PERSPECTIVE

Evolutionary individual-based model for the recruitment of anchovy (*Engraulis capensis*) in the southern Benguela

Christian Mullon, Philippe Cury, and Pierrick Penven

Abstract: Evolutionary simulations are developed to explore environmental constraints that select observed spatial and temporal spawning patterns for anchovy (*Engraulis capensis*) in the southern Benguela. They couple a realistic three-dimensional hydrodynamic model with an individual-based model in which an evolutionary-based reproductive strategy for adult fish and a passive transport for early life stages are implemented. The evolutionary success of spawning is quantified when patterns at the population level emerge after many generations from constraints at the individual level through a selective process. As a result, several self-sustaining populations are identified considering different sets of selective constraints. Simulated spawning patterns better match the observed mean spawning pattern when two selective environmental constraints are associated: a threshold temperature of 14°C, above which the development of early life stages is ensured, and the avoidance of offshore currents that constitute a loss of spawning products. Simulated recruitment patterns are more realistic when considering the constraint of reaching the nursery area. This modeling experience can help to identify, temporally and spatially, environmental factors important for fish recruitment and to establish a hierarchy of these factors. The probable coexistence in nature of several self-sustaining populations of pelagic fishes is shown to be important for recruitment studies.

Résumé : Nous avons mis au point des simulations évolutives pour étudier les contraintes environnementales qui agissent sur la sélection des comportements de ponte que l'on observe chez l'anchois (*Engraulis capensis*) dans le sud Benguela. Les simulations associent un modèle hydrodynamique 3-D avec un modèle centré sur l'individu; elles représentent les effets évolutifs du couplage entre la stratégie de reproduction des adultes et le transport passif lors des jeunes stades (oeufs et larves). Nous nous intéressons à l'apparition au niveau de la population de patterns spatio-temporels de ponte causés par un processus de sélection dans lequel des contraintes s'exercent au niveau individuel pendant plusieurs générations. Plusieurs populations autosuffisantes, correspondant à ces patterns, peuvent être identifiées et associées à différentes séries de contraintes évolutives. Les patterns de ponte simulés s'accordent mieux avec le pattern de ponte observé lorsque deux contraintes sélectives de l'environnement sont associées: un seuil de température de 14°C et l'évitement des courants au large. Les patterns de recrutement simulés sont plus réalistes si on tient compte de la nécessité d'atteindre la zone de nourricerie. Une telle expérience de modélisation aide à identifier dans le temps et l'espace les facteurs environnementaux les plus importants pour le recrutement et à les hiérarchiser. Il nous apparaît alors que la coexistence probable en nature de plusieurs populations autosuffisantes de poissons pélagiques est un facteur important à considérer dans les études sur le recrutement.

[Traduit par la Rédaction]

Introduction

The marine fish egg and larvae studies carried out under the direction of Committee A of the International Council for the Exploration of the Sea between 1902 and 1907 generated a paradigm shift that is still highly influential today (Sinclair 1997). The results of studies on the geography of spawning led to a new working hypothesis in evolution

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(Sinclair 1988) because patterns in spawning locations and the geographical scale of the larval distributions provided a new image of species. This new interpretation was dependent on the recognition that species comprise self-sustaining stocks or populations (Wyatt et al. 1991; Sinclair 1997). In fact, spawning occurs in very restricted and distinct areas relative to the distribution of the species as a whole. Moreover, fish spawn once or several times every year but generally over a limited period of time (see www.fishbase.org for further details). This reproductive strategy in marine fishes is thought to have evolved as a mechanism to synchronize the occurrence of larval stages with environmental conditions that are optimal for their survival (Roy et al. 1992). Food availability is an obvious factor that determines larval survival (Cushing 1996). However, microscale and mesoscale oceanographic events, related to retention, concentration, and enrichment processes, have been identified more recently as playing a major role in recruitment success (Bakun 1996).

Given the difficulties in assembling all of the temporally flexible physical attributes and biological processes into a single spatially explicit framework (Boisclair 2001), it is scientifically challenging to estimate environmental risks with different habitats during the various early life stages of pelagic fish (Hutchings et al. 1998). The potential of considering spatial and temporal dynamics in ecological studies to explain recruitment variability in fish populations is promising (Frank and Leggett 1994; Hinckley et al. 1996; Rose et al. 1999). However, this presents new methodological difficulties such as how to evaluate the relative beneficial or detrimental effects of several environmental factors acting simultaneously or independently during the different phases of larval life histories. Moreover, theoretical difficulties in the study of the variability of fish populations have underlined the necessity of taking into account the evolutionary process that they derive from (Frank and Leggett 1994). An integrated approach is needed that would conciliate evolutionary and ecological constraints.

In this paper, we explore the viability of self-sustaining spawning populations under selective environmental constraints. For this purpose, we develop evolutionary simulations that associate environmental constraints with spatial and temporal spawning patterns for anchovy (*Engraulis capensis*) in the southern Benguela. A realistic three-dimensional hydrodynamic model is coupled with an individual-based model (IBM) in which an evolutionary-based reproductive strategy for adult fish and passive transport for early life stages are modeled. Finally, a methodology is derived from this modeling study to identify sets of environmental factors that are important for self-sustaining populations and fish recruitment.

Background and hypotheses

### Pelagic fish reproductive strategy in the Benguela ecosystem and environmental constraints

Pelagic fish usually spawn in the nursery area. In two known cases, the Canary and Benguela ecosystems, anchovy spawn in an area from which the eggs are jetted to a distinct nursery area in which the larvae develop further (Wyatt et al. 1991). In the southern Benguela, anchovy spawn on the

Fig. 1. (*a*) Spawning patterns for anchovy as depicted by spatial egg distribution. The map is a composite calculated from the egg distribution obtained during scientific surveys conducted during November between 1983 and 2000 (van der Lingen et al. 2001); 100- and 200-m isobaths are shown. (*b*) Empirical model of anchovy eggs and larvae dynamics in the southern Benguela derived from field studies. The eggs and larvae are transported by a strong jet current from the spawning area in the western Agulhas Bank to the nursery area located on the west coast (from Hutchings 1992).
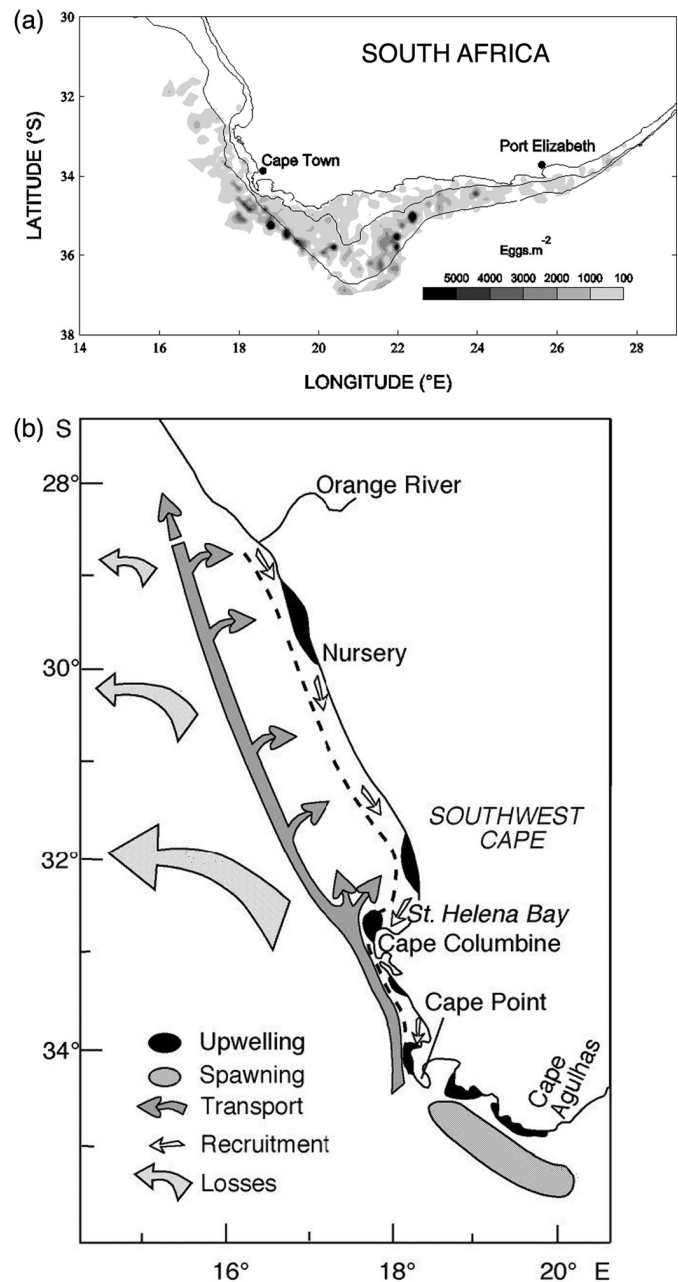
Agulhas Bank between September and December (Fig. 1) with a peak season during mid-November (Huggett et al. 1998). Eggs and larvae are then advected by a strong jet current to a nursery habitat on the west coast of South Africa where they grow as larvae and juveniles (Fig. 1*b*). Transport of anchovy eggs and larvae from the western Agulhas Bank

Fig. 2. Temporal pattern of anchovy recruitment in the Benguela. (*a*) Biomass X_t from 1984 to 2001 derived from acoustic estimates (Barange et al. 1999, M&CM data); (*b*) rate of recruitment, i.e., $X_{t+1}/X_t \times 100$.
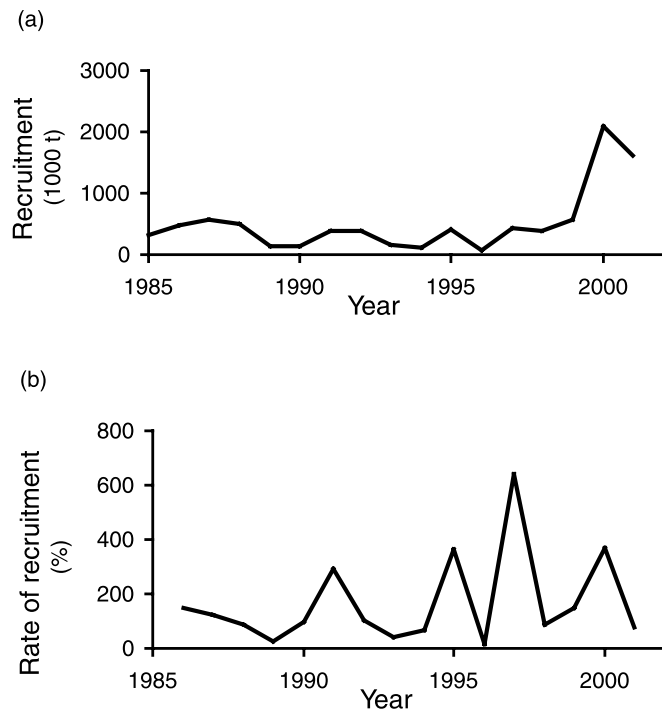
to the nursery grounds on the Cape West Coast has been investigated in numerous field, empirical, and modeling studies. All of these studies aimed at trying to understand and predict the observed large fluctuations of anchovy recruits (Fig. 2). The predominant role of environmental factors on the early life stages has long been noticed (Hutchings 1992).

Multiple factors affect the early life stages of South African anchovy in the spawning, transport, and nursery areas in which environmental constraints to larval survival appear to be different (Hutchings et al. 1998). For anchovy in the Benguela, we will focus on two environmental factors known to have direct effects on eggs or larvae and regarded as surrogates for ecological factors that are strongly linked to environmental fluctuations (Hutchings et al. 1998). These are wind (direction, intensity, and frequency, all related to transport and enrichment processes) and temperature (related to spawner biomass, development, and growth, food availability, and spawning intensity). These two factors have many biological and ecological consequences that can be tested for fish larval survival.

In the southern Benguela, strong southerly winds produce stronger upwelling, currents, and offshore transport, resulting in an increased loss of eggs and larvae from the coastal upwelling system (Shannon et al. 1992; Huggett et al. 1998). Empirical studies revealed a strong negative correlation between southeasterly winds and anchovy recruitment success in the transport area off the east coast, indicating that such winds were not conducive to good recruitment during the 1980s and 1990s (Hutchings et al. 1998). Strong southeasterly winds (Boyd et al. 1998) and advective losses as a result of an Agulhas ring (Duncombe-Rae et al. 1992) could account for the reduced recruitment in 1988–1989 (see Fig. 2).

Losses during the transport phase may be significant (Hutchings et al. 1998), and the extension offshore of the 16°C isotherm has been used as a proxy for evaluating transport success (Cochrane and Hutchings 1995).

Incubated eggs of anchovy survived experimentally a temperature of 11–31°C, but the minimal temperature for anchovy normal development in Cape waters was found to be above 14°C (King et al. 1978). The optimum temperature range for spawning has been determined to be between 16 and 19°C in the upper mixed layers (Anders 1965). This temperature range also constitutes a suitable spawning habitat for adult fish, associated with optimal production of large copepods on the western Agulhas Bank (Richardson et al. 1998). High gonad atresia was also observed in anchovy found in cool, inshore waters in January 1994 (Hutchings et al. 1998).

These studies were dedicated to identifying key environmental factors to explain distribution or patterns of abundance of pelagic fish. The impacts of spawning distributions and advection processes on larval survival were modeled by Shannon (1998).

In our study, we would like to extend this exploration to better understand the selective pressures imposed by the environment on spawning dynamics. Therefore, we implement a model that simulates the reproductive strategy in relation to the physical environment.

An evolutionary reproductive strategy to relate spawning and the environment in the Benguela

Pelagic fishes are thought to have developed opportunistic reproductive strategies, i.e., they spawn when environmental conditions are favourable. This seems a tautological definition, as one might question what "favourable" means at an individual level. From an ecological point of view, favourable could mean a favourable food environment for the larvae, a suitable temperature for egg development, or a suitable retention area to avoid losses, factors that were discussed previously. From an evolutionary point of view, it means not only life history survival, survival from birth to adulthood, but also survival over the generations that face environmental changes or evolutionary success (Michod 1999). Using evolutionary and ecological arguments, Cury (1994) proposed an extended homing strategy within which homing is viewed as part of a continuum of reproductive strategies, all relying on imprinting. This Darwinian way of looking at the "imprinting" mechanism provides, at the individual level, a basic mechanism for coupling adult fish reproductive strategy to the surrounding environment (Le Page and Cury 1997). Using the concept of "extended homing", Cury (1994) generalized this reproductive strategy for marine fish species (in particular pelagic fish) and its importance for the viability of self-sustaining populations.

In the Benguela, if location, timing, and duration of anchovy spawning have a strong ecological meaning, then one may consider that spawning in another place at a different time is detrimental and has been counterselected by one or more environmental factors. Recurrent spawning patterns for anchovy are observed in restricted areas (Hutchings et al. 1998) and their apparent slight spatial changes do not appear to be related to environmental changes (van der Lingen et al. 2001). Therefore, one may consider that individuals "home" to specific locations at particular times to spawn. This re-

Fig. 3. Hydrodynamic model. Examples of model outputs: sea surface temperature (°C) on 1 November for year 5 (left) and year 7 (right). Notice the presence of cold water owing to upwelling along the west coast, the plumes and filaments extending offshore, the mesoscale eddies, and the warm Agulhas Current flowing along the eastern Agulhas Bank. Also notice the differences between the two years regarding shapes of the eddies appearing in the central part of the area and the jet intensity.
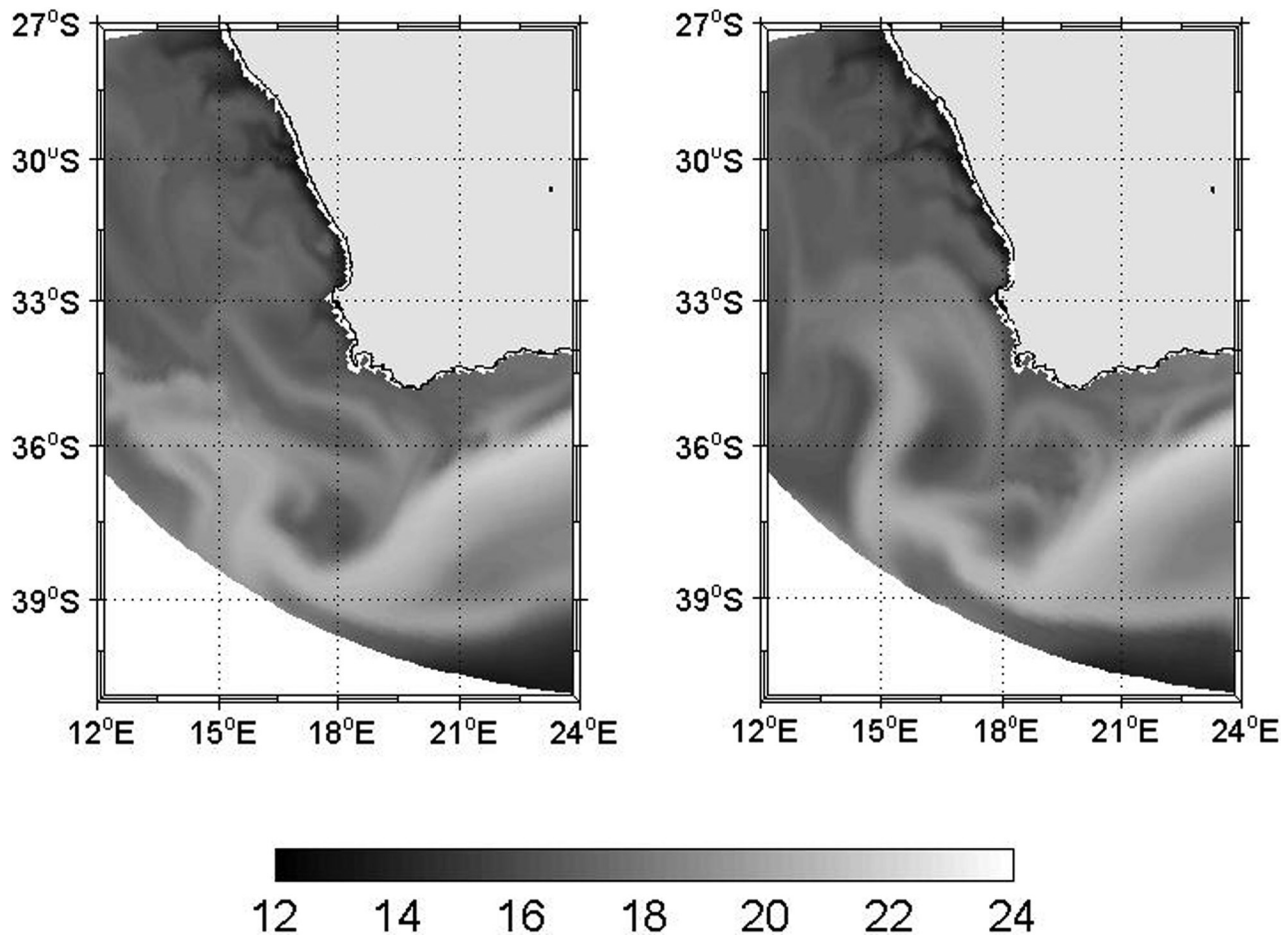
mains a hypothesis, as we do not know what determines the spawning process at the individual level. However, we consider it useful for assigning spatial and temporal coordinates in a dynamical way to spawning individuals.

Considering this reproductive strategy in the present modeling framework can help to identify the environmental factors that determine the timing and location of the observed spawning and its renewal through successive generations. It is thus necessary to integrate this reproductive strategy into a realistic and dynamical environment.

Materials and methods

A realistic three-dimensional hydrodynamic model is coupled with an IBM by considering an evolutionary-based reproductive strategy for adult fish and passive transport for early life stages. It is implemented to understand the spawning strategy of anchovy in the southern Benguela upwelling system. The evolutionary success of spawning is quantified when patterns at the population level emerge after many generations from constraints at the individual level through a selective process.

A hydrodynamic model to simulate a realistic and dynamical environment

A numerical oceanic model of the dynamics in the southern Benguela has been set up in the coastal area between 28 and 40°S and 10 and 26°E (Penven 2000; Penven et al. 2001*b*). It relies on the regional ocean modeling system (ROMS) developed at the State University of Rutgers (New Brunswick, N.J.) and at the University of California at Los Angeles. It resolves the hydrostatic primitive equations with a variable free surface. A specific open-boundary scheme has been developed for long-term integration of the model on limited size regional domains (Marchesiello et al. 2001; Penven et al. 2001*a*). The model uses a horizontal curvilinear coordinates system and a variable vertical coordinates system that is able to keep a high vertical resolution in the boundary layers (e.g., at the surface of the ocean). The horizontal grid is pie-shaped to follow the southwestern corner of the African continent (Fig. 3). The horizontal resolution ranges linearly from 9 km at the coast to 16 km offshore. Twenty vertical levels preserve a high vertical resolution near the surface. These modeling choices (spatial extension, spatial resolution, and time resolution) have been made to generate mesoscale circulation features important for the transport and retention of pelagic fish (Bakun 1996).

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The model is integrated for 10 years, using yearly climatologic data for the surface-forcing and open-boundary conditions. After a spinup of 2 years, the model results are stored at 2-day intervals to provide a high temporal sampling for the IBM. The model develops an important mesoscale activity produced by intrinsic instability processes of the ocean dynamics (Penven 2000; Penven et al. 2001a): it provides realistic patterns in the Benguela system like the coastal upwelling, coastal jet, eddies, filaments, and plumes extending from the major capes (Fig. 3). It also generates a realistic circulation in the Agulhas Current area (Penven 2000). Despite being forced by the same averaged conditions every year, the model generates an important year-to-year variability (Fig. 3). For example, simulated temperature depth distributions exhibit interannual variability comparable with the one observed in several points of measurements on the shelf of the Agulhas Current. It affects, both in time and space, the hydrodynamic structures (jets, filaments, and eddies) of interest for eggs or larvae transport.

An evolutionary IBM: a reproductive strategy evolving in a physical environment under different selective constraints

An IBM is a bottom-up approach that starts with the parts (i.e., individuals) of a system (i.e., population) and then tries to understand how the properties of a system emerge from the interactions between the parts (Grimm 1999). An evolutionary approach attempts to express how patterns at the population level emerge from constraints at the individual level through a Darwinian selective process (i.e., relative selective advantages).

In our model, individuals are particles released and advected in the currents of the hydrodynamic model. They can be considered eggs, larvae, or juveniles. They have a memory that encodes their spawning strategy, i.e., date and location. Individuals are subject to a set of constraints under which they survive or die. The surviving individuals are able to spawn again at the place where they were born and in the same time period. These dynamics generate a new population. This algorithm can be viewed as a simple genetic algorithm (Mitchell and Taylor 1999) where the "genotype" is an encoded spawning strategy and the "fitness" corresponds to the recruitment success. This is an elementary IBM: the individuals only differ by their spawning strategy, date, and location.

The algorithm for the IBM is implemented as follows. (i) Choose a set of selective environmental constraints for survival, expressed in terms of offshore advection, sensitivity to temperature, reaching of the recruitment area, etc. (ii) Create a population of N_I individuals with random spawning strategies. (iii) Repeat during N_G generations (each generation equals 1 year): (a) randomly choose one year among the seven years of the three-dimensional hydrodynamic model output, (b) allow the individuals to be passively advected in the currents and temperature fields corresponding to that particular year during 60 days after their birth date, (c) observe which ones have fulfilled the constraints, (d) create a new population of N_I individuals by allowing successful individuals to spawn eggs in the neighbourhood of their natal spawning area (around N_K km) at the same date of their birth (within plus or minus N_D days) (the

number of eggs per recruit is then N_I/S, where S is the number of successful individuals; this ensures a constant population level), and (e) visualize the spawning pattern after each generation. (iv) Plot the results of the simulation: the spatial distribution of spawning locations at generation 60 is plotted. The recruitment index during the first N_G generations is defined as the number of eggs and larvae that survived under the chosen constraints.

Assumptions

The assumptions of the evolutionary IBM are as follows. (i) The output of the three-dimensional hydrodynamic model provides realistic dynamics of the environment: they present sufficient seasonal and interannual variability to test the environmental changes experienced by eggs and larvae. (ii) We can consider eggs and larvae to be analogous to passive drifters (particle tracking without diffusion) in this virtual environment; other abilities (swimming) and biological processes (feeding and predation) are assumed to be negligible for recruitment success. (iii) An extended homing mechanism drives the spawning process: this implies that successful adults try to spawn in the same place and at the same time of the year in which they were born.

Design of the simulations

The present model is aimed at illustrating how a combination of environmental constraints can explain recruitment variability. The following procedure ensures that hypotheses, model population dynamics, and model results are the following. (i) Observable: visualization of the hypotheses, of the different dynamics, and of the results is an important outcome of the approach; hypotheses, selective constraints, and the resulting dynamics are observable and easily interpreted from graphical displays and outputs. (ii) Comparable: we start by enunciating a null hypothesis; this allows comparison of any simulation using environmental selective constraints with a null hypothesis where no selective constraints are imposed. (iii) Testable: we follow a pattern-oriented approach (Grimm et al. 1996; Grimm 1999). First, a set of observed patterns is defined at the global level. Subsequently, alternative models are compared according to their ability to produce matching patterns. This constitutes a powerful way to infer the mechanisms by which individuals respond to their environment. (iv) Believable: we follow a KISS principle (keep it simple stupid) after A. Okubo (Slobodkin 1999), adopting simple and tractable rules and hypotheses. This is the way to compare and learn from hypotheses and simulations to make a model understandable and believable.

We have chosen two specific patterns derived from the field surveys to be compared with the output of the simulations: spawning pattern and recruitment pattern. The spawning pattern has a spatial component that is compared with the observed egg distribution (Fig. 1a). It also has a temporal component, i.e., spawning dates. Simulated spawning patterns are compared with the results of surveys that indicate summer (i.e., November–December) as the most probable period for spawning. The number of surviving eggs or larvae at the end of each generation can be considered as a recruitment-like pattern that is compared with the observed recruitment time series (Fig. 2b).

Fig. 4. Example of a simulation showing how anchovy spawning patterns emerge through time. Each dot represents the spawning location of an individual. The colour indicates the month of spawning according to the legend on the figure. The solid area corresponds to our definition of the nursery grounds. In some of the forthcoming simulations, eggs and larvae are considered to be recruited when they reach this area. (*a*) At time = 0, eggs are randomly spread over the grid; (*b*) spawning pattern after two generations; (*c*) spawning pattern after five generations; (*d*) spawning pattern after 60 generations.
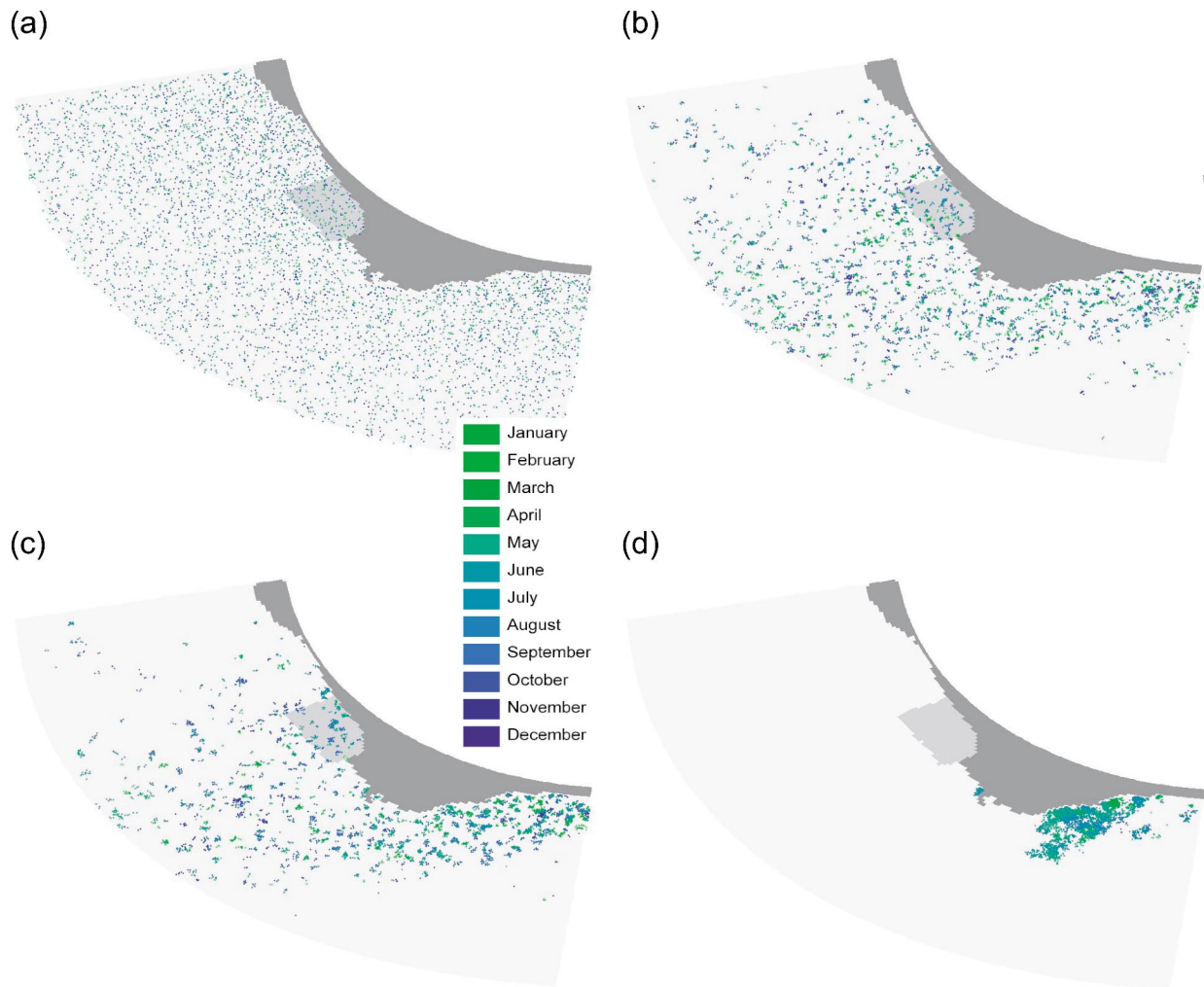
This approach results in a series of experiments. Each one simulates dynamics associated with one or a set of environmental constraints that have been previously recognized to have an effect on recruitment. Tested environmental constraints are as follows: (*i*) no environmental constraint: the null hypothesis, (*ii*) avoiding offshore advection, (*iii*) avoiding offshore advection and being successively transported, (*iv*) avoiding offshore advection and staying in temperatures greater than 14°C, (*v*) avoiding offshore advection, staying in temperatures greater than 14°C, and being successively transported, and (*vi*) avoiding offshore advection, staying in temperatures between 16 and 19°C, and being successively transported.

Results

### Assigning values to the parameters

As for any genetic algorithm, a compromise has to be found between the size of population, the selective pressure,

and the number of generations according to limitations imposed by computer time for simulations. After many preliminary attempts, we have chosen the following for use in this study: N_I (number of individuals) = 5000, N_K (distance from natal and spawning locations) < 5 km, N_D (difference between birth and spawning anniversary dates) < 10 days, and N_G (number of generations) = 60. It appears that the resulting patterns do not change substantially after 60 generations. Using this algorithm, we are able to observe how patterns emerge spatially and temporally under chosen selective constraints (Fig. 4).

Checking the stability of the algorithm

There are three sources of stochasticity in the algorithm: (*i*) the random initial distribution of spawners in time and space, (*ii*) at each generation, the random choice of a particular year of the output of the hydrodynamic model, and (*iii*) the spawning positions randomly chosen close to the natal site. To deal with this stochasticity and test the robustness

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Fig. 5. Resulting anchovy spawning patterns for four trials of simulation 6: individuals do not reproduce when advected offshore, experience water temperatures below 14°C, or do not reach the nursery area after 30 and before 60 days.
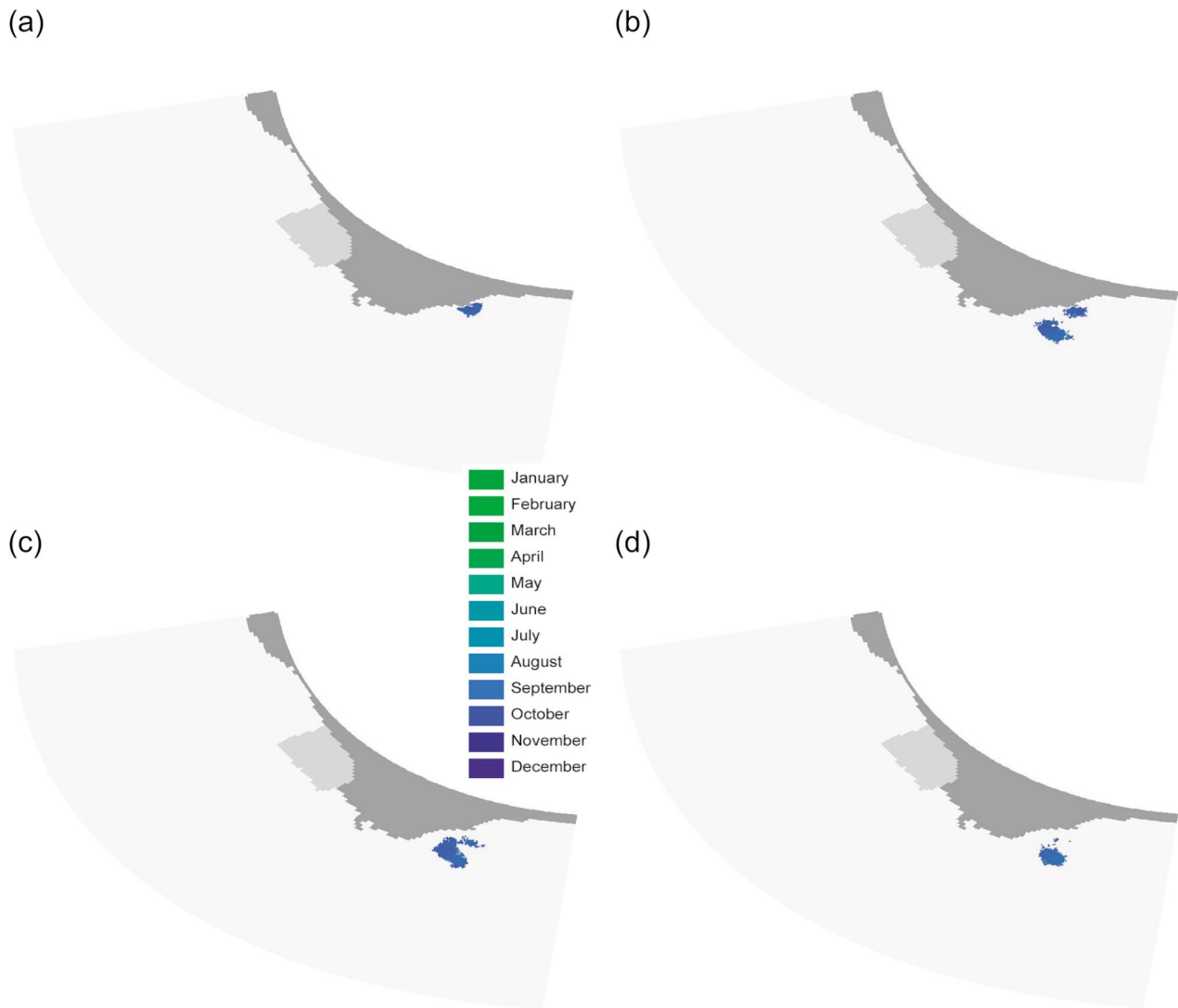
of the resulting patterns, we proceed for each simulation with four independent runs of the algorithm. Different patterns can emerge from the same set of constraints (Fig. 5). However, most emerging patterns appear to be robust to stochasticity, as indicated by the four replicates that were performed for each simulation. We only present one output of each simulation in forthcoming figures of the spawning patterns.

Simulation 1. Null hypothesis: no environmental constraint on larval survival

In this first simulation, we consider that the environment has no selective effects on egg or larval survival. There are no constraints on advection or temperature and no criteria for recruitment success. The probability of being able to spawn is 50%. Spawning patterns are "structured" by homing behaviour, but no realistic spawning patterns emerged (see Fig. 6a). This special situation of "genetic drift" illustrates that a neutral Darwinian process can create patterns.

The recruitment index is almost constant at the defined probability level of 50% (Fig. 7a).

Simulation 2. Where should anchovy spawn to avoid offshore advection?

This simulation explores where spawning should occur to avoid offshore advection. Individuals do not reproduce when advected offshore (i.e., distance from the coast greater than 400 km). No other criterion is considered here as an environmental constraint. The probability of being able to spawn is 75% for individual surviving to reproductive age.

This simulation (see Fig. 6b) gives a realistic spatial spawning pattern in comparison with the observed one (Fig. 1a). However, the simulation results in spawning activity during winter (May–July), which is not realistic. Moreover, the recruitment pattern (Fig. 7b) appears to be much less variable than the observed one (Fig. 2b). During the first several years, the recruitment index steadily increases and finally reaches a plateau with a value of about 70% (Fig. 7b).

Fig. 6. Simulated anchovy spawning patterns produced by the evolutionary model considering the following environmental constraints: (*a*) simulation 1: null hypothesis where individuals that reproduce are randomly chosen; (*b*) simulation 2: individuals do not reproduce when advected offshore; (*c*) simulation 3: individuals do not reproduce when advected offshore or do not reach the nursery area after 30 and before 60 days; (*d*) simulation 4: individuals do not reproduce when advected offshore or experience water temperatures below 14°C; (*e*) simulation 5: individuals do not reproduce when advected offshore, experience water temperatures below 14°C, or do not reach the nursery area after 30 and before 60 days; (*f*) simulation 6: individuals do not reproduce when advected offshore, experience water temperatures below 14°C, or do not reach the nursery area after 30 and before 60 days.

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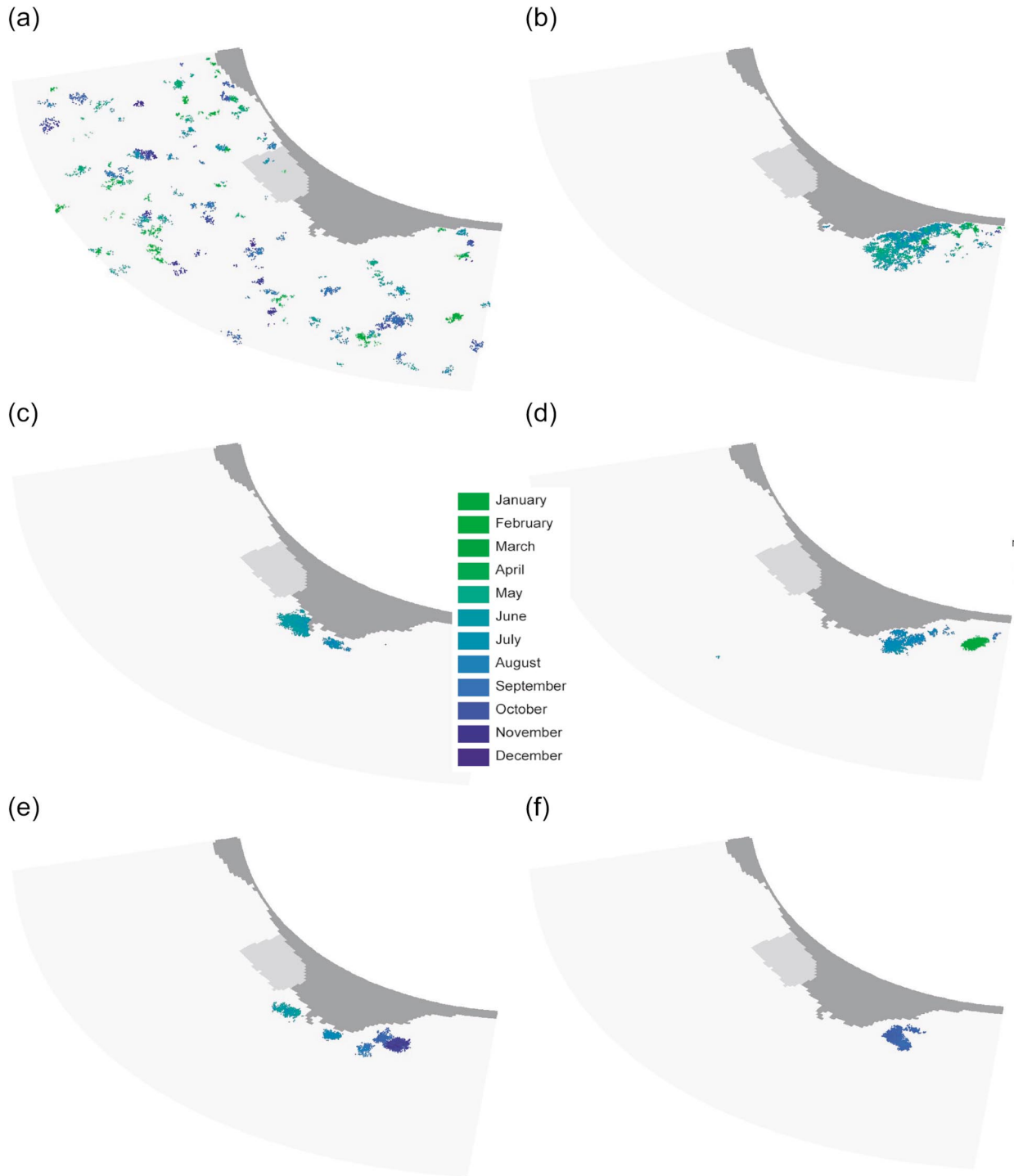
Fig. 7. Simulated anchovy recruitment variability measured as the number of surviving eggs and larvae at the end of each generation: (*a*) simulation 1; (*b*) simulation 2; (*c*) simulation 3; (*d*) simulation 4; (*e*) simulation 5; (*f*) simulation 6.
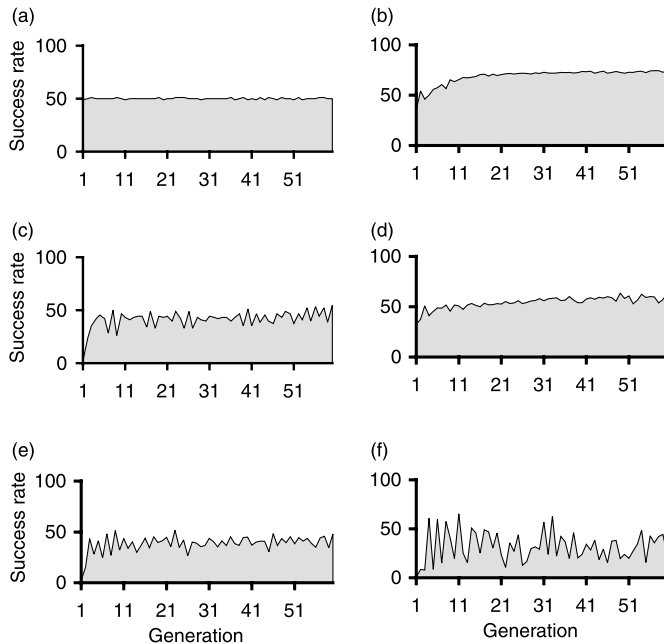
In fact, the population progressively adapts itself to environmental constraints through generations and finally finds an appropriate spawning location under this selective constraint. Thus, it seems that the evolutionary process results from an effective trial-and-error strategy at the population level.

Simulation 3. Where should anchovy spawn to avoid offshore advection and to reach the nursery area?

In this simulation, the individuals are considered successful when they avoid offshore advection and when they reach the nursery area between 30 and 60 days. If those two conditions are fulfilled, then they become adults and reproduce again at the same location and in the same time period during which they were produced.

The resulting spawning patterns are not stable. According to the different replicates, they correspond to a small confined area located off Cape Point for replicates 1, 2, and 3 (Fig. 6*c*) or in the nursery area in St. Helena Bay for replicate 4. In addition, in all four replicates, some spawning occurs in winter. The fourth replicate suggests a possible persistent spawning area within the nursery area, which is something that has not been observed in field surveys (Fig. 1*a*). As stressed in the Introduction, spawning and nursery areas of anchovy are distinct and remote from one another in the Benguela. The discrepancy between the evolutionary model and the observed pattern tells us that the environmental constraint "to avoid offshore advection" should not be the only one that controls anchovy spawning. Another

factor must also be important, for example, temperature, which is explored in simulation 4.

Simulated recruitment shows quite high variability, but variation (standard deviation/mean) is low when compared with the observed recruitment. In this simulation, the population progressively detects a spawning habitat that is subject to high environmental variability. This is detrimental to recruitment, which varies from 30 to 65% (Fig. 7*c*). In this case, the population finds a spawning pattern that ensures its persistence through time. However, it is not then able to detect any environmental patterns that will improve its fitness, as a trial and error strategy is no longer effective.

Simulation 4. Where should anchovy spawn to avoid offshore advection and cool waters (<14°C)?

In simulation 4, individuals do not reproduce when advected offshore or encountering a temperature below 14°C. Then the probability of spawning for an individual that is still alive after 30 days is 0.75.

The resulting spawning pattern appears to be realistic (see Fig. 6*d*) according to the observed egg distribution (Fig. 1*a*). Two groups that spawn at two different time periods can be identified (Fig. 7*d*): on the eastern Agulhas Bank during January–February and on the western Agulhas Bank during November–December. This corroborates the observed temporal pattern of spawning for anchovy in the Benguela (Hutchings et al. 1998).

The resulting pattern of recruitment variability shows a slow but progressive convergence to optimal conditions (Fig. 7*d*). This observed pattern of recruitment variability is different from the observed one, which appears more erratic (Fig. 2*b*). Here again, it seems that the evolutionary process results from an effective trial-and-error strategy at the population level.

Simulation 5. Where should anchovy spawn to avoid offshore advection and cool waters (<14°C) and to reach the nursery area?

To the constraints of simulation 4, we add now the constraint of reaching the nursery area within 30–60 days (see Fig. 6*e*). This simulation appears quite unstable, as replicates produce slightly different patterns. As a common feature, the resulting spawning pattern is a set of confined areas off the Cape peninsula. For some of these areas, the corresponding spawning dates are in spring (September) and autumn (April), which is not in agreement with field studies (van der Lingen 2001). The resulting pattern of recruitment variability exhibits erratic fluctuations (Fig. 7*e*). Because of environmental variability, recruitment is highly variable, but here again, variation is low when compared with the observed recruitment.

Simulation 6. Where should anchovy spawn to avoid offshore advection, to stay in waters between 16 and 19°C, and to reach the nursery area?

Here, we consider a small interval of temperatures (16–19°C) according to ecological arguments that were discussed in the Introduction and are related to food availability on the Agulhas Bank. Offshore advection and being able to reach the nursery area are additional constraints.

Table 1. Summary of the results of the six simulations for anchovy regarding their stability and their fit to observed data.

	Environmental constraints: eggs and larvae randomly die when	Stability of convergence of the algorithm	Simulated vs. observed spawning pattern	Simulated vs. observed recruitment pattern
1	there are no environmental constraints		Grounds: no fit Dates: no fit	No fit
2	they are advected offshore	High	Grounds: good fit Dates: poor fit	No fit
3	they are advected offshore they do not reach the nursery area after 30 and before 60 days	Low	Grounds: no fit Dates: no fit	Poor fit
4	they are advected offshore they experience water temperatures below 14°C	High	Grounds: good fit Dates: good fit	Poor fit
5	they are advected offshore they experience water temperatures below 14°C they do not reach the nursery area after 30 and before 60 days	Medium	Grounds: poor fit Dates: good fit	Poor fit
6	they are advected offshore they experience water temperatures between 16 and 19°C they do not reach the nursery area after 30 and before 60 days	Medium	Grounds: poor fit Dates: good fit	Good fit

Table 2. Anchovy recruitment strength (percentage of successfully transported individuals) according to the different hydrodynamic years considered in the simulations.

Year	Simulation 1	Simulation 2	Simulation 3	Simulation 4	Simulation 5	Simulation 6
3	49	70	42	57	43	13
4	50	63	42	54	38	34
5	49	71	37	53	41	32
6	49	71	38	53	31	33
7	49	72	43	56	37	55
8	50	67	35	54	44	26
9	49	64	43	53	39	30

The resulting spawning pattern that emerges from these selective constraints is a small area located in the central Agulhas Bank around mid-December (Fig. 6*f*). This spawning pattern has not been extensively sampled during this time period in field studies. Therefore, it would be interesting to explore if this pattern is real.

Associated with this pattern is high recruitment variability, which can be compared with the observed one (Fig. 7*f*). When compared with simulation 2, this simulation does not constitute an optimal spawning area, as recruitment variability is always very high (Fig. 7*f*). However, this may be viewed as a persistent spawning area, as the population maintains itself through time (for every generation, recruitment is good enough to ensure the survival of the population).

Summary of the results

We summarize results of the six simulations according to their characteristics in terms of stability and their ability to reproduce the observed spawning and recruitment patterns (Table 1). It appears that none of these simulations gives a "perfect" fit to both the spawning and recruitment patterns observed in the field. Considering avoidance of offshore advection and cold waters results in fairly realistic spawning patterns in time and space. Attempting to reach the recruit-

ment area results in highly variable recruitment, similar to the observed one.

We compute for each simulation the mean recruitment success according to the hydrodynamic year (Table 2). It appears that recruitment strength depends on the hydrodynamic year when taking into account the constraint of reaching the nursery area (simulations 3, 5, and 6), especially when a temperature constraint is added (simulations 5 and 6).

Discussion

Tools from individual-based modeling provide new and refreshing views in recruitment studies (Rose et al. 1999). For example, Hermann et al. (1996) have considered individuals advected in the currents of an oceanic model and differing by many biological and ecological attributes. We have used concepts from evolutionary ecology, which are efficient for considering the adaptation of organisms to their environment (Frank and Leggett 1994; Fox et al. 2001), and have carried out an IBM with very simple individuals, but in an evolutionary perspective.

The proposed evolutionary model, which is not predictive but exploratory in essence, illustrates how selective constraints can affect spawning and recruitment patterns. It is aimed at promoting transfer between two different scales:

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the individual in its surrounding environment and the emerging spawning pattern of a pelagic fish in an upwelling area. We believe that this modeling experience can help to identify environmental factors important for fish recruitment and establish a hierarchy for these factors.

A hierarchy for the selective environmental constraints

The results, especially those from simulation 6, suggest some independence between two types of constraints, namely (*i*) avoiding offshore advection and cold waters, and (*ii*) being successfully transported to the nursery area. To survive, anchovy must satisfy the first set of constraints, which apparently drives their spawning behaviour, and then the recruitment success largely depends on the specific hydrodynamic features of the current year.

Concerning the nature of effective selective constraints, a paradox should be discussed when comparing results from simulations 2 and 3. Environmental constraint for simulation 2 is a subset of the constraints of simulation 3. In that case, as a result, one would expect to observe the resulting spawning pattern of simulation 3 to be found among the solutions obtained with simulation 2. This is not the case: adding one constraint to another drastically modifies the emerging pattern. Adding one environmental constraint means defining new viable spawning patterns, as it changes the hierarchy of the relative advantages of the spawning strategies. In other words, spawning location and timing result from specific interactions between environmental and ecological processes. Adding one selective constraint to another means changing the whole functional relationship between the environment and the ability of the species to evolve.

Identifying self-sustaining populations

As Lewontin (1983) noticed, "by its behaviour—its genetically determined use of habitats and resources—an animal largely defines the selective pressures to which it is subject". The choice of a spawning location has major consequences for recruitment success and evolution, as it defines the choice of the present and future habitats for the eggs and early life stages, and consequently, associated selective constraints. Simulated persistent spawning patterns can be viewed as virtual self-sustaining populations. Several of them were identified, and when related to observed spawning and recruitment patterns, some of them appeared to be more realistic than others. A simulated spawning pattern was found to match better the mean observed pattern when two selective environmental constraints were associated: a threshold temperature of 14°C, above which the development of early life stages is ensured, and the avoidance of offshore currents that constitute a loss of spawning products. Thus, two environmental constraints seem to have shaped the main reproductive pattern of anchovy in the southern Benguela. On the other hand, the recruitment variability is related to the constraint of reaching the nursery area and facing interannual environmental changes.

Systematic acoustic surveys have shown that from one year to another, observed spawning patterns exhibit recurrent patterns and also slow and consistent spatial changes. Thus, it appears that in recent years, more anchovies are spawning on the eastern Agulhas Bank (van der Lingen et al. 2001). The dynamics at the whole-population level can then be seen

as the result of the dynamics of numerous self-sustaining subpopulations that react differently to given environmental conditions. Our modeling experiment can provide a framework for understanding changing spawning patterns. Observed spawning patterns might be viewed as a combination of several self-sustaining populations, like the ones emerging in simulations 4, 5, and 6. Thus, recognizing differences in spawning strategy (location and date) between individuals and considering their adaptation to environmental constraints may explain some diversity (i.e., coexistence of self-sustaining populations) and some population dynamics features. For certain years, in a certain environmental context, one or the other self-sustaining population is selected in a differential way, which will lead to varying strength in recruitment.

Self-sustaining populations have long been recognized in marine fish populations (Hjort 1914). Their importance for fish population dynamics and fisheries management is only recent (Sinclair 1997; Page et al. 1999). To recognize their importance emphasizes the need for promoting recruitment studies that will focus on spawning patterns and their spatial dynamics. According to Sinclair (1988), geographical differences in the retention of eggs and larval distribution areas are key processes in the regulation of fish abundance. However, temporal changes in spawning patterns are mostly seen as anecdotal, and the link between recruitment strength and spatial dynamics is rarely addressed. A recurrent topic in the fisheries literature is to question empirical relationships between recruitment and environmental indices that fail through time (Myers 1998). However, recognizing the heterogeneous character of fish populations could help to understand the changing nature of such relationships. Recognizing the diversity and coexistence of persistent spawning patterns can potentially have major consequences for recruitment studies and fish exploitation.

Our modeling experience can help to better understand the role of diversity for fish spawning dynamics. Recognizing diversity, the essence of life, as the basic principle for recruitment studies can also stimulate our imagination and provide new and refreshing views to old problems.

Acknowledgements

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