

Management Implications In Using Spawning Stock Biomass As A Proxy For Total Egg Production In Highly Fecund Species: The Swordfish Case.

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ABSTRACT

Swordfish is one of the most economically important highly migratory species in the northwestern Atlantic. The high level of fishing and declining catches in recent years fish have prompted managers to impose regulatory measures to avoid recruitment overfishing. The lack of adequate data has prevented the development of more precise management regulations. Spawning stock biomass is often used as a proxy for total egg production in spawner-per-recruit analysis, but this type of analysis does not take into consideration the dynamics of egg production. In highly fecund species, like swordfish, changes in egg production increase with age, thus the use of spawning stock biomass fails to recognize the higher seasonal fecundity of older fish. To demonstrate this, the effect of fishing on the reproductive potential of the northwestern Atlantic swordfish stock on a per-recruit basis was analyzed using the Spawning Potential Ratio (*SPR*) based in terms of spawning stock biomass-per-recruit ($SPR_{SSB/R}$) and as egg production-per-recruit ($SPR_{EP/R}$). Pronounced differences were observed in the estimation of $SPR_{SSB/R}$ and $SPR_{EP/R}$, due to the non-linear nature of the egg production curve over the lifetime of an individual swordfish. This results in a reduction of the $SPR_{EP/R}$ with respect to the $SPR_{SSB/R}$ and causes an overestimation up to 1.5 times of any target $F_{\%SPR}$ (i.e., fishing mortality of a % of *SPR*). The effect on other highly fecund species, like billfish, is also discussed. Another aspect considered was the effect of fishing effort (deployed by the U.S. and Venezuelan longline fleet) spatial distribution on the spawning stock. It was observed that the seasonal fishing effort was clustered from January to May in the oceanic area, time when most of the spawning takes place in that area. It became evident that the reproductive output of the swordfish stock will be strongly affected by the high concentration of the fishing effort on the spawning grounds.

KEY WORDS: Spawning Potential Ratio, swordfish, fishery management.

INTRODUCTION

In fisheries management it is necessary to establish proximate goals to guide the decision processes to achieve certain socioeconomic benefits while preserving the production potential of the fishery resource (Pope 1983). These proximate goals are referred to as biological reference points by institutions concerned with fisheries management (ICES 1984). Most biological reference points based on reproductive output are derived from spawner-per-recruit or spawning stock biomass per recruit (*SSBPR*) analysis, which are an extension of the yield-per-recruit model (Gabriel et al. 1989). Goodyear (1990) presented a rationale for using *SSBPR* as a biological measure of the reproductive potential of the stock, where the ratio of the spawning stock-per-recruit of the population under exploitation (*SSBPR_{fished}*) to that in the absence of fishing (*SSBPR_{unfished}*) represents the spawning potential ratio (*SPR*). Consequently, it can be used as an index of the resilience of a population to fishing and other compensatory changes, where the basic assumption lies in the requirement for the existence of density dependence in population renewal. Reference points from *SPR* analysis can be expressed as the fishing mortality rates that result in a given percentage of the maximum *SPR* ($F_{\%SPR}$) and are commonly used as targets or thresholds in fisheries management strategies (Mace and Sissenwine 1993).

The fish stocks that are currently managed based on $F_{\%SPR}$ measures in the northwestern Atlantic are mostly based on the spawning stock biomass per recruit method (Rosenberg et al. 1994). This approach tends to ignore the details of the reproductive dynamics of the stock in species exhibiting multiple spawning, and the increase in the number of seasonal spawns with age. In highly fecund species, like swordfish, spawning stock biomass per recruit does not take into consideration the higher seasonal fecundity of older fish, as fecundity is not always linearly related to body weight, and body weight is affected by seasonal exploitation (Arocha 1997). Therefore, the full potential reproductive output may not be adequately measured by spawning stock biomass computations. Consequently, it is preferable to use *SPR* ratios in terms of actual egg production, rather than in terms of spawning stock biomass.

In this paper, biological reference points based on the reproductive output of swordfish will be used to measure the effect of fishing on the reproductive potential of the stock on a per-recruit basis. The effect on other highly fecund species, like billfish, is also discussed. The influence of spatio-temporal dynamics of fishing effort on swordfish spawning will also be considered and their implications for management will be discussed.

METHODS

To measure the effect of fishing on the reproductive potential of the stock on a per-recruit basis, the rationale developed by Goodyear (1993) is used. This is done first in terms of spawning stock biomass-per-recruit (*SSBPR*) and second as egg production-per-recruit (*EPR*). *SSBPR* is calculated as the total spawning stock biomass (*SSB*) divided by number of initial recruits and total *SSB* is obtained by summing *SSB* over all ages,

$$SSB = \sum_{i=1}^n SSB_i = m_i \overline{N}_i \overline{W}_i \quad (1)$$

where m_i is the maturity fraction at age i for a given age (Arocha 1997) expressed as,

$$m_i = \frac{1}{1 + e^{-1.236(\text{Age} - 5.03)}} \quad (2)$$

\overline{N}_i is the average abundance in numbers at age i and \overline{W}_i is average weight at age i . \overline{N}_i is calculated by assuming an exponential mortality function such that,

$$\overline{N}_i = \frac{N_i(1 - e^{-(F_i + M)})}{(F_i + M)} \quad (3)$$

where M is the instantaneous rate of natural mortality, F_i is the instantaneous fishing mortality at age i , and N_i is the number of survivors to age i .

When estimating *SPR* in terms of egg production-per-recruit (*EPR*) equation (1) can be substituted by total potential fecundity (E), such that egg production (*EP*) can be calculated as,

$$EP = \sum_{i=1}^n EP_i = m_i \overline{N}_i \overline{E}_i \quad (4)$$

where the new variable is average total potential fecundity (\overline{E}_i) at age i , and is estimated as the product of batch fecundity at age i (Bf) given as,

$$Bf_i = 1846990 + 77.407 \text{ Age}^{4.637} \quad (5)$$

and the average spawning frequency for swordfish during the main spawning season (Arocha 1997).

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The spawning potential ratio (*SPR*) was then calculated as the ratio of spawning stock biomass-per-recruit in the fished population ($SSBPR_{Fished}$) or as the ratio of egg production-per-recruit in the fished population (EPR_{Fished}), to that of the population in the absence of fishing ($SSBPR_{F=0}$ or $EPR_{F=0}$). Computations were made using a modified version of the yield-per-recruit model (Thompson and Bell 1934). The model required four sets of data entry: the average weight at age i (\bar{W}_i), the maturity fraction of females at age i (m_i), the total potential fecundity at age i (E_i) and the proportion of fish susceptible to capture from the gear at age i (s_i) which was used in computing age-specific fishing mortalities as $F_i = s_i AF$. The average weight at age (\bar{W}_i) and the total potential fecundity at age (E_i) were varied between 0.5 and 1.5 times the input values, such that the uncertainty in the *SPR* estimates would be approximated by 1000 bootstraps.

To estimate *SPR* based on *SSBPR*, the model uses the maturity fraction of females at age i (m_i) and the average weight at age i (\bar{W}_i) that is obtained by a two step process: 1) obtain length-at-age from the sex-specific growth function, and 2) convert length-at-age to weight-at-age from the weight-length equation. The parameters used in the sex-specific growth function and the weight-length equation were those obtained by Ehrhardt et al. (1996).

The proportion of fish which is susceptible to capture by the gear at age (s_i) was the average partial recruitment for 1992 - 1993 (PR_{92-93}) used in ICCAT's 1994 swordfish stock assessments (ICCAT 1995). A constant natural mortality rate (M) of 0.2 per year was assumed to be uniformly distributed over the year and over the ages throughout the cohort. It follows that the total mortality rate is, $Z_i = F_i + M$, which is used to compute the number of survivors between consecutive age classes:

$$N_{i+1} = N_i e^{-Z_i} \quad (6)$$

The analysis began at the age of entry to the fishery (age 1) and comprised 20 age classes with $N_1 = 1$ swordfish.

The effort in number of hooks deployed by the U.S. and Venezuelan longline fleet targeting swordfish during the 1990-1995 period, the relative gonad index (*RGI*) values and the mean diameter of mature oocytes in spawning areas obtained from Arocha (1997) were contrasted to view the effects of fishing on the northwestern Atlantic swordfish spawning stock. The northwestern Atlantic was divided latitudinally into temperate (35 - 55° N) and subtropical (13 - 35° N) areas, the latter was subdivided into two subareas: the offshore and the inshore (Fig. 1).

Since most of the effort deployed by the Venezuelan longline fleet targeting swordfish is localized south of 13°N, the majority of the effort deployed in the temperate and subtropical area is originated by the U.S. longline fleet.

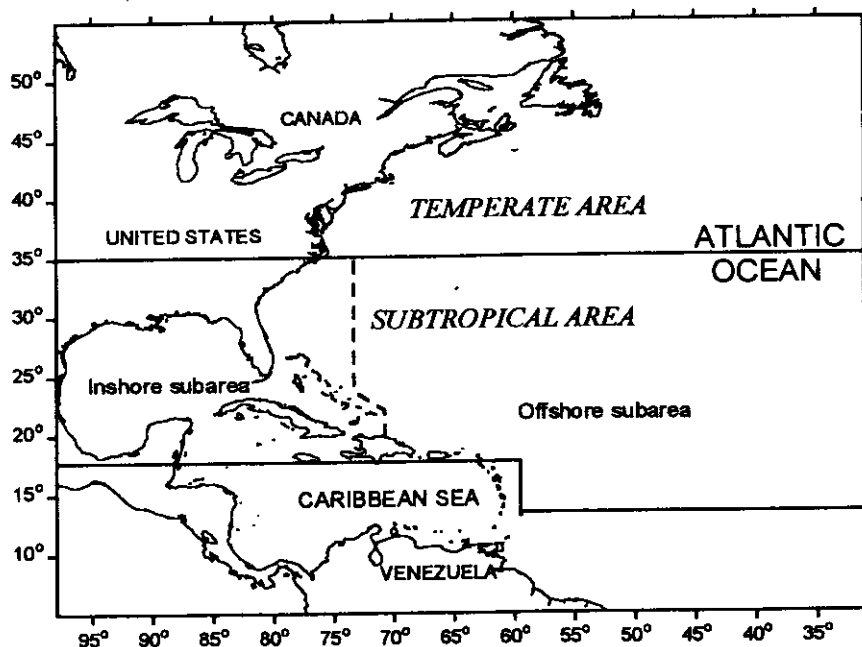


Figure 1. Map showing the limits of the temperate and subtropical areas and the limits of the two subareas within the subtropical area: the offshore and the inshore subareas.

RESULTS

Spawning Potential Ratio

The results of the *SPR* analysis produced a pronounced difference in the estimation of *SPR* using spawning stock biomass-per-recruit (*SSBPR*) compared to egg production-per-recruit (*EPR*) (Figure 2a,b; Table 1). As can be

observed from these figures, the highest difference between the *SPR* based on spawning biomass and that of *SPR* based on egg production occurs when fishing mortality reaches 0.13 which is close to ICCAT's $F_{0.1}$ estimate of 0.164 (ICCAT 1995). As fishing mortality increases further, the difference between SPR_{SSBPR} and SPR_{EP} declines monotonically as both ratios converge to zero. This is caused by the non-linear nature of the egg production curve over the lifetime of an individual swordfish in terms of relative spawning (Figure 3a). In swordfish, prior to full age at maturity, the increase in batch fecundity at age is minimal but increases markedly once full maturity is attained at age 8, while the relative *SSB* is linear throughout the life span of an individual.

As the numbers of older fish are removed from the fishery, the reproductive potential of the cohort will decline significantly due to the lesser ability of younger fish to produce larger number of eggs. This situation becomes more evident when the egg production of a cohort is contrasted against the *SSB* of a cohort under different fishing mortality rates (Figure 3b). Using three biological reference points based on fishing mortality rates ($F_{0.1}$, F_{max} and F_{1993}) obtained from ICCAT's swordfish stock assessments (ICCAT, 1995). At low levels of fishing mortality ($F_{0.1}$), cohort egg production at older ages remains high with respect to SSB_{cohort} at similar ages. As fishing mortality increases, the reduction in egg production at older ages becomes more conspicuous. At a high fishing mortality ($F_{1993} = 0.506$), it almost parallels the decline in SSB_{cohort} beyond age 7. At this level of exploitation the contribution of egg production of older fish (> age 8) becomes almost extinguished due to the absence of older fish, contributing to the sharp decline in the reproductive potential of the cohort (Figure 3b). The high mortality (F_{1993}) causes swordfish to concentrate reproduction at an earlier age, in this case shifting the age at maximum egg production from age 6 at low F levels ($F_{0.1}$) to age 5 at high F levels (F_{1993}).

Effect of Fishing Effort on the Spawning Stock

Another factor that needs to be considered in management is the effect of spatial distribution of fishing effort on the spawning stock. Examining the spatio-temporal distribution of effort in the study area with respect to the spatio-temporal spawning pattern, the fishing effort may change the reproductive potential of the stock in the near future (Figure 4).

In the northwestern Atlantic, the effort (*i.e.*, number of hooks) deployed by the U.S. longline fleet for the period of 1990 - 1995 showed marked seasonal concentration in the temperate and subtropical areas (Figure 5a,b). In the temperate area, the effort is clustered during the summer and fall months (June - November), while the effort for the remainder of the year is below 5% of the total effort for this area (Figure 5a). Because no spawning activity is observed in this

area as demonstrated by the low mean *RGI* across all months, the fishing effort does not seem be inflicting pressure on the reproductive output of the stock present in this area.

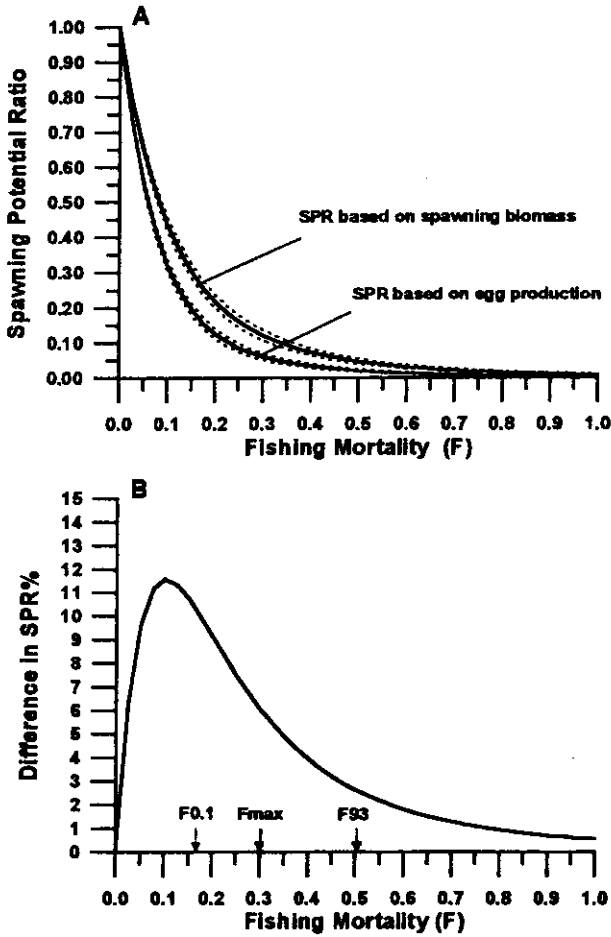


Figure 2. (A), Spawning potential ratio (*SPR*) of northwestern Atlantic swordfish at different levels of fishing mortality (*F*) based on spawning biomass and egg production estimates. (B), Percent difference in *SPR* (i.e., $SPR_{SSBPR} - SPR_{EP}$) at different biological reference points based on fishing mortality rates.

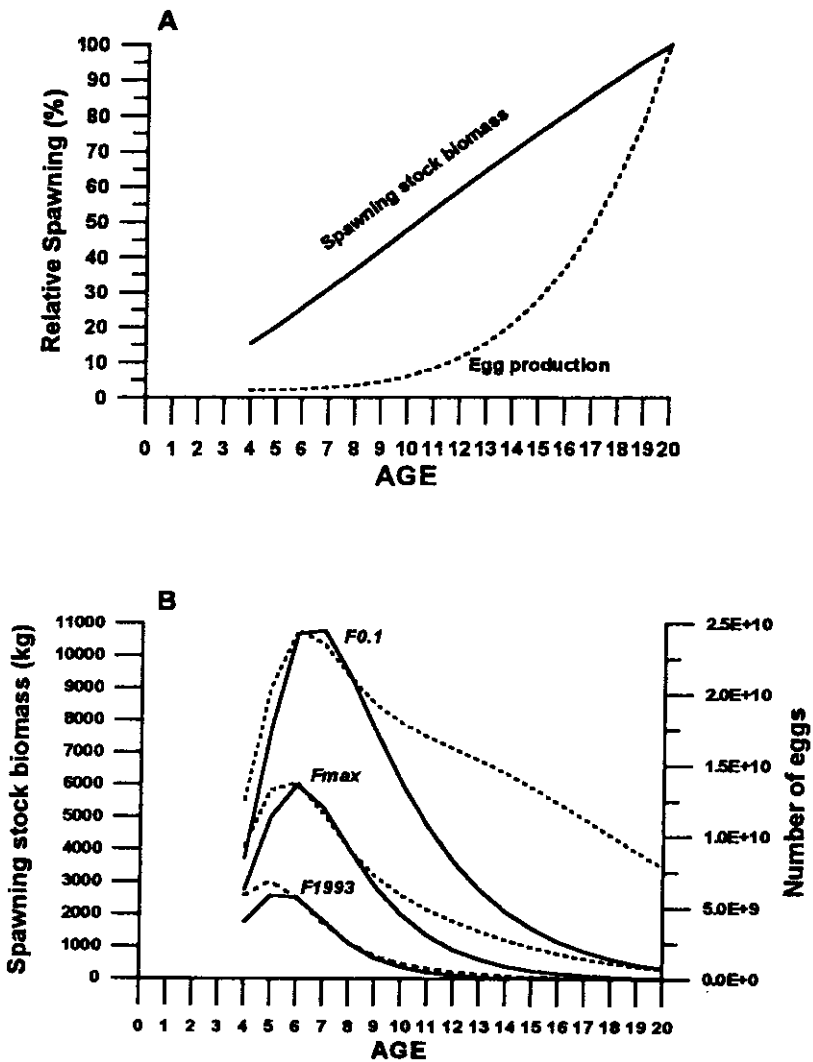


Figure 3. (A), Relationship between age and relative spawning, based on spawning stock biomass and egg production. (B), Reduction of egg production and spawning stock biomass under different biological reference points based on fishing mortality rates over the age structure of a cohort.

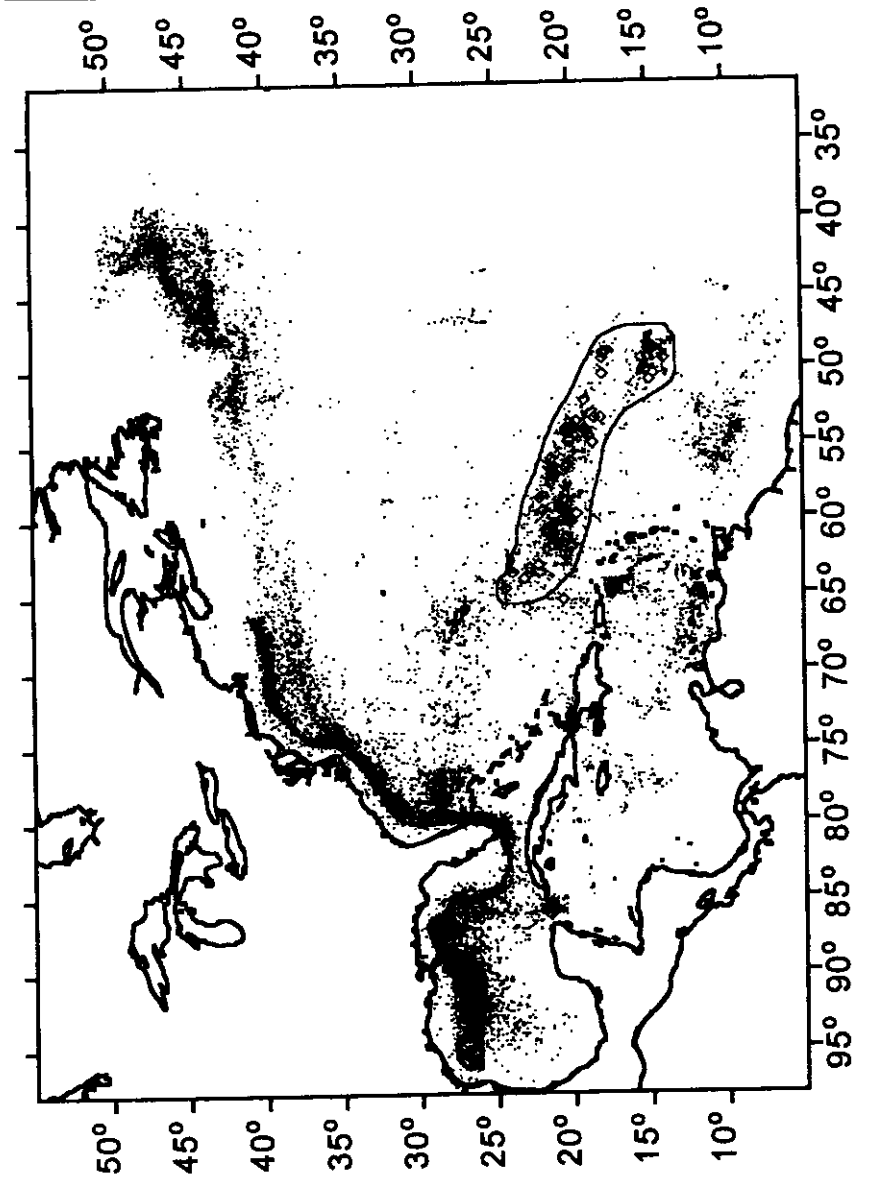


Figure 4. Map showing the spatial distribution of the fishing effort represented as positive swordfish sets (small dots) during 1990-1995, and the spawning areas (open rhombs and circled area).

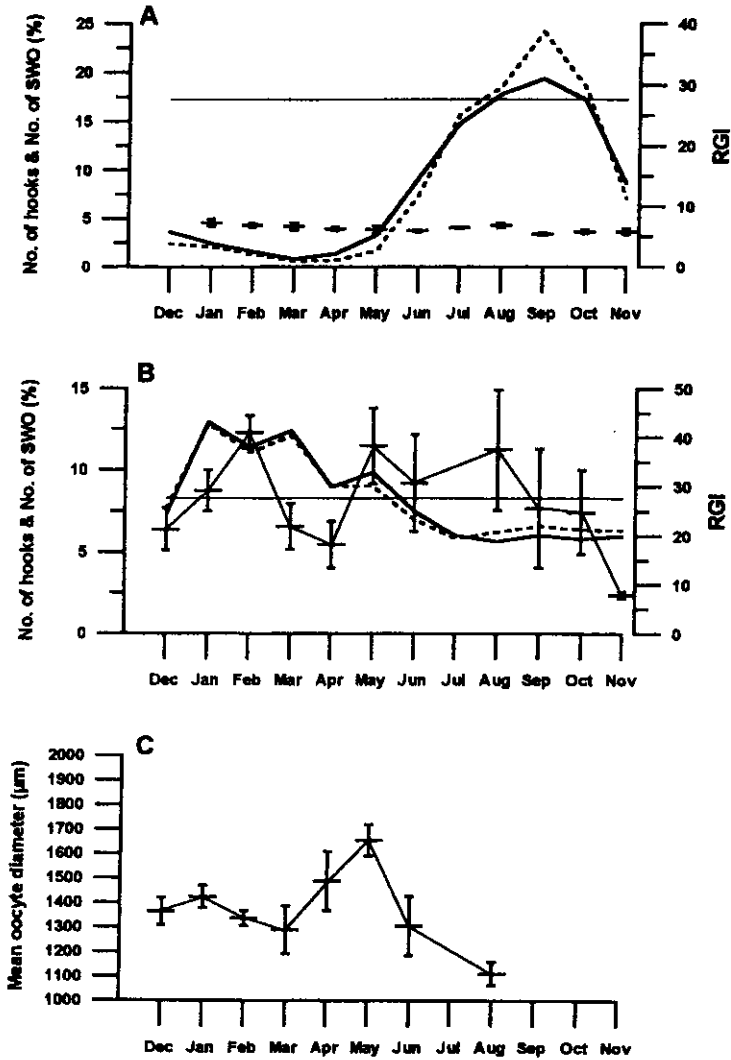


Figure 5. Monthly variation of the number of hooks in percentage (solid line) and the number swordfish in percentage (dashed line) caught by the U.S. longline fleet between 1990 and 1995, and monthly variation in the mean monthly RGI for the temperate (A) and subtropical (B) areas. $RGI_{spawning}$ is represented by the dotted line in each area. (C), Monthly mean diameter of the most developed group of oocytes in sexually active female swordfish in the subtropical area. Means are denoted by a wide bar and *s.e.* by a narrow bar.

Table 1. Spawning Potential Ratios (%) based on spawning stock biomass (*SSB*) and egg production (*EP*) assessments under different biological reference points based on fishing mortality rates (BRP_F) obtained from ICCAT (1995) swordfish stock assessments.

BRP_F	<i>SPR</i> (%) based on <i>SSB</i>	<i>SPR</i> (%) based on <i>EP</i>
$F_{0.1} = 0.164$	27.71	17.32
$F_{max} = 0.300$	12.18	6.07
$F_{1993} = 0.506$	4.54	1.95

In the subtropical area, the seasonal fishing effort is clustered around winter and spring (January - May), while the amount of effort concentrated in the area during the rest of the year accounts for less than 7% (Figure 5b). Spawning in this area appears high during most of the year as mean *RGI*s are close to $RGI_{spawning}$ (27.64; Arocha 1997). However, when the seasonality of imminent spawning (represented by the mean diameter of the most developed group of oocytes) is taken into consideration, the spawning seasonality coincides with that of the highest concentration of effort (Figure 5c). The distribution of effort with respect to spawning becomes clearer when it is separated into the two subareas within the subtropical area: the offshore and the inshore subareas. Over 20% of the total effort in the offshore subarea is clustered between January and March, coinciding with the incidence of females with high mean oocyte diameters which indicates imminent spawning (Figure 6a,b). A similar situation occurs in the inshore subarea. Although effort does not show a clear maximum as it does in the offshore subarea, it is higher between January and June which coincides with the increased incidence of females in state of imminent spawning (Figure 7a,b).

DISCUSSION

Spawning Potential Ratio

It has become evident that when estimating *SPR* based on egg production, the reduction in the spawning potential of a cohort is reduced to a lower value than when it is estimated based on spawning stock biomass. This results in an overestimation of any target $F_{\%SPR}$ that managers may wish to consider to maintain the stock above a given replacement level. The level commonly used as a basis for defining overfishing threshold in the U.S. is to maintain on average a 20% *SPR* (i.e., $F_{20\%SPR}$), but this level may change depending on the life history of the species subjected to exploitation (Mace and Sissenwine 1993).

Mace (1995) using data from 1992 swordfish stock assessments estimated that median %*SPR* was 8.1% and indicated that compared to other species in which the median *SPR* has been calculated, the value obtained was relatively low. The same author suggested that species with large body sizes that mature late (e.g., Atlantic cod, swordfish) seem to have low replacement %*SPR*.

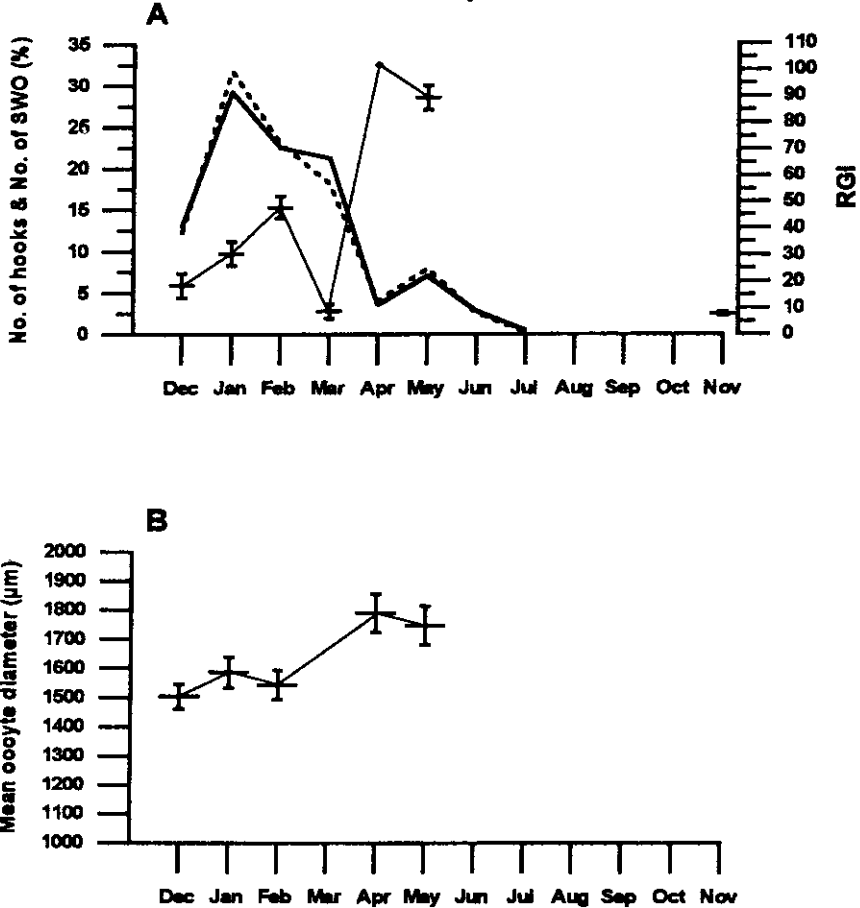


Figure 6. (A), Monthly variation of the number of hooks in percentage (solid line) and the number swordfish in percentage (dashed line) caught by the U.S. longline fleet between 1990 and 1995 in the offshore subarea, and monthly variation in mean *RGI*. (B), Monthly mean diameter of the most developed group of oocytes in sexually active female swordfish in the offshore subarea. $RGI_{spawning}$ is represented by the dotted line in each area. Means are denoted by a wide bar and *s.e.* by narrow bars.

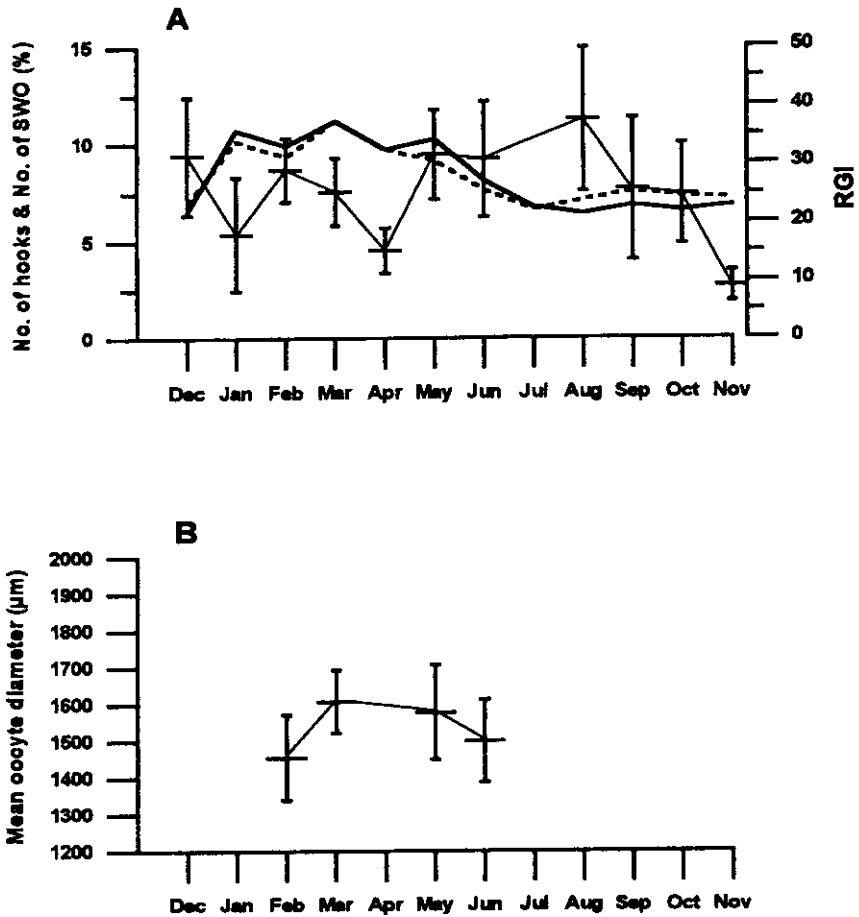


Figure 7. (A), Monthly variation of the number of hooks in percentage (solid line) and the number swordfish in percentage (dashed line) caught by the U.S. longline fleet in the inshore subarea between 1990 and 1995, and monthly variation in mean *RGI*. (B), Monthly mean diameter of the most developed group of oocytes in sexually active female swordfish in the inshore subarea. *RGI*_{spawning} is represented by the dotted line in each area Means are denoted by a wide bar and *s.e.* by narrow bars.

Assuming that swordfish may have a low replacement %*SPR* located around 10%. The corresponding *F* derived from *SSB* will be overestimated by 1.5 times relative to those derived from egg production. Clearly, if these replacement levels are to be considered as overfishing thresholds, the stock may be subjected to high levels of exploitation that may exhaust much of its compensatory capacity. Thus, the overestimation of $F_{10\%SPR}$ caused by SPR_{SSB} may be risk-prone.

In other highly migratory species like billfish and bluefin tuna, little is known about their reproductive output with the same detail as in swordfish, with the exception of sailfish from the Straits of Florida (Jolley 1977). Nevertheless, in billfish and bluefin tuna, there is little information about their reproductive spawning pattern, *i.e.*, whether the species have determinate or indeterminate fecundity (Hunter and Macewicz 1985).

However, from the published literature on blue marlin (Erdman 1968), white marlin (Baglin 1979), sailfish (Jolly 1977) and bluefin tuna (Baglin 1981), and from frequency distributions of oocyte diameters from mature, ripe and regressing ovaries in sailfish, bluefin tuna, longbill spearfish and blue marlin from the western central Atlantic (personal observations), it can be deduced that the above species can be considered highly fecund species, as they all have ripe gonads weighing more than 8 kg. Furthermore, their fecundity pattern can be considered indeterminate. This is based on the absence of a gap between the permanent stock of oocytes and the maturing batch, which can have several modes (3 - 4) as observed in the frequency distributions of oocyte diameters of the species considered (personal observations).

It can be inferred from the characteristics above, that billfish and bluefin tuna may have a similar spawning pattern as swordfish. That is, a relative low fecundity at ages prior to full maturity (100%); once full maturity is reached – fecundity increases markedly with increasing age (Arocha 1997). Thus, the removal of fully mature fish by the fishery will severely impact the reproductive output of these species, which may exhaust much of its compensatory capacity. This situation may be the cause why the bluefin tuna stock from the North Atlantic has not been able to fully recuperate.

Effect of fishing effort on the spawning stock

Based on the results presented here, the reproductive output of the stock may be strongly affected by a high concentration of fishing effort in the spawning grounds. The fact that fishing effort is clustered in the reproductive season imposes major concern to managers. This should be viewed in the context of a recent re-distribution of effort: fishing that was concentrated in the southern Gulf of Mexico, Venezuelan Basin and off the northeastern coast of South America

from 1987 to 1989 (Cramer 1996), shifted and became concentrated after 1990 in the areas where most of the spawning occurs (Arocha 1997).

Seasonal area closures are used by managers as a tool to achieve various objectives, including the protection of reproductively active individuals. Such closures, or at least a limit on effort, could be considered by managers as a conservation measure for swordfish. From the observed spatio-temporal pattern of the fishing effort on the spawning areas it can be deduced that an effort limit or a closure would be most effective in the offshore subarea between January and May, in terms of protecting active spawners. It should be noted, however, the realized benefits from such a management tactic would be difficult to evaluate under current circumstances. Because swordfish undergo seasonal movements throughout the entire region (Jones 1996), some would-be spawners would certainly be caught elsewhere, even if the offshore subarea is entirely closed to fishing. A quantitative evaluation of spatio-temporal management measures would require detailed knowledge about the spatio-temporal distribution of the population and of the landings. This would require the implementation of spatially-structured stock assessments methods that utilize information on transfer rates (by sex and age) between the various subareas, as well the seasonal distribution of landings and fishing effort. Nevertheless, despite the current impediments to quantitative analysis, seasonal area closures or effort limitations seem to be a potentially useful tool to provide increased protection to spawning swordfish in the northwestern Atlantic.

The analysis presented in this paper demonstrates that management advice based on *SPR* ratios derived from *SSB* analysis are inadequate, because of the overestimation of target *F*. It also revealed the need to have a complete understanding of swordfish movement in the North Atlantic before the actual reproductive output of the entire stock can be quantified. However, it is evident that a substantial proportion of the effort is deployed in the area and season where much of the spawning activity takes place. A technical conservation measure to protect the spawners could include a seasonal effort limitation in the offshore subarea of the subtropical area to protect the spawning potential of the northwestern Atlantic swordfish.

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