Tuna natural mortality as a function of their age: the bigeye tuna case

By Alain Fonteneau[1] and Pilar Pallares[2]

Summary

This document reviews the age specific levels and variability of natural mortality (M_i) in tuna populations. Based on a review of the literature concerning this fundamental parameter, the U shape curve of M_i expected for all living as a function of their sizes and ages is discussed. High levels of M_i are a biological rule for larvae and juvenile: minimal rate of M_i tend to be observed before first spawning, followed by increasing M_i during spawning and for older fishes due to biological senescence. The biological factors contributing to M_i variability of tunas are presented and discussed. The paper later compares the profiles and levels of M_i presently used for bigeye tuna by tuna Commissions. The biological validity of differences in the M_i at juvenile ages between different species is discussed (for instance small yellowfin and small bigeye). VPA are conducted on catch at age vectors typical of bigeye fisheries, using various vectors of M_i. A subsequent yield per recruit analysis tends to confirm that the potential negative effects of catching large amount of small bigeye tuna are highly dependant of the M_i vector. It is concluded that this major biological uncertainty should be better taken into account for bigeye by scientists.

Key Words: tuna, bigeye, natural mortality, senescence, age, yield per recruit.

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[1] Fonteneau, IRD scientist, UR THETIS, IRD, BP 171, 34203 Sète cedex (E Mail: FONTENEAU@IRD.FR)

[2] Pallares Pilar, IEO scientist, IEO, Corazon de Maria 8, 28002 Madrid, Spain (E Mail: pilar.pallares@md.ieo.es)

Résumé

Ce document fait un bilan des niveaux et des variations de la mortalité naturelle (M_i) dans les populations de thons. En se basant sur la littérature spécialisée sur ce paramètre, un profil de M_i en fonction de la taille et de l'age en forme de U est attendu pour toutes les créatures vivantes. De hauts niveaux de M sont une règle biologique classique pour les larves et les juvéniles, alors que des taux minima de M_i sont souvent observés avant la première ponte. Il s'ensuit pour les poissons plus âgés un accroissement de M_i du à la reproduction et à la sénescence. La validité biologique de ces variations de M_i chez les juvéniles des différentes espèces de thons est discutée (par exemple chez les petits patudos et albacores). Des analyses séquentielles des populations sont conduites sur des prises par tailles typiques des pêcheries de patudo en utilisant divers vecteur de M_i. Une analyse subséquente de production par recrue est conduite et tend à confirmer que les conséquences des fortes captures de patudo juvéniles sont très dépendantes du Mi retenu. L'article conclut que cette majeure incertitude biologique devrait être mieux prise en compte dans les recherches sur le patudo.

Mots clefs :
Thons, patudo, mortalité naturelle,sénescence,age, production par recrue

1- Introduction

The correct estimation of natural mortality as a function of age probably remains one of the most elusive parameter in fishery science. For tunas in general, this problem is even worse, since all the estimates of natural mortality are obtained from fishery data, knowing that most of these data are highly biased by multiple and permanent changes in the fisheries. In population of bigeye tuna worldwide, natural mortality is a widely uncertain parameter despite the great importance of this parameter in stock assessment and management. This uncertainty is related to the great difficulties to estimate this biological parameter as a function of age during the entire exploited life of the species. Tagging and recovery results are probably the best source of reliable information on this parameter, but their results tend to remain widely uncertain for bigeye stocks due to the low number of bigeye presently tagged, and to the various bias common to tagging and recovery investigations. This paper will examine the variability of natural mortality as a function of age (so called later M_i). It will also discuss the hypothesis used in the Atlantic during the last 20 years (An. ICCAT 1984) that small tunas at a given size living in the same habitat and showing similar behavior should show similar levels of M_i, regardless of the species. It should be noted that the importance of correctly estimating the profile of M_i has been reinforced world wide for bigeye following the recent major increase of juvenile bigeye catches taken under Fish Aggregating Devices (or FADs) by purse seiners as well as by the steady increase of catches by longliners (figure 1, 2). The final step of this work will be to better evaluate the potential effect of the present uncertainties in the M_i patterns and levels on the stock assessment analysis, especially when evaluating the potential interaction between the surface and longline fisheries.

2- M_i following a U shape curve: a universal biological rule

Various general biological rules should be kept in mind concerning the variability of M_i as a function of age, these rules being valid for all living animals, including tunas; this universal biological rule has been well described for terrestrial animals nearly two centuries ago (Gompertz 1825):

(1) Young and small individuals tend to face a much higher M than the adults because of a strong pressure by natural selection (the weak individuals being eliminated early) and by multiple sources of predation, including by cannibalism. Fish larvae and juveniles can be eaten by a wide range and great numbers of predators (fig. 3). Formation of schools of larvae and juveniles may limit predation on young tunas, but the general rule that this group of very small fishes is heavily targeted by a wide range of predators, including tunas remains valid. This pressure tends to decrease at increasing sizes, through better escapement capacities and progressive reduction in the numbers of potential predators as well as through increased biological capacity to efficiently occupy the habitat (vertically and geographically).

(2) Natural mortality tends to a plateau of minimal M at preadult stages.

(3) At the age of first spawning, M_i tends to increase for most animals (probably including fishes and tunas) in relation with the biological expenditure of energy invested in this spawning, especially for females but also for males: building of mature gonads necessitate a lot of metabolic energy, added to the movement patterns and migrations of pre spawning fishes that is often observed for tunas. As spawning tends to be concentrated in a given time and areas, tunas need to abandon their feeding areas to move towards these spawning areas (most often in warm waters). Such migration tend to necessarily increase their output of energy and reduce their potential for feeding, then possibly increasing the rate of natural mortality.

(4) For ageing individuals, the universal rule faced by most animals[3] (in both terrestrial and marine life) is that each individual in the population will face a process of “senescence” leading to increasing M (Finch 1990). This senescence can be described as the organic process of growing older and showing the negative effects of increasing age. Such a senescence of the ageing organisms is generally characterized by the declining ability to respond to stress, increasing homeostatic imbalance, increased risk of disease and parasitism and decreasing ability to repair biological damages. It can also be noted that all the parts of the body do not necessarily become senescent at the same time or age at the same rate, but it is simple to understand that the consequences of cumulative deficiencies in various critical functions or organs such as vision, or thermoregulation and an excessive rate of internal parasites, will increase the probability of “natural death”. While such a biological senescence tend to be acknowledged by fishery scientists, it is still rarely estimated.

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[3] Including man , at least during pre modern times.

3- Overview of M_i estimated or hypothesized for various stocks world wide

The various tuna bodies that are doing stock assessment of bigeye tuna using analytical models are working on a wide range of values concerning M_i of bigeye (figure 4). These M_i can be classified in three groups of methods and results:

(1) ICCAT and IOTC M_i

These natural mortalities are purely hypothetical and firmly established at a stable level from one year to the other. The ICCAT M hypothesis was established by SCRS since 1984 (ICCAT working group on tropical tunas, An. ICCAT 1984) at a level of 0.8 during the first 2 years of the bigeye life, followed quite abruptly by a constant level of M=0.4 during the entire life of the fish. The reasons of this pattern of M were (1) that the adult M was probably quite low for a long living and quite temperate species such as bigeye and (2) that M for juvenile bigeye was probably at similar levels for yellowfin, skipjack and bigeye when these 3 species are living in mixed schools in shallow equatorial waters (this hypothesis will be later discussed, chapter 4).

(2) IATTC:

Stock assessment of bigeye has been done only recently in the Eastern Pacific as this species was of minor importance in the Eastern Pacific Ocean purse seine fisheries. The first virtual population analysis conducted for the first time on bigeye in 1999 was using, among other values, a constant and low hypothetical M of 0.4 (Tomlinson 1999). Since 2000, the IATTC has used its new stock assessment model, A-SCALA, recently developed by Maunder et al (Maunder et al 2003), and this model has been working on a best vector of M at age. This vector of M at age has been showing each year some variability from one analysis to the other. The Mi presently used tends to be decreasing between maximum levels of 0.8 and 0.7 (at the age of early recruitment) and age 1, decreasing to a level of 0.4 at age 2.5; this early decline is followed by an increase to about 0.6 at 4 years, followed by an moderate decline to 0.4 for older fish (Figure 4).

(3) SPC:

Scientists from the Oceanic Fisheries Program of the Secretariat of the Pacific Community (SPC) (Hampton, this symposium) have been running, during recent years, various stock assessments on the bigeye stocks fished in the western and whole Pacific ocean, primarily using their statistical model MULTIFAN-CL (Fournier et al. 1998). This comprehensive statistical model that is stratified by area, estimates the “statistically best vector of M” at age, this best result being estimated in terms of its consistency with all the available fishery and tagging/recovery data available. This M is estimated independently in each run of the model, but the patterns of M profiles tend to be consistent and similar to the results shown figure 4: the shape of the M at age vector is similar to the IATTC pattern, but M is reaching a lower level of 0.25 at 2.5 years, and a higher peak of M after the age of 1st spawning (M=0.7 at age 5), followed after age 7 by a quite low M (M<0.4).

(4) Comparative overview of M_i vectors used for assessment:

Introduction: Figure 4 shows that the 3 vectors of M presently used by the various tuna bodies are quite similar in shape and relative levels. The major pending question at this stage is if the real patterns of bigeye M_i are well described by the levels and patterns of M described by figure 4. It should be fully recognized that the scientific knowledge about both M_i of early juvenile and M_i of very large adult bigeye are probably quite weak, as all these estimations of M were obtained in the absence of fishery independent data and as the age structure of adult catches remains poorly estimated in all stock assessments (due to the low levels of bigeye tagging). Presently none of the M_i patterns used for stock assessment is showing the typical biological expectation of the U shaped curves, with high M at small sizes and increasing M for the ageing fishes.

Mi of small bigeye: at this stage it could be stressed that the levels of M_i estimated by MULTIFAN-CL (Hampton 2003) on small yellowfin (based on better size sampling and on more tagging) are quite high compared to those estimated for bigeye: three times greater for the very small fishes and twice for the larger ones (70cm). This point is shown in figure 5 giving the M_i patterns of yellowfin and bigeye estimated for small yellowfin and small bigeye (<70cm) in 2003 by the same model MULTIFAN-CL for the western Pacific stocks. It could also be noticed that these levels of best M_i estimated for juvenile yellowfin are higher than the levels presently assumed for yellowfin and bigeye by the ICCAT scientists (maximum M=0.8 during 2 years).

The main conclusion of this comparative overview is that if the patterns of M_i presently used by the tuna bodies for bigeye in their assessments are quite similar, these M are very different between the various species. This potential biological inconsistency will be examined and discussed thereafter in section 4.

#**M_i of large fishes**: another question still pending in the patterns of Mi presently estimated or used is that none of them is measuring or using a significant increase of natural mortality for the aging fishes. This flat curve of natural mortality rates of the oldest fishes assume that tunas are not facing senescence. It has often been noticed in the VPA results obtained on bigeye in the Atlantic and Indian oceans that the estimated catchability of the adult stock to the longline fisheries was often decreasing with age (this decline being clear for purse seiners).

It is unclear at this stage if this decreased catchability is real, or if it is biased, for instance due to the VPA method used, or to a bias in the catch at age table or in the Mi vector assumed in the VPA. Such pattern could also be explained by a decline in the availability of the older bigeye to the longline fisheries (for instance these fishes being deeper or more scattered)

The comparison of **M_i used by the various tuna bodies for their stock assessment** is based on a biological understanding of the biological phenomena that are underlying the levels and changes in natural mortality as a function of age. These vectors of natural mortality at age have been selected and used by each group of scientists based on various criteria, but not on the biological rules that are conditioning natural mortality as a function of age. This point will then need further discussion.

4- Discussion

4-1- How much M_i is size specific, independently of the tuna species?

There is a general tendency in the various tuna bodies doing stock assessment to do their analysis independently for each species. The only exception to this rule is the stock assessment of tropical tunas done by the ICCAT since 1984 and by the IOTC, as scientists working in these two commissions have been working on an hypothesis widely promoted in the ICCAT forum during the early eighties by John Gulland (various verbal interventions during the SCRS meetings): small tunas living in mixed schools in the same ecosystem, having the same food available and facing the same risk of predation, should suffer similar levels of natural mortality. This hypothetical rule was then applied to bigeye and yellowfin, as these two species are very difficult to identify at small sizes, sharing the same equatorial habitat and living in the same schools closely associated with yellowfin; this observation is valid only at sizes smaller than 80 cm, as the adult bigeye tend to show a very different vertical, geographical and schooling behavior.

Similarities in the yellowfin and bigeye sizes taken in the Indian and Atlantic ocean are striking (Fig. 6), as well as the consistency in the fishing zones of these two species taken at small sizes by the purse seine fishery (Fig. 7). The fact that small bigeye tunas are never caught in pure schools but always in mixed schools with yellowfin and skipjack (examples taken from the Atlantic and Indian Ocean, figure 8) is a further confirmation that these three species are most often living in very close association when they are small, then facing similar predation risks. Given these similarities in the early life history of such co-occuring tuna species, comparable levels of natural mortality at small sizes should be anticipated.

On the other hand, the other tuna commissions have not paid attention to this heterogeneity in the natural mortality estimated for these small yellowfin and small bigeye (when these levels of M tend to be widely different, Fig. 5), simply because all stock assessment works are done independently in each body.

What is the biological validity of the ICCAT hypothesis? Is there any consistency among the various tropical tunas in their natural mortality, and especially for small tunas. The overall review of natural mortality as a function of fish sizes or weight, for instance by various authors such as Beverton and Holt 1957, Ricker 1975, Peterson & Wrobleski 1984 (Fig. 9), McGurk 1986 (Fig. 10), Finch 1990, Hampton 2000, tend to indicate that natural mortality is driven by sizes, and much less by the species (at least in a given habitat).

As a conclusion, if the ICCAT hypothesis remains unsubstantiated by comparative studies, it appears to a logical consequence of similarities in life history of young bigeye and yellowfin tunas. In this context it should at least be an interesting goal to further explore its validity for small tunas. This work could be done for instance in a double track: (1) better analysis of all the potential factors contributing to the natural mortality of small tunas, for instance small yellowfin and bigeye, in order to better understand why they could be either similar, lower or greater for a given species, and (2) through an intensive simultaneous tagging of very small and small tunas caught in mixed schools (yellowfin, skipjack and bigeye).

4-2- M_i , behavior changes and levels of catchability during the life of a bigeye cohort

It is interesting and important to keep in mind the fact that bigeye tunas worldwide show similar changes in their behavior during their life, and subsequently in their patterns of availability to various fishing gear.

In summary, it appears that the life of a bigeye cohort can be classified as following:

a) Pre recruitment stages, for instance for a small bigeye less than 28cm or 1 pound (about 6 months), remain unknown for scientists: the areas where larvae and early juveniles are concentrated have never been sampled nor studied by scientists. The schooling behavior of small bigeye tuna remains unknown to scientists, but it seems likely that having a pelagic habitat inhabited by a wide range of predators including their parents, such fish probably school at very early stages (like the southern bluefin schools of larvae observed and described by Davis et al 1991).

b) At sizes between 30 and 80 cm (0.5 to 10 kg, e.g. during a period of about 1 year), it is well known from fishery data that bigeye tend to concentrate in mixed schools with skipjack and yellowfin of the same sizes (Fig. 7). During this schooling phase, the peak in the availability to fisheries tends to be observed between 46 and 50 cm (e.g. fishes between 2 and 3 kg, figure 2). During this period of their life, small bigeye show a shallow schooling behavior, eating in shallow layers during the day (Brill 1994) . It appears that during this period small bigeye tunas are never caught in pure bigeye schools but always mixed with the two other species (Fig. 7). This behavioral tendency has been typically observed world wide for bigeye in most equatorial areas, but the real fraction of the bigeye stocks showing such schooling behavior remains unknown. It could well be envisaged that all the population of juvenile bigeye is available to the purse seine fisheries during a large part of this juvenile stages (this is the hypothesis commonly used in stock assessment), but the alternate hypothesis that only an unknown fraction of this population is available to the surface fleets, should also be envisaged. Such hypothesis would reduce the potential for interaction between the surface and longline fisheries. It should also be noted that the massive recent development of the FAD fishery has reinforced world wide this tendency of bigeye to form mixed schools that are increasingly available to surface fisheries (Harley et al this symposium, An. IOTC 2003, An ICCAT 2003).

c) This schooling stanza will be followed by a decline in catchability to purse seiners, probably due to fish dispersal outside the area where mixed schools are concentrated in surface layers. During this intermediate pre-adult period, there is a progressive decline of availability to the purse seine fishery, and a corresponding increase of the availability to the long line gear (fish between 80 and 110 cm).

d) At sizes larger that about 110cm, bigeye tunas are reaching their sexual maturity, these fishes have fully adopted the behavior of an adult bigeye: a quite dispersed life, with biomass seasonally concentrated (but rarely schooling in pure bigeye schools nor mixed with other species) in feeding or spawning zones, showing a deep feeding during the day, and a shallow feeding during the night. This stanza of the bigeye life is heavily longliners using deep longli,es, when these large tunas are seldom available to surface fisheries.

This biological life cycle of bigeye tunas seems to be quite consistent world wide, as bigeye tuna do show during its life a wide range of behavior described in the previous paragraph, that are very distinct from the behavior shown by other tuna species such as yellowfin and skipjack. As a consequence, the changes in sizes and in schooling behavior that are observed world wide for bigeye tuna are probably an additional factor contributing to the variability of natural mortality as a function of its sizes and ages.

4-3- Is there a senescence for tunas?

The biological phenomenon of senescence seems to be universal, but it remains poorly studied for most fishes (with a few interesting exceptions, such as sturgeons or rockfishes, two groups of species showing a surprisingly low level of senescence, Bennet 1982) and for all tuna species. It appears that the real functional form and strength of senescence in fishes and especially in tunas, remains to be established: the biological process of ageing for tunas remains widely unexplored by tuna scientists. The hypothesis that M of older tunas, because of their biological characteristics, are not facing a significant rate rate of senescence (for instance a plateau of natural mortality in relation with their late spawning, as in Mueller and Rose 1996) cannot be eliminated. However, the alternate hypothesis that tunas could face an ageing process and an increased natural mortality at old ages, is still valid and would be an interesting hypothesis worth to explore, this hypothesis being potentially an important one for the modelling and management of tuna stocks. One of the major difficulty remains that the real age structure of the fished population remains widely uncertain for large and old tunas. These difficulties in tuna studies are worsened by weak data allowing to evaluate changes in natural mortality: lack of recoveries for old tagged tunas, lack of a good table of catch by age and by sex available, and lack of biological studies on changes in the biological condition of old tunas.

However, as this pattern of senescence is quite universal in the living world, this question would need further studies for tunas and for bigeye. One step would be to study the biological condition of very large bigeye (for instance by experts in senescence). In parallel, the stock assessment studies could also incorporate some sensitivity analysis of the M at age vector assuming such senescence and steadily increasing M, especially for female after their first spawning, but also for males (as they have no reason to stay young forever). The results of such investigations would also improve all the estimates of bigeye yield per recruit.

4-4- M_i : constant or variable from one year to another?

All the bigeye stock assessments done world wide are conducted under the hypothesis that $\mathbf{M_i}$ is invariant from one year to the next. This working hypothesis is a necessary simplification, but on the other hand there are many biological reasons to hypothesize or to consider that natural mortality is variable from one year to the next. This variability may be of two types:

- Natural mortality may first be variable from year to year as a function of the environment, for instance in relation with a lower (or a higher) natural mortality of larvae and juveniles during years with large environmental anomalies such as El Niño/La Niña events, or during cold or warm long term environmental cycles such as the NAO cycles (Polovina et al 1995, Ravier and Fromentin 2001), thus temporarily leading to low or high recruitments in the adult stock. Such variability remains difficult to evaluate, as the biological mechanism causing the year clkass strength variability remain poorly understood.
- Natural mortality may also show long term trends in relation with changes in the biomass of top predators. Knowing that the total biomass of large predators (sharks, tunas, billfishes) has been seriously declining in the open oceans during the last 50 years (Fonteneau et al 2002) due to a steadily increasing fishing pressure of most large pelagic fishes such as tunas, billfishes and sharks (their catches being multiplied by a factor of 10 during the last 10 years, and their biomass most often widely depleted). It could then be envisaged that natural mortality of all juvenile tunas, including bigeye, has been subsequently declining. This conclusion would be a valid one only if the predation by tunas, billfishes and sharks is a significant component of natural mortality of juvenile tunas, such hypothesis being quite well accepted by most tuna experts, as these predators correspond to the majority of predators in the offshore pelagic ecosystems. Of course, this top down effect and potential decline of M on juvenile tunas remains purely hypothetical, but there is little doubt that this ecosystem hypothesis should, at least, be seriously envisaged as an alternate of the constant M hypothesis that is now universally used in all stock assessments.

5- Yield per recruit analysis & the importance to correctly estimate juvenile $\mathbf{M_i}$ for bigeye

5-1- Introduction

The main question in most bigeye stock assessments is to evaluate, in terms of yield per recruit, the theoretical competition between surface fisheries catching small bigeye and the longline fisheries catching the adults. Natural mortality used in this type of analysis is probably one of the most critical parameters to estimate and to use in all analytical stock assessments. The goals of this chapter is to take a typical figure of bigeye catch at age, and to run various *ad hoc* VPA (Tomlinson 1970) and Yield per recruit analysis (Ricker 1975) in a two gear fishery (typical case for bigeye), using various sets of vectors of natural mortality at age. The goal of this small scale sensitivity analysis will be to provide a better understanding of the consequences, in term of yield per recruit, of changes in the pattern and levels of natural mortality assumed in this analysis. Potential effects of senescence will not be studied in these calculations, because this analysis would need to develop a complex and new procedure allowing to obtain a new catch at age matrix based on senescence. If senescence does occur significantly for bigeye, it would mean that many of the the old fishes would be less abundant than expected, the large fishes taken by fisheries being simply on a group of young adults showing a large individual L infinity and a fast growth. As a results, there could be in a given catch at size table fewer old fishes than in the constant M hypothesis. It is acknowledged that these calculations are qualitative and give only general guidance, but they should help to promote better and wider sensitivity analyses to evaluate the effects of uncertainties concerning natural mortality in bigeye stock assessment (such as the analysis planned in the FEMS research project, Pallares this symposium).

5-2- Data and method used in the analysis

Data used in the analysis is a synthetic data set and a set of biological and fishery parameters that are typical of the bigeye stocks and fisheries world wide. The analysis will be doing the following calculations (summarized in figure 11) :

- First, various virtual population analyses (VPA) were conducted on a typical bigeye stock sequentially exploited by purse seine and longline fisheries (the transition between these 2 fisheries being at 80 cm e.g. at an age of about 1.5 years), each fishery exerting exploitation rates that are typical of these fisheries (in terms of selectivity and levels). The average pattern of catch at age has been estimated using the average size distribution of bigeye taken world wide by purse seine and longline fisheries during recent years (See Fontenau et al this symposium), converting by slicing this catch at size into a vector of catch at age (using the Stequert et al 2003 Indian Ocean growth curve). This analysis was conducted using variable time steps: short intervals of time corresponding to 2 cm intervals for young bigeye between 30 and 80 cm, followed by yearly intervals after 80 cm.

- Second, the weight at age of unfished cohorts, and the corresponding optimal weight at which a cohort should be taken in order to maximize its yield per recruit, has been calculated in each hypothesis of M.
- Third, a simplified multigear yield per recruit analysis (Ricker method) has been conducted on the hypothesis (exploitation rates, growth, and Mi) and results (F at age) estimated from these VPA, (this analysis being also conducted using the same variable time intervals).
- These two sets of combined analysis are conducted under 3 hypothesis of natural mortality at age: (1) using a constant low yearly Mi of 0.4, (2) using the ICCAT value of M at age and (3) using during the 2 first years the SPC vector of Mi estimated for yellowfin in 2003 (followed by a M=0.4). These 3 sets of VPA were conducted under an hypothesis of a constant given recruitment at 80 cm in the longline fisheries, and then a given stable fishing mortality on the adults (independently of M assumed).

5-3- Results

The weight of an unfished cohort and the corresponding optimal weight are shown Fig. 12. This optimal weight is quite independent of natural mortality assumed and is located at an age of about 4 years (e.g. an individual weight of about 40 kg)

Fishing mortalities as a function of age estimated on bigeye in the present analysis are shown in figure 13 . These results have been chosen among the infinite numbers of VPA potential solutions as they are estimated to show a pattern and level of F that are typically estimated for the adult bigeye of the most recent assessment done by the ICCAT, the IOTC, the IATTC and SPC: however, it can be noted that the maximum levels of this estimated fishing mortality exerted on juvenile bigeye tend to be higher than fishing mortality on the adults, but this high sharply dome shaped fishing mortality is exerted only during a short period of time (as there is only a short duration between sizes taken by purse seiners, 40 to 65 cm, when the adult bigeye are available and fished by longliners). This result, a high dome shaped F at young ages, may seem to be contradictory with the flat and low fishing mortalities that have often been estimated by the ICCAT (An ICCAT 2003) and the IOTC (an. IOTC 2003): this apparent contradiction is simply due to the very wide yearly time units used in these stock assessment analysis, and to the very short time intervals (less than a month) used for juvenile bigeye in this analysis. It is considered that these short intervals are much more realistic to describe the rapid changes in the life cycle and fisheries of small bigeye, and when possible they should be preferred to the yearly time steps in all sequential population analysis done on bigeye. Such short interval are already used in the quarterly analysis conducted by the A-SCALA and Multifan-CL analysis (Harley et al. this volume, , Hampton et al, this volume) and such variable intervals should easily be incorporated in all sequential analysis that are now using yearly intervals (Tomlinson 1970)

On the opposite, the fishing mortality exerted on the adults by longline fisheries takes place during several years. These VPA were done on the hypothesis of a given known recruitment in the longline fisheries at 80 cm (see figure 13), as well as a given level of fishing mortality exerted by longliners, independently of levels of M on juvenile. This working rule was accepted in the present calculations because the longline catches are de facto always widely dominating all VPA analysis done on bigeye tuna.

The subsequent yield per recruit analysis done on these three vectors of juvenile M can be summarized by the following table:

Natural mortality	Recruitement at 6 months (million of fishes)	Present Yield (1000t)	Yield without F<80cm (1000t)	Change in Yield (1000t) without F<80cm	Corresponding change in yield in %
M low 0.4	83	380	436	+56	14,74
M ICCAT	133	384	407	+23	5,99
M juvenile yellowfin SPC	220	380	396	+16	4,21

If Juvenile M is low (constant 0.4), then the fishery on small fishes less than 80 cm reduces the yield per recruit of about 15%. If M on juvenile is higher (two other hypothesis), the absolute recruitment levels are higher and then the negative impact of the small fish fishery is estimated to be much lower (here a range between 4.2 and 6%). It should also be kept in mind in these changes of yield per recruit, that in these calculations, the yield per recruit interactions between the purse seine and longline fisheries are always much more important than the changes in total yield per recruit: as the catches of small bigeye (less than 80 cm) in these calculations correspond to a total catch of about 75.000 t. This means than in each case, the benefit for the longline fisheries to eliminate all catches of bigeye less than 80 cm are much higher, in a range between 43% (low M hypothesis) and 30% (higher M) of potential yield per recruit gain for the adult fishery if all the bigeye catches smaller than 80 cm were eliminated.

5-5- Conclusions about the uncertainty in the bigeye interactions

The type of catch at size figures observed for all the bigeye fisheries (a typical pattern that is more or less equally observed world wide) clearly suggest a potential for great interaction between purse seine fisheries and longliners. However, the age specific analysis conducted on this data set is much less conclusive. It appears that there is, of course, a potential for interaction between the two fisheries because small bigeye taken by purse seiners are well under the optimum sizes of this species (figure 12). However, this negative impact tends to be widely dependant of the natural mortality. This F also tends to be quite low, as the purse seine fishery takes place during a short period of the bigeye life (<1 year), and a period during which natural mortality is probably quite high. This negative impact of the purse seine fishery will be highly dependent of exploitation rates, but this type of uncertainties has not been explored. At this stage, the present calculations are only indicative, and there is no doubt that this type of sensitivity analysis should be generalized for the various bigeye stocks, taking into account the real uncertainties in M at age (including the uncertainties due to a potential senescence of old fishes), as well as the uncertainties related to the exploitation rates of the bigeye stocks.

6- Conclusion

Natural mortality as a function of age remains for bigeye a fairly unknown parameter, despite of its fundamental importance in the modelling and management of every bigeye stock. There is thus a serious need to improve the knowledge upon this parameter, for instance developing a more comprehensive biological thinking upon the biology and mechanism conditioning the age specific natural mortality (for both juveniles and adult bigeye), and developing coordinated international research programs targeting this parameter. One of the practical goals of these coordinated researches should be to validate or to abandon the hypothesis that natural mortality of small tunas should be at similar levels as long as these species are living in the same schools and in the same habitat. There is clearly a need to reinforce the international cooperation between tuna scientists and tuna regional fishery organizations as well as with biologists experts in natural mortality, in order to reduce the multiple uncertainties on M at age. This conclusion also tends to reinforce the need to conduct large scale tagging programmes targeting simultaneously the major tuna species, as tagging is the best way to estimate levels and changes of natural mortality as a function of age. Another conclusion after the present overview of the uncertainties in the knowledge of M at age should, at least, be that these major uncertainties should be fully recognized for bigeye tuna. Subsequently, stock assessments done on bigeye should not be based on a single best M at age level but on a wide range of potential levels of biologically plausible levels of M at age. This sensitivity analysis would probably be complex and time consuming to run, but its result would be essential to estimate the present levels of uncertainties in natural mortality of juvenile and adult bigeye and to conduct realistic analysis of fishery interactions.

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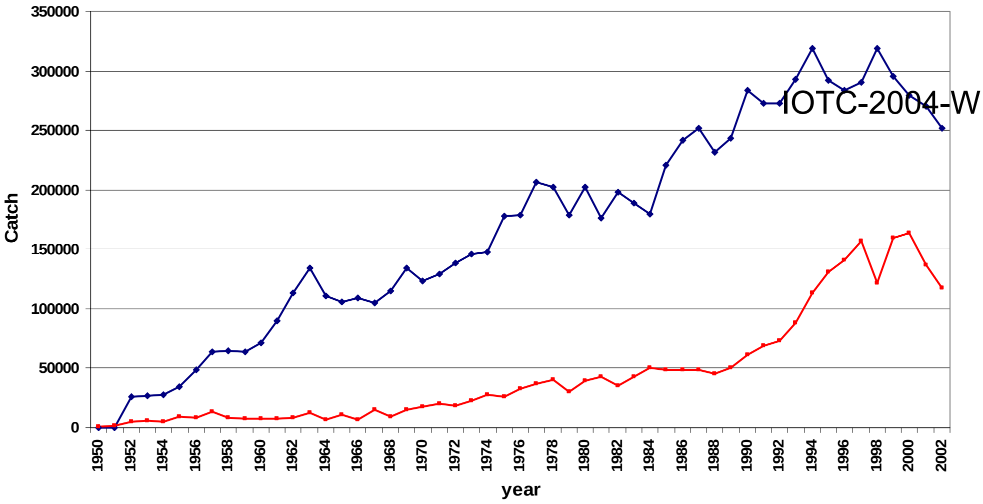


Figure 1: Yearly catches of bigeye tuna taken world-wide by purse seiners and by longliners

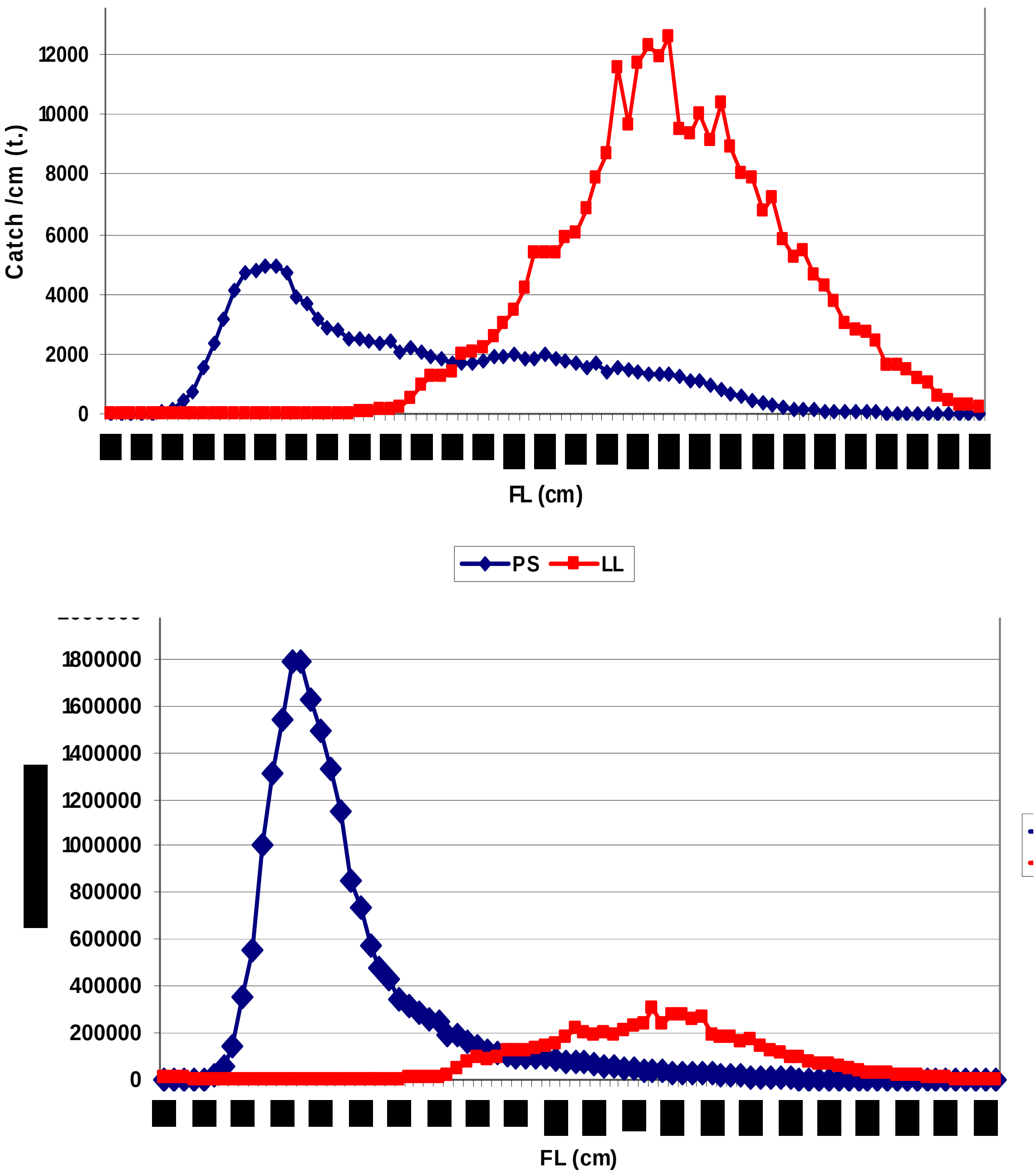


Figure 2: Average catches of bigeye tuna taken world-wide as a function of their sizes by purse seiners (PS) and by longliners (ll), in numbers of fishes (left) and in weight by sizes classes of 2 cm.

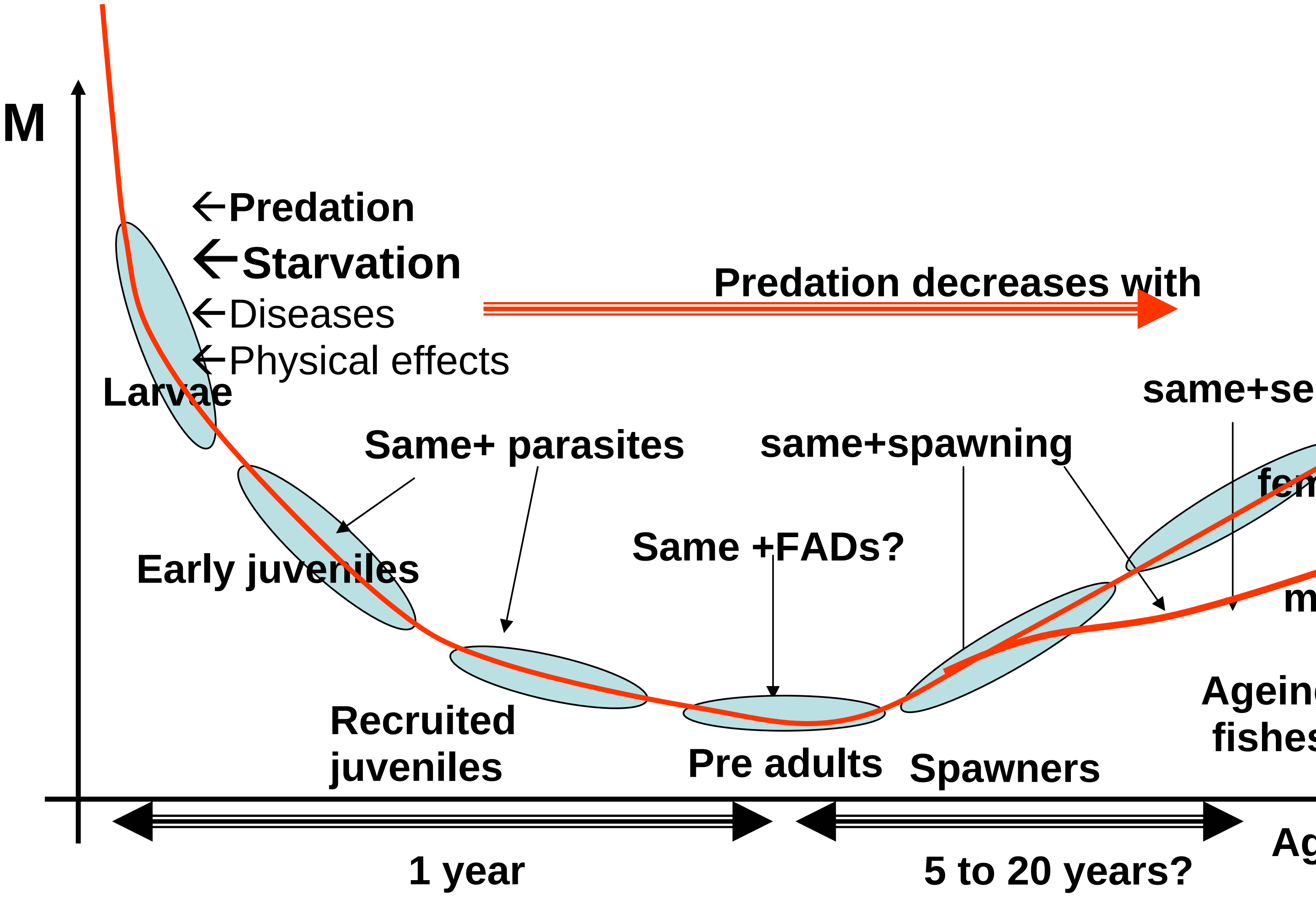


Figure 3: Conceptual figure showing the biological patterns in natural mortality as a function of age, that could b
tropical tunas as a function of their age.

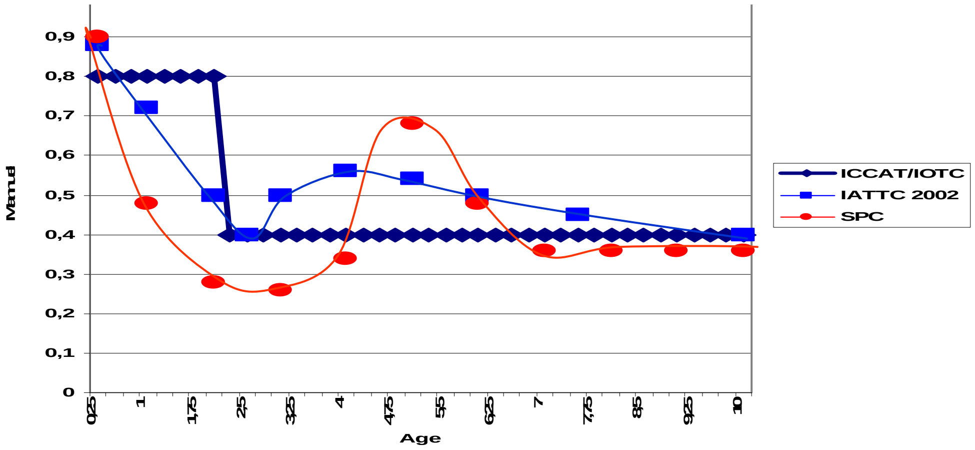


Figure 4: Yearly natural mortality of bigeye as a function of age used by the various tuna bodies in their assessment. *NB: The IATTC and SPC secondary peak of natural mortality at about age 4 years tend to be related by the authors to first spawning, although this age seems to be lower than the 50% levels of firts spawning; this point should be clarified.*

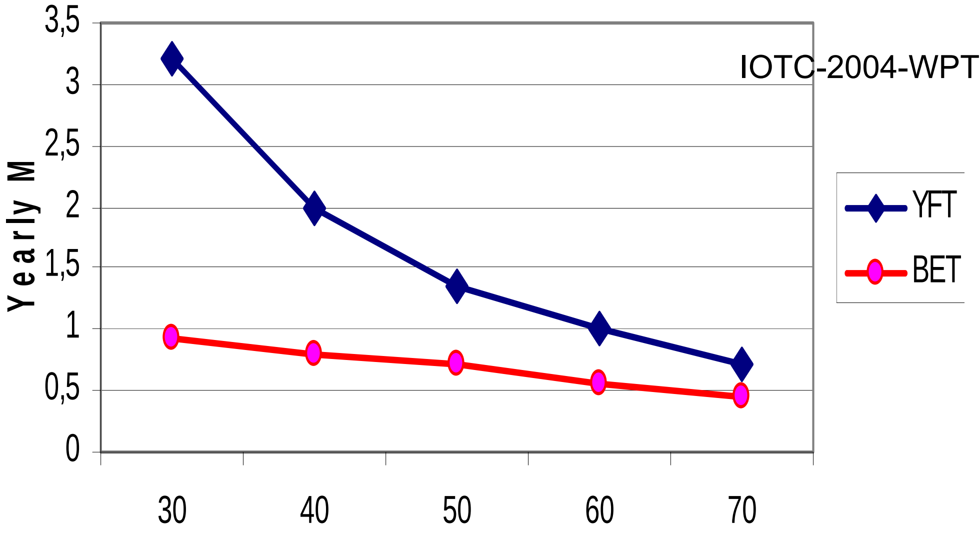


Figure 5: Size specific natural mortalities estimated for small yellowfin (YFT) and small bigeye (BET) in the western Pacific by Multifan CL (Hampton 2003).

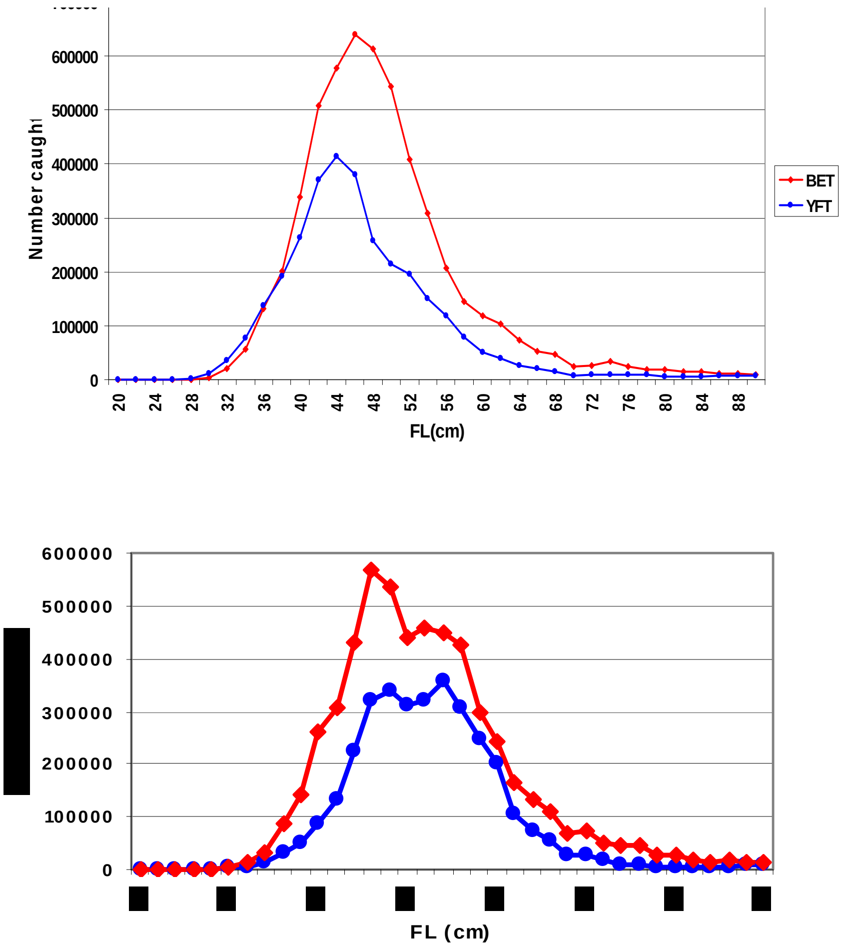
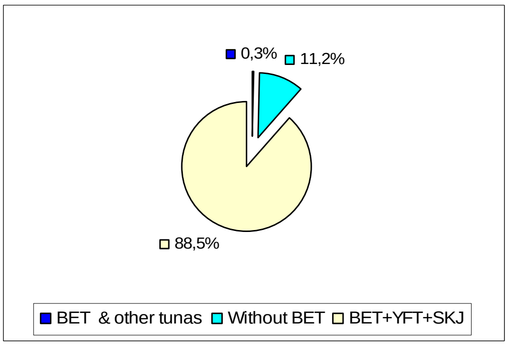


Figure 6: Average numbers of yellowfin and bigeye taken by purse seiners in the Atlantic (upper) and Indian oceans (lower) during recent years (period 1997-2002)



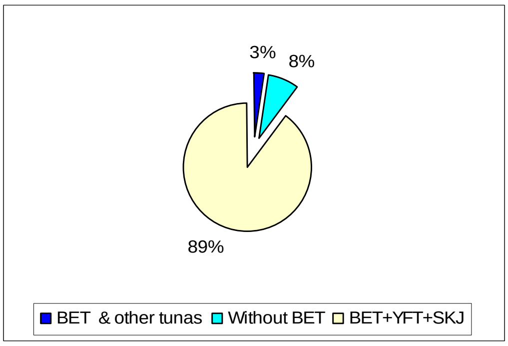


Figure 7: Overview of the species composition estimated by the multispecies schemes developped during the period 1991-2002 in the Atlantic (right, 9000 samples taken) and in the Indian Ocean (left, 8500 samples). These figures show that in these 2 oceans bigeye has been sampled in association with yellowfin and skipjack in 89% (Atlantic) and 88% (Indian) of the sampled schools.

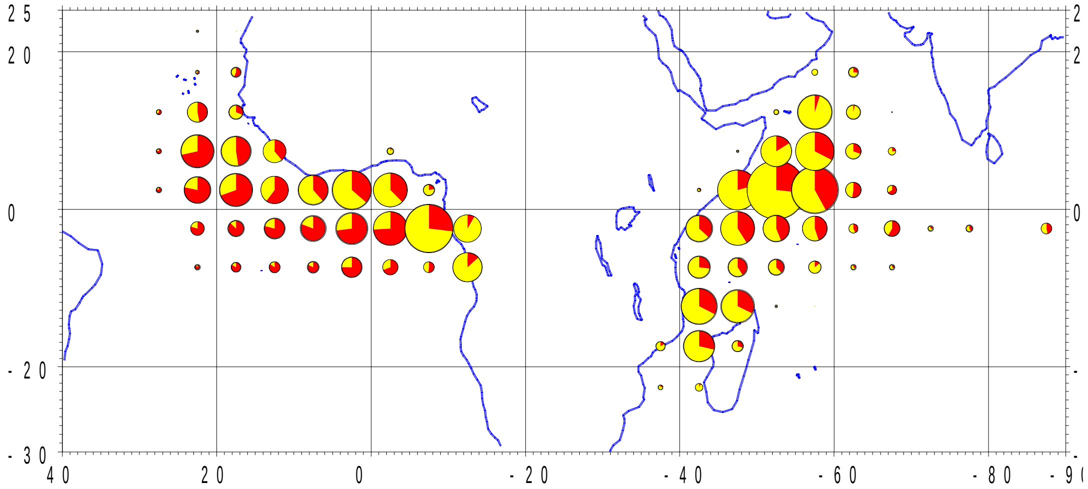
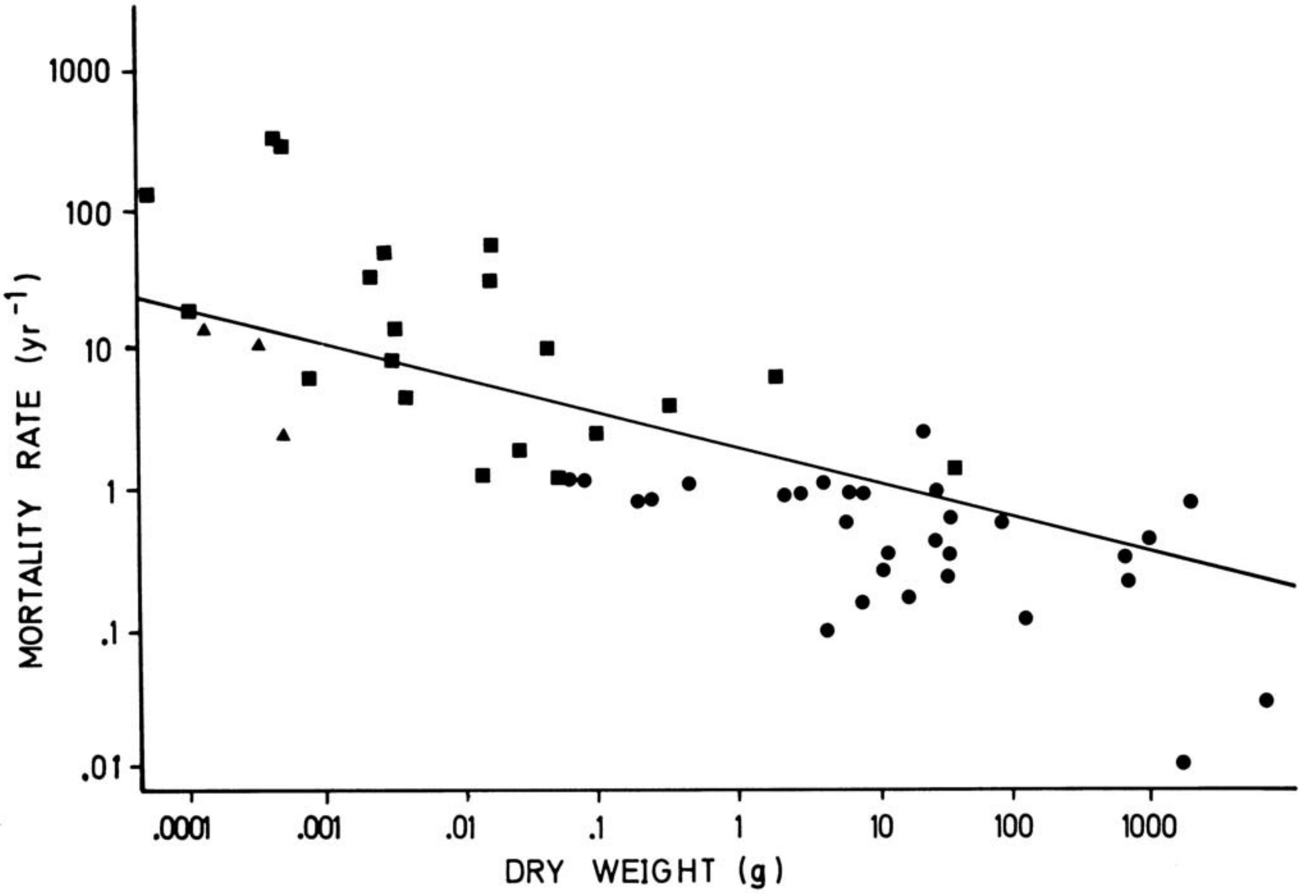


Figure 8: Average catches by 5° squares of small yellowfin (grey) and small bigeye (dark), both species with an individual weight less than 5kg, taken by purse seiners in the Atlantic and Indian oceans during recent years (period 1998-2002)

Figure 9: Yearly natural mortality as a function of individual dry weight estimated for pelagic species by Peterson and Wroblewski 1984 (for larvae and early juveniles) .



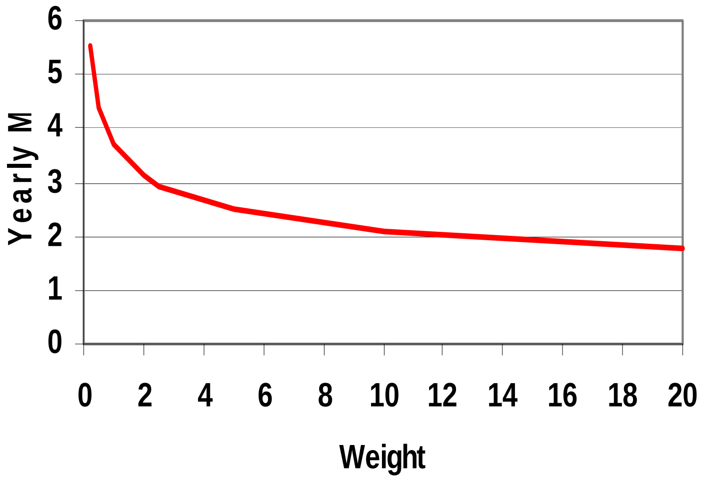


Figure 10: Yearly natural mortality as a function of individual weight estimated by McGurk 1986 for pelagic species.

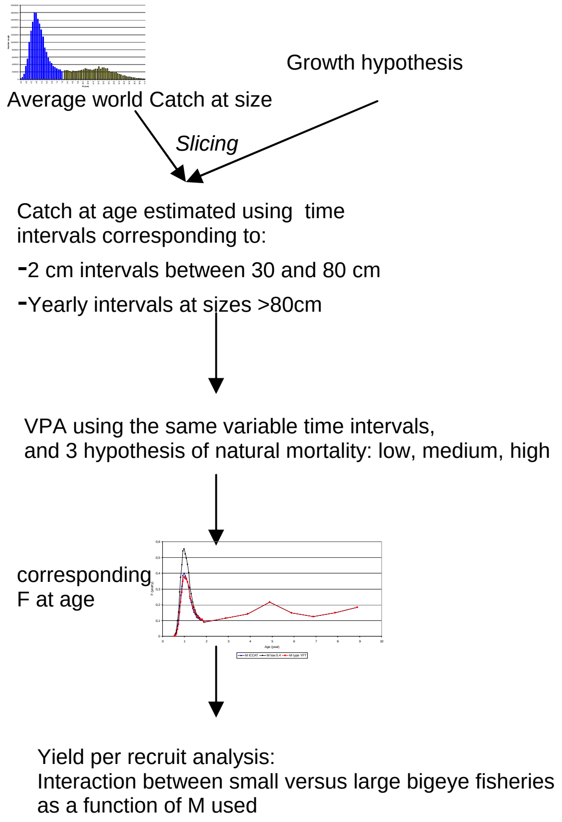


Figure 11: Diagram showing the data processing done in order to estimate the sensitivity of the yield per recruit results to the uncertainties in natural mortality of juvenile bigeye.

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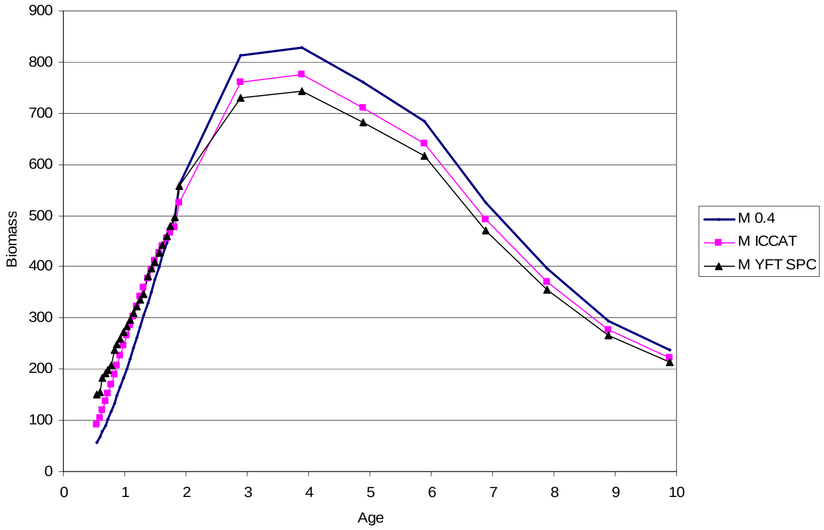

Figure 12: Typical pattern of optimal biomass estimated for bigeye tuna for various hypothesis of natural mortality

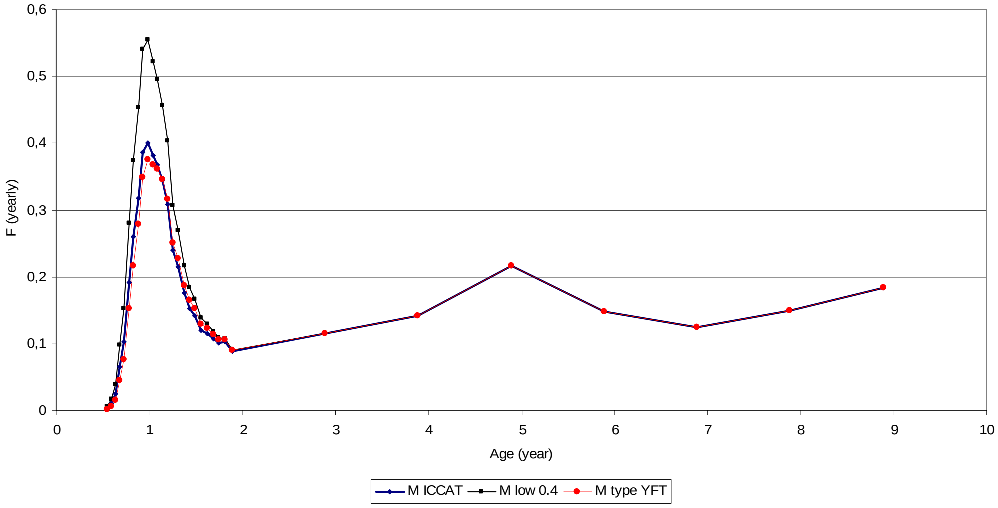

Figure 13: Typical patterns of fishing mortality at age estimated for the world bigeye stocks and fisheries. Fishing mortality for fishes younger than   years are taken only by purse seiners, when fishes than this age are taken in wide majority by longliners.