested to occur in the same range as *S. japonica*; however, the distribution in the Sea of Japan was limited (Figure 2b, S2b). *Saccharina cichorioides* was also predicted to occur both in the Pacific Ocean and Sea of Japan, but only at 43°N or higher (Figure 2c, S2c). *Agarum clathratum* was estimated to occur between 42 and 44°N in the Pacific. In the Sea of Japan, presence at 45°N was predicted by the summer model, but not by the winter model (Figure 2d, S2d). Another seven species were estimated to occur only along the Pacific coast. *Alaria crassifolia* was estimated between 39 and 43°N (Figure 3a, S3a), *Systata*

TABLE 2 Environmental variables used for the species distribution models

Environmental variable	Unit	Time period	Resolution	Source
Coldest and warmest month sea surface temperature	Degree Celsius	1982–1990	25 km (0.25°)	^a
Mean significant height of wind waves	m	Jan. 1990–Dec. 1999	150 km (1.5°)	^b
Length of natural and semi-natural rocky coasts	km/grid	1984–1993	5 km	^c

^aNational Climatic Data Center (2007). GHRSSST Level 4 AVHRR_OI Global Blended Sea Surface Temperature Analysis. Ver. 1.0. PO.DAAC, CA, USA. Dataset accessed [2013-Feb-20th] at doi:10.5067/GHAAO-4BC01.

^b40 years reanalysis, Wave model, Analysis data ECMWF (European Centre for Medium-Range Weather Forecasts).

^cEnvironmental Agency (1994). The report of the coast line survey in the 4th national survey on the natural environment.

TABLE 3 Predicted number of grids for 11 cold temperate species based on different climate scenarios in the winter and summer models

Model	Family	Species	1980s	RCP4.5 2040s	RCP4.5 2090s	RCP8.5 2040s	RCP8.5 2090s
Summer	Alariaceae	<i>Alaria crassifolia</i>	117	62	57	58	0
Model	Costariaceae	<i>Agarum clathratum</i>	176	106	34	77	0
		<i>Costaria costata</i>	216	81	68	69	0
	Laminariaceae	<i>Arthrothamnus bifidus</i>	28	0	0	0	0
		<i>Saccharina angustata</i>	70	81	25	65	0
		<i>Saccharina cichorioides</i>	127	88	64	71	0
		<i>Saccharina coriacea</i>	34	0	0	0	0
		<i>Saccharina gyrata</i>	27	0	0	0	0
		<i>Saccharina japonica</i>	313	284	111	124	0
		<i>Saccarina longissima</i>	34	0	0	0	0
		<i>Saccharina sculpera</i>	47	28	2	4	0
		All species ^a	531	426	160	205	0
Winter	Alariaceae	<i>Alaria crassifolia</i>	135	132	101	122	52
Model	Costariaceae	<i>Agarum clathratum</i>	128	89	48	76	0
		<i>Costaria costata</i>	196	129	91	116	45
	Laminariaceae	<i>Arthrothamnus bifidus</i>	30	0	0	0	0
		<i>Saccharina angustata</i>	61	85	50	68	0
		<i>Saccharina cichorioides</i>	131	127	99	116	31
		<i>Saccharina coriacea</i>	32	0	0	0	0
		<i>Saccharina gyrata</i>	30	0	0	0	0
		<i>Saccharina japonica</i>	320	319	160	177	84
		<i>Saccarina longissima</i>	34	0	0	0	0
		<i>Saccharina sculpera</i>	50	40	28	36	2
		All species ^a	521	415	264	300	128

^aAll species; total number of grids in which more than one species occurred.

angustata between 42 and 43°N (Figure 3b, S3b) and *Saccharina sculpera* between 41 and 43°N (Figure 3c, S3c). The estimated distributions of *A. bifidus*, *S. coriacea*, *S. gyrata* and *S. longissima* were very limited, occurring only around 43°N of eastern Hokkaido (Figure 3d-g, S3d-g). The winter and summer models showed similar results except that the summer model predicted a higher occurrence of *A. clathratum* and *C. costata*.

The distribution of 11 kelp species were well predicted by the combination of three environmental variables with mean AUC of 0.89 in both the winter and summer models (Table 4). The SSTs explained nearly 50% to more than 70% of the SDMs for *A. clathratum*, *A. bifidus*, *S. angustata*, *S. coriacea*, *S. gyrata* and *S. longissima*. In contrast, the length of natural/semi-natural rocky coasts was the most influential factor for *C. costata* and *S. japonica*, and mean significant wind wave height was most significant for *A. crassifolia*, *S. cichorioides* and *S. sculpera*. For *S. angustata*, SST and wave height equally contributed to the estimated distribution.

The species richness of cold temperate Laminariaceae, estimated by the summation of SDMs for each species, was highest along the coast of the Pacific Ocean from 42 to 43°N. In the Sea of Japan, it was highest at 45°N (Figure 4, S4).

3.2 | Future projections

All of the species were predicted to decline in distribution by 2040s and 2090s under the two different future carbon emission scenarios (Table 3). The summer model with RCP 8.5 forecasted severe decline in which all of the 11 species disappeared from Japanese waters by the 2090s. Including all the 11 species, suitable habitats would decrease 42% (from 521 to 300 grids) and 61% (from 531 to 205) by the 2040s, and 75% (from 521 to 128) and 100% (from 531 to 0) by the 2090s in the worst case scenario (RCP 8.5) of the winter and summer models, respectively (Table 3).

For the dominant *S. japonica*, the winter model (RCP 8.5) predicted a 300 km northern shift along the coast of

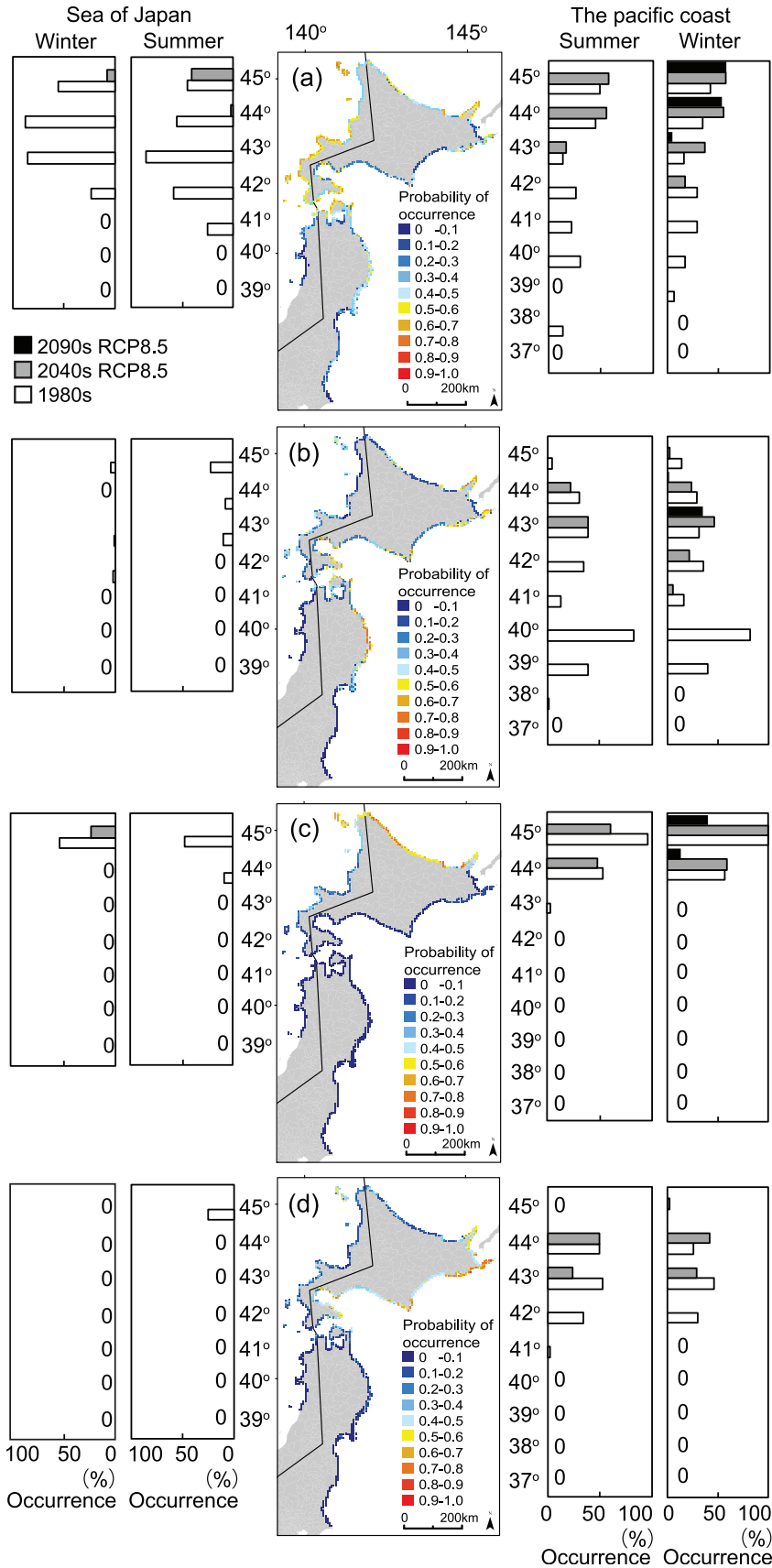


FIGURE 2 Estimated distribution of four kelp species that occur both along the Pacific coast and in the Sea of Japan. The maps show their distribution in the 1980s; the bar graphs represent occurrence (%) by latitude in the Sea of Japan (left) and the Pacific Ocean (right) in the 1980s (white column), and predicted distribution in the 2040s (gray column) and 2090s (black column) based on the RCP 8.5 scenarios. (a) *Saccharina japonica*, (b) *Costaria costata*, (c) *Saccharina cichorioides*, (d) *Agarum clathratum*

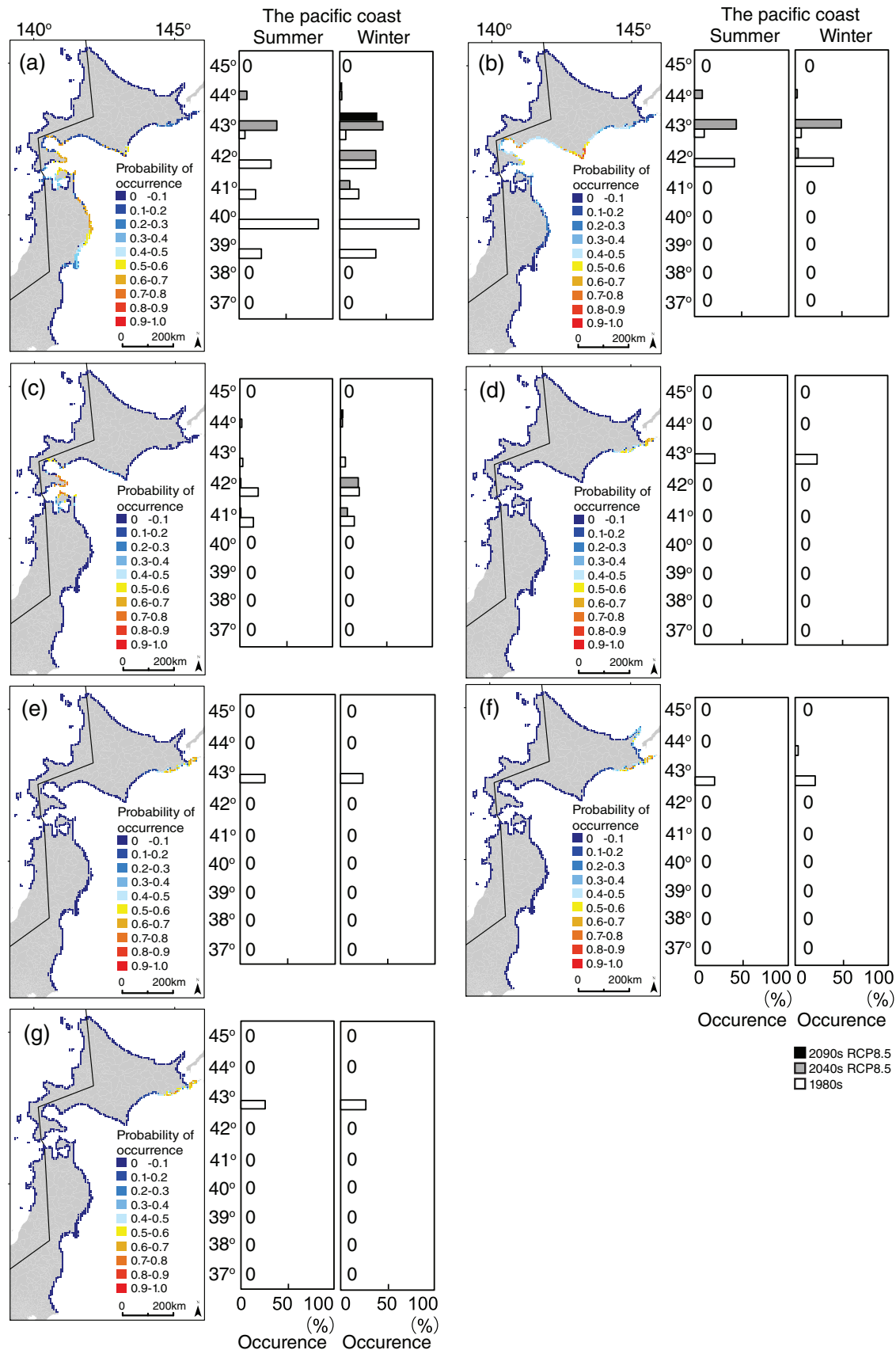


FIGURE 3 Estimated distribution of seven kelp species that were found only along the Pacific coast. The maps show their distribution in the 1980s; the bar graphs represent occurrence (%) by latitude in the 1980s (white column), and predicted distribution in the 2040s (gray column) and 2090s (black column) based on the RCP 8.5 scenarios. (a) *Alaria crassifolia*, (b) *Saccharina angustata*, (c) *Saccharina sculpera*, (d) *Arthrothamnus bifidus*, (e) *Saccharina coriacea*, (f) *Saccharina gyrata*, (g) *Saccarina longissima*

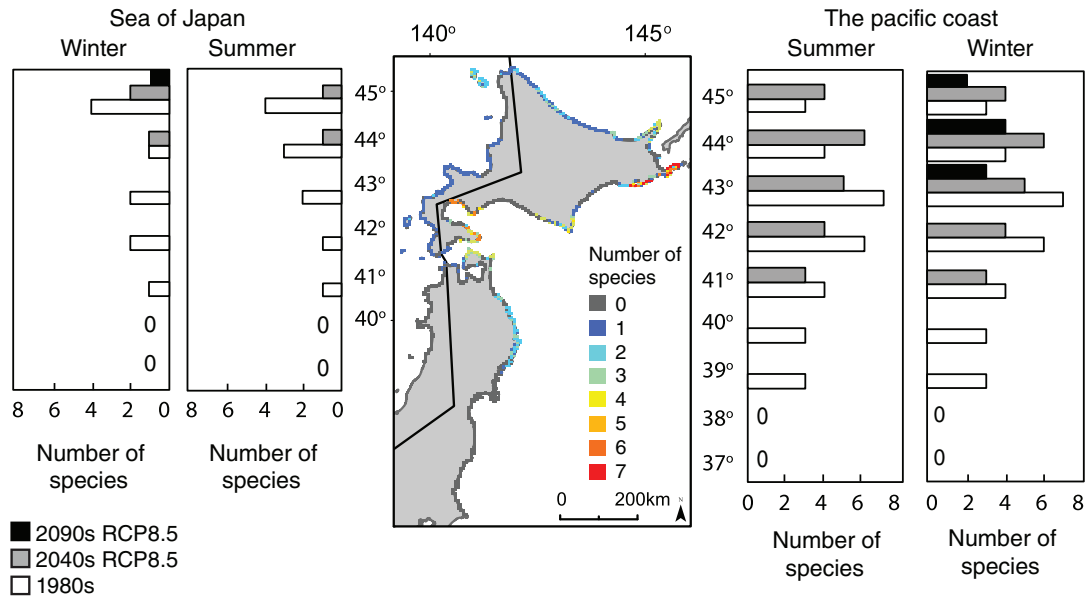


FIGURE 4 Estimated species richness of the cold temperate kelps. The maps show the species richness in the 1980s; the bar graphs represent number of species by latitude in the Sea of Japan (left) and the Pacific Ocean (right) in the 1980s (white column), and predicted richness in the 2040s (gray column) and 2090s (black column) based on the RCP 8.5 scenarios

TABLE 4 Contribution (%) of each environmental variable and AUC of the species distribution models for 11 species of Laminariaceae

Family	Species	Summer model			AUC	Winter model			AUC	
		SST	Mean significant height of wind waves	Length of natural/semi-natural rocky coasts		SST	Mean significant height of wind waves	Length of natural/semi-natural rocky coasts		
Alariaceae	<i>Alaria crassifolia</i>	30.4	38.6	31.0	0.90	25.0	42.3	32.7	0.89	
Costariaceae	<i>Agarum clathratum</i>	71.8	14.1	14.1	0.80	71.2	12.6	16.2	0.80	
	<i>Costaria costata</i>	41.4	9.7	49.0	0.78	32.8	17.2	50.0	0.78	
Laminariaceae	<i>Arthrothamnus bifidus</i>	58.0	30.7	11.3	0.97	46.5	38.3	15.3	0.97	
	<i>Saccharina angustata</i>	52.9	41.4	5.7	0.92	47.3	47.2	5.5	0.92	
	<i>Saccharina cichorioides</i>	14.4	80.8	4.8	0.87	9.2	85.4	5.4	0.85	
	<i>Saccharina coriacea</i>	57.8	32.5	9.7	0.97	48.0	38.3	13.8	0.97	
	<i>Saccharina gyrata</i>	77.1	10.2	12.7	0.97	56.4	23.6	20.0	0.97	
	<i>Saccharina japonica</i>	38.3	16.3	45.4	0.69	34.7	10.8	54.5	0.69	
	<i>Saccharina longissima</i>	58.4	33.7	8.0	0.97	49.0	39.7	11.3	0.97	
	<i>Saccharina sculpera</i>	3.4	74.5	22.1	0.94	2.0	75.5	22.5	0.95	
	Mean		45.8	34.8	19.4	0.89	38.4	39.2	22.5	0.89

Abbreviations: AUC, area under the curve; SST, sea surface temperature.

Pacific Ocean by the 2040s and 400 km by the 2090s. The summer model (RCP 8.5) predicted a 500 km shift north by the 2040s and extinction by the 2090s (Figure 2a, S2a). *Costaria costata* was predicted to also shift north along the Pacific coast, 200 km by the 2040s and 400 km by the 2090s, in the winter model with RCP 8.5; it would disappear from the Sea of Japan by the 2040s with RCP 8.5 in both models (Figure 2b, S2b). In the winter model with RCP 8.5, *S. cichorioides* maintained its distribution of the 1980s along the Pacific coast until the 2090s, but disappeared from both sides of the coast with RCP 8.5 in the summer model (Figure 2c, S2c). *Agarum clathratum* was predicted to occur between 43 and 44°N in the Pacific by the 2040s and to totally disappear from the study area by the 2090s with RCP 8.5 (Figure 2d, S2d).

Alaria crassifolia, *S. angustata* and *S. sculpera* were also predicted to shift north in both models (Figure 3a-c, S3a-c). In contrast, minor species, such as *A. bifidus*, *S. coriacea*, *S. gyrata* and *S. longissima* were predicted to go extinct by the 2040s with RCP 4.5 in both models (Figure 3d-g, S3d-g). *Saccharina coriacea* and *S. longissima* were predicted to go extinct by the 2090s even with RCP 4.5 models and by the 2040s with RCP 8.5 (Table 3).

Forecasts of kelp species richness based on the results of a species-by-species distribution model showed a sharp decline in diversity from both the winter and summer models (Figure 4, Fig. S4). The reduction of species richness was most remarkable between 39 and 43°N along the coast of the Pacific and in the whole of the Sea of Japan. The summer model predicted a more severe decline in species diversity than the winter model.

4 | DISCUSSION

This study estimated past and future distributions of kelp species in northern Japan where previous information on their distribution is scattered. The fit of the SDMs was generally high and similar to another kelp study in the Atlantic Ocean (Franco et al. 2018). The coldest and warmest month SSTs significantly contributed to the estimation for many species. This study highlighted that the distribution range and species diversity of cold water kelps in Japanese waters would greatly decrease with ongoing climate change.

4.1 | Species distribution and biodiversity of Laminariaceae

Each kelp species occurs over different latitudinal ranges, leading to gradients in species composition from temperate to polar regions (Müller et al. 2009). Water temperature is one of the key variables determining the global biogeography of many kelps (Franco et al. 2018; Khan et al. 2018;

Müller et al. 2009). For example, water temperature explains the biomass patterns of *S. japonica* in northern Japan (Kamiya et al. 2006; Kirihaara et al. 2003). In addition, ocean currents also affect the horizontal and latitudinal distribution of algal species, including kelps (Kumagai et al. 2018). It is likely that cold ocean currents affect the diversity of the cold temperate species studied here, as shown by the fact that the highest species richness in the 1980s was estimated in eastern Hokkaido where the influence of the Oyashio Current is strongest. At the same latitudes, species diversity was higher along the Pacific Ocean coast affected by the Oyashio than the Sea of Japan, which is influenced by the warm Tsushima Current.

The coldest and warmest month SSTs were selected as key environmental factors for the SDMs in our study, which agrees with previous studies on kelp distribution in the northern Atlantic Ocean (Assis et al. 2018; Franco et al. 2018). For the family Laminariaceae, found along the Atlantic coast of Europe, the coldest SSTs contributed more than 50% and the warmest SSTs 25% to the model using MaxEnt (Franco et al. 2018). The SST was also the most important factor for several kelp species in the North Atlantic when distribution was estimated with boosted regression tree models (Assis et al. 2018). In our study, however, the distribution of some species, such as *S. cichorioides* and *S. sculpera*, was not well explained by SST. These species occurred in very limited areas around Hokkaido. The spatial variation in SSTs may be too broad to predict the distribution of these endemic species.

Kelp species have evolved large and flexible thalli to endure high wave energy and current stresses (Friedland and Denny 1995). They sometimes exhibit higher diversity and abundance at sites with strong wave energy because they can avoid the feeding pressure of herbivores, such as sea urchins (Akaike et al. 2002; Kawamata 2001). Wind wave height was also important in the models for some species, but the effects varied. *Saccharina cichorioides* and *S. sculpera* occur mostly inside a breakwater or deep water with low wave energy (Gouda and Kawai 2012; Kawashima 2012; Tani et al. 2015) and, thus, wave height likely affects their distribution negatively. In contrast, *S. angustata* and *S. longissima* are found along the Pacific coast where wave disturbance is high. For these species, wave height is positively correlated with the probability of their occurrence.

As kelps generally grow on rocky substrate, the length of natural/semi-natural rocky coasts also contributed to the models of many species. The occurrence of temperate kelp species, such as *Laminaria digitata*, *Laminaria hyperborean* and *Laminaria ochroleuca*, on the northeast Atlantic coast is a result of seafloor substrate and sediment conditions (Gorman et al. 2013). In our study, rocky coast length was the most important factor for *S. japonica* and *C. costata*, two

of the most abundant species. The relative influence of habitat type is likely more important than temperature for species with wide distributions that have a broad temperature tolerance.

4.2 | Future projections

The distribution of kelps expanded and contracted with glacial and interglacial cycles because of the influence of temperature fluctuations (Assis et al. 2016). Ongoing water temperature increases with global climate change is predicted to shift kelp distribution toward higher latitudes, as revealed in this study and others (Assis et al. 2016; Assis et al. 2017; Assis et al. 2018; Franco et al. 2018; Khan et al. 2018; Müller et al. 2009; Raybaud et al. 2013; Takao et al. 2015). In fact, shifts in the global distribution of kelp species have already been observed over the last five decades (Araújo et al. 2016; Assis et al. 2013; Filbee-Dexter et al. 2016; Kumagai et al. 2018; Krumhansl et al. 2016; Wernberg et al. 2016). Additionally, habitat changes, predicted by SST-based ocean current models, are in good agreement with observed chronological changes from Japanese historical data (Kumagai et al. 2018).

Our forecast showed that kelp species found offshore northern Japan are predicted to shift northward at 40 km/decade from the 1980s to the 2090s (winter model of RCP 8.5) and >70 km/decade (summer model). Similarly, Takao et al. (2015) estimated that *Ecklonia cava*, which inhabits the temperate region of Japan south of our study site, would shift north by 45 km/decade (RCP 8.5) by the 2090s, although this model did not take seasons into account. A faster distribution shift was predicted by the summer model because water temperature increases in our study area are predicted to be much higher in summer than in winter (Fig. S1). Summer heat stress can directly cause biomass decrease in kelps in Hokkaido and can also negatively affect the discharge of zoospores in this region (Kamiya et al. 2006).

Species with limited distributions are predicted to disappear from our study area instead of shifting north. This is particularly true for *A. bifidus*, *S. coriacea*, *S. gyrata* and *S. longissima* where extinction by the 2040s was predicted even with the moderate RCP 4.5 scenario. For these species, their suitable habitats, such as lower wave energy for *S. gyrata*, and more exposed areas for *A. bifidus*, *S. coriacea* and *S. longissima*, are less available than those species with a broader distribution, such as *S. japonica*. It is thus likely that after significant climate change suitable habitats for these species would not exist at higher latitudes.

The past (1980s) distribution of kelps estimated by the winter and summer models generally agreed, whereas the future (2040s and 2090s) distributions differed between the models with a greater decline in distribution predicted by the

summer models. Previous studies have shown that both winter and summer temperatures play important roles in determining kelp abundance, growth and production by affecting different life phases (Kamiya et al. 2006, Kawai et al., 2014, Kirihara et al., 2003, 2006). Past studies on marine algae distribution shifts mostly take seasonal variation into account (e.g., Assis et al. 2018; Franco et al. 2018; Khan et al. 2018; Kumagai et al. 2018; Takao et al. 2015). Summer water temperature increases in northern latitudes was predicted to be much higher than winter (Figure S1) and thus comparisons of models using the SSTs of different seasons may lead to more accurate predictions of future changes in marine biodiversity.

4.3 | Implications for conservation and resource management

The present study demonstrated that the distribution of cold temperate kelp species in northern Japan would drastically decrease in area and all 11 species would disappear by the end of this century under the most extreme climate scenario (RCP 8.5). This result offers very important implications for the conservation of endangered kelps and resource management of commercially important kelps, such as *S. japonica*, *S. longissima* and *S. angustata*.

Species with narrow distribution ranges, such as *A. bifidus*, *S. angustata*, *S. cichorioides*, *S. coriacea*, *S. gyrata*, *S. longissimi* and *S. sculpera* were predicted to drastically decrease and face the risk of local extinction from northern Japanese waters. Among them, *S. cichorioides* occurs in only the northern part of Hokkaido and its status is near threatened (Ministry of the Environment Japan 2018). This species was predicted to disappear from Japan by the 2090s (summer models with RCP 8.5). As other habitats outside of Japan are unknown for this species, the implication of this finding could be extinction. In this study, we excluded other endangered species, such as *Saccharina longipedalis*, *Saccharina yendoana* and *Saccharina kurilensis* because there was insufficient data for the models, but these species would also face a high risk of extinction. In our models, we did not include nearby colder climate regions, such as the eastern coast of the Kamchatka Peninsula (Russia), which could be a potential refuge for the species studied here. A future study should include information on these regions to examine the species-specific risk of extinction for the cold temperate kelp species.

Economically important species, such as *S. japonica*, would also decline greatly with ongoing climate change because SSTs have a large influence on the species distribution, according to the models. Additional kelp species adapted to higher temperatures could shift northward and become dominant in our study area (Takao et al. 2015). For

example, *Undaria pinnatifida*, is another commercially important species adapted to a wide range of water temperatures and currently is found from 31 to 45°N in Japan. The depth range preference of *U. pinnatifida* is similar to *S. japonica* and other species (Epstein & Smale 2017). Thus, economically important species, such as *S. japonica*, could be replaced with others, such as *U. pinnatifida*, in northern Japan, which has already been observed in northern Honshu (Kirihara et al. 2006). Furthermore, northern shift and increasing of grazing pressure from dominant sea urchin of *Strongylocentrotus nudus* also becomes important driver of local disappearance for the cold temperate species (Fishery agency Japan 2017; Kawai and Yotsukura 2018). Further studies incorporating the effects of species interaction among plants and between plants and animals on the changes in the distribution and abundance of algal community would be necessary to elucidate the community-wide impact of climate changes in kelp forest (Bertocci et al. 2015 Seeley & Schlesinger 2012; Smale et al. 2013).

Finally, our SDMs can be utilized to find suitable sites for the reintroduction of endangered species and aquaculture of commercially important species. For example, our models predict Rebun and Rishiri Islands in the northern part of Hokkaido would be suitable habitats for *S. cichorioides*, which have not been recorded in this region (Figure 2c). In fact, the Hokkaido Fisheries Experiment Station has carried out aquaculture tests of *S. cichorioides* around these islands and produced some successful yield (Gouda and Kawai 2011; Nabata et al. 2003). For the conservation of endangered species, conducting field surveys in areas where previous records are absent is worthwhile to accumulate more precise knowledge on the status of cold temperate kelp species.

5 | CONCLUSIONS

Our integrated analysis of 11 cold temperate kelp species in the coastal areas of northern Japan revealed that species diversity was highest around southern and eastern Hokkaido along the Pacific Ocean coast. Diversity was influenced by the cold ocean current and strong wave exposure to the rocky substrate. Forecasts based on models using winter and summer SST changes predicted a rapid northward shift of major species, similar to what has been predicted for kelps in the Atlantic Ocean and other marine organisms. As a result, species diversity would greatly decline by the end of the 21st century even in the modest IPCC scenarios. Some kelp species have high economic value and are important ingredients in traditional Japanese cuisine. In addition, kelp provides habitats and food to various marine animals, including economically important species such as sea urchin and abalone. Thus, the declines in kelp species predicted in


this study would greatly affect marine biodiversity and coastal ecosystem dynamics, as well as coastal fisheries and the economy and culture of Japan. The findings of the present study could be used to help plan management options for fisheries and other coastal ecosystem services that are rapidly changing with ongoing climate change.

ACKNOWLEDGMENTS

We thank Ms. Ayako Ohira, Ms. Kiko Unjo, Ms. Marina Hashimoto, Ms. Mie Kawamura and Ms. Natsumi Hayashi for their assistance in database construction. We are grateful to Dr. Yumiko Yara (JAMSTEC) for preparing sea surface temperature data for future projection, and to Dr. Naoki H. Kumagai (NIES) for the valuable comments on the manuscript. We thank Kara Bogus, PhD, from Edanz Group (www.edanzediting.com/ac) for editing a draft of this manuscript. We also thank the three reviewers for their comments which help to improve the manuscript. This study was supported by the Environment Research and Technology Development Funds (S-9: Integrated study on monitoring, evaluation and prediction of biodiversity at Asia, and S-15: Predicting and assessing natural capital and ecosystem services) of the Ministry of the Environment, Japan, and by the Belmont Forum Collaborative Research Action on Scenarios of Biodiversity and Ecosystem Services (TSUNAGARI) by JST.

ORCID

Kenji Sudo  <https://orcid.org/0000-0001-5392-0976>

Masahiro Nakaoka  <https://orcid.org/0000-0002-5722-3585>

REFERENCES

- Aguirre-Gutiérrez, J., Carvalheiro, L. G., Polce, C., van Loon, E. E., Raes, N., Reemer, M., & Biesmeijer, J. C. (2013). Fit-for-purpose: Species distribution model performance depends on evaluation criteria—Dutch hoverflies as a case study. *PLoS One*, 8(5), e63708. <https://doi.org/10.1371/journal.pone.0063708>
- Akaike, S., Tsuda, F., & Kuwahara, H. (2002). Formation and maintenance of the natural *Laminaria* bed on the coast of Iwanai, Hokkaido, Japan. *Scientific Reports of Hokkaido Fisheries Experimental Station*, 63, 41–54. (In Japanese).
- Assis, J., Coelho, N. C., Alberto, F., Valero, M., Raimondi, P., Reed, D., & Serrão, E. A. (2013). High and distinct range-edge genetic diversity despite local bottlenecks. *PLoS One*, 8(7), e68646. <https://doi.org/10.1371/journal.pone.0068646>
- Assis, J., Lucas, A. V., Bárbara, I., & Serrão, E. A. (2016). Future climate change is predicted to shift long-term persistence zones in the cold-temperate kelp *Laminaria hyperborea*. *Marine Environmental Research*, 113, 174–182. <https://doi.org/10.1016/j.marenvres.2015.11.005>
- Assis, J., Bercibar, E., Claro, B., Alberto, F., Reed, D., Raimondi, P., & Serrão, E. A. (2017). Major shifts at the range

- edge of marine forests: The combined effects of climate changes and limited dispersal. *Scientific Reports*, 7, 44348. <https://doi.org/10.1038/srep44348>
- Assis, J., Araújo, M. B., & Serrão, E. A. (2018). Projected climate changes threaten ancient refugia of kelp forests in the North Atlantic. *Global Change Biology*, 24(1), e55–e66. <https://doi.org/10.1111/gcb.13818>
- Araújo, R. M., Assis, J., Aguillar, R., Airoldi, L., Bárbara, I., Bartsch, I., ... Sousa-Pinto, I. (2016). Status, trends and drivers of kelp forests in Europe: An expert assessment. *Biodiversity and Conservation*, 25(7), 1319–1348. <https://doi.org/10.1007/s10531-016-1141-7>
- Bartier, P. M., & Keller, C. P. (1996). Multivariate interpolation to incorporate thematic surface data using inverse distance weighting (IDW). *Computers & Geosciences*, 22(7), 795–799.
- Beaugrand, G., Edwards, M., Raybaud, V., Goberville, E., & Kirby, R. R. (2015). Future vulnerability of marine biodiversity compared with contemporary and past changes. *Nature Climate Change*, 5(7), 695–701. <https://doi.org/10.1038/nclimate2650>
- Bennett, S., Wernberg, T., Connell, S. D., Hobday, A. J., Johnson, C. R., & Poloczanska, E. S. (2016). The 'Great Southern Reef': Social, ecological and economic value of Australia's neglected kelp forests. *Marine and Freshwater Research*, 67(1), 47–56. <https://doi.org/10.1071/MF15232>
- Bertocci, I., Araújo, R., Oliveira, P., & Sousa-Pinto, I. (2015). Potential effects of kelp species on local fisheries. *Journal of Applied Ecology*, 52(5), 1216–1226. <https://doi.org/10.1111/1365-2664.12483>
- Connell, S. D., Russell, B. D., Turner, D. J., Shepherd, S. A., Kildea, T., Miller, D., ... Cheshire, A. (2008). Recovering a lost baseline: Missing kelp forests from a metropolitan coast. *Marine Ecology Progress Series*, 360, 63–72. <https://doi.org/10.3354/meps07526>
- Dormann, C. F., Elith, J., Bacher, S., Buchmann predictive, C., Carl, G., Carré, G., ... Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, 36(1), 27–46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>
- Elith, J., Graham, C. H., Anderson, R. P., Dudík, M., Ferrier, S., Guisan, A., ... Zimmermann, N. E. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29(2), 129–151. <https://doi.org/10.1111/j.2006.0906-7590.04596.x>
- Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E., & Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, 17(1), 43–57. <https://doi.org/10.1111/j.1472-4642.2010.00725.x>
- Environment Agency Japan. (1994). Report of the marine biotic environment survey in the 4th National Survey on the natural environment. Vol. 2 Algal and sea-grass beds. (In Japanese).
- Environment Agency Japan. (1999). Report of the survey on Important Coastal Zone Organisms in the 5th National Survey on the Natural Environment. (In Japanese).
- Epstein, G., & Smale, D. A. (2017). *Undaria pinnatifida*: A case study to highlight challenges in marine invasion ecology and management. *Ecology and Evolution*, 7(20), 8624–8642. <https://doi.org/10.1002/ece3.3430>
- Fielding, A. H., & Bell, J. F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, 24(1), 38–49. <https://doi.org/10.1017/S0376892997000088>
- Filbee-Dexter, K., Feehan, C. J., & Scheibling, R. E. (2016). Large-scale degradation of a kelp ecosystem in an ocean warming hotspot. *Marine Ecology Progress Series*, 543, 141–152. <https://doi.org/10.3354/meps11554>
- Franco, J. N., Tuya, F., Bertocci, I., Rodríguez, L., Martínez, B., Sousa-Pinto, I., & Arenas, F. (2018). The 'golden kelp' *Laminaria ochroleuca* under global change: Integrating multiple eco-physiological responses with species distribution models. *Journal of Ecology*, 106(1), 47–58. <https://doi.org/10.1111/1365-2745.12810>
- Fishery agency Japan. (2017). Guidelines on fishing ground improvement measures corresponding to climate change. PP112. (In Japanese). Retrieved from http://www.jfa.maff.go.jp/j/gyoko_gyozyo/g_hourei/attach/pdf/index-42.pdf.
- Friedland, M. T., & Denny, M. W. (1995). Surviving hydrodynamic forces in a wave-swept environment: Consequences of morphology in the feather boa kelp, *Egregia menziesii* (Turner). *Journal of Experimental Marine Biology and Ecology*, 190(1), 109–133. [https://doi.org/10.1016/0022-0981\(95\)00038-S](https://doi.org/10.1016/0022-0981(95)00038-S)
- García Molinos, J., Halpern, B. S., Schoeman, D. S., Brown, C. J., Kiessling, W., Moore, P. J., ... Burrows, M. T. (2016). Climate velocity and the future global redistribution of marine biodiversity. *Nature Climate Change*, 6(1), 83–88. <https://doi.org/10.1038/nclimate2769>
- Gouda, H., & Kawai, T. (2011). Aquaculture technology development experiment of *Saccharina cichorioides*. Annual report of 2010 Fiscal year. Wakkanai Fisheries research institute Hokkaido research organization. (In Japanese).
- Gouda, H., & Kawai, T. (2012). Growth and maturation of *Saccharina cichorioides* Miyabe on the coast of soya, northern Hokkaido, Japan. *Algal Resources*, 5, 53–60.
- Gorman, D., Bajjouk, T., Populus, J., Vasquez, M., & Ehrhold, A. (2013). Modeling kelp forest distribution and biomass along temperate rocky coastlines. *Marine Biology*, 160(2), 309–325. <https://doi.org/10.1007/s00227-012-2089-0>
- Graham, C. H., Elith, J., Hijmans, R. J., Guisan, A., Townsend Peterson, A., Loisele, B. A., ... Zimmermann, N. (2008). The influence of spatial errors in species occurrence data used in distribution models. *Journal of Applied Ecology*, 45(1), 239–247. <https://doi.org/10.1111/j.1365-2664.2007.01408.x>
- Harley, C. D. G., Hughes, A. R., Hultgren, K. M., Miner, B. G., Sorte, C. J. B., Thornber, C. S., ... Williams, S. L. (2006). The impacts of climate change in coastal marine systems. *Ecology Letters*, 9(2), 228–241. <https://doi.org/10.1111/j.1461-0248.2005.00871.x>
- Hijmans, R. J., & Graham, C. H. (2006). The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology*, 12(12), 2272–2281. <https://doi.org/10.1111/j.1365-2486.2006.01256.x>
- Johnson, C. R., Banks, S. C., Barrett, N. S., Cazassus, F., Dunstan, P. K., Edgar, G. J., ... Taw, N. (2011). Climate change cascades: Shifts in oceanography, species ranges and subtidal marine community dynamics in eastern Tasmania. *Journal of Experimental Marine Biology and Ecology*, 400(1–2), 17–32. <https://doi.org/10.1016/j.jembe.2011.02.032>
- Kamiya, T., Wada, A., & Hasegawa, K. (2006). Relationships between habitats, production of kelp *Laminaria japonica* and two factors (water temperature and substratum). *Proceedings of Hydraulic Engineering*, 50, 1477–1482. (In Japanese).

- Kawamata, S. (2001). Effect of waves on grazing by sea urchins and abalone on the coast of northern Japan. *Bulletin of Fisheries Research Agency*, 1, 59–107. (In Japanese).
- Kawashima, S. (2012). *Morphology and taxonomy of the laminariaceous algae in cold water area of Japan*. Tokyo, Japan: Seibutsu kenkyusha. (in Japanese).
- Kaschner, K., Kesner-Reyes, K., Garilao, C., Rius-Barile, J., Rees, T., & Froese, R. (2016). AquaMaps: Predicted range maps for aquatic species. World wide web electronic. Publication. Retrieved from <https://www.aquamaps.org/>.
- Kawai, T., & Yotsukura, N. (2018). Recent study on saccharinan kelp in northern Japan. *Aquabiology*, 236, 40(3), 286–291. (in Japanese).
- Kawai, T., Galanin, D., Tskhay, Z., Latokovskaya, E., Nagai, N., & Yotsukura, N. (2014). Relationship between occurrence of kelp species and water temperature in northern Hokkaido, Japan, and southern Sakhalin, Russia. *Algal Resources*, 7, 107–116.
- Khan, A. H., Levac, E., Van Guelphen, L., Pohle, G., & Chmura, G. L. (2018). The effect of global climate change on the future distribution of economically important macroalgae (seaweeds) in the north-west Atlantic. *Facets*, 3(1), 275–286. <https://doi.org/10.1139/facets-2017-0091>
- Kirihara, S., Nakamura, S., & Notoya, M. (2003). Effect of water temperature on the growth of *Laminaria japonica* (Laminariales, Phaeophyceae) at the Coast of Shiriyazaki, Shimokita Peninsula, Japan. *Aquaculture Science*, 51(3), 273–280. <https://doi.org/10.11233/aquaculturesci1953.51.273>
- Kirihara, S., Nakamura, T., Kon, N., Fujita, D., & Notoya, M. (2006). Recent fluctuations in distribution and biomass of cold and warm temperature species of Laminariales algae at Cape Ohma, northern Honshu, Japan. *Journal of Applied Phycology*, 18(3–5), 521–527. <https://doi.org/10.1007/s10811-006-9057-3>
- Krumhansl, K. A., Okamoto, D. K., Rassweiler, A., Novak, M., Bolton, J. J., Cavanaugh, K. C., ... Byrnes, J. E. K. (2016). Global patterns of kelp forest change over the past half-century. *Proceedings of the National Academy of Sciences*, 113(48), 13785–13790. <https://doi.org/10.1073/pnas.1606102113>
- Kumagai, N. H., Yamano, H., Fujii, M., & Yamanaka, Y. (2016). Habitat-forming seaweeds in Japan (fucoids and temperate kelps). *Ecological Research*, 31(6), 759–759. <https://doi.org/10.1007/s11284-016-1404-5>
- Kumagai, N. H., García Molinos, J., Yamano, H., Takao, S., Fujii, M., & Yamanaka, Y. (2018). Ocean currents and herbivory drive macroalgae-to-coral community shift under climate warming. *Proceedings of the National Academy of Sciences of the United States of America*, 115(36), 8990–8995. <https://doi.org/10.1073/pnas.1716826115>
- Kuwahara, H., Aketa, S., Kobayashi, S., Takeshita, A., Yamashita, Y., & Kido, K. (2006). Estimation of geographical changes in target species of fisheries in Japan by global warming. *Global Environment*, 11, 49–57. (in Japanese).
- Meteorological Agency Japan. (2017). Climate change monitoring report 2017. pp. 87.
- Ministry of the Environment Japan. (2018). Ministry of the Environment red list 2018. Retrieved from <https://www.env.go.jp/press/105504.html>.
- Moss, R. H., Edmonds, J. A., Hibbard, K. A., Manning, M. R., Rose, S. K., Van Vuuren, D. P., ... Wilbanks, T. J. (2010). The next generation of scenarios for climate change research and assessment. *Nature*, 463(7282), 747–756. <https://doi.org/10.1038/nature08823>
- Moy, F. E., & Christie, H. (2012). Large-scale shift from sugar kelp (*Saccharina latissima*) to ephemeral algae along the south and west coast of Norway. *Marine Biology Research*, 8(4), 309–321. <https://doi.org/10.1080/17451000.2011.637561>
- Müller, R., Laepple, T., Bartsch, I., & Wiencke, C. (2009). Impact of oceanic warming on the distribution of seaweeds in polar and cold-temperate waters. *Botanica Marina*, 52(6), 617–638. <https://doi.org/10.1515/BOT.2009.080>
- Nabata, S., Takiya, A., & Tada, M. (2003). On the decreased production of natural kelp, *Laminaria ochotensis* in Rishiri Island, northern Hokkaido. *Scientific Reports of Hokkaido Fisheries Experiment Station*, 64, 127–136. (in Japanese).
- Nakaoka, M., Watanabe, K. and Yotsukura, H. (2017). Kelp occurrence data around Japanese water extracted from literature. Retrieved from http://www.godac.jamstec.go.jp/bismal/j/dataset/S9-5_Kelp.
- Nishimura, S. (1981). *Sea and life on earth introduction to marine biogeography*. Tokyo: Kaimeisha. (In Japanese).
- Orr, J. C., Fabry, V. J., Aumont, O., Bopp, L., Doney, S. C., Feely, R. A., ... Yool, A. (2005). Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature*, 437, 681–686. <https://doi.org/10.1038/nature04095>
- Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190(3–4), 231–259. <https://doi.org/10.1016/j.ecolmodel.2005.03.026>
- Poloczanska, E. S., Burrows, M. T., Brown, C. J., García Molinos, J., Halpern, B. S., Hoegh-Guldberg, O., ... Sydeman, W. J. (2016). Responses of marine organisms to climate change across oceans. *Frontiers in Marine Science*, 3, 62. <https://doi.org/10.3389/fmars.2016.00062>
- Raes, N., & ter Steege, H. (2007). A null-model for significance testing of presence-only species distribution models. *Ecography*, 30(5), 727–736. <https://doi.org/10.1111/j.2007.0906-7590.05041.x>
- Raybaud, V., Beaugrand, G., Goberville, E., Delebecq, G., Destombe, C., Valero, M., ... Gevaert, F. (2013). Decline in Kelp in West Europe and climate. *PLoS One*, 8(6), e66044. <https://doi.org/10.1371/journal.pone.0066044>
- Ready, J., Kaschner, K., South, A. B., Eastwood, P. D., Rees, T., Rius, J., ... Froese, R. (2010). Predicting the distributions of marine organisms at the global scale. *Ecological Modelling*, 221(3), 467–478. <https://doi.org/10.1016/j.ecolmodel.2009.10.025>
- Sasaki, M. (2017). Status of kelp fishery of Hokkaido. *Hokkaido Fisheries Research Institute Letter*, 94, 5–9. (In Japanese).
- Seeley, R. H., & Schlesinger, W. H. (2012). Sustainable seaweed cutting? The rockweed (*Ascophyllum nodosum*) industry of Maine and the Maritime Provinces. *Annals of the New York Academy of Sciences*, 1249(1), 84–103. <https://doi.org/10.1111/j.1749-6632.2012.06443.x>
- Smale, D. A., Burrows, M. T., Moore, P., O'Connor, N., & Hawkins, S. J. (2013). Threats and knowledge gaps for ecosystem services provided by kelp forests: A northeast Atlantic perspective. *Ecology and Evolution*, 3(11), 4016–4038. <https://doi.org/10.1002/ece3.774>
- Steneck, R. S., Graham, M. H., Bourque, B. J., Corbett, D., Erlandson, J. M., Estes, J. A., & Tegner, M. J. (2002). Kelp forest ecosystems: Biodiversity, stability, resilience and future.

- Environmental Conservation*, 29(4), 436–459. <https://doi.org/10.1017/S0376892902000322>
- Stocker, T. F., Qin, D., Plattner, G. K., Tignor, M., Allen, S. K., Boschung, J., ... Midgley, P. M. (2013). *Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change. Climate change 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (p. 1535). Cambridge, England; New York, NY: Cambridge University Press. <https://doi.org/10.1017/CBO9781107415324>
- Swets, J. A. (1988). Measuring the accuracy of diagnostic systems. *Science*, 240(4857), 1285–1293. <https://doi.org/10.1126/science.3287615>
- Takao, S., Kumagai, N. H., Yamano, H., Fujii, M., & Yamanaka, Y. (2015). Projecting the impacts of rising seawater temperatures on the distribution of seaweeds around Japan under multiple climate change scenarios. *Ecology and Evolution*, 5(1), 213–223. <https://doi.org/10.1002/ece3.1358>
- Tanaka, K., Taino, S., Haraguchi, H., Prendergast, G., & Hiraoka, M. (2012). Warming off southwestern Japan linked to distributional shifts of subtidal canopy-forming seaweeds. *Ecology and Evolution*, 2(11), 2854–2865. <https://doi.org/10.1002/ece3.391>
- Tani, T., Kawagoe, C., Matsumoto, S., Mizuta, H., & Yasui, H. (2015). Seasonal variations and morphological changes of sporophytes of *Saccharina sculpera* (Laminariales, Phaeophyceae) from Hakodate, Hokkaido. *Aquaculture Science*, 63(3), 235–244. <https://doi.org/10.11233/aquaculturesci.63.235>
- Taylor, K. E., Stouffer, R. J., & Meehl, G. A. (2012). An overview of CMIP5 and the experiment design. *Bulletin of the American Meteorological Society*, 93(4), 485–498. <https://doi.org/10.1175/BAMS-D-11-00094.1>
- Teagle, H., & Smale, D. A. (2018). Climate-driven substitution of habitat-forming species leads to reduced biodiversity within a temperate marine community. *Diversity and Distributions*, 24(10), 1367–1380. <https://doi.org/10.1111/ddi.12775>
- Tittensor, D. P., Mora, C., Jetz, W., Lotze, H. K., Ricard, D., Berghe, E. V., & Worm, B. (2010). Global patterns and predictors of marine biodiversity across taxa. *Nature*, 466(7310), 1098–1101. <https://doi.org/10.1038/nature09329>
- Vásquez, J. A., Zuñiga, S., Tala, F., Piaget, N., Rodríguez, D. C., & Vega, J. A. (2014). Economic valuation of kelp forests in northern Chile: Values of goods and services of the ecosystem. *Journal of Applied Phycology*, 26(2), 1081–1088. <https://doi.org/10.1007/s10811-013-0173-6>
- Yara, Y., Oshima, K., Fujii, M., Yamano, H., Yamanaka, Y., & Okada, N. (2011). Projection and uncertainty of the poleward range expansion of coral habitats in response to sea surface temperature warming: A multiple climate model study. *Galaxea, Journal of Coral Reef Studies*, 13(1), 11–20. <https://doi.org/10.3755/galaxea.13.11>
- Yara, Y., Vogt, M., Fujii, M., Yamano, H., Hauri, C., Steinacher, M., ... Yamanaka, Y. (2012). Ocean acidification limits temperature-induced poleward expansion of coral habitats around Japan. *Biogeosciences*, 9(12), 4955–4968. <https://doi.org/10.5194/bg-9-4955-2012>
- Yoshida, T., Suzuki, M., & Yoshinaga, K. (2015). Check list of marine algae of Japan (revised in 2015). *The Japanese Journal of Phycology (Sôru)*, 63, 129–189. (in Japanese).
- Watanabe, S., Hajima, T., Sudo, K., Nagashima, T., Takemura, T., Okajima, H., ... Ise, T. (2011). MIROC-ESM 2010: Model description and basic results of CMIP5-20c3m experiments. *Geoscientific Model Development*, 4(4), 845–872. <https://doi.org/10.5194/gmd-4-845-2011>
- Wernberg, T., Bennett, S., Babcock, R. C., De Bettignies, T., Cure, K., Depczynski, M., ... Wilson, S. (2016). Climate-driven regime shift of a temperate marine ecosystem. *Science*, 353(6295), 169–172. <https://doi.org/10.1126/science.aad8745>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

How to cite this article: Sudo K, Watanabe K, Yotsukura N, Nakaoka M. Predictions of kelp distribution shifts along the northern coast of Japan. *Ecological Research*. 2020;35:47–60. <https://doi.org/10.1111/1440-1703.12053>