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Mackerel egg predation by cannibalism during the spawning season

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Consuming one's own viable offspring is common among species that share the same distribution area for all their different life stages. The objective of this paper is to describe the role of mackerel as prey and as predator in the Cantabrian Sea (ICES Division VIIIc) during its spawning season. Mackerel is classified as a serial spawner as the female spawn several times during spawning season. The southern component of northeast Atlantic mackerel stock spawns between March and April. The information used in this paper are: diet composition from stomach content analyses, stage-specific production values derived from pelagic trawl hauls and ichthyoplankton surveys conducted on cruises in March and April from 2000 to 2003 . Temperature of the water column and abundance of juvenile and adult mackerel at each sampled station were also collected. The analysis of all these data allowed us to evaluate temporal changes in the predation process and their possible causes. These results are also discussed under the perspective of cannibalism's role in the estimated mackerel recruitment.

INTRODUCCIÓN

The predation is widely accepted as the most important cause of mortality during the egg state (Hunter, 1984: Bailey and Houde, 1989). However, until rates of egg production were established, estimates of the impact of cannibalism on fish eggs remained largely incalculable (Bunn *et al*., 2000). Cannibalism on eggs is common in some clupeoid fishes, either by incidental filter-feeding or by selective consumption, and it is reported in literature (Alheit, 1987; Rankine & Morrison, 1989; Ellis & Nash, 1997; Köster & Möllmann, 2000). Egg mortalities by cannibalism greater than 20 % have been reported in sardines (*Sardinops spp*) and anchovies (*Engraulis spp*.) in upwelling ecosystems (Houde, 2002). The fact that mackerel eat mackerel eggs is a known phenomenon but there are very few data on this. Fish predation on Atlantic mackerel eggs in the North of Spain, Cantabrian Sea, has not been studied yet, and there are very few data of its food habits. The Cantabrian Sea is an area that belows to the southern spawning component of northeast Atlantic mackerel stock. We know that the adult northeast Atlantic mackerel from the south and west area migrate to feed in the Norwegian Sea and the North Sea during the second half of the year. They then return during the first half of the year towards Southern Europe (March and April) in order to carry out the spawning during the spring (Villamor *et a*l., 1997; Uriarte & Lucio, 2000; Reid, 2001; Reid *et al*., 2001). Mackerel arrives at the beginning of the spring at the Bay of Biscay, Cantabrian Sea concretely.

Mackerel is classified as a multiple spawner as the female spawn several times during spawning season, and the spawning pike of the southern component of the stock is in April. *Scomber scombrus* is closely related with the zooplankton, and various feeding studies have been carried out on their larvae (Peterson & Ausubel, 1984; Conway *et al.*, 1999; Fortier & Villeneuve, 1996), as well as their adults (Gregoire & Castonguay, 1989; Macy *et al*., 1998). However, specifically in the Bay of Biscay and along the coast of Portugal, no study has been undertaken on the feeding of this species, except for an accurate study on stomach repletion carried out by Lucio (1997), and other on seasonal diet changes in the coast of Portugal (Cabral and Murta, 2002). In the spring surveys we found eggs upon the stomachs of adult mackerel (Olaso *et al*., in preparation) on the spawning grounds in Cantabrian Sea, and we suspect that this might be a major source of mortality for these eggs, although there is very little knowledge about interannual variation in both the magnitude and the spatial structure of total mackerel egg production.

The main objective of our study was (is) to estimate preliminary data on total consumption of mackarel eggs by *S. scombrus*. We know that the methods to assess predation mortality are very difficult to develop, since besides to determine and to quantify egg prey, we need to estimate the abundance of mackerel and the number of eggs as prey. For it, in addition to analyze the stomach contents of this study, we used all the information available about mackerel in this area. To the being a preliminary study, we made numerous assumptions to determine the main objectives previously indicated. With the information used in this paper we also considered (estimate) the food daily ration of mackerel in April. Therefore, we give a first step on the cannibalism that can exert mackerel with its own eggs in the Cantabrian Sea, and we discuss the cannibalism predation as a factor that may regulate levels of recruitment or generate variations in it.

MATERIAL AND METHODS

Sampling

The samples were obtained on board R/V Thalassa during the acoustic surveys carried out in the North of Spanish continental shelf area in 2000 (PELACUS 00, 28 March – 13 April), 2001 (PELACUS 01, 3 April – 21 April), 2002 (PELACUS02, 14 March - 2 April) and 2003 (PELACUS03, 23 March – 11 April). The survey track consisted of parallel transects, eight nautical miles apart. Fishing stations, both for species identification and biological sampling were undertaken on selected echo-traces. Most of the samples were taken by day and by night using a pelagic gear (25 m vertical opening). Pelagic trawling was for the most part concentrated in the upper 150 m of the water column, but some hauls in deeper waters were also made. In addition , when the fish were detected in shallow waters (less than 30 m depth), we used samples from commercial boats, purse seiners operating at the same time that the surveys, due to the impossibility of using the pelagic trawling. Each haul lasted for about 30 minutes.

From each haul, 10 mackerel stomachs were randomly selected. If there was any evidence of predation during the haul the predator was not considered and, whenever possible, another specimen of the same length range was taken. For each fish predator, the following were noted: total length (rounded down to the nearest cm), sex, maturity stage and stomach fullness (with food, empty or regurgitated).

Stomach analysis

The fresh stomachs were analyzed within one hour after being captured, and were kept cool (< 8 °C) prior to the investigation. The volume of total stomach contents (cc) was measured using a trophometer, a calibrated instrument consisting of several different-sized half-cylinders built into a tray, so that they formed horizontal cylindrical moulds (Olaso 1990; Olaso et al*.* 1998). Prey were identified to the lowest taxonomic level for fish, crustaceans and cephalopods, whereas invertebrates were classified to higher family or order to account for differences in taxonomic resolution between the sampling periods. For each prey type the following data were taken: the percentage of stomach volume, the state of digestion (1 intact. prey: 2 partially digested prey: 3 very digested and skeletal material), and number of specimens. Fish, decapod crustaceans and cephalopods were measured to the mm. Eggs of fish species in stomach were enumerated. After obtaining the total volume of the contents, these were placed in a Petri dish and examined under a dissecting microscope. Each prey item was classified to the lowest practical taxonomic level. The relationship between estimated volume and actual weights of the stomach contents was as described in Olaso (1990) derived from a potential model (a=0.932735, b=0.99324, r^2= 0.99; p<0.01).

Most of the eggs found were of mackerel, although there also were eggs of horse mackerel, anchovy and pilchards (very few eggs in these two last species). We know that most species produce fish eggs between 0.8 and 1.6 mm in diameter, average is 1.2 mm ± 0.12 (Worley, 1933), and that the egg mackerel diameter is between 1 and 1.38 mm (Russell, 1976). In order to consider the number of eggs found in each stomach, we have considered that the average diameter of eggs is 1.2 mm, and considering that the eggs are spherical, we have applied the formula of Archimedes on the volume of the sphere, (4/3)*pi*r^3, and consequently an egg is 0.00090478 cc. Transformed to weight, an egg is 0.0008486 g (1 g = 1105 eggs). Mackerel eggs were subsampled as number of eggs per g. By multiplying the wet weight of mackerel eggs contained in each stomach by the number of eggs per g, the total number of mackerel eggs in each stomach was estimated.

Data Analysis

The juvenile (21 - 29 cm) and adult mackerels (30 - 48 cm) were differentiated in all analyses. The methods used to assess the relative importance of individual prey taxa were the frequency of occurrence percentage, FO%, volume percentage, V%, and weight percentage, W% (Hyslop, 1980). The stomach contents were expressed as a percentage of the body weight (BW%), which allowed a comparison of the quantities of the prey in the *S. scombrus* stomachs of various sizes. This was achieved by applying the relationship between the body weight and the total size using the potential model $W = aL^b$ (W = total weight in g and L = size in cm) with a = 0.00669 and b = 3.01 (Villamor, IEO, Santander, Spain, pers. comm.). We calculated the weight of each predator caught during the surveys.

Food daily ration

To study the daily feeding of *S. scombrus*, the percentage of empty stomachs and the %BW index in periods of six hours were considered separately (e.g. 0 - 6, 6 - 12, 12 - 18, 18-24). We considered the application of a method to evaluate gastric evacuation with limited food data for *S. scombrus*, Eggers (1977). This model uses the mean quantity of food in the stomach throughout a 24 h period, and the daily total ration corresponds to the sum of the time intervals; in a more simplified way the consumption, *C*, in 24 hours is $C = F_{24} \times R$, with F_{24} being the mean of the stomach repletion index in 24 hours, and *R* the evacuation rate. *R* was not determined experimentally, since the existing formula $R = 0.0406\, e^{0.111T}$ was used (Durbin *et al.* 1983), where *T* is the temperature.. In the Cantabrian Sea continental shelf, the temperature in the upper part of the column ranges (10 – 50 m) in April between 2000 – 2004 was 12.75 º ± 0.398 (Lavin *et al*., 2003). The rate of digestion that were used was related to this water temperature, but do not have any effect of predator size; therefore *R* = 0.1671. This formula has been employed for a large variety of marine fish that eat small easily digestible preys (e.g. worms, crustaceans and diatoms).

F_{24} is expressed in %BW/hour and wet weight average/hour. We used %BW/hour to avoid the effect of predator size on the rate of gastric evacuation and to consider the changes that occurred in the feeding habits with growth. In addition, we used the wet weight average/hour to calculate daily comsumption in weight eggs: C_{Wegg}

$C_{Wegg} = F_{24} \times R \times W\%_{egg} / 0.00090478$, with C_{Wegg} being daily comsumption of eggs in weight , and W% the weight percentage of mackerel eggs. We changed the daily ration in egg biomass to a daily ration in egg numbers multiplying C_{Wegg} by the number of eggs per g.

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We also considered the daily proportion of eggs consumption as a percentage of body weight. Then, incorporating the biomass estimates for mackerel in North of Spain from 2003, and the number of incubation days for mackerel eggs in 2001, we calculated the total weight of eggs consumed to $Ct = Bg \times Cw \times I$.

This estimate of egg biomass consumed was applied to the biomass estimates of eggs spawned in the North of Spain in 2001 to obtain a percentage of the total mackerel eggs cannibalizeds. This was an approximation to obtain a preliminary estimate until the abundance (length structure) of mackerel in the study area during the spawning season in 2001 be available.

RESULTS

Mackerel diet and eggs stomachs

A total of 1305 stomach contents of Atlantic mackerel were analyzed. The Table 1 summarizes mackerel diet at spawning time in years 2000 – 2003. In the juveniles almost half of the prey correspond to small crustaceans (44%), the rest being gelatinous preys and eggs and larvae of fish; most of the eggs correspond to mackerel. In the adults the importance of gelatinous prey increases while the importance of crustaceans and fish prey decreases; as in the case of juveniles most of eggs are of mackerel (13.5%), being also horse mackerel eggs of some importance (7.2 %). The feeding intensity in the adults is almost the half that in the juveniles.

In the juveniles the average number of mackerel eggs per stomach was 222, and in adults 277. Every year appeared stomachs with more than 1000 mackerel eggs in a single stomach, and the largest recorded number of mackerel eggs in a single stomach was 6332 in juveniles and 5526 in adults

The analyses of mackerel stomach contents have indicated that they cannibalise its own eggs in the four years of sampling, although there are annual variations: the eggs appear in more than 70% of the stomachs contents in 2001 and 2002, that percentage decreases in 2003, whereas in 2000 they have little incidence (Table 2). Regarding the percentage of empty stomachs the minimum was found in 2001 (9.1 %), while the maximum was found in 2002 (44.1%).

Daily feeding pattern

With relation to the time of day, we appreciated that there are stomachs with mackerel eggs during the 24 hours, but the number of stomachs with mackerel eggs is smaller during the night, while between noon and midnight more than 50% of the stomachs contain mackerel eggs.

In the juvenile predators the largest vacuity index occurs during the night (66%), when it is also found the minimum mean stomach content in weight (Table 3). From dawn the percentage of empty stomachs decreases, increasing simultaneously the average stomach content. From dusk twilight to midnight we found all the stomachs with more food.
The opposite happens in the adult fish, in which during the night the percentage of empty stomachs is at its minimum (Table 3). There seemed to be a daily pattern of percentage vacuity, decreasing during the night when the fish ate more, and increasing during the day when feeding whether ceased completely or the fish fed at intervals (?).

Daily rations and annual food consumption

The rate of gastric evacuation (*R*) was estimated as 0.1671 g/h, by extrapolation from the formula of Durbin *et al.* (1983) at a temperature of 12.75 ºC. The values of mean repletion, including the fish with empty stomachs and expressed in %BW, were used to estimate the mean feeding rate for periods of six hours during 24 h. The estimates of the daily ration for Eggers method are summarised in Table 3, and they show that the ingestion estimates in each interval fluctuated considerably, showing both positive and negative values. The daily ration estimates obtained were 3.089 ± 0.675 % BW in the juveniles and 1.559 ± 0.437 % BW in the adults.

Regarding daily egg consumption in number of eggs, in the juveniles we estimate 885 mackerel eggs and 73 horse mackerel eggs; while in the adults they were 824 mackerel eggs, 438 horse mackerel eggs, 3 pilchard eggs and 1 anchovy egg. The daily mackerel egg consumption in body weight was estimated in the juveniles, 0.85 % BW and 0.33% in the adults.

DISCUSSION

Daily comsumption estimation

In this experience we find a high incidence of egg cannibalism by mackerel (*Scomber scombrus*) on the spawning grounds in the North of Spain. This results are new in the southern component of Northeast Atlantic mackerel. Egg cannibalism by mackerel (*Scomber scombrus*) was found to occur during the spawning, and we thought that this work is a good opportunity to make a general estimation of mackerel egg consumption, since there is very little knowledge about interannual variation in both the magnitude and the spatial structure of mackerel egg production.

The Egger`s model used assumes that the weight of the stomach content does not change significantly between the beginning and the end of the study period. In other words, the ingested food is constant in time and therefore the method can underestimate the daily ration if a feeding rhythm exists. The values of daily consumption in juveniles (3.1 % BW) can be considered as an amount enough to guarantee the energetic expenses of metabolism energy, growth and locomotion; but in the adults, 1.6 % BW, the feeding intensity is small. In theory these estimates are smaller than the forecasts of Priede & Watson (1997) on the food intake; since they consider that approximately 3% of body weight per day is required to maintain body weight and spawning.

Consequently, the Egger model was used given the lack of data in some time intervals of 3 hours of the daily cycle, we decided to add the data in intervals of 6 hours. We considered that 6 hours is time enough to develop this work of egg predation, since the capsule of a fish egg is relatively resistant to digestion up to 12 h. (Daan *et al*., 1985). However, Hunter & Krimbell (1980) reported that anchovy digest anchovy eggs in about 3 h. We have not estimated the larval consumption because the digestion rates for fishes feeding on larvae are very fast, 15-30 minutes (Hunter & Kimbrell, 1980; Christensen 1983).

Mackerel egg mortality by cannibalism

This preliminary paper is going to consider a large series of assumptions to be able to determine roughly the impact that could produce the egg cannibalism of mackerel (i.e. the annual variations are not considered). We are conscious of the important limitations that we have and that these can produce great bias in the final results. In the parameters in which we needed to make assumptions, we used verified measures. For example it was assumed that all the eggs had a size of 1,2 mm (in bibliography 1.1 mm), and its number by gram was a little inferior to the considered by other authors.

Acoustic estimates of mackerel abundance (numbers) and biomass from the study area in 2003 were obtained after applying the methodology described in Carrera et al. (2000). Previous biomass estimates from acoustic surveys since 1999 are available but we have not been able to obtain the information on length structure at the moment of writing this contribution. The biomass estimates in 2000, 2001, 2002 and 2003 were: 706000, 399000, 1383000 and 1137283 tonnes respectively. In 2002 and 2003 the target strength changed for mackerel (TS from –82 to –88) as recommended by the Planning Group on Aerial and Acoustic Surveys for Mackerel. The surveys since 1999 to 2001 used the old target strength for mackerel (-82) and the mackerel acoustic data was not revised with the new target strength (-88) (ICES, 2004). On the other hand in 2001 was carried out the triennal egg surveys for mackerel and horse mackerel, along the Northeast Atlantic. The total egg production estimated for mackerel in the study area was: 28.31 x 10^{13} eggs (CV: 16.53%) which corresponded to a spawning biomass of 371279 tonnes (CV: 20.7%) (ICES, 2002). We assumed for every years the estimations of abundance of the stock mackerel 2003, and the number of eggs of mackerel obtained in 2001 by the method of egg production, since are the only data available at this moment.

To calculate the total amount of eggs consumed, it is first necessary to estimate the proportion of the mackerel stock that preys on eggs, and for how long this predation takes on. In the North of Spain is around 85% of total mackerel estimates, 2707497871 juveniles and 1971906768 adults in 2003. If we assume that all mackerel preys on its eggs, then multiplying the specimen estimates by the daily ration as number of mackerel egg consumption estimate (885 in juveniles and 824 in adults), we obtain the number of eggs of mackerel cannibalized by the southern component of the Northeast Atlantic Stock per day. The spawning season lasts about 100 days but individual fish probably spawn over a period of 60 days (Priede & Watson 1993, Solá et al., 1990). We considered that the spawning peak is in April (Comm. Pers.), and multiplying by 30 days we have estimated the number of cannibalized mackerel eggs each year. On the other hand, we know that incubation time is 5 or 6 days (Lockwood *et al*, 1977), therefore the rest of the eggs stages are also available to be eaten. Then we considered that the total number of eggs is that obtained by 2001 egg production methods multiplied by ten. Moreover, we have to take into account that the estimated abundance of eggs at sea (considering all the egg stages at the same time) is probably overestimated. We have the abundance of eggs in stage I, but we do not know with certainty the egg mortality rate by stage or by day, which probably will be available in the next future. In this way we have assumed a rather low total egg mortality through the different stages in order to be more cautious for the estimation of cannibalism rate. If we compared the number of eggs depredated with the egg total number estimation, the mackerel juveniles would have consumed 2.99 % of the total mackerel deposited, and the mackerel adults 2.03%.

Altogether, the number of mackerel eggs eaten by mackerel at the spawning period (April) was a 5% of the total egg production of the mackerel stock spawning in this area. This paper is a first approximation to the total mortality rates of mackerel eggs, since the total mortality would also include the effect of all predators (Rijnsdorp & Jaworski, 1990), and the eggs of fish are vulnerable to small invertebrates, fishes and other vertebrates (Hunter, 1984; Bailey & Houde, 1989). The recruitment variability is the central problem of fishery science and a major source of uncertainly in management science (Sissenwine, 1984). About 50% of the variability in the Atlantic mackerel recruitment may be explained by means of environmental variables, such as turbulence (Borja *et al*., 2002). However, predation appears to be the principal factor to generate high mortality rates during the earliest eggs stages. In this paper we have displayed data that allow us to roughly estimate the mortality produced by mackerel cannibalism on its own eggs, and we suspect that cannibalism might be a major source of mortality for these eggs. We suggest here that the pattern and magnitude of total egg production on Northern Spain is highly variable from year to year. In the short term, it must of be considered of high-priority to advance in the resolution of egg determinations, and to try to differentiate as much as possible the mackerel egg development stages (Bunn *et al*., 2000).

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Tables

Table 1. Prey groups found in stomach of mackerel (*Scomber scombrus*) in spring surveys (2000 - 2003) off northern Spain (%V, percentage by volume, V% BW, Volume percentage by body. wight. ± 95% of confidence limits.

	JUVENILS		ADULTS	
Prey	%V	BV%	%V	BV%
Crustacea	44.1	0.301	19.1	0.060
Amphipoda	+	+	+	+
Copepoda	5.7	0.043	9.3	0.027
Decapoda	29.5	0.193	6.2	0.082
Natantia	+	+	0.3	0.002
Anomura			0.2	0.003
Macrura			+	
Brachyura	4.02	0.021	1.8	0.005
Euphausiacea	7.8	0.060	2.36	0.009
Isopoda		+	+	+
Mysidacea	0.5	0.002	+	+
Crustacea undetermined	0.2	0.003	0.3	0.001
Stomatopoda		+	+	+
Cephalopoda	+	+	0.3	0.001
Plankton undetermined	4.3	0.022	4.47	0.012
Tunicata undetermined	16.6	0.112	36.4	0.116
Fish	34.9	0.295	39.8	0.175
Fish egg undeterminated	2.4	0.021	2.6	0.007
Trachurus trachurus egg	1	0.009	7.2	0.022
Engraulis encrasicholus egg		+	+	+
Sardina pilchardus egg		+	+	+
Scomber scombrus egg	23.7	0.199	13.5	0.033
Sardina pilchardus larval	1	0.007		+
Fish scale		0.002	0.1	0.001
TOTAL	100	0.731	100	0.363

Table 2. Number of stomachs sampled by year and time day by the juvenils (21 - 29 cm) and the adults (30 - 48 cm)

		YEAR			
JUVENILS		2000	2001	2002 #	2003
	EGG TAXA PREY	FO %	FO %	FO %	FO %
	Fish egg undet.	32.9		14.4	25.3
	T. trachurus egg	21.1	9.3	11.5	12.1
	S. scomber egg		81.4	76.0	37.4
	E. encrasicholus				
	S. pilchardus			4.8	
	Total stomach	95.0	50.0	155.0	158.0
	Empty %	25.3	14.0	41.3	22.8
ADULTS					
	Fish egg undet.	19.2	0.5	21.9	23.0
	T. trachurus egg	53.2	9.7	22.5	8.2
	S. scomber egg	0.1	70.5	73.5	29.5
	E. encrasicholus		1.8		
	S. pilchardus		3.2	0.6	
	Total stomach	192.0	239.0	286.0	130.0
	Empty %	26.6	9.2	44.1	36.2

		TIMES OF DAY (hours)			
JUVENILS		00 - 06	06 - 12	12 - 18 #	18 - 24
	EGG TAXA PREY	FO %	FO %	FO %	FO %
	Ffish egg undet.	15.4	14.1	35.3	1.5
	T. trachurus egg		12.5	12.6	14.9
	S. scomber egg	7.7	31.3	53.8	52.2
	E. encrasicholus				
	S. pilchardus				
	Total stomach	38.0	194.0	135.0	91.0
	Empty %	65.8	34.0	11.9	0.0
ADULTS					
	Fish egg undet.		14.7	21.6	9.9
	T. trachurus egg		30.0	22.2	14.1
	S. scomber egg	25.0	45.1	51.5	65.3
	E. encrasicholus			2.4	
	S. pilchardus		0.3	3.6	5.0
	Total stomach	22.0	415.0	220.0	190.0
	Empty %	9.1	2.9	24.1	36.3

Table 3 . Mean of food (% BW) presents in the stomach of *Scomber scombrus* stomachs (x/ ± 95% of confidence limits), and estimated mean amount of food ingested during each 6-h period. BW=body weight. % BW: oncluding the fish with empty stomachs.

STOMACH CONTENTS, INCLUDING THOSE WITH EMPTY STOMACHS						
	Nº of predators	Empty %	Mean ±95% C.L. (% BW)	Minimun (% BW)	Maximun (% BW)	Ingestion (%BW)
21-29 cm						
00 - 06	38	65.8	0.162 ± 0.140	0.075	1.738	-0.486
06 - 12	194	34.0	0.886 ± 0.237	0.075	5.851	1.304
12 - 18	135	11.9	0.761 ± 0.156	0.075	6.300	0.690
18 - 24	91	0.0	1.277 ± 0.309	0.054	6.018	1.580
30 - 48 cm						
00 - 06	22	9.1	0.693 ± 0.261	0.024	2.008	0.872
06 - 12	415	2.9	0.022 ± 0.034	0.019	3.548	-0.051
12 - 18	220	14.1	0.252 ± 0.052	0.020	3.707	0.270
18 - 24	190	36.3	0.388 ± 0.132	0.019	7.702	0.468