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AQUATIC ECOSYSTEM SERVICES

Jellyfish blooms challenge the provisioning of ecosystem services in the Korean coastal waters

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Abstract Temperate fisheries grounds are exposed to compound effects of jellyfish proliferations and fishing pressure, which affect local fisheries, cause economic losses, and threaten seafood supply. Here, we quantify the interlink between climate variability and jellyfish blooms and their impact on the Japanese anchovy (*Engraulis japonicus*), in the Korean coastal waters. We used a bioclimate dataset (2010–2019) that includes quantitative information of two major bloom-former species, *Aurelia coerulea* and *Nemopilema nomurai*, in the Korean Peninsula. We show that climate phenomena governing East Asia regions explain circa half of jellyfish variability. In turn, jellyfish blooms have a significant negative effect on anchovy interannual changes ($r = -0.47$, $P < 0.01$), which varies along with the bloom magnitude. Our results indicate that the intensity of jellyfish blooms, more than their duration, has a predominant effect on anchovy and coastal fisheries production. We also suggest the possibility of using climate signals for assessing and eventually predicting, interannual abundance changes of jellyfish in the Korean Peninsula. These results stress the challenge posed by jellyfish blooms to the provisioning of ecosystem services via their influence on marine harvested fish and further highlight the need for their integration into ecosystem-based management.

Keywords Anchovy · Gelatinous carnivores · Fisheries · East Asian marginal seas · Climate variability

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Introduction

Safeguarding marine resources constitutes a fundamental concern to balance food security and ecosystem health and therefore bears vast management and economic implications. The East Asian marginal seas (EAMSs) are among the world's most productive fisheries grounds and likely the main world's area for aquaculture, producing up to 90% of the world's aquaculture products (FAO, 2022). However, the region is exposed to varied anthropogenic stressors, i.e., rapid coastal population growth, overharvesting of marine resources, warming, hypoxia, and pollution (Uye, 2008), which threaten ecosystem services and pose major risks for marine sustainability and therefore for human welfare (Lomartire et al., 2021).

South Korea shows in the upper ranking of seafood consumption in the world, with a national seafood production expanded by 3.5% of annual growth in the last decade, i.e., 2000–2018 (FAS, 2021). In addition, the national annual seafood demand has been 2.5-fold higher than the world average consumption, i.e., 54.97 and 20.3 kg/capita/year in 2017, respectively (FAO, 2020). Seafood is the preferred source of daily protein intake in the country, which causes proteins consumption being twice the world's average level: 38.7% vs. 16.7% (MOF, 2018). Such a high demand is expected to increase to 64.3 kg/capita/year by 2025 (Kim et al., 2018). However, stock assessments indicate that the capable amount of domestic fish catch exhibits a restrained capacity to increase, for which the sustainable management of fishery resources is fundamental to warrant food security (Kim et al., 2018). Climate-driven environmental changes may further enhance adverse conditions thus jeopardizing the sustainable provision of marine resources in the EAMSs. Indeed, Korean waters have experienced a warming rate ~ 2.5 times faster than the average mean global sea surface temperature (SST) in the last 50 years (Han & Lee, 2020). Such temperature changes are driven by climate phenomena that shape regional hydrographic conditions, such as Pacific Decadal Oscillation (PDO) and the East Asian Winter Monsoon (EAWM) (Jung et al., 2017). In addition, frequent coastal eutrophication and hypoxia events have been documented in the last decades (Lee et al., 2018). Climate change and anthropogenic disturbances alter marine ecosystems, thereby opening novel ecological spaces for the proliferation of opportunistic, harmful populations, such as jellyfish, which constitute warning ecological signals of perturbed marine ecosystems (sensu Jackson, 2008).

Since the late 1990s, massive jellyfish aggregations in Korean waters have been reported causing damages in broad socio-economical fields, e.g., stinging sea users, impairing coastal power plants, and fisheries. The latter being affected through spoiling fish catches and as bycatch in fishing nets. According to national fishery sales, these massive proliferations may cause heavy economic losses valued in ca. 141,233 billion KRW (≈117 million USD) and their damages have reached up to 7.04% of national fishery industries (Kim et al., 2014a). There is no doubt about the negative impact jellyfish proliferations have on fisheries, for which their broad implications in ecosystem services call for an integrative socio-ecological approach to effectively balance food security and ecosystem health.

The Japanese anchovy (*Engraulis japonicus*, Temminck and Schlegel, 1846) is a common forage species in the northwest Pacific, widespread distributed in the East Sea (Sea of Japan), Yellow Sea, and East China Sea and one of the main harvested species in Korea. Ranked in the top ten of consumed seafood, together with Alaska pollock, squid, mackerel, shrimp, crabs, monkfish, flatfish, oyster, and octopus (FAS, 2021), the production of anchovy fishery has increased in the last six decades, ca. six times, from < 40,000 metric tons in the 1950s to > 212,000 metric tons in the 2010s (MOF, 2019). Despite the economic value of the species, however, mainstream studies have focused on the influence of univariate environmental stressors and life history traits, e.g., SST, dissolved oxygen (DO), eggs spatial distribution, and larval survival and growth (Lee & Kim, 2007; Jung et al., 2008; Kim et al., 2013b; Yoo et al., 2018). Hence, a multi-stressors approach is required to consider the potential effects of external forces, such as hydroclimate dynamics and ecological feedback, potentially interfering in anchovy recruitment (Takasuka et al., 2008).

Proliferation events of jellyfish warn on scenarios of high ecological competition, where it is plausible their dominance over forage fishes (Lynam et al., 2006; Uye, 2011). By virtue of their survivalist life history traits, massive proliferations of jellyfish are signs of prominent changes in the state of marine ecosystems and have been proposed as ecological warnings for food security and management of socio-ecological systems (Aubert et al., 2018). In this study, we explore the influence of climate on jellyfish blooms to assess their impact on coastal food provisioning. Our hypothesis is that the climate may shape the blooming season by promoting suitable environmental conditions (i.e., temperature, food availability) under which the fast growth of jellyfish can double their population size within short periods, thereby enhancing the intensity of blooms. The impact of this mechanism magnifies fisheries pressure on harvested populations and develops a feedback, due to the decline of competition for food promoted by the fish harvest. The compound effect of jellyfish and fisheries might then shape interannual variations of forage fish, such as anchovy.

Methods

Study site

The Korean peninsula is bordered by three large marine ecosystems (LMEs). The Yellow Sea surrounding the western coast and characterized by the Yellow Sea Warm Current (YSWC). The southern region, Namhae, belonging to the East China Sea, which also influences the western and southeastern Korean regions through a branch of the Tsushima Warm Current and the East Sea surrounding the eastern coast and characterized by cold and warm currents, the northward East Korea Warm Current (EKWC), and the southward North Korean Cold Current (NKCC), a branch of the Liman Current that flows southward from Russia and North Korea. In turn, these three LMEs are influenced by the Kuroshio Current, which is characterized by high temperature, 20–30°C, and high salinity, 34–34.8‰, and is the second-largest warm ocean current, after the Gulf Stream.

Biological data

Jellyfish data were obtained from the Korea jellyfish monitoring program (KoJeM) operated by the National Institute of Fisheries Science (NIFS), Korea. The KoJeM was launched in 2006 as a weekly survey to track jellyfish biomass changes in coastal waters of South Korea. These data inform on the spatial distribution of jellyfish and serve as warning signals for beach users and fisheries. We focused on two common bloom-former Scyphozoan jellyfish, *Aurelia coerulea* (von Lendenfeld, 1884) and *Nemopilema nomurai* (Kishinouye, 1922), which are known to cause major detrimental effects on coastal socio-ecological systems due to their recurrent blooms and their broad spatial extent lasting from late spring to the beginning of winter. In this study, we assessed jellyfish data over the period 2010–2019 as it matches the years with the best sampling resolution (available online at www.nifs.go.kr). In addition, the total catches of anchovy were extracted from the annual marine and fishery statistics report, Statistical Yearbook of Oceans & Fisheries, Ministry of Oceans and Fisheries (MOF) (MOF, 2019). Data on catches were collected by administrative districts of Korea from 2010 to 2019.

Environmental data

Three climate indices were selected because of their influence on the Korean Peninsula. These climate signals shape seasonal and interannual weather patterns, i.e., El Niño -Southern Oscillation (ENSO), East Asia Winter Monsoon (EAWM) and Pacific Decadal Oscillation (PDO). We used the Niño-3.4, which is defined as a 5-month running mean SST over the region (5°N-5°S, 170–120°W) to describe El Niño and La Niña events (Trenberth & Stepaniak, 2001). The EAWM index has been used to explain the influence of the winter monsoon in the East Asia regions and is based on the variability of the pressure gradient between the Aleutian low and Siberian high (Jhun & Lee, 2004). The PDO index is the leading empirical orthogonal function (EOF) of SST variability in the North Pacific Ocean (Mantua, 2002) and its influence on plankton communities in the East China Sea has been reported (Rebstock & Kang, 2003; Molinero et al., 2018; Ma et al., 2019). The hydrological data were acquired from the coastal water quality survey operated by the Environment monitoring network for coastal sea by the Ministry of Oceans and Fisheries, South Korea.

Statistical analyses

Prior to statistical analysis, all biological and environmental data were rescaled to normalize the unit variance of the distributions at zero mean and the standard deviation to be 1, and standardized values were used for analysis. The statistical procedure was based on a three-step procedure as follows:

Step 1: We first evaluated climate effects on jellyfish bloom intensity. Jellyfish data refer to bloom spatial coverage along Korean coasts. These data were used as a proxy of jellyfish bloom intensity and were averaged by month from the original weekly data. Generalized additive models (GAMs) were used to assess how climate variability shapes temporal patterns of jellyfish bloom intensity. GAM is a semi-parametric extension of a generalized linear model that uses additive functions and smoothly components to depict non-linear and non-monotonic relationships between response and predictor variables (Guisan et al., 2002). The GAM equation employed is as follows:

$$y_{i=}\beta_0 + \sum_{j=1}^{p} f_j\left(x_{ij}\right) + \in_i, \tag{1}$$

where y_i is the response of jellyfish bloom intensity (e.g., *A. coerulea, N. nomurai*), β_0 is the intercept, and f_j denotes a smooth function for each predictor variable. The symbol x_{ij} stands for an interaction value of the climate variable and $\in_i$ is an error term with unit variance and zero mean. We used the three climate indices (i.e., PDO, ENSO, EAWM) as explanatory variables, while the jellyfish bloom intensity was assessed as the response variable. GAMs were run using monthly observations, from 2010 to 2019. We tested the strength of climate forcing on jellyfish, and how it varies over time. To do so, we used different lags, e.g., 0, 1, 3, 6, and 12 months.

Step 2: We assessed whether the influence of both environment and jellyfish on anchovy varies and under which circumstances any of these factors dominate anchovy interannual changes. A proxy of environmental conditions was extracted by principal component analysis (PCA), applied to the ensemble of climate indices (PDO, ENSO, EAWM; PC1: 71.23% of the total variance) and regional hydrographic variables (SST, Salinity, DO, Chl-*a*; PC1: 59.35% of the total variance). In turn, jellyfish bloom intensity denotes the average bloom intensity of the two species, *A. coerulea* and *N. nomurai*. We then assessed the relationship jellyfish vs. anchovy, and local environment vs. anchovy, by Pearson's product moment correlations with bootstrap resampling, as in Casini et al. (2009). This analysis involved a random pairwise sampling with replacement, where each time series was resampled 1000 times. In each bootstrap sample, we made even the number of elements as in the original data set. Then, the density distribution of the corresponding correlation coefficients was computed using nonparametric Kernel smoothing.

Step 3: We assessed the overall effect of jellyfish bloom duration and magnitude on anchovy interannual changes. Jellyfish bloom metrics are based on cumulative curves from which we identified the start, middle, and end of bloom, as in Lee et al. (2021). These temporal points in the evolution of the bloom corresponded to the 15%, 50%, and 85% of cumulative curves. The bloom duration was computed as the difference (in days) from the start and end of jellyfish bloom metrics. We additionally assessed the relative contribution of anchovy fishery with respect to the coastal fishery. To quantify this ratio, the coastal fishery production was used as representative of the maximum value among fishery types, and the anchovy percentage was computed as follows:

$$\begin{aligned} &\mathit{Anchovy\,fishery\,percentage}\,(\%)\\ &\quad = (\mathit{Anchovy\,catches}/\mathit{coastal\,fishery\,production}) \times 100. \end{aligned} \tag{2}$$

Equation (2) provides the importance of anchovy by a measure of the percentage of anchovy fishery in the Korean fishery.

Data were analyzed using the R software tool (R core team, 2021), with the package "mgcv" (v1.8–40; Wood, 2017) and using Matlab (MATLAB. 2020a, The MathWorks, Natick, 2020). Additionally, Grapher18 (Grapher™ from Golden Software) was used for visualization.

Results

Hydroclimate conditions in Large Marine Ecosystems bordering the Korean Peninsula

The interannual variability of dominant climate phenomena and hydrological conditions governing Korea is shown in Fig. 1. The PDO displayed both positive and negative phases. The negative PDO lasted until late 2013 and shifted in 2014 to positive values,

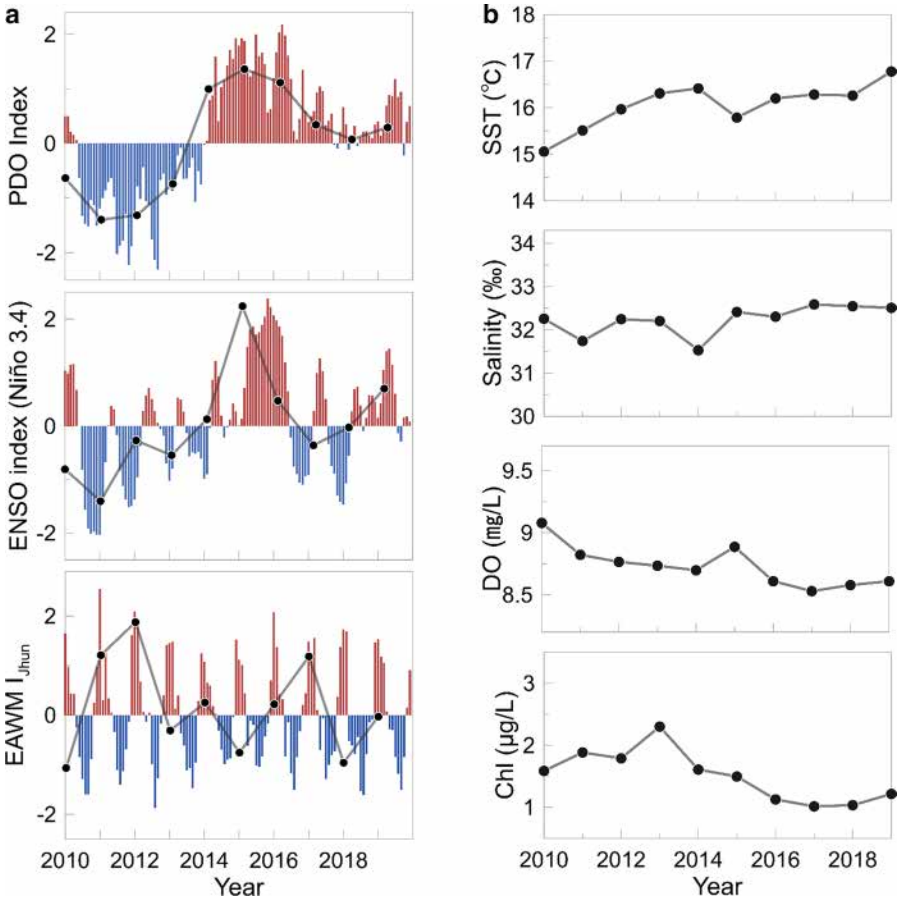

Fig. 1 Interannual variability of **a** climate indices (black dots denote anomalies calculated over the study periods), Pacific Decadal Oscillation (PDO), El Niño-Southern Oscillation (ENSO index), East Asia Winter Monsoon Index from Jhun 2004 (EAWM I_{Jhun}) and **b** local hydrology (annual average of in situ raw data) in the Korean coastal waters over the period 2010–2019. Data were extracted from annual coastal water quality survey operated by the Environment monitoring network for coastal sea (Ministry of Oceans and Fisheries, MOE, Republic of Korea)

which promoted a dominance of cold temperatures in the NW Pacific Ocean. The interannual changes of ENSO showed enhanced variance during 2011–2015, almost threefold higher compared to the average of the study period, followed by a dropping phase during 2015–2017 and positive values dominating the last years. In turn, larger fluctuations were detected in the interannual variability of EAWM. Higher values were observed in 2011 and 2012, followed by alternated peaks (2014, 2017) and valleys (2013, 2015, and 2018).

SST showed an overall upward trend, characterized by two periods of consecutive years of increasing temperatures. The first covering 2010–2014 and the second spanning from 2016 to 2019, which were separated by a marked temperature decrease in 2015. The highest SST was observed in 2019 showing values ca. 1.72 °C higher than the records observed in 2010. Salinity showed marked drops in 2011 and 2014, followed by rising values that remained high after 2015. DO showed three peaks in 2010, 2012, and 2018 and noticeable low values over consecutive years from 2014 to 2017, when DO concentrations were lower than 8.75 mg/l. In turn, a relatively higher concentration of chlorophyll was observed in three consecutive years, i.e., 2011–2013, followed by a marked decrease in 2014. Afterward, interannual changes of chlorophyll showed low variations until the end of the study period (Fig. 1).

Climate and the jellyfish bloom intensity

The interannual variability of the two jellyfish displayed marked changes. *A. coerulea* showed an average spatial coverage of 47%, with two major peaks observed in 2010 and 2016, when the species covered up to 63.64 and 64.60% of the Korean coastline, respectively. In turn, annual patterns of *N. nomurai* displayed larger differences than *A. coerulea* with an average spatial coverage of 36%, although the highest bloom event, 2012, reached up to 70% of the Korean coastlines (Fig. 2). We found that the climate influence differs by species and changes over time; GAM results showed significant links between climate indices and the bloom intensity of the two jellyfish species at different lags. An influence of hemispheric-wide climate, ENSO and EAWM, was found for both jellyfish species; however, *A. coerulea* was strongly linked with the regional climate variability ascribed to the effect of EAWM (Table 1). The climate influence on *A. coerulea* was detected at 0-, 1-, 3-, 6- and 12-month lag, with a leading role of EAWM at zero lag ($r^2 = 0.38$; 41% deviance explained by the model). However, the strongest influence was noticed at 6-month lag with the leading role of EAWM and ENSO ($r^2 = 0.69$; 70.7% deviance explained by the model) (Fig. 3, upper panels). In contrast, we found that the influence of ENSO and EAWM on *N. nomurai* was noticeable except for a 6-month lag; the strongest link with the climate indices was detected at 1-month lag ($r^2 = 0.25$; 28.2% deviance explained by the model) (Fig. 3, bottom panels).

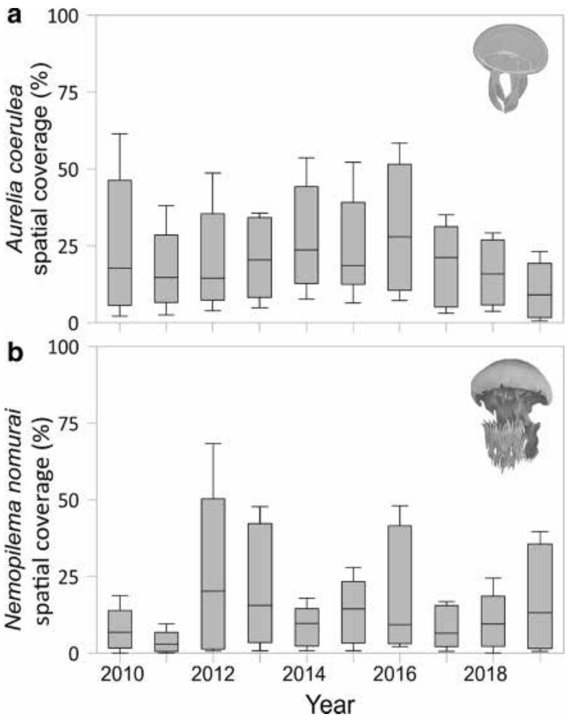

Fig. 2 Interannual variability of the spatial coverage of bloom-former Scyphozoan **a** *Aurelia coerulea* and **b** *Nemopilema nomurai* in the Korean coastal waters from 2010 to 2019. Jellyfish data were gathered from the annual report on the jellyfish appearance in Korean coastal waters established the Korean Jellyfish Monitoring Network (KoJeM)

Effects of environmental factors and jellyfish proliferations on anchovy variance

The strength of the link between anchovy, environmental variability, and jellyfish was quantified by the density distribution of correlation coefficients obtained through bootstrap resampling (Fig. 4). Hydroclimate variability, as indexed by the East Asia climate signal, PC1 Climate (71.23% of total variance), and the temporal pattern of hydrological conditions in Korean waters, PC1 Hydrology (59.35% of total variance) displayed positive correlations with anchovy interannual changes: $r = 0.34$, $P < 0.05$ and $r = 0.71$, $P < 0.01$, respectively. SST showed instead a significant negative correlation with anchovy interannual changes: $r = -0.69$, $P < 0.05$ (Fig. 4a). Figure 4b shows the species-specific jellyfish impact on anchovy interannual changes, as well as the overall jellyfish effect, when averaging the bloom intensity of the two species. We found that the overall effect of jellyfish, PC1 Jellyfish (63.64%) showed a negative correlation ($r = -0.47$, $P < 0.01$), although at the species level a clear negative impact of *N. nomurai* on anchovy was observed, $r = -0.65$, $P < 0.01$, whereas *A. coerulea* displayed a broad variance and not significant relationship.

Changes in catches under jellyfish scenarios

Fisheries production in Korea appeared related to jellyfish bloom scenarios, which are indicative of prominent changes in both quantitative and qualitative catches (Fig. 5). Annual anchovy catches varied under jellyfish scenarios (Fig. 5a), with lower yields observed under in case of blooms of high magnitude, when a decrease of 11.32% was recorded. In contrast, under low bloom magnitude, anchovy catches increased up to 26%. Likewise, a similar pattern was observed in the national fishery production, which showed a decline in the gross weight and economic value under strong magnitude of jellyfish blooms (Fig. 5b). These results show a clear influence of jellyfish blooms on fishery production, the impact

Table 1 Results of generalized additive models (GAM) of leading climate influence on monthly variations of *Aurelia coerulea* and *Nemopilema nomurai* in Korean coastal waters over the period 2010–2019

Response variables	Explanatory variables					
	Time lag (month)	Variable	edf	*p*-value	Adj. R^2	Deviance (%)
Aurelia coerulea	0	PDO	2.328	0.376	0.371	41.0
		ENSO	1.042	0.122		
		EAWM***	1.578	<0.001		
	1	PDO	3.545	0.073	0.319	39.7
		ENSO	3.427	<0.001		
		EAWM***	2.075	0.050		
	3	PDO	1.000	0.988	0.521	55.9
		ENSO*	1.000	0.027		
		EAWM***	4.369	<0.001		
	6	PDO	1.000	0.244	0.668	70.7
		ENSO*	3.599	0.036		
		EAWM***	4.715	<0.001		
	12	PDO	1.001	0.782	0.315	34.5
		ENSO*	1.000	0.015		
		EAWM***	1.457	<0.001		
Nemopilema nomurai	0	PDO	1.000	0.977	0.224	28.3
		ENSO*	3.957	0.035		
		EAWM**	1.000	0.003		
	1	PDO	1.000	0.848	0.328	35.7
		ENSO	1.482	0.668		
		EAWM***	1.000	<0.001		
	3	PDO	1.000	0.060	0.248	28.2
		ENSO***	1.549	<0.001		
		EAWM***	1.000	<0.001		
	6	PDO	1.675	0.749	0.064	12.0
		ENSO	2.005	0.084		
		EAWM	1.000	0.107		
	12	PDO	2.814	0.080	0.260	32.8
		ENSO	3.375	0.170		
		EAWM**	1.000	0.004		

edf indicates the effective degrees of freedom

Significant relationships are indicated with asterisks (*$P<0.05$; **$P<0.01$; ***$P<0.01$)

of which was higher in coastal fishery than at the national scale.

These two factors provide varied configurations that shape the main trend of interannual anchovy catches, although the intensity of the bloom appears as the main driver (Fig. 6a). Indeed, high anchovy catches were observed regardless the duration of the bloom, such as in 2010 and 2011. In the two cases, however, the intensity of the bloom was low. This contrasts with anchovy catches observed under high bloom intensity, where a dramatic decrease of catches was noticed (Fig. 6a). In line with this result, we found a noticeable opposed pattern of interannual variations of anchovy catches and bloom intensity where peaks of anchovy catches occurred during years of low intensity of jellyfish blooms (Fig. 6b).

Discussion

We investigated the interplay between climate, jellyfish, and anchovy in Korean waters. Our findings highlight that massive jellyfish proliferation affects local fisheries production and such interaction can magnify the negative impact that overfishing and warming have on harvested populations.

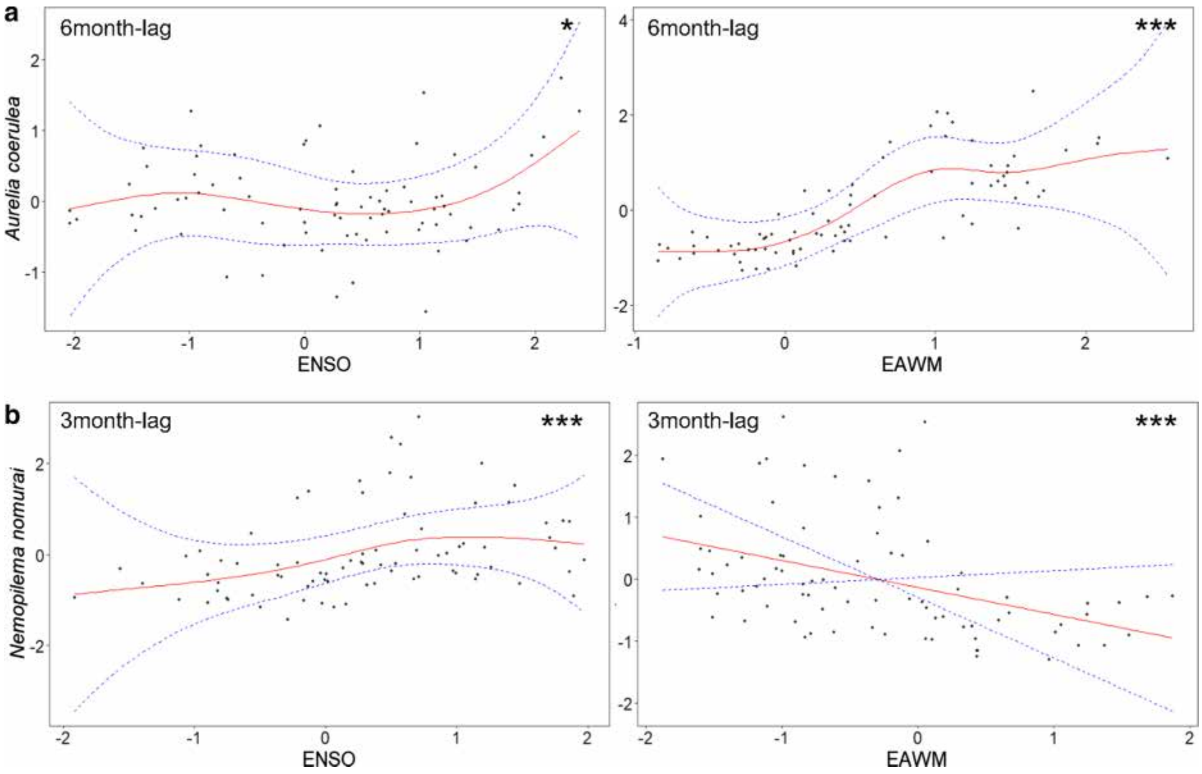

Fig. 3 Climate influence on the two jellyfish species, **a** *Aurelia coerulea* (top panels) and **b** *Nemopilema nomurai* (bottom panels). Top panels correspond to the significant links observed at 6-month lag for *A. coerulea*, while bottom panels show the significant link observed at 3-month lag for *N. nomurai*. Lags denote the time delayed climate effect on monthly variability of jellyfish. Red-thick lines represent the spline fit and blue-dotted lines indicate the 95% confidence interval. Results of GAM are reported in Table 1 and S. Figure 1; $^{*}P < 0.05$; $^{***}P < 0.01$

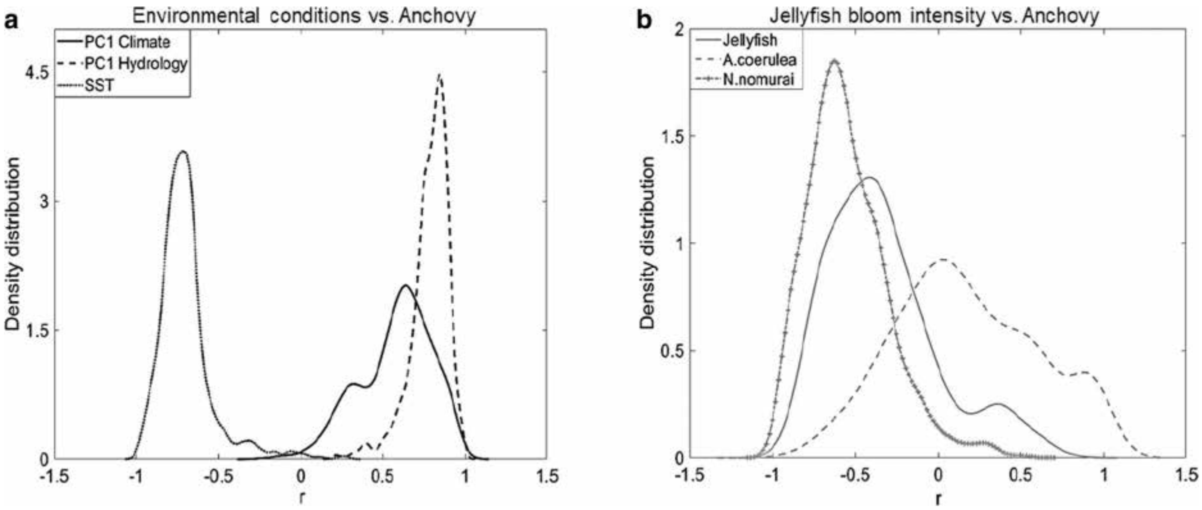

Fig. 4 Assessment of the relationships between **a** anchovy and hydroclimate and **b** anchovy and jellyfish over the period 2010–2019. Link strength is illustrated by the density distribution of correlation coefficients obtained through bootstrap resampling (1000 times)

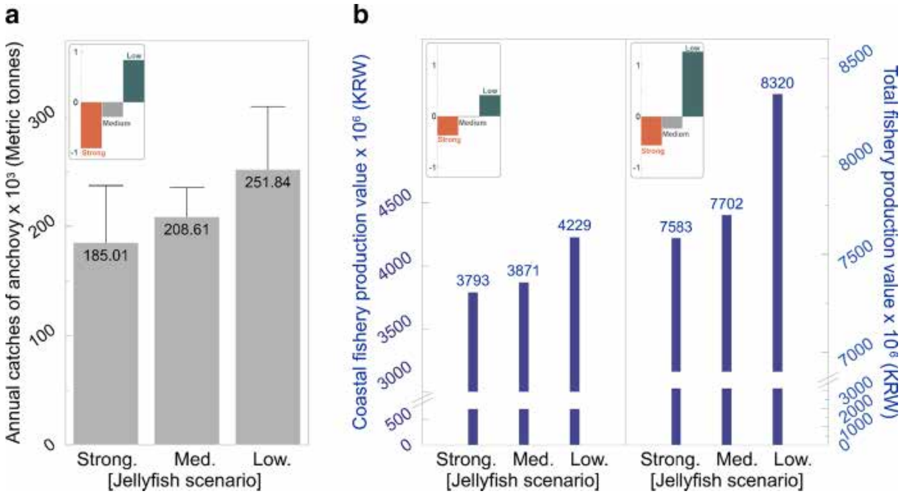

Fig. 5 Assessment of annual changes in Korean fishery production under three jellyfish bloom scenarios, from 2010 to 2019. Assessments are made for **a** Anchovy, coastal, and total fishery catches and **b** Economic value of fishery production in the Korean Peninsula. Inset charts denote the anomalies of fishery production under three jellyfish bloom scenarios: strong–orange, medium–gray, and low–green. Jellyfish bloom scenarios were defined using quantiles of the overall maximum jellyfish bloom intensity (BI_m) during study period. We plotted the three jellyfish scenarios grouped by phase for strong (2012 and 2016, $BI_m > 50.73\%$, Q3) and low (2011 and 2017, $BI_m < 29.52\%$, Q1) magnitude years over the study period. Rest of years were classified as of medium magnitude

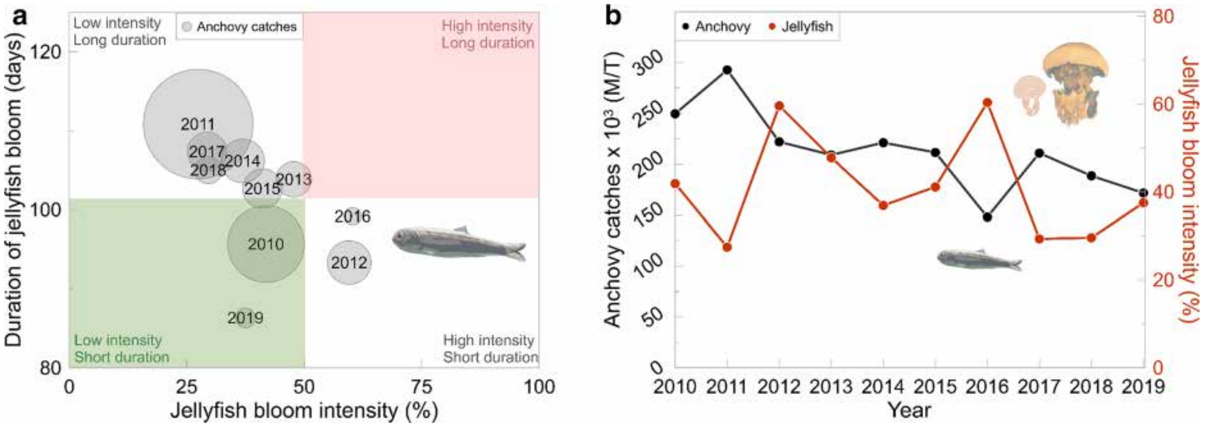

Fig. 6 Interannual variation of anchovy catches relative to **a** jellyfish bloom parameters (intensity and duration). Circles size denotes the relatively magnitude of annual catches. Quadrants indicate the midpoint of each parameter (intensity: 50% of coastal coverage and duration: 102 days); **b** interannual variability of anchovy catches and jellyfish bloom intensity in the Korean coastal waters

Climate variability and East Asian marginal seas

Temporal patterns of oceanographic conditions in the EAMSs are shaped by climate phenomena developing in the subtropical and north Pacific Ocean. Underlying mechanisms are related to the enhanced influence of the Aleutian Low dynamics and westerlies during the positive phase of PDO, which favors lower temperatures in the northern and mid-latitude northwestern Pacific (Huo et al., 2008). PDO represents the leading atmospheric force shaping environmental conditions in the North Pacific (e.g., precipitation, surface air temperature) due to the interaction with large-scale currents and regional wind (Wu &

Li, 2007) and is therefore a useful proxy for the variability of regional hydrological patterns. During the period investigated, we found similar interannual patterns in PDO and ENSO with a dominance of positive values around 2014–2016 (Fig. 1). The concurrence of the positive phase in these major climate patterns influenced local hydrology, promoting a conspicuous decline of chlorophyll after 2014, along with an increase of temperature and salinity. These results agree with former investigations that showed a major influence of PDO, El Niño, and EAWM on local temperature in Korean coastal waters (Kim et al., 2014b; Jung et al., 2021).

Marine ecosystem dynamics is shaped by climate variance through its influence on the pelagic physical environmental, which molds trophic interactions among successive trophic levels. Warming scenarios are expected to disturb plankton communities and marine food webs, i.e., eroding ecosystem structure and resilience, which will likely magnify the impact of growing fishing stress on harvested fish (Möllmann et al., 2021; Scotti et al., 2022). Such scenarios of ecosystem health degradation also promote ecological spaces for opportunistic species, such as jellyfish, which impair harvested populations and rise uncertainties on the governance of coastal marine resources. Our results showed that the close covariation of climate phenomena and local hydrological system leads to cascading effects from climate to jellyfish dynamics in the EAMS and therefore suggest the possibility of using such climate signals for assessing and eventually predict, interannual abundance changes of jellyfish in the Korean Peninsula.

Jellyfish blooms and climate variability

Jellyfish blooms have raised awareness due to their enhanced frequency and magnitude in recent decades (Condon et al., 2013). One of the underlying factors promoting such jellyfish increase is warming, which shapes the water column structure and has been suggested to favor gelatinous taxa (Boero et al., 2016). A close relationship between jellyfish and climate variability has been observed in many regions, such as in the North Sea (North Atlantic Oscillation, NAO, Attrill et al., 2007), the northwestern Mediterranean (NAO, Molinero et al. 2008), the northwest Pacific (PDO, ENSO, and Aleutian Index, AI, Zavolokin, 2011), the northern Gulf of Mexico (PDO, ENSO, and Atlantic Multidecadal Oscillation, AMO, Robinson and Graham, 2012), and the southeastern Pacific Ocean (ENSO, Quiñones et al., 2018; Canepa et al., 2020), although responses are species specific. In EAMSs, the time-varying hydroclimate influence promotes dissimilar responses, as observed in the close link existing between *A. coerulea* and local hydroclimate conditions, while *N. nomurai* is influenced by dominant atmospheric phenomena at larger scales (Lee et al., 2021).

The observed lagged response of *A. coerulea* to climate is likely due to the SST effect on the benthic phase, e.g., polyp strobilation and ephyra release (Wang et al., 2015; Goldstein et al., 2017). Empirical studies have shown that warmer temperatures are a primary factor promoting asexual reproduction of *A. coerulea* polyps, e.g., budding and earlier/number of replicated strobilation (Willcox et al., 2007, Xing et al., 2020) and enhance podocysts production (Han and Uye, 2010; Suzuki et al., 2019). Anomalously strong EAWM reduce the intensity of the Kuroshio Current, thereby weakening thermal mixing and promoting mild winters (Oct–Dec) and warmer spring conditions (Feb–April) in the adjacent Korean waters (Yin et al., 2018). Such hydrographic configuration mainly affects the Yellow Sea and the East China Sea, major nursery areas of *A. coerulea* polyps in the Korean Peninsula and therefore favors their survival, ultimately resulting in the enhancement of bloom intensity. This mechanism explains the positive relationship between this species and EAWM (Fig. S1). Indeed, we have observed that years with higher bloom intensity were concurrent with anomalous, higher winter temperatures, e.g., 2014–2016 (Kwon et al., 2013; Kim et al., 2014b). In addition, salinity changes during spawning seasons have been suggested to induce a delayed settlement and higher mortality of *A. coerulea* planulae due to their weak tolerance to lower salinities (Takao and Uye, 2018). Indeed, marked drops in the population size of *A. coerulea* have been observed concurrently with strong precipitation events during spawning seasons in summers of the year before, e.g., 2013 and 2019 (Fig. 2).

The lagged response shown by *N. nomurai* is due to a wider distributional area coupled with regional hydrographic patterns (Lee et al. 2021). Temperature conditions the year prior the bloom have been shown to favor asexual reproduction and strobilation along with suitable prey fields (Feng et al., 2015; Sun et al., 2015; Lee et al., 2017). In agreement with this influence, we observed a decline of *N. nomurai* during the positive phase of EAWM at three-month lag (Fig. 3) and at 1-year lag (Fig. S1). This response is likely due to the influence of an anomalously strong EAWM that weakens the water mass transport in the following year from February to April (Yin et al., 2018). Temporal patterns of this species are further controlled by the dominant wind field promoting *N. nomurai* transport from its seeding ground (e.g., west China coast) over the Yellow Sea and East China Sea, including the Korea Peninsula (Moon et al., 2010; Yoon et al., 2014; Choi et al., 2018). Hence, the intensity of *N. nomurai* bloom is closely intertwined with climate-driven effects, i.e., weakening of current dynamics and enhanced thermal changes (Fig. S1).

Interplay between jellyfish and forage fish

Our results provide evidence on the magnitude of jellyfish blooms on ecosystem provisioning services. These results are in line with previous reports and advocate for external forces, other than only hydrographic variations, as main drivers of anchovy recruitment (Yoo et al., 2018). Indeed, the hydrological differences in July 2015 and July 2016 did not explain a strong decline ca. 88% observed in anchovy small size classes (Yoo et al., 2018). Instead, the anchovy decline was concurrent with the observed massive bloom of *N. nomurai* that covered ca. 50% of the South Korean coast in July 2016 (National Institute of Fisheries Science, 2019). We hypothesize that strong blooms of *N. nomurai* act as a superposed top-down effect on both fish eggs and zooplankton, the main food item for anchovy larvae (Lee et al., 2017; Wang et al., 2022). Similar negative impacts of jellyfish have been reported on the relative biomass of anchovy in the Eastern Bering Sea, the Northern California Current, and the Northern Peruvian Current (Decker et al., 2013; Quiñones et al., 2013). Such observational evidence suggests that jellyfish are an essential indicator of the ecosystem state and should be considered in local fish stock assessments.

Ecological interactions driving the relationship between jellyfish and forage fish are mostly ascribed to diet overlaps. One well-known example is given by the intraguild competition between the comb jelly *Mnemiopsis leidyi* and anchovy in the Black Sea, which helps understanding why gelatinous zooplankton tends to prevail over forage fishes (Bodini et al., 2018). The competitive advantage is partly explained by the positive effect of warming on jellyfish growth. Moreover, these latter are more effective than forage fish in consuming shared prey (e.g., copepods), and the predation of jellyfish over the larvae of forage fishes strengthens the food web prevalence of these gelatinous carnivores. Furthermore, the jellyfish predation impacts the development of fish larvae due to their similar prey spectrum, e.g., zooplankton (Boero et al., 2016).

Another factor favoring jellyfish is the overlapping of the critical period for anchovy annual recruitment, from spring to summer (Lee & Kim, 2007; Takasuka et al., 2008; Kim et al., 2013b), with the recurrent timing of jellyfish blooms in the Korean Peninsula (Lee et al., 2021). This match suggests severe adverse conditions for anchovy due to the potential reduction of food availability, i.e., prey diversity and amount, which is critical for its recruitment (Fig. 4b). Indeed, it has been shown that fish recruitment is affected by both food amount and quality (Durant et al., 2005). In this line, stable isotope analysis has provided support on the competition for the same prey between anchovy and the two Scyphozoans here investigated (Shoji et al., 2009; Wang et al., 2022). These implications are likely to induce lower reproduction rates and higher mortality of anchovy due to the reduction of food availability or food quality (Báez et al., 2022). Furthermore, jellyfish impact also occurs on anchovy eggs, which reach up to 77% of total plankton biomass in the Korean coast and estuaries during summer (National marine ecosystem monitoring program; MOF, 2020). This may explain the observed opposite interannual trends of anchovy catches and jellyfish (Fig. 6b and Fig. S2).

The spatial co-occurrence of anchovy eggs and larvae with coastal jellyfish blooms warns on the risks of dramatic impacts during massive blooms. During strong jellyfish blooms the loss of coastal fishery economic value reached ca. 435,616 million KRW (≈36.3 million USD) (Fig. 5b). Eggs predation by jellyfish may thus explain the decline in anchovy catches concurrent with bloom periods, e.g., 2016 (Fig. S3). Hence, massive jellyfish proliferations not only impeded fish recruitment but also precluded the fishing activity, as observed during the recurrent interference of jellyfish with the most employed devices in coastal fishery, i.e., the set-net fishery, which is the main gear used in summer (Kim et al., 2013a), for example, over the period 2006–2010, jellyfish caused a drop of 26.8% in set-net catches (Kim et al., 2012).

The ecological interaction between the forage fish reduction and large jellyfish productivity has been assessed by numerical simulations that have shown negative feedbacks, i.e., the removal of forage fish being concurrent with high jellyfish productivity (Chiaverano et al., 2018). Our results are further in line with the proposed "jellyfish-spiral" concept (Uye, 2011), where a dominance of jellyfish impairs the energy flow to high trophic levels, thereby affecting the ratio fish: primary production (Sommer and Stibor, 2002; Ruzicka et al., 2012), ultimately weakening fish production. Hence, a predominance of jellyfish should be regarded as one of the additive factors in heavily reduced fish recruitment, hampering not only the resilience of the ecosystems but also jeopardizing the provisioning ecosystem services provided by fishery (Lynam et al., 2006; Purcell, 2012; Graham et al., 2014; Schnedler-Meyer et al., 2016).

Challenges for provisioning ecosystem services and sustainable fisheries

Jellyfish blooms affect fisheries in various ways. Jellyfish may in fact modify marine food web structure by reducing food availability for fish larvae and planktivorous fish. Moreover, they prey on fish eggs and larvae, thereby affecting fish recruitment. Massive proliferations interfere with fishing operations, i.e., clogging and bursting nets, increasing the sorting time of fish catches and stinging fishermen (Uye, 2008 and references therein). In South Korea, the annual direct damage caused by jellyfish has been estimated to be between US$ 68.2 million and US$ 204.6 million and, under massive blooms, they have caused a drop of ca. 25% of the annual fisheries production (Kim et al., 2012).

By virtue of their ecological role, structural changes in forage fish populations can destabilize the trophic balance in food webs (Roux et al., 2013) and therefore imperil fundamental ecosystem services. From a socio-ecological perspective, the benefit of forage fish as source of nutrients to humans has been economically estimated in 7.1 billion USD per year (Konar et al., 2019). However, projected scenarios forewarn that the fish stock availability may downslope under growing global anthropogenic stressors, e.g., warming, overexploitation, and pollution (Pauly et al., 2002; Lotze et al., 2019), which are further magnified by the synergies of these factors and jellyfish. This is likely occurring in the Korean Peninsula, a highly productive fisheries ground, but heavily exposed to climate change and anthropogenic stressors.

We engage in global conservation for safeguarding oceans and their resources to balance food security and ecosystem health, as stated in the UN Sustainable Development Goal 14. Since growing coastal societies and projected high population densities suggest a larger demand for marine ecosystem services in future, there is a pressing need to develop holistic approaches to preserve the health and productive use of exploited resources (Kim et al., 2018). Building a strategic framework beyond current fishery management is therefore a major challenge that requires incorporating pertinent human-driven environmental degradation factors and the synergetic interplay of ecological feedback and climate change, along with multilateral cooperation (Takasuka et al., 2008). By showing the prominent role of jellyfish on the provisioning of ecosystem services in the Korean Peninsula, our findings shed light on the importance of this group as a critical indicator in fish stock assessment. Hence, integrating jellyfish into ecosystem-based management is essential for achieving sustained resources management and secure healthy seas and their governance.

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Data availability Data used to support the findings of this study are included in the manuscript and the Supplementary Material.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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