A new hypothesis concerning the nature of small pelagic fish clusters
An individual-based modelling study of Sardinella aurita dynamics off West Africa

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Abstract
Coastal populations of small pelagic fish display nested aggregation levels. Above the level of the school structure, clusters are observed the nature of which has not been definitively determined. We hypothesized that these clusters corresponded to a materialisation of the microcohorts originating from successive spawnings of fish populations in their vital domain.

A candidate individual-based model was developed to investigate this hypothesis. This model is based on pattern-oriented modelling of a concrete documented case: the dynamics of the round sardinella (Sardinella aurita) population living off the West African coasts and subject to environmental fluctuations caused by seasonal upwelling. The simulated agents were round sardinella microcohorts situated and moving in a discretised physical environment. The combined effects of environmental forcing (temperature, wind, retention) and inner biological dynamics (reproduction, growth and mortality, competition) condition the dynamics of this population.

The modelled behaviour generated realistic dynamic patterns (population distribution, spawning zones, periods and plasticity, biomass fluctuations), which were obtained simultaneously and successfully compared with observations. The steady-state number of microcohorts obtained after simulation convergence was similar to the number of clusters observed in situ in this area for this population.

The realism and diversity of the patterns simultaneously simulated suggested the cluster-microcohort equivalence hypothesis as a candidate framework accounting for the origin of the clusters observed in situ.

Within this preliminary exploration, we discuss the consistency of the hypothesis and the accuracy of the model. If the correspondence between clusters and microcohorts proves to be real, it may be transient and progressively modified by other environmental factors. If stable over time, as simulated in the model, the number of observed clusters should be related to the number of spawning events in the species’ lifetime.

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1. Introduction

Animal aggregation is a general natural phenomenon (Allee, 1927, Wilson, 1975 in Viscido et al., 2004) that may generate high-level structures such as schools, flocks, swarms or herds (DeAngelis and Mooij, 2005) or less complex gatherings (clusters, concentrations, crowds). Aggregation mechanisms may have a broad range of possible biological or environmental causes (Allee, 1927) or both (Levin, 1994); patterns may in particular be accounted for by self-organisation (Detrain and Deneubourg, 2006). However, aggregation patterns may occur in the absence of adaptation or functional reasons, and aggregative structures may also appear as epiphenomena (Flierl et al., 1999) resulting from the configuration of the individuals (Young et al., 2005), the complexity of the inanimate environment (Parrish and Edelstein-Keshet, 1999), multi-scale effects (Rietkerk and van de Koppel, 2008) or noise (D’Odorico et al., 2007).

Small pelagic fishes are the world’s main marine resources (FAO, 2005) and are therefore of primary economic importance. They also provide a good model of gregarious behaviour (Fréon and Misund, 1999) with practical consequences for fishing practices (Petitgas, 2003) or stock assessment (Petitgas et al., 2001). Species of this biological group are indeed characterised by embedded aggregative structures at various spatial scales, ranging from dense nuclei of individuals within a school to substocks (Bertrand et al., 2008). At the local level, schooling behaviour has been studied in most detail. It involves several adaptive traits, such as response to predation, feeding, reproduction, hydrodynamic properties (Gerotto

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and Paramo, 2003; Fréon et al., 2005; Breherm et al., 2007). At the upper aggregative level, acoustic pelagic survey studies and geostatistical analyses have shown that individual schools aggregate into clusters (Petitgas and Levèzene, 1996; Fréon and Misund, 1999). Clusters are now considered to be a real phenomenon in small pelagic fishes (Swartzman, 1997) with temporal span scale of weeks in some cases (Mackinson et al., 1999). Reid et al. (2000) also suggested that clusters may be more robust aggregations than schools, which may be more labile and opportunistic structures (Breherm et al., 2007). However, the underlying reasons for cluster formation remain unclear, probably due to the difficulties involved in studying these structures (Swartzman, 1997; Haugland and Misund, 2004). Swartzman (1997) showed that temperature, depth, the height of the school and the number of schools within a cluster were related, whereas Petitgas et al. (2001) concluded that relationship between abundance and school clustering was unclear. A number of interpretations and hypotheses concerning the origin of small pelagic fish clusters have also been put forward, such as responses to hydroclimatic conditions (Swartzman, 1997), environment patchiness (Fréon and Misund, 1999) communication between schools (Haugland and Misund, 2004) or meso-scale (10 s km) food availability (Bertrand et al., 2008). Several reviews have concluded that the reasons for school clustering remain a matter of speculation (Fréon and Misund, 1999; Haugland and Misund, 2004) or are not unique (Fréon et al., 2005).

In this work, we suggest that, in the observed aggregation and distribution patterns of small pelagic fish populations, clusters may correspond to an observable trace of the microcohorts generated at each spawning event at a given location. The observed cluster structure may therefore partly reflect the history of successive spawning events in the population.

There are arguments to support this cluster-microcohort equivalence hypothesis. Small pelagic fishes, particularly those living in upwelling areas, are highly susceptible to environmental fluctuations (Bakun, 1996; Cury et al., 2000). Major environmental effects (temperature, wind, current) operate on a meso-scale (Fréon et al., 2005; Bertrand et al., 2008; D’Orgeval et al., 2005) and leave a few degrees of freedom for population dynamics, such as restricted spawning windows (Cury and Roy, 1989; Bakun, 1996). This global forcing may lead to a conservative environment with identical responses of the organisms or groups of organisms to fluctuations. The cohesion of microcohorts may then persist for longer periods in such situations than in populations living in more fragmented and ‘dissipative’ habitats (Latore et al., 1999; Flather and Bevers, 2002).

In this study, we carried out a preliminary exploration of the realism of the cluster-microcohort equivalence hypothesis. The selected modelling approach fits into the framework of individual-based ecology (Grimm and Railsback, 2005): we test the hypothesis by evaluating how realistically a candidate microcohort-based model reproduces patterns observed at population level. The emergent feature proposed by the individual-based formalism (e.g., Railsback, 2001; Hölker and Breckling, 2005) can be used to separate the level formalised (the microcohorts) and the level of the resulting patterns (the population dynamics) used for validation (Grimm et al., 1996, 2005). Reproduction of the patterns observed at population level is then used as a criterion for evaluating the accuracy of the assumptions underlying the model.

As a test case, we chose to model the spatio-temporal dynamics of the population of round sardinella, Sardinella aurita (Valenciennes, 1847), a clupeoid pelagic fish species that lives along the coasts of Senegal and Mauritania in an upwelling-driven environment. The East-Atlantic upwelling is an Ekman-type upwelling (Cury and Roy, 1988; Roy et al., 1988) caused by wind stress, generating an environment in which water temperature and richness in nutrients fluctuate over time. We carried out a simulation based largely on data from the 1980s. Indeed, this period was particularly rich in field studies on this population (Boëly, 1980, 1982; Boëly et al., 1982a,b; Conand, 1977a,b; Cury and Roy, 1988, 1989; Demarcq, 1998; Demarcq and Samb, 1991; Fréon et al., 1979; Fréon, 1988; Garcia, 1982; Maxim and Maxim, 1988; Rebert, 1983; Roy, 1989, 1991; Roy et al., 1989), providing both knowledge relating to the various sets of processes formalised and data for calibration and validation of the model.

We integrate all the available information on both the biological features of this species and on the physical environment dynamics into a single individual-based model. The model describes the creation and evolution of a spatially and temporally overlapping set of fish microcohorts living in a simulated coastal area. The simulations results should determine whether this hypothesis and its associated aggregation level can generate the global patterns observed in situ: migration, sites and periods of reproduction, estimated biomass levels and fluctuation, plasticity of the population response to environmental fluctuations.

2. Model description

Individual-based formalism (e.g., DeAngelis and Mooij, 2005) was selected for the emergent feature it proposes and the validation criteria it constitutes. We also chose to use this formalism because it can generate realistic field models. Indeed, this approach can simultaneously account for (i) composite, heterogeneous factors and interactions (Breckling et al., 2006), (ii) intrapopulational variability through individualised fates of the components (Huston et al., 1988), and (iii) spatially distributed mechanisms in heterogeneous space (Bascompte and Solé, 1995; Parrot and Kok, 2000; Bartsch and Coombs, 2001).

The individual-based formalism used is a derived multi-agent modelling scheme (Ginot et al., 2002; Bousquet and Le Page, 2004) in which agents are computer objects with abilities in terms of perception, deliberation, action, interaction, goals and behaviour within a simulated environment (Ferber, 1999).

The description of the model follows the ODD protocol (Overview, Design concepts, Details) proposed by Grimm et al. (2006) for describing individual-based models. According to this scheme, an overview is first presented, explaining the purpose of the model, its state variables, scales and process scheduling. The design concepts are then described (emergence, fitness, interaction, etc.), followed by details concerning its implementation (initialisation, input, submodels).

2.1. Purpose

The model aims to explore, as a preliminary assessment, the realism of a hypothesis that suggests equivalence between the age classes (microcohorts) of a small pelagic fish population and the aggregated structures (clusters) observed in situ for that population.

The individual-based model implements this hypothesis. It simulates the spatio-temporal dynamics of a small pelagic fish population composed of various individualised age classes.

The model combines, in a simplified and integrated scheme, (i) the spatial heterogeneity and dynamic fluctuations of a discretised physical environment, the coastal waters off West Africa and (ii) the main life traits of S. aurita’s biological cycle (longevity, growth, reproduction).

2.2. State variables and scales

Two types of object classes are defined in the model: one describing spatial areas and one formalizing the sardinella microcohorts. A supplementary class defining the biological characteristics of the species is also implemented.
The sardinella population migrates seasonally between Senegal and Mauritania, apparently driven by spatio-temporal fluctuations in upwelling (Fréon, 1988; Roy, 1989). The simulated area therefore corresponds to the habitat range of this population (Fig. 1). Space is discretised using a set of 14 contiguous ‘marine zone’ objects in which hydroclimatic characteristics vary independently over time.

Each ‘marine zone’ object covers 0.65° in latitude and the whole continental shelf in longitude. Each object is defined by its location and area, water temperature, hydrodynamic retention value, wind speed, and coastal upwelling index, a proxy for biotope enrichment. Hydroclimatic characteristics are individualised and uniform within each ‘marine zone’ object. The meaning of the abiotic environment variables and the data sets from which their values were obtained are described in Section 2.6.

A fortnightly time step was used to account for the propagation of upwelling along the coast and its possible effects on the sardinella population.

The ‘microcohort’ class defines the active agents; each corresponds to a set of individuals born at the same time step and in the same ‘marine zone’ object. The variable set characterizing a microcohort consists of its name, the species to which it belongs, its location (x, y and marine zone), age, birth date, the length and the number of individuals.

The ‘species’ class includes general items relating to the specific characteristics of the microcohort agents. In this model, only S. aurita agents are considered. The attributes of the species class are its name, life time, parameters for growth, length-weight and weight-fecundity relationships, mortality rate and sex-ratio vectors, number of spawnings per year, duration of the sexual rest period, ages at which particular maturation points are reached, swimming speed and abiotic parameter preferences. The use of these parameters is detailed in Section 2.7.

2.3. Process overview and scheduling

The characteristics and behaviour of fish change during the course of the life cycle. To account for these differences a system composed of three microcohort agent sub-classes has been formalised: ‘juvenile’, ‘youngster’ and ‘adult’. Youngsters are young fishes of reproductive age that remain in or near their nurseries until they first reproduce (Boëly, 1980). Adults are ‘mature’ reproducers able to migrate according to the intensity of the upwelling. The different functions attributed to each sub-class are used to differentiate between them. The life cycle of sardinella is formalised by successive added functions that each agent has to accomplish (Fig. 2).

At birth, the fish belongs to the juvenile class. Their only ‘functions’ are growth and death. When they reach the age of sexual
maturity, they become youngsters. They retain their previous function and take on a new one: waiting for favourable conditions for reproduction. After their first spawning, youngsters become adults, with the added function of remaining within a favourable temperature range. They follow a succession of directional movements resulting in migration (emergent pattern) toward favourable upwelling conditions.

The overall simulation schedule is summarised in Fig. 3, and each step is described in detail in Sections 2.6 and 2.7.

At the beginning of each time step, the environmental conditions (see Section 2.6) are input into the model, using field data. Thereafter, information concerning the sardinella agents is updated, modifying data for age, weight (using the growth procedure) and the number of individuals (agent size, the agent being a group of fish at the same stage of development), using the natural mortality procedure. The agents are then allowed to act, their actions depending on their status (e.g., how many times they have spawned), the environmental conditions in which they are situated and their ‘function’ (moving, spawning).

2.4. Design concepts

2.4.1. Emergence

This study is based on a pattern-oriented modelling approach (Grimm et al., 2005; Reuter et al., 2005) in which the model generates patterns that are not explicitly coded, but which result instead from the collective interactions of the elements comprising the model.

Following the IBM/multi-agent bottom-up approach methodology (e.g., Reuter et al., 2005; Grimm et al., 2005), we only selected as simulation results the upper level patterns that could be compared with observations made in situ. We first considered the spatial distribution of the resource, with migration occurring as a result of local movement. Population spawning periods and areas were also simulated as the sum of microcohort ‘choices’ bound to biological state and local environmental conditions. The third simulated pattern relates to the distribution and dynamics of the population biomass. This pattern results from (i) collective individual growth, linked to size, (ii) environmental conditions and (iii) the individual history of the microcohort agents.

Lastly, the number of microcohorts at the end of the simulation reflects all the mechanisms and inputs of the model. This variable is compared with the number of clusters observed in situ.

2.4.2. Adaptive traits

Two adaptive traits are formalised to improve the agents’ fitness; the first concerns the ability of reproducers’ agents to evaluate the favourability of environmental conditions for spawning. The second concerns the ability of adults to move from one ‘marine zone’ to another in search of optimal conditions. This last trait is an indirect adaptive trait, as the search for better conditions do not provide any advantage (e.g., better growing condition) but the possibility of discovering better areas for spawning.

2.4.3. Fitness

The search for favourable reproduction conditions is a key aspect of population fitness in sardinella. For Ekman-type upwelling-dependent species, Cury and Roy (1989) demonstrated the existence of an optimal environmental window in the form of a dome-shaped relationship between larval survival success and wind speed, reflecting a trade-off between hydrodynamic turbulence and nutrient enrichment. According to Shin et al. (1998), three environmental conditions are assumed necessary for spawning to occur: a convenient retention zone (in this case, the identified spawning areas), a wind speed within an optimal environmental window and a maximum upwelling index. In the model, if the agents’ ‘marine zone’ meets these requirements, spawning is simulated. Otherwise, the agent may move to surrounding areas if it detects more suitable conditions elsewhere.

A simple process was implemented to formalise movement of the population in the domain. By superimposing the migration pattern (Boëly et al., 1982b) and sea surface temperatures, Pauly (1994) suggested that adults may have different thermal preferences and migration distances as a function of their weight. Nevertheless, for the sake of simplicity, we assumed that all adults migrate according to the same thermal preference, corresponding to an interval of water mass temperatures ($T_{optimal}$).

2.4.4. Interaction

Interactions between agents concern only competition for food between juveniles in a given area. This feature was included in the model to account for the sensitivity of juveniles to the amount of food available during their development (Cushing, 1973).

Fig. 2. Round sardinella biological life cycle model. Rectangle: agent class, ellipse: formalised process associated with the agent class. Agents change their status during their life cycle, thereby gaining the ability to perform new actions.

Fig. 3. Simplified flowchart of the processes involved in the model. Each step is applied sequentially to each set of agents (juveniles, adults, etc.). Within each set the agents are activated in the order in which they were generated (i.e., oldest first). Variables are updated immediately (asynchronous updating). The procedure for changing class (named ‘biological cycle’ in Section 2.7) between juveniles, youngsters and adults is not shown.
2.4.5. Sensing

In the model, sensing is not explicitly formalised as a process. Nevertheless, agents obtain information from their current environment and adults may also obtain information about adjacent areas (suggesting that they may be able to sense gradients). The agents sense wind speed, water temperature and food availability—factors affecting reproduction and the search for optimal conditions. These parameters are described in Section 2.6. Moreover, the sensing ability of the agents does not necessarily result in good or bad adaptation. For example, depending on their cruising speed (a calibrated parameter), they may arrive 'too late' in a favourable area.

2.4.6. Stochasticity

No stochastic processes are used in the model to optimise the control and capture of causal relationships between factors and dynamics.

2.4.7. Collectives

The sardinella population was formalised using the ‘super-individual’ concept (Scheffer et al., 1995) according to which 'agents' correspond to groups, in this case, microcohorts of the simulated population. Under the study hypothesis, each agent also formalises an observed concrete cluster assumed to be a set of schools, each of which (i) belongs to the same age class and (ii) is subjected to the same simulated spatio-temporal environmental conditions. Spatio-temporal processes beneath this level (such as school dispersion or aggregation within a cluster) are not considered.

2.4.8. Observation

The type of observations used for simulation are of the ‘omniscient’ (Grimm et al., 2006) type, with graphical display of the simulated population's patterns over space and time. Sensitivity analyses are carried out on subsets of parameters (e.g., preference values, longevity) and input data (initial number and type of agent). Functions (e.g., moving, spawning) are also turned on and off to investigate their influence on the resulting patterns.

2.5. Initialisation

Initialisation involves establishing the species object state variables, loading the marine zone object and a collection of microcohorts' agents. Various combinations of initial agent sets were tested during analyses of the relationship to the number of clusters. However, for results and sensitivity analysis for other factors, we used the same set of agents in each case, consisting of 6 juvenile, 1 youngster and 52 adult microcohorts spread over five of the existing 14 marine zones (this arbitrary composition corresponds to a steady-state configuration arising from the simulations; it does not significantly alter the resulting patterns, see sensitivity analysis, Fig. 9).

2.6. Input

The main input concerns the Upwelling hydroclimatic dynamics: in the study area (Fig. 1), the north Mauritanian upwelling is continuous, but fluctuates in intensity. The Senegalese coast is subject to a seasonal upwelling, with a cold and a warm season (Roy, 1989). The cold season starts around the end of October on the north coast and mid November on the south coast; it depends on the arrival of the trade winds. Decreases in wind speed towards the end of May lead to the arrival of warm masses of water with low levels of nutrients from Guinea to the south of Mauritania (Robert, 1983; Cury and Roy, 1988).

Four factors appear to influence sardinella dynamics. Temperature, as an indicator of oxygen availability, may drive migration (Pauly, 1994). Water turbulence and hydrodynamic retention may drive larval settlement and development (Porch, 1998). Finally, upwelling intensity, as an indicator of food availability, influences dynamics. Available observed data were used to account for these factors. Their spatio-temporal variation and discretisation are presented as latitude-time diagrams in Fig. 4.

Sea surface temperature was used as an indicator of water mass temperature. Values were derived from biweekly Meteosat satellite data (Demarcq, 1998). The temperature in each 'marine zone' object corresponds to the mean observed between the northernmost and southernmost latitudes of the zone.

Wind stress was used as an indicator of turbulence. Wind speed data were obtained from the COADS datasets, from a network of survey samplers providing monthly data for each degree of latitude (Roy and Mendelissohn, 1998).

Retention is a local hydrodynamic process dependent on the topographic characteristics of a marine area. It results in water circulation cells in particular conditions that limit the drift of the superficial water layer offshore and therefore favour the retention of larvae and food (Bakun, 1996). As hydrodynamic processes were not formalised in this model, the retention ability of a marine zone was formalised as a Boolean field of the 'marine zone' class. Known nursery grounds are considered to be favourable places for retention (see Fig. 1), whereas other areas are considered to correspond to unfavourable retention conditions for spawning.

Food availability is calculated using the coastal upwelling index (CUI). This index is calculated from the Ekman transport equation, which estimates water mass transport by the wind. This index is a standard indirect indicator of environmental enrichment through an Ekman-type upwelling: the higher the CUI value, the higher the level of environmental enrichment (Roy, 1991).

At the beginning of each time step, environmental values specific for each area are averaged on the particular marine zone corresponding surface and input in the corresponding marine objects.

2.7. Submodels

2.7.1. Growth

The current size of the individuals composing a simulated microcohort is calculated by means of the Von Bertalanffy equation (Table 1).

2.7.2. Mortality

From a review of direct and indirect evaluation methods, Maxim and Maxim (1988) proposed an average mortality rate of between 0.49 and 0.57 for the Senegalese/Mauritanian population (fully recruited age classes). Moreover, mortality rates in sardinella are highest at the start of the life cycle and lowest when the fishes reach maturity, increasing thereafter as the fish get older (combination of increased fishing mortality and senescence). Based on this pattern, a rough hyperbolic curve has been discretised to obtain a mortality rate vector with a new value every 6 (simulated) months in the sardinella life cycle (Table 1). At each time step, a corresponding percentage is removed from each agent. As suggested by Maxim and Maxim (1988), the lifetime of the round sardinella was assumed to be 6 years. The mortality rate is updated for each agent, based on their current 'age' in the simulation.

2.7.3. Competition between juvenile agents

Competition for food was taken into account using the concept of carrying capacity ($K$). $K$ is considered here to be the number of individuals that a given area can support. The carrying capacity of a 'marine zone' object $j$ is expressed as $K_{CUIj}$, where $K$ is a fixed multiplier applied to the whole field and $CUIj$ is the local upwelling...
2.7.4. Moving

If the temperature of the ‘marine zone’ object in which an adult agent is situated is not within \( [\theta_{\text{optimal}}] \), the agent scans the ‘marine zone’ objects it can reach, given a cruising speed of \( d_{\text{max}} \) (maximum distance it can ‘swim’ in a time step). It selects the nearest such object within \( [\theta_{\text{optimal}}] \), whatever its direction, and moves towards it. If its current ‘marine zone’ is the most favourable, it does not move.

2.7.5. Reproduction

If the current location of an adult reproducer is not favourable for spawning but the agent ‘detects’ suitable conditions in one of the surrounding patches, the agent moves towards it and spawns.

index, the parameter used in the model to account for enrichment. Competition is assumed to occur when \( \sum_{ij} N_{ij} > K \cdot \text{CUI}_{j} \), i.e., when the total number of fish in the ‘marine zone’ object \( j \) exceeds the carrying capacity. At that time, a proportion \( K \cdot \text{CUI}_{j}/\sum_{ij} N_{ij} \) is then removed from the number of individuals for each juvenile agent in the ‘marine zone’ object.
We assumed, as suggested by Boëly (1982), that youngsters ‘reproduce’ only once between the first and second simulated levels of sexual maturity. In the model, if adults have spawned less than their maximum number of spawning per year (Fontana, 1969) and if youngsters have not yet spawned, they continue to search for spawning conditions.

2.7.6. Spawning

All females (given by the sex ratio) for a given reproducer agent spawn at the same time. In the model, the number of eggs produced by a given reproducer agent depends on female fecundity and the microcohort sex ratio. Fecundity is proportional to female weight. Weight and Fecundity are calculated using standard relationships (Table 1).

Mortality is high after spawning due to predation, cannibalism and unfertilised eggs (Cushing, 1973). For Senegalese, mortality has been estimated at 65% during the first few days after spawning (Conand, 1977a). We accounted for this high level of mortality by simulating 10% larval survival to the end of the spawning time step (15 days).

2.7.7. Biological cycle

When an adult or youngster agent spawns, it ‘creates’ a new juvenile agent, which thereafter develops on its own. The transition between the juvenile and reproducer conditions depends on the individual size of the agents. In the model, juvenile agents become youngster agents when their individuals reach this size. Youngster agents become adult agents once they have spawned for the first time.

The state variables used in the model are summarised in Table 1. The other simulation parameters are obtained from the calibration step and are described in the following section.

3. Parameters identification

As described in the model section, life cycle parameters were obtained from previous studies and environmental parameter values were observed data of various origins. The parameters to be calibrated are those governing the behaviour of round sardinelas within their simulated environment. The first calibration phase simultaneously identified the cruising speed and the optimal temperature interval \[ T_{\text{optimal}} \]. The data used for calibration were the observed migration patterns (from Conand, 1977b; Boëly et al., 1982b; Fréon, 1988) for the whole simulation period. The cruising speed and \[ T_{\text{optimal}} \] parameters were determined within a set of values with realistic intervals (e.g., 13 values between 18° and 25° for temperature). The values retained are those providing the best overall visual agreement when combined, between observed and simulated migration paths (see Fig. 5).

The optimal temperature interval obtained for the model lies within the range of published values (Table 2). However, it is difficult to compare calibration results for cruising speed with in situ data because this parameter depends on various factors, such as the size of the fish (Breen et al., 2004), maturity and temperature (Blaxter, 1969). Speed also varies during fish migration, with various phases observed (Vilhjálmsson, 1994). For similar species, Bainbridge (1958), Blaxter (1969), Hara (1987) suggest cruising speeds of around one knot (24 nm/d). Nevertheless, these speeds were measured during the day, and only for a few hours, and fish may slow down during the night. An average value of 3–11 nm/d may be more realistic (P. Fréon, personal communication, 2006).

Retaining values obtained for cruising speed and temperature preference, we carried out a new set of simulations to calibrate environmental conditions for spawning. We simultaneously modified various sets of wind speed ‘optimal windows’ and minimum CUIs. The values retained were those giving the best agreement between observed and simulated spawning areas (mapped in Fig. 1).

The values obtained for the parameters calibration phase are reported in Table 2; the joint set of values obtained has been found consistent with known values intervals for the real case.
the only quantified estimate available for this area during the time period studied. The resulting multiplier parameter was estimated at $30 \times 10^8$.

4. Simulation results

We deal with two aspects in the presentation of the results for this model. We first try to determine the extent to which the microcohort-based model reproduces the spatio-temporal pattern observed at population level. We then try to characterise the possible link between the microcohort structure and the observed clusters.

4.1. Simulation of observed patterns

The resulting overall dynamics obtained here concern migration patterns, spawning dynamics and biomass dynamics and levels. As necessary for this type of model, results are presented for each pattern together with the corresponding description of in situ observations.

4.1.1. Migration pattern

Adult agents local moves result in a migration pattern which is presented in Fig. 5 along with the classically observed empirical pattern. Simulated sardinella leave the Mauritanian coast in October and November, spend the cold season along the south coast and return to Mauritania when the simulated warm season begins in Senegal, between July and August. The migration scheme is often disturbed when adult agents arrive at the extreme south of their area in February–June. Adult agents then move back and forth between Cape Vert and Cape Roxo.

The northward movement observed in March 1985 is explained by water masses at 20–22°C around Cape Vert surrounded by colder water masses (20°C) (the preference is 21–25°C, see calibration above). The northward movement to Fass-Boye in March 1990 is explained by a break in upwelling at this time: adults start migrating northward but return when upwelling restarts.

4.1.2. Spawning dynamics

The overall spatio-temporal patterns of spawning have been established by several authors. The results obtained in simulations were compared with available data from previous studies (Fig. 6).

The in situ observations were as follows: reproduction occurs throughout the year along the Senegalese/Mauritanian coast, but with a peak period. In Mauritania, breeding takes place in July–October between Banc d’Arguin and Cape Timiris. In Senegal, the main breeding peak occurs on the south coast in May–June (Boély, 1982). A similar peak was also observed in March for the years 1987, 1988 (Fréon, 1988). In October–November, a secondary spawning peak occurs (Conand, 1977b). The overall spawning time and location pattern is reproduced by the model, but with a spatial lag for the spring spawning on the south coast, a time lag for the Mauritanian spawning and poor representation of autumn spawning on the south coast.

Reproduction has been studied more precisely along the ‘south coast’ during the cold season, by means of a gonado-somatic index.
study (Fréon, 1988), allowing more detailed comparison. The simulated spawning dynamics for this area is presented along with the environmental dynamics in Fig. 7. In the model, a major spawning peak usually occurs in May–June, when upwelling is continuous. In 1987, simulated spawning occurred in April–May, due to a sudden slackening of trade winds at the end of April (from sea surface temperature data). In 1988, it occurred in March in relation to an upwelling break. This was observed in situ by Fréon (1988).

The model also includes a secondary autumn spawning period. This spawning peak involves only youngsters, other than in 1988 and 1989, when it corresponded to adults reproducing late. Conand (1977b) and Fréon (1988) reported such a pattern and similarly attributed the secondary spawning to young reproducers reaching the second level of sexual maturity, as the adults have already moved northward and are not observed in this area at this time of year.

The simulated cold season spawning (1.2E12 individuals) was 12 times greater than the simulated warm season spawning (0.1E12 individuals). These results are consistent with published results: Conand (1977b) estimated that 10^{12} larvae were obtained from the spawning peak and Conand (1977a) reported spring spawning to be 10 times greater than the secondary autumn spawning.

In the model, these two simulated microcohorts develop in different environmental conditions: the smaller number of juveniles produced by the secondary spawning benefit from high food availability with the beginning of the upwelling season, whereas the juveniles produced by the main spawning at the end of the cold season face competition for food, due to both the large number of juveniles and decreases in the carrying capacity of the environment. Finally, these two spawnings of different sizes result in similar recruitments, as predicted by the simulation results. This result was reported by Boëly (1980), based on in situ observations.

Fig. 7. Simulation results: spawning intensity and hydroclimatic proxies for the south coast area (see map in Fig. 1). Spawning production (number of individuals) in black simulated from September 1984 to August 1990, wind speed in white, coastal upwelling index in grey. Striped squares: spawning periods observed in situ (from Conand, 1977b; Boëly, 1980; Boëly et al., 1982b; Fréon, 1988).
The model finally displays the flexibility in the spawning calendar observed on the south coast by Roy et al. (1989): spawning at the end of a strong upwelling (1985) and in the middle of a disturbed two-peak upwelling (1988 and 1990).

4.1.3. Biomass dynamics

The changes in total biomass simulated in the Senegalese area are shown by the grey area in Fig. 8. Over the time range simulated, the overall biomass curve is dome-shaped, peaking in the 1987–1988 cold season. Annual biomass fluctuations result principally from upwelling fluctuations and secondarily from variations in recruitment efficiency during preceding seasons.

Sardinella biomass for this period and area was evaluated by Do Chi (1994), using a virtual population analysis model which provides biomass estimates from fishing data on a yearly basis. This last model also gives a dome-shaped curve with a peak in 1987. These two methods, based on different input data, thus give results that are consistent overall.

4.2. Accuracy and robustness of the aggregation level

With respect to the explored hypothesis, we tried to relate the simulated microcohorts to the clusters observed in this area. A single dedicated acoustic survey program carried out during the study period (Petitgas and Samb, 1998) gave a field estimate of the number of small pelagic fish clusters in the Senegalese area. This study suggested that the sardinella population was, at the time, composed of 57 clusters of various shapes and sizes, and 34 solitary schools.

For the observed environmental conditions and parameters set based on published results or calibrations, the simulated population stabilised itself, with an almost constant number of agents (fluctuating between 55 and 65 agents).

The modelled domain is larger, but the 55–65 microcohort agents resulting from simulation remain within an order of magnitude and are similar to the number of clusters observed in the field.

Sensitivity analyses were conducted on the initial set of microcohorts and simulations were carried out, starting with small, large, young or equilibrated populations (Fig. 9). Whatever the initial scenario, the number of microcohorts converged towards this steady-state attractor, corresponding to a set of 17% juvenile, 1% youngster and 82% migrant adult microcohorts in the vital domain of the simulated population.

The steady-state number of microcohorts obtained is an overall result of the model, arising from the combination of life-cycle parameters, formalised behaviour and particular environmental conditions imposed in the model. The sensitivity of steady-state microcohort number (MN) to these three types of factor was studied. The results are not shown, but the main features of the analysis are summarised below.

Shorter life times were found to lower MN. Changing the number of yearly spawnings also changed MN, but the relationship between these two factors was not uniform. Moreover, a maximum was reached with a value of three ‘maximum spawning a year’, beyond which productivity did not change. This level may be bound to a limited time window during which environmental conditions are favourable for spawning.

Environmental conditions also had an effect, with particularly large decreases or increases in wind over the domain stopping reproduction and leading to extinction of the simulated population. A general increase or decrease in temperature decreased MN, but had no direct effect on biomass production (e.g., decrease when general temperature fell, offset in the response curve when the overall temperature increased). Changes in enrichment index (CUI)
had no significant effect on MN but did lead to proportional differences in biomass.

Preventing the microcohorts from moving led to contrasting patterns, depending on the area to which the initial microcohorts were assigned. The simulated population became extinct if microcohorts were placed in areas in which retention was unfavourable for spawning. Assigning microcohorts to two types of area (with and without favourable retention), resulted in a higher MN. This may be due to the static population being settled permanently in a favourable area with better spawning conditions than the migrant population with long phases of transit to favourable areas during which spawning cannot take place. Nevertheless, this situation appears counterintuitive, as the migrant population would be expected to have greater fitness, and may simply reflect the simplicity of the model.

5. Discussion

The model developed here simultaneously reproduces the major spatio-temporal dynamics patterns observed in populations of S. aurita off West Africa: the adult migration pattern, a major spawning period at the end of the cold season, a secondary spawning period at the end of the warm season on the south coast, spawning during the northward migration, an intensity of the major spawning event ten times greater than that of the secondary spawning and a dome-shapes dynamics curve during the study period. This mutual corroboration (Popper, 1959, in Oreskes et al., 1994) indicates strong coherence between the underlying processes formalised. This empirical validity (Grimm, 1994, 1999) highlights the importance of the microcohort hierarchical level among the factors influencing the overall dynamics of the population. In this scenario, microcohorts would play a structuring and key role in the population dynamics and durability at a global level. In this case, the concrete materialisation of the microcohorts of the population appears to be a legitimate consequence.

5.1. Consistency of the cluster-microcohort equivalence

The values of state variables used in the model were taken from published case studies. The environmental variability incorporated is also derived from field data. Finally, the identification phase leads to a set of parameters (swimming speed, optimal wind speed window and temperature interval), with values similar to those reported in previous studies for the stock considered. In this context of realistic simulation, the stabilised number of microcohorts obtained by simulation was of the same magnitude as the number of clusters observed in situ. Cluster aggregation level therefore constitutes the observed structure closest in size and number to the microcohorts simultaneously moving about in the vital domain of the population. The size and number of clusters observed in situ thus indicates that this aggregation level is a good candidate level for correspondence to microcohorts, providing support for the hypothesis of cluster-microcohort equivalence.

5.2. Ecological justification of the hypothesis

The correspondence between microcohorts and clusters may reflect a mechanism described by Haugland and Misund (2004) as “comparable strategies to comparable challenges”. Indeed, microcohorts produced in a spawning ground during a given season are likely to undergo the same constraints, to have similar temporal and spatial fates and, as such, may constitute a particular cluster. The observed clusters may reflect this phenomenon, with grouping thus corresponding to an epiphenomenon (Flierl et al., 1999): the simultaneous release, in highly constrained locations, of the various spawnings may lead to the microcohorts produced having a similar fate in a forcing environment; the greater the environmental constraint – and the upwelling environment represents a highly constraining environment (Fréon, 1988; Bakun, 1996) – the more visible initial microcohort aggregation is likely to be in the field. As a possible illustration, a given cluster may include several small pelagic species (Fréon and Misund, 1999) and this could be due to the simultaneous hatching of microcohorts of different species sharing the same local origin, age, type of behaviour and fate.

A study on clupeid clustering by Haugland and Misund (2004) suggested that clusters may provide a kind of superstructure within which schools can communicate and join together in response to predators. Swartzman (1997) studied Pacific gadoids and also concluded that interactions between schools within a cluster were probably effective, whereas schools in different clusters would be unlikely to interact. The hypothesis of cluster-microcohort equivalence is not inconsistent with this interpretation. Moreover, the advantage provided by clustering would favour the persistence of the initial cluster structure over time.

This raises questions about the visibility and permanence of microcohort-cluster equivalence. Indeed, successive events over time may decrease the consistency of the original cluster, for example by mixing it with other microcohorts, making identification increasingly difficult over time. Bertrand et al. (2008) showed that the Peruvian anchovy, Engraulis ringens, spontaneously organises into ‘opportunistic’ clusters as a function of the spatial and temporal scales at which plankton swarming events occur. Cluster-microcohort equivalence may thus weaken over time, as successive environmental forcing and historical events affecting the microcohort gradually erase the initial structure. In this case, if the suggested equivalence is real, it may correspond to a transient structure of the population of small pelagic fishes holding only for the juvenile and young individual microcohorts. This may also be the case in highly disturbed environments, such as the Benguela upwelling system, in which strong hydrodynamic forces play a major role (Lett et al., 2007). Cluster-microcohort equivalence would therefore be sustainable only in the most homogeneous and conservative upwelling situations.

5.3. Suggested means of confirming or rejecting the hypothesis

The lack of data for clusters makes it difficult to distinguish between these scenarios and this preliminary exploration can only suggest ways of testing the proposed hypothesis and deciding whether to accept or reject it. If biological microcohorts and the cluster structures observed in natural populations of small pelagic fishes are truly related, then sensitivity analyses we conducted provide clues as to the value of the attractor, the steady-state number of microcohorts moving about in the vital domain of the population (Fig. 9): This factor seems to be related to the biological characteristics of the species concerned, in terms of a combination of the number of possible spawning events per year and the life expectancy of the simulated species. However, these factors appear to be underlying determinants affected by spatial heterogeneity and fluctuating environmental conditions (within a viable range of variation). As such, the spatial origin and mobility of the clusters may determine their number. The overall wind and temperature in the simulated field also had various effects on the number of clusters. In light of the results obtained with this model, species longevity is the only feature directly related to the number of clusters found in the simulated domain: as the number of spawning events in the life time of a species increases, so should the number of clusters observable in its habitat, all other things being equal.
5.4. Model accuracy

The model presented is based on coarse microcohort granularity. This approach was used to keep as close as possible to the population level, but the validity of the results obtained may be called into question due to the oversimplification of reality inherent in this model. Some studies have presented more detailed (i.e., at the individual level) approaches to spatially explicit models accounting for the environment fluctuations, migration and reproduction processes of small pelagic fishes. Using an optimisation scheme, Huse and Giske (1998) simulated semi-theoretical fish populations based on various factors (physical environment, food, bioenergetics, etc.). Although reproduction was a key parameter in their model, the aggregation patterns obtained were not clustered or patched, but global and associated with either predation (itself related to temperature) or plankton abundance. Mannon et al. (2002) also proposed a model of anchovy (Engraulis capensis) first-stage evolutionary dynamics in Benguela. The model was linked to detailed 3D hydrodynamics and took into account transport and reproduction processes. In this case, aggregation was also obtained as a single concentrated patch of fish in the domain, and spatial clustering of the simulated population was observed only in certain cases considered either unrealistic or transient. These two studies were based on formalisms focusing on evolution and fitness-based selection of the population; these features were not related to cluster formation. It is therefore difficult to draw conclusions concerning the realism of these models with respect to clustering.

The studied fish population dynamics also depend on complex sources of variability, which, due to the granularity chosen, were taken into account in a simplistic manner in this study. For the spawning process alone, for example, one shows the complexity and importance of juvenile competition (Harris, 1975), the critical role of retention (Porch, 1998) or the complexity of factors involved in egg and larvae survival in upwelling systems (Santos et al., 2007) such as buoyancy (Parada et al., 2004) or coastal topography (Giannoulaki et al., 2006). The attempts made in previous studies to account for these sources of variation in the modelling of small pelagic fishes also cannot readily be compared with the model developed here, as previous studies have generally focused on particular factors affecting dynamics, such as the jet current transport of eggs and larvae in the case of the Benguela upwelling (Parada et al., 2004), vertical movements of fish (Strand et al., 2002) or the effects of the trophic web and fishing (Shannon et al., 2004). In our study, the associated use of environmental proxies was primarily intended to ensure compatibility with the microcohort level studied. These proxies and the coarse granularity used should make it possible to encompass some of the many sources of variation and to ensure the validity of the model for investigations at population level.

6. Conclusion

This microcohort-based simulation model satisfactorily reproduces the observed population patterns of round sardinella. The resulting microcohort set size converges towards a steady-state attractor that can be linked to the number of clusters observed within the population. In the context of this simulation study, the equivalence of clusters and microcohorts thus appears to be a parsimonious hypothesis, with no functional explanation other than the history of spawning events to account for the observed clusters. The cluster-microcohort equivalence may be either progressively masked by successive aggregation factors or a permanent structure. In the first case, size classes within a given cluster are expected to be similar, at least for the youngest groups. In the latter case, then the number of clusters observed in the habitat of the population should be related to the number of spawning events in the species’ lifetime. Further insight into the hypothesis would then consist either to determine the size spectrum of clusters in field trawling survey data or to estimate and compare the numbers of clusters in various habitats of small pelagic species.

These conclusions should be interpreted with caution as they stem from a simple model. Going further in modelling would either consist in providing more details of the spatio-temporal fluctuation of processes such as hydrodynamic retention or decrease the granularity of the model, to allow clusters to emerge.

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