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

Jean Le Fur [a,*], Patrick Simon [b]

[a] *Institut de Recherche pour le Développement, UMR Centre de Biologie et de Gestion des Populations (CBGP), Campus international Baillarguet, CS 30016, 34988 Montferrier-sur-Lez cedex, France*
[b] *COACH-IS, 58, Chemin de la Bruyère, 69570 Dardilly, France*

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.

© 2009 Elsevier B.V. All rights reserved.

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 (Gerlotto

---

* Corresponding author. Tel.: +33 4 99 62 33 02; fax: +33 4 99 62 33 45.
E-mail address: lefur@ird.fr (J. Le Fur).

and Paramo, 2003; Fréon et al., 2005; Brehmer 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 Levenez, 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 (Brehmer 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., 1989) 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.