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ORIGINAL RESEARCH

Improvements in length structure, reproductive indices, and spawning biomass following strengthened fisheries management: evidence from the common sardine (*Strangomera bentincki*) off central-southern Chile

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ABSTRACT. Fisheries management measures are expected to enhance the demographic structure and reproductive capacity of exploited fish populations, particularly in short-lived, fast-growing small pelagic species. We evaluated long-term changes in key demographic traits of common sardine (*Strangomera bentincki*) off central-southern Chile in relation to major regulatory milestones implemented between 1991 and 2023. Biological data from fishery monitoring programs were analyzed across three management periods (1991-2000: open access, 2001-2012: political decisions, and 2013-2023: scientifically supported decisions), focusing on length-structure, spawning biomass (SSB), fishing mortality (F), reproductive activity, condition factor, and length-based indicators. Significant differences were observed among the three periods. The second period was characterized by a reduced median length, delayed reproductive peak, high F, and low SSB, consistent with overfishing. In contrast, the most recent period exhibited consistently lower fishing mortality, increased spawning biomass, improved length-structure with a higher proportion of large and repeat spawners, and an earlier and more intense winter reproductive peak. Length-based indicators showed improved conservation of immature and large individuals and improved alignment with optimal yield benchmarks. Results demonstrate that strengthened, science-based fisheries management has positively influenced the demographic structure and reproductive dynamics of common sardine, underscoring the importance of sustained low fishing mortality in short-lived pelagic fisheries in the region.

Key words: Fisheries management, small pelagic fish, reproductive dynamics, length-based indicators.

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Mejoras en la estructura de talla, índices reproductivos y biomasa de desove tras el fortalecimiento de la gestión pesquera: evidencia de la sardina común (*Strangomera bentincki*) frente a la costa centro-sur de Chile

RESUMEN. Es de esperar que las medidas de ordenación pesquera mejoren la estructura demográfica y la capacidad reproductiva de las poblaciones de peces explotadas, particularmente en especies pelágicas pequeñas de vida corta y crecimiento rápido. Evaluamos los cambios a largo plazo en los rasgos demográficos clave de la sardina común (*Strangomera bentincki*) frente al centro-sur de Chile en relación con los principales hitos regulatorios implementados entre 1991 y 2023. Los datos biológicos de los programas de monitoreo pesquero se analizaron en tres períodos de gestión (1991-2000: acceso abierto, 2001-2012: decisiones políticas y 2013-2023: decisiones con respaldo científico), enfocándonos en la estructura de talla, biomasa reproductora (SSB), mortalidad por

pesca (F), actividad reproductiva, factor de condición e indicadores basados en la talla. Se observaron diferencias significativas entre los tres períodos. El segundo período se caracterizó por una longitud media reducida, un pico reproductivo retrasado, F alta y SSB baja, consistente con sobrepesca. En contraste, el período más reciente exhibió una mortalidad por pesca consistentemente menor, una mayor biomasa reproductora, una mejor estructura de tallas con una mayor proporción de desovantes grandes y repetidos, y un pico reproductivo invernal más temprano y más intenso. Los indicadores basados en la talla mostraron una mejor conservación de individuos grandes e inmaduros y una mejor alineación con los puntos de referencia de rendimiento óptimos. Los resultados demuestran que una gestión pesquera fortalecida y con base científica influyó positivamente en la estructura demográfica y la dinámica reproductiva de la sardina común, lo que subraya la importancia de una mortalidad por pesca baja y sostenida en las pesquerías pelágicas de corta duración en la región.

Palabras clave: Manejo pesquero, pequeños peces pelágicos, dinámica reproductiva, indicadores basados en talla.

INTRODUCTION

The implementation of fishery regulations and management measures is expected to have a positive effect on the demographic traits of fish populations, which is particularly relevant in fast-growing small pelagic fish species due to their short life span, where the interplay between growth and recruitment overfishing can have undesirable consequences even under recruitment dependence and climate-driven variability (Pinsky and Bayler 2015; Peck et al. 2021). Hilborn et al. (2020) found that in regions with intensive management, stocks are largely stable or recovering, indicating that perceptions of worldwide decline are shaped by the spatial and temporal frame of assessment.

In fast-growing small pelagic fish, growth overfishing occurs when fishing pressure is high and concentrated on growing juveniles before they reach an optimal length-at-age, i.e. when the biomass of a cohort is the highest (Feltrim and Ernst 2010; Hountcheme and Montcho-Simon 2024). One simple regulation to minimize the impact on growing juveniles is to change the age (length) selectivity (Ben-Hasan et al. 2021) or close the fishery during the months when they are growing. Nevertheless, intensive fishing tends to selectively remove the oldest and largest fish (Beamish et al. 2006; Hixon et al. 2014), which can have a significant impact on the demographic structure and reproductive capacity of the population; that is, recruitment overfishing occurs when high exploitation rates reduce the abundance of mature individuals such that recruitment is impaired (Myers et al. 1994). Indeed, larger females exhibit higher fecundity, produce higher-quality eggs, and experience more intense and extended spawning periods than smaller females (Trippel et al. 1997; Hixon et al. 2014).

The common sardine (*Strangomera bentincki*) is a small pelagic fish (< 20 cm total length, TL) inhabiting Chilean waters. It grows rapidly, has a short life cycle, seasonal growth rate, and high natural mortality rate (Cubillos et al. 1999, 2002). The common sardine is an iteroparous fish with undetermined fecundity, reaching 50% of gonadal maturity at 11 cm TL at the end of its first year of life (Cubillos et al. 1999; Bustos and Cubillos 2016). Juvenile common sardines are recruited to fishing grounds between 4 and 6 months after spawning in July (Cubillos et al. 2001; Arteaga et al. 2014), and the fishery is closed during January and February to protect the growing juveniles recruited to the fishing grounds. Thus, the fishing season starts in March, when juveniles have reached 8-9 cm TL, and is closed again between July and September (or mid-October) to protect the main reproductive season (Cubillos and Claramunt 2009; Arteaga et al. 2014).

The fleet targeting common sardine consists of industrial (> 18 m, > 80 m^3 storage capacity) and artisanal purse-seiners. Industrial vessels were authorized to operate within the central-southern fishery unit, geographically limited between Val-

paraíso and Los Lagos (Figure 1 A). At present, the artisanal fleet is the largest (approximately 400 boats) and operates only within the administrative regions where they are registered. Although the industrial fleet must operate beyond a 5 nm limit, only artisanal fishers have been active since 2020, as industrial vessel owners have begun transferring their quotas to artisanal ownership. The implementation of fishery regulations and management measures has progressively evolved from open access to a highly regulated system (Porobic et al. 2018).

Currently, the management of the common sardine fishery is based on a biologically controlled exploitation framework integrating access regulations, catch limits, and technical measures. Access to fisheries is restricted by suspending the registration of new fishing vessels. Total removals are regulated by a Biologically Acceptable Catch (BAC) recommended by a Scientific Technical Committee (STC) to the Undersecretariat of Fisheries and Aquaculture (SUBPESCA), which determines the allocated catch quota (Aedo et al. 2020). Biological closures are implemented to protect spawning and recruitment processes, complemented by regulations on authorized fishing gear. Measures to protect the first nautical mile include transitional authorizations allowing limited access for larger artisanal vessels in specific areas under legal conditions. Discard and bycatch are addressed through sector-specific management strategies. Institutional governance is supported by the STC and a Management Committee (MC) that provides advice based on annual stock assessments conducted by the Instituto de Fomento Pesquero (IFOP).

In the most recent history of the fishery, three distinct periods can be identified based on key milestones in its regulation: open access (1991-2000), politically driven decisions (2001-2012), and scientifically supported decisions (2013-2023) (Figure 1 B). The first corresponds to a phase of open-access fishing without restrictive measures, and the industrial fleet was authorized to operate within 5 nm of specific areas. In the second period, the fishery was declared under a fully exploited administrative regime, allowing control through a global catch quota and individual quotas under

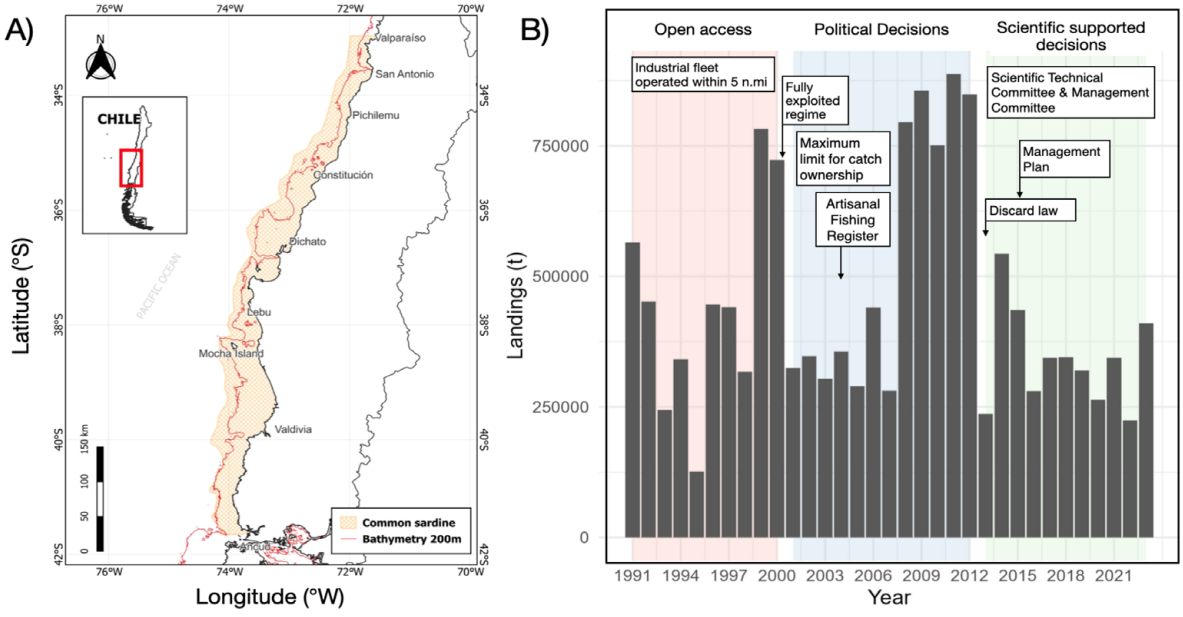

Figure 1. Study area corresponding to the common sardine fishery unit in central-southern Chile (A), and annual landings from 1991 to 2023 showing blocks of years associated with major fisheries management milestones in Chile (B) (see Table 1).

the administrative regime known as the Maximum Limit for Catch Ownership for the industrial fleet and Artisanal Fishing Register regime (Dresdner et al. 2010; Chávez-Estrada et al. 2018). However, quotas were decided by a politically representative institution known as the National Fishing Council (Leal et al. 2010). During the third period, the establishment of binding scientific-technical committees linked to catch quotas, and the Discard Law were key milestones. The Discard Law, among other objectives, seeks to prevent the discarding of fish in undesirable conditions (e.g. length below sexual maturity). During these periods, there were also variations in common sardine landing patterns, with annual averages of 443, 540, and 340 thousand tons for periods I, II, and III, respectively (Figure 1 B). Additionally, Cubillos et al. (2014) reported changes in the seasonal reproductive cycle between the 1990s and 2000s due to increased fishing pressure.

Accordingly, we hypothesized that increased implementation of fisheries regulations and management measures would have a positive effect on key demographic traits, such as the spawning-season peak and length, the proportion of larger specimens during the spawning season and their better condition, the length structure, and the spawning biomass and fishing mortality.

The objective of this study was to compare demographic aspects of the common sardine regarding length-structure, reproductive activity, condition factor, spawning biomass, and fishing mortality across three periods defined by regulatory milestones in the fishery of the central-southern zone of Chile.

MATERIALS AND METHODS

Study area and data sources

The study area corresponded to the fishery unit in the central-southern zone off Chile, extending from the northern boundary of the Valparaíso administrative region to the southern limit of the Los Lagos administrative region (Figure 1 A). The study spanned from 1991 to 2023, which was grouped into three blocks of years (management periods) based on major milestones in fisheries regulations: Period I: open access (1991-2000), Period II: politically driven decisions (2001-2012), and Period III: scientifically supported decisions (2013-2023) (Table 1).

Biological data were obtained from the Pelagic Fisheries Monitoring Program of IFOP, which included monthly length-frequency data collected from daily landings at main ports, as well as biological data on TL, total weight (W), sex, and ovary weight (G) for each sampled specimen. In addition, estimates of spawning biomass, recruitment, and fishing mortality rate from the official stock assessment conducted by Zuñiga and Bucarey (2024) were obtained. Spawning biomass (t) and recruitment (age 0) are referenced to July 1 of each year because the stock assessment model was based on a biological year extending from July 1 of a given year to June 30 of the following year.

Data analysis

Length-frequency data from the peak reproductive season (July to September) of 1991-2023 were selected to compare changes in median total length, a length-based indicator of fishing effects on the spawner length structure after the main fishing season (March-July). Kruskal-Wallis and Dunn's *post hoc* tests were applied to evaluate significant differences between management period pairs because the data did not meet normality assumptions required for parametric analyses.

Changes in reproductive activity were assessed using the Gonadosomatic Index (GSI), computed as the percentage of ovary weight (G) relative to the body weight (W) of each fish:

$$\mathrm{GSI} = \left[\frac{G \times 100}{(W - G)} \right]$$ (Cubillos and Claramunt 2009).

Table 1. Chronology of fisheries regulations and management affecting the common sardine fishery in central-southern Chile. GFAL: General Fishing and Aquaculture Law, SD: supreme decree, VMS: Vessel monitoring system

Periods	Year	Milestones
1991-2000	1991	General Fishing and Aquaculture Law (GFAL 18.892 and 19.079)
	1991	Ratification of the National and Zonal Fisheries Councils
	1992	Creation of the artisanal fishing register
2001-2012	2001	Fishery declared as Fully Exploited Regime (SD 440)
	2001	Maximum catch limit per owner for individual quotas (GFAL 19.713) ending in 2012
	2003	Exclusive five nautical miles from the coast for artisanal fishers, southward of Valparaíso administrative Region (GFAL 19.907 and 19.849)
	2004	Artisanal Fishing Register for individual quotas (GFAL 19.849)
2013-2023	2012	Transferable Fishing Licenses for a renewable 20-year period, with a focus on sustainability, individual catch quotas, and penalties for discarding, and first nautical mile exclusive for artisanal boats smaller than 12 m, certification of landings, and implementation of a satellite
	2013	surveillance VMS (GFAL 20.625)
	2016	Implementation of scientific-technical committees and management committees (Law 20.657 Management Plan for the common sardine and anchovy fisheries

In addition, changes in the condition factor (CF) were compared. It was computed for each specimen as $CF = 100 \cdot WE/L^3$ where WE is the observed eviscerated weight and L is the total length (cm) of the fish (Fulton 1904). Data were obtained from biological monitoring components of the Pelagic Fisheries Monitoring Program of IFOP conducted between 1991 and 2023.

Modeling changes in GSI and CF

To evaluate changes in reproductive activity and body condition across management periods, the GSI and CF were separately modeled using generalized linear mixed models fitted with the glmmTMB package in R (Brooks et al. 2017). Because both response variables were positive and right-skewed, models were fitted assuming a Gamma error distribution with a log-link function (see Appendix for statistical details). Management periods were included as a fixed effect. Seasonality was represented using Fourier terms based on calendar month, allowing seasonal patterns to differ among management periods. Fish length was included as a covariate using a natural cubic spline to account for non-linear effects, and a season × length interaction was incorporated because reproductive investment and body condition may vary seasonally with fish size (see Appendix for details). Temporal dependence among monthly observations was modeled using a first-order autoregressive (AR1) structure at the month-year level within each management period. Four nested candidate models were compared using ΔAIC, residual diagnostics, and biological interpretability (Burnham and Anderson 2002). The final model was selected when it minimized AIC, showed no relevant residual autocorrelation, and adequately represented seasonal and size-related patterns.

Spawning biomass, recruitment, and fishing mortality

Fishing mortality (F), spawning biomass (SSB), and recruitment among management periods were compared using Kruskal-Wallis and Dunn's *post*

hoc tests to evaluate significant differences between management periods pairs. In addition, a lagged cross-correlation between SSB and R was applied to test whether recruitment was associated with subsequent changes in SSB over lags of one or more years. It was assumed that recruitment was modulated by environmental effects and, in turn, drives spawning biomass (Szuwalski et al. 2015; Kurota et al. 2020). Cross-correlation functions (CCF) between SSB and R were computed on rank-transformed series to reduce sensitivity to outliers and departures from normality (Zuur et al. 2007; Box et al. 2015). The CCF was estimated between rank(SSB_{t+k}) and rank(R_t) for integer lags $k \in [-5, +5]$ due to the short life cycle of the common sardine. A positive lag $k > 0$ tests whether prior recruitment pulses modulate current biomass. Instead, a negative lag $k < 0$ indicates that the current spawning biomass at time *t* is associated with recruitment k years later. Cross-correlations for the full series and separately within each management period were computed to detect structural changes in the biomass-recruitment relationship. Similarly, to test the effects of fishing mortality on spawning stock biomass, a CCF between rank(F_{t+k}) and rank(SSB_t) was performed, with the expectation that negative correlations at lag $k > 0$ indicate that prior fishing mortality influences future SSB.

Length-based indicator

The Length-Based Indicators (LBI) method was used to evaluate conservation objectives (large and juvenile specimens), yield enhancement (optimal length), and maximum sustainable yield (MSY) benchmarks (Cousido-Rocha et al. 2022; Pennino et al. 2022). The LBI approach depends on annual length-composition data and life-history parameters, such as von Bertalanffy asymptotic length (Linf = 18.1 cm), growth coefficient (K = 0.745 $year^{-1}$), maturity length (Lmat = 11.5 cm), and natural mortality (M = 0.98 $year^{-1}$); therefore, M/K = 1.3. The von Bertalanffy parameters were obtained from Cubillos et al. (2001), maturity length from Aranis et al. (2006), and natural mortality from Cubillos et al. (2002). Indicators of large individuals included the mean length at the 5th percentile of individuals in the catch (Lmax5%), length at 95th percentile of the individuals in the catch (L95%), and proportion of mega-spawners (Pmega). Indicators of immature specimens were both the length at 25th percentile (L25%) and the length at first capture (Lc), while the optimal yield and MSY (maximum sustainable yield) were related to the mean length (Lmean). A catch with more than 30-40% mega-spawners was considered a sign of a healthy population (Jardim et al. 2015; ICES 2018). To assess the optimal yield, the mean length was compared with the length at maximum biomass in the catch (Lopt) using the ratio Lmean/Lopt, which should be close to 1 (> 0.9). The mean length of the catch above Lc (Lmean/$L_{F=M}$) when the fishing mortality rate (F) equals the natural mortality rate (M) was used as a proxy for MSY, with $L_{F=M}$ = 0.75Lc + 0.25Linf (Jardim et al. 2015; ICES 2018). Annual LBI values were computed using the guidelines of ICES (2018) and the application available at https://scott.shinyapps.io/LBIndicator_shiny/, and then compared to reference points consisting of specific ratios or values (Table 2).

RESULTS

Demographic traits

The length structure during the main reproductive season (July to September) differed between the first and second periods, with the modal length shifting toward smaller individuals, from 14 to 10 cm TL (Figure 2). During the third period, we observed a higher frequency of specimens with TL > 11 cm. Regarding the median, individuals in the third period had a greater total length than in the second period (12 versus 11 cm TL, respectively) but a median lower than the 14 cm TL observed in the first period (Figure 2 and Table

Table 2. Indicators, description, reference points, and length-based indicator performance that were utilized to determine fishing effects on the length structure of common sardine across management periods.

Indicator	Description and computation	Reference point	Indicator ratio	Expected value	Property
$L_{max5\%}$	Mean length of largest 5%	L_{inf}	$L_{max5\%}/L_{inf}$	> 0.8	Conservation (large matures)
$L_{95\%}$	95th percentile		$L_{95\%}/L_{inf}$		
P_{mega}	Proportion of individuals above L_{opt} + 10%	0.3-0.4	P_{mega}	> 0.3	
$L_{25\%}$	25th percentile of length distribution	L_{mat}	$L_{25\%}/L_{mat}$	> 1	Conservation (immatures)
L_c	Length at first catch (length at 50% of mode)	L_{mat}	L_c/L_{mat}	> 1	
L_{mean}	Mean length of individuals > L_c	$L_{opt} = \frac{3}{3 + M/k} \times L_{inf}$	L_{mean}/L_{opt}	≈ 1	Optimal yield
L_{max_y}	Length class with maximum biomass in catch	$L_{opt} = \frac{3}{3 + M/k} \times L_{inf}$	L_{maxy}/L_{opt}	≈ 1	
L_{mean}	Mean length of individuals > L_c	$L_{F=M} = (0.75L_c + 0.25L_{inf})$	$L_{mean}/L_{F=M}$	≥ 1	MSY

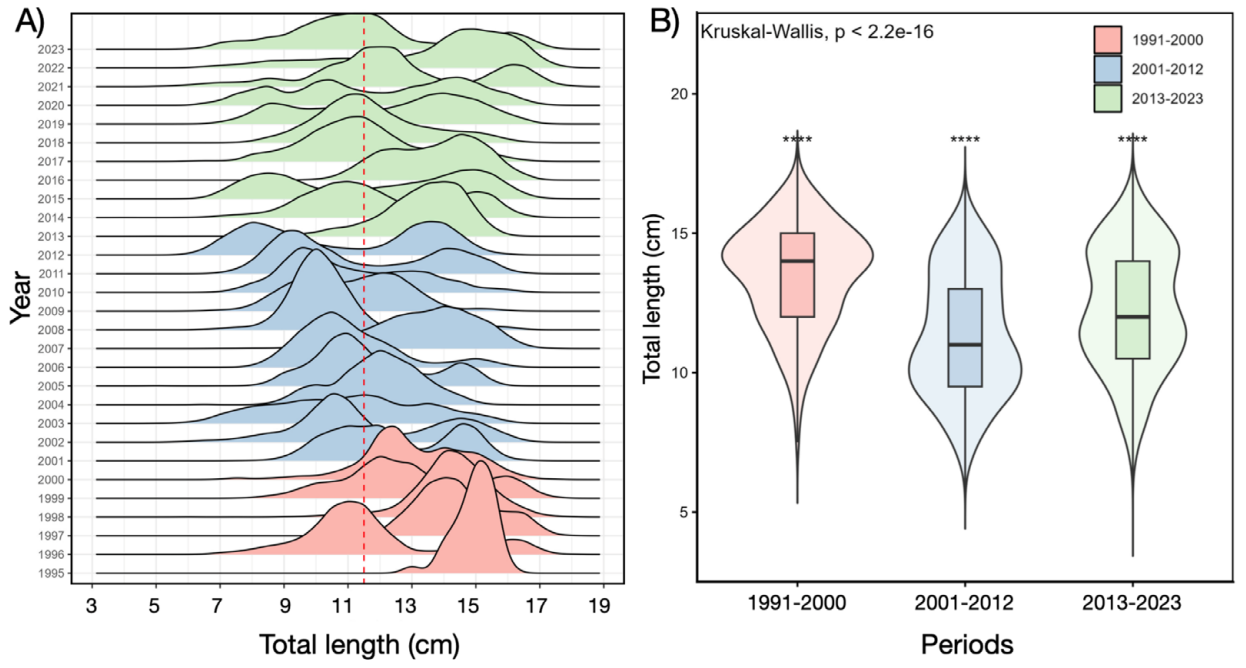

Figure 2. Annual changes in the length structure of common sardine landings during the main reproductive season (July-September) (A), and violin plots showing the results of the Kruskal-Wallis test comparing length distributions among fishery management periods (B). In panel A, the red dashed line indicates the length at sexual maturity.

3). The Kruskal-Wallis test revealed significant differences among periods. Dunn's *post hoc* test determined that the length-structure varied across periods (Table 3).

The period of higher observed reproductive activity fluctuated between July and September over the three periods that were analyzed. During the first period, the reproductive peak occurred in July, whereas during the second period, it occurred in September. In the last period, the peak occurred again in July (Figure 3).

Modeling changes in GSI and CF

For both GSI and CF, Model M4 best explained variation in reproductive activity and body condition (Table 4). Model M4 included period-specific effects, body length, the season × length interaction, and a between-month autoregressive random effect (AR1). The AR1 structure accounted for temporal dependence among consecutive monthly observations, indicating that elevated GSI values were not independent between adjacent months, which was consistent with a temporally extended spawning season.

The estimated AR1 autocorrelations for GSI (φ_1 = 0.66) and CF (φ_1 = 0.50) indicated substantial autocorrelation in population-level condition and reproductive investment over time. The management periods had significant effects on the mean GSI (likelihood ratio test: $P < 0.001$). Using 1991-2000 as the reference period, the period 2001-2012 showed a significant increase in mean GSI ($\exp(\hat{\beta}) = 1.28$; 95% CI: [1.03, 1.59]; $P = 0.026$). This suggested that, in the presence of seasonality, body length, and temporal autocorrelation, mean reproductive investment was significantly higher during periods of high fishing pressure than at the minimally regulated baseline. By contrast, the period 2013-2023 did not differ significantly from 1991-2000 in mean GSI ($\exp(\hat{\beta}) = 0.992$; 95% CI: 0.80, 1.23; $P = 0.943$), suggesting that quota-based management was associated with a return to reproductive investment levels similar to those observed during the first, less intensively fished period.

The modeled seasonal cycles in GSI differed among the three management periods (Figure 4 A). In all periods, GSI exhibited a pronounced unimodal annual cycle, peaking in austral winter and extending into austral spring. The amplitude and timing of the seasonal cycle differed among periods. During 1991-2000, the seasonal cycle started early and peaked in mid-July. In 2001-2012, the reproductive cycle peaked in August and extended into the austral spring. In 2013-2023, the onset of the seasonal cycle resembled that observed during 2001-2012, whereas the post-peak decline more closely resembled the pattern observed during 1991-2000.

Table 3. Central statistics for the length composition of common sardine across management periods during the main spawning season (July-September), and results of Kruskal-Wallis (K-W) test and Dunn's *post hoc* test.

	Periods		
Statistics	1991-2000 (I)	2001-2012 (II)	2013-2023 (III)
Mean (cm)	13.5	11.4	12.3
Median (cm)	14.0	11.0	12.0
Mode (cm)	14.0	10.0	11.5
K-W Test	P < 0.001	P < 0.001	P < 0.001
Dunn test (z)	124.5 (I versus II)	71.3 (II versus III)	-94.7 (I versus III)
Dunn test-P(adj.)	P < 0.01	P < 0.01	P < 0.01

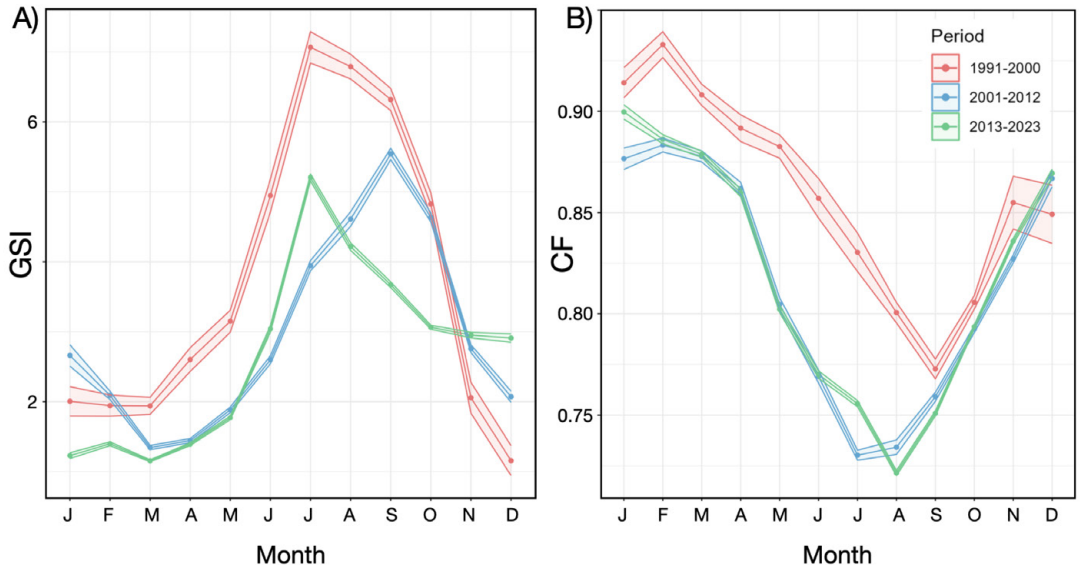

Figure 3. Observed mean seasonal changes in the gonadosomatic index GSI (A) and condition factor (CF) (B) of common sardine across fishery management periods.

Table 4. Comparison of models utilized to model changes in the gonadosomatic index (GSI) and condition factor (CF) of common sardine across management periods with generalized linear mixed models (glmmTMB). The best model is shown in bold according to the Akaike criterion information (AIC).

Response	Model	AIC	ΔAIC	Description
GSI	M1	867,351.90	112,245.60	Seasonal × period + AR1
	M2	867,353.80	112,247.50	M1 + within-month random intercept
	M3	764,101.80	8,995.50	M2 + individual length
	M4	**755,106.30**	**0**	**M3 + season × length interaction**
CF	M1	-589,472.60	9,029.20	Seasonal × period + AR1
	M2	-589,485.60	9,016.20	M1 + within-month random intercept
	M3	-594,856.70	3,645.10	M2 + individual length
	M4	**-598,501.80**	**0**	**M3 + season × length interaction**

The effect of body length on GSI was positive (Figure 4 B; likelihood-ratio test: $P < 0.001$), consistent with allometric scaling of ovary mass. In addition, the interaction between season and length was significant (likelihood-ratio test: $P < 0.001$), indicating that the seasonal amplitude of GSI varied with female length (Figure 4 C).

Management periods had a significant effect on the mean condition factor (likelihood-ratio test: $P < 0.001$). The CF declined during 2001-2012 relative to the first period ($\exp(\beta) = 0.950$, 95% CI: [0.925, 0.977]) and remained significantly lower during 2013-2023 ($\exp(\beta) = 0.967$, 95% CI: [0.941, 0.994]). The CF also exhibited a clear seasonal cycle, but with a seasonal phase shift relative to GSI (Figure 5 A), consistent with the expected

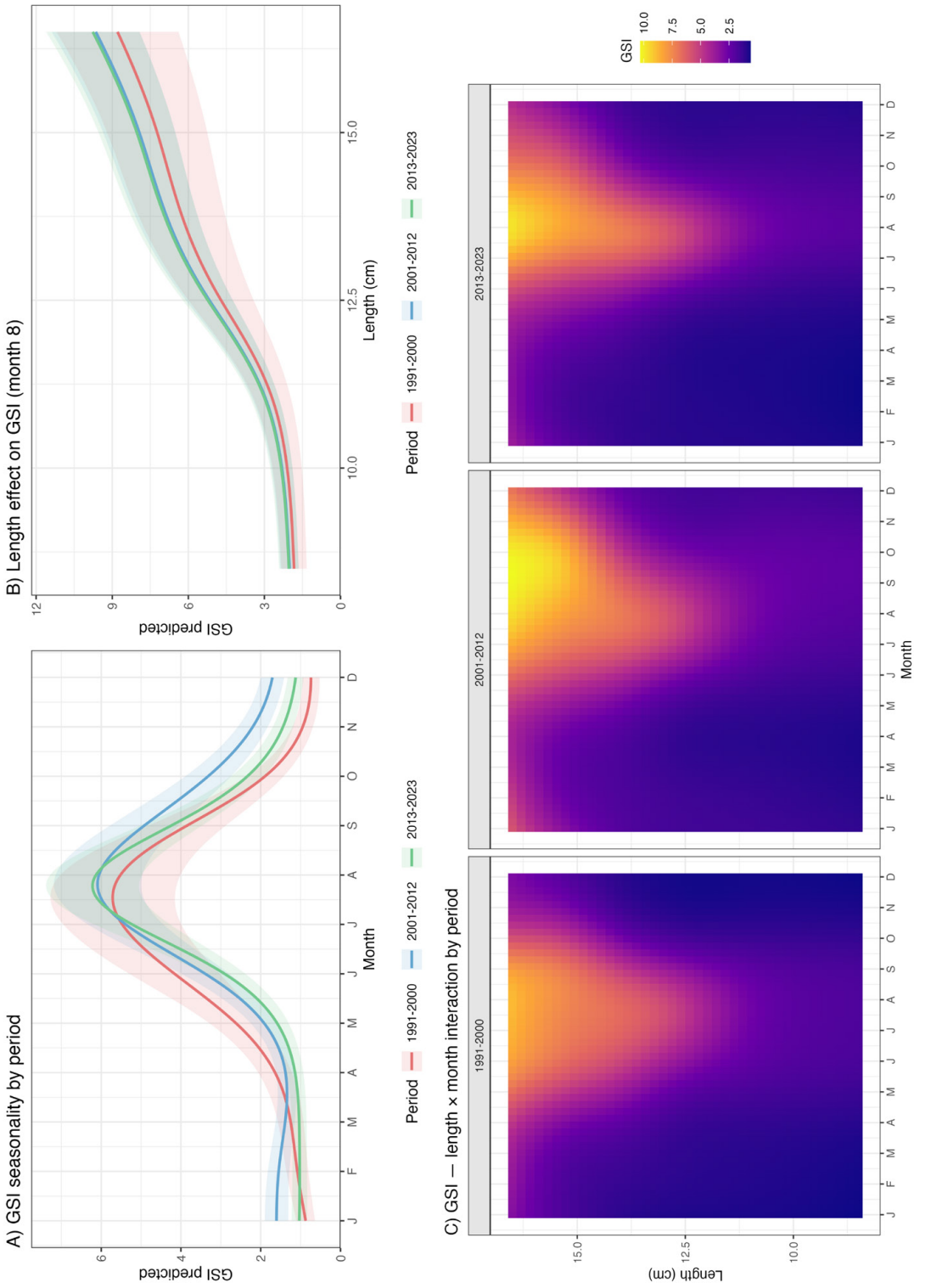

Figure 4. Modeled seasonal changes of the gonadosomatic index (GSI) (A) across management periods, with effects of female length (B), and the season-length interaction (C) with an autoregressive term (AR1) for changes in month across management periods (Model M4).

trade-off between energy storage and reproductive investment (Claramunt et al. 2007). In all three periods, CF reached its annual minimum during the peak spawning season, when energy reserves are mobilized to support gonadal growth and spawning activity. In addition, CF was higher in January-February (austral summer), corresponding to the post-spawning recovery and lipid accumulation phase. The CF showed a positive relationship with female length (likelihood-ratio test: $P < 0.001$), indicating relatively higher body condition in larger females (Figure 5 B). The season-length interaction was significant (likelihood-ratio test: $P < 0.001$), indicating that seasonal variation in body condition depended on fish length, with patterns differing among management periods (Figure 5 C).

Spawning stock biomass and fishing mortality

During the first period, the fishing mortality rate (F) fluctuated widely, with higher values recorded in 1997 and 2000 (~ 0.75 $year^{-1}$), whereas in the second period, it peaked near the estimated natural mortality rate (M ~ 1 $year^{-1}$) by 2003 (Figure 6 A). A declining trend in F was observed from the middle of the second period (mid-2000s). Of the three periods analyzed, the last consistently maintained F values below 0.3 $year^{-1}$, showing less variability between years. Regarding spawning stock biomass (SSB), the average was 606.1 thousand tonnes during the second period, 750.6 thousand tonnes during the first period, and 1,100.5 thousand tonnes during the third period (Figure 6 B). Recruitment was generally below 200 million individuals during the first period, increased markedly but remained highly variable during the second period, probably influencing the recovery of the biomass, and was intermediate and variable during the third period (Figure 6 C). There were significant differences among management in both F and SSB (Kruskal-Wallis $P < 0.01$). Subsequently, Dunn's *post hoc* analysis identified that only the second period differed significantly from the third period in both SSB and F ($P < 0.01$). By contrast, there were no significant differences in R across management periods (Kruskal-Wallis, $P = 0.103$).

The cross-correlation analysis between rank-transformed SSB and R showed that spawning biomass was positively associated with recruitment at zero and positive lags ($k > 0$), with the strongest association occurring at lag + 1 (Figure 7 A). This pattern was consistent with recruitment preceding increases in spawning stock biomass, suggesting that stronger recruitment was followed by higher spawning biomass approximately one year later. A similar pattern was observed within management periods, particularly during periods II and III (Figure 7).

Regarding cross-correlation analysis between rank-transformed F and SSB ($n = 32$), there was a negative correlation in phase ($r = -0.437$, $P < 0.05$) and significant negative correlations in all lags $k > 0$, increasing from lag 1 ($r = -0.375$) to lag 4 ($r = -0.606$), $P < 0.05$) consistent with the negative effects of fishing mortality on current and future spawning stock biomass.

Length-based indicator

The poorest performance of the length-based indicator (LBI) was observed during the first (1991-2000) and second period (2001-2012), whereas performance improved during the third period (2013-2023), particularly with respect to the conservation of immature and large spawners, as indicated by P_{mega} values exceeding 0.3 during 2020-2021 (Figure 8 A). Similarly, the optimal yield indicator improved during the most recent period, particularly in the L_{mean}/L_{opt} ratio (Figure 8 B). The LBI for maximum sustainable yield fluctuated near 1 in most years (Figure 8 C).

DISCUSSION

This study provides evidence that the progressive strengthening of fisheries management in the common sardine fishery was accompanied by

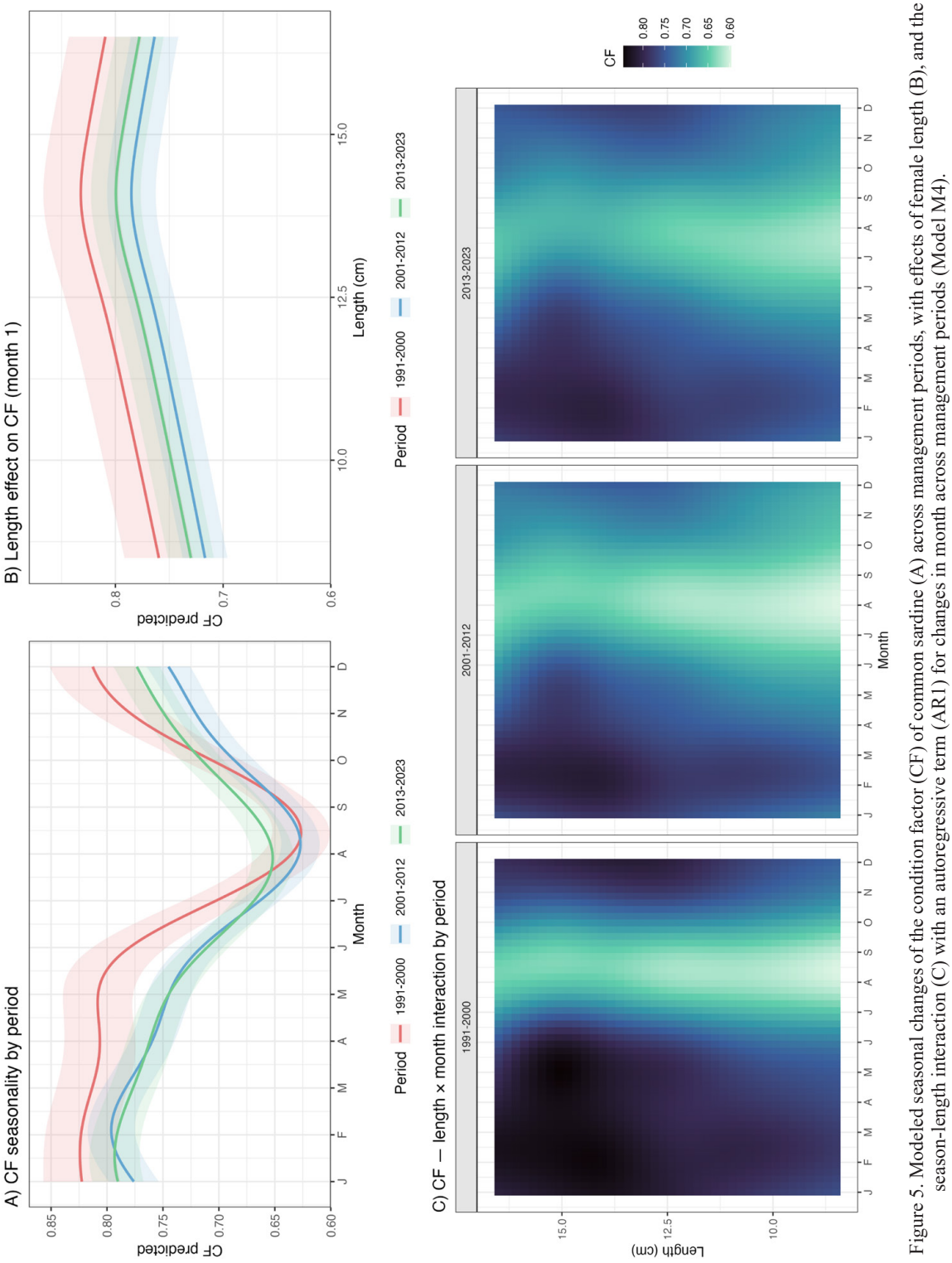

Figure 5. Modeled seasonal changes of the condition factor (CF) of common sardine (A) across management periods, with effects of female length (B), and the season-length interaction (C) with an autoregressive term (AR1) for changes in month across management periods (Model M4).

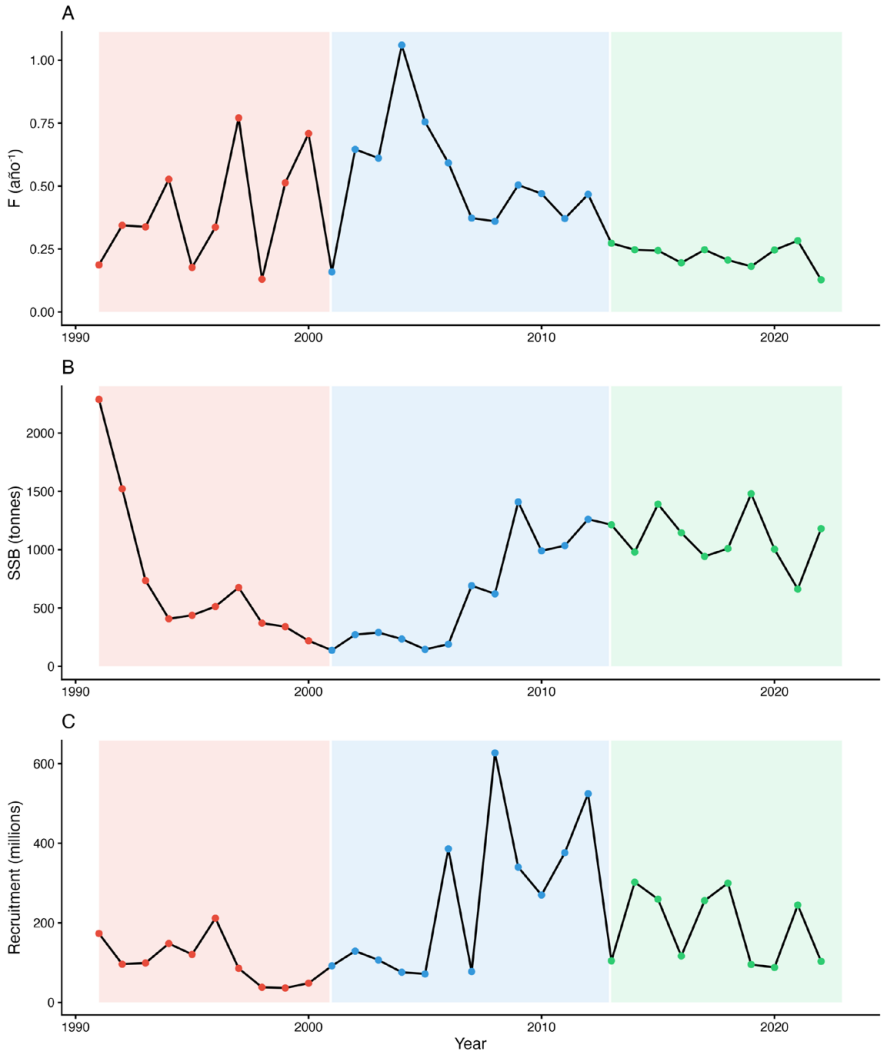

Figure 6. Annual changes in fishing mortality rate (A), spawning stock biomass (B), and recruitment (C) of common sardine across fishery management periods in central-southern Chile (after Zuñiga and Bucarey 2024).

substantial changes in key demographic and reproductive traits. The period characterized by science-based, quota-driven management (2013-2023) exhibited lower fishing mortality, higher spawning biomass, a greater proportion of large and repeat spawners, improved length-based indicators, and an earlier reproductive peak compared with the previous management periods. These results suggest that sustained regulation of fishing pressure can contribute to rebuilding the demographic structure and reproductive capacity, even in short-lived, environmentally variable small pelagic species.

The common sardine fishery has undergone progressive management reforms, evolving from open access to a science-based regulatory framework. Based on major regulatory milestones, three management periods were identified. Period I was characterized by open-access fishing. In Period II (from 2001 onward), the fishery was declared fully exploited, annual catch quotas were implemented,

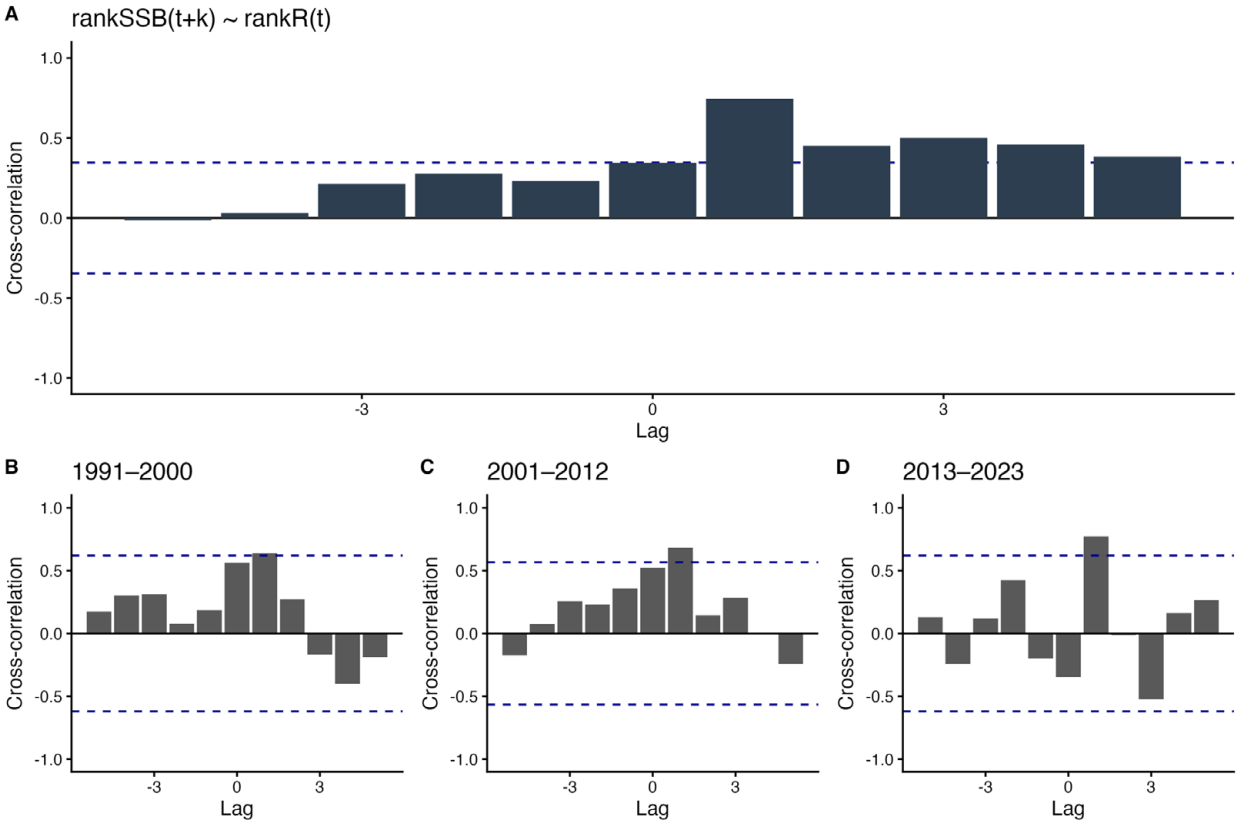

Figure 7. Rank-based cross-correlation between spawning biomass (SSB) and recruitment for the full-series (lag ± 5) (A); and cross-correlation within each management period (lag ± 5) in panels B, C, and D. Dashed horizontal lines represent 95% confidence bands. Note: lag < 0 means SSB drives R, while lag > 0 means R precedes SSB.

and access regulations were strengthened through measures such as vessel-owner catch limits and the allocation of quotas between the industrial and artisanal sectors (Leal et al. 2010; Zuñiga and Bucarey 2024).

The transition from Period I to Period II was particularly critical for the common sardine fishery because of major changes in the jack mackerel (*Trachurus murphyi*) fishery, resulting from overexploitation and the unusually higher presence of small-sized individuals associated with the 1997-1998 El Niño event (Arcos et al. 2001). This resulted in distorted landing patterns for common sardine and anchovy during 1999-2001 as fishing efforts shifted away from jack mackerel, leading to greater reported catches of these small pelagic species (Zuñiga and Bucarey 2024). Thus, the impact of fishing on small pelagic fish populations, such as common sardine and anchovy (*Engraulis ringens*), increased substantially. Nevertheless, the anchovy was overexploited during Period II, but its biomass recovered notably during Period III, likely associated with the implementation of strengthened science-based management of both common sardine and anchovy fisheries (Zuñiga and Bucarey 2024).

During Period III (after 2012), additional reforms included the implementation of discard reduction measures (Araya et al. 2022), modifications to the artisanal extraction regime, and the establishment of Fisheries Scientific Technical Committees and Fisheries Management Committees, which provide scientific advice and play a

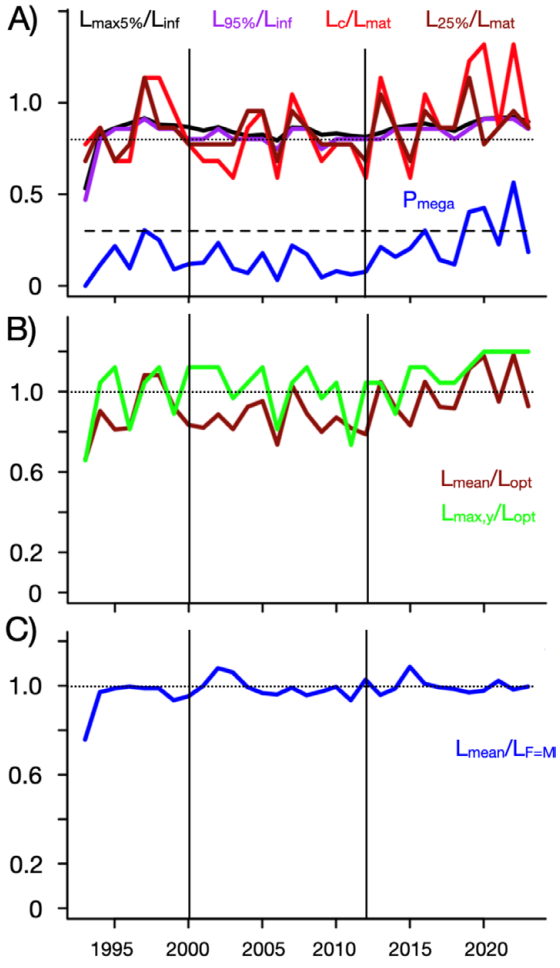

Figure 8. Length-based indicators for the conservation of immature and mature specimens (A), optimal yield (B), and maximum sustainable yield (C). Black vertical lines separate management periods. Dotted and segmented horizontal lines represent reference values for each indicator, and the dashed horizontal line in panel A indicates the reference value for P_{mega} (see Table 2).

binding role in setting biologically acceptable catch quotas and developing management plans.

The recovery of larger individuals during the third management period is particularly relevant because size and age structure are key components of stock reproductive potential. Larger and older females generally exhibit higher fecundity, produce larger eggs and larvae, and often contribute disproportionately to recruitment stability compared with first-time spawners (Berkeley et al. 2004; Wright and Trippel 2009; Hixon et al. 2014). Similar patterns have been documented in several small pelagic species, including sardines and anchovies, where repeat spawners can extend the spawning season and increase reproductive output through multiple spawning events (Claramunt et al. 2007), consistent with the demographic changes observed during Period III. Indeed, age truncation due to fishing can alter the timing and duration of annual reproduction (Scott et al. 2006). Maintaining larger and older fish (repeated spawners) associated with reproductive processes has been widely reported (Hixon et al. 2014; Koenigbauer and Höök 2023).

Large, long-lived, fat, and fecund females (hereafter referred to as BOFFFF) have relatively higher fecundity per unit of specific weight, produce larger eggs and larvae with a better ability to withstand starvation (Wright and Trippel 2009; Hixon et al. 2014), and generate more egg batches over longer periods per season, as reported for anchoveta and sardine (Claramunt et al. 2007). Furthermore, it has been shown that BOFFFF individuals have earlier and/or longer spawning periods than smaller and younger individuals (Lambert 1987; Millán 1999; Bobko and Berkeley 2004).

Consistent with this framework, the present study found that in the third period, when the length-structure showed a high frequency of repeat spawners (individuals with greater reproductive experience, > 13 cm TL), the observed gonadal maturity index indicated greater reproductive activity during the early austral winter than during the spring, when the length-structure was dominated by first-time spawners (< 13 cm TL). Finally, it has been documented that BOFFFF specimens may spawn in different locations, which may contribute to risk diversification and buffering of short-term environmental variability (Hsieh et al. 2010). Although the present study did not analyze the spatial variability of spawning by length, future studies could explore this relationship, in which large, long-lived females might select spawning sites to maximize reproductive success and larval survival.

The modeled GSI and CF differed significantly among management periods, particularly between Periods I and II, revealing that mean reproductive investment was significantly higher during the high-fishing-pressure period relative to the minimally regulated baseline. In addition, the reproductive peak was delayed toward austral spring. During Period III and the recovery of larger individuals, the decline of the reproductive cycle more closely resembled that observed during Period I. The modeled condition factor reflected the reproductive strategy of the common sardine, with higher body mass during the austral summer and minimum during the spawning season, reflecting the energetic trade-off in which somatic reserves are mobilized during reproduction (Claramunt et al. 2007). Modeled seasonal changes in GSI differed from the observed monthly averages, a consequence of the modeling approach using a mixed-effects generalized linear model. The mixed-effects framework estimates population-level seasonal patterns after accounting for differences in female length, season × length interactions, and temporal autocorrelation, while reducing the influence of observation error and unbalanced sampling. The modeling approach extends that of Cubillos and Claramunt (2009), by explicitly accounting for temporal autocorrelation and management-period effects.

Spawning biomass declined from the late first period through the second period, then recovered and stabilized at approximately 1,100 thousand tonnes during the third period. This recovery coincided with the implementation of major management reforms between 2012 and 2013, including the Discard Law and the establishment of binding Fisheries Scientific Technical Committees to advise on biologically acceptable catch levels. These measures were associated with reduced fishing mortality, reflected in both lower interannual variability in fishing mortality and higher spawning biomass levels during the third period compared with the previous management periods. Recruitment varied throughout the time series, with no significant changes across management periods. In addition, the significant positive correlation at lags + 1 indicates that stronger recruitment was consistently followed by higher spawning stock biomass one year later, consistent with recruitment contributing to subsequent biomass. Similarly, spawning biomass showed significant negative correlations with fishing mortality at lag + 1, consistent with the expectation that sustained reductions in fishing mortality favor higher spawning biomass over time. Therefore, these results suggest that both stronger recruitment and lower fishing mortality contributed to the recovery of spawning biomass. Indeed, an exclusive attribution to fisheries management may oversimplify the dynamics of a small pelagic species whose population fluctuations are also strongly influenced by environmental variability (Kurota et al. 2020). Hilborn et al. (2022) found that the abundance of small pelagic fish appears relatively insensitive to changes in fishing pressure. Even in well-managed fisheries, the strong natural fluctuations characteristic of small pelagic fish stocks can overwhelm management interventions such as catch reductions (Hilborn et al. 2022). Consequently, the benefits of reduced fishing pressure for stock recovery may be limited or context dependent.

Evidence from Georges Bank Atlantic herring indicates that stock recovery under reduced fishing pressure was accompanied by increases in biomass and a broadening of age and size structure, with greater representation of older spawners and multiple year classes (Melvin and Stephenson 2006). A similar pattern has been reported for Bay of Biscay anchovy, where the collapse of the fishery prompted the implementation of a science-based management plan integrating stock assessments, recruitment monitoring, and harvest control rules. Following stock recovery, fishing mortality was maintained at substantially lower levels than historical values, while spawning biomass remained close to historical maxima, supporting the effectiveness of science-based management in rebuilding short-lived pelagic fish populations (Uriarte et al. 2023).

Environmental conditions favoring recruitment

may also have contributed to the increase in spawning biomass observed during the third period. Small pelagic fish populations are strongly influenced by environmentally driven variability in recruitment and juvenile survival (Tommasi et al. 2017; Peck et al. 2021, 2024). A global meta-analysis of marine fish stocks found that only 14% of stocks exhibited clear evidence that recruitment was driven by spawning biomass, whereas 57% showed recruitment dynamics primarily associated with environmental variability. Furthermore, 29% of stocks displayed patterns in which recruitment influenced subsequent spawning biomass more strongly than spawning biomass influenced recruitment, and nearly half of environmentally influenced stocks exhibited shifts in recruitment regimes over time. Those findings suggest that changes in stock productivity can result from environmentally driven recruitment processes that subsequently propagate through the population and affect spawning biomass. This pattern appears particularly common in short-lived pelagic species such as anchoveta and sardines, where recruitment pulses can rapidly modify population size and structure (Szuwalski et al. 2015; Sellinger et al. 2024).

Consistent with this view, the increase in spawning biomass observed during the third period may reflect reduced fishing mortality, and favorable/unfavorable environmental conditions may contribute to variability around a given level modulated by SSB. Indeed, the evidence suggests that the spawning period is associated with environmental conditions conducive to the development of early life stages in offspring, providing a window of enhanced survival opportunities in the presence of SSB (Cury and Roy 1989; Arteaga et al. 2024). In the case of common sardine, the recruitment period overlaps with the onset of coastal upwelling events, which enhance the food supply for early life stages (Gomez et al. 2012). However, the onset of upwelling in the main spawning area between 38°S-40° S showed very low variability (less than 26 days) over an extensive time series from 1966 to 2020 (Muñoz et al. 2023), which does not fully explain the observed difference of approximately two months in the reproductive peak between the evaluated periods.

Results obtained in this study indicate that consistently lower fishing mortality over the last decade (period III: scientifically supported decisions) has likely contributed to an improved length structure, with larger females likely sustaining spawning during the austral winter. These findings are consistent with previous simulation analysis of fishing-induced changes in size structure and reproductive timing in common sardine (Cubillos et al. 2014). Future studies should evaluate changes in oceanographic conditions (e.g. upwelling activity and sea surface temperature anomalies) as potential influences on the observed biological changes. Such studies will contribute to a better understanding of how fishing pressure and environmental variability jointly influence the reproductive dynamics of common sardines.

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Declarations of use of AI

During the preparation of this work, the author(s) used Grammarly to improve English grammar.

Conflict of interest

All authors declare no conflicts of interest. The author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

Ethical approval

Not applicable.

Author contributions

Eveling Monsalve Tequén: conceptualization; methodology; supervision; data curation; investigation; original draft; writing, review, and editing. Luis A. Cubillos: conceptualization; methodology; formal analysis; software; validation; visualization; writing, review, and editing. Sebastián I. Vásquez: conceptualization; writing, review, and editing.

REFERENCES

Aedo G, Garcés C, Niklitschek E, Musleh S, Cubillos LA, Quiñones RA. 2020. Spatial distribution of small pelagic fishes: implications for fishing quota allocations. Mar Policy. 120: 104147. DOI: https://doi.org/10.1016/j.marpol.2020.104147

Akaike H. 1973. Information theory and an extension of the maximum likelihood principle. In: Petrov BN, Csáki F, editors. Second International Symposium on Information Theory. Akadémiai Kiadó. p. 267-281.

Aranis A, Caballlero L, Böhm G, Cerna F, Bocic V, Vera C, Gomez A, Rossow G. 2006. Informe Final Programa de Seguimiento del Estado de Situación de las Principales Pesquerías Nacionales. Investigación Situación Pesquería Pelágica Zona Centro-Sur 2005. IFOP. https://www.ifop.cl/laboratorioedadycrecimiento/informes-tecnicos/.

Araya A, Bernal C, Gertosio A, Palta E, Tapia-Jopia C, Trejo P. 2022. La ley de descarte en Chile. Revisión comparada y análisis de su implementación. Nuevo Mundo Mundos Nuevos. DOI: https://doi.org/10.4000/nuevomundo.86961

Arcos DF, Cubillos LA, Núñez S. 2001. The jack mackerel fishery and El Niño 1997-98 effects off Chile. Prog Oceanogr. 49 (1-4): 597-617. DOI: https://doi.org/10.1016/S0079-6611(01)00043-X

Arteaga M, Ernst B, Vásquez S, Gatica C. 2014. Conceptual bases for implementing a management strategy evaluation (MSE) for common sardine (*Strangomera bentincki*) and anchovy (*Engraulis ringens*) in south-central zone of Chile. Lat Am J Aquat Res. 42 (3): 445-467. DOI: https://doi.org/10.3856/vol42-issue3-fulltext-6

Arteaga M, Vásquez SI, Neira S, Cubillos L. 2024. Effect of wind variability on the recruitment of anchovy *Engraulis ringens* in the southern Humboldt upwelling ecosystem. Fish Oceanogr. 33 (5): e12677.

Beamish RJ, McFarlane GA, Benson A. 2006. Longevity overfishing. Prog Oceanogr. 68 (2): 289-302. DOI: https://doi.org/10.1016/j.pocean.2006.02.005

Ben-Hasan A, Walters C, Hordyk A, Christensen V, Al-Husaini M. 2021. Alleviating growth and recruitment overfishing through simple management changes: insights from an overexploited long-lived fish. Mar Coast Fish. 13 (2): 87-98. DOI: https://doi.org/10.1002/mcf2.10140

Berkeley SA, Chapman C, Sogard SM. 2004. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. Ecology. 85 (5): 1258-1264. DOI: https://doi.org/10.1890/03-0706

Bobko SJ, Berkeley SA. 2004. Maturity, ovarian cycle, fecundity, and age-specific parturition of black rockfish (*Sebastes melanops*). Fish Bull. 102 (3): 418-429. DOI: http://hdl.handle.

net/1834/30917

Box GEP, Jenkins GM, Reinsel GC, Ljung GM. 2015. Time series analysis: forecasting and control. 5th ed. Wiley. 720 p.

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Mächler M, Bolker BM. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated data. The R Journal. 9 (2): 378-400.

Burnham KP, Anderson DR, editors. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. New York: Springer. 488 p.

Bustos B, Cubillos LA. 2016. Cambios interanuales en la talla de madurez de sardina común, *Strangomera bentincki*, en la zona centro-sur de Chile (2007-2012). Rev Biol Mar Oceanogr. 51 (2): 317-325. DOI: https://dx.doi.org/10.4067/S0718-19572016000200009

Chávez-Estrada GA, Quiroga Suazo MÁ, Dresdner Cid JD. 2018. The effect of collective rights-based management on technical efficiency: the case of Chile's common sardine and anchovy Fishery. Mar Resour Econ. 33 (1): 87-112. DOI: https://doi.org/10.1086/696130

Claramunt G, Serra R, Castro LR, Cubillos L. 2007. Is the spawning frequency dependent on female size? Empirical evidence in *Sardinops sagax* and *Engraulis ringens* off northern Chile. Fish Res. 85 (3): 248-257. DOI: https://doi.org/10.1016/j.fishres.2007.01.009

Cousido-Rocha M, Cerviño S, Alonso-Fernández A, Gil J, Herraiz IG, Rincón MM, Ramos F, Rodríguez-Cabello C, Sampedro P, Vila Y, Pennino MG. 2022. Applying length-based assessment methods to fishery resources in the Bay of Biscay and Iberian Coast ecoregion: stock status and parameter sensitivity. Fish Res. 248: 106197. DOI: https://doi.org/10.1016/j.fishres.2021.106197

Cubillos LA, Canales M, Bucarey D, Rojas A, Alarcon R. 1999. Época reproductiva y talla media de primera madurez sexual de *Strangomera bentincki* y *Engraulis ringens* en el período 1993-1997, en la zona centro-sur de Chile. Invest Mar. 27: 73-85. DOI: https://doi.org/10.4067/S0717-71781999002700008

Cubillos LA, Arcos DF, Bucarey DA, Canales MT. 2001. Seasonal growth of small pelagic fish off Talcahuano, Chile (37°S, 73°W): a consequence of their reproductive strategy to seasonal upwelling? Aquat Living Resour. 14 (2): 115-124.

Cubillos LA, Bucarey DA, Canales MT. 2002. Monthly abundance estimation for common sardine *Strangomera bentincki* and anchovy *Engraulis ringens* in the central-southern area off Chile (34-40°S). Fish Res. 57 (2): 117-130. DOI: https://doi.org/10.1016/S0165-7836(01)00340-X

Cubillos LA, Claramunt G. 2009. Length-structured analysis of the reproductive season of anchovy and common sardine off central southern Chile. Mar Biol. 156 (8): 1673-1680. DOI: https://doi.org/10.1007/s00227-009-1202-5

Cubillos LA, Claramunt G, Castro LR. 2014. Simulation of fishery-induced changes on the reproductive cycle of common sardine, *Strangomera bentincki*, off central southern Chile. Fish Res. 160: 103-111. DOI: https://doi.org/10.1016/j.fishres.2013.12.003

Cury P, Roy C. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. Can J Fish Aquat Sci. 46 (4): 670-680. DOI: https://doi.org/10.1139/f89-086

Dresdner J, Campos N, Chávez C. 2010. The impact of individual quotas on technical efficiency: does quality matter? Environ Develop Econ. 15 (5): 585-607. DOI: https://doi.org/10.1017/S1355770X10000215

Feltrim M, Ernst B. 2010. Inter-cohort growth variability and its implication for fishery management of the common sardine (*Strangomera bentincki*) stock off the coast of south-central Chile. Fish Res. 106 (3): 368-377. DOI: https://doi.org/10.1016/j.fishres.2010.09.006

Fulton TW. 1904. The rate of growth of fishes.

Fisheries board of Scotland. Annual Report 22. Part 3. p. 141-241.

Gomez F, Montecinos A, Hormazabal S, Cubillos LA, Correa-Ramirez M, Chavez FP. 2012. Impact of spring upwelling variability off southern-central Chile on common sardine (*Strangomera bentincki*) recruitment. Fish Oceanogr. 21 (6): 405-414. DOI: https://doi.org/10.1111/j.1365-2419.2012.00632.x

Hsieh CH, Yamauchi A, Nakazawa T, Wang WF. 2010. Fishing effects on age and spatial structures undermine population stability of fishes. Aquat Sci. 72 (2): 165-178.

Hilborn R, Amoroso RO, Anderson CM, Baum JK, Branch TA, Costello C, De Moor CL, Faraj A, Hively D, Jensen OP, et al. 2020. Effective fisheries management instrumental in improving fish stock status. Proc Natl Acad Sci. 117 (4): 2218-2224. DOI: https://doi.org/10.1073/pnas.1909726116

Hilborn R, Buratti CC, Acuña ED, Hively D, Kolding J, Kurota H, Baker N, Mace PM, Muko S, Osio GC, et al. 2022. Recent trends in abundance and fishing pressure of agency-assessed small pelagic fish stocks. Fish Fish. 23 (6): 1313-1331. DOI: https://doi.org/10.1111/faf.12690

Hixon MA, Johnson DW, Sogard SM. 2014. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. ICES J Mar Sci. 71 (8): 2171-2185. DOI: https://doi.org/10.1093/icesjms/fst200

Hountcheme C, Montcho-Simon A. 2024. Understanding overfishing: a literature review. Asian J Fish Aquat Rese. 26 (1): 61-71. https://ssrn.com/abstract=4707384.

ICES. 2018. Technical Guidelines - ICES reference points for stocks in categories 3 and 4. ICES Technical Guidelines. Report. DOI: https://doi.org/10.17895/ices.pub.4128

Jardim E, Azevedo M, Brites NM. 2015. Harvest control rules for data limited stocks using length-based reference points and survey biomass indices. Fish Res. 171: 12-19. DOI: https://doi.org/10.1016/j.fishres.2014.11.013

Koenigbauer ST, Höök TO. 2023. Increased offspring provisioning by large female fish and consequences for reproductive efficiency. Ecol Evol. 13 (10): e10555. DOI: https://doi.org/10.1002/ece3.10555

Kristensen K, Nielsen A, Berg CW, Skaug H, Bell BM. 2016. TMB: automatic differentiation and Laplace approximation. J Stat Softw. 70 (5): 1-21.

Kurota H, Szuwalski CS, Ichinokawa M. 2020. Drivers of recruitment dynamics in Japanese major fisheries resources: effects of environmental conditions and spawner abundance. Fish Res. 221: 105353. DOI: https://doi.org/10.1016/j.fishres.2019.105353

Lambert TC. 1987. Duration and intensity of spawning in nerring *Clupea harengus* as related to the age structure of the mature population. Mar Ecol Progr Ser. 39: 209-220.

Leal CP, Quiñones RA, Chávez C. 2010. What factors affect the decision-making process when setting TACs?: The case of Chilean fisheries. Mar Policy. 34 (6): 1183-1195. DOI: https://doi.org/10.1016/j.marpol.2010.04.002

Melvin GD, Stephenson RL. 2007. The dynamics of a recovering fish stock: Georges Bank herring. ICES J Mar Sci. 64 (1): 69-82. DOI: https://doi.org/10.1093/icesjms/fsl018

Millán M. 1999. Reproductive characteristics and condition status of anchovy *Engraulis encrasicolus* L. from the Bay of Cadiz (SW Spain). Fish Res. 41 (1): 73-86. DOI: https://doi.org/10.1016/S0165-7836(99)00010-7

Muñoz R, Vergara OA, Figueroa PA, Mardones P, Sobarzo M, Saldías GS. 2023. On the phenology of coastal upwelling off central-southern Chile. Dyn Atmos Oceans. 104: 101405. DOI: https://doi.org/10.1016/j.dynatmoce.2023.101405

Myers RA, Rosenberg AA, Mace PM, Barrowman N, Restrepo VR. 1994. In search of thresholds for recruitment overfishing. ICES J Mar Sci. 51: 191-205.

Pennino MG, Cousido-Rocha M, Maia C, Rocha A, Figueiredo I, Alonso-Fernández A, Silva C, Izquierdo F, Castro J, Teruel Gomez J, et al. 2022. This is what we know: assessing the stock status of the data-poor common sole on the Iberian coast. Estuar Coast Shelf Sci. 266: 107747. DOI: https://doi.org/10.1016/j.ecss.2022.107747

Peck MA, Alheit J, Bertrand A, Catalán IA, Garrido S, Moyano M, Rykaczewski RR, Takasuka A, Van der Lingen CD. 2021. Small pelagic fish in the new millennium: a bottom-up view of global research effort. Prog Oceanogr. 191: 102494. DOI: https://doi.org/10.1016/j.pocean.2020.102494

Peck MA, Catalán IA, Garrido S, Rykaczewski RR, Asch RG, McDowell JR, Hazen EL, Kaplan IC. 2024. Small pelagic fish: new frontiers in ecological research. Mar Ecol Progr Ser. 741: 1-6. DOI: https://doi.org/10.3354/meps14648

Porobic J, Fulton EA, Frusher S, Parada C, Haward M, Ernst B, Stram D. 2018. Implementing ecosystem-based fisheries management: lessons from Chile's experience. Mar Policy. 97: 82-90. DOI: https://doi.org/10.1016/j.marpol.2018.08.037

Pinsky ML, Byler D. 2015. Fishing, fast growth and climate variability increase the risk of collapse. Proc Biol Sci B. 282 (1813): 20151053. DOI: https://doi.org/10.1098/rspb.2015.1053

R Core Team. 2024. R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org.

Sellinger EL, Szuwalski C, Punt AE. 2024. The robustness of our assumptions about recruitment: a re-examination of marine recruitment dynamics with additional data and novel methods. Fish Res. 269: 106862. DOI: https://doi.org/10.1016/j.fishres.2023.106862

Szuwalski CS, Vert-Pre KA, Punt AE, Branch TA, Hilborn R. 2015. Examining common assumptions about recruitment: a meta-analysis of recruitment dynamics for worldwide marine fisheries. Fish Fish. 16 (4): 633-648. DOI: https://doi.org/10.1111/faf.12083

Scott BE, Marteinsdottir G, Begg GA, Wright PJ, Kjesbu OS. 2006. Effects of population size/age structure, condition and temporal dynamics of spawning on reproductive output in Atlantic cod (*Gadus morhua*). Ecol Model. 191 (3): 383-415. DOI: https://doi.org/10.1016/j.ecolmodel.2005.05.015

Tommasi D, Stock CA, Pegion K, Vecchi GA, Methot RD, Alexander MA, Checkley DM. 2017. Improved management of small pelagic fisheries through seasonal climate prediction. Ecol Appl. 27 (2): 378-388. DOI: https://doi.org/10.1002/eap.1458

Trippel EA, Kjesbu OS, Solemdal P. 1997. Effects of adult age and size structure on reproductive output in marine fishes. In: Chambers RC, Trippel EA, editors. Early life history and recruitment in fish populations. Netherlands: Springer. p. 31-62. DOI: https://doi.org/10.1007/978-94-009-1439-1_2

Uriarte A, Ibaibarriaga L, Sánchez-Maroño S, Abaunza P, Andrés M, Duhamel E, Jardim E, Pawlowski L, Prellezo R, Roel BA. 2023. Lessons learnt on the management of short-lived fish from the Bay of Biscay anchovy case study: satisfying fishery needs and sustainability under recruitment uncertainty. Mar Policy. 150: 105512. DOI: https://doi.org/10.1016/j.marpol.2023.105512

Wood S. 2017. Generalized additive models: an introduction with R. Boca Raton: Chapman and Hall/CRC. 410 p.

Wright PJ, Trippel EA. 2009. Fishery-induced demographic changes in the timing of spawning: consequences for reproductive success. Fish Fish. 10 (3): 283-304. DOI: https://doi.org/10.1111/j.1467-2979.2008.00322.x

Zuñiga MJ, Bucarey D. 2024. Estatus y posibilidades de explotación biológicamente sustentables de sardina común, Región de Valparaíso a la Región de Los Lagos, año 2024. https://www.ifop.cl/wp-content/contenidos/uploads/Reposi

torioIfop/InformeFinal/2024/P-483272.pdf.
Zuur AF, Ieno EN, Smith GM. 2007. Analyzing ecological data. Series Statistics for Biology and Health. Springer: New York. 672 p. https://link.springer.com/content/pdf/10.1007/978-0-387-45972-1.pdf.

APPENDIX

Detailed implementation of generalized linear mixed models

We used glmmTMB (Brooks et al. 2017) to determine significant changes in the gonadosomatic index (GSI) and condition factor (CF) across management periods. Both variables, GSI and CF, followed a Gamma distribution and a log link function. The GSI and CF data had values > 0 (IGS: CV = 87.5%, skewness = 1.278, excess kurtosis = 1.550; CF: CV = 16.5%, skewness = 0.332, excess kurtosis = 0.099), and both followed a Gamma distribution according to the Anderson-Darling (GSI: $A^2 = 226.5$, $P < 0.001$; CF: $A^2 = 4.87$, $P = 0.003$) and Cramér-von Mises (GSI: $W^2 = 42.85$, $P = 0$; CF: $W^2 = 0.76$, $P = 0.009$) statistical tests.

We included the season × length interaction because it has a significant effect on the reproductive cycle and condition factor (Cubillos and Claramunt 2009). Therefore, the general linear predictor for the log-transformed conditional mean of individual i sampled in month m of year y in period p was:

$$\log(\mu_i) = \alpha + \alpha_p + f_p(m) + g(\text{Lcent}_i) + h(m, \text{Lcent}_i) + b_p(\tau)$$

where α is the grand intercept, α_p is the fixed effect of management period, $f_p(m)$ is a period-specific seasonal smooth, g(Lcent) is the length effect, h(m, Lcent) is a season-length interaction, and $b_p(\tau)$ is a monthly autocorrelation random effect, AR(1).

The annual seasonal cycle within each management period was represented by a truncated Fourier series with K = 3 harmonics:

$$f_p(m) = \Sigma_{v=1^3} [\beta c^0_{s,j,p} \cos(2\pi jm/12) + \beta_{s^{pn},j,p} \sin(2\text{-}jm/12)]$$

where $m \in \{1, \ldots, 12\}$ is calendar month, j is harmonic order, and $\beta c^0_{s,j,p}$ and $\beta_{s^{pn},j,p}$ are period-specific harmonic coefficients. Three harmonics (six basis functions per period, 18 in total) provide a sufficiently flexible approximation to the cyclic cubic spline s(month, bs = 'cc', k = 12) used in GAM analyses (Wood 2017), capturing seasonal shapes up to the sixth subharmonic of the annual cycle. Period-specific coefficients allow the seasonal pattern to differ in amplitude, phase, and shape among the three management periods.

All length values were mean-centered before analysis (Lcent = L - $\bar{L}$) to reduce collinearity between the Fourier basis functions and the natural spline. The effect of individual body length on each index was represented by a natural cubic spline with five degrees of freedom, ns(Lc, df = 5), computed using the R function ns() from the splines package. Knots were placed at the default quantile positions of Lc across the pooled sample. This parametric spline approximates the GAM smooth s(length, k = 8) and avoids the computational overhead of penalized estimation for this fixed-effects component.

The interaction between the seasonal cycle and body length was approximated by forming cross-products of the first two Fourier harmonics ($\cos_1$, $\sin_1$, $\cos_2$, $\sin_2$) with the first three natural-spline basis vectors (ns_{l1}, ns_{l2}, ns_{l3}), yielding 12 additional predictor columns. This construction approximates the tensor-product interaction ti(month, length, bs = c('cc', 'tp')) estimated in the companion GAM models (Cubillos and Claramunt 2009).

The between-month temporal autocorrelation implies that the observations collected within the same calendar month share the same environmental context and are therefore not independent. Indices such as GSI or CF tend to exhibit positive autocorrelation between consecutive months (e.g.

high reproductive activity in one month predicts high activity in the next). Thus, we introduce an AR(1) random effect specified as ar1(time-month-*f* + 0 | period). Here, time-month-*f* is a factor whose levels index the ordered sequence of unique year-month combinations within each management period. This specification assigns a shared random intercept bτ to all individuals sampled in the same month-year cell and period, and imposes an AR(1) correlation structure (with autocorrelation coefficient φ_1) on the sequence of intercepts over consecutive months. The '+ 0' suppresses an overall random intercept per period (which would be confounded with the fixed period effect), so only the AR(1) component is estimated.

To identify the most parsimonious model structure for each response variable, four nested candidate models were compared using the Akaike information criterion (AIC; Akaike 1973):

- M1: period + Fourier harmonics (× period) + AR1(month).
- M2: M1 + within-month random intercept.
- M3: M1 + ns(length, df = 5).
- M4: M3 + season × length (12 terms).

After, we computed ΔAIC as AIC_i - AICmin within each fitting framework. Models with ΔAIC > 2 were considered substantially inferior (Burnham and Anderson 2002). Residual temporal autocorrelation was assessed by computing Pearson residuals, aggregating them to monthly means, and examining the autocorrelation function (ACF) and partial ACF (PACF). Adequate model fit was indicated by residual ACF and PACF values lying within the $\pm 1.96/\sqrt{N}$ confidence bounds for all lags ≥ 1.

All analyses were conducted in R (R Core Team 2024). Generalized linear mixed models were fitted with glmmTMB (Brooks et al. 2017), which uses Template Model Builder (Kristensen et al. 2016) for fast automatic differentiation and maximum-likelihood estimation of mixed-effects models with complex random-effect structures. Fourier basis functions were computed using base-R trigonometric functions. Natural cubic splines were generated with the splines package (R Core Team 2024).