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RECRUITMENT VARIABILITY AND ENVIRONMENT: ISSUES RELATED TO STOCK ASSESSMENTS OF ATLANTIC TUNAS

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SUMMARY

Variations in recruitment and year-class strength of fish populations is a well known feature which can be related to three main factors: 1) human activity, mainly through over-exploitation of the spawning stock, but also through pollution of the spawning and nursery areas; 2) biological processes, such as predation, cannibalism and competition and 3) environmental events. Life history traits of Atlantic tuna make the probability of a stable recruitment much higher for tropical tuna than temperate ones, but the latter are more adapted to the risks of recruitment failures than the former. As noise in the recruitment can lead to pseudo-cyclic variations in SSB and yields, trends in stock size and catches are also more likely in temperate Atlantic tuna. All these stochastic processes, however, make difficult (and in some cases impossible) the choice of a pertinent deterministic stock-recruit relationship, such as the Ricker or Beverton and Holt models. A way forward is to move to a stock-recruitment relationship that would integrate environmental influence; a step which should be tempered by careful thinking about the physical, biological, physiological and behavioral processes affecting Atlantic tuna.

RÉSUMÉ

Les fluctuations du recrutement des populations de poissons sont un fait bien connu, pouvant être liées à 3 types de facteurs: 1) l'activité humaine, au travers de la surexploitation des reproducteurs mais aussi de la pollution des aires de croissance des jeunes recrues ; 2) les processus biologiques tels que la prédation, le cannibalisme et la compétition et 3) les événements environnementaux. Les caractéristiques biologiques des différents thonidés de l'Atlantique font que les populations tropicales ont une probabilité de recrutement stable bien supérieure aux populations tempérées, qui, par ailleurs, sont mieux adaptés aux échecs de recrutement. Comme le bruit du recrutement peut générer des fluctuations pseudo-cycliques du stock reproducteur et des captures, des tendances dans ces deux composantes sont elles aussi plus probables chez les thons tempérés. Tous ces processus stochastiques rendent difficile (voire impossible) le choix d'un modèle stock-recrutement déterministe, tel qu'un modèle de Ricker ou de Berverton et Holt. Pour sortir de ce dilemme, une possibilité serait d'intégrer les facteurs environnementaux influents au sein de ces modèles; une étape qui nécessite au préalable un examen critique des processus physiques, biologiques, physiologiques et comportementaux affectant les thonidés de l'Atlantique.

RESUMEN

Las variaciones en el reclutamiento y la fuerza de la clase anual de las poblaciones de peces son características bien conocidas que pueden estar relacionadas con tres principales factores: 1) la actividad humana, principalmente la sobreexplotación del stock reproductor, y también la contaminación de las zonas de desove y cría; 2) los procesos biológicos, como la depredación, canibalismo y competencia, y 3) fenómenos del medio ambiente. Las características del ciclo vital de los túnidos atlánticos hacen que la probabilidad de un reclutamiento estable sea mucho más alta en el caso de los túnidos tropicales que en el de los de aguas templadas, si bien estos últimos están mejor adaptados a los riesgos de fallo en el reclutamiento que los primeros. Igual que el ruido en el reclutamiento puede conducir a variaciones pseudo-cíclicas en SSB y rendimientos, las tendencias en el tamaño del stock y las

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capturas son también más probables en túnidos atlánticos de aguas templadas. Todos estos procesos estocásticos, sin embargo, dificultan (y en algunos casos imposibilitan) la elección de una relación determinista stock-reclutamiento pertinente, como por ejemplo los modelos Ricker o Beverton-Holt. Una forma de avanzar sería adoptar una relación stock-reclutamiento que integrase la influencia del medio ambiente. Este paso debería decidirse considerando bien los procesos físicos, biológicos, fisiológicos y de comportamiento que afectan a los túnidos atlánticos.

MOTS CLÉS

Recruitment, environmental effects, stochastic processes, population dynamics, life history, tuna fisheries

INTRODUCTION

The scientific literature has shown, since more a century, that variations in recruitment is a common feature of most exploited (and non-exploited) fish populations (e.g., Caley et al. 1996, Cushing 1975, Hjort 1914, Hjort 1926, May 1974, Wooster and Bailey 1989). The understanding of the processes controlling these variations is not only important on an ecological viewpoint, but also (and mainly?) on a conservation and management one. The long-term consequences of a management regime are, for instance, closely related to the ability of the stock assessment working groups to adequately model the stock-recruit relationship .

In this manuscript, we first presented a brief review on the recruitment of fish. Then, we tried to evaluate the possible implications of the differences in life history traits between tropical and temperate Atlantic tunas on the recruitment. Finally, we discussed the present limits and some perspectives about the spawner-recruit modelling in the frame of the stock assessment and management of the Atlantic tunas.

1. A BRIEF REVIEW ON THE RECRUITMENT ISSUE OF FISH

At the beginning of the century, Hjort (1914) stated, on the basis of historical observations, that " *a characteristic feature of all branches of the fishing industry has been the fluctuations of their respective yields from year to year, …/… with a series of years of profitable fishery succeeding and succeeded by several years of dearth*". Studying cod, herring and haddock, Hjort (1914, 1926) put forward that these variations are mainly due to fluctuations of the year classes (and not migration), which are themselves determined at a very early stage. The author proposed two main mechanisms for his hypothesis : (i) the former postulates that the strength of the year-class is set by the availability of planktonic food shortly after the larval yolk supply has been exhausted, i.e. what has been called the 'Hjort's critical concept', see also (May 1974) and (ii) the latter suggests that the eggs and larvae might be carried far away out by wind and current, so that they could not return and reach their nursery grounds. These two features thus consider that the starvation of the fish larvae is the crucial process determining the year-class strength.

Larval starvation, which has been demonstrated in laboratory experiments but not in natural populations (May 1974), has been currently explained by two popular mechanisms. The first and most well known one is the 'match-mismatch hypothesis' (Cushing 1990), which postulates that the larval mortality is determined by the match-mismatch in the seasonal availability of food of fish larvae (i.e., mainly zooplanktonic food such the copepods, an hypothesis which has been confirmed by further studies, e.g., Fortier et al. 1995, Gotceitas et al. 1996, Mertz and Myers 1994). Some studies showed that the year-class strength could be also established after the critical period and even during the early juvenile stages, so that the match-mismatch hypothesis has to be taken in a less restrictive sense and understood as a general correspondence between larval production and planktonic food (Myers et al. 1993, Peterman et al. 1988). The second hypothesis (Lasker 1975), postulates, on the basis of a study on anchovy larvae, that fish larvae need dense concentration of proper-sized food which are attained when ocean is calm and when there is a stable mixed layer. This hypothesis has been further developed by Cury and Roy (1989), who showed that the optimal environmental window for pelagic fish recruitment success is actually dome-shaped and more recently by Bakun (1996), who suggested that the recruitment success in upwelling areas is mainly determined by three variables: the planktonic production, the turbulence and the retention.

Beside starvation, other processes have been put forward to explain variation in recruitment and year-class strength. Among them, predation by other fish species or jelly fish, cannibalism and competition resulting from food and/or habitat limitation have recently shown to be an important source of mortality of eggs and fish larvae (Bogstad et al. 1994, Cushing 1995, Paradis et al. 1996, Shepherd and Cushing 1980, Wootton 1990). These processes could further induce density-dependent-mortality/growth, which are known to reduce the variability induced by stochastic factors during the early stages (Fromentin et al. in press, Myers and Cadigan 1993) but also to generate cycles and/or long-term fluctuations in fish stocks (Bjørnstad et al. 1999, Bjørnstad et al. 1999, Caley et al. 1996, Fromentin et al. 2000b, Knell 1998). It was further shown that the mortality of the eggs and fish larvae was dependent on the age and size of the spawners; older individuals producing offspring with higher rates of survival, so that the recruitment is not only proportional to the spawning stock biomass but also the age-classes structure of the spawning stock (Cardinale and Arrhenius 2000). This implies that recruitment overfishing (Myers and Barrowman 1996) become more probable, for a given level of SSB, when the population structure is strongly truncated.

Variations in recruitment and year-class strength appear thus to be related to three main classes of factors: 1) human activity, mainly through over-exploitation of the spawning stock, but also through pollution of the spawning and nursery areas; 2) biological processes, such as predation, cannibalism and competition and 3) environmental events. Environmental factors mainly affect fish recruitment through changes in: (i) sea temperature, which influences the daily development and mortality of the eggs and fish larvae (Pepin 1991, Planque and Frédou 1999, Rätz et al. 1999) and (ii) the food availability, i.e., the match-mismatch hypothesis and/or the impact of the wind and current at a large scale (the dispersal of the eggs and fish larvae and the Bakun's triad) and at a small scale (the turbulence which plays a role on the prey encounter rates, (Kiørboe and MacKenzie 1995, MacKenzie and Leggett 1991, MacKenzie et al. 1994). This brief review shows that there is no simple and unifying mechanism to explain variations in recruitment and year class. The processes differ between species and depend on the local environments. The following section attempts to list the most probable mechanisms that could affect recruitment of Atlantic tuna populations, considering their differences in life history traits and geographical areas.

2. THE RECRUITMENT ISSUE FOR THE ATLANTIC TUNAS

2.1. life history traits of Atlantic tunas

The table 1 sums up the life history traits of Atlantic tunas and tuna-like species related to:

i. The geographical distribution of the population as well as the main spawning places (information being obtained from the literature, see legend of table 1)
ii. The spawning duration (i.e., the number of months per year during which spawning usually occurs) and the age-at-maturity (age at which 50% of the individuals are mature) were also collected from the literature.
iii. The maximum age, which was derived from tagging data (Fromentin and Fonteneau in press) and defined as the longest observed duration between a mark and a recapture, plus the age of the fish when marked (suspect or incomplete information was not considered).
iv. A growth index was computed as: $$\frac{\left(\frac{Length-at-maturity}{Maximum-length}\right)*100}{Age-at-maturity}$$. This index corresponds to the mean juvenile growth scaled by the maximum length. We did not deduce growth and

maximum length from the parameters *K* and L_∞ of the von Bertalanffy growth equation because of large differences between various estimates.

Skipjack (SKJ, *Katsuwonus pelamis*), Atlantic little tuna (LTA, *Euthynnus alletteratus*) and yellowfin tuna (YFT, *Thunnus albacares*) are typical tropical tunas, mainly distributed from 20°N to10°S for the two first species and from 35°N to 20°S for the latter. SKJ and LTA can be considered as opportunistic spawners, since these two species can spawn all year long in the equatorial waters and some tropical areas (Table 1). YFT has a more restrictive spawning season in time, about 6 months, but not in space. Bigeye tuna (BET, *Thunnus obesus*), Atlantic sailfish (SAI, *Istiophorus albicans*) and Atlantic white marlin (WHM, *Tetrapturus albidus*) are subtropical species, having a wider distribution than tropical tunas (from 50°N to 40°S). Their spawning seasons are more restricted in time, 2 to 4 months, but the spawning places are still very large (Table 1). Albacore (ALB, *Thunnus alalunga*) and swordfish (SWO, *Xiphias gladius*) are common in sub-tropical and temperate waters. Typically, their spawning season spread over 3 months in some more limited areas of the western and central Atlantic and Mediterranean Sea (Table 1). Although Bluefin tuna (BFT, *Thunnus thynnus thynnus*) and southern bluefin tuna (SBF, *Thunnus maccoyii*) have a very wide geographical distribution (from the sub-polar to the sub-tropical waters of the Atlantic), their spawning season and spawning places are the most restricted ones. Note also that these two typical temperate tunas probably perform the greatest migrations, since they reproduce in warm waters (the Indonesian waters, South of Java, for SBF and the Western Mediterranean Sea and the Gulf of Mexico for BFT) but mainly feed in temperate and cold waters (Mather et al. 1995).

2.2. Main differences between tropical and temperate tunas

All the tropical, sub-tropical tunas and temperate tunas have wide geographical distribution. However, the spawning season becomes shorter as soon as we consider a gradient from the equatorial to the temperate populations. This feature could be related to the physiological ecology of these species (Bard et al. 1998, Sharp 1978). All tunas and tuna-like species need warm waters for reproduction and larval growth (around 24°c for tuna larvae, (Nishikawa et al. 1985). In that sense, the tropical waters provide an optimum habitat for tunas in term of reproduction and growth (juvenile growth being much more rapid for tropical and sub-tropical tunas than temperate ones, Table 1). Because SBF and BFT mainly live and feed in temperate waters (Mather et al. 1995), their spawning season in warmer locations is automatically shorter than for tropical tunas, which roughly live and reproduce in the same waters. A similar observation can be made in the spatial domain: the spawning areas are wider for tropical than temperate tunas. This is probably due to the same physiological constraint, which allows an opportunistic strategy in tropical waters (i.e., a more or less continuous spawning as soon as favourable conditions are encountered) that the temperate waters do not permit. These two features make, in theory, the probability of a stable recruitment much higher for tropical than temperate tunas (see also (Fonteneau 1992).

Another point of interest of table 1 is given by the age-at-maturity and the maximum age. Briefly, temperate tunas have a late age-at-maturity but a long life span, so that their spawning stock include numerous year-classes (> 10). In contrast, tropical tunas display an early age-at-maturity but a short life span. Their spawning stock is, thus, constituted by a few number of year class. This difference in life history traits makes temperate tunas more adapted to the risks of recruitment failures than tropical ones; BFT could easily support 10 years of recruitment forced to zero, whereas the SKJ dynamics was disrupted if the period with no recruitment persisted for more than 2 years, see (Fromentin and Fonteneau in press). The dynamical features of the tropical tunas populations are, thus, mainly determined by a continuous recruitment and a rapid juvenile growth, i.e., an opportunistic strategy which is possible in warm waters. Conversely, temperate tunas are rather resistant to recruitment failure, but they display a later age-at-maturity and a slower growth. For these species, the core of their dynamics is related to the reserve that constitutes their spawning stock, i.e., a conservative strategy related to a colder and more variable environment.

2.3. Variation in recruitment and in stock size

Noise in recruitment can lead to pseudo-cyclic fluctuations in the SSB and in the yields, with a main period depending on the life span of the species, i.e., ~ 5 yr for SKJ and ~ 20 yr or more for BFT, Fig. 1). This feature is probably due to the autocovariance generated by the sum of the noises in the recruitment of each year. Analysing historical data of the trap fisheries, Ravier and Fromentin (pers. comm.) showed that the temporal variability in these catches may be decomposed firstly into pseudo-secular cycles (see also (Fromentin et al. 2000a), secondly into cyclic variations between 15 and 30 years, then into year-to-year fluctuations. The cycle of about 20 years, which approximately corresponds to the life span of the Atlantic bluefin tuna (Table 1), could result from variation in the recruitment. We have not sufficient results to valid such a hypothesis, but it is interesting to note that the Nordic fisheries, which suddenly collapsed in the mid 60's (Marsac 1999, Tiews 1978), recently reappeared after 30 years (Ólafsdóttir and Ingimundardóttir 2000). However, further investigations are needed by comparing, for instance, the amplitude and the frequency of the variations in the abundance (or the catches corrected from fishing effort) of the tropical *versus* the temperate tunas.

3. MODELLING SPAWNERS-RECRUIT RELATIONSHIP (SRR)

Modelling of the spawner-recruit relationship (SRR) plays an important role in the application of population dynamics theory in support of fisheries management. It is only with some assumptions about this relationship that scientists can state something about the likely long-term consequences of a management regime, i.e., to make projections to forecast the state of the exploited stock during the next years.

3.1. SRR used in fisheries management

The SRR models most typically used in the fisheries world are those due to Ricker (1954) and Beverton and Holt (Beverton and Holt 1957). However, many other relationships have been advocated, such as "generalized" ones (Schnute et al. 1989), or ad-hoc ones (Barrowman and Myers 2000). The fitting of SRRs in stock assessments could be classified in three categories as follows:

(1) In models that make implicit use of a SRR. A good example of this is stock production models, in which the stock´s growth in biomass one year depends partially on the recruitment of new biomass which is itself a function of the previous year´s stock biomass.
(2) In age-structured models, independently of the assessment of catch/effort data. The typical example is taking the results of a VPA to calculate time series of stock biomass and recruitment, and carrying out some sort of nonlinear regression or nonparametric smoothing to the S-R data.
(3) In age-structured models, simultaneously with the fitting of the catch/effort data.

In principle, there should be no reason why one of the approaches above should be preferable to the others, given that all models are simplifications of reality. Some scientists may prefer (1) or (3) because they lead to a higher degree of consistency in the analyses, since they are done internally. For example, if the tuning of the VPA also estimates the SRR parameters which are, in turn, used to estimate B_{MSY}, it is relatively straightforward to estimate the variance of B_{MSY} based on the covariance matrix for the VPA model fit. Others may, however, argue that it is preferable to carry out the VPA-tuning and SRR-fitting exercises separately, so that one will not affect the results of the other in some unknown fashion.

3.2. Limits of the deterministic SRR and possible alternatives

Whether or not to fit an SRR simultaneously in the assessment is often not as big a question as whether to fit it at all. Many scientists are simply put off by the "shotgun pattern" typical from a plot of recruitment against stock size and quickly rush to stating that, on the basis of visual evidence, there is no relationship between recruits and stock size. And, indeed, a statistical test will more often than not fail to reject the hypothesis that the slope of the S-R plot is zero. On the other hand, those scientists that are more familiar with computer simulation will be aware of how easy it is to create the shotgun patterns in the presence of a little noise, even when there is an underlying stock-recruitment relationship. Thus, much of the difference in perception may be simply due to unfulfilled expectations for a deterministic relationship in a stochastic world. Even at a low level, stochastic forces can totally blur the underlying SRR, so that it becomes difficult (sometimes impossible) to choose a deterministic SRR on statistical criteria (see e.g., the case of the Northeast Atlantic bluefin tuna, (Anonymous 1999, Fromentin 1999), leading the scientists to +/- arbitrary choices.

Clearly a way forward is to move from a stock-recruitment relationship (SRR) to a stock-environment-relationship (SERR) in which recruitment is modelled as a function of both explanatory variables. Most attempts to do this deal with allowing an environmental variable to effect the "height" of the relationship (e.g., the asymptote), as opposed to having an effect on the slope at the origin of the relationship. It is also important to remember, however, that there is always a good chance (difficult to measure) of finding a spurious correlation between recruitment and some environmental variables, because of various violations of the basic statistical assumptions due to the dependence between observations, autocorrelation and long-term trends (Legendre and Legendre 1998). Furthermore, some authors, e.g., (Walker et al. 1994), have issued strong warnings that such correlative studies can actually provide a disservice to fisheries management when they are not done carefully and that more certainty about the relationships can only be gained from manipulative experiments that change the size of the stock. We hold the view that progress can be made to include environmental covariates in the modelling of recruitment as a function of stock size (e.g., (O'Brien et al. 2000), or in eggs-production models when this additional step appears necessary (Cardinale and Arrhenius 2000). However, this progress should be tempered by careful thinking about the physical, biological, physiological and behavioral processes affecting Atlantic tunas.

DISCUSSION

The scientific literature has shown that variations in the recruitment is a common feature of marine populations, including fish (e.g., (Bailey and Houde 1989, Cushing 1975, Hjort 1926, Lasker 1975, May 1974, Planque and Frédou 1999, Uda 1957). Listing some of the main life history traits of several tuna populations, we further postulated that variations in the recruitment are probably higher for temperate than tropical tunas. As variations in the recruitment is likely to lead to variations in the spawning stock and yields, this question is not only interesting on a theoretical viewpoint, but also in a stock assessment and management one. Therefore, we propose to that ICCAT organises in the near future a workshop on this topic, during which several questions may be explored, including:

1. Age-slicing, which is used to construct the catch-at-age matrices for the VPA analyses of many tuna stocks, can mask interannual fluctuations in year-class strength. What alternative approaches are available to assess recruitment variability?
2. Can we identify fluctuations in the yields and SSB due to variations in the recruitment? And is the frequency different between temperate and tropical tunas?
3. Which SERR could be the most relevant for the different Atlantic tunas?
4. Does the inclusion of variations in the recruitment due to environmental influences within the stock assessment change significantly the biomass estimates and the predictions or the levels of the biological reference points?
5. Following the match-mismatch hypothesis, variations in recruitment should increase as the spawning and recruitment period decreases, i.e., should be higher within temperate tunas (BFT) than tropical (SKJ, YFT). Can we get reliable data to test such an hypothesis?

6. Relationship between large-scale climatic events, the North Atlantic Oscillation (NAO), and the recruitment of albacore and bluefin tuna have been recently put forward in the last SCRS meetings (Bard and Santiago 1999, Marsac 1999, Santiago 1998). Can further analyses help to identify the possible mechanisms linking the NAO to the success of the recruitment?
7. Transport is particularly important for species having nurseries in localized areas. Which are the Atlantic tuna populations concerned, BFT, ALB?, SBF?
8. Tropical and subtropical species may also be "prey-sensitive" because of their high metabolic rates and short time of starvation (another difference between tropical and temperate tunas). Is that testable?
9. Is there any ecological evidence of regime shifts in terms of the recruitment of Atlantic tunas?

REFERENCES

Alves, A., P. de Barros and M.R. Pinho. 1998. Age and growth of bigeye tuna, *Thunnus obesus*, captured in Madeira archipelago. ICCAT scientific papers. 48; pp. 277-283.

Amorim, A.F., C.A. Arfelli, J.N. Antero-Silva, L. Fagundes, F.E.S. Costa and R. Assumpçao. 1998. Blue marlin (*Makaira nigricans*) and white marlin (*Tetrapturus albidus*) caught off the Brazilian coast. ICCAT scientific papers. 47; pp. 163-172.

Anonymous. 1996. Report of the final meeting of the ICCAT Albacore research program. ICCAT scientific papers. 43; pp. 1-116.

Anonymous. 1997. 1996 SCRS detailed report on bluefin tuna. ICCAT scientific papers. 46(1); pp. 1-301.

Anonymous. 1998. 1997 SCRS detailed report on bigeye tuna. ICCAT scientific papers. 48(2); pp. 109-176.

Anonymous. 1998. Report of the third ICCAT billfish workshop. ICCAT scientific papers. 47; pp. 1-128.

Anonymous. 1999. 1998 SCRS detailed report on bluefin tuna. ICCAT scientific papers. 49(2); pp. 1-191.

Antoine, L., P. Cayré and J. Mendoza. 1982. Etude de la croissance du listao (*Katsuwonus pelamis*) de Atlantique au moyen des rayons de la nageoire dorsale. Mise au point d'une méthodologie - Résultats préliminaires. ICCAT scientific papers. 17; pp. 195-208.

Arocha, F. and D.W. Lee. 1996. Maturity at size, reproductive seasonality, spawning frequency, fecundity and sex ratio in swordfish from the Northwest Atlantic. ICCAT scientific papers. 45(2); pp. 350-357.

Baglin, R.E. 1977. Maturity, fecundity and sex composition of white marlin (*Tetrapturus albidus*). ICCAT scientific papers. 6; pp. 408-416.

Baglin, R.E. 1979. Sex composition, length-weight relationship and reproduction of the white marlin (*Tetrapturus albidus*) in the westernnorth Atlantic ocean. Fisheries Research. 76; pp. 919-925.

Bailey, K.M. and E.D. Houde. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. Adv. Mar. Biol. 26; pp. 1-83.

Bakun, A. 1996. Patterns in ocean: ocean processes and population dynamics. California Sea Grant. San Diego-La Jolla (CA).

Bard, F.X. 1984. Croissance de l'Abacore (*Thunnus albacores*) Atlantique d'après les données de marquages. ICCAT scientific papers. 20; pp. 104-116.

Bard, F.X. and C. Capisano. 1991. Actualisation des connaissances sur la reproduction de l'albacore (*Thunnus alalunga*) en océan atlantique. ICCAT scientific papers. 36; pp. 182-204.

Bard, F.X. and G. Compean-Jimenez. 1980. Conséquences pour l'évaluation du taux d'exploitation du germon (*Thunnus alalunga*) nord atlantique d'une courbe de croissance déduite de la lecture des sections de rayons épineux. ICCAT scientific papers. 9(2); pp. 365-375.

Bard, F.X., E. Josse and P. Bach. 1998. Habitat et écophysiologie des thons : Quoi de neuf depuis 15 ans? ICCAT scientific papers. 50(1); pp. 319-342.

Bard, F.X., S. Kume and L. Antoine. 1983. Données préliminaires sur la croissance, les migrations et la mortalité du listao (*Katsuwonus pelamis*) en Atlantique-est obtenues à partir du marquage. ICCAT scientific papers. 18; pp. 271-294.

Bard, F.X. and J. Santiago. 1999. Review of the albacore (*T. alalunga*). Historical surface fisheries data (1920-1975) for possible relationship with North Atlantic Oscillation. ICCAT scientific papers. 49(4); pp. 311-323.

Barrowman, N.J. and R.A. Myers. 2000. Still more spawner-recruitment curves: the hockey stick and its generalizations. Can. J. Fish. Aquat. Sci. 57; pp. 665-676.

Beverton, R.J.H. and S.J. Holt. 1957. On the dynamics of exploited fish populations. Fish. Investigat. London Serie 2. 19; 533 pp.

Bjørnstad, O., J.-M. Fromentin, NC. Stenseth and J. Gjøsæter. 1999. Cycles and trends in cod populations. Proc. Nat. Acad. Sci. US. 96; pp. 5066-5071.

Bjørnstad, O.N., J.-M. Fromentin, N.C. Stenseth, T. Johannessen and J. Gjosaeter. 1999. A test for density-dependent survival in juveniles stages of cod. Ecology. 80; pp. 1278-1288.

Bogstad, B., G.R. Lilly, S. Mehl, O. Palsson and G. Stefansson. 1994. Cannibalism and year-class strength in Atlantic cod (*Gadus morhua*) in Arcto-boreal ecosystems (Barents Sea, Iceland and eastern Newfoundland). ICES mar. Sci. Symp. 198; pp. 576-599.

Caley, M.J., M.H. Carr, M.A. Hixon, T.P. Hughes, G.P. Jones and B.A. Menge. 1996. Recruitment and the local dynamics of open marine populations. Annu. Rev. Ecol. Syst. 27; pp. 477-500.

Capisano, C. 1989. Le voilier de l'Atlantique est, *Istiophorus albicans* (Latreille, 1804) : Quelques aspects de la biologie et de la reproduction. ICCAT scientific papers. 30; pp. 392-430.

Capisano, C. and A. Fonteneau. 1991. Analyse des fréquences de longueur, du sex-ratio et des zones de reproduction de l'albacore, *Thunnus albacores*, de l'Atlantique. ICCAT scientific papers. 36; pp. 241-279.

Cardinale, M. and F. Arrhenius. 2000. The relationship between stock and recruitment: are the assumptions valid? Mar. Ecol. Prog. Ser. 196; pp. 305-309.

Cayré, P. 1981. Maturité sexuelle, fécondité et sex ratio du listao (*Katsuwonus pelamis*) des côtes d'Afrique de l'Ouest (20°N-0°N) étudiés à partir des débarquements thoniers (1977 à 1979), au port de Dakar, Sénégal. ICCAT scientific papers. 15; pp. 135-149.

Cayré, P., J.B. Amon Kothias, J.M. Stretta and T. Diouf. 1988. Biologie des thons. In: Fonteneau, A. and J. Marcille (eds) Ressources, pêche et biologie des thonidés tropicaux de l'Atlantique centre-est, FAO Doc. Tech. Pêches. Rome. 292: 157-268

Cayré, P. and T. Diouf. 1981. Croissance de la thonine, *Euthynnus alletteratus* (Rafinesque 1881) établie à partir des coupes transversales du premier rayon de la nageoire dorsale. ICCAT scientific papers. 15; pp. 337-345.

Cayré, P. and T. Diouf. 1984. Croissance du thon obèse (*Thunnus obesus*) de l'Atlantique d'après les résultats de marquage. ICCAT scientific papers. 20; pp. 180-187.

Cayré, P. and H. Farrugio. 1986. Maturité sexuelle du listao (*Katsuwonus pelamis*) capturé aux Açores de 1980 à 1982. Proceedings of the ICCAT conference on the international skipjack year program. Costero de Canarias, 21-29 June 1983. ICCAT scientific papers. pp. 252-272.

Cayré, P. and F. Laloë. 1986. Relation poids-longueur du listao (*Katsuwonus pelamis*) de l'océan Atlantique. Proceedings of the ICCAT conference on the international skipjack year program. Costero de Canarias, 21-29 June 1983. ICCAT scientific papers. pp. 335-340.

Champagnat, C. and R. Pianet. 1974. Croissance du patudo (*Thunnus obesus*) dans les régions de Dakar et de Pointe-Noire. ICCAT scientific papers. 2; pp. 141-144.

Chur, V.N., V.B. Grudinin and V.L. Zharov. 1980. Data on length-age composition and gonad maturity stages of skipjack (*Katsuwonus pelamis*) of the eastern tropical Atlantic. ICCAT scientific papers. 9(1); pp. 245-254.

Clay, D. 1991. Atlantic bluefin tuna (*Thunnus thynnus thynnus* (L.)): a review. World meeting on stock assessment of bluefin tunas: strengths and weaknesses. La Jolla, California, USA. IATTC. pp. 89-180.

Coan, A. 1976. Length, weight and age conversion tables for Atlantic tunas. ICCAT scientific papers. 5; pp. 64-66.

Cort, J.L. 1991. Age and growth of the bluefin tuna *Thunnus thynnus* (L.) of the Northeast Atlantic. ICCAT scientific papers. 35; pp. 214-230.

Cury, P. and C. Roy. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. Can. J. Fish. Aquat. Sci. 46; pp. 670-680.

Cushing, D.H. 1975. Marine ecology and fisheries. Academic Press. London.

Cushing, D.H. 1990. Plankton production and year class strength in fish populations: an update of the match/mismatch hypothesis. Adv. Mar. Biol. 26; pp. 249-293.

Cushing, D.H. 1995. Population production and regulation in the sea: a fisheries perspective. Cambridge University Press. Cambridge.

Diouf, T. 1991. Les pêcheries thonières d'albacore de l'Atlantique. Bilan de l'évolution durant la période récente. ICCAT scientific papers. 36; pp. 289-325.

Draganik, B. and J. Cholyst. 1988. Temperature and moonlight as stimulators for feeding activity by swordfish. ICCAT scientific papers. 27; pp. 305-314.

Ehrardt, N.M. 1991. Review of the age and growth of swordfish (*Xiphias gladius*) in the Northwestern Atlantic. ICCAT scientific papers. 35; pp. 362-371.

Ehrardt, N.M., R.J. Robbins and F. Arocha. 1996. Age validation and growth of swordfish, *Xiphias gladius*, in the Northwest Atlantic. ICCAT scientific papers. 45(2); pp. 358-367.

Farber, M.L. 1988. An overview of available information pertinent to interpreting possible stock structure of sworfish in the Atlantic ocean. ICCAT scientific papers. 27; pp. 240-255.

Farrugio, H. 1981. Exploitation et dynamique des populations de thon rouge, *Thunnus thynnus* (Linné 1758), Atlanto-Méditéranéennes. Montpellier: Université des Sciences et Techniques du Languedoc, pp. 266

Fonteneau, A. 1980. Croissance de l'Albacore (*Thunnus albacores*) de l'Atlantique est. ICCAT scientific papers. 9(1); pp. 152-168.

Fonteneau, A. 1992. A comparative study of yellowfin tuna in the Eastern Pacific and in the Eastern Atlantic. Int. Am. Trop. Tuna Com. Int. Rep. 22; pp. 1-71.

Fortier, L., D. Ponton and M. Gilbert. 1995. The match/mismatch hypothesis and the feeding success of fish larvae in ice-covered southeastern Hudson Bay. Mar. Ecol. Prog. Ser. 120; pp. 11-27.

Fromentin, J.-M. 1999. Bluefin Tuna stock assessment in the Northeast Atlantic. Problems related to data, methods and knownledge. ICCAT scientific papers. 49(2); pp. 388-399.

Fromentin, J.-M. and A. Fonteneau. in press. Fishing effects and life history traits: a case-study comparing tropical *versus* temperate tunas. Fish. Res.

Fromentin, J.-M., A. Fonteneau and H. Farrugio. 2000a. Biological reference points and natural long-term fluctuations: the case of the Eastern Atlantic bluefin Tuna. ICCAT scientific papers. 51; pp. 2072-2084.

Fromentin, J.-M., J. Gjøsæter, O. Bjørnstad and N.C. Stenseth. 2000b. Biological processes and environmental factors regulating the dynamics of the Norwegian Skagerrak cod populations since 1919. ICES J. Mar. Sci. 57; pp. 330-338.

Fromentin, J.-M., R.M. Myers, O. Bjørnstad, N.C. Stenseth, J. Gjøsæter and H. Christie. in press. Effects of density-dependent and stochastic processes on the stabilization of cod populations. Ecology.

Gotceitas, V., V. Puvanendran, L.L. Leader and J.A. Brown. 1996. An experimental investigation of the 'match/mismatch' hypothesis using larval Atlantic cod. Mar. Ecol. Prog. Ser. 130; pp. 29-37.

Hjort, J. 1914. Fluctuations in the great fisheries of northern europe. Viewed in the light of biological reseach. Rapp. P.-v Réun. Cons. int. Explor. mer. 20; pp. 1-228.

Hjort, J. 1926. Fluctuations in the year classes of important food fishes. J. Cons. Int. Explor. Mer. 1; pp. 5:38.

Hoey, J. and A. Bertolino. 1988. Review of the U.S. fishery for swordfish, 1978 to 1986. ICCAT scientific papers. 27; pp. 267-282.

Kiørboe, T. and B. MacKenzie. 1995. Turbulence-enhanced prey encounter rates in larval fish: effects of spatial scale, larval behaviour and size. J. Plank. Res. 17; pp. 2319-2331.

Knell, R.J. 1998. Generation cycles. Trends in Ecology and Evolution. 13; pp. 186-190.

Lasker, R. 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull. 3; pp. 453-461.

Legendre, P. and L. Legendre. 1998. Numerical ecology. ed., S.E. Elsevier. Amsterdam.

MacKenzie, B.R. and W.C. Leggett. 1991. Quantifying the contribution of small-scale turbulence to the encounter rates between larval fish and their zooplankton prey: effects of wind and tide. Mar. Ecol. Prog. Ser. 73; pp. 149-160.

MacKenzie, B.R., T.J. Miller, S. Cyr and W. Leggett. 1994. Evidence of a dome-shaped relationship between turbulence and larval fish ingestion rates. Limnol. Oceanogr. 39; pp. 1790-1799.

Marsac, F. 1999. Changements hydroclimatiques observés dans l'Atlantique depuis les années 50 et impacts sur quelques stocks de thons et leur exploitation. ICCAT scientific papers. 49(4); pp. 346-370.

Mather, F.J., J.M. Mason Jr and A. Jones. 1995. Historical document: life history and fisheries of Atlantic bluefin tuna. NOAA Technical Memorandum N.M.F.S. Miami.

May, R.C. 1974. Larval mortality in marine fishes and the critical period concept. In 'The early life history of fish'. Blaxter, J.H.S. (Eds). pp. 3-19. Springler-Verlag. New York.

Mejuto, J. and B. Garcia. 1997. A preliminary analysis of gonadal indices of the swordfish (*Xiphias gladius*) in the Atlantic ocean. ICCAT scientific papers. 46(3); pp. 336-344.

Mertz, G. and R.A. Myers. 1994. Match/mismatch predictions of spawning duration versus recruitment variability. Fish. Oceanogr. 3:4; pp. 236-245.

Miyake, M. 1990. Manuel d'opérations pour l'échantillonnage des thonidés et espèces voisines dans l'océan atlantique. ICCAT Documents.

Myers, R.A. and N.J. Barrowman. 1996. Is fish recruitment related to spawner abundance? Fish. Bull. 94; pp. 707-724.

Myers, R.A. and N.G. Cadigan. 1993. Is juvenile natural mortality in marine demersal fish variable? Can. J. Fish. Aquat. Sci. 50; pp. 1591-1598.

Myers, R.A., G. Mertz and C.A. Bishop. 1993. Cod spawning in relation to physical and biological cycles of the northern North-west Atlantic. Fish. Oceanogr. 2:3/4; pp. 154-165.

Nishikawa, Y., M. Honma, S. Ueyanagi and S. Kikawa. 1985. Average distribution of larvae of oceanic species of scombroid species, 1956 - 1981. Bull. Far Sea Fish. Lab. S. Series. 12; pp. 99 pp.

O'Brien, C.M., C.J. Fox, B. Planque and J. Casey. 2000. Climate variability and North Sea cod. Nature. 404; pp. 142.

Ovchinnikov, V.V., M.E. Grudtsev and S.V. Kholodkova. 1980. Length-age composition of the tropical Atlantic swordfishes (*Xiphias gladius*, L.). ICCAT scientific papers. 9(2); pp. 620-623.

Ólafsdóttir, D. and T. Ingimundardóttir. 2000. Preliminary report on experimental fisheries and biological research on bluefin tuna *(Thunnus thynnus*) within the Islandic EEZ in 1996-98. ICCAT Scientific Papers. 51; pp. 827-838.

Paradis, A.R., P. Pepin and J.A. Brown. 1996. Vulnerability of fish eggs and larvae to predation: review of the influence of the relative size of prey and predator. Can. J. Fish. Aquat. Sci. 53; pp. 1226-1235.

Pepin, P. 1991. Effect of temperature and size on development, mortality and survival rates of the pelagic early life history stages of marine fish. Can. J. Fish. Aquat. Sci. 48; pp. 503-518.

Peterman, R.M., M.J. Bradford, N.C.H. Lo and R.D. Methot. 1988. Contribution of early life stages to interannual variability in recruitment of Northern anchovy (*Engraulis mordax*). Can. J. Fish. Aquat. Sci. 45; pp. 8-16.

Planque, B. and T. Frédou. 1999. Temperature and the recruitment of Atlantic cod (*Gadus mohrua*). Can. J. Fish. Aquat. Sci. 56; pp. 2069-2077.

Porter, J.M. and S.C. Smith. 1991. Literature review of differential growth and mortality in Atlantic swordfish, *Xiphias gladius*. ICCAT scientific papers. 35; pp. 445-448.

Rätz, H.-J., M. Stein and J. Lloret. 1999. Variation in growth and recruitment of Atlantic cod (*Gadus morhua*) off Greenland during the second half of the twentieth century. J. Northw. Atl. Fish. Sci. 25; pp. 161-170.

Ricker, W.E. 1954. Stock and recruitment. J. Fish. Res. Bd. Can. 11; pp. 559-623.

Santiago, J. 1998. The North Atlantic Oscillation an recruitment of temperate tunas. ICCAT Scientific papers. 48(3); pp. 240-249.

Schnute, J.T., L.J. Richards and A.J. Cass. 1989. Fish survival and recruitment: Investigations based on a size-structured model. Can. J. Fish. Aquat. Sci. 46; pp. 743-769.

Sharp, G.D. 1978. The physiological ecology of tunas. Sharp, G.D. and A.E. Dizon. Academic Press. London.

Shepherd, J.G. and D.H. Cushing. 1980. A mechanism for density-dependent survival of larval fish as the basis of a stock-recruitment relationship. J. Cons. int. Explor. Mer. 39; pp. 160-167.

Souza, R.C., R. Lessa and F. Hazin. 1994. First observations on reproductive biology of billfishes (*Tetrapturus albidus*, *Istiophorus albicans* and *Tetrapturus pfluegeri*) in southwestern equatorial Atlantic (Brazil). ICCAT scientific papers. 42(2); pp. 329-334.

Tiews, K. 1978. On the disapperance of bluefin tuna in the North Sea and its ecological implications for herring and mackerel. Rapp. P.-v. Réun. Cons. int. Explor. Mer. 172; pp. 301-309.

Uda, M. 1957. A consideration on the Long Years trend of the Fisheries fluctuation in relation to sea conditions. Bull. Jap. Soc. Sci. Fish. 23; pp. 368-372.

Walker, M.D., P.J. Webber, E.H. Arnold and D. Ebert-May. 1994. Effects of interannual climate variation on aboveground phytomass in Alpine vegetation. Ecology. 75; pp. 393-408.

Weber, E. 1980. An analysis of Atlantic bigeye tuna (*Thunnus obesus*) growth. ICCAT scientific papers. 9(2); pp. 303-307.

Wooster, W.S. and K.M. Bailey. 1989. Recruitment of marine fishes revisited. In 'Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models'. Beamish, R.J. and G.A. McFarlane (eds). pp. 153-159. Can. Spec. Pub. Fish. Aquat. Sci. 108

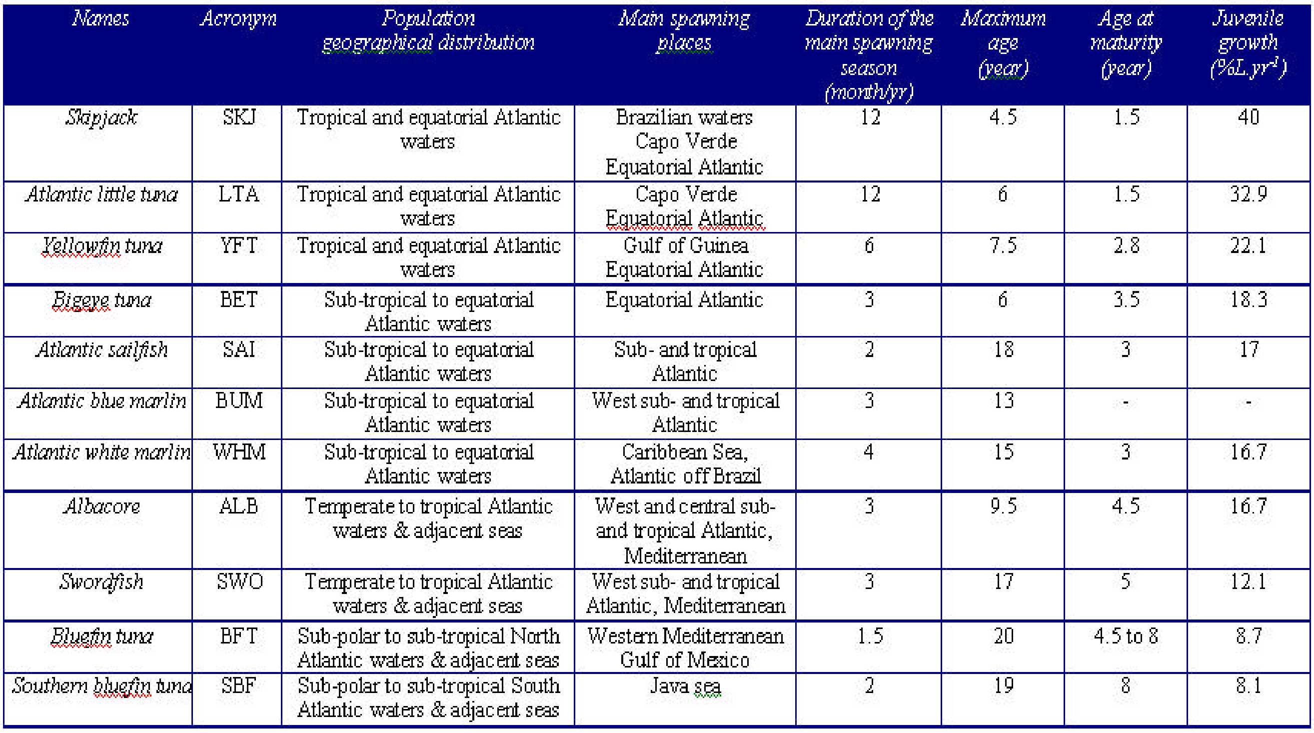
Wootton, R.J. 1990. Ecology of Teleost fishes. Chapman & Hall. London.

Table 1

Life history traits of the 10 selected tunas and tuna-like species. Information on life span (i.e., maximum length, weight and age) as well as minimal SST was derived from catch-at-age and tagging data (see ‘Data section’).

Growth was computed as:
$$\frac{\left(\frac{Length-at-maturity}{Maximum-length}\right)*100}{Age-at-maturity}.$$

Information on spawning duration and maturity was collected from the literature; references: 1. Alves et al. (1998); 2. Amorim et al. (1998); 3. Anonymous (1996); 4. Anonymous (1997); 5. Anonymous (1998a); 6. Anonymous (1998b); 7. Antoine et al. (1982); 8. Arocha and Lee (1996); 9. Baglin (1977); 10. Baglin (1979); 11. Bard (1981); 12. Bard (1984); 13. Bard and Compean-Jimenez (1980); 14. Bard and Capisano (1991); 15. Bard et al. (1983); 16. Capisano (1989); 17. Capisano and Fonteneau (1991); 18. Caton et al. (1991); 19. Cayré (1981); 20. Cayré and Diouf (1981); 21. Cayré and Diouf (1984); 22. Cayré and Farrugio (1986); 23. Cayré and Laloë (1986); 24. Cayré et al. (1988); 25. Champagnat and Pianet (1974); 26. Chur et al. (1980); 27; Coan (1976); 28. Cort (1991); 29. Diouf (1991); 30. Draganik and Cholyst (1988); 31. Ehrardt (1991); 32. Ehrardt et al. (1996); 33. Farber (1988); 34. Farrugio (1981); 35. Fonteneau (1980); 36. Hoey and Bertolino (1988); 37. Mather et al. (1995); 38. Mejuto and Garcia (1997); 39. Ovchinnikov et al. (1980); 40. Porter and Smith (1991); 41. Souza et al. (1994); 42. Weber (1980)



Names	*Acronym*	*Population geographical distribution*	*Main spawning places*	*Duration of the main spawning season (month/yr)*	*Maximum age (year)*	*Age at maturity (year)*	*Juvenile growth (%L.yr^{-1})*
Skipjack	SKJ	Tropical and equatorial Atlantic waters	Brazilian waters Capo Verde Equatorial Atlantic	12	4.5	1.5	40
Atlantic little tuna	LTA	Tropical and equatorial Atlantic waters	Capo Verde Equatorial Atlantic	12	6	1.5	32.9
Yellowfin tuna	YFT	Tropical and equatorial Atlantic waters	Gulf of Guinea Equatorial Atlantic	6	7.5	2.8	22.1
Bigeye tuna	BET	Sub-tropical to equatorial Atlantic waters	Equatorial Atlantic	3	6	3.5	18.3
Atlantic sailfish	SAI	Sub-tropical to equatorial Atlantic waters	Sub- and tropical Atlantic	2	18	3	17
Atlantic blue marlin	BUM	Sub-tropical to equatorial Atlantic waters	West sub- and tropical Atlantic	3	13	-	-
Atlantic white marlin	WHM	Sub-tropical to equatorial Atlantic waters	Caribbean Sea, Atlantic off Brazil	4	15	3	16.7
Albacore	ALB	Temperate to tropical Atlantic waters & adjacent seas	West and central sub- and tropical Atlantic, Mediterranean	3	9.5	4.5	16.7
Swordfish	SWO	Temperate to tropical Atlantic waters & adjacent seas	West sub- and tropical Atlantic, Mediterranean	3	17	5	12.1
Bluefin tuna	BFT	Sub-polar to sub-tropical North Atlantic waters & adjacent seas	Western Mediterranean Gulf of Mexico	1.5	20	4.5 to 8	8.7
Southern bluefin tuna	SBF	Sub-polar to sub-tropical South Atlantic waters & adjacent seas	Java sea	2	19	8	8.1

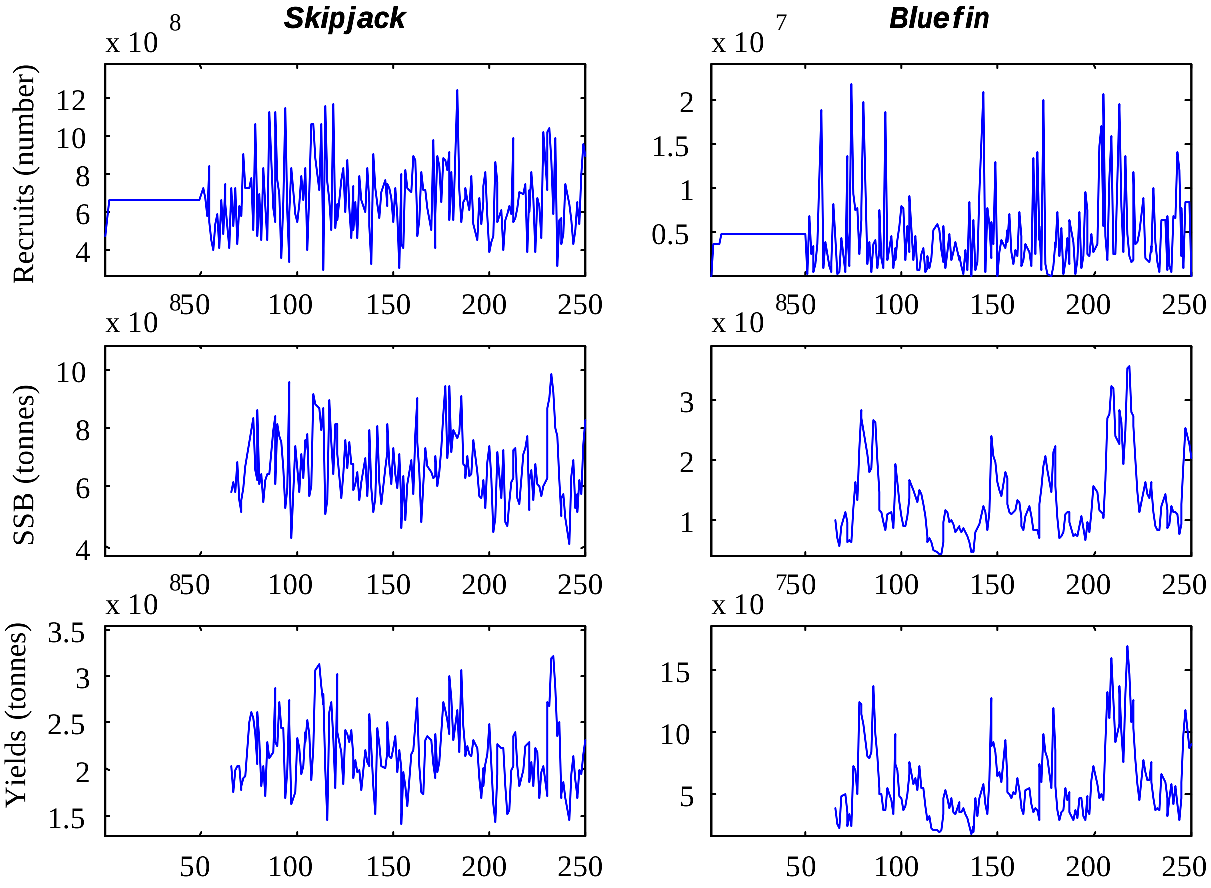


Figure 1

Figure 1. Outputs from a simulation modelling (see Fromentin and Fonteneau in press) with a constant fishing mortality of 0.5 during the last 200 years. The first 50 years is the transition period during which there is no fishing mortality. After t=50, random noise was added to the recruitment. Fishing mortality started at age 1 for skipjack (left panel) and bluefin tuna (right panel). Top graphs: recruitment, medium graphs: spawning stocks biomass (SSB) and bottom graphs: total yields. Time series of SSB and yields only start at time t=65 to avoid scaling problems.