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Nonstationary response of commercially pelagic species in the Humboldt current ecosystem to climate variability

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Abstract In this study, the four most important species in the Humboldt Current System (HCS), *Engraulis ringens, Sardinops sagax, Trachurus murphyi*, and *Dosidicus gigas* were linked to four climate indices, sea surface temperature (SST) and wind speed (WS) based on multivariate statistical analyses, aiming to explore their nonstationary responses to climate variability. Significant decadal variations in the catches were identified, with regime shifts in the mid-1970s, early 1990s, and late 1990s. These shifts corresponded well to climatic and environment regime shifts during these periods. However, the response patterns to climate and environmental variations varied among species. Compared with other physical drivers, seawater temperature, wind

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X. Chen · Y. Li · W. Yu National Engineering Research Center for Oceanic Fisheries, Shanghai Ocean University, Shanghai 201306, China speed, the Pacific Decadal Oscillation (PDO), and the North Pacific Gyre Oscillation (NPGO) had greater ecological importance in driving changes in the four pelagic species. The variations in the important climate events influenced seawater temperature and wind speed fluctuations within the HCS, impacting on these commercially important pelagic species. Furthermore, non-stationarity was identified in the relationships between climate/environment and species catches, with different species showing different threshold years. The non-stationarity may be attributed to the transitions between warm and cold periods within the HCS, as well as shifts between strong and weak phases of pressure system. This study helps further understand changes in the HCS caused by fluctuations in climate and environment.

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Introduction

An increasing number of studies emphasize the presence of non-stationary relationships between individuals, populations, or ecosystem structure and climate/ environment in complex marine ecosystem. These findings highlight the relationship between biology and climate factors characterized by discontinuous nonlinear dynamics (Wolkovich et al. 2014; Vasilakopoulos et al. 2017; Litzow et al. 2018; Damalas et al. 2021). For instance, in the North Sea ecosystem, the relationship between cod and sea surface temperature (SST) shifted in the 1970s, associated with nonlinear changes in ecological thresholds and nutrient amplification within the ecosystem (Kirby and Beaugrand 2009). In the Gulf of Alaskan, relationship between biological abundance and climate was evaluated, it weakened or reversed in the late 1980s, consistent with increased variance in the North Pacific Gyre Oscillation (NPGO) (Puerta et al. 2019). With regard to the North Pacific Ocean, non-stationarity in climate and ecosystem was found, as well as spatial difference in non-stationary between northwest and northeast Pacific (Ma et al. 2020). Therefore, analyzing the nonstationary relationship between biological and abiotic factors, as well as the underlying mechanisms, is crucial for elucidating the effects of climate variability on species or ecosystem changes. This process is essential for formulating adaptive management strategies based on the consideration of the ongoing changes in climate conditions (Williams and Jackson 2007; Dormann et al. 2013; Litzow et al. 2018; Ma et al. 2020).

The Humboldt Current System (HCS) is a highly productive eastern boundary upwelling ecosystem, influenced by seasonal or permanent coastal upwelling (Fig. 1) (Cruz et al. 2022). This ecosystem is characterized by its susceptibility to El Niño–Southern Oscillation (ENSO) events; high productivity of pelagic fishes; and presence of shallow, intense oxygen minimum zones (OMZ) (Gutiérrez et al. 2016; Ramos et al. 2022; Yu and Wen 2022). The HCS is abundant in four typical, pelagic important economic species (PIES), *Engraulis ringens*,



Fig. 1 Schematic diagram of the currents and distribution of four important pelagic species within the study area. Both solid and dashed arrows indicate ocean currents, with blue representing cold currents and red representing warm currents.

Sardinops sagax, Trachurus murphyi, and Dosidicus gigas (Cruz et al. 2022; Ramos et al. 2022). These species are crucial energy pathways in the ecosystem, exerting wasp-waist control that influence the stock dynamics of both zooplankton and top predators, such as large fishes, seabirds, and marine mammals (Cury et al. 2000; Fréon et al. 2009). Significant fluctuations in the abundance of these species often affect the community composition, and even the entire ecosystem structure variations (Salvatteci et al. 2019; Gonzalez-Pestana et al. 2022; Yu and Wen 2022). Therefore, these four species have been the primary research focus for understanding the long-term ecosystem dynamics in the HCS driven by climate variability (Alheit and Niquen 2004; Alheit et al. 2009; Salvatteci et al. 2019).

Regarding to the four important pelagic species in the HCS, *E. ringens* primarily inhabits the coast of south America, covering the upwellings and other coast cold water masses with high productivity, which is directly affected by the changes in the trophic dynamic relationship of diatoms, large copepods, and euphausiids (Bertrand et al. 2011; Moron et al. 2019; Salvatteci et al. 2019; Briceno-Zuluaga et al. 2023). *S. sagax* primarily inhabits waters with higher sea water temperature and abundant biomass of small phytoplankton and zooplankton (Bertrand et al. 2004; Politikos et al. 2018; Moron et al. 2019; Salvatteci et al. 2019). T. murphyi and D. gigas are both the highly migratory species, adapting well to a wide temperature range. Specially, T. murphyi tends to favor habitats with higher dissolved oxygen concentrations (Bertrand et al. 2016; Li et al. 2016; Yu and Chen 2018; Yu et al. 2019, 2021). Numerous studies indicates that the life history characteristics including growth and reproduction, of these four species are highly sensitive to environmental variables, such as seawater temperature, wind field (referring to the 3D spatial patterns of the winds, including direction, intensity, and variations across different altitudes), etc (Bertrand et al. 2016; Li et al. 2016; Yu et al. 2021, Belkin and Shen 2023). Climate and environmental changes can drive variations in abundance and distribution of these species (Yu et al. 2021; Flores-Valiente et al. 2023). For example, El Niño and Pacific Decadal Oscillation (PDO) events influenced the spawning, distribution and catch of E. ringens and S. sagax, leading to shifts in dominant species during the early to mid-1970 (Alheit and Niquen 2004; Niquen and Bouchon 2004; Hernández-Santoro et al. 2019; Salvatteci et al. 2019). Under the cold phased of ENSO and PDO, changes in sea surface temperature and sea surface height within the HCS induced the expansion of suitable habitat area for D. gigas (Yu et al. 2019, 2021). Additionally, composition variations of plankton within the HCS can affect the abundance and distribution of T. murphyi (Bertrand et al. 2016).

However, current research on PIES within the HCS has primarily considered the responses to climate and environmental factors to be stable, and the non-stationarity in the relationships between these factors over time has not been evaluated (Salvatteci et al. 2014, 2018; Li et al. 2016). Therefore, to further analyze the response of PIES in the HCS to climate and environment variations, E. ringens, S. sagax, T. murphyi, and D. gigas were selected as the research targets in this study, on the basis of their total annual catch exceeding 1 million tons and extremely climatesensitive life history characteristics. The combination of PIES catch data with climate, SST, and wind speed (WS) data was used to analyze the long-term trends in catches of these species and their nonstationary responses to climate stressors. Furthermore, the potential mechanisms by which climate variability drives the regime shifts in PIES catches were also explored. The main objectives of this study are as follows: (1) to analyze the long-term changes in climate, regional environment, and PIES catches in the HCS; (2) to identify regime shifts in climate, environmental variables, and PIES catches; and (3) to investigate the non-stationarity in the evolving relationship between PIES catches and abiotic factors such as climate and regional environment in the HCS. The findings of this study can provide essential insight for the scientific management of fisheries resources and ensuring the resilience of long-term predictions concerning the impacts of climate change.

Materials and methods

Climate, environment, and biology data

PDO index (http://research.jisao.washington.edu/pdo/ PDO.latest.txt), Southern Oscillation Index (SOI, https://www.esrl.noaa.gov/psd/enso/dashboard.html), NPGO (http://www.o3d.org/npgo/), sea surface temperature in the Niño 1+2 region (Niño 1+2, https:// www.esrl.noaa.gov/psd/enso/dashboard.html), as well as SST and WS, were chosen to characterize the variations in large-scale climate, regional seawater temperature and wind field conditions in the HCS. These climate indices and environmental variables are well documented and have been associated with the responses of species, fish communities, and ecosystem structures to variations in climate and environment in the Pacific region (Bertrand et al. 2004; Salvatteci et al. 2018; Li et al. 2022; Tam et al. 2021). Monthly climate indices data were obtained from publicly available datasets from 1950 to 2019. The monthly SST and WS grid data, with a resolution of $0.5^{\circ} \times 0.5^{\circ}$, were derived from the Hadley Centre observations datasets (https://www.metoffice.gov.uk/ hadobs/hadisst/) and reanalysis datasets (https://psl. noaa.gov/data/gridded/data.ncep.reanalysis.html), respectively, covering the spatial range of 71-90°W, 4-54°S during the same period (Gutiérrez et al. 2016).

The reconstructed catch data for these four PIES were sourced from the Large Marine Ecosystem (LME) dataset within the Sea Around US (http://www.seaaroundus.org/; Zeller et al. 2016; Liang et al. 2018), covering the period from 1950 to 2019.

These data were derived from the fisheries database of the Food and Agriculture Organization (FAO) and national datasets from countries bordering this ecosystem, taking into account discards during the fishing processes (Pauly and Zeller 2016; Zeller et al. 2016; Liang et al. 2018). Compared with previous studies on biomass or resource abundance changes for these species, the biomass trends relatively align well with the catch trends within the subset of the time series in this study, which indicates that these catch data could well reflect the changes in the true population dynamics (Fig. S1) (Arancibia and Neira 2008; Cahuin et al. 2015; Oliveros-Ramos et al. 2017; Yatsu and Kawabata 2017; Oozeki et al. 2019). Therefore, the reconstructed catch data were used for the analysis of regime shift related to the climate variability.

Dominant patterns of the regional environment

An empirical orthogonal function (EOF) analysis was employed to examine the primary variation patterns of SST and WS in the HCS (Litzow et al. 2018; Wang et al. 2022). EOF analysis, also known as eigenvector analysis or principal component analysis (PCA), decomposes a physical field containing m spatial points that vary with time into nontemporal spatial modes and temporal patterns (Hannachi et al. 2007; Litzow et al. 2018). This enables the spatiotemporal analysis of irregularly distributed grid points within a limited area (Litzow et al. 2018). In this study, spatial modes and time coefficients (shortened as EOFs) were calculated and the first two principal components for each were retained to focus on the dominant variation patterns of SST and WS within the HCS.

Regime shift detection

In this study, regime shift is defined as dramatic, abrupt changes in species catch association with multiple variables (Alheit and Niquen 2004; Conversi et al. 2015; Heymans and Tomczak 2016; Tian et al. 2023). Multiple regime shift detection methods were employed to detect trends and regime shifts in the time series of climate indices, EOFs, and PIES catches, including a sequential *t*-test analysis of regime shift (STARS), change point analysis, and Bayesian change point analysis (Zeileis et al. 2003; Rodionov 2004, 2006; Aminikhanghahi and Cook 2017; Tian et al. 2023). After exploratory analyses

with STARS, the cut-off length (L) and Huber weighting factor were set to 15 and 1, respectively, with a significant level of 5%. Additionally, sensitivity analyses of L for STARS and h for change point analysis were conducted to identify uncertainty in the results of STARS and change point analysis. Specifically, L was varied from 10 to 20 in equal increments over 1000 runs of STARS, and h was varied from 0.1 to 0.3 in equal increments over 1000 runs of change point analysis. Subsequently, the time nodes with higher frequencies were identified as regime shifts in climate indices, EOFs, and PIES catches. The STARS was conducted using the code provided by Stirnimann et al. (2019), while the change point analysis and the Bayesian change-point analysis was carried out using 'strucchange' and 'bcp' packages in R, respectively.

Relationship between species catch and physical drivers

A correlation analysis was employed to explore the linear relationships among climate indices, EOFs, and PIES catches (Tian et al. 2006; Litzow et al. 2018; Ma et al. 2019, 2020). In the correlation analysis, the impact of autocorrelation is mitigated by adjusting the degrees of freedom in the significance test of the correlation coefficient (Chelton 1984; Pyper and Peterman 1998; Litzow et al. 2018). The specific methods are as follows (Chelton 1984; Pyper and Peterman 1998; Litzow et al. 2018):

$$\frac{1}{N^*} \approx \frac{1}{N} + \frac{2}{N} \sum_{j=1}^{\infty} \frac{(N-1)}{N} r_{XX} r_{YY}$$
(1)

where N* and N represent effective degree of freedom and the length of time series, respectively. The r_{XX} and r_{YY} represent the autocorrelations of variable X and Y at a lag of j years, respectively.

A random forest (RF) analysis was employed to determine the contribution of climate and environmental changes to the variations in each PIES catch within the HCS (Howard et al. 2014). RF is an extension of decision trees, generating a large number of bagged decision trees through randomization and combining their outputs using voting or averaging (Breiman 2001; Xu et al. 2024). This method reveals significant interactions and nonlinear effects of predictor variables, and measures the relative importance of predictor variables on the response variable (Siroky 2009; Luan et al. 2020). In this study, the predictor variables for RF included climate indices and EOFs of environmental variables, while the response variable was each PIES catch. After exploratory analysis, the number of trees (n_{tree}) and the m_{try} were set to 500 and 2 for all PIES, respectively. Additionally, predictive performances were evaluated using a five-fold cross-validation approach, in which the predictor and response datasets were randomly partitioned into five equal-sized folds. During the cross-validation, 4/5 of the data was used for model training and the remaining 1/5 for testing, repeated 100 times for each PIES. The RF was conducted using the 'randomForest' package in MATLAB.

Generalized additive models (GAM) and threshold generalized additive models (TGAM) were employed to assess the response relationships between PIES catches in the HCS and climatic and environmental variations (Tsimara et al. 2021; Polo et al. 2022). GAM assumes an additive and stationary relationship between the response variables and explanatory variables, while TGAM captures abrupt changes in their relationship during specific years (Ciannelli et al. 2004; Casini et al. 2009; Damalas et al. 2021; Hidalgo et al. 2022; Polo et al. 2022). For both GAM and TGAM, the response variables were the PIES catches in the HCS, while the predictors included climate indices and EOFs. To avoid the issue of collinearity among predictor variables and to identify whether there is a non-stationary response of species catch to each predictor variable, only one predictor was considered in each model run for GAM and TGAM. The distribution family and link function for both GAM and TGAM were Gaussian and identity, respectively. A "stationary" relationship formulated by GAM is more suitable for fitting a single function across the entire time series (Ciannelli et al. 2004):

$$Y = \alpha + s(X) + \in \tag{2}$$

where Y represent the response variables, X represent the predictors, and *s*, α and ϵ represent smooth function (with k \leq 3 to avoid overfitting), intercept, and error terms, respectively. On the contrary, a "non-stationary" relationship assumed by TGAM is better for fitting different functions across different time periods (Puerta et al. 2019):

$$Y(t) = \begin{cases} \alpha + s(X) + \in_t, & \text{if} t < y \\ \alpha + s(X) + \in_t, & \text{if} t \ge y \end{cases}$$
(3)

y is the threshold year that separates different time period with response variables to predictors, which is selected by minimizing the generalized cross validation (GCV) after running the model for every possible threshold year between the 0.1 lower and the 0.9 upper quantiles of the time series (Casini et al. 2009; Vasilakopoulos et al. 2017). The "genuine" cross-validation squared prediction error (gCV), proposed by Cianelli et al. (2004), was used to compare the fitness of GAMs and TGAMs with the response and explanatory variables and select the optimal model, which considered the estimation of the threshold line and the degrees of freedom for the functions in all stationary and nonstationary formulations (Vasilakopoulos et al. 2017; Hialgo et al. 2022). The basic GAM and TGAM functions used are included in the R package mgcv.

Results

Climate and regional environment variability

There were substantial variations in the climate indices on a decadal scale except SOI and Niño 1+2 (Fig. 2). The PDO phase showed negative and positive fluctuations, with regime shift in 1975/76. A transition from a negative phase before an abrupt change to a positive phase occurred in NPGO, corresponding to regime shift in 1997/98. SOI and Niño 1+2 both remained stable from the 1950s to the 2010s, displaying significant interannual fluctuations but without regime shifts. The correlation results showed that PDO was positively correlated with Niño 1+2 (r = 0.54, p < 0.001) but negatively correlated with SOI (r = -0.63, p < 0.001); SOI were negatively correlated with Niño 1+2 (r = -0.64, p < 0.001) and positively correlated with NPGO (r = 0.39, p < 0.05), respectively.

The first two modes of the SST in the HCS had a cumulative explanation of 72.69% of seawater temperature variance, while that of WS was 50.99% (Fig. 3). EOF1SST revealed a long-term upward trend, whereas EOF2SST shifted from a negative phase before the regime shift node to a positive afterward, with regime shifts in 1976/77 and 1997/98,

Fig. 2 Variations in climate indices A, the sensitivity results of STARS and change point analysis B (up-panel), and posterior probability and the 95% confidence intervals from 1000 model runs of Bayesian change point analysis B (low-panel). The bars represent the climate indices and time nodes with considerable probability of regime shifts, while the line graphs represent the regime means of the climate index detected by the sequential t-test analysis of regime shifts (STARS) in section A. The red and black bars represent the sensitivity results of STARS to cut-off length and h to change point analysis for climate indices in section B (uppanel), respectively. The black lines represent the posterior probability from 1000 model runs of Bayesian change point analysis, while gray and blue lines represent upper confidence and lower confidence from 1000 model runs of Bayesian change point analysis in section B (low-panel), respectively.



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respectively. EOF1WS shifted from a negative phase before the mid-1990s to a positive phase afterward, while EOF2WS transitioned from a negative phase before the 1980s to a positive phase afterward, with regime shifts in 1975/76 and 1995/96 for EOF1WS, and in 1972/73 for EOF2WS, respectively. The correlation results indicated that EOF1SST showed a positive correlation with PDO (r = 0.67, p < 0.001) and Niño 1+2 (r = 0.74, p < 0.001), but a negative correlation with SOI (r = -0.61, p < 0.001), whereas EOF2SST exhibited a negative correlation with Niño 1+2 (r = -0.42, p < 0.05) and a positive correlation with SOI (r = 0.40, p < 0.05).

Variations in species catch

The proportion of pelagic species in the total pelagic group catch was highest for *E. ringens*, followed by *S. sagax*, *T. murphyi*, and then *D. gigas*. The cumulative catch of these four species accounted for more than 94% from 1950 to 2019 (Fig. 4A-left). In line with the overall trend in pelagic group catch, the total catch of PIES showed a long-term increase from the late 1960s to the mid-1990s, followed by a decline (Fig. 4A-right).

The variations in catch volumes of PIES in different countries or regions exhibited notable disparities (Fig. 4B-left). For E. ringens, Peru had significant interdecadal variations, with an increase in the 1960s and from the mid-1980 to the early 1990s, and a decline in other periods. In Chile, changes in catch were relatively small, ranging from 0 to 3 million tons overall. Regarding S. sagax, catch volumes were high in both Peru and Chile, exhibiting a synchronized upward trend in the mid-1970s followed by a decline in Peru from the early 1990s and in Chile from the late 1980s. For T. murphyi, Chile had the highest catch volumes, showing a prolonged increase from the mid-1970s to the mid-1990s, followed by a gradual decline in the other periods. In contrast, the changes in catch in Peru were relatively small, with the highest annual catch being less than 1 million tons. For D. gigas, Peru had the highest catch of all countries and regions, experiencing a significant increase since the late 1990s, followed by a decrease in the mid-2010s. Chile was next, with the catch increasing in the early 2000s and the 2010s, reaching an annual peak about 310,000 tons. Meanwhile, the catch in China showed a long-term increase since 2000, with the highest annual catch being 130,000 tons in 2014.

The variations in catch of PIES exhibited significant difference (Fig. 4B-right and C). Catch for *E. ringens* showed significant interdecadal changes with two regime shifts in 1971/72, and 1991/92. *S. sagax* catch volumes increased from the mid-1970s to the mid-1980s, followed by a decline, with regime shifts occurring in 1975/76 and 1991/92. The catch volume of *T. murphyi* exhibited an overall increase from the mid-1970s to the mid-1990s, followed by a decline, with two regime shifts in 1976/77 and 1997/98. In contrast, the catch of *D. gigas* showed a significant increase from the early 2000s, with a regime shift in 1998/99.

Effects of climate and environment on changes in species catch

Regime shifts in the PIES catches in the HCS revealed a synchronic response to climate and environmental variations (Table 1). In the mid-1970s, the regime shifts in catches of *S. sagax* and *T. murphyi* corresponded to EOF1SST, EOF1WS, and PDO regime shifts. In the late 1990s, the regime shifts in catches of *T. murphyi*, and *D. gigas* corresponded to EOF2SST and NPGO regime shifts. Additionally, the correlation results between climate, environment, and species showed that the catch of *D. gigas* was positively correlated with EOF2SST (r = 0.43, p < 0.01) and EOF1WS (r = 0.73, p < 0.001).

RF analysis results showed difference in the importance of climate indices and environment on the variations in the PIES catch (Fig. 5). The important climate indices and environmental variables were EOF2WS, EOF1WS, and EOF2SST for E. ringens catch ($R^2 = 0.6704$, RMSE = 0.2143), while that is EOF1WS, EOF2WS, and PDO for S. sagax catch (\mathbb{R}^2) = 0.7212, RMSE = 0.1729). For the variation in T. murphyi catch, the importance climate and environment were EOF2WS, PDO, and EOF1SST ($R^2 =$ 0.7014, RMSE = 0.2048), while the major driving factors affecting the D. gigas catch were EOF1WS, EOF2SST, and NPGO ($R^2 = 0.7429$, RMSE = 0.181).TGAMs provided a better fit for the relationship between PIES catches and physical drivers than GAMs (Fig. 6). Different years were distinguished by the threshold year based on the variations in GCV, indicating an alteration in the relationship between



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Fig. 3 Variations in the first two modes of sea surface temperature and wind speed within the Humboldt current system (HCS) A, the sensitivity results of STARS and change point analysis B (up-panel), and posterior probability and the 95% confidence intervals from 1000 model runs of Bayesian change point analysis B (low-panel). The bars represent the empirical orthogonal functions (EOFs) of the environment and time nodes with considerable probability of regime shifts, while the line graphs represent the regime means of the EOFs detected by the sequential t-test analysis of regime shifts (STARS) in section A. The red and black bars represent the sensitivity results of STARS to cut-off length and h to change point analysis for EOFs in section **B** (up-panel), respectively. The black lines represent the posterior probability from 1000 model runs of Bayesian change point analysis, while gray and blue lines represent upper confidence and lower confidence from 1000 model runs of Bayesian change point analysis in section B (low-panel), respectively.

PIES catches and physical drivers (Fig. 7). The bestfitted model for the catch of *E. ringens* was non-stationary, with EOF2WS as the driver and the threshold year identified as 1991/92. Similarly, For the catches of *S. sagax*, *T. murphyi*, and *D. gigas*, the best-fitted models exhibited non-stationary, with EOF1WS as the driver and threshold years identified as 1975/76, 1980/81, and 2002/03, respectively. The best-fitted TGAM curves exhibited distinct patterns before and after the selected threshold years, indicating a shift in the relationship between PIES catches and physical drivers across these threshold years.

Discussion

PIES response to climatic and environmental variations

To explore the long-term variations in PIES catches in the HCS and the response patterns to driving factors, four PIES with relative high catches were chosen as the research targets, *E. ringens*, *S. sagax*, *T. murphyi*, and *D. gigas*, in combination with climate and environment data. Significant interannual and interdecadal variations in the PIES catches were identified, which strongly respond to climate and environmental changes, but the response patterns showed both similarities and differences (Table1, Figs. 4 and 5).

In the mid-1970s, regime shifts in *S. sagax* and *T. murphyi* catches mainly responded to their important influencing factors such as EOF1SST, EOF1WS,

and PDO, characterized by higher catches of them (Table 1, Figs. 4 and 5). The spatial modes of EOF-1SST and EOF1WS both demonstrated strong consistency, reflecting the long-term variations in sea surface temperature and wind speed within the HCS region (Figs. 3 and S2). In the HCS region, resources abundance and distribution of species may be primarily related to physical processes such as upwelling transport (Montecinos and Gomez 2010). Sea temperature and wind are key driving factors influencing the variability in upwelling intensity (Shi et al. 2023; Yari et al. 2023). Generally, higher wind speeds and lower sea temperatures promote Ekman transport, thereby enhancing upwelling intensity (García-Reyes and Largier 2010; Putri et al. 2021; Shi et al. 2023; Yari et al. 2023). For S. sagax, PDO and EOF1WS, as the importance influencing factors for its catch variation, exhibited opposite change trends, indicating that the HCS exhibited regional environment characterized by lower upwelling intensity and warmer conditions (Figs. 2, 3 and 5) (Quintana and Aceituno 2012; Jacques-Coper and Garreaud 2015; Tam et al. 2021; Cruz et al. 2022). Affected by warmer waters, biomass of large phytoplankton and zooplankton such as diatoms, large copepods, and euphausiids sharply declined, while the biomass of small phytoplankton (such as dinoflagellates) increased (Alheit and Niquen 2004; Van der Lingen, et al. 2006; Rykaczewski and Checkley 2008; Bertrand et al. 2011). This transformation created favorable conditions for the growth of S. sagax, leading to higher catch of this species (Alheit and Niquen 2004; Bertrand et al. 2004, 2011). The catch of T. murphyi was influenced by cold coast water and surface subtropical water (Dioses 2013). As the important influencing factors, PDO and EOF-1SST showed same change trends, indicating that the southeast Pacific subtropical anticyclone weakened due to the transition of PDO (Figs. 2, 3, and 5) (Alheit and Niquen 2004; Bertrand et al. 2004). This change further led the oceanic subtropical water masses with warm temperature to shift into the coastal areas. As a result, warm, low-salinity equatorial and tropical surface waters dominated the ecosystem regions, favoring the development of the T. murphyi and consequently increasing its catch (Alheit and Niquen 2004; Bertrand et al. 2004, 2016; Dioses 2013; Ancapichún and Garcés-Vargas 2015).

Moreover, under the effects of climate variability, species interactions may also influence the population



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◄Fig. 4 The proportion of total catch of pelagic important economic species (PIES) in the pelagic group total catch A (left), interannual variations in total catch of PIES and pelagic group total catch A (right), catch variations in fishing countries or regions of PIES B (left), decadal variations in PIES catch anomalies of B (right), the sensitivity results of STARS and change point analysis for PIES catches C (up-panel), and the 95% confidence intervals from 1000 model runs of Bayesian change point analysis C (low-panel). The bars represent PIES catches anomalies and time nodes with considerable probability of regime shifts, while the line graphs represent the regime means of catches anomalies detected by the sequential t-test analysis of regime shifts (STARS) in section B (right). The red and black bars represent the sensitivity results of STARS to cut-off length and h to change point analysis for PIES catches anomalies in section C (up-panel), respectively. The black lines represent the posterior probability from 1000 model runs of Bayesian change point analysis, while gray and blue lines represent upper confidence and lower confidence from 1000 model runs of Bayesian change point analysis in section C (low-panel), respectively.

dynamics of these PIES. As the rise in seawater temperatures and the coastal advancement of the warm oceanic subtropical water mass also expanded the overlapping areas in the spatial distribution of E. ringens, S. sagax, and T. murphyi (Muck and Sanchez 1987). This expansion increased the chances of T. murphyi preying on E. ringens juveniles and adults, and S. sagax consuming E. ringens eggs, negatively affecting the *E. ringens* population (Muck and Sanchez 1987; Alheit and Niquen 2004). Conversely, for T. murphyi and S. sagax, the enhancement of favorable environmental conditions and increased feeding opportunities have a positive impact on their populations. This further influences the asynchronous pattern within this period, characterized by low E. ringens resources and high resources of S. sagax and T. murphyi (Arcos et al. 2001; Gutiérrez et al. 2016, 2017, 2019; Salvatteci et al. 2018).

In the late 1990s, regime shifts in *T. murphyi* and *D. gigas* catches mainly responded to their important influencing factors such as EOF2SST and NPGO, characterized by an increase in *D. gigas* but a decrease in *T. murphyi* (Table 1, Figs. 4 and 5). EOF-2SST was largely consistent with NPGO oscillations, reflecting the complex eddy structures in the convergence zones of ocean currents. Additionally, it may also reflect changes in the intensity of the southeast Pacific subtropical anticyclone (Figs. 2, 3, and S2). During this period, NPGO shifted from a negative phase to a positive phase, with EOF2SST showing decreasing trend, indicating that the HCS exhibited regional environment characterized by higher intensity upwelling and colder conditions (Figs. 2 and 3). As a result, the catch of *T. murphyi* decreased as the intensity of the subtropical water masses weakened (Bertrand et al. 2004; Diose, 2013; Bertrand et al. 2016). Conversely, the variation in the catch of *D. gigas* was opposite. Lower seawater temperatures and stronger coastal cold-water masses enhanced the habitat suitability of *D. gigas*, leading to an increase in its catch (Yu and Chen 2018; Yu et al. 2019, 2021).

Non-stationarity between species catches and climate/environment

Previous studies have provided clear evidence of the nonstationary relationship between the North Pacific climate/environment and species or ecosystem changes (Litzow et al. 2018, 2019; Ma et al. 2020, 2023; Wang et al. 2022). In this study, TGAMs better fitted the relationship between PIES catches in the HCS and variations in climatic and environmental factors (Fig. 6). This implied that the non-stationarity in the response relationship was found between species catches and driving factors such as climate/ environment within the HCS. The non-stationarity observed in the relationship between species and climate/environmental changes in this study was evident through distinct threshold years and varying fitting trends within specific periods (Fig. 7). These findings highlighted the asynchronous non-stationarity in PIES in the HCS, which could be attributed to the different sensitivities in the biological characteristics of each species to climate variability (Kirby and Beaugrand 2009; Beaugrand 2015; Ma et al. 2020).

The threshold years of the nonstationary relationship between the catch of *E. ringens* and *S. sagax*, and climate/environment corresponded to the regime shift in their catch, coinciding with a sharp increase in both species catch (Table 1, Figs. 4 and 7). This change may be associated with the shifts between cold and warm periods in the HCS. These transitions directly influence the composition and biomass of planktonic organisms within the HCS, thereby affecting the key species shift between the "cold period-*E. ringens*" and the "warm-*S. sagax*" within the HCS region (Alheit and Niquen 2004; Bertrand et al. 2004, 2011, 2016). In the early 1970s, despite the HCS entering a warm period, it was still dominated
 Table 1
 The correlation among climate indices, region environmental variables, and species regime shift

		1960s	1970s	1980s	1990s	2000s
Climate	PDO		1976			
	NPGO				1998	
	SOI					
	Niño 1+2					
Environment	EOF1SST		1977			
	EOF2SST				1998	
	EOF1WS		1976		1996	
	EOF2WS		1973			
Species	E. ringens		1972		1992	
	S. sagax		1976		1992	
	T. murphyi		1977		1998	
	D. gigas				1999	

by *E. ringens* (Fig. 4). However, with the strengthening and southward shift of the Aleutian Low in the mid-1970s, the warm state intensified, leading to a



Fig. 5 The importance of climate indices and EOFs of environment ranked by the feature importance of the random forest analysis for each PIES.

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significant increase in the biomass and catch volumes of *S. sagax*, while those of *E. ringens* decreased substantially (Fig. 4) (Alheit and Niquen 2004; Bertrand et al. 2004; Oliveros-Ramos et al. 2017; Oozeki et al. 2019). This marked the period of *S. sagax* dominance in the HCS (Alheit and Niquen 2004; Bertrand et al. 2004, 2011; Alheit et al. 2009). By the early 1990s, with the complete end of the warm period in the HCS and a notable increase in *E. ringens* catch, the ecosystem shifted back to a period dominated by *E. ringens* (Ballón et al. 2011; Bertrand et al. 2004, 2011; Salvatteci et al. 2018).

The regime shifts in the catch of T. murphyi occurred in the mid-1970s, while the threshold year of the nonstationary relationship emerged in the 1980s (Table 1, Fig. 7). This may be related to the transitions between strong and weak phase of pressure system (Litzow et al. 2018; Wang et al. 2022; Ma et al. 2023). During the 1980s, PDO showed decreased correlations with EOF1WS and EOF2WS, while NPGO exhibited increased correlations with them (Fig. S3). This suggested that the phenomenon that the Aleutian Low-forced change in the relative importance of PDO and NPGO to the regional environment variability may also exist within the HCS. The changing relative importance of PDO and NPGO may result in consistent alterations in regional oceanic physical processes such as seawater temperature fields and ocean currents within the Pacific ecosystem region. These changes subsequently impacted the PIES catches in the HCS (Alheit and Niquen 2004; Yeh et al. 2009; Di Lorenzo et al. 2010; Litzow et al. 2018; Ma et al. 2020). The correlation results showed



Fig. 6 Model comparisons between stationary and nonstationary models. Gray bars show the "genuine" cross-validation squared prediction error (gCV) of stationary models (GAMs)

and light gray column chart with black border bars show the gCV of non-stationary models (TGAMs), respectively.

a significant relationship between the catch of *D. gigas* and EOF2SST and EOF1WS, respectively, suggesting that climate variability primarily influenced the catch of *D. gigas* through regulating environmental conditions (Fig. 5). From the late 1990s to the early 21st century, NPGO exhibited a positive trend, with EOF2SST and EOF1WS showing decreasing and increasing trend (Figs. 2 and 3). This indicated that the cold and high upwelling intensity regional environment in the HCS during this period was conducive to *D. gigas* stock.

This study investigated the nonstationary relationship between PIES in the HCS and climate/environment, and preliminarily analyzed and discussed the potential mechanism for this non-stationarity. However, the causes of a nonstationary relationship between species or ecosystem structure and the physical drivers are complex, apart from quantifiable abiotic factors such as variations in climate and environment, which might also be correlated with specific ecological interactions within the ecosystem or between species, as well as fishing activities (Schmidt et al. 2014; Litzow et al. 2018). Therefore, the influence of biological and ecological factors on longterm changes in species catch or ecosystem structure must also be considered. This will help us better understand the mechanisms behind the nonstationary relationship between species or ecosystems and the influencing factors. This understanding will provide support for stock assessment and ecosystem-based fisheries management (Dorman et al. 2011; Schmidt et al. 2014).

Implications for fisheries management of pelagic species in the HCS

The HCS is a typical upwelling ecosystem, where changes in ecosystem structure become more prominent and rapidly evident than in other types of ecosystems under the influence of climate variability, especially in the synchronous response of PIES catches (Cahuin et al. 2015; Salvatteci et al. 2018). Therefore, clarifying the historical response of PIES to driving factors is crucial for formulating adaptive measures



Fig. 7 Generalized cross-validation score (GCV) paths of the best-fitted models in model comparison and the relationships were fitted by the best-fitted models. The black lines represent threshold years that are characterized by concave GCV paths.

Blue and purple represent different eras with distinguished models, while the dashed line represents the confidence interval. Figures represent the years from 1950 to 2019.

efforts should be intensified to explore the mecha-

to cope with future climate change. As highlighted by the results of this study, species with diverse biological characteristics demonstrated varying sensitivities to climate and environmental variations.

For these four important species, the interdecadal fluctuations in their catch synchronize with the shifts between warm and cold phases of the HCS, emphasizing the critical importance of monitoring the regional environmental conditions of the ecosystem. For example, long-term monitoring of seawater temperature, upwelling intensity, and the biomass of various planktonic organisms is particularly crucial for *E. ringens* and *S. sagax* (Bertrand et al. 2004, 2011, 2016). This helps us more effectively identify periods of cold and warm phase in the ecosystem, thereby distinguishing between *E. ringens* and *S. sagax* regimes. Of course, the key driver behind this nonstationary relationship is climate variability, so nisms of climate variability, given the uncertainty associated with it (Damalas et al. 2021). Analyzing regime shifts in PIES catches driven by climate variability can help establish early warning indicators for species abundance variations, aiding fisheries management at the species, community, and ecosystem levels (Litzow and Hunsicker 2016; Polo et al. 2022). The total allowable catch (TAC) can be optimized based on these indicators, and corresponding fisheries management policies can be adjusted for interannual or decadal climate changes in the future. Additionally, considering the cascading effects, this approach promotes the development of an adaptive ecosystem management framework and supports the dynamic resilience of ecosystems (Litzow and Hunsicker 2016; Damalas et al. 2021; Hidalgo et al. 2022).

There were no other long-term time series available for fishery-independent or dependent biomass indices to be supplemented to give more confidence on the results of this study. Therefore, the catch data for these four species were utilized in this study as proxies for species relative abundance or supplementary indicators to analyze the response of species fishery resources to large-scale climate and regional environmental variations. The variations in species catch are affected by many factors, fishery factors (such as fishing intensity, fishing methods, etc.), and biological characteristics of species (such as migration, etc.) also influence the catch except climate and environment. There is the potential controversy regarding whether catch data reflect the abundance of marine species (Pauly et al. 2013). However, the catch data may provide a better description of the actual trends of different species under appropriate conditions (Froese et al. 2012; Pauly and Zeller 2016; Tsimara et al. 2021).

The PIES catch data used in this study belonged to reconstructed data, and the variation trends in catch among different fishing countries or regions for various species were basically consistent. Moreover, the recovery of E. ringens catch following different intensities of El Niño events, with slower recoveries after the El Niño events in 1972/73 and 1982/83 but faster recoveries after the El Niño event in 1997/98 (Fig. 4). This variation is consistent with previous findings on the recovery of E. ringens biomass following different intensities of El Niño events (Bakun and Broad 2003; Alheit and Niquen 2004). Additionally, the biomass and resource abundance trends of S. sagax, T. murphyi, and D. gigas relatively align well with the catch trends within the subset of the time series covered by our study (Fig. S1) (Arancibia and Neira 2008; Cahuin et al. 2015; Oliveros-Ramos et al. 2017; Yatsu and Kawabata 2017; Oozeki et al. 2019). Therefore, the changes in species catches can reflect the variations in species biomass in the study area to a certain extent. Thus, while the present study documented a nonstationary response for PIES catches within the HCS to large-scale climate and regional environment, we believe that it could reflect the response patterns of the species biomass to climate and environment to a certain degree.

Conclusions

A combination of large-scale climate data, regional environment data, and catch data of PIES in the HCS were analyzed to identify regime shifts in climate indices, environmental variables, and PIES catches, and to explore the potential mechanisms of climate variability impacts on variations in PIES catches. The conclusions were as follows: (1) Synchronic regime shifts were identified in climate, environmental variables, and PIES catches, occurring in the mid-1970s and late 1990s; (2) In the mid-1970s, the regime shifts in catches of S. sagax and T. murphyi corresponded to EOF1SST, EOF1WS, and PDO regime shifts; In the late 1990s, the regime shifts in catches of T. murphyi, and D. gigas corresponded to EOF2SST and NPGO regime shifts; (3) The important climate and environmental factors influencing the variations in the PIES catches exhibited both similarities and differences. (4) Nonstationary relationships were identified between climate/environment and species catches, with different species showing different threshold years; (5) The non-stationarity between climate/ environment and species catches may be attributed to the transitions between warm and cold periods within the HCS driven by the phase transition of climate, as well as shifts between strong and weak phases of the pressure system. This study furthers our understanding of the changes in ecosystem structure in the HCS driven by climate variability, emphasizing the significance for the management of marine biological resources within this ecosystem. The effects of climate variability should be fully considered in the formulation of fisheries management strategies for this ecosystem in the future.

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Author contributions Zhiping Feng and Wei Yu conceptualized the study. Zhiping Feng, Nan Li, Wei Yu and Yunkai Li designed the methodology, and provided the software used to analyze data used in the present study. Zhiping Feng and Wei Yu wrote the original draft. Wei Yu, Jie Cao and Xinjun Chen revised the manuscript. Wei Yu and Xinjun Chen were involved in the funding acquisition. All authors approved the final version of the manuscript. **Data availability** Data would be made available upon request from the corresponding author.

Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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