Local overfishing and fishing tactics: theoretical considerations and applied consequences in stock assessment studied with a numerical simulator of fisheries

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Abstract − Intense local fishing pressure is likely to induce significant local decreases in both resource biomass and fishing yields. This is what we term ‘local overfishing’. Such a phenomenon and its consequences for stock assessment are investigated with the fisheries simulator SHADYS (Simulateur halieutique de dynamiques spatiales: spatialized simulator of fisheries dynamics). In SHADYS, resource dynamic is based on an advection–diffusion–reaction equation. After a brief presentation, the simulator is used to characterize the ‘local overfishing’ phenomenon as a ‘wound’ of the population. The latter is subsequently able to ‘heal’ and to recover its initial distribution. We show that, associated with cooperation tactics of the fishing fleets, local overfishing may induce non-linear relationships between catches per unit of effort (CPUE) and fishing effort calculated locally. In particular, it is shown that there is a strictly decreasing relationship between catchability and effort when fishing vessels apply intense local fishing pressure but do not cooperate; that the relationship may increase when vessels cooperate but do not apply intense local fishing pressures; and finally, that it may go through a maximum when, simultaneously, ships cooperate and have high local exploitation rates. These three main types of theoretical relationships correspond well with those observed in reality. The existence of such relationships could be an important source of biases in stock assessment. © 2001 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

advection–diffusion / biomass nonlinearity / CPUE / fishermen cooperation / local fish depletion / spatial model / stock assessment

Résumé − « Surexploitation locale » et tactiques de pêche : considérations théoriques et conséquences pratiques en évaluation des stocks étudiés avec un simulateur numérique de pêcheries. De fortes pressions de pêche locales sont susceptibles d’entraîner des diminutions locales significatives de la ressource et des rendements de pêche. C’est ce que nous appelons la « surexploitation locale ». Le phénomène et ses conséquences en évaluation des stocks sont étudiés à l’aide du simulateur de pêcheries « Shadys » (Simulateur halieutique de dynamiques spatiales) où la dynamique de la ressource est fondée sur une équation d’advection–diffusion–réaction. Après avoir été rapidement présenté, le simulateur est utilisé pour caractériser le phénomène de « surexploitation locale » qu’on décrit ici comme une « blessure » de la population. Celle-ci peut, ensuite, « cicatriser » et retrouver sa répartition initiale. Associé à des stratégies de coopération des flottilles de pêche, le phénomène de surexploitation locale est susceptible d’entraîner l’existence d’une relation non linéaire entre les captures par unité d’effort (CPUE) et l’effort de pêche, calculés localement. En particulier, nous montrons qu’il existe une relation entre la capturabilité et l’effort de pêche, et que cette fonction est strictement décroissante quand les navires développent de fortes pressions de pêche locales mais ne coopèrent pas entre eux, qu’elle peut être croissante si les navires coopèrent mais ne développent pas de fortes pressions de pêche locales, et qu’elle peut passer par un maximum si les navires coopèrent et développent de fortes pressions de pêche locales. Ces trois grands types de relations obtenues théoriquement correspondent aux relations observées dans la réalité. L’existence de telles relations est une source de biais potentiellement importants en évaluation des stocks. © 2001 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS

advection-diffusion / non linéarité de la relation CPUE–biomasse / coopération des pêcheurs / surexploitation locale / modèle spatial / évaluation des stocks

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1. INTRODUCTION

Usually in exploited fish population dynamic models, commercial captures per unit of effort, CPUEs, are supposed to be proportional to stock abundance (Palheimo and Dickie, 1964). The reality is far from such ideal conditions. In practice, it is well known that, due to the resource heterogeneous density-dependent distribution and to fishermen search tactics, the relationship linking CPUE to stock abundance may be non-linear (Clark and Mangel, 1979;GREEN and Overholtz, 1990; Gauthiez, 1997; HILBORN and Walters, 1987, 1992). Thus, the use of CPUE as a stock abundance index becomes tricky when such relationships are considered. Nevertheless, it is generally accepted that CPUEs calculated for a small area can be considered as being proportional to local fish density, and used as a local stock abundance index as is frequently done to draw fish density maps for instance.

What we aim to show is that local dynamic phenomena linked to the diffusive behaviour of fish population and to the fishermen searching tactics have to be taken into account when using CPUE as abundance indices. Indeed, localized fishing effort can induce important local fish depletions (Fonteneau et al., 1998) which may cause a dramatic local decrease in the CPUE. This is what we call the ‘local overfishing’ phenomena: due to the non instantaneous mixing of the population, local fish density estimated with local CPUE can be modified by the local fishing intensity. At the same time, fishermen cooperation or spaying tactics is likely to induce local modifications of vessels’ individual fishing power, which becomes linked with the total number of vessels operating in the area. What we show is that both phenomena can be analysed by considering the statistical relationship between local CPUE and local fishing effort. A non linear statistical analysis of the yellowfin tuna (Thunnus albacares) CPUE in the Atlantic ocean brought to the fore such non linear relationships between local CPUE and local fishing effort. A non linear statistical analysis of the yellowfin tuna (Thunnus albacares) CPUE in the Atlantic ocean brought to the fore such non linear relationships between local CPUE and local fishing effort. A non linear statistical analysis of the yellowfin tuna (Thunnus albacares) CPUE in the Atlantic ocean brought to the fore such non linear relationships between local CPUE and local fishing effort. (Maury et al., 2001b). In this paper, different simulations of the simulator SHADYS (Simulateur halieutiques de dynamiques spatiales) are reported to elucidate such non-linear relationships. SHADYS attempts the realistic representation and study of complex spatial fisheries behaviours at different spatiotemporal scales (Maury, 1998; Maury and Gascuel, 1999).

After a short presentation of the simulator, different simulations are conducted to address the problem of local overfishing and its practical consequences in stock assessment. From a general point of view, the first simulation presented in this paper leads to a conceptual framework to interpret the local overfishing phenomenon, in terms of ‘wound and healing’ of a fish population. From an assessment point of view, the second set of simulations allows the interpretation of the non-linear relationships observed between the local CPUE and the local fishing effort as a consequence of local overfishing phenomena and fishermen’s fishing tactics (Maury et al., 2001b).

2. MATERIAL AND METHODS

The work presented here is an application of the SHADYS simulator. SHADYS is a spatialized fishery simulator based on a Geographic Information System (GIS) interface (Savane software © Orstom 1995). In this paper, SHADYS is briefly presented. We focus on its important features and avoid details useless for understanding the text. For a more complete presentation, the reader can refer to Maury and Gascuel (1999) where the simulator is fully presented.

In the simulator, the fishery modelled is made up of subsystems whose dynamics are coupled together by means of simple and well-known properties and ecological mechanisms. In this way, SHADYS joins together three fundamental entities in a fully explicit spatiotemporal way: the environment, which is mainly responsible for the spatiotemporal population structuration, the populations considered, and the fishing fleet, each elements being spatially distributed in a two dimensional square space.

2.1. Environment modelling

The habitat of fish can be functionally characterized by its favourableness for fish living: its local suitability as perceived by fish. This is what we call the ‘biotic affinity’ of the environment. As suggested by MacCall (1990), fish habitat can be represented as a basin topography whose altitude is equal to the opposite of the biotic affinity: the lower the altitude, the stronger the biotic affinity and the more favourable the place. In SHADYS, according to this representation, fish habitat is modelled as large-scale basin topography where mesoscale patchy structures (square holes or bumps) are randomly distributed to simulate local environmental heterogeneity. In the simulator, the basin location varies to mimic seasonal oscillations of the environment, and patch number and size can be changed to model various levels of environment heterogeneity.

2.2. Fish population dynamics modelling

An advection–diffusion–reaction model is used to represent the spatial dynamics of recruited fishes. In such a model, fish movements have two components: a random one, the diffusion term, which characterizes ‘dispersive’ movements, and a directed one, the advection term, which describes movements directed along the habitat suitability gradient. Both components are included in a partial differential equation (PDE), continuous in time and space (Okubo, 1980; Sibert et
which represents the spatial dynamics of one cohort over its full lifetime (10 years).

\[
\frac{\partial N}{\partial t} = \frac{\partial}{\partial x} \left( D \cdot \frac{\partial N}{\partial x} \right) + \frac{\partial}{\partial y} \left( D \cdot \frac{\partial N}{\partial y} \right) - \frac{\partial}{\partial x} \left( ba \cdot \frac{\partial N}{\partial x} \right) - \frac{\partial}{\partial y} \left( ba \cdot \frac{\partial N}{\partial y} \right) - Z \cdot N \quad (1)
\]

with \( N = \frac{N}{x, y} \) the fish density of the considered cohort at point \((x, y)\) at time \( t \), \( D \) the diffusivity coefficient, \( ba = ba_{x, y} \), the biotic affinity (the altitude of the environmental basin) and \( Z = Z_{x, y} \), the local mortality rate including the natural \( M \) and the local fishing mortality rate \( F_{x, y} \).

Such models have a long history in ecology [Skelham, 1951; Holmes et al., 1994; Okubo, 1980; Sibert et al., 1999], but their use in fishery science has grown recently [Breiteneder, 1998; MacCall, 1999; Maury et al., 2001a; Sibert and Fournier, 1994; Sibert et al., 1996, 1999]. To be realistic in our case, they must reflect the heterogeneous distribution and movements of the fish population linked to the environment heterogeneity. Thus, in equation (1), the advective component of the model is related to the local gradient of biotic affinity (the slope of the habitat basin) to transport the fish population towards a more suitable environment. Then, like a liquid, the fish population ‘flows’ into canyons towards the bottom of the biotic affinity landscape’s valleys (figure 1).

A numerical solution of equation (1) is obtained using an ‘alternating direction implicit method’ [Press et al., 1994] on the SHADYS 10 000 cells (100 \times 100) square grid with 6 time steps a month. Closed reflective boundaries (Neumann conditions: \( \frac{\partial N}{\partial x} = \frac{\partial N}{\partial y} = 0 \) at boundaries) are used to model an impassable frontier, such as a shore for instance. The initial population distribution is obtained from a uniform distribution of the fish population by running the model during one year without mortality.

2.3. Fishing fleet modelling

A fishing fleet of \( n \) vessels is simulated. Fishing gear selectivity is the same for all boats. At each period in time, each boat is fishing in a particular cell chosen in the whole grid. Fishing tactics used by fishermen to choose their fishing area are too complex to be explicitly represented here. Then, a simple stochastic process is used to characterize the vessels’ capacity to detect fish. In each time period, each vessel is assumed to explore randomly a fraction \( \alpha \) of the total number of spatial cells and to apply its fishing effort in the most abundant cell found [Gauthiez, 1997]. \( \alpha \) varies from 0% to 100%. If \( \alpha = 0 \), fishing effort is attributed randomly in the grid. If \( \alpha = 100\% \), abundance of fishes in all cells are known by the fishermen and fishing effort is exerted in the cell with the highest abundance.

SHADYS also allows the cooperative (or spying, which is equivalent in term of effects) behaviour of fishermen to be simulated. In this case, all the others use the search capacity of a vessel. In the case of cooperation, each vessel is individually endowed with a low capacity of detection of high fish concentrations, which enables it to be hardly more effective than if it was fishing randomly. On the other hand, when several vessels fish in the same area, their effort is allocated to the most abundant cell found by all the vessels. Under these conditions, the more numerous the ships are in a zone, the more their capacity in finding fish concentrations increases. The increase in fishing effort then has a positive effect on local fishing power [Laurec, 1977] of each ship.

Given the distribution of fishing effort, catches are calculated in each cell with a simple catch equation:

\[
C_{i,t} = \frac{q \cdot n_{i,t} \cdot \left( 1 - e^{-q \cdot n_{i,t} - M} \right)}{q \cdot n_{i,t} + M} \quad (2)
\]

with \( C \) the catches in the cell \( i \) and the time step \( t \), \( q \) the individual fishing efficiency for one vessel during one time step, \( n \) the total number of vessels in the cell \( i \) and the time step \( t \), and \( M \) the natural mortality during one time step.

2.4. Simulations

- The first simulation presented here is designed to describe qualitatively the general behaviour of a population submitted to very high, localized exploitation rates. For that purpose, the habitat is simply constituted of nine unfavourable square patches (bumps in the habitat basin) without seasonal oscillations, and the fish population is highly diffusive. The fishing pressure is characterized by very high, localized mortality levels, almost randomly distributed (\( \alpha = 0.03\% \)).

- To characterize potential biases linked to the use of CPUE as a local abundance index, different simulations are carried out. To induce heterogeneous distribution of the fish population, 54 randomly distributed patches (holes) are supposed to model the heterogeneous distribution of favourable places. A seasonal
oscillation of the basin is also implemented, which causes the population to move seasonally, encountering suitable distinct zones that cause high local concentrations of fish. Diffusion and advection coefficients are chosen so as to result in a realistic heterogeneity of the population’s spatial distribution. Fishing effort varies from 1 to 40 vessels whose position is changed every 15 days (3 numerical time steps). Vessels can cooperate, and their individual catching capacity varies depending on the simulation. Monthly CPUEs are calculated (one month corresponds to 6 time steps). Because the simulations concern a single cohort exploited from the beginning to the end of its life (and hence presenting variable abundances according to age), the CPUEs at different ages cannot be compared and used to measure vessels efficiency. In order to quantify the latter, we use the coefficient of global catchability defined as the ratio of monthly CPUE to the monthly abundance of the stock on the whole spatial grid:

$$Q_m = \frac{CPUE_m}{N_m} = \frac{6 \sum_{i=1}^{1000} \sum_{k=1}^{n} C_{m,i,k}}{n \sum_{i=1}^{1000} \sum_{k=1}^{n} N_{m,i,k}/6} \quad (3)$$

with $Q$ the global catchability coefficient, $C$ the catches, $N$ the fish number, $m$ the considered month, $t$ the time step, $i$ the grid cell number, $k$ the subscript for vessels and $n$ the total number of vessels (i.e. the fishing effort).

In order to study the catchability $Q$ as a function of fishing effort $n$, the whole cohort simulation is reprocessed for different number $n$ of fishing vessels, and $Q$ is calculated for each simulation as the mean value for $Q_m$ during one simulation.

3. RESULTS

3.1. The dynamics of local overfishing

In the general case of intense localized fishing pressure, the fishing activity induces local fish population depletions, which progressively are replenished by the diffusion of fish from adjacent places when the fishing vessels leave. Thus, the fish population behaves like an organism injured by fishing and who, more or less rapidly, heals and recovers its initial distribution (Figure 2). Of course, our simulation may appear to be too much of a caricature to be realistic. Nevertheless, the main feature is that local fishing pressure may cause a local resource exhaustion, which will adjust more or less rapidly, depending on the resource’s displacement capacity.

3.2. Non linearity of the local CPUE–effort relationship

Simulations characterized three main relationships between local CPUE and fishing effort:

- When vessels do not cooperate and are individually endowed with a high capacity for detection of fish concentrations ($\alpha = 0.5\%$, which corresponds for each vessel to the exploration of 50 cells in the grid every 15 days) and with a high individual fishing efficiency, catchability as a function of effort is strictly decreasing and tends asymptotically towards zero (Figure 3a).
- When vessels cooperate and are individually endowed with a low capacity for the detection of fish concentrations ($\alpha = 0.01\%$) and with a low individual fishing efficiency, catchability as a function of effort increases towards a maximal asymptotic value (Figure 3b).
- When ships cooperate and are individually endowed with a low capacity for the detection of fish concentrations ($\alpha = 0.01\%$) and with an intermediate individual fishing efficiency, catchability in function of effort reaches a maximum before decreasing (Figure 3c).

The interest of these caricatural scenarios is in bringing to the fore situations where local effort and catchability are not independent and to characterize various possible shapes of the local CPUE–effort relationship.

4. DISCUSSION

4.1. Population as an open system: wound and healing, a matter of scale

By exploiting the analogy with a liquid, MacCall (1990) proposes to characterize the displacement ca
pacity of populations by their viscosity. The viscosity of a population is then a function of diffusion and advection coefficients as well as of the functional connectivity (Baudry and Merriam, 1988) of the environmental landscape. The more viscous the population is, the slower it will respond to the modification of its environment. The more fluid it is, the faster it will adapt its distribution to changes in habitat suitability and fill up the relative depletions of the biotic affinity landscape. In our case, using the analogy with a wounded organism, the more 'fluid' the exploited population, the faster it will heal up and the more 'viscous' it is, the slower it will heal. On a broad spatial scale, strong local fish depletions due to fishing are well known, for instance in tuna fisheries (Fontneau et al., 1998). This is what we call local overfishing phenomena.

Such 'wound and heal' phenomena can be interpreted from an open system perspective. Indeed, because populations are open systems, their dynamics exhibit two interesting characteristic properties (Von Bertalanffy, 1968):

- The existence of an attractive state independent of time: a limit behaviour (which is probably never reached because the population, continuously constrained by its moving environment, is in a perpetual state of transition [Frontier and Pichod-Viale, 1993]). In our simulation, fishes always swim towards the moving optimal valleys of their biotic affinity landscape.
- The principle of equi-finality, which drives different initial states to the same attractor: the system forgets its past and the perturbations it encountered, the population heals up and its scars vanish.

According to Weinberg (1975) in Allen and Starr (1982), systems may be split into three categories: small number systems, which can appropriately be modelled with differential equations systems (e.g. planets), large number systems for which a probabilistic approach replaces the trajectory approach (e.g. statistical mechanic, gas laws) and middle number systems (e.g. living systems), where there are too few parts to average their behaviour easily and too many parts to manage each separately with its own equation. Because populations are middle number systems, statistical properties of large number systems must be cautiously extended to them. Nevertheless, probabilistic models such as advection–diffusion models seem to

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**Figure 3.** On the first line, the mean monthly simulated catchability (average value for a ten year simulation, see text for details) as a function of fishing effort (ship number). a. Case of ships high capacity of individual search ($\alpha = 0.5\%$) and a high individual catch capacity (high rates of local exploitation). b. Case of a null individual search capacity ($\alpha = 0.01\%$) and a low individual catch capacity. c. Case of a low individual search capacity ($\alpha = 0.01\%$) and a medium individual catch capacity. On the second line, results of generalized additive modelling (GAM) regression (solid lines) of fishing effort on ln(CPUE + 1) of yellowfin tuna (Thunnus albacares) in the Atlantic Ocean (Maury et al., 2001b) with the 95% standard error boundary confidence limits (dashed lines) around the covariate effects. Tick marks on the x-axis show the location of data points. d. Relationships obtained for longliners exploiting old fish that can be subject to important local overexploitation. e. Relationships characterizing the purse seiners obtained for young fish slightly affected by local depletions because they are numerous in the environment. f. Relationships characterizing the purse seiners obtained for old fish being subject to high local exploitation rates and which might experience local depletion phenomena.
fit quite well to biological reality [Bertignac et al., 1998; Holmes et al., 1994; Maury et al., 2001a; Okubo, 1980; Sibert et al., 1999] Such models apply only at the population scale when advection and diffusion emerge from complex local behaviours of individuals and schools (including aggregation behaviours). At this level, the population can be understood from a probabilistic point of view, in terms of expected density. The image of a population wounded and healed is then a matter of scale and cannot be extended to local scales concerning schools and individuals where the population concept is not accurate. At the same time, such a representation must not hide the potential risk of overfishing local endemic and non-interchangeable subpopulations [Curry, 1994; Curry and Anneville, 1998]. In such a case of intraspecific biodiversity being undermined, healing could be impossible and local overexploitation irreversible.

4.2. Local overfishing, fishing tactics and CPUE as local abundance indices

When vessels are individually endowed with a great capacity to detect high densities of fish and with a high fishing power (inducing high local rates of exploitation), catchability as a function of effort is strictly decreasing. As ships are individually capable of detecting favourable zones for fishing and because they do not cooperate, the fishing efficiency of the fleet does not increase with the number of ships. As ships are endowed with a high catch capacity, they deplete the fishing area quite rapidly and their yields (and hence the catchability coefficient $Q$) fall markedly when effort increases. Because vessels exert their effort during three consecutive time periods at the same place, the local decrease of abundance that they cause is partly compensated for by the arrival of fishes by diffusion or advection. If vessels always fished in the same place and exerted a very high local fishing mortality, they would catch at each time step all the fish diffusing from the unfished zones.

When fishing vessels are individually of little efficiency but cooperate, catchability grows rapidly when effort increases (local fishing power increases due to cooperation), and then reaches a maximum level when the number of vessels is sufficient to almost always detect the highest fish concentrations. As local exploitation rates remain low despite increasing effort (at least in the explored range of effort), fish coming by diffusion compensate for the catches and local biomass remains stable: CPUE does not decrease. If vessels are more efficient, catchability grows first with effort (local fishing power increases owing to cooperation) and then, the increase in local fishing power and effort leads to an increase in local exploitation rates and induces the phenomenon of local overexploitation (catches are higher than the diffusive flux) and decreasing catchability.

Different types of fisheries may be concerned with local overfishing phenomena. For example, they are well known for tuna fisheries [Fonteneau and Pallares, 1995; Fonteneau et al., 1998]. With the use of general additive models (GAM), which are non-parametric generalizations of multiple linear regression techniques based on empirical transformations by local smoothing techniques [Hastie and Tibshirani, 1990], whose main feature is that they enable multivariate analysis with no a priori assumptions of linearity, thus making them useful to characterize non linear relationships, Atlantic yellowfin tuna (Thunnus albacares) CPUE have been studied for different fleets in order to characterize potential non linear relationships between CPUE and various covariates [Maury et al., 2001b]. This study clearly brings to the fore three types of non-linear relationships between CPUE and fishing effort, whose shapes correspond exactly to the ones simulated by SHADYS (figure 3a). The interpretation of such observed relationships is completely consistent with the theoretical framework developed in this article:

- For the longliners fleet considered, exploiting old fish that can be subject to important local overexploitation, the relationship CPUE–effort is strictly decreasing (figure 3a) and exhibits a shape like the one obtained by SHADYS (figure 3a).
- For the purse seiners fleet considered whose cooperation behaviour is well known [Foucher, 1994], CPUEs are systematically growing for low effort values. Then, for higher values of effort, either they reach a plateau in the case of young fish probably little affected by local depletions because they are very numerous in the environment (figure 3b) compared with figure 3b), or they decrease for old fish subject to high local exploitation rates which are likely to experience local depletion phenomena (figure 3f) compared with figure 3f).

There is remarkable agreement between observed and simulated CPUE–effort relationships. Thus, the simulations carried out using SHADYS enable the non-linear relationships observed in reality to be interpreted as resulting from the antagonistic effects on the one hand of cooperation tactics (or spying tactics) between vessels to locate tuna concentrations, and on the other hand, of the local decrease in the biomass due to local overexploitation phenomenon (high local rates of exploitation compared to diffusive replenishment, figure 4).

5. CONCLUSION

The use of a simulator like SHADYS enables a clear formal representation of complex phenomena, which are difficult to observe in reality. Based on simple and well identified mechanisms, SHADYS enables the potential consequences of hypotheses made about the way fisheries function to be explored.

The question of the local overexploitation of a stock, which is addressed in this article, has crucial implications in fisheries science. SHADYS permits a fish population to be represented as a meta-organism that
The object of systematic preliminary study before using high local exploitation rates are exerted and should be established simulations enable the consequences of a local overfishing phenomenon on the estimation of local CPUEs to be simply shown. Therefore, the non linear relationships between local CPUEs and effort that are observed in reality [Maury et al., 2001b] can be recognized and explained. Such relationships are interpreted as resulting from the antagonistic effects on the one hand of the strategies of effort distribution in fish-abundant zones and of cooperation tactics (positive effects) and, on the other hand, of local overfishing phenomena (negative effect).

Such non linearities in the local CPUE–effort relationship are obviously important for fisheries where high local exploitation rates are exerted and should be the object of systematic preliminary study before using the CPUE as an index of local abundance.

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