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Variability of the growth parameters of the skipjack tuna (*Katsuwonus pelamis*) among areas in the eastern Atlantic: analysis from tagging data within a meta-analysis approach

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Abstract – In order to assess the latitudinal variability in growth of the eastern Atlantic skipjack (*Katsuwonus pelamis*), conventional tagging data collected by the International Commission of the Conservation of Atlantic Tunas (ICCAT) since the 1960s are reanalyzed using a modified version of the von Bertalanffy-Fabens growth model. An analysis of the latitudinal patterns of recaptures showed that the lowest mixing rate between northern and southern regions was evidenced at 10° N Latitude. Since it is theoretically admitted that growth parameters L_∞ and K are negatively correlated, we substituted L_∞ into the growth equation model by a simple bioenergetic function of K fitted from existing studies on skipjack growth parameters. The likelihood for the meta-analysis of growth is combined with the likelihoods from the two regional tagging data with the aim of estimating simultaneously K in both areas and to transfer adequately uncertainties associated with the different data sets. From this study, it was showed that fish inhabiting waters south of 10° N latitude can be expected to grow generally larger but at slower rate than in the North (L_∞ = 112.34 cm vs. 89.38 cm, and K = 0.14 vs. 0.38, respectively). Our results are consistent with the range of growth estimates obtained in the Atlantic Ocean and in different parts of the World's oceans. In contrast, the estimates of L_∞ and K done in the Senegalese region in the 1980s within the framework of the Skipjack Year Program, and traditionally applied by ICCAT, are not supported by the present study. The findings concerning the phenotypic plasticity exhibited by growth of skipjack among latitudinal regions suggest potential differences in fish population productivity and consequently imply that non-conventional stock assessment methods such as catch-at size/growth transition matrix per region could be used to assess the responses of skipjack to exploitation.

Key words: Skipjack tuna / Growth rate / Conventional tagging / Combined likelihood / Bioenergetic function

Résumé – Variabilité de la croissance du listao (*Katsuwonus pelamis*) entre les secteurs de l'Atlantique Est : utilisation de données de marquage-recapture dans un contexte de méta-analyse. Dans le but d'évaluer la variabilité latitudinale de la croissance du listao (*Katsuwonus pelamis*) dans l'Atlantique Est, les données de marquage traditionnel collectées par l'ICCAT depuis le début des années soixante ont été reanalysées à l'aide d'une version modifiée du modèle de croissance de von Bertalanffy-Fabens. L'analyse des taux de recaptures par strates longitudinales montre que les échanges sont minima entre le Nord et le Sud au niveau de la latitude 10° N. Etant donné qu'il est admis que les estimations des paramètres de la courbe de croissance L_∞ et K sont corrélées, nous proposons de substituer, dans l'équation de croissance, L_∞ par une simple fonction bioénergétique de K ajustée à partir des paramètres de croissance obtenus dans la littérature sur le sujet. La fonction de vraisemblance pour ces données de méta-analyse est combinée aux vraisemblances des deux jeux de données de marquage afin d'estimer K de manière simultanée dans les deux régions, tout en conservant de manière correcte les incertitudes attachées à chaque jeu de données. Nous montrons dans cette étude que les listaos qui vivent dans les eaux situées au Sud de la latitude 10° N peuvent atteindre des longueurs maximales plus élevées que ceux vivant dans le Nord mais avec un taux de croissance inférieur (L_∞ = 112,34 cm contre 89,38 cm,

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et $K = 0{,}14$ contre 0,38, respectivement). Nos estimations sont comprises dans la gamme de variation des paramètres de croissance reportés pour le listao dans l'océan Atlantique et dans d'autres océans. Au contraire, les estimations de L_∞ et de K faites au Sénégal au début des années 1980 dans le cadre du Programme international « Année Listao », et utilisées traditionnellement par l'ICCAT, ne sont pas confirmées par notre étude. Ces résultats, relatifs à la plasticité phénotypique de la croissance du listao en fonction de la latitude, suggèrent de possibles différences régionales au niveau de la productivité du stock et en conséquence l'intérêt que représentent les méthodes non-conventionnelles d'évaluation des stocks, telles que des matrices de transition des prises par taille par régions, pour analyser les réponses du listao vis-à-vis de l'exploitation.

Introduction

It is admitted that growth rate of skipjack tuna (*Katsuwonus pelamis*) depicts substantial differences according to the latitude in the Atlantic Ocean (Bard and Antoine 1986), as well as in the Pacific Ocean (Sibert et al. 1983; Bayliff 1988). There remains, however, considerable uncertainty about the variability of the growth parameters between areas and consequently the ICCAT Standing Committee on Research and Statistics (SCRS) considers that it is a priority to gain more knowledge on the growth patterns of this species.

Tag-recovery studies facilitate the collection of a variety of types of information on the species under study, such as stock structure, growth rate, gear selectivity, migrations, survival/mortality, immediate mortality due to tagging, etc. (Gaertner et Hallier 2004; Gaertner et al. 2004; Hallier et al. 2005). Consequently, conventional tagging is one of the research tools widely used by tuna commissions to increase the biological understanding of spatially structured populations and to gauge the effects of fishing activities on these populations. Between the early 1960s and 2002 a total of 35 965 skipjacks were tagged with conventional "spaghetti" tags within the framework of different tagging programs conducted by ICCAT scientists with the collaboration of fishermen.

A re-analysis of the tagging data collected in the Senegalese area during the research program termed "Mattes Associées aux Canneurs" (MAC) (Hallier et al. 2001) showed that the parameters of the growth curve obtained in this region were closer to values estimated in the Gulf of Guinea or in other oceans (Hallier and Gaertner 2006) than those previously reported in Senegal (Cayré and Farrugio 1986). With the aim to reinforce previous findings and to explore whether the growth of skipjack exhibits phenotypic plasticity in different regions of the eastern Atlantic Ocean (i.e., longitude <= 30° W) we explored the entire release-recovery information available into the ICCAT tagging database.

In this paper, (1) we take advantage of skipjack growth parameters estimated from existing studies in the world's oceans within a meta-analysis framework. Since von Bertalanffy's growth parameters K and L_∞ are negatively correlated, existing growth information from numerous studies is used to expressed L_∞ as a bioenergetic function of K, whose equation is incorporated into the von Bertalanffy-Fabens growth model. (2) Instead of modelling northern and southern tagging data separately, we incorporate the three data sets into a combined likelihood to estimate simultaneously the two regional growth parameters K conditional on all types of information.

Material and methods

Measurements of the fish were taken, with callipers, from the tip of the snout to the fork of the tail to the nearest centimetre or half-centimetre. Only fish with accurate size and known dates and positions at tagging and at recapture are used for growth study in the eastern Atlantic (i.e., excluding data with longitude >= 30° W longitude). From a subset of 4084 data, recaptures of fish at liberty for less than 30 days as well as fish with growth less than –2 cm have been omitted (1356 fish). The first limitation is to take into account possible stress of the fish that will disrupt the growth and slight measurement errors as tuna were measured directly on the tagging cradle. The second limitation is directly related to measurement errors that can be done negatively or positively.

A comparative analysis of growth rates between different regions supposes low amounts of mixing. To assess the level of non-mixing between northern and southern regions, we developed a series of 2*2 contingency tables of release-recapture per region, each corresponding to a particular latitude from 20° N latitude to 5° S latitude. The latitude for which the chi-square test of non-mixing (Latour et al. 2001) is the largest will be used to discriminate the tagging data into two geographic regions. Then, only non-mixed skipjacks (i.e., tagged and recovered in the same region) were analyzed.

Growth was modelled using the translation of the von Bertalanffy curve formalized by Fabens (1965) to account for the sort of information obtained from tagging programmes (i.e., tag release and recapture lengths and time at liberty data):

$$\Delta L = (L_\infty - L_t)\left(1 - e^{-K\Delta t}\right)$$
$$\Delta L = L_{t+\Delta t} - L_t$$

where the increment in length ΔL through the period Δt (i.e., the time at liberty) is calculated as the difference between the size at recapture $L_{t+\Delta t}$ and the size at tagging L_t; K and L_∞ are the conventional growth rate coefficient and the asymptotic average maximum length of the von Bertalanffy curve, respectively (Haddon 2001).

Assuming normal random errors, the likelihood function L can be represented by:

$$L = \prod\left(\frac{1}{\sigma\sqrt{2\pi}}\, e^{-\frac{\left(\Delta L - \Delta\hat{L}\right)^2}{2\sigma^2}}\right).$$

The maximum likelihood estimates of L_∞ and K, are obtained by minimising the negative logarithm of L (LL), which is:

$$LL = -\sum Ln\left(\frac{1}{\sigma\sqrt{2\pi}}\, e^{-\frac{\left(\Delta L - \Delta \hat{L}\right)^2}{2\sigma^2}}\right)$$

where σ is the standard deviation which can be obtained analytically (as in the present study) or estimated as a free parameter in the likelihood function.

This method is termed hereafter the conventional von Bertalanffy-Fabens method. However, it is generally admitted that (1) there is a high negative correlation between the estimates of K and L_∞ and (2) these estimates are sensitive to the size range of the population sampled. That is to say that from a sample composed mainly of young fish one can expect a reasonable estimate of K and a weak estimate of L_∞ (and vice versa). In the case of tagging data, methods to take into account the fact that the proportion of short-term returns can be very large compared with the long-term returns of tagged fish have been proposed by Joseph and Calkins (1969). When there are some doubts, there is still the possibility to perform sensitivity analysis, e.g., fixing one parameter and calculating the objective function for different values of the second (Bayliff 1988) or, based on expert knowledge, fixing the asymptotic length at a value corresponding to an average maximum size observed in the catch (Bard and Antoine 1986). However, in such a situation Hilborn and Liermann (1998) highlighted the application of meta-analysis in order to summarize and to quantify variability of population parameters among numerous isolated studies.

For all of these reasons, we endorsed this approach by incorporating existing growth information in the tagging analysis within a meta-analysis approach based on Beverton and Holt's considerations about several patterns in growth and mortality parameters across fish species. Following these authors, Jensen (1997) stated that the relation between asymptotic length and the growth coefficient might occur as the result of a constraint on growth, and consequently can be expressed as a simple bioenergetic growth equation, such as:

$$L_\infty = CK^{-h}$$

where C and h represent metabolic and growth parameters whose interpretation is beyond the scope of this paper.

Although, these metabolic considerations were originally used for the comparison of life history parameters across species or across taxonomic groups, we considered that growth parameters of skipjack obtained from isolated studies reflect the variability across the different stocks of this species in the world's oceans (Table 1), and consequently may be useful to provide inferences on the parameters C and h.

Substituting L_∞ by this function of K, into the conventional Fabens' equation gives:

$$\Delta L = \left(\left(CK^{-h}\right) - L_t\right)\left(1 - e^{-K\Delta t}\right)$$

One advantage of the likelihood theory is the possibility to integrate multiple types of data (Maunder 2001; Hallier et al. 2005). Assuming independence between the observations, the combined log likelihood of the three types of data is:

$$LL = -\left[\Sigma_{j=1}^{2}\Sigma_{i=1}^{nj} Ln\left(\frac{1}{\sigma_j\sqrt{2\pi}}e^{-\frac{\left(\Delta L_{ij} - \Delta\hat{L}_{ij}\right)^2}{2\sigma_j^2}}\right) + \Sigma_{l=1}^{nk} Ln\left(\frac{1}{\sigma_k\sqrt{2\pi}}e^{-\frac{\left(L_{\infty l} - \hat{L}_{\infty l}\right)^2}{2\sigma_k^2}}\right)\right]$$

where $j = 1{,}2$ represents the tagging region, either the northern region or the southern region ($i = 1, ..., n_j$ with $n_j = 632$ and 629 fish in each region, respectively) and k = the existing pairs of estimated growth parameters K and L_∞ (Table 1, $l = 1, ..., n_k$ with $n_k = 29$).

The estimates of the growth parameters from the combined approach are compared with the growth estimates obtained by separately fitting the two tagging data sets from the conventional von Bertalanffy-Fabens model. Confidence intervals (95% C.I.) of the parameters of interest were estimated by bootstrapping the residuals ($B = 1000$). It should be noted that other approaches that permit simultaneous quantitative analysis of growth, such as Bayesian methods, have also been proposed for estimating variability among individuals (Pilling et al. 2002) or among populations within a species (Helser et al. 2007).

Results

Tagging data were examined by latitude to investigate whether skipjacks were more likely recaptured in the region of their release. The calculated χ^2 statistics depict a maximum value at 10° N latitude which can be considered as the latitude which maximizes the non-mixing between the northern and southern regions in the eastern Atlantic Ocean (Fig. 1). On the 2409 skipjacks released North of 10° N latitude, only 36 (i.e., 1.5%) were recaptured in the South and no fish tagged in the South was recaptured in the northern region (Table 2).

The ranges of lengths at release are approximately similar for the two regions considered (i.e., 42–60 cm FL for latitudes north of 10° N latitude, and 36–62 cm for equatorial areas; Fig. 2). First, with the aim of comparing the different approaches, growth curves were fitted separately to each region with the use of the conventional von Bertalanffy-Fabens method. Conventional regression diagnostic plots were used to identify outliers and influential observations and then the tagging data in each geographic set were fitted again with outliers removed. The estimates of the asymptotic length (L_∞), the growth rate coefficient (K) and the corresponding bootstrapped C.I. are shown in Table 3.

The asymptotic average maximum length of the von Bertalanffy curve appears very similar between fish tagged and recovered at latitudes more northern than 10° N latitude and fish

Table 1. Estimates of growth parameters from isolated studies for skipjack in the world's oceans used for modelling the bioenergetic function expressing L_∞ as a function of K used into the integrated approach.

Area	L_∞	K	Method	Reference
E. Atlantic G. of Guinea	80	0.322	Tagging	Bard and Antoine 1986
E. Atlantic N. trop	80	0.601	Tagging	Bard and Antoine 1986
E. Atlantic G. of Guinea	86.7	0.307	Spines	Chur and Zharov 1983
E. Atlantic Senegal	62	2.080	Tagging	Cayré et al. 1986
E. Atlantic Cap Vert	60	1.537	Tagging	Cayré et al. 1986
E. Atlantic Senegal	97.26	0.251	Tagging	Hallier and Gaertner 2006
W. Atlantic Caribbean sea	94.9	0.340	Length frequency	Pagavino and Gaertner 1995
W. Atlantic Brasil	87.12	0.219	Spines	Vilela and Costello 1991
Indian Ocean	60.6	0.930	Length frequency	Marcille and Stequert 1976
Indian Ocean Maldives	64.3	0.550	Tagging	Adams 1999
Indian Ocean Maldives	82	0.450	Length frequency	Hafiz 1987, in Adams 1999
Indian Ocean Sri Lanka	85	0.620	Length frequency	Amarasiri and Joseph 1987
Indian Ocean Sri Lanka	77	0.520	Length frequency	Sivasubramanium 1985; in Adams 1999
Indian Ocean Minicoy	90	0.490	Length frequency	Mohan and Kunhikoya 1985; in Adams 1999
E. Pacific	75.5	0.770	Tagging	Sibert et al. 1983
E. Pacific	79	0.640	Tagging	Josse et al. 1979
E. Pacific N	96.3	0.515	Tagging	Bayliff 1988
E. Pacific S	66.5	1.806	Tagging	Bayliff 1988
E. Pacific	73	0.820	Tagging	Joseph and Calkins 1969
E. Pacific	107	0.420	Length frequency	Joseph and Calkins 1969
W. Pacific	61.3	1.250	Tagging	Sibert et al. 1983
W. Pacific	65.5	0.945	Tagging	Josse et al. 1979
W. Pacific Vanuatu	60	0.750	Length frequency	Brouard et al. 1984
W. Pacific Trop. & Jap.	93.6	0.430	Otolith	Tanabe et al. 2003
W. Pacific Japan	76.6	0.600	Length frequency	Yao 1981; in Wild and Hampton 1994
W. Pacific Taiwan	103.6	0.302	Vertebrae	Chi and Yang 1973; in Wild and Hampton 1994
Central Pacific	102.2	0.550	Otolith	Uchiyama and Struhsaker 1981
Central Pacific	80	0.950	Grouped L-frequency	Brock 1954; in Adams 1999
Central Pacific West	74.8	0.515	Length frequency	Wankowski 1981

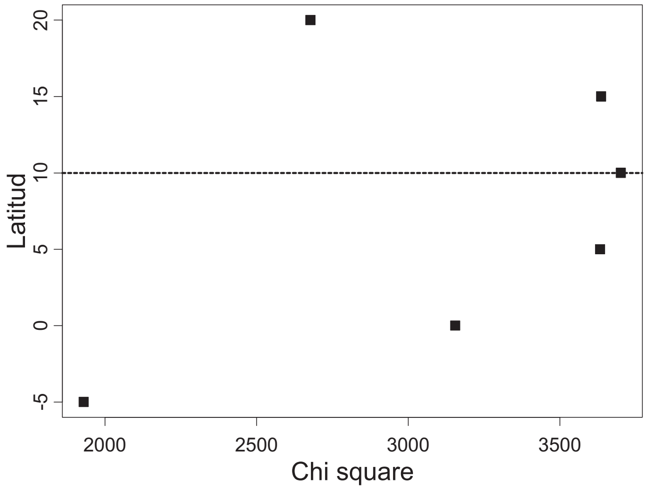

Fig. 1. Application of the χ^2 test to 2*2 contingency tables of release-recaptures per region to explore the latitude which maximizes the non-mixing rate of skipjack between the North and the South in the eastern Atlantic.

Table 2. Contingency table for the released-recaptured skipjack separated by 10°N latitude in the eastern Atlantic Ocean.

		Captured at Lat>=10° N	Captured at Lat<10° N
Released at Lat>=10° N	Observed	2373	36
	Expected	1484.4	924.6
Released at Lat<10° N	Observed	0	1442
	Expected	88.6	553.4

tagged and recovered in more southern areas (96.78 cm vs. 99.88 cm, respectively). However, the difference in the growth rate coefficients (0.35 vs. 0.20 per year) suggests that skipjack grow faster in the northern region of the eastern Atlantic Ocean than in the equatorial areas. Support for the latitudinal gradient in growth is reinforced by the results obtained from the combined likelihood (0.38 vs. 0.14 per year, Table 3). The corresponding value of the asymptotic length L_∞ (89.38 cm, and 112.34 cm, respectively) are calculated a posteriori based on the estimated parameters C (71.81) and h (0.22) of the bioenergetic function relating L_∞ and K which is embedded into the combined likelihood (Fig. 3). It must be stressed that both the conventional and the combined methods provided a similar finding (i.e., slower growth rate in the South), but bootstrapped confidence intervals of K were substantially narrower for the integrated method (Fig. 4).

Table 3. Summary of bootstrapped statistics for the von Bertalanffy-Fabens model per region and for the integrated likelihood approach combining the two eastern Atlantic regional tagging data and the meta-analysis on existing studies on growth parameters of skipjack in the world's oceans. * = estimated a posteriori based on the *C* and *h* estimates of the bioenergetic function relating L_∞ at *K*; NA = non estimable.

Method	Area	Estimate	*K*	L_∞	*C*	*h*
Fabens	North	mean	0.35	96.78	NA	NA
		median	0.35	91.82	NA	NA
		C.I.	0.14–0.56	76.96–145.35	NA	NA
	South	mean	0.20	99.88	NA	NA
		median	0.22	85.00	NA	NA
		C.I.	0.07–0.34	72.49–167.13	NA	NA
Combined	North	mean	0.38	89.38*	71.81	0.22
		median	0.37	89.10*	71.78	0.22
		C.I.	0.28–0.53	78.18–99.89	66.74–76.41	0.15–0.29
	South	mean	0.14	112.34*	71.81	0.22
		median	0.14	111.08*	71.78	0.22
		C.I.	0.10–0.18	96.07–134.35	66.74–76.41	0.15–0.29

Table 4. Summary statistics for the environmental factors in both areas considered in the analysis (from the World Ocean Database 2005, NODC; period: 1980–2005). The limits of latitude and longitude for each region contain 90% of the tagging at release and at recapture. * To minimize the effect of seasonality in the northern region, environmental data were restricted to May-November, i.e., the period of the year which represents 90% of the released-recaptured fish.

Area	Latitude / Longitude	Temperature (°C) (90% CI)	Salinity (‰) (90% CI)	Dissolved Oxygen (ml L^{-1}) (90% CI)
North*	28°N – 14°N	20.2	36.3	5.1
	19°W – 16°W	(17.8–24.6)	(35.9–36.8)	(4.5–5.8)
South	5°N – 3° S	26	35.1	4.6
	12°W – 8° E	(22.6–29.1)	(32.3–35.9)	(4.5–5.3)

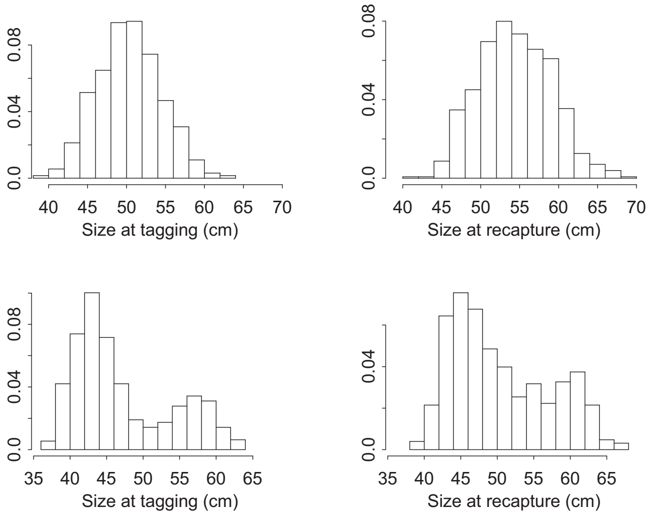

Fig. 2. Frequency of recoveries for different lengths at release (left panel) and lengths at recapture (right panel) for eastern Atlantic skipjack tagged and recaptured at latitudes > 10° N latitude (upper panel) or at latitudes <=10° N latitude (lower panel).

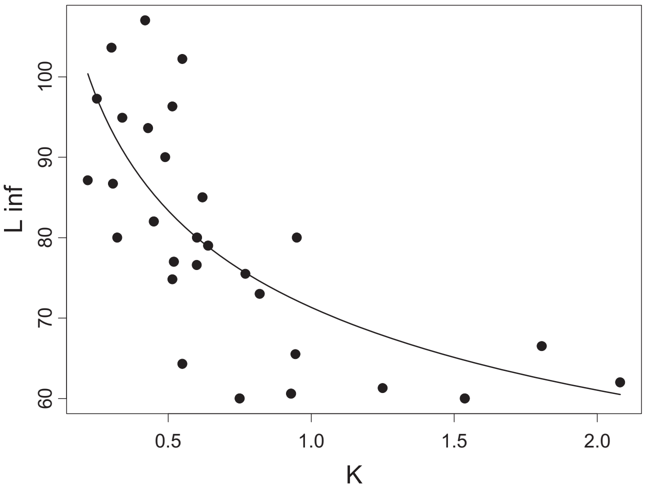

Fig. 3. Distributions of skipjack growth parameters L_∞ and *K* estimated from existing studies in the world's oceans (see, Table 1) and fitted values (solid line) of the Jensen's bioenergetic function from the integrated likelihood approach.

Discussion and conclusion

In the present analysis, rather than ignoring everything ever learnt from previous growth studies, we summarized all the information contained in the historic data set into the functional relationship between growth parameters for different stocks of skipjack. It must be noted that fitting different tagging data separately makes the assumption that there is no relationship among the growth parameters of the populations under study which, in light of previous analyses, seems unrealistic. In contrast, (1) accounting for plausible growth

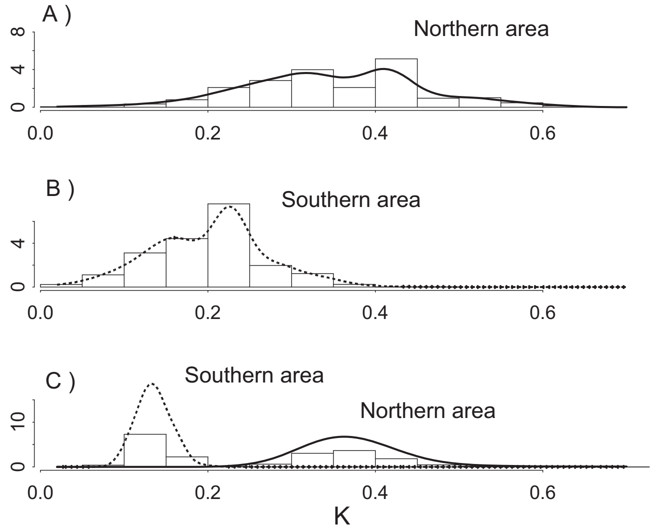

Fig. 4. Bootstrapped values of the growth parameter K for eastern Atlantic skipjack based on the conventional von Bertalanffy-Fabens model fitted separately for fish tagged and recaptured either North of 10° N latitude (A), or South (B), and based on the integrated likelihood approach combining the two tagging data sets and the meta-analysis on existing studies on growth parameters in the world's oceans (C).

parameters values within a meta-analysis framework has the advantage of borrowing strength from other populations to improve parameter estimation for a given population with weaker data (Hilborn and Liermann 1998); and (2) integrating these data into a combined likelihood reduces the loss of information and the risk that uncertainty be inadequately transferred between the different equations (Maunder 2001).

Our results are in agreement with the estimates of the growth parameters obtained from skipjacks tagged during the MAC activities in the Senegalese area (Hallier and Gaertner 2006), in the Gulf of Guinea (Chur and Zharov 1983; Bard and Antoine 1986), in the western Atlantic (Vilela and Castello 1991; Pagavino and Gaertner 1995), as well as in other parts of the world's oceans. In contrast, we found substantial differences in the growth parameters between the present study and the estimates reported by Cayré et al. (1986) for the Senegalese region (62 cm for L_∞ and 2.080 for K; Table 1).

The fact that growth parameters of skipjack may vary with latitude has been pointed out several authors (Bard and Antoine 1986; Bayliff 1988, among others). Our findings suggest that skipjack inhabiting waters south of 10° N latitude can generally be expected to grow larger but at a slower rate than skipjack inhabiting North of 10° N latitude.

Since conventional tagging data do not provide detailed information on the migratory behaviour of the fish when they are at liberty, integrating environmental indicators with conventional tagging data to infer habitat of tropical tuna remains uncertain. That is that individual migrations are more complex than directed movements with straight trajectories, and consequently the residence time within a specific area between the location at release and the location at recapture is unknown. In addition, one can argue that movements of skipjack are not constrained by surface water environmental factors within the geographic confines of their distribution. However taking these limitations into account, a comparison was made of the average physical environmental factors (i.e., sea surface temperature, dissolved oxygen and salinity) between each area from oceanographic data of the World Ocean Database 2005 (NODC[1]) (Table 4).

Even if skipjack do penetrate into cooler waters of thermocline as deep as 200 m, laboratory and field studies indicate that skipjack can live in a wide range of water temperatures (20–29 °C), and that only fish less than 1 kg can tolerate temperatures over 30 °C. The range of sea surface temperatures observed in both regions coincides with these values and consequently there is no evidence that growth is temperature-limited in the area South of 10° N latitude. Dissolved oxygen concentration may be a limiting factor for skipjack, specifically at concentrations below 2.8 ml L^{-1}, and would confine the fish to fairly shallow layers in some tropical areas. Evans et al. (1981) showed that a combination of an 18 °C isotherm and depth contours of the 3.5 ml L^{-1} dissolved oxygen surface was considered as a proxy of skipjack habitat depth to hypothesize areas of vulnerability of skipjack to surface gears in the Atlantic Ocean. Based on this approach, and bearing in mind that oxygen requirements may vary with fish size, skipjack habitat depth is greater in the southern region than in the 10° N latitude region. Since fish growth faster in the northeastern Atlantic, the restriction of habitat suitable for skipjack in this region does not negatively affect its growth rate.

Regarding the productivity of the two regions considered, and their respective richness in tuna forage, there is evidence that surface waters of the northern region are strongly enriched with nutrients by wind-induced upwellings off the Senegalese and Mauritanian coasts. However, in a non-tropical upwelling situation (such as the Mauritania area), the rich forage should attract tunas but the low temperatures may exclude them (Sund et al. 1981). During the winter months, when surface temperatures are below 20 °C, skipjack can only reach the fringes of the concentration of their prey. As the upwelling regime decays, the food-rich areas become warm enough for the tunas to penetrate them. This period of transition corresponds, in effect, to the start of the fishing season (approximately May in Senegal and June in Mauritania; Stretta 1988). On the other hand, the southern area is under the influence of numerous physical processes that may enrich near-surface waters with nutrients in different places and periods of the year: the Ghanaian upwelling and the equatorial upwelling (both in July-September), the vertical mixing over a ridge in the thermocline along the North Equatorial Countercurrent (January-February) and, for the eastern-most waters of this region, the proximity of the Cape Lopez front. Even if movements into relatively productive areas may have survival value for tunas, and the fact that they probably aggregate around any rich patches of food that they find in waters of suitable temperature and dissolved oxygen (Sund et al. 1981), it is unclear how to relate the food available in a given area to tunas' food requirements and finally to their growth rate.

Whatever the environmental factors affecting the growth of skipjack, two conclusions can be made from our study: (1) the

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[1] National Oceanographic Data Center, NOAA
http://www.nodc.noaa.gov/OC5/WOD05/pr_wod05.html

growth parameters for the two groups of skipjack separated by 10° N latitude could differ as much as 23 cm and 0.24 per year for L_∞ and K, respectively; and (2) because of growth correlation to other life history parameters (e.g., size at first maturity and mortality) one can expect substantial differences in fish population productivity. This feature and certain other key aspects of its biology (e.g., opportunistic spawning throughout the year, and over large areas, resulting in widespread recruitment but heterogeneous in space and time; Cayré and Farrugio 1986) make it difficult to conduct an assessment using current methods. As catch-at-age matrix would not be consistent because fish of the same age can exhibit different sizes depending on their past movement patterns, catch-at-size analysis and a growth-transition matrix by large geographical entities could be an alternative to assess the status of skipjack stocks.

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