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REPRODUCTIVE ACTIVITY OF SWORDFISH (*Xiphias gladius*) IN THE PACIFIC OCEAN ON THE BASIS OF DIFFERENT MACROSCOPIC INDICATORS

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ABSTRACT

A total of 23,639 swordfish females were analysed. The percentage of females larger that 145 cm shows important differences among areas. Maximum percentages were obtained in temperate waters South of 25º S and the lowest values in warm areas where small females were observed. The overall sex-ratio obtained was 51%. The sex-ratios at size suggest that females are predominant as of 170 cm although different patterns of sex-ratio at size were obtained between zones. The gonad index detects areas as producing the most intense maturation activity in females, ranging from the central Pacific between 10ºN and 10ºS to the West of 120ºW where the greatest gonad development was observed. The results would indicate that reproductive activity is mostly carried out in certain areas of the central-western Pacific but that there may also be sporadic-seasonal or moderate reproductive events in some of the other areas adjacent to these. At the same time, the SE Pacific show resting females with active feeding behaviour. The most active areas with maturity events are linked to warm waters where the characteristic spawning patters of sex-ratio at size are caused by the higher abundance/catchability of males over females within particular size ranges. The results match well with similar indicators observed for the Atlantic swordfish. However, the Pacific shows somewhat broader warm areas than the Atlantic, suggesting that the potential spawning areas for the Pacific swordfish could be relatively broader and eastern than those reported for the Atlantic.

Key words: swordfish, reproduction, gonad index, Pacific

1. INTRODUCTION.

Although the swordfish population would appear to be structured into different stocks in the different oceans -and probably even within each ocean- (Alvarado *et al.* 2005; Kotoulas *et al*. 2007; Kasapidis *et al*. in press) it is very likely that this species has similar biological-physiological components associated with the oceanographic requirements in all of these oceans. Therefore, information on the biology and behaviour of this species in a region or an ocean, regardless of whether it is geographically different from our preferential area of interest, may provide the key to the interpretation of these biological, physiological and behavioural characteristics, both on a local and global level. The reproduction of the swordfish has been studied in the Pacific and Atlantic for decades. A broad range of up-to-date information on swordfish reproduction from the Atlantic would also be useful for the purpose of comparing these data with results from the Pacific.

The gonads of female swordfish are paired organs located ventrally on either side of the intestinal sac and the large natatory bladder in the anterior anal area. With a little experience, it is easy to distinguish the sex of these animals, but males and females may be misidentified especially in small fish, when observers lack sufficient training and the identification criteria are not standardized. An analysis of quantitative and qualitative macroscopic indicators of the gonad developmental stage and maturity of the females offers the advantage of presenting information on the general status of maturation in the gonads of each female specimen without having to preserve the samples. This option is a good initial approach for the study of several different reproductive variables of this species (areas, times, spawning sizes, etc.) with a broad populational focus, which requires substantial and representative sampling sizes. This means that it would be feasible to carry out studies on long distance commercial vessels in which the mass preservation of samples is impossible for this type of species. This approach is an especially useful step and would be advisable prior to conducting histological studies targeting areas with intensive reproduction activity. Recent analyses on the reproduction of swordfish have attempted to focus on these aspects in a broad geographical perspective, including data from the North and South Atlantic regions (Mejuto and García-Cortés in press) and from the West Indian Ocean and the East Pacific (Mejuto *et al.* 1995; García-Cortés and Mejuto 2003; Mejuto and García-Cortés 2003a) pointing, in some cases, to common characteristic patterns among oceans.

Although the swordfish is a solitary species, rarely forming schools per se, there have been reports indicating that they may "*pair up*" for reproductive purposes (Goode 1883; Palko *et al.* 1981). These observations initially made by fishermen were recently explained using different indicators (Mejuto and García-Cortés in press). Most of the information available from the Atlantic areas is relatively recent and largely originates from the northwestern regions (Arocha 1997, 2002, 2007; Arocha and Lee 1995, 1996; Arocha *et al*. 1994; Mejuto and García-Cortés 2003b, in press; Palko *et al.* 1981; Rey 1988; Taylor and Murphy 1992). One of the most comprehensive papers on these regions, focusing chiefly on histological studies (Arocha 1997), detected reproduction areas-times in some of the subtropical regions observed in the Northwest Atlantic as far as 35ºN. The first study with a broad spatial coverage conducted in the NE Atlantic highlighted the lack of maturation and reproductive processes between 35º-45ºN and 10º-40ºW, on the basis of microscopic data and gonad indices, in addition to showing the systematic difference in weight and its biometric relationship between both female gonads. The study also made fertility estimations and provided other variables of reproductive interest (García and Mejuto 1988). In the South Atlantic, the first indicators of swordfish reproduction between 20º-33ºS and 40º-50ºW were described by Brazilian researchers (Amorin and Arfelli 1984). Later studies broadened our knowledge on reproduction in these oceanic areas (Mejuto and García 1997; Mejuto and García-Cortés 2003b; Mejuto 2007; Mejuto and García-Cortés in press). In the Indian Ocean studies on the reproductive processes of this species have only been carried out recently (García-Cortés and Mejuto 2003; Mejuto and García 1997; Mejuto *et al.*1994, 1995, 2006; Poisson *et al.* 2001; Poisson and Taquet 2000).

The Pacific swordfish has also been studied in terms of its developmental processes for reproduction (Hinton *et al.* 1997; Kume and Joseph 1969; Matsumoto and Kazama 1974; Miyabe and Bayliff 1987; Nakano and Bayliff 1992; Nishikawa and Ueyanagi 1974; Nishikawa *et al.* 1978, 1985; Young *et al.* 2003) while other studies have reported on the absence of said processes (Ramón and Castro-Longoria 1994; Weber and Goldberg 1986; Wang *et al.* 2003; Mejuto and García-Cortés 2003a). Several studies have also described the spawning of the swordfish in the Pacific Ocean in spring-summer north of the Equator; in winter south of the Equator and all year round in equatorial latitudes, with cut-off points between 25º-30º N and 10º S. Spawning did not take place to the east of 100º W (Kume and Joseph 1969; Miyabe and Bayliff 1987; Nakano and Bayliff 1992), nor did these fish spawn on the East Pacific coast (Weber and Goldberg 1986; Ramon and Castro-Longoria 1994). Similar observations were obtained in previous works on the Spanish longline fleet fishing in these eastern areas (see previous references). Other works suggest that the reproductive activities and distribution of swordfish larvae are more prevalent in equatorial waters west of 120ºW with sea surface temperatures (SST) above 23º-24ºC, which would indicate that the fishes have a preference for the tropical Western Pacific as spawning grounds (Matsumoto and Kazama 1974; Nishikawa and Ueyanagi 1974; Nishikawa *et al.* 1978, 1985).

While some authors postulate that the reproductive processes of this species would mainly occur within the entire intertropical band of the different oceans (Rey 1988), the available information would suggest that the intense reproductive processes and larval distribution of swordfish appear to be mostly restricted to the intertropical and, to a lesser extent, the subtropical regions. But both generally occur in the western margins of the respective oceans with seawater temperatures (SST) generally higher than 23º-24ºC. The reported preference of swordfish for spawning grounds within tropical or subtropical zones in the western regions of the oceans is not new. This behaviour has also been reported in the Northwest and Southwest Atlantic as well as the in West Indian Ocean (Mejuto *et al.* 1994, 1995; Arocha and Lee 1996; Mejuto and García 1997; García-Cortés and Mejuto 2003; Mejuto 2007; Mejuto and García-Cortés 2003b, in press). In the Atlantic, it has been also suggested that some very sporadic and exceptional events may be possible in July off the Atlantic areas of Açores Islands (Simoes 2001), although, in general, the gonadosomatic indices observed in these areas would confirm the absence of reproductive activity all year round. Similarly, some individuals with a relatively high gonad index have been observed in restricted regions of the NE Atlantic near the Strait of Gibraltar (De la Serna *pers. comm.*) even though the mean gonad index values are normally low and might even pertain to fishes of Mediterranean origin.

Recent studies have also focussed jointly on alternatives aimed at determining and validating, in the case of female swordfish, the relationship that exists between the histological observations and the biometric indicators (gonad weight) suggesting that both indicators can define areas where the reproduction of the swordfish is happening (Hinton *et al.* 1997; Wang *et al.* 2003). Using this strategy previously described (Cayre and Laloe 1986) it is possible to establish threshold values of the biometric indicators of maturity in females and to relate them to the histological observations of a smaller-sized sub-sampling.

In any case, most of the studies that include histological data have been based on limited sampling sizes and restricted areas-times, which reduce the degree to which the results may be representative of all of the potentially reproductive areas. Moreover, given the fact that swordfish reproduction grounds are generally believed to be restrictive, the selection of samples from a particular zone-time may very well play an important role in terms of conditioning the results obtained.

Additionally, we will attempt to shed light on the overall sex ratio (*SRo*) in specific areas of the Pacific Ocean. The SRo is not generally considered to be a good indicator for the detection of spatial-temporal differences in the distribution of the swordfish by sex because it is very much affected by the size range available in the samples. Hoey (1986) put forth a migratory hypothesis differentiating between male and female swordfish called "*size- temperature mediated sexual segregation*", which was later confirmed in works by other authors. The sex ratios at size of the swordfish (*SRs*) were studied and postulated as a better alternative to explain the spatial and temporal variability of swordfish and size-sex stratification (Becket 1974; García and Mejuto 1988; Hoey 1986, 1991; Lee 1992). These SRs patterns are very useful for comparison with other data previously reported from other oceans. The differences in SRs have been considered as probably being due to possible natural differential growth and/or mortality by age between males and females (see Anonymous 1986, 1988 for details) (Arocha and Lee 1993; Arocha *et al*. 1994, De la Serna *et al*. 1992, 1993, Guitart-Manday 1964, Hoey 1986, Mejuto *et al.* 1994, 1995; Restrepo 1998). However other factors, such as differential migratory behaviour and differential spatial-temporal distribution by sex, owing to the different oceanographic requirements of the swordfish associated with their size-sex and reproductive physiology, have been able to explain the characteristic spatial and temporal variations that have been found in some oceans. A broad overview of the SRs in different areas and oceans pointed to three general patterns in sex ratios at size, linked basically to the geographic-oceanographic-physiological aspects, known generically as "*spawning*", "*feeding*" and "*transitional*" patterns (Mejuto *et al*. 1998). These patterns defined in the SRs have brought about the definition of the so-called "*biological regions*" for the Atlantic swordfish with a view to draw up data on preliminary stock assessment by sex (Anonymous 1999). The assessment results were similar to those using sex-combined alternatives, such as production modelling or virtual populations analyses after a complete data stratification by area-time-sex.

This work approaches the reproductive study of the swordfish in some Pacific areas using, as a first step, certain macroscopic-quantitative indicators (gonad index and CPUEs by sex between areas) in addition to macroscopic-qualitative indices (gonad stages). All of the above could improve our knowledge of the reproduction areas used by this species in the Pacific as a whole and will make it possible to determine the reproductive condition of the females by regions and times. The data collected and presented in this paper come exclusively from a scientific research project done in collaboration with the Spanish surface longline vessels in the Pacific Ocean. A comparison with research from other areas-fleets is essential in order to draw general conclusions on the behaviour of this species in the Pacific.

2. MATERIAL AND METHODS.

The records were obtained through an observer program in the Pacific carried out in the year 1990 and during the period 1998-2007. Observations were obtained in some commercial activities as well as during experimental trips that took place in zones-times when the activity of the Spanish surface longline fleet was generally sporadic or non-existent. Catch data by sex, fishing effort (in number of hooks set) and other biological data of the swordfish caught were collected on a total of 46,063 swordfish specimens of both sexes, of which 23,639 females were analysed biologically in terms of their reproduction parameters. The observations were tentatively classified by geographic areas: PAC40, PAC42, PAC43, PAC44, PAC46 and PAC47 (figure 1). A total of 1,098, 12,476, 968, 1,004, 3,632 and 4,456 females were observed in areas PAC42, 43, 44, 45, 46 and 47, respectively. A few females were sampled in area PAC40, which were omitted from the analysis. During the dissection of the swordfish on board the vessel (gutting, removal of gills, fins, head, etc.) the sex and other variables were recorded. The overall sex ratios (SRo) for combined sizes, the (SRo) by zone and the sex ratio at size (SRs) by zone were obtained. Sex ratios were defined as: SR= Sample [females/(males + females)]*100, (Mejuto *et al.* 1995). The standard size lower-jaw-fork-length (LJFL) was measured and grouped into 5 cm size classes (50<=LJFL<=350) adjusted to the lower limit (MIYAKE 1990).

The female gonads were weighed and the gonad stage observed. The maturity stage of the females was established by means of two types of macroscopic indicators: quantitative and qualitative. The quantitative maturity index of each female sampled, called the "*gonad index"* (GI) was based on the weight of the two gonads and their relation to the size of the female, equivalent to its body weight: GI2 = (ln Wg) / (ln LJFL), modified from the equation used for this species (HINTON *et al*. 1997). Wg = weight of the two female gonads, in grams. LJFL = standard length from the lower jaw to the fork in cm (lower jaw- fork length).

Previous studies done in some Pacific areas have suggested that a gonad index >= 1.375 would be an indication of females in active stages of maturation or spawning, based on the weight of female gonads and eye-fork length (EFL) size (Hinton *et al*. 1997). The equivalent of this threshold would correspond to GI2>= 1.346 when the LJFL size is used (Mejuto and García-Cortés 2003a). GI2 values less than this threshold value would be considered as indicating an insignificant activity of gonad development, maturation or spawning whereas values equal to or greater than the threshold would point to gonad development, maturation and reproductive activity. The GI2 values were mapped into 5ºx5º squares for the different size ranges (50<=LJFL<=350 and LJFL>=145 cm) classifying the observations into three GI2 ranges: 1) no significant reproductive processes or gonad rest stage (GI2<1.346), 2) maturation-reproductive activity (1.346=< GI2 =<1.5) and 3) extreme maturation-reproductive activity (GI2>1.5). Box-plots were also constructed on the GI2 (S-PLUS 1997) for sizes LJFL>=145 cm and by monthly periods in each zone to detect possible monthly patterns. This could be helpful in the identification of the regions with a great likelihood of presenting maturation and spawning processes and the regions where this activity may be only sporadic or non-existent. The size at first maturity of females ($LJFL_{50}$) was obtained at 145 cm LJFL for areas of the Atlantic having a consistently high reproductive pattern throughout the year (Mejuto 2007; Mejuto and García-Cortés in press). For this reason some analyses were tentatively restricted to sizes >=145 cm LJFL, although previous studies have suggested a size of first maturity of 143 cm (EFL), equivalent to 160 cm LJFL (DeMartini 1999).

The catch per unit of effort (CPUE) by sex, in number (CPUEn) and in weight (CPUEw) per thousand hooks, for the observations as a whole, were calculated for each of the defined zones. The CPUEn was divided into four size ranges and labelled as L1, L2, L3 and L4, respectively: (50<= LJFL <125), (125<= LJFL <170), (170<= LJFL <205), (205<=LJFL<=350+). The first of both groups would define individuals of the two sexes in the earliest juvenile stages, with a similar ratio being expected between males and females. The second would define the juvenile female fraction and most males in potentially reproductive sizes. The third was designed to define the potential female breeders and large males. The fourth singled out almost exclusively the large females. The CPUE (R_CPUE) ratios between males (M) and females (F) and the anomalies found in terms of the presence of each sex (Anomaly R_CPUEn) for each zone were defined as: (R_CPUE) = CPUE males / CPUE females, and Anomaly R_CPUE = R_CPUE – 1.

The subjective-qualitative index called the "*gonad stage*" was established for females in 6 levels on the basis of visual criteria: 1: "primordial"; 2: "developing"; 3: "developed, hydrated with visible opaque oocytes"; 4: "very developed, oocytes of around 1 mm, transparent"; 5: "evident-spontaneous spawning at the time of capture, when gutted"; 6: "post-spawning, flaccid, bloody gonads, visible interior lumen, post-spawning residues".

In the paper, Eastern Pacific refers to areas closer to the coasts of America. Western Pacific was used to refer to areas closer to Oceania and Asia.

3. RESULTS AND DISCUSSION

A total of 23,639 female swordfish specimens were analysed to obtain their gonad index. The majority of the samples were taken in the area PAC43 that has been the usual fishing region of the Spanish fleet since 1990. Therefore, for the most part, the overall overview represents mostly this region. The availability of samples from other areas is more limited and recent. Hence the conclusions reached here must be considered preliminary until more representative sampling coverage can be obtained, especially from the westernmost regions not covered yet. The size range of the females sampled is broad, ranging from juveniles to large adult females and accurately represents the sizes captured by the surface longline fleets in these sea temperatures. Females larger that 300 cm are observed quite frequently while males are generally smaller in size, although larger than regularly observed in the Atlantic areas (figure 2).

The number of total swordfish females sampled by zone and their size distribution, as well as the number of females LJFL>=145 cm sampled are provided (figure 3). The percentage of females LJFL>=145 cm in relation to the total number of females observed shows important differences among areas. Maximum values of 85% and 80% are observed in areas PAC46 and 47, respectively, both with latitudes south of 25º S and mostly within temperate waters. Intermediate values of 52%, 60% and 50% are observed in areas PAC42, 43 and 44, respectively. The lowest value 19% is observed in area PAC45, where an abundance of small females (60<= LJFL<=120 cm) were observed. The 5ºx5º geographic coverage of females and the number of observations with an available gonad index value (GI2), for all sizes and years combined, are also shown (figure 4).

The overall SRo obtained for the whole Pacific was 51%. This value is similar to those found in other oceans. The SRo by zone were: 61% (PAC42), 51% (PAC43), 36% (PAC44), 34% (PAC45), 55% (PAC46) and 59% (PAC47). Although SRo is not considered to be an appropriate indicator to detect differences in distribution by sex, in some cases it could outline different sex distributions based on the specimens caught using surface gear. The SRs values by size class for the entire Pacific ocean indicate that females are generally predominant as of 170 cm (figure 5), similar to the findings recorded in other oceans. However, as in other Oceans too, the SRs also suggest different-characteristics patterns between zones. The SRs were much less than 50% in zone PAC45 and also in PAC44 for sizes 110-185 cm LJFL and 115-245 cm LJFL, respectively. For the rest of the zones the SRs were around 50% for sizes 105-170 cm LJFL and more abundant females in size classes of over 170 cm LJFL (figure 5). The SRs pattern from zones PAC44 and PAC45 could be interpreted as being similar to the SRs pattern defined as being characteristic of the reproduction zones in other oceans (Mejuto *et al.* 1994, 1995, 1998; García-Cortés and Mejuto 2003; Mejuto et al. 2006; Mejuto 2007; Mejuto and García-Cortés, in press). However, the patterns observed in both regions suggest some differences between their respective size ranges that will be further explained. A lower proportion of females is observed in PAC44 *vs* PAC 45 for sizes LJFL>170 cm suggesting a possible mixing sex-size mechanism between both areas, considering their different thermal characteristics.

Previous papers on the Pacific areas indicate that female swordfish are normally predominant in higher latitudes and the proportion between sexes should be different between regions (Sakagawa 1989). Other studies (Kume and Joseph 1969) indicate that the ratio between sexes was similar for fishes 130-160 cm (EFL) in all EPO regions, except between 10ºN-5ºS and 100ºW and also in coastal areas of America where females were more prevalent during the first quarter for sizes greater that 170 cm. Weber and Godlberg (1986) indicate that only 26% of 90 swordfish observed near the South California were males, while DeMartini *et al.* (2000) reports an increase in the mean size with latitude and an increase in the male:female ratio only during the spawning periods. Young (2003) indicates that the size of the swordfish and the season are the main factors affecting the sex ratio in the areas of Eastern Australia where females were predominant. In other words, as in the case of the historical research from the Atlantic regions, the different authors have reported the specific observations made in their respective fishing areas-times. The overview of SRs patterns available from recent works suggest similar events in the SRs patterns among Oceans using data from surface longline fleets. The SRs indicator was largely studied for more than a decade in the case of the Atlantic swordfish before obtaining a general and acceptable overview.

A preliminary analysis of the mean GI2, all areas combined, shows values that are generally lower than the threshold of 1.346 for most of the females observed (figure 6). The smallest females found to reach this threshold measured 125 cm LJFL. A large number of females with a maximum GI2 greater than this threshold were observed in the 155 cm LJFL size class. However, the overall mean GI2 at 155 size class was quite low when all the data are combined because most of the observations come from feeding areas where only immature-resting females are observed.

The 145 cm LJFL selected for this preliminary overview was based on the most recently reported first maturity ogive from the intertropical-western Atlantic areas where the most intensive reproductive processes and characteristic SRs patterns –with a high concentration of males– were detected all year round. This size was found to be lower than $LJFL_{50}$ observed in some western subtropical areas of the North Atlantic where seasonal or sporadic reproduction events had been previously reported, but it was higher and closer than the $LJFL_{50}$ range described for the Mediterranean Sea. Size 145 cm is also lower than the L_{50} regularly reported for the Pacific areas using different methodologies: 150 cm EFL (Young *et al* 2003), 144 cm EFL (DeMartini *et al.* 2000), 170 cm EFL in the eastern Pacific (Kume and Joseph, 1969), 160 cm EFL in the North Pacific (Sosa-Nishizaki, 1990), 150-170 cm EFL in the western Pacific (Yabe *et al.* 1959), 168 cm LJFL (Wang *et al.* 2003), etc. This L_{50} size range is generally similar to or above those described by several authors for the Atlantic. However, as in the Atlantic, most of these studies from the Pacific refer to areas where limited or even non existent maturity-reproductive activities were prevalent. Nakano and Bayliff (1992) indicate the observation of a ripe female of around 110 cm EFL.

The occurrence of each of the three GI2 gonad index classifications defined in each 5ºx5º square, restricted to fishes LJFL>=145 cm, makes it possible to detect some areas as producing the most intense maturation activity in females (figure 7). The 5ºx5º areas ranging from the central Pacific between 10ºN and 10ºS to the West of 120ºW exhibited the greatest gonad development observed and a very advanced stage of gonad maturation. The 5ºx5º square (0ºN-145ºE) observed Northern of Australia represents only one female observed. The infrequent maturation processes observed in females East of 120ºW would probably rule out the generalization that the reproduction of this species occurs equally throughout the whole intertropical band (REY 1988). Although the SSTs in this intertropical band are apparently quite homogeneous, which is what led to this assumption, a substantial difference in temperature is observed between the surface layers on both sides of the Atlantic as well as in the Pacific, although to a lesser extent. These thermal factors would explain the results obtained for the Atlantic areas and probably the preliminary results obtained here, as well. The high GI2 values observed in this paper suggest that, as in the case of the Atlantic, the most active areas for swordfish reproduction are linked to warm waters and they would be expected in the central intertropical band observed and are likely to be found in the westernmost part of the Pacific, where samples are not yet available. The availability of new samples from the most potentially active areas could modify our general overview of the reproduction of this species in the Pacific, as occurred in the Atlantic Ocean when the spatial coverage was improved. At the same time, the samples from the SE Pacific generally show resting females with very active feeding behaviour. This situation is similar what was observed on the African-Atlantic coasts (around the Gulf of Guinea). The greatest genetic similarity in the Atlantic was found when samples from the respective feeding vs. spawning grounds were compared (Alvarado-Bremer *et al.* 2005). Additionally, another gonadal index (GI1) (Mejuto and García-Cortés 2003a; in press) based on Kume and Joseph (1969) was tested for comparison. This index in general provides a similar overview, especially for areas where the active maturity-reproductive events were detected using GI2. However, the areas closer to the coasts of South America and some other squares 5ºx5º where a minor portion of maturity events had been identified using GI2, they were not identify within the same range when GI1 was used (figure 8). The resting conditions of large females observed in the eastern most areas of the South Pacific, also reported by other authors (Weber and Goldberg 1986; Ramon and Castro-Longoria 1994) suggest that the GI2 threshold used could misclassify some of the resting large females sampled in some of these 5ºx5º areas.

Simple box-plot diagrams of the GI2 by region, restricting the analysis to females with LJFL>=145 cm, would point to differences between zones. The results support the previous conclusions, but they also provide additional information on the distribution of the observations obtained in the different zones with a considerable number of positive outlier GI2 values in some of the areas (figure 9). The analysis of the GI2 data by month would also suggest the presence of monthly-seasonal reproductive behavior in some of the areas (figure 10). Zones PAC42 and 43 generally show low GI2 in all months. Zones PAC46 and 47 also exhibit low GI2 values in all months but with relevant positive outliers suggesting sporadic maturation events. However zones PAC44 and 45 show the highest GI2 in most of the available months. Zone PAC45 has high GI2 values from April to July and they are lower in September-October, which could suggest that this zone may be potentially reproductive under certain circumstances related to temperature, at least during the austral spring-summer. Unfortunately there is a lack of observations from other months. The gonad index by zone obtained in this paper, as well as the SRs patterns, indicate that the reproductive processes observed, particularly in PAC45, could explain the concentration of males in the catch of this zone. Similar, although more moderate events are also possible in zone PAC44. The lack of data from some of the months prevents us from obtaining final conclusions.

Data from the fleet of Hawaii would suggest a spawning period between March-July probably around the areas located at 17º-41ºN-141º-180ºW (De Martini et al. 2000). Kume and Joseph (1969) summarize information and indicate "*that swordfish move northwards form Chile to Peru during June to September* (austral winter). *Since all swordfish taken off Chile are immature females* (resting females?) *it has been further postulated that they move seaward to spawn from November through February*". They go on to say that "*it is obvious that some spawning occurs throughout every quarter of the year; it appears to be confined to the area west of 100ºW and, except for the southern summer, is infrequent between 10º north and south of the equator- since sampling coverage is extremely sparse north of 10ºN and south of 10ºS we cannot comment on the spawning activities of swordfish in these areas.* De Martini *et al.* (2000) indicate higher values of GIs during the first quarter than in the last quarter and reproductive activity was detected around Baja California between May-August (Northern spring-summer). Hinton and Deriso (1998) also indicate that the swordfish is active for reproduction between May-August in Baja California. Yabe *et al.* (1959) inferred that swordfish spawn throughout the wide area of the southern waters of the Subtropical Convergence Zone in the North Pacific Ocean –in Melanesia to the NE of Papua– (see figure 9 of this document) based on the information gathered from the collection of ripe ovaries, larvae and juveniles. Matsumoto and Kazama (1974) "*believed that there was evidence of a difference in spawning time in various parts of the Pacific, which was reflected by the seasonality of occurrence of larvae and juveniles. Spawning occurs in spring and summer (March-July) in the central Pacific and in spring (Sept-Dec) in* *the western South Pacific. They note that spawning takes place all year in equatorial waters and begins and ends 1 or 2 months earlier in the western Pacific in the Philippine-Formosa areas compared with the Hawaiian Islands area.*"

Other authors also indicate that "*larvae of swordfish occur in waters with SST hither than 24ºC*" (Nishikawa and Ueyanagi 1974). In the spawning area of swordfish evaluated by Yabe *et al.* (1959), historical SSTs (Igoss 2001) were always higher than this limiting temperature of 24ºC. In addition, observations indicate that larvae of swordfish are widely distributed over the southern waters of the Subtropical Convergence Zone and are more concentrated around tropical areas (Nishikawa and Ueyanagi 1974). Larval distribution was suggested as another indicator of spawning areas, and the authors described their respective findings and hypothesized about larvae drifting (Yabe *et al*. 1959, Nishikawa and Ueyanagi 1974, Lalli and Parsons 1993, Yabe *et al*. 1959, Sosa-Nishizaki and Shimizu 1990). In general, larval distribution coincides with the warmer water masses or warm currents drifting from intertropical areas to the western subtropical-temperate areas, which would even suggest a possible continuity or geographical proximity as regards larval distribution between the Pacific and Indian Oceans at the intertropical level. The latter work pointed out that most of the larvae were obtained in areas equivalent to PAC45 and smaller amounts in the western part of area PAC44. Areas equivalent to those located North of PAC45 also presented some larvae, owing probably to the Kuro Sivo drifting, as is the case of Gulf Stream in the North Atlantic (Palko *et al*. 1981). Young swordfish (<80 mm SL) were also located in similar latitude areas of the Pacific Ocean (Matsumoto and Kazama 1974).

The CPUE data by sex between zones would suggest that the CPUEs of females in PAC45 do not differ substantially from the CPUEs of females found in PAC44 (table 1). Both zones have warm temperatures at a sea layer of 50 m deep (mean annual temperature was taken from NOAA web page) although differences between the temperature ranges are obvious between the two (warmer in PAC45) and especially in relation to the other adjacent zones of the Pacific. However, a comparison of the CPUEs between zones did not provide a suitable interpretation of the data and the ratios between sexes (R_CPUE) by zones would appear to be a better approach to explain possible segregation processes associated with the reproduction of this species. The CPUE ratios by sex (R_CPUEn and R_CPUEw) indicate positive ratios for areas PAC44 and especially PAC45, differing from those of other zones (table 1). Additionally, the CPUE for zone PAC45 by size class clearly points to size group 125-165 cm LJFL (R_CPUEL2) as being the cause of the high CPUEn of males in this area, with R_CPUEL2 values showing that abundance-catchability of males is 7.7 times greater than females while, at the same time, exhibiting lower CPUEL2_F values in this zone than in other adjacent areas. These values would therefore suggest that the abundance-catchability of females in the range 125-165 cm LJFL in this area having a maturation-reproduction pattern could be somewhat lower than what was observed in other adjacent zones, especially in relation to temperate regions. At the same time, the CPUE by sex for zone PAC44 by size class also suggests that size group 125-165 cm LJFL (R_CPUEL2) may be the cause of the higher CPUEn of males, with R_CPUEL2 more moderate values (only 1.5 times grater) but also showing that larger males are 2.7 times more abundant than females for size group 170-205 cm LJFL (R_RCPUEL3). The segregation of males by size ranges, probably linked to the different temperature ranges of preference, would explain the different spawning patterns of the SRs observed between regions PAC45 and PAC 44. These values would therefore suggest that the abundance/catchability of females in the size ranges 125-165 cm LJFL in PAC45 as well as size range 170-205 cm LJFL in PAC44, having a maturation-reproduction pattern, could be somewhat lower than those observed in other zones, especially in relation to temperate regions. However, the abundance/catchability of males seems to be several times greater than females in these areas for specific size ranges where most of the reproductive male fraction is included (figure 11). These results shed light on the reproductive processes that take place in these regions as well as on the characteristic spawning-related sex-ratio at size (SRs) values (figure 5). Almost mimetic behaviour was observed for the Atlantic (Mejuto and García-Cortés 2003b; Mejuto 2007; Mejuto and García-Cortés in press).

In the areas where intensive reproductive processes are observed, mature females may sometimes be caught on the longline, and it is common to see one or more males chasing or courting the hooked mature female, right up to the side of the vessel until the female is hauled on board. These marauding males are often easily caught even with a simple harpoon. The reproductive behaviour of this species is therefore much more complicated that was previously thought. Elements such as external stimuli of attraction and courting behaviour in the reproduction zones should not be ruled out, in keeping with the descriptions of the many fishermen who have given these zones names alluding to this courting activity that had no scientific explanation. Quantitative data suggest that the females of this species spawn in specific areas and at certain times, the duration of which varies depending on the zone. The zones in which intense reproductive activity occurs are clearly dominated by males in the surface longline catch, especially in certain size ranges that include most of the reproductive fraction of males (figure 11).

The “gonad stage” of a total of 23,639 females was also examined as qualitative indicator. An analysis of all the sizes combined (50<=LJFL<=350 cm) revealed that the primordial stage and the stages not showing significant maturity (stages1, 2 and 3) dominated the observations in most regions. This may be attributed to the prevalence of juvenile females or resting adult females in most of the areas. Nevertheless, the qualitative analysis is capable of distinguishing between zones having very little or no maturation activity and zones with apparent reproductive activity. The occurrence of stages 4 and 5 in zones PAC44 and PAC45 was only 5.9% and 3.4% of the total females examined, respectively. In the other zones the occurrence of these stages is even lower and in zone PAC43 this occurrence is almost 0% (figure 12). There was a shift in the results when the analysis was restricted to only specimens LJFL>=145 cm. The occurrence of stages 4 and 5 in areas PAC44 and PAC45 reaches values of 11.5% and 18.0 % of the females examined, respectively (figure 12). These values are quite low in relation to those found in the high reproductive areas of the Atlantic with a similar approach, suggesting that the areas covered in this paper are probably not the most relevant maturity-spawning areas of the Pacific Ocean or reproduction process are more widespread geographically in the Pacific than in the Atlantic. Zone PAC43 continues to have an occurrence close to 0%. In any case, these results would indicate that reproductive activity is mostly carried out in certain areas (PAC45 and PAC44) and that there may also be sporadic or moderate reproductive events in some of the other areas adjacent to these. The observations would suggest that the macroscopic-qualitative identifications in general correlate quite well with the gonad index obtained (figure 13).

The preliminary results obtained for the Pacific match similar indicators observed for the Atlantic. However, the Pacific shows somewhat broader warm areas than the Atlantic, suggesting that the potential spawning areas of the Pacific could be expanded to include broader areas, especially to the east, than those reported for the Atlantic. Therefore, the potential SSB (*SSBp*) are more likely to become effective SSB (*SSBe*) than in the Atlantic because more favourable thermal conditions are generally observed in the Pacific for these processes. This situation could be even more wide-ranging during El Niño events. Some of the intertropical areas not yet covered by the sampling -west of 170º W- would probably concentrate an important fraction of the reproduction processes of the Pacific swordfish, but this should be confirmed in future research if observations are available. The intertropical central Pacific areas (PAC45–44) show important reproductive processes. Additionally, some sporadic-seasonal maturity processes could also be possible in some areas, taking advantage of the seasonal-local expansions of the warm isotherms. However, these maturation events would be minor in these areas in relation to warmer areas located within the central and western part of the intertropical band. Studies done to establish the reproduction parameters of swordfish should avoid areas with sporadic maturation events, or areas near the limits of the maturity-spawning regions affected by the local-temporal abundance of resting females or just the sporadic presence of larger mature females, because some of these reproductive parameters obtained - such as $LJFL_{50}$- could be biased, as was pointed out in the case of the Atlantic.

The suitability of macroscopic indices of gonadal development as indicators for defining the potential reproductive areas of swordfish has sometimes been questioned, suggesting that the areas where female gonad development takes place could be different from those areas where the spawning processes eventually occur. The wealth of literature on the reproductive behaviour of the swordfish in the different oceans (see previous references and the introduction) has confirmed that the macroscopic indicators of females are linked to the oocytarian development observed histologically, with good approximations being found between both types of indicators and the thresholds defined. Moreover, unlike other species, the swordfish exhibits a characteristic and highly visible reproductive behaviour distinguished by the greater prevalence of reproductive males in addition to the practice of “marauding males” and “pairing up” in these zones. This reveals that the reproductive behaviour of this species is a complex and efficient process which makes good use of the favourable environmental variables, when the availability of energy is adequate prior to development. Furthermore, from the standpoint of biological energy efficiency, it is rather implausible that the gonadal development processes of this species would not to be related spatially and temporally to maturation-spawning processes, particularly if we consider that the finales stages of these processes take place within a short time frame, through successive spawning in batches with gonads weighing several kilograms in their final stages of maturity (Arocha 1997, 2002, 2007). In contrast, larval distribution is strongly affected by the drift produced by surface currents, which means that in some areas influenced by the strong warm currents, this larval drift might give rise to a geographically biased picture of the potential reproductive areas of this species.

The results obtained support the hypothesis of a very broad and probably *quasi continuous* maturity-spawning region linked to the warm waters of the central-western intertropical band (using 50 m deep temperature as a proxy indicator) as it was also observed in the Atlantic. At the same time, some sporadic or seasonal events may also take place the adjacent areas, taking advantage of the seasonal expansion of the isotherms northward and eastward during their respective periods in restricted areas of the North and South hemispheres, as was also pointed out for the Atlantic. These sporadic reproduction areas could be broader and more eastward in the Pacific than in the Atlantic. The thermal structure and larval distribution described by several authors suggest a plausible communication of spawners and/or larvae between Pacific and Indian regions throughout the intertropical band of both oceans because the continental barrier allows this communication *vs.* the case of Africa or America. Recent genetic studies done by several authors comparing samplings from different oceans have suggested a unique “Indo-Pacific” clustering (Kasapidis *et al*. 2008a, b). The stock structure for the assessment-management of the Pacific swordfish should consider, at least, the different fractions within each unit that are highly reproductive, feeding and transitional, which probably require broad geographical assumptions.

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Table 1. CUE in number (CPUEn), CPUE in weight (CPUEw), by sex (Males =”M”, Females=”F”) and ratios between CPUE by sex (males/females) in the Pacific, by zone and for each of the four size ranges defined: CPUEL1 = (50<=LJFL<125), CPUEL2 = (125<=LJFL<170), CPUEL3= (170<=LJFL<205), CPUEL4 = (205<LJFL<=350+).

Zone	CPUEN_F	CPUEW_F	CPUEL1_F	CPUEL2_F	CPUEL3_F	CPUEL4_F
PAC42	3,710	137,77	0,743	1,858	0,808	0,301
PAC43	7,051	302,00	0,537	4,173	1,578	0,763
PAC44	2,455	108,50	0,761	0,877	0,446	0,370
PAC45	2,700	49,64	2,063	0,266	0,247	0,124
PAC46	3,731	244,82	0,331	1,115	1,283	1,003
PAC47	6,999	474,16	0,404	1,845	2,727	2,023

Zone	CPUEN_M	CPUEW_M	CPUEL1_M	CPUEL2_M	CPUEL3_M	CPUEL4_M
PAC42	2,375	73,87	0,605	1,291	0,382	0,098
PAC43	6,776	219,75	0,734	4,843	0,947	0,253
PAC44	4,303	177,78	0,928	1,757	1,204	0,413
PAC45	5,131	100,08	2,670	2,057	0,366	0,038
PAC46	3,083	134,21	0,402	1,532	0,839	0,310
PAC47	4,903	234,27	0,449	2,092	1,776	0,586

Zone	R_CPUEn	R_CPUEw	R_CPUEL1	R_CPUEL2	R_CPUEL3	R_CPUEL4
PAC42	0,640	0,536	0,814	0,695	0,473	0,326
PAC43	0,961	0,728	1,367	1,161	0,600	0,332
PAC44	1,753	1,639	1,219	2,003	2,700	1,116
PAC45	1,900	2,016	1,294	7,733	1,482	0,306
PAC46	0,826	0,548	1,215	1,374	0,654	0,309
PAC47	0,701	0,494	1,111	1,134	0,651	0,290

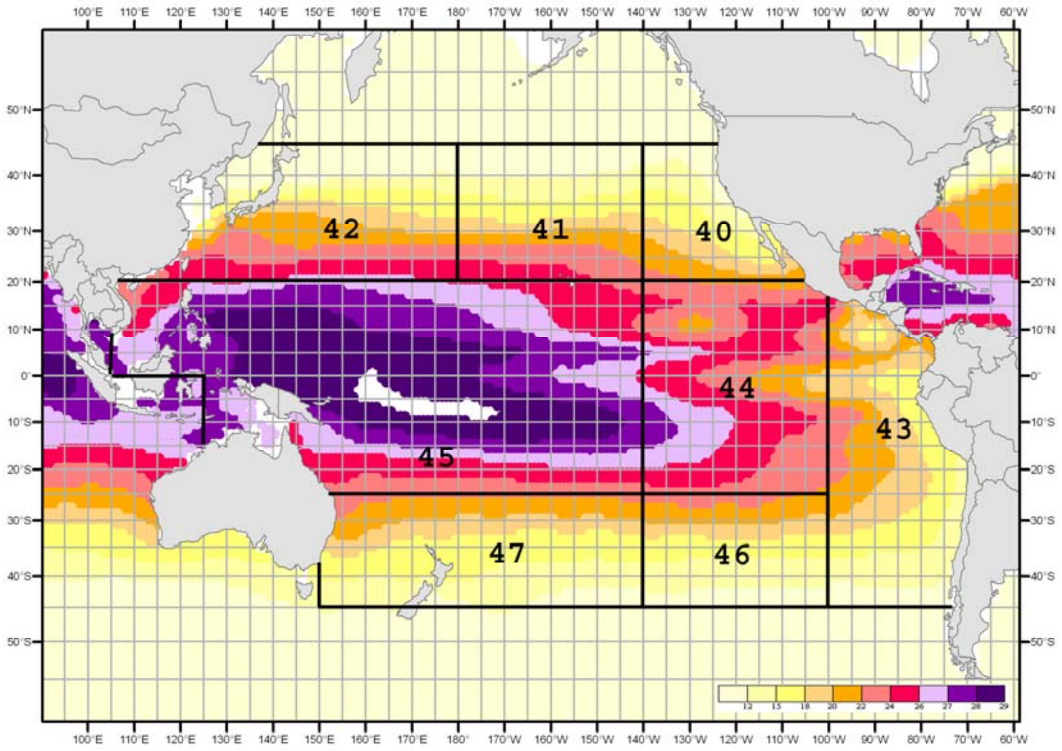


Figure 1. Definition of the different zones of the Pacific ocean used in the analyses and isotherms of sea temperature at 50 m deep (NOAA web page).

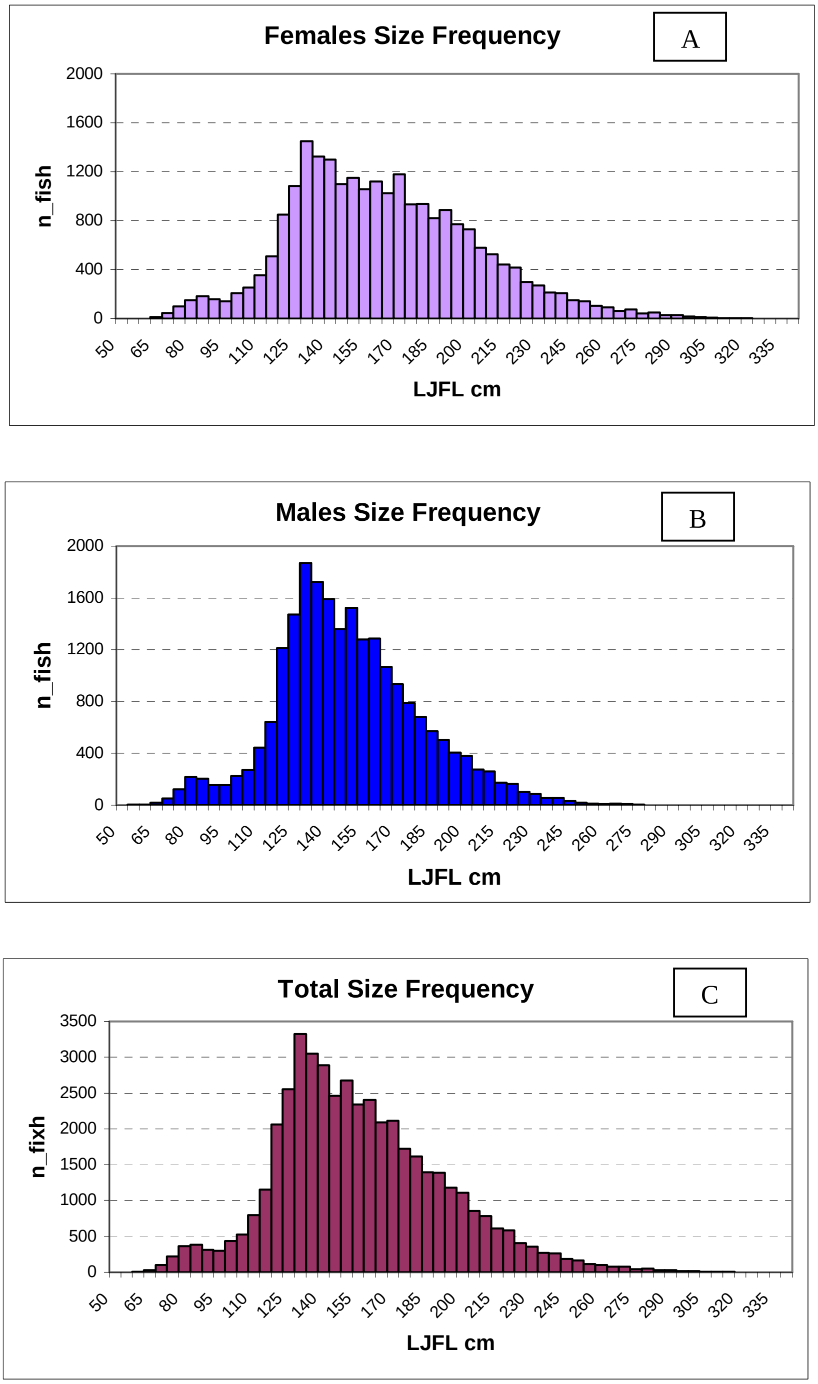


Figure 2. For all the Pacific zones combined and by size class (LJFL), (A): Histogram of the frequency (number of fish) of swordfish females examined for gonad index and sex-ratio. (B): Histogram of the frequency of swordfish males for sex-ratio. (C): Histogram of the frequency of total swordfish (males+females).

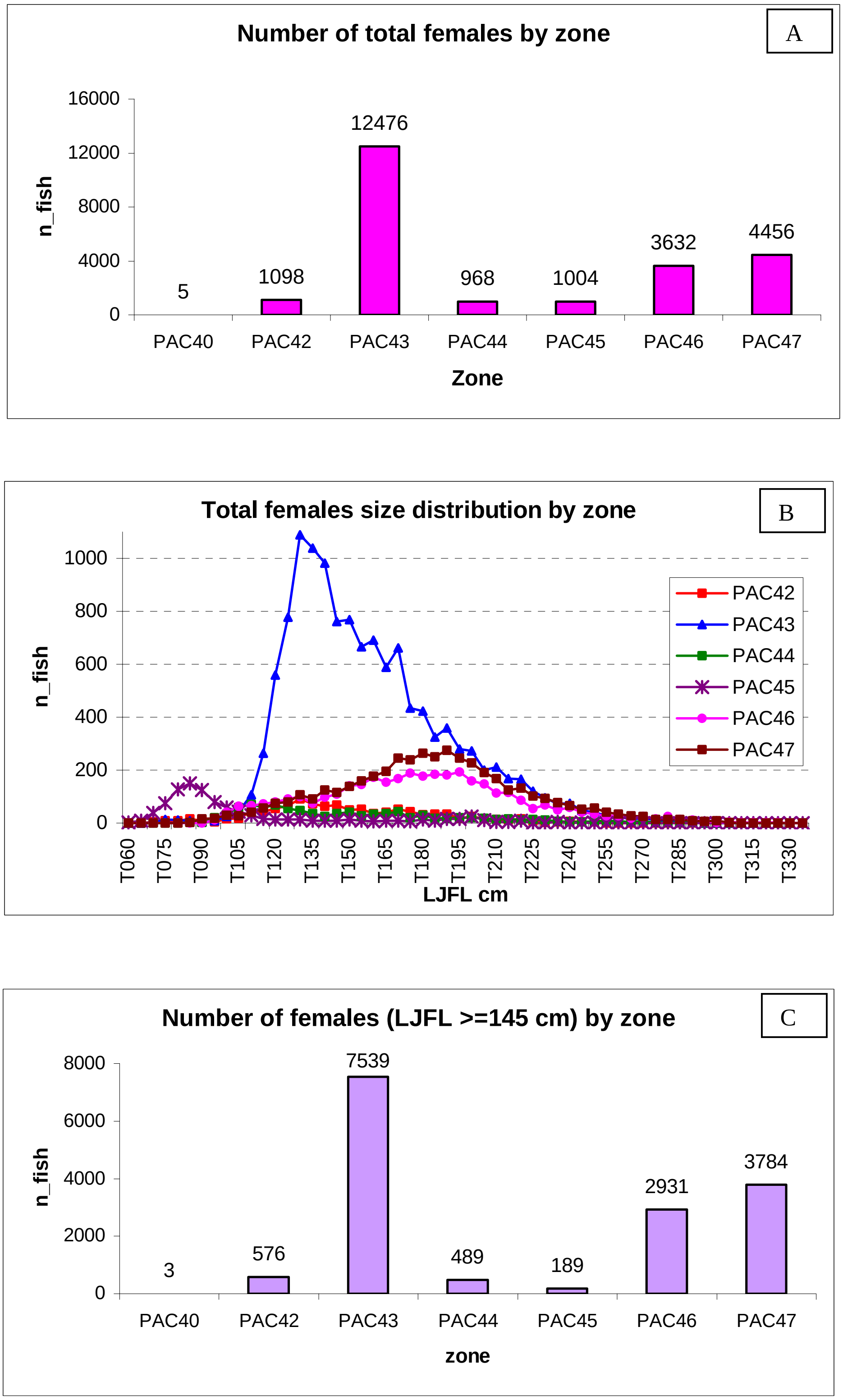


Figure 3. Number (A), size distribution (B) of total swordfish females sampled in the Pacific by zone and (C) number of swordfish females LJFL>=145 cm by zone.

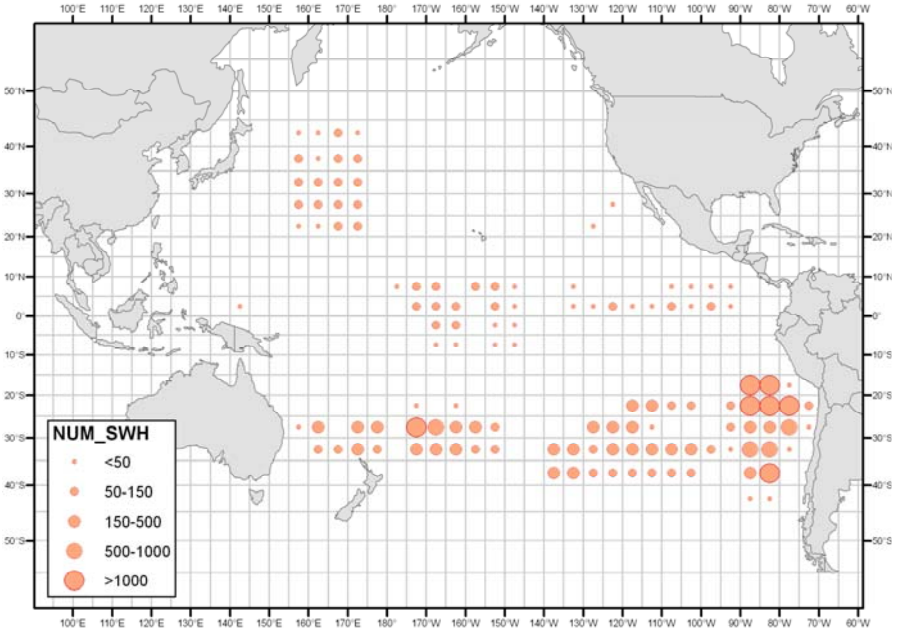


Figure 4. Geographic location and number of observations in the Pacific, in 5ºx5º squares, of females with available gonad index (GI2) data, for all years and months combined.

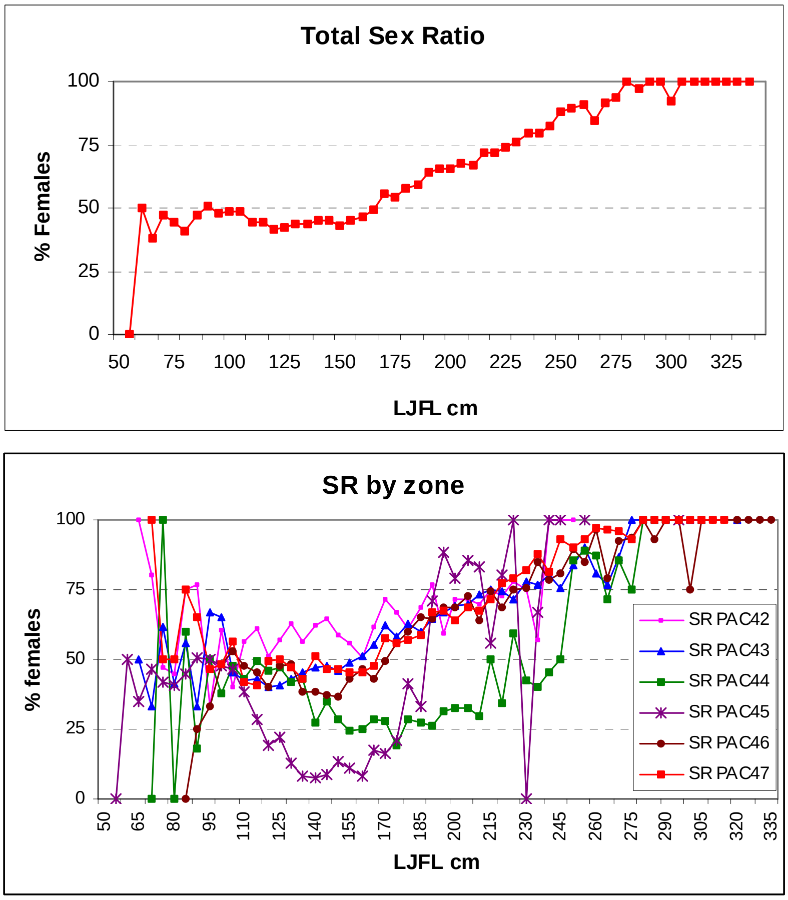


Figure 5. Sex-ratio at size for all zones combined (upper) and sex-ratio at size by zone (lower) in the Pacific areas defined.

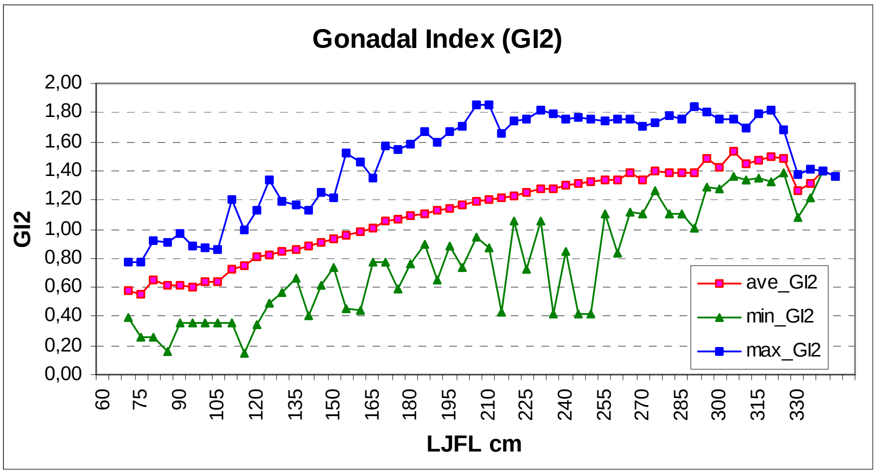


Figure 6. Gonad index (GI2)(ave_GI2: average GI2; min_GI2 :minimum GI2, max: maximum GI2) in relation to female size (50=<LJFL<=350 cm) obtained in the Pacific ocean. All observations combined.

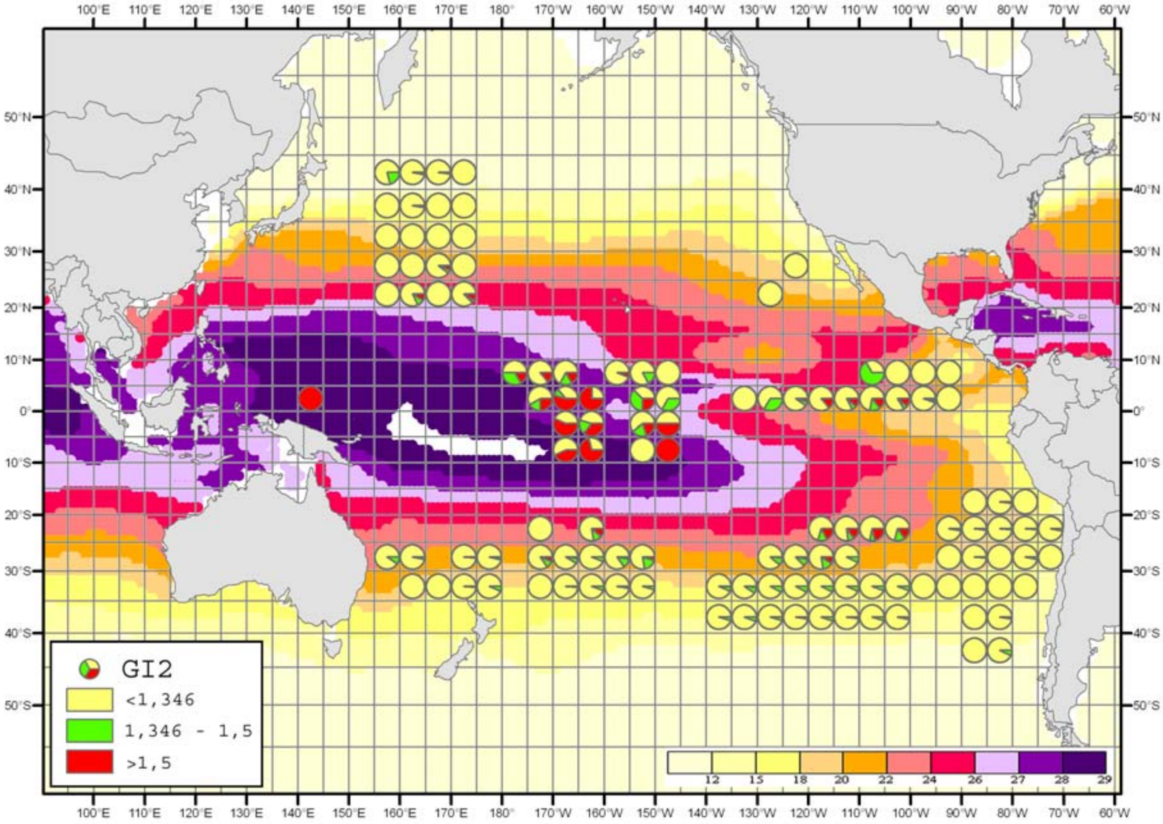


Figure 7. Ocurrence of each of the three gonad index (GI2) ranges defined, in each 5°x5° square observed in the Pacific ocean, for females with sizes LJFL>=145 cm and for all observations combined.

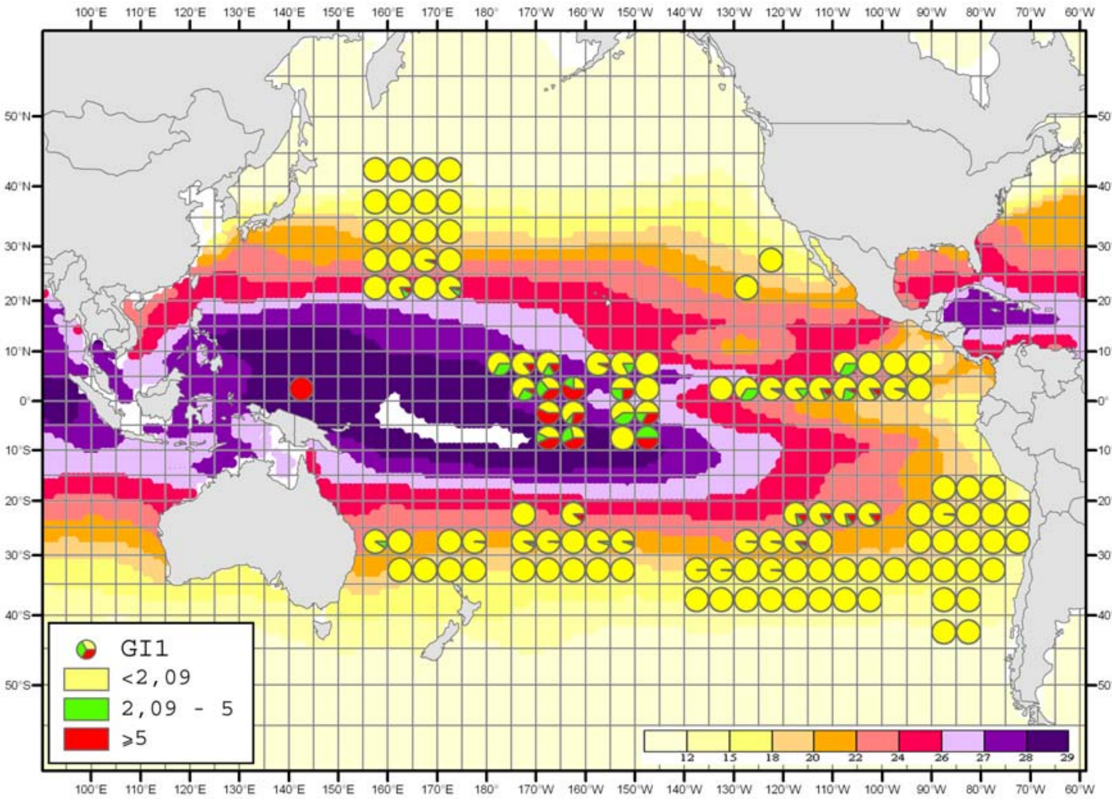


Figure 8. Ocurrence of each of the three GI1 gonad index ranges defined (GI1 from Mejuto and García-Cortés 2003a, in press), in each 5ºx5º square observed in the Pacific ocean, for females with sizes LJFL>=145 cm and for all observations combined.

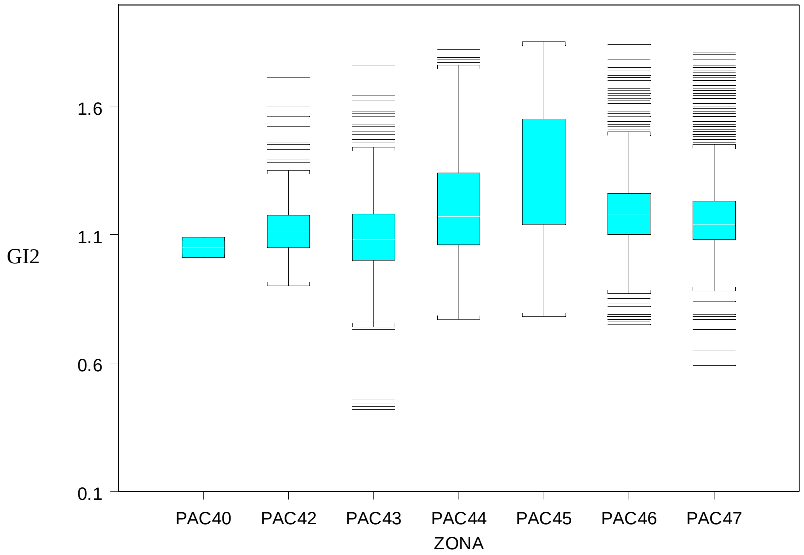


Figure 9. Box-plot of the GI2 gonad index values by zone for females with sizes LJFL>=145 cm, for all the months and years combined (S-PLUS 1997).

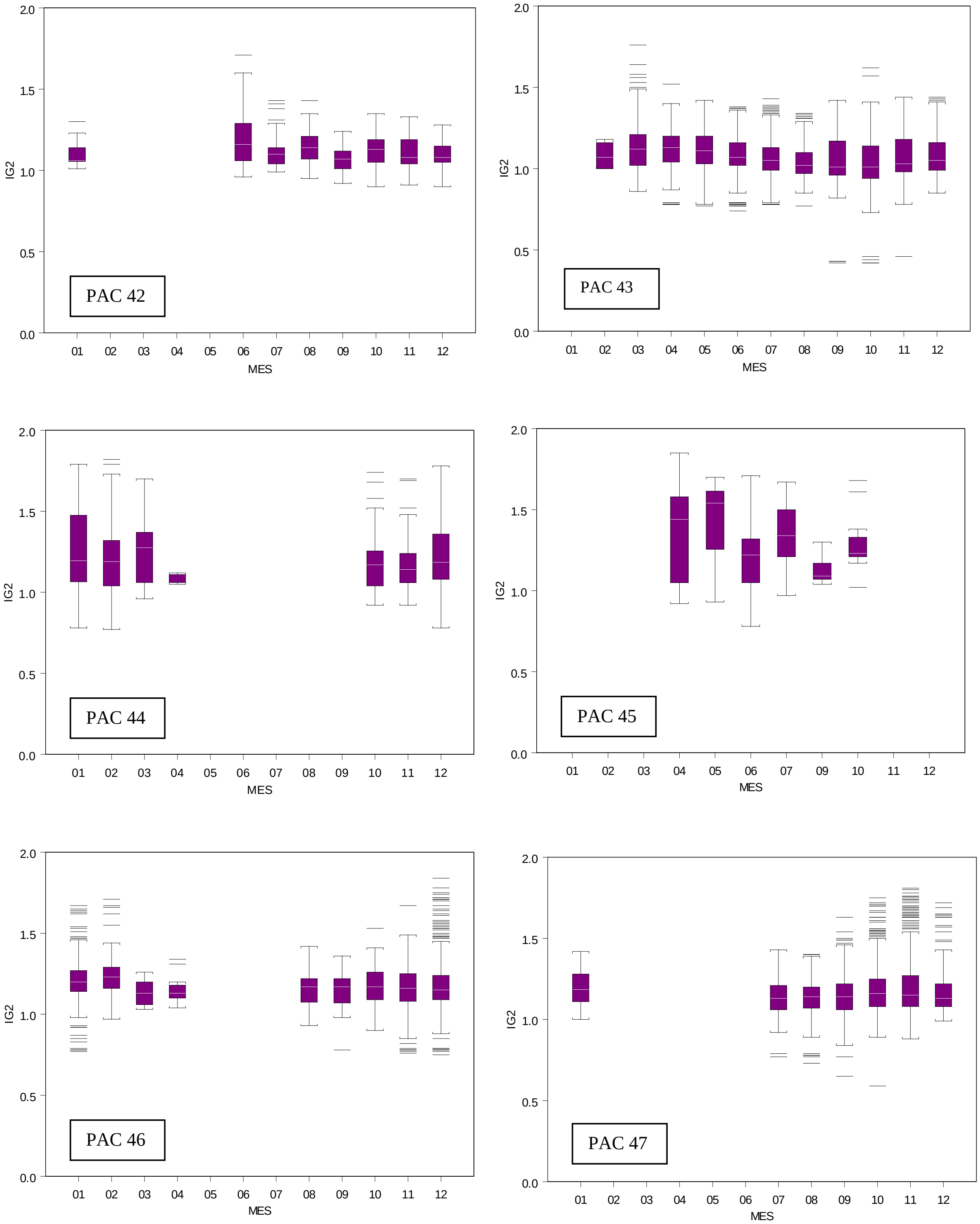
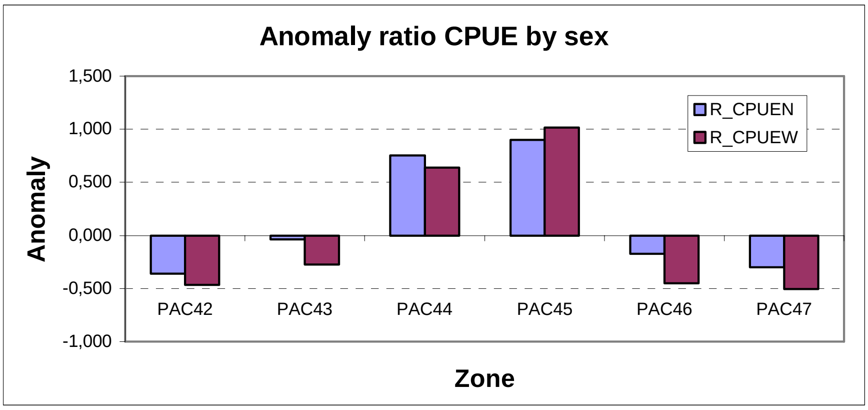


Figure 10. Box-plot of the GI2 (=IG2) gonad index for females with sizes LJFL>=145 cm, by month (=mes) and zone defined (S-PLUS 1997).



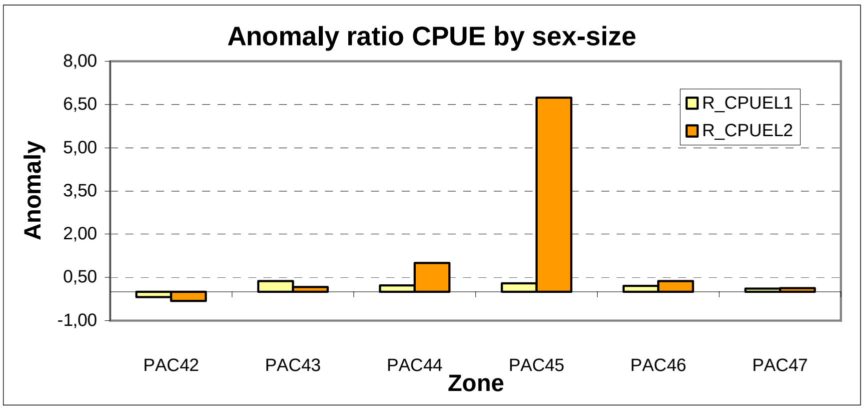


Figure 11. Anomalies by zone of the ratio between CPUEs by sex (males/females) in number of swordfish (R_CPUEN) and in kilograms of round weight (R_CPUEw) (upper). Anomalies of the ratio between CPUEs in number of swordfish for size class of 50-120 cm LJFL (R_CPUEL1) and 125-165 cm LJFL (R_CPUEL2) (lower).

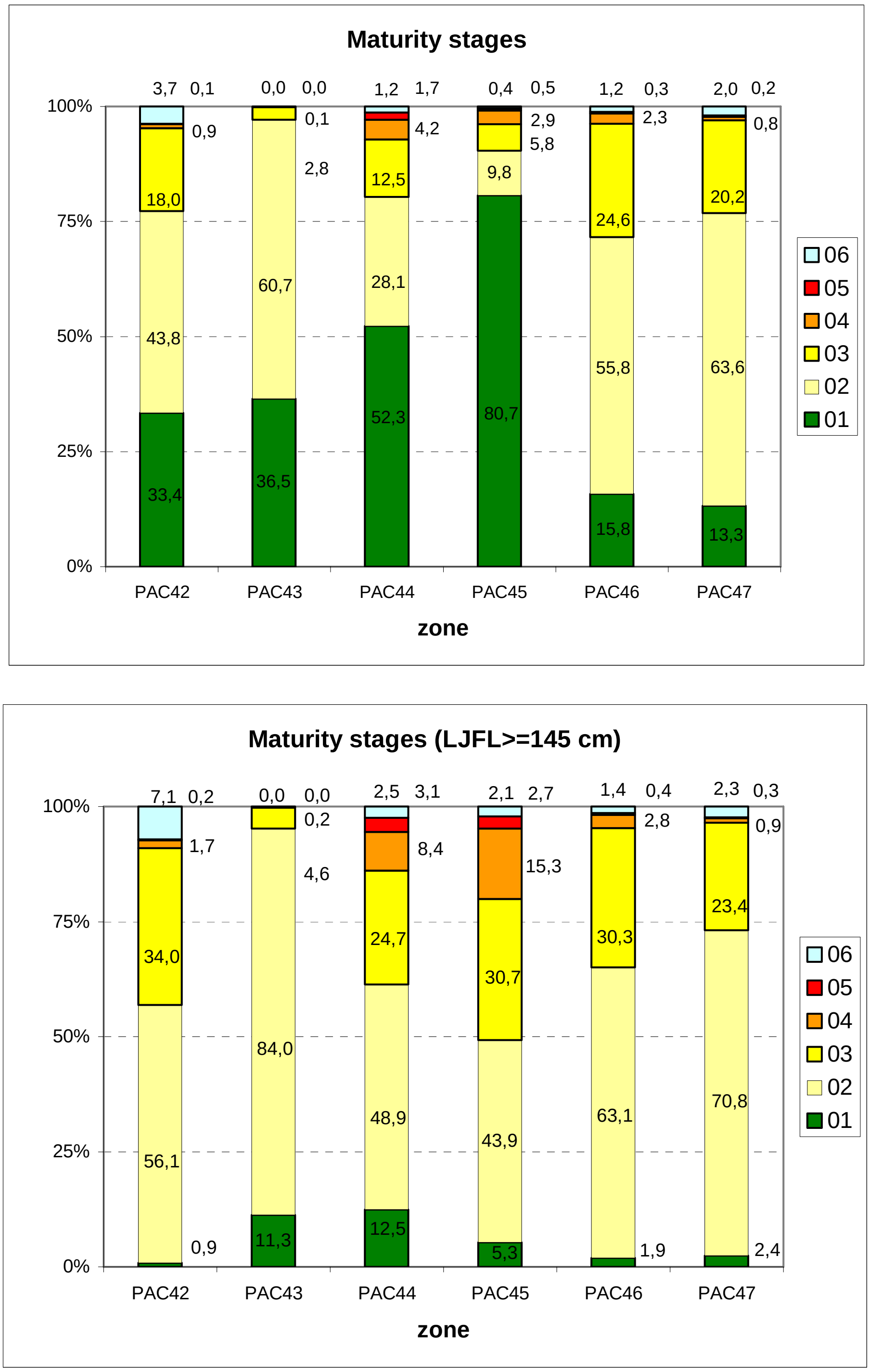


Figure 12. Percentage of swordfish females presenting each of six maturity stages in each of the defined zones in the Pacific. Upper panel: all sizes included. Lower panel: sizes LJFL>=145 cm.

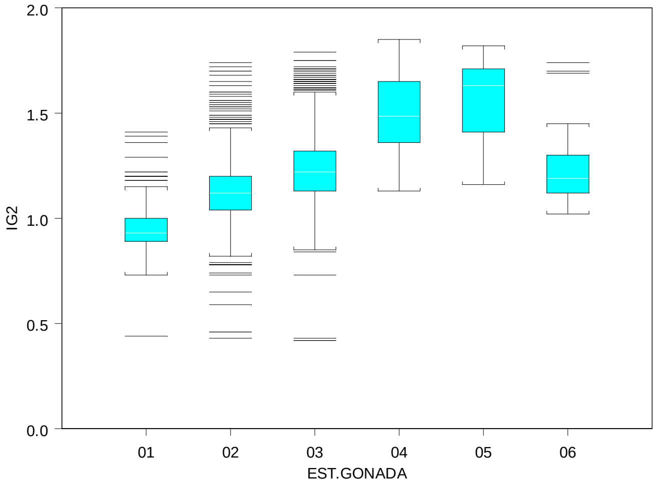


Figure 13. Box-plot diagram of the gonad index (GI2=IG2)) in relation to each of the 6 different maturity stages (EST_GONADA) identified in sizes LJFL>=145 cm in the Pacific ocean.