Dynamics of a migratory population under different fishing effort allocation schemes in time and space

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Abstract: Many exploited fish populations migrate or are confined to some preferential habitats at certain stages of their life cycle. Fishermen may follow some of these spatial and seasonal patterns, in which case the spatio-temporal distribution of fishing effort is closely tied to that of fish abundance. We investigated the dynamics of a population that migrates seasonally in relation to reproduction. Using a two-patch, two-season model, we compared population and catch levels obtained under different spatio-temporal allocations of fishing effort. The model mimics the dynamics of the saithe fishery in the west of Scotland in the 1980s. Results show that better biomass and catch levels could be attained by changing the allocation of fishing effort between seasons and patches, so that the effective age at entry in the fishery is optimized. Similar biomass levels could be obtained through an 80% reduction in total effort without changing its allocation, but catch levels would be much lower. Describing the dynamics of a fishery at a finer spatio-temporal scale thus allows us to explore management measures like openings and closures of zones or seasons.

Résumé : Beaucoup de populations de poissons exploitées migrent ou résident dans des habitats préférentiels à certaines époques de leur cycle vital. Les pêcheurs s'adaptent parfois à ces particularités, et dans ce cas la distribution spatio-temporelle de l'effort de pêche est étroitement liée à celle de l'abondance du poisson. Nous avons étudié ici la dynamique d'une population qui migre chaque année pour aller se reproduire. Grâce à un modèle à deux saisons et deux compartiments, nous comparons les niveaux de population et de captures obtenus pour une gamme d'allocations spatio-temporelles de l'effort de pêche. Le modèle décrit la pêcherie de lieu noir de l'ouest de l'Écosse, telle qu'elle existait à la fin des années 1980. Les résultats montrent que des niveaux de biomasse et de capture plus élevés pourraient être atteints en réallouant un effort total donné entre les compartiments et les saisons, de manière à optimiser l'âge d'entrée dans la pêcherie. Un niveau de biomasse comparable pourrait être obtenu en réduisant l'effort total de 80% sans le réallouer, mais les captures s'en trouveraient nettement diminuées. Cette description spatio-temporelle de la dynamique d'une pêcherie permet d'explorer des mesures de gestion par fermetures ou ouvertures de zones ou de saisons.

Introduction

Most exploited fish populations migrate between some preferential habitats at certain stages of their life cycle. For demersal species living in temperate zones, migration is periodic and closely tied to the seasons. For instance, many demersal species migrate en masse toward spawning areas to reproduce in winter. Thus, reproduction can give rise to high fish concentrations in particular areas. Fishermen often take advantage of this behaviour and target the population at that time.

Therefore, because the spatio-temporal distribution of fishing effort is closely tied to that of fish abundance, ignoring spatial features when estimating fish abundance from commercial catch per unit effort data may lead to substantial biases (Beverton and Holt 1957; Gulland 1977; Pelletier et al. 1993). Also, a population dynamics model that neglects spatial and

seasonal features is likely to yield an erroneous stock assessment. Yet there are few attempts to explicitly model the spatial and temporal dynamics of effort and abundance to evaluate alternative management measures (Walters et al. 1993). In most cases, spatial dynamics are not accounted for in operational assessment models, and these models do not allow one to explore management measures like seasonal and spatial openings and (or) closures.

The purpose of this paper is to investigate the dynamics of a population that migrates seasonally to reproduce. We built a model with two seasons and two patches that allows us to consider spatio-temporal management measures, in addition to global measures. This model is used to compare population and catch levels obtained under different allocations of fishing effort between seasons and patches. The model mimics the dynamics of the saithe (*Pollachius virens*) fishery in the west of Scotland that prevailed during the 1980s.

We first describe the saithe population and fishery, then construct a spatio-temporal population model, and compare it with a global (nonspatial) model. Fishing mortalities are modelled as a function of total effort, patch surface areas, catchabilities, and effort allocation parameters. The model is then applied to the data to explore a variety of effort allocation schemes using indicators like population growth rates, biomass, and catch levels. The sensitivity of the results to several parameters is also studied. Finally, we discuss the im-

Fig. 1. Management area for the saithe stock in the west of Scotland. The broken line represents the 200-m isobath, i.e., roughly the limit of the continental shelf. Patches A and B are located west and east of this isobath, respectively. The patches correspond to ICES zone VIa. Indeed, the regulatory area (ICES VI zone) for saithe also includes a more western zone (VIb), but saithe catches are negligible there.
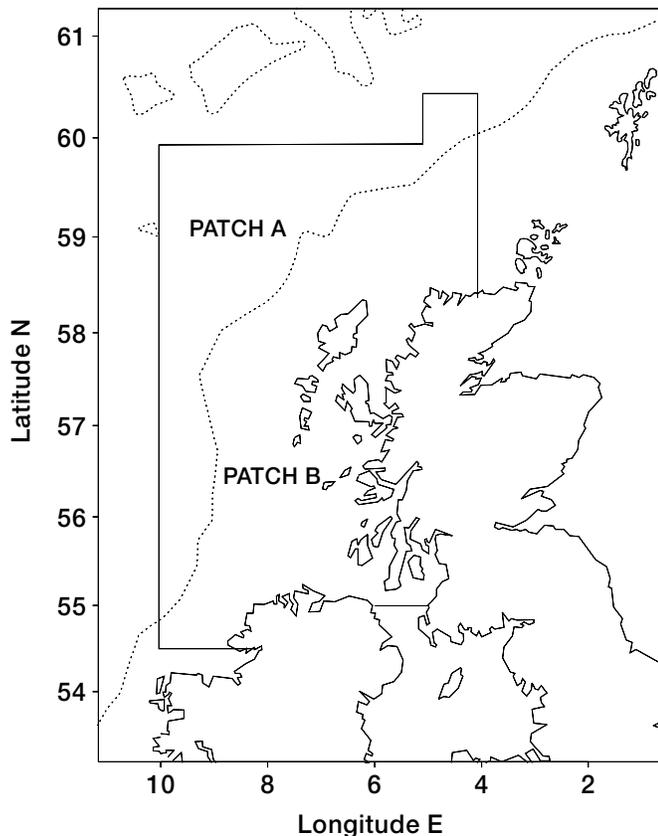
plications of the results in terms of spatio-temporal management measures and compare these with global measures like total effort limitation.

The saithe stock in the west of Scotland

Saithe (*Pollachius virens*) exhibits a widespread distribution in the northeast Atlantic, ranging from the west of Scotland to the Arctic Sea. For the purpose of management, five stocks are considered and assessed separately by the International Council for the Exploration of the Sea (ICES): the Arcto-Norwegian, North Sea, Faroe, Icelandic, and west of Scotland stocks. This paper focuses on the latter (Fig. 1), which is the most southern. Mainly exploited by Scottish and French fleets, it has substantially declined in recent years, to the extent that the catch quotas have not been met since 1989 (Anonymous 1992).

Saithe is a highly migratory species; even though stocks are assessed independently, there is evidence of movements between them. Migration studies using tagging experiments have primarily focused on exchanges between the Arcto-Norwegian stock (the largest stock) and the North Sea stock (Jakobsen

1982; Jakobsen and Olsen 1987). The only mark–recapture experiment carried out northwest of the North Sea and west of Scotland indicated a global migration of spawners northeastwards, along the continental slope, toward the North Sea stock (Fontaine et al. 1985). Only occasional migrants could be detected in the opposite direction (from the North Sea toward the west of Scotland). There is apparently no significant exchange with the Icelandic and Faroe stocks. According to current knowledge, the west of Scotland stock can be considered as contributing to the other saithe stocks and there is no evidence for immigration to the area from the other stocks. In this paper, we consider this stock as a biological population, i.e., a self-reproducing group of individuals of the same species.

During the first quarter of the year, spawning adults congregate along the continental slope for reproduction (notice the 200-m isobath in Fig. 1). After spawning, they partially disperse toward more inshore areas. Some migrate northeastwards as indicated earlier. In the western part of the area, the population distribution is limited by depth, which increases sharply beyond the continental slope. Immature fish remain near the coast until they mature, at age 5 approximately. For the purpose of this study, we assume that the area of distribution of the population roughly coincides with the area currently used for assessment and management (Fig. 1).

From January until April, saithe is heavily exploited by large trawlers along the continental slope, where the mature adults congregate to spawn (Fig. 2). We will refer to this fleet as industrial, although these vessels are not factory trawlers. This designation refers rather to their mode of ownership. During this period, the industrial fleet allocates little effort in patch B. During the rest of the year, this fleet's fishing effort is much lower and more evenly distributed over the whole area; often, fishermen do not specifically target saithe, even though they catch some. On average, exploitation by the fleet of large trawlers constitutes up to 80% of the landings, but saithe is also exploited on the continental shelf by a fleet of smaller boats. This effort is allocated closer to the coast; thus, the catch is of more immature fish. Saithe is not necessarily a target species for this fleet. These exploitation features prevailed during the 1980s, but recently the emergence in nearby areas of new resources like deep-water species has modified fishing strategies in the region. We use this example because of the striking relationship between the seasonal distributions of fish and fishing effort.

Population model and assumptions

Biological parameters
The population model is age structured with 11 age groups, the first corresponding to the young-of-the-year, generally called the 0 group. We make the following assumptions: (1) reproduction takes place before fishing, (2) natural mortality is independent of age and equal to 0.2, (3) fishing mortality is age dependent, and (4) knife-edge maturity occurs at age 5.

Assumptions 2 and 4 are not a requirement of the analysis, but rather simplify the equations. Assumptions 1–4 are those on which current ICES assessments are based. Regarding recruitment, there are no research survey indices to study the relation between parental stock and the abundance at age 1.

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Fig. 2. Allocation of fishing effort and corresponding catch between patches and months for the industrial fleet in 1988.
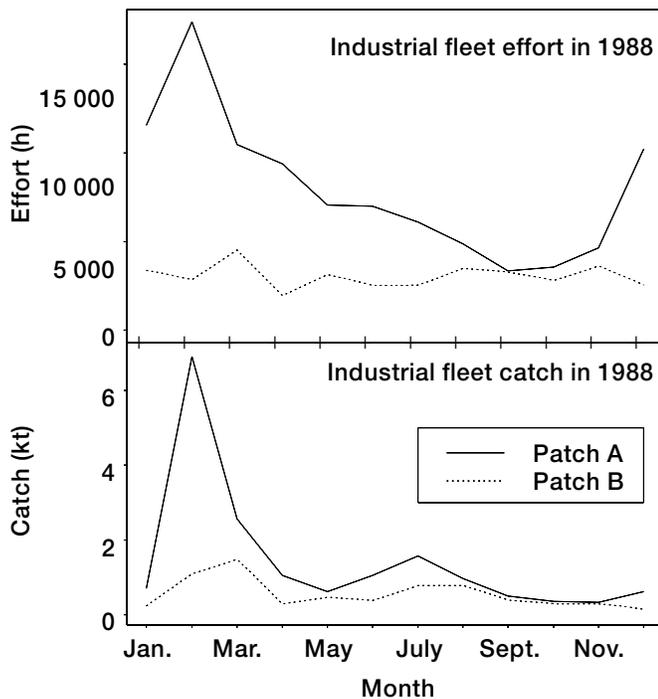
The time series of historical virtual population analysis (VPA) estimates in Anonymous (1992) is short and offers little insight on this issue. We will therefore consider two alternative hypotheses about reproduction: (*i*) a linear relationship between the abundance at age 1 and the parental stock and (*ii*) a constant abundance at age 1. Assumption *i* corresponds to a situation where there is recruitment overfishing and the stock is low, so that compensatory effects do not affect the survivorship of the young of the year. This assumption could be justified in this application by the intense exploitation level of the stock. Assumption *ii* corresponds to a population with sufficient reproductive capacity, so that the number of young fish surviving the larval phase can be considered as independent of the size of the adult population within certain biomass levels.

These assumptions allow us to build a relatively simple model of the population. At the same time, they are not fundamental for the population dynamics with respect to the question of seasonality and spatial patterns we want to study in this paper. Since there is no information to test hypotheses about reproduction, we will investigate the sensitivity of the results to each of these assumptions.

In addition to the above assumptions, we consider a constant migration rate *m* for mature age groups migrating from patch A to patch B in spring. We will also explicitly account for the emigration of mature fish toward the northern North Sea to be consistent with the exchanges observed between the different saithe populations (see previous section). The sensitivity of the results to migration parameters will be studied.

Global model
We first consider a model in which patches and seasonality are

not taken into account. This model is actually rather close to the current assessment model. Let $N(t)$ be the vector of population size at age at time t. For each age group, fishing mortality at time t and natural mortality are supposed to be independent Poisson processes with respective parameters $F(a,t)$ and M (Seber 1989). The emigration of some mature fish northeastwards outside of the area of interest takes place after reproduction during a short period. A model without seasons cannot capture this feature correctly, so we assume in this model that emigration takes place before fishing. This has consequences for catch rates, but not for survival rates. Let e denote this emigration rate for mature fish, and $p_a(t)$ the survival rate for age a at time t. Under these assumptions, the survival rates are as follows:

$$(1) \quad \begin{cases} p_a(t) = \exp\left(-(M + F(a,t))\right), & \forall a = 1,\dots,4 \\ p_a(t) = (1 - e)\exp\left(-(M + F(a,t))\right), & \forall a = 5,\dots,10 \end{cases}$$

The date at which animals are counted is the 1st day of the year. Every fish changes age group immediately after this date. Therefore, there exists an age group 0 (0 group) comprising the young of the year at time t. Under these conditions, the evolution of stock sizes between t and $t + 1$ is given by

$$N_a(t + 1) = p_a(t)N_{a-1}(t), \quad \forall a = 1,\dots,10$$

Under the assumption of a constant recruitment rate at age 1, the abundance of the young-of-the-year at time $t + 1$ is

$$(2) \quad N_0(t + 1) = \sum_{a=5}^{10} b_a N_{a-1}(t)$$

where b_a is the individual fecundity coefficient at age a. Indeed b_a is an effective fecundity coefficient that combines individual fecundity and 0-group survival rate. Note that fish of age 4 at time t contribute to $N_0(t + 1)$ because of the conventional date for changing age groups. Under the alternative assumption of a constant recruitment at age 1, $N_0(t + 1)$ is simply a constant value R. With respect to fish of the last age group, we assumed they still contribute to reproduction for year $t + 1$, i.e., after their 11th birthday; they then die of natural causes, and thus they do not contribute to catches. There are very few fish in this age group, and the hypothesis is not crucial to the model.

By convention, catch $C_a(t)$ represents the catch realized between $t - 1$ and t from fish of age $a - 1$ at $t - 1$, and individuals in the last age group are not totally fished. Consequently, the catch equation is written as

$$C_a(t) = f_a(t)N_{a-1}(t - 1), \quad \forall a = 1,\dots,10$$

where

$$\begin{cases} f_a(t) = \dfrac{F(a,t)}{F(a,t) + M}\left(1 - \exp\left(-(F(a,t) + M)\right)\right), \\ \hspace{6cm} \forall a = 1,\dots,4 \\ f_a(t) = \dfrac{F(a,t)}{F(a,t) + M}(1 - e)\left(1 - \exp\left(-(F(a,t) + M)\right)\right), \\ \hspace{6cm} \forall a = 5,\dots,10 \end{cases}$$

Spatio-temporal model

To take into account the spatio-temporal dynamics of the system, we now consider a model with two patches and two seasons. The first season corresponds to the reproductive season, i.e., January to April on average. Patch A corresponds to the spawning area, i.e., the continental shelf between 55 and 60°N latitude (Fig. 1). Patch B corresponds to the inshore zone where immature fish are assumed to reside until age 4. Patch A is substantially smaller than patch B, hence a given number of fish yields a higher density when living in patch A than when living in patch B. The way patches and seasons were precisely determined in practice is described in the section on application.

Reproduction takes place during the first season in patch A exclusively. After spawning, some of the spawners migrate toward patch B, and others definitively migrate northeastwards outside the zone studied. To avoid unnecessary complexity of the model, these migrations are assumed to take place instantaneously at the end of the first season. During the second season, from May to December, every fish remains in the same patch, basically for feeding. At the end of the year, every future spawner migrates toward patch A. At the same time, young-of-the-year arrive in patch B where they stay until maturity. These migrations are also assumed to occur instantaneously.

Fishing activity follows the seasonal and spatial patterns of the population described above. During the first season, we assume that the industrial fleet fishes exclusively for big spawning fish concentrated in patch A. This is a simplification, since data indicate that the industrial fleet also allocates some effort (although little) during the first season in patch B (Fig. 2). After spawner dispersion, this fleet distributes its effort between patches until the end of the year. The inshore fleet is assumed to fish in a uniform way throughout the year in patch B. To construct the spatio-temporal model, it is convenient to consider the dynamics in each patch for each season separately, and then combine them over a 1-year interval (see Appendix for details). Finally, the evolution of stock sizes between t and $t + 1$ follows the same equations as in the global model:

$$(4) \quad \begin{cases} N_0(t + 1) = \displaystyle\sum_{a = 5}^{10} b_a N_{a - 1}(t) \ \text{ or } \ N_0(t + 1) = R \\ N_a(t + 1) = p_a(t)N_{a - 1}(t), \quad \forall a = 1,...,10 \end{cases}$$

but with survival rates at age a given by

$$(5) \quad \begin{cases} p_a(t) = \exp\left(-(F_1^B(a,t)l_1 + F_2^B(a,t)l_2 + M)\right), \\ \qquad\qquad\qquad\qquad\qquad\qquad \forall a = 1,...,4 \\ p_a(t) = (1 - m - e) \exp\left(-(F_1^A(a,t)l_1 + F_2^A(a,t)l_2 + M)\right) \\ \qquad + m \exp\left(-(F_1^A(a,t)l_1 + F_2^B(a,t)l_2 + M)\right), \\ \qquad\qquad\qquad\qquad\qquad\qquad \forall a = 5,...,10 \end{cases}$$

where F_i^j denotes fishing mortality for season i in patch j, l_i is the length of season i, and m is the migration rate from patch A to patch B at the end of the first season. As explained in the appendix, b_a is the number of young-of-the-year (per spawner capita at age a) surviving after 1 year. Therefore, b_a has exactly the same meaning in the spatio-temporal and in the global model.

The catch equation is the same as eq. 3 with catch rates given by

$$(6) \quad \begin{cases} \forall a = 1,...,4, \\ f_a(t) = \left\{ \dfrac{F_1^B(a,t)}{F_1^B(a,t) + M} \left(1 - \exp\left(-(F_1^B(a,t) + M)l_1\right)\right) \right. \\ \qquad + \exp\left(-(F_1^B(a,t) + M)l_1\right) \dfrac{F_2^B(a,t)}{F_2^B(a,t) + M} \\ \qquad \left. \left(1 - \exp\left(-(F_2^B(a,t) + M)l_2\right)\right) \right\} \\ \forall a = 5,...,10, \\ f_a(t) = \left\{ \dfrac{F_1^A(a,t)}{F_1^A(a,t) + M} \left(1 - \exp\left(-(F_1^A(a,t) + M)l_1\right)\right) \right\} \\ \qquad + \exp\left(-(F_1^B(a,t) + M)l_1\right) \\ \qquad \left\{ (1 - m - e) \dfrac{F_2^A(a,t)}{F_2^A(a,t) + M} \right. \\ \qquad \left(1 - \exp\left(-(F_2^A(a,t) + M)l_2\right)\right) \\ \qquad \left. + m \dfrac{F_2^B(a,t)}{F_2^B(a,t) + M} \left(1 - \exp\left(-(F_2^B(a,t) + M)l_2\right)\right) \right\} \end{cases}$$

Evaluation of the dynamics of catch and population

To evaluate the dynamics of both population and catch for a given fishing mortality, we assume that biological parameters and fishing mortality remain unchanged for a number of years, say at least for a generation time, and we compute indicators of population dynamics, catch, and biomass levels in these conditions.

Under the additional assumption of a constant recruitment rate at age 1, the population model can be framed into a Leslie matrix with constant coefficients (Caswell 1989). The evolution of the population over an infinite time horizon is then described by the asymptotic growth rate and the stable age distribution of the matrix. If the growth rate is larger than 1, the population size increases forever, and if it is smaller than 1, the population continuously decreases. The stable age distribution describes the age structure of the population. These measures are independent of initial population values and approximate the population dynamics after a sufficiently long amount of time. Biomass and catch trajectories are also computed to illustrate the evolution of the resource. Because they are computed for a given Leslie matrix, with constant biological parameters and fishing mortalities, these trajectories correspond to equilibrium projections from this standpoint, but catches and biomasses do not stabilize over time, because the population growth rate is never strictly equal to 1. Because of this behaviour, the model is only used for diagnostic purposes on a limited time horizon, and not for prediction purposes. In these conditions, it may be assumed that the parameters of the model remain constant.

Alternatively, under the assumption of constant recruitment, the population reaches equilibrium after a generation, so that both population size and catch become constant and independent of initial population values. In this case, the equilibrium biomass and catch may be computed to provide a diagnostic of the resource. The equilibrium population size is easily expressed as

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$$N^{\text{eq}} = R \begin{bmatrix} 1 \\ p_1 \\ p_1 p_2 \\ \vdots \\ p_1 p_2 \cdots p_{10} \end{bmatrix}$$

so that the equilibrium biomass can be written as

$$(7) \qquad B^{\text{eq}} = \sum_{a=0}^{10} w_a N_a^{\text{eq}}$$

From eq. 3, we get the equilibrium catch:

$$(8) \qquad C^{\text{eq}} = \sum_{a=0}^{10} w_a f_a N_a^{\text{eq}}$$

C^{eq}/R corresponds to an equilibrium yield per recruit.

Modelling fishing mortality and fishing effort allocation

The purpose of the paper is to study the consequences on population and catch of the intensive exploitation of fish concentrations during one season. More generally, we want to explore the population and catch levels obtained under different allocations of fishing effort between patches and seasons. Therefore, we need to define the relationship between fishing mortality and a given fishing effort allocation. Let F denote the vector of instantaneous fishing mortality rates in the global model, each rate being expressed in years^{-1}. In many assessment models, it is assumed that fishing mortality is proportional to fishing effort E:

$$(9) \qquad F = qE$$

where q is a constant vector of individual catchability coefficients q_a. Considering the fishing mortality as a Poisson process, q_a represents the probability that an individual fish of age a present in the area of distribution will be caught by a unit of effort during the time interval chosen. Fish of a given age are thus assumed to be equally vulnerable to fishing. However, the assumption of a constant q may be invalidated in several instances such as density-dependent catchability, spatial heterogeneities, and technological developments in the fleet. In this study, we focus on spatial heterogeneities at the scale of the seasonal changes in fish distribution.

Introducing the spatio-temporal model allows us to account for the differences in both patch sizes and season lengths. Because patch B is substantially larger than patch A, individual catchability is higher in the latter, all other things being equal. In these conditions, catchabilities in patches A and B, say q^{A} and q^{B}, should be related to overall catchability q through the ratio of patch surface area (where a given unit of effort is applied) to the total area of fish distribution:

$$\begin{cases} q^{\text{A}} = ((s_{\text{A}} + s_{\text{B}}) / s_{\text{A}}) q \\ q^{\text{B}} = ((s_{\text{A}} + s_{\text{B}}) / s_{\text{B}}) q \end{cases}$$

To explore the effects of patch sizes, catchability per unit of surface is assumed to be constant throughout the area of distribution of the population. Thus, the assumption of eq. 9 does not hold at the global scale but is used within a patch for a given season. This means that fishing gears have a constant efficiency whatever the patch and the fleet, and that fish are randomly distributed within each patch. With this model, a given fishing effort E generates a higher mortality in the smallest patch (where fish congregate for reproduction).

In addition, the two seasons have different lengths, the first one comprising only one third of the year. Fishing effort is measured in numbers of trawled hours (and not in numbers of boats, for instance) per time interval. All other things being equal, a given number of fishing hours must imply the same relative decrease in stock sizes at the end of the season, regardless of season length. Therefore, it is necessary to rescale fishing efforts with respect to the length of each season when expressing fishing mortalities.

Let E_1^{A}, E_2^{A}, E_1^{B}, and E_2^{B} be the fishing efforts allocated in each patch, A and B, during each season, 1 and 2. Let us denote s_j the surface areas of patch j, and l_i the length of season i. Fishing mortalities are finally formulated as

$$(10) \quad \begin{cases} F_1^{\text{A}} = q^{\text{A}} E_1^{\text{A}} / l_1 = (s_{\text{A}} + s_{\text{B}}) / s_{\text{A}} q E_1^{\text{A}} / l_1 \\ F_2^{\text{A}} = q^{\text{A}} E_2^{\text{A}} / l_2 = (s_{\text{A}} + s_{\text{B}}) / s_{\text{A}} q E_2^{\text{A}} / l_2 \\ F_1^{\text{B}} = q^{\text{B}} E_1^{\text{B}} / l_1 = (s_{\text{A}} + s_{\text{B}}) / s_{\text{B}} q E_1^{\text{B}} / l_1 \\ F_2^{\text{B}} = q^{\text{B}} E_2^{\text{B}} / l_2 = (s_{\text{A}} + s_{\text{B}}) / s_{\text{B}} q E_2^{\text{B}} / l_2 \end{cases}$$

We will consider a constant total fishing effort E for the year over the whole area and explore a range of possible allocations of E over patches and seasons. We make two additional assumptions to obtain a simple model of effort allocation: (*i*) the inshore fleet generates a constant mortality rate all year long in patch B (recall that this fleet fishes exclusively in patch B) and (*ii*) during the second season, the industrial fleet generates the same mortality rate in both patches. These assumptions imply rescaling corresponding fishing efforts with respect to season length and patch surfaces, respectively. Alternatively, we may have considered equal nominal efforts rather than equal mortality rates in the previous assumptions. The assumption of equal mortality rates facilitates the comparison with the global model because from the population standpoint, the spatial heterogeneity then strictly pertains to the concentration of fishing effort during the first season in patch A.

Under assumptions *i* and *ii*, effort allocation over patches and seasons is parameterized as follows :

$$(11) \quad \begin{cases} E_1^{\text{A}} = (1 - \beta) \, \alpha E \\ E_1^{\text{B}} = \beta l_1 E \\ E_2^{\text{A}} = (1 - \beta)(1 - \alpha) \dfrac{s_{\text{A}}}{s_{\text{A}} + s_{\text{B}}} E \\ E_2^{\text{B}} = \beta l_2 E + (1 - \beta)(1 - \alpha) \dfrac{s_{\text{B}}}{s_{\text{A}} + s_{\text{B}}} E \end{cases}$$

with $E_1^{\text{A}} + E_1^{\text{B}} + E_2^{\text{A}} + E_2^{\text{B}} = E$. Parameters β and α quantify the total effort corresponding to the inshore fleet and the fraction of the industrial fleet's effort allocated in patch A during the first season, respectively. In terms of survival rates, the global model is equivalent to $\alpha = 0$ and $\beta = 0$. This parameterization does not capture all possible allocation schemes of fishing effort between seasons and patches, but it accounts for the existence of the two fleets: a highly seasonal industrial fleet and a nonseasonal inshore fleet. Because total effort E is constant, fishing effort allocation is simply determined by α and β.

Fig. 3. Population growth rate as a function of β, the importance of the nonseasonal inshore fleet, and α, the concentration of fishing effort on the continental shelf in winter. The empty planes correspond to the growth rate in the global model (broken line) and to a growth rate of 1 (solid line).
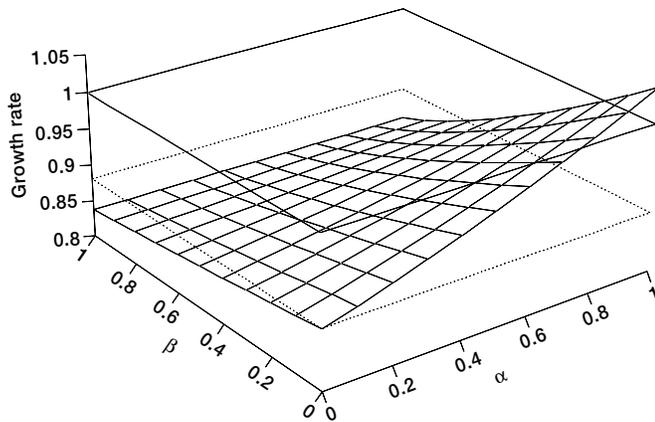
Application and results

To compare population and catch obtained under different fishing effort allocations, we computed the indicators of population and catch levels defined in the subsection entitled Evaluation of the dynamics of catch and population. We studied how migration rate m and effort allocation parameters influence the dynamics of both population and catch. We also examined the sensitivity of the results to several parameters and assumptions. We successively present results in the case of a linear stock-recruitment relationship, i.e., a constant recruitment rate at age 1 (termed the constant b case) and in the case of a constant recruitment at age 1 (termed the constant R case).

The dynamics of both spatial and global models are studied in the case of the saithe stock, whose biological characteristics were described in a previous section. Natural mortality and weights at age are taken from Anonymous (1992). Regarding recruitment, there is unfortunately no information available from surveys or previous studies about the biology of this population. Therefore, we consider the two alternative assumptions mentioned in the previous paragraph. In the constant b case, there is not enough information to estimate age-dependent fecundity coefficients without additional arbitrary hypotheses; therefore, we assume $b_a = b$ and crudely compute b from VPA stock size estimates as the ratio of the mean number of fish of age 1 to the mean number of mature fish in the previous year. This is consistent with the definition of b_a in eq. 2. In the constant R case, recruitment R is estimated as the historical mean value of VPA stock size estimates at age 1 in Anonymous (1992). Initial population sizes used for computing trajectories correspond to 1988 VPA estimates in Anonymous (1992). As for migration rates, there is no information nor are there experimental results concerning the value of the between-patch migration rate m, which we assume to be unknown. Conversely, the emigration rate e is set equal to 0.4 following Fontaine et al. (1985). Since no uncertainty was attached to this estimation in the latter study, we will study the sensitivity of the results to this parameter.

Definition of patches

To define precisely the extent of each patch, logbook data for the industrial fleet were used. The information reported in the logbooks consists of catch, fishing effort (in numbers of trawled hours), and fishing location for each vessel on a per trip basis. Fishing location is defined by a statistical rectangle that is the finest subdivision of ICES regulatory areas. The dimensions of a statistical rectangle are 30° latitude and 1° longitude, which in this zone roughly corresponds to a 30 nautical mile square. Multivariate data analyses were carried out with the logbook data on a monthly basis and for each statistical rectangle. This way, statistical rectangles could be grouped into two patches and two seasons according to their profiles of effort and catch (see for instance Fig. 2). Rectangles that represented negligible catch and effort levels were excluded from the application, particularly west of the continental slope.

Exploitation and effort allocation parameters

Exploitation characteristics are taken from Anonymous (1992). Since the early 1990s, exploitation by the industrial fleet has undergone thorough changes, in particular with the emergence of fishing for deep resources. Therefore, our study is based on the 1988 patterns of fishing mortality and fishing effort. A vector of catchabilities at age q is simply derived as $q = F/E$ where F is the fishing mortality vector for 1988 estimated from the VPA model used for the assessment in 1992 and E is the total effort of the industrial fleet in trawled hours for 1988. Parameter α can be computed from the industrial fleet effort data as approximately 0.2. The computation of β requires effort data for the inshore fleet. However, these data were not considered here because the effort measures of the industrial and inshore fleets are not comparable: neither the boat sizes, nor the gears used (different trawl types), nor the fishing techniques, nor the fishermen tactics (particularly the degree of targetting for saithe) are similar. No information is available to intercalibrate effort data by rescaling catchabilities. As the inshore fleet catch amounts to about 10% of total catch, it is more reasonable to neglect its effort when computing catchabilities, rather than combine incompatible data. This will probably introduce a slight error in the computation of catch and biomass levels in the real case situation. However, global and spatial models will be affected in the same way, and this approximation will be of little consequence when comparing different spatio-temporal allocations of fishing effort. The impact of the coastal fishing activity will rather be investigated through the parameter β (see eq. 11). Since the inshore fleet catch amounts to only 10% of the total catch, β is likely to be small, probably between 0.1 and 0.3.

Population dynamics

The first (and unexpected) result is the general insensitivity of the dynamics to the value of the migration rate m whatever the assumption about reproduction. Therefore, only results for $m = 0.3$ will be presented.

In the constant b case, the population dynamics is illustrated by the population growth rate, the biomass trajectories, and the stable age distribution. Under the effort allocation prevailing in 1988 (termed actual effort allocation), i.e., $\alpha = 0.2$ and plausibly $0.1 < \beta < 0.3$, the population growth rates in the spatial model and in the global model are very similar, around 0.89.

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Fig. 4. Evolution of the biomasses over a 20-year period for several values of α and β: α = 1 and β =0.2, α = 1 and β = 0.4, α = 0.2 and β = 0.2, and α = 0.2 and β = 0.4. The trajectories for the global model are very close to those of the last case (α = 0.2 and β = 0.4).

Fig. 5. Total biomass and total catch as a function of β and α after a generation time (constant *b* case). The broken line corresponds to the global model.
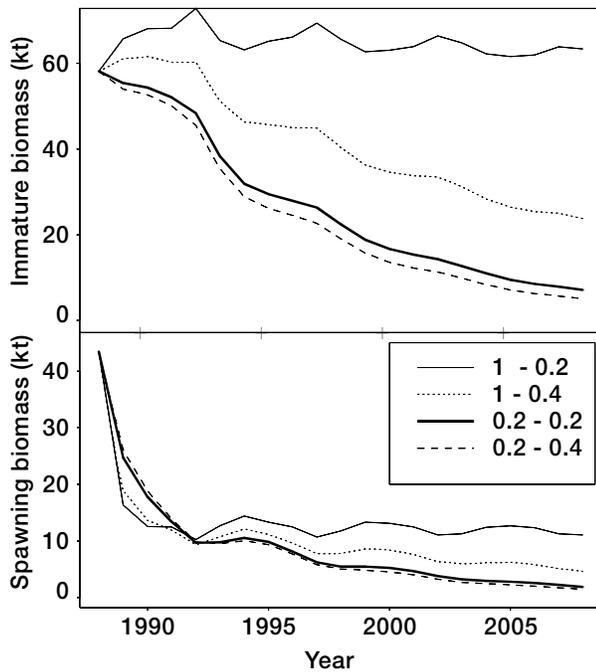
Table 1. Immature biomass in tonnes after a generation time for several values of β and α (constant *b* case).

β	α		
	0	0.2	1
0	16 694	22 880	111 465[a]
0.2	14 887	18 887[b]	62 679
0.4	13 331	15 743	36 313
1	9 869	9 869	9 869

Note: The corresponding biomass in the global model is 16 694 t.
[a]The effort allocation that maximizes both population and catch levels.
[b]The actual effort allocation.

Table 2. Mature biomass in tonnes after a generation time for several values of β and α (constant *b* case).

β	α		
	0	0.2	1
0	5277	6322	21 134[a]
0.2	4860	5462[b]	13 316
0.4	4515	4803	8 584
1	3876	3876	3 876

Note: The corresponding biomass in the global model is 5277 t.
[a]The effort allocation that maximizes both population and catch levels.
[b]The actual effort allocation.

From this standpoint, the population is overexploited. The population growth rate in the spatio-temporal model becomes

larger than in the global model roughly when α is larger than β (Fig. 3). Under these conditions, the spatial growth rate becomes more sensitive to changes in α and β. Logically, the influence of α is mainly apparent at small β values, i.e., when the industrial fleet effort constitutes the major component of exploitation. The largest growth rates are observed for simultaneously high α and low β values. They become even larger than 1 when α ≥ 0.8 and β ≤ 0.2. These results indicate that for a constant total effort, when fishing concentrates even more on spawners (α increases), the population growth rate does not decrease. In contrast, allocating more effort to catching immature fish (by increasing β) drastically affects the whole population. In fact, the population growth rate is driven primarily by the survival rate of the immature fish. Note that the intensive exploitation of the spawners takes place after reproduction (the consequences of this assumption will be evaluated later).

In general, the absolute magnitude of the growth rate does not vary much according to the parameters considered, but a small variation in the growth rate may induce large changes in population sizes as exemplified by biomass trajectories (Fig. 4). Recall that such trajectories are not predictions of future biomasses, but only represent equilibrium projections, in that all parameters remain constant over the projection horizon. Monotonically decreasing trajectories correspond to growth rates smaller than 1. Steadily increasing biomasses can be observed for α = 1 and β ≤ 0.2 (not represented here). Note that the general decrease in spawning biomass in the first years is sharp only because of the initial stock sizes.

Table 3. Age distributions obtained from the spatial model for two different effort allocations (β = 0.2 in every case).

Effort		Age group (years)						
allocation (α)	Reproduction	0	1	2	3	4	5	6–10
0.2	Constant b	0.284	0.261	0.203	0.125	0.071	0.033	≤0.015
0.2	Constant R	0.323	0.264	0.191	0.115	0.065	0.027	≤0.010
1	Constant b	0.295	0.230	0.180	0.141	0.110	0.035	≤0.009
1	Constant R	0.293	0.240	0.187	0.136	0.096	0.034	≤0.010

Note: The age distributions correspond to equilibrium in the constant R case, and to the stable age distributions in the constant b case.

Fig. 6. Equilibrium biomass and catch as a function of β and α (constant R case). The broken line corresponds to the global model. Note the difference between scales when comparing with Fig. 5.

Table 4. Immature catch in tonnes after a generation time for several values of β and a (constant b case).

	α		
β	0	0.2	1
0	4911	5467	0[a]
0.2	4688	5121[b]	5489
0.4	5974	5607	6142
1	3901	3901	3901

Note: The corresponding catch in the global model is 5094 t.
[a]The effort allocation that maximizes both population and catch levels.
[b]The actual effort allocation.

Table 5. Mature catch in tonnes after a generation time for several values of β and α (constant b case).

	α		
β	0	0.2	1
0	1227	3289	32 015[a]
0.2	1010	2414[b]	16 432
0.4	821	1734	8 319
1	380	380	380

Note: The corresponding catch in the global model is 1272 t.
[a]The effort allocation that maximizes both population and catch levels.
[b]The actual effort allocation.

Examining biomass levels after a generation time stresses the influence of β and α (Fig. 5, Tables 1 and 2). Biomass variations may of course be very high when comparing extreme values of the parameters, but it appears that slightly modifying the values of α and β from the actual effort allocation may produce significant changes in biomass values. Immature biomass is much more sensitive to changes in effort allocation than mature biomass. Again, results show that what matters to the population is not fishing on spawners, but fishing pressure on immature fish. Thus, when all the fishing pressure is concentrated on mature fish during the first season (α = 1 and β = 0), mature biomass is maximal, and after a generation time it is 2–5 times as high as under any other allocation scheme considered (Table 2). Under these conditions immature biomass is maximal too (Table 1). Therefore, it seems that in the long term, the persistence of the population is not af-

fected by a very high fishing pressure on spawners. Biomasses relative to the actual situation (α = 0.2 and 0.1 < β < 0.3) are substantially larger in the spatial model than in the global model, although corresponding population growth rates were found to be similar.

In the constant R case, the equilibrium biomass (reached after a generation) shows qualitatively similar variations with fishing effort allocation, being maximal for α = 1 and β = 0 (Fig. 6). However, on the whole it is less sensitive to α and β.

Note finally that whatever the assumption about recruitment, the age structures of the population are similar in most cases because the stable age distribution is not sensitive to parameters α, β, and m (Table 3). The spatial and global models yield similar results.

Catch dynamics

Similarly to the situation for biomasses, catch is not sensitive to the migration rate m, and mainly varies according to α and β (Figs. 5 and 6). Whatever the assumption about reproduction, total catch after a generation is maximal for β = 0 and α = 1, but it is much less sensitive to these parameters in the

Fig. 7. Sensitivity of the asymptotic growth rate to the relative surfaces of the patches for several values of α and β: $\alpha = 1$ and $\beta = 0.2$, $\alpha = 1$ and $\beta = 0.4$, $\alpha = 0.2$ and $\beta = 0.2$, and $\alpha = 0.2$ and $\beta = 0.4$. The vertical line indicates the real value ($s_B/(s_A + s_B) = 0.75$).
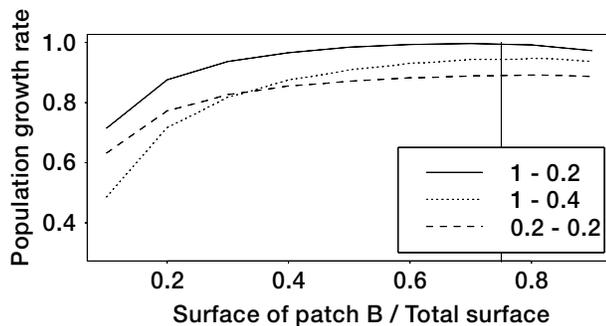
constant R case than in the constant b case. In the latter case, it may vary from 4281 t for $\beta = 1$ (independently of the value of α) to 32 015 t for $\beta = 0$ and $\alpha = 1$ (Tables 4 and 5). Moving from the actual effort allocation (7535 t) to the one that maximizes total catch (referred to hereafter as best effort allocation) would expand total catch fourfold. Recall that these values do not stabilize over years in the constant b case. Similarly to the situation for biomasses, catch trajectories (results not shown) emphasize descending or increasing trends in the case where population growth rates are smaller or greater than 1, respectively. In the constant R case, total catch is at equilibrium after a generation and roughly varies from 14 000 to 18 000 t. In this case, moving from the actual effort allocation to the best one would raise total catch from 14 588 to 17 721 t, i.e., an increase of only 21%. Considering mature and immature catches separately, we show that in any case, catch variations above all reflect changes in mature catch levels. As was found for biomass, a maximal catch is obtained when fishing effort exclusively targets mature fish during the first season.

Sensitivity analyses

At this point, it is necessary to investigate carefully the importance of some parameters and assumptions to (*i*) thoroughly understand why catch and population dynamics vary so much with the spatio-temporal allocation of effort and (*ii*) ensure that our results are not too sensitive to parameters that were crudely estimated or may undergo random fluctuations, or to assumptions that may prove difficult to check. Several parameters may a priori be important in investigating effort allocation between patches and seasons: the between-patch migration rate m, the emigration rate e, the ratio of the patch sizes, and season lengths. Migration rate m has proved to be a minor parameter throughout the analysis, and therefore will not be studied further. Note also that our results do not depend upon the relative lengths of the seasons because fishing effort is measured in hours per season. Hence, instantaneous fishing mortalities depend upon the lengths of the seasons, but not the mortality rates integrated over a given season. It would be different if effort were measured in number of boats (or gears) used during a season.

We considered the sensitivity of the results to the emigration parameter e. Unreported results show that the population growth rate is systematically affected in the same way regard-

less of effort allocation. Thus, the value of the emigration rate e does not generate qualitative changes in the results.

We then examined the influence of relative patch size in the constant b case. Population growth rates were computed over a range of values of $s_B/(s_A + s_B)$ (Fig. 7). Recall that as $s_B/(s_A + s_B)$ increases, the fishing mortality induced by a given effort decreases if this effort is applied in patch B and increases if it is applied in patch A. The values explored range between 0.1 and 0.9 to avoid unreasonably high fishing mortalities by reducing patch sizes too much. Results show that whatever the allocation of fishing effort, increasing F on spawners is not a problem: if patch A were even smaller, growth rates would not be much affected. In contrast, it would be harmful to the population to increase F on immature fish (for instance if patch B were smaller), since the growth rate would quickly drop below 0.8. This decrease would be mitigated in the case of moderate fishing pressure on immature fish, approximately when $\beta \leq 0.2$ and $\alpha \geq 0.8$ (cf. thin solid line in Fig. 7). In these cases, patch B should theoretically be smaller than patch A (i.e., $s_B/(s_A + s_B) < 0.5$) for the growth rate to drop below 0.9. Relative patch size is thus a sensitive parameter, because it is important for the relationship between fishing mortality and fishing effort. This result may be helpful if we want to discuss our results from a more general standpoint (see next section).

We also checked the consequences of assumption 1 (reproduction takes place before fishing). Reproduction takes place during the first quarter and there certainly exists some overlap in time between reproduction and fishing. To check the consequences of this possible overlap for our analysis, we assumed that the date at which reproduction takes place is uniformly distributed during the first season. Subsequent growth rates are only slightly modified (results not shown), and the relative performances of different effort allocation schemes are not qualitatively affected.

Finally, we checked the sensitivity of our results to recruitment parameters and to assumptions regarding the stock-recruitment relationship, assumptions that are likely decisive for the results.

The effective fecundity coefficient b, or alternatively the recruitment R, could only be crudely estimated. Also, these parameters may fluctuate randomly in relation to environmental conditions. We investigated these effects in the constant b case by carrying out 200 Monte-Carlo simulations, assuming a lognormal distribution for b with an arbitrary coefficient of variation (CV) of 50%. We found that the sensitivity of the population growth rate to random fluctuations in b is low and almost independent of α and β with a CV of approximately 7%. Logically, biomass and catch projections are much more sensitive, particularly as the time horizon for projections increases. After a generation time, biomass and catch CVs are approximately 94 and 89% under the actual allocation, versus 100 and 86% when $\alpha = 1$ and $\beta = 0$. Unlike catches, biomasses are slightly more sensitive for allocation schemes that yield the highest population growth rates. In the constant R case, C^{eq} and B^{eq} are proportional to R (see eqs. 7 and 8). Therefore, if R is a random variable with a given CV, C^{eq} and B^{eq} have the same resulting CV, which determines their sensitivity to R.

In the application, we considered an age-independent b because of a lack of information for estimating this parameter. We investigated the sensitivity of the results to a possible age

Fig. 8. Comparison between estimated real catch (real) and catch obtained from the models: global model (global), and spatio-temporal model for $\alpha = 0.2$ and $\beta = 0.2$ under the constant b assumption (spatial b) and under the constant R assumption (spatial R).
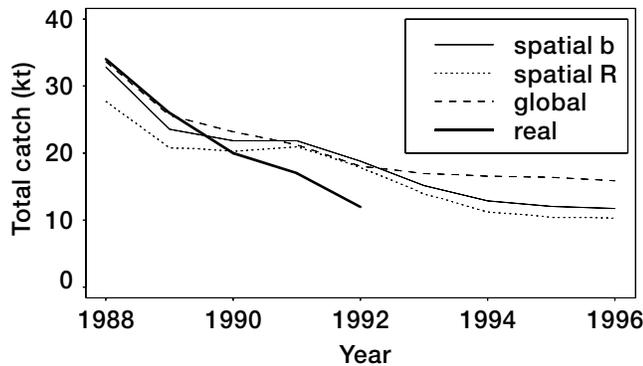
dependence of b considering that b_a is likely to be linked to individual weight at age a. There are different ways to achieve this and we explored several of them, so we only report qualitative results. Introducing age dependence for b amounts to increasing it for old age groups and decreasing it for young ones. Since the latter are more numerous in the population, this has the same effect as decreasing an age-independent b. Unreported results show that better allocation schemes, which used to have the highest population growth rates (α close to 1 and β close to 0), are more affected by a change in b than the other allocation schemes. When b diminishes, or equivalently when it is age dependent, population growth rates corresponding to better effort allocation schemes become closer to those of the other schemes, but still remain higher in any case.

In the analysis, we investigated two contrasting stock-recruitment relationships, a linear one and a constant recruitment. We also examined the dynamics of the model under a compensatory stock-recruitment relationship, e.g., a Ricker relationship (results not shown). As might be expected, the addition of a compensatory effect reduces the biomass and catch levels that can be observed for better allocation schemes. Biomass and catch trajectories are similar to those observed with a low constant coefficient b.

We conclude from these additional computations that our results about the relative performances of a range of fishing effort allocations are not qualitatively dependent upon the assumptions about reproduction, nor upon the value of the emigration rate or the fecundity coefficient. However, absolute levels of catch and biomass may be affected. In particular, the biomasses and catches presented above in the constant b case for better allocation schemes may be overly optimistic if (*i*) the overall reproduction level of the population is overestimated in the model, (*ii*) b depends upon age in reality, or (*iii*) there is a compensatory stock-recruitment relationship.

Discussion

Although this was not the main objective of the paper, available information allowed us to provide a diagnostic about the saithe stock in the west of Scotland under the exploitation regime prevailing during the 1980s. Under the constant b assumption, the level of fishing effort and its allocation between

seasons and patches in 1988 corresponds to a population growth rate of 0.89; therefore, the population should become extinct over an infinite time horizon if biological parameters and effort features remain unchanged. The population growth rate in the global model is close to that in the spatial model. Under the constant R assumption, the population cannot become extinct; the catch model is then close to an equilibrium yield per recruit model and only allows a possible diagnostic of growth overfishing (see below).

Catch projections are obtained from constant exploitation features; they may be compared on the short term with catches in 1988–1992. Both exhibit a similar descending trend (Fig. 8). The deviation between catches obtained from the model and real catches increases from 1991 onwards, probably in relation to changes in fishing strategies. As mentioned earlier, fishermen started to target deep resources after 1990.

The performances of the spatio-temporal model and the global model may also be compared. In general, the growth rate is higher in the first case. The difference in growth rates between the two models increases as the seasonality and heterogeneity of the exploitation increases, i.e., as the nonseasonal fleet becomes marginal (β diminishes) and the industrial fleet concentrates more on spawner aggregates during winter (α increases). This is because in the spatial model, the relationship between fishing effort and fishing mortality is described more accurately. In particular, because this model accounts for the fact that the industrial fleet mainly targets spawners during the first season, corresponding fishing effort does not induce mortality on immature fish.

Exploration of alternative allocation schemes for fishing effort

The spatio-temporal model presented above was mainly helpful in investigating catch and population dynamics under a range of fishing effort allocation schemes over patches and seasons, although the parameterization used does not capture all possible schemes. We showed that concentrating effort on spawners should not be harmful to the population, even if it were to occur within a small area (thus inducing very high fishing mortalities). In contrast, the population level is substantially affected by the mortality rate of immature age groups. This is all the more striking since patch B (where immature saithe live) is three times as large as patch A, so that a given fishing effort yields a mortality rate in patch B approximately one third of what it would be in patch A.

Under this model, the best allocation of fishing effort, i.e., the one that maximizes both population and catch levels, would be to fully concentrate on mature fish during the spawning season. This is true regardless of which assumption about reproduction is chosen among those considered in the analysis. Under the best allocation, immature age groups are simply not exploited. The age of recruitment to the fishery is thus increased from 2 to 5 years, which prevents recruitment overfishing in the constant b case. In the constant recruitment case, our model is a spatio-temporal version of the classical yield per recruit model (Thompson and Bell 1934; Beverton and Holt 1957). In this case, increasing the age of recruitment to the fishery prevents growth overfishing. Beverton and Holt (1957) also showed that for a fast growing species intensely exploited, it is desirable to delay the age of recruitment, so as to take full advantage of the fast growth during the first years.

Fig. 9. Biomass and catch trajectories obtained when introducing the best allocation scheme ($\alpha = 0$ and $\beta = 1$) after 6, 10, or 14 years (constant b case). The thick solid line corresponds to a status quo situation ($\alpha = 0.2$ and $\beta = 0.2$). Dots correspond to introducing the best allocation scheme in the 1st year.

Fig. 10. Biomass and catch trajectories obtained in the constant b case: for the actual situation, the best allocation scheme, and two levels of reduction of total effort: 95% (reduction 1) and 72% (reduction 2). Reduction 1 yields a growth rate close to that obtained from the effort allocation that maximizes both population and catch levels, whereas reduction 2 yields a growth rate of 1.

In addition, only large fish are caught, which may be desirable for commercial reasons. Under the best allocation of fishing effort, both biomass and catch are maximal whatever the assumption about reproduction, but the contrast in catch between the different effort allocations is much less striking in the constant recruitment case (Figs. 5 and 6). Moving from the actual allocation to the best one would result in multiplying total catch by 4 in the constant b case, but would only increase it by 21% in the constant R case.

In the constant b case, catch and biomass levels have to be considered with caution, because they depend on both initial population sizes and projection horizon. So it is interesting to study what would happen in a transient situation and at different population levels. We assumed that the actual situation corresponds to α and β equal to 0.2, and let stock sizes adjust for a few years. We then modified the fishing effort allocation so that it corresponds to the best scheme ($\alpha = 1$ and $\beta = 0$). This change was introduced in different years to evaluate the efficiency of the best scheme at several population levels (Fig. 9). The best allocation scheme always allows the population to rebuild because the population growth rate does not depend upon initial population sizes. More interesting are catch trajectories (Fig. 9). Moving from the actual effort allocation to the best effort allocation induces a short-term loss in catch. When this change occurs early enough, catch loss is limited to ca. 15%, but if it takes place when the population level is already very low, it may be higher. In general, the short-term loss in catch is found to affect the first 2 or 4 years following the change. This may be compared with short-term losses resulting from total effort reductions (see next section).
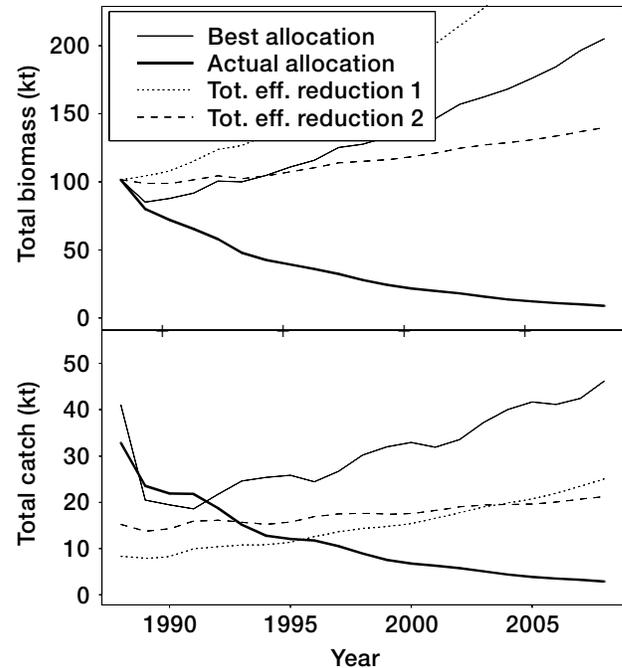
Evaluation of spatio-temporal management measures

By accounting for seasons and patches, our model explicitly describes the seasonal segregation of successive population stages in relation to the population life cycle. This enables us to contemplate a wider range of management measures, including openings and closures of fishing zones and (or) fishing seasons. Such spatio-temporal measures may be compared with a global measure like total effort limitation, for instance.

Consider the best allocation scheme found in the analysis, i.e., fishing exclusively on spawner concentrations. In these conditions, the population growth rate is around 1.05. To attain this growth rate under the current allocation scheme, it would be necessary to decrease total effort by 95%, whereas under the best allocation scheme, total effort would remain unchanged. If we were only aiming at a growth rate of 1, a 72% reduction of total effort would still be required. Biomass trajectories exemplify the differences in growth rates (Fig. 10). In fact, the best allocation scheme is very conservative for the stock. Under this scheme, total effort may even be substantially increased without decreasing the population growth rate below 1.

Regarding catch, the advantage of reallocating effort is even more striking. First, although population growth rates are similar, catch is always much lower under the global measure than under the best allocation scheme (Fig. 10). In addition, global measures induce short-term losses in catches (with respect to the status quo) that last longer (7 or 8 years) and are more severe than those implied by reallocating effort (bottom of Fig. 10). Recall that the magnitude of short-term loss is to

Fig. 11. Equilibrium catch (constant R case) as a function of total effort multiplier (1 corresponding to actual total effort) for two fishing effort allocations: $\alpha = 0$ and $\beta = 1$ (Best), and $\alpha = 0.2$ and $\beta = 0.2$ (Actual).
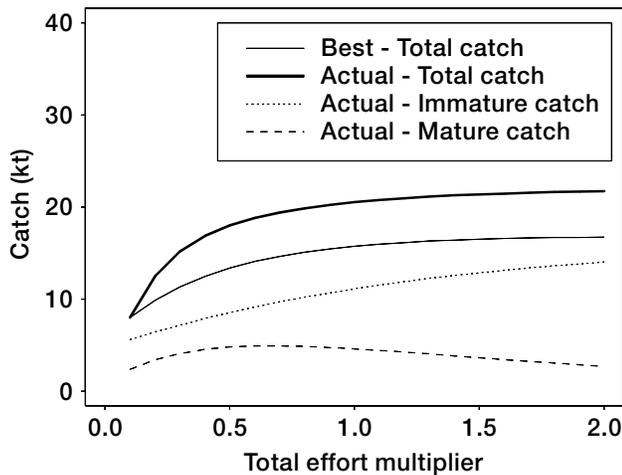
some extent tied to the initial conditions for the stock (see previous section).

Let us consider this question under the assumption of a constant recruitment R. Then, biomass level is not an issue any longer. Equilibrium catches were computed for a range of effort multipliers under the best and the actual effort allocation (Fig. 11). In the actual situation, the actual equilibrium catch is ca. 14 500 t, as opposed to a maximum of ca. 19 500 t under the best allocation scheme. This catch level cannot be attained by increasing the total effort under the actual effort allocation (the maximal catch for the actual allocation is only around 16 000 t). Therefore, changing effort allocation and total effort enables an increase of 30% in total catch at equilibrium. In this case, short-term losses in catch are minor.

In general, the global measure performs poorly with respect to catch because the exploitation pattern remains the same and there is no change in the age composition of catches. In contrast, when moving to the best allocation scheme, only mature fish are caught and immature fish are no longer exploited. Therefore, the short-term loss in total catch is moderate. Avoiding or mitigating short-term losses in catch is a desirable property for any management measure that aims at reducing overexploitation. Such transitional phases have for instance been studied by Beverton and Holt (1957) and Pelletier and Laurec (1992).

Conclusions

With this model, it is thus possible to show how effective some spatio-temporal management measures may theoretically be. They entail simultaneously a better state of the population and higher catches, when compared with a global measure like total effort limitation. These conclusions have been made possible because this model explicitly accounts for the dependence of exploitation features upon the population life cycle. The main feature, the concentration of fishing on spawners during winter, is captured by a rather simple two-patch, two-season model with migration, which suffices to depict the es-

sentials of the fishery dynamics. Congregation of spawners for reproduction is a frequent feature of the life cycle of many demersal species. What may vary is the extent of the spawning area with respect to the total distribution area. The concentration of exploitation at a place or a moment where fish are more vulnerable because they are grouped also occurs in other instances. In these situations, it is thus important to assess the stock from a model that explicitly accounts for these relationships between exploitation and population. When there is a diagnostic of overexploitation, it may sometimes be possible to address this problem at least partially by resorting to spatiotemporal management measures like opening and closing sensitive zones during a given period of the year. In this paper, we did not evaluate the technical and political feasibility of such measures, which is beyond our competence.

Lastly, the above analysis may be improved in two respects. First, the evaluation of the effort allocation prevailing in the 1980s would be more accurate if data for the inshore fleet had been included. This would require a standardization of fishing effort and catchabilities between the industrial and the inshore fleet, which would probably prove difficult to achieve. Second, some biological parameters are only crude estimates, like the effective fecundity coefficient, recruitment coefficient, and natural mortality coefficient. Note incidentally the insensitivity of our results to the migration rate. Although this depends to some extent on certain characteristics of the system studied, this insensitivity is noteworthy because the difficulty of estimating migration rates is sometimes presented as an impediment to developing spatial models.

The spatio-temporal model presented includes several strong assumptions (particularly about reproduction), the consequences of which were evaluated in the previous section. Among these assumptions, this model is a static description of the system, in that biological parameters and survival rates are constant over time and independent of population sizes. In the constant recruitment case, this leads to an equilibrium situation after a generation time. But in the constant b case, the possible population dynamics emphasize that this model should be used only for diagnostic purposes over a limited time horizon. It is not appropriate for predicting population and catch dynamics, nor for exploring long-term diagnostics. In this analysis, we use it to compare fishing effort allocations, mostly over a generation time. Besides, it is likely that catchabilities, effective fecundity coefficients, and recruitment are affected by density-dependent effects when population levels are drastically modified. In this respect, the strongly contrasting biomasses and catches obtained under extreme effort allocations are probably too optimistic. Unfortunately, no information about possible density-dependent effects is available because of the lack of contrast in exploitation features over years. Another shortcoming of this static description is that this model cannot capture possible effort dynamics with respect to the abundance of the target population, unlike predator–prey type models (Allen and McGlade 1986). This is illustrated by the change in fishing strategies observed in the data after 1991, when fishermen started to target deep species in addition to saithe. It is likely that in most cases, fishing strategies will depend upon the abundances of several species and not only one. Therefore, any model that accounts for effort dynamics should include multispecific considerations. This seems to be a major avenue for future fisheries modelling.

Acknowledgements

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Appendix

Construction of the spatio-temporal model

Consider the two-patch, two-season dynamics described in the second section. Let $N^{AB}(t)$ be the vector of population sizes in each patch at time t:

$$^t N^{AB}(t) = \left(N_0^A(t), N_1^A(t),..., N_{n-1}^A(t), N_0^B(t), N_1^B(t),..., N_{n-1}^B(t) \right)$$

where n is the number of age groups (including 0 group) and $^t N^{AB}(t)$ denotes the transposed vector of $N^{AB}(t)$.

Under the assumption of a constant recruitment rate at age 1, the evolution of $N^{AB}(t)$ may be described via a Leslie matrix L:

(A.1) $\quad N^{AB}(t+1) = L N^{AB}(t)$

In general, L can be written as:

$$L = \begin{pmatrix} L_A & Q_{BA} \\ Q_{AB} & L_B \end{pmatrix}$$

where the block matrices L_A, L_B, Q_{AB}, and Q_{BA} correspond to the survival and movement of the individuals present in patch A who survive and stay in patch A, those present in patch B who survive and stay in patch B, those present in patch A who survive and migrate to patch B, and those present in patch B who survive and migrate to patch A, respectively.

To construct the population matrix L for the entire year, we consider each season separately. To avoid a tedious presentation of every intermediate matrix, we only express population sizes in each patch at the end of each season, i.e., $N^{AB}(t + l_i)$ and $N^{AB}(t + 1)$ where l_i denotes the length of season i.

First season (January to April)

By convention, the fish change age groups right after time t at the beginning of the year. Reproduction takes place before fishing at the beginning of this season, so that the number of young-of-the-year at the end of this season is given by:

$$N_0^A(t + l_1) = \sum_{a=5}^{10} b_a^* N_{a-1}^A(t)$$

where b_a^* is the effective fertility coefficient at the end of the first season for individuals of the ath age group, so that b_a^* accounts for the natural mortality of the juveniles during that season. The lag in indices between b_a^* and N_{a-1}^A in the previous equation is due to the convention for changing age groups. Individuals of age 4 at time t are 5 years old and therefore spawn at time $t + l_1$.

The other immature age groups are confined to and exploited in patch B:

$$N_a^B(t + l_1) = N_{a-1}^B(t) \exp\left(-(F_1^B(a,t) + M) l_1 \right), \quad \forall a = 1,...,4$$

Mature fish are first confined to and exploited in patch A, and then some of them migrate instantaneously at the end of the season (i) toward patch B (m) and (ii) northeastwards (e), so that

$$\begin{cases} N_a^A(t + l_1) = N_{a-1}^A(t)(1 - m - e) \\ \qquad \exp\left(-(F_1^A(a,t) + M) l_1 \right) \\ N_a^B(t + l_1) = N_{a-1}^A(t)\, m \exp\left(-(F_1^A(a,t) + M) l_1 \right), \\ \qquad \forall a = 5,...,10 \end{cases}$$

Note that $m + e$ has to be smaller than 1.

Second season (May to December)

During this season, the number of young-of-the-year only decreases as a result of natural mortality. They migrate toward the coastal patch (patch B) at the end of the year, so that

$$N_0^B(t + 1) = p_0 N_0^A(t + l_1)$$

where p_0 is the survival rate of the young-of-the-year during the second season. With the exception of age group 4, the other immature fish remain in patch B:

$$N_a^B(t + 1) = N_a^B(t + l_1) \exp\left(-(F_2^B(a,t) + M) l_2 \right), \quad \forall a = 1,...,3$$

At the end of the season, all future spawners migrate instantaneously toward patch A:

$$\begin{cases} N_4^A(t+1) = N_4^B(t+l_1) \exp\left(-(F_2^B(4,t)+M)\,l_2\right) \\ N_a^A(t+1) = N_a^A(t+l_1) \exp\left(-(F_2^A(a,t)+M)\,l_2\right) \\ \qquad + N_a^B(t+l_1) \exp\left(-(F_2^B(a,t)+M)\,l_2\right), \\ \qquad\qquad\qquad\qquad\qquad \forall a = 5,\dots,10 \end{cases}$$

Annual dynamics of the population

The population is counted at time t, i.e., the beginning of the year, when immature fish and fish that will spawn are segregated in patches B and A, respectively. Thus, the population at time t may be entirely described by the following vector:

$$N(t) = \begin{bmatrix} N_0^B(t) \\ N_1^B(t) \\ \vdots \\ N_3^B(t) \\ N_4^A(t) \\ \vdots \\ N_{10}^A(t) \end{bmatrix}$$

Then, eq. A.1 simplifies to

$$N(t+1) = LN(t)$$

where L is the following Leslie matrix:

$$L = \begin{pmatrix} 0 & 0 & 0 & 0 & b_5 & \cdots & b_{10} \\ p_1 & 0 & 0 & \cdots & \cdots & \cdots & 0 \\ 0 & p_2 & 0 & & & & \vdots \\ 0 & 0 & \ddots & \ddots & & & \vdots \\ \vdots & & \ddots & \ddots & \ddots & & \vdots \\ 0 & & & 0 & \ddots & 0 & 0 \\ 0 & 0 & \cdots & 0 & 0 & p_{10} & 0 \end{pmatrix}$$

and

$$\text{(A.2)} \begin{cases} b_a = p_0 \cdot b_a^*, \quad \forall a = 5,\dots,10 \\ p_a = \exp\left(-(F_1^B(a,t)\,l_1 + F_2^B(a,t)\,l_2 + M)\right), \\ \qquad\qquad\qquad\qquad \forall a = 1,\dots,4 \\ p_a = (1-m-e)\exp\left(-(F_1^A(a,t)\,l_1 + F_2^A(a,t)\,l_2 + M)\right) \\ \qquad + m\exp\left(-(F_1^A(a,t)\,l_1 + F_2^B(a,t)\,l_2 + M)\right), \\ \qquad\qquad\qquad\qquad \forall a = 5,\dots,10 \end{cases}$$

Note that b_a is the effective fecundity coefficient after 1 year. The model can accommodate alternative maturity curves by changing the first row of the matrix appropriately.

In the case where recruitment is constant, the population dynamics cannot be framed into a Leslie matrix; survival rates remain unchanged (cf. eq. A.2) but the number of young-of-the-year is simply given by:

$$N_0^B(t+1) = R$$