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Population structure of the Chilean jack mackerel *(Trachurus murphyi)* in the South Pacific Ocean

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ABSTRACT

The Chilean Jack Mackerel (*Trachurus murphyi* Nichols), is one of the most important among the exploited stocks in the world. Its area of distribution covers the sub-tropical waters of the South Pacific Ocean, from South America up to New Zealand and even Australia. It is subject to strong variation in its biomass, and the world catches varied from less than 1 million tons to 5 million tons. Its management requires a correct understanding of the population structure. Although several hypotheses have been submitted, suggesting up to 4 independent populations, the genetic analysis of the fish shows a single population in the whole Pacific Ocean.

We consider the two most probable structures for this population: a "superpopulation" where all the fish belong to a single population that expands and contracts depending on the biomass; and a metapopulation, where a source population creates several subpopulations that can remain independent during a long period, depending on the environmental conditions. The conditions for these hypotheses to represent the real case are studied. It is difficult to adapt the definitions of metapopulations to this large pelagic stock, and we suggest some adaptation of the concept to pelagic gregarious species.

Using the knowledge obtained from a considerable amount of data from fisheries and acoustic survey on spatial distribution, demographic structure and dynamics, spawning areas, etc., we analyze the two hypotheses. None can be fully rejected. We present a model for metapopulation structure and conclude that, although no final choice can be done between the two hypotheses, the metapopulation is likely to better describe the stock; moreover it represents a safer definition as far as stock assessment is concerned.

INTRODUCTION

The jack mackerel *Trachurus murphyi* (Nichols) or Chilean Jack Mackerel (CJM) presents a particular case in its genus: on the one hand it has the common characteristics of most *Trachurus* species: rather long life (more than 15 years), mature at around 30 cm (3 years), predator on micronekton and especially Euphausids, etc. (see www.fishbase.org). On the other hand it has the widest area of extension, as it can be found in the whole sub-tropical area of the Southern Pacific Ocean and even in some occasion has been encountered in the Indian and Atlantic Oceans in their southern subtropical areas (Riede, 2004; Nakamura et al, 1986). Its fishery is one of the biggest in the world, with catches reaching 5 million tons in the years of highest production (1995): CJM is indeed one of the three most exploited fish species in the world, with the Peruvian anchovy *Engraulis ringens* and the walleye Pollock *Theragra chalcogramma* (see www.fao.org). Since the late 90s, the CJM has suffered a strong decrease of the total catches that fell to less than 1 million tons (figure 1), which is likely to reflect a similar decrease of its abundance.
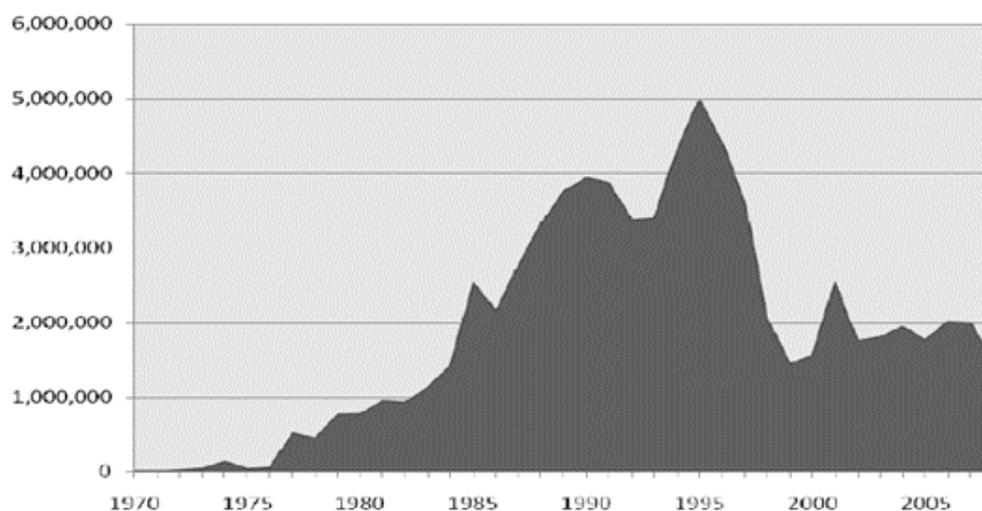

Figure 1. Total annual catches of CJM from 1970-2008 (from SPRFMO).Catches in tons

The CJM presents three characteristics that have a strong impact in management policy: (i) a huge potential biomass (it has been evaluated at until 20 million tons: Konchina and Pavlov, 1999), which made this fish an essential target for industrial fisheries, as for example the soviet during 1978-1992; (ii) a strong variability in the overall biomass depending on some strong cohorts that occurs or not according to

the environmental conditions (Konchina and Pavlov, 1999), which increases the risk of overfishing when the stock decreases; and (iii) a wide extension in international unregulated waters, making the species available for any country, the main fishing fleets coming from Chile, Peru, Russia, China, European Union, New Zealand, Australia, etc. These unfavorable conditions make a regulation agreement indispensable. For that purpose the CJM became a concern for the South Pacific Region Fisheries Management Organization (SPRFMO: www.southpacificrfmo.org). Scientific studies have been undertaken, the first and prioritary objective being to define the actual population structure of the CJM stocks in the South Pacific, in order to draw sound regulation rules. This consideration was stated during a meeting of SPRFMO dedicated to CJM in Santiago, Chile, 2008 (Anonymous, 2008), with the objective to start "*urgent work to develop working stock structure hypotheses upon which to base future stock assessments of Chilean Jack Mackerel (*Trachurus murphyi*) in the SPRFMO area, and (…) to discuss and develop agreed working hypotheses, and to consider assessment requirements and inputs under such stock structures hypotheses*".

A large series of works have been achieved and a series of hypotheses about stock structures have been presented, from a single global stock to "*up to four separate stocks: a Chilean stock which is a straddling stock with respect to the high seas; a Peruvian stock which is also a straddling stock with the high seas; a central Pacific stock which exists solely in the high seas; and, a southwest Pacific Ocean stock which straddles the high seas and both the New Zealand and Australia EEZs. However, further collaborative work is required to confirm and/or clarify this hypothesized stock structure as a basis for effective management regimes*" (Anonymous, 2008). The 4 principal hypotheses are summarized in Figure 2.

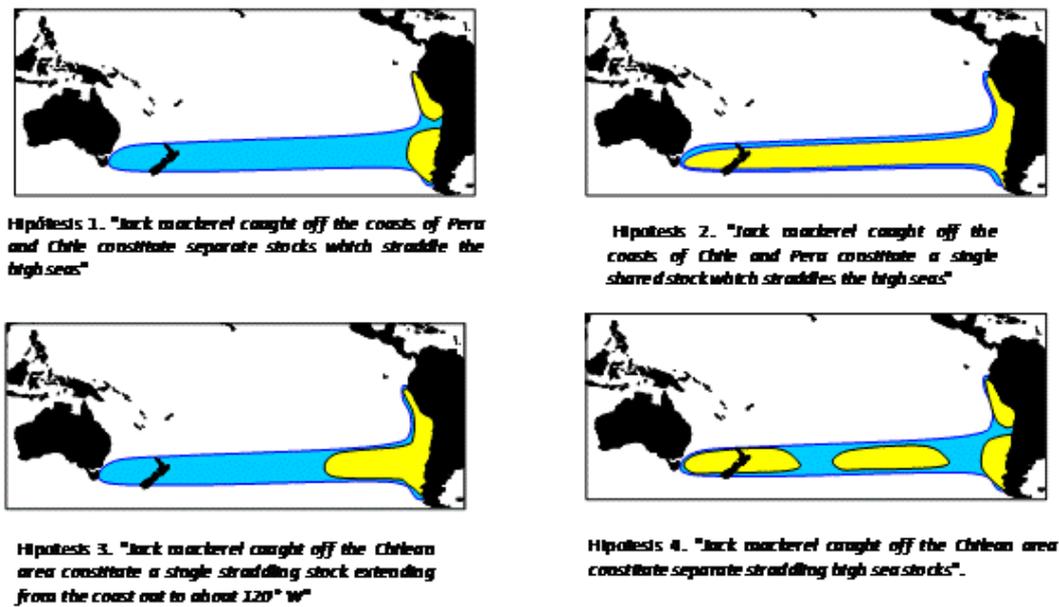As can be seen, there is still no general agreement on one hypothesis on the stock structure of the CJM.

Figure 2. Schematic diagram of the 4 hypotheses on population structure for the CJM
Blue: the CJM "Pacific Belt"; yellow: high density stocks

However, genetic studies have demonstrated very clearly that there is a single global genetic population in the Pacific Ocean (Cardenas et al, 2009; fig. 3).
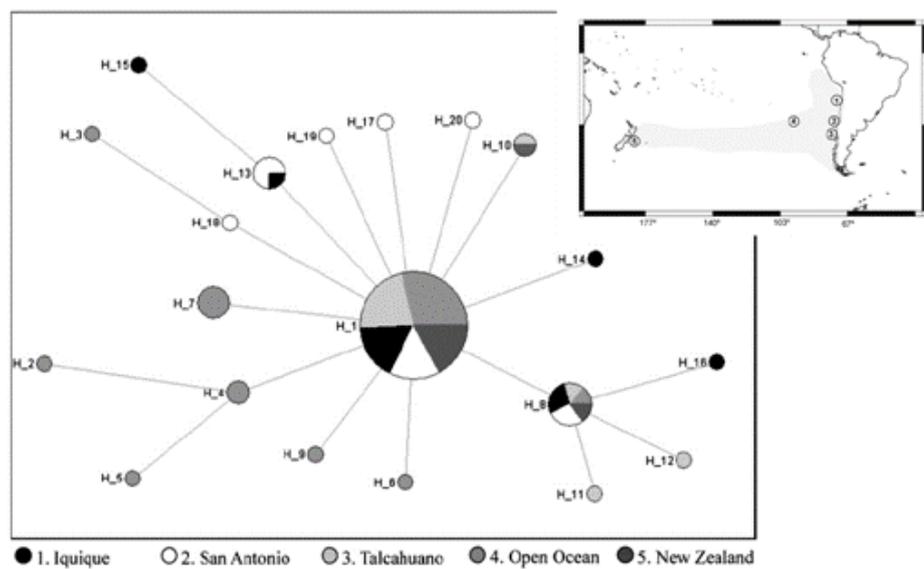

Figure 3. Haplotype network for 173 control region sequences of CJM. The numbers of population are in accordance with the simple locations displayed on the map (from Cardenas et al, 2009)

We can cite the major conclusion of these authors: *The present results [indicates] little or no genetic differentiation in the Chilean jack mackerel T. murphyi across its entire distribution range. Both mtDNA and microsatellite markers failed to detect any*

significant differences among localities. This result supports the hypothesis that a single population of T. murphyi inhabits the entire South Pacific.

This shows that defining multiple independent populations does not fit with the observed genetic structure. From this observation, we can reduce the possible population structure to two major hypotheses: a superpopulation hypothesis and a metapopulation hypothesis.

Defining which one of these two hypotheses is better describing the CJM population structure is important, because fish stock management would be different depending on the population characteristics. A superpopulation requires a unique global management, while the metapopulation, at least in the phase of existing independent sub-populations, allows for separate management policies adapted to each sub-population. Therefore it is important to investigate this point and define the best hypothesis. This is the objective of our paper.

1. MATERIAL AND METHODS

1.1. Bibliographical data

In order to help defining what the proper structure is, we can take advantage of a general synthesis of biological observations of the populations in the South Pacific produced by SPRFMO. We present below the table 1 summarizing the works presented in 2008 (Anonymous, 2008). We added recent results to this table.

Table 1

Synthesis of biological observations on the CJM: (1) papers presented at the SPRFMO scientific Workshop on CJM, 30 June-4 July, Santiago, Chile and not included in the bibliography; (2) SSP: Subsecretatia de Pesca, Gov. of Chile

Population characteristics	Supporting hyp. of different pop	Supporting hyp. of single pop.	Comments
parasites	Oliva (1999) A central-northern Peru population separated from a Chilean stock (lack of data from southern Peru)		Parasites are not a proof of different populations, but the demonstration that a given fish has been living in a given place during a given moment
Genetics	Koval (1996) Analysis with allozymes (but grey literature, low nb of loci, no peer review	Poulin et al (2004) FIP-IT96-15 (grey literature) Zhang et al (paper SPRFMO 3). Low sampling, peer review needed Cardenas et al. (2009)	Genetics shows clearly that there is a single recent population in the whole SPO

Spawning grounds	Evseenko (1987); Serra (1991); Nesterov et al (2007): two main spawning grounds Peru-central Chile. Santander & Flores (1983); Gorbunova et al (1985); Dioses (pers.comm): presence of spawning activity in Peruvian waters every year. Braun & Valenzuela(1): low egg and larvae density in the northern Chilean waters, increasing towards southern Iquique Nuñez et al (1); Ruiz et al (1); SSP(2) (1): main spawning ground in Chilean waters 35-40ºS	Braun & Valenzuela (1): important spatial and interannual changes in egg distribution in northern Chile. Evseenko (1987); Cubillos et al (2008); Nuñez et al (1): spawning of jack mackerel in the main reproductive region from Chilean extended up to 110ºW	The CJM spawning ground is not strictly delimited; eggs and larvae can be found almost everywhere. Existence of major areas, at least 3 of them in periods of large distribution: Peru, central south Chile, "source" (90-110ºW); conditions for separate life cycles including spawning are present; although there is no hydrological constraints, CJM focus the spawning in the "source" area mostly. Balance: the main spawning characteristics of CJM allow drawing the two hypotheses.
Abundance distribution	Castillo (1); Gutierrez (1): acoustic biomass concentrated northern to 17ºS and southern 20ºS. Existence of a "no-fish zone" between north and south populations. Soldat et al (1): 3 populations groups in the Central Pacific based on discontinuities of distribution, 105-125; 125-155; 155-175ºW (data 1982-1991, not currently available)	Castillo (1): continuous CJM distribution through the northern coast of Chile before El Niño 83. Cordova et al (1): biomass distribution by acoustic in water masses salinity between Peru and central-south Chile.	Abundance and distribution show a patchy distribution, with 4 major focuses: Peru and northern Chile; central-south Chile; "source"; west 110ºW, although no discrete distribution, existence of continuous distribution all over the CJM area.
Demographic structures	Soldat et al (1): in the three areas defined from the soviet fishery, there is spawning activity and complete range of ages from juvenile to adults (same remarks as above on data availability). Espinoza et al (1); Ñiquen & Peña (1); Ojeda et al (1); Bernal et al (1): distribution patterns different in Peru and Chilean waters, with larger fish towards the North in Peru and the South in Chile; complete size-age structure in both Peruvian and Chilean waters.	Espinoza et al (1); Ñiquen & Peña (1); Ojeda et al (1); Bernal et al (1): similarity in catch at length composition in N Chile and S Peru; similarity in recruitments since 1998 from S Peru to S Chile; presence of juveniles in N Chile and S Peru	A global vision of demographic structures shows that there is possibility of independent cycles of life until 1998. Possibility of a juvenile area S Peru to N Chile (but contradictory with abundance distribution). No clear idea of demographic and recruitment independence of the different sub-populations.
fisheries	Castillo (1); Cordova et al (1); Gutierrez et al	Zhang et al (1); Corten (1): presence of	Four separate fisheries have existed until 1998 (Peruvian,

	(1): fisheries based on a permanent and large concentration and biomass off Chile and Peru (at least until 1998).	continuous catches by Chinese and EU vessels 878-110ºW); the seasonal movements. INPESCA (2008)(1): the spatial distribution of central-south purse seine fleet shows the continuous distribution and the seasonal patterns of CJM off central Chile, from coast to areas beyond Chilean EEZ	Chilean, International, New-Zealand) in 4 separate areas. Since 1998 the coastal fisheries are decreasing; in 2008-2009 the Peruvian has almost disappeared; in 2009 the NZ has almost disappeared; the Chilean fishery is every year more focused on the international sector. It seems that during high abundance periods populations behave separately. The international area is the less affected by the global decrease of the abundances.
Environmental conditions	Gutierrez et al (1); Dioses (pers.comm): differences in water masses between Peru and central-south Chile. Soldat et al (1): existence of permanent eddies in the western areas.	Arcos et al (2001): global influence of El Niño events in distribution patterns.Northern Chile as an important nursery area.	Environmental conditions do not seem to play a role in the discretization of populations (high plasticity of fish in regard to physical conditions)
Trends and Cycle life	Soldat et al (1): in the three areas defined from the soviet fishery, there is spawning activity and complete range of ages from juvenile to adults (same remarks as above on data availability). (paper already presented in line "demographic structures"). Espinoza et al (1); Ñiquen & Peña (1); Ojeda et al (1); Bernal et al (1): complete size/age structure in both Chilean and Peruvian waters.	Penney and Taylor (1): Coincident trends in catches between Chilean and New Zealand areas.	3 major remarks: - There is synchrony in many cases for recruitment and variations in abundance. - There is a complete set of ages in each one of the sub-population areas. - There is a coincident trend in the catches. Here too the conditions for a metapopulation to exist are existing but do not proof the existence of a metapop.
alimentation		Cordova et al (1): existence of feeding grounds (*for Chilean CJM?*) in Peruvian coastal area. Bertrand et al. (2004, 2006), distribution of CJM more driven by the distribution of prey than by the oceanographic conditions.	Here too investigation shows that there is an important plasticity of CJM as far as feeding is concerned. Not a good criterion for population discrimination.

1.2. The two major hypotheses

- **The superpopulation hypothesis**

The superpopulation hypothesis considers a single population that expands and contracts according to its abundance, but with a single biological cycle, as schematized in figure 4. When the abundance is important, some parts of the distribution area act as subpopulations, at least for exploiting new feeding areas. In this case the authors defined a unique area for juveniles and several potential areas for spawning and feeding adults. The idea underneath this model is that the adults can colonize favorable areas, while the general biological cycle remains unchanged: same and single spawning area and juvenile area.
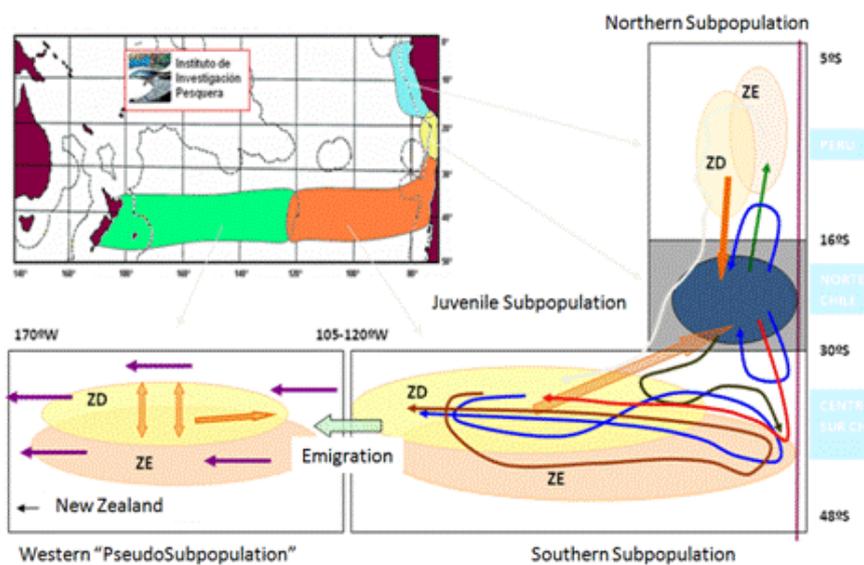

Figure 4. Diagram of the "superpopulation hypothesis" (from INPESCA).
ZD = spawning area; ZE = feeding area.

This hypothesis implies synchrony in the different subpopulations as far as reproduction is concerned, and the difference in space occupation, i.e. the existence of "subpopulations", is directly linked to the global abundance. There is no possible genetic or biological divergence between the subpopulations that are completely synchronous. This hypothesis was submitted by the Chilean from IFOP and INPESCA (Anonymous, 2008), and a general drawing of the hypothesized CJM superpopulation has been presented (figure 4).

- **The metapopulation hypothesis.**

The metapopulation hypothesis considers that sub-populations can have independent (and eventually divergent) lives. We present a diagram of this

hypothesis in the case of the CJM (figure 5) where independence between the "subpopulations" is assumed. In this case the fish subpopulations can diverge, at least during a period. This requires a series of conditions that will be studied more in details below. Each subpopulation is linked to a particular spawning area.
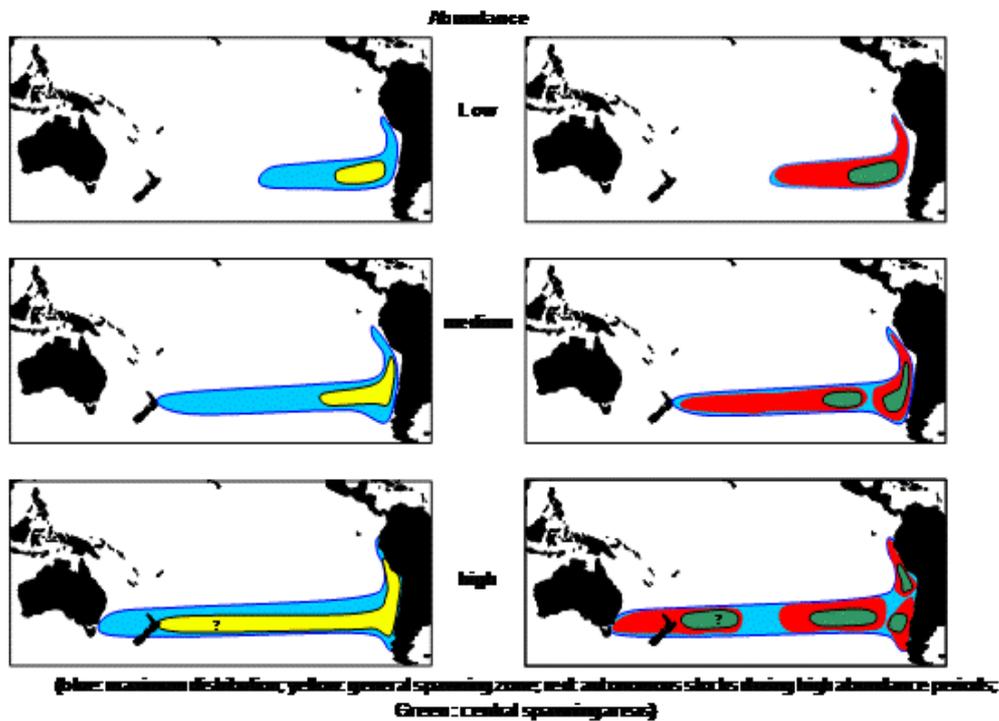

Figure 5. Diagram of the metapopulation hypothesis in the Pacific Ocean. Depending on the area of distribution the metapopulation can be formed of one (low abundance), two (medium abundance) of up to 4 (high abundance) sub-populations, each one centered on a particular spawning area. Blue: the CJM belt; yellow: areas of main concentrations; red: subpopulations; green: spawning areas

Our methodology will be then to consider the possibility of existence of a metapopulation, comparing the results and constraints with relation to a superpopulation structure.

1.3.   The metapopulation concept.

This concept was first defined by Levins (1968) as: "*a population of local populations which were established by colonists, survive for a while, send out migrants, and eventually disappear. The persistence of a species in a region depends on the rate of colonisation successfully balancing the local extinction rate".* The concept has been proved heuristic and was substantially enriched during the last decades. McQuinn (1999) presented a remarkable synthesis of these ideas when applying them to the populations of Atlantic herring, and synthesized Levin's ideas as: "*The population structure of many species can be considered as an array of local*

populations linked by variable degrees of gene flow (Wade and McCauley, 1988). This metapopulation concept, extensively explored by Montgomery Slatkin and others, was developed to study selection, genetic differentiation, extinction and recolonization events (Slatkin and Wade, 1978; Gilpin, 1991; Gotelli, 1991; McCauley, 1991). Levins (1968) first defined the metapopulation as:

(1) There is a large number of sites, each supporting a single local population;

(2) Each local population has a probability of going extinct that may depend on its genetic composition;

(3) The allele frequencies are governed by the classical genetic equations; and

(4) Vacant sites are recolonized by migrants from within the metapopulation (Slatkin and Wade, 1978)."

First developed for terrestrial ecology, the metapopulation concept was enriched by adding some characteristics and definitions to Levins' first description, e.g. the fact that a metapopulation is discontinuous in distribution, and even distributed "*over spatially disjunct patches of suitable habitat "patches" separated by intervening unsuitable habitat in which the animal cannot survive*" (McCullough, 1997). This first history on terrestrial ecosystems made the series of definitions inside the metapopulation concept difficult to precisely adapt to marine organisms, and especially pelagic fish which, by definition, do not occupy a geographically fixed ecosystem. McQuinn (1999) was among the first scientists to apply the metapopulation concept to pelagic fish (the Atlantic herring) and succeeded in explaining the contradictions between the two former hypotheses presented on this species, i.e. the "discrete population" concept (Iles & Sinclair, 1982) and the "dynamic and unstructured assemblages" (Smith & Jamieson, 1986). Nevertheless the herring is a particular case among the pelagic fish as it is a demersal spawner and spawning areas are strictly located on hard bottom substratum: a sort of territoriality, or at least homing, exists in the herring, which is not the case for most of the other pelagic species. McQuinn's elegant demonstration of the existence of a metapopulation was done through the existence of a straying and learning behaviour, balancing the homing and allowing for gene flow between the different local populations. Recently, Johannessen et al (2009) found evidence of straying and entrainment hypothesis for this species, by identifying herrings of two different populations mixed in a single school. Secor (2001) studied the possibility for Atlantic bluefin tuna to be organised into a metapopulation. He compared the results of two models to the actual population, the "diffusion model", which represents the "true" metapopulation, where transatlantic migrants of bluefin become expatriate and join

the other population, and the "overlap model", where migration occurs on an annual or cyclic basis but migrants go back to their natal region after the migration process. He concluded that the bluefin was not organised into a metapopulation but more likely followed the "overlap model". Nevertheless the question "*Connectivity of marine populations: open or closed?*" (Cowen et al, Science, 2000) is important and not completely answered.

Another point has been considered, i.e. that continuous populations cannot be considered as metapopulations. Kritzer & Sale (2004) define a metapopulation as "*a system of discrete local populations, each of which determines its own internal dynamics to a large extent, but with a degree of identifiable and nontrivial demographic influence from other local populations through dispersal of individuals*"; "[in fisheries research] *the unique feature of a metapopulation is the need to adopt two spatial scales to fully understand system dynamics: the local patch scale and the regional patch network scale. If the dynamics of each individual population can be modelled in isolation without reference to external influences, then metapopulation concepts are not appropriate. If, however, the inner workings of these local populations largely dictate their fate, but there is also a degree of replenishment from outside the population that affects population size and structure to an extent that it cannot be ignored, then metapopulation concepts are relevant*".
But on the contrary, *"if interpopulation exchange is sufficiently high, all populations equally affect all others and the system experiences regionally correlated population fluctuations, despite patchy distribution of individuals within the region. Metapopulation concepts are not appropriate for these "patchy populations". Grimke et al (2003) argue that the general "openness" of marine populations is not adequate justification for conferring metapopulation structure upon a system, because dispersal can be sufficiently widespread and recruitment sufficiently homogenised to remove the distinction between local- and regional-scale processes".*
"An important component of metapopulation dynamics is asynchrony in local populations dynamics because of partial closure of local populations that counteract homogenization of regional dynamics".

The same authors give a theoretical example of three spatially structured populations: at one extreme, the network of closed populations (A), at the other the patchy population (C). Neither of them can be accepted as metapopulation contrarily to the intermediate case (B) (fig 6)
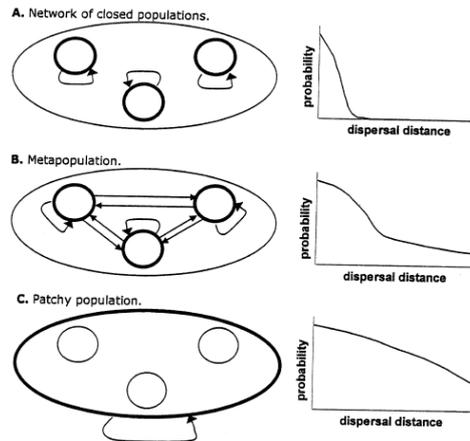
Figure 6. Three types of spatially structured populations with generalized dispersion curves for each local population. A: close local population with no exchange between them; B: metapopulation; C: patchy population inside a single "superpopulation". From Kritzer & Sale (2004)

Another series of definitions relates to distribution: "*given species may have the following types of distribution: 1) small and non-differenciated (species consisting of only one population without a clear spatial structure); 2) large and differentiated into numerous populations; and 3) large but almost non-differenciated (a super-population)*" (Camus & Lima, 2002).

Thorrold et al (2001) stressed also the fact that there is a need of non-genetic information to be sure that differences exist. They used otoliths of weakfish (*Cynoscion regalis*) to identify natal origins of individuals that cannot be differentiated through genetics. Although the genetics studies "*detected no genetic differentiation among the 5 estuaries (..) there is much more spatial structure than is currently assumed by fisheries managers*", they conclude that " *it may be useful to consider weakfish population dynamics from a metapopulation perspective*".

Some other definitions have been added afterward by other authors, e.g. the fact that there is a population "source" and that the others are assumed to "sink" at any moment.

Pelagic fish populations present specificities in their distribution strategies, because of the wideness of the potential area, the lack of precise borders in the habitats, and the year-to-year variability of the environmental conditions. Therefore it seems important to consider the metapopulation concept in the case of these large pelagic stocks. The CJM has adopted an evolutionary strategy of surviving through a series of particularly efficient recruitments that colonize the whole usable area, where –if

metapopulation exists- populations become independent in that point that they have their own spawning grounds, their own growing and hatching areas, etc. These sub-populations live on their own (and eventually develop particular characteristics) until a strong ENSO or decadal event reset the ecosystem and force them to leave the region and/or collapse.

This scheme is extremely common in the marine fish (and probably in other terrestrial or aquatic ecosystems) where demographic explosions are frequent. Bakun (2006) gave a series of examples in the Atlantic and Pacific Oceans. Moreover, this expansive behaviour is not restricted to pelagic species such as sardine and anchovies (Schwartzlose et al, 1999), or sardinella (Bard & Korentang, 1995), but also to demersal fish such as the grey triggerfish *Balistes capriscus* (Caverivière, 1991; Caverivière et al, 1980); the spinefish *Macroramphosus scolopax* (Aristegui et al, 2006); the file fish *Pervagor spilosoma* (Hobson & Chess, 1996). More surprisingly for at least one of these demersal fish, *Balistes capriscus*, the expansion was accompanied by a complete change in its behaviour, and this solitary and territorial benthic species became pelagic, gregarious, changed its diet from crustaceans and echinoderms to plankton, etc. (Burczynski et al, 1979; Caverivière et al, 1980). Then after a couple of years, the actual abundance went back spontaneously to the "standard" of the species which recovered its usual behaviour. The importance of these changes shows clearly that demographic explosions do not represent an accident but are part of the evolutionary strategy of the species. In the case of the grey triggerfish, a confirmation of this remark is (1) that these expansions have been reported even since 1853, relating the discovery of triggerfish caught in the Irish waters (Went**,** 1948); and (2) that some members of the family Balistidae are permanent pelagic species, living in tropical high seas below FADs or any floating object: the pelagic phenotype is not exceptional in this family.

Therefore this strategy of demographic explosions and invasions can be considered inside a metapopulation framework, although the precise mechanism is not completely identical to the "classical" scheme: here one single "source" invades all the potential life zone of the fish. This invasion process can take generations, as huge schools of juvenile triggerfish have been observed during the early 80s in Senegal while the original explosion began in the early 70s off Ivory Coast (Aggrey-Fynn, 2007). Its biomass is usually so important that it becomes predominant compared to the local populations (in the case of Balistes, for instance, the density

in one hour trawling shifted from less than 10 kilos to more than 200 kilos: Caverivière, 1991). Colonization was general and all the potential habitats were occupied. Then after several years the overall biomass fell down spontaneously to previous low levels. (fig. 7).
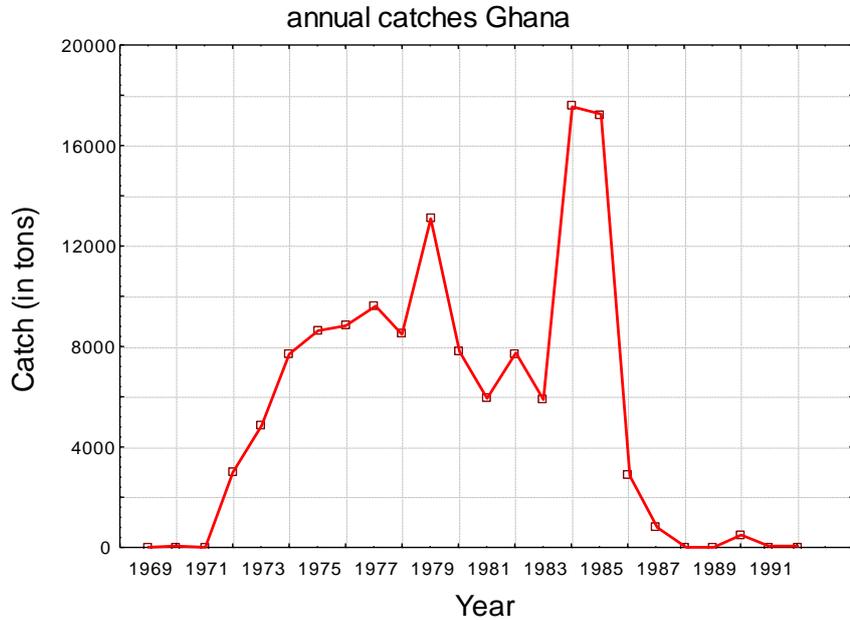

Figure 7. Catch statistics of *Balistes capriscus* in Ghana, 1969-1992
(from Aggrey-Fynn, 2007)

Many pelagic species present the same characteristics of a wide expansion phase followed by stable periods organised in local populations, and eventually a decrease to a lower level. This strategy shares with the metapopulation the ability to recolonize lost areas, to exchange genes between populations, maintain a source population at a consistent level, etc. Differently from metapopulations, the importance of the invasion produces a synchronous history of the different local population at least during a few years, blurs the limits of each populations making discrete areas recognition impossible, and homogenises completely the genetic pool of the species. Such invasions seem to present a very low frequency in most of the species (since the late 40s no invasion of Balistes was reported by scientists before that of 1973-1985).

Another important comment is presented by Petitgas (2010), applying the "migration triangle" (Harden Jones, 1968) where 4 particular locations can be encountered in a life cycle: area of spawning adults; of larvae; of juveniles; of feeding adults (figure 8). Changes in the migration triangle for environmental reasons (climatic change, overexploitation) may have heavy consequences.
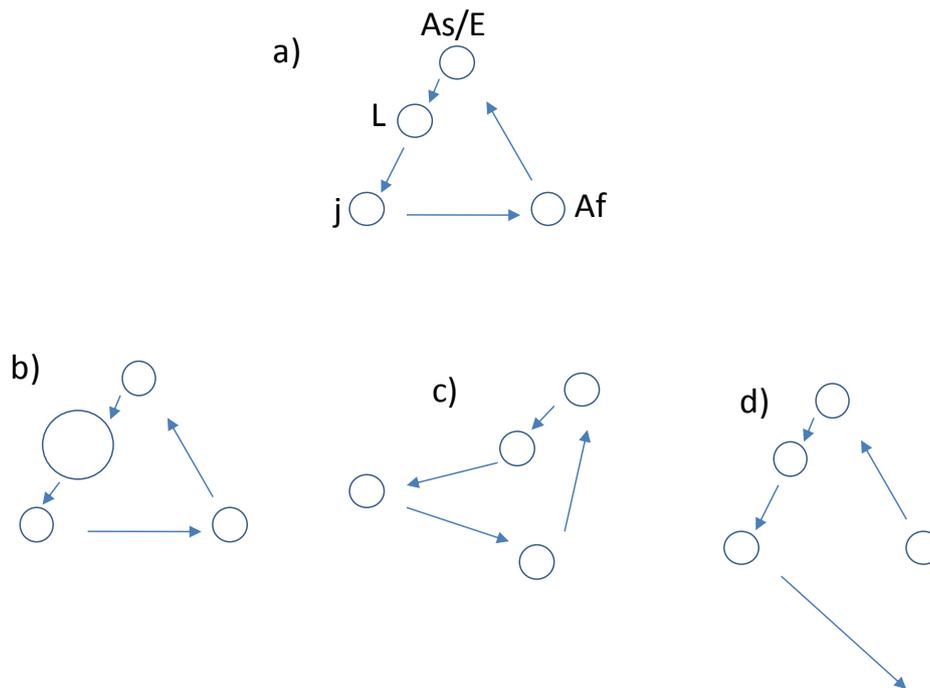
Figure 8. a) scheme of a life cycle (migration triangle) and possible impacts of a climatic change on: b) the availability of an habitat; c) the modification of the geographical location of an habitat or d) the discontinuity of habitats. Af: feeding adults; As/E: spawning adults and eggs; L: larvae; j: juveniles (from Petitgas, 2010)

On the base of this description, Petitgas et al (2010) "*argue that stock collapses not only involve biomass loss, but also the loss of structural elements related to life-cycle diversity (contingents) as well as the breakdown of socially transmitted traditions*". Contacts between generations are essential to "train" the juveniles and take them to the proper spawning and feeding areas. When a stock recovers after a severe collapse, no old adult can play this role and the population has to discover again these old territories, through the emergence of a contingent of migrant phenotype. These particular fish, usually presenting a higher growth rate and a delay in reaching the maturity, are able to explore the ecosystem and encounter favourable areas. We found some similar thoughts expressed by Cury (1994) describing the "Obstinate Nature".

If this hypothesis is confirmed, it explains how sub-populations can disappear and appear again in areas outside the "source" zone. The concept allows envisaging that population and life cycle structures are dynamical over time, e.g., they change from one structure to the other (possibly with a predefined sequence). In particular, in a superpopulation, mixing between reproducing adults is greater than in a metapopulation where isolation is greater.

2. **RESULTS**

Defining a population is extremely difficult from a strictly ecological point of view (e.g. Frontier, 2004). But our objective is different and the fact that we have to provide recommendations to managers is an argument for accepting a pragmatic definition of what our population is. As said Cowen et al (2000), despite the fact that "*genetic studies have suggested that many populations of marine species are homogeneous over large spatial scales (...), management decisions based on open population models might overestimate the level of population exchange. Such overestimates might lead to a false sense of security among managers of 'downstream' resources*".

2.1. **Results from the literature**

The definitions and description of the metapopulation concept shows that conditions for a metapopulation to exist are more restrictive than those for a superpopulation. Then we hypothesize that if the CJM characteristics do not fit with the metapopulation conditions, the structure is more likely a superpopulation. Within this framework, in order to define which, between superpopulation and metapopulation, describes better the CJM distribution and dynamics, we listed the conditions for a metapopulation to exist; then list in what extent the CJM fulfils these requirements or not; and eventually decide if this hypothesis is applicable.

Hanski (1999) gives a list of 12 conditions that we listed in table 2 (conditions 1 to 12). Since Hanski's list is not completely exhaustive we added four other conditions expressed by other authors (Table 2).

Table 2. Description of the populations

	population characteristics	The case of the CJM
1	*Population size or density is significantly affected by migrations*	Yes, obviously (large movements between populations at environmental changes).
2	*Population density is affected by patch areas and isolation*	?
3	*Existence of asynchronous local dynamics*	Apparently no, but characteristics possibly within (hidden by) a global synchrony due to strong basin-scale environmental signals
4	*Population turnover, local extinctions and establishment of new populations*	Probably, the case of New Zealand where CJM was unknown before the 70s is a good example
5	*Presence of empty habitats*	Yes if we consider again the case of NZ and

		Tasmania
6	*Metapopulations persist despite population turnover*	Yes. Fisheries have always showed the presence of fish in the central area, Chilean and Peruvian areas. Presence of small groups of very large sedentary adults along the South America coastline
7	*Extinction risk depends on patch area*	Yes probably
8	*Colonization rate depends on patch isolation*	? this condition probably does not fit with the case of a large pelagic population
9	*Patch occupancy depends on patch area and isolation*	? this condition probably does not fit with the case of a large pelagic population
10	*Spatially realistic metapopulation models can be used to make prediction about metapopulation dynamics in particular fragmented landscape*	? no modelling exercise done so far
11	*Metapopulation coexistence of competitors*	Yes. Presence of mackerel in overlapping with the CJM at least in the Peruvian waters
12	*Metapopulation coexistence of prey and its predator*	? this condition probably does not fit with the case of a large pelagic population
13	*Evidence of genetic linkage*	yes
14	*Genetic or morphometric, meristic or biological/behavioural differences*	Not studied. The recent history of the population as evidenced by genetic studies suggests that such differences are unlikely
15	*Existence of source/sink populations*	Yes, the central offshore population is clearly the source, Peruvian and western Pacific being "sink" populations
16	*Discrete local populations*	Clearly no

This table shows a series of interesting points.

The first one is that there are few but critical conditions that apparently do not fit with metapopulation definition in the case of CJM. Actually two of them are rather clearly in contradiction with the metapopulation definition: (*Condition 16*) the different populations cannot be considered as discrete and it is impossible to draw clear borders between the populations with the existing data. The CJM has a strong plasticity (Bertrand et al, 2003), and can be encountered in the whole "Pacific belt". (*Condition 3*) there is no independence between the apparent changes in the different population (synchrony of variations in abundance, migrations, etc.). This is particularly the case in the present time where all the sub-populations are shrinking together, from Peru and Chile to New Zealand.

Our second observation is that most of the other essential requirements are fulfilled. This is particularly the case for the genetic linkage (condition 13), as demonstrated by the genetic analyses (Cardenas et al, 2009), which show first that there is a single species and a single genetic population in the South Pacific Ocean (SPO), but also that there are differences in the colonization dates, the arrival in New Zealand being more recent than for populations along the coastline (fig. 3).

The third observation is that some of the conditions cannot apply for the particular characteristics of CJM which is a pelagic population covering a large area, where no absolute separation between patches or populations can be described, as small quantities of CJM are encountered in any place of the whole "jack mackerel belt"; environmental conditions are also specific. The importance in the SPO of strong climatic signals at interannual (e.g. El Niño southern oscillation: Barber and Chavez, 1983), decadal (Chavez et al., 2003) and centennial (Sifeddine et al., 2008; Gutiérrez et al., 2009) scales, is well known and they have a strong impact on the whole ecosystem, *ergo* on fish stocks. It is especially interesting to note that the CJM has developed a strategy of a few successful recruitments (in average 1 every5 years) that lead the whole population and its exploitation (Konchina and Pavlov, 1999). It is too soon to know if these recruitments are synchronous with one or several of these signals.

2.2 Critical analysis of the metapopulation concepts in the case of the CJM

The major difficulties in most of the cases of metapopulation studies relate to the difficulty to demonstrate the existence of gene flow or the risk of extinction of individual populations. Paradoxically these two conditions are the easiest to put in evidence in the case of the CJM. In our case the question is mostly on the likeliness of independence of the different patches and the existence of a clear synchrony in collapses and recoveries. Most of the conditions listed for metapopulation recognition come from studies on small sedentary populations e.g. shrimp in estuaries. We can suspect that the conditions for metapopulation existence are rather different in the case of any circum-oceanic species. One trivial example is that the distances of coverage of this "super-population" are so wide that the usual definition of a single population, i.e. "*the population concept assumes that all individuals in a population interact equally with all the other individuals*" (Hanski, 1999), does not make any sense in the case of the CJM, where it would take close to one year for a fish to travel from the eastern to the western borders of the Pacific belt considering the usual speed of fish and the distance in the SPO. For evident geographical reasons, subpopulations must behave separately. This is also the case of European jack mackerel (*Trachurus trachurus*) where there is no practical possibility for individuals in Aegean Sea to permanently interact with those of the Norwegian Sea (*see EU Project HOMSIR, http://www.homsir.com/*). Then the question of the synchrony of reactions should be studied. Interestingly we can find synchrony not only between the CJM populations, but with other completely different

species. During the last decades we observed a clear in-phase synchrony between the jack mackerel (*Trachurus murphyi*), the mackerel (*Scomber sp*) and the sardine (*Sardinops sagax)* populations, and out-of-phase with the Peruvian anchovy (*Engraulis ringens*), etc. (fig. 9).
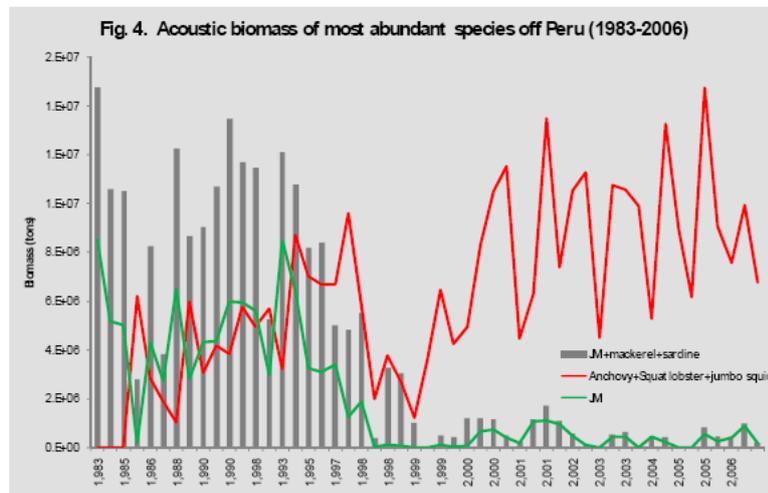

Figure 9: acoustic estimates of biomass for CJM, anchovy, sardine and mackerel in Peru, 1985-2008.

Nevertheless, paleo-studies (Gutiérrez et al., 2009) demonstrate that sardine-CJM-Mackerel are not always strictly out of phase with anchovy. A hypothesis of simple coincidence in cycles cannot be rejected for long periods (e.g. centuries).

Anyway, this shows, at least for the present period, the peculiarity of the Humboldt Current System and more widely the Southeast Pacific Ocean, which is completely driven by the ENSO, decadal and centennial oscillations. Environmental shifts act as a reset of the whole ecosystem. Synchrony in this case is not due to single population behaviour, but to reaction of the ecosystem to these climatic events. Interestingly these synchronies have been discussed for other species (Freon et al, 2003) and for other periods of the CJM life (Ortlieb, ref), and when one enters in the details they become less evident. We will not enter in this difficult discussion, but we can conclude that either there is synchrony and in the CJM case it is likely due to environmental signals and not to the unity of the population; or there is no synchrony or the apparent synchrony is coincidental. In both cases, the argument of existence of synchrony between the different parts of the populations cannot be received as an argument against the metapopulation hypothesis. Although we observed that (Condition 3: *Existence of asynchronous local dynamics*) was not apparently

respected, this may not be sufficient a reason to reject the hypothesis of metapopulation.

The CJM presents the strong characteristics of a wide expansion phase followed by stable periods with local populations, and eventually a decrease to a lower level. This strategy shares with the metapopulation structure the ability to recolonize lost areas, to exchange genes between populations, maintain a source population at a consistent level, etc. Differently from metapopulations, the importance of the invasion produces a synchronous history of the different local population at least during a few years, blurs the limits of each populations making discrete areas recognition impossible, and homogenises completely the genetic pool of the species. Such invasions seem to present a very low frequency in most of the species. In the particular case of the CJM, such strategy might have a shorter rhythm, likely related to the South Pacific oscillations.

Another requirement, i.e. the discrete population (condition 16), is also extremely difficult to apply in an "open" pelagic population such as the CJM. This question of the "open-close dilemma" (Camus & Lima, 2002; Cowen et al, 2000) has been extensively addressed and forced the scientists to define more precisely the populations. Camus & Lima (2002) show how this definition has evolved with the advance of understanding. They insist on the difficulty to define clearly the concepts: "*Each species has a population spatial structure of its own, ranging from a single population, to a population of populations or to a super-population (Beklemishev, 1960). Although metapopulation theory can be a very useful approach, one has to define clearly what is the definition of "local" populations and its relationships with populations and metapopulation systems*" (Camus & Lima, 2002). This is particularly complicated in the case of the CJM, where the actual limits of extension for each subpopulation cannot be easily defined or observed

2.3. Characteristics of the spawning areas

We assume that the main characteristics that would give sound information is the variation in demographic strategy of the sub-population. Therefore it is important to have a clear idea of the spawning areas and cycles, and on the demographic structure of the subpopulations. Many works have been done on these points for the CJM and we give below a synthesis of the results.

- The CJM spawning areas are not neatly depending on environmental conditions. Works from Cubillos et al (2008) show in the case of the centre-south population that the sea surface temperature (SST) varies significantly from one year to the other in the spawning ground (figure 10).
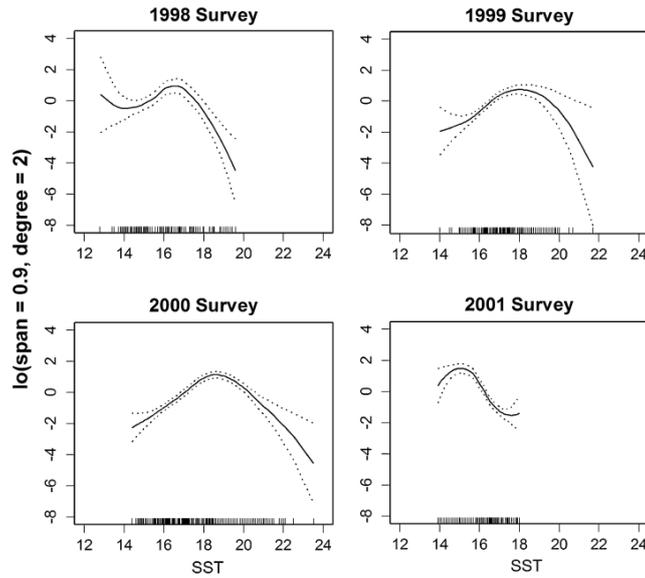

Figure 10. Relationships between jack mackerel eggs density and sea surface temperature (SST) obtained by GAM models from 1998 to 2001 in the centre south Chile (from Cubillos et al, 2008)

- Interestingly, CJM tends to scatter in the spawning areas (Barbieri et al, xx: figure 11). Several hypothesis can explain this paradox, e.g. cannibalism or difficulty for acoustics to observe scattered fish close to the surface.
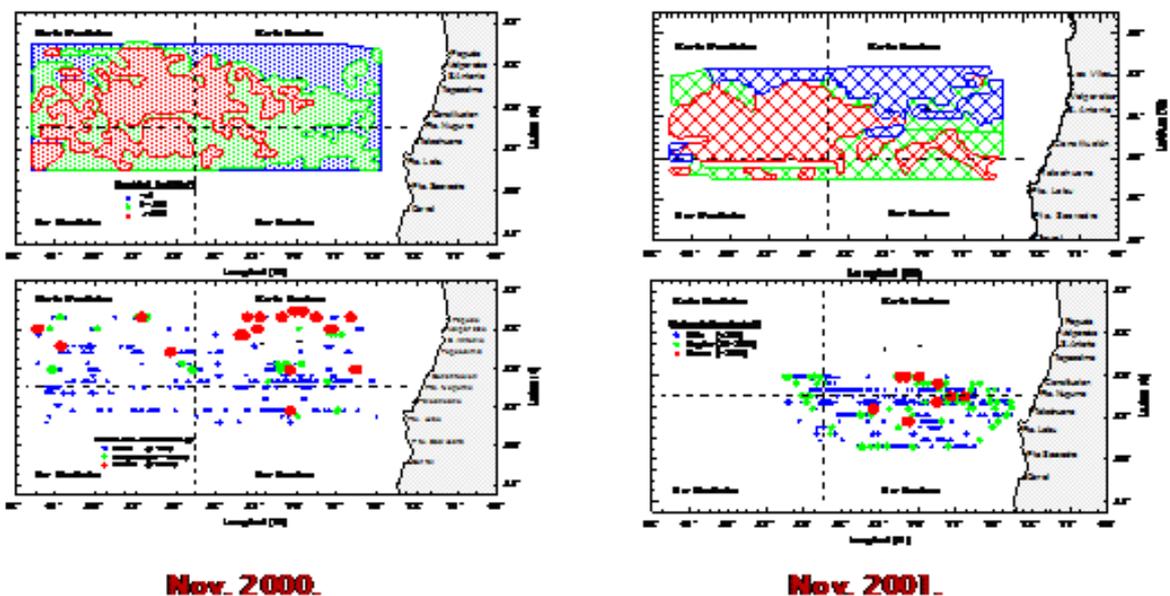

Figure 11. Comparison of egg distribution (above) and fish concentration (below) in November, 2000 and 2001. The highest concentration of fish observed (using acoustics)

occured in the less dense egg area. Concentrations in relative units, from blue (low) to red (high) (from Barbieri et al, xx)

- The major spawning ground has been surveyed each year since 1997 using hired fishing ships ("Rastrillo" surveys, ref.). Results show a rather good stability in geographic position, but a wide variability in density of eggs (figure 12). Confirming the former results from Cubillos et al (2008), we can see that according to the years (and maybe the abundance), the higher egg densities can be found in waters warmer (1999) or colder (2000-2007) than 17º.
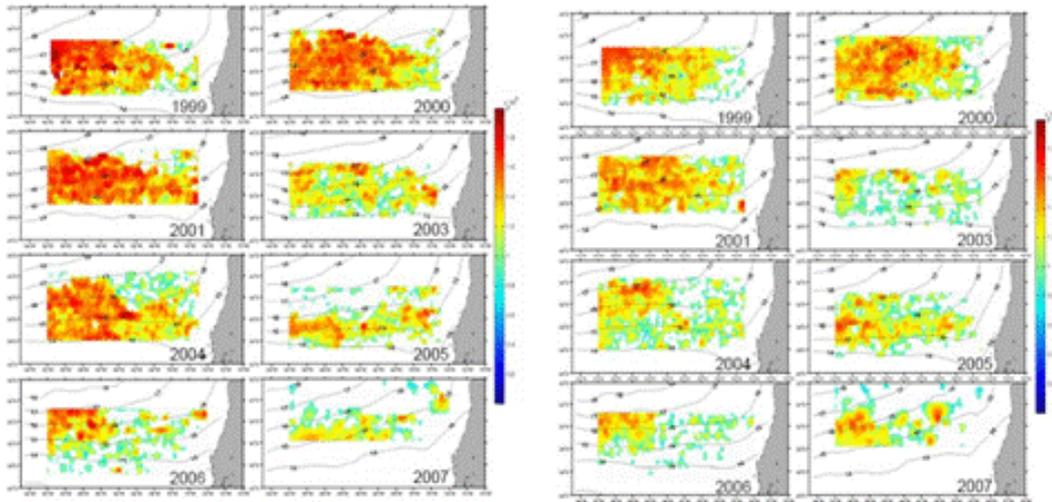

Figure 12. Distribution of eggs in the centre south spawning area (from Sepulveda et al, xx). This point reinforces the observation that the CJM does not require precise environmental conditions to spawn.

- The overall observation of eggs and larvae in the CJM distribution area, as observed adding the Russian fishing fleet data and the Chilean dedicated surveys (figure 13) shows a wide distribution of eggs, demonstrating that opportunistic spawning grounds are likely to appear wherever adult fish stocks are present. The spawning area can extend up to 15ºS off Peru, while it is generally situated between 30ºS and 40ºS off Chile. This map shows that there are two focus of egg distribution: a large one centered on 30ºSD-40ºS off Centre-South Chile and a smaller one centered on 15ºS-25ºS off South Peru and North Chile. The latitude 25ºS seems to be poorer in eggs than any other and could delimitate two major areas.
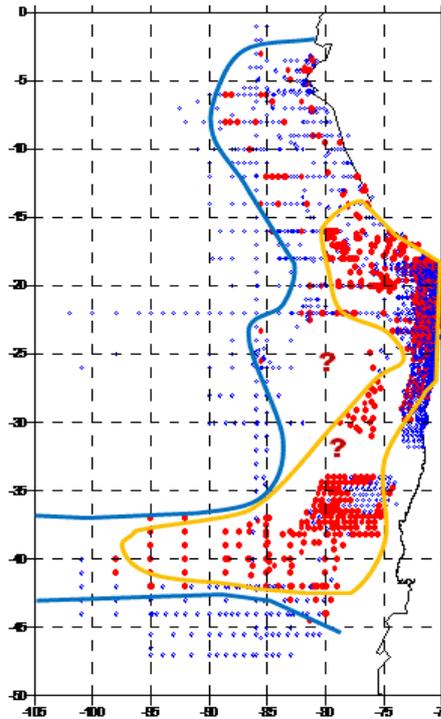
Figure 13. General distribution fo CJM eggs in the SE Pacific, as observed during the period xxxx-xxxx (from xx). Blue dots: sampling stations with no eggs; red dots: sampling stations with eggs. Oorange line shows the limits of the major spawning areas. Blue line shows the extreme limits where eggs were found. Note the lack of data from 25ºS to 35ºS in the Russian data base, this area belonging to the Chilean EEZ (represented by the question marks)

In conclusion, the fish egg distribution, the fish requirement for spawning and the CJM behaviour are the following: no major specific requirement in terms of temperature (SST) for the spawning area (SA); wide and permanent SA in international waters off Chile; during high abundance periods, besides the principal SA W of 80ºW between latitudes 35-40ºS, existence of one (or several) coastal SA between 12ºS and 40ºS, and sporadic spawning over the whole distribution area; during low abundance periods, one major SA off Chile (same as above), marginal SA in Peru and Chile EEZ; CJM tends to scatter in the SAs.

2.4. Demographic structure of the CJM stocks in Chile and Peru

As we explained before, the best evidence of the existence of metapopulation would be if specific demographic strategies, implying different recruitments, could appear in the different sub-population areas. The figure 14 shows the general information of the demographic structure of the catches in Peru and Chile for the period 1996-2007.
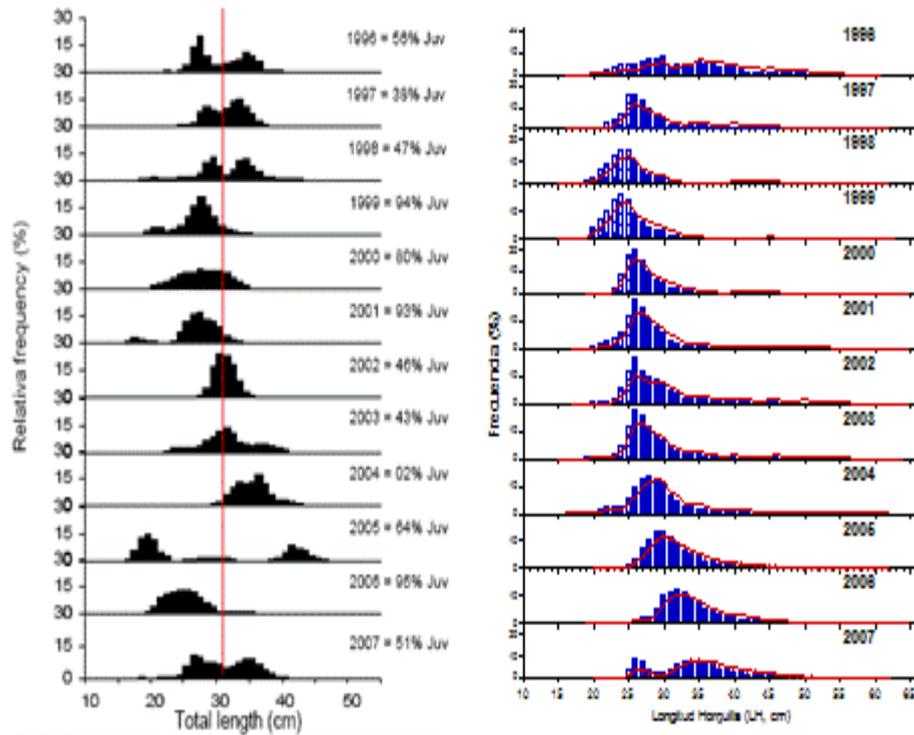
Figure 14. Comparative diagram of demographic structures (length frequencies) in the catches of CJM in the Peruvian (left) and Chilean (right) sub-populations. From xxx

If these diagrams represent correctly the actual structures of the sub-population and their respective abundances per cohort, it appears that, as hypothesized, different demographic dynamics occur in the two sub-populations. For instance, an important cohort is recruited in the Peruvian fishery in 2005 that only appears in a much lower abundance in 2007 in Chile.

Superposing the mode values extracted from figure 13 in Peru and Chile, we can observe better the possible common and specific dynamics (figure 15).
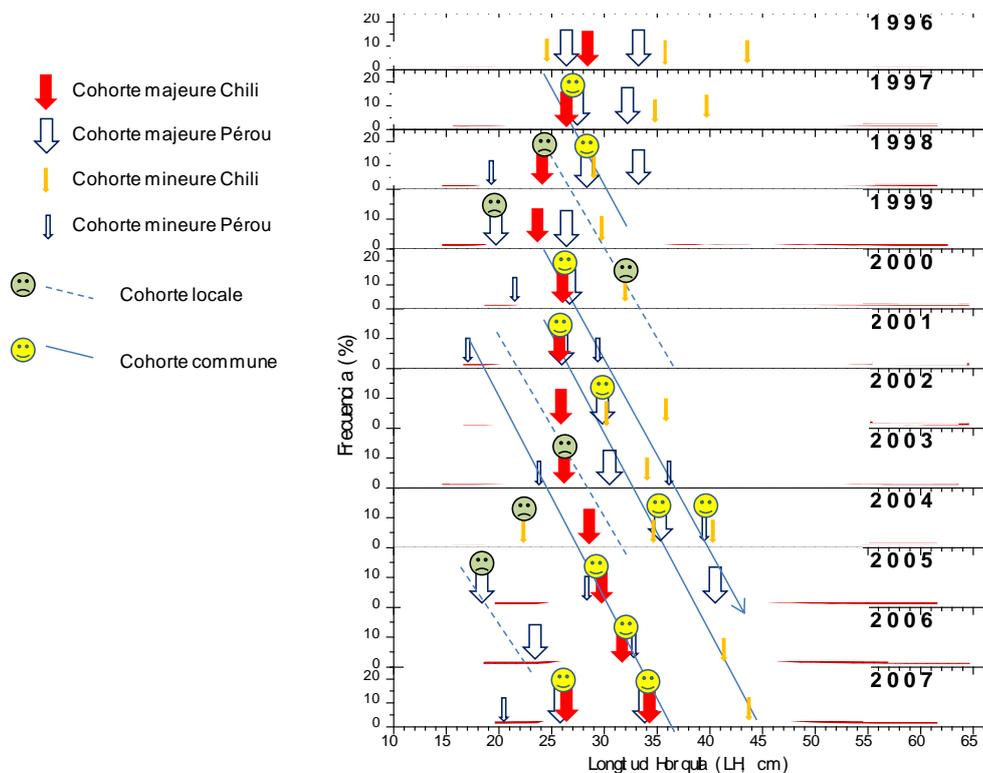
Figure 15. Synthesis of the mode values observed on a yearly base in Chilean and Peruvian fisheries.

An annual histogram is by construction hiding the intra-annual growth. This, plus the regulation of the fishery that forbids fishing individuals of less than 20 cm, explains why most of the catch is performed on fish between 20 and 40 cm FL. Nevertheless we can extract three principal types of results.

- Some year classes, among the most abundant, are common to the two fisheries. Contradictorily to what could be expected, they often appear in the Peruvian fishery (e.g. new cohorts in 1999, 2001, 2005). It is difficult to know whether this is related to the catches, the sampling, or the biology. In any cases, these cohorts (e.g. 2001) are equally exploited by the two fisheries. We may suspect that this is typically source recruitment.

- Some others, e.g. 1998, 2003, 2004, are specific. These three cohorts appeared in the Chilean fishery and not in the Peruvian one. We may assume that they are issued of the southern subpopulation.

- Finally some ones, e.g. 2005, appear first and in a great abundance only one subpopulation (north in this case) and are represented only a couple of years later in the other one.

3. DISCUSSION

We have seen that although most of the conditions are fulfilled to consider that the Chilean Jack Mackerel populations observed in the Southern Pacific Ocean could belong to a metapopulation, two essential requirements are not: that the populations form discrete patches, and that they evolve independently. In a first lecture, and following strictly the metapopulation definitions, we should then reject the hypothesis, these two conditions being the ones differentiating a metapopulation from a "superpopulation".

However the description of this "superpopulation" does not seem fully convincing either, for several reasons: (i) the juveniles cannot present the status of a particular subpopulation as the North subpopulation is; (ii) there is not only one growth zone according to the length structure of the catches, and juveniles have been encountered west of 112ºW ; (iii) the description of the superpopulation (figure 4) takes into account the existence of separate feeding areas, which fits with the superpopulation hypothesis, but also separate spawning areas related to each sub-populations, which is somehow contradictory with the definition of a superpopulation. On the contrary, the fact that, as is observed nowadays, all the sub-populations seem to evolve synchronously (general decrease of the abundances from New Zealand to Peru and Chile) is rather in favour of a superpopulation structure.

We saw that the metapopulation hypothesis is not fully satisfactory either, but we must note that several definitions in the table are not simply applicable to the CJM population, because of the dimension of the populations. It is important to enter more in details in these particular cases, following Hanski (1999): "*perhaps most striking is the virtual lack of unambiguous evidence for the threshold condition for metapopulation persistence*". Considering this point, the discussion on the organisation in metapopulation or in other structure must be leaded by empirical observation and practical needs: *"The context-specific applicability of metapopulation theory reinforces Hanski's argument that the metapopulation concept is more of an analytical approach to be used when appropriate rather than a set of strict criteria and definitions (Hanski 1999)."* Kritzer & Sale (2004).

We see that pelagic populations present some particular characteristics that make uneasy the application of the list of conditions established from a literature review of the main authors in this field. It is likely that we might have to draw a particular series of definitions that fit to the pelagic fish.

In any case, it seems clear that the most convincing condition that could show whether a species is organised into a metapopulation or not is that the different sub-populations present different (independent) traits of life. Such differences are the result of different selective environmental pressures that eventually lead to genetic divergence in the sub populations. Here too, differently from the other cases, some particular traits that are significantly linked to a given subpopulation are not necessarily the demonstration of different sub-populations: given the ability of fish to move along considerable distances, the fact that a fish present, for instance, a difference in the proportions of parasite species that infest it may just show that it has passed (or is provisionally living) in a region where these parasites are present. Alimentation too, for such an opportunistic species as is the CJM, can be the demonstration of the adaptation of the fish to a given area, not a divergent preferendum. Then our objective is to evaluate, synthesizing the observation listed in the former chapters, what are the significant characteristics and to which point they show real differences in the populations.

We consider that the main characteristics that would give sound information is the variation in demographic strategy of the sub-population. Indeed we propose the following scheme. A "source" population is the most important in term of abundance and produces "demographic pulsations", linked to environmental signals, which gives periodic high recruitments invading the whole potential area of the CJM. These high recruitments should impact all the subpopulations, with some delay (time for invasion). If the CJM is organised in a "superpopulation", then these high recruitments coming from the source are the only ones. If it is organised into a metapopulation, then some other demographic pulsation can appear in the different sub-populations, and these local high recruitments should be independent from each other, and above all independent from the source. If they are absolutely synchronous with the source pulsations, then we may suspect environmental synchrony, and not invasion. In this case we cannot conclude which one of the two hypotheses is the correct one.

The egg-larvae characteristics are not contradictory with a metapopulation model as displayed in figure 10. They are not in contradiction either with the superpopulation hypothesis, provided this extended spawning area remains a single area with an equal probability for any fish to spawn in any part of it. Whether there are one or several spawning areas can only be answered using tagging surveys.

We give in figure 16 a schematic model of the differences that are likely to occur in the CJM distribution and dynamics depending on the type of population, limiting the diagram to the two subpopulations south and north to 20ºS. We use the "migration triangle" suggested by Petitgas et al (2010) and drawn in figure x.
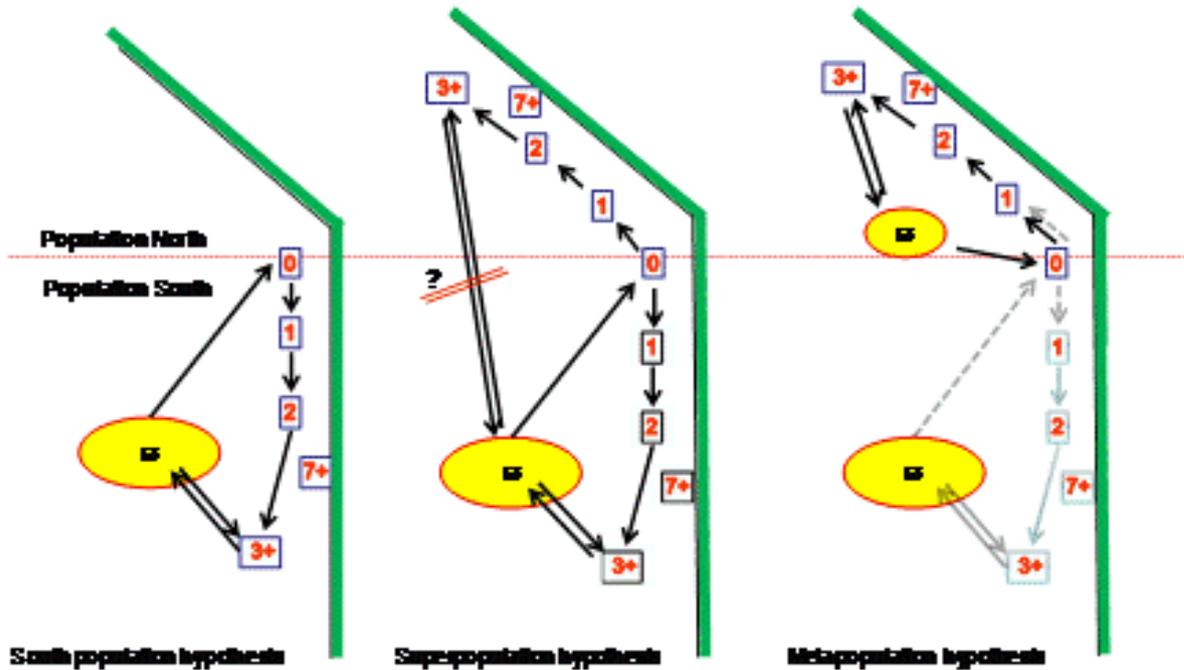

Figure 16. Diagram showing the theoretical differences in the biological cycles of CJM in the case of a superpopulation (centre) or metapopulation (right structure of teh populations, using the actual migration diagram of the centre-south stock as a basis. Π = spawning ground; 0 to 7: year classes

The left part of the diagram shows the observed cycle of the Centre-South population off Chile and in the Chilean EEZ, which could be considered as the "source" population. The cycle is simple: the larvae leave (actively or passively) the spawning area to go to a "growing" area. Then the fish go slowly southward when growing. At age of 3, the young adult begins an annual migratory cycle between the feeding ground and the spawning area. We can add that an almost sedentary old year class is observed along the coastline, very close to the shore (fish above 60 cm FL). This model is in agreement with the observation of the spatiotemporal behaviour of the centre-south population, which is the best known: the observation of the fisheries data allowed Arcos et al (2001) designing its migratory cycle, both in position of the stock and demographic structure of the fish (figure 17). It is this diagram that we used in our model.
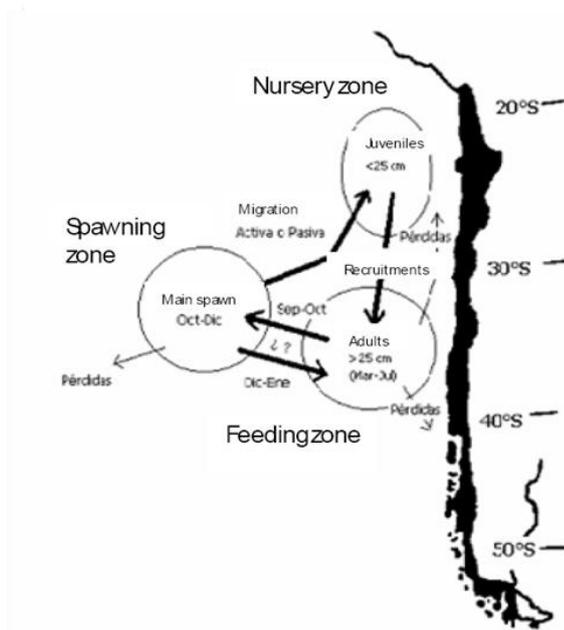
Figure 17. Schematic diagram of CJM migrations in the centre-South area, from catch data and egg-larvae surveys (from Arcos et al, 2001)

The central diagram shows what would be the situation when adding the Peruvian (North) population in the framework of a superpopulation hypothesis: the major difference with the first diagram consists in a migration northward of part of the young fish, symmetric to the southward one. Once reaching age 3, the young adults in the North develop the same migration behaviour as the southern population, going to the common spawning ground for spawning, and back to the north of Peru for feeding. It is interesting to notice a contradiction between the superpopulation model and the diagram given in figure 4 which displays several spawning areas, while the model cannot accept but a single one, otherwise genetic divergence is likely to occur. Moreover it is difficult to imagine that this symmetric colonisation would have no different effect on these two parts of the stock, considering the ecosystems north and south of 20ºS are not similar in many aspects, particularly in the SST, the OMZ, etc. and would have different selective impacts on the biology of the two stocks. If the effects are distinct, then some independence in the traits of life of the CJM in Chile and Peru should happen sooner or later.

The diagram on the right shows the same case under a metapopulation hypothesis. In this case a specific cycle appears in the north, different from the south one, where the young adults, instead of going to the common spawning ground, create a new one specifically for their population. Indeed a specific spawning ground for each subpopulation is essential in the definition of a

metapopulation, as it is the only way for them to be able to diverge genetically from the parent population. In this case the cycle becomes independent and metapopulation can occur. This metapopulation model is also in agreement with the general hypotheses from Petitgas et al (2010), who observed the existence of different emerging behaviours in a population that produce migrant and non migrant groups. The fact that the fish share a common juvenile growth area is also observed in the demographic structures of the stocks in Peru and Chile, where the distribution of year classes are symmetric in latitude: therefore it is likely that exchanges occur between individuals from the two sub-populations, as stated by McQuinn (1993) for the herring and Petitgas et al (2010) for the anchovy in the Bay of Biscay.

The next step is to determine which one of these models is better representing the actual situation. The simplest way to test them is evaluating whether the existing spawning grounds and demographic structures observed from surveys and from the fisheries are or are not in contradiction with the superpopulation and/or the metapopulation hypotheses. We have seen that there are different cohort histories, some being common to the two areas while some others remain localised in only one area.

Here too, as in the case of the egg distribution and spawning areas, the results are not in contradiction with the metapopulation hypothesis. Nevertheless whatever the result is, the frequent resetting of the ecosystem (by the ENSO and decadal cycles?) does not give enough time for the subpopulations to diverge. The metapopulation can be effective but with no genetic results. Therefore considering the CJM as leaded by a superpopulation strategy will not drive to very different conclusions.

The major reason of the difficulty to decide whether the CJM belongs to a superpopulation or a metapopulation is likely due to a non adapted definition of metapopulations to the case of large pelagic stocks. When considering the possible evolution of the population structure of the CJM, and taking advantage of the mechanisms suggested by Petitgas (2010), we may present a diagram that could resolve this contradiction. Indeed, the observation of figure 16 shows that there is a continuum between the cases of a superpopulation and a metapopulation: when the global stock expands, for instance after the successful recruitment of a cohort, fish can be seen successively as a population, then a superpopulation and eventually a metapopulation depending on mixing and connectivity between

contingents. The figure 18 shows the application of a simplified version of the migration triangle (Harden Jones, 1968) to show how the CJM metapopulation can appear.
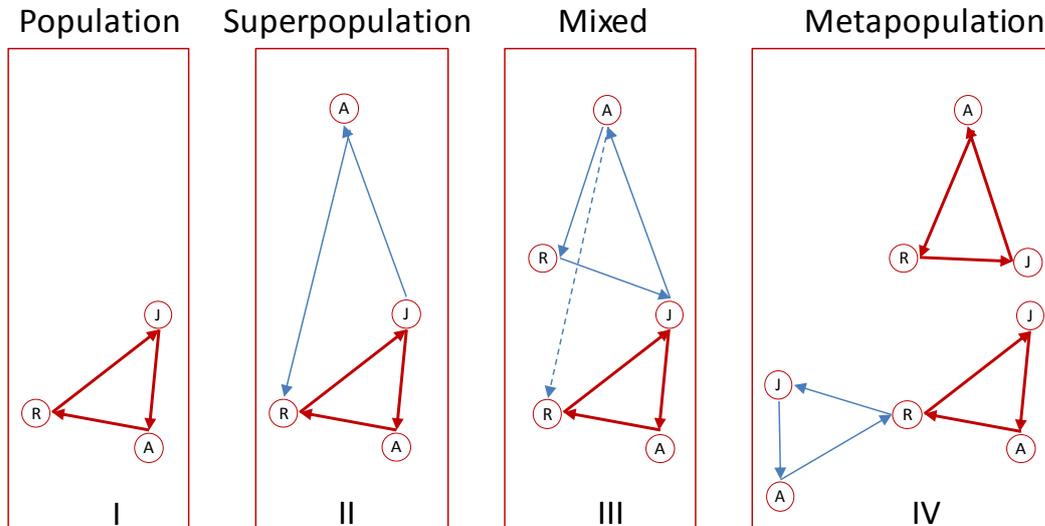
R = reproduction (spawning); A = adult (feeding); J = juveniles

Figure 18. Model of population structure evolving for the CJM.
I: Source population. II: extension towards new areas, under the structure of a superpopulation (where the two adult colonies share common spawning and juvenile areas). III: Organization into a "mixed" structure, when the two adult colonies still share a common spawning area but where "migrant phenotypes" explore and find particular spawning areas. IV: typical metapopulation structure where two populations have autonomous areas. A new sub-population can begin to appear

In this diagram, a superpopulation is defined by a single reproduction area and different nutrition (in the diagram) or larvae-juvenile areas. As long as all the fish share a reproduction zone, i.e. as long as there is possibility of genetic mixing between any adult and any other, we remain in the case of a superpopulation. Such case is typical, for instance, of the European eel, which reproduces in the Sargasso Sea, but then occupies all the rivers of Europe.

When the migrant phenotype (Petitgas, 2010; Cury, 1994), finds a new reproductive zone, then a "mixed" situation occurs, where fish from the second subpopulation are spawning either in the original or in the new spawning ground. Finally when all the fish of the second subpopulation choose to spawn in the new spawning ground, a metapopulation is formed, as genetic drift can occur between the two sub-populations.

This new metapopulation is then the result of an expansion of the global abundance, producing searching for new feeding areas, and the existence of new distinct spawning areas selected by migrant fish. Once this formed, the system evolves as a classical metapopulation, one subpopulation having s distinct probability to collapse. The way back to single (source) population is not requiring to go through superpopulation. Indeed the construction of metapopulation requires a superpopulation plus migrant exploratory fish. Once the local feeding and spawning ground recognised, the fish will use them until the sub-population disappears. The dynamics of the system is therefore a cycle (source => superpopulation => metapopulation => source), and not a way back (source ⇔ superpopulation ⇔ metapopulation).

The major result of this analysis is that the stable and opposite concepts of population structure are not necessarily pertinent. As observed each time more often, things are dynamic in the nature, and a species is not condemned to live permanently under a given situation. Then our question at the beginning of the paper has to be changed from "Is the CJM organised into a metapopulation?" to "Is the CJM, AT THE PRESENT TIME, organised into a metapopulation?"

From an empirical as well as theoretical point of view we might conclude that the CJM can be still represented by such metapopulation structure. This can change soon if the decreasing of the different subpopulations (Peru, coastal Chile, offshore, New Zealand) reaches a level of collapse. In this case we will be put into a situation of a single population (the source, remaining the only one), until a new expansion colonises again the whole potential area. Nevertheless as long as these subpopulation, and particularly the Peruvian, exist, we are under the case of a metapopulation, which means that each one of these subpopulations needs a particular assessment strategy. We present in figure 19 a schematic diagram of the different stages of development of such metapopulation.
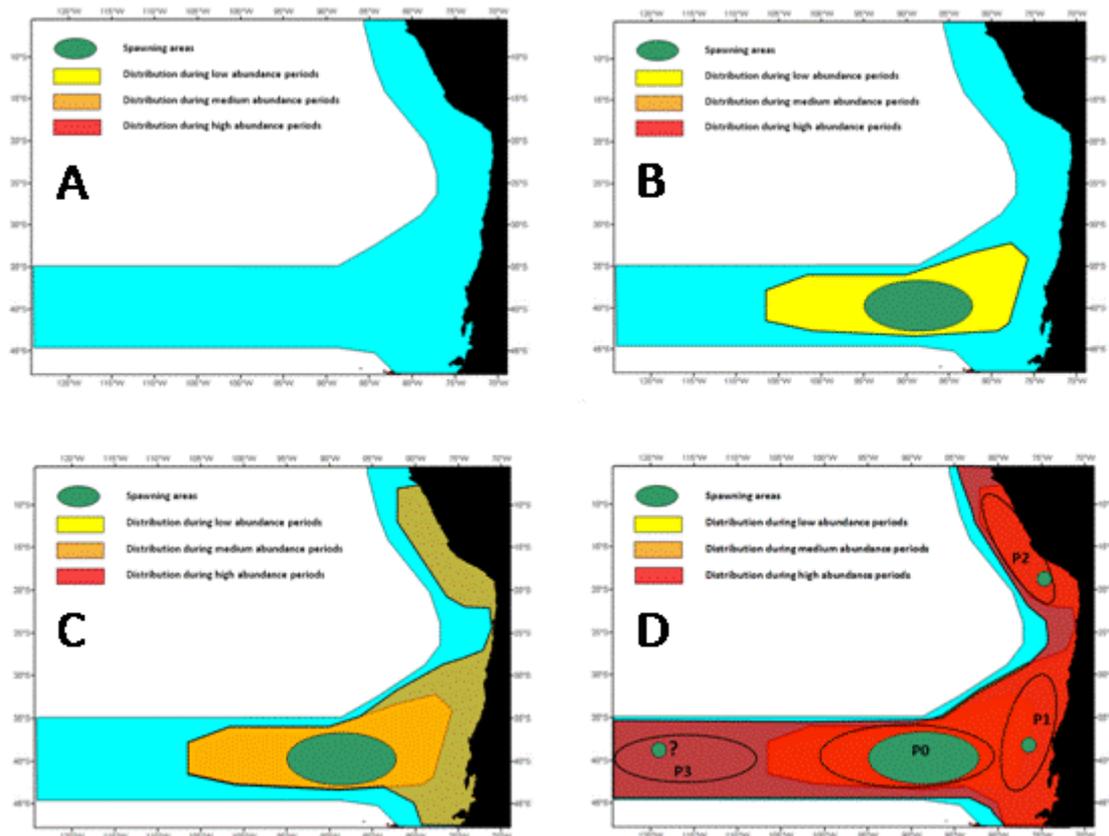
Figure 19. Diagram of the different stages of the metapopulation of CJM.
A : delimitation of the "CJM Pacific belt" and its extension along the coast of South America; B: location of the main and permanent spawning area and the minimum fish distribution ("Source") during low abundance periods. We are in situation of a single population; C: fish distribution during medium abundance periods: this is the period of superpopulation; D: fish distribution during high abundance periods. The CJM is then organised into a metapopulation with 4 major local populations, each one centred on a spawning zone: population P0, "source", off Chile; population P1, along the centre-south Chilean coastline (P0 and P1 are probably a single sub population); population P2, along northern Chile and Peru; population P3, west of 120ºW.

4.   CONCLUSION: THE CJM METAPOPULATION

It seems that, as discrete population are quite unlikely and as there is no way to spatially delimitate them, we will not be able to get real proofs of whether the CJM is or is not strictly speaking a metapopulation, if we apply the definitions from the literature. Therefore one can ask the reason why such question is important. The answers to this question are related to the use of this concept. The need for defining as precisely as possible the organization type of the CJM comes from the managers. Indeed as said in the former chapters the whole population is in a dangerous position, if we consider that the "source" of the total population is located in unregulated international waters where everybody can exploit it. As long as the other subpopulations (mostly Peruvian and Chilean) were in good shape, the bulk of

the catch was taken from them and the "source" was protected by the highest cost of going to fish offshore. This is no longer the case, and as pointed out by several authors (e.g. Hanski, 1999), a practical and heuristic definition is needed before any management decision be taken. In this case, assuming the CJM as forming a metapopulation is a precautionary approach, which considers the central offshore stock as the source and therefore as particularly important. Management of this particular part of the metapopulation becomes a priority.

Another conclusion is on the concept and definitions of metapopulation in the case of such widely distributed pelagic stocks. There is need for a set of definitions that apply better to these stocks, and especially on the effect of non-discrete populations and single genetic structure. Although one first question could be to wonder if there is any interest in such case to study the metapopulation, this concept has been proved extremely rich and heuristic in the few cases of pelagic stocks to which it has been applied (especially the herring). The major question of demographic explosions and expansion could get an answer with these studies. Expansions are a mechanism included in the phenotypical "toolbox" of many species (if not all of them), and an answer to losses of territories, genetic divergence, local adaptation and learning. So far they have not been studied in this perspective, and the inclusion of explosions in the metapopulation hypothesis adapted to large marine stocks could provide us a series of important understandings.

The major reason of the difficulty to decide whether the CJM belongs to a superpopulation or a metapopulation is due to a non adapted definition of metapopulations to the case of large pelagic stocks. We may propose a definition for these stocks, where we consider that the most important effects of a metapopulation and the evolutionary reasons of its existence are the following:
- It allows a species to colonise most of the favourable areas for its expansion, these areas being optimal for one or several of the "migration cycle" functions (Petitgas, 2010): feeding, growing, spawning.
- It produces independent smaller sub-populations as far as reproductive areas are concerned and makes them able to select efficient mutation in a much easier way as could occur in a single wide population. Then, when genetic exchanges occur, these efficient mutation can be "exported" to the whole species.
- It prevents the sub-populations to drift too far away from the holotype, and therefore maintain a specific homogeneity: this allows to re-introduce into

the specific group those populations that were isolated during a long time. The expansion of *Balistes capriscus* is a good example of such phenomenon.

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