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Fishing ground hotspots reveal long-term variation in chub mackerel *Scomber japonicus* habitat in the East China Sea

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ABSTRACT: The global warming trend has altered the ocean environment, but space-time changes in the oceanic distribution of small pelagic fishes have been difficult to identify due to their extensive ranges. Using detailed Japanese fishery logbooks, we reconstructed the main location of chub mackerel *Scomber japonicus* fishing grounds (hotspots) in the East China Sea over 328 consecutive months (27 yr). Our analyses revealed that the chub mackerel hotspots migrated seasonally over the continental shelf of the East China Sea, and demonstrated multi-year and decadal shifts in location, changing according to the spatial variation in the surface temperatures of the East China Sea. Spatial variation in sea surface temperatures was correlated with the volume transport of ocean currents, indicating that temperature and flow fields affected chub mackerel distribution both directly and indirectly. We also found that long-term fluctuations in climate were associated with chub mackerel hotspots, suggesting that atmosphere–ocean interactions may drive chub mackerel distribution variability. This empirical evidence regarding wide-ranging and long-term changes in chub mackerel distribution implies that future management measures need to enhance information sharing among relevant countries around the East China Sea.

KEY WORDS: Small pelagic fish · Fish distribution · Fishery · Climate change · Migration · Home range · Catch per unit effort · CPUE

INTRODUCTION

Small pelagic fish comprise approximately one-quarter of the world's fish catch. Just 5 species, i.e. *Engraulis ringens* (anchovy off Peru and Chile), *Clupea harengus* (Atlantic herring), *Scomber japonicus* (chub mackerel), *Trachurus murphyi* (Chilean jack mackerel), and *E. japonicus* (Japanese anchovy), represented approximately 18% of the total marine fish catch in 2008 (FAO 2010). In addition, small pelagic fish play an important role in the diets of top marine predators, including large pelagic fish, seabirds, and marine mammals. Therefore, responses of small pelagic fish to the ocean environment may provide baseline information for the future management of small pelagic fish stocks and marine ecosystems (Smith et al. 2011, Cury et al. 2011).

Warming trends on a global scale may alter ocean environments, marine fish distributions, and fish abundances (Genner et al. 2004, Perry et al. 2005). Sea temperatures may be key determinants of large oscillations in the abundance of small pelagic fish (Chavez et al. 2003, Takasuka et al. 2007, Alheit et al. 2009). However, empirical evidence demonstrating how long-term environmental variability affects the distribution of small pelagic fish is not available (Bakun 2009). Temperature affects many physiological processes of ectotherms, including metabolic rate and muscle contraction rate (Schmidt-Nielsen 1997). Therefore, thermal variability should influence the distributions of small pelagic fish (Sabatés et al. 2006) and their interactions with predators (Cairns et al. 2008). However, our understanding of long-term variations in small pelagic fish distributions with

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respect to temperature is limited due to the difficulty of observing fish across their extensive spatial and temporal ranges.

Information collected from Japanese large-scale pelagic fisheries in the East China Sea may help overcome such problems. The East China Sea lies across a transition zone between temperate and subtropical areas, and is one of the largest shelf regions in the world (Fig. 1). Continent-derived waters and oceanic currents create complicated temperature and flow fields along the continental shelf (Ichikawa & Beardsley 2002). Recent meteorological reports indicate that sea surface temperatures (SSTs) in the East China Sea have increased by 0.7 to 1.3°C over the past century, and that the volume of water transported by the Kuroshio Current fluctuates in a decadal cycle (Japan Meteorological Agency 2012); thus, the distribution of marine fishes might also have similar fluctuations. Japanese large- and medium-type purse seiners operate throughout the continental shelf, where the boundaries between water masses might be subject to variation. More importantly, the fishing vessels maintain meticulous logbooks of their operations.

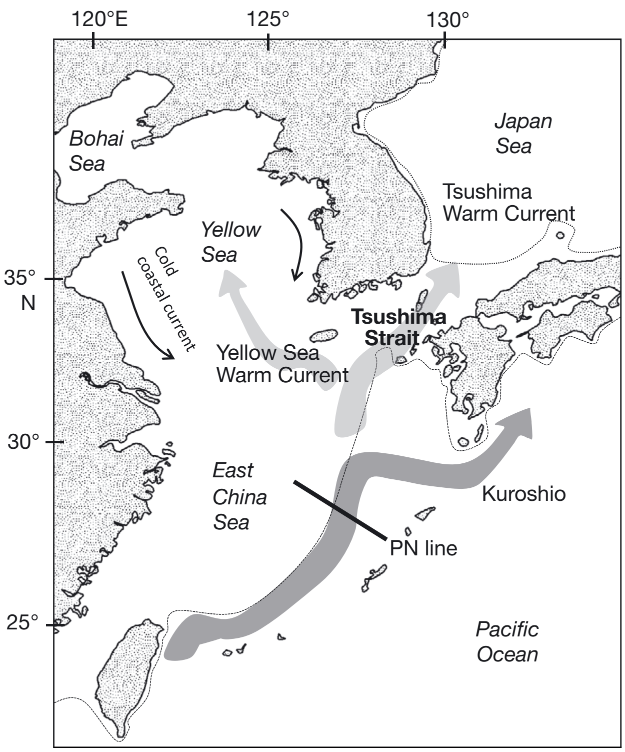

Fig. 1. Study region showing the major currents likely to influence the waters of the East China Sea. Solid line represents the PN line that is the fixed observation line of the Nagasaki Marine Observatory, administered by the Japan Metrological Agency. Thin black lines: 200 m isobaths

Within this framework, we examined the spatial distribution dynamics of a small pelagic fish, the chub mackerel *Scomber japonicus*, using 27 yr of logbook data. The specific objective of this study was to address the question of whether chub mackerel habitat locations shift in relation to the long-term variability of the SST field in the East China Sea.

MATERIALS AND METHODS

Study species and fisheries data

Scomber japonicus is a circumglobal pelagic fish species (Hernández & Ortega 2000). Two stocks have been identified in Japan: (1) the Pacific stock, which spawn near the margin of the Kuroshio Current (Kawabata et al. 2012), and (2) the Tsushima Warm Current (TWC) stock, which spawn in the East China Sea (Yukami et al. 2012). This study examined the TWC stock. Spawning in the TWC stock occurs between February and June (Yukami et al. 2009). The TWC stock of chub mackerel is assumed to be distributed mainly in the East China Sea, with seasonal migrations occurring within the East China Sea and across the Yellow Sea and the Japan Sea (Hasegawa et al. 1991, Hiyama et al. 2002). The TWC stock is thought to inhabit the northern part of the area in summer and the southern part of the area in winter (Limbong et al. 1991).

Japanese large- and medium-type purse seine fisheries catch small pelagic fish in the East China Sea. They identify 7 species of small pelagic fish and record the quantity of each species caught during each operation. Chub mackerel is a major target species, representing approximately 40% of the total catch for the East China Sea and the Japan Sea purse seine fisheries (Yukami et al. 2012). Fishermen divide chub mackerel into 4 body size classes: large (ca. >40 cm), medium (ca. 35 to 39 cm), small (ca. 29 to 34 cm), and very small (ca. <28 cm); catch amounts for each size class are recorded.

In this study, we focused on the distribution of adult chub mackerel. Because adult chub mackerel are highly mobile, it was assumed that it would be easy to detect behavioural responses to thermal environmental variability. Large and medium body-size classes represent mature chub mackerel (Yukami et al. 2012); therefore, these body size classes were analysed. In the present study, we only analysed data from January 1973 to December 1999, in order to exclude the effects of regulation measures that were introduced in both the Japan-Korea and Japan-China fisheries treaties in 2000.

Spatial distributions of chub mackerel and fishing effort

The spatial distribution of chub mackerel was established by generating kernel density maps using the ESRI® ArcGIS 10.0 Spatial Analyst Density tool, with a search radius of 0.5° (Fig. 2). Areas with >50% utilization distribution of kernel density were defined as areas of relatively high abundance for chub mackerel (hereinafter termed 'hotspots'). The gravity centre of each hotspot (°N and °E) was calculated and used to delineate the main chub mackerel habitat location. To estimate the kernel density distribution of adults, location data were weighted according to catch per unit effort (CPUE, tonnes per number of nets cast), using the 'population field' tool in Spatial Analyst. The logbook data provided a resolution of 0.16° (°N and °E). CPUE analysis was performed to reveal areas of relatively high adult chub mackerel abundance in a given month. To develop a data sequence of chub mackerel distribution dynamics, separate kernel density maps were generated for each month, and the kernel densities for each month were normalized. Since changes in fishing effort might change the apparent fish distribution, we simultaneously investigated kernel density maps of fishing effort. Although there may have been fleet-wide improvements in fisheries engineering (such as improvements in nets and vessels), this study was unable to consider these engineering factors.

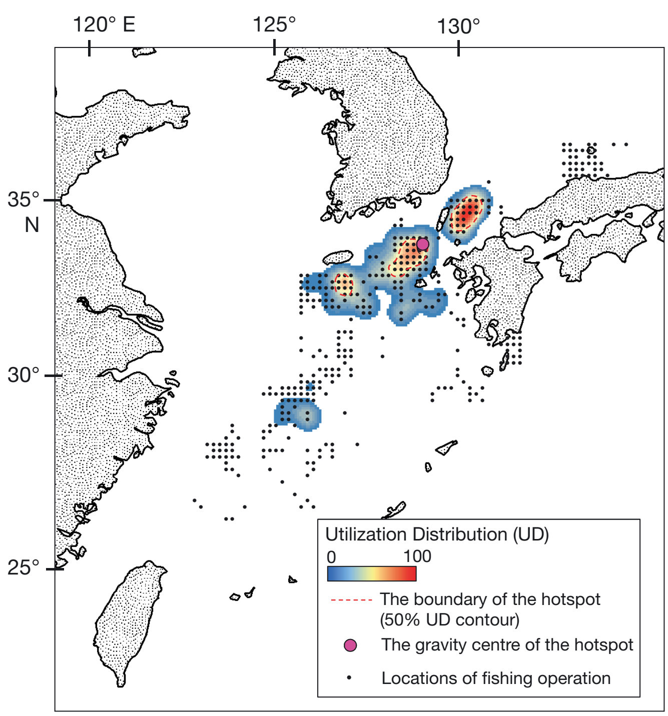

Fig. 2. *Scomber japonicus*. Kernel density distribution estimated using catch per unit effort data for each chub mackerel fishing operation location in January 1985

To determine periodicity of the chub mackerel hotspot locations, we estimated the spectral density, based on a fast Fourier transformation of a signal in the time-series location data. Before estimating spectral density, we removed the linear trend of hotspot location that was observed across the study period. This analysis was conducted using procedures built into IGOR Pro version 6.12 (WaveMatrix).

Space–time variability of the thermal environment

Monthly satellite-derived SSTs (Pathfinder version 5.0, 4.4 km resolution) were used to represent the thermal environment within chub mackerel habitats. We used 1 mo composite SST data from December 1981 to December 1999, publicly available via the National Oceanic & Atmospheric Administration (NOAA) website (http://coastwatch.pfel.noaa.gov/coastwatch/CWBrowserWW180.jsp). Mean SSTs within chub mackerel habitat hotspots were calculated for each month using Spatial Analyst in ArcGIS.

To represent the space-time variability of SSTs across the continental shelf, we constructed isotherms from December to the subsequent March — the high season for the chub mackerel fishery (Yukami et al. 2012). We focused on 15°C isotherms because visual inspection of the SST maps indicated that these were representative of the space-time variability of SSTs in the study area. In addition, 15°C SST is thought to be a good indicator of the lower thermal threshold of chub mackerel reproduction (Yukami et al. 2009).

The meridional positional deviance of 15°C isotherms (hereafter termed MPD15) at month K in year N (denoted $\text{MPD15}^{K,N}$) in the East China Sea was used to represent the space-time variability in SST, and was calculated according to the method described by Yasuda & Watanabe (1994). Monthly SST maps for the winters (December to the following March) between 1982 and 1999 were used to determine the monthly MPD15s. To cover areas for which there was no SST data, SST data were interpolated from neighbouring areas using the inverse distance weighted method, at a resolution of 0.5°. Next, 15°C isotherms were drawn. We marked all latitudes that intersected the 15°C isotherms along 14 longitudinal lines, which were spaced at intervals of 0.5° between 123.0°E and 129.5°E. The latitude of the ith point was labelled as $\mathrm{lat}_{i,j}^{K,N}$ for the jth longitudinal line. On each longitudinal line, segments warmer than 15°C were removed by adding $\Delta\mathrm{lat}_{i,j}^{K,N}$, i.e. $\mathrm{lat}_{2i+1,j}^{K,N} - \mathrm{lat}_{2i,j}^{K,N}$ to the latitude at the southern limit, $\mathrm{lat}_{1,j}^{K,N}$. Consequently, the latitude of the 15°C isotherms for the jth longitudinal line, $\mathrm{lat}_{j}^{K,N}$, were obtained as follows:

$$\mathrm{lat}_{j}^{K,N} = \mathrm{lat}_{1,j}^{K,N} + \sum_{i=1}^{I_j}\left(\mathrm{lat}_{2i+1,j}^{K,N} - \mathrm{lat}_{2i,j}^{K,N}\right) \tag{1}$$

The mean latitude over an 18 yr period from 1982 to 1999 (MLatKj) was then calculated for each longitudinal line for each month:

$$\mathrm{M\,lat}_{j}^{K} = \frac{1}{18}\sum_{N=1982}^{1999}\mathrm{lat}_{j}^{K,N} \tag{2}$$

$\mathrm{MPD15}^{K,N}$ was obtained by averaging the deviation of $\mathrm{lat}_{j}^{K,N}$ from $\mathrm{M\,lat}_{j}^{K,N}$ between 123.0° and 129.5° E, using the following equation:

$$\mathrm{MPD15}^{K,N} = \frac{1}{14}\sum_{j=1}^{14}\left(\mathrm{lat}_{j}^{K,N} - \mathrm{M\,lat}_{j}^{K}\right) \tag{3}$$

We excluded data from 5 months (December, February and March of 1984, February of 1988, and January of 1998) from the analysis, because of a large number of missing values in the SST data.

To evaluate the importance of SSTs for chub mackerel habitat selection, SDs of mean SSTs for each month between 1982 and 1999 were calculated within chub mackerel hotspots. In a similar way, monthly SDs between 1982 and 1999 were calculated for all 0.5° grids across the continental shelf (25 to 34° N, 123 to 130° E).

To delineate the main chub mackerel habitat location, we used the gravity centre of hotspots. The gravity centre of these high-abundance areas allowed us to determine how fish distribution changed relatively over time, as well as in relation to shifts in the temperature field (Lehodey et al. 1997). However, the presence of more than one hotspot for chub mackerel might give rise to inaccurate results due to increasing distances between patches. In this study, the mean number of hotspot patches in the monthly chub mackerel kernel distribution maps was 1.97 ± 1.16 (range: 1 to 8) with 45% of all maps containing a single hotspot. The total hotspot area increased as the number of hotspot patches increased (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m501p239_supp.pdf). The coefficient of variation (CV) of SSTs within hotspots increased with the number of hotspot patches or total area of the hotspot patches (Figs. S2 and S3 in the Supplement). However, the average value of the CV for the entire hotspot dataset was only 0.04 ± 0.03 (range: 0.01 to 0.15), and the effect of these independent factors on the CV of SSTs within hotspots was weak. Such small variations in SST within hotspots may be caused by the temperature-related habitat selection of chub mackerel. Therefore, use of the processed data (hotspot position and MPD15) may be reasonable to support the temperature-related variation in chub mackerel distribution in this case study of the East China Sea.

Ocean currents and climate indices

Other possible oceanic environmental factors that affect chub mackerel distribution were represented by the volume transports of the Kuroshio Current along the PN line (Fig. 1). The Kuroshio Current volume transport was observed at quarterly intervals (i.e. seasonally) by the Nagasaki Marine Observatory, administered by the Japan Metrological Agency.

To determine the correlation between air–sea environmental interactions and chub mackerel distribution, we used the multivariate El Niño-Southern Oscillation (ENSO) Arctic Oscillation (AO) indices. Data for the ENSO index were obtained via NOAA's Earth System Research Laboratory (www.esrl.noaa.gov/psd/enso/mei/), and the data for the AO index were obtained from the Climate Prediction Center (www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/ao_index.html). Monthly ENSO and AO data for 1973 through 1999 were used.

Statistics

We examined the effects of month and year on MPD15 using 2-way analysis of variance (ANOVA). MPD15 was used as a dependent variable, and month and year were used as categorical independent variables.

Relationships between the hotspot locations and environmental factors were examined using 3-way ANOVA. In this analysis, we did not use the volume transports of the Kuroshio Current because the location of chub mackerel hotspots, MPD15, AO, and ENSO were determined monthly, whereas the Kuroshio volume transports were seasonal data. Relationships among environmental factors in the winter were inferred from multiple regression analysis using Akaike's Information Criterion (AIC) and a simple

Pearson's correlation approach. In this analysis, we used the average monthly values of MPD15, AO, and ENSO for December through March, and the winter observation values of the Kuroshio volume transports.

We compared the SST SD between 1982 and 1999 for each month in the chub mackerel hotspots to those in the 0.5° grids using paired *t*-tests.

In order to clarify associations between long-term changes in climate and chub mackerel hotspots, we used multiple regression analysis of hotspot data and climate indices over the entire study period from 1973 to 1999. In this analysis, we focused on the relationship between chub mackerel hotspot location and climate on multi-year and decadal scales. The 3 yr moving average of hotspot location was calculated from the monthly dataset and was used as a dependent variable. Similarly, the ENSO index and the winter AO index were calculated from the monthly dataset and were used as independent variables. The best-fit regression model was determined by a stepwise method based on the minimum AIC. These statistical analyses were conducted using JMP version 9.0 (SAS Institute).

RESULTS

Spatial distributions of chub mackerel, fishing effort, and SST field

Scatter plots of the location of chub mackerel hotspots across the study period extended along the continental shelf in the East China Sea (Fig. 3). There was a strong positive correlation between the location of chub mackerel hotspots on the latitudinal axis and that on the longitudinal axis ($r = 0.63$, $n = 324$, $p < 0.0001$), indicating that the location of hotspots moved along an axis from the northeast to the southwest.

Time-series data also showed that the location of hotspots exhibited clear temporal trends (Fig. 4a,b). Correlation analysis indicated that the mackerel hotspots gradually moved south-westward with time (latitude: $r = -0.19$, $n = 324$, $p = 0.0007$; longitude: $r = -0.36$, $n = 324$, $p < 0.0001$). Moreover, 3 yr moving mean curves indicated the presence of long-term fluctuations. Indeed, results of periodogram analysis indicated that the hotspots fluctuated in both seasonal (i.e. 1 yr) and multi-year cycles (Fig. 4c,d). However, time-series profiles of fishing activity hotspots were considerably different from those of adult chub mackerel. Neither a linear trend nor multi-year cycles were observed in the fishing effort time-series (Fig. 5).

We found changes in oceanographic SST fields in the East China Sea during the winter with respect to the position of the 15°C isotherms (Fig. 6a). There was an interannual difference in MPD15 ($F = 5.927$, df = 17, $p = 0.0033$), whereas there was no significant difference in MPD15 between months of the same year ($F = 0.027$, df = 3, $p = 0.9746$). Overall, the MPD15 gradually moved northward between 1982 and 1999 (adjusted $r^2 = 0.29$, $F = 5.936$, df = 20, $n = 67$, $p = 0.0087$; Fig. 6b).

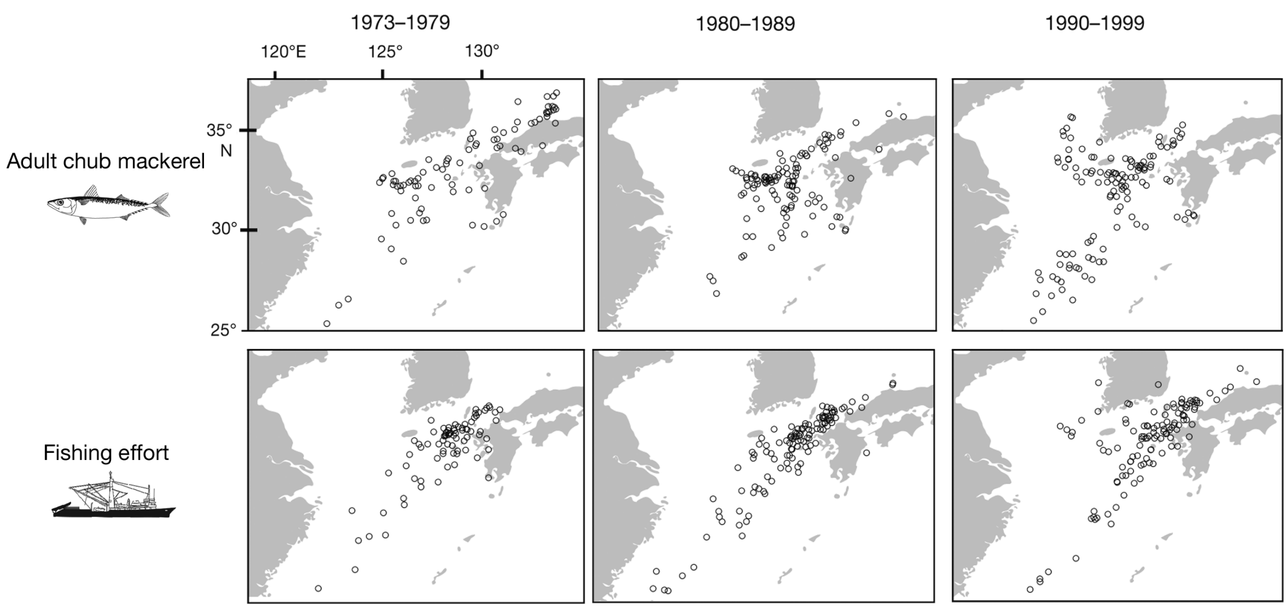

Fig. 3. *Scomber japonicus*. Scatter plots of chub mackerel and purse seine fishing effort hotspot locations

Relationships between chub mackerel or fishing effort hotspots and environmental factors

We found significant correlations between SST and the location of chub mackerel hotspots during the winter. There was a significant effect of MPD15 on the location of chub mackerel hotspots along the longitudinal axis (Table 1). However, on the latitudinal axis, no significant effect was found. There was no effect of MPD15 on the location of fishing activity hotspots (latitude: $F = 2.5045$, n = 68, p = 0.1185; longitude: $F = 3.5696$, n = 68, p = 0.0634). There was also no significant correlation between the location of chub mackerel hotspots and ocean current indices or climate indices.

MPD15 was correlated with the volume transports of the Kuroshio Current, but was less correlated with climate indices (Table 2). This result had a AICc of ca. 2, relative to models that did and did not include the transport volume of the Kuroshio Current. This suggests that there is not enough evidence to select the more complex model, which may be a result of small sample size. We found the Kuroshio volume transports correlated with AO (r = −0.58, p = 0.011, n = 18), suggesting an indirect correlation between MPD15 and AO. There was no correlation between the ENSO index and the AO index during the winter (r = −0.09, p = 0.73, n = 18).

The ENSO and AO indices were correlated with chub mackerel distribution over a long temporal scale: from 1973 to 1999, both of these climate indices were associated with the location of chub mackerel hotspots (Table 3). However, no significant association with the location of fishing effort hotspots was observed (latitude: $r^2 = 0.01$, $F = 1.0371$, n = 25, p = 0.3712, longitude; $r^2 = 0.18$, $F = 2.3495$, n = 25, p = 0.1189).

SSTs within the gridded 50% kernel density of chub mackerel fluctuated to a lesser degree than SSTs over the East China Sea, and exhibited clear seasonality (Fig. 7a) despite the presence of >1 hotspot patch (cf. Fig. 2). However, the SDs of SSTs between 1982 and 1999 within chub mackerel hotspots were larger than that of each 0.5° grid in the East China Sea (Paired t-test, $t = -9.902$, df = 11, n = 12, p < 0.0001; Fig. 7b).

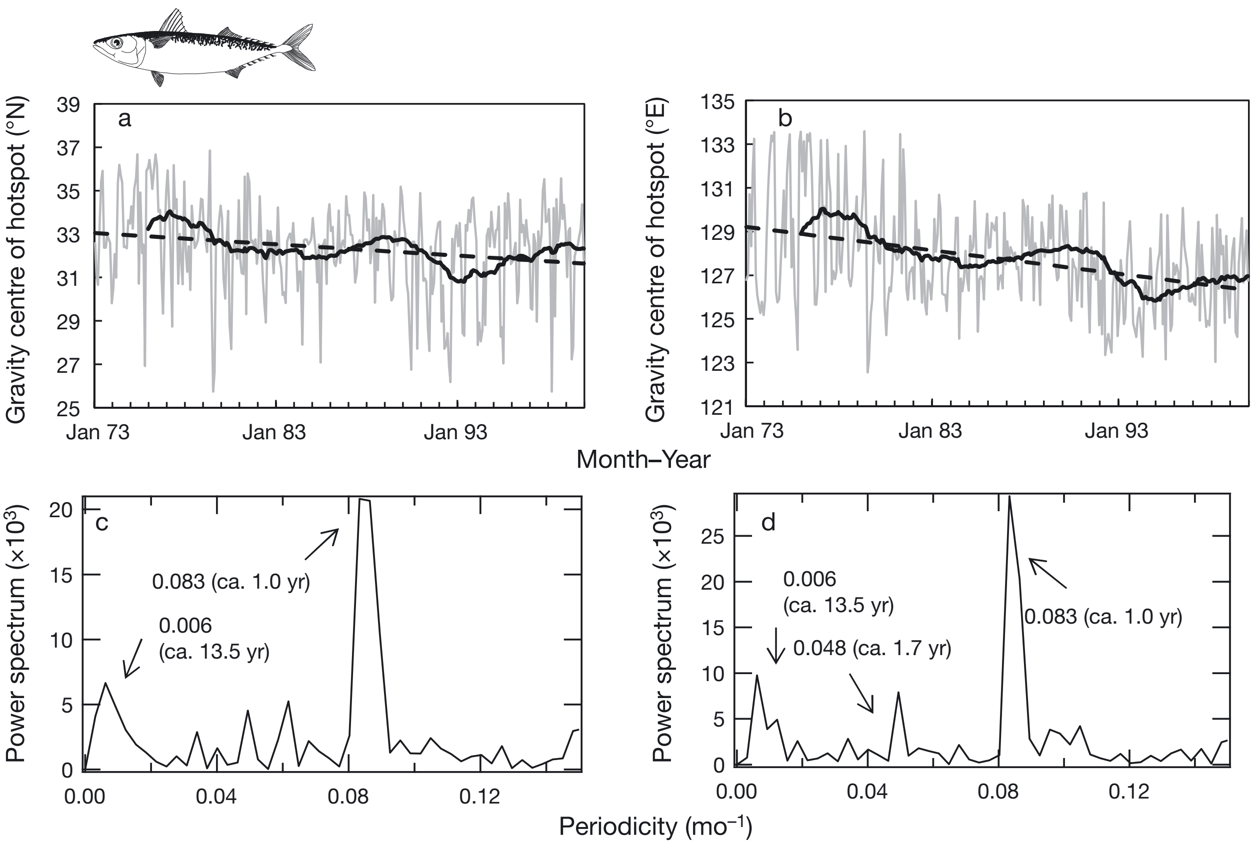

Fig. 4. *Scomber japonicus*. (a,b) Time-series of (a) latitudinal and (b) longitudinal locations of chub mackerel hotspots. Grey lines indicate location time-series. Bold black lines and dashed lines show 3 yr running means and linear regression lines, respectively. Power spectrum densities of (c) latitudinal and (d) longitudinal chub mackerel hotspot locations

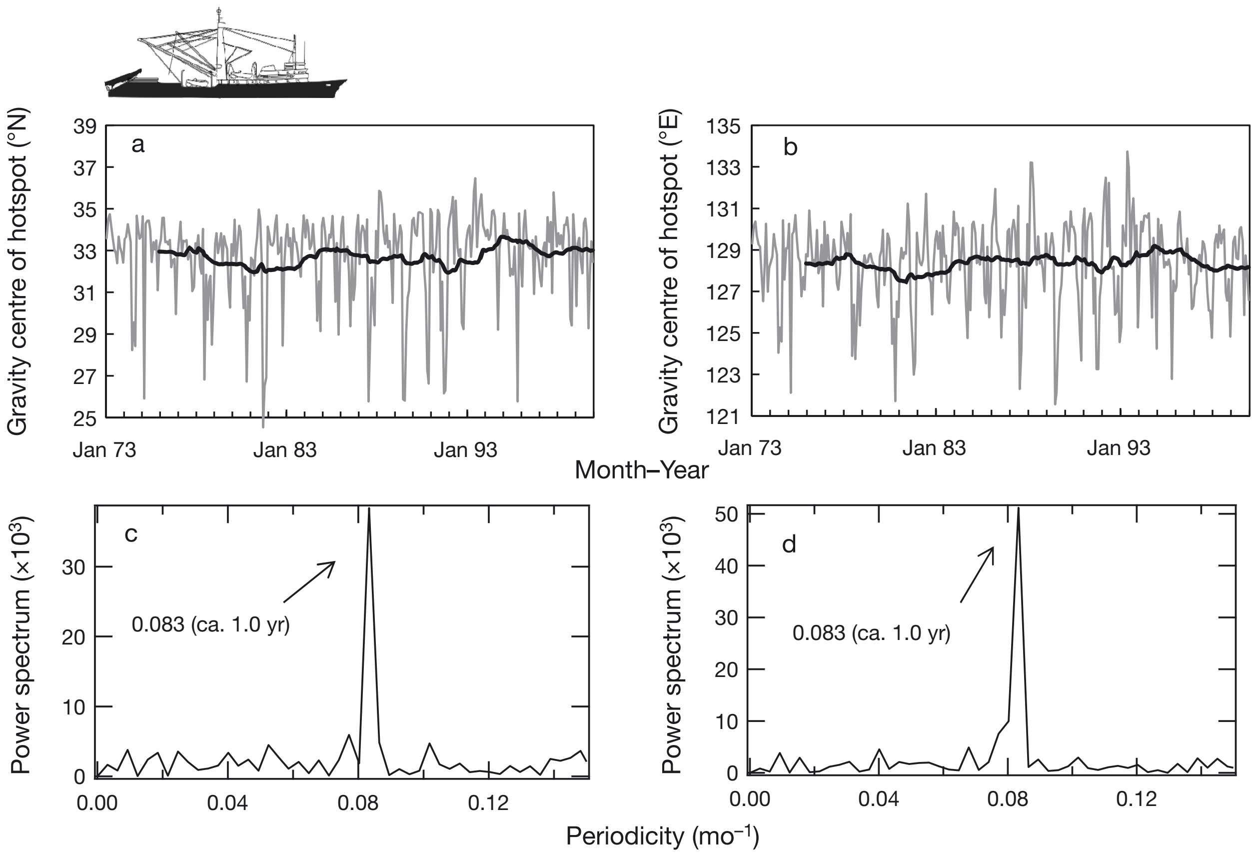

Fig. 5. Time-series of the (a) latitudinal and (b) longitudinal locations of fishing effort hotspots. Grey lines indicate location time-series. Bold black lines show 3 yr running means. Power spectrum densities of the (c) latitudinal and (d) longitudinal locations of fishing effort hotspots

Table 1. *Scomber japonicus.* 3-way analysis of variance ANOVA indicating the effects of environmental factors on the chub mackerel hotspot locations in the winter season between 1982 and 1999. MPD15: meridional positional deviance of 15°C isotherms; AO: Arctic Oscillation Index; ENSO: multivariate El Niño-Southern Oscillation Index

Dependent variable	Independent variables	Parameter estimate	*F*	p	n
Latitude	MPD15	–0.41	0.8422	0.3622	68
	AO	–0.03	0.0365	0.849	73
	ENSO	–0.07	0.1779	0.6746	73
Longitude	MPD15	–1.09	4.8474	0.0113	68
	AO	–0.12	0.6952	0.4075	73
	ENSO	–0.22	1.521	0.222	73

DISCUSSION

We found that the fishing ground hotspots for adult chub mackerel, as estimated from Japanese fisheries' logbook data, oscillated over the 27 yr study period in relation to spatial changes in SSTs on the continental shelf. Because the spatial changes in SSTs varied with ocean current transports and climate conditions, our results suggest that the locational shifts of chub mackerel hotspots were both directly and indirectly affected by broad-scale environmental changes in temperature and ocean currents.

Effects of temperature and other environmental factors on chub mackerel distribution

The present study revealed that the gravity centre of chub mackerel hotspots moved with an index of spatial and temporal variations in SST in the East China Sea. SST fields during the winter varied from year to year. Nonetheless, the SSTs at chub mackerel hotspots retained clear seasonality. This is empirical evidence that relates chub mackerel distribution to the ocean temperature field.

For ectothermic fish, water temperature affects growth, mortality, and locomotion (Wootton 1990), and it is thought that individuals (or shoals) select temperatures that are physiologically advantageous,

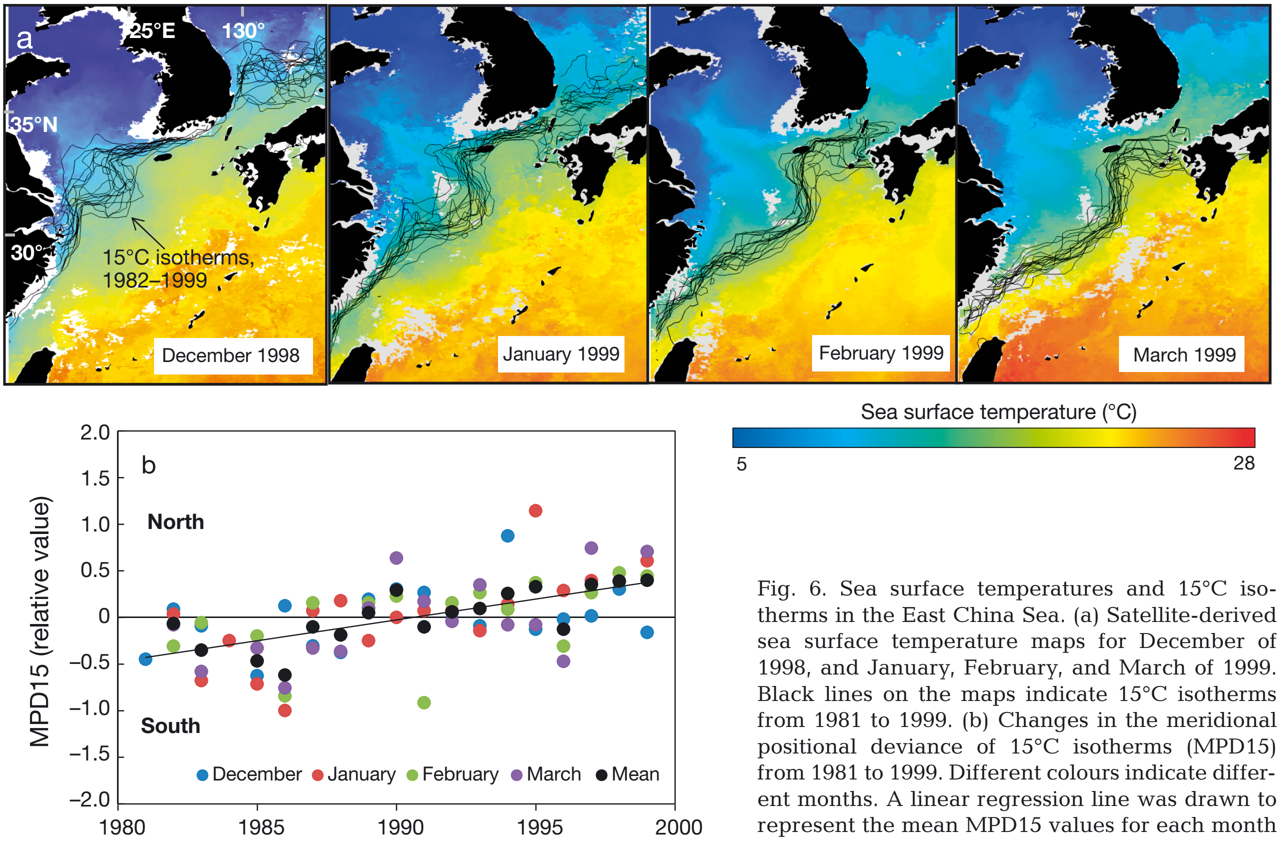

Fig. 6. Sea surface temperatures and 15°C isotherms in the East China Sea. (a) Satellite-derived sea surface temperature maps for December of 1998, and January, February, and March of 1999. Black lines on the maps indicate 15°C isotherms from 1981 to 1999. (b) Changes in the meridional positional deviance of 15°C isotherms (MPD15) from 1981 to 1999. Different colours indicate different months. A linear regression line was drawn to represent the mean MPD15 values for each month

Table 2. *Scomber japonicus*. Relationships among environmental factors in the winter seasons from 1982 to 1999. MPD15: meridional positional deviance of 15°C isotherms; AO: Arctic Oscillation Index; ENSO: multivariate El Niño-Southern Oscillation Index; AICc: Akaike's Information Criterion with a correction for finite sample sizes

Dependent variable	Model	Adjusted r^2	AICc
MPD15	Kuroshio (n = 18)	0.19	14.48
(n = 17)	Null		16.20
	AO (n = 18)	0.08	16.63
	Kuroshio + AO	0.15	17.69
	Kuroshio + ENSO	0.14	17.85
	ENSO (n = 18)	0.00	19.01
	AO + ENSO	0.04	19.71
	Kuroshio + AO + ENSO	0.09	21.61

Table 3. *Scomber japonicus*. Multiple regression analysis indicating the relationship between long-term changes in 3 yr moving averages of climate indices and that of chub mackerel hotspot locations from 1973 to 1999. AO: Arctic Oscillation Index; ENSO: multivariate El Niño-Southern Oscillation Index; AICc: Akaike's Information Criterion with a correction for finite sample sizes

Dependent variable	Model	Adjusted r^2	AICc
Latitude	ENSO + AO	0.64	35.89
(n = 25)	ENSO (n = 25)	0.46	44.14
	AO (n =25)	0.12	56.65
	Null		58.25
Longitude	ENSO + AO	0.57	60.53
(n = 25)	ENSO	0.47	63.64
	Null		78.11
	AO	0.04	78.55

or that individuals move to avoid the disadvantages associated with environmental changes in the habitat (e.g. Wurtsbaugh & Neverman 1988, Wildhaber & Crowder 1990, Krause et al. 1998, Sims et al. 2004, 2006, Yasuda et al. 2010). Even if the water temperature is within the physiological range for a given species, it may still affect the species' distribution through restriction of productivity and the distribution of prey (Fujioka et al. 2012).

In chub mackerel, laboratory experiments have revealed a significant effect of temperature on metabolic costs (Shadwick & Steffensen 2000, Dickson et al. 2002), locomotion performance (Dickson et al. 2002, Rome et al. 2000), and mortality (Schaefer 1986). Further, the spawning season of chub mackerel in the East China Sea occurs from February to June (Yukami et al. 2009). Temperatures during this

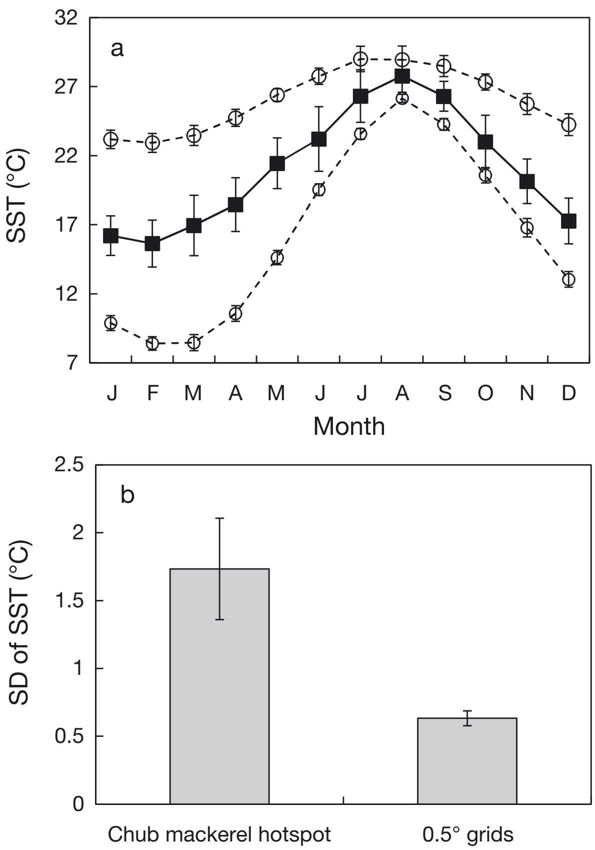

Fig. 7. *Scomber japonicus.* (a) Black squares: mean monthly sea surface temperatures (SSTs) within chub mackerel hotspots from 1982 to 1999. Open circles: monthly maximum and minimum SST in 0.5° grids of the East China Sea (range: 25 to 34° N, 123 to 130° E). (b) Mean of the monthly SD of SSTs within chub mackerel hotspots (grey) and in 0.5° grids of the East China Sea (white). Error bars: SD in both (a) and (b)

period might affect biomass of adults and/or larvae (Hiyama et al. 2002). Therefore, effects of temperature on mackerel abundance and distribution can be inferred through the relationship between SST conditions and CPUE in Japanese, Argentine, and Taiwanese chub mackerel fisheries (Limbong et al. 1991, Perrotta et al. 2001, Sun et al. 2006).

Our results indicate that chub mackerel hotspots shifted seasonally between the western part of the Japan Sea and the southern part of the East China Sea. During the winter season, the locations of the hotspots varied with the location of the 15°C isotherms. Because these isotherms extended from the Tsushima Strait to the boundary area between the East China Sea and the Yellow Sea, this result may indicate that the winter SST in these areas is a key determinant of the annual distribution of adult chub mackerel. The relationship between MPD15s and Kuroshio volume transports observed in this study suggest that the Yellow Sea and the Tsushima Strait oceanography may be influenced by the Kuroshio Current at the shelf break of the East China Sea (Kondo 1985, Naimie et al. 2001). The Yellow Sea Warm Current, a tongue of Kuroshio Current origin, flows northward over the central trough of the Yellow Sea as far as the Bohai Sea during the winter (Naimie et al. 2001). In order to compensate for these transports, cold coastal currents flow southward along the Chinese and Korean coasts (Kondo 1985, Naimie et al. 2001). Therefore, oceanic fronts develop between the Yellow Sea Warm Current and the Korean coastal currents that might offer optimal thermal conditions for adult chub mackerel. Variability of the flow path and volume transports of the Tsushima Warm Current may affect the spatial distribution of oceanic fronts in the East China Sea and the Yellow Sea (Kondo 1985) and, consequently, may affect adult chub mackerel distribution.

If the mackerel's distribution is determined by the selection of certain preferential temperatures, small variations in seasonal SSTs between years within chub mackerel hotspots would be expected. However, the variation of mean SSTs within chub mackerel hotspots was slightly larger than that of each grid in the East China Sea. This then raises the question as to why chub mackerel hotspots moved with the location of the 15°C isotherm. First, fish movement may also be generally limited by the magnitude or rate of water temperature changes, rather than the absolute temperature of the water (Brill 1994). Therefore, adult chub mackerel might move to avoid differences in temperature and retain thermal seasonality. Second, the Kuroshio Current may affect the formation of water masses in the East China Sea (Isobe & Beardsley 2006, Lee & Matsuno 2007). The Kuroshio Current may change both temperature and flow fields in the East China Sea, and thus the location of the 15°C isotherms may represent changes in both temperature and flow fields. We showed an indirect correlation between shifts in the hotspots of adult chub mackerel and the volume transport of the Kuroshio Current. Therefore, variations in ocean currents may also affect the distribution of chub mackerel.

Association with climate change

Long-term periodicity in the locations of chub mackerel hotspots might reflect changes in global climate. We found that the locations of chub mackerel hotspots changed on multi-year and decadal scales. Long-term fluctuations in the AO and ENSO indices were indirectly correlated with chub mackerel habitat. Structural changes in atmospheric pressures in the northern hemisphere (i.e. the AO) during the winter may produce quasi-decadal changes in SST conditions of the East China Sea and the adjacent Japan Sea with a periodicity of roughly 10 yr (Gong et al. 2001, Minobe et al. 2004, Isobe & Beardsley 2007). ENSO events have 2 to 3 and 5 to 6 yr cycles, and may be associated with both the Asian monsoon system (Kawamura 2008) and the Kuroshio volume transport (Hwang & Kao 2002), both of which affect the temperature and flow fields in the East China Sea (Isobe & Beardsley 2006, Lee & Matsuno 2007, Kawamura 2008). Hwang and Kao (2002) noted that characteristics of the Kuroshio volume transport differed between the northeast and southeast regions of Taiwan, and that the Kuroshio Current at these 2 spots was correlated with ENSO in different ways. Although the cycle of periodicity in long-term spatial shifts in the chub mackerel population may be roughly consistent with that of climatic changes, further intensive research on atmosphere–ocean interactions in the East China Sea are necessary.

Evaluation of methods

A previous tagging study suggested that chub mackerel migrate over a wide range between the East China Sea and the Japan Sea (Hasegawa et al. 1991). However, no effect of isotherm movement on hotspot location was shown along the latitudinal axis. One reason for this lack of correlation is that the topography and oceanography of the study area is complex. Another reason is that our data was limited. Because our data did not include fishing operations in the north and middle parts of the Japan Sea, we might not have detected partial migrations beyond the study area. Although the mean proportion of annual adult chub mackerel catch in the north and middle parts of the Japan Sea to the sum of the Japan Sea and the East China Sea catches from 1978 to 1999 was only 8.9% (range: 1.6 to 20.2), expansion of the study area might be useful in future studies.

In this study, we used SST maps as temperature field data. Because thermoclines develop in the East China Sea during summer, summer SSTs might not be a good indicator of temperature conditions. Further, we used the MPD15 as an index of single isotherm movements during the winter season to elucidate chub mackerel movements. However, ocean temperature fields in the East China Sea exhibit seasonal, annual, and more long-term variations, and these are often complex (Kondo 1985). Therefore, more elaborate indices using multiple isotherms may be useful in future studies.

Higher fishing pressure and fluctuation in CPUE in a local area might manifest as an apparent shift in hotspots to another local area. The CPUE of chub mackerel of all size classes in the East China Sea and the Japan Sea fluctuated during the study period (Hiyama et al. 2002). However, we did not consider the relationship between distribution and abundance indices because more detailed work may be needed to determine whether the apparent shift in the habitat range of this highly migratory species was environmentally driven or caused by local CPUE fluctuations. For example, due to changes in fisheries resource compositions (Tian et al. 2006, Ohshimo et al. 2009), fisheries-engineering techniques, and socioeconomic parameters of marine products (Seikai National Fisheries Research Institute 2010), the operation of purse seine fisheries in these seas might change. Effects of these biological and fisheries factors on fishing operations may be important aspects of spatial-temporal fluctuations in CPUE. The effect of abundance on distribution may be a topic for further study of chub mackerel distribution.

In this study, spatio-temporal changes in chub mackerel habitat were investigated using fishery-dependent data. Although fishery-dependent data provided us with valuable large-scale data sets, there are limitations to our analysis. For example, the increase in fishing effort in the southern Yellow Sea in the 1990s may have influenced the location of hotspots (Fig. 3). However, we could not determine whether fishing effort moved to follow the chub mackerel or if the movement was due to other factors. Therefore, an integrated approach, including use of research vessel survey data, would be required to better understand the spatio-temporal variability of chub mackerel. The recent development of new tagging techniques has enabled the collection of more fine-resolution behavioural and environmental data for marine organisms, and might help to determine proximate factors that regulate fish migration and distribution (e.g. Kitagawa et al. 2000, Tanaka et al. 2000, Yasuda et al. 2010, Righton et al. 2010).

Implications for the management of chub mackerel

We conclude that adult chub mackerel in the East China Sea respond to long-term variations in the oceanographic environment, which implies that environmental variability affects recruitment (Hiyama et al. 2002), growth (Watanabe & Yatsu 2006), and larval and juvenile distributions (Sassa & Tsukamoto 2010) of chub mackerel populations. We suggest that atmosphere–ocean interactions drive the variability in chub mackerel distribution. If the current warming trend continues, chub mackerel distributions may shift substantially, not only at the adult stage, but also at the larval and juvenile stages. Although stock assessments and closures in specific areas will help to manage local chub mackerel populations, the wide-ranging and long-term movement of chub mackerel hotspots requires future management measures, including enhanced information sharing among the relevant countries around the East China Sea.

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