SCRS/2004/103

REPRODUCTIVE AND DISTRIBUTION PARAMETERS OF THE BLUE SHARK *PRIONACE GLAUCA*, ON THE BASIS OF ON-BOARD OBSERVATIONS AT SEA IN THE ATLANTIC, INDIAN AND PACIFIC OCEANS

Jaime Mejuto[1] & Blanca García-Cortés[1]

SUMMARY

On the basis of 81560 observations of <u>*Prionace glauca*</u> *carried out on board surface longline vessels between 1993 and 2003 in the Atlantic, Indian and Pacific Oceans, the basic reproductive parameters of this species are presented. Thirty-five percent of the specimens observed were females, showing a clear prevalence of males in the catches. The identification of 28733 females allow us to provide sex ratio data, both overall and at size, as well as the prevalence of females on the basis of different signs of fecundation. The results revealed important differences between zones-regions in terms of sizes, CPUEs and sex ratios. Of the total number of females observed, 50.34% showed signs of fecundation; of these 39.2% were found to be gravid and 11.1% exhibited mating injuries. Stages associated with reproduction were detected in most of the zones studied, although considerable differences were seen among zones-regions-seasons.*

*The mean litter size was estimated to be 37.1 pups, with an average FL size of 19.7 cm, with levels of development depending on the region. The significance of the relationship between female size and litter size was determined (No. embryos= -61.605 + 0.470403*FL female), (P < 0.01). A significant relationship (P < 0.01) between the size of the embryos and month-zone predictor variables was also established into each region. The models fitted explain between 22.2% and 71.7% of the variability in embryo size, depending on the region under consideration.*

RESUMEN

A partir de 81560 observaciones de <u>*Prionace glauca*</u> *obtenidas a bordo de palangreros de superficie entre los años 1993 y 2003 en los océanos Atlántico, Índico y Pacífico, se presentan parámetros reproductivos básicos de esta especie. El 35% de los ejemplares observados fueron hembras, indicando una clara prevalencia de los machos en la captura. A partir de la identificación de 28733 hembras se ofrecen datos de sex ratio (overall y por talla) y prevalencias de las hembras según distintos síntomas de fecundación. Los resultados sugieren importantes diferencias entre zonas-regiones en cuanto a sus tallas, CPUEs y sex ratios. El 50.34% del total de hembras observadas presentaron síntomas de fecundación, de las cuales el 39.2% estaban preñadas y el 11.1% presentaban heridas de los procesos de acoplamiento, detectándose diversos estados ligados con la reproducción en la mayoría de las zonas analizadas aunque con importantes diferencias entre zonas-regiones-épocas.*

*El número medio del tamaño de la camada se estimó en 37.1 crías, con una talla media de 19.7 cm FL, con diferente grado de desarrollo según la región. La relación entre la talla de las hembras y el tamaño de su camada fue significativamente establecido (No.embrios = -61.605 + 0.470403 * FL female), (P < 0.01. Fue también establecida dentro de cara región definida una relación significativa (P < 0.01) entre la talla de los embriones y las variables mes-zona. Los modelos ajustados explicaron entre el 22.2% y el 71.7 % de la variabilidad observada en la talla de los embriones, según la región considerada.*

KEY WORDS: blue shark, reproductive cycle, sex ratio, CPUE, long lining.

[1] Instituto Español de Oceanografía, P.O. Box. 130, 15080 A Coruña. Spain.

1. Introduction.

The blue shark *Prionace glauca* (PGO) belongs to the pelagic ecosystem and could probably be considered as one of the most successful species in this system. PGO has a broad geographic distribution, with preferences for tropical and temperate areas in the Atlantic (including the Mediterranean Sea), Pacific and Indian Oceans, most commonly found between 50º N and 50º S, however it has been known to appear at higher latitudes (COMPAGNO 1984).

Historically this species has been caught by sport and commercial fleets all over the world, although this fishery is believed to have become more intense starting in the 1960s as a result of the improved technologies used by the fleets and their expansion whereby they started targeting several species of tuna and tuna-like species. Although data on targeted fisheries is generally rather scarce, it would appear that the great historical catches of PGO have occurred mainly as by-catches of other species, since the economic importance of this species has been either limited to local level exploitation, or of relatively minor importance, up until recent decades at which point the globalisation of the markets aroused world-wide interest in the meat of this and other shark species and their derivatives. Therefore, the historical international catches are quite likely underestimated or unreported, for a number of reasons, such as the large amount of discards, which have generally been poorly documented.

The data available on the catch per unit of effort (CPUE) of several fleets in both number and biomass suggest that the abundance of this species in the pelagic system is high, equal or in many cases even higher than that of other large pelagic species of bony and cartilaginous fish. These would include species of tuna, billfish (including swordfish) and other large pelagic sharks. The high prevalence of this shark species in the catches of many of the oceanic fleets whose activity includes a wide variety of fishing gears in different fishing zones and seasons in fisheries carried out over the course of decades may be attributed to the great abundance of this species in the pelagic system and its probable high renovation rate, as has been corroborated by the observations of many fleets and available biological studies. Consequently, the broad geographic distribution of this species in the pelagic ecosystem in addition to its complex and efficient reproductive cycle are elements that have clearly been conducive to its success as a species and to its consideration as one of the key elements in the oceanic pelagic ecosystem.

Catches of PGO have been landed by the Spanish fleets probably for centuries, particularly in the regions of the South of Spain and the Mediterranean. This species must also have been caught on a smaller scale from as early as the 1950s to the 1970s. However, a substantial increase in the catches would have been expected in the early 1980s, coinciding with the deployment of the surface longline fleets in the oceanic zones (MUÑOZ-CHAPULI 1985, REY *et al*. 1988, MEJUTO *et al*. 1989, MORENO & MORON 1992, REY & MUÑOZ-CHAPULI 1992, BUENCUERPO *et al*. 1998), during which time the fleet targeting swordfish caught this species as a by-catch. At that time, PGO discards were estimated as being substantial and related to the limited on-board preservation systems as well as to the duration-catch per trip of the target species (MEJUTO & GARCES 1984; MEJUTO 1985).

However, in more recent times, the fleet has changed the methods used to preserve fish on board ship as well as its fishing strategy (MEJUTO 2000, CASTRO *et al*. 2000, MEJUTO *et al.* 2002, MEJUTO *et al*. 2003) so that during the 1990s and at the beginning of this century, the discards of the Spanish fleet have gradually declined to the point where they may be considered scarce or sporadic, since the market has placed an economic value on the meat of this species for human consumption, in addition to the use of other parts of the fish. This has given rise to the integral use of the catches which is probably proportionally greater than that of most bony fish destined for human consumption (MEJUTO *in press*).

Information on the reproduction of PGO in different oceans is relatively abundant and has recently been summarised and compared (NAKANO & SEKI 2003). Previous studies (CASTRO & MEJUTO 1995) have allowed us to advance in our knowledge of these reproductive parameters and compare them to data reported by other authors. However, the information from most of the available studies by the different authors is more often than not patchy and local in scope (NAKANO & SEKI o.c.).

The wide geographic distribution of the Spanish surface longline fleet and its scientific monitoring with on board observers have provided us with sporadic and specific observations of some shark species. On the basis of these observations, this document aims to supplement the information presented previously, offering broader spatial coverage, and focusing on the reproductive parameters of PGO observed in different zones of the Atlantic, Indian and Pacific Oceans.

2. Material and methods.

The biological observations were made on board commercial surface longliners targeting swordfish from 1993-2003. The observers had received previous training and the criteria used had been standardised. Since the biological observations of PGO were made sporadically in some of the sets, the areas, months and trips observed were not selected strictly adhering to a random design. However, the specimens chosen for sampling in each set were randomly selected.

The observations were carried out in areas targeted by the Spanish surface longline fleet and in no case did the observers prompt any changes in the commercial fishing strategy of the vessel. The areas examined were located between 40ºN-35ºS: 55ºW-15ºE in the Atlantic, between 5ºS-30ºS : 35ºE-75ºE in the Indian Ocean and between 25ºN-40ºS : 85ºW-135ºW in the Pacific Ocean. The observations were initially grouped into 5ºx5º squares. Subsequently, to accommodate the different analyses, the data were tentatively classified into 22 zones (figure 1) and also into 5 regions: North Atlantic Region (ATLN): zones 01,02,03,04,06,91,92,93. Central Atlantic Region (ATLC): zones 07,08,09,10. South Atlantic Region (ATLS): zones 11,12,13,15. Indian Ocean Region (INDI): zones 52,53,54,55. Pacific Ocean Region (PACI): zones 40,44.

The size of the sharks caught and the embryos found to be present in females were measured in a straight line to the lowest cm, from the anterior end of the head to the fork of the caudal fin (fork length, FL cm). This type of FL size was considered to be the most appropriate since the total length (TL) (COMPAGNO 1984) may be affected by the position of the caudal fin and it is more difficult to standardise, particularly in shark species whose caudal fin is rather stiff and hard to handle, such as the Alopiidae and Lamnidae sharks, among others. Moreover, the FL measurement offers greater operational advantages on board commercial vessels where limited space is available. In addition, FL is the standard measurement adopted by the ICCAT for most of the species other than billfishes. For this reason, it would also be advisable to adopt the FL size as a standard measurement for sharks under the ICCAT protocols.

The sharks were sexed visually, on the basis of the presence or absence of claspers on the pelvic fin, with special care being taken by the observers on examining juvenile specimens where an observation at first sight might lead to sexing errors because juvenile males could mistakenly be classified as females, since their claspers may not extend beyond the posterior edge of the pelvic fin.

Of all the females sexed, most were able to be analysed specifically to detect internal or external signs of fecundation. The external signs of fecundation were based on the identification of the external tooth cuts (mating injuries) inflicted by the males on females during the mating process (PRATT 1979) and no embryos were detected into the uteri. The internal signs of fecundation in females were defined by dissection and internal observation to detect the presence of embryos in the uteri, leading, therefore, to their classification as pregnant females. On some occasions, when embryos were found, it was possible to count the number of embryos in the litter and/or measure them to estimate their stage of development.

The FL size of the individuals caught during the fishing activity was later grouped into 5 cm classes. The FL size of the embryos was analysed using 1 cm classes. In both cases the size classes were defined using their respective lowest cut-off points.

The mean values of the number of embryos per female (litter size) and the mean size of the embryos per female, zone and region were calculated. GLM procedures (Statgraphics Plus 5.1) were applied by region to the observations to explain the variability in the mean embryo size in relation to the variables of month and zone.

The sex ratio values – by zone and region- were calculated as the percentage of females present relative to the total number of specimens sexed. The sex ratios were obtained for all the sizes combined –overall sex ratio (SRo)- as well as for sex ratio at size (SRs).

The respective yields per thousand hooks let out in the sets observed or catches per unit of effort (CPUE), by sex and combined sexes were calculated for the purpose of identifying the possible areas of PGO concentration. The CPUE was calculated, in both kg of dressed weight (CPUEw) and number of fishes (CPUEn), as well as for each size categories: Juveniles CAT1= 50-120 cm, sub-adults CAT2= 125-165 cm, adults CAT3= 170-200 cm, large adults CAT4= 205+ cm.

3. Results and discussion.

Table 1 presents a summary of the number of specimens observed by zone and region in addition to some of the general variables related to the presence of females in the different stages. A total of 81560 fishes averaging 178 cm FL in size were identified and sexed during the 1993-2003 period in all the areas (figure 1). Of this total, 50542 specimens pertained to the Atlantic Ocean (62%), 7779 specimens to the Indian Ocean (9%) and 23239 individuals to the Pacific Ocean (28%). In the Atlantic Ocean the total number of fishes sampled per region can be broken down as follows: 11352 in the ATLN (13%), 29889 specimens in the ATLC (37%) and 9301 specimens in the ATLS (11%).

Of the total number of fishes sampled, 28733 specimens were identified as females (35.23%), 18176 of which belonged to the Atlantic Ocean (63%) (ATLN = 4202, ATLC = 11733, ATLS = 2241), 1656 females were found in the Indian Ocean (6%) and 8901 in the Pacific (31%).

Out of the total number of 28733 females observed, 23244 specimens were also specifically analysed to check for internal or external fecundation signs. The results were 11702 females with internal or external fecundation signs (50.34%), of these 9110 (39.19%) contained embryos (pregnant females) and 2592 (11.15%) exhibited external mating injuries.

A comparison of size distributions in cumulative % of the specimens observed in each region for the two sexes combined and females alone, respectively, highlights the difference between the size distributions in the 5 regions, for both the two sexes combined and females alone (figures 2 and 3). The smallest specimens –sexes combined- appeared in regions PACI, ATLN and ATLS, respectively and the largest sharks in regions INDI and ATLC, respectively. A similar conclusion was drawn after examining the size distribution of females alone. The mean size of the specimens caught fluctuated greatly in an analysis of the data on the basis of both zone and region (table 2). Taking only the Atlantic regions into account, the largest specimens were clearly observed in region ATLC, for both sexes combined and females alone and the smallest individuals in region ATLN. These size differences are probably related to the spatial segregation by size occurring in this species as a result of its migratory-biological cycle associated with environmental variables (biotic and abiotic), which is a pattern of behaviour that has been observed in other ocean pelagic species as well.

In all the regions the SRo was under 50% and the SRo for all the regions combined was 35%. The highest SRo values by region were found in ATLC, ATLN and PACI, respectively and the lowest figures came from regions ATLS and INDI, respectively (figure 4). In most of the zones the SRo values pointed to the predominance of males, to a greater or lesser extent, except in ATL02, ATL93 and ATL08 which showed SRo values of around 50% or slightly higher (figure 5). Nonetheless, similar to what has been observed in other large pelagic fishes evidencing spatial-temporal segregation by size and sex, the SRo value must be interpreted with caution, since it is affected by the size range included in the observations and therefore it is generally more advisable to base comparisons on the SRs.

The SRs, values by both region and zone are highly variable in pattern. The SRs by region suggest that there are broad fluctuations with different patterns and characteristics depending on the region being analysed (figure 6). These SRs patterns by region, however, tend to smooth the considerable variability observed in the SRs by zone, even in zones located within the same region, although there were also detected some similarities between zones (figure 7). These SRs patterns by zone are influenced by the spatial definition used, and are also very likely affected by the temporal variability which has not been taken into account in this analysis. Moreover, the different SRs by zone may also be affected by the depth-dependent segregation of males and females, since this effect may have a greater or lesser consequence, depending on the seawater temperature in the zone (NAKANO & SEKI, o.c.).

The different SRs patterns observed would also be explained by the nominal CPUE data collected in each zone. The CPUEs (combined sizes) by zone, sex, or sexes combined, generally suggest a greater prevalence of males versus females in this surface longline catch, particularly if we consider the CPUEw of most of the zones (figure 8). The zones having the highest CPUEn were found in ATL01, ATL02, ATL03, ATL91 and ATL92 of region ATLN and in zone ATL15 of region ATLS. This high CPUEn was often due to the greater prevalence of males, as specifically observed in zones ATL15, ATL91 and ATL92. The CPUE data by size class and sex would point to a complex geographic distribution of specimens by size and sex, with a surprisingly greater prevalence of males in some zones, which could be related to mating processes. Furthermore, the data suggest that there is widespread cohabitation among the different size groups in most zones, with an alternating predominance of some of the size groups depending on the zone. Nevertheless, the comparison of the CPUEs among zones must be interpreted with caution, since the targeting intensity of the fleet may not be the same in all the zones. In this sense, in some zones-seasons the fishery may target the prevalent species -swordfish and blue shark-, or it may even focus preferentially on the latter species. Therefore, a comparison of the CPUEs by sex within each zone would appear, a priori, to be more appropriate than the comparison of nominal CPUEs among zones.

Pregnant females were large in size, exceeding the mean sizes of females with mating injuries, which might imply that many of the females close to adulthood had already mated, but had not yet produced embryos (figure 9). Although there have been occasional records of extremely small-sized pregnant females (some records of around 110 cm), small females with embryos begin to appear in significant numbers when they reach roughly 150 cm. Fifty percent of the size distributions of these females generally fall within the 180 to 215 cm size class, depending on the zone. The largest gravid females measured were between 265 and 290 cm, depending on the region. Table 2 gives the mean sizes of females identified as gravid and their respective confidence intervals (95%), by zone and region.

Figures 10, 11 and 12 indicate the % of females showing fecundation signs (internal or external), the % of gravid females (with embryos) and the % of females with mating injuries only, relative to the total number of females observed by zone and month. In region ATLN a wide variety of situations were found according to the zone-month observed (figure 10). In zones ATL01 (not already included in the figure) and ATL02 it was unusual to see females with fecundation signs and, when they were sighted, it was only during occasional months. In zone ATL02 some injured females with mating signs appeared only in the month of August. In contrast, however, in zones ATL03, ATL06, ATL91 and ATL93 high percentages of females with fecundation signs were observed, particularly from March to April and from July to November in zones with a prevalence of females exhibiting internal or external fecundation signs. The prevalence of gravid females is higher in some months-zones while in other months-zones it is the presence of females with mating injuries.

In region ATLC there is a strong percentage of females with fecundation signs across all the zones (figure 11). Moreover, in most of the zones-months, gravid females predominate over females with mating injuries, except in some zones-months, generally during the first half year, where the opposite occurs. A similar conclusion can be drawn from region ATLS, particularly zones ATL11 and ATL12 from August to November and in zones ATL13 and ATL15 in some of the months analysed.

In region INDI there is a high % of females with fecundation signs in most of the zones, especially during some months (figure 12). The April-November period revealed a greater presence of gravid females in most of the zones. In region PACI, zone PAC40 counted a high % of females showing signs of mating, which would clearly suggest that seasonality exists between the mating period (June-September) and the pregnancy period (October-February).

Data regarding the % of pregnant females relative to the number of females analysed for the entire Atlantic Ocean and month pointed to seasonality. The highest percentages appeared from May-September (figure 13). These results resemble those found in region ATLC, since a great many observations were carried out in this region, conditioning the final outcome when the three Atlantic regions were combined. However, within the Atlantic regions, different multimonthly patterns were observed. In region ATLC the greatest prevalence of gravid females occurred chiefly from April to September. Region ATLS also gave rise to relatively high prevalence between the months of July and September. The prevalence of gravid females in region ATLN, on the other hand, was generally much lower, with the prevalence peaking during two periods, February-March and August-September.

It was possible to count the mean number of embryos per gravid females (litter size) in a total of 5068 females. The mean values fluctuated between 25 and 43 embryos depending on the zone, resulting in a mean value of 37.1 embryos per female for all the zones combined (CI95%:36.7-37.5), (table 3, figure 14). These results confirm the findings of previous studies for the same fleet (CASTRO & MEJUTO o.c.) and fall within the ranges reported previously by several authors (NAKANO & SEKI o.c.).

The mean embryo size of the gravid females would suggest that there are substantial differences between zones and regions (table 4, figure 15). The mean value obtained for all the zones combined was 19.7 cm FL (CI95%:19.5-20.0) (figure 16).

For the purpose of facilitating a global interpretation of some of the above results, the data are presented by region (figure 17). In region ATLN only 27% of the females examined presented fecundation signs (internal or external), roughly 7% of which had mating injuries and only 19% of the females analysed contained embryos (mean litter size =39), although with a relatively high mean size (mean FL= 23.6 cm).

In region ATLC 83% of the females analysed presented fecundation signs (internal or external), only 12% of which exhibited mating injuries and approximately 70% were gravid (mean litter size= 37) with embryos in early stages of development (mean FL= 14.9 cm).

In region ATLS 38% of the females studied exhibited fecundation signs (internal or external), 11% with mating injuries and 27% had embryos (mean litter size =34) with a relatively high mean size (mean FL= 27.1 cm).

In region INDI 70% of the females analysed exhibited fecundation signs (internal or external), 41% of which had mating injures and only 29% of the females examined were found to have embryos (mean litter size =38) with a relatively high mean size (mean FL= 26.2 cm).

In region PACI only 12% of the females analysed presented fecundation signs (internal or external), 7% of which showed mating injuries and only 6% of the females examined had embryos (mean litter size =34) with a relatively high mean size (mean FL= 23.0 cm).

The mean size of the embryos of a total of 5092 females was measured. Mean size by zone and region was obtained (table 4) as well as the mean embryo size by region and month (figure 18). In region ATLN the largest sized embryos, around 30 cm FL or greater, were seen between February-June, whereas the smallest sized embryos were observed between July-September, and tended to increase during the following months. The pattern seen in this region would point to somewhat of a seasonal cycle in embryo size.

In region ATLC the mean embryo sizes were overall relatively low when compared with other regions, with values of generally under 20 cm FL during all the months studied and minimums in March-April. This would imply that this region is probably used mostly for gestation but not for parturition, at least in the oceanic areas under observation.

In region ATLS the mean embryo sizes were overall relatively high especially during the months of January and from June-November, reaching values of around 40 cm FL. Minimum size values were found between February-May, which would also point to a seasonal cycle.

In region INDI the mean embryo sizes were overall relatively high from July to November, attaining values of around 30 cm FL. Minimum values were recorded between March and June, also suggesting a possible seasonal cycle.

In region PACI the mean embryo size values were generally low, roughly 20 cm FL, except during the month of January.

On the basis of the mean embryo size by quarter, in the Atlantic zones the females would be close to parturition in the first or second quarter in region ATLN and in the third and fourth quarter in region ATLS. In region INDI the highest mean embryo sizes were attained in the third quarter, which might mark the time of birth, and in region PACI the animals would be expected to give birth preferably during the second quarter.

To assess the significance of the predictive factors month and zone relative to the mean embryo size, GLM procedures were tested within each region and for all the Atlantic regions combined. The results point to a statistically significant relationship between the size of the embryos and both predictor variables at the 99% confidence level in almost all regions, except ATLS where the effect of the zone was not statistically significant at the 90% or higher limit. However, when the GLM was conducted for the total observations made in the Atlantic (ATLN+ATLC+ATLS) a statistically significant relationship between the size of the embryos and both predictor variables at the 99% confidence level was also obtained. The R-squared statistic indicates that the models fitted explain 51.7%, 22.2%, 64.4%, 31.4%, 71.7% and 61.3 % of the variability of the embryo size, for regions ATLN, ATLC, ATLS, ATL (all), PACI and INDI, respectively (figure 19).

With a view to verify the proposed relationship between female size and their litter size (CASTRO & MEJUTO o.c.) a linear model was applied to the Atlantic data: No. embryos= -61.605 + 0.470403*(FL female). The ANOVA indicates that there is a statistically significant relationship ($P < 0.01$). The correlation coefficient (0.5983) indicates a moderately strong relationship between the variables. The R-squared statistic indicates that the model as fitted explains 36% of the variability in litter size (figure 20).

A total of 138839 embryos (69891 males and 68948 females) belonging to 3729 pregnant females were sexed in all the zones combined, resulting in an embryo sex ratio of 0.4966, very close to the theoretical value of 0.50 as indicated for this species by several authors (CASTRO & MEJUTO o.c., NAKANO & SEKI o.c).

A controversial issue is the definition of the reproduction and gestation period in females, covering the mating processes up until birth. Obviously, it is not easy to pinpoint the period between mating-gestation-birth. However, the definition of the period between mating and the presence of embryos it could help us to suggest a minimum period around which different alternatives could be estimated and tested. On the basis of female size data in all of the Atlantic zones combined where signs of fecundation -internal vs. external- have been observed (FL_pregnant vs. FL_ mating), (table 2), the difference between their respective mean sizes weighted with their respective number of observations would be estimated at roughly 19 cm FL between both sets of females. This mean difference would be around 13 cm FL if we use the data for all the zones combined. Taking into account several growth equations defined for different size types for the Atlantic (sexes combined) and Pacific (females), (NAKANO & SEKI o.c.,), and transforming them into FL by means of the appropriate conversions (NAKANO *et al.* 1985, CASTRO & MEJUTO o.c), we would find that period of time expected to pass between the mean sizes of both sets of females would be estimated at between 1.1 and 1.2 years if we use only the observations from the Atlantic, and between 0.8 and 1.1 years if we use all the observations combined. However, we must remember that the total number of gravid females observed did not contain embryos in a predominantly advanced developmental stage in all zones (table 4), so an additional brief period of gestation must be estimated until the embryos reach a viable birth size.

Taking into consideration the information available on mean embryo size per month from the North and South Atlantic regions (ATLN and ATLS) and considering some monthly periods with increased size trend between August-December and March-November, respectively (figure 18), the results suggest very similar monthly increases in mean embryo size between both regions, with growth rates of 4.15 and 4.58 cm per month, respectively. The longest series from the ATLS region points to a monthly growth increase explained by the linear equation FL embryos (cm) = 3.7393 + 3.394 * months (R^2 = 0.769). This equation would allow us to estimate that birth size could be attained after 10 or 11 months of embryonic development. However, the estimated growth rates based on these monthly mean values may be underestimated in slope because no cohorts or individually tagged embryos were actually tracked. The possible entry into the area-month under observation of new pregnant females carrying small embryos could produce a systematic underestimation of the growth rates obtained. In such a case, the real growth rates of the embryos could be higher and the time needed to reach the viable birth size shorter than previously defined.

The higher prevalence of males in the catch in most of the zones is not easy to explain in a population with a sex ratio of embryos and in pups at birth amounting to 1:1. The possibility of a differential natural mortality by sex might be able to partially explain these differences observed in the catches by sex. However, other more plausible causes must not be ruled out, namely the reduced catchability of females in the surface longline gear, owing, among other causes, to the different depth distribution of the specimens depending on the size, sex, temperature and area (NAKANO & SEKI o.c.). However, diametrically opposed phenomena have also been reported. Females appear to be distributed somewhat closer to the surface than males in some tropical zones (HAZIN *et al.* 1994),which would a priori make them more vulnerable to being caught with this surface gear and local abundances of a seasonal nature in temperate waters have been reported with females dominating the regions in the vicinity of the British Islands (STEVENS 1974, VAS 1990).

The total data obtained would suggest that the behaviour of this species in the Atlantic is complex and would encourage future studies of a more specific nature, focusing on shedding light on some of the questions outlined in this paper. It will be necessary a revision through the available records in a more in-depth study to detect possible outlayers and probably try out new definitions of the zones-regions depending on the most important environmental conditions, such as temperature in the respective areas. Nevertheless, on the basis of our findings here, we have been able to draw general and preliminary conclusions, that will serve as a starting point.

The zones-seasons involved in the reproduction processes of this species appear to be broad and much less restrictive that the ones first considered on the basis of other data sources from more limited scope. The results from the Atlantic would suggest that in some of the temperate zones of the North Atlantic (ATLN) there is an abundance of juveniles and sub-adults of both sexes, although female adults also inhabit the area. Only a small portion of the females show fecundation signs, with pregnancy prevailing over mating injuries. Males were also found to be plentiful and, on occasion, clearly dominant. While, in these zones only some females were gravid, they did however contain embryos in a relatively advanced stage of development. In the warm waters of the Central Atlantic (ATLC), on the other hand, adult specimens were observed as well as large adults with a high

SRo, and an extremely high percentage of females with fecundation signs dominated by gravid females although with relatively small embryos. The South Atlantic zones (ATLS) exhibited a wider diversity of results, perhaps owing to the fact that some of the observations cover warm water zones while others include temperate waters, with oceanographic regimes that differ greatly between East and West. This oceanographic situation did not generally occur in the ATLN observations since data on the warm water areas of the West were not available. However, the situation found in region ATLS could be described as midway between the two defined above, although, it is in fact quite similar to what occurs in the North Atlantic zones in some aspects.

Therefore, ATLN and ATLS are regions having a lower prevalence of females in stages of reproduction than the region ATLC, although with large-sized embryos and the presence of specimens from both sexes with a possible higher number of juveniles and sub-adults than in region ATLC. The warm zones analysed in region ATLC appear to be used preferentially for gestation, and not parturition. If this were found to be the case, in view of the size of the embryos observed in the different regions, the final processes of embryo development and birth, at least for a part of the female population, would probably take place in the temperate water zones of the North or South, where food is more readily available. This would account for the wide-ranging and complex migratory pattern observed in this species. On the basis of this thesis, the animals might carry out two migrations in opposite directions during the mating-gestation or gestation-parturition processes. However, other zones should not be ruled out as alternative places for parturition in some coastal areas of region ATLC, as previously suggested in the Gulf of Guinea where a gradient of the embryos size from West to East was reported (CASTRO & MEJUTO o.c.) and corroborated in this paper, with its highly productive surface layers of temperate water linked to the coastal upwelling areas about which we have no available data.

An analysis of this complex pattern of behaviour could be based on different of studies, such as a good description of the different fisheries and their biological observations, tagging-recapture data from the programs that have been underway for decades, multimonthly electronic tagging, etc. In addition, the presence of concentrations of juveniles in highly productive temperate zones with an abundance of available food, as occurs in some of the North Atlantic regions, will help support this thesis. In this way tagging-recapture data by sex, size class and time periods will be able to help clarify some of these behavioural questions in the future from join research projects (MEJUTO *et al*. in press).

Acknowledgements.

We would like to express our gratitude to the crews of the Spanish surface longliners for their collaboration and voluntarily allowing scientific observers on board their vessels for scientific purposes. We are especially grateful to the many scientific observers who contributed to the processing of the data used in this paper. Special thanks go to the I.E.O staff involved on this tasks into the projects SWOATL, SHKLL and SHKLL03, between 1993 and 2003, in alphabetic order, Isabel González, Ángel Lamas, Manuel Quintans and Ana Ramos-Cartelle.

References.

BUENCUERPO, V., S. Ríos, J. Morón. 1998. Pelagic sharks associated with the swordfish, Xiphias gladius, fishery in the eastern North Atlantic Ocean and Strait of Gibraltar. Fishery Bulletin 96(4):667-685.

CASTRO, J. A., J. Mejuto. 1995. Reproductive parameters of blue shark, *Prionace glauca*, and other sharks in the Gulf of Guinea. Mar. Freshwater Res., 46:967-73.

CASTRO J. , J. M. dela Serna, D. Macías, J. Mejuto. 2000. Estimaciones científicas preliminares de los desembarcos de especies asociadas realizadas por la flota española de palangre de superficie en 1997 y 1998. ICCAT. Col. Vol. Sci. Pap. Vol. LI:1882-1894.

COMPAGNO L. J. V. 1984. Sharks of the world. FAO species catalogue. Carcharhiniformes. FAO Fisheries Sinopsis N 125. Vol 4. Part. 2.

HAZIN F. H. V., C. E. Boeckman, E. C. Leal, R. P. T. Lessa, K. Kihara, K. Otsuka. 1994. Distribution and relative abundance of the blue shark, *Prionace glauca*, in the southwestern equatorial Atlantic Ocean. Fish. Bull.92(2),474-480.

MEJUTO, J. 1985. Associated catches of sharks, *Prionace glauca, Isurus oxyrhinchus* and *Lamna nasus*, with NW and N Spanish swordfish fishery, in 1984. ICES C.M. 1985/H:42

MEJUTO, J. in press. Preliminary relationship between the wet fin weight and the body weight of some pelagic sharks caught by the Spanish surface longline fleet. ICCAT. Col. Vol. Sci. Pap. (SCRS2003/085).

MEJUTO, J. 2000. Standardized catch rates by age and biomass for the North Atlantic swordfish (*Xiphias gladius*) from the Spanish longline fleet for the period 1983-1998 and bias produced by changes in the fishing strategy. ICCAT Col. Vol. Sci. Pap. Vol. LI (SCRS 99/056, CD Version).

MEJUTO, J., B. García-Cortés, A. Ramos-Cartelle. in press. Tagging-recapture activities of large pelagic sharks carried out by Spain or in collaboration with the tagging programs of other countries. ICCAT Col. Vol. Sci. pap. (SCRS/2004/104).

MEJUTO, J., A. G. Garcés 1984. Shortfin mako, *Isurus oxyrhinchus*, and porbeagle, *Lamna nasus*, associated with longline swordfish fishery in the NW and N Spain. ICES C.M. 1984/G:72.

MEJUTO, J., B. García-Cortés, J. M. De la Serna. 2002. Preliminary scientific estimations of by-catches landed by the Spanish surface longline fleet in 1999 in the Atlantic Ocean and Mediterranean Sea. ICCAT. Col. Vol. Sci. Pap., Vol. LLIV: 1150-1163.

MEJUTO, J., B. García-Cortés, J.M. de la Serna. 2003. Standardized catch rates for the North and South Atlantic swordfish (*Xiphias gladius*) from the Spanish longline fleet for the period 1983-2001. ICCAT. Col. Vol. Sci. Pap. Vol. LV: 1495-1505.

MEJUTO, J., S. Iglesias, B. García. 1989. La pesquería española de pez espada y especies asociadas, en Galicia: Presente y futuro de una pesquería en expansión. Jornadas sobre economía y sociología de las comunidades pesqueras. M.A.P.A.:223-239.

MEJUTO J., J.M. de la Serna, B. García, M. Quintans, E. Alot. 1994. Sex ratio at size of the swordfish (*Xiphias gladius*) in the Atlantic and Mediterranean sea. Similarity between different spatial-temporal strata. ICCAT. Col. Vol. Sci. Pap. (SCRS/93/113).

MORENO, J., J Moron. 1992. Comparative study of the Genus Isurus (Rafinesque, 1810) and description of a form ('marrajo criollo') apparently endemic to the Azores. Aust. J. Mar. Freshwater Res. 43:109-122.

MUÑOZ-CHAPULI, R. 1985. Análisis de las capturas de escualos pelágicos en el Atlántico nororiental (15º-40º N). Inv. Pesq. 49(1):67-79

NAKANO, H. 1994. Age, reproduction and migration of blue shark in the North Pacific Ocean. Bull. Mat. Res. Inst. Far. Seas. Fish, 31:141-256.

NAKANO H., M. Makihara, K. Shimazaki. 1985. Distribution and biological characteristics of the blue shark in the central North Pacific. Bull. Fac. Fish. Hokkaido Univ. 35(3):99-113.

NAKANO H., M. P. Seki. 2003. Synopsis of biological data on the blue shark, *Prionace glauca* Linnaeus. Bulletin of Fisheries Research Agency. Nº 6, March 2003.

PRATT H. W. JR. 1979. Reproduction in the blueshark, *Prionace glauca*, Fish Bull., 77 (2):445-470.

REY J.C., J. Mejuto, S. Iglesias. 1998. Evolución histórica y situación actual de la pesquería española de pez espada, *Xiphias gladius*. ICCAT. Col. Vol. Sci. Pap. Vol.XXVII:202-213.

REY, J.C., R. Muñoz-Chapuli. 1992. Intra and interspecific association of large pelagic fishes inferred from catch data of surface longline. Environmental Biology of Fishes 35:95-103.

STEVENS, J.D. 1974. The occurrence and significance of tooth cuts on the blue shark (Prionace glauca) from British waters. J. Mar. Biol. Assoc. U.K. 54:373-378.

VAS, P. 1990. The abundance of the blue shark, *Prionace glauca*, in the western English Channel. Environmental Biology of Fishes 29:209-225.

Table 1. Number of fish sexed (No.(Ma+Fem)), number of females sampled (No.Fem.), overall sex ratio (SRo), number of females specifically analysed to determine the presence of fecundation signs (No.analiz.Fem), number of females showing internal or external signs of fecundation (No.Fec.Fem.), percentage of females with fecundation signs relative to the females analysed (% Fecun.), number of pregnant females (No.Pre.Fem), percentage of pregnant females (% Pre.Fem) relative to females with fecundation signs and the percentage of females with mating injuries (% Mat.Fem) relative to females with signs of fecundation; for each zone and region defined.

ZONE	Nº (Ma+Fem)	No. Fem.	SRo	No.analiz. Fem.	No. Fec. Fem.	% Fecun	No. Pre. Fem	% Pre.Fem	% Mat.Fem
ATL01	439	205	46,70	204	3	1,47	3	1,47	0,00
ATL02	801	415	51,81	405	3	0,74	-	0,00	0,74
ATL03	2187	601	27,48	295	107	36,27	88	29,83	6,44
ATL04	158	76	48,10	75	0	0,00	-	0,00	0,00
ATL06	2600	1036	39,85	970	447	46,08	366	37,73	8,35
ATL91	4550	1573	34,57	1273	231	18,15	154	12,10	6,05
ATL92	127	35	27,56	35	5	14,29	5	14,29	0,00
ATL93	490	261	53,27	249	136	54,62	67	26,91	27,71
ATLN	**11352**	**4202**	**37,02**	**3506**	**932**	**26,58**	**683**	**19,48**	**7,10**
ATL07	249	121	48,59	113	81	71,68	36	31,86	39,82
ATL08	1711	947	55,35	898	819	91,20	627	69,82	21,38
ATL09	15876	7742	48,77	6793	6060	89,21	5396	79,43	9,77
ATL10	12053	2923	24,25	2438	1509	61,89	1166	47,83	14,07
ATLC	**29889**	**11733**	**39,26**	**10242**	**8469**	**82,69**	**7225**	**70,54**	**12,15**
ATL11	2574	762	29,60	580	308	53,10	261	45,00	8,10
ATL12	738	125	16,94	92	56	60,87	55	59,78	1,09
ATL13	1315	404	30,72	396	94	23,74	79	19,95	3,79
ATL15	4674	950	20,33	870	283	32,53	130	14,94	17,59
ATLS	**9301**	**2241**	**24,09**	**1938**	**741**	**38,24**	**525**	**27,09**	**11,15**
IND52	87	43	49,43	41	34	82,93	31	75,61	7,32
IND53	3182	230	7,23	148	129	87,16	61	41,22	45,95
IND54	3601	1141	31,69	750	481	64,13	152	20,27	43,87
IND55	909	242	26,62	166	131	78,92	72	43,37	35,54
INDI	**7779**	**1656**	**21,29**	**1105**	**775**	**70,14**	**316**	**28,60**	**41,54**
PAC40	3424	926	27,04	658	546	82,98	133	20,21	62,77
PAC44	19815	7975	40,25	5795	239	4,12	228	3,93	0,19
PACI	**23239**	**8901**	**38,30**	**6453**	**785**	**12,16**	**361**	**5,59**	**6,57**
ALL	**81560**	**28733**	**35,23**	**23244**	**11702**	**50,34**	**9110**	**39,19**	**11,15**

Table 2. Mean size by sexes combined (FL(Ma+Fe)), mean female size (FL Fem.), mean size and confidence interval of pregnant females (FL Pre.Fem) and mean size and confidence intervals for females with mating injuries (FL Mat.Fem); for each zone and region defined.

	FL(Ma+Fem)	FL Fem	FL Pre.Fem			FL Mat.Fem		
ZONE	Mean	Mean	Mean	LCI(95%)	UCI(95%)	Mean	LCI(95%)	UCI(95%)
ATL01	135	139	201	97,2	305,5	-	-	-
ATL02	140	139	-	-	-	195	-	-
ATL03	166	155	219	215,2	223,3	177	167,4	187,6
ATL04	142	132	-	-	-	-	-	-
ATL06	180	181	219	217,4	221,3	200	194,7	205,8
ATL91	160	155	223	219,7	226,4	203	196,6	209,8
ATL92	148	149	232	223,6	240,8	-	-	-
ATL93	222	213	222	217,2	226,5	204	199,2	208,6
ATLN	**165**	**162**	**219**	**217,1**	**220,7**	**201**	**197,7**	**203,9**
ATL07	205	196	208	201,7	214,6	186	181,6	190,8
ATL08	208	207	213	211,4	214,8	200	198,1	203,1
ATL09	205	202	206	205,7	206,6	194	192,8	195,5
ATL10	192	191	206	204,4	206,5	183	180,3	184,8
ATLC	**200**	**200**	**210**	**209,3**	**210,4**	**192**	**190,7**	**192,8**
ATL11	196	189	199	197,2	200,8	186	181,7	189,9
ATL12	192	192	202	197,6	206,9	196		
ATL13	202	187	203	199,6	206,3	189	179,5	198,9
ATL15	168	150	207	201,6	212,1	171	166,6	175,2
ATLS	**182**	**172**	**206**	**203,8**	**208,6**	**176**	**172,5**	**179,1**
IND52	214	216	227	216,9	237,9	193	141,6	245,0
IND53	212	203	220	214,3	225,9	202	197,4	206,6
IND54	209	188	226	223,1	229,4	201	198,0	203,1
IND55	217	200	212	209,0	216,5	205	198,8	212,1
INDI	**211**	**192**	**222**	**219,8**	**224,5**	**201**	**119,2**	**203,4**
PAC40	183	189	190	186,9	192,7	220	215,3	225,5
PAC44	135	135	204	201,5	205,7	209	202,3	216,3
PACI	**140**	**137**	**186**	**183,8**	**187,6**	**192**	**179,1**	**205,3**
ALL	**178**	**173**	**207**	**206,7**	**207,5**	**194**	**193,5**	**195,4**

Table 3. Number of females (n) specifically sampled to estimate litter size (No.Embryos), mean, median, minimum, maximum and confidence intervals of the number of embryos present in the two uteri by pregnant female; for each zone and region defined.

	No. Embrios						
ZONE	n	Mean	Median	Min.	Max.	UCI(95%)	LCI(95%)
ATL01	2	28	-	-	-	-	-
ATL02	-	-	-	-	-	-	-
ATL03	54	36	36	5	71	38,7	32,2
ATL04	-	-	-	-	-	-	-
ATL06	252	43	42	2	96	44,1	40,5
ATL91	99	30	30	5	80	34,3	28,4
ATL92	5	37	40	15	60	60,9	13,1
ATL93	46	32	40	1	63	43,9	36,7
ATLN	**458**	**39**	**39**	**1**	**96**	**37,5**	**40,2**
ATL07	11	31	25	18	48	37,8	22,9
ATL08	276	40	38	2	86	39,6	36,4
ATL09	2858	36	35	1	108	37,3	36,3
ATL10	580	35	37	1	107	39,4	37,1
ATLC	**3725**	**37**	**36**	**1**	**108**	**36,7**	**37,5**
ATL11	139	30	30	1	65	32,1	27,7
ATL12	36	36	30	5	71	37,4	28,4
ATL13	27	31	30	17	64	37,6	28,1
ATL15	57	42	47	3	94	52,5	42,6
ATLS	**259**	**34**	**32**	**1**	**94**	**32,6**	**36,5**
IND52	22	31	29	18	58	36,1	27,4
IND53	32	32	40	10	82	45,6	34,9
IND54	78	30	38	16	82	43,8	37,1
IND55	28	32	34	19	50	36,5	29,7
INDI	**160**	**38**	**36**	**10**	**82**	**35,8**	**40,1**
PAC40	293	38	32	6	74	35,5	32,2
PAC44	173	25	42	3	71	43,8	39,8
PACI	**466**	**34**	**33**	**3**	**71**	**32,8**	**35,5**
ALL	**5068**	**37**	**36**	**1**	**108**	**36,7**	**37,5**

Table 4. Number of females (n) sampled specifically to estimate the mean embryo size (FLemb), minimum, maximum and confidence intervals of the size of the embryos found in pregnant females; for each zone and region defined.

	FLemb					
ZONE	n	Mean	Min.	Max.	LCI(95%)	UCI(95%)
ATL01	-	-	-	-	-	-
ATL02	-	-	-	-	-	-
ATL03	62	28	16	45	25,1	31,1
ATL04	-	-	-	-	-	-
ATL06	283	17	2	41	15,5	18,7
ATL91	7	35	33	41	31,7	39,0
ATL92	-	-	-	-	-	-
ATL93	51	20	2	28	16,8	22,9
ATLN	**403**	**23,6**	**2**	**45**	**22,0**	**25,2**
ATL07	33	12	3	29	8,0	14,9
ATL08	441	10	1	36	8,7	12,2
ATL09	2824	20	1	43	18,5	20,6
ATL10	545	24	3	37	23,0	25,5
ATLC	**3843**	**14,9**	**1**	**43**	**13,3**	**16,5**
ATL11	134	26	9	48	24,9	29,3
ATL12	36	34	26	41	32,4	34,9
ATL13	27	20	5	48	17,4	23,4
ATL15	57	26	12	45	22,8	29,6
ATLS	**254**	**27,2**	**5**	**48**	**25,4**	**28,9**
IND52	22	26	6	37	22,4	29,8
IND53	31	23	6	38	20,0	26,9
IND54	78	33	24	43	31,4	34,5
IND55	28	31	23	40	28,9	32,6
INDI	**159**	**26,2**	**6**	**43**	**24,3**	**28,1**
PAC40	264	15	1	42	11,9	17,5
PAC44	169	32	3	36	30,6	34,3
PACI	**433**	**23**	**1**	**42**	**21,4**	**24,4**
ALL	**5092**	**20**	**1**	**48**	**19,5**	**20,0**

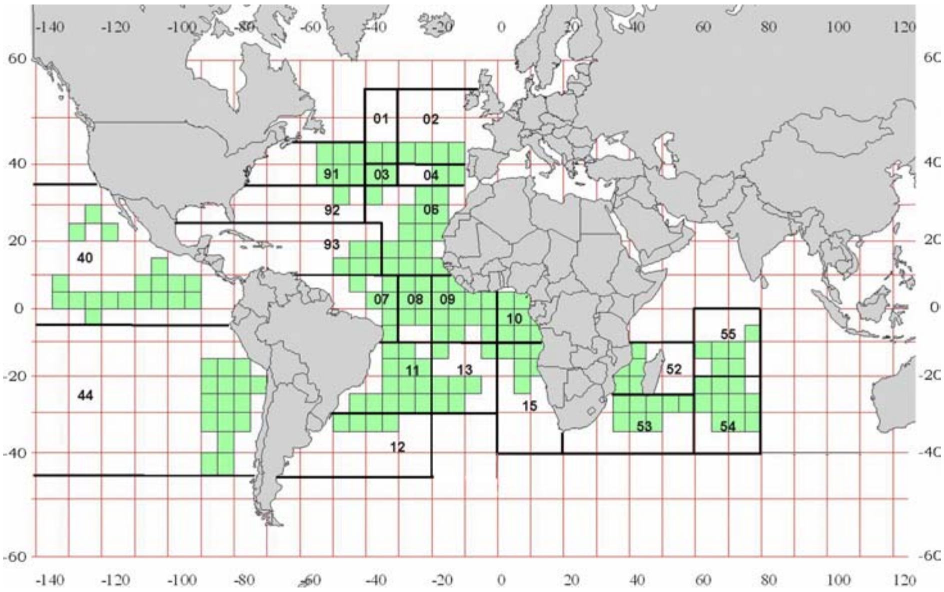


Figure 1. Map of the areas where observations of *Prionace glauca* (coloured squares) were carried out and definition of the zones considered in the analyses.

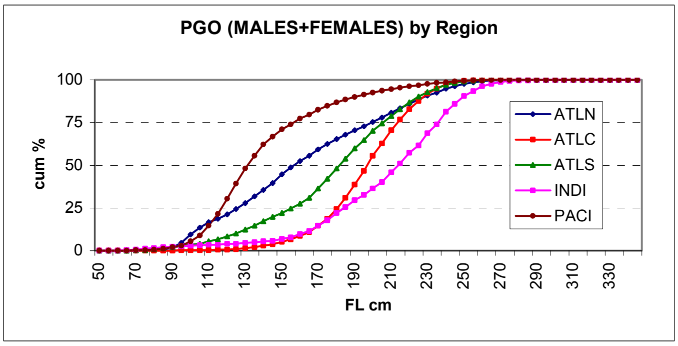


Figure 2. Size distribution in cumulative percentage of the specimens sampled (sexes combined), by region.

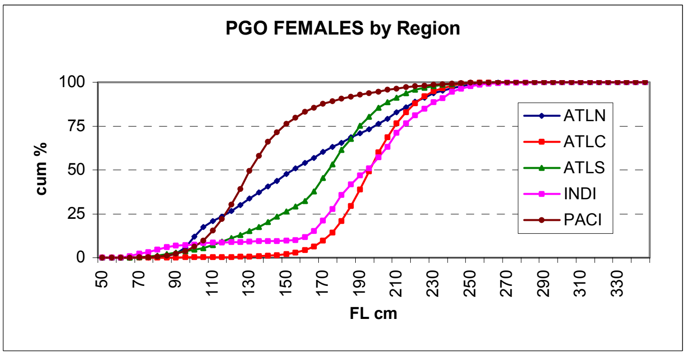


Figure 3. Size distribution in cumulative percentage of the specimens sampled (females), by region.

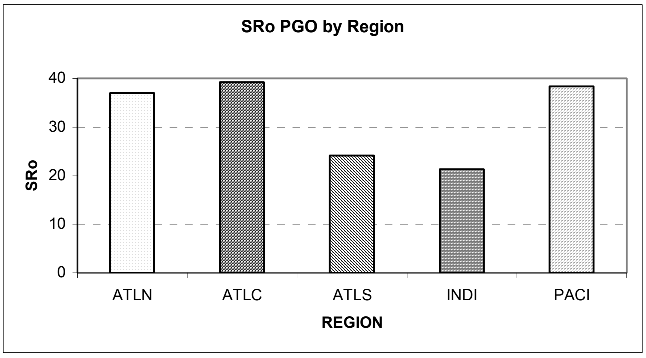


Figure 4. Overall sex ratio (SRo) obtained for each of the regions defined.

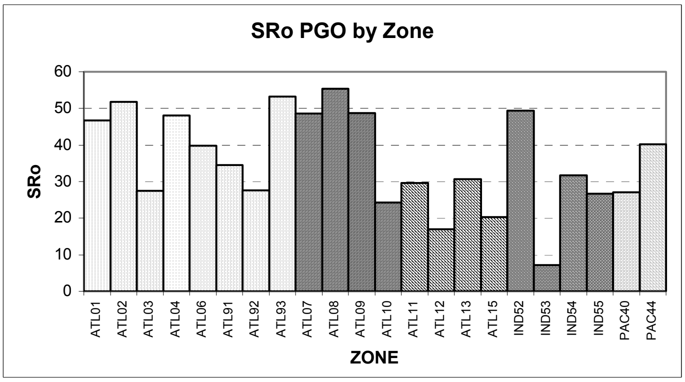
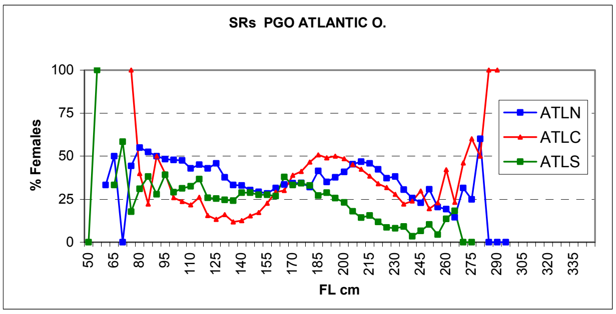


Figure 5. Overall sex ratio (SRo) obtained for each of the zones defined.



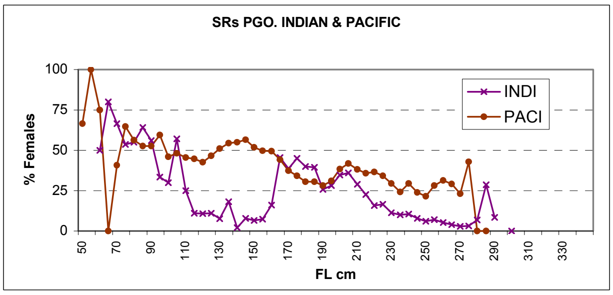


Figure 6. Sex ratio at size (SRs) values obtained for each of the regions defined.

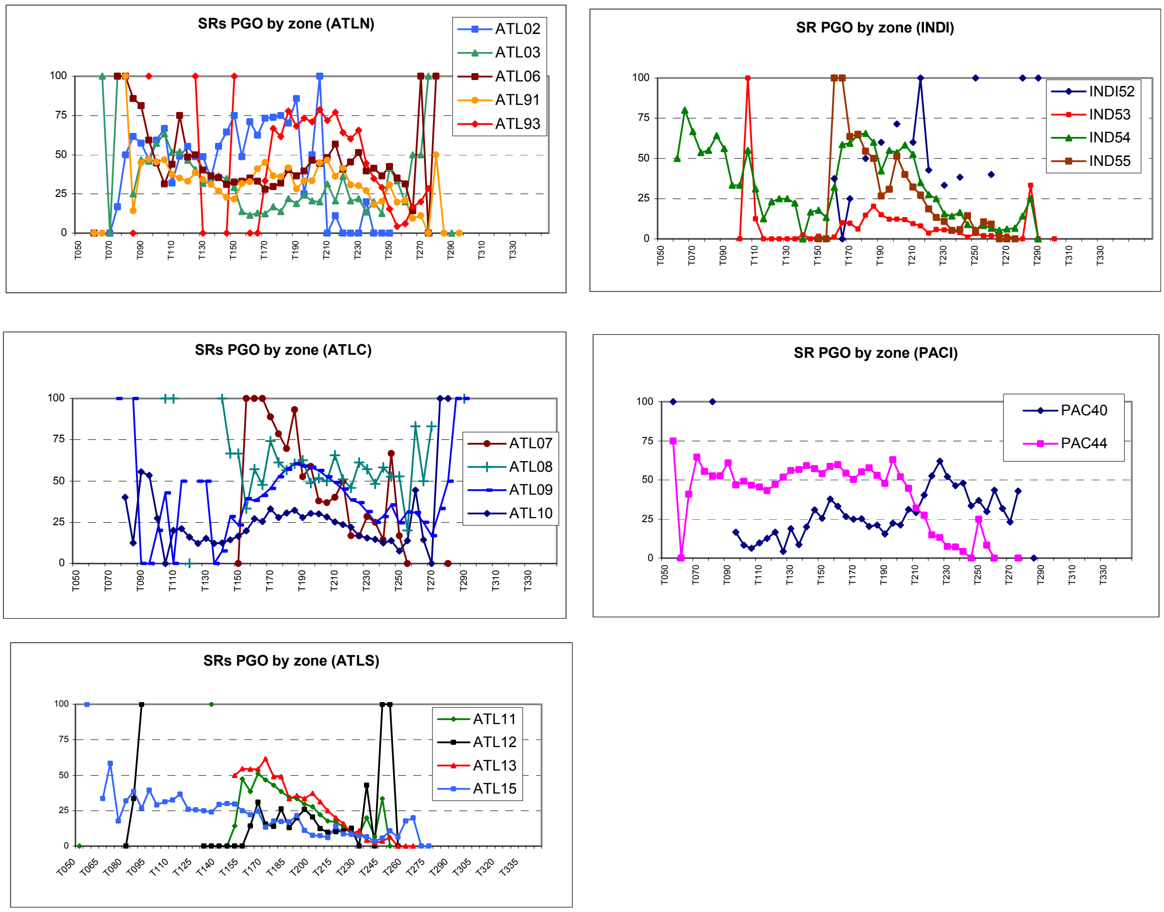


Figure 7. Sex ratio at size (SRs) values obtained for each of the zones defined.

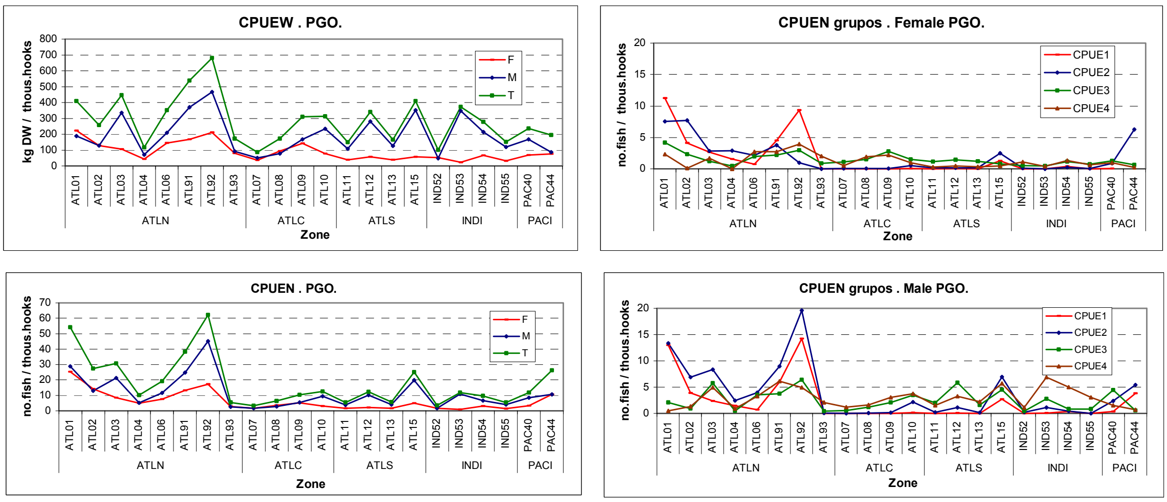


Figure 8. Nominal catch per unit of effort (CPUE), in number of fishes and in kg of dressed weight, for sizes combined, by zone, sex and sexes combined (left). CPUE in number of fishes by size categories (CAT), by zone, sex and sexes combined (right).

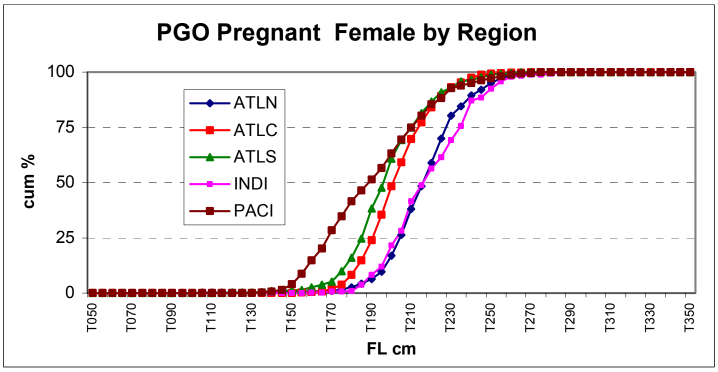


Figure 9. Size distribution in cumulative percentage of pregnant females, by region.

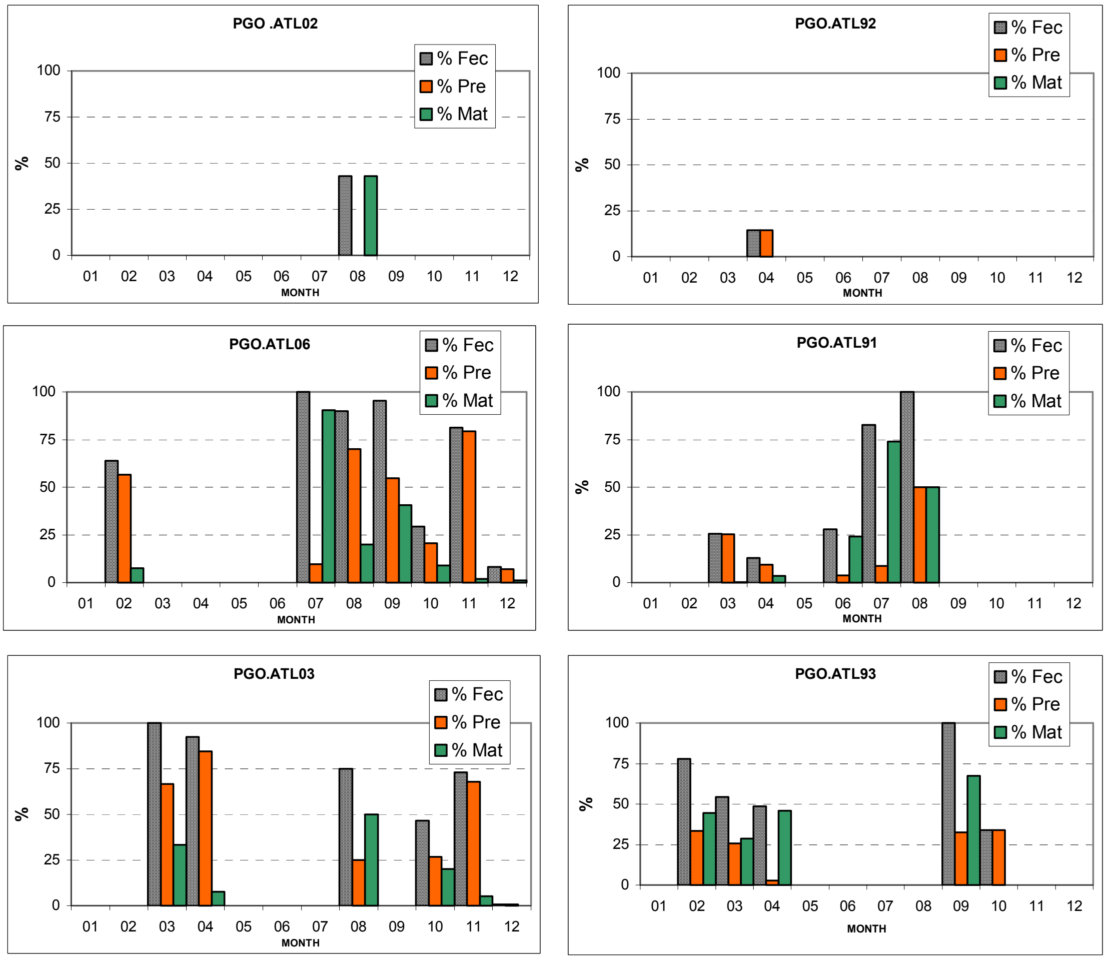


Figure 10. Prevalence of females showing signs of fecundation (%Fec), of the females with mating injuries (%Mat) and pregnant females (%Pre), relative to the total number of females specifically analysed, by zones and months, in zones belonging to region ATLN.

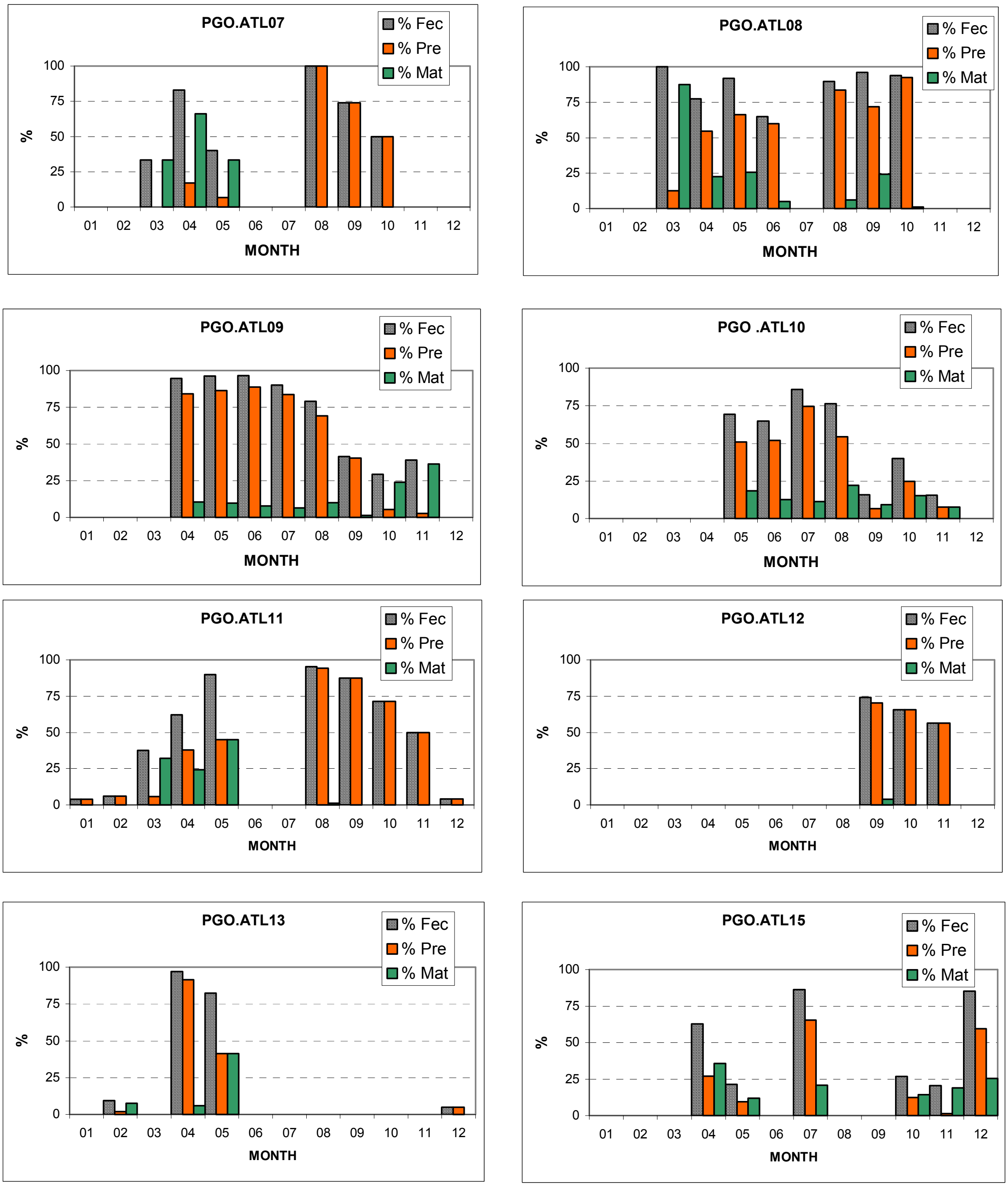


Figure 11. Prevalence of females showing signs of fecundation (%Fec), of the females with mating injuries (%Mat) and pregnant females (%Pre), relative to the total number of females specifically analysed, by zones and months, in zones belonging to region ATLC (ATL07-10) and ATLS (ATL11-15).

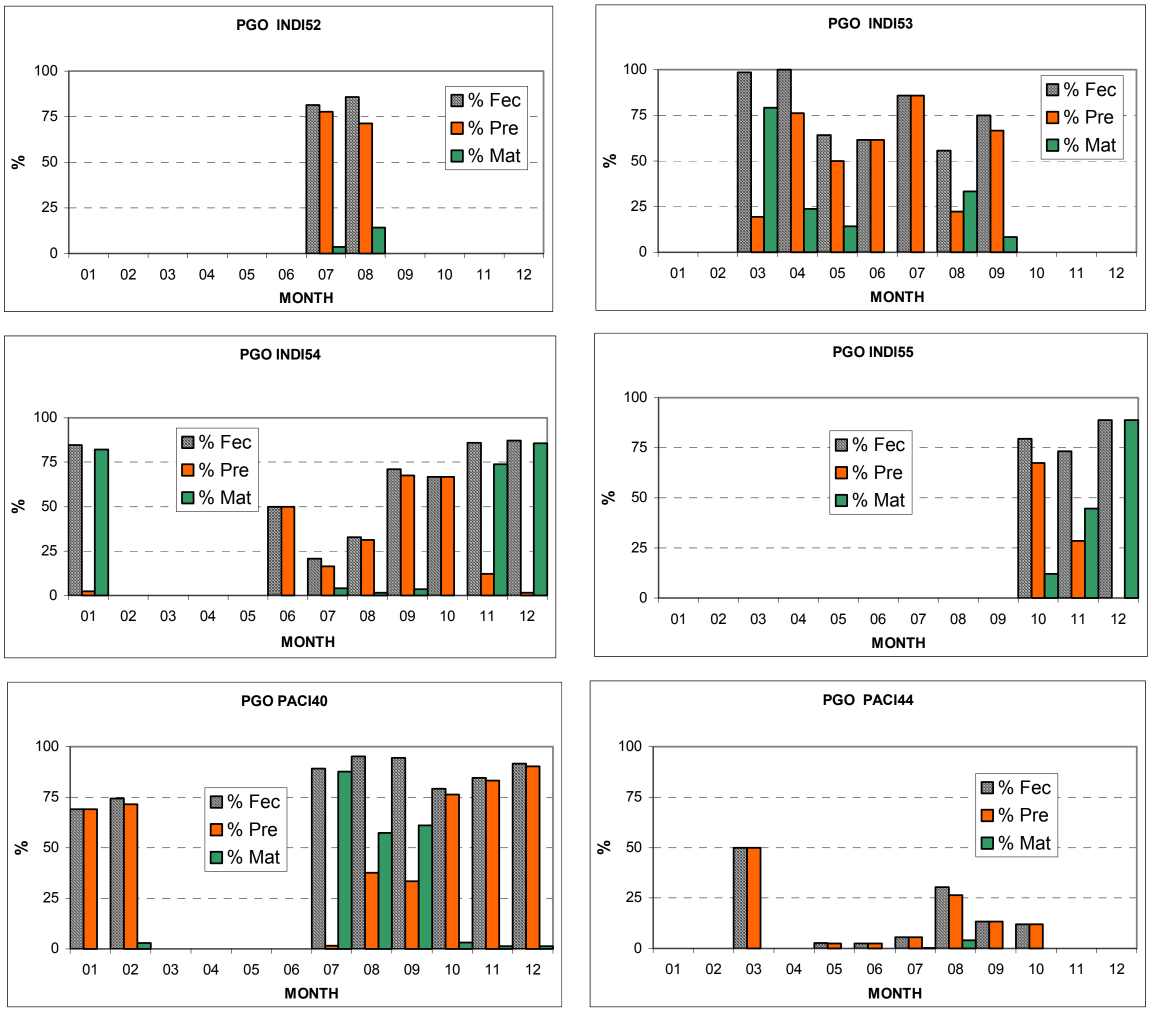


Figure 12. Prevalence of females showing signs of fecundation (%Fec), of the females with mating injuries (%Mat) and pregnant females (%Pre), relative to the total number of females specifically analysed, by zones and months, in zones belonging to region INDI (INDI52-55) and PACI (PAC40-44).

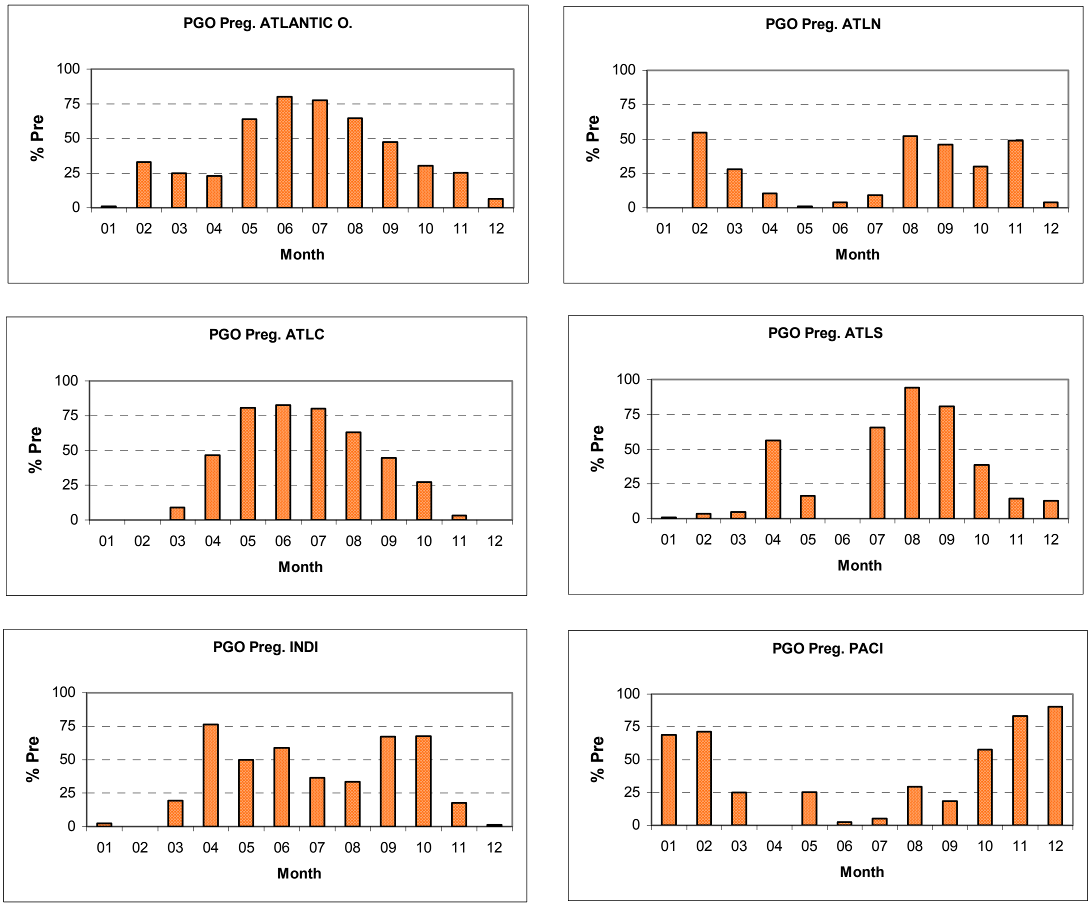


Figure 13. Prevalence in percentage of pregnant females (%Pre) relative to females showing signs of fecundation by region-month and for the whole Atlantic-month.

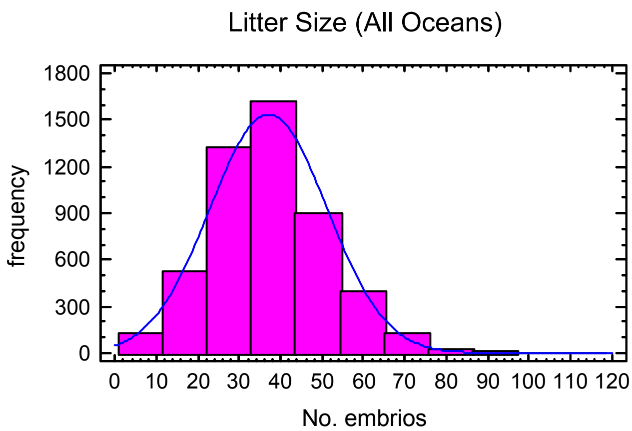


Figure 14. Histogram of the frequency of the litter-size per pregnant female for all the areas combined (N= 5068).

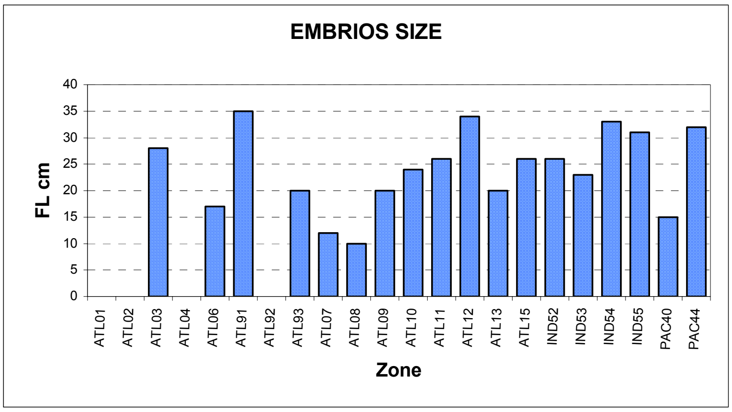


Figure 15. Mean embryo size observed in pregnant females, by zone.

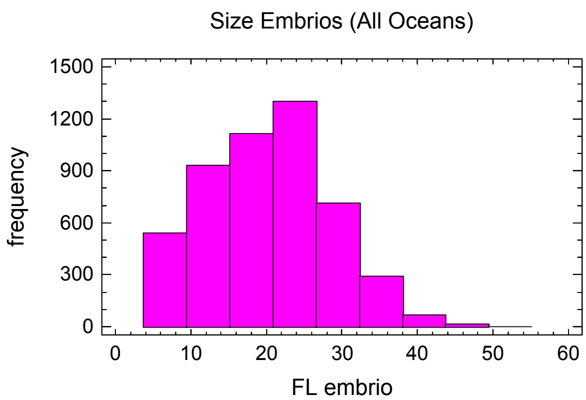


Figure 16. Histogram of the frequency of mean embryo size found in pregnant females for all the areas combined (N= 5092).

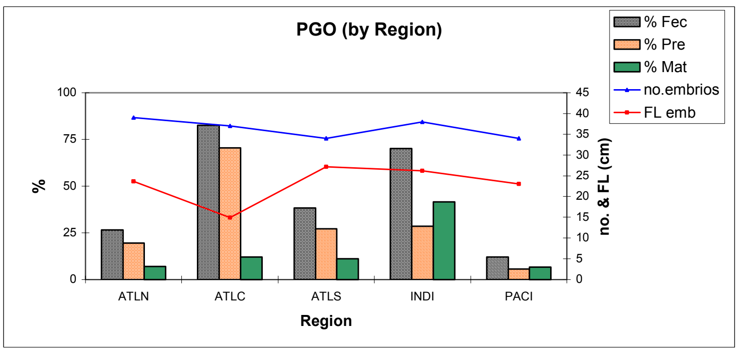


Figure 17. Summary of some of the basic reproductive parameters of *Prionace glauca*, by region, relative to the number of females analysed: Prevalence in % of females showing internal or external signs of fecundation (%Fec), prevalence in % of pregnant females (%Pre) and females with mating injuries (%Mat); (left axis). Mean number of embryos per female (No. embryos) and mean embryo size (FL emb); (right axis).

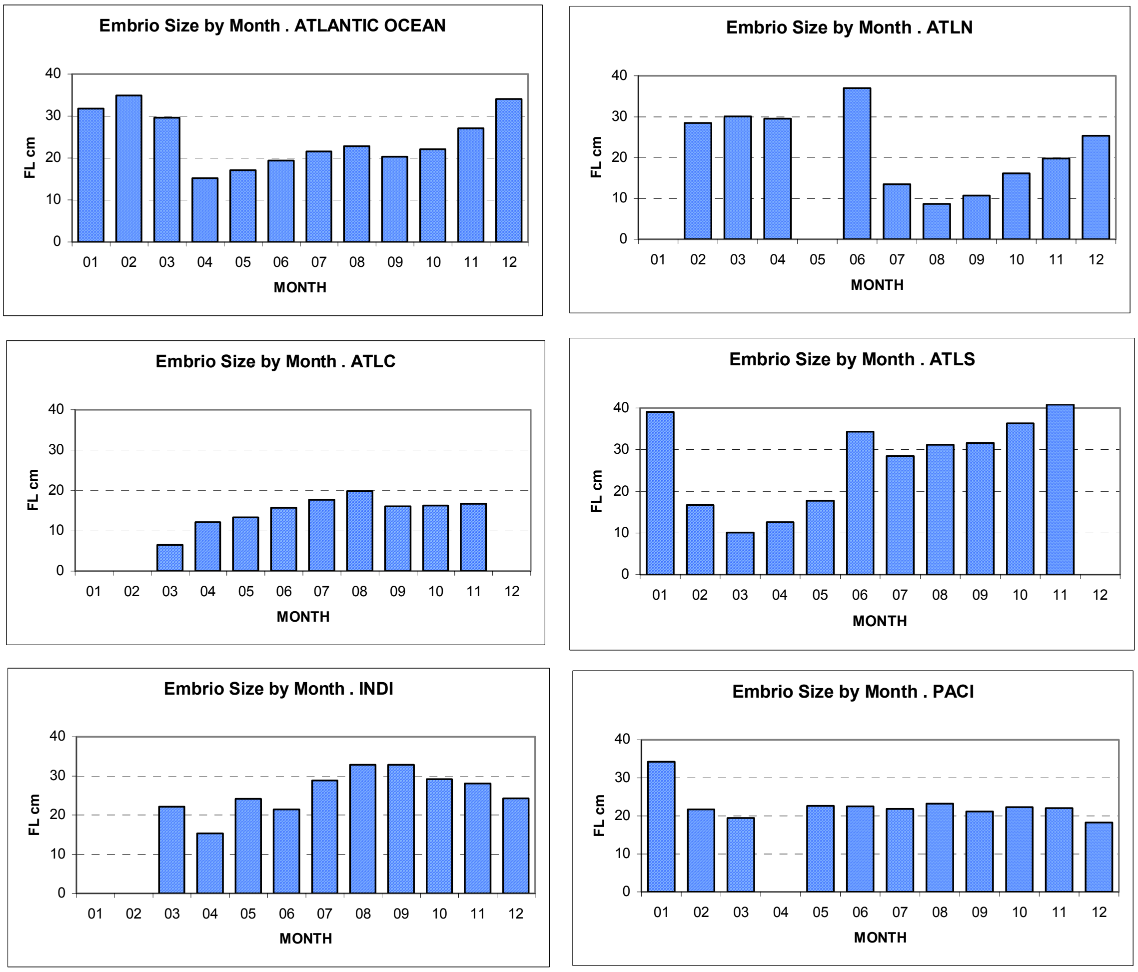
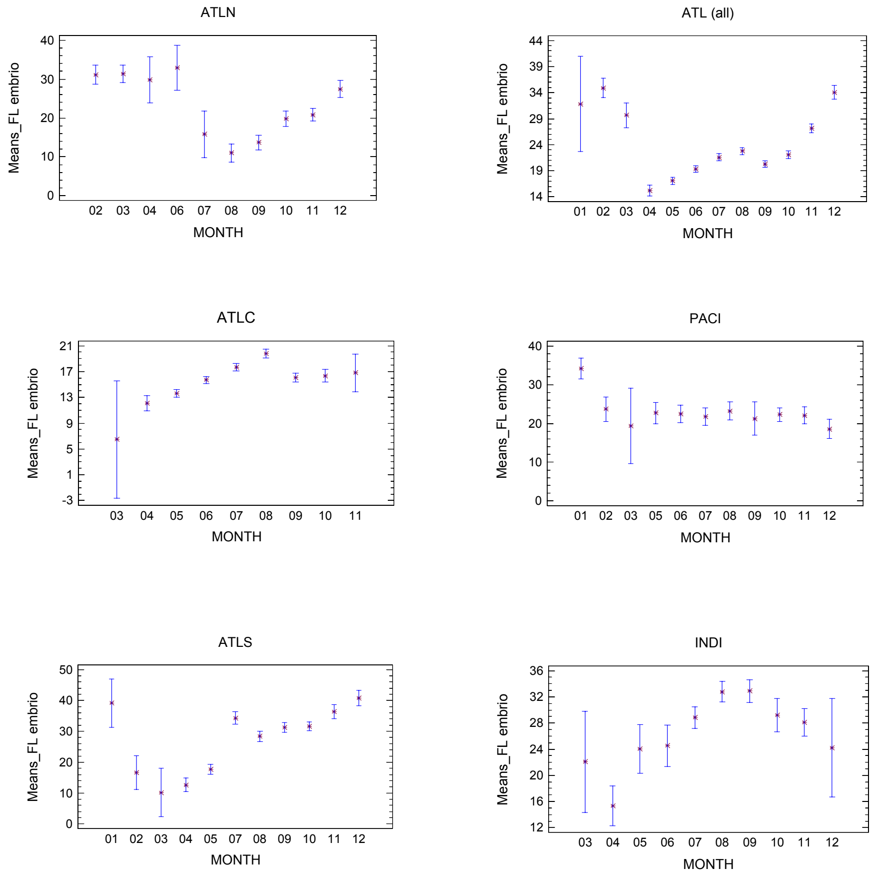


Figure 18. Mean embryo size (FL cm) by month, by region and for the whole Atlantic.

(A:Month)



(B:Zone)

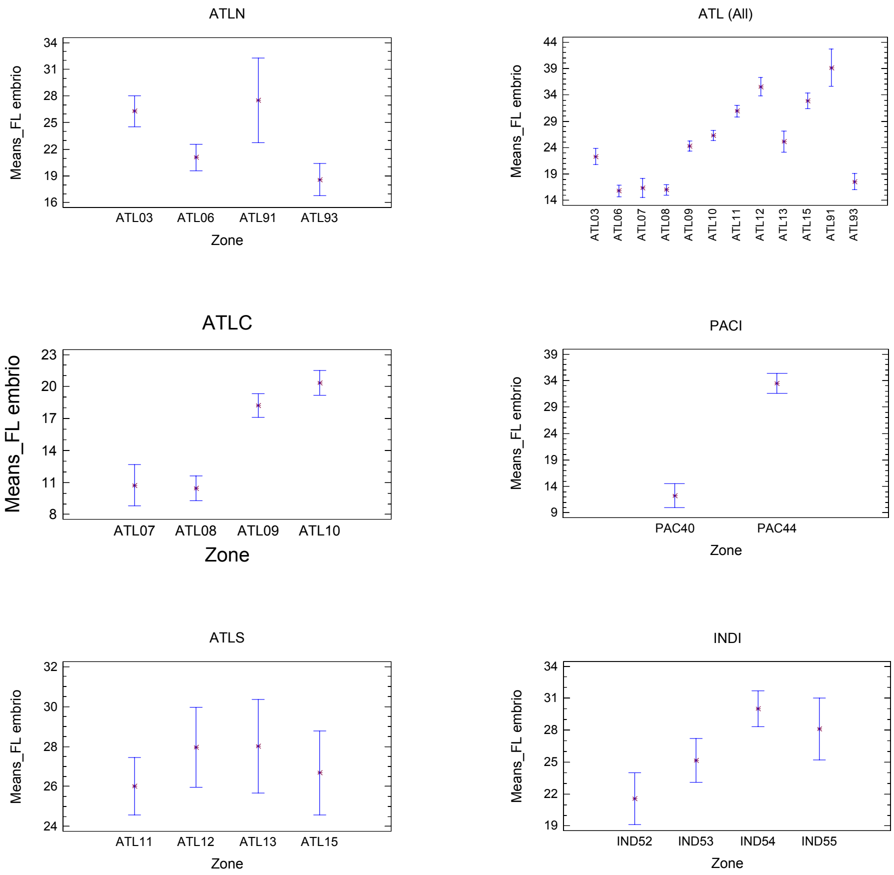


Figure 19. Effect of the variables month and zone on mean embryo size (and 95% confidence intervals), within each of the regions defined.

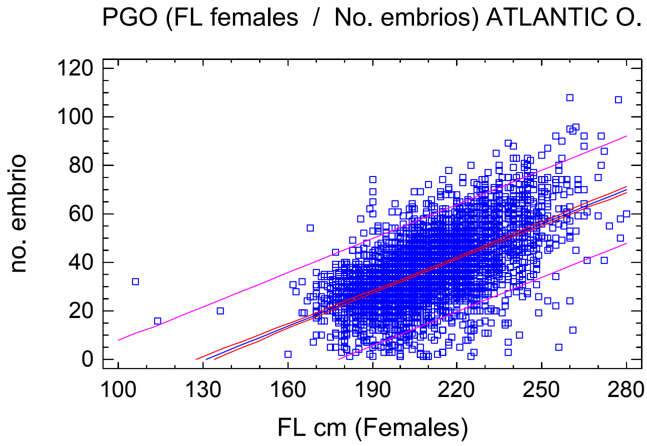


Figure 20. Relationship between the size of pregnant females and their litter size, based on a linear model applied to the Atlantic observations.