A review of the Reproductive biology of the Swordfish (*Xiphias gladius*) in the Indian Ocean

H. Murua[1], J. Farley[2], I. Zudaire[3], P.L. Luque[3], I. Artetxe-Arrate[3], E. Romanov[4], F. Marsac[5], I. Fraile[3], G. Merino[3]

Abstract

This paper review the reproductive biology of swordfish (*Xiphias gladius*) in the Pacific, Atlantic and Indian Oceans as well as the Mediterranean Sea, with particular focus in the Indian Ocean to inform the next swordfish stock assessment scheduled for 2023, as part of the 'GERUNDIO' project. The review focuses on the reproductive strategy, seasonal and geographical spawning activity, maturity patterns and fecundity of swordfish. In general, available literature on swordfish reproductive biology is scarce, with most of the studies located in the Atlantic and Pacific Oceans. Swordfish is characterised as a multiple spawner species showing an asynchronous oocyte development and indeterminate fecundity. Swordfish size at maturity and fecundity studies have revealed significant variation both between and within oceans depending on sex, geographical area and environmental conditions. However, the differences could also stem from the different techniques used to determine the maturity status of individual fish among studies and estimate fecundity and/or the limited samples used.

Swordfish stock assessment is sex-disaggregated to account for a number of sex-specific population characteristic such as, among others, growth and maturation. Although the swordfish maturity ogives for the Indian Ocean (Poisson and Fauvel, 2009a) and South-West Pacific Ocean (Farley et al., 2016) had a similar 50% length, following recommendations from WPB15, the assessment used the age-based logistic ogive from Farley et al. (2016) (applying the new otolith-based growth from SW pacific). However, considering that (i) there are clear differences in growth and maturation by sexes, (ii) Farley et al. (2016) did not estimate maturity ogives for males but Poisson and Fauvel (2009a) did, (iii) length based maturity ogive for females estimated by Farley et al. (2016) and Poisson and Fauvel (2009a) are similar, (iv) Poisson and Fauvel (2009a) maturity ogive was estimated using samples from the South-West Indian Ocean; it is recommemded to explore the possibility of using the Poisson et al. (2009a) length-based maturity ogives by sex, converted to age-based maturity ogives using Farley et al. (2016) growth curves by sex.

[1] International Seafood Sustainability Foundation, 1440 G Street NW, Washington, DC 20005, USA.
[2] CSIRO Oceans and Atmosphere, Hobart, Australia
[3] AZTI, Marine Research, Basque Research and Technology Alliance (BRTA), Pasaia- Gipuzkoa, Spain
[4] CAP RUN - CITEB (Centre technique de recherche et de valorisation des milieux aquatiques). Île de la Réunion,
[5] IRD, UMR MARBEC, Sète, France

Introduction

In 2020, an IOTC collaborative research project was launched on the "Development and implementation of a sampling scheme to support the collection of biological samples and conduct analysis on these samples to provide improved estimates of age, growth and reproduction of tropical tunas, swordfish, and blue sharks for the Indian Ocean". The project is being led by AZTI (EU-Spain), with the participation of research institutions with experience in the IOTC area, and is funded by the European Union through FAO-IOTC (FAO Contract No. 2020/SEY/FIDTD/IOTC - CPA 345335"). The aim of the project is to produce updated estimates of age, growth and reproduction parameters for the stock assessments of Indian Ocean tropical tunas (bigeye, skipjack and yellowfin), swordfish and blue shark.

The state of exploitation of the five species of interest for this project is evaluated using Stock Synthesis (Methot and Wetzel, 2013), a highly parameterized age-structured stock assessment software. Stock Synthesis explicitly describes the key fish dynamics and key processes of the population dynamic such as growth and reproduction, with equations that need accurate parameters from biological studies. The lack of knowledge on biological processes can reduce the reliability and confidence in stock assessment outcomes and undermine the sustainable management of fish stocks and fisheries. Therefore, age/growth and reproduction parameters are key to improve the stock assessment of those species. As such, the project plans to develop a sampling scheme to collect samples of otoliths, gonads and other body parts, and analyse them for age, growth and reproduction (in combination with samples collected in previous research initiatives) to produce updated estimates of key biological parameters using samples from the Indian Ocean for five important commercial species (three tropical tunas, swordfish and blue shark). Here, we present a review of swordfish, *Xiphias gladius*, reproductive strategy and potential to inform the next swordfish stock assessment scheduled for 2023.

The swordfish is a highly migratory large meso-pelagic species with a circumglobal distribution found throughout tropical and temperate waters from latitudes of about 45°N to 45°S (Arocha, 2007) and is the most widely distributed species of billfish. It is mainly distributed up to depths of about 350 m, however, deeper dives down to 1,100 m have been also recorded (Abascal et al., 2010). It generally forages in deep water during the day and stays in the mixed layer at night (Abascal et al, 2010; Sepulveda et al., 2017). The swordfish makes large-scale migrations, including complex horizontal and vertical movement patterns (Sepulveda et al., 2017).

Swordfish in the Indian Ocean are mainly caught by longlines (around 85% of the total catches) and to a lesser extent by driftnet fisheries (around 15% of the total catches). In the Indian Ocean, swordfish catches have continuously increased since 1950 and they markedly increased after 1990 to reach the historic highest catch record of 40,000 t in 2004. Since then, catches have decreased until 2011 when they started to steadily increase again up to around 34,000 t in 2019. The average annual swordfish landings reported to IOTC over the 2015–2019 period was around 30,000 tonnes (IOTC, 2021).

The latest stock assessment for the Indian Ocean swordfish was carried out in 2020 and the IOTC determined that the stock was not overfished and was not subject to overfishing; however, the IOTC suggested catches should not exceed 2018 levels (31,000 tonnes) to ensure high probability of maintaining spawning biomass above MSY reference levels (SB>SBMSY) over the next years.

Understanding life history strategies of fish species such as age and growth, reproduction, maturity and mortality is required to determine population productivity and, hence, resilience to fisheries (King and McFarlane, 2003; Morgan et al., 2009) and how a species might respond to fishing pressure (Jennings et al., 1998; Juan-Jordá et al., 2013). Reproductive biology is particulary important as, in conjunction with other life history characteristic, it determines the productivity of the species and contributes to the recruitment of new individiuals to the population (Murua et al., 2003).

Understanding the relative importance of factors responsible for interannual variation in recruitment is a primary objective of fisheries science and management (Chambers and Trippel, 1997) and the relationship between population and recruitment is the central, and generally most difficult, outstanding problem in the study of population dynamics and the management of marine fish stocks (Hilbornand Walters, 1992).

Despite its commercial importance, information available on the reproductive biology of swordfish is scarce in the Indian Ocean (Mejuto et al., 2006; Poisson and Fauvel, 2009a,b). More reproductive biology studies of swordfish are available for the Pacific (Uchiyama et Shomura 1974; Miyabe and Bayliff 1987; DeMartini et al. 2000; Wang et al. 2003; Young et al. 2003; Farley et al., 2016) and Atlantic Oceans (Taylor and Murphy 1992; Hazin et al. 2001; Arocha, 2007; Abid et al., 2019) and the Mediterranean Sea (De la Serna et al. 1996). The study of the reproductive biology of swordfish is complicated by the fact that it is a highly migratory species with a very large distribution and, thus, a large number of samples across its geographical distribution is needed. The reproductive studies available for the Indian Ocean, and other oceans, reported the reproductive strategy, the spawning activity based on gonadosomatic index, sex-ratio of catches, and size at 50% maturity of swordfish with a few studies also providing batch fecundity estimations.

The original aim of this study was to collect and analyse swordfish samples and report on the reproductive biology of swordfish, including the sex-ratio, reproductive strategy, duration and location of the reproductive season, size/age at maturaty, and fecundity; however, due to the pandemic and access of observers to fishing vessels, it has not been possible to collect swordfish gonad samples under the IOTC "Development and implementation of a sampling scheme to support the collection of biological samples and conduct analysis on these samples to provide improved estimates of age, growth and reproduction of tropical tunas, swordfish, and blue sharks for the Indian Ocean" project. Thus, we review the reproductive biology of swordfish based on the literature published for the Indian Ocean and elsewhere. This review could inform on the reproductive parameters to be included in the next swordfish stock assessment schedules for 2023.

Reproductive biology

The swordfish is a gonochoristic species, that is their sexes are separate, possess no external sexual dimorphism and exhibit external fertilization (Palko et al. 1981). As in most fishes, the paired gonads are located ventrally on both sides of the intestinal sac and the large swim bladder in the anterior anal area.

Reproductive strategy

The swordfish is characterised as a multiple spawner species showing an asynchronous oocyte development (Arocha 2002; Poisson and Fauvel, 2009a), where oocytes of all stages are simultaneously present in reproductively active ovaries; which has been interpreted as providing evidence for swordfish indeterminate annual fecundity (Arocha 2002). The term 'indeterminate' refers to species in which the potential annual fecundity is not fixed prior to the onset of spawning (Hunter et al., 1992; Murua et al., 2003). In such species, pre-vitellogenic oocytes can develop and be recruited into the yolked oocyte stock at any time during the season (de novo vitellogenesis) (Hunter and Goldberg, 1980). Estimation of total fecundity in the ovary, prior to the onset of spawning, is meaningless if during the spawning season oocytes are recruited to the vitellogenic oocyte stock. In these species, annual fecundity should be estimated from the number of oocytes released per spawning (batch fecundity), the percentage of females spawning per day (spawning frequency) and the duration of the spawning season (Hunter and Macewicz, 1985; Murua et al., 2003).

Spawning seasonality/location

The seasonal and spatial spawning patterns of swordfish have been inferred from a variety of methodological approaches, from larval surveys to gonadosomatic index and microscopic/macroscopic examination of oocytes development stages. In the Atlantic Ocean, the main spawning period for swordfish was defined between December to June (Taylor and Murphy, 1992; Arocha, 2007), with some individuals also showing spawning activity in August, based on the examination of the size of the most advanced group of oocytes (MAGO) in the ovary. However, in different regions of the temperate and sub-tropical Atlantic Ocean, spawning activity based on Relative Gonad Index (RGI) was inferred to take place outside the main spawning seasons, which suggested that swordfish has year round spawning with different peak seasons, in different locations (Arocha, 2007). The main spawning areas of swordfish in the Atlantic Ocean are identified in the Gulf Mexico, south of the Sargasso Sea, in the Strait of Florida and along the south-eastern coast of the USA and in the south tropical equatorial Atlantic between 10° and 5°S and west of 20°W (Arocha, 2017).

In the Pacific Ocean, extended spawning seasons from September to March, with a main spawning peak between December to February, have been identified (Young et al., 2003). However, reproductively active individuals have also been observed between March and July in other regions of the Pacific Ocean (e.g. Hawaii) (De Martini et al., 2000) and, similarly, a protacted spawning season over summer in other temperate regions of the Pacific has been inferred (Yabe et al. 1959; Nishikawa et al. 1974).

In the Indian Ocean, Poisson and Fauvel (2009a) identified an extended spawning season from October to April, with a peak in February-March, similar to the findings of Young et al. (2003). Mejuto et al. (2006) reported high values of gonadal activity between 10°N and 5°S and 40°E and 55°E during the second quarter and third quarter of the year, suggesting that this area could be a potential spawning area. On the other hand, Varghese et al. (2013) observed mature ripening females around Indian waters in the north Indian Ocean from December to April and Yabe et al. (1959) collected matured ovaries between the equator and the Bay of Bengal in April, which may also suggest spawning activity in that region from December to April.

Various works in the literature indicated that the extent and duration of spawning is related to sea surface temperature, with greatest spawning activity in surface water temperature greater than 24°C (Arocha 1997; Young et al., 2003; Poisson and Fauvel, 2009a), which could explain the regional and seasonal differences of spawning activity.

Size at maturity

There are various studies that have presented maturity ogives (i.e., proportion mature by length/age) of swordfish in the Indian, Pacific and Atlantic Oceans and in the Mediterranean Sea. Those studies have revealed significant variation in maturity schedule both between and within oceans, depending on sex, geographical area and environmental conditions (**Table 1**). However, the differences could also stem from the different techniques used to determine the maturity status of individual fish among studies; some studies use microscopic maturity staging via histological analysis (Taylor & Murphy 1992; DeMartini et al. 2000; Young and Drake 2002; Wang et al. 2003) and others use gonadosomatic index and/or macroscopic maturity staging of ovaries (De la Serna et al. 1996; Arocha 1997; Hazin et al. 2002; Arocha 2007; Poisson and Fauvel 2009a; Varghese et al. 2013; Mejuto & Garcia-Cort.s 2014).

For example, in the Atlantic Ocean the estimated size at 50% maturity for female swordfish was estimated at 178.7 cm lower jaw-to-fork length (LJFL) in the north-western tropical area using gonadosomatic index (Arocha et al., 2007), 182.0 cm LJFL in the north-western sub-tropical area of the Straits of Florida using microscopic staging (Taylor and Murphy, 1992), 156.0 cm LJFL in the south-western equatorial using macro/microscopic staging (Hazin et al., 2002), 146.5 cm LJFL in the south-western and central sub-tropical area based (Mejuto and Garcia-Cortes, 2014), and 142.2 cm LJFL in the Mediterranean Sea using gonadosomatic index (De la Serna et al., 1996).

In the Pacific Ocean, the estimated size at 50% maturity for female swordfish was 189 cm LJFL in the eastern Pacific (Kume and Joseph, 1969) and 178 cm LJFL in the North Pacific (Sosa-Nishizaki, 1990) both studies using gonadosomatic index, 161.9 cm LJFL (originally 143.6 cm EFL- eye-to-fork length) in the central north region based on histological classification of maturity (DeMartini et al., 2000), 216.6 and 222.9 cm LJFL (originally 193.6 – 199.8 cm EFL) depending on the model applied using microscopic staging of oocyte development for the southwest (Young and Drake, 2002), 175.1 cm UFL in the western South Pacific (Young et al., 2000), and 168.2 cm LJFL in the northwest using histology (Wang et al., 2003).

In the Indian Ocean, only two work is available describinig the maturity pattern. Poisson and Fauvel (2009a) estimated size at 50% for female swordfish at 170.4 cm LJFL in the southwest and Varghese et al. (2013) at 164.0 cm LJFL for females collected around India in the north; both studies were based on gonadosomatic index.

The size-at-maturity of Mediterranean swordfish is the smallest estimated (142.2 cm LJFL; De la Serna et al. 1996) compared to any any other region/population. This difference has been linked to the longer explotation period of swordfish in the Mediterranean Sea where larger individuals have been substantially reduced (Arocha et al., 2007), which may have produced fishery-induced genetic evolution toward earlier maturation in this population (Heino et al., 2015).

In general, all the authors agreed that there is a sexual dimorphism in swordfish maturation, which has been also observed in growth, with males maturing earlier than females (Table 1). The size at maturity estimates for males varies from 112 to 130 cm LJFL in the Atlantic Ocean, between 100 and 117 cm LJFL in the Pacific Ocean, and it was estimated at 120 cm LJFL in the Indian Ocean (Poisson and Fauvel, 2009a).

Table 1. Estimates of length at 50% maturity (L_{50}) for female and male swordfish, batch fecundity (BF), relative batch fecundity (RBF) – number of oocytes per female body gram-, and spawning frequency (S) found in the literature. All lengths have been converted to lower jaw fork length (LJFL), in cm.

Ocean	Region	L_{50} Males (LJFL cm)	L_{50} Females (LJFL cm)	Method	Average BF (range) * 10^6 oocytes	Average RBF (range)	S (days)	Reference
Pacific	Eastern	-	189*	GSI	-	-	-	Kume and Joseph, 1969
	Southwest	-	181.5*	Histology	-	-	-	Farley et al., 2016
	Southwest	99.7-117.3*	216.6 – 222.9*	Histology	1.7 (1.2-2.5) (n=9)	11.4 (n= 9)	3 (1.78¨)	Young & Drake (2002)
	Central North	117.1*	161.9*	Histology	-	-	-	DeMartini et al. (2000)
	North	-	178*	GSI	-	-	-	Sosa-Nishizaki (1990)
	Northwest	-	168.2	Histology	-	-	-	Wang et al. (2003)
Mediterranean	Western	-	142.2	GSI	5.9 (2.14-9.91) (n=16)	113 (52.5-189.4)	-	De la Serna et al. (1996)

Atlantic	Western North	129	179.0	Macroscopic	3.9 (0.99-9.0) (n=29)	-	2.31	Arocha and Lee (1996)
	Western North	-	178.7	GSI & oocyte diameter	3.9 (0.99-9.0) (n=29)	-	-	Arocha (2007)
	Western North	112.0	182.0	Histology	3.1 (1.4-4.2) (N=7)	21.3 (12.6-44.5) (N=7)	-	Taylor & Murphy (1992)
	Western tropical	120-130	156.0	Macroscopic & histology	5.1 (2.00 - 8.60) (n=10)**	-	-	Hazin et al. (2002)
	North-east	95	170	Macroscopic & histology				Abid et al. (2019)
	Western tropical	-	146.5	GSI & Macroscopic	-	-	-	Mejuto & Garcia-Cortés (2014)
Indian	North	-	164.0	Macroscopic & histology	4.5	37.5 (n=5)	-	Varghese et al. (2013)
	Southwest	119.9	170.4	GSI	3.2 (0.9°9-4.3)	44.1 (25.1-71.8) (n=7)	2.77	Poisson & Fauvel (2009a,b)

* Originally estimated using EFL (eye-to-fork length) and converted to LJFL by LJFL = 1.0753*(OFL + 6.898).
** For batch fecundity the reference is Hazin et al., (2001).
¨ If the analysis is restricted to mature females during the peak spawning.

The different maturity schedules observerd among and within oceans could be due to regional variation in size at maturity, but it could also be due to different methodological approaches used (micro- vs macroscopic staging) and/or different criteria used to identify individual maturity status. Histological based microscopic maturity staging is considered the most precise technique to determine ovary development stage (West 1990), however, even in such cases it is not easy to distinguish immature virgin females from mature post-spawning females as the latter are histologically similar to immature females because their reabsorb all vitellogenic oocytes. For example, using the same histological samples, Farley et al. (2016) updated the estimate of L_{50} for swordfish in the southwest Pacific to 181.7 cm LJFL using revised histological criteria to identify post-spawning females; this was considerably lower than the original estimate by Young and Drake (2002) (216.6 – 222.9 cm LJFL).

Fecundity

Swordfish batch fecundity, the number of eggs laid in each spawning act, increases with fish size. Although there are few studies, linear relationships were generally estimated even when the number of samples were low (Hazin et al. 2001, Poisson and Favel, 2009b, Young et al., 2003). Non-linear relationships have also been obtained with batch fecundity increasing more rapidly with increasing fish size (Arocha and Lee, 1996; de la Serna et al. 1996).

Swordfish batch fecundity estimates in the Atlantic ranged from around 1.0 and 9.0 million oocytes and are comparable among studies (Arocha and Lee, 1996; Hazin et al., 2001; Taylor and Murphy, 1992), however, the values estimated by Taylor and Murphy (1992) for samples collected in the Straits of Florida are in the lower-middle of that range (Table 1). For the Mediterranean Sea, batch fecundity was estimated to be around 2 and 9.9 million of oocytes, which are comparable to the estimates reported for the Atlantic. However, for the Indian and Pacific Oceans, batch fecundity was estimated to be lower than in the Atlantic, ranging from 1 to 4.3 million oocyets in the Indian Ocean (Poisson and Fauvel, 2009b), which is a value similar to Taylor and Murphy (1992) for the Atlantic Ocean, and 1.2 and 2.5 million of oocytes for the Pacifc (Young et al., 2003); which is the lowest estimated batch fecundity (Table 1).

Some of the differences in batch fecundity estimates could be due to the oocyte size threshold used to separate oocytes that will spawn in the batch and those remaining in the ovary. That is, using oocytes larger than a particular size (e.g. advance vitellogenic oocytes) instead of counting only hydrated oocytes, which are the ones clearly separated from the rest of the oocytes that will be spawned in the next imminent batch. For example, the estimated swordfish batch fecundity in the Mediterranean (De la Serna et al., 1996) counted oocytes larger than 0.65 mm which most likely included oocytes that will not enter the hydration phase for the next batch and, therefore, the batch fecundity was overestimated. This can explain the large batch fecundity estimation for the Mediterranean Sea while the size of the fishes sampled (as well as maturity) is smaller.

There are few studies providing information on the relative batch fecundity (i.e. number of oocytres per female body gram) of swordfish (Table 1). The relative batch fecundity was estimated to be on average 11.4 oocytes per female body gram in the Pacific Ocean, on average 21.3 (with a range 12.6-44.5) in Atlantic Ocean, on average 113 (range 52.5-189.4) in the Mediterranean Sea, and on average 44.1 (range 25.1-78.1) in the Indian Ocean. The values for the Mediterranean Sea are likely to be understimates, given their methodological approach to count oocytes in the advanced vitellogenic stage, which may include oocytes not entering the hydration phase.

Only three studies, one per ocean, reported spawning frequency (i.e., the interval between spawning events) for swordfish, and all three showed compable values (Table 1): 3.0 days for the Pacific Ocean, 2.8 for the Indian Ocean, and 2.3 days for the Atlantic Ocean.

Implications for Stock Assessmennt

Most of the aforementioned studies on reproduction of swordfish were based on samples obtained from relatively limited areas-seasons and for some of the parameters, e.g. batch fecundity, with low numbers of samples. Their results inform various hypotheses on the reproductive biology of this species, but when using those results to inform stock assessment the limitation of those studies should be taken into account.

The most recent assessment was undertaken in 2020 using stock synthesis with fisheries data up to 2018. This assessment used a spatially disaggregated, sex explicit and age structured model. Swordfish exhibit fast growth in the first year of life and there is a marked difference in growth rates between males and females, which can be potentially important in the right-hand tail of the size distribution often estimated to consist predominantly of large mature females. Thus, the stock assessment model separates the Indian Ocean swordfish population into two sex groups to account for a number of sex-specific population characteristic such as growth and maturation among others.

Farley et al. (2016) undertook a growth study for swordfish in southwest Pacific waters comparing the use of both fin-rays and otolith samples and found that age estimates from fin rays and otoliths produce different growth curves in the southwest Pacific, with discrepancies evident in age classes >7 years for females and >4 years for males than previous estimates. The otolith-based growth curves indicate slower growth and a higher maximum age for both males and females, compared to previous growth curves used in the assessment (Young and Drake, 2004). Consequently, the Working party on Billfished in 2017 (WPB15) agreed that the stock assessment for swordfish in the Indian Ocean should use the new otolith-based growth estimates for the southwest Pacific from Farley et al. (2016).

The stock assessment also used the age-based logistic maturity ogive from Farley et al. (2016) (applying the new otolith-based growth from the southwest Pacific) following recommendations from WPB15. The swordfish maturity ogives for the Indian Ocean (Poisson and Fauvel, 2009a) and southwest Pacific Ocean (Farley et al., 2016) have a similar estimate of 50% length. And considering that (i) there are clear differences in growth and maturation by sexes, (ii) Farley et al. (2016) did not estimate maturity ogives for males but Poisson and Fauvel (2009a) did, (iii) length based maturity ogive for females estimated by Farley et al. (2016) and Poisson and Fauvel (2009a) are similar as pointed out by WPB15, (iv) Poisson and Fauvel (2009a) maturity ogive was estimated using samples from the South-West Indian Ocean; it would be worth exploring the possibility of using the Poisson et al. (2009a) length-based maturity ogives by sex converted to age-based maturity ogive using Farley et al. (2016) growth curves by sex in the next stock assessment.

Acknowledgements

The project is supported by financial assistance of the European Union (contract no. 2020/SEY/FIDTD/IOTC - CPA 345335) and FAO-IOTC. The views expressed herein can in no way be taken to reflect the official opinion of the European Union.

References

Abid, N., Laglaoui, A., Arakrak, A., & Bakkali, M. (2019). The reproductive biology of swordfish (Xiphias gladius) in the Strait of Gibraltar. Journal of the Marine Biological Association of the United Kingdom, 99(3), 649-659. doi:10.1017/S0025315418000346

Abascal F.J., Jaime Mejuto, Manuel Quintans, Ana Ramos-Cartelle, Horizontal and vertical movements of swordfish in the Southeast Pacific. (2010). ICES Journal of Marine Science, Volume 67 (3): 466–474, https://doi.org/10.1093/icesjms/fsp252

Arocha, F. and D. Lee. (1996). Maturity at size, reproductive seasonality, spawning frequency, fecundity, and sez-ratio in swordfish from the Northwest Atlantic. ICCAT Collective Volume of Scientific Papers 45(2)350-357.

Arocha F (1997) The reproductive dynamics of swordfish Xiphias gladius L. and management implications in the northwestern Atlantic. Ph.D. thesis, University of Miami, Miami, FL.

Arocha, F. 2002. Oocyte development and maturity classification of swordfish from the north-western Atlantic. Journal of Fish Biology 60: 13-27.

Arocha F (2007) Swordfish reproduction in the Atlantic Ocean: An overview. Gulf ad Caribbean Research 19: 21–36.

Chambers, R. C., and Trippel, E. A. (1997). In “Early Life History and Recruitment in Fish Populations” (R. C. Chambers and E. A. Trippel, eds.). Champman and Hall, London.

De la Serna JM, Ortiz JM, Macias D (1996) Observations on sex ratio, maturity and fecundity by length-class for swordfish (Xiphias gladius) captured with surface longline in the western Mediterranean. Collect Vol Sci Pap ICCAT 45: 115–140.

DeMartini EE, Uchiyama JH, Williams HA (2000) Sexual maturity, sex ratio, and size composition of swordfish, Xiphias gladius, caught by the Hawaii-based pelagic longline fishery. Fish Bull 98: 4 89-506.

Farley J., N. Clear, D. Kolody, K. Krusic-Golub, P. Eveson, J. Young. (2016). Determination of swordfish growth and maturity relevant to the southwest Pacific stock. R 2014/0821 Report. CSIRO Oceans & Atmosphere, Hobart. ISBN 978-1-4863-0688-6.

Hazin, E, H. Hazin, C. Boeckmann, and P. Travassos. 2001. La reproduction de l'cspadon (Xiphias gladius) dans l' Atlantique sud-ouest equatorial: La ponte et la fecondite. ICCAT, Collective Volume of Scientific Papers 52: 1233- 1240.

Hazin FHV, Hazin HG, Boeckmann CE, Travasson P (2002) Preliminary study on the reproductive biology of swordfish, Xiphias gladius (Linnaeus, 1758), in the southwestern equatorial Atlantic Ocean. ICCAT Col Vol Sci Pap 54 (5): 1560-1569

Heino M., B. D. Pauli, U. Dieckmann (2015). Fisheries-Induced Evolution. Annual Review of Ecology, Evolution, and Systematics 2015 46:1, 461-480

Hilborn, R., and Walters, C. J. (1992). Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. Chapman and Hall, New York.

Hunter, J. R., and Goldberg, S. R. (1980). Spawning incidence and batch fecundity in Northern anchovy, Engraulis mordax. Fish. Bull. 77(3), 641–652.

Hunter JR, Macewicz BJ (1985) Rates of atresia in the ovary of captive and wild northern anchovy, Engraulis mordax. Fish Bull 83: 119-136.

Hunter, J. R., Macewicz, B. J., Lo, N. C. H., and Kimbrell, C. A. (1992). Fecundity, spawning, and maturity of female Dover sole, Microstomus pacificus, with an evaluation of assumptions and precision. Fish. Bull. USA 90, 101–128.

IOTC (2021). Nominal catches by fleet, year, gear, IOTC area and species. IOTC-2021-WPEB17(AS)-DATA03_R.

Jennings, S., Reynolds, J.D., Mills, S.C., 1998. Life history correlates of responses to fisheries exploitation. R. Soc. London B Biol. Sci. 265, 333–339. https://doi.org/10.1098/rspb.1998.0300.

Juan-Jordá, M.J., Mosqueira, I., Freire, J., Dulvy, N.K., 2013. Life in 3-D: life history strategies in tunas, mackerels and bonitos. Rev. Fish Biol. Fish. 23, 135–155. https://doi.org/ 10.1007/s11160-012-9284-4.

King, J.R., McFarlane, G.A., 2003. Marine fish life history strategies: applications to fishery management. Fish. Manag. Ecol. 10, 249–264. https://doi.org/10.1046/j.1365-2400.2003.00359.x.

Kume, S., and P.J. Josheph.1969. Size composition and sexual maturity of billfish caught by the Japanese longline fishery in the Pacific Ocean east of 130oW. Bulletin of the Far Seas Fisheries Research Laboratory 2: 115-162.

Mejuto J, Garcia-Cortes B, Ramos-Cartelle A. (2014). An overview of research activities on swordfish (Xiphias gladius) and the by-catch species, caught by the Spanish longline fleet in the Indian Ocean. IOTC-2006-WPEB-11

Mejuto J, Garcia-Cortes B (2014) Reproductive activity of swordfish Xiphias gladius, in the Atlantic Ocean inferred on the basis of macroscopic indicators. Revista de Biología Marina y Oceanografía 1493): 427-447.

Methot, R. D. and C.R. Wetzel (2013). Stock synthesis: A biological and statistical framework for fish stock assessment and fishery management. Fisheries Research, 142: 86-99. https://doi.org/10.1016/j.fishres.2012.10.012.

Miyabe N., Bayliff W.H., 1987, A review of the Japanese longline fishery for tunas and billfishes in the eastern Pacific Ocean, 1981– 1987. Bull. IATTC 19.

Morgan, M.J., Murua, H., Kraus, G., Lambert, Y., Marteinsdo´ ttir, G., Marshall, C.T., O'Brien, L., Tomkiewicz, J., 2009. The evaluation of reference points and stock productivity in the context of alternative indices of stock reproductive potential. Can. J. Fish. Aquat. Sci. 66, 404–414. https://doi.org/10.1139/F09-009.

Murua H, Saborido-Rey F (2003) Female reproductive strategies of marine fish species of the North

Atlantic. J Northwest Atl Fish Sci 33: 23-31

Nishikawa, Y., and Euyenagi, S. (1974). The distribution of the larvae of swordfish, Xiphias gladius, in the Indian and Pacific Oceans. In 'Proceedings of the International Billfish Symposium. Kailua-Kona, Hawaii, 9–12 August 1972. Part 2. Review and Contributed papers'. (Eds R. S. Shomura and F.Williams.) pp. 261–64. NOAATechnical report, NMFS ssRF–675.

Palko, B.J., G. Beardsley, and W.J. Richards. 1981. Synopsis of the biology of the swordfish, Xiphias gladius Unnaeus. National Oceanographic and Atmospheric Administration, Technical Report, National Marine Fisheries Service Circular 441, 21 p.

Poisson F, Fauvel C (2009a) Reproductive dynamics of swordfish (Xiphias gladius) in the southwestern Indian Ocean (Reunion Island). Part 1: oocyte development, sexual maturity and spawning. Aquat living Resour 22: 45-58.

Poisson F, Fauvel C (2009b) Reproductive dynamics of swordfish (Xiphias gladius) in the southwestern Indian Ocean (Reunion Island). Part 2: fecundity and spawning pattern. Aquat living Resour 22: 59-68.

Sepulveda, CA, Aalbers, SA, Heberer, C, Kohin, S, Dewar, H. Movements and behaviors of swordfish Xiphias gladius in the United States Pacific Leatherback Conservation Area. Fish Oceanogr. 2018; 27: 381– 394. https://doi.org/10.1111/fog.12261

Sosa-Nishizaki, O. 1990. A Study on the Swordfish Xiphius gladius Stocks in the Pacific Ocean. Ph. D. Thesis, Department of Fisheries, Faculty of Agriculture. Tokyo, University of Tokyo: 246 p.

Taylor RG, Murphy M (1992) Reproductive biology of the swordfish Xiphias gladius in the Straits of Florida and adjacent waters. Fish Bull 90: 809–816.

Uchiyama JH, RS Shomura. 1974. Maturation and fecundity of swordfish, Xiphias gladius, from Hawaiian waters. In RS Shomura, F Williams, eds. Proceedings of the International Billfish Symposium, part 2. Review and contributed papers. US Dept. Comm., NOAA Tech. Rep. NMFS SSRF-675. U.S. Government Printing Office, Washington, D.C., pp. 142-148.

Varghese SP, Vijayakumaran, K, Anrose A, Mhatre VD (2013) Biological aspects of swordfish, Xiphias gladius Linnaeus, 1758, caught during tuna longline survey in the Indian seas. Turkish J Fish Aquat Sci 13: 529-540.

Wang S-P, Sun C-L, Yeh S-Z (2003) Sex ratios and sexual maturity of swordfish (Xiphias gladius L.) in the waters of Taiwan. Zool Stud 42: 529–539.

West, G. 1990. Methods of assessing ovarian development in fishes: A review. Australian Journal of Marine and Freshwater Research 41: 199-222.

Young, J., A. Drake, T. Carter, and J. Farley. 2000. Reproductive dynamics of broadbill swordfish (Xiphias gladius) in the eastern Australian AFZ: prelintinary results. 13th meeting of the standing committee on tuna and billfish, Noumea, New Caledonia, 5-12 July 2000, p. 1-12

Young J, Drake A (2002) Reproductive dynamics of broadbill swordfish (Xiphias gladius) in the domestic longline fishery off eastern Australia. FRDC Final Report for project 1999/108.

Young J, Drake A (2004) Age and growth of broadbill swordfish (Xiphias gladius) from Australian waters. FRDC Final Report for project 2001/014.

Young JW, Drake A, Brickhill M, Farley JH, Carter T (2003) Reproductive dynamics of broadbill swordfish, Xiphias gladius, in the domestic longline fishery off eastern Australia. Mar Freshwat Res 54: 315-32.