REPRODUCTIVE CYCLE OF THE PACIFIC SARDINE, SARDINOPS SAGAX MUSICA (GIRARD, 1854) FROM THE FISHERY AREA OF TALCAHUANO, CHILE (1983-1984)

CICLO REPRODUCTIVO DE LA SARDINA ESPAÑOLA, SARDINOPS SAGAX MUSICA (GIRARD, 1854) EN EL AREA PESQUERA DE TALCAHUANO, CHILE (1983-1984)

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ABSTRACT

This report describes the spawning cycle of the Pacific sardine Sardinops sagax musica (Girard, 1854) during 1983-1984, in the Talcahuano fishery area (36°41'S; 73°06'W), using gonadic histological analysis. Information on gonosomatic index and the presence of eggs and larvae in the plankton are also used.

The results show Pacific sardine to be a serial spawner with continuous breeding throughout the year, and two peaks of reproductive activity-a main peak during winter and early spring (june to september), and a secondary peak in february.

The implications of this two spawning peaks, and an index of larval survival index in relation to environmental biotic and abiotic conditions are discussed.

First maturity sizes were found to be 29.5 cm total length for males and 30.0 cm for females, which aproximately corresponds to 5 year of age.

The reproductive cycle in Talcahuano is similar to that found in the north of Chile. This could mean that the southern stock originated from the northern stock, but the reproductive differences between the both areas (e.g. first maturity size) migth indicate the existence of at least two populations along the Chilean coast.

Keywords: Fish reproduction, Sardinops sagax musica, Histological analysis, first maturity, Chile.

RESUMEN

En este trabajo se describe el ciclo reproductivo de la sardina española Sardinops sagax musica (Girard, 1854) en el área de Talcahuano (36°41'S; 73°06'W) durante 1983-1984, mediante análisis histológico de gónadas, índice gonosomático y verificación de la presencia de huevos y larvas en el plancton.

Los resultados indican que la sardina española es un desovante parcial y se reproduce todo el año, con un máximo de actividad reproductiva en invierno y principio de primavera (junio a septiembre), y un máximo secundario en febrero. Se discuten las implicancias de ambos máximos de desove, y de un índice de sobrevivencia larvario, en relación con características ambientales bióticas y abióticas.

Se determina la talla de primera madurez a los 29.5 cm de longitud total en machos y de 30,0 cm en hembras, longitudes que equivalen aproximadamente a 5 años de edad.

Se determina que el ciclo reproductivo tiene un patrón similar al de la zona norte de Chile, por lo que el stock del sur podría haberse originado a partir de aquél, pero las diferencias reproductivas entre estos dos stocks, tales como talla de primera madurez, podría estar evidenciando la existencia de a lo menos dos stock poblacionales en la costa de Chile. Palabras claves: Reproducción de peces, Sardinops sagax musica, análisis histológico, primera madurez, Chile.

INTRODUCTION

The Pacific sardine, Sardinops sagax musica (Girard, 1854), is the main pelagic fishery resource in Chile (SERNAP, 1984; 1985). In the Talcahuano area, this species was entirely unknown to the fishermen before 1973 (Serra, 1983). Since 1973 it begun to be signi-

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ficant in the landigs, becoming the second pelagic fishery resource in this area after the jack mackerel (*Trachurus murphyi*, Nichols, 1920). In 1984, the catch of *S. sagax* in the Talcahuano area reached 93,885 ton from a total of 2.57×10^6 ton for the whole country (SERNAP, 1984); while in 1985, landings were 67,648 ton for Talcahuano from a total of 2.89×10^6 ton (SERNAP, 1985).

The Pacific sardine S. sagax musica is distributed in Chile from $18^{\circ}S$ (De Buen, 1958) to 42°S (Chiloé Island) (C. Oyarzún unpublished data). From ichthyoplankton surveys, carried out in 1981-1982, three spawning areas can be recognized: a large northern area (18° to 26°S), a small central area (around 30°S), and a southern area (32° to 40°S) (Rojas et al., 1983). The existence of these areas, could represent a mechanism for relative reproductive isolation associated to the maintenance of diferents stocks (Cushing 1975; Iles & Sinclair, 1982).

All previous studies on the reproduction of Sardinops sagax musica in Chile have been conducted in the northern zone. They describe a continuous spawning from april-may to november-december following a bimodal cycle, with the main peak around august (Serra et al., 1979). However, the timing of the secondary peak is conflictive. Serra (1983) locates it around february, using macroscopic gonadic analysis and based upon the gonosomatic index. A recent study in the same zone using gonadic histology and gonosomatic index, indicates that the principal peak extends from august to september but the secondary peak was not reported, probably because of the occurrence of an "El Niño" event during the study period (Retamales & González, 1984; 1985). On the other hand, Martínez et al., (1984) based upon macroscopic observations, reported the existence of two peak of reproductive activity, the main from july to september and the secondary one between january and february, but they also report that during the "El Niño" event of 1982-1983 the secondary peak was not observed. These authors also reported that the proportion of monthly mature females never fell below 60%.

Ichthyoplankton surveys from Valparaíso Bay (33°S) indicate the presence of eggs and larvae in the plankton all over the year (Balbontín & Garretón, 1977), meaning that S. sagax is a serial spawner at that latitud.

The present investigation was carried out

with the following aims: i) to know the reproductive cycle of *Sardinops sagax musica* (Girard, 1854), in the Talcahuano fishery area, the southernmost spawning area known for this species; ii) to determine the spawning pattern; iii) to determine first maturity size; and iv) to compare the information obtained with the information available for the northern area.

MATERIALS AND METHODS

Samples were obtained in commercial landings from the Talcahuano fishery area (36°41'S; 73°06'W), since april 1983 to september 1984. A total of 851 individuals were used to determine total length, total weight and gonad weight. A cross-section piece from the mid region of each gonad, was preserved in 10% fomalin/sea water for histological analysis. Ovary tissues were embedded in paraffin, cut in slices 7 and 10 μ m thick and stained with Meyer's Hematoxyline and 1% Eosine. Gonosomatic Index (Nikolsky, 1963) was expressed as: (gonad weight/(Total weight-gonad weigth)) × 100.

Homogenous gonadic maturation was checked in both males and females at different stages of maturity. Five sections from diferent portions along of both gonads were analyzed in 11 males and 11 females, which were between 25.7 to 36.4 cm of total length, following histological procedure described before for each section.

Ovaries were histologically classified in five stages (plate 1):

I. Inactive. Containing primary oocytes about 0.12 mm in diameter, with basophilic cytoplasm, and a large nucleous with many nucleoli under the nuclear membrane.

II. Previtellogenic. Containing enlarged oocytes 0.25 mm in diameter, with a ring of lipidic vacuoles under the cytoplasm membrane.

III. Vitellogenic. Containing oocytes 0.30 mm in diameter in yolk accumulation process. Nuclei are larger and irregular, the granulate and radiate zones of the follicles are clearly distinguished.

IV. Mature. Containing oocytes 0,49 mm in diameter in which the yolk accumulation process has been completed. Polar position of the nucleous or hydrating eggs sometimes present.

V. Mature post batch spawning. Presence of postovulatory follicles is verified. These structures can be detected only up to 48 hr



Plate I. Gonadal development stages in females of Sardinops sagax musica. (a) Inactive ovary with primary oocytes;
(b) Previtellogenic ovary with vacuolated oocytes; (c) Vitellogenic ovary with yolked oocytes; (d) Mature ovary with mature oocytes with accumulation yolk process finished; (e) Mature post batch-spawning ovary with postovulatory follicles and vitellogenic oocytes, sometimes mature oocytes; and (f) Postovulatory follicle.



Figure 1. Gonosomatic Index of Sardinops sagax musica of males and females pooled, and separated sexes.



Figure 2. Female frecuency of Sardinops sagax musica, mature plus mature post batch-spawning (with postovulatory follicles).

after spawning (Alarcón et al., 1984; Goldberg et al., 1984).

For the analysis of monthly maturity frecuencies, stages IV and V were considered as mature and fishes smaller than first maturity size were not considered for histological analysis and Gonosomatic Index analysis.

Testicles maturity was classified according to the criteria of Oliva et al. (1982).

First maturity for both males and females

was determined by interpolation as the size with at least 50% mature specimens.

Fulton's Condition Factor was expresed as $(total weight/(total length)^3) \times 100$.

Age of the fishes were estimate according to the size-age determinations done in the northern zone of Chile (Aguayo *et al.*, 1984).

Sea Surface Temperature data was obtain from Navarro (1984).



Figure 3. Relationships between reproductive activity expressed as mature female frecuency and Gonosomatic Index with superficial sea temperature, in Sardinops sagax musica.

RESULTS

Considering the pooled samples, the sexual ratio was 49.94% of females (426 males: 425 females), indicating positively a 1: 1 sexual ratio (Chi square test with P <0.05), however, the sexual ratio was not 1: 1 in 11 out of 17 of the individual samples (P> 0.05) (Table 1).

Size frecuency distributions indicated that samples were composed by fishes between 24.5 and 37.5 cm (aproximately 3 to 12 years old) and the more frecuent sizes were between 29.5 cm. and 35.5 cm (aproximately 6 to 9 years of age), summer samples were composed mainly by fishes below the size of first maturity (29.5 - 30.0 cm total length).

Fulton's Condition factor reached high values (aproximately 1.5) during Summer, being around 1 during the other seasons (Table 1).

Gonosomatic Index Analysis

Trends of Gonosomatic Indeces (GSI) (Fig. 1) did not show large diferences for males, females or pooled mean monthly values, and they are inter-correlated (Kendall Concordance W = 0.93). From july to october 1983, a large and fast increase of GSI in females was observed, followed by a decrease during the next four months. GSI in males increased and decreased more gradually. Pooled GSI values were low from november 1983 to january 1984; they increased in february, only to decrease in march, increasing again in winter 1984 (june to september) to reach a higher value than the one from february. This means that the reproductive cycle determined by GSI shows two speak of high activity (bimodal curve), being the main peak placed during winter.

Histological Analysis

The histological analysis of all the sections obtained throughout the both gonads indicated that maturity process was homogeneous for both males and females, independently of the maturity stage or fish-size.

Histological analysis of the gonads showed the occurrence of high frecuencies of pre-and postspawned mature females during the whole sampling period, indicating continuous spawning (Fig. 2, Plate 1), accordingly the Pacific sardine off Talcahuano behave as a multiple or serial spawner. Thus 42.9% females were mature in the month of lowest reproductive activity, period when early maturity stages were also dominant (Table 2). During the main reproductive period, up to 100% of females in the sample were mature. During 1983 the main spaw-

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Monthly composition of the samples Sardinops sagax musica from Talcahuano, Chile

Month	Sample date	N° ind. sample	Female frecuency (%)	Fulton's Conditions Factor	
April '83	26/04/83	18	50.00	0.98	
July '83	15/07/83	40	70.00*	0.92	
	20/07/83	33	48.50	0.92	
Sept '83	13/09/83	27	44.44	0.91	
	28/09/84	28	28.57*	0.94	
Oct '83	03/10/83	24	45.83	0.88	
Nov '83	04/11/83	34	64.71*	0.93	
Jan '84	05/01/84	25	48.00	0.97	
	11/01/84	14	71.43*	1.08	
Feb '84	01/02/84	31	74.19*	1.46	
	24/02/84	26	73.08*	1.30	
	29/02/84	16	68.75*	1.15	
March '84	29/03/84	88	60.23*	1.02	
June '84	20/06/84	100	64.00*	0.95	
July '84	28/07/84	111	49.55	0.87	
Aug '84	24/08/84	80	60.00*	0.91	
Sept '84	22/09/84	156	14.10*	0.89	

* Sexual ratio different from 1: 1, with Chi square test significative at P < 0.05

TABLE 2

Frecuency of the differents maturity stages in females S. sagax musica from Talcahuano, Chile.

Month	Sample date	N	Ovary Maturity Stage				
			I	Р	v	М	POF
April '83	26/04/83	7	0.0	0.0	14.3	85.7	42.9
July 83	15/07/83	13	0.0	0.0	0.0	100.0	15.4
Sept '83	13/09/83	10	0.0	10.0	0.0	90.0	10.0
•	28/09/83	7	0.0	0.0	0.0	100.0	57.1
Oct '83	03/10/83	10	0.0	0.0	0.0	100.0	20.0
Nov '83	04/11/83	19	0.0	15.8	10.5	73.7	0.0
Jan '84	05/01/84	6	0.0	16.7	16.7	66.7	0.0
•	11/01/84	7	14.3	28.6	14.3	42.9	14.3
Feb '84	01/02/84	2	0.0	0.0	0.0	100.0	50.0
	24/02/84	11	0.0	0.0	0.0	100.0	9.1
	29/02/84	3	0.0	0.0	0.0	100.0	33.3
March '84	29/03/84	21	19.0	14.3	14.3	52.4	4.8
June '84	20/06/84	23	0.0	0.0	0.0	100.0	4.4
July '84	28/07/84	20	5.0	0.0	0.0	95.0	15.0
Aug '84	24/08/84	21	0.0	0.0	0.0	100.0	23.8
Sept '84	22/09/84	20	0.0	0.0	0.0	100.0	35.0

I = Inactive ovary stage

P = Previtellogenic ovary stage

V = Vitellogenic ovary stage

M = Mature ovary stage

POF = Ovary with Postovulatory Follicles

ning peak was from april to october, after a drastic decrease of the frequency of mature females in november. During summer reproductive activity was low, except for february, when a secondary reproductive peak was observed. Reproductive activity was low again in march, only to rise again in winter and early spring, 1984 (from june to september).

Size of first maturity —with 50% mature fishes— was estimated to be 29.5 cm total length in males and 30.0 cm total length in females. That size would correspond to fishes averaging 5-6 years old. the smallest male and female reaching maturity in this study were 28.3 and 26.4 cm total length respectively (aproximately 5 and 4 years old).

Monthly ichthyoplankton hauls from a station located 8 nautical miles West off Concepción Bay, and sporadic observations from the Arauco Gulf and Concepción Bay, indicate the presence of eggs and larvae in the plankton throughout the year (G. Herrera pers. comm.).

An inverse relationship between spawning incidence and sea surface temperature (SST) (Fig. 3) was observed during this study using either GSI or histologicallydetermined maturity.

DISCUSSION

Maturity stages shows no histological differences with previous descriptions (Macer, 1974; Scott, 1974; Crossland, 1977; Hodgkiss & Man, 1978; Hunter & Goldberg, 1980; De Martini & Fountain, 1981; Treasurer & Holliday, 1981), and the only changes done here refers to the nomenclature of stages.

Asynchronous gamete development indicates that Pacific sardine S. sagax is a serial or multiple spawner at this latitud. Continuous gamete releasing was demonstrated by the presence of postovulatory follicles during the whole sampling period, since this structures can only be recognized up to 48 hr after spawning (Alarcón et al., 1984; Goldberg et al., 1984). The observation of eggs and larvae in the plankton all year around in the area further confirm the continuous character of spawning activity in this species.

The sexual ratio on the average was 1: 1 for the whole sampling period. However, the monthly variations observed might indicate that some specific reproductive behaviour is taking place, characterized by partial spatial

segregation by sex during spawning. This has been previously recorded for other Clupeiform species (Hunter & Goldberg, 1980; Blaxter & Hunter, 1982). The numerical dominance of males in the spawning schools may represent a mechanism to ensure a high rate of fertilization, a situation that would be favoured by natural selection (Conover, 1984; Conover & Kinard, 1984). High male dominance was observed in Sardinops sagax musica during september 1984, when only 14.9% of all fishes sampled were females. Besides, both males and females were mature. Males presented a high GSI (8.9 ± 1.3), and 35% of the females showed evidence of recent spawning (Postovulatory follicles).

Determinations of first maturity sizes of 23.0 cm by Vidai in 1967 (fide Serra et al., 1979), and 26.0 cm by Retamales & González (1985) for sardine from the north of Chile are not consistent with our estimations for the Talcahuano area, which, could suggest the existence of at least two populations.

GSI information appears to be consistent with histological data, but great care is necessary when using it as the main tool of analysis. A non-linear relationship between gonad weigth and body weigth has been reported in serial spawners (De Vlaming et al., 1982). Also GSI might not be a suitable index because experimental evidence has shown variations of this index with non histological correlates in the gonad (Lam, 1983). Available information indicates the same for Sardinops sagax musica (Aguilera, 1984). Even GSI is open to misinterpretation, however, as it is influenced not only by changes in gonad weigth, but also by change in somatic weigth; it is thus necessary to have an estimate of change in somatic weigth; in that sense the conventional Fulton's Condition Factor is useful.

Gametes were released during the whole year. Nevertheless, a main peak was observed during winter and early spring (june to september), and a secondary peak during frebruary, although this last peak is not as notorious using GSI as with histologycal analysis. Spawning activity would to be less intense the rest of the year.

Fulton's condition factor was uncoupled with the main winter reproduction activity, while it exhibited a peak in february, coincident with the secondary reproductive peak of sardine this situation could faced the GSI variation. In the northern zone of Chile the sardine population spawns every night and a single female could spawn every 5-6 days (Retamales & González, 1984). It is possible that in Talcahuano female spawning has a lower frecuency because of lower SST.

In the Talcahuano area, the main spawning peak is uncoupled with the production cycle (Bernal et al., 1982; Castillo et al., 1985) and represents a clear example of mis-match in the sense of Cushing (1975); the secondary reproductive peak lags 1 or 2 months those of primary and secondary production. On the contrary, in the north of Chile there exists a close coupling between spawning and the production cycle, because upwelling also occurs in winter (Bernal et al., 1982). The main winter reproductive peak in Talcahuano is associated with low SST (Fig. 3), low surface Ekman transport, and moderate turbulence, while in the northern area this peak is associated with low SST, low turbulence but high Ekman transport. Condition's that are consistent with the criteria of Smith & Lasker (1978) regarding optimun for larval survival. The secondary summer reproductive peak is associated in Talcahuano, with high SST, high Ekman transport, and high turbulence while in the northern zone it is associated with high SST, low Ekman transport, and low turbulence (Bakun & Parrish, 1982; Parrish et al., 1983; Bakun, 1985).

A comparison of apparent survival ratios of sardine for both north (18°S) and south (37°S) (Castillo *et al.*, 1985), suggests that the southern larvae spawned in winter have a higher probability of survival than those spawned in summer, despite the low SSTs found in the area, which sometimes reacher critical low temperature for the development of larval sardines (Garretón & Balbontín, 1982). Also, both winter and summer larval survival are higher for the northern area than in Talcahuano (Castillo *et al.*, 1985), a fact that reflects the "border" character of the local population off Talcahuano with respect to the geographical range of the species.

Thus, of course to Smith & Lasker hypothesis (1978), only the winter reproductive peak at Talcahuano would to be successful because the environmental conditions are favourable for larval development in this season, while in the northern area both reproductive peaks would succeed, because of better environmental conditions over the whole year. Results indicate a "northern-like" spawning pattern (timming) for the Talcahuano sardine, despite large differences of environmental conditions. This could indicate that the southern stock originated from the northern stock, but differences in some demographic characteristics, e.g. the larger size at first maturity, could represent adaptations of a local population, suggesting the existence of a relatively isolated southern stock of *Sardinops sagax musica*, hypothesis that needs

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REFERENCES

further testing

- AGUAYO, H.M.; V. ERBS G.; E. ESTAY M.; R. GILI V. & M. STEFFENSA. 1984. Elaboración de claves edad-talla de sardina española, jurel, anchoveta y caballa para el año 1982. Corporación de Fomento de la Producción. Gerencia de Desarrollo. Instituto de Fomento Pesquero, Chile AP 83-3.
- AGUILERA, E.A. 1984. Ciclo reproductivo de la sardina española, Sardinops sagax musica (Girard, 1854), en el área de Talcahuano. Unidad de Investigación para obtener el Grado de Licenciado en Biología Marina, Universidad de Concepción, Chile, Departamento de Zoología, 83 pp.
- ALARCÓN, V.H.; S.R. GOLDBERG & J. ALHEIT. 1984. Histología de folículos postovulatorios de la sardina (Sardinops sagax) del Perú. Boletín del Instituto del Mar del Perú-Callao, 8(1): 1-16.
- BALBONTÍN, F. & M. GARRETÓN. 1977. Desove y primeras fases de desarrollo de la sardina española, Sardinops sagax musica, en Valparaíso. Revista de Biología Marina, Valparaíso, Chile, 16(2): 171-181.
- BAKUN, A. & R.H. PARRISH. 1982. Turbulence, transport, and pelagic fish in the California and Perú Current System. CalCOFI Reports, 23: 99-112.
- BAKUN, A. 1985. Comparative studies and the recruitment problem: searching for generalizations. Cal-COFI Reports, 26: 30-40.
- BERNAL, P.A.; F.L. ROBLES & O. ROJAS. 1982. Variabilidad física y biológica en la región meridional del sistema de corrientes Chile-Perú. Monografías Biológicas, 2: 75-102.
- BLAXTER, J.M.S. & J.R. HUNTER. 1982. The biology of the Clupeoid fishes. Advances in Marine Biology, 20: 1-223.
- CASTILLO, G.; E. AGUILERA; G. HERRERA; P.A. BERNAL; J.L. BUTLER; J. CHONG; H. GONZÁLEZ; C. OYARZÚN & C. VELOSO. 1985. Larval growth rates of the Pacific sardine Sardinops sagax off Central Chile, determina-

ted by daily ring counts in otoliths. Biología Pesquera (Chile), 14: 3-10.

- CONOVER, D.O. 1984. Adaptative significance of temperature dependent sex determination in a fish. American Naturalist, 123: 297-313.
- CONOVER, D.O. & B.E. KYNARD. 1984. Field and laboratory observation of spawning periodicity and vehaviour of a northern population of the atlantic silverside, *Menidia menidia* (Pisces: Atherinidae). Environmental Biology of Fishes, 11(3): 161-172.
- CROSSLAND, J. 1977. Seasonal reproductive cycle of snapper Chrysophrys auralus (Forster) in the Hauraki Gulf. New Zealand Journal of Marine and Freshwater Research, 11(1): 37-60.
- CUSHING, D.H. 1975. Marine Ecology and Fisheries. Cambridge University Press, Great Britain, 278 pp.
- DE BUEN, F. 1958. Peces de la superfamilia Clupeoidae en aguas de Chile. Revista de Biología Marina, Valparaíso, Chile, 8: 83-110.
- DE MARTINI, E.E. & R.K. FOUNTAIN. 1981. Ovarian cycling frecuency and batch fecundity in the queenfish, *Seriphus politus*: attributes representatives of serial spawning fishes. Fishery Bulletin, 79(3): 547-560.
- DE VLAMING, V.; G. GROSSMAN & F. CHAPMAN. 1982. On the use of gonosomatic Index. Comparative Biochemistry and Physiology, 73A(1): 31-39.
- GARRETÓN, M. & F. BALBONTÍN. 1982. Efecto de la temperatura en el desarrollo embrionario y crecimiento inicial de las larvas de la sardina española, Sardinops sagax musica en condiciones de laboratorio. Revista de Biología Marina, Valparaíso, Chile, 18 (1): 57-71.
- GOLDBERG, S.R.; V.H. ALARCÓN & J. ALHEIT. 1984. Postovulatory follicle histology of the pacific sardine, *Sardinops sagax*, from Peru. Fishery Bulletin, 82(2): 443-445.
- HODGKISS, I.J. & H.S.M. MAN. 1978. Reproductive biology of Sarotherodon mossambicus (Cichlidae) in Plover Cove Reservoir, Hong Kong. Environmental Biology of Fishes, 3(3): 287-292.
- HUNTER, J.R. & S.R. GOLDBERG. 1980. Spawning incidence and batch fecundity in Northern Anchovy, Engraulis mordax. Fishery Bulletin, 77(3): 641-652.
- ILES, T.D. & M. SINCLAIR. 1982. Atlantic herring: stocks discreteness and abundance. Science 215: 627-633.
- LAM, T.J. 1983. Environmental influences on gonadal activity in fish. *in*: Fish Fisiology, 9B: 65-116, Edited by W.S. Hoar, D.J. Randall and E.M. Donaldson. Academic Press, Orlando, U.S.A. 477 pp.
- MACER, C.T. 1974. The reproductive biology of the horse mackerel *Trachurus trachurus* (L.) in the North Sea and English Channel. Journal of Fish Biology, 6: 415-438.
- MARTÍNEZ F. C.; C. SALAZAR Z.; G. BOHM S.; A. ARANIS R.; J. MENDIETA V. & A. TORRES G. 1984. Estado de situación de las pesquerías pelágicas: Análisis de las pesquerías pelágicas 1978-1983. Corporación de Fomento de la Producción. Gerencia de Desarrollo. Instituto de Fomento Pesquero, Chile AP 84-26.
- NAVARRO, N. 1984. Variabilidad de los procesos de surgencia en el área de Talcahuano, Chile. Unidad de

Investigación para optar al Grado de Licenciado en Biología Marina, Universidad de Concepción, Chile, Depto. de Oceanología, 22 pp. + anexos.

- NIKOLSKY, G.V. 1963. The ecology of fishes. Academic Press, New York, 352 pp.
- OLIVA N.J.; W. CARBAJAL V. & A. TRESIERRA A. 1982. Reproducción e Histología de gónadas en peces. Universidad Nacional de Trujillo, Perú. Depto. de Ciencias Biológicas, Sección de Recursos Acuáticos. 93 pp.
- PARRISH, R.H.; A. BAKUN; D.M. HUSBY & C.S. NELSON. 1983. Comparative climatology of selected environmental processes in relation to eastern boundary current pelagic fish reproduction. In: Sharp, G.D. & J. Csirke (eds). Proceedings of the Expert Consultation to examine changes in abundance and species of neritic fish resources. FAO Fish. Rep., (291), 3: 731-777.
- RETAMALES, R. & L. GONZÁLEZ. 1984. Fecundidad de sardina española (Sardinops sagax musica). Programa Estudio de Recursos Pelágicos. Corporación de Fomento de la Producción. Gerencia de Desarrollo. Instituto de Fomento Pesquero, Chile AP 84-5.
- RETAMALES, R. & L. GONZÁLEZ. 1985. Incidencia del fenómeno El Niño 1982-1983 en el desove de sardina española (Sardinops sagax). Investigaciones Pesgueras (Chile), 32: 161-165.
- ROJAS J. O.; A. MUJICA R.; M. LABRA C.; G. LEDERMANN J. & H. MILLES U. 1983. Estimación de la abundancia relativa de huevos y larvas de peces. Corporación de fomento de la Producción. Gerencia de Desarrollo. Instituto de Fomento Pesquero, Chile AP 83-31.
- SCOTT, D.B.C. 1974. The reproductive cycle of *Mormy*rus kannaume Forsk. (Osteoglossomorpha, Mormyriformes) in Lake Victoria, Uganda. Journal of Fish Biology, 6: 447-454.
- SERNAP. 1984. Anuario Estadístico de Pesca. Servicio Nacional de Pesca. Ministerio de Economía, Fomento y Reconstrucción. Chile. 82 pp.
- SERNAP. 1985. Anuario Estadístico de Pesca. Servicio Nacional de Pesca. Ministerio de Economía, Fomento y Reconstrucción. Chile. 180 pp.
- SERRA, J.R. 1983. Changes in the abundance of pelagic resources along the Chilean coast. in: G.D. Sharp & J. Csirke (eds), Proceedings of the Expert Consultation to examine changes in abundance and species of neritic fish resources. FAO Fish. Rep. (291), 2: 553 pp.
- SERRA, J.; O. ROJAS; M. AGUAYO; F. INOSTROZA & J. CAÑÓN. 1979. Estado actual de las principales pesquerías nacionales. Sardina española. Bases para un desarrollo pesquero. Corporación de Fomento de la Producción. Gerencia de Desarrollo. Instituto de Fomento Pesquero, Chile AP 79-18.
- SMITH, P.E. & R. LASKER. 1978. Position of larval fish in an ecosystem. Rapports et Procs-Verbaux des Réunions du Conseil International pour L'Exploration de la Mer, 173: 77-84.
- TREASURER, J.W. & F.G.T. HOLLIDAY. 1981. Some aspects of the reproductive biology of perch *Perca fluviatilis* L. A histological description of the reproductive cycle. Journal of Fish Biology, 18: 359-376.