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Expansion and contraction of the *Engraulis ringens* spawning area in northern Chile

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Summary: Many studies have considered the temporal patterns of reproduction of *Engraulis ringens*, but little attention has been given to the spatial patterns of reproduction (spawning areas), which have shown great variability in both location (geographical position) and extent (the area covered by positive stations), without a satisfactory explanation. Along the Chilean coast, the daily egg production method (DEPM) has been used for several years to estimate spawning biomass in the northern Chile *E. ringens* population, with 24 surveys being carried out from 1992 to 2020. The most fluctuating parameters estimated in the DEPM have been the location and extent of the spawning area and the average female weight. In the last few years the eggs were distributed near the coast, whereas in the first few years they showed a more oceanic distribution. The average female weight has fallen from 30 g in the 1990s to 11 g in the last few years. In the present study, we analysed the relationship of the location and extent of spawning areas with female size and abundancy in *E. ringens* from northern Chile. According to the results, periods of high abundancy of eggs are positively correlated with larger females that spawn in more oceanic zones and to the south, expanding the spatial egg distribution and increasing the egg density. By contrast, in years with low abundance of eggs, the spawning was located north and towards the coast, with a smaller spawning area and smaller female size.

Keywords: anchovy; reproduction; spawning areas.

Expansión y contracción del área de desove de *Engraulis ringens* en el norte de Chile

Resumen: Han habido muchos estudios sobre los patrones temporales en la reproducción de *Engraulis ringens*, sin embargo, se ha prestado poca atención a los patrones espaciales de reproducción (áreas de desove), que han mostrado una gran variabilidad tanto en la ubicación (posición geográfica) como en la extensión (área cubierta por estaciones positivas), sin tener explicación satisfactoria. A lo largo de la costa chilena, el método de producción diaria de huevos (MPDH) se ha utilizado durante varios años para estimar la biomasa desovante de *E. ringens* del norte de Chile, con 24 aplicaciones desde 1992 hasta 2020. Los parámetros más fluctuantes estimados en el MPDH han sido la zona de desove, tanto en localización como en extensión y el peso medio de las hembras. En los últimos años los huevos se han distribuido cerca de la costa en contraste con los primeros años con una distribución más oceánica. El promedio del peso de las hembras se ha reducido de 30 g en la década de los 90 a 11 g en los últimos años. En el presente estudio analizamos la relación entre la ubicación y extensión de las áreas de desove, con el peso de las hembras y su abundancia en *E. ringens* del norte de Chile. Según los resultados, los períodos de alta abundancia de huevos se correlacionan positivamente con hembras más grandes que desovan en zonas más oceánicas y hacia el sur, expandiendo la distribución espacial de huevos y aumentando la densidad de huevos. Por el contrario, en años donde se registró baja abundancia de huevos, el desove se ubicó al norte y hacia la costa con menor área de desove y menor tamaño de las hembras.

Palabras clave: anchoveta; reproducción; áreas de desove.

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INTRODUCTION

The anchoveta, *Engraulis ringens* Jenyns 1842, from northern Chile has a short life cycle, a fast growth rate and therefore a naturally high mortality rate (Cubillos and Arancibia 1993, Cubillos et al. 2001). Juveniles typically recruit to the fisheries around five months after hatching (Castillo and Plaza 2016). The spawning season of the species tends to occur in winter (Southern Hemisphere) and extends from July to September with a peak between August and September (Claramunt et al. 2014). Many studies have considered the temporal patterns of reproduction of the anchoveta (Cubillos and Claramunt 2009, Claramunt et al. 2014, Hernández et al. 2013), but little attention has been given to the spatial patterns of reproduction (spawning areas), which have shown great variability in both location (geographical position) and extent (the area covered by positive stations), without a satisfactory explanation. According to Castillo-Jordán et al. (2007), GAM models indicate that in southern Chile egg density distribution is better explained by a bivariate function of longitude and latitude together with bottom depth. However, since in this case egg densities depend exclusively on parameters that are not directly sensitive for fish, the results are not satisfactory from a biological point of view (Castillo-Jordán et al. 2007). For northern populations there is no explanation yet for the changes in the location or extent of their spawning areas. In a study of spawning habitat preferences, Claramunt et al. (2012) concluded that chlorophyll concentration could be a relevant variable in female spawning habitat selection, but this does not explain interannual expansion and contraction of the spawning area.

Along the Chilean coast, the daily egg production method has been used for several years to estimate spawning biomass in the northern Chile *E. ringens* population, with 24 surveys being carried out from 1992 to 2020. One of the great advantages of this method is that in addition to abundance estimates it provides valuable information about the reproductive biology of the stocks, through intensive sampling of the ichthyoplankton and adult females (Claramunt et al. 2019, Claramunt et al. 2012). The most fluctuating parameters estimated in the daily egg production method have been location and extent of the spawning area and the average female weight. In the spawning area, changes occurred in latitude and coast-ocean directions. In the last few years the eggs were distributed near the coast, whereas the first few years they showed a more oceanic distribution. The average female weight has fallen from 30 g in the 1090s to 11 g in the last few years. In the present study, we analysed the relationship of the location and extent of the spawning areas with female size and abundancy in *E. ringens* from northern Chile.

MATERIALS AND METHODS

This study used information found in the database of the daily egg production method programme, which consisted of research cruises carried out during the peak spawning season from 1992 to 2020, except the years 1993, 1994, 1998 and 2010, making a total of 25 cruises (Table 1). The study area covered the northern region of Chile, from 18°20'S (Arica) to 26°03'S (Carrizalillo), and from the coast to 60 or 80 nautical miles (nm) seaward, with transects every 10 nm and stations every 5 nm. At every station, eggs were collected using a CalVET plankton net with a 0.05 m^2 mouth area equipped with a 250 µm mesh size net. Simultaneously purse-seine boats were used for annual adult surveys, which sampled a minimum of 30 females in each of the 40 hauls.

For the purpose of exploring the changes in the location of the spawning areas, the centre of gravity for each year was calculated using the following equation.

$$CG = \frac{\sum h * Lat}{\sum h}$$

where h is the number of eggs at a given station and Lat is the position of the station in either latitude or longitude (Bez 1997, Gutierrez et al. 2012). The egg density was calculated as the average number of eggs per 0.05 m^2 at the positive stations (i.e. at least one egg).

For each survey the area regarded as the main spawning area encompassed all positive stations (i.e. with anchovy eggs) as well as negative stations embedded between positive stations. All negative stations outside the positive area were omitted from the area estimate. To overcome interannual differences in the total amount of surveyed area, the spawning area was standardized by the ratio with the total area of each survey: spawning area/survey area (Table 1).

The annual catch (Table 1) was used as an abundance index for the stock. The database of industrial fleet landing was obtained from the national fisheries service (SERNAPESCA; www.SERNAPESCA.cl).

The relationships between variables were tested by means of multiple and simple linear regressions and the significance of the coefficients by t test.

RESULTS

In the northern zone a high variability in both location (geographical position) and extent (the area covered by positive stations) of the spawning area was observed (Fig. 1). In terms of locations, changes occurred in latitude and coast-ocean directions. In some years (e.g. 2015, 2017 and 2019) the eggs were distributed near the coast, whereas in others (2000, 2002) they showed a more oceanic distribution. Latitudinally within the spawning area in northern Chile, in some years (e.g. 2013) the main spawning zones were north of 20°S, while in other years (e.g. 2011, 2015) they were south of 21°S.

Female length frequency distribution shows a clear reduction pattern (Fig. 2). In the first years the mode is centred near 16 cm, falling to 12 cm in the last years. The extent of the spawning area is correlated with annual landings (Fig. 3A, Table 2), latitude (Fig. 3B) and longitude (Fig. 3D, Table 2). An expansion of the

Table 1. – Information used in the study. Stations (+): number of stations with anchovy eggs. CG, centre of gravity in latitude (°S) and longitude (°W); A, survey area; A(+), spawning area; A(+)/A, spawning area/survey area.

	Stations	Stations (+)	Egg density	Survey area	Spawning area	A(+)/A	Female weight	CG Latitude	CG Longitude	Annual catch
Year	N°	N°	N°/0.05 m^2	mn^2	mn^2		g	°S	°W	t*1000
1992	542	212	20.2	18341.8	9966.5	0.54	21.0	19.94	70.61	954
1995	578	209	13.3	18794.6	8710.3	0.46	29.0	22.40	70.76	1482
1996	752	176	8.9	19668.5	6422.9	0.33	30.0	21.10	70.66	840
1997	800	209	10.1	28713.7	10328.2	0.36	21.7	21.92	70.72	1317
1999	598	132	12.7	28018.7	7182.8	0.26	23.0	21.72	70.53	809
2000	502	212	20.9	20186.8	10212.8	0.51	30.9	21.59	70.64	1154
2001	514	60	14.5	25630.9	3481.3	0.14	32.4	21.93	70.33	640
2002	589	310	31.0	29947.1	17781.3	0.59	21.3	21.43	70.60	1216
2003	537	129	17.2	26799.6	7498.3	0.28	25.2	21.18	70.42	418
2004	649	211	19.1	32006.8	11694.9	0.37	23.6	20.78	70.59	1394
2005	658	215	25.9	32581.1	12239.6	0.38	23.0	21.33	70.77	1008
2006	799	226	14.3	40771.6	14804.0	0.36	22.5	20.89	70.52	513
2007	799	113	5.9	38206.6	7611.9	0.20	21.7	19.40	70.64	745
2008	717	136	14.4	34860.3	8912.6	0.26	21.8	21.24	70.33	648
2009	773	41	6.1	38234.8	3036.6	0.08	18.0	19.47	70.30	440
2011	730	292	19.1	35033.2	17316.6	0.49	23.4	21.34	70.51	958
2012	564	211	19.1	34823.7	18326.2	0.53	20.1	21.72	70.51	710
2013	770	201	8.2	35874.6	11141.7	0.31	24.5	20.37	70.50	691
2014	632	128	11.8	29581.5	6937.7	0.23	17.0	19.82	70.41	729
2015	659	150	9.4	31814.3	9689.9	0.30	13.2	21.12	70.41	633
2016	791	64	7.6	41102.6	4175.2	0.10	11.5	18.89	70.46	243
2017	819	108	5.4	42508.7	7095.8	0.17	15.7	19.63	70.51	530
2018	799	203	16.9	40732.0	12783.0	0.31	15.9	20.84	70.48	751
2019	782	117	14.3	41757.0	8366.0	0.20	11.1	20.28	70.35	516
2020	789	52	5.4	39272.9	3890.8	0.10	11.7	19.79	70.29	268

spawning area is associated with an increase in egg density (Fig. 3C, Table 2).

The eggs' centres of gravity show a trend over time to be located north and towards the coast (Fig. 4A). The years with centres of gravity located south and towards the ocean are associated with high annual landings (Fig. 4B). Low landings are associated with centres of gravity located north and towards the coast. A multiple linear regression of annual landings as a function of centres of gravity in latitude and longitude was adjusted (Table 3), resulting in an equation with predicted values very close to the observed ones (Fig. 5).

Female size is correlated with centre of gravity in latitude and longitude (Fig. 6, Table 2). Larger females spawn in more oceanic areas and southwards. Summarizing the results, years with high catch are associated with larger females that spawn in more oceanic zones and to the south, expanding the eggs' spatial distribution.

DISCUSSION

According to the results, years with high annual catches of anchovy show high egg density, an extended spawning area and a good range of female size distribution, with females over 31 g or 16 cm. By contrast, years with low annual catches show lower egg density, the spawning area is restricted to the coastal zone and the female size distribution is restricted to smaller females (<31 g or 16 cm).

The egg distribution area could be used as a proxy for the adult fish distribution area, as tested by Barange et al. (2009), indicating that if the eggs samples are taken during the peak period of the species' spawning season, the distribution area of the eggs is proportional (but not equivalent) to that of the adults, thus validating the use of either eggs or adults to estimate the relationship between distribution area and stock size (Barange et al. 2009). Therefore, we can postulate that spawning area is a proxy of adult distribution, so the expansion and contraction of the spawning area of the anchoveta

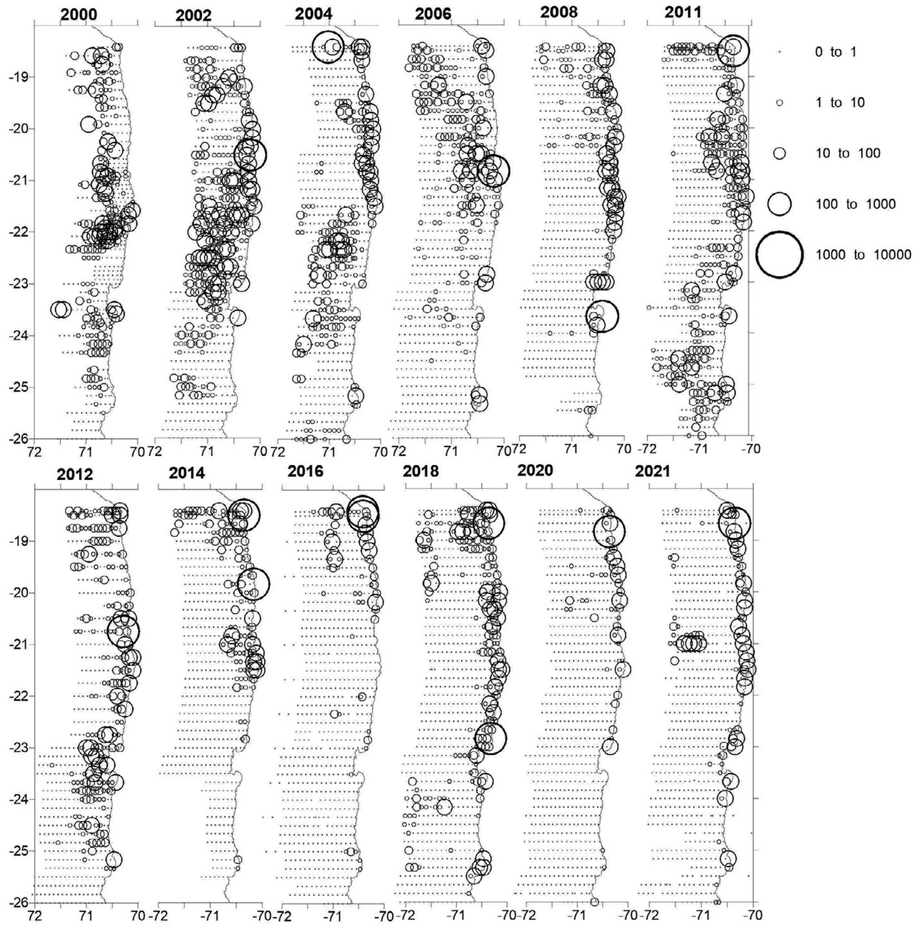

Fig. 1. – Anchovy egg distribution from 2000 to 2021. Diameter of the circles are proportional to the eggs numbers (N°/0.05 m²). Circles in eggs number/0.05 m².

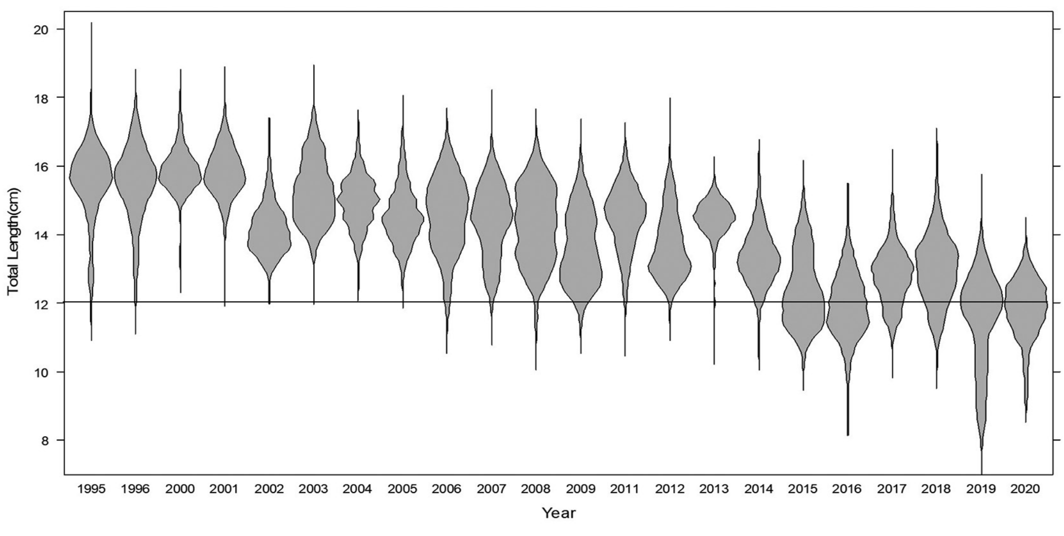

Fig. 2. – Distribution of female total length (cm). Horizontal line indicates 12 cm total length (maturity).

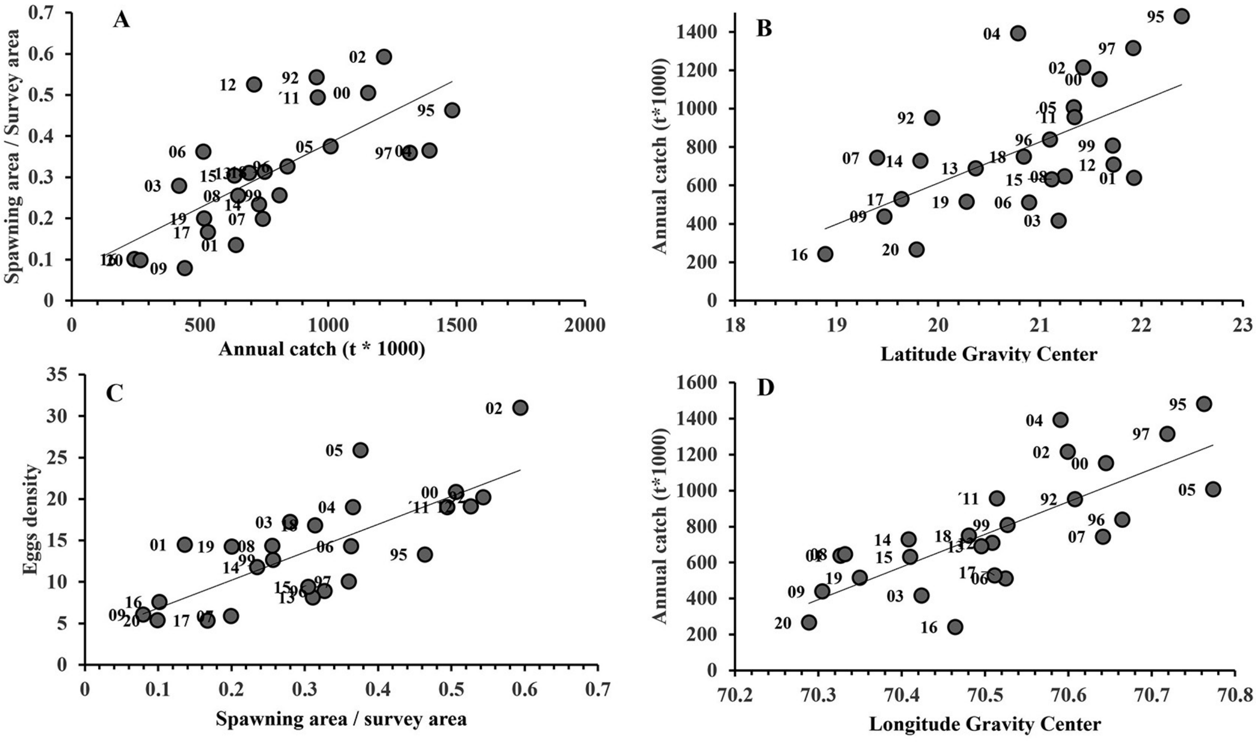

Fig. 3. – Relationship between annual catch and spawning area (as a proportion of the survey area) (A). Egg distribution latitude (°S), centre of gravity and annual catch (B). Spawning area and egg density (N°/0.05 m^2) (C). Egg distribution longitude (°W), centre of gravity and annual catch (D). Numbers indicate year.

Table 2. – Results of the linear regressions between independent (X) and dependent (Y) variables. CG, Gravity Centre; a, Intercept; b, slope; Sa and Sb, standard error. Prob, probability parameter = 0.

Independent	Dependent	a	Sa	Prob	b	Sb	Prob	R^2	n
Annual catch	Spawning area	0.069	0.055	0.219	0.0003	10^{-5}	7.08 10^{-5}	0.50	25
Spawning area	Egg density	3.47	2.11	0.114	33.7	6.11	1.30 10^{-5}	0.57	25
GC latitude	Annual catch	–3672	1250	0.007	214	60.04	0.0016	0.36	25
GC longitude	Annual catch	–127179	22658	1.03 10^{-5}	1814.7	321.3	9.50 10^{-6}	0.58	25
GC latitude	Average female weight	–62.9	21.27	0.007	4.04	1.02	0.0006	0.41	25
GC longitude	Average female weight	–1343	550.2	0.023	19.4	7.80	0.021	0.21	25

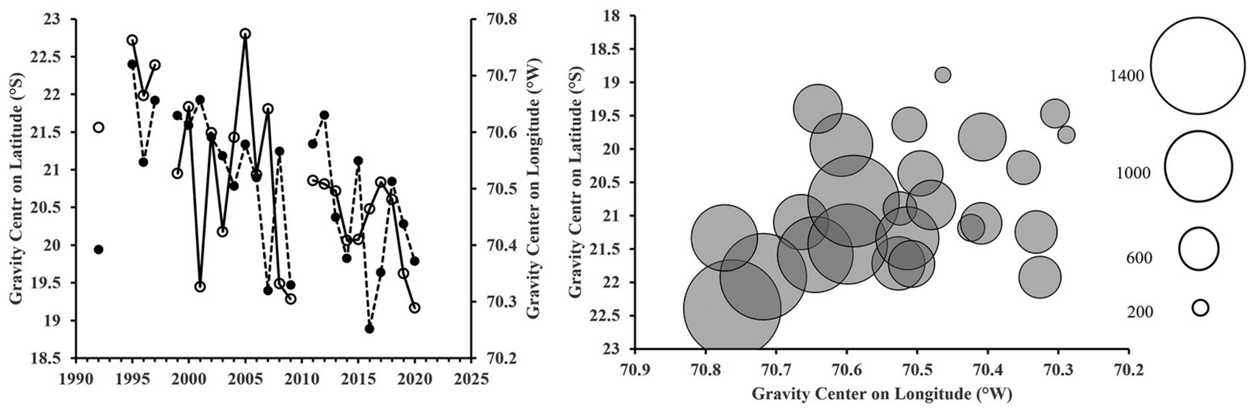

Fig. 4. – A, centre of gravity of egg distribution. B, centre of gravity of egg distribution and annual catch (diameter of the circles).

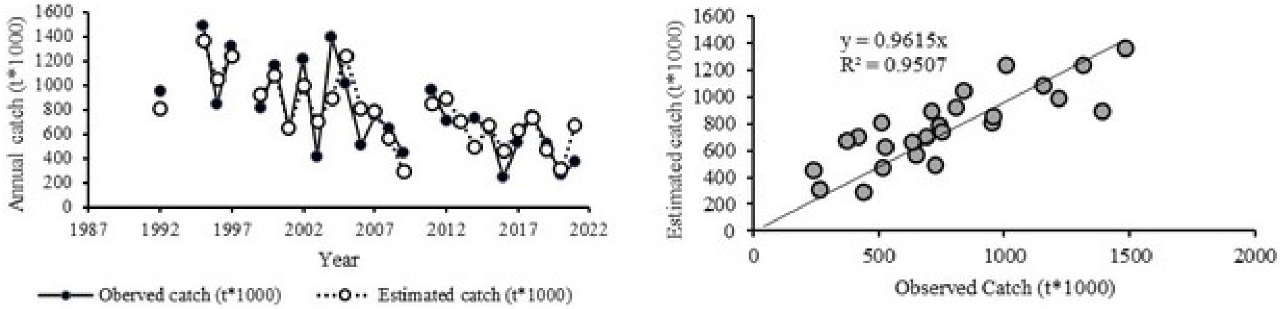

Fig. 5. – Left: Observed annual catch from 1992 to 2020 and estimated annual catch (t*1000) by a multiple linear regression with egg distribution centre of gravity in latitude (°S) and longitude (°W). Right: Linear regression between observed and estimated annual catch.

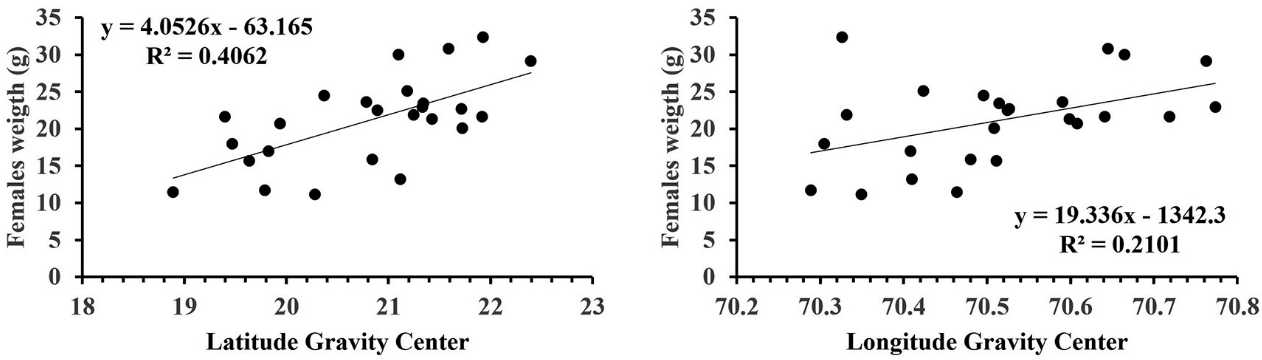

Fig. 6. – Relationship between average female weight and latitude (°S) and longitude (°W) of the centre of gravity of egg distribution.

Table 3. – Results of the linear multiple relationship between annual catch and centre of gravity in longitude (CGLong) and latitude (CGLat). SD, standard deviation.

Coefficient	SD	Probability
Intercept	–107329.9	3.6758E-05
CGLong	1494.4	5.568E-05
CGLat	131.5	0.0082
r^2	0.84	
n	25	

in the northern region of Chile follow the changes in abundance of eggs to adults.

The results show that the spawning area location is influenced by female weight distribution. Bigger females have a more oceanic and southward spawn, expanding the egg distribution. These results contrast with the proposal of Swartzman et al. (2008) that the Peruvian stock of anchoveta is restricted to the cold waters of coastal upwelling, regardless of their abundance. Barange et al. (2009) suggest that in anchoveta the available habitat determines the size of the stock of the anchoveta. The causes of female size reduction in the northern anchovy population are as yet unknown. Natural and fishery mortality and changes in growth rate could be involved.

Three basic models describe the relationship between stock size, distribution area and local density (Petitgas 1998, Barange et al. 2009): (i) the constant density model, in which density stays constant and the area covered by the stock varies with abundance; (ii) the proportional model, in which the area occupied stays constant and local density varies proportionally to abundance; and (iii) the basin model, in which density and area vary with abundance. According to our results, anchovy off northern Chile shows a type (iii) model, density and area varying with abundance.

Although the mechanisms and environmental aspects that cause fluctuations in anchoveta populations have received considerable attention around the world (Alheit and Bakun 2010, Alheit et al. 2019, McCall 2009), these studies have not yet been sufficient to determine the environmental aspects or mechanisms that regulate the changes in abundance and the density-dependent processes that might be involved. In fishes, changes in time and space in reproduction, namely, changes in spawning periods and spawning areas, affect growth and early stage survival because they also determine the kind of environment in which the fish populations will develop (Secor 2007). In the Japanese pacific, fluctuations in the abundance of the stock of *Sardinops melanosticus* were followed by changes in the spawning period (Itoh et al. 2009, Takahashi et al. 2008, Watanabe et al. 1996, 1997), which in turn changed the environment encountered by the early stages (i.e. temperature, food availability and predator evasion), which affects early growth.

This strategy of a density-dependent use of space could be a mechanism for avoiding cannibalism upon their own eggs. This also signifies that, if the appropriate conditions are met in more oceanic sites, the population could undergo a phase of expansion. Something similar happens with the anchoveta *Engraulis encrasicolus* in the Adriatic Sea, where apparently they seem to change their spawning centres during the reproductive period according to the favourable environmental conditions, beginning the spawning process in the northern and more shallow part of the Adriatic, where they first find the appropriate conditions for survival of the early stages of life (Zorica et al. 2018). Examples of periodic habitat expansion and contraction are reported in the literature for small pelagic populations in different ecosystems (Bakun 2005, 2006, Barange et al. 2009). These expansions have been linked to predator-prey interactions or competitive advantages, which determine or are determined by an increase in population size (Bakun 2006, Barange et al. 2009). This density-dependent relationship assumes that the number of progenies recruited to a fishery is proportional to the number of eggs spawned until an environmental carrying capacity is reached. Departures from this relationship are density-independent and attributed to the environment. Implicitly, the stock-recruit relationship does not account for climate variability and change, although environmental terms can be added to expand this type of model (Checkley et al 2017).

In conclusion, the expansion and contraction of spawning areas in *E. ringens* of northern Chile depend on the abundance and size of females. Abundance is more related to extent and female size to the location of the spawning areas.

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