Research Article

Detecting *Opisthonema libertate* (Günther, 1867) phenotypic stocks in northwestern coast of Mexico using geometric morphometrics based on body and otolith shape

[1]Carlos I. Pérez-Quiñonez, [1]Casimiro Quiñonez-Velázquez & [1]Francisco J. García-Rodríguez
[1]Instituto Politécnico Nacional, Centro Interdisciplinario de Ciencias Marinas
Departamento de Pesquerías y Biología Marina, La Paz, Baja California Sur, México
Corresponding author: Casimiro Quiñonez-Velázquez (cquinone@ipn.mx)

ABSTRACT. Stock discrimination is essential for biomass population assessment and essential for the fisheries management. The analysis of shape differences in anatomical structures (*e.g.*, body shape, otoliths, scales) has been relevant issue in the study of population structure. We evaluated the hypothesis on the existence of a stock-structured population of Pacific thread herring *Opisthonema libertate* in the northwestern coast of Mexico. Geometric morphometric methods were used to analyze body and otolith shape. Samples come from at three commercial fishery-landing sites: Magdalena Bay, Guaymas, and Mazatlan, Mexico. Results based on body and otolith shape support the existence of different morphotypes by location. Body shape allowed better discrimination than otolith shape. The differences observed between the phenotypic stocks suggest seasonal movements, which are linked to the marine current system in this region, particularly to the California Current and the North Equatorial Counter Current.

Keywords: *Opisthonema libertate*, stock, morphotypes, anatomical structure, shape, fisheries management.

INTRODUCTION

Related to the management of marine resources, the differentiation of stocks in an exploited population is critical in fishery biology (Begg & Waldman, 1999; Cadrin *et al.*, 2005). According to Ihssen *et al.* (1981) stock is an intraspecific group of individuals that mate randomly and maintain spatial and temporal integrity. An approach for stock identification has been centered on the detection of groups based on the quantification of morphometric differences (Cadrin, 2000; Waldman, 2005). This approach is founded on the assumption that individuals with high similarity (similar morphotypes) must be closely related biologically and ecologically (Cadrin *et al.*, 2005). The origins of individuals and the environmental variables associated with their distribution provide a source of additional information to justify the natural integrity of stocks.

Stock identification, mainly of commercial fishes, has usually been addressed on the analysis of body shape (Silva, 2003; De La Cruz-Agüero & García-Rodríguez, 2004; Tzeng, 2004; Ibáñez-Aguirre *et al.*, 2006; García-Rodríguez *et al.*, 2011; Vergara-Solana *et al.*, 2013) and of *sagitta* otolith shape (Campana & Casselman, 1993; DeVries *et al.*, 2002; Félix-Uraga *et al.*, 2005; Stransky *et al.*, 2008; Ramírez-Pérez *et al.*, 2010), or on the analysis of the shape of both structures (Vergara-Solana *et al.*, 2013). Results obtained based on body morphology could be different from those obtained based on otolith shape (Félix-Uraga *et al.*, 2005; García-Rodríguez *et al.*, 2011; Vergara-Solana *et al.*, 2013), as the morphometric variability between the two structures could vary (Vergara-Solana *et al.*, 2013) due to environmental and/or genetic causes. For this reason, the use of both structures could provide a better understanding of population dynamics. Comparative analyses are therefore relevant and more informative (Waldman, 1999).

To date, the study of small pelagic fishes based on morphometric analyses in northwestern Mexico has been carried out mainly on the Pacific sardine *Sardinops sagax* (De La Cruz-Agüero & García-Rodríguez, 2004; Félix-Uraga *et al.*, 2005; García-Rodríguez *et al.*, 2011; Vergara-Solana *et al.*, 2013).

These studies support the existence of different phenotypic stocks, which have been associated with water masses with different sea surface temperature (SST) (Félix-Uraga *et al*., 2005; García Rodríguez *et al*., 2011; Vergara-Solana *et al*., 2013). On the other hand, there are two main marine current systems in northwestern Mexico: the California Current (CC) and the North Equatorial Counter Current (NECC). The CC intensifies in winter-spring, and the NECC is most influential in summer-fall (Pavlova, 1966; Hickey, 1979; Talley, 1993; Parés-Sierra *et al*., 1997; Pérez-Brunius *et al*., 2007; García-Morales *et al*., 2012). It has been observed that the intensification or weakening of these current systems modifies the latitudinal distribution of marine fauna (Bograd & Lynn, 2003; Félix-Uraga *et al*., 2004; Lluch-Belda *et al*., 2005; Gaxiola-Castro *et al*., 2008; Durazo, 2009). In particular, the existence of a well-defined anticyclonic circulation occurring from February to July and cyclonic circulation occurring from August to January has been proposed for the Gulf of California (Marinone *et al*., 2011; Marinone, 2012). The western coast of Baja California is influenced by the CC in winter-spring, whereas in summer-fall it is influenced by the NECC. Under this scenario, it is reasonable to hypothesize some influence of oceanographic circulations patterns in the population structure of fishes. This could be true of the Pacific thread herring *Opisthonema libertate* (Günther, 1867), a species widely distributed from northern Peru to the western coast of the Baja California Peninsula and the Gulf of California, Mexico.

The Pacific thread herring is one of the most abundant species of small pelagic fishes in the northwestern Mexican Pacific and is an essential component in the diet of a wide variety of high trophic level species (Holt, 1975; Rodríguez-Domínguez, 1987; Pérez-Quiñonez *et al*., 2017). The Pacific thread herring, along with slender thread herring *Opisthonema bulleri* (Regan, 1904*)* and middling thread herring *Opisthonema medirastre* (Berry & Barrett, 1963), constitute important economic resources in Mexico due to their significant catch rates (1,333,786 ton total catch during 2006-2014), and currently represents one of the most stable fisheries in Mexico (Acal, 1990; Nevárez-Martínez *et al.,* 2006; Jacob-Cervantes, 2010; SAGARPA-CONAPESCA, 2013). The fishery is only regulated by a 160 mm SL minimum catch size. Despite its importance as a fishery resource, the information necessary to evaluate the population status of this species within the *Opisthonema* genus in northwestern Mexico is limited. Even its taxonomic situation is controversial until recently (Csirke, 1980; Stevenson & Carranza, 1981; Lagúnez-Moreno, 1989; Vega-

Corrales, 2010; Vallarta-Zárate, 2012). However, the taxonomic validity of the three entities (*O. libertate, O. bulleri* and *O medirastre*) was recently supported by morphometric and genetic data (Pérez-Quiñonez *et al*., 2017).

Consequently, the official records do not discriminate by species in the catch records, studies by Ruiz & Lyle (1992) and Jacob-Cervantes *et al*. (2007) indicate that of the three species, *O. libertate* comprises the highest catch volumes. Consequently, it is crucial to provide biological information on this species to obtain a better understanding of its population dynamics.

In the present study, we carried out a morphometric comparison (body and otoliths) of the Pacific thread herring *O. libertate* to detect the existence of morphotypes or phenotypic stocks in the northwestern coast of Mexico. Taking into account the movement pattern dynamics of other sardine species and the oceanographic characteristics of the region, we evaluated the hypothesis on the existence of a population structured in stocks (different morphotypes) of Pacific thread herring in northwestern Mexico.

MATERIALS AND METHODS

Sampling

Two hundred and four Pacific thread herring specimens were obtained from the commercial catch. The herring comes from winter (January-February) and summer (July, August and September) landings in the ports of Bahía Magdalena (BM), Guaymas (GYM), and Mazatlan (MZ), the fish caught during these months were selected for the analysis, because at this time the smallest (winter) and largest (summer) differences in SST among the three fishing zones are recorded. These SST conditions, a consequence of the influence of the two current systems in the region (CC and CCNE), would promote the expansion and concentration of the distribution of the herring population in the northwest of the Mexican Pacific. (Fig. 1). The sample size was 94 individuals (BM, n = 33; GYM, n = 31; MAZ, n = 30) in winter, and 110 individuals (BM, n = 39; GYM, n = 37; MAZ, n = 34) in summer. All individuals were sampled in 2014, except the Mazatlán winter sample, which was collected in 2013.

Specimens were frozen and transferred to the Population Dynamics Laboratory of CICIMAR-IPN (http://www.cicimar.ipn.mx) in La Paz, B.C.S., Mexico, where they were processed, and their taxonomic status was confirmed based on the works by Berry & Barret (1963), Torres-Ramírez (2004), and Pérez-Quiñonez *et al*. (2017). The size of individuals was recorded taking into account standard length. All the individuals analy-
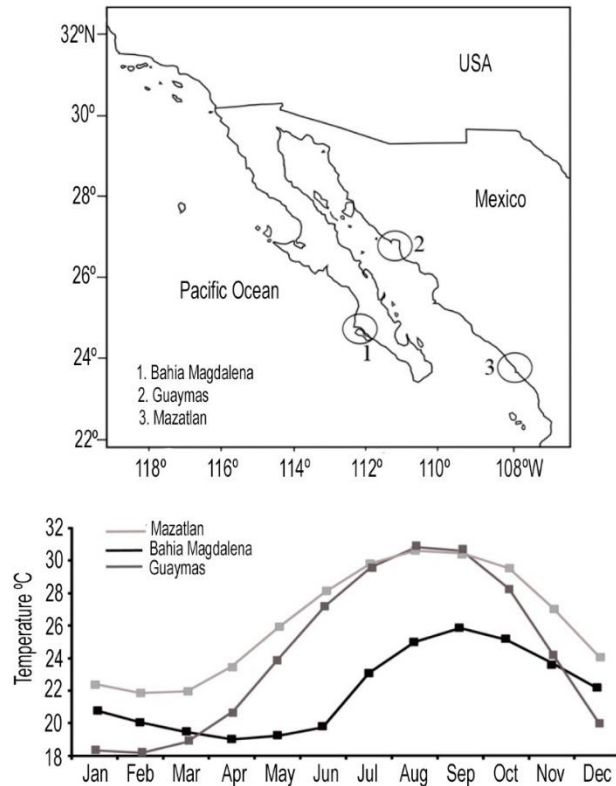
Figure 1. Northwestern coast of Mexico showing the geographic location of the landing ports of the purse-seine fleet fishing small pelagic fish, and SST monthly variation by zone.

zed were adults (≥120 mm SL), according to the relationship between length and sexual condition (Berry & Barrett, 1963; Jacob-Cervantes & Aguirre-Villaseñor, 2014, Pérez-Quiñonez *et al*., 2017), the range of size varies between 140 to 210 mm LE.

Image acquisition and location of landmarks

The left side of each´s body was photographed next to a size-scale using a Cannon Power Shot Sx5001S digital camera mounted on a fixed base. The *sagitta* otoliths were later extracted using dissecting forceps and washed with water and phosphate-free soap. The sulcus face of the right otolith of each was photogra-phed using a Sony Hyper HAD CCD-IRIS/RGB Model DXC-151a digital camera connected to a stereoscopic microscope using reflected light (Olympus SZX-ILLK100). All otolith images were recorded along with a size-scale using 16.5x magnification.

Morphometric comparisons were based on configure-tions generated from digitizing homologous anato-mical landmarks. As landmarks were insufficient to represent the body and otolith shapes, we generated templates of the digital images to provide guidelines of equal angular spacing to identify points (semiland-

marks) along the structure´s curves using the MakeFan program (Sheets, 2004). For the body shape first, a template was constructed based on the landmarks at the tip of snout, and at the origin of the pectoral and dorsal fin. A second template was based on landmarks located at the end of the dorsal fin, and the origin of the anal fin and at the origin of the upper part of the caudal fin. Moreover, a third template was based on landmarks located at the origin of the dorsal and anal fin, and at the origin of the lower part of the caudal fin. Semi-landmarks were digitized at the intersection of the curve and the lines of the fans. For the otolith shape first were located three natural marks; the antirostrum tip, the focus and the right posterior border of the otolith then two templates was cons-tructed based on these marks; one for the otoliths ventral part and another for the dorsal part.

A total of 13 body landmarks and semi-landmarks, and 20 otolith landmarks and semi-landmarks were used in our analysis (Fig. 2). All marks were digitized using the program TpsDig 1.4 (Rohlf, 2004).

Data analysis

We carried out morphometric comparisons, separating the winter and summer data because migratory movements can confound the origin of stocks, as has been suggested for other pelagic fish (Félix-Uraga *et al*., 2005; García-Rodríguez *et al*., 2011).

Geometric configurations were translated, scaled and rotated for each season using the generalized least squares Procrustes superimposition (Gower, 1975) in the Coordgen 6 program (Sheets, 2004). The Partial Procrustes Distance (PPD) was calculated between the mean shapes of the two groups to perform paired comparisons. The significance of the test was based on bootstrapping to determine whether the observed F-value could have been produced by chance, taking into account the distribution of bootstrapped F-values. We carried out this analysis using the TwoGroup6 software (Sheets, 2004).

For each structure separately, partial warp scores were obtained from the Thin-Plate Spline interpolation function (Bookstein, 1989), and used for quantifying differences between groups by means of a canonical variate analysis (CVA), which is a method of finding the set of axes (or linear combination of variables) that allows for the greatest possible ability to discriminate between two or more groups. The significance of the CVA scores was based on Wilk's lambda (λ) values, using Bartlett's test, a statistic that has an appro-ximately chi-squared distribution. The CVA scores were used to obtain an *a posteriori* assignment of individuals based on Mahalanobis distances between
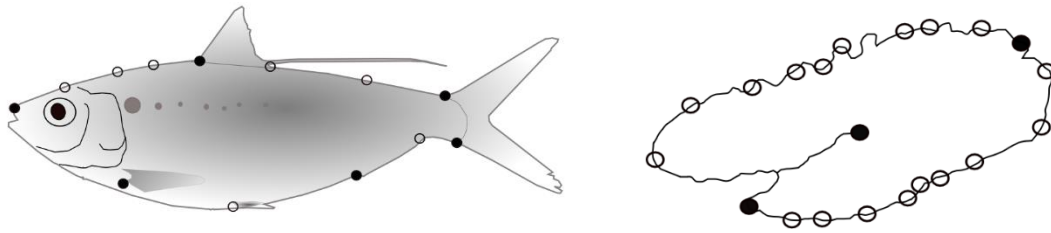
Figure 2. Location of 13 marks used to represent the thread herring (*Opisthonema libertate)* body shape; 20 marks were used for otoliths. Black dots: landmarks, white dots: semi-landmarks.

the means of the *a priori* groups. Bias classification was determined using the Jackknife method with 1000 bootstrap iterations; this provides a sense of how effective the discrimination and assignment can be expected to be, given a specific data set. Previous analyses were performed in the CvaGen6o program (Sheets, 2004). Mahalanobis distances were estimated using Statistica v.8 (www. Statsoft.com) and used to construct an unrooted tree based on Neighbor-Joining (Saitou & Nei, 1987) using the Neighbor module in Phylip Ver 3.6 module (Felsenstein, 2005).

A total of 13 body landmarks and semi-landmarks, and 20 otolith landmarks and semi-landmarks were used in our analysis (Fig. 2). All marks were digitized using the program TpsDig 1.4 (Rohlf, 2004).

Data analysis

We carried out morphometric comparisons, separating the winter and summer data because migratory movements can confound the origin of stocks, as has been suggested for other pelagic fish (Félix-Uraga *et al*., 2005; García-Rodríguez *et al*., 2011).

Geometric configurations were translated, scaled and rotated for each season using the generalized least squares Procrustes superimposition (Gower, 1975) in the Coordgen 6 program (Sheets, 2004). The Partial Procrustes Distance (PPD) was calculated between the mean shapes of the two groups to perform paired comparisons. The significance of the test was based on bootstrapping to determine whether the observed F-value could have been produced by chance, taking into account the distribution of bootstrapped F-values. We carried out this analysis using the TwoGroup6 software (Sheets, 2004).

For each structure separately, partial warp scores were obtained from the Thin-Plate Spline interpolation function (Bookstein, 1989), and used for quantifying differences between groups by means of a canonical variate analysis (CVA), which is a method of finding the set of axes (or linear combination of variables) that allows for the greatest possible ability to discriminate

between two or more groups. The significance of the CVA scores was based on Wilk's lambda (λ) values, using Bartlett's test, a statistic that has an approximately chi-squared distribution. The CVA scores were used to obtain an *a posteriori* assignment of individuals based on Mahalanobis distances between the means of the *a priori* groups. Bias classification was determined using the Jackknife method with 1000 bootstrap iterations; this provides a sense of how effective the discrimination and assignment can be expected to be, given a specific data set. Previous analyses were performed in the CvaGen6o program (Sheets, 2004). Mahalanobis distances were estimated using Statistica v.8 (www. Statsoft.com) and used to construct an unrooted tree based on Neighbor-Joining (Saitou & Nei, 1987) using the Neighbor module in Phylip Ver 3.6 module (Felsenstein, 2005).

RESULTS

Morphometric differences based on body shape

The analysis based on the F-test indicated significant differences between each paired Partial Procrustes Distance (PPD) in winter (F = 5.23, *P* = 0.002, PPD = 0.0218, for BM-GYM; F = 3.77, *P* = 0.011, PPD = 0.0202, for GYM-MAZ; F = 7.42, *P* = 0.001, PPD = 0.0238, for BM-MAZ). The two canonical variables indicated statistically significant differences between the groups (Wilk's lambda = 0.15, *P* < 0.001 for CV1; Wilk's lambda = 0.50, *P* < 0.001 for CV2), giving support to the existence of different Pacific thread herring morphotypes in winter (Fig. 3). The percentage of correct assignment (PeCoAs) was 72.3% on average. The highest value was obtained for MAZ (76.6%), and the lowest was obtained for GYM (67.7%) (Table 1). The lowest average assignment error occurred between fish from BM-MAZ and the highest between fish from GYM-MAZ and GYM-BM (Table 1).

The two canonical variables indicated statistically significant differences between the groups (Wilk's lambda = 0.23, *P* < 0.001 for CV1; Wilk's lambda =
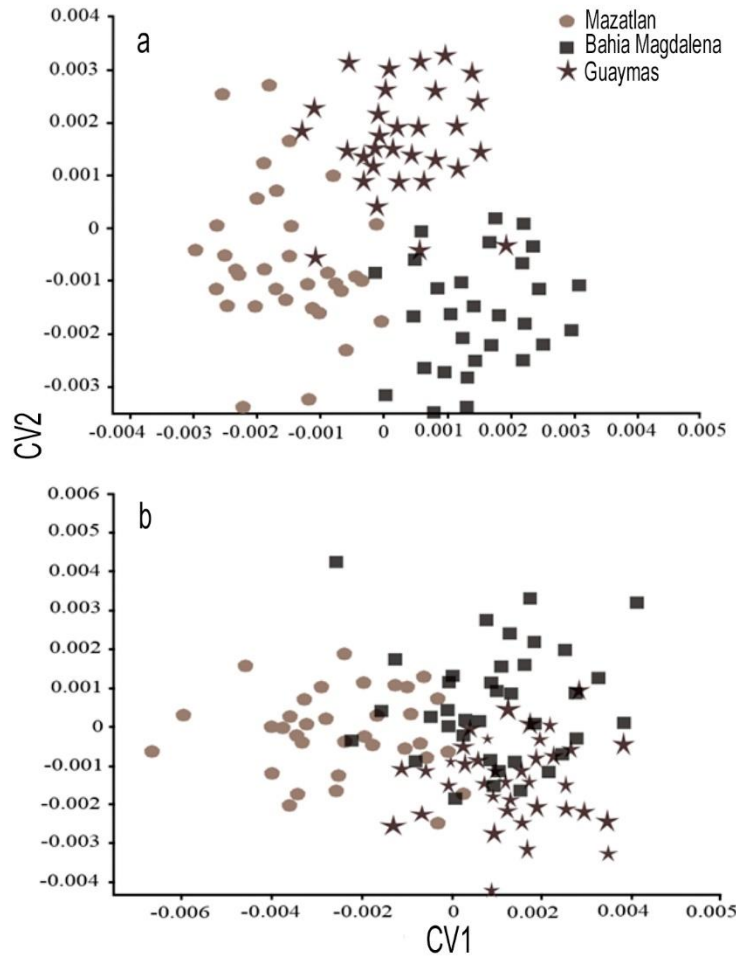
Figure 3. Scatter diagram generated from CV1 and CV2 scores for body shape in a) winter and b) summer.

Table 1. Allocation matrix (%) generated from the CVA for body shape. Upper matrix values correspond to winter body shape analysis (PeCoAs = 72.3%); bottom matrix values correspond to summer body shape analysis (PeCoAs = 62.7%). Values in bold on diagonal of each matrix show correct classification percentages per zone. Sample size: number of individuals analyzed per data set.

Zone	Mazatlán (MAZ)	Bahía Magdalena (BM)	Guaymas (GYM)	Sample size
Mazatlán (winter)	**76.6** (n = 23)	6.66 (n = 2)	16.6 (n = 5)	94
Bahía Magdalena (winter)	9.09 (n = 3)	**72.7** (n = 24)	18.1 (n = 6)	
Guaymas (winter)	16.1 (n = 5)	16.1 (n = 5)	**67.7** (n = 21)	
Mazatlán (summer)	**67.4** (n = 23)	14.7 (n = 5)	17.6 (n = 6)	110
Bahía Magdalena (summer)	12.8 (n = 5)	**66.6** (n = 26)	20.5 (n = 8)	
Guaymas (summer)	18.9 (n = 7)	27 (n = 10)	**54** (n = 20)	

0.52, $P < 0.001$ for CV2), suggesting the existence of different Pacific thread herring morphotypes in summer (Fig. 3). Figure 4 shows the morphological affinity between the three groups based on Mahalanobis distances and indicates that fish from GYM-MAZ had the lowest morphological differences, whereas fish from BM-MAZ showed the highest differences.

During summer the analysis indicated significant differences between each paired PPD (F = 3.73, P = 0.014, PPD = 0.0200, for BM-GYM; F = 2.91, P = 0.024, PPD = 0.0196, for GYM-MAZ; F = 6.96, P = 0.001, PPD = 0.0223, for BM-MAZ).
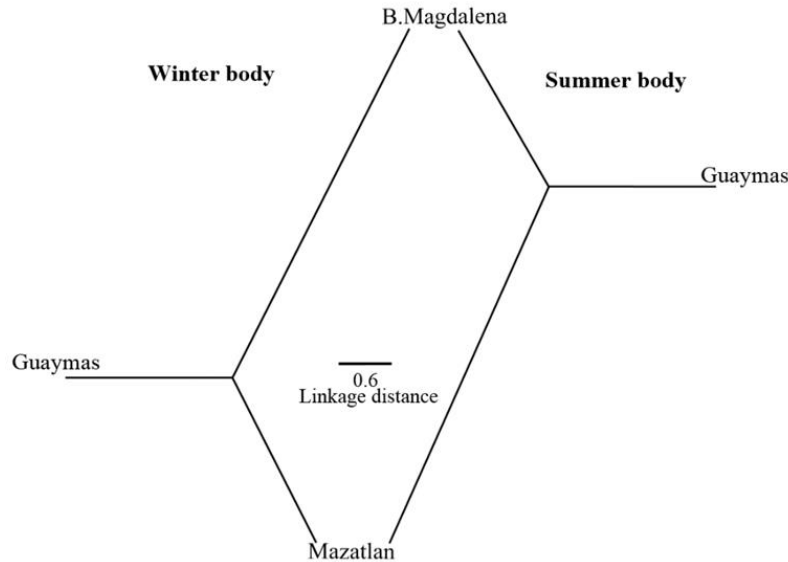
Figure 4. Dendrogram generated for each season with the UPGMA algorithm, using the Mahalanobis distance matrix of the body shape.

The PeCoAs was 62.7% on average. The highest value was obtained for MAZ (67.4%), and the lowest for GYM (54.0%). Similarly to what occurred in winter, there was a lower average assignment error between fish from BM-MAZ and higher error between fish from GYM-MAZ and GYM-BM (Table 1). Taking into account Mahalanobis distances, individuals captured during summer in GYM showed a stronger morphological relationship with fish from BM. The highest differences between fish occurred in BM and MAZ during both seasons (Fig. 4). According to the Mantel test, there was no correlation between the matrix based on body shape in winter and summer ($P = 0.677$).

Morphometric differences based on sagitta otolith shape

Results obtained using otoliths were relatively similar to those found based on body shape. The analysis based on the F-test indicated significant differences between paired PPD in winter between fish from BM-GYM (F = 7.52, $P = 0.001$, PPD = 0.0640) and BM-MAZ (F = 12.48, $P = 0.001$, PPD = 0.721), but not between fish from GYM-MAZ (F = 1.98, $P = 0.062$, PPD = 0.0188). However, based on the significant differences found using body shape, we considered these groups different; consequently, we performed a CVA for otoliths considering the three groups to maximize possible morphometric differences. The two canonical variables indicated statistically significant differences between the groups (Wilk's lambda = 0.12, $P < 0.001$ for CV1; Wilk's lambda = 0.43, $P < 0.001$ for CV2), supporting the existence of different morphotypes, according to otolith characteristics in winter (Fig. 5). The PeCoAs

was 67.3% on average, lower than that found based on body shape. The highest value was obtained for fish from MAZ (78.3%), and the lowest for fish from GYM (57.1%) (Table 2).

The lowest average assignment error occurred between the BM-MAZ fish and the highest between the GYM-MAZ and GYM-BM fish (Table 2). Based on Mahalanobis distances, fish from GYM and MAZ had the lowest morphological differences, and fish from BM and MAZ showed the highest differences (Fig. 6).

For data corresponding to summer, the analysis based on the F-test indicated significant differences between each paired PPD (F = 6.29, $P = 0.001$, PPD = 0.0601, for BM–GYM; F = 25.86, $P = 0.001$, PPD = 0.1212, for GYM-MAZ; F = 12.10, $P = 0.001$, PPD = 0.0853, for BM-MAZ). There were statistically significant differences between the groups only for the first canonical variable (Wilk's lambda = 0.14, $P < 0.001$), giving support to the existence of different morphotypes when taking into account Pacific thread herring otolith characteristics in summer (Fig. 5). The PeCoAs was 56.8% on average, lower than that found in winter and that found for the same season based on body shape. The highest value was found in fish from MAZ (77.1%), and the lowest in fish from BM (41.6%) (Table 2). Similar to what occurred in winter, and to what was found for both seasons based on body shape, the lowest average assignment error occurred between fish from BM-MAZ and the highest between fish from GYM-MAZ and GYM-BM (Table 2). Based on Mahalanobis distances, fish from GYM-BM had the lowest lowest morphological differences, and similarly to what
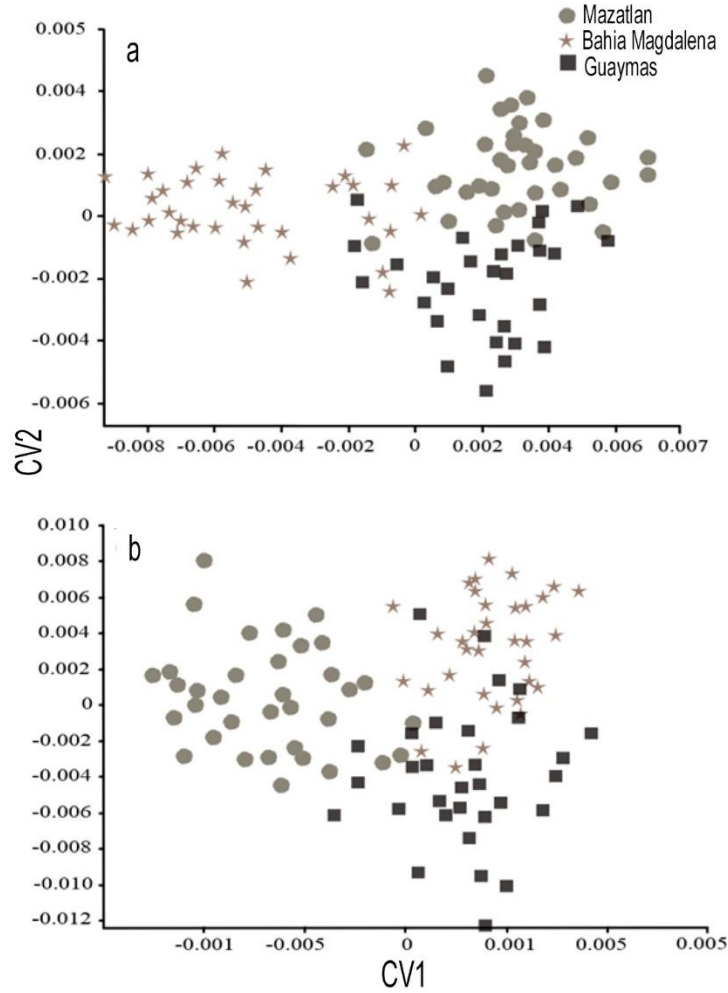
Figure 5. Scatter diagram generated from CV1 and CV2 scores for otolith in a) winter and b) summer.

Table 2. Allocation matrix (%) generated from the CVA for the otolith shape. Upper matrix values correspond to winter otolith shape analysis (PeCoAs = 67.6%); bottom matrix values correspond to summer otolith shape analysis (PeCoAs = 56.8%). Values in bold on diagonal of each matrix show correct classification percentages per zone. Sample size: number of individuals analyzed per data set.

Zone	Mazatlán (MAZ)	Bahía Magdalena (BM)	Guaymas (GYM)	Sample size
Mazatlán (winter)	**78.3** (n = 29)	5.40 (n = 2)	16.2 (n = 6)	102
Bahía Magdalena (winter)	22.8 (n = 8)	**57.1** (n = 20)	20 (n = 7)	
Guaymas (winter)	20 (n = 6)	13.3 (n = 4)	**66.6** (n = 20)	
Mazatlán (summer)	**77.1** (n = 27)	8.5 (n = 3)	14.2 (n = 5)	102
Bahía Magdalena (summer)	11.1 (n = 4)	41.6 (n = 15)	**47.2** (n = 17)	
Guaymas (summer)	9.67 (n = 13)	38.7 (n = 12)	**51.6** (n = 16)	

occurred in winter, fish from BM-MAZ had the highest differences (Fig. 6). The Mantel test showed no significant correlation between the matrix based on the otolith shape in winter and summer ($P = 0.985$).

DISCUSSION

It was possible to identify differences in the body and otolith shape of the Pacific thread herring *O. libertate*
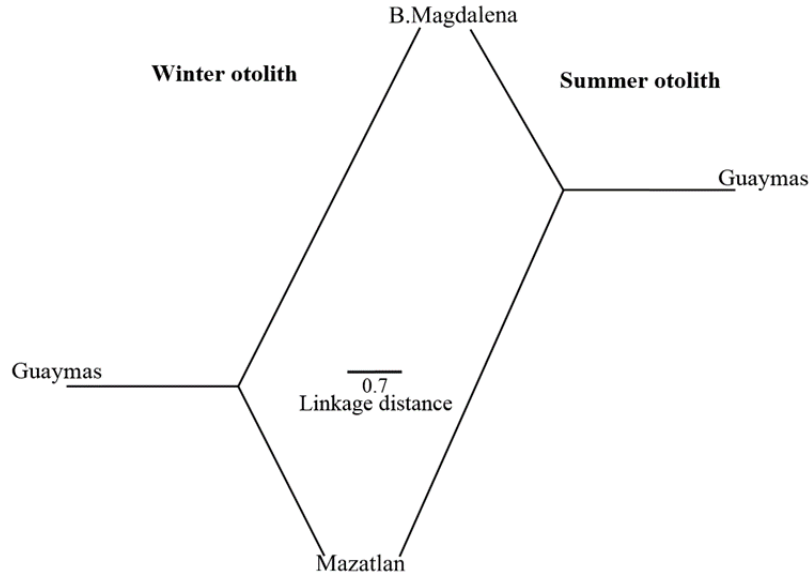
Figure 6. Dendrograms generated for each season with the UPGMA algorithm, using the Mahalanobis distance matrix of the otolith shape.

using geometric morphometry, supporting the existence of three different morphotypes or phenotypic stocks in the northwest Mexican Pacific. Body shape had a higher discriminant power than otolith shape. In all cases, for analyses based on body shape the Partial Procrustes Distance, and the two Canonical Variables were significant, whereas for analyses based on otolith shape differences between Pacific thread herring landed in GYM and MAZ were non-significant (although marginal $P = 0.06$) in winter. Only one Canonical Variable was statistically significant in summer. The results obtained from the *a posteriori* assignation matrix (based on Mahalanobis distances) also concur with the previous observations (Vergara-Solana *et al*., 2013). An explanation of these differences could be related to the amount of cover provided to each structure by the landmarks and semi-landmarks because the morpho-space can be affected by an increase in the number of marks, and the differentiation among groups can be more precise (Farré *et al*., 2016). However, since a higher number of marks were used for otolith analysis, we consider that otolith shape was not over-represented compared with body shape. In all cases, we considered a number of specimens bigger than the number of landmarks, considering that extra landmarks could be redundant. Thus, we believe that our results are not indicative of more than a methodological effect and that otoliths are less variable structures than body shape, as has been observed in other species (Vergara-Solana *et al*., 2013).

Despite the lower resolution in the detection of differences between groups when using otoliths, both structures used provided congruent results, indicating that body shape and otolith shape of Pacific thread herring *O. libertate* allow the detection of different morphotypes in the sampled areas of northwestern Mexico. Both indicated that the Guaymas Pacific thread herring shared the highest morphological affinity with Pacific thread herring from Bahía Magdalena and Mazatlán and that Pacific thread herring from Bahía Magdalena and Mazatlán presented the highest differences.

Variations in the shape of anatomical structures are associated with the age of individuals in species with individual growth tending towards allometry (Gould, 1966; Alberch *et al*., 1979; Klingenberg, 1998). In the present study all analyzed individuals were adults ($\geq$120 mm SL) (Berry & Barret, 1963; Jacob-Cervantes & Aguirre-Villaseñor, 2014; Pérez-Quiñonez *et al*., 2017), so that differences found were not related to the allometric effect (Félix-Uraga *et al*., 2005; Ramírez-Pérez *et al*., 2010) In addition, one of the characteristics of the use of geometric morphometry is that it eliminates differences between configurations that are attributable to differences in location, scale, and orientation, leaving only differences in shape (Kendall, 1977; Zelditch *et al*., 2004). Other factors related to genetic differences due to the presence of different populations, or due to local environmental factors impinging on phenotypic plasticity should be consi-
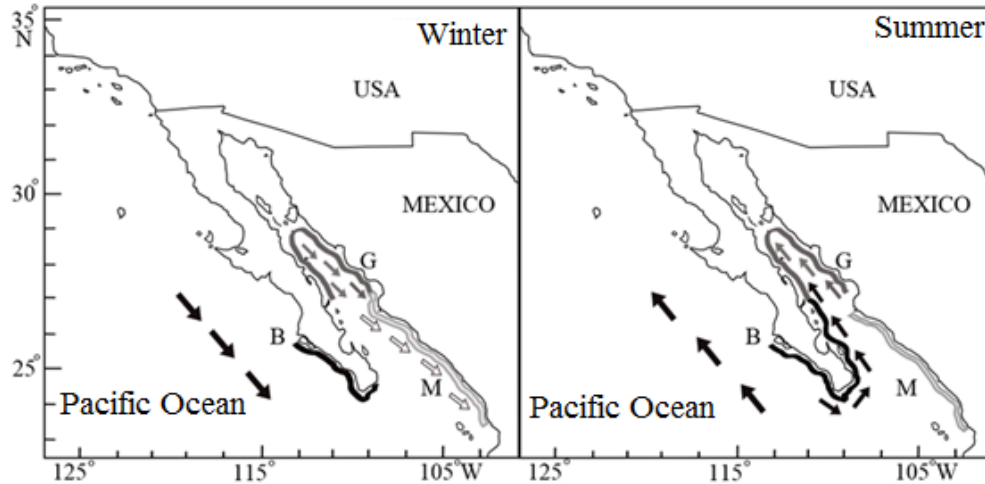
Figure 7. Time-space distribution model of the three-stock hypothesis for sardina crinuda (*O. libertate*): B: Bahía Magdalena stock, G: Guaymas stock and M: Mazatlan stock. The sizes of the arrows do not represent intensities of the current; they are indicative of the main direction.

dered to explain the differences found between the morphotypes (Lin & Dunson, 1999).

Potential stock movements could be linked to latitudinal and longitudinal migration patterns having to do with feeding and spawning (Sokolov, 1974; Lluch-Belda *et al*., 1986). Based on this, we suggest a conceptual model of spatial displacement of Pacific thread herring explain the morphometric similarities and dissimilarities of the shape of fish structures from the three fishing zone. Seasonal changes in the wind pattern play a dominant role in the formation of fish groups (Sokolov, 1974). Winds blow from north to south in winter, and the California Current (CC) is stronger in spring in the study area. During this period the influence of the North Equatorial Counter Current (NECC) over the coast of the Baja California Peninsula decreases (Pavlova, 1966; Hickey, 1979; Talley, 1993; Parés-Sierra *et al*., 1997; Pérez-Brunius *et al*., 2007) favors the upwelling of sub-superficial cold and nutrient-rich waters, resulting in the formation of areas with high biological productivity off the western coast of the Baja California Peninsula and eastern coast of the Gulf of California. Consequently, favorable conditions are created for feeding by pelagic species such as herring, sardines, and anchovies (Sokolov, 1974). These physical and biological conditions could allow the migration of individuals from Guaymas towards areas to the south along the eastern gulf coast, allowing the mixing of fish from GYM and MAZ. At the same time, the BM individuals initiate their displacement towards the south along the western peninsula coast, limiting their displacement towards the mouth of the Gulf of California (Fig. 7).

There is a weakening of the CC, and strengthening of southerly winds and of the NECC flow in summer (Fig. 7) (Pavlova, 1966; Hickey, 1979; Talley, 1993; Parés-Sierra *et al*., 1997; Pérez-Brunius *et al*., 2007). Coastal areas with high biological productivity appear on the western part of the Gulf of California, creating favorable conditions for BM Pacific thread herring, which had started their displacement towards the south to continue along the west coast until they reach the middle part of the gulf. The individuals that were concentrated in the MAZ area move towards the north along the coast until they reach the middle part of the gulf, and the Pacific thread herring has its maximum reproduction (Saldierna-Martínez *et al*., 1995). These authors point out that the highest spawning rates of this species occur in summer, with maximum spawning in the central part of the gulf, in the area between GYM and Punta Lobos, and could explain the high morphological similarity between fish from BM and GYM in summer. A similar migration mechanism has been observed in the Pacific sardine *Sardinops sagax* (Sokolov, 1974; Félix-Uraga *et al*., 2004, 2005) and in the jumbo squid *Dosidicus gigas* in the Gulf of California (Ehrhardt *et al*., 1983), with movements along both gulf coasts and along the western coast of the peninsula, depending on conditions in the marine environment.

The results found in this study using body shape and otolith shape could have considerable potential effects on the detection of phenotypic groups. The use of otoliths has been favored in previous studies, mainly due to its dual use for age determination as well as comparison with other structures (Blood, 2003; Edwards *et al*., 2005; Polat *et al*., 2005; Vergara-Solana

et al., 2013). However, body shape has been shown to be useful for species discrimination (De La Cruz-Agüero *et al*., 2015; Pérez-Quiñonez *et al*., 2017) and stock delimitation in structured populations (Ramírez-Pérez *et al*., 2010; García-Rodríguez *et al*., 2011; Vergara-Solana *et al*., 2013). Our results suggest that at least three Pacific thread herring morphotypes are distributed in the northwestern Mexican Pacific and that the GYM morphotype has the highest similarity with the other two groups (BM and MAZ), depending on the time of year. Future analyses should focus on the identification of a morphological criterion to distinguish among individuals according to the morphotypes found, as well as on the evaluation of whether the identified phenotypic stocks correspond to different populations using molecular analyses. It could provide a better understanding of this species´ biology and reinforce the management of its fishery.

ACKNOWLEDGMENTS

REFERENCES

Acal, D.E. 1990. Biomass and potential yield of the thread herring (*Opisthonema* spp.) off the coasts of Sinaloa and Nayarit. Cienc. Mar, 16: 61-73.

Alberch, P., S.J. Gould, G.F. Oster & D.B. Wake. 1979. Size and shape in ontogeny and phylogeny. Paleobiology, 5: 296-317.

Begg, G. & J.R. Waldman. 1999. A holistic approach to fish stock identification. Fish. Res., 43: 35-44.

Berry, D.H. & I. Barret. 1963. Gillraker analysis and speciation in the thread herring genus *Opisthonema*. Bull. Inter-Amer. Trop. Tuna Comm., 7: 137-190.

Blood, C.L. 2003. Age validation of Pacific halibut. II. Comparison of surface and break-and-burn otoliths methods of aging Pacific halibut. IPHC Tech. Rep., 47: 32 pp.

Bograd, S.J. & R.J. Lynn. 2003. Long-term variability in the southern California Current System. Deep-Sea Res. II, 50: 2355-2370.

Bookstein, F.L. 1989. Principal warps: thin-plate splines and the decomposition of deformations. IEEE Trans. Patt. Anal. Mach. Intel., 11: 567-585.

Cadrin, S.X. 2000. Advances in morphometric identification of fishery stocks. Rev. Fish Biol. Fish., 10: 91-112.

Cadrin, S.X., K.D. Friedland & J.R. Waldman. 2005. Stock identification methods -an overview. In: S.X. Cadrin, K.D. Friedland & J.R. Waldman (eds.). Amsterdam stock identification methods applications in fishery science. Elsevier Academic Press, London, pp. 3-8.

Campana, S.E. & J.M. Casselman. 1993. Stock discrimination using otolith shape analysis. Can. J. Fish. Aquat. Sci., 50: 1062-1083.

Csirke, J. 1980. Introducción a la dinámica de poblaciones de peces. FAO Doc. Téc. Pesca, 203: 82 pp.

De La Cruz-Agüero, J. & F.J. García-Rodríguez. 2004. Morphometric stock structure of the Pacific sardine *Sardinops sagax* (Jenyns, 1842) off Baja California, Mexico. In: A.M.T. Elewa (ed.). Morphometrics applications in biology and paleontology. Springer-Verlag, New York, pp. 115-127.

De La Cruz-Agüero, J., F.J. Vergara-Solana & F.J. García-Rodríguez. 2015. Geometric morphometrics supports the proposed molecular taxonomy for three *Eucinostomus* species (Perciformes: Gerridae) along the coasts of Mexico. Zoomorphology, 134: 125-134.

DeVries, D.A., C.B. Grimes & M.H. Prager. 2002. Using otolith shape analysis to distinguish eastern Gulf of Mexico and Atlantic Ocean stocks of king mackerel. Fish. Res., 57: 51-62.

Durazo, R. 2009. Climate and upper ocean variability off Baja California, México: 1997-2008. Prog. Oceanogr., 83: 361-368.

Ehrhardt, N.M., P.S. Jacquemin, B.F. García, D.G. González, B.J.M. López, C.J. Ortiz & N.A. Solís. 1983. On the fishery and biology of the giant squid *Dosidicus gigas* in the Gulf of California, Mexico. In: J.F. Caddy (ed.). Advances in assessment of world cephalopod resources. FAO Fish. Tech. Pap., 231: 306-340.

Edwards, K.R., Q.E. Phelps, J.L. Shepherd & D.W. Wills. 2005. Comparison of scale and otolith age estimates for two south Dakota bluegill populations. Proc. South Dakota Acad. Sci., 84: 181-186.

Farré, M., J. Narayan, G.T. Slavov, J. Damas, L. Auvil, C. Li, E.D. Jarvis, D.W. Burt, D.K. Griffin & D.M. Larkin. 2016. Novel insights into chromosome evolution in birds, archosaurs, and reptiles. Genome Biol. Evol., 8: 2442-2451.

Félix-Uraga, R., V.M. Gómez-Muñoz, C. Quiñonez-Velázquez, F.N. Melo-Barrera & W. García-Franco. 2004. On the existence of Pacific sardine groups off

the west coast of Baja California and southern California. CalCOFI Rep., 45: 146-151.

Félix-Uraga, R., V.M. Gómez-Muñoz, C. Quiñonez-Velázquez, F.N. Melo-Barrera, K.T. Hill & W. García-Franco. 2005. Pacific sardine (*Sardinops sagax*) stock discrimination off the west coast of Baja California and southern California using otolith morphometry. CalCOFI Rep., 46: 113-121.

Felsenstein, J. 2005. Using the quantitative genetic threshold model for inferences between and within species. Philos. Trans. Roy. Soc. B, 360: 1427-1434.

García-Morales, R., B. Shirasago-German, R. Félix-Uraga & E.L. Pérez-Lezama. 2012. Conceptual models of Pacific sardine distribution in the California Current System. Curr. Dev. Oceanogr., 5(1): 23-47.

García-Rodríguez, F.J., S.A. García-Gasca, J. De La Cruz-Agüero & V.M. Cota-Gómez. 2011. A study of the population structure of the Pacific sardine *Sardinops sagax* (Jenyns, 1842) in Mexico based on morpho-metric and genetic analyses. Fish. Res., 107: 169-176.

Gaxiola-Castro, G., B. Durazo-Lavaniegos, M.E. De-la-Cruz-Orozco, E. Millán-Nuñez, L. Soto-Mardones & J. Cepeda-Morales. 2008. Pelagic ecosystem response to interannual variability off Baja California. Cienc. Mar., 34: 263-270.

Gould, S.J. 1966. Allometry and size in ontogeny and phylogeny. Biol. Rev., 41: 587-638.

Gower, J.C. 1975. Generalized procrustes analysis. Psy-chometrika, 40: 33-51.

Hickey, B.M. 1979. The California current system. Hypotheses and facts. Progr. Oceanogr., 8: 191-279.

Holt, S.J. 1975. Los recursos alimenticios del océano. Oceanografía. Madrid: selecciones del Scientific American, sardinagolfodecalifornia.org/wp-content/uploads/2013/08/, pp. 400-414.

Ibáñez-Aguirre, A.L., E. Cabral-Solís, M. Gallardo-Cabello & E. Espino-Barr. 2006. Comparative morphometrics of two populations of *Mugil curema* (Pisces: Mugilidae) on the Atlantic and Mexican Pacific coasts. Sci. Mar., 70: 139-145.

Ihssen, P.E., H.E. Booke, J.M. Casselman, J.M. McGlade, R.N. Payne & F.M. Utter. 1981. Stock identification: material and methods. Can. J. Fish. Aquat. Sci., 38: 1838-1855.

Jacob-Cervantes, M. 2010. La pesquería de peces pelágicos menores en el sur del Golfo de California. Análisis de la temporada de pesca 2008. Cienc. Pesq., 18(2): 47-58.

Jacob-Cervantes, M.L. & H. Aguirre-Villaseñor. 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. Cienc. Pesq., 22(1): 61-68.

Jacob-Cervantes, M.L., M.A. Valdez-Ornelas, O. Chapa-Morales, R.E. Gastelum-Villareal, I. López-Nuño & P. Valdez-Ledón. 2007. La variabilidad de las capturas en la pesquería de peces pelágicos menores en Sinaloa, Nayarit y Jalisco durante el 2006. CRIP-Mazatlán, INP, SAGARPA. Doc. Interno, 23 pp.

Kendall, D. 1977. The diffusion of shape. Adv. Appl. Probab., 9: 428-430.

Klingenberg, C.P. 1998. Heterochrony and allometry: the analysis of evolutionary change in ontogeny. Biol. Rev., 73: 79-123.

Lagúnez-Moreno, L.M. 1989. Identificación de razas geográficas de *Opisthonema* sp. en las costas de Baja California Sur. Tesis Maestría en Ciencias, Centro de Ciencias Interdisciplinario de Ciencias Marinas, La Paz, 46 pp.

Lin, H.C. & W.A. Dunson. 1999. Phenotypic plasticity in the growth of the self-fertilizing hermaphroditic fish *Rivulus marmoratus.* J. Fish. Biol., 54: 250-266.

Lluch-Belda, D., F.J. Magallon & R.A. Scwartzlose. 1986. Large fluctuations in the sardine fishery in the Gulf of California: possible causes. CalCOFI Rep., 27: 136-140.

Lluch-Belda, D., D.B. Lluch-Cota & S.E Lluch-Cota. 2005. Changes in marine faunal distributions and ENSO events in the California Current. Fish. Oceanogr., 14: 458-467.

Marinone, S.G. 2012. Seasonal surface connectivity in the Gulf of California. Estuar. Coast. Shelf Sci., 100: 133-141.

Marinone, S.G., M.F. Lavín, A. Parés-Sierra. 2011. A quantitative characterization of the seasonal Lagran-gian circulation of the Gulf of California from a three dimensional numerical model. Cont. Shelf Res., 31: 1420-1426.

Nevárez-Martínez, M.O., M.A. Martínez-Zavala, C.E. Cotero-Altamirano, M.L. Jacob-Cervantes, Y. Green-Ruiz, G. Gluyas-Millán, A. Cota-Villavicencio & J.P. Santos-Molina. 2006. La pesquería de pelágicos menores. In: F. Arreguín-Sanchez, L. Beléndez-Moreno, I. Méndez Gómez-Humaran, R. Solana-Sansores & C. Rangel-Dávalos (eds.). Sustentabilidad y pesca res-ponsable en México: evaluación y manejo. Instituto Nacional de la Pesca, SAGARPA, México, pp. 263-295.

Parés-Sierra, A., M. López & E.G. Pavia. 1997. Oceanografía física del Océano Pacífico Nororiental. In: M.F. Lavín (ed.). Contribuciones a la oceanografía física en México. Unión Geofísica Mexicana, Monografía, 3: 1-24.

Pavlova, Y.V. 1966. Seasonal variations of the California Current. Oceanology, 6: 806-814.

Pérez-Brunius, P., M. Lopez, A. Pares-Sierra & J. Pineda. 2007. Comparison of upwelling indices off Baja California derived from three different wind data sources. CalCOFI Rep., 48: 204-214.

Pérez-Quiñonez, C.I., C. Quiñonez-Velázquez, J.S. Ramírez-Pérez, F.J. Vergara-Solana & F.J. García-Rodríguez. 2017. Combining geometric morphemetrics and genetic analysis to identify species of *Opisthonema* Gill, 1861 in the eastern Mexican Pacific. J. Appl. Ichthyol., 33: 84-92.

Polat, N., D. Bostanci & S. Yilmaz. 2005. Differences between whole otolith and broken-burnt otolith ages of red mullet (*Mullus barbatus ponticus* Essipov, 1927) Sampled from the black sea (Samsun Turkey). Turk. J. Vet. Anim. Sci., 29: 429-433.

Ramírez-Pérez, J.S., C. Quiñonez-Velázquez, F.J. García-Rodríguez, R. Félix-Uraga & F.N. Melo-Barrera. 2010. Using the body shape of *Sagitta* otoliths in the discrimination of phenotypic stocks in *Scomberomorus sierra* (Jordan & Starks, 1895). J. Fish. Aquat. Sci., 5(2): 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. Tesis de Maestría, CICESE, Ensenada, 87 pp.

Rohlf, F.J. 2004. TpsDIG Version 1.40. Department of Ecology and Evolution, State University of New York at Stony Brook, New York.

Ruiz, L. & F. Lyle. 1992. Periodic fluctuations capture thread herring (*Opisthonema* spp.) in the Gulf of California, 1972-1990. CalCOFI Rep. 33: 124-129.

SAGARPA-CONAPESCA. 2013. Anuario estadístico de acuacultura y pesca 2013. Secretaría de Agricultura, Ganadería y Desarrollo Rural, Pesca y Alimentación. Comisión Nacional de Pesca. Mexico. [http://www. conapesca.sagarpa.gob.mx/wb/cona/cona_anuario_est adistico_de_pesca]. Reviewed: 5 July 2017.

Saldierna-Martínez, R.J., G. Vera-Alejandro, F. Lachica-Bonilla & M.E. Hernández-Rivas. 1995. Estrategias reproductivas de *Sardinops caeruleus* y *Opisthonema libertate* (Pisces: Clupeidae) en el Golfo de California, México. Memorias del Talles de Pelágicos Menores, La Paz, B.C.S., noviembre 1995.

Saitou, N. & M. Nei. 1987. The neighbor-joining method: a new method for reconstructing phylogenetic trees. Mol. Biol. Evol., 4: 406-425.

Sheets, H.D. 2004. IMP: integrated morphometrics package. Canisius College, Buffalo. [http://www3. canisius.edu/~sheets/morphsoft.html]. Reviewed: 10 July 2017.

Silva, A. 2003. Morphometric variation among sardine (*Sardina pilchardus*) populations from the northeastern Atlantic and the western Mediterranean. ICES J. Mar. Sci., 60: 1352-1360.

Sokolov, D.V. 1974. Investigaciones biológico pesqueras de los peces pelágicos del Golfo de California. All-Union Research Institute of Marine Fisheries and Oceanography, 17, Krasnoselskaya. Moscow B-140, USSR.

Stevenson, D.K. & F. Carranza. 1981. Maximum yield estimates for the Pacific thread herring, *Opisthonema* spp., fishery in Costa Rica. Fish. Bull., 79: 689-703.

Stransky, C., A.G. Murta & C. Zimmermann. 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.

Talley, L.D. 1993. Distribution and formation of the North Pacific Intermediate Water. J. Phys. Oceanogr., 23: 517-537.

Torres-Ramírez, M.N. 2004. Nueva clave de identificación para la sardina crinuda del género *Opisthonema* (Gil, 1861) en el Pacífico mexicano. Tesis de Licenciatura, Universidad Autónoma de Sinaloa, Mazatlán, 19 pp.

Tzeng, T.D. 2004. Morphological variation between populations of spotted mackerel (*Scomber australasicus*) off Taiwan. Fish. Res., 68: 45-55.

Vallarta-Zárate, J.R. 2012. Distribución y abundancia de la sardina crinuda (*Opisthonema* spp.) en el sur del Golfo de California asociada a la variabilidad ambiental durante el periodo 1996-2010. Tesis Maestría, Universidad Nacional Autónoma de México, Mazatlán, 119 pp.

Vega-Corrales, L.A. 2010. Population assessment of exploitable stock *Opisthonema* complex (Pisces: Clupeidae) in the Gulf of Nicoya, Costa Rica. Rev. Mar. Cost., 2: 83-94.

Vergara-Solana, F.J., F.J. García-Rodríguez & J. De la Cruz-Agüero. 2013. Comparing body and otolith shape for stock discrimination of Pacific sardine, *Sardinops sagax* Jenyns, 1842. J. Appl. Ichthyol., 29: 1241-1246.

Waldman, J.R. 1999. The importance of comparative studies in stock analysis. Fish. Res., 43: 237-246.

Waldman, J.R. 2005. Definition of stocks: an evolving concept. In: S.X. Cadrin, K.D. Friedl & J.R. Waldman (eds.). Stock identification methods applications in fishery science. Elsevier Academic Press, Amsterdam, pp. 7-16.

Zelditch, M.L., D.L. Swiderski, H.D. Sheets & W.L. Fink. 2004. Geometric morphometrics for biologists: a primer. Elsevier Academic Press, London, 443 pp.