



# Temporal changes in the body shape of the Pacific thread herring *Opisthonema libertate* on the Western Baja California Sur coast

Carlos Iván Pérez-Quiñonez<sup>1</sup> · Jorge Guillermo Chollet-Villalpando<sup>2,3</sup> · Casimiro Quiñonez-Velázquez<sup>2</sup> · Dana Isela Arizmendi-Rodríguez<sup>4</sup>

Received: 29 January 2024 / Revised: 2 July 2024 / Accepted: 26 July 2024  
© The Author(s), under exclusive licence to Senckenberg Gesellschaft für Naturforschung 2024

## Abstract

Over the past few decades, analyzing body shape changes and their application to population dynamics has allowed the quantitative and qualitative evaluation of morphological changes associated with phenotypic expression. However, the physiological conditions of organisms need to be considered in the analyses of body shape variation. We address changes in the body shape of the Pacific thread herring *Opisthonema libertate* (Günther, 1867) on the western coast of Baja California Sur during an annual cycle using landmark data and geometric morphometric methods. Pacific thread herrings were collected from commercial landings of small pelagic fish in Bahía Magdalena. Morphometric analyses were based on the multivariate comparison of 22 reference points that characterize fish body shape. All comparisons in the multivariate analysis of variance revealed significant differences between the monthly means (a priori groups), as indicated by the ten significant CV axes. Furthermore, the pattern of body shape variation was consistent with reproductive changes in Pacific thread herring. The most helpful shape variation for distinguishing among the groups was in the dorsal and ventral profiles of the truncal region of the body shape. These results support the hypothesis that fish physiological condition is a temporal factor that helps us discriminate intra-population units based on body shape variation and is a potential bias in inter-population comparisons.

**Keywords** Fish · Geometric morphometrics · Physiological condition · Body shape variation

## Introduction

The classification of individuals is based on morphological characteristics and models that summarize the best characteristics of the population (Landi and Quiroz-Valiente 2011). Comparisons between groups or populations have traditionally been based on analyzing differences in linear dimensions (Strauss and Bookstein 1982; Winemiller 1991; Klingenberg and Ekau 1996). However, body shape is considered a quality of the structure that can be described in detail but cannot be analyzed quantitatively (Toro-Ibacache et al. 2010). Technological advances have led to quantitative descriptions of body shape and other structures. Beginning in the twentieth century, with the collaboration of statisticians and biometricians, intra and intergroup patterns of morphological variation have been described, leading to the development of multivariate morphometrics (Marcus 1990; Rohlf and Marcus 1993; Adams et al. 2004; Zelditch et al. 2012). Since then, this approach has been used in several studies, and it has been suggested as a useful tool to better understand the mechanisms that promote species

---

Communicated by S. E. Lluch-Cota

---

✉ Jorge Guillermo Chollet-Villalpando  
chiguas@gmail.com

- 1 Conservación Sostenible de los Recursos Marinos y Acuáticos A.C. (COSOREMA), Calle 30 de Octubre 630, Col. Benito Juárez, C.P.80210 Culiacan, Sinaloa, México
- 2 Instituto Politécnico Nacional, Centro Interdisciplinario de Ciencias Marinas, Departamento de Pesquerías y Biología Marina, Avenida Instituto Politécnico Nacional s/n, Colonia Playa Palo de Santa Rita, La Paz, Baja California Sur, México
- 3 Consejo Nacional de Humanidades, Ciencias y Tecnologías (CONAHCYT), Av. Insurgentes Sur 1582, Col. Crédito Constructor, Alcaldía Benito Juárez, C.P. 03940 Ciudad de México, México
- 4 Centro Regional de Investigación Acuícola y Pesquera Guaymas, Instituto Nacional de Pesca y Acuicultura, Calle 20 Sur 605, Colonia Cantera, CP 85400 Guaymas, México

coexistence, to infer ecological strategies (e.g., Gatz 1979; Bellwood et al. 2006) and to investigate the fluctuations in biomass and diversity within communities due to natural or anthropogenic perturbations (Villéger et al. 2010).

Geometric morphometrics have been increasingly used in fisheries management for species identification (Pérez-Quiñonez et al. 2017) or identification of population units (morphotypes) through the analysis of body shape (Silva 2003; De La Cruz-Agüero and García-Rodríguez 2004; Tzeng 2004; Ibáñez-Aguirre et al. 2006; García-Rodríguez et al. 2011; Vergara-Solana et al. 2013; Cronin-Fine et al. 2013; Pérez-Quiñonez et al. 2018; Chollet-Villalpando et al. 2024) and otolith shape (Campana and Casselman 1993; DeVries et al. 2002; Félix-Uraga et al. 2005; Stransky et al. 2008; Ramírez-Pérez et al. 2010; Pérez-Quiñonez et al. 2018; Chollet-Villalpando et al. 2019). However, the physiological conditions of these organisms are often not considered in fish body shape studies (Hedgecock et al. 1989; Pérez-Quiñonez et al. 2017). Most of these studies do not consider the species breeding cycle, so the results could reflect differences that are not the result of shape as a distinctive characteristic of the population or species studied but of the physiological condition of the organism. As an alternative to reduce this shape effect, Rodríguez-Mendoza et al. (2019) proposed eviscerating fish to avoid the influence of gonad size or stomach fullness on body shape.

In the Mexican Pacific, most studies that have used body shape through geometric morphometric methods applied to pelagic fish have focused on the Pacific sardine *Sardinops sagax* (De La Cruz-Agüero and García-Rodríguez 2004; García-Rodríguez et al. 2011; Vergara-Solana et al. 2013). The collapse of the Pacific sardine fishery in California and northern Mexico at the beginning of the 1950s (Wolf 1992) resulted in the movement of the Mexican fishery to new fishing areas to the south, such as Bahía Magdalena (Félix-Uraga et al. 1996). The ecological and commercial importance of other small pelagic species in this area, such as the Pacific thread herring *Opisthonema libertate* (Günther, 1867), has led to increased interest in the population dynamics of this species through the use of morphometric analysis to differentiate the sympatric species of the genus (*O. libertate*, *O. bulleri*, and *O. medirastre*) (Pérez-Quiñonez et al. 2017) and population structure (Pérez-Quiñonez et al. 2018; Ruiz-Domínguez and Quiñonez-Velázquez 2018).

The Pacific thread herring is the most abundant pelagic species in the region after the Pacific sardine. This species is also of great economic and ecological importance due to its catch volume (3,387,012 t total catch between 1972 and 2016, SAGARPA-CONAPESCA 2017) and is prey for a wide variety of fish, mollusks, birds, and marine mammals (Holt 1975). On the coasts near and even within Bahía Magdalena and Baja California Sur, the breeding season of *O. libertate* occurs during the summer months (Torres-Villegas

and Pérez-Gómez 1988; Matus-Nivón et al. 1989), the rest of the year presenting gonads in stages of immaturity and sexual indifference. These characteristics have made the Pacific thread herring a species of interest for applied research to obtain information on its biology and population structure and to propose better resource management strategies.

In this study, we analyzed the temporal variation in the body shape of the Pacific thread herring *O. libertate* from Bahía Magdalena using Cartesian coordinate 2D and geometric morphometric methods. The aim of this study was to determine whether the reproductive cycle directly affects body shape. In addition, we tested the hypothesis that changes in gonadal condition significantly affect the body shape of Pacific thread herring.

## Materials and methods

### Sampling

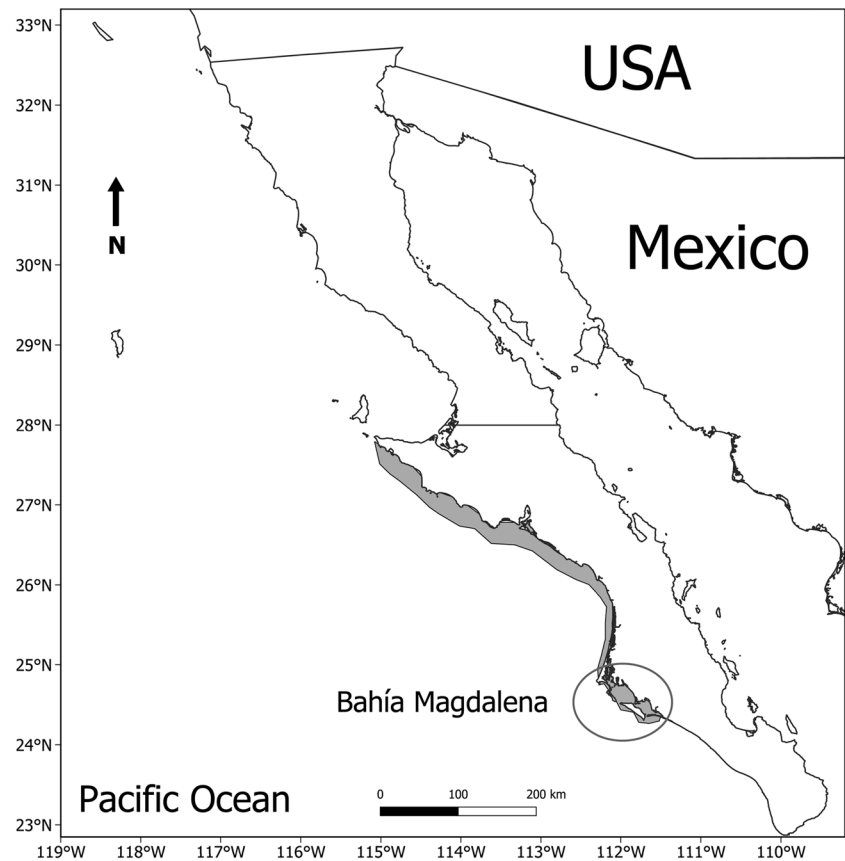
Pacific thread herring specimens were collected monthly from January to November 2016 (during December, boats usually reduce fishing trips) from commercial small pelagic fish landed in Bahía Magdalena (Fig. 1). The total sample size was 326 specimens ( $n = 30$  except for August,  $n = 26$ ). The sea surface temperature (SST) was obtained monthly from the MODIS sensor on the AQUA satellite (NASA Ocean Color website: <https://oceancolor.gsfc.nasa.gov/13>) for the area comprising between 24°N and 26°N and between 111.5°W and 113°W, which includes Bahía Magdalena and its surrounding fishing area.

The taxonomic identification of specimens was performed based on the methods of Berry and Barret (1963), Torres-Ramírez (2004), and Pérez-Quiñonez et al. (2017). The size (SL mm), weight (TW g), and sex of each specimen were recorded. Maturity was determined using a morphochromatic scale (Holden and Raitt 1975), with five development stages: undifferentiated (1), immature (2), in the process of maturation (3), mature (4), and spawned (5). All specimens analyzed were adults ( $\geq 120$  mm LE; Berry and Barret 1963; Jacob-Cervantes and Aguirre-Villaseñor 2014), reducing the potential contribution of the allometric component to the variation in fish shape.

### Digitalization and location of landmarks and semi-landmarks

The left side of each specimen was photographed along with a metric scale, using a Canon Power Shot Sx50001S digital camera fixed on a base. Outline shape variation of the fish body was registered using a combination of 11 landmarks and 11 semi-landmarks (22 points in total; Fig. 2), with 2D data coordinates (X, Y). The 11 landmarks defined were as

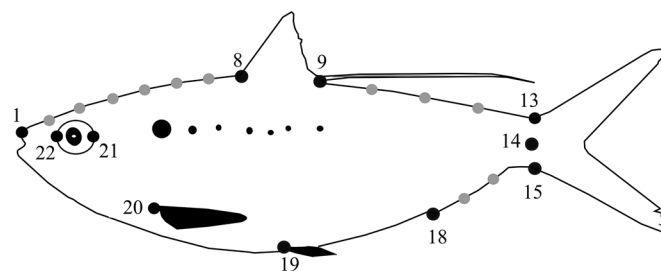
**Fig. 1** Geographical location of Bahía Magdalena (circle empty) on the western coast of the Baja California Peninsula, Mexico. The shaded region is the fishing area for the purse seine fleet landing in Bahía Magdalena



follows: the tip of the snout (LM 1), the first spine of the dorsal fin (LM 8), the last radius of the dorsal fin (LM 9), the first upper principal caudal radius (LM 13), the midpoint of the caudal fin base (LM 14), the first lower principal caudal radius (LM 15), the first spine of the anal fin (LM 18), the first spine of the pelvic fin (LM 19), the first spine of the pectoral fin (LM 20), and the ocular orbit (LM 21 and 22).

Since landmarks were insufficient to represent body shape and to obtain the best representation of shape variation, we generated “fans” in the digital images to provide

guidelines of equal angular spacing, helping us to locate semi-landmarks along the curves using MakeFa8 software (Sheets 2014). We created three open curves to capture the body shape of the thread herring. First, a triangular fan was constructed based on the landmarks located at the tip of the snout (point 1), the first spine of the dorsal fin (point 8), and the first spine of the pectoral fin (point 20), using the landmark of the pectoral fin as the origin of the lines. This first fan helped to locate semi-landmarks two to seven, obtaining a curve composed of two landmarks and six semi-landmarks



**Fig. 2** Location of the 22 points used to represent the Pacific thread herring (*Opisthonema liberate*) body shape. Black dots, landmarks; gray dots, semi-landmarks. Landmarks: the tip of the snout (LM 1), the first spine of the dorsal fin (LM 8), the last radius of the dorsal fin (LM 9), the first upper principal caudal radius (LM 13), the midpoint

of the caudal fin base (LM 14), the first lower principal caudal radius (LM 15), the first spine of the anal fin (LM 18), the first spine of the pelvic fin (LM 19), the first spine of the pectoral fin (LM 20), and the ocular orbit (LM 21 and 22)

(eight points in total). A second fan was constructed using the landmarks located on the last radius of the dorsal fin (point 9), the first spine of the anal fin (point 18), and the first upper principal caudal radius (point 13), using the spine of the anal fin landmark as the origin of the lines. The second curve was used to locate semi-landmarks ten to twelve, obtaining a curve composed of two landmarks and three semi-landmarks (five points in total). Finally, a third fan was based on landmarks located on the first spine of the dorsal fin (point 8), the first lower principal caudal radius (15), and the first spine of the anal fin (point 18), using the spine of the dorsal fin landmark as the origin of the lines. This third fan helped locate semi-landmarks 16 and 17, resulting in a curve composed of two landmarks and two semi-landmarks (four points total). All landmarks and semi-landmarks were digitized using the program TpsDig 1.4 (Rohlf 2004).

### Superimposition and alignment

We superimposed the sample data based on a generalized Procrustes analysis (GPA). This procedure removed the differences produced by the position, orientation, and scale between all configurations of landmarks and semi-landmark points (Rohlf and Bookstein 1990; Rohlf and Slice 1990) using Coordgen8 software (Sheets 2014). The semi-landmarks were then aligned according to their corresponding curve by sliding points using the minimum distance criterion in the semiLand8 software (Sheets 2014).

### Shape data analysis

Before the statistical analyses, we assessed the dependence of shape on size via regression analysis using Regress8 software (Sheets 2014). We examined whether the fish body shape variation among the months was allometric because there was variation in size among the specimens sampled. We used body shape as the dependent variable ( $Y$ ) and centroid size log-transformed (CS-log) values as the independent variable ( $X$ ) following the equation described by Zelditch et al. (2012). The superimposed and aligned Procrustes coordinates of all months were used to compute the partial warp scores using the three smallest specimens as a reference. We used 2500 replicates in a bootstrap permutation test to estimate the significance of the regression parameters. The regression slope ( $m$ ) defined the deviation ratio of body shape to the corresponding deviation of the CS-log. A low value indicates that the size effect on shape might not be significant. In addition, if size accounts for very little shape variation, size provides weak insight into fish body shape (Sheets 2014).

We performed a principal component analysis (PCA) using the partial warp scores produced from the superimposed and aligned coordinates to examine the generalized

body shape variance among all specimens in PCAGen8 (Sheets 2014). The results of this analysis were used to determine the number of components (PCs) that accounted for 95% of the total variance. Using this procedure, we reduced the number of variables used to perform canonical variate analysis (CVA) of shape variation in CVAGen8 software (Sheets 2014). The multivariate analysis of variance (MANOVA) for the shape variation of the fish body included the first 14 PCA-shaped axes (95.45% of the total variance) and discarded the last 26 PCA components (4.55% of the total variance). The significance of the CVA scores was based on Wilk's lambda ( $\lambda$ ) values determined using Bartlett's test, which has an approximately chi-squared distribution (Zelditch et al. 2012).

Body fish shape changes explained by the first two canonical variates (CVs) were visualized in a scatterplot using thin-plate spline deformation grids and vectors on landmarks and semi-landmarks for the positive and negative sides of CV1 and CV2. The percentage of correct posterior classification and the CVA performance were tested by jackknifing up to 500 trials of the total sample, with 10% (33 specimens) used as unknowns and testing 16,500 specimens randomly. The hierarchy of the greatest differences in shape discriminated by the CVA axes was visualized via cluster analysis using the unweighted pair group method using arithmetic averages (UPGMA). The pattern of body shape similarity was determined using the matrix of Procrustes distances derived from the CVA between the 11 months as a priori groups in the NTSYSpc 2.11 (Rohlf 2005).

The results obtained were compared with the Pacific thread herring reproductive cycle and with the SSTs recorded during 2016 in the fishing area. Considering that the reproductive cycle of the species is closely related to the arrival of the equatorial warm water mass to the Bahía Magdalena area (Torres-Villegas and Pérez-Gómez 1988), it could be that the SST influences the degree of gonadal maturity. Therefore, larger gonad size could be associated with body shape changes.

## Results

Based on the regression analysis results, it is suggested that there is no statistically significant allometric component relationship between size (CS-log) and shape variation. The value for the regression slope ( $m$ ) was 0.007, with only 1.50% of the variation in shape explained by variation in size (CS-log) based on summed squared Procrustes distances.

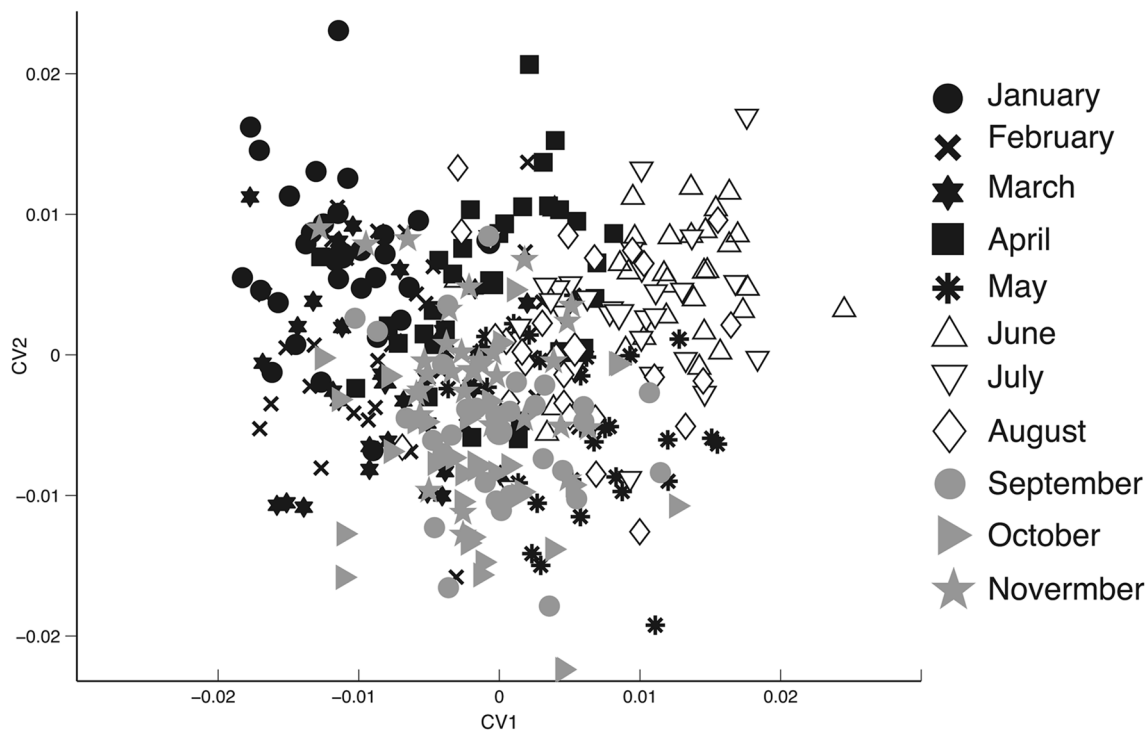
Shape variation in the fish body showed a dispersion pattern that added up to 95.45% of the total variance with the first 14 PCA-shaped axes. The first component explained 41.95% of the total variance, the second component explained 17.45%, and 8.69% of the variance was related to

the third component. These results were useful for reducing the number of variables included in the CVA of shape variation. The analyses carried out to evaluate the monthly variation in body shape showed significant differences among the 11 mean shapes of the 11 months as a priori groups, with ten significant CV axes in the MANOVA performed with the 14 PCA-shaped axes (CV1: Wilk's  $\lambda=0.082$ , Chisq = 785.402, df = 110,  $P < 0.001$ ; CV2: Wilk's  $\lambda=0.226$ , Chisq = 466.721, d.f. = 90,  $P < 0.001$ ; CV3: Wilk's  $\lambda=0.373$ , Chisq = 309.241, df = 72,  $P < 0.001$ ). Based on the Procrustes distances among the total samples, a considerable percentage of the specimens was correctly assigned to their a priori group. A posteriori classification from the CVA scores was 6717 (40.7%) correct and significant, and only 10 (0.1%) were correct and nonsignificant for all specimens analyzed.

The shape variation of the fish body showed a spatial dispersion pattern in the morphospace, with the shapes of June and July on the positive side. In contrast, the shapes of January and February are positioned on the negative extreme along CV1. The shape of April was located most in the positive extreme and October in the negative of the CV2 (Fig. 3). These results reveal shape changes in the Pacific thread herring body shape over the months (a priori groups). CV1 showed the most significant shape variation between January and June (Fig. 3). This result concurs with

the greatest percentage of Pacific thread herring exhibiting advanced gonadal maturity between June and July (Fig. 4a). Additionally, the greatest gradient of monthly SST changes over the year occurred in these months. The SST showed a seasonal pattern defined by the lowest values (approximately 21 °C) during the first semester, with the greatest increase occurring from June to July. In the subsequent months, the SST was approximately 25 °C (Fig. 4b).

The graphical representation of morphological variations indicated seasonal changes, with June showing the most significant morphological variations. Visualizing the morphological distinction of shapes for the body over the 11 months showed two main groups of shapes as the most different (Fig. 5). One shape was present in June, and the second shape was observed in the remaining months. A more elevated and robust body was present in the first shape (Fig. 6a, with the mean shape as a reference in the grid) with a greater body depth. The second group of shapes shows a slenderer and enlarged body shape (Fig. 6b, with the mean shape as a reference in the grid). Within the second shape group, January, February, and March are separated from the rest of the months, with January having the most different shape (Fig. 5). Consequently, within this second shape group, April is distinguished from the rest of the species, with September and October being the most similar months in shape.

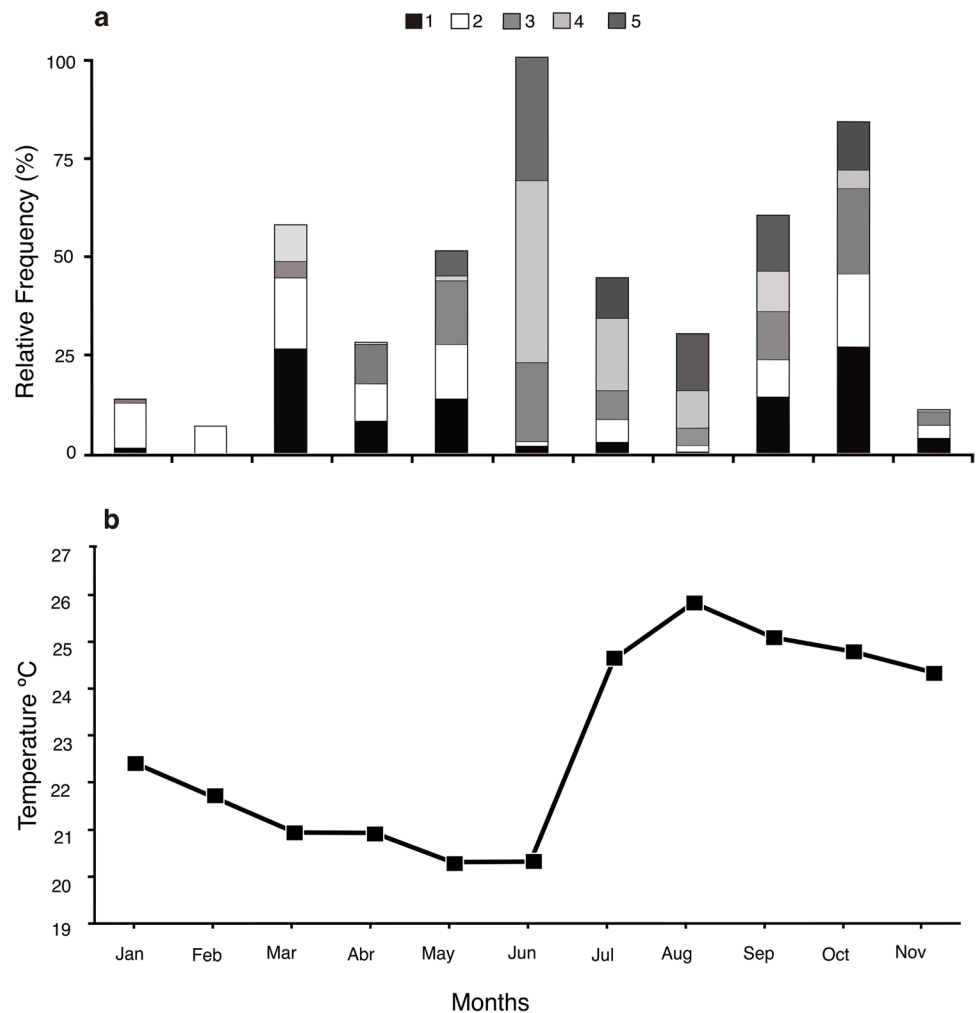


**Fig. 3** Morphospace of the body shape of the Pacific thread herring *Opisthonema libertate*. The scatter plot depicted the distribution of the specimens in the multivariate space of CV1 and CV2. Symbols are as follows: filled black circle, January; black equis, Febru-

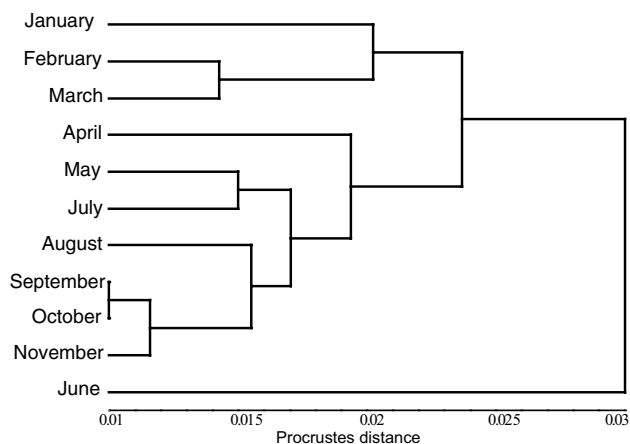
ary; filled black star, March; filled black square, April; black asterisk, May; empty triangle, June; inverse empty triangle, July; empty rhombus, August; filled gray circle, September; filled gray triangle, October; filled gray star, November



**Fig. 4** Monthly variation of the sexual maturity in the Pacific thread herring and SST for Bahía Magdalena during 2016. **a** Relative frequency according to developmental stages by month: undifferentiated (1), immature (2), in the process of maturation (3), mature (4), and spawned (5); **b** SST by month for the area, including Bahía Magdalena and its surrounding fishing area



The shape changes occurred in the month before the SST increased to its maximum in the area and when the organisms were at their maximum spawning activity (Fig. 4),

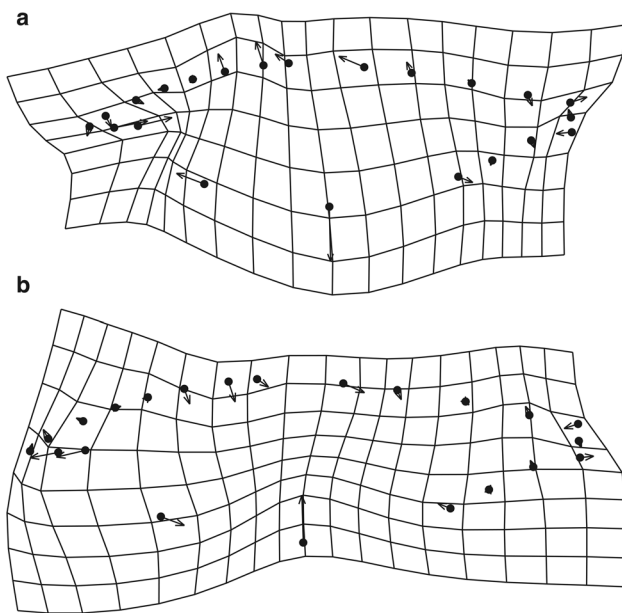


**Fig. 5** Dendrogram derived from the unweighted pair-group method with arithmetic mean (UPGMA), based on Procrustes distances between the defined a priori groups (months)

with a more prominent ventral area. During the remaining months, mainly September and October, differences between the body shapes of the dorsal and ventral regions of the organisms were smaller, as revealed by the dendrogram. This body compression coincides with the months when the SST decreased, and the fish presented an increase in gonads in the undifferentiated development stage (Fig. 4).

## Discussion

Using geometric morphometric analysis, the results of this study indicate a highly variable shape in the body of the Pacific thread herring *Opisthonema libertate*, mainly in the dorsal and ventral portions of the body. Shape changes were associated with the seasonal gonadal maturity of the Pacific thread herring in Bahía Magdalena. According to the canonical variate analysis, the differences between the months' shapes were significant in all cases. The spatial dispersion of the groups in the scatterplot indicated that



**Fig. 6** Deformation grids. **a** Body shape of specimens in June compared with the global mean. Pacific thread herring showed the most significant morphological differences in height in June compared with the remaining months; **b** Body shape of specimens in January compared with the global mean. This month, Pacific thread herring showed a more compressed body shape than the rest of the year. Grids and vectors represent the direction and magnitude of deformations, referencing the overall mean configuration (black dots)

the specimen most significant body shape changes occurred between January and June (Fig. 3). These 2 months coincided to the time when the fish showed greater relative frequencies in the immature and mature developmental stages (Fig. 4a). Our results support previous findings that it is possible to obtain useful information to identify intra-population levels of organization through geometric morphometric studies (e.g., Murta et al. 2008; Pérez-Quñonez et al. 2018). In this case, the results provide reliable data on seasonal body shape variation using geometric morphometrics.

Changes in scaling relationships between traits explain to a great extent variation in the shape of structures and, in turn, can be explained by variations in body shape associated with allometric growth (e.g., Klingenberg 1998; Delgado-Calvillo et al. 2012). However, in this study, allometric effects on morphological variations were reduced because all individuals analyzed were adults ( $\geq 120$  mm SL) (Berry and Barret 1963; Jacob-Cervantes and Aguirre-Villaseñor 2014; Ruíz-Domínguez 2015; Pérez-Quñonez et al. 2017, 2018). Another potential factor could be that the specimens belonged to different age classes since the recruitment of Pacific thread herring to fishing occurs at one year of age (approximately 120 mm SL) (Ruíz-Domínguez 2015), and different life histories and population dynamics may translate into distinct levels of intraspecific body shape variation.

According to the previously mentioned causes of variation, potential biases were reduced by the methodology and the sampling strategy used in this study. We presume that gonadal conditions were the most significant source of body shape variation in the Pacific thread herring *O. libertate* collected on the western Baja California Sur coast. This species is characterized by asynchronous oocyte development, which results in a partial spawner (Torres-Villegas and Pérez-Gómez 1988), reaching maximum spawning in the study area in June (Rodríguez-Domínguez 1987; Torres-Villegas and Pérez-Gómez 1988). The most distinct body shape of all a priori-determined groups for the Pacific thread herring specimens analyzed occurred in this month (Figs. 5, 6). Additionally, the greatest SST variation (20 to 25 °C) was recorded between June and July. This temperature change could stimulate the maximum spawning of the adult population, as suggested in previous studies (Torres-Villegas and Pérez-Gómez 1988; Lluich-Belda et al. 1991; Castro-González et al. 1996) (Fig. 4b).

Hedgecock et al. (1989) indicated that the gonadal maturity state was independent of differences in Pacific thread herring body shape for the same study area. This result was probably due to the temporal origin of these authors' samples, which consisted of two specimens collected in July and 198 in March. Our results indicated that Pacific thread herring presented mainly undifferentiated and immature gonads between January and March, whereas in June–July, it presented gonads at the pre-spawning stage (large-sized gonads; Fig. 4a), resulting in marked body shape differences in height and depth, as we reported (Fig. 6). Therefore, our geometric morphometrics analysis results support the hypothesis that the physiological conditions of specimens should be considered when discriminating species or populations. If analyses are based on samples collected at different times of the year, and physiological conditions are not considered, the interpretation of results could easily find a potentially non-biological shape variation, especially in species with long reproductive periods and a spawning peak.

## Conclusions

Our constructed morphometric protocol allowed us to capture and analyze the variation in the body shape of the Pacific thread herring *Opisthonema libertate* from the west coast of Baja California Sur, Mexico. There was no dependence of shape variation on fish size in the samples studied. The body shape changes significantly during the annual cycle, with those in January and June being the most different. However, during June, the greatest changes in body shape were observed (more elevated and robust body shape), coinciding with the maximum gonadal maturity and higher sea surface temperature.

**Acknowledgements** The authors are indebted to the boat crew and fish canning plant staff of Baja California Sur's western coast for their help in obtaining biological samples. We also thank our colleague E. Álvarez-Trasviña for assisting us with the map edition. Finally, we thank the two anonymous reviewers for their constructive criticisms of the manuscript.

**Funding** This study was funded by the Secretaria Académica y de Investigación of the Instituto Politécnico Nacional (SIP: 20160837). C.I.P.Q. was a recipient of a graduate fellowship and a grant from the Consejo Nacional de Ciencia y Tecnología (México) and Programa de Estímulo Institucional de Formación de Investigadores del IPN (México). J.G.C.V. is thankful for the fellowship of "Estancias Posdoctorales por México" 2022(3) (grant number 349241) from the Consejo Nacional de Humanidades, Ciencias y Tecnologías (CONAHCyT) and the support provided by the program SNI. C.Q.V. is thankful for the support provided by the EDI, COFAA, and SNI programs.

## Declarations

**Conflict of interest** The authors declare no competing interests.

**Ethics approval** No animal testing was performed during this study.

**Sampling and field studies** All necessary permits for sampling and observational field studies were obtained by the authors from the competent authorities and are mentioned in the acknowledgments, if applicable. The study complied with the CBD and Nagoya protocols. Fish specimens are cataloged in the ichthyological collection of the IPN-CICIMAR.

**Data availability** The datasets supporting these findings are available at <https://www.doi.org/https://doi.org/10.17632/fdkbx9jmxp.2>.

**Author contribution** C.Q.V.: funding acquisition; C.Q.V and C.I.P.Q.: project administration; C.Q.V., C.I.P.Q., and J.G.C.V.: formal analyses; C.Q.V., C.I.P.Q., J.G.C.V., and D.I.A.R.: conceptualization and writing — original draft; J.G.C.V., C.Q.V., C.I.P.Q, and D.I.A.R.: writing, review and editing.

## References

- Adams WM, Aveling R, Brockington D, Dickson B, Elliot J, Hutton J, Roe D, Wolmer W (2004) Biodiversity conservation and the eradication of poverty. *Science* 306:1146–1149. <https://doi.org/10.1126/science.1097920>
- Bellwood RD, Wainwright PC, Fulton CJ, Hoey AS (2006) Functional diversity supports coral reef biodiversity. *Proc Biol Sci* 273:101–107. <https://doi.org/10.1098/rspb.2005.3276>
- Berry DH, Barret I (1963) Gillraker analysis and speciation in the thread herring genus *Opisthonema*. *Inter-Am Tropical Tuna Comm Bull* 7:113–190
- Campana SE, Casselman JM (1993) Stock discrimination using otolith shape analysis. *Can J Fish Aquat Sci* 50:1062–1083. <https://doi.org/10.1139/f93-123>
- Castro-González JJ, Lizárraga-Rodríguez HM, Chapa-Morales O (1996) Fecundidad de la sardina crinuda *Opisthonema bulleri* (piscis: Clupeidae) entre las costas de Sinaloa y Nayarit, México. *Rev Biol Trop* 44:659–661
- Chollet-Villalpando JG, García-Rodríguez FJ, De Luna E, De La Cruz-Agüero J (2019) Geometric morphometrics for the analysis of character variation in size and shape of the sulcus acusticus of sagittae otolith in species of Gerreidae (Teleostei: Perciformes). *Mar Biodiv* 49:2323–2332. <https://doi.org/10.1007/s12526-019-00970-y>
- Chollet-Villalpando JG, García-Rodríguez FJ, De La Cruz-Agüero J (2024) Character variation in separate body regions of Gerreidae (Osteichthyes: Teleostei) fishes inferred from geometric morphometrics. *J Fish Biol* 104:723–736. <https://doi.org/10.1111/jfb.15615>
- Cronin-Fine L, Stockwell JD, Whitener ZT, Labbe EM, Willis TV, Wilson KA (2013) Application of morphometric analysis to identify Alewife stock structure in the Gulf of Maine. *Mar Coast Fish* 5:11–20. <https://doi.org/10.1080/19425120.2012.741558>
- De La Cruz-Agüero J, García-Rodríguez FJ (2004) Morphometric stock structure of the Pacific sardine *Sardinops sagax* (Jenyns, 1842) off Baja California, Mexico. In: Elewa AMT (ed) *Morphometrics: Applications in biology and paleontology*. Springer, Berlin, pp 115–127. [https://doi.org/10.1007/978-3-662-08865-4\\_9](https://doi.org/10.1007/978-3-662-08865-4_9)
- Delgadillo-Calvillo AC, Martínez-Palacios CA, Barruecos-Villalobos JM, Ulloa-Arvizu R (2012) Caracterización de la curva de crecimiento en dos especies de pez blanco *Chirostoma estor*, *C. promelas* y sus híbridos. *Vet Méx* 43:113–121
- DeVries DA, Grimes CB, Prager MH (2002) Using otolith shape analysis to distinguish eastern Gulf of Mexico and Atlantic Ocean stocks of king mackerel. *Fish Res* 57:51–62. [https://doi.org/10.1016/S0165-7836\(01\)00332-0](https://doi.org/10.1016/S0165-7836(01)00332-0)
- Félix-Uraga R, Alvarado-Castillo RM, Carmona-Piña R (1996) The sardine fishery along the western coast of Baja California, 1981 to 1994. *Calif Coop Ocean Fish Rep* 37:188–192
- Félix-Uraga R, Gómez-Muñoz VM, Quiñonez-Velázquez C, Melo-Barrera FN, Hill KT, García-Franco W (2005) Pacific sardine (*Sardinops sagax*) stock discrimination off the west coast of Baja California and southern California using otolith morphometry. *Calif Coop Ocean Fish Rep* 46:113–121
- García-Rodríguez FJ, García-Gasca SA, De La Cruz-Agüero J, Cota-Gómez VM (2011) A study of the population structure of the Pacific sardine *Sardinops sagax* (Jenyns, 1842) in Mexico based on morphometric and genetic analyses. *Fish Res* 107:169–176. <https://doi.org/10.1016/j.fishres.2010.11.002>
- Gatz AJJ (1979) Ecological morphology of freshwater stream fishes. *Tulane Stud Zool Bot* 21:91–124
- Günther A (1867) Descriptions of some new or little-known species of Fishes in the collection of the British Museum. *Proc Zool Soc Lond* 99–104
- Hedgecock D, Hutchinson ES, Li G, Sly FL, Nelson K (1989) Genetic and morphometric variation in the Pacific sardine, *Sardinops sagax caerulea*: comparisons and contrasts with historical data and with variability in the northern anchovy. *Engraulis Mordax Fish Bull* 87:653–671
- Holden M, Raitt D (1975) Manual de ciencia pesquera Parte 2 - Métodos para investigar los recursos y su aplicación. FAO, Roma
- Holt SJ (1975) Los recursos alimenticios del océano. In: Moore JR (ed) *Oceanografía*. Blume, Barcelona, pp 400–414
- Ibáñez-Aguirre AL, Cabral-Solís E, Gallardo-Cabello M, Espino-Barr E (2006) Comparative morphometrics of two populations of *Mugil curema* (Pisces: Mugilidae) on the Atlantic and Mexican Pacific coasts. *Sci Mar* 70:139–145. <https://doi.org/10.3989/scimar.2006.70n1139>
- Jacob-Cervantes ML, Aguirre-Villaseñor H (2014) Inferencia multimodelo y selección de modelos aplicados a la determinación de L50 para la sardina crinuda *O. libertate* del sur del Golfo de California. *Cien Pesq* 22:61–68
- Klingenberg C, Ekau W (1996) A combined, morphometric and phylogenetic analysis of an ecomorphological trend: Pelagization in Antarctic fishes (Perciformes: Nototheniidae). *Biol J Linn Soc* 59:143–177. <https://doi.org/10.1111/j.1095-8312.1996.tb01459.x>
- Klingenberg CP (1998) Heterochrony and allometry: the analysis of evolutionary change in ontogeny. *Biol Rev* 73:79–123. <https://doi.org/10.1017/S000632319800512X>



- Landi V, Quiroz-Valiente J (2011) Advances in genetic technologies and their application in animal selection. *Actas Iberoam Conserv Anim* 1:33–43
- Lluch-Belda D, Lluch-Cota DB, Hernández-Vázquez S, Salina-Zavala CA (1991) Sardine and anchovy spawning as related to temperature and upwelling in the California Current system. *Calif Coop Ocean Fish Rep* 32:105–111
- Marcus LF (1990) Traditional morphometrics. In: Rohlf FJ, Bookstein FL (eds) Proceedings of the Michigan morphometrics workshop, Special Publication Number 2. The University of Michigan Museum of Zoology. Ann Arbor, pp 77–122
- Matus-Nivón E, Ramírez-Sevilla R, Ortiz-Galindo JL, Martínez-Pecero R, González-Acosta B (1989) El huevo y la larva de la sardina crinuda del Pacífico *Opisthonema libertate* (Günther). *Rev Biol Trop* 37:115–125
- Murta AG, Pinto AL, Abaunza P (2008) Stock identification of horse mackerel (*Trachurus trachurus*) through the analysis of body shape. *Fish Res* 89:152–158. <https://doi.org/10.1016/j.fishres.2007.09.026>
- Pérez-Quiñonez CI, Quiñonez-Velázquez C, Ramírez-Pérez JS, Vergara-Solana FJ, García-Rodríguez FJ (2017) Combining geometric morphometrics and genetic analysis to identify species of *Opisthonema* Gill, 1861 in the eastern Mexican Pacific. *J Appl Ichthyol* 33:84–92. <https://doi.org/10.1111/jai.13051>
- Pérez-Quiñonez CI, Quiñonez-Velázquez C, García-Rodríguez FJ (2018) Detecting *Opisthonema libertate* (Günther, 1867) phenotypic stocks in northwestern coast of Mexico using geometric morphometrics based on body and otolith shape. *Lat Am J Aquat Res* 46:779–790. <https://doi.org/10.3856/vol46-issue4-fulltext-15>
- Ramírez-Pérez JS, Quiñonez-Velázquez C, García-Rodríguez FJ, Félix-Uraga R, Melo-Barrera FM (2010) Using the shape of *Sagitta* otoliths in the discrimination of phenotypic stocks in *Scomberomorus sierra* (Jordan and Starks, 1895). *J Fish Aquat Sci* 5:82–93. <https://doi.org/10.3923/jfas.2010.82.93>
- Rodríguez-Domínguez G (1987) Caracterización bioecológica de las tres especies de sardina crinuda (*Opisthonema libertate*, *O. bulleri* y *O. medirastre*) del Pacífico mexicano. Dissertation, CICESE
- Rodríguez-Mendoza R, Muñoz M, Saborido-Rey F (2019) Structure and connectivity of bluemouth, *Helicolenus dactylopterus*, populations in the NE Atlantic and Mediterranean. *Fish Res* 213:56–66. <https://doi.org/10.1016/j.fishres.2019.01.006>
- Rohlf FJ (2004) TpsDIG Version 1.40. Department of Ecology and Evolution, State University of New York at Stony Brook, New York. <https://sbmorphometrics.org/soft-dataacq.html>. Accessed 15 December, 2023.
- Rohlf FJ (2005) NTSYSpc, Numerical Taxonomy and multivariate analysis System, Version 2.11. New York: Applied Biostatistics Inc.
- Rohlf J, Bookstein F (1990) Proceedings of the Michigan morphometrics workshop. University of Michigan Museum of Zoology, Ann Arbor
- Rohlf J, Slice D (1990) Extensions of the Procrustes method for the optimal superimposition of landmarks. *Syst Zool* 39:40–59. <https://doi.org/10.2307/2992207>
- Rohlf FJ, Marcus LF (1993) A revolution in morphometrics. *Trends Ecol Evol* 8:129–132. [https://doi.org/10.1016/0169-5347\(93\)90024-J](https://doi.org/10.1016/0169-5347(93)90024-J)
- Ruíz-Domínguez M (2015) Enfoque multimodelo en la descripción del crecimiento de la sardina crinuda (*Opisthonema libertate*) en la zona sur del Golfo de California. Dissertation, CICIMAR
- Ruíz-Domínguez M, Quiñonez-Velázquez C (2018) Age, growth, and mortality of *Opisthonema libertate* on the coasts of northwestern Mexico. *Cienc Mar* 44:235–250. <https://doi.org/10.7773/cm.v44i4.2908>
- SAGARPA-CONAPESCA (2017) Anuario estadístico de acuicultura y pesca 2017. Secretaría de Agricultura, Ganadería y Desarrollo Rural, Pesca y Alimentación. Comisión Nacional de Pesca. México. [https://nube.conapesca.gob.mx/sites/cona/dgpppe/2017/ANUARIO\\_ESTADISTICO\\_2017.pdf](https://nube.conapesca.gob.mx/sites/cona/dgpppe/2017/ANUARIO_ESTADISTICO_2017.pdf). Accessed 17 November 2023.
- Sheets HD (2014) IMP8: integrated morphometrics package. Computer program and documentation. [http://www.filogenetica.org/cursos/Morfometria/IMP\\_installers/index.php](http://www.filogenetica.org/cursos/Morfometria/IMP_installers/index.php). Accessed 6 August 2023.
- Silva A (2003) Morphometric variation among sardine (*Sardina pilchardus*) populations from the north-eastern Atlantic and the western Mediterranean. *ICES J Mar Sci* 60:1352–1360. [https://doi.org/10.1016/S1054-3139\(03\)00141-3](https://doi.org/10.1016/S1054-3139(03)00141-3)
- Stransky C, Murta AG, Zimmermann C (2008) Otolith shape analysis as a tool for stock separation of horse mackerel (*Trachurus trachurus*) in the Northeast Atlantic and Mediterranean. *Fish Res* 89:159–166. <https://doi.org/10.1016/j.fishres.2007.09.017>
- Strauss RE, Bookstein F (1982) The truss: body form reconstructions in morphometrics. *Syst Zool* 31:113–135. <https://doi.org/10.1093/sysbio/31.2.113>
- Toro-Ibacache V, Soto MG, Suazo I (2010) Morfometría Geométrica y el Estudio de las Formas Biológicas: De la Morfología Descriptiva a la Morfología Cuantitativa. *Int J Morphol* 28:977–990. <https://doi.org/10.4067/S0717-95022010000400001>
- Torres-Ramírez MN (2004) Nueva clave de identificación para la sardina crinuda del género *Opisthonema* (Gill, 1861) en el Pacífico mexicano. Dissertation, Universidad Autónoma de Sinaloa
- Torres-Villegas JR, Pérez-Gómez L (1988) Variación de la fecundidad de *Opisthonema libertate* (Günther, 1866) (Pisces: Clupeidae) de 1983 a 1985 en Bahía Magdalena, Baja California Sur, México. *Invest Pesq* 52:193–206
- Tzeng TD (2004) Morphological variation between populations of spotted mackerel (*Scomber australasicus*) off Taiwan. *Fish Res* 68:45–55. <https://doi.org/10.1016/j.fishres.2004.02.011>
- Vergara-Solana FJ, García-Rodríguez FJ, De la Cruz-Agüero J (2013) Comparing body and otolith shape for stock discrimination of Pacific sardine, *Sardinops sagax* Jenyns, 1842. *J Appl Ichthyol* 29:1241–1246. <https://doi.org/10.1111/jai.12300>
- Villéger S, Ramos-Miranda J, Flores-Hernández D, Mouillot D (2010) Contrasted changes in taxonomic and functional diversity of tropical fish communities after habitat degradation. *Ecol Appl* 20:1512–1522. <https://doi.org/10.1890/09-1310.1>
- Winemiller KO (1991) Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. *Ecol Monogr* 61:343–365. <https://doi.org/10.2307/2937046>
- Wolf P (1992) Recovery of the Pacific sardine and the California sardine fishery. *Calif Coop Ocean Fish Rep* 33:76–86
- Zelditch ML, Swiderski DL, Sheets HD (2012) Geometric morphometrics for biologists: a primer, 2nd edn. Elsevier Academic Press, New York

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.