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Predicting skipjack tuna forage distributions in the equatorial Pacific using a coupled dynamical bio-geochemical model

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ABSTRACT

Skipjack tuna (*Katsuwonus pelamis*) contributes ≈70% of the total tuna catch in the Pacific Ocean. This species occurs in the upper mixed-layer throughout the equatorial region, but the largest catches are taken from the warmpool in the western equatorial Pacific. Analysis of catch and effort data for US purse seine fisheries in the western Pacific has demonstrated that one of the most successful fishing grounds is located in the vicinity of a convergence zone between the warm (>28–29°C) low-salinity water of the warmpool and the cold saline water of equatorial upwelling in the central Pacific (Lehodey *et al.*, 1997). This zone of convergence, identified by a well-marked salinity front and approximated by the 28.5°C isotherm, oscillates zonally over several thousands of km in correlation with the El Niño–Southern Oscillation. The present study focuses on the prediction of skipjack tuna forage that is expected to be a major factor in explaining the basin-scale distribution of the stock. It could also explain the close relation between displacements of skipjack tuna and the convergence zone on the eastern edge of the warmpool. A simple bio-geochemical model was coupled with a general circulation model, allowing reasonable predictions of new primary production in the equatorial Pacific from mid-1992 to mid-1995. The biological transfer of this production

toward tuna forage was simply parameterized according to the food chain length and redistributed by the currents using the circulation model. Tuna forage accumulated in the convergence zone of the horizontal currents, which corresponds to the warmpool/equatorial upwelling boundary. Predicted forage maxima corresponded well with high catch rates.

INTRODUCTION

Since 1991, the annual catch of tuna and tuna-like species in the Pacific Ocean has approached 70% of the global catch of these species (Shomura *et al.*, 1994). Skipjack tuna (*Katsuwonus pelamis*) is the most important species in terms of catch weight and more than 90% of the Pacific skipjack tuna catch is taken west of 150°W longitude within the so-called 'warmpool' (Lehodey *et al.*, 1997). Despite large catches (almost 1 million tonnes, SPC, 1995), skipjack tuna exploitation rates are estimated to be low to moderate (Kleiber *et al.*, 1987), and the western Pacific stock is believed to be capable of sustaining even higher catches. This high productivity is sustained by a high growth rate (Wild and Hampton, 1994), rapid turnover (Kleiber *et al.*, 1987) and early onset of reproductive maturity (≈1 year, ≈45 cm fork length). Such a rapid development demands very high energetic requirements. Several studies (e.g. Kitchell *et al.*, 1978) suggest that skipjack tuna consume 10–15% of their body weight each day. Thus, being opportunistic feeders, skipjack tuna would be expected to be concentrated in areas where suitable food is abundant. As direct observations of zooplankton and micronekton distributions at the scale of the region are not available, it is worth attempting to test this hypothesis through a modelling approach. Skipjack tuna are known to consume epipelagic prey items ranging from larger zooplankton, such as euphausiids, amphipods and other small crustaceans, to baitfish, such as the oceanic anchovy *Stolephorus buccanneeri* (Hida, 1973, later called *Encrasicholina punctifer*). Ideally the simulation of skipjack tuna forage would integrate the

dynamics of all the different trophic levels from the primary producers to these prey species. Such explicit modelling of the trophic chain, and moreover at the scale of a whole basin, is a long and difficult task (Ekman, 1994). Considerable progress has nevertheless been made during the last decade in the modelling of ocean physics and of the bio-geochemical aspects of marine ecosystem dynamics (Sarmiento et al., 1993). The present study is an attempt to take advantage of this progress for modelling the relationships between tuna and their environment. In a simple and practical way, we try to predict skipjack tuna forage (F) spatial distributions using the current and primary production fields simulated by a coupled 3D-dynamical/bio-geochemical 'JGOFS' model (Stoens et al., 1998 this Vol.). The predicted F will be used as an input in a spatial population dynamics model based on habitat (Bertignac et al., 1998, this volume). Within the simulation, we were also interested in assessing the influence of oceanic circulation in aggregating forage in the convergence zone on the eastern edge of the warmpool, the location of which is related to the El Niño–Southern Oscillation (ENSO) conditions and correlated to high abundance of skipjack tuna (Lehodey et al., 1997).

MATERIALS AND METHODS

Fishing Data

Skipjack tuna catch and fishing effort data from the western and central Pacific Ocean (west of 150°W) were available from the Secretariat of the Pacific Community databases (SPC, 1997). Commercial fisheries data currently represent the only means of estimating tuna distribution on a large scale. In particular, catch rates (CPUE) are assumed to provide a better index of stock abundance than the catch. For the present study, and for the reasons discussed in Lehodey et al. (1997), only the CPUE (metric tonnes per fishing day on a 1 week time resolution) of the US purse seiners ($\approx$25% of the annual purse seine skipjack tuna catch in the region) were used.

General circulation model

A general circulation model (OGCM) called 'OPA' and developed by the LODYC (Laboratoire d'Océanographie Dynamique et de Climatologie), was used to predict the water dynamics in the tropical Pacific. A high-resolution version of OPA (1/3°longitude × 1/3°latitude, 16 levels in the upper 150 m; Blanke and Delecluse, 1993) was forced at the surface with the 5 day winds deduced from the ERS 1 scatterometer (Grima et al., in press) and with water and heat fluxes based on these winds, on Reynolds' SST (Reynolds and Smith, 1994), and on ouput-fields of the atmospheric model Arpège-Climat (Dequé et al., 1994). This forcing allowed a 3 year simulation during a period (April 1992 to June 1995) of marked interannual variations in the equatorial Pacific.

Bio-geochemical model

The OGCM was coupled to a bio-geochemical model to predict primary production (Stoens et al., this Vol.). In this model, new production (P) is simply approached as nitrate consumption modulated at each depth by chlorophyll content and by available light. The NO_3 consumption obeys Michaelis–Mentens kinetics, and is controlled by the NO_3 level and two parameters – the maximum absorption rate of NO_3 and the half-saturation constant for its assimilation – which were assigned their best values by fitting with *in situ* ^{15}N-production data obtained during the JGOFS cruises in the area. Chlorophyll is predicted at the surface from the NO_3 concentration using an empirical relationship based on an *in situ* data regression and its vertical profiles are deduced from the surface value (using also a statistical relation). Nitrogen balance is ensured in the model by assuming that the equivalent of the new production within the whole euphotic layer is instantaneously remineralized below the euphotic layer. In spite of its simplicity, this model provided very reasonable P estimates, as validated against *in situ* measurements (further details: Stoens et al., 1998, this volume).

Modelling the distribution of skipjack tuna food
Skipjack tuna forage (F)

The model developed in the present study to predict the distribution of skipjack tuna potential food items in the tropical Pacific makes the following assumptions: (1) skipjack tuna forage originates from the trophic conversion of primary production to secondary production and more precisely from the nitrate-based new production within the euphotic zone (Iverson, 1990); (2) during the period of trophic conversion, redistribution of primary/secondary production occurs under the influence of surface currents (as predicted by the OPA OGCM); and (3) a nominal diffusive process reproduces both the diffusion of the water masses and a diffusion pattern attributed to the random movements of the organisms. It is clear from these assumptions that we are seeking a general, Pacific-wide representation of F distribution. In particular, we do not take into account swarming (zooplankton) or schooling (anchovy) behaviour.

The variation in time of F can be expressed as:

$$\frac{dF}{dT} = \text{Transport} - \text{Loss} + \text{Source} \quad (1)$$

In the present study, transport in the two dimensions x and y is described by the diffusion–advection equation, with σ, the diffusion coefficient and u, v the zonal and meridional components of the current in the euphotic layer. The loss term depends on the loss coefficient λ and the source term is the biomass recruited in the forage production after a characteristic time T_r. During this period T_r, P (in the euphotic zone) is redistributed according to the same model transport used for F, and with a loss coefficient m_r. This is described under a mathematical form by equations 2 and 3:

$$\frac{\partial F}{\partial t} = \sigma\left(\frac{\partial^2 F}{\partial x^2} + \frac{\partial^2 F}{\partial y^2}\right) - \frac{\partial}{\partial x}(uF) - \frac{\partial}{\partial y}(vF) - (\lambda F) + S \quad (2)$$

$$\frac{\partial S}{\partial t} = \sigma\left(\frac{\partial^2 S}{\partial x^2} + \frac{\partial^2 S}{\partial y^2}\right) - \frac{\partial}{\partial x}(uS) - \frac{\partial}{\partial y}(vS) - (m_r S) \quad (3)$$

Selecting the parameter values
A value of 10 000 m^2 s^{-1}, assumed constant in time and space, was selected for the diffusion coefficient σ. The value attributed to the diffusion of water itself is estimated from drifting buoys to be on the order of 6000 m^2 s^{-1} (Flament *et al.*, 1996a). In order to assign reasonable values to the biological parameters, equation 2 for F was first integrated over a year assuming no x,y-dependent processes, so that F depends only on the source and loss terms:

$$\frac{dF}{dt} = S - (\lambda F) \quad (4)$$

with:

$$S = P \, exp(-m_r T_r) \quad (5)$$

Assuming that P is constant in time over the year and that $F_0 = 0$ at $t = 0$, the solution of equation 4 is:

$$F(t) - \frac{S}{\lambda}(1 - exp(-\lambda t)) \quad (6)$$

For a life cycle of tuna forage assumed to be achieved within 1 year, a value of 4.6 year^{-1} was given to λ (i.e. approximated by $e^{-\lambda t} = 0.01$). Using equations 5 and 6, the annual skipjack tuna forage production (F_{yr}) is therefore given by:

$$F_{yr} = 1/\lambda P_{yr}e^{(-m_r T_r)} \quad (7)$$

where P_{yr} is the annual new N production. According to Iverson (1990), the annual production of pelagic fish at trophic level n can be estimated as $P_{yr}E^n$, where E is an energy transfer coefficient estimated to 2.8. On the basis of results from different studies (Roger and Grandperrin, 1976; Pauly and Christensen, 1995), a value of $n = 2.5$ would be representative of the tuna forage in the Pacific. Therefore,

$$F_{yr} = 0.04 \, P_{yr} \quad (8a)$$

and

$$1/\lambda P_{yr}exp(-m_r T_r) = 0.04 \, P_{yr}. \quad (8b)$$

Thus m_r is given by:

$$m_r = \ln(\lambda * 0.04)/T_r \quad (9)$$

A nominal value of 90 days was chosen for the characteristic time of recruitment in F, T_r. Such a value is representative of the minimum age for organisms upon which skipjack tuna can feed.

Numerical resolution
The transport of F and S is based on the advection–diffusion equation (Okubo, 1980). The differential equations are numerically solved by finite-difference techniques using a network of regularly spaced grid points, as in Sibert and Fournier (1994). Equation 2 is applied over a time step of 5 days and a spatial resolution of one degree square. The predicted P (mMolN m^{-2} day^{-1}) was integrated within the euphotic zone and the predicted currents (m s^{-1}) averaged on the same layer. Euphotic depths are typically 80–90 m in the (oligotrophic) warmpool in the western part of the basin and 50–60 m in the relatively richer waters of the equatorial upwelling. In practice, the model was run over 6 years (twice the 3 year period) before predictions were recorded for analysis.

RESULTS

An example of the spatial distribution of P as predicted by the OPA-bio-geochemical coupled model is shown in Fig. 1. The major feature on this figure is the enrichment in the area of the equatorial upwelling contrasting with the low production levels in the subtropical gyres and within the western Pacific warmpool, as delineated on Fig. 1 by the 28.5°C isotherm (further details: Stoens *et al.*, 1998, this

Figure 1. Spatial distribution of new primary production (P) simulated by the coupled OPA-bio-geochemical model for the month of June 1994 in the equatorial Pacific Ocean. The delineation of the warmpool is approximated by the (simulated) 28.5°C isotherm and the contours of US purse seiners' CPUE > 10 t day^{-1} are superimposed.


New Primary Production (P)

$(mMol\ N\ m^{-2}\ d^{-1})$
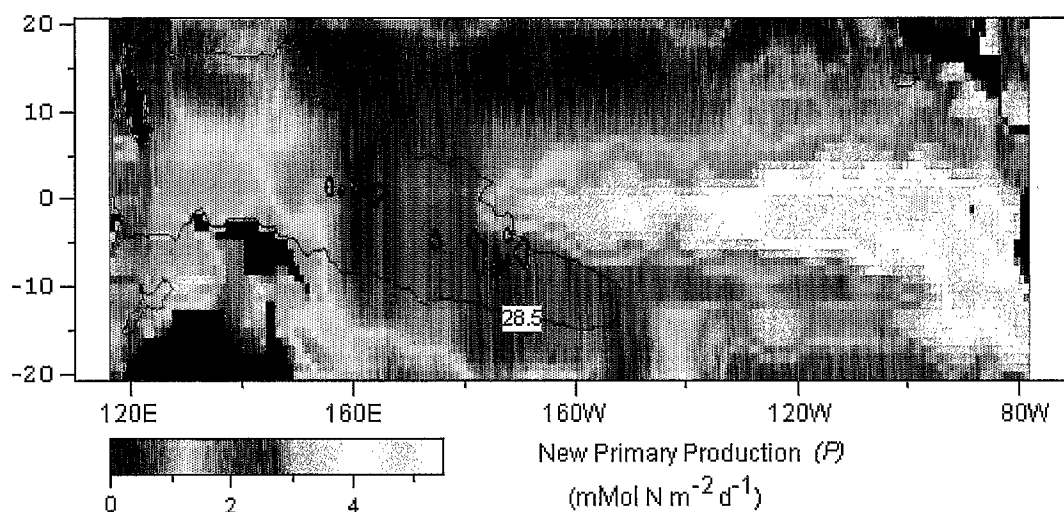
volume). Overlaying skipjack tuna CPUE on the spatial distribution of P for the same month indicates that skipjack tuna abundance would be highest within the oligotrophic warmpool, particularly in a small area at the eastern edge of the warmpool. This pattern appears to be constant in time, as shown in Fig. 2, which gives the temporal evolution within the 5°N–5°S latitudinal band of CPUE and physical parameters simulated by the model OPA. High skipjack tuna catch rates (Fig. 2a) remain confined to the warmpool, which is delimited by a well-marked salinity front (Fig. 2b) and the 28.5°C isotherm (Fig. 2d). Moreover, the displacement of the area of skipjack tuna abundance is correlated with the displacement of the eastern edge of the warmpool (Fig. 2a), as already demonstrated from observed surface temperature (SST) (Lehodey et al., 1997). This displacement is well marked by SST and salinity (SSS) predicted by the OPA model (Fig. 2b,c) and is closely related to ENSO (Picaut et al., 1996). In fact, the front highlighted by SST and SSS corresponds to a convergence of currents as shown on Fig. 2(c), which gives the simulated zonal velocity in the surface (euphotic) layer.

Figure 3(a) shows that P directly responds to the physics. In particular, the physical front between the equatorial upwelling and the warmpool also corresponds to a well-marked gradient in primary production (Stoens et al., 1998, this volume). Figure 3(b) presents the distribution of the modelled skipjack tuna forage F, predicted on the basis of currents and P. A major feature on this figure is the westward extension of the front in the tuna forage distribution compared

with the P front. This spatial uncoupling occurs because the trophic transfer from the primary producers (most active within the equatorial upwelling) into the forage compartment proceeds as the water is advected westward by the equatorial currents (Fig. 2c). Figure 3(c) presents the enrichment in tuna forage relative to the primary production level. The inner edge of the warmpool where currents converge appears to be the zone of maximum relative enrichment. Overlaying skipjack tuna CPUE on this figure shows fairly good agreement with the maximum relative enrichment in forage, and both of them move in phase zonally. However, a shift in time appears between the two series during the El Niño phase in the second half of 1994. This time lag was already apparent between the distribution of CPUE and the physical delimitation of the eastern edge of the warmpool by surface salinity and temperature (Fig. 2b, 2d). On the other hand, the displacement of skipjack tuna abundance (as indicated by CPUE) appears in phase with the eastward advection, which is particularly marked during this period in the surface layer of the warmpool (Fig. 2c). Clearly, this feature requires further detailed investigation.

Figure 4 compares the skipjack tuna forage distribution with the distribution of P (Fig. 1). The westward extension of the F front compared with the P front (Fig. 1) is a striking feature. In the eastern Pacific, zones with high primary production conserve high levels of secondary production. On the other hand, the equatorial divergence results in a low F contrasting with high P along the equator. Another

Figure 2. Time–longitude plots of aggregated data for the latitudinal band 5°N–5°S for the period April 1992 – June 1995. (a) Weekly mean CPUE of the US purse seine fleet in the western Pacific. The longitudinal gravity centre ± 1 SD calculated according to Lehodey et al. (1997) is represented with the Southern Oscillation Index (SOI). (b) Sea surface salinity simulated by the OPA general circulation model showing a well-marked front between the warmpool and the central equatorial upwelling. (c) East–west component (U) of the current in the surface (euphotic) layer simulated by the OPA general circulation model showing the convergence zone of currents. Positive values are eastward currents, negative values are westward currents. (d) Sea surface temperature simulated by the OPA general circulation model showing the delineation of the warmpool approximated by the 28.5°C isotherm. Contours of CPUE > 10 t day^{-1} are superimposed on (b), (c) and (d).
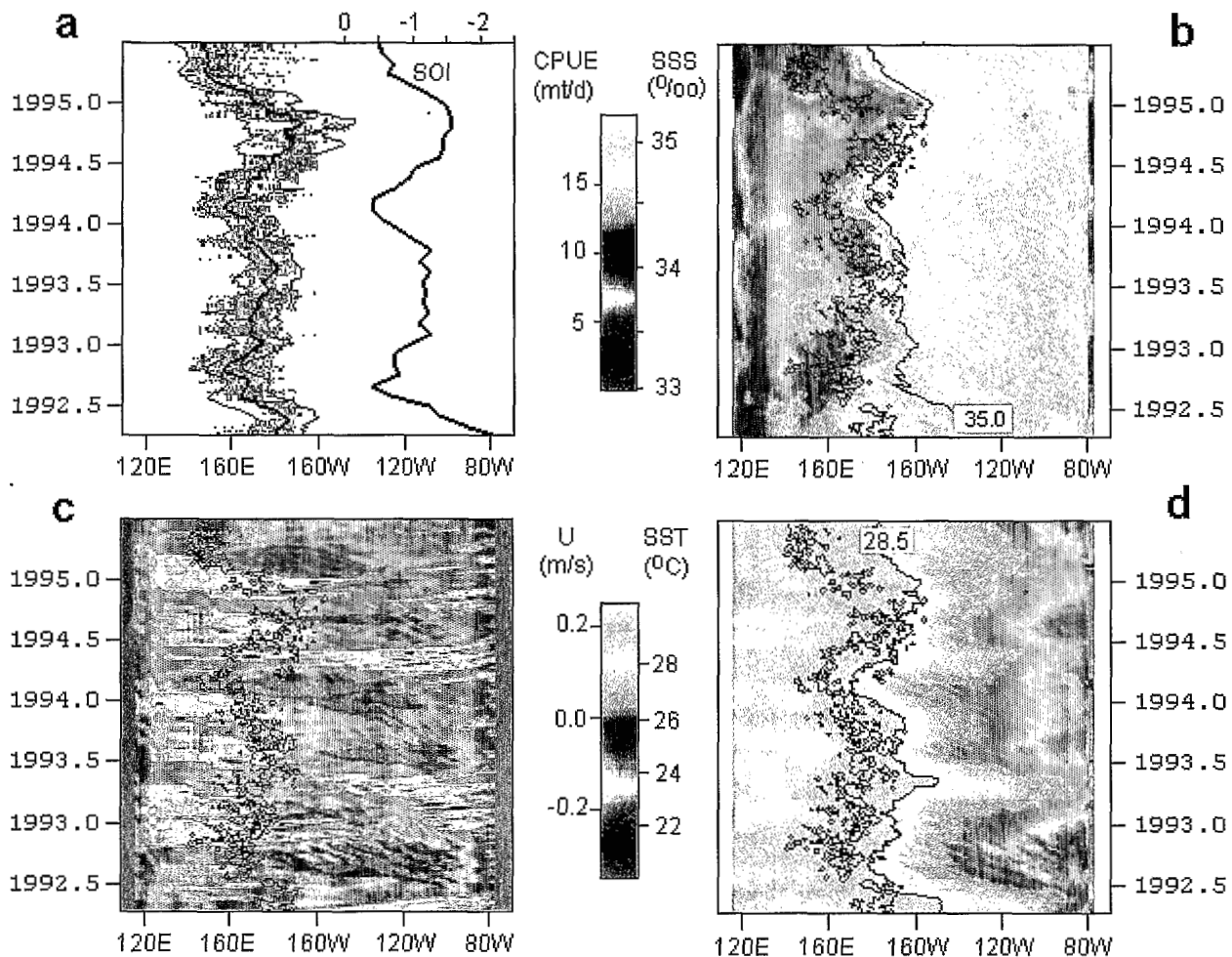
major feature produced by the divergence is the accumulation of high levels of F on both sides of the equator. Though this result is highly consistent with the observations of distribution of plankton biomass in the equatorial region (Fig. 5), the concentration of F along the southern side of the central equatorial upwelling is likely to be overestimated. This overestimation could be due to the bio-geochemical model (Stoens et al., 1998, this volume) and also because the skipjack tuna forage model does not take into account the vertical dimension. This can lead to an unrealistic accumulation of forage in certain regions where downwelling transport is important. Whereas the relation between P and skipjack tuna CPUE is poor (Fig. 1), the distribution of the simulated F (Fig. 4) is much more in agreement with the location of high skipjack tuna CPUE in the warmpool. It is worth noting that high levels of CPUE occur in an area combining both high forage levels and high temperature.

Figure 3. Time–longitude plots of aggregated data for the latitudinal band 5°N–5°S for the period April 1992 – June 1995. (a) New primary production expressed over 5 days (mMol N m^{-2} per 5 days). (b) Skipjack tuna forage (mMol N m^{-2}). (c) Enrichment in tuna forage relative to the new primary production level. Contours of CPUE > 10 t day^{-1} are superimposed.
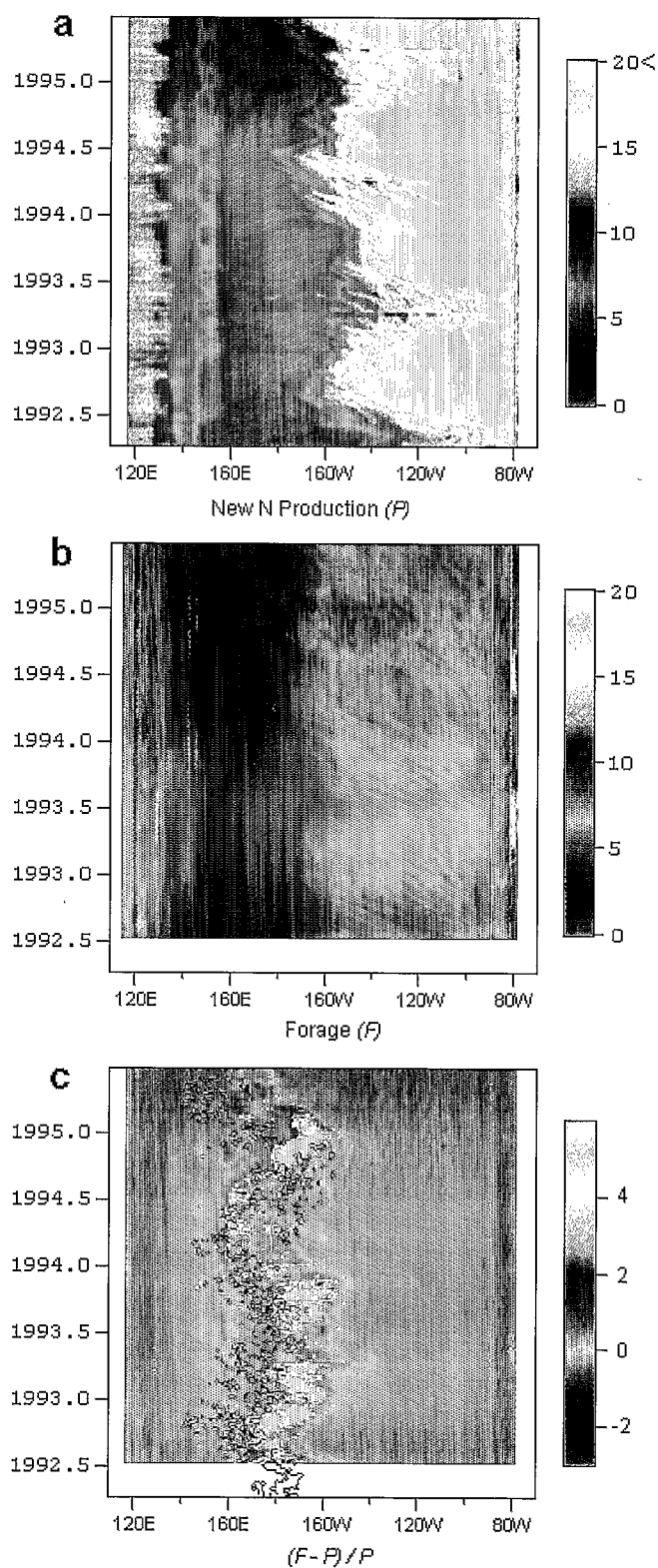
DISCUSSION

In the present study, the skipjack tuna forage was modelled in a simple way, although the trophic pathways that link the primary producers to high-rank predators are likely to be complex and variable. The advantage of a modelling scheme that relies on a few parameters (i.e. four), is that the sensitivity of the results is easily analysed. In addition to its simplicity, the forage adequately integrates various organisms at various trophic levels, in a fair representation of the large spectrum of prey items observed in the tuna diet. In this respect, the characteristic recruitment time T_r is a central parameter as its value will determine the constitution of the forage 'population'. The forage is composed of organisms accumulated through time according to a decreasing exponential function; therefore, a low value of T_r will produce forage that is predominantly composed of organisms such as zooplankton that developed shortly after P becomes available. Conversely, a high value will emphasize the importance of organisms of upper trophic levels. These effects were tested and the results (not shown) indicated that the spatial distribution produced with $T_r < 30$ days resembles the zooplankton distribution in the equatorial system, and showed also that the predicted forage became poorly sensitive to the T_r values when T_r was >90 days. Variation of the diffusion coefficient in the range of 2000–20 000 m^2 s^{-1} appears to have a low influence on the general features of the model output, at least in the region under investigation (20°N–20°S). Of course a constant diffusion is likely a simplistic approach, particularly in regions of high shear near the equator which could produce local transient gradients in forage density. The sensitivity of the predicted F distributions to the selected value of λ was also tested. This parameter has a significant impact on the F-value at a given point but a rather minor impact on the spatial features of the distributions. In the western Pacific, skipjack tuna forage consists mainly of the zooplanktivorous oceanic anchovy (Hida, 1973; Hampton and Bailey, 1993). This species, as well as other stolephorid anchovies, has a short life cycle of less than 1 year, grows rapidly and attains maturity in 3–4 months (Dalzell, 1993). These life history characteristics indicate that the mean values given to the biological parameters T_r (90 days) and λ (life cycle $\approx$ 1 year) are realistic.

Although the restriction of our analysis to US purse seine data reduces considerably the possible sources of variability in the CPUE, the question of high capturability in the convergence zone owing to specific environmental conditions could be posed. Indeed, conditions for successful purse seining in the western and central Pacific appear much less favourable than in the eastern Pacific. There is in effect no easily remarkable association with marine mammals, and both a relatively deep thermocline and very clear water allow tuna to avoid the encircling net by diving beneath the seine. In these conditions, the CPUE is expected to be well representative of the actual abundance of the skipjack population. However, a bias could be introduced in the abundance index by an increased vulnerability of surface tuna to purse seine

Figure 4. Spatial distribution of the simulated skipjack tuna forage production (F) for June 1994 in the equatorial Pacific Ocean. The delineation of the warmpool is approximated by the (simulated) 28.5°C isotherm and the contours of US purse seiners' CPUE > 10 t day^{-1} are superimposed.
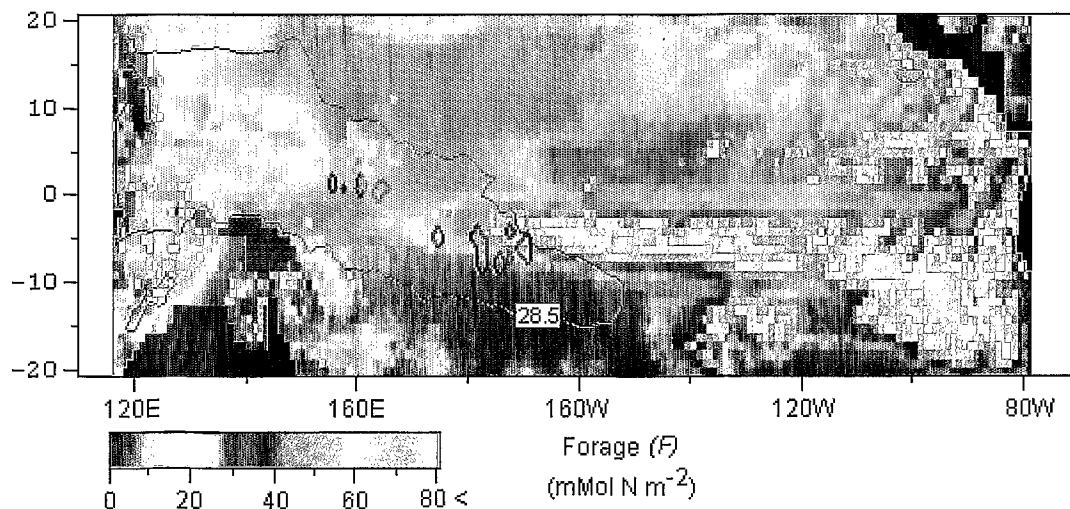
Figure 5.   Distribution of plankton biomass (ml m^{-3}) in the 0–100 m layer in the equatorial region of the Pacific (reprinted from Vinogradov, 1981, by permission of the publisher Academic Press).
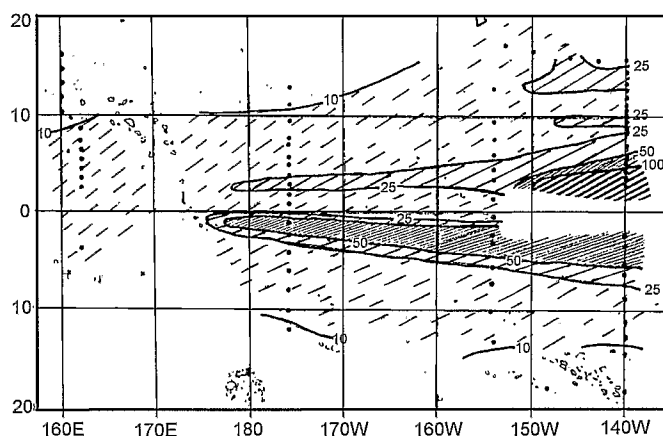
gear due to their feeding behaviour. As a matter of fact, fishermen take advantage of the distraction of fish, when they are feeding on large surface concentrations of forage, which allows the setting and pursing of a purse seine.

Large tuna fisheries (and presumably high tuna abundance) may occur close to highly productive upwelling zones (e.g. in the eastern Pacific Ocean) as well as in oligotrophic tropical waters (e.g. in the western Pacific Ocean). It is clear that primary production *per se* does not aggregate tuna, rather it is the 'downstream' development of secondary production that provides attractive habitat for skipjack tuna and other tunas. For that reason, tuna aggregations are often found close to convergence zones and fronts (Laurs *et al.*, 1984) which are important aggregating mechanisms of plankton and micronekton (Flament *et al.*, 1996b; Power, 1996). However, it has proved difficult to formally test this relationship with data, because basin-scale distributions of zooplankton and micronekton cannot be monitored at appropriate spatial and temporal scales using classical observation methods. The modelling approach may be the only practical way to describe such distributions in the foreseeable future.

Most of the work on the spatio-temporal changes in plankton communities in the equatorial Pacific was carried out by Vinogradov (1981), and the observed features were modelled by Vinogradov *et al.* (1972). Their model, however, included only a rudimentary treatment of horizontal movement. In this respect, the use of the OPA OGCM for the prediction of the horizontal currents is a significant improvement. The horizontal currents were averaged over the euphotic

layer and the trophic transfer leading to the term source in the *F* equation was predicted accordingly. This is consistent with the exclusive feeding of skipjack tuna on epipelagic prey (review: Matsumoto *et al.*, 1984). However, possible overestimation of *F* could occur in regions of high vertical exchanges. This would be considered in a further development of a multilayer model.

Given the data uncertainties and the simplicity of the model, these initial results are encouraging. They show the potential value of using new primary productivity and surface current data to model the large-scale distribution of aggregated secondary/tertiary production. The distribution pattern of the simulated skipjack tuna forage production is in agreement with both limited observations of zooplankton distributions and the time–space sequence of plankton community evolution in the equatorial Pacific. Zonal transport appears to create an enrichment in secondary production of the warmpool, where a longer residence time is more advantageous than in the region of equatorial upwelling. The simulated forage combined with other environmental parameters, such as temperature and dissolved oxygen concentration (Barkley *et al.*, 1978) should lead to a realistic habitat index (MacCall, 1990) useful for large-scale spatial models of tuna populations (Bertignac *et al.*, 1998, this volume).

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A spatial population dynamics simulation model of tropical tunas using a habitat index based on environmental parameters

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ABSTRACT

We are developing a spatial, multigear, multispecies population dynamics simulation model for tropical tunas in the Pacific Ocean. The model is age-structured to account for growth and gear selectivity. It includes a tuna movement model based on a diffusion–advection equation in which the advective term is proportional to the gradient of a habitat index. The monthly geographical distribution of recruitment is defined by assuming that spawning occurs in areas where sea surface temperature is above 25°C. During the first 3 months of their life, simulated tunas are transported by oceanic currents, after which movement is conditioned by gradients in the habitat index. Independent estimates of natural mortality rates and population size from large-scale tagging experiments carried out by the Secretariat of the Pacific Community are used in the simulations. The habitat index consists of components due to forage density and sea surface temperature, both of which are suspected to play major roles in determining tuna distribution. Because direct observations of forage are not available on a basin scale, we developed a submodel to simulate the surface tuna forage production (Lehodey *et al.*, 1998). At present, only skipjack (*Katsuwonus pelamis*; a surface tuna species caught by purse seine and by pole-and-line) is considered, at a 1°-square resolution and on a monthly climatological time series. Despite the simplicity of the model and the limitations of the data used, the simulation model is able to predict a distribution of skipjack catch rates, of the different fleets involved in the fishery, that is fairly consistent with observations.

INTRODUCTION

Tuna fisheries of the western tropical Pacific are among the most valuable in the world. Catches of skipjack (*Katsuwonus pelamis*) have more than doubled since the beginning of the 1980s; they reached a peak of about 1 000 000 tonnes (t) in 1991 and have remained between 800 000 and 1 000 000 t annually since then. Yellowfin (*Thunnus albacares*) catches have also increased up to 430 000 t in 1993. Only bigeye (*Thunnus obesus*) catches have remained fairly stable, at about 75 000 t. Most of the increase in the catch has been due to the development of the purse seine fishery, which in 1994 accounted for 65% of the total skipjack catch and 50% of the total yellowfin catch. Furthermore, most of the purse seine catch is taken inside the EEZs (exclusive economic zones) of the western Pacific Island nations. It has thus become important for those countries to know the 'optimal' number of licences that should be allocated for purse seiners and other vessel types.
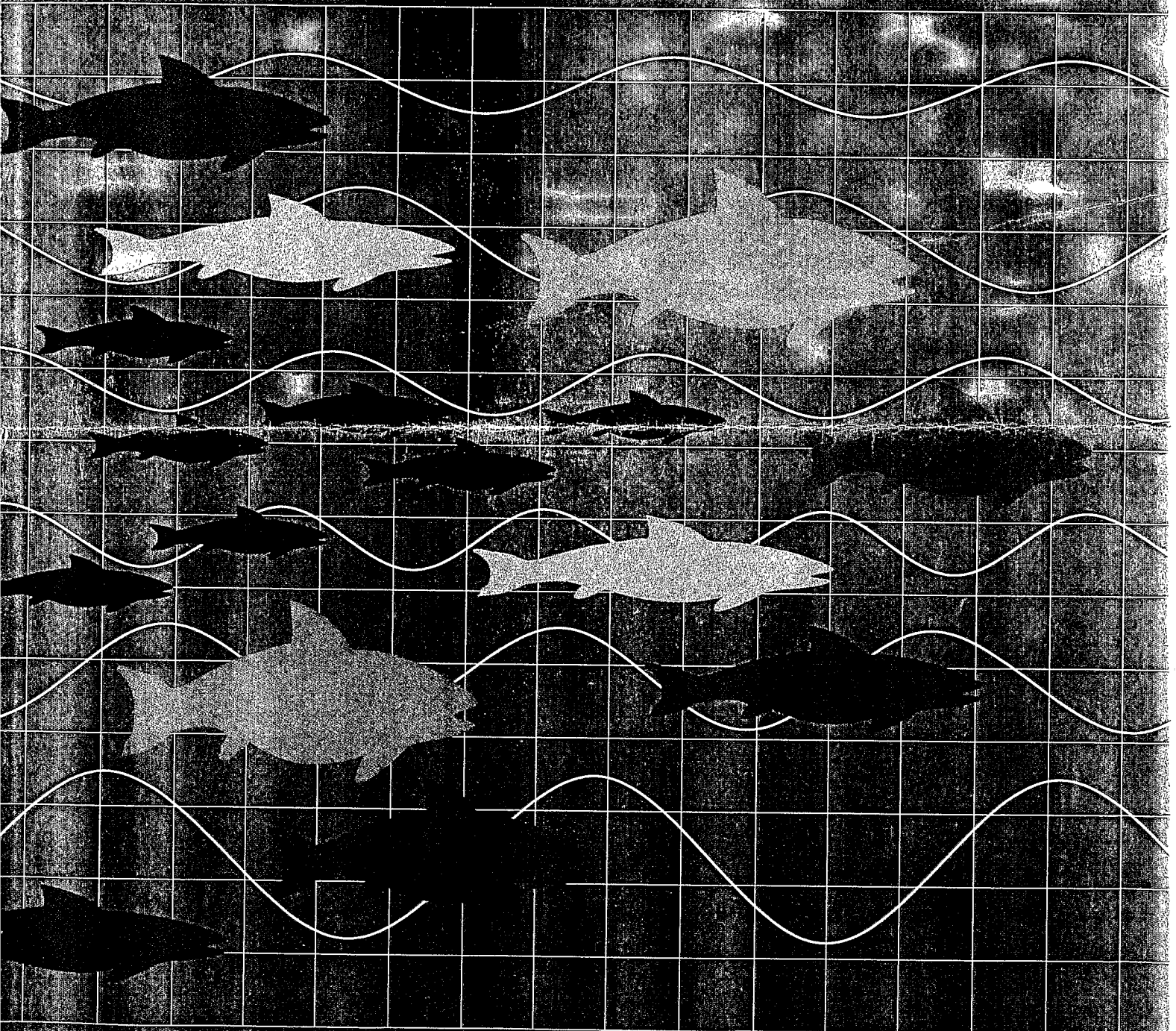
To investigate such issues, we are developing a simulation model for tropical tunas in the Pacific Ocean. The tuna fishery in that region is typically a multispecies and a multigear fishery in which interactions can occur. Tuna species caught by the purse seiners (i.e. mainly skipjack, yellowfin and bigeye) are also caught by several other gears such as pole-and-line or longline. Tunas are also known to have a wide distribution and the model has to incorporate spatial structure to account for the distribution of fishing effort, the movements of fish and environmental variations. To be realistic, it should also specify gear selectivity and take into account the growth of fish; this can be done by incorporating an underlying age structure for the fish population.

The purpose of this paper is to give a preliminary account of the characteristics of the model, which is still under development. After a short review of several approaches used to deal with fish movements and a description of the main components of the model,