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Insight on Population Structure

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Insight on population structure of the Chilean Jack Mackerel (*Trachurus murphyi* N.)

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ABSTRACT

The Chilean Jack Mackerel (*Trachurus murphyi*, Nichols), is one of the most important fish exploited population 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, with world catches varying from less than 0.5 to almost 5 millions of tonnes. 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 depicted a single population in the South Pacific Ocean.

Here, we consider the two most probable structures for this population: a “patchy population” 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 prolonged periods, depending on the environmental conditions. The conditions for these hypotheses to represent the real case are studied, and especially the demographic structure and the existence of different spawning areas.

Using the knowledge obtained from fisheries and acoustic surveys we show that if we apply strictly their definitions, none of the two hypotheses can be fully rejected. Nevertheless some particular spatial characteristics observed recently between the Peruvian and centre-south Chilean parts of the distribution induce us to conclude that the metapopulation is likely to better describe the stock. The consequences of each population structure for fisheries management are listed. They allow considering that the metapopulation hypothesis represents a safer definition as far as stock assessment is concerned. The paper concludes that *T. murphyi* can be described as a metapopulation, but also that the definitions proposed in the literature for metapopulation are not fully adapted to fish pelagic populations presenting a basin-scale range of distribution, and suggests specific research that could be done in this field.

Keywords: metapopulation, patchy population, *Trachurus murphyi*, fisheries management, Southern Pacific Ocean

1. Introduction

The Chilean Jack Mackerel *Trachurus murphyi* (Nichols) presents most of the common characteristics of *Trachurus* species: rather long life (around 15 years), mature at around 30 cm (3 years), predator on macro-zooplankton and micronekton, especially copepods, euphausiids, and mesopelagic fish (Konchina, 1981). However it has the widest area of extension (Cardenas et al., 2005) and is observed in the whole sub-tropical area of the Southern Pacific Ocean, from South America up to New Zealand, Australia (Serra, 1991; Grechina, 1998) and even in some occasion in the Indian and Atlantic Oceans in their southern subtropical areas (Riede, 2004; Nakamura et al, 1986). Its fishery has been one of the biggest in the world, with catches reaching almost 5 millions of tonnes in the year of highest production (1995). Since the late 1990s, *T. murphyi* has suffered a strong decrease of the total catches that dropped to close to 0.5 million of tonnes, which decrease is likely to reflect a similar decrease in its abundance (see www.southpacificrfmo.org).

During high abundance periods, the overall biomass of *T. murphyi* has been evaluated at around 20 millions of tonnes by Konchina and Pavlov (1999). Such biomass made this fish an essential target for the industrial fisheries. The biomass is related to a few strong cohorts which occurrence depends on environmental conditions (Konchina and Pavlov, 1999). *T. murphyi* presents also a wide extension in international unregulated waters, making the species available for any fishery. So far the main fishing fleets come from Chile, Peru, Russia, China, European Union, New Zealand and Australia. The demographic strategy and the geographical situation of *T. Murphyi* increase the risk of overfishing when the stock decreases. These conditions make a regulation agreement indispensable. For that purpose *T. murphyi* became a concern for the South Pacific Region Fisheries Management Organization (SPRFMO: www.southpacificrfmo.org). Scientific studies have been undertaken, one objective being to define the actual population structure of *T. murphyi* stocks in the South Pacific and recommend sound regulation rules. Indeed fish stock management would be different depending on the population characteristics. A single population requires a unique global management, while separate populations, either independent or linked by exchange of individuals, may require separate (albeit not independent) management policies adapted to each subpopulation. Defining which structure is better describing *T. murphyi* population is important as far as management policies are concerned. This is the objective of this paper.

2. Definition of population structures

Description of T. murphyi spatial distribution

A series of works has been achieved and hypotheses about *T. murphyi* stock structure were presented showing no general agreement, 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” (Anonymous, 2008). We give in Figure 1 a schematic diagram of the major locations of the potential populations and the area of extension of the “Chilean Jack Mackerel Belt” in periods of low to high abundances. Usually authors describing metapopulations call “source” the limited population occupying one particular and permanent area (that would be represented by the region A in Figure 1) during low abundance periods. It is supposed to be the only permanent population area and to be the “source” of any other patch existing during high abundance periods.

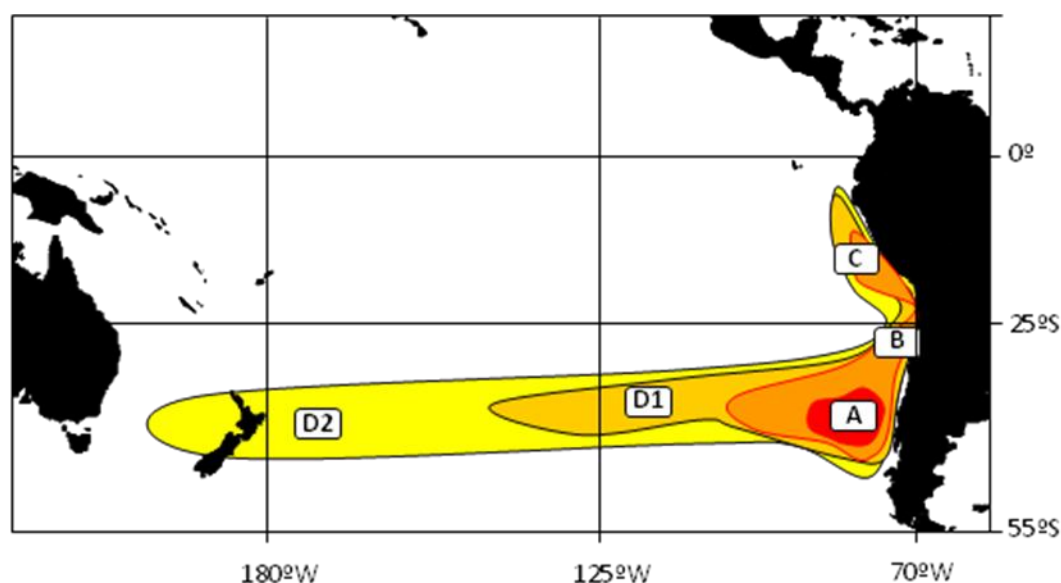


Figure 1. Extension and abundance of the Chilean Jack Mackerel, during periods of low (red surface) to high abundance (yellow surface). The letters inside rectangles show the major patches of density. A: Central Pacific-Centre South Chilean stock; B: Northern Chilean stock; C: Peruvian stock; D1 and D2: Central South and Southwest Pacific Ocean stocks.

The three major types of population distribution.

Populations can occupy space in different way. Kritzer and Sale (2004) classified the different structures that populations can take in a given space in three groups from highly separated subpopulations to a single homogeneous global population (Fig. 2).

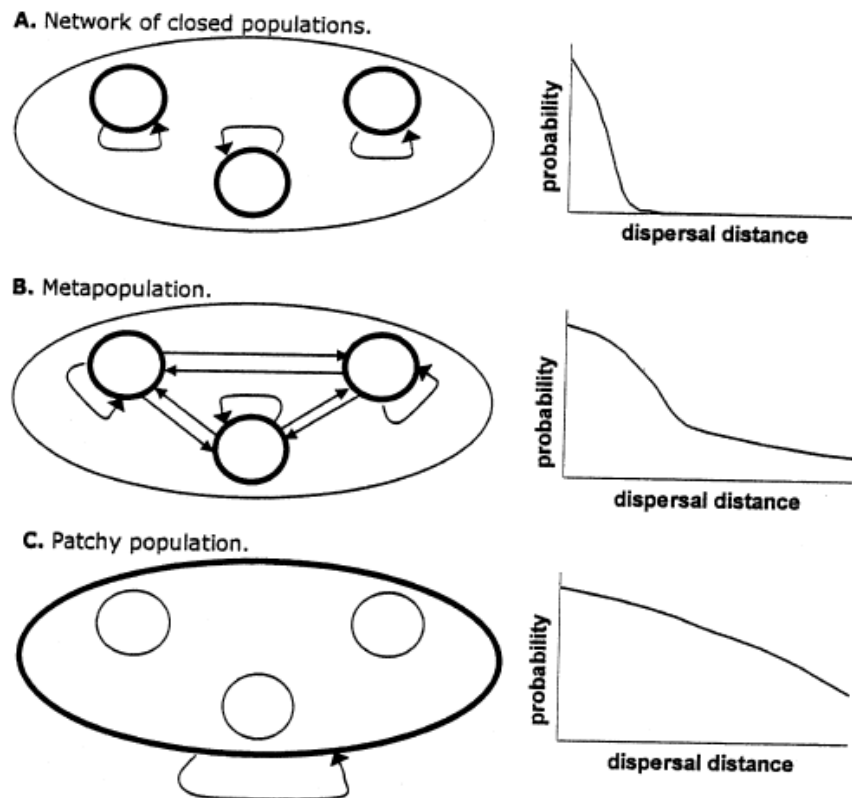


Figure 2. Three types of spatially structured populations with generalised dispersion curves for each local population. A: close local populations with no exchange between them; B: metapopulation; C: Patches of high density inside a single “patchy population”. From Kritzer and Sale (2004).

The criteria used by these authors were related to the biological cycles that are observed. These cycles can be described by the “migration triangle” (Harden Jones, 1968) where three particular locations can be encountered in a life cycle: area of spawning adult, larvae and juveniles, and feeding adults.

The three groups defined by Kritzer and Sale (2004) are the followings:

- A “**network of closed populations**”, where each subpopulation in the area has a particular cycle and where no exchange between subpopulations exists. Populations are completely independent and have a separate life. This can lead to speciation.
- A “**patchy population**”, where there is a single cycle for the whole population and where the individuals “*move frequently among habitat patches and may reproduce in several patches during their lifetime*” (Ovaskainen and Hanski, 2004). This last group requires either a common spawning area for the whole population or the possibility for every individual to spawn in any spawning grounds, and implies that the “patches” are mostly growing/feeding areas.

- A “**metapopulation**”, where the subpopulations have particular cycles but where some exchange between them still occur: “*individuals remain all their life in their natal population, and movements among populations are infrequent, though migration rate is high enough to allow eventual recolonization of habitat patches where a local population has gone extinct*” (Ovaskainen and Hanski, 2004). Each subpopulation is autonomous but a few individuals maintain links between the different populations (genetic mixing).

Using samples from centre-south Chile, northern Chile, Peru, mid ocean (at point 91°20'W, 32°30'S) and New Zealand, genetic studies on mitochondrial DNA and microsatellites identified a single global genetic population in the Pacific Ocean (Poulin et al., 2004; Cardenas et al., 2009). These results were confirmed by a recent work from Ashford et al. (2011): comparing the chemistry of the otolith nucleus between the western and eastern South Pacific Ocean, Chile and Peru, these authors observed a significant heterogeneity among population sampling areas, but no consistent differences and conclude that “*discrete population hypotheses do not account for the data*”. In synthesis they consider that all the fish from New Zealand come mostly from the spawning area off central Chile. Things are less clear for the Peruvian area, where, if at least “*half of the adults have spent their early life further south,*” another part of this adult stock would represent “*fish that were spawned in a protected area inshore*”.

Using migration studies and egg and larvae distributions, Arcos et al. (2001) applied Harden Jones' migration triangle in the Chilean area and give a schematic diagram of the *T. murphyi* migratory behaviour in this part of its distribution area (Fig. 3).

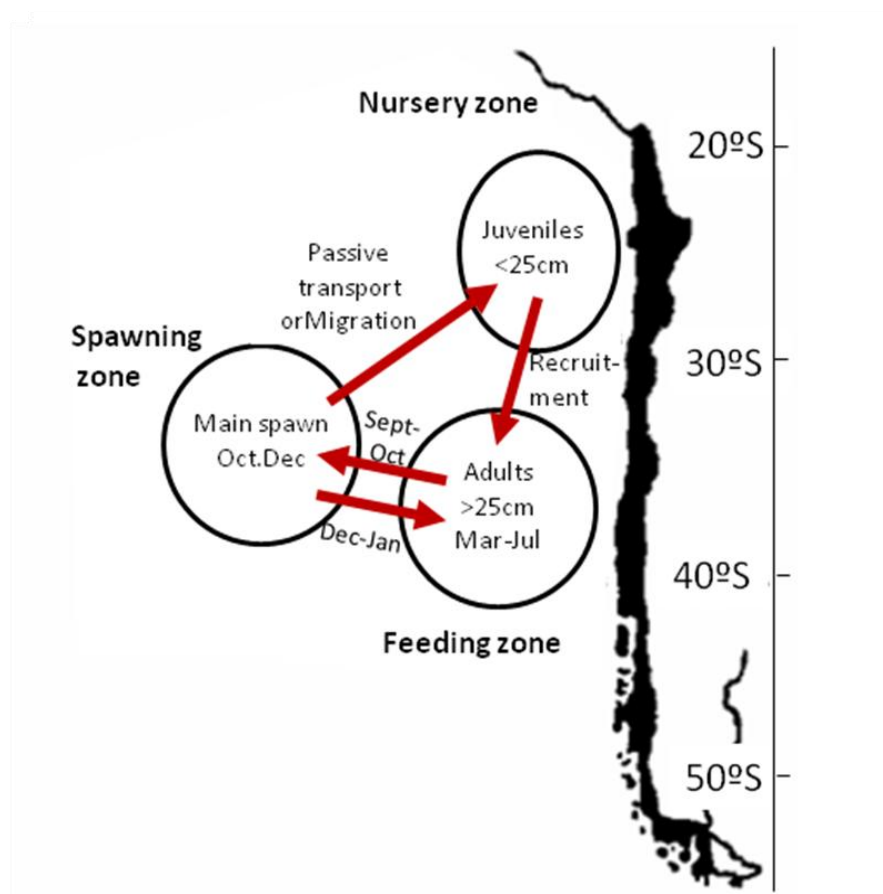


Figure 3. Schematic diagram of *T. murphyi* migrations in the centre-South area, from catch data and egg-larvae surveys (from Arcos et al, 2001)

The results of these population analyses, based on genetics, otolith chemistry and egg and larvae surveys, refute convincingly the possibility of completely independent discrete self-recruiting populations. So the hypothesis of a network of closed population can rather safely be rejected. The question remains as whether *T. murphyi* is organised into a unique patchy population or a metapopulation.

The patchy population hypothesis

The patchy population hypothesis (Ovaskainen and Hanski, 2004) considers a single population that expands and contracts according to its abundance, but with a single biological cycle, as schematized in Figure 2. When the abundance is large, some parts of the distribution area act as subpopulations, at least for exploiting new feeding areas. The idea underneath this model is that the adults can colonize favourable areas, while the general biological cycle remains unchanged.

This patchy population hypothesis implies generally the existence of a common spawning area for the different subpopulations as far as reproduction is concerned. According to Ashford et al

(2011), various spawning areas can exist together as long as there is no particular preferendum from the adults towards one of them. Also, a major characteristic of a patchy population is the absence of “source population”: any part of the population that is reproducing is theoretically able to “regenerate” the whole population after a collapse. The difference in space occupation, i.e. the existence of “feeding subpopulations”, is by definition directly linked to the global abundance. There is no possible genetic or biological divergence between the subpopulations. From this hypothesis we propose a general drawing of the hypothesized *T. murphyi* patchy population (Fig. 4A).

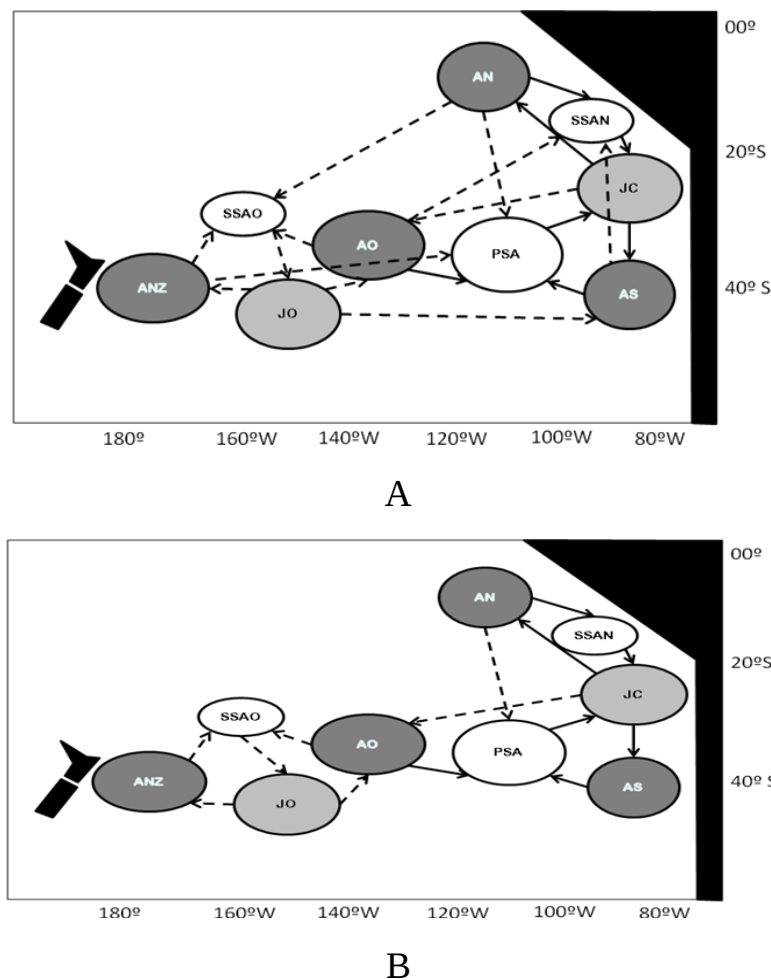


Figure 4. (A) Diagram of the patchy population hypothesis applied to *T. murphyi*. Adult individuals present an equal probability to live and spawn in any one of the feeding and spawning areas. (B) Diagram of the metapopulation hypothesis applied to the *T. murphyi*. Adults come from a single spawning area where they reproduce. Depending on the area of distribution, the metapopulation can be formed of one (low abundance), two (medium abundance) or up to four (high abundance) subpopulations, each one centred on a particular spawning area. PSA: principal spawning area; SSAN: secondary spawning area north; SSAO: secondary spawning area, oceanic (hypothetical); JC: juveniles, coastline; JO: juveniles, oceanic (hypothetical); AS: Adults, south; AN: Adults, north; AO: adults, oceanic; ANZ: Adults, New Zealand. Solid lines: observed migrations. Dotted lines: hypothesized migrations.

The metapopulation hypothesis

The metapopulation hypothesis (Levin, 1969) considers that subpopulations can have autonomous (and eventually divergent) lives. We present a diagram of this hypothesis in the case of *T. murphyi* (Fig. 4B) where independence between the subpopulations is assumed. In this case the fish inside the subpopulations can diverge genetically, at least during a period. This requires a series of conditions that will be studied more in details below. Each subpopulation is mostly linked to a particular spawning area, but a small, albeit significant, quantity of adults may move from one spawning area to the other. Contrarily to the patchy population, the existence of a source population is one key characteristic of a metapopulation. This source requires particular attention in terms of stock assessment and management.

3. The *T. murphyi* population structure: the biological evidences

A general synthesis of unpublished data has been presented by the SPRFMO describing the state of the art for the main characteristics of the biology of *T. murphyi* (see www.southpacificrfmo.org for the list of reports). Using this set of knowledge, and taking the “migration triangles” (Harden Jones, 1968) as a methodological basis for extracting from the complete set of key biological patterns those useful for differentiating populations, we can describe the three major biological areas for *T. Murphyi*, in a comparative approach between patchy vs. metapopulation structures:

- The spawning areas: whether there is a single or multiple spawning areas is a strong indication of the possibility or not of separate triangles, therefore of separate subpopulations;
- The larvae-juvenile areas, related to environmental conditions;
- The adult feeding and growing areas. The “patches” of high density can be related to larger abundance of prey, or to non-trophic characteristics. Therefore knowledge of the alimentation regime and plasticity of the *T. murphyi* behaviour is important (see Konchina, 1981; Konchina and Pavlov, 1996; Bertrand et al, 2004, 2006).
- The general life cycle, including demographic structures, migrations, genetics, parasitism, etc.

Characteristics of the spawning areas

The existence (or absence) of quasi-independent spawning areas is a key characteristic to determinate the existence of a metapopulation or a patchy 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 and we give below a synthesis of the results.

The synthesis of eggs and larvae observations in the *T. murphyi* distribution area, as observed from both the Russian fishing fleet data, the Chilean dedicated surveys and the Peruvian surveys (see SPRFMO annual reports for a synthesis) shows that eggs are distributed over a large range (Fig. 5). This demonstrates that opportunistic spawning grounds are likely to appear wherever adult fish stocks are present. Evseenko (1987), Serra (1991), Grechina et al. (1994) and Nesterov et al. (2007) argued on the existence of two main spawning areas, respectively in Peru and central Chile (Fig. 5). Concerning Peru, the presence of spawning activity in Peruvian waters has been observed every year during the 1980-1990s (Santander and Flores, 1983; Gorbunova et al., 1985). Most of these observations were achieved two-three decades ago, but despite a strong variability of fish abundance (extremely low during the period 2000-2010 in Peruvian waters), recent results still unpublished confirmed that spawning was always observed even in recent years (T. Dioses, pers. com., for inshore observations; M. Gutierrez, pers. comm., for offshore observations of high abundance of larvae west to the Peruvian waters by R/V Kayo Maru in 2010). In synthesis, it appears that the spawning areas are not strictly delimited (Sepúlveda et al., 2008). Eggs and larvae can be found almost everywhere, although the major abundances are observed in two main areas: Peru-North Chile and central south Chile (90-110°W). It is important to note that around latitudes 25°S the abundance of *T. murphyi* is low along the coastline (see IFOP reports of acoustic surveys, www.ifop.cl): there is a “no jack mackerel zone” in this area, which can be considered as the border between the Peruvian and the Chilean spawning zones as well as between the juvenile (Northern Chile) and adult (Centre-South Chile) concentrations.

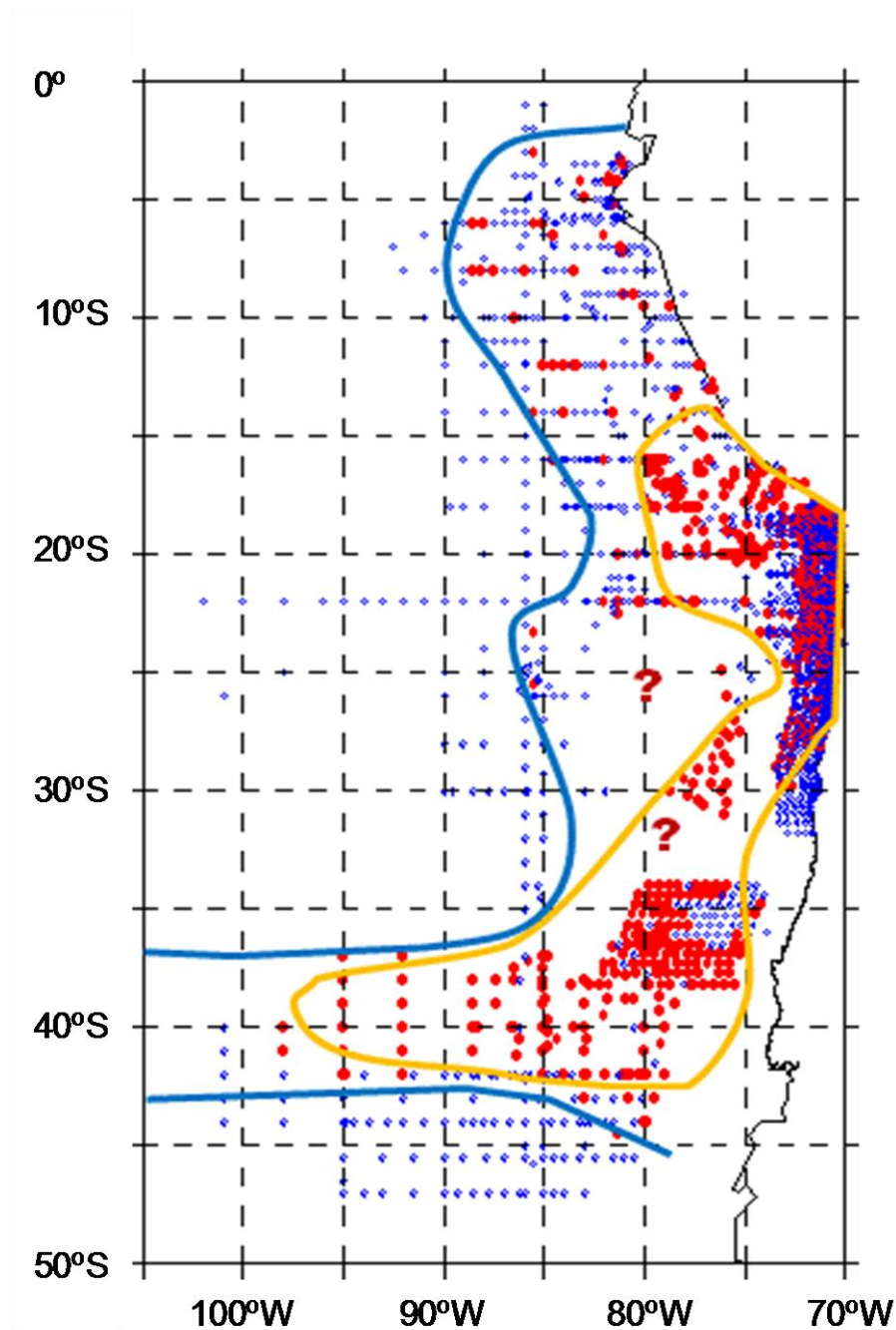


Figure 5. General distribution of *T. murphyi* eggs in the SE Pacific, as synthesized from historical and recent data by Sepúlveda et al. (1998). Blue dots: sampling stations with no eggs; red dots: sampling stations with eggs. Orange line shows our vision of the limits of the major spawning areas (redrawn from Grechina et al, 1994). Blue line shows the extreme limits where eggs were found. Note the lack of data from 25°S to 35°S in the Russian data base, this area belonging to the Chilean EEZ (represented by the question marks).

Spawning activity is not strictly driven by abiotic environmental conditions. Cubillos et al (2008) showed, 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 areas, centred on waters from 15°C (2001) to 19°C (1999). Actually the range of distribution for *T. murphyi*'s eggs (Fig. 5) covers a variety of environmental conditions in terms of water masses, temperature and other

environmental factors (Cubillos et al., 2008; Barbieri et al., 2004; Dioses, 1995; Grechina et al., 1994; Sepúlveda et al., 1998, 2007, 2009), although always inside the subtropical waters.

The major spawning area off Chile has been surveyed each year since 1997 using hired fishing ships (“Rastrillo” surveys: Barbieri et al., 1999, 2001, 2004; Sepúlveda et al., 2007, 2009). Results show a rather good stability in geographic position, but a wide variability in density of eggs, confirming the former results from Cubillos et al. (2008).

As far as spawning is concerned, from results published in the literature, the major conclusions are the following: (i) *T. murphyi* has no major specific requirement in terms of temperature (SST) for its spawning area, as long as it is included in the subtropical waters; (ii) a principal and permanent spawning area occurs in Chilean EEZ and adjacent international waters between latitudes 30°S and 42°S; (iii) during high abundance periods, besides the principal spawning area west of 75°W between latitudes 35-40°S, coastal spawning areas between 12°S and 40°S are observed, with a major concentration along the coastline between 15°S and 25°S, and sporadic spawning over the whole distribution area (from 4°S to 45°S); (iv) during lower abundance periods, it remains only the major spawning area off centre-south Chile and a more reduced spawning area in south Peru-north Chile; (v) *T. murphyi* tends to scatter in the spawning areas (Barbieri et al., 2004). We can conclude that the Chilean Jack Mackerel spawning strategy is adaptive and not strictly depending on homing: the fish will spawn in the first convenient area encountered, then will keep this new spawning area as long as it remains “favourable”. We still do not know precisely what a “favourable” spawning area for the Chilean jack mackerel is, and research should be undertaken in this field.

Demographic structure of T. murphyi stocks in Chile and Peru

- A good evidence for the existence of metapopulation is that specific demographic strategies implying different recruitments appear in the different subpopulation areas. Figure 6 shows the general information of the demographic structure in age, calculated by SPRFMO (2011) from the catches in three regions: North Chile (NC, lat 18-23°S) and centre-south Chile (CSC, 30-45°S, 79-90°W) for the period 1975-2011; far north (FN, mostly Peru and marginally Equator, north of 18.5°S) for the period 1980-2011. The high sea Soviet then Russian fishery is difficult to compare with the three other ones because it suffered a long interruption (from 1992 to 2002) and the fishing gears are different (pelagic trawls instead of purse seines). It will not be considered in this study.

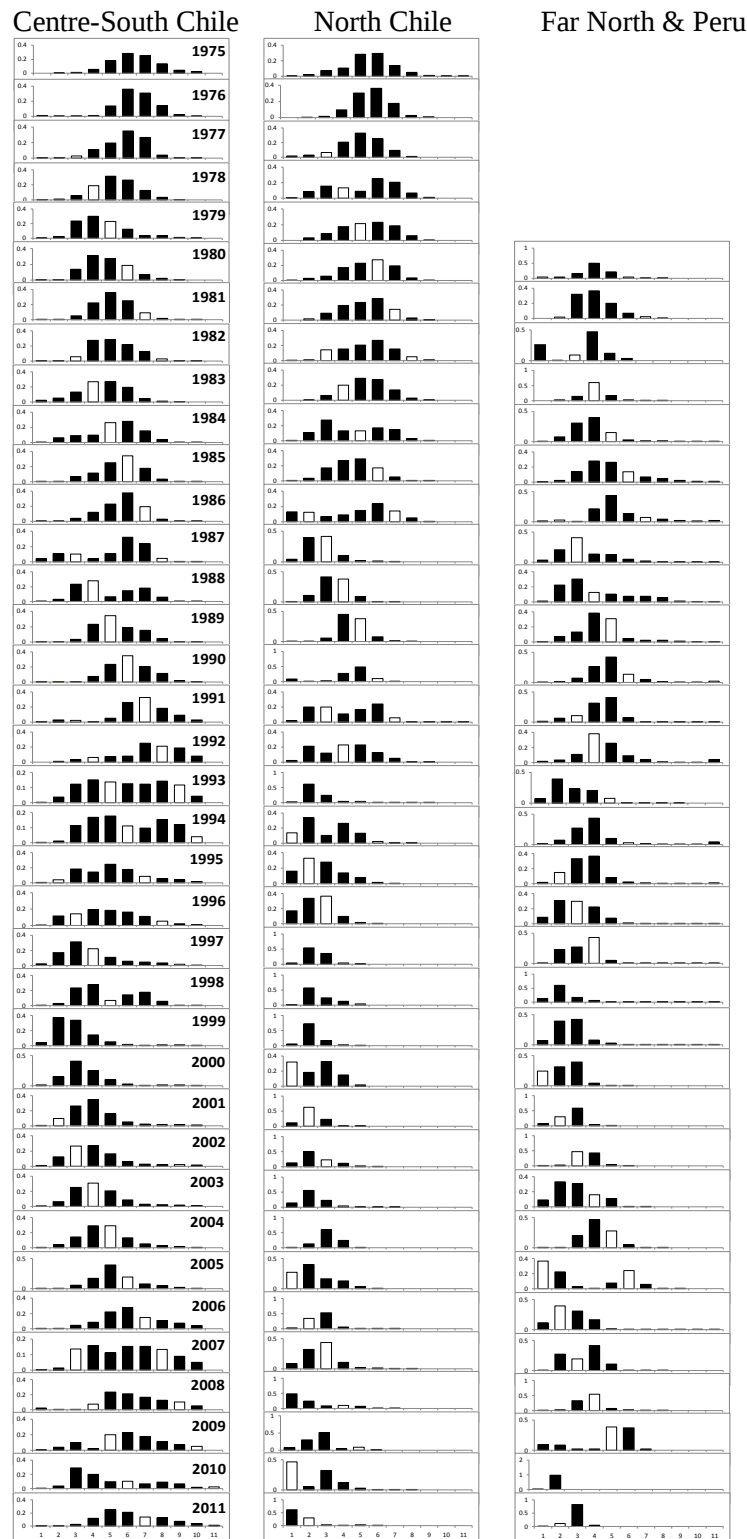


Figure 6. Age composition of catches for the Chilean South-central (CSC, left), the Chilean northern (NC, centre) and the Peruvian “far north” (FN, right) purse seine fisheries. Histogram in standardized proportions of abundance for year classes 3 (1st recruited class) to 13 (11th recruited class). White cohorts are those born immediately after an ENSO event that are recruited two years later. From SPRFMO (2011, www.southernpacificrfom.org)

From these histograms (Fig. 6), we can extract the following observations:

- When comparing the different fishing areas, one can split the period into 4 sub-periods: (i) before 1986 no clear evolution is visible in the demographic structures in the four fisheries; (ii) in 1986-1993 a clear evolution of classes recruited in 1985 and 1986 is observed, and these year classes are visible in the four regions and represent the bulk of the catches in the whole sub-period; (iii) in 1994-2003 a difference is visible between North Chile (NC) and Centre-South Chile (CSC) where the juveniles are only present in NC and the young adults disappear from NC at age 4 and appear at this same age in CSC, while no such separation can be seen in the far north (Peruvian) fishery (FN); and (iv) during the period after 2003 clear cohort dynamics appear in the Peruvian zone but are less clear in the Chilean fisheries. We must note that this period (until 2009) corresponds to a period of very low abundance and catches of *T. murphyi* off Peru. Almost no jack mackerel were observed offshore during acoustic survey and fishing operation. Only few very coastal jack mackerel were observed.
- The CSC fishery is exploiting the widest distribution of year classes, with the most regular evolution. Except in two occasions (1989, 1998-1999), juveniles were not significantly present in the catches in this area. This reinforces the idea that CSC represents the "source population" where most adults occurs and spawn.
- The NC fishery is clearly the area of concentration for juveniles in the Chilean fisheries (NC+CSC), since 1994. From this observation, we can assume that the adult zone for the CSC group moved southward in the early 1990s. After this year, CSC and FN became completely distinct areas of adults, separated by the NC juvenile area. Two successive high recruitments appeared recently in the NC fishery: one in 2008 and another in 2009.
- The FN, mostly represented by the Peruvian fishery, presents distinct characteristics. The juveniles were observed during all the period but always mixed with adults (although in recent years juveniles were encountered northward from the adults), and the difference between NC and FN from this point of view has been especially remarkable since 2005: fish of age 7 are observed in 2005 in the FN, while jack mackerels of this age have not been observed in the NC catches since 1992. The year 2005 is also interesting because an important new cohort appeared in the FN and represented the most important exploited from 2005 to 2009 while it was not significantly different from former cohorts in the NC. Contrarily, it rapidly disappeared in the NC, probably moving to the CSC where it did not represent any strong class either. Recruitment in 2005 was much stronger in the FN than in the NC-CSC. Finally a very strong cohort born in 2007 appeared in 2009 and was heavily exploited in 2011, giving almost half of the total catch of *T. murphyi* in this year. This fact is unexpected because if routine surveys performed by observers in the different fisheries

showed a strong spawning, it actually occurred in 2008. Catches in Peru during January-June 2011 reached 240 000 tons of 28-32 cm long fish. The same year class (born in 2007) was also recorded in Centre-South Chile and Central Oceanic area, but in smaller quantities and catch statistics provided to SPRFMO by the fishing fleets showed that it remained almost insignificant (www.southpacificrfmo.org). This cohort distribution in FN is different from the one observed in NC where the most recent important cohort was born in 2008 and appeared in the fishery in 2010.

It is worthwhile to notice that the ENSO (El Niño Southern Oscillation) events are almost always followed by a strong recruitment, as stated by various authors (Muck and Sanchez 1987; Diones 1995; Ganoza 1998; see a general comment by Bertrand et al, 2004). We put in white the cohorts born during ENSO events (Fig. 6) i.e. 2 years before their recruitment. They show that even though in some periods no strong biomass was observed after El Niño, these cohorts almost always dominated in the population structures. Most of the ENSO cohorts can be observed longer in average than the others. Interestingly this could be linked with an observation done on school type proportions in the Chilean waters during the period 1991-1999, where the dense structures (big schools and dense layers) decreased in proportions during the ENSO events (Gerlotto and Barbieri, 2000). If we remind that *T. murphyi* disperses during spawning, the coincidence of these high recruitments 2 years after ENSOs and the fact that during ENSOs fish tend to scatter is a good confirmation that high recruitments of *T. murphyi* could be partly linked to ENSO events.

4. Discussion

Population concepts

The patchy population concept presents one simple strong requirement, i.e. each individual is equivalent to any other. There are no identified group or sub-population (and consequently no “source” population) among the patches that would have a particular dynamics. This has a consequences as far as spawning is concerned: either there is a single common spawning area where all the adults spawn, or, if there are different spawning areas, individuals are not linked to a particular one and can spawn in any one of them, which results in (1) an absence of genetic divergence in the whole distribution area, and (2) a homogeneity in demographic structures in all the patches. The description of *T. murphyi*’s distribution as a “patchy population” does not seem fully convincing because the huge distances between some adult feeding areas and spawning areas are contradictory with the definition. It is unlikely that *T. murphyi* could indifferently spawn in any place inside the whole spawning area. The differences in

demographic structures between the patches are also against the patchy population hypothesis. *T. murphyi* thus does not present the characteristics of the patchy population except maybe as a transitional stage in periods of extension of the stock.

On the contrary, a metapopulation presents a series of specificities and characteristics that have been widely discussed in the literature, and we need to enter more in details in order to know whether this concept can fit with *T. murphyi* characteristics.

The metapopulation was first defined by Levin (1969) 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 (1997) presented a remarkable synthesis of these ideas when applying them to the populations of Atlantic herring, and synthesized Levin’s ideas in four characteristics:

- “(i) *There is a large number of sites, each supporting a single local population;*
- (ii) Each local population has a probability of going extinct that may depend on its genetic composition;*
- (iii) The allele frequencies are governed by the classical genetic equations; and*
- (iv) Vacant sites are recolonized by migrants from within the metapopulation”* (McQuinn, 1997).

Grimm et al. (2003) indicated also that there is asynchrony in local population dynamics because of partial closure of local populations that counteract homogenization of regional dynamics.

The definitions and description of the metapopulation concept show that conditions for a metapopulation to exist are more restrictive than those for a patchy population. It is therefore important to list the conditions for a metapopulation to exist, then evaluate whether *T. murphyi* fulfils these requirements or not (Table 1). To achieve this list we used the twelve conditions proposed by Hanski (1999) that we completed by adding four more conditions (Table 1).

Table 1. Conditions for a metapopulation to exist (extended from Hanski, 1999) applied to the case of the CJM.

	Population characteristics	The case of the CJM
1	Population size or density is	Yes, obviously: large movements between subpopulations

	significantly affected by migrations	related to environmental changes
2	Population density is affected by patch areas and isolation	Yes: CJM obviously presents a patchy distribution since its density is not constant all along its range of distribution. Small groups of old adults are always observed by the artisanal fishery along the shore
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 1970s is a good example. Also paleoecological results show a series of rise and fall in Peru during the last centuries and a strong increase during the 1970s (Gutiérrez et al., 2009)
5	Presence of empty habitats	Yes if we consider again the case of New Zealand and Tasmania
6	Metapopulations persist despite population turnover	Probably: fisheries have always showed the presence of fish in the central area, Chilean and Peruvian areas. Sporadic 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 testing the metapopulation hypothesis. Models have been constructed on the basis of the patchy population hypothesis (e.g. SPRFMO 2010)
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 (Cardenas et al., 2005, 2009)

14	Genetic or morphometric, meristic or biological/behavioural differences	No: although genetics suggests that there is a single biological group Ashford et al. (2011) show some local differences
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

Selection of the most adapted population structure

Considering the metapopulation hypothesis, we can see that most of the essential requirements of Table 1 are fulfilled by *T. murphyi*. Nevertheless there are few but critical conditions that apparently do not fit with the metapopulation definition. Actually two of them, conditions 3 and 16, are in some way contradictory with Levin’s definition. Indeed the different populations cannot be considered as discrete and it is impossible to draw clear borders between them with the existing data (condition 16): *T. murphyi* has a high plasticity (Bertrand et al, 2004, 2006), and can be encountered in the whole “Pacific belt”. Condition 3 should also be discussed because we observed contradictory results: on the one hand local differences did occur in the demographic structures; on the other hand there is no complete independence between the major dynamics in the different populations as synchrony of variations in abundance, migrations, etc. is frequently observed. This was obvious in the late 1990s-early 2000s where all the subpopulations decreased synchronously, from Peru and Chile to New Zealand. In the South Pacific Ocean the 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 are known to have a strong impact on the whole ecosystem, *ergo* on fish stocks. In this highly dynamic context (see Chavez et al., 2008), *T. murphyi* has developed a strategy of a few successful recruitments (in average 1 every 5 years) that lead the whole population and consequently its exploitation (Konchina and Pavlov, 1999). However we cannot determine if all the recruitments are depending on one or several of these signals.

We believe that those requirements for metapopulation (Table 1) that are not fulfilled by *T. murphyi* are not applicable to pelagic populations and especially jack mackerel, because of their dimensions and spatiotemporal variability. Pelagic populations with large ranges of distribution present particular characteristics that make uneasy the application of some items from the list of conditions for a patchy vs. a metapopulation to exist as established from the literature. Table 1 represents a series of conditions that have been defined mostly for small population of rather

sedentary species, and in the future we should draw a particular series of definitions that fit to pelagic fish with large range of distribution. This remark has been done earlier by 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 metapopulation concept is more of an analytical approach to be used when appropriate rather than a set of strict criteria and definitions (Hanski 1999)*” (cited by Kritzer and Sale, 2004).

The Chilean jack mackerel appears more likely organised into a metapopulation than a patchy population and we will focus on this structure for evaluating its consequences in terms of management. The first point is that the population located off central Chile is the most important in terms of abundance and produces “demographic pulsations” linked, among other, to ENSO signals which induce periodic high recruitments invading the jack mackerel belt. This population is certainly the source population and this fact will require particular modelling (Kritzer and Sales, 2006) and specific recommendations for management policy.

A model of metapopulation for the Chilean Jack Mackerel

Under a metapopulation hypothesis, a specific cycle, different from the south one, appears in the north where the young adults, instead of going to the common spawning area, create a new one specifically for their population. Indeed a specific spawning area 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. This creation is made easy considering that *T. murphyi* is rather opportunistic and tends to spawn as soon as the conditions are favourable: we have seen that no real homing exists as far as spawning is concerned and local spawning areas can appear and remain at any place compatible with the main environmental requirements for spawning. In this case the cycle becomes autonomous and metapopulation can appear. This metapopulation model is 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 may 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. Nevertheless exchanges still can occur between individuals from the two sub-populations, as stated by McQuinn (1997) for the herring and Petitgas et al. (2010) for the anchovy in the Bay of Biscay.

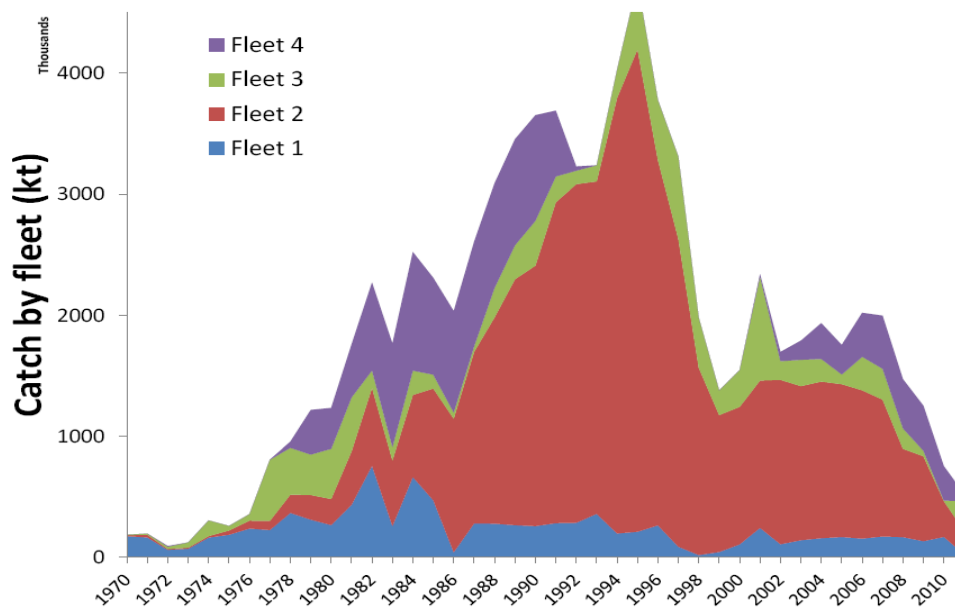
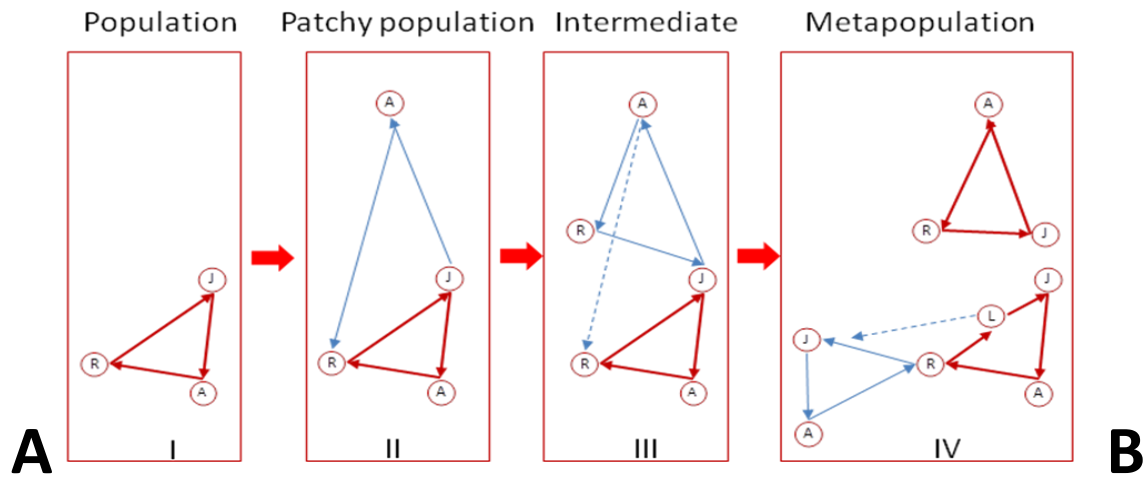


Figure 7.

- A. Description of the different stages of organization depending on overall abundance: I Single population; II Patchy population; III Intermediate; IV Metapopulation.
- B. Diagram of catches for *T. murphyi* during the period 1970 (beginning of the fishery)-2011. The 4 main fleets are the North Chile (fleet 1), Centre-South Chile (fleet 2), Peru (fleet 3) and USSR-Russia (Fleet 4). 5 main periods are visible: 1970-1985, increasing of the catches due to the development of the fisheries; 1985-1995, period of very high abundance and catches by all the fisheries (the end of the USSR catches was due to political decisions, until the Russian fleet came back in 2002); 1996-2000, strong decrease of the fisheries; 2001-2008, relative stability of the catches; since 2008, new decrease and quasi collapse of the stocks.

We propose a schematic model (Fig. 7A) describing the possible way population structures evolve according to the overall abundance of fish. We defined 4 stages:

- I. Single population. This structure represents a small population without any relationships with others. This case may occur with *T. murphyi* and represents the source population in period of collapse of the stocks.
- II. Patchy population. This structure appears when new feeding grounds are colonized by fish during periods of increasing abundance (e.g. high recruitment periods).
- III. Intermediate structure. This is an hypothetical intermediate stage between patchy and metapopulation, when patches of adults encounter favorable conditions to spawn outside the source spawning zone but still a consistent proportion of adults go back to the original spawning zone.
- IV. Metapopulation. Requires a period of high abundance to be created by colonization of feeding and spawning areas, then metapopulations can remain even when the overall biomass drops off, as long as conditions for surviving of the subpopulation exist: the return to the single population stage is not necessarily linked to decreases in abundance and metapopulation would remain even during low global abundance periods, until a given threshold is reached, and during this period the different sub-population have specific histories. On the opposite, some particular sub-population can also vanish even in periods of high abundance, if biotic or abiotic conditions in its own area become unfavourable.

Considering the huge variability of *T. murphyi* abundance (figure 7B), it is likely that this pattern has existed several times in the life of this species. Indeed when observing the total catches for jack mackerel during the period 1970 (beginning of the fishery) to 2011, 5 main periods are visible: 1970-1985, increasing of the catches due to the development of the fisheries during a period of increasing population; 1985-1995, period of very high abundance and catches by all the fisheries (the end of the USSR catches was due to political problems, until the Russian fleet came back in 2002); 1996-2000, strong decrease of the global abundance and catches; 2001-2008, relative stability of the catches; 2008-2010, new decrease and quasi collapse of the stocks. Actually a change in this last dynamics has been observed since 2011 where *T. murphyi* was particularly abundant in the FN fishery. It is too soon to draw new conclusions but the next years will be especially interesting to study.

If we take our model into consideration, a particular attention should be given to the overall biomass and the local abundances in order to define which one of the situations are present and what management rules should be selected. This means that the recruitment in the whole potential distribution area must be surveyed yearly.

5. Conclusion

The question asked in this paper was: which one of the two models, metapopulation vs. patchy population, is better representing the current situation. We have seen that there are different cohort histories, some being common to the two areas: [NC + CSC] and FN, while some others remain located in mostly one area. As in the case of spawning areas, the results tend to favour the metapopulation hypothesis. Nevertheless the frequent resetting (Bakun and Broad, 2003) of the ecosystem (e.g. by ENSO and decadal cycles) is unlikely to give enough time for the subpopulations to stabilize and diverge genetically.

The need for defining as precisely as possible how *T. murphyi* is organized is particularly important for management purposes. In the present context of overfishing and low population state, if we keep in mind that a significant part of the total adult population is located in unregulated international waters, then the whole population is in danger. As long as the global abundance was high enough to fill-up the Chilean EEZ, and the other populations (mostly Peruvian and oceanic) were in good shape, the bulk of the catch was taken from them while the “source” was protected by the highest cost of going offshore for fishing. This is no longer the case. As pointed out by several authors (e.g. Hanski, 1999), a practical and heuristic definition is needed before any management decision be taken. In a metapopulation perspective, the central offshore stock represents the source and therefore is particularly important. Specific management of this part of the metapopulation becomes a priority, and in case of collapse of the other sub-populations it could be recommended to close or strictly restrict the fishing activity in this particular area. The “source area” can be geographically defined as the rectangle surrounding the major spawning area, i.e. from 30°S to 40°S and from 82°W and 98°W. An important research effort should be devoted to this area and especially as far as eggs and larvae are concerned, as it appeared that the *T. murphyi* population strategy is leaded by the occurrence of strong recruitments: during low recruitment periods the fishery should be strongly limited. In any case, the source population should be carefully monitored with precautionary regulations since the whole population depends on the health of the source population. The other areas (Peruvian area, coastal Centre-South Chile and oceanic –west of 98°W) should be considered as supporting separated subpopulations that have a weak impact over the source. When the global population is high and these subpopulations are important (e.g. during the 1980-1990s; since 2010), specific regulations should be designed for each one of them, different from the regulation inside the source area. However managers of all regions must work together and build specific regulations according to the joint analysis of the international scientific

community, using the best available information (including the access to data collected by fishing vessels).

Considering the population as organised into a metapopulation structure is both a “precautionary” approach (the source is considered as the most important part of the global population and its safety is essential) and an optimal approach (allowing an optimised management of each one of the different parts of the population), therefore it permits the best exploitation scheme. This leads us to recommend as a precautionary approach to assume that *T. murphyi* is organized in a metapopulation. Eventually we must point out the importance of pre-recruitment surveys: we have seen that the recruitment is a key factor in jack mackerel dynamics and that its magnitude is still unpredictable. This is feasible through the use of fishers’ observation data.

Another conclusion can be drawn: the concept of metapopulation has been designed on cases from terrestrial and rather small sedentary populations of animals. It is not surprising that the definition and some of the conditions defined do not apply to a world-wide highly versatile and migrating pelagic fish population. Application of the concept to such animals has always been difficult and if in some case it gave remarkable results (e.g. on herring, probably due to the homing behaviour of herring as benthonic spawners, see McQuinn, 1997), in several other no clear conclusion could be obtained. This was the case for the European horse mackerel *Trachurus trachurus* which also presents a wide distribution area (from Norway to Mauritania and Greece) but where the genetic analysis showed, as in the case of *T. murphyi*, no difference in the different geographically separated populations (EU Project HOM SIR: www.homsir.com).

In order to go further in the analysis of this metapopulation application to large pelagic stocks, there is need for some theoretical work to evaluate how these populations can be analysed inside the framework of the metapopulation concept, and probably to write adapted definitions for these species.

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