

*Research Article*

## Sexual maturity effects on the relative growth of the central stock of northern anchovy *Engraulis mordax* (Clupeiformes: Engraulidae) off the west coast of Baja California, Mexico

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**ABSTRACT.** The objective of this study was to analyze the standard length-total weight (SL-WT) relationships of the central stock of northern anchovy (*Engraulis mordax*) off Baja California to determine its relative growth pattern (isometric or allometric) and its variation in relation to size at maturity. The length-weight relationship was determined by fitting somatic growth to the observed SL-WT data using a polyphasic model, segmented into two phases (stanzas), which estimates a stanza change length (SCL). Student's t-tests were used to assess the type of growth. Likewise, the SL at maturity (SL<sub>50</sub>) was estimated using a polyphasic model to compare and identify changes in relative growth. Females were more frequent in large sizes (>95 mm SL), whereas males dominated the smaller size classes in the sample. Growth exhibited significant allometry according to the polyphasic model, showing hyperallometric ( $b = 3.17$ ) growth in the first stage and hypoallometric ( $b = 2.64$ ) growth in the second. The SCL in relative growth was estimated at 97.51 mm for males and 99.03 mm for females. These values correspond to SL<sub>50</sub> and also coincide with the minimum legal size (MLS = 100 mm SL) established as a management measure. The process of sexual maturity may be associated with changes in relative growth, suggesting that the energetic demands linked to reproductive function at the onset of adulthood influence somatic growth. The use of the polyphasic regression model represents a promising approach when information on sexual maturity is scarce, as SCL estimates can serve as a useful indicator of fish maturation.

**Keywords:** small pelagic; maturation; somatic relationship; polyphasic model; adulthood onset; fishery management

### INTRODUCTION

The northern anchovy (*Engraulis mordax*) is distributed from Canada to Mexico along the California Current. This species comprises three subpopulations: a northern stock ranging from Haida Gwaii, Canada, to northern California; a central stock extending from San

Francisco Bay to central Baja California, Mexico; and a southern stock distributed from central Baja California to the Gulf of California (Sydeman et al. 2020). The central stock, or subpopulation, is the most abundant and the most extensively studied (Checkley Jr. et al. 2017, Rykaczewski 2019).

In Mexico, the northern anchovy was the most abundant species during the 1970s and mid-1980s, contributing up to 50% of the total small pelagic production; however, it subsequently accounted for only about 2-3% of the total catch (Nevárez et al. 2014). In recent years, the volume of its catch has increased substantially, now representing more than 10% of total landings (DOF 2022). In the Baja California small pelagic fishery, northern anchovy has exhibited marked fluctuations, with annual landings ranging from less than 5,000 to 260,000 t. The most substantial decline occurred between 1990 and 2014. However, the fishery has shown significant signs of recovery since 2015 (Escudero & Castellanos 1990, Pedrín-Osuna et al. 1992, Álvarez-Ramírez 2003, DOF 2023).

Variability in this type of resource occurs on both annual and decadal scales (Lluch-Belda et al. 1989, Checkley Jr. et al. 2017, Ma et al. 2019, Castro-Gutiérrez et al. 2022). Such variability is driven by changes in environmental conditions and fishing pressure (Lluch-Belda et al. 1989). Key challenges for sustainable management and the prevention of over-fishing include biomass variability, susceptibility to climatic fluctuations, and the difficulty of determining the onset and duration of productivity regimes (Peck et al. 2021). As previously mentioned, northern anchovy catches off western Baja California exhibit high variability, underscoring the need to examine biological characteristics to understand the current status of the fishery.

Determining biological characteristics, such as reproductive traits, growth patterns, age structure, and somatic relationships, is essential for effective management of species of high ecological and economic value, particularly those vulnerable to fishing pressure (Oliveira et al. 2012). In this context, understanding population aspects such as structure size, length-weight relationships, spawning, and size at sexual maturity ( $L_{50}$ ) is a key component of biological characterization. It provides valuable information for fisheries management (Froese et al. 2011).

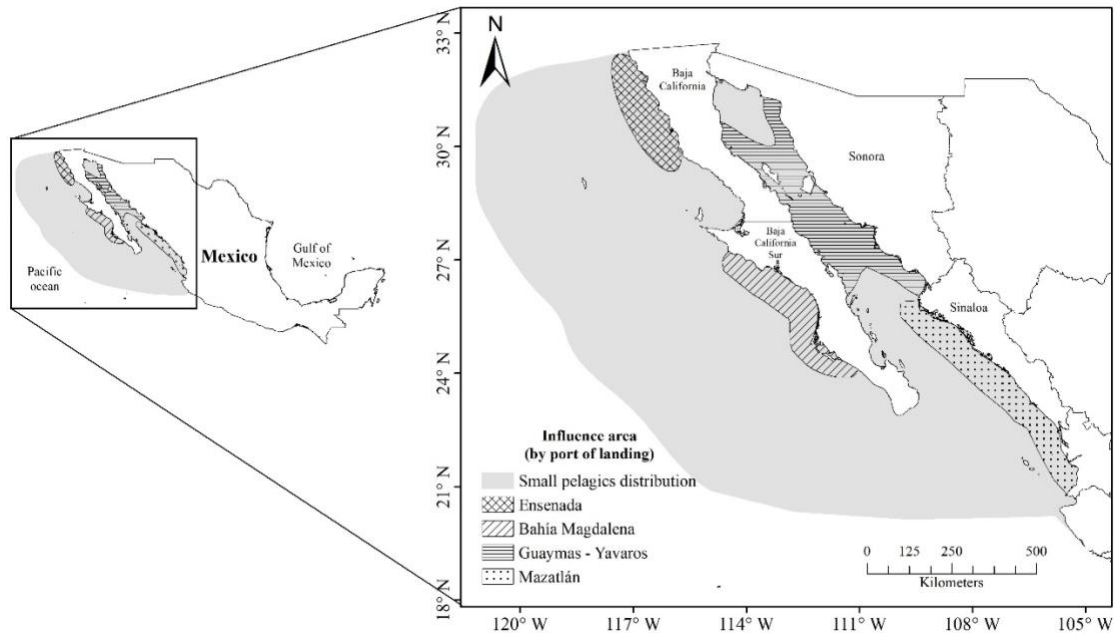
Some studies on *E. mordax* have reported negative allometric growth, indicating that individuals grow more in length than in weight (Tapia-Vázquez et al. 1988, Rodríguez-Romero et al. 2007). In addition, reproductive studies have identified two spawning peaks: one occurring from late spring to early summer and another in late autumn. Estimates of length at maturity ranged from 85 to 120 mm standard length (SL) (Tapia-Vázquez et al. 1988, Escudero & Castellanos 1990, Schwartzkopf et al. 2021).

The high variability may be attributed to the way the data are arranged, as maturity-at-length data often show proportions either above 0.6 or below 0.5 across most length intervals. In such cases, it is possible to estimate  $L_{50}$  by accumulating the proportion of sexually mature individuals (Flores-Anaya et al. 2024). However, this approach tends to estimate  $L_{50}$  within the length class where the maturity mode occurs, which may not correspond to the length at which 50% of individuals are sexually mature, as expected under a binomial distribution. Under such circumstances, an allometric model describing relative growth in two stages may provide a better fit and more accurate estimates of length at maturity (Bervian et al. 2006, Fontoura et al. 2009, Lanzoni et al. 2018, Borrego-Durán et al. 2024). Accordingly, differential relative growth can be detected through a marked change in the allometric exponent  $b$ , which may occur when sexual maturation promotes increased somatic growth associated with reproduction. Therefore, the objective of this study was to analyze the length-weight relationships of the central stock of northern anchovy off Baja California to determine its growth pattern (isometric or allometric) in relation to reproduction, thereby contributing to sustainable fisheries management.

## MATERIALS AND METHODS

### Study area

Mexico's small pelagic fishery is mainly concentrated in the northwest of the country, where four key landing zones are recognized: Ensenada (Baja California), Magdalena Bay (Baja California Sur), Guaymas-Yavaros (Sonora), and Mazatlán (Sinaloa) (Fig. 1). In the Ensenada region, located along the western coast of the Baja California Peninsula between 29-33°N and 115-117°, the small pelagic fishery has historically exhibited oscillations in catches, characterized by alternating dominance between Pacific sardine (*Sardinops sagax*) and northern anchovy (*E. mordax*). However, in recent years, northern anchovy has become the most frequently harvested species (DOF 2023). This area lies within the California Current System, which is bounded to the north by the Subarctic Gyre and to the south by the North Equatorial Current, and flows southward (Parés-Sierra et al. 1997, Venrick 2000). Vertical movement characterizes this system, generating upwelling that brings nutrient-rich waters to the surface and promotes high levels of primary productivity (Espinosa-Carreón 2005).



**Figure 1.** Distribution of Mexico's small pelagic fishery and coverage area by landing port.

### Sample collection

Samples of northern anchovy were taken from the commercial purse seine fishery landing in Ensenada, Baja California, Mexico. All biological information was recorded by the Mexican Institute for Sustainable Fisheries and Aquaculture Research (IMIPAS, by its Spanish acronym). A total of 7,827 organisms were collected from August 2015 to September 2023.

Once in the laboratory, fish were measured for SL (mm) and weighed for wet weight (WT, g). Subsequently, organisms were dissected and examined to determine sex and gonadal phases (Cotero-Altamirano 1987). Yearly and monthly sex ratios were estimated, and a chi-square test was performed to assess the null hypothesis of a 1:1 male-to-female sex ratio (Sokal & Rohlf 1981, Zar, 1999). Differences in length and weight between sexes were evaluated using the Mann-Whitney rank sum test after performing a Kolmogorov-Smirnov test for normality and an F-test for homogeneity of variances. In addition, a Kruskal-Wallis test was conducted to determine statistical differences in length across years; once differences were confirmed, they were further examined using a *post-hoc* Tukey-Kramer HSD test. All tests were performed at the 95% confidence level (Zar 1999).

The SL data were grouped into 5-mm intervals, and the proportion of mature individuals was estimated for each analyzed year. A logistic model (Lysack 1980) was then fitted to the data:

$$P_i = \frac{1}{1 + e^{-b(SL_i - SL_{50})}}$$

where SL represents standard length,  $b$  is the rate of maturity, and  $SL_{50}$  is the standard length-at-sexual-maturity. The parameters were estimated by minimizing the negative log-likelihood function assuming a binomial distribution (Brouwer & Griffiths 2005), using the following formula:

$$-LL(\theta|data) = -\sum_{i=1}^n \left[ m_i \times \ln\left(\frac{p}{1-p}\right) + n \times \ln(1-p) + \ln\binom{n_i}{m_i} \right]$$

where LL is the negative log-likelihood,  $p$  is the proportion of individuals in length class  $SL_i$ ,  $n_i$  represents the total number of individuals in class  $SL_i$ , and  $m_i$  is the number of mature individuals in class  $SL_i$ .

A bootstrap procedure was used to generate one thousand random samples with replacement; each sample was fitted, and parameter uncertainty was estimated using nonparametric (95%) confidence intervals based on the bias-corrected percentile method (Haddon 2011).

The length-weight relationship was obtained by adjusting somatic growth to the observed SL-WT data using the potential growth model proposed by Bervian et al. (2006) and Fontoura et al. (2010). These authors suggested that polyphasic growth can be segmented into distinct phases, each characterized by a consistent power function. This biphasic structure was assumed

for the length-weight relationship to represent the juvenile and adult stages, which constitute the main ontogenetic transitions in small pelagic species with short life cycles, such as *E. mordax*. Accordingly, the following equation was used:

$$WT_{poly} = (\alpha_1 \times SL^{\beta_1}) \times \left( \frac{1}{1 + e^{(Tx \times (SL - SCL))}} \right) + (\alpha_2 \times SL^{\beta_2}) \times \left( \frac{1}{1 + e^{(-Tx \times (SL - SCL))}} \right)$$

where WT represents the expected weight corresponding to a given SL. The parameters  $\alpha_1$  and  $\alpha_2$  are the proportionality coefficients for the first and second stanzas, respectively, while  $\beta_1$  and  $\beta_2$  are the associated allometric coefficients. Tx denotes the transition rate between the first and second stanzas, and SCL refers to the stanza (stage) change length, that is, the point at which the growth pattern shifts.

A Student *t*-test was applied to test the null hypothesis that the coefficient  $\beta = 3$  (isometric growth) (Pauly 1983):

$$t = \frac{SD_x}{SD_y} \times \frac{|b - 3|}{\sqrt{1 - r^2}} \times \sqrt{(n - 2)}$$

where:  $SD_x$ : standard deviation of log (SL) and  $SD_y$ : the standard deviation of log (WT);  $n$  is the sample size, and  $R^2$  is the coefficient of determination.

The polyphasic model was fitted by minimizing the negative log likelihood function:

$$LL = -\frac{n}{2} [\ln 2\pi + 2 \times \ln \sigma + 1]$$

By using additive error:

$$\sigma = \sqrt{\frac{(WT_{obs} - WT_{est})^2}{n}}$$

Confidence intervals (95% CI) for the parameters  $a$ ,  $b$ , and SCL (polyphasic model) were estimated using the approach of Venzon & Moolgavkar (1988), which is based on chi-square distribution with  $d$  degrees of freedom (Hilborn & Walters 1992).

## RESULTS

A total of 7,827 northern anchovies were sampled between 2015 and 2023 (2,811 males, 4,718 females, and 298 unidentified). SL ranged from 65 to 150 mm, with an overall mean of  $107.89 \pm 11.29$  mm, while the WT ranged from 2.8 to 37.8 g, with a mean of  $13.99 \pm 4.80$  g. Mean length and weight values were significantly higher in females than in males (Mann-Whitney test: length  $T = 10335369.0$ ,  $P = 0.006$ ;

weight:  $T = 10262591.0$ ,  $P = 0.001$ ). Most individuals were within the 65-145 mm length range, with males exhibiting a narrower size range than females. Mean SL values for males and females were  $107.83 \pm 9.97$  and  $108.75 \pm 11.53$  mm, respectively. SL showed an increasing trend from 2015 to 2023, as confirmed by statistical analyses ( $P < 0.05$ ), indicating that the mean length in the final year was significantly higher than in all previous years for both sexes (Table 1).

### Sex ratio

The chi-square test did not detect significant differences between observed and expected sex ratios during the first three years, indicating no significant differences between males and females during that period. However, in subsequent years, statistically significant differences ( $P < 0.05$ ) were detected, with females consistently more abundant than males. Additionally, when considering the entire dataset (i.e. all years combined), females were significantly more abundant than males ( $X^2 = 724.8$ ,  $P < 0.05$ ) (Table 2). Monthly sex ratios significantly deviated from the 1:1 expectation in most months ( $P < 0.05$ ), indicating consistent female dominance, except in February and November, where no significant differences were detected (Table 3).

### Reproductive activity

Two reproductive peaks were observed over the annual cycle. The first occurred in females from February to April. From March to April in males, while the second occurred from October to December in females and from November to December in males (Fig. 2). Given that the species exhibits synchronous gonadal maturation, the apparent bimodal pattern and minor differences between sexes should be interpreted with caution. They may partially reflect sampling effects rather than true reproductive asynchrony.

In female anchovies, reproductive activity showed interannual variability, with the highest proportion (90%) recorded in 2016 and the lowest (12%) in 2019. The proportion of mature individuals was generally close to or above 0.5 across most years; however, during the middle years of the dataset, maturity levels were notably low in two years. In male anchovies, reproductive activity showed a similar interannual pattern, except that the lowest proportion (21%) occurred in 2021 (Fig. 2).

The size structure during the first reproductive peak showed that mature individuals were concentrated in the larger size classes for both sexes (Fig. 3, top). In contrast, during the second peak, a higher proportion of immature individuals was observed (Fig. 3, bottom).

**Table 1.** Summary statistics of *Engraulis mordax* from the west coast in Baja California (N: sample size, SD: standard deviation). KW-TK: Kruskal-Wallis test followed by *post-hoc* Tukey-Kramer comparisons; different letters indicate significant differences.

Sex	Year	Weight (g)				Standard length (mm)			
		n	Range	Mean	SD	Range	Mean	SD	KW-TK
Males	2015	129	3.4-16.3	12.0	2.17	70-117	104.2	6.45	CD
	2016	72	8.6-22.3	13.2	2.87	99-125	109.1	5.52	B
	2017	248	5.3-32.1	13.4	5.53	86-139	107.6	12.2	B
	2018	295	4-27.6	11.8	4.63	76-130	102.0	10.8	D
	2019	253	6.6-26.6	14.3	4	84-130	109.0	9.51	B
	2020	89	5.6-18.1	11.0	2.43	81-120	100.9	7.91	CD
	2021	570	5.5-23.3	12.3	2.61	80-130	104.1	7.35	C
	2022	459	4.7-26.8	14.3	3.47	80-135	108.8	8.69	B
	2023	696	6.1-32.2	16.3	4.27	85-144	113.7	9.19	A
	Total	2811	3.4-32.2	13.8	4.21	70-144	107.8	9.97	-
Females	2015	142	5.4-20.7	12.4	2.82	82-132	105.0	8.06	CD
	2016	62	8.8-25.9	15.2	4.45	97-135	113.6	9.23	AB
	2017	273	5.3-35.3	14.4	7.52	81-143	108.2	16.2	C
	2018	397	3.5-36.1	13.9	5.67	72-145	106.4	11.5	C
	2019	1032	2.9-35.9	12.0	3.48	70-145	103.2	9.15	D
	2020	234	5.1-23.4	10.9	2.68	75-126	99.8	7.84	E
	2021	822	5.4-26.9	13.3	3.13	84-139	106.8	8.21	C
	2022	684	4.3-25.9	15.2	4.08	76-135	110.8	10.2	B
	2023	1072	3.5-31.9	18.2	5.11	76-147	117.5	10.5	A
	Total	4718	2.9-36.1	14.4	5.01	70-147	108.8	11.5	-

**Table 2.** Yearly results of the chi-square test assessing sex ratio equality in northern anchovy (*Engraulis mordax*) on the west coast of Baja California.

Year	Observed			Expected hypothesis 1:1	$X_i^2$	P
	Males	Females	Total			
2015	129	142	271	135.5	0.6	0.430
2016	72	62	134	67	0.7	0.388
2017	248	273	521	260.5	1.2	0.273
2018	295	397	692	346	15.0	0.000
2019	253	1032	1285	642.5	472.2	0.000
2020	89	234	323	161.5	65.09	0.000
2021	570	822	1392	696	45.6	0.000
2022	459	684	1143	571.5	44.3	0.000
2023	696	1072	1768	884	80.0	0.000
Total	2811	4718	7529	3764.5	724.8	0.000

### Sexual maturity

SL<sub>50</sub> ranged from 98.04 to 121.54 mm in males, with a mean value of 108.5 mm, and from 99.37 to 123.4 mm in females, with an estimated mean of 109.54 mm. Values for both sexes followed similar trends: an increase from 2015 to 2019, a decline in 2020, and a subsequent recovery that has remained stable over the last three years (Fig. 4).

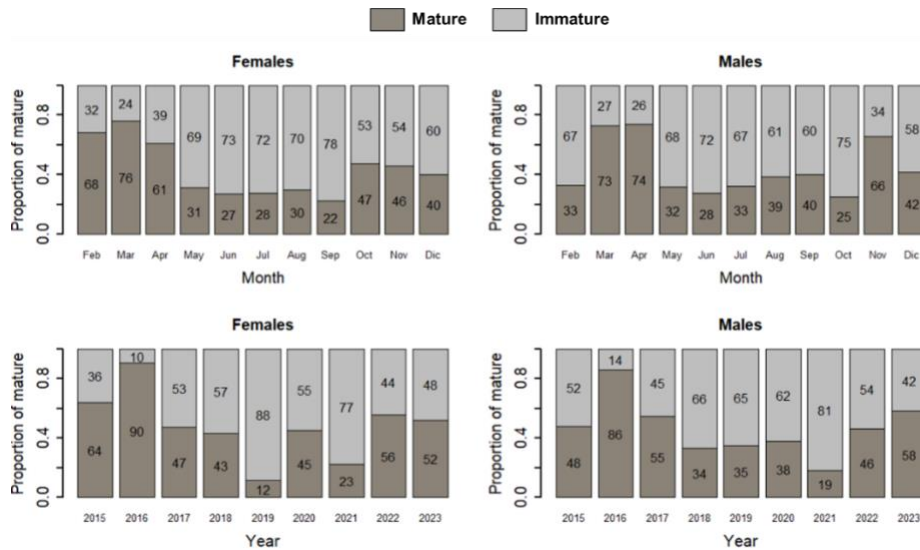
### Traditional power and polyphasic model

Length-weight relationships were significant and well-fitted ( $R^2 > 0.90$ ). The allometric coefficient (b) showed interannual variation, shifting from positive to negative allometry, with overall values indicating near-isometric growth in both sexes (Table 4).

Northern anchovy in this region exhibited relative allometric growth in both sexes, with hyper-allometry prevailing in the first stanza and hypo-allometry in the

**Table 3.** Monthly results of the Chi-square test assessing sex ratio equality in northern anchovy (*Engraulis mordax*) on the west coast of Baja California.

Month	Observed			Expected Hypothesis 1:1	X <sub>i</sub> <sup>2</sup>	P
	Males	Females	Total			
Feb.	85	111	196	98	3.4	0.063
Mar.	300	357	657	328.5	4.9	0.026
Apr.	392	558	950	475	29.0	0.000
May	748	1360	2108	1054	177.7	0.000
Jun.	423	657	1080	540	50.7	0.000
Jul.	381	694	1075	537.5	91.1	0.000
Aug.	204	553	757	378.5	160.9	0.000
Sep.	117	184	301	150.5	14.9	0.000
Oct.	84	133	217	108.5	11.1	0.001
Nov.	41	46	87	43.5	0.3	0.592
Dec.	36	65	101	50.5	8.3	0.004
Total	2811	4718	7529	3764.5	483.0	0.000



**Figure 2.** Monthly (top) and annual (bottom) proportions of mature males and females of northern anchovy (*Engraulis mordax*) on the west coast of Baja California. Numbers within the light- and dark-gray bars indicate the percentages of mature individuals.

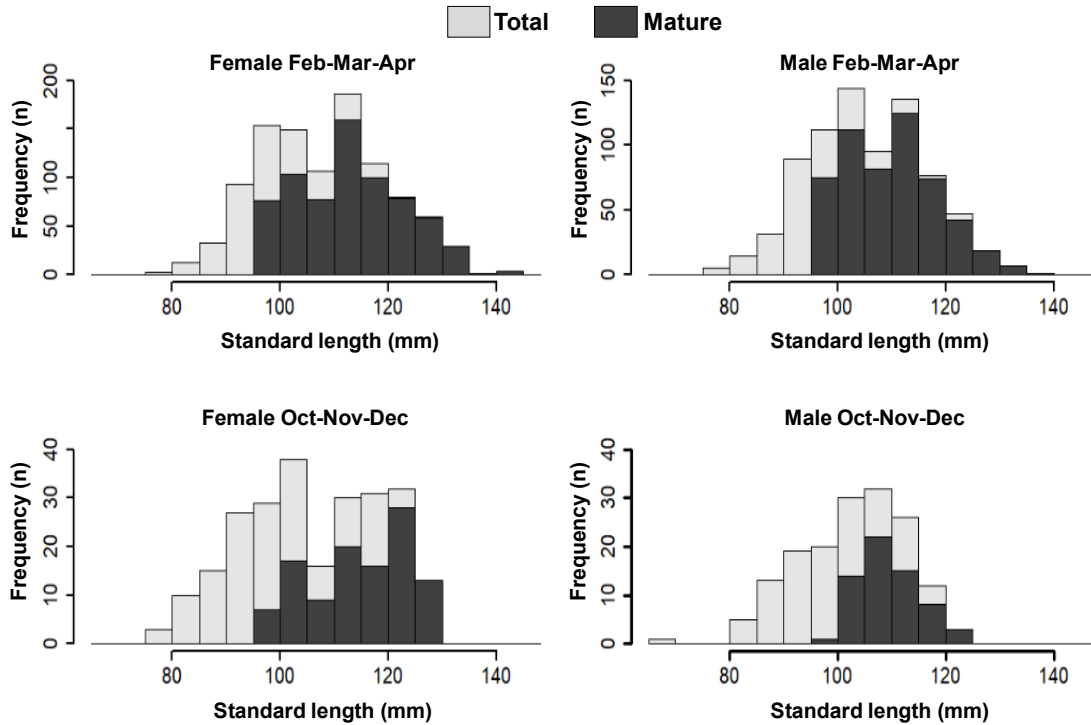
second. However, in some years, isometric growth was observed in both stanzas. The SCL showed interannual variation between sexes, ranging from 97.72 to 113.06 mm SL in males and 97.61 to 111.50 mm SL in females, with mean standard lengths across all years of 104.1 mm SL for males and 103.4 mm SL for females (Table 5).

By comparing the standard length distribution with the results of the polyphasic model for males and females, it was observed that the SCL (97.51 mm SL for males and 99.03 mm SL for females) coincided with the length at which the maturation process begins to

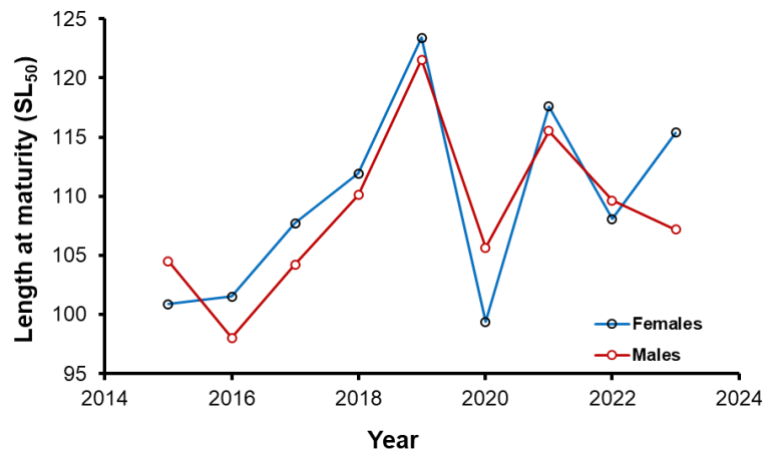
increase in both sexes. A similar pattern was observed in the results obtained for 2023 (Fig. 5).

### DISCUSSION

In the size structure of the catch, females predominated over males at both the annual and pooled time-series levels. In most years, females exhibited a wider length range and higher mean length and weight than males. These findings are consistent with those reported by Pike (1951) for the northern stock of *E. mordax* off the coast of British Columbia, who reported larger mean



**Figure 3.** Standard length structure during the first (top) and second (bottom) reproductive peaks of northern anchovy (*Engraulis mordax*) on the west coast of Baja California.



**Figure 4.** Yearly standard length at sexual maturity ( $SL_{50}$ ; mm) of northern anchovy (*Engraulis mordax*) from the west coast of Baja California.

sizes for females than for males; however, the sizes reported in that study were larger than those observed in the present study. In addition, INAPESCA (1985) reported mean sizes of 120 and 110 mm for females and males of *E. mordax* during the 1975 and 1976 fishing seasons in Baja California, consistent with the sex-related size differences observed in this study. Similarly, Cotero-Altamirano (2000) reported larger

mean sizes for *E. mordax* females than for males in the Gulf of California. More recently, Orona-Díaz et al. (2024), working in the same area and on the same species, reported sizes ranging from 48 to 138 mm. Although sex-specific separation was not determined, these lengths are comparable to those observed in the present study.

**Table 4.** Results of the traditional power model and relative growth patterns for northern anchovy (*Engraulis mordax*) from the west coast of Baja California. \*Negative allometric; \*\*positive allometric; \*\*\*isometric. CI: confidence interval.

Group	Year	<i>a</i>			<i>b</i>			R <sup>2</sup>	n	<i>t</i>	<i>P</i>
		Value	CI 95% (lower-upper)		Value	CI 95% (lower-upper)					
Males	2015	1.46E-05	1.45E-05	1.48E-05	2.9295	2.9271	2.9319	0.92	129	4.36	*
	2016	2.77E-07	2.71E-07	2.83E-07	3.7649	3.7602	3.7697	0.93	72	80.33	**
	2017	5.68E-07	5.62E-07	5.75E-07	3.6149	3.6126	3.6174	0.93	248	56.73	**
	2018	1.30E-06	1.29E-06	1.33E-06	3.4531	3.4517	3.4583	0.93	295	38.65	**
	2019	1.21E-05	1.20E-05	1.23E-05	2.9749	2.9724	2.9774	0.94	253	2.23	*
	2020	5.66E-05	5.57E-05	5.75E-05	2.6378	2.6343	2.6412	0.91	89	20.22	*
	2021	2.56E-05	2.54E-05	2.58E-05	2.8127	2.8113	2.8142	0.92	570	12.86	*
	2022	1.69E-05	1.68E-05	1.70E-05	2.9062	2.9047	2.9077	0.93	459	7.64	*
	2023	9.25E-06	9.19E-06	9.31E-06	3.0341	3.0327	3.0354	0.94	696	3.43	**
	Total	8.37E-06	8.34E-06	8.40E-06	3.0503	3.0495	3.0510	0.93	2811	4.31	**
Females	2015	4.24E-05	4.18E-05	4.29E-05	2.7025	2.6997	2.7053	0.92	142	19.55	*
	2016	4.99E-06	4.89E-06	5.20E-06	3.1502	3.1461	3.1591	0.94	62	16.08	**
	2017	1.20E-06	1.19E-06	1.21E-06	3.4590	3.4566	3.4614	0.94	273	46.85	**
	2018	1.01E-06	9.95E-07	1.02E-06	3.5119	3.5096	3.5142	0.93	397	52.39	**
	2019	1.44E-05	1.43E-05	1.45E-05	2.9365	2.9351	2.9379	0.92	1032	4.46	*
	2020	1.89E-05	1.87E-05	1.91E-05	2.8794	2.8770	2.8818	0.91	234	7.41	*
	2021	2.04E-05	2.03E-05	2.05E-05	2.8629	2.8617	2.8641	0.93	822	10.47	*
	2022	1.87E-05	1.86E-05	1.88E-05	2.8862	2.8849	2.8874	0.94	684	9.52	*
	2023	1.11E-05	1.10E-05	1.12E-05	2.9978	2.9966	2.9990	0.95	1072	0.25	***
	Total	7.84E-06	7.81E-06	7.86E-06	3.0663	3.0656	3.0669	0.94	2812	6.02	**

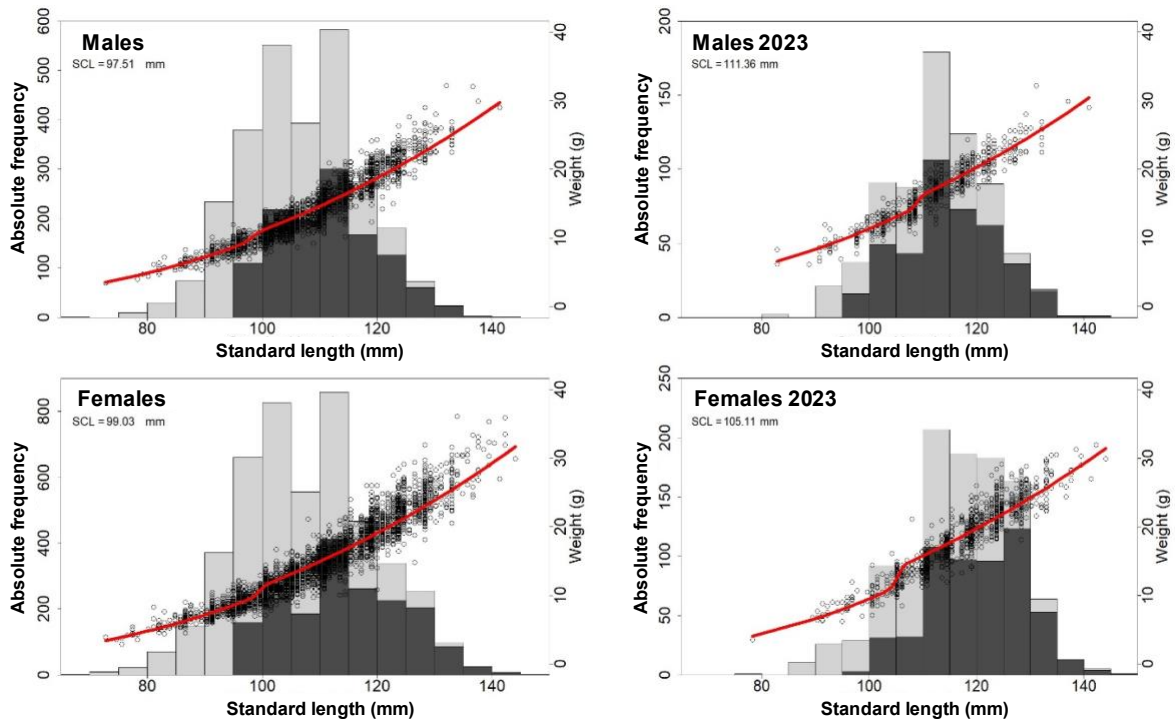
The annual sex ratio was consistent with the null hypothesis of a 1:1 male-to-female ratio during the first three years of the study. A similar annual equilibrium in sex proportions was reported for *Engraulis encrasicolus* in the Cadiz Bay (Millan 1999), suggesting a balanced population structure. However, in subsequent years, the sex ratio became female-dominated, which may be related to several factors, including higher post-spawning survival of females, differential environmental stressors affecting the sexes, or an adaptive reproductive strategy in *E. mordax*. This behavior has also been documented for *E. ringens* (Alheit et al 1984), *E. mordax* (Klinbeil 1978, Parrish et al. 1986), and *E. encrasicolus* (Millan 1999). Although synchronous spawning species are often expected to exhibit balanced sex ratios during reproductive aggregations, a female-biased sex ratio may confer reproductive advantages at the population level. In externally fertilizing fishes, reproductive success is rarely limited by the number of males, whereas egg production depends directly on the abundance and condition of females. Consequently, female dominance may enhance reproductive output and provide reproductive insurance under conditions of high mortality and environmental variability (Hunter & Leong 1981, Lowerre-Barbieri et al. 2011, Checkley Jr.

et al. 2017). Monthly sex ratio analysis revealed female dominance in 9 of the 11 months, which is consistent with findings reported for *E. encrasicolus* in the Mediterranean Sea and Cádiz Bay (Giraldez & Abad 1995, Millan 1999).

Monthly patterns in maturity suggest two apparent reproductive peaks; however, these patterns do not necessarily indicate discrete spawning events. Previous studies on *E. mordax* in the California Current System have consistently described a prolonged spawning season extending from late winter to spring, rather than clearly separated reproductive pulses (Hunter & Goldberg 1980, Checkley Jr. et al. 2009). In this context, the bimodal pattern observed here is more likely explained by ontogenetic structuring within a continuous reproductive period. The first peak, characterized by larger individuals and a higher proportion of mature fish, likely represents the adult spawning stock, whereas the second peak, dominated by smaller individuals and a lower proportion of mature fish, may reflect the progressive incorporation of first-time spawners into the reproductive population. This interpretation is consistent with the reproductive strategies of small pelagic fishes, in which extended spawning seasons and size-dependent reproductive participation are common (Lowerre-Barbieri et al. 2011,

**Table 5.** Results of the polyphasic growth model, relative growth patterns, and standard length at sexual maturity  $SL_{50}$  estimates for northern anchovy (*Engraulis mordax*) from the west coast of Baja California. \*Negative allometric; \*\*positive allometric; \*\*\*isometric. CI: confidence interval, LL: Log-likelihood; AIC: Akaike information criterion.

Sex	Year	Polyphasic model					CI 95%		LL	AIC	Allometry t-test						L <sub>50</sub> model	CI 95%		b	LL	AIC	
		$\alpha_1$	$\alpha_2$	$\beta_1$	$\beta_2$	Tx	SCL	Lower			Upper	t <sub>1</sub>	df <sub>1</sub>	p <sub>1</sub>	t <sub>2</sub>	df <sub>2</sub>		p <sub>2</sub>	Lower				Upper
Males	2015	5.40E-06	3.31E-05	3.1	2.8	0.3	97.8	86.8	100.4	-149.1	310.1	6.4	12	**	4.24	113	**	104.5	102.2	106.9	0.2	-10.5	24.9
	2016	1.34E-05	6.87E-06	2.9	3.1	0.4	111.6	109.9	113.2	-118.0	248.0	2.0	48	**	0.13	20	*	98.0	97.5	101.5	0.2	-9.6	23.2
	2017	4.71E-06	2.58E-05	3.2	2.8	0.5	113.1	111.8	116.6	-422.1	856.2	5.7	156	**	2.67	84	**	104.2	101.9	106.5	0.1	-31.3	66.6
	2018	1.11E-06	2.40E-04	3.5	2.4	0.9	109.9	106.8	110.6	-496.4	1004.7	15.4	226	**	4.42	65	**	110.1	106.8	114.9	0.1	-47.7	99.4
	2019	2.35E-05	1.62E-05	2.8	2.9	0.2	104.70	100.6	111.2	-449.7	911.5	4.6	73	**	1.67	176	*	121.5	114.7	127.5	0.2	-22.2	48.3
	2020	1.32E-06	3.47E-05	3.5	2.7	0.2	91.05	88.5	92.5	-116.6	245.2	7.4	10	**	5.07	75	**	105.7	101.1	113	0.3	-19.1	42.2
	2021	1.15E-05	1.68E-05	3	2.9	0.4	97.72	95.4	107.9	-830.3	1672.6	0.1	104	*	3.16	462	**	115.5	113.5	118.5	0.3	-15.0	34.0
	2022	1.21E-05	3.22E-05	3	2.8	0.3	99.41	98.2	100.3	-713.4	1438.7	0.7	48	*	8.62	407	**	109.7	107.5	112.1	0.2	-26.1	56.2
	2023	1.42E-05	1.02E-04	2.9	2.5	0.4	111.4	111.1	111.6	-1241.6	2495.3	1.3	237	*	12.3	455	**	107.2	103.8	109.7	0.1	-31.2	66.4
	Pooled	8.91E-06	5.63E-05	2.7	3	0.6	97.51	97.4	97.6	-15893.0	31797.9	1.0	423	*	26.8	2388	**	110.4	109.5	111.3	0.1	-92.3	188.7
Females	2015	3.28E-06	8.04E-05	3.3	2.6	0.1	101.4	96.7	105.9	-206.1	424.2	5.0	40	**	9.41	98	**	100.9	98.91	102.5	0.3	-14.7	33.3
	2016	1.50E-05	1.47E-04	2.9	2.5	0.1	111.5	110.8	115.2	-120.5	253.0	1.7	26	*	3.36	32	**	101.5	97.5	100.9	0.4	-6.2	16.3
	2017	3.77E-05	3.19E-06	2.7	3.3	0.5	101.3	99.0	106.1	-528.8	1069.5	6.1	126	**	9.77	143	**	107.7	105.3	110.3	0.1	-35.4	74.9
	2018	4.60E-06	5.54E-05	3.2	2.7	0.5	103.3	102.8	103.8	-790.5	1593.0	3.3	165	**	11.7	228	**	111.9	107.2	119.5	0.2	-85.7	175.5
	2019	2.70E-05	1.71E-05	2.8	2.9	0.2	99.13	99.0	99.3	-1921.1	3854.1	11.1	291	**	1.7	736	**	123.4	120.2	128	0.2	-24.9	53.8
	2020	8.27E-05	8.84E-06	2.6	3	0.1	97.61	83.2	111.7	-320.4	652.7	22.4	81	**	1.83	149	*	99.4	98.11	100.8	0.3	-19.8	43.6
	2021	2.74E-05	1.28E-05	2.8	3	0.4	108.8	100.5	122.3	-1268.6	2549.2	7.6	443	**	0.66	375	*	117.6	115.8	120.1	0.3	-20.1	44.2
	2022	1.25E-05	2.23E-04	3	2.4	0.9	102.4	100.8	103.0	-1171.2	2354.5	1.3	112	*	28.4	568	**	108.1	106.7	109.4	0.1	-24.8	53.5
	2023	4.67E-06	2.04E-04	3.2	2.4	0.5	105.1	104.8	105.5	-2193.0	4398.1	2.0	157	**	22.2	911	**	115.4	113.7	117	0.1	-38.2	80.4
	Pooled	6.37E-06	7.01E-05	3.1	2.6	0.5	99.03	99.0	99.1	-8948.7	17909.4	4.9	899	**	39.1	3815	**	113.8	113.1	114.5	0.1	-104.5	212.9



**Figure 5.** Comparison of the standard-length structure and polyphasic model for males and females of northern anchovy (*Engraulis mordax*) from the west coast of Baja California, pooled data (left) and 2023 (right). SCL: stanza change length.

Ganias 2014). Therefore, rather than indicating a shift in reproductive timing, the observed pattern likely reflects cohort-specific contributions to spawning activity within a single, extended reproductive season.

$SL_{50}$  estimates showed broadly similar trends between sexes, with an apparent inverse relationship with the annual maturity proportion, such that lower  $SL_{50}$  values coincided with years of higher maturity. However, this pattern is likely influenced by the dominance of smaller individuals participating in reproductive activity, which may shift maturity ogives toward smaller sizes without reflecting a true change in maturation dynamics (Lowerre-Barbieri et al. 2011). When interpreted within the context of a prolonged reproductive season extending from late autumn to early spring, this pattern supports the hypothesis that the participation of smaller, first-time spawners contributes to reduced  $SL_{50}$  estimates, rather than indicating discrete spawning seasons or a shift in size at maturity (Hunter & Goldberg 1980).

Although there are a limited number of studies estimating the allometric growth of *E. mordax* in the southern region of the California Current, particularly off Baja California, Mexico, most have relied on the traditional power model (Gallardo-Cabello 1985,

Rodríguez-Romero et al. 2007), which has limited ability to detect size-related changes in relative growth. In the present study, analysis of historical data from 2015 to 2023 showed that allometry varied over time, shifting from positive to negative during the first four years and remaining predominantly negative thereafter. This pattern may be driven by multiple factors, including climatic variability, habitat conditions, ontogenetic changes, oceanographic dynamics, food availability, interspecific competition, and fishing pressure (Bilgin et al. 2016, Brosset et al. 2016, Lappalainen et al. 2016, Bilgin & Solak 2020). In addition, part of the observed temporal variability may reflect sampling-related effects, such as differences in sample size, size selectivity, and temporal or spatial coverage among years. Seasonal variation in the length-weight relationship associated with reproductive condition may also play an important role, as shifts in maturity composition across sampling periods can influence relative growth patterns.

Results from the polyphasic approach indicated significant allometry in nearly all years analyzed. In addition, values  $>$  (positive allometry and isometry) were more frequent in the first stage of the model than in the second, where negative allometry predominated.

This pattern may be linked to a shift in energy allocation across ontogeny: during the first stage, when *E. mordax* individuals are relatively small, energy is primarily allocated to survival and somatic growth, resulting in proportional or positive increases in weight relative to length. In contrast, during the second stage, as individuals grow larger, a greater proportion of energy is allocated to reproductive processes. Although gonadal maturation involves substantial energetic investment and an increase in gonad mass, this investment does not translate into proportional increases in total body weight relative to length. Instead, reproductive allocation may constrain somatic growth in length, leading to negative allometry in the weight-length relationship. During reproductive and spawning phases, energy typically reserved for somatic maintenance and growth is redirected toward lipid accumulation in the gonads and oogenesis (Sinovčić & Zorica 2006), which can result in reduced somatic condition and lower relative weight at a given length, as reflected by declining condition factor and  $\beta$  values (Armstrong & Shelton 1990, Kozłowski 1996).

The application of this methodological approach to small pelagic species remains largely unexplored; however, it has been successfully implemented in other fish taxa (Bervian et al. 2006, Fontoura et al. 2010, Lanzoni et al. 2018, Borrego et al. 2024). In those studies, the main findings suggest an association between the identified inflection points and the processes of sexual maturation and reproduction. In the present study, mean SCL values were 97.51 mm SL for males and 99.03 mm SL for females, indicating inflection points in the respective models. These values represent the inflection points on the respective models. In males, SCL values declined over time, whereas in females they increased. In *E. mordax*, the spawning season tends to increase in duration with female size, weight, and age. Although most individuals attain sexual maturity within their first year, older females contribute substantially more to total annual egg production than younger, first-time spawners (Parrish et al. 1986, Schwartzkopf et al. 2022). This pattern may account for the differences observed in  $\beta_1$  (stage 1) and  $\beta_2$  (stage 2) values within the polyphasic approach. It is therefore plausible to suggest that these variations in length in *E. mordax* are associated with intensified sexual development.

When comparing SCL values with  $SL_{50}$  estimates for *E. mordax* in this region, it is noteworthy that Tapia-Vázquez et al. (1988) reported an overall  $SL_{50}$  value of 85 mm for female *E. mordax*, based on samples collected between 1981 and 1983. Comparable results

were obtained from cumulative sexual maturity curves by Escudero & Castellanos (1990), who estimated  $SL_{50}$  ranging from 106 to 126 mm, with a downward trend observed from 1975 to 1983. These values are quite similar to the SCL values obtained in this study. Although such similarities may suggest that sexual maturation is a primary factor in determining SCL, multiple factors can influence SCL, underscoring the need for further studies to disentangle the relationship between SCL and  $SL_{50}$  better. Fontoura et al. (2010) noted that their findings revealed shifts in growth patterns linked to the energetic demands of reproduction. While such biological changes may also reflect the influence of adverse environmental factors, they recommended using this method as a complementary tool for fisheries management.

Comparison of Akaike information criterion (AIC) values between the polyphasic and  $L_{50}$  models showed a consistent pattern across all years and both sexes, with the  $L_{50}$  model yielding substantially lower AIC values, indicating a better statistical fit. However, despite this difference in performance, the polyphasic model remains particularly valuable in contexts where maturity data are unavailable. Unlike the  $L_{50}$  approach, which requires explicit information on reproductive status, the polyphasic model relies solely on length-weight relationships to identify growth shifts associated with ontogenetic changes. Therefore, although it may be less parsimonious under the AIC criterion, the polyphasic model provides a practical and informative alternative for inferring biological transitions, especially in data-limited scenarios where direct estimates of size at maturity are unavailable.

In conclusion, females attained larger sizes (>95 mm SL) than males. Growth exhibited significant allometry when analyzed using the polyphasic approach. Positive allometry and isometry predominated during the first stage, whereas negative allometry characterized the second stage. The estimated standard length at sexual maturity (SCL) was 97.51 mm for males and 99.03 mm for females, suggesting a close relationship with the maturation process. The application of polyphasic regression represents a promising alternative when direct information on sexual maturity is scarce, as SCL estimates derived from growth patterns may serve as a proxy for the onset of maturation. Given that growth and maturity are key metrics for fisheries assessment and management, the development and application of complementary analytical approaches to compensate for unavailable biological information remain central and ongoing tasks for fisheries biologists in evaluating exploited resources.

### Credit author contribution

J.R. Rendón-Martínez: methodology, formal analysis, interpretation, writing-original draft and editing; J. Payán-Alejo: conceptualization, methodology, formal analysis, and writing-original draft and editing; C. Enciso-Enciso: project administration, conceptualization, methodology, writing-original draft and editing; M.O. Nevarez-Martínez, J.S. Ramírez-Pérez & R. Sánchez-Cárdenas: methodology, interpretation, review and editing. All authors have read and accepted the published version of the manuscript.

### Conflict of interest

The authors declare no conflict of interest regarding this research article.

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### REFERENCES

- Alheit, J., Alarcon, V.H. & Macewicz, B.J. 1984. Spawning frequency and sex ratio in the Peruvian anchovy *Engraulis rigens*. California Cooperative Oceanic Fisheries Investigations Reports, 25: 43-52.
- Álvarez-Ramírez, I.M. 2003. Análisis comparativo de la morfometría de la anchoveta norteña (*Engraulis mordax*, Girard, 1856. Clupeiformes: Engraulidae) de la costa occidental de Baja California y Golfo de California. M.Sc. Thesis, Instituto Politécnico Nacional, La Paz.
- Armstrong, M.J. & Shelton, P.A. 1990. Clupeoid life-history styles in variable environments. Environmental Biology of Fishes, 28: 77-85.
- Bervian, G., Fontoura, N.F. & Haimovici, M. 2006. Statistical model of variable allometric growth: otolith growth of *Micropogonias furnieri* (Actinopterygii, Sciaenidae). Journal of Fish Biology, 68: 196-208. doi: 10.1111/j.1095-8649.2005.00890.x
- Bilgin, S. & Solak, E. 2020. Weight-length relationships (WLRs) of anchovy, *Engraulis encrasicolus* with the evaluation of overfishing effects on the slope (b) in the Black Sea (Turkey). Journal of Anatolian Environmental and Animal Sciences, 5: 253-259. doi: 10.35229/jaes.726961
- Bilgin, S., Sümer, Ç., Bektaş, S., et al. 2016. Evaluation of anchovy (*Engraulis encrasicolus*) population dynamics studies (1985-2015) in terms of fisheries management in the Black Sea. Ege Journal of Fisheries and Aquatic Sciences, 33: 169-182. doi: 10.12714/egejfas.2016.33.2.12
- Borrego-Durán, J.Z., Pérez-González, R., Rodríguez-Domínguez, G., et al. 2024. Crecimiento alométrico de *Panulirus gracilis* (Decapoda: Palinura) asociado a la fase de madurez gonádica. Ecosistemas y Recursos Agropecuarios, 11: e3861. doi: 10.19136/era.a11n1.3861
- Brosset, P., Lloret, J., Muñoz, M., et al. 2016. Body reserves mediate trade-offs between life-history traits: new insights from small pelagic fish reproduction. Royal Society Open Science, 3: 60202. doi: 10.1098/rsos.160202
- Brouwer, S.L. & Griffiths, M.H. 2005. Reproductive biology of carpenter seabream (*Argyrozona argyrozona*) (Pisces: Sparidae) in a marine protected area. Fishery Bulletin, 103: 258-269. doi: 10.1146/annurev-marine-122414-033819
- Castro-Gutiérrez, J., Cabrera-Castro, R., Czerwinski, I.A., et al. 2022. Effect of climatic oscillations on small pelagic fisheries and their economic profit in the Gulf of Cadiz. International Journal of Biometeorology, 66: 613-626. doi: 10.1007/s00484-021-02223-9
- Checkley Jr., D.M. & Barth, J.A. 2009. Patterns and processes in the California Current System. Progress in Oceanography, 83: 49-64. doi: 10.1016/j.pocean.2009.07.028
- Checkley Jr., D.M., Asch, R.G. & Rykaczewski, R. 2017. Climate, anchovy, and sardine. Annual Review of Marine Science, 9: 469-493. doi: 10.1146/annurev-marine-122414-033819
- Cotero-Altamirano, C.E. 1987. Ciclo reproductivo, madurez y fecundidad de la anchoveta (*Engraulis mordax*): Análisis comparativo en el período 1981-1983. MSc Thesis, CICESE, Ensenada, B.C.
- Cotero-Altamirano, C.E. 2000. Dinámica de la población de la anchoveta (*Engraulis mordax*) del Golfo de California. Ph.D. Thesis, CICESE, Ensenada, B.C.
- Diario Oficial de la Federación (DOF). 2022. Acuerdo mediante el cual se da a conocer la actualización de la Carta Nacional Pesquera. Secretaría de Agricultura y Desarrollo Rural (SADER). Diario Oficial de la Federación, Ciudad de México.
- Diario Oficial de la Federación (DOF). 2023. Acuerdo mediante el cual se da a conocer el Plan de Manejo Pesquero para la pesquería de Pelágicos Menores (sardinas, anchovetas, macarelas y afines) del noroeste

- de México. Diario Oficial de la Federación, Ciudad de México.
- Escudero, M. & Castellanos, C. 1990. Estudio de la pesquería de anchoveta norteña (*Engraulis mordax*) en aguas mexicanas. *Ciencia Pesquera*, 7: 35-37.
- Espinosa-Carreón, T.L. 2005. Producción primaria en relación a procesos físicos de mesoescala en la región sur de la Corriente de California. Ph.D. Thesis, Centro de Investigación Científica y de Educación de Ensenada Ensenada, B.C.
- Flores-Anaya, R.J., Quiñonez-Velázquez, C., Arizmendi-Rodríguez, D.I., et al. 2024. Estimation of age, growth, and length at first maturity of the round herring *Etrumeus acuminatus* (Gilbert, 1890) on the western coast of Baja California Sur, Mexico. *Latin American Journal of Aquatic Research*, 52: 713-726. doi: 10.3856/vol52-issue5-fulltext-3201
- Fontoura, N.F., Braun, A.S. & Milani, P.C.C. 2009. Estimating size at first maturity ( $L_{50}$ ) from gonadosomatic index (GSI) data. *Neotropical Ichthyology*, 7: 217-222. doi: 10.1590/S1679-62252009000200013
- Fontoura, N.F., Jesus, A.S., Larre, G.G., et al. 2010. Can weight/length relationship predict size at maturity? A case of two species of Characidae. *Neotropical Ichthyology*, 8: 835-840. doi: 10.1590/S1679-62252010005000013
- Froese, R., Tsikliras, A.C. & Stergiou, K.I. 2011. Editorial note on weight-length relations of fishes. *Acta Ichthyologica et Piscatoria*, 41: 261-263. doi: 10.3750/AIP2011.41.4.01
- Gallardo-Cabello, M. 1985. Análisis del crecimiento de la anchoveta *Engraulis mordax* Girard, en aguas de Baja California Norte (Pisces: Engraulidae). *Anales del Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México (UNAM)*, 12: 235-252.
- Ganias, K. (Ed.). 2014. *Biology and ecology of sardines and anchovies*. CRC Press, Boca Raton.
- Giraldez, A. & Abad, R. 1995. Aspects of the reproductive biology of the western Mediterranean anchovy from the coasts of Malaga (Alboran Sea). *Scientia Marina*, 59: 15-23.
- Haddon, M. 2011. *Modeling and quantitative methods in fisheries*. Chapman & Hall, London.
- Hilborn, R. & Walters, C.J. 1992. *Quantitative fisheries stock assessment: choice, dynamics & uncertainty*. Chapman & Hall, London..
- Hunter, J.R. & Golberg, S.R. 1980. Spawning incidence and batch fecundity in northern anchovy. *Fishery Bulletin*, 77: 641-652.
- Hunter, J.R. & Leong, R. 1981. The spawning energetics of female northern anchovy *Engraulis mordax*. *Fishery Bulletin*, 79: 215-230.
- Instituto Nacional de la Pesca (INAPESCA). 1985. *Anchoveta: Diagnóstico y perspectivas*. Información resumida. Instituto Nacional de la Pesca - Secretaría de Pesca. [<https://inapesca.gob.mx/portal/Publicaciones/Series/1985-RI-Diagnostico/1985-RI-2-Anchoveta.pdf>]. Reviewed: July 12, 2025.
- Klinbeil, R.A. 1978. Sex ratios of northern anchovy (*Engraulis mordax*) in southern California. *California Fish and Game*, 64: 210-218.
- Kozłowski, J. 1996. Optimal allocation of resources explains interspecific life-history patterns in animals with indeterminate growth. *Proceedings of the Royal Society B*, 263: 559-566. doi: 10.1098/rspb.1996.0084
- Lanzoni, M., Aschonitis, V., Milardi, M., et al. 2018. A method to identify bimodal weight-length relations: Possible ontogenetic diet and/or metabolism shift effects in *Anguilla anguilla* (Actinopterygii: Anguilliformes: Anguillidae). *Acta Ichthyologica et Piscatoria*, 48: 163-171. doi: 10.3750/AIEP/2400
- Lappalainen, A., Saks, L., Šuštar, M., et al. 2016. Length at maturity as a potential indicator of fishing pressure effects on coastal pikeperch (*Sander lucioperca*) stocks in the northern Baltic Sea. *Fisheries Research*, 174: 47-57. doi: 10.1016/j.fishres.2015.08.013
- Lowerre-Barbieri, S.K., Ganias, K., Saborido-Rey, F., et al. 2011. Reproductive timing in marine fishes: variability, temporal scales, and methods. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*, 3: 71-91. doi: 10.1080/19425120.2011.556932
- Lluch-Belda, D., Crawford, R., Kawasaki, T., et al. 1989. Worldwide fluctuations of sardine and anchovy stocks: The regimen problem. *South African Journal of Marine Science*, 8: 195-205.
- Lysack, W. 1980. 1979 Lake Winnipeg fish stock assessment program. Department of Natural Resources, Manitoba.
- Ma, S., Cheng, J., Li, J., et al. 2019. Interannual to decadal variability in the catches of small pelagic fishes from China Seas and its responses to climatic regime shifts. *Deep-Sea Research Part II*, 159: 112-119. doi: 10.1016/j.dsr2.2018.10.005
- Millan, M. 1999. Reproductive characteristics and condition status of anchovy *Engraulis encrasicolus* L. from the Bay of Cadiz (SW Spain). *Fisheries Research*, 41: 73-86.

- Nevárez-Martínez, M.O., Martínez-Zavala, M.A., Cotero-Altamirano, C.E., et al. 2014. Peces pelágicos menores. In: Beléndez-Moreno, L.F.J., Espino-Barr, E., Galindo-Cortes, G., et al. (Eds.). Sustentabilidad y pesca responsable en México. Evaluación y manejo. Instituto Nacional de la Pesca, Ciudad de México, pp. 84-137.
- Oliveira, M.R., Costa, E.F.S., Araújo, A.S., et al. 2012. Sex ratio and length-weight relationship for five marine fish species from Brazil. *Journal of Marine Biology & Oceanography*, 1: 1-3. doi: 10.4172/23248661.1000103
- Orona-Díaz, D.A., Vallarta-Zárate, J.R., Payán-Alejo, J., et al. 2024. Edad y crecimiento de anchoveta norteña (*Engraulis mordax*) en la costa occidental de la península de Baja California y en el Golfo de California. XXXII Taller de pelágicos menores. Agricultura-IMIPAS-CRIAP-Mazatlán, Mazatlán.
- Parés-Sierra, A., López, M. & Pavía, E. 1997. Oceanografía física del Océano Pacífico nororiental. In: Lavín, M.F. (Ed.). Contribuciones a la oceanografía física en México. Unión Geofísica Mexicana, 3: 1-24.
- Parrish, R.H., Mallicoate, D.L. & Klingbeil, R.A. 1986. Age dependent fecundity, number of spawnings per year, sex ratio, and maturation stages in northern anchovy, *Engraulis mordax*. *Fishery Bulletin*, 84: 503-517.
- Pauly, D. 1983. Algunos métodos simples para la evaluación de recursos pesqueros tropicales. FAO Documentos Técnicos de Pesca 234. FAO, Rome.
- Peck, M.A., Alheit, J., Bertrand, A., et al. 2021. Small pelagic fish in the new millennium: A bottom-up view of global research effort. *Progress in Oceanography*, 191: 1-34. doi: 10.1016/j.pocean.2020.102494
- Pedrin-Osuna, O.A., Granados-Gallegos, M.L. & Cota-Villavicencio, A. 1992. Tasas de explotación y mortalidad por pesca de la anchoveta norteña (*Engraulis mordax*) para el periodo de 1974 a 1989. *Ciencias Marinas*, 18: 97-113.
- Pike, G.C. 1951. Age, growth and maturity studies on the Pacific anchovy (*Engraulis mordax*) from the coast of British Columbia. M.Sc. Thesis, University of British Columbia, British Columbia.
- Rodríguez-Romero, J., Palacios-Salgado, D.S., López-Martínez, J., et al. 2007. The length-weight relationship parameters of demersal fish species off the western coast of Baja California Sur, Mexico. *Journal of Applied Ichthyology*, 25: 114-116. doi: 10.1111/j.1439-0426.2008.01175.x
- Rykaczewski, R.R. 2019. Changes in mesozooplankton size structure along a trophic gradient in the California Current Ecosystem and implications for small pelagic fish. *Marine Ecology Progress Series*, 617-618: 165-182. doi: 10.3354/meps12554
- Schwartzkopf, B.D., Dorval, E., James, K.C., et al. 2021. A summary report of life history information on the central subpopulation of northern anchovy (*Engraulis mordax*) for the 2021 stock assessment. U.S. Department of Commerce, NOAA Technical Memorandum NOAA-TM-NMFS-SWFSC-665U.S. doi: 10.25923/jv24-1539
- Schwartzkopf, B.D., Dorval, E., James, K.C., et al. 2022. A summary report of life history information on the central subpopulation of northern anchovy (*Engraulis mordax*) for the 2021 stock assessment. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-SWFSC-659. doi: 10.25923/ckvg-va49
- Sinović, S. & Zorica, B. 2006. Reproductive cycle and minimal length at sexual maturity of *Engraulis encrasicolus* (L.) in the Zrmanja River estuary (Adriatic Sea, Croatia). *Estuarine Coastal and Shelf Science*, 69: 439-448.
- Sokal, R.R. & Rohlf, F.J. 1981. *Biometry: The principles and practice of statistics in biological research*. Freeman, New York.
- Sydemann, W.J., Dedman, S., García-Reyes, M., et al. 2020. Sixty-five years of northern anchovy population studies in the southern California Current: a review and suggestion for sensible management. *ICES Journal of Marine Science*, 77: 486-499. doi: 10.1093/icesjms/fsaa004/5734670
- Tapia-Vázquez, O.M., Cotero-Altamirano, C.E. & García-Cuellar, C.M. 1988. Determinación de madurez gonadal y fecundidad en anchoveta (*Engraulis mordax*) de la subpoblación central. *Ciencia Pesquera*, 6: 69-101.
- Venrick, E.L. 2000. Summer in the Ensenada Front: The distribution of phytoplankton species, July 1985 and September 1988. *Journal of Plankton Research*, 22: 813-841.
- Venzon, D.J. & Moolgavkar, S.H. 1988. A method for computing profile-likelihood-based confidence intervals. *Applied Statistics*, 37: 87-94.
- Zar, J. 1999. *Biostatistical analysis*. Prentice Hall, Upper Saddle River.

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