

Estimating abundance, fishing mortality and migration rates by area, using the spatial VPA methodology. Application to yellowfin tuna in eastern and western Atlantic

MAURY O ⁽¹⁾, GASCUEL D ⁽¹⁾, FONTENEAU A. ⁽²⁾

(1) ENSAR halieutique, 65 rue de Saint-Brieuc, F 35042 Rennes cedex, Email : maury@rozahon.inra.fr

(2) ORSTOM-HEA, 911 Av Agropolis, BP 5045, 34032 Montpellier cedex 1, Email : fontenea@melusine.mpl.orstom.fr

Résumé :

L'évaluation et la gestion des stocks halieutiques à une échelle spatiale plus fine que celle du stock butent généralement sur l'estimation des paramètres démographiques dans les différentes zones considérées. On propose ici une méthode dite de "VPA spatiale", qui permet d'estimer les effectifs du stock et les taux de mortalité par pêche dans différentes zones géographiques, ainsi que les taux d'échange entre zones.

La méthode s'appuie sur les données de captures par âge et d'effort de pêche dans chaque zone, et sur une estimation de la surface occupée par le stock dans chaque zone. A partir d'une estimation de la mortalité par pêche totale, issue d'une analyse des cohortes concernant l'ensemble du stock, ces données permettent de calculer des taux locaux de mortalité par pêche. Ces taux sont eux-mêmes utilisés dans un modèle discret en boîte afin d'estimer les effectifs et les taux de migration par zone.

A titre d'illustration, la méthode est appliquée aux fractions Est et Ouest du stock d'albacores de l'Atlantique, en considérant une cohorte moyenne sur la période récente. Deux méthodes d'approximation des surfaces occupées par le stock sont proposées ; elles permettent de borner la réalité et les estimations de mortalité correspondantes. La méthode de VPA spatiale met clairement en évidence les migrations transocéaniques de fractions importantes du stock, avec des taux d'échange qui atteignent *****

Abstract:

Spatial approaches of fish stock dynamics remain most of the time impossible in practice, because of the lag of parameter estimates at a scale smaller than the whole stock. This paper proposes a method to estimate fish numbers and fishing mortality in discrete spatial zones, and migration rates between these zones. The method needs catches at age and fishing effort by zone data only. It takes into account the surface of the stock in each zone too. It is based on a calculation of the fishing mortality in each zone from the total fishing mortality estimated by VPA. Fishing mortality in each zone is then used by a temporally discrete boxes model to estimate fish numbers and migration rates in each zone.

As an illustration, the method is applied to eastern and western part of the Atlantic yellowfin stock. Two estimates of the surfaces occupied by the stock are proposed. The spatial VPA methodology clearly show the transoceanic migration of a large fraction of the stock, with migration rates *****

INTRODUCTION

Since the agreement of a single Atlantic yellowfin stock (Anon., 1993), current yellowfin stock assessment and management advice are based on population dynamic modelling at the global stock distribution scale. In this way, those methods do not allow spatially heterogeneous assessments. Nevertheless, yellowfin tunas migrate massively at different scales (Bard et Hervé 1994 ; Foucher 1995 ; Fonteneau 1994a ; Fonteneau *et al.* 1997). Many studies underline the importance of spatial heterogeneity and fish movement for both stock assessment (***) and fleet interaction studies (**). Spatial models do exist and could profitably be applied to Atlantic yellowfin tuna stock. Such models have already been used for different tuna stocks (Porch 1996 ; Sibert et Fournier 1994 ; Kleiber et Fonteneau 1994 ; Butterworth **, ...). But most of them deal with stocks with available tagging data. Unfortunately, because of such data scarceness for Atlantic yellowfin stock, fish migration rates are unknown and spatial stock assessment and modelling remain inapplicable in practice.

This paper uses the spatial VPA to assess fishing mortality rates, fish numbers and migration rates between ICCAT east and west Atlantic zones. Spatial VPA is a method to estimate fish abundance and local fishing mortality coefficients in spatial zones and migration rates between these zones (Maury *et al.* 1997). The method only needs data of catches at age and fishing effort by zone and it takes into account the surface of the stock in each zone. Stock surface is estimated here by long liners catches spatial interpolation using a GIS (Geographical Information System).

1. DATA AND MÉTHOD

1.1. The spatial VPA methodology

The method used here is described in detail in Maury *et al.* (1997a). The basic model used is a discrete model. It is analogous to the boxes model whose differential formulation was presented by Beverton and Holt in 1957, and is based on the assumption of an instantaneous migration of fishes at the end of each time step (Punt et Butterworth., 1994). Here, the method is applied for two distinct boxes but could be easily extended to more boxes.

$$(1) \quad \begin{cases} N_{1,t+1} = N_{1,t} e^{-(F_{1,t} + M_{1,t})} \cdot (1 - T_{12,t}) + N_{2,t} e^{-(F_{2,t} + M_{2,t})} \cdot T_{21,t} \\ N_{2,t+1} = N_{2,t} e^{-(F_{2,t} + M_{2,t})} \cdot (1 - T_{21,t}) + N_{1,t} e^{-(F_{1,t} + M_{1,t})} \cdot T_{12,t} \\ C_{1,t} = \frac{F_{1,t}}{F_{1,t} + M_{1,t}} \cdot N_{1,t} \cdot (1 - e^{-(F_{1,t} + M_{1,t})}) \\ C_{2,t} = \frac{F_{2,t}}{F_{2,t} + M_{2,t}} \cdot N_{2,t} \cdot (1 - e^{-(F_{2,t} + M_{2,t})}) \end{cases}$$

with $N_{1,t}$ and $N_{2,t}$, the fish numbers in zones 1 and 2 during time step t ; $F_{1,t}$ and $F_{2,t}$, the fishing mortality coefficients in zones 1 and 2 corresponding to numbers of fish and efforts in each zone during the time step t ; $M_{1,t}$ and $M_{2,t}$, the natural mortality coefficients in zones 1 and 2 during the time step t ; $T_{12,t}$ the migration rate from zone 1 to zone 2 during time step t and $T_{21,t}$, the migration rate from zone 2 to zone 1 during time step t .

No hypothesis is made about the distance between zones or their connexity. The model is not spatially explicit, it is based on the fundamental assumption of homogeneity within each zone (each zone is supposed to behave as a whole). The case of a single cohort only is considered in the following of the paper. In the case of a single cohort, the time t is redundant with the age.

System (1) has two unknown state variables $N_{1,t}$ and $N_{2,t}$, two measurable output variables $C_{1,t}$ and $C_{2,t}$ and six parameters ($M_{1,t}$, $M_{2,t}$, $F_{1,t}$, $F_{2,t}$, $T_{12,t}$ et $T_{21,t}$). Without external information, natural mortality coefficients $M_{1,t}$ et $M_{2,t}$ can be arbitrarily set as it is normally done in cohort analysis. The fishing mortality applied to the whole stock F_t is estimated by VPA and is used to determine the fishing mortality in each zone $F_{1,t}$ et $F_{2,t}$. By using the catchability per surface unit q'

(Laurec and Le Guen, 1981) and the assumption of spatial homogeneity of fish density in each zone⁽¹⁾, we can write:

$$(2) \quad q'_t = q_{i,t} \cdot S_{i,t} = \frac{F_{i,t} \cdot S_{i,t}}{f_{i,t}}$$

with $S_{i,t}$, the surface covered by the stock in zone i during time step t (see 1.3.). Because q'_t is constant in space, we can write:

$$\frac{F_{1,t} \cdot S_{1,t}}{f_{1,t}} = q'_t = \frac{F_{2,t} \cdot S_{2,t}}{f_{2,t}}$$

then:

$$(3) \quad F_{2,t} = \frac{S_{1,t} \cdot f_{2,t}}{S_{2,t} \cdot f_{1,t}} \cdot F_{1,t}$$

⁽¹⁾ The catchability per surface unit q'_t is defined as being equal to the local CPUE $U_{s,t}$ divided by the local density $D_{s,t}$, both calculated on a unit surface ds during time t :

$$(2) \quad q'_t = \frac{U_{s,t}}{D_{s,t}} = \frac{U_{s,t}}{N_{s,t}} \cdot ds = q_{s,t} \cdot ds$$

with $N_{s,t}$ and $q_{s,t}$, the fish number and the catchability in the unit surface ds during time t .

Contrary to the catchability q_t , the assumption that the coefficient q'_t is spatially constant at a given time t can be done. Then, catch per unit effort in each zone i at time t can be expressed as follow:

$$CPUE_{i,t} = \frac{C_{i,t}}{f_{i,t}} = \frac{q'_{i,t} \cdot \oint_{S_i} D_{s,t} \cdot f_{s,t} \cdot ds}{\oint_{S_i} f_{s,t} \cdot ds}$$

with $f_{s,t}$ the effort in the elementary surface ds at time t .

With the assumption of spatial homogeneity of fish density in each zone i ($D_{s,t} = D_{i,t}$), the previous equation can be simplified:

$$CPUE_{i,t} = q'_t \cdot D_{i,t} = q'_t \cdot \frac{N_{i,t}}{S_{i,t}} = q_{i,t} \cdot N_{i,t} \quad \text{with } N_{i,t}, \text{ the number of fish in zone } i \text{ at}$$

time t . Such a simplification could be made at the global stock level only under the generally false hypothesis of equality of fish densities in all zones at a given time t :

$$CPUE_t = \frac{C_t}{f_t} = \frac{\sum_i^n C_{i,t}}{\sum_i^n f_{i,t}} = \frac{q' \cdot \sum_i^n (D_{i,t} \cdot f_{i,t})}{\sum_i^n f_{i,t}}$$

Using the conservativity of the number of fish ($N_{1,t}+N_{2,t}-N_t=0$), system (1) gives:

$$(4) \quad g(F_{1,t}) = \frac{C_{1,t} \cdot (M_{1,t} + F_{1,t})}{F_{1,t} \cdot (1 - e^{-(F_{1,t} + M_{1,t})})} + \frac{C_{2,t} \cdot (M_{2,t} + F_{2,t})}{F_{2,t} \cdot (1 - e^{-(F_{2,t} + M_{2,t})})} - \frac{C_t \cdot (M_t + F_t)}{F_t \cdot (1 - e^{-(F_t + M_t)})} = 0$$

with $F_{2,t}$ given by equation (3), $M_{1,t}$, $M_{2,t}$, $C_{1,t}$, $C_{2,t}$ and C_t already known and F_t estimated by VPA.

Equation (4) is solved numerically with the hybrid method proposed by Press *et al.* (1994). When $F_{1,t}$ is assessed, equation (3) is used to calculate $F_{2,t}$. Next, fish numbers $N_{1,t}$ and $N_{2,t}$ are calculated using the catch equations in each zone of the system (1).

The only remaining unknown parameters are $T_{12,t}$ and $T_{21,t}$. But system (1) is still not identifiable, as far as infinity of couples ($T_{12,t}$, $T_{21,t}$) can be a solution. It is under-determined and must be simplified (*i. e.* : a relation between $T_{12,t}$ and $T_{21,t}$ has to be found). For this, fish movement is supposed to have two components: a random one D_t (diffusion) which is spatially isotropic (brownian motion) and depends only on age and time t , and a deterministic one T'_t (advection) which is spatially directed (Okubo, 1980 ; Deriso *et al.*, 1991 ; Kleiber and Fonteneau, 1994). With such assumptions, transfer coefficients $T_{12,t}$ and $T_{21,t}$ can be expressed as follows:

$$(5) \quad a \begin{cases} T_{12,t} = D_t + T'_{12,t} \\ T_{21,t} = D_t \end{cases} \quad \text{or} \quad b \begin{cases} T_{12,t} = D_t \\ T_{21,t} = D_t + T'_{21,t} \end{cases}$$

$T'_{12,t}$ and $T'_{21,t}$ can not be simultaneously positive because advection is considered as an homogeneous and univocal phenomenon. Now, the unknown parameters are: (D_t , $T'_{12,t}$) or (D_t , $T'_{21,t}$). In the present study, the coefficient D_t is supposed to be estimated with an auxiliary method (Kleiber *et al.*, 1994 ; Porch, 1996), neglected compared to $T'_{i,t}$, or bounded in an interval. Migration rates at terminal age $T_{12,T}$ and $T_{21,T}$ are supposed to be equal to values at the previous time step : $T_{12,T-1}$ and $T_{21,T-1}$. For all the other time steps, equations (1) and (5) are used to estimate $T_{12,t}$ and $T_{21,t}$:

$$\begin{cases} T_{12,t} = \frac{N_{2,t+1} + N_{2,t} \cdot e^{-(F_{2,t} + M_{2,t})}}{N_{1,t} \cdot e^{-(F_{1,t} + M_{1,t})}} \cdot (D - 1) \\ T_{21,t} = D_t \end{cases}$$

If $T_{12,t} \leq D_t$ ($\Leftrightarrow T'_{12,t} \leq 0$ which is impossible by definition), symmetrical equations are used to estimate $T_{12,t}$ et $T_{21,t}$.

1.2. Extending the method to several fleets

For $i = 1 \dots n$ fleet, fishing mortality on the whole stock can be split up into fishing mortality for each fleet :

$$F_i = \frac{C_i}{C} \cdot F$$

So, equation (3) can be used for each fleet :

$$F_{i,2,t} = \frac{S_{1,t} \cdot f_{i,2,t}}{S_{2,t} \cdot f_{i,1,t}} \cdot F_{i,1,t}$$

with $F_{i,j,t}$ the fishing mortality exerted by fleet i in zone j (on the local stock $N_{j,t}$) at time t .

And equations (3) is changed in a n equations systems (6) :

$$(6) \quad \begin{cases} F_{1,2,t} = \frac{S_{1,t} \cdot f_{1,2,t}}{S_{2,t} \cdot f_{1,1,t}} \cdot F_{1,1,t} \\ \vdots \\ F_{i,2,t} = \frac{S_{1,t} \cdot f_{i,2,t}}{S_{2,t} \cdot f_{i,1,t}} \cdot F_{i,1,t} \\ \vdots \\ F_{n,2,t} = \frac{S_{1,t} \cdot f_{n,2,t}}{S_{2,t} \cdot f_{n,1,t}} \cdot F_{n,1,t} \end{cases}$$

then,

$$(7) \quad F_{2,t} = \sum_i F_{2,i,t} = \sum_i \frac{S_{1,t} \cdot f_{2,i,t}}{S_{2,t} \cdot f_{1,i,t}} \cdot F_{1,i,t} = \sum_i \left(\frac{S_{1,t} \cdot f_{2,i,t}}{S_{2,t} \cdot f_{1,i,t}} \cdot \frac{C_{1,i,t}}{C_{1,t}} \right) \cdot F_{1,t}$$

Equation (4) and (7) are fully determined and can be numerically solved.

1.3. Application to Atlantic yellowfin tuna

To illustrate the method, it is applied to yellowfin tuna of Atlantic considering the eastern and western fractions of the stock. At the time of the present work the most

recent fisheries statistics was not reliable and the present run must be considered as a first one, which purpose is just to check the method. More analysis are actually performed and will be further presented.

ICCAT catches and effort data are used. Age decomposition is performed by month for the for first age groups (0-1-2-3) using the age-length adjustment method developed by Gascuel (1994) with a two stage growth model (Gascuel *et al.*, 1992). Because the yellowfin mean size at age is close for older age groups, slicing is used to distinguish the two last age groups (4-5+) with ICCAT limit. Catches and effort data are averaged on the period 198***-199 for the eastern fleet and 198-199 for the western fleet. A backward VPA is then runned with a quarterly time step as it is usually performed by ICCAT working groups.

The spatial VPA methodology also needs an estimation of stock surface in each zone as an auxiliary information (equation (3)). Stock surface is a theoretical concept as far as a stock has no clear delimited geographic frontiers. To avoid variations with total abundance, it can be defined as the surface of a given fraction of the stock (Swain and Sinclair, 1993) but it is most of the time considered as the area of the stock where density is higher than a given threshold (Swain and Wade, 1992, Marshall and Frank, 1994). In the present study, long line catches were used to estimate yellowfin stock surface in both east and west ICCAT zones. Catches were cumulated by month and 5°x5° square over the whole 1956-1993 period. The total catches were spatially interpolated to produce a continuous map and two catches level (150 and 300 tons by 5°.month) were arbitrarily defined as the stock limit. Such levels were used to calculate yellowfin stock surface in each side of the Atlantic ocean (fig. 1). This method was used because the surface of a 5°x5° square varies with latitude and then the number of 5°x5° square can't be used. All calculations were computed with a GIS (savane software ©orstom, 1995).

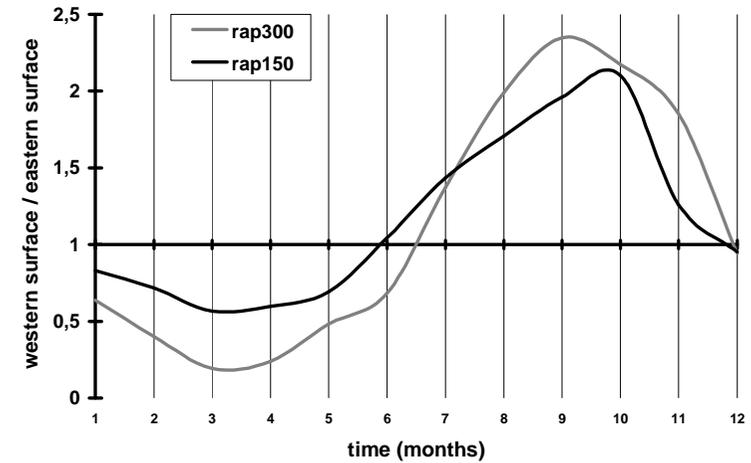
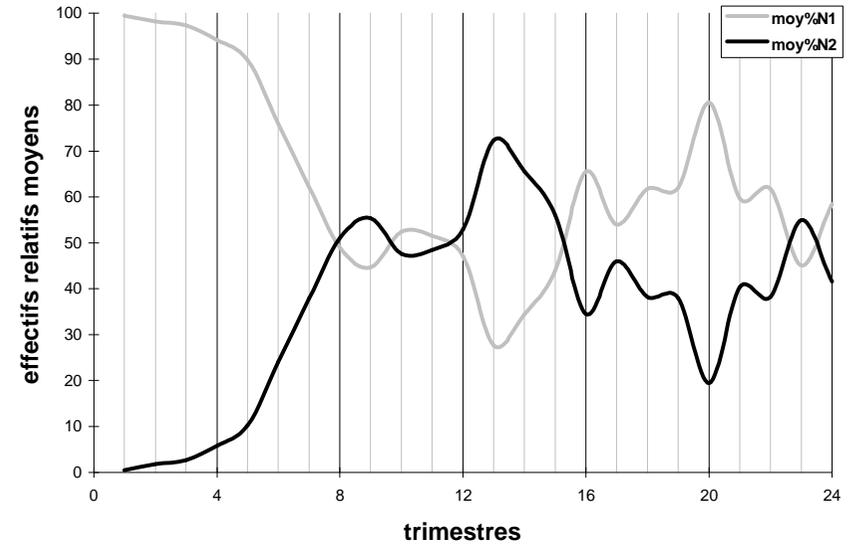
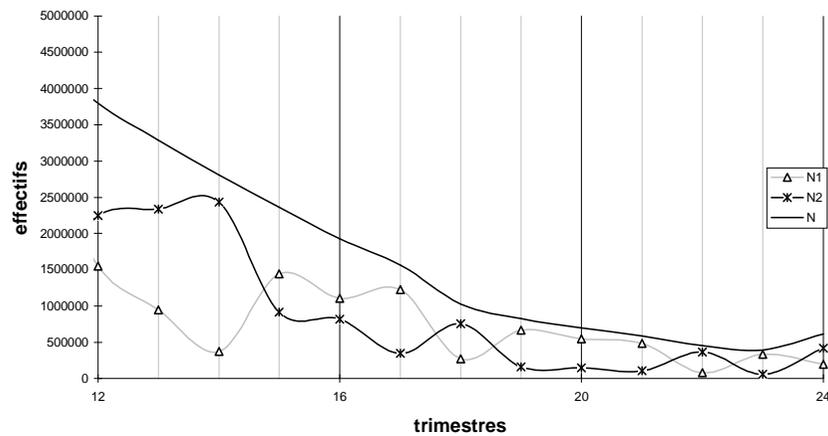
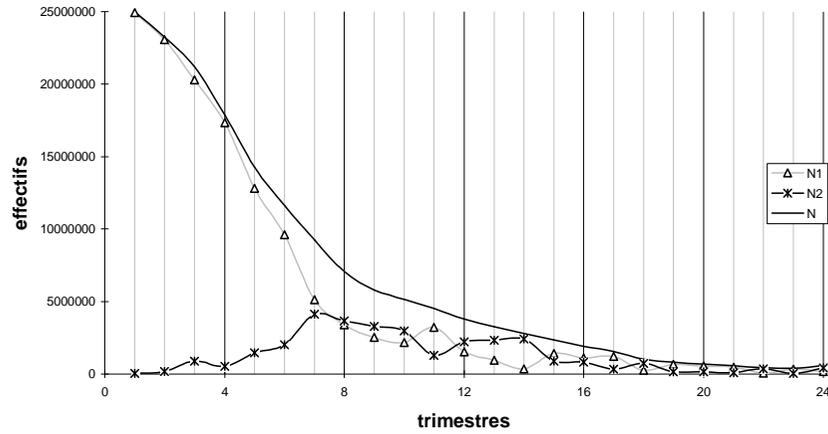


fig 1. Surfaces ratio for both threshold levels.

2. RESULTS

2.1. Global and local fishing mortalities

2.2. Fish numbers in each zone and migration rates



3. DISCUSSION AND CONCLUSION

*** A monthly basis is certainly more accurate for the VPA performed at the global stock level (Fonteneau, 1994b) and a short time step is necessary for the spatial VPA because of the important time variability of migration phenomena.***

Spatial VPA results emphasize the hypothesis of massive migrations across the Atlantic ocean. Mark recapture data (Bard) and length frequency analyses (Fonteneau) already suggested such an hypothesis. Foucher (199) give a first rough approximation of exchange rates but the method he uses is only based on purse seiners catches and doesn't take into account stock surface. Our results suggest that yellowfin recruitment is on average not equally distributed between east and west atlantic. % of the recruitment comes from in eastern zone, very likely from the main reproduction area of the gulf of Guinea (Fonteneau, 1993) and probably from accessory breeding areas such as Cape Verde islands (Santa Rita Vieira, 199). % of the recruitment could come from western zones,

The relationship between commercial vessels CPUE and stock abundance is generally not a simple linear function. Many well known phenomena lead to a non linear relationship between CPUE and fish abundance. They are generally attributed

to the resource spatial heterogeneity and to the fishermen search behaviour (Clark *et al.*, 1979 ; Hilborn and Walters, 1987 ; Hilborn and Walters, 1992 ; Gauthiez, 1997). The consequences of such phenomena on the spatial heterogeneity of catchability at age q_t (and more precisely on the variability of the catchability by surface unit q'_t at a given time t between different given zones) are less studied.

The catchability q'_t generally varies with stock abundance (its variations are density-dependant) and with fishermen behaviour (Hilborn and Walters, 1992 ; Gauthiez, 1997). Because fish density is spatially heterogeneous, catchability $q'_{z,t}$ also varies in space. These aspects are not detailed here, but it is important to keep in mind the potential consequences of violation of the spatial catchability $q'_{z,t}$ homogeneity hypothesis.

Nevertheless, simulations show that in many cases the spatial VPA method is reliable (Maury *et al.*, 1997 a and b). It seems to be biased when simultaneously fishing effort is highly deterministic and fish density is highly heterogeneous and density dependent. Different statistical tools such as mean/variance relationship (Gauthiez, 1997) or geostatistical selectivity curves (Petitgas, 1994) may allow to identify such « dangerous » cases. In those cases, the use of different stock surface estimates allows to bound spatial VPA outputs between a high and a low value (Maury *et al.* 1997 a and b).

CONCLUSION

The method and its underlying hypothesis are tested for two zones on several data sets simulated with the advection-diffusion based simulator SHADYS (Simulateur HALieutique de DYnamiques Spatiales) (Maury and Gascuel, 1997).

The proposed method enables to estimate local parameters which are usually estimated at the global stock level (fish numbers and fishing mortality coefficients).

Le découpage n'est pas biologiquement pertinent, il ne l'est que pr estimer des taux d'interaction entre pêcheries est et ouest , le schema de migration non plus. Il faut changer de modele

RÉFÉRENCES

- Beverton R. J. H., S. J. Holt 1957. On the dynamic of exploited fish populations. Fishery Invest., Lond., ser. 2, **19**:553 p.
- Bard F.X., A. Hervé 1994 Structure de stock de l'albacore (*Thunnus albacares*) atlantique d'après les marquages comparés aux lieu de ponte. Groupe de Travail

ICCAT sur l'évaluation de l'Albacore de l'Atlantique. *Rec. Doc. Sci. ICCAT*, **XLII** (2), SCRS/93/41, 204-208.

Brethes J.-C. 1996. The canadian atlantic groundfish experience and the constraints to the conservation of fisheries resources: a perspective. *Oc. coast. manag.* sous presse.

Clark C. W., M. Mangel 1979. Aggregation and fishery dynamics : a theoretical study of schooling and the purse seine tuna fisheries. *Fish. Bull.*, **77**, no. 2.

Cury P., O. Anneville 1997. Fisheries as diminishing assets : Marine diversity threatened by anecdotes. *in* La surexploitation. Third symposia of the Association Française d'Halieumétrie. Montpellier, 1-3 juillet 1997.

Deriso R. B., R. G. Punsly, W. H. Bayliff 1991. A markov movement model of yellowfin tuna in the eastern Pacific ocean and some analyses for international management. *Fish. Res.*, **11**: 375-395.

Fonteneau A. 1994a. Structure de la population d'albacore de l'Atlantique : quelques considérations sur les migration et la modélisation. Groupe de Travail ICCAT sur l'évaluation de l'Albacore de l'Atlantique. *Rec. Doc. Sci. ICCAT*, **XLII** (2), SCRS/93/43, 215-218.

Fonteneau A. 1994b. Time units to be used in yellowfin VPAs. Groupe de Travail ICCAT sur l'évaluation de l'Albacore de l'Atlantique. *Rec. Doc. Sci. ICCAT*, **XLII** (2), SCRS/93/42, 215-218.

Fonteneau A., D. Gascuel, P. Pallares Soubrier 1997. Vingt cinq ans d'évaluation des ressources thonières dans l'Atlantique : quelques réflexions méthodologiques. *in* : Ouvrage du Symposium ICCAT, Les Açores, Juin 1996. In press.

Foucher E. 1995. Dynamique saisonnière et spatiale de la ressource dans les pêcheries thonières de l'Atlantique Tropical Est. Thèse de doctorat, ENSA-Rennes, ORSTOM éd., TDM **131**, 127 p. + annexes.

Foucher E., A. Fonteneau, D. Gascuel, T. Diouf 1996. Quantification des migrations d'albacore (*Thunnus albacares*) entre les façades est et ouest de l'Atlantique tropical. Ouvrage du Symposium ICCAT, Les Açores, Juin 1996. In press.

Gascuel D. 1994. Une méthode simple d'ajustement des clés taille/âge : application aux captures d'albacores (*Thunnus albacares*) de l'Atlantique Est. *Can. J. Fish. Aquat. Sci.*, **51** : 723-733.

- Gascuel D., A. Fonteneau, C. Capisano 1992. Modélisation d'une croissance en deux stances chez l'albacore (*Thunnus albacares*) de l'Atlantique Est. *Aquat. Liv. Res.* **5** : 155-172.
- Gauthiez F. 1997. Structuration spatiale des populations de poissons marins demersaux. Caractérisation, conséquences biométriques et halieutiques. Thèse de doctorat. ENGREF.
- Hilborn R., C. J. Walters 1987. A general model for simulation of stock and fleet dynamics in spatially heterogeneous fisheries. *Can. J. Fish. Aquat. Sci.*, **44**.
- Hilborn R., C. J. Walters 1992. Quantitative fisheries stock assessment. Choice, dynamics and uncertainty. Chapman and Hall, 570p.
- Kleiber P., A. Fonteneau, 1994. Assessment of skipjack fishery interaction in the eastern tropical atlantic using tagging data. Proceedings of the first FAO expert consultation on interactions of Pacific ocean tuna fisheries. Vol. 1. R. S. Shomura, J. Majkowski and S. Langi (eds) *FAO fisheries technical paper* **336/1** 326p.
- Laurec A., J. C. Le Guen 1981. Dynamique des populations marines exploitées. Publi. CNEXO., rapp. scient. tech. 45.
- Marshall and Frank, 1994
- Maury O., D. Gascuel 1997. Short term yield and effort impacts of a precautionary management strategy based on marine refugia. Simulations with SHADYS (Simulateur HALieutique de DYNAMIQUES Spatiales). ICES Annual Science Meeting. CM 1997/V:08, 8 p.
- Maury O., D. Gascuel, D. Pelletier 1997. Estimating fish numbers, fishing mortality and migration rates between different spatial zones : the VPA methodology. ICES Annual Science Meeting. CM 1997/DD:09, 7 P.
- Mac Call A. D. 1990. Dynamic geography of marine fish populations. Univ. of Washington Press, 153p.
- Okubo A. 1980. Diffusion and ecological problems : mathematical models. Biomathematics Vol.10. Springer-Verlag. 254p.
- Paloheimo J. E., L. M. Dickie 1964. Abundance and fishing success. Rapp. P. V. Reun. CIEM 155: 152-163.
- Petitgas P. 1994. Spatial strategies of fish populations. ICES Annual Science Meeting. Statistics committee. C.M. 1994/D:14.
- Punt A. E., D. S. Butterworth 1994. Use of tagging data in a VPA formalism to estimate migration rates of bluefin tuna across the north atlantic. ICCAT working document SCRS/94/72.
- Porch C. E. 1996. A theoretical comparison of the contributions of random swimming and turbulence to absolute dispersal in the sea. *Fish. Bull.* sous presse.
- Press W. H., S. A. Teukolsky, W. T. Vetterling, B. P. Flannery 1994. Numerical recipes in C. The art of scientific computing. Second edition. Cambridge University Press. 994p.
- Sibert J.R., D.A. Fournier 1994 Evaluation of advection-diffusion equations for estimation of movement patterns from tag recapture data. *FAO Tech. paper*, **336**, 108-121.
- Swain and Sinclair, 1993
- Swain and Wade, 1992