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Review of sexual maturity in Atlantic bluefin tuna, *Thunnus thynnus* (Linnaeus, 1758)

Aldo Corriero^a, Gilad Heinisch^b, Hanna Rosenfeld^c, Ivan Katavić^d, Letizia Passantino^a, Rosa Zupa^a,
Leon Grubišić^d, Molly E. Lutcavage^b

^aDepartment of Emergency and Organ Transplantation, Section of Veterinary Clinics and Animal Production, University of Bari Aldo Moro, Valenzano (Bari), Italy

^bLarge Pelagics Research Center, School for the Environment, University of Massachusetts Boston, Gloucester, Massachusetts, USA

^cNational Center for Mariculture, Israel Oceanographic and Limnological Research, Eilat, Israel

^dInstitute of Oceanography and Fisheries, Split, Croatia.

Contact: Aldo Corriero. Department of Emergency and Organ Transplantation (D.E.T.O.), Section of Veterinary Clinics and Animal Production, University of Bari, S.P. per Casamassima km. 3, I-70010 Valenzano (BA), Italy. Email address: aldo.corriero@uniba.it.

Abstract

The age of sexual maturity of the Atlantic bluefin tuna (*Thunnus thynnus*; ABFT) is a reference point for stock assessment and management. The International Commission for the Conservation of Atlantic Tunas (ICCAT) recognizes a western and an eastern Atlantic ABFT stock, based on the assumptions of separate, exclusive spawning grounds, i.e., the northern Gulf of Mexico and the Mediterranean Sea, with different ages of sexual maturity, 8-12 years vs 3-5 years, respectively. Multiple line of evidences indicate that spawning is not restricted to the Gulf of Mexico and the Mediterranean Sea, and reconsideration of historical documents, as well as results from recent studies, indicate that sexual maturation schedules of the two proposed stocks are similar (3-5 years). The present review of classical and recent literature suggests that ABFT have more complex reproductive behaviour than previously considered: on eastern spawning grounds 50% of ABFT females reproduce at three years of age and 100% are sexually mature at five years of age. In the western management area, younger adults (age ≥ 5 years) and some larger adults apparently spawn in the northwest Atlantic Ocean across the Slope and Caribbean Seas, whereas the Gulf of Mexico spawners are mostly large adults (age ≥ 8 years).

Keywords: Bluefin tuna; reproduction; puberty; length at sexual maturity; age at sexual maturity.

Introduction

Atlantic bluefin tuna *Thunnus thynnus* (Linnaeus, 1758) (ABFT) have a wide geographical distribution (Bard et al., 1998; Fromentin and Fonteneau, 2001; Fromentin and Powers, 2005) ranging (in the western Atlantic) from Newfoundland to Brazil and (in the eastern Atlantic) from Iceland and the Lofoten Islands off Norway to the Canary Islands (Mather et al., 1995). The International Commission for the Conservation of Atlantic Tunas (ICCAT) currently manages ABFT assuming western- and eastern-Atlantic stocks with limited mixing (Magnuson et al., 1994), differential sexual maturation schedules, and strict spawning fidelity to two natal areas: the northern Gulf of Mexico (for western-Atlantic stock) and the Mediterranean Sea (for the eastern-Atlantic stock) (Rooker et al., 2008; Arrizabalaga et al., 2019). These assumptions are supported by electronic tagging data (Block et al., 2005), otolith micro-constituent analysis (Rooker et al., 2006, 2008), and fisheries data indicating the presence of ABFT schools on the presumed spawning grounds during the presumed spawning period (Di Natale and Tensek, 2016; Di Natale et al., 2018).

In contrast, other studies provide information rejecting the separated-stocks assumption. Results from conventional and electronic tagging studies have documented trans-oceanic movements of both juveniles and adults (Mather et al., 1995; Turner and Powers, 1995; Lutcavage et al., 1999; Block et al., 2001, 2005; Galuardi et al., 2010; Galuardi and Lutcavage, 2012). The populations have been reported to overlap in north Atlantic feeding grounds (Lutcavage et al., 1999; Block et al., 2001, 2005; Rooker et al., 2008; Dickhut et al., 2009), and stomach contents, stable isotope analyses and age determination studies confirm similarities in diets (Logan et al., 2011) and growth rates (Restrepo et al., 2010). Other investigators have, moreover, concluded that opportunistic spawning occurs occasionally outside the northern Gulf of Mexico (Muhling et al., 2011) and the classically recognized Mediterranean spawning grounds when suitable oceanographic conditions are present (Karakulak et al., 2004; Di Natale, 2006; Piccinetti et al., 2013). These alternate spawning areas include locations off western Africa, as well as around Madeira and Canary Islands (Mather et al., 1995). Other studies

have identified complex migration routes (Galuardi et al., 2010) and diverse reproduction behaviour in the North Atlantic (Westman and Neville, 1942; Mather et al., 1995; Goldstein et al., 2007) which further question the natal homing hypothesis and the current ICCAT two-stock assumption. (Fromentin and Powers, 2005; Galuardi et al., 2010; Galuardi and Lutcavage, 2012).

Atlantic bluefin tuna are iteroparous spawners with an asynchronous ovarian development, showing ovaries with oocytes at all development stages during spawning season (Medina et al., 2002; Corriero et al., 2003, 2005). Batch fecundity, spawning frequency and spawning season duration as well as sexual maturity are key life history traits that contribute to determine the productivity and resilience of a population, and require accurate depiction in stock assessment (Maunder and Deriso, 2013; Brodziak et al., 2015; Lowerre-Barbieri et al., 2016). The available data indicate for ABFT a batch fecundity between 28-93 eggs g^{-1} body weight (Medina et al., 2002; Aranda et al., 2013; Knapp et al., 2014), a spawning frequency of 1.2 days and a spawning duration of approximately one month (Medina et al., 2002); the age/length at maturity of the two ABFT populations is a matter of debate.

Our objective in this review is to analyse critically the available literature on ABFT reproduction in an attempt to confirm or reject the proposed differences in a key life history trait, age at sexual maturation, between individuals from the western- and eastern-Atlantic stocks so that they are correctly defined in ABFT stock assessment.

Sexual maturity of the Atlantic bluefin tuna from the eastern spawning grounds

Atlantic bluefin tuna spawning is temperature dependent (≥ 20 °C), and rapid larval development is the successful outcome of spawning (Reglero et al., 2012). In the Mediterranean Sea, recurrent spawning areas have been localized in the waters around the Balearic Islands, Malta, Aeolian Islands and in the Levantine Sea. Spawning begins in May in the Levantine Sea (Karakulak et al., 2004) and lasts until the end of July in the western spawning grounds of the Balearic Islands (Susca et al., 2001; Corriero et al., 2003; Abascal et al., 2004; Heinisch et al., 2008). The existence of additional spawning

grounds in the Mediterranean have been repeatedly proposed (Mather et al., 1995; Piccinetti et al., 2013; Di Natale et al., 2018). The Adriatic Sea has been considered as a nursery area for juvenile ABFT up to the age of 3 years (Tičina and Kačić, 1998); however, the presence of adult individuals during the spawning season suggested the Adriatic Sea as another possible spawning ground (Di Natale et al., 2018; Piccinetti et al., 2013; Katavić et al., 2017).

Efforts to ascertain ABFT size and age at sexual maturity have been made using different methods since the first decades of the 20th century. For the eastern Atlantic, studies on sexual maturity have been mostly carried out on individuals caught during their dispersal towards the known spawning grounds in the Mediterranean Sea. These studies were initially based on the evidence that ABFT gonads, like those of other fish, undergo significant seasonal changes in their volume and mass, as well as in their macroscopic appearance during the different phases of the reproductive cycle. Based on these seasonal changes, macroscopic gonad classification and the gonadosomatic index (GSI), i.e. the percentage of the gonadal mass in respect to the body mass, have been widely used to obtain information on ABFT reproductive state, and to determine size/age at maturity, reproductive periods and spawning grounds (Sella, 1929a, b; Rodríguez-Roda, 1964, 1967; Scaccini, 1965; Arena, 1988; Heinisch et al., 2008). The capacity to determine fish reproductive state was subsequently improved thanks to the use of light microscopy, that allows detection of the germ cell types and the histological signs of recent as well as remote reproductive activity (e.g. postovulatory follicles and atretic oocytes) (Susca et al., 2001; Medina et al., 2002; Santamaria et al., 2003; Corriero et al., 2003, 2005). More recently, further and more powerful tools have been made available to determine ABFT reproductive state, including quantitative assays for sex steroids, vitellogenin (egg yolk precursor) (Heppell and Sullivan, 2000; Susca et al., 2001) and gonadotropins (GTHs) (Rosenfeld et al., 2012) as well as pituitary GTHs transcripts (Berkovich et al., 2013). All these approaches and methods employed for the assessment of ABFT reproductive state established that, in the Mediterranean Sea, ABFT reproduce for the first time between ages of three to five years. Incidentally, ABFT age is commonly determined through the count of growth bands observed in cross sections of the first spiniform ray of

the first dorsal fin (Corriero et al., 2005; Santamaria et al., 2009, Luque et al., 2014; Santamaria et al., 2015, 2018).

Vitellogenesis (i.e. the process of hepatic synthesis of the egg yolk precursor vitellogenin) in vertebrates is controlled by 17- β estradiol, whose synthesis and secretion are stimulated by follicle stimulating hormone (FSH) (Patiño and Sullivan, 2002; Lubzens et al., 2010). Consequently, the presence of vitellogenic oocytes is evidence of an active reproductive axis and is often used as marker of sexual maturity in fishes, including tunas (Schaefer, 1998, 2001). Based on the presence of vitellogenic oocytes as sign of sexual maturity, ABFT larger than 110 cm FL (age ≥ 3) sampled in the Mediterranean Sea during the reproductive season were found to be sexually mature (Susca et al., 2001; Medina et al., 2002; Corriero et al., 2003).

The use of vitellogenic oocytes as marker of sexual maturity may introduce a bias in the sexual maturity estimate because vitellogenic oocytes may potentially undergo massive degeneration (i.e., atresia) before completion of the oogenic process. This condition results in omission of spawning (Rideout et al., 2005, 2011). The hypothetical mechanism of energy allocation to somatic growth over reproduction, and its relation to life history and reproductive strategies is well described (e.g., Roff, 1983; Rijnsdorp, 1990) especially for species with short lifespans. In long-lived fish species, young adults might omit spawning more frequently than older adults due to energetic limitations (Jørgensen et al., 2006; Chapman et al., 2011). Nonetheless, skipping one or more reproductive seasons may increase survival probability and egg production in the following reproductive seasons (Houston and McNamara, 1999; Clark and Mangel, 2000; Roff, 2002; Jørgensen et al., 2006).

Zupa et al. (2009), analysed the ovaries of 326 ABFT females captured in the Mediterranean Sea during the spawning season and found extensive atresia of vitellogenic oocytes in only three large (FL > 200 cm) individuals. This finding suggests that oocyte atretic degeneration followed by skipped spawning is not a normal component of ABFT reproductive schedules and does not occur on a systematic basis in young adults once they have achieved sexual maturity and reached an area with ecological conditions suitable for larval survival and development.

Further insight on ABFT sexual maturity came from experimental and commercial tuna farming. In the framework of ABFT domestication studies, ABFT females older than four years were able to complete oogenesis and spawn spontaneously, or did so after hormonal induction (Corriero et al., 2007; Aranda et al., 2011). In tuna farming, the availability of fish of different size classes supported development of new tools for analysing sexual maturation (Mylonas et al., 2007; Rosenfeld et al., 2012). In a notable study, Berkovich et al. (2013) showed that the pituitary FSH/LH ratio of age three, captive-reared female ABFT was like that of older, mature individuals and significantly lower than that of age one juveniles. Moreover, since the FSH/LH ratio is a reliable indicator for sexual maturation in humans (e.g., Oerter et al., 1990) and other vertebrates (e.g., Desjardins et al., 1968; Ito et al., 1993), its validation for ABFT via captive-based individuals confirmed that this bio-marker identifies sexual maturation in this species.

Corriero et al. (2005) classified the reproductive state of 501 specimens captured in the Mediterranean Sea based on ovary histological analysis (Figure 1) [Figure 1 near here] and reported that 50% of female bluefin tuna reached sexual maturity at 104 cm FL and all females above 135 cm FL were mature (Figure 2) [Figure 2 near here]. Moreover, based on age determination estimates, 50% of the ABFT sampled in the Mediterranean Sea were found to reach sexual maturity at the age of three years and 100% maturity is reached by the age of five (Corriero et al., 2005) (Figure 3) [Figure 3 near here]. Recently, the presence of age 3 females with hydrated oocytes was observed also in the central Adriatic Sea in late May-early June (I. K., unpublished data) and spontaneous spawning of age 3-4 ABFT reared in captivity in the central Adriatic have been documented (Džoić et al., 2017).

Taken together, the negligible occurrence of atretic individuals in the Mediterranean Sea spawning grounds, and the proven capacity of ABFT to mature oocytes and spawn in the wild and in captivity at the age of three-four years, confirm that vitellogenic oocytes are a reliable markers of sexual maturity, and exclude the possibility that a systematic massive atresia of vitellogenic oocytes in younger adults as a normal element of the reproductive pattern of the species. Consequently, evidence

supports the conclusion that ABFT females begin to reproduce in the Mediterranean Sea at three years of age and reach 100% maturity at the age of five.

Although reliable criteria to distinguish between mature and immature males through the histological analyses of the testes are not as extensive as those for females, there is clear evidence that males achieve sexual maturity at the age of 3 years in the Mediterranean Sea. Abascal et al. (2004) documented sexual maturity in individuals of 20 kg in body weight (~100 cm LF; 3 years of age) with GSI over 5 and histological features indicative of full maturity. Active spermatogenesis was also reported in the testes of ABFT with FL \geq 120 and 127 cm (estimated age 4-5 years) by Santamaria et al. (2003) and Zupa et al. (2013), respectively. In the western Atlantic, milt was recorded in the testis of 5-year old males (Heinisch et al., 2014). Spermatogenic activity, together with a pituitary FSH/LH ratio indicative of sexual maturity, was reported in captive-reared ABFT captured at the age of 2 years and confined in captivity until sampling one year later (Berkovich et al., 2013).

The existence of additional spawning grounds in the eastern Atlantic also need to be considered, based on historic, albeit sparse observations (Mather et al., 1995). Although electronic tagging studies have shown that some presumably mature ABFT fail to enter the Mediterranean Sea during the known spawning season, which could imply skipped spawning behaviour, new studies documenting ABFT larvae in the western Atlantic pelagic realm, beyond enclosed seas (Richardson et al., 2016), suggest that some fish may likewise be spawning also in the eastern Atlantic, if oceanographic conditions consistent with ABFT larval habitat characteristics occur (Rypina et al., 2019), but where research to confirm the reproductive status of adult fish is lacking.

Sexual maturity of the Atlantic bluefin tuna from the western spawning grounds

In comparison with the eastern Atlantic, a central issue regarding the size and age at sexual maturity of the Atlantic bluefin tuna from the western spawning grounds is that until recently,

biological studies were limited and a maturity ogive based on the analyses of biological samples is not available. Current ICCAT management assumptions on size and age at maturity of ABFT from the western stock mainly relied on fishery dependent data such as size at catch of ABFT in the northern Gulf of Mexico, its presumed exclusive spawning ground (Nemerson et al., 2000; Diaz and Turner, 2007), and interpretations of tagging experiments (Block et al., 2005; Boustany et al., 2008) rather than on reproductive biology investigations. Until recently, based upon size-frequency of fish captured in the Gulf of Mexico and electronic tagging, it was proposed that the western spawning stock is comprised of larger, late-maturing individuals compared with the eastern stock. Electronic tagging of ABFT captured and released in the western Atlantic showed that only individuals larger than or equal to 200 cm fork length (FL) (mean FL = 241 ± 28 cm, corresponding to age 11), entered the Gulf of Mexico during the spawning season (Block et al., 2005), although a later study confirmed that smaller individuals also dispersed there (Galuardi et al., 2010). Diaz and Turner (2007) analysed size-frequency data from fish caught in the Gulf of Mexico and estimated that 50% of the fish were mature at 12 years and 100% at 16-17 years of age (Figure 2). Nevertheless, current ICCAT assumptions examine two maturation scenarios: the first similar to the eastern stock and the second assumes 50% maturation at the age of ten and 100% maturation at 15 years (ICCAT 2018a, b).

In contrast, historical documents based on macroscopic observations of the gonads (Westman and Neville 1942; Wilson and Bartlett, 1967; Mather et al., 1995) and early histological evaluations (Rivas, 1954) suggested that sexual maturity is attained at five-six years. In a historical survey, ABFT were visually sampled on the MV Delaware of Cape Hatteras from 30 March to 23 April 1965, and fish from 78 to 169 kg were found in “spawning condition” (Wilson, 1965). Unfortunately, histological results from that study were apparently lost (Peter C. Wilson, personal communication, 2001). Baglin (1982), in a study based on GSI and gonadal histological analysis, reported “little development towards maturity in age 1 through age 7 fish from the Middle Atlantic Bight” and well developed ovaries in giants (FL > 207 cm) from the Gulf of Mexico and Florida Straits, suggesting that sexual maturity in western ABFT is attained at 8-10 years of age. A careful reading of Baglin’s

data suggests that some of his samples might have been misclassified: his classification scale did not take into the due account the presence of atretic oocytes as sign of previous reproductive activity. In addition, some small fish in his sample with GSI around 0.4-0.5 were classified as immature, inconsistent with his GSI scale indicating that gonad reproductive development begins at GSI = 0.5, consistent with Corriero et al. (2005). The possible errors in Baglin's gonad histological classification may have led him to categorize some mature specimens as immature, consequently, overestimating age at sexual maturity. Goldstein et al. (2007) examined gonads of commercial size ABFT (≥ 185 cm CFL) landed in New England and found evidence for asynchronous reproduction behaviour and possible younger age at maturity than eight or nine years, based on the presence of post ovulatory follicles in smaller fish. The authors suggested three scenarios that could explain the observed histological condition of sampled ovaries and testes: natural variation in spawning schedules, different spatio-temporal patterns of spawning with size, and skipped spawning. Skipped spawning was discounted as being unlikely for adult fish found in good somatic condition, typical of fish leaving the foraging ground (Estrada et al., 2005; Goldstein et al. 2007; Golet et al., 2007). Notably, ABFT smaller than 185 cm CFL, the minimum size limit for commercial catches, were not sampled. Two recent studies pioneering endocrine approaches for sexual maturation and reproduction provide additional evidence for the younger age at maturity for western ABFT. Heinisch et al. (2014) measured pituitary gonadotropins, follicle stimulating hormone (FSH) and luteinizing hormone (LH), in ABFT of various size classes from the Gulf of Maine and off Maritime Canada during the 2008-2010 foraging seasons. The comparative analysis of FSH/LH ratios with young of the year (YOY) ABFT sampled off Virginia Beach, VA, consistent with a larger sample size of juvenile and adult ABFT from the Mediterranean Sea (Berkovich et al., 2013), led the authors to conclude that age at sexual maturity in the two ABFT stocks is similar at three to five years. In a comprehensive examination of the gonadotropin axis involved in sexual determination and maturation in ABFT, Berkovich (2013), provided functional details of the endocrine cascade, showing maturation as the result of a complex of feedback and feed-forward neuro-endocrine systems, also involving lipid

transport and energy status. Endocrine research and advances in understanding of sexual maturity in fishes is largely focused on aquaculture species (e.g., Bhatta et al., 2012), and components of the endocrine complex in ABFT were found to be consistent with other fish, amphibian and reptilian species (Nagahama, 1994; Nagahama and Yamashita, 2008; Mylonas et al., 2010; Rosenfeld et al., 2012). The use of molecular markers of sexual maturity seems to confirm historical observations of age 4 and 5 individuals with intra-testicular milt and apparently mature ovaries in the north-western Atlantic off Massachusetts (Mather et al., 1995 and references therein cited). In future studies molecular markers of sexual maturity should be complemented with the analysis of histological markers of realized ovulation and spawning (Farley et al., 2014) in order to confirm that all endocrinologically competent adult individuals actually mature and release gametes.

Multiple studies (Lutcavage et al., 1999; Galuardi and Lutcavage, 2012; Heinisch et al., 2014) noted that the apparent absence of smaller, young spawners in Gulf of Mexico longline catches may be explained by the existence of alternative spawning ground(s) and age-structured spawning migrations similar to confirmed reproductive patterns of Pacific bluefin tuna (Itoh, 2006; Ohshimo et al., 2018). Evidence supporting this was recently provided with the multi-year confirmation of small ABFT larvae spawned across multiple areas of the Slope Sea in summer, through August (Richardson et al., 2016; Rypina et al., 2019).

Skipped spawning in ABFT has been hypothesized (Secor et al., 2007) but never demonstrated, except for three individuals captured in the Mediterranean Sea that showed atretic ovaries during the spawning period (Zupa et al., 2009). Most females larger than 134 cm FL sampled in the northwest Atlantic had only oocytes at the primary growth stage (Heinisch et al., 2014). This was expected since the fish were captured during the foraging season after absorbing the gonads. An alternative explanation for the presence of small, mature fish in the north-western Atlantic could be that these are eastern individuals skipping that reproductive season. They would then be assigned to the “resting” category of Rideout et al. (2005). The advantage of the skipped spawning is directing energy reserves to body growth in order to ensure higher fecundity in the following reproductive season

(Rideout et al., 2005; Secor, 2007). This could produce higher somatic growth rates in the population fraction delaying reproduction or skipping one or more reproductive seasons (Roff, 1983; Folkvord et al., 2014). However, eastern and western ABFT have similar growth rates (Restrepo et al., 2010), and population fractions showing significantly different lengths-at-age are not documented. It cannot be excluded, however, that after trans-oceanic migrations, young adults with energy reserves below a threshold level do not activate the reproductive axis during the reproductive season following the migration.

An individual energy-based model for ABFT (Chapman et al., 2011) suggests that younger fish conduct shorter spawning migrations than larger fish. Smaller fish are expected to forage closer to their spawning grounds relative to larger fish, as do cod in the northeast Atlantic (Jørgensen and Fiksen, 2006). A scenario where fish utilizes several spawning grounds during their life time, as demonstrated for ABT spawning in the Mediterranean Sea (Heinisch et al., 2008) and Pacific bluefin tuna (Itoh, 2006; Ohshimo et al., 2018), is likely to be the case for western ABFT. Moreover, it is argued that, by combining the results of the historical data, physiological findings, tagging, migration and larvae sampling with the results of energy-based models and growth curves, a larger, more realistic overview emerges (Figure 4). It is likely that ABFT utilize a larger area of the Atlantic Ocean and its basins for foraging and reproduction, like other temperate tunas. [Figure 4 near here]

Conclusions

Recent findings from investigations carried out using advanced molecular technologies challenged the current paradigm indicating that the two recognised Atlantic bluefin tuna stocks reproduce in the Gulf of Mexico and in the Mediterranean at diverse ages. It is argued that a comprehensive analysis of historical studies and recent biomolecular evidences indicates that ABFT have more complex reproductive biology and spawning behaviour patterns than previously considered. First, on eastern spawning grounds 50% of ABFT females reproduce at three years of age and 100% are sexually

mature at five years of age. Second, mostly large adults (age ≥ 8 years) reproduce in the Gulf of Mexico. Third, younger adults (≥ 5 years old) as well as large adults spawn in the northwest Atlantic Ocean across the Slope and Caribbean Seas. There is little biological evidence that ABFT reproduce according to a non-annual schedule, or that a relevant fraction of the population delays sexual maturity and reproduce at an older age than the rest of the population. Since the available information is biased by studies having been carried out in known spawning areas and periods, further studies on the reproductive status of ABFT beyond known spawning areas and periods, while being consistent with oceanographic conditions of spawning areas, are recommended. This would help confirm whether ABFT spawn annually, or whether a fraction of the adult population can skip reproduction for one or more consecutive years. The question of sexual maturation schedules is a part of a bigger picture of ABFT life history, much of which remains unresolved, including lifespan and natural mortality. Integrating results of tagging studies, migration, mixing, larvae sampling, energetics and growth with sexual maturation results argues that the current separation of ABFT as two exclusive stocks, adopted by ICCAT during the 1970's for statistical purposes might no longer be appropriate to explain ABFT behaviour and population structure. Alternative scenarios for characterizing ABFT as a single stock with substructure, or a meta-population, must be explored to generate a more realistic paradigm for understanding and managing ABFT fisheries.

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References

Abascal, F. J., C. Megina, and A. Medina. Testicular development in migrant and spawning bluefin tuna (*Thunnus thynnus* (L.) from the eastern Atlantic and Mediterranean. *Fish. Bull.*, **102**: 407–417 (2004).

- Aranda, G. A., L. Aragón, A. Corriero, C. C. Mylonas, F. de la Gándara, A. Belmonte, and A. Medina. GnRHa-induced spawning in cage-reared Atlantic bluefin tuna: an evaluation using stereological quantification of ovarian post-ovulatory follicles. *Aquaculture*, **317**: 255–259 (2011).
- Aranda, G., A. Medina, A. Santos, F. J. Abascal, and T. Galaz. Evaluation of Atlantic bluefin tuna reproductive potential in the western Mediterranean Sea. *J. Sea. Res.*, **76**: 154–160 (2013).
- Arena, P. Rilevazioni e studi sulle affluenze del tonno nel Tirreno e sull'andamento della pesca da parte delle “tonnare volanti” nel quadriennio 1984-1988. Report to: ESPI, Ente Siciliano per la Promozione Industriale, Palermo. pp. 1-55 (1988).
- Arrizabalaga, H., I. Arregui, A. Medina, N. Rodríguez-Ezpeleta, J.-M. Fromentin, and I. Fraile. *Life History and Migrations of Mediterranean Bluefin Tuna*, Chapter 3. **In:** *The Future of Bluefin Tunas Ecology, Fisheries Management, and Conservation* (Block B. A., Ed.). Baltimora, MD: Johns Hopkins University Press (2019).
- Baglin, R. E. Reproductive biology of western Atlantic bluefin tuna. *Fish. Bull.*, **80**: 121–134 (1982).
- Bard, F. X., P. Bach, and E. Josse. Habitat et écophysiole des thons: Quoi de neuf depuis 15 ans? *ICCAT Col. Vol. Sci. Pap.*, **50**: 319-342 (1998).
- Berkovich, N., A. Corriero, N. Santamaria, C. C. Mylonas, R. Vassallo-Agius, F. de la Gándara, A. Belmonte, I. Meiri-Ashkenazi, H. Gordin, C. R. Bridges, and H. Rosenfeld. The intra-pituitary relationship of follicle stimulating hormone and luteinizing hormone during pubertal development in Atlantic bluefin tuna (*Thunnus Thynnus* Linnaeus, 1758). *Gen. Comp. Endocrinol.*, **194**: 10-23 (2013).
- Bhatta, S., T. Iwai, C. Miura, M. Higuchi, S. Shimizu-Yamaguchi, H. Fukada, and T. Miura. Gonads directly regulate growth in teleosts. *PNAS*, **109**: 11408-11412 (2012).
- Block, B. A., H. Dewar, S. B. Blackwell, T. D. Williams, E. D. Prince, C. J. Farwell, A. Boustany, S. L. H. Teo, A. Seitz, A. Walli, and D. Fudge. Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. *Science*, **293**: 1310-1314 (2001).

- Block, B. A., S. L. H. Teo, A. Walli, A. Boustany, M. J. W. Stokesbury, C. J. Farwell, K. C. Weng, H. Dewar, and T. D. Williams. Electronic tagging and population structure of Atlantic bluefin tuna. *Nature*, **434**: 1121-1127 (2005).
- Boustany, A. M., C. A. Reeb, and B. A. Block. Mitochondrial DNA and electronic tracking reveal population structure of Atlantic bluefin tuna (*Thunnus thynnus*). *Mar. Biol.*, **156**: 13–24 (2008).
- Brodziak, J., M. Mangel, and C.-L. Sun. Stock-recruitment resilience of North Pacific striped marlin based on reproductive ecology. *Fish. Res.*, **166**: 140–150 (2015).
- Chapman, E. W., C. Jorgensen, M. E. Lutcavage, and R. Hilborn. Atlantic bluefin tuna (*Thunnus thynnus*): a state-dependent energy allocation model for growth, maturation, and reproductive investment. *Can. J. Fish. Aquat. Sci.*, **68**: 1934–1951 (2011).
- Clark, C. W., and M. Mangel. *Dynamic state variable models in ecology*. New York, US: Oxford University Press (2000).
- Corriero, A., S. Desantis, M. Deflorio, F. Acone, C. R. Bridges, J. M. de la Serna, P. Megalofonou, and G. De Metrio. Histological investigation on the ovarian cycle of the bluefin tuna in the western and central Mediterranean. *J. Fish Biol.*, **63**: 108-119 (2003).
- Corriero, A., S. Karakulak, N. Santamaria, M. Deflorio, P. Addis, S. Desantis, F. Cirillo, A. Fenech-Farrugia, R. Vassallo-Agius, J. M. de la Serna, Y. Oray, A. Cau, and G. De Metrio. Size and age at sexual maturity of female bluefin tuna (*Thunnus thynnus* L. 1758) from the Mediterranean Sea. *J. Appl. Ichthyol.*, **21**: 483-486 (2005).
- Corriero, A., A. Medina, C. C. Mylonas, F. J. Abascal, M. Deflorio, L. Aragón, C. R. Bridges, N. Santamaria, G. Heinisch, R. Vassallo-Agius, A. Belmonte, C. Fauvel, A. Garcia, H. Gordin, and G. De Metrio. Histological study of the effects of treatment with gonadotropin-releasing hormone agonist (GnRHa) on the reproductive maturation of captive-reared Atlantic bluefin tuna (*Thunnus thynnus* L.). *Aquaculture*, **272**: 675-686 (2007).
- Desjardins, C., and H. D. Hafs. Levels of pituitary FSH and LH in heifers from birth through puberty. *J. Anim. Sci.*, **27**: 472–477 (1968).

- Diaz, G., and S. C. Turner. Size frequency distribution analysis, age composition, and maturity of western bluefin tuna in the Gulf of Mexico from the U.S. (1981-2005) and Japanese (1975-1981) longline fleets. *ICCAT Col. Vol. Sci. Pap.*, **60**: 1160-1170 (2007).
- Dickhut, R. M., A. D. Deshpande, A. Cincinelli, M. A. Cochran, S. Corsolini, R. W. Brill, D. H. Secor, and J. E. Graves. Atlantic bluefin tuna (*Thunnus thynnus*) population dynamics delineated by organochlorine tracers. *Environ. Sci. Technol.*, **43**: 8522–8527 (2009).
- Di Natale, A. Sensitive and essential areas for large pelagic species in the Mediterranean Sea. Report of the STECF-SGMERD-06-01 Sensitive and Essential Fish Habitats in the Mediterranean. pp 165-180 (2006).
- Di Natale, A., and S. Tensek. ICCAT Atlantic-wide Research programme for bluefin tuna (GBYP): activity report for the last part of Phase 4 and the first part of Phase 5 (2014-2015). *ICCAT Collect. Vol. Sci. Pap.*, **72**: 1477-1530 (2016).
- Di Natale, A., J. A. Cañadas, S. Vázquez-Bonales, A. Tensek, and A. Pagá García. Report of the ICCAT GBYP aerial survey for Bluefin spawning aggregation in 2017. *ICCAT Collect. Vol. Sci. Pap.*, **74**: 3172-3204 (2018).
- Džoić, T., G. Beg Paklar, B. Grbec, S. Ivatek-Šahdan, B. Zorica, T. Šegvić-Bubić, V. Čikeš Keč, I. Lepen Pleić, I. Mladineo, L. Grubišić, and P. Verley. Spillover of the Atlantic bluefin tuna offspring from cages in the Adriatic Sea: A multidisciplinary approach and assessment. *PLoS ONE*, **12**:e0188956 (2017).
- Estrada, J. A., M. Lutcavage, and S. Thorrold. Diet and trophic position inferred from stable carbon and nitrogen isotopes of Atlantic bluefin tuna (*Thunnus thynnus*). *Mar. Biol.*, **147**: 37-45 (2005).
- Farley, J. H., S. D. Hoyle, J. Paige Eveson, A. J. Williams, C. R. Davies, and S. J. Nicol. Maturity ogives for South Pacific albacore tuna (*Thunnus alalunga*) that account for spatial and seasonal variation in the distributions of mature and immature fish. *PLoS ONE*, **9**:e83017 (2014).

- Folkvord, A., C. Jørgensen, K. Korsbrekke, R. D. M. Nash, T. Nilsen, and J. E. Skjæraasen. Trade-offs between growth and reproduction in wild Atlantic cod. *Can. J. Fish. Aquat. Sci.*, **71**: 1106–1112 (2014).
- Fromentin, J. M., and A. Fonteneau. Fishing effects and life history traits: a case-study comparing tropical versus temperate tunas. *Fish. Res.*, **53**: 133-150 (2001).
- Fromentin, J. M., and J. E. Powers. Atlantic bluefin tuna: Population dynamics, ecology, fisheries, and management. *Fish Fish.*, **6**: 281-306 (2005).
- Galuardi, B., and M. Lutcavage. Dispersal routes and habitat utilization of juvenile Atlantic bluefin tuna, *Thunnus thynnus*, tracked with mini PSAT and archival tags. *PLoS ONE*, **7**: e37829 (2012).
- Galuardi, B., F. Royer, W. Golet, J. Logan, J. Neilson, and M. Lutcavage. Complex migration routes of Atlantic bluefin tuna (*Thunnus thynnus*) question current population structure paradigm. *Can. J. Fish. Aquat. Sci.*, **67**: 966–976 (2010).
- Goldstein, J., S. Heppell, A. Cooper, S. Brault, and M. Lutcavage. Reproductive status and body condition of Atlantic bluefin tuna in the Gulf of Maine, 2000–2002. *Mar. Biol.*, **151**: 2063–2075 (2007).
- Golet, W. J., A. B. Cooper, R. Campbell, and M. Lutcavage. Decline in condition of northern bluefin tuna (*Thunnus thynnus*) in the Gulf of Maine. *Fish. Bull.*, **105**: 390–395 (2007).
- Heinisch, G., A. Corriero, A. Medina, F. J. Abascal, J. M. de la Serna, R. Vassallo-Agius, A. Belmonte Ríos, A. García, F. de la Gándara, C. Fauvel, C. R. Bridges, C. C. Mylonas, S. Karakulak, I. Oray, G. De Metrio, H. Rosenfeld, and H. Gordin. Spatio-temporal pattern of bluefin tuna (*Thunnus thynnus* L. 1758) gonad maturation across the Mediterranean Sea. *Mar. Biol.*, **154**: 623-630 (2008).
- Heinisch, G., H. Rosenfeld, J. M. Knapp, H. Gordin, and M. E. Lutcavage. Sexual maturity in western Atlantic bluefin tuna. *Sci. Rep.*, **4**: 7205 (2014).
- Heppell, S. A., and C. V. Sullivan. Reproduction of bluefin tuna: assessing maturity using sex specific compounds present in muscle. *ICCAT Coll. Vol. Sci. Pap.*, **51**: 860-865 (2000).

- Houston, A. I., and J. M. McNamara. *Models of adaptive behaviour: an approach based on state*. Cambridge, UK: Cambridge University Press (1999).
- ICCAT. Recommendation by ICCAT establishing a multi-annual management plan for bluefin tuna in the eastern Atlantic and the Mediterranean Sea. ICCAT recommendation [18-02], pp. 46 (2018a).
- ICCAT. Compendium management recommendations and resolutions adopted by ICCAT for the conservation of Atlantic tunas and tuna-like species. pp. 388 (2018b).
- Ito, J., T. Tanaka, R. Horikawa, S. Morita, M. Kokaji, M. Satoh, A. Tanae, and I. Hibi. Changes in serum and urinary LH/FSH ratio during puberty. *Pediatr. Res.*, **33**: S86 (1993).
- Itoh, T. Sizes of adult bluefin tuna *Thunnus orientalis* in different areas of the western Pacific Ocean. *Fisheries Sci.*, **72**: 53–62 (2006).
- Jørgensen, C., B. Ernande, Ø. Fiksen, and U. Dieckmann. The logic of skipped spawning in fish. *Can. J. Fish. Aqua. Sci.*, **63**: 200–211 (2006).
- Jørgensen, C., and Ø. Fiksen. State-dependent energy allocation in cod (*Gadus morhua*). *Can. J. Fish. Aqua. Sci.*, **63**, 186–199 (2006).
- Karakulak, S., I. Oray, A. Corriero, M. Deflorio, N. Santamaria, S. Desantis, and G. De Metro. Evidence of a spawning area for bluefin tuna (*Thunnus thynnus* L.) in the eastern Mediterranean. *J. Appl. Ichthyol.*, **20**: 318–320 (2004).
- Katavić, I., L. Grubišić, V. Tičina, T. Šegvić-Bubić, J. Maleš, I. Talijančić, I. Žužul. Catch structure of purse seine bluefin tuna fishing in the Adriatic Sea: the first age frequency distribution estimate based on spine age-length key. *ICCAT Collect. Vol. Sci. Pap.*, **73**: 2535-2542 (2017).
- Knapp, J. M., G. Aranda, A. Medina, and M. Lutcavage. Comparative assessment of the reproductive status of female Atlantic bluefin tuna from the Gulf of Mexico and the Mediterranean Sea. *PLoS ONE*, **9**: e98233 (2014).

- Logan, J. M., E. Rodríguez-Marín, N. Goñi, S. Barreiro, H. Arrizabalaga, Golet, W., and M. Luctavage. Diet of young Atlantic bluefin tuna (*Thunnus thynnus*) in eastern and western Atlantic foraging grounds. *Mar. Biol.*, **158**: 73–85 (2011).
- Lowerre-Barbieri, S. K., S. L. Walters Burnsed, and J. W. Bickford. Assessing reproductive behavior important to fisheries management: a case study with red drum, *Sciaenops ocellatus*. *Ecol. Appl.*, **26**: 979–995 (2016).
- Lubzens, E., G. Young, J. Bobe, and J. Cerdá. Oogenesis in teleosts: how fish eggs are formed. *Gen. Comp. Endocrinol.*, **165**: 36–389 (2010).
- Luque, P. L., E. Rodriguez-Marin, J. Landa, M. Ruiz, P. Quelle, D. Macias, and J. M. Ortiz De Urbina. Direct ageing of *Thunnus thynnus* from the eastern Atlantic Ocean and western Mediterranean Sea using dorsal fin spines. *J. Fish Biol.*, **84**: 1876–1903 (2014).
- Lutcavage, M., R. W. Brill, G. B. Skomal, B. C. Chase, and P. W. Howey. Results of pop-up satellite tagging of spawning size class fish in the Gulf of Maine: do North Atlantic bluefin tuna spawn in the mid-Atlantic? *Can. J. Fish. Aquat. Sci.*, **56**: 173-177 (1999).
- Magnuson, J. J., B. A. Block, R. B. Deriso, J. R. Gold, W. S. Grant, T. J. Quinn, S. B. Saila, L. Shapiro, and E. D. Stevens. An Assessment of Atlantic Bluefin Tuna, 148pp. *National Research Council*. Washington, D.C.: National Academy Press (1994).
- Mather, III, F. J., J. M. Mason, and A. C. Jones. Historical document: life history and fisheries of Atlantic bluefin tuna. U.S. Dep. Comm., NOAA Tec. Mem., NMFS-SEFSC 370 (1995).
- Maunder, M. N. and R. B. Deriso. A stock-recruitment model for highly fecund species based on temporal and spatial extent of spawning. *Fish. Res.*, **146**: 96-101 (2013).
- Medina, A, F. J. Abascal, C. Megina, and A. García. Stereological assessment of the reproductive status of female Atlantic northern bluefin tuna during migration to Mediterranean spawning grounds through the Strait of Gibraltar. *J. Fish Biol.*, **60**: 203-217 (2002).
- Mylonas, C. C., C. R. Bridges, H. Gordin, A. Belmonte Ríos, A. García, F. de la Gándara, C. Fauvel, M. Suquet, A. Medina, M. Papadaki, G. Heinisch, G. De Metrio, A. Corriero, R. Vassallo-Agius,

- J. M. Guzmán, E. Mañanos, and Y. Zohar. Preparation and administration of gonadotropin-releasing hormone agonist (GnRHa) implants for the artificial control of reproductive maturation in captive-reared Atlantic bluefin tuna (*Thunnus thynnus*). *Rev. Fish. Sci.*, **15**: 183–210 (2007).
- Mylonas, C. C., A. Fostier, and S. Zanuy. Broodstock management and hormonal manipulations of fish reproduction. *Gen. Comp. Endocrinol.*, **165**: 516–534 (2010).
- Muhling, B. A., J. T. Lamkin, J. M. Quattro, R. H. Smith, M. A. Roberts, M. A. Roffer, and K. Ramírez. Collection of larval bluefin tuna (*Thunnus thynnus*) outside documented western Atlantic spawning grounds. *Bull. Mar. Sci.*, **87**: 687–694 (2011).
- Nagahama, Y. Endocrine regulation of gametogenesis in fish. *Int. J. Dev. Bio.*, **38**: 217–229 (1994).
- Nagahama, Y., and M. Yamashita. Regulation of oocyte maturation in fish. *Dev. Growth Differ.*, **50**: S195–S219 (2008).
- Nemerson, D., S. Berkeley, and C. Safina. Spawning site fidelity in Atlantic bluefin tuna, *Thunnus thynnus*: the use of size-frequency analysis to test for the presence of migrant east Atlantic bluefin tuna on Gulf of Mexico spawning grounds. *Fish. Bull.*, **98**: 118–126 (2000).
- Oerter, K. T., M. Uriarte, S. Rose, K. M. Barnes, and G. B. Cutler. Gonadotropin secretory dynamics during puberty in normal girls and boys. *J. Clin. Endocr. Metab.*, **71**: 1251–1258 (1990).
- Ohshimo, S., T. Sato, Y. Okochi, S. Tanaka, T. Ishihara, H. Ashida, and N. Suzuki. Evidence of spawning among Pacific bluefin tuna, *Thunnus orientalis*, in the Kuroshio and Kuroshio–Oyashio transition area. *Aquat. Living Resour.*, **31**: 33 (2018).
- Patiño, R., and C. V. Sullivan. Ovarian follicle growth, maturation, and ovulation in teleost fish. *Fish Physiol. Biochem.*, **26**: 57–70 (2002).
- Piccinetti, C., A. Di Natale, and P. Arena. Eastern bluefin tuna (*Thunnus thynnus*, L.) reproduction and reproductive areas and seasons. *ICCAT Collect. Vol. Sci. Pap.*, **69**: 891–912 (2013).
- Reglero, P., L. Ciannelli, D. Alvarez-Berastegui, R. Balbín, J. L. López-Jurado, and F. Alemany. Geographically and environmentally driven spawning distributions of tuna species in the western Mediterranean Sea. *Mar. Ecol. Prog. Ser.*, **463**: 273–284 (2012).

- Restrepo, V. R., G. A. Diaz, J. F. Walter, J. D. Neilson, S. E. Campana, D. Secor, and R. L. Wingate. Updated estimate of the growth curve of Western Atlantic bluefin tuna. *Aquat. Living Resour.*, **23**: 335–342 (2010).
- Richardson, D. E., K. E. Marancik, J. R. Guyonc, M. E. Lutcavage, B. Galuardi, C. H. Lam, H. J. Walsh, S. Wildes, D. A. Yates, and J. A. Hare. Discovery of a spawning ground reveals diverse migration strategies in Atlantic bluefin tuna (*Thunnus thynnus*). *P. Natl. Acad. Sci. USA*, **113**: 3299–3304 (2016).
- Rideout, R. M., G. A. Rose, and M. P. M. Burton. Skipped spawning in female iteroparous fishes. *Fish Fish.*, **6**: 50–72 (2005).
- Rideout, R. M. and J. Tomkiewicz. Skipped spawning in fishes: more common than you might think. *Mar. Coast. Fish.*, **3**: 176–189 (2011).
- Rijnsdorp, A. D. The mechanism of energy allocation over reproduction and somatic growth in female North Sea plaice, *Pleuronectes platessa* L. *Neth. J. Sea Res.*, **26**: 279–290 (1990).
- Rivas, L. R. A preliminary report on the spawning of the western North Atlantic bluefin tuna (*Thunnus thynnus*) in the Straits of Florida. *B. Mar. Sci.*, **4**: 302–322 (1954).
- Rodríguez-Roda, J. Biología del atún, *Thunnus thynnus* (L.), de la costa sudatlántica de España. *Invest. Pesq.*, **25**: 33–164 (1964).
- Rodríguez-Roda, J. Fecundidad del atún, *Thunnus thynnus* (L.), de la costa sudatlántica de España. *Invest. Pesq.*, **31**: 33–52 (1967).
- Roff, D. A. An allocation model of growth and reproduction in fish. *Can. J. Fish. Aquat. Sci.*, **40**: 1395–1404 (1983).
- Roff, D. A. *Life history evolution*. Sunderland, MA: Sinauer (2002).
- Rooker, J. R., D. H. Secor, G. De Metro, and E. Rodriguez-Marin. Evaluation of population structure and mixing rates of Atlantic bluefin tuna from chemical signatures in otoliths. *ICCAT Col. Vol. Sci. Pap.*, **59**: 813–818 (2006).

- Rooker, J. R., D. H. Secor, G. De Metrio, R. Schloesser, B. A. Block, and J. D. Neilson. Natal homing and connectivity in Atlantic bluefin tuna populations. *Science*, **322**: 742-744 (2008).
- Rosenfeld, H., C. C. Mylonas, C. R. Bridges, G. Heinisch, A. Corriero, R. Vassallo-Aguis, A. Medina, A. Belmonte, A. Garcia, F. de la Gándara, C. Fauvel, G. De Metrio, I. Meiri-Ashkenazi, H. Gordin, and Y. Zohar. GnRHa-mediated stimulation of the reproductive endocrine axis in captive Atlantic bluefin tuna, *Thunnus thynnus*. *Gen. Comp. Endocrinol.*, **175**: 55–64 (2012).
- Rypina, I. I., K. Chen, C. M. Hernández, L. J. Pratt, and J. K. Llopiz, Investigating the suitability of the Slope Sea for Atlantic bluefin tuna spawning using a high-resolution ocean circulation model. *Ices J. Mar. Sci.*, fsz079, (2019).
- Santamaria, N., G. Bello, A. Corriero, M. Deflorio, R. Vassallo-Agius, T. Bök, and G. De Metrio. Age and growth of Atlantic bluefin tuna, *Thunnus thynnus* (Osteichthyes: Thunnidae), in the Mediterranean Sea. *J. Appl. Ichthyol.*, **25**: 38-45 (2009).
- Santamaria, N., G. Bello, C. Pousis, R. Vassallo-Agius, F. de la Gándara, and A. Corriero. Fin spine bone resorption in Atlantic bluefin tuna, *Thunnus thynnus*, and comparison between wild and captive-reared specimens. *PLoS ONE*, **10**: e0121924 (2015).
- Santamaria, N., G. Bello, L. Passantino, M. Di Comite, R. Zupa, C. Pousis, R. Vassallo-Agius, V. Cicirelli, G. Basilone, S. Mangano, and A. Corriero. Micro-anatomical structure of the first spine of the dorsal fin of Atlantic bluefin tuna, *Thunnus thynnus* (Osteichthyes: Scombridae). *Ann. Anat.*, **219**: 1-7 (2018).
- Santamaria, N., A. Corriero, S. Desantis, D. Zubani, R. Gentile, V. Sciscioli, M. de la Serna, C. R. Bridges, and G. De Metrio. Testicular cycle of the Mediterranean bluefin tuna (*Thunnus thynnus* L.). *Cah. Opt. Medit.*, **60**: 183-185 (2003).
- Scaccini, A. Biologia e pesca dei tonni dei mari italiani. Memoria n. 12, Ministero della Marina Mercantile, Direzione Generale della Pesca Marittima, Roma. pp. 1-101 (1965).
- Schaefer, K. M. Reproductive biology of yellowfin tuna (*Thunnus albacares*) in the eastern Pacific Ocean. *Inter-Amer. Trop. Tuna Comm. Bull.*, **21**: 201-272 (1998).

- Schaefer, K. M. Reproductive biology of tunas, pp. 225-270. **In:** *Tuna: Physiology, Ecology and Evolution* (Block B. A. and E. D. Stevens, Eds.). San Diego, CA: Academic Press (2001).
- Secor, D. Pacific Ocean. Inter-Amer Trop Tuna Comm, Bull 21: 201-272. Do some Atlantic bluefin tuna skip spawning? *ICCAT Col. Vol. Sci. Pap.*, **60**: 1141-1153 (2007).
- Sella, M. Migrazione e habitat del tonno (*Thunnus thynnus* L.) studiati col metodo degli ami, con osservazioni sull'accrescimento, sul regime delle tonnare ecc. *Mem. R. Com. Talassogr. Ital.*, **156**: 1-24 (1929a).
- Sella, M. Biologia e pesca del tonno (*Thunnus thynnus* L.). Atti Conv. Biol. Mar. Appl. Pesca, Messina, Giugno 1928, pp. 1-32 (1929b).
- Susca, V., A. Corriero, C. R. Bridges, and G. De Metro. Study of the sexual maturity of female bluefin tuna: purification and partial characterization of vitellogenin and its use an enzyme-linked immunosorbent assay. *J. Fish Biol.*, **58**: 815-831 (2001).
- Tičina, V., and I. Kačić. Preliminary data on age determination of bluefin tuna (*Thunnus thynnus* L.) caught in the Adriatic Sea. *Rapp. Comm. Int. Mer Medit.*, **35**: 486-487 (1998).
- Turner, S. C, and J. E. Powers. Review of information related to Atlantic bluefin tuna east-west movement. *ICCAT Col. Vol. Sci. Pap.*, **44**: 191-197 (1995).
- Westman, J. R., and W.C. Neville. The tuna fishery of Long Island, New York. A survey conducted by the United States Department of the Interior, Fish and Wildlife Service, in cooperation with the County Executive and the Board of Supervisors, Nassau County. Long Island, New York. *Board of Supervisors*, Nassau County, Long Island, New York. pp. 1-31 (1942).
- Wilson, P. C., and M. R. Bartlett. Inventory of U.S. exploratory longline fishing effort and catch rates for tunas and swordfish in the northwestern Atlantic 1957-1965. *U.S. Fish and Wildlife Special Scientific Report-Fisheries*, **543**: 1-52 (1967).
- Wilson, P. C., R. A. Bruce, W. H. Stevenson, and E. Dixwell Chase. Cruise report, MV Delaware cruise 65-3; March 30 - April 23, 1965. Gloucester, MA: *Exploratory fishing and gear research base* (1965).

- Zupa, R., A. Corriero, M. Deflorio, N. Santamaria, D. Spedicato, C. Marano, M. Losurdo, C. R. Bridges, and G. De Metrio. A histological investigation of the occurrence of non-reproductive female bluefin tuna *Thunnus thynnus* in the Mediterranean Sea. *J. Fish Biol.*, **75**: 1221–1229 (2009).
- Zupa, R., C. Fauvel, C. C. Mylonas, N. Santamaria, L. Valentini, C. Pousis, M. Papadaki, M. Suquet, F. de la Gándara, G. Bello, G. De Metrio, and A. Corriero. Comparative analysis of male germ cell proliferation in wild and captive Atlantic bluefin tuna *Thunnus thynnus*. *J. Appl. Ichthyol.*, **29**: 71-81 (2013).

Captions

Figure 1. Micrographs of the ovaries from adult Atlantic bluefin tuna (*Thunnus thynnus*) captured in the Mediterranean Sea during the reproductive season. (a) Ovary from a mature non-spawning specimen with advanced yolk oocytes. (b) Ovary from a spawning specimen showing hydrated oocytes. (c) Ovary from a spawning individual showing both oocytes at migratory nucleus and post-ovulatory follicles. (d) Ovary from an inactive mature fish showing extensive atresia of vitellogenic follicles. Magnification bars = 500 μm in a), b) and c); 300 μm in d). All sections were stained with haematoxylin-eosin. Arrow, post-ovulatory follicle; arrow, advanced stage of atresia of yolked oocyte; h, hydrated oocyte; mn, oocyte at the migratory nucleus stage; yo, advanced yolked oocyte.

Figure 2. Maturity ogives for Atlantic bluefin tuna (*Thunnus thynnus*) according the present assumptions of the International Commission for the Conservation of Atlantic tunas. Estimates for the eastern Atlantic are based on histological analysis of ovaries from fish captured in the Mediterranean Sea (Corriero et al., 2005). Estimates for the western Atlantic are based on size-frequency data of unsexed individuals captured in the Gulf of Mexico (Diaz and Turner, 2007) and do not include maturity data obtained through the analyses of gonads and pituitaries of fish captured in the north-western Atlantic indicating an age at maturity similar to that of the eastern stock.

Figure 3. Micrographs of Atlantic bluefin tuna spine sections used for age determination of mature individuals sampled in the Mediterranean Sea during the spawning season. (a) Age 3, 103 cm FL; two rings are visible and one ring was reabsorbed. (b) Age 5, 138 cm FL; four rings are visible and one ring was reabsorbed. Arrows indicate visible rings. Magnification bars = 2 mm. *Modified from Corriero et al. (2005).*

Figure 4. Distribution and sexual maturity of Atlantic bluefin tuna. The figure integrates distribution data from Figure 11 of Rooker et al. (2007) with data on sexual maturity in the ascertained spawning grounds (Mediterranean, Gulf of Mexico and north-western Atlantic).