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The Concept of “Pelagic metapopulation” as exemplified by the case of jack mackerel *Trachurus murphyi* in the South Pacific Ocean

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Introducing the concept of "Pelagic metapopulation" as exemplified by the case of jack mackerel *Trachurus murphyi* in the South Pacific Ocean

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Abstract

The way fish populations are structured is a key question for various reasons including fisheries management and ecological research. Indeed depending on its structure, a population may present different adaptive capacities to climate change or overexploitation. Among the different cases of population structures, metapopulation is particularly interesting as it allows to adapt to changing conditions and to recover lost niches, inducing a strong resilience to regime shifts. The question of whether pelagic populations can be organized in metapopulation has been studied since the 1990s, but remains unanswered in a large part and still controversial, due to the difficulty to apply to these large and moving populations the standard definitions of metapopulation, originally conceived on small terrestrial sedentary groups. To evaluate the capacity of pelagic fish populations to be structured into metapopulation, this paper explores first the case of the Chilean jack mackerel *Trachurus murphyi.* After analysing the biological and ecological characteristics of this species and the structure of its habitat in the South Pacific Ocean, we concluded that the species fulfils most of –but not all- the standard conditions required to be considered a metapopulation. From the results of this case study we suggest a new definition of metapopulation adapted to pelagic population, differentiating between "Territory-Bounded Habitat" metapopulations and "Environment-Bounded Habitat" metapopulations, this last one corresponding specifically to pelagic populations. The TBH is mostly defined by the existence of geographically limited habitat (e.g. an island) while EBH habitats are limited by local conditions inside a large moving environment. The effects on population dynamics of these two distinct types of habitat structures and their evolutionary consequences are suggested.

Keywords Metapopulation, population structure, small pelagics, South Pacific Ocean, connectivity

1. Introduction

Since the 1990s, series of works have been published on the population structure of pelagic fish populations (see Kritzer & Sale 2004 for a synthesis). The question of the existence of metapopulations (Levins 1969; 1970) has been studied by various authors on a variety of pelagic fish species, but no final conclusion was given. McQuinn (1997) was the first who presented the hypothesis that north Atlantic herring (*Clupea harengus*) was organized as a metapopulation.

Although absolutely convincing, his work was performed on a non-genuine pelagic species, as herring is known to spawn on geographically identified bottom habitats. This result was completed by Secor et al. (2009) who studied the stability of an Atlantic herring metapopulation and by Hintzen et al. (2015) who analysed the effect of the metapopulation structure of British herring on management policies. Wright et al. (2006) concluded that Scotland and North Sea cod populations were indeed also a metapopulation. Smedbol and Wroblewski (2002) studied the problems of recovery and interdependency inside the cod metapopulation. Cod is not a pelagic species either and when the metapopulation approach is applied on genuine pelagics, conclusions are more controversial. Petitgas et al. (2010) assumed that metapopulations are common in large pelagic fish populations, but their research focused on the behavioural tools allowing colonisation and recovery of lost niches. However they did not clearly explain how they could draw such conclusion for anchovy (*Engraulis encrasicholus*) in the Bay of Biscay, capelin (*Mallotus villosus*) in the Barents Sea, and the Californian sardine (*Sardinops sagax*). Secor (2010) studied the North Atlantic bluefin tuna (*Thunnus thynnus*) and concluded that this species was not organized in metapopulation. Gerlotto et al. (2012), Hintzen et al. (2014) and Bertrand et al (2016) concluded that metapopulation is the most likely structure for the South Pacific jack mackerel (*Trachurus murphyi* Nichols, 1920), whereas Gretchina et al. (2013) found that this species was rather a "superpopulation". Kritzer and Sale (2004) in their synthesis on marine fish populations concluded that metapopulation for pelagics should not be defined for biological research but for use in management methods.

The question of population structure of pelagic populations is not trivial. Indeed, they suffer huge and fast changes in their abundances, provoking economic crisis, as most of the largest fisheries in the world depend on these populations (www.FAO.org) It becomes urgent to make a step forwards on understanding population structures for these species, in order to design adapted models.

For answering this question we chose to study the case of the South Pacific -or Chilean- jack mackerel *Trachurus murphyi* (CJM), which represents an ideal case study.

Indeed, the CJM is an intriguing species. It has been exploited by industrial fisheries since the late 1970s, and in the 1980s and 1990s the population became one of the biggest exploited stock in the world, with catches reaching almost 5 million tonnes and a biomass being evaluated to more than 22 million tonnes (SPRFMO, 2015). During this period the fish occupied large areas of the subtropical waters in the South Pacific Ocean and was exploited from the South American coastline (Ecuador to south Chile) to New Zealand by different international and national fisheries. After the strong increase in the 1980s to 1990s, landings showed a substantial drop since the late 1990s. In the recent years catches remained below 0.5 million tonnes (Figure 1). Such fluctuations are likely to impact the worldwide economy and food security. To analyse these phenomena the "South Pacific Region Fisheries Management Organization" (SPRFMO) was created in 2006, having among its major objectives the management of the CJM.

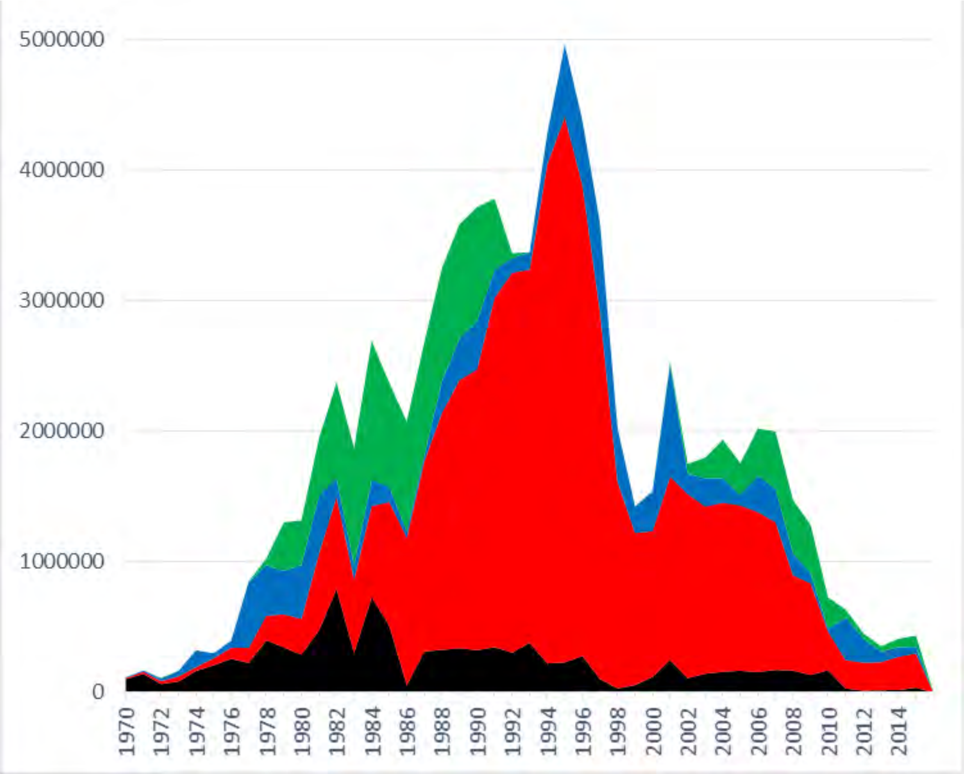

Figure 1. Catch data for the Chilean jack mackerel *Trachurus murphyi*, 1970-2014, by fishery, in tonnes. Green: USSR (until 1992) and Russia (after 2000); Blue: Far north (Peruvian and international fisheries); Red: centre-south Chile (Chilean and international fisheries); Black: North Chile (Chilean fishery). Fishing gear: purse seine in Chile and Peru; pelagic trawl in others cases. www.sprfmo.int

As it often occurs on pelagic populations, available knowledge on CJM is insufficient to accurately model its dynamics. Specifically, understanding is lacking regarding the key interactions of CJM with its environment, and the spatial structure and organisation of the population. These two elements are linked and lead to specific spatial distribution and population organization (Gerlotto and Dioses 2013.) Defining these key interactions and modelling their effect on CJM will allow research to obtain insight into the population structure of CJM. One way to define them is through the study of the fish habitat.

The role of the habitat, mainly defined by hydrographical conditions, has been of interest for more than 30 years (Barange et al. 2009), but new perspectives arose when SPRFMO (2012) applied the concept of “potential habitat” (Zwolinski et al. 2010) to the CJM distribution. This concept has three major practical applications:

- It allows a-priori definitions of the distribution area for a given species, in order to adapt the sampling or the fishery exploration to a limited area and save research effort (Zwolinski and Demer 2012);
- It is a method to extrapolate the abundance measured in the “window” of an acoustic survey to obtain biomass estimates of the species over its entire distribution (SPRFMO 2012);

- It is a way to analyse how the extension or the shrinking of the habitat may affect the abundance and distribution of a fish (Bertrand et al. 2012).

Studying CJM population structure is difficult however as the population resides in the Humboldt Current System which is one of the most impacted by climate variability (Chavez et al., 2008), where periodic and non-periodic variations in hydrological conditions and food availability (e.g. Chavez et al. 2008; Ayón et al. 2011; Bertrand et al. 2011) may induce strong changes in abundance and spatial distribution of fish populations. To investigate CJM population structure, we make use of the conceptual framework developed by Kritzer and Sale (2004) who synthesised the variety of possible spatially structured populations into three principal types:

- A network of closed populations, where each population inside a global distribution area is independent and no exchange of fish between populations exists. Spawning and feeding area are attributed to one single population, where the latter one may overlap with others but has no exchange of individuals;

- The metapopulation, adding exchanges between different populations to the framework of closed populations; usually, each population has access to an own spawning and feeding area, but some individuals can move from one population to the other, e.g. through entrainment (McQuinn 1997).

- The patchy population, where fish can occupy several feeding areas inside the global distribution area (patches), but where either a single spawning area is common to all the adults, or spawning can occur indifferently in any place of the habitat.

The definition of the most likely population structure requires an in-depth understanding of the environment a pelagic species lives in. For instance Bertrand et al (2016) indicate that a multi-parameter approach taking into account the physical, chemical and trophic environment is needed to describe a 3D habitat, from which population structure can be inferred.

For such a goal and still using CJM as a case study, we will first describe the main biological characteristics of the fish that have a potential impact on the population structure (Section 2); then we will define the habitat of the species, taking into account the environment characteristics and the biology (Section 3); finally we will define the most likely population structure (Section 4). On this basis, we will analyse how a large pelagic population can fit within a metapopulation scenario and present some suggestions for the possible definition of “pelagic metapopulations” (Section 5).

2. Main biological characteristics of the CJM throughout its distribution area

Trachurus murphyi (Nichols, 1920) is one of the 16 species of genus *Trachurus,* anatomically very similar to the holotype *Trachurus trachurus* (www.fishbase.org). Most *Trachurus* species are characterized by wide extensions in the subtropical or tropical areas. They have a rather long life, reaching 15-30 years old or above. Fish are mature at length 20-30 cm (2-4 years old) (Abramov and Kotlyar 1980; Nekrasov 1994; Perea et al. 2013), and spawning is pelagic. *Trachurus spp.* display daily vertical movements, being observed in deep layers by day (up to 150-300 m deep depending on the depth of the continental shelf or the oxycline) and close to the surface by night (Hancock et al. 1995; Bertrand et al. 2004a). All species feed on crustacean, micronekton, fish larvae and small cephalopods.

T. murphyi presents several differences with the average biology of the genus. Contrarily to the other species (excepting *T. symmetricus*), *T murphyi* is mostly distributed in high seas where it has by far the widest extension (Elizarov et al. 1992), covering most of the subtropical area of the Southern Pacific from the South America coastline of Ecuador to Chile and up to Argentinean Patagonia on east (Nakamura et al. 1986), to New Zealand (Paulin et al. 1989) and Australia (OBIS: www.fishbase.org) on west. *T. murphyi* is probably the biggest among *Trachurus* species. Individuals as large as 80 cm are regularly observed along the South American coast, with sizes up to 1 m according to fisheries observations in the early 20th century in Peru (Coker 1908). Still bones of the largest known individual, with length estimated 150 cm, have been encountered in a 4200 year old archaeological site in Peru (Vasquez et al. 2012).

In the early 1990s Elizarov et al. (1993) defined the “Jack mackerel belt” representing the overall area of distribution of CJM in the South Pacific Ocean (figure 2).

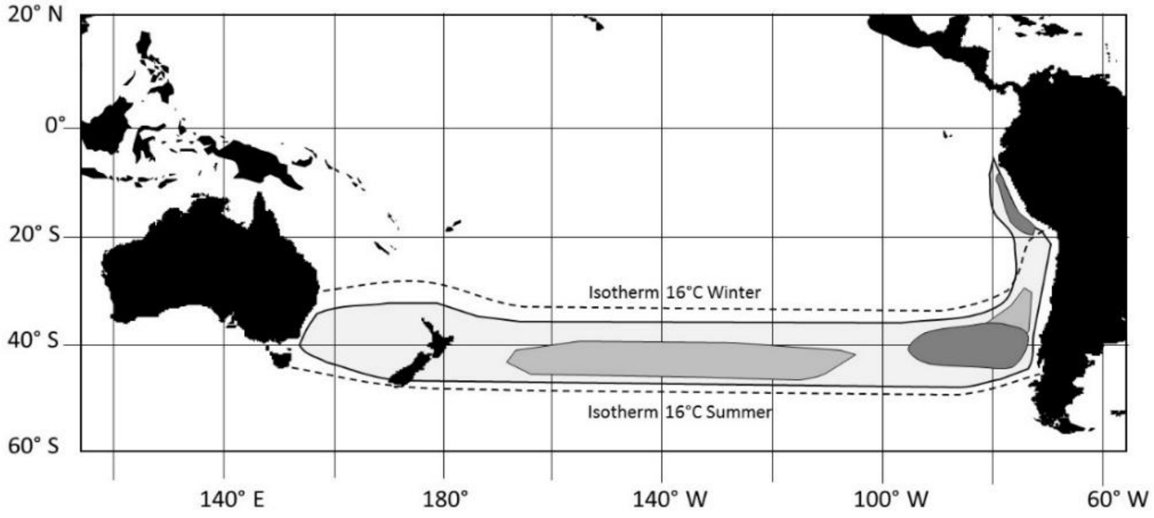

Figure 2. The CJM belt in the South Pacific Ocean, limited by the north (winter) and south (summer) extensions of the 16° isotherm presented in dashed lines. On the same figure are represented the main spawning areas. Pale grey: maximum extension of the spawning areas; mid-grey: medium density spawning areas; dark grey: the two major permanent spawning areas.

2.1. Reproductive patterns

2.1.1. Spawning periods

The CJM has a standard sexuality with external fertilization and no sexual dimorphism. Andrianov (1985) calculated a sex-ratio with 51% males. Histology (Dioses et al. 1989; Ruiz et al. 2008) shows that fish usually spawn from the beginning (August) to the end (March) of the austral warm season, spring (December to February) being the most important period

(Santander and De Castillo 1971; Santander and Flores 1983; Peña and Mariátegui 1988; Leal et al. 2012; Perea et al. 2013).

2.1.2. Spawning areas

There are three major spawning areas: centre-south Chile, Peruvian waters and, less important, the high seas areas (figure 2). In longitude, the spawning area is observed all along the subtropical front in the South Pacific Ocean, and up to New Zealand (170ºE) (Barbieri et al. 2004; Gretchina 2009; Vasquez et al. 2013).

The centre-south region of Chile represents the largest and most important spawning area. In Chile observations during large surveys (Barbieri et al. 2004) allowed to define and follow this wide sector, limited approximately by 31ºS to 40ºS and 74ºW to 89ºW, although there is no fixed border and a high variability between years (Cubillos et al. 2008).

The major spawning area in Peru is the coastal sector (outside of the continental shelf) between 14º00'S and 18º30'S (Santander y Flores 1983; Dioses et. al 1989), inside a front limited by the cold coastal waters and the subtropical surface waters (with salinities above 35.1 psu). The location of spawning areas changed throughout the years, being located mostly south of 12°S until 1980; north of 12°S during the period 198-1995; and rather dispersed (6-17°S) after 1995 (Ayon and Correa 2013)

Offshore, Dejnik and Nevinskyi (1994) and Dejnik et al. (1994) studied the ichtyoplankton inside the North and South subdivisions (separated by latitude 15ºS) of the Southern Pacific Ocean. For the first time CJM eggs were observed in equatorial waters at 1º57'S. Eggs and larvae were encountered in the whole studied area, with SST between 17.5ºC and 22.3ºC and SSS between 34.9 psu and 35.6 psu. The average abundances of eggs were around 0.3 to 6.6 eggs.m^{-2}, and the abundance of larvae from 0.3 to 9 larvae.m^{-2}, i.e. two orders of magnitude lower than in coastal spawning grounds.

2.2. Spatial distribution

The spatial distribution of *T. murphyi* has been studied from acoustic surveys and fisheries data. Results allowed getting a rather good understanding of its general distribution in the three dimensions. The studies were performed separately in three different fisheries: the Chilean fishery (along the Chilean coastline and offshore - up to 300 NM from the coast) in the area limited by the latitudes 35ºS - 45ºS; the Peruvian fishery, mostly located in the jurisdictional waters of Peru (from the coastline up to 200 NM from the coast, between latitudes 4ºS - 17ºS); and the high sea fishery, from the EEZ of Chile until New Zealand, between latitudes 30ºS - 45ºS. (Gerlotto and Dioses 2013)

2.2.1. Vertical migrations

CJM vertical migrations are linked to the diel cycle and prey accessibility. Several works have been performed, using acoustic devices (e.g. Hancock et al. 1995; Bertrand et al. 2006) and conclude that the jack mackerel is performing daily vertical movements, from the sub-surface (between 15 and 100 m) by night to the depth of the oxycline by day. These vertical movements are likely related to the micronekton migrations and availability as shown by the behavioural model elaborated by Bertrand et al. (2006). Indeed, unable to penetrate the oxycline, CJM “awaits in the pelagics” (Bertrand et al., 2006) just above the oxygen minimum zone (OMZ) all the day until micronekton appears during its dusk upwards migration, to feed on. Migration amplitude, as well as the depth of the oxycline, is generally related to the distance to the coast and the latitude: around 50 m deep at distances inferior to 10 nm from the coast, until over 100-200 m for distances farther than 30 nm; deeper oxycline (Helly and Levin 2004) so higher range of vertical migration off Chile than off Peru.

2.2.2. Horizontal distribution and migrations

Variation of the horizontal overall distribution**.** During its period of highest abundance, the CJM occupied almost the whole subtropical waters of the Southern Pacific Ocean. The first approach to this distribution analysis was performed in the 1990s by the Soviet scientists analysing the movements of the fishing fleet and the eggs and larvae collection aboard the fishing and research vessels. According to the data of the soviet fishery (1977-1990) and the more recent Russian fishery, the CJM southern extension is limited by the subantarctic cold waters: depending on the year, the fish can be observed more south than 45ºS, or remains north of 40ºS.

In periods of lower abundance, the distribution area shrinks and the fish tend to concentrate in the South-East Pacific. Gretchina (2008) showed that the overall distribution of CJM shrank from 1999 to 2008 in the western (170ºW to 140ºW), southern (50ºS to 40ºS along the Chilean coast) and northern (4ºS to 15ºS along the Peruvian coast) limits of its area

Migrations. Few studies have been published in the literature using tagging (e.g. Torres 1986), and none of them gave any consistent result on fish migration. Therefore the easiest results are obtained by observing the movements of the fishing fleet. For instance, Corten (2008; 2009) studied migrations from the EU catch data and showed that the fishery outside Chile's EEZ presents a cyclic movement in its centre-south region during the fishing season. The same author presented hypotheses on the movements of the 2008 year class (Corten 2014) between the centre-south Chile fishing grounds and the Peruvian fishery.

2.2.3. General models of fish spatial dynamics.

In the 1990s the Soviet scientists constructed a conceptual model of migration defined from the USSR catch data. They described cyclic North (spawning) to South (feeding) migrations accompanied with a general westward drift of the cohorts (Gretchina 2008). Arcos et al. (2001) presented the first schema of migration within the Centre-South Chile population which follows the “triangle” scenario proposed by Harden Jones (1968), with spawning offshore, juveniles in the North Chile and feeding adults in the Centre-south.

Besides migrations *sensu stricto*, CJM develops phases of expansion and shrinking depending on the abundance and the hydrology. From this series of works, Gretchina (2008) proposed a conceptual model where the relationships between the juvenile area and the adult spawning and feeding areas change depending on the overall abundance. Gretchina (2008) concluded to “a probable contraction of the whole distribution area since 2002”. Spatial dynamics in Peruvian waters are harder to characterise since the acoustic and catch data show that the location of adults and juveniles in the Peruvian EEZ vary according to the year and climatic conditions (Gutierrez 2014). Some works intended to define a migratory circuit in the northern zone of the CJM distribution. Espinoza et al. (2008) noted that the CJM, which was mostly distributed in the north-Peru and south Ecuador in the 1990s, moved toward the south since 2000, and has almost disappeared from the north since 2002 and until 2011 (see also Gutiérrez et al., 2012).

Gretchina (2013) synthesized these observations in his conceptual model of superpopulation in which two cases are proposed: before and after the year 2000. Before 2000 adults were moving northward (from centre Peru up to the Equator) to the feeding zone. This northward expansion disappeared after 2000, the fish remaining south of 15° S (Gerlotto and Dioses, 2013). The authors do not give any reason for this change in distribution. However, as discussed in section 3, Bertrand et al. (2016) showed that the 'door' connecting the Chilean and Peruvian areas was likely closed after 2000 when the OMZ get more shallow.

Gretchina (2013) points out the fact that the juveniles from the Peruvian area are concentrated in the south of the region (from 16°S to 27°S), in an area shared with the juveniles born in the centre-south Chile region. Although this point is in agreement with the fishing data, the question of whether it is a single juvenile area or two juvenile areas overlapped or separated still remains. Indeed this area is characterized by a minimum abundance zone of *Euphausia mucronata*

(Antezana 2008) and low catches of CJM around the 22ºS-25°S latitudes (Nesterov and Chur 2006; Gerlotto & Dioses, 2013; see FAO catch statistics e.g. http://www.fao.org/fishery/species/2309/en).

2.3. Interactions with pelagic species.

CJM is an opportunistic predator foraging on a high variety of prey that belong to the mesopelagic community, in particular euphausiids and mesopelagic fishes (Konchina et al., 1996; Alegre et al., 2015). Subtropical waters are clearly the core of CJM habitat. Nevertheless the plasticity of this species should permit it to occupy other water masses: actually, most of the carangids and many of the *Trachurus* species are tropical (e.g. *T. lathami, T. trecae, T. indicus*). We hypothesize that the restriction of *T. murphyi* mostly to subtropical waters could be at least in part due to interactions with other pelagic species, and principally tunas. Indeed the southern distribution of tuna as observed through longline catches (Fonteneau, 1997) in the period of maximum extension of the CJM (1994-1997) coincides with the northern border of the CJM belt. The overlap between the two groups is very limited, except with albacore *Thunnus alalunga*, which were found foraging on juveniles over the northern border of the CJM belt between 130º and 170ºW (Bailey, 1989). When comparing CJM spatial behaviour with tunas, which occupy all oligotrophic tropical oceans despite having among the highest metabolisms of fish species (Holland et al., 1992), we may wonder why CJM, with a lower metabolism and sharing tuna diet, is limited to subtropical waters.

Some pieces of answer can be found by comparing observations on the trophic behaviour of tunas in French Polynesia (Bertrand et al., 1999; 2002) and CJM in the South East Pacific (Alegre et al., 2015). Micronekton abundance is orders of magnitude lower in the central Pacific gyre than where CJM distributes, but in the two areas it performs similar vertical diel migrations. In the subtropical waters this migration added to the presence of a shallow OMZ makes prey out of reach for CJM by day since micronekton distribute inside the OMZ (Bertrand et al., 2006), and only accessible by night in surface. On the contrary considering the vertical profiles of temperature and oxygen, prey are theoretically always accessible in the inter-tropical area. Can the low abundance be compensated by a permanent availability? This is linked to another question: is CJM behaviour adapted to day and night hunting? We have no answer yet. Anyway, we hypothesize that additional factors, such as predation, likely matter to restrict their range of distribution and tuna may exert a predation pressure reducing habitat suitability for CJM in tropical areas.

Another potential predator of CJM is the jumbo squid *Dosidicus gigas*. An extensive study on *D. gigas* diet revealed a low predation effect since CJM occurrence in squid stomachs was <0.3 % (Alegre et al., 2014). Jumbo squid is more a competitor than a predator of jack mackerel. Interestingly jumbo squids flourish when the OMZ extends (Bograd et al., 2008) so its biomass increased when the CJM's reduced being expulsed from low oxygen areas since the late 1990s (Bertrand et al., submitted). Finally we must mention that whales, foraging in euphausiids, have also been proposed as competitors (Konchina et al., 1996).

2.4. Population patterns

2.4.1. Biological markers

<u>Genetic discrimination of populations</u>**.** Four studies were achieved on CJMgenetic structure (Poulin et al., 2004; Cárdenas et al., 2005; 2009). The first one was done in 1986 with samples from north and south Chile and Juan Fernandez Island. The second study covered southern Chile. The third one was performed in 1996 using molecular techniques based on nuclear DNA, on samples collected in coastal and insular places of Chile as well as in New Zealand and Tasmania. The fourth and last study was done in 2002 in Talcahuano, San Antonio and Iquique in Chile. Both confirm the existence of a single genetic population of CJM in the South Pacific Ocean.

More recently, a new series of works, have been undertaken (Afanasiev et al., 2012). Both sides of the Pacific Ocean were sampled. The effort was principally focused on the finding of proper loci for a correct representation of the CJM genetic diversity. The work depicted "*significant differences between localities*" in two of the four loci selected.

Otholith biogeochemistry**.** Thorrold et al (2001) consider that there is a need of non-genetic information for observing differences in population structure. They studied the case of weakfish (*Cynoscion regalis*) with otholiths data to identify natal origins of individuals and conclude that despite the lack of genetic differentiation, "there is much more spatial structure than is currently assumed by fisheries managers".Ashford et al. (2011) used the biochemical properties of otholiths for population identification. Their objective was first to evaluate whether otholiths were a consistent tool for evaluating variations in the populations characteristics. The authors defined a series of sampling location all along the Chilean coastline and islands. These markers enable differentiating among locations and significant differences appeared. A main result is that no major difference exists within sampling areas (e.g. between two samples taken in Puerto Montt), while strong significant differences occur between the coastal and oceanic areas (e.g. between Chiloe oceanic vs. coastal areas of Talcahuano, North Coquimbo, Iquique). The data could not find consistent differences marking a population boundary between Chile and Peru.

In conclusion, the authors state that "the chemistry laid down in otholiths nuclei showed considerable spatial heterogeneity" that should exclude the hypothesis of a single randomly mixing population with fish off New Zealand, Peru and Chile, recruiting from a single spawning area in oceanic waters off Central Chile.

Parasites. Parasitism presents two interesting characteristics for the discrimination of populations (Avdeyev, 1992): (i) some parasites are extremely selective, at the level of species and even populations in their choice of host; and (ii) some parasites are also very selective in their geographical location, being unable to survive in other waters than their endemic area. Due to these two characteristics, a variety of parasite species are used as markers for identifying fish species or populations (MacKenzie. and Longshaw, 1995; Brown and Colgan, 1986; Cox, 1990; Fréon et al., 2005). The Chilean Jack mackerel is a-priori a good case study, due to its extreme dispersion in a vast area, its potential distribution in sub-populations, a rather easy access to samples from the industrial fisheries all over the South Pacific, and even its co-existence with other *Trachurus* species, especially in the western South Pacific (*T. novaezelandiae*, *T. picturatus*).

A review of works has been published by the SPRFMO (Anonymous, 2008). Metazoan parasites of CJM were analyzed along the Chilean and Peruvian coast (Oliva, 1999) and from Iquique to Valdivia (George-Nascimento, 2000). Results, based on univariate analyses, strongly suggest two populationss (Centre-North Peru and along the Chilean coast) as well as two stocks in north and south Chilean waters respectively. However, when adding fish length to parasites as explanatory variable it appears that the stock differences are more likely due to fish length differences between sampling sites.

Glubokov (2008), showed evidence for a population in the central south Pacific Ocean based on reproductive distribution, morphological and parasite information (Evseenko 1987a, b; Duran and Oliva 1983, Romero and Kuroki 1985, Storozhuk et al. 1987, Kalchugin 1992, and Adveyev 1992)".

Ashford et al (2011), find that Chilean jack mackerel caught off Peru may come from a separate self-recruiting population (Serra, 1991).

2.4.2. Demography

Growth. Studies on the growth of the CJM and establishment of growth curves were achieved mostly through otholiths observation and studies of the modal distribution (Kaiser, 1973; Pavez & Saa, 1978; Castillo & Arizaga, 1987 Nosov & Kalguchin, 1990;; Arcos & Gretchina, 1994;

Cubillos & Arancibia, 1995; Li et al., 2011; Dioses, 2013). Results show a rather wide variety of growth curves attributed mostly to the areas where the studies were performed.

Csirke (2013) notes that in its the northern range of distribution, off Peru, CJM grows faster and larger than in the southern part (central-south Chile), likely due to a higher metabolism linked to warmer waters in the North. Dioses (2013) compared CJM growth in Peru and Chile based on otholiths readings and showed that the Peruvian CJM is 35% longer than the Chilean at the same age. Diaz (2013) reached a same conclusion by comparing growth parameters for the Chilean and the Peruvian CJM calculated from different methods and (Table 1)

Demographic structure. Studies on demographic structures have been developed on the base of the fisheries data. Therefore they produce results for exploited stocks more than for specific populations or sub-populations. SPRFMO calculated age structure and dynamics for four major fisheries.

The CENTRE-SOUTH CHILE fishery (CSCF), limited by the Chilean coastline between latitudes 30ºS and 45ºS, and reaching 100ºW. This fishing area is exploited by Chile with purse seines and the international fleet (outside Chilean EEZ) with pelagic trawls.

The NORTHERN CHILE fishery (NCF), from 17ºS to 30ºS, limited by the coastline and the longitude 80ºS. This area is more concentrated along the coast than the former one, and is almost exclusively exploited by Chile.

The FAR NORTH fishery (FNF), located north of the former one, and mostly inside the jurisdictional waters of Peru. Practically the only exploitation is performed by the purse seine fishery of Peru, and marginally west of the 200 NM limit.

The HIGH SEAS fishery (HSF), gathering all the south Pacific area, but mostly located west of 100ºW, between latitudes 35ºS and 45ºS, and with no defined limit westward, although no fishery exists or existed west of New Zealand. Most of the vessels are equipped with pelagic trawls.

The data of these fisheries allowed describing demographic histories for each one of these fisheries, using the growth curves listed above. Gerlotto et al. (2012) analysed in detail the demographic dynamics of these 4 fisheries and concluded that the different fisheries/areas present different histories, split into four main periods:

(a) Before 1986 all the fisheries present approximately the same pattern, characterized by a stable age histogram with no visible cohort evolution. The mean age is different for each fishery: around 6-7 years old in CSCF and NCF, younger in FNF (5 years old) and older in HSF (7-8 years old)

(b) 1986-1993. This period is characterized by the presence of a very strong cohort, visible in all the fisheries, which represents the bulk of the catches. We can observe some delays in the occurrence of the cohort, present since 1986 in FNF and NCF, and only after 1988 in CSCF and HSF. This cohort is the clearest in NCF.

(c) 1993-2003. This period is characterized by important differences between fisheries. CSCF is mostly catching adults of age 3-7 (younger than in the first period), with no clear cohort evolution; NCF is almost exclusively catching young fish (age 2-5), centred on age 3; FNF is exploiting both young fish and adults (age 3-6). No data describe the HSF, as this period corresponds to the end of the Soviet fishery, and the international fishery in HSF began to operate in 2000. Note that the only cohort evolution that is visible occurs in CSCF and FNF, between 1999 and 2003.

(d) 2003-present. This period is characterized by the occurrence of a series of cohorts, with differences between the fisheries. CSCF and HSF are exploiting exclusively adults, the mean age being similar to that of the first period (age 5-8) and the NCF continues exploiting only young fish (age 3-4). The FNF presents an original pattern, where several cohorts are clearly visible and where the fishery exploits successively each of them, from age 2 to age 7.

We can see that since 1986 CJM population is driven by a series of strong cohorts which usually represent the bulk of the catches. In the CSCF for instance, according to Bernal et al. (2007), a strong year class was observed from 1986 to 1991, and some others (although less evident) during the periods 1998-2000; 2000-2004; 2005-2007. This is explained by the authors as a possible relationship between an ENSO event (El Niño) and the occurrence of a strong recruitment. The results of the EU fishery show an interesting phenomenon. This fishery is much younger than the former ones, and the length composition is given since 2007 by Corten and Janusz (2011), who mention that only one year class is observed and followed from 2007 to 2011. In this particular case, the cohort growth was from 31 cm in 2007 to 41 in 2010.

Corten and Janusz (2011), Corten (2014) observed a new abundant year class, presumably born in 2008, which appeared in the fishery in 2010 and was observed again in 2011 although at a lower level of abundance. This year class became much less abundant in 2011 and disappeared almost completely from the catches in 2012. However, fish of the same length appeared in large numbers in the waters of northern Peru and Ecuador in late 2010, and it is likely that these fish belonged to the same group that was observed half a year earlier in the waters off Chile. The second half of 2010 was characterized by a strong La Niña in the eastern Pacific. The increased residual current and cooling of surface waters may have influenced the distribution of juvenile jack mackerel, either by increasing their passive northward transport by an intensified Humboldt Current, or by stimulating the fish to actively migrate further north in search of warmer waters. Corten (2014) hypothesizes that juvenile jack mackerel recruit to the adult population in the area where they find themselves at the time of first maturation. In this way, descendants from the population off central Chile could incidentally recruit to the adult population in Peruvian/Ecuadorian waters, thereby providing an occasional boost to this population.

3. The CJM Habitat

The characteristics of the habitat are driving the fish spatial distribution and the existence of separated groups, which leads to the potential organization into sub-populations. Studying the habitat of the CJM is a way to get a description of its population structure.

3.1. The main factors affecting the habitat

The Humboldt Current Ecosystem presents a huge variability in climate (Espino and Yamashiro, 2012). Number of environmental characteristics have a clear effect on the CJM habitat.

3.1.1. Climatic events.

ENSO events. Gretchina (2008) shows that the habitat limits of the CJM are related to the ENSO events, following the variations of the subtropical front from south to north when an ENSO occurs (Arcos et al., 2001). The author showed that the overall distribution of CJM shrank since 1999 in the western, southern and northern limits of its area, the western limit, for instance, moving from New Zealand (170ºE) in the 90s to east of 130ºW in 2003. Apart the population movements, these ENSO affect also the egg and larvae distribution, as stated by Barbieri et al (2004) who show a strong difference of this index between 1998 (el Niño) and the years before (1997) and after (1999: La Niña).

Dissolved oxygen. The south-east Pacific is characterised by the presence of an intense and shallow oxygen minimum zone (OMZ) (Helly and Levin, 2004; Fuenzalida et al., 2009). This OMZ has strong impacts on the vertical and horizontal distribution of the CJM (Bertrand et al., 2016) since this fish is unable to live in waters with oxygen concentrations below 1 $ml.l^{-1}$ (Bertrand et al., 2006). This tolerance to oxygen depends on fish concentration, dense schools being unable to survive in water with DO less than 4 ml.l^{-1} while scattered fish can tolerate DO as low as 2 ml.l^{-1} (Fig. 3).

Recently another limitation related to oxygen has been evidenced: the need for a sufficient vertical range of oxygenated water. Indeed besides a minimum DO, the CJM requires a vertical range of oxygenated waters greater than 30 m (Bertrand et al., 2016).

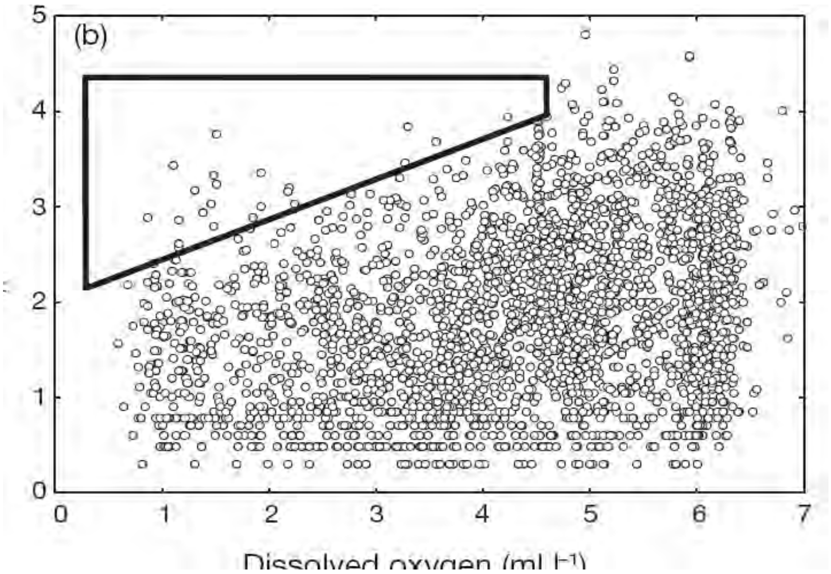

Figure 3. Jack mackerel aggregations (represented by Log-transformed acoustic area scattering coefficient s_A, in m^2.nautical mile^{-2} of CJM echo traces) relative to dissolved oxygen (in ml.l^{-1}), during the day. Log(s_A) represents the fish density and is a proxy for the type of aggregation, from dense schools (s_A >3) to scattered fish (s_A <1). The polygon illustrates the “exclusion zone” where almost no fish were observed. Each point represents one aggregation referring to its corresponding hydrological values as interpolated from CTD stations during the acoustic surveys (from Bertrand et al 2006).

Salinity. There are few works on salinity, which should not play a significant role in the definition of the CJM habitat since the range of tolerance of CJM remains much above the maximum variation of salinity in the distribution area]33-36[: Bertrand et al. (2004a, 2006).

Productivity. *T. murphyi* is an active predator with a high metabolism (Konchina, 1983). Food availability and quality are thus critical for its distribution (Serra, 1991; Bertrand et al., 2004b; Alegre et al. 2013). Chlorophyll-a is often used as a proxy for prey abundance (e.g. Li et al., 2016). CJM is found on the external border of the high Chl-a concentration above 0.07 mg m^{-3}. Such value is not independent from temperature as metabolism, i.e. energetic requirement, increases with temperature (Kooijman, 2010). CJM can be encountered in areas with lower productivity in its cold water southern distribution (< 0.1mg m-3) than in the warmer north (Bertrand et al., submitted).

We present in the table 2 a synthesis of the limits and preferenda of the main hydrological parameters observed and defined for the CJM as detailed above (chapters 1 and 2).

2.2 The 3D habitat of the Chilean Jack Mackerel: a conceptual model

A key publication was produced by Bertrand et al (submitted) who present a model of habitat for the CJM defined by the dynamics of its horizontal and vertical distribution.

2.2.1. Horizontal distribution. This model is based on interactions between SST and CHL-a for the horizontal distribution. This model fitted a maximum probability of jack mackerel presence between SST = 11.5°C and SST = 24°C and CHL-a > 0.5 mg m^{-3}. It presented two clear seasonal patterns (fig. 4): an important contraction of the favourable habitat towards the coast in austral summer and a temporal discontinuity in spatial distribution at ~19ºS - 22ºS from January to April.

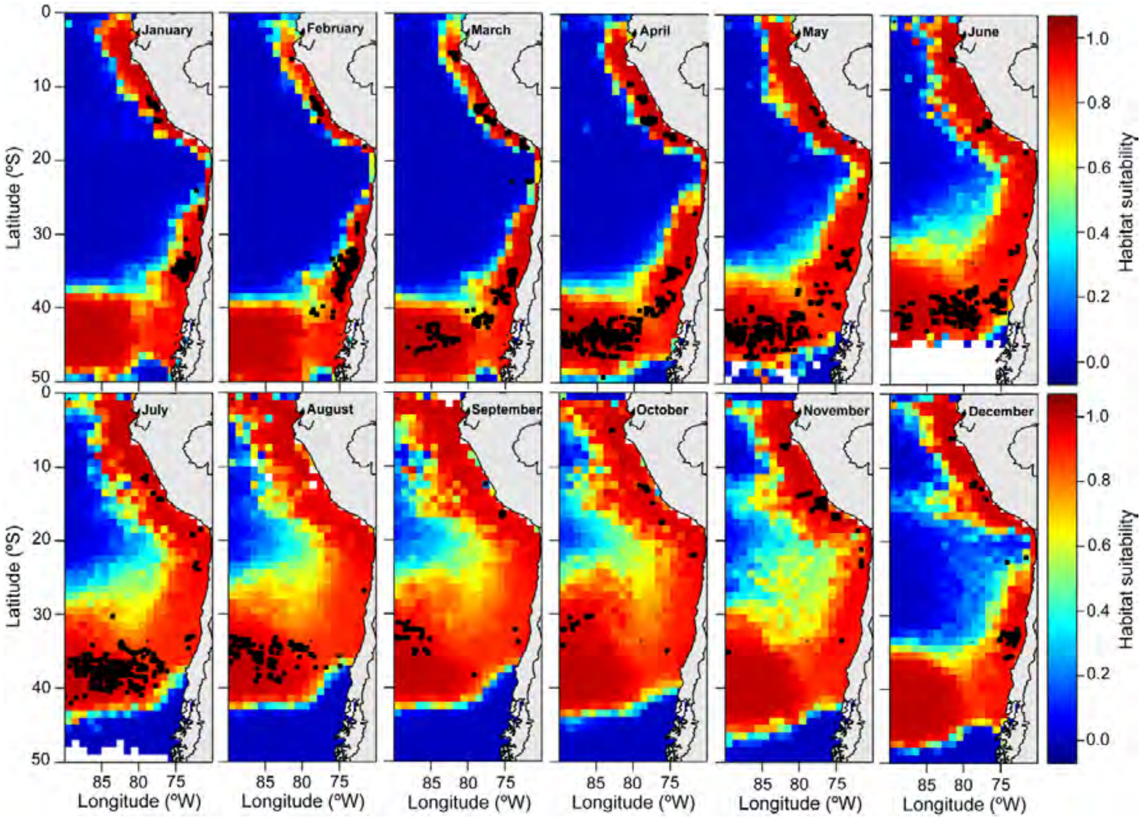

Figure 4. Zoom on the Humboldt Current system of the climatological jack mackerel habitat probability maps from January to December. High probabilities in red; low probabilities in blue. Catch observations are superimposed as black dots (from Bertrand et al., 2016).

2.2.2. Vertical distribution. The 9°C is defined by the authors as the lower thermal limit for jack mackerel and thus the limit of its vertical habitat range from the surface is selected as the depth of the 9°C isotherm. Additionally the vertical limit is also dependent on the minimal depth of oxygenated water (dissolved oxygen >2 ml l^{-1}) as described in the former chapter.

2.2.3. Conceptual model in 3D. Using these criteria the authors built a 3D model of CJM habitat horizontally and vertically limited by temperature, productivity and oxygen (fig. 5).

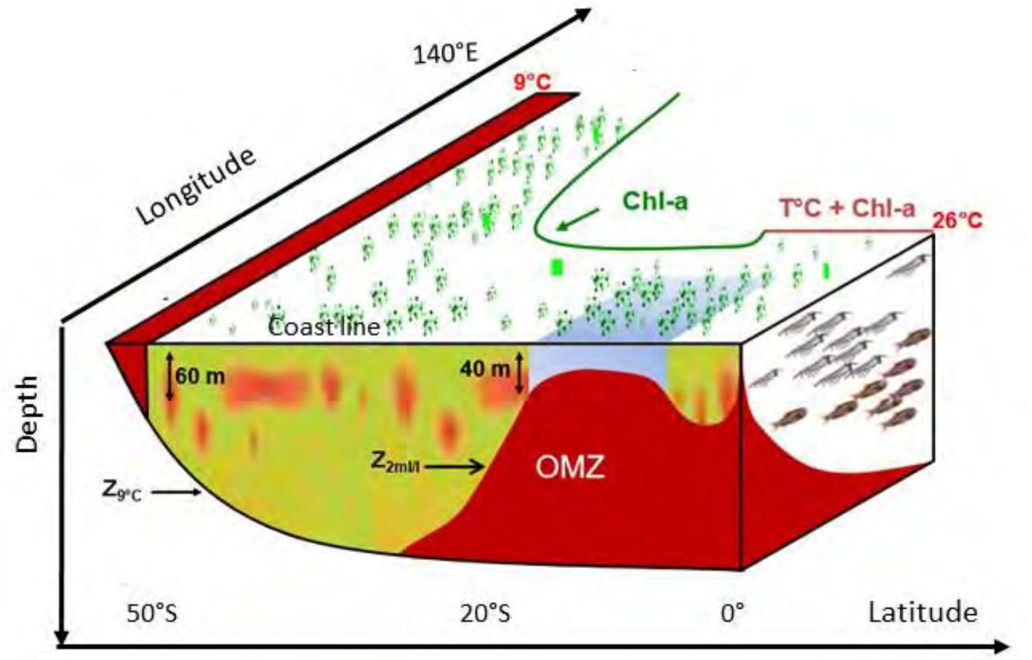

Figure 5. 3D conceptual model of the Jack mackerel habitat in the South Pacific. The habitat is limited by temperature (9ºC), productivity (Chl-a), concentration (2ml/l) and depth (40m) of the dissolved oxygen. Red surfaces correspond to unfavorable habitat delimited in the south by the 9ºC SST isoline and a minimum depth of 60 m for the 9ºC isotherm (9ºC) and in the north by the 26ºC SST isoline. Blue volume represents the “door”, closed for CJM when the oxycline is above 40 m. The horizontal limits are represented by a green (tropical gyre) or red (9°

isotherm) lines. Primary production is represented by patches, mesopelagic fish and euphausiids by drawings (from Hintzen et al., 2014; Bertrand et al., 2016).

It presents two schematic cases. The first situation corresponds to a case where the suitable habitat along the Chilean and Peruvian coast is low and presents a “closed door” between north and south caused by a gap in the horizontal habitat at ~19-22°S and a shallow oxycline off south-centre Peru. This usually happens during austral summer (December to April: fig. 4), when the oxycline is shallow. This period corresponds to the spawning period for CJM (see chapter 2). During the other part of the year (austral winter, May to November) the deeper oxycline off south-centre Peru and the absence of the gap in the horizontal suitable habitat “open the door” between North and South.

2. Jack mackerel and metapopulation

The various authors who defined the metapopulations often presented different although complementary series of conditions for a metapopulation to exist. Gerlotto et al. (2012) encountered 16 major conditions in the literature. A few of them are always mentioned as obligatory conditions: space is discrete; ecological processes take place at local and/or metapopulation scales; the discrete spatial units of habitat are large and permanent enough to enable the persistence of local breeding populations for at least a few generations (Hanski, 1999). To these three major conditions Hanski (1999) added: possibility of recolonization and asynchrony in local dynamics.

From the literature we may also add, for the special case of pelagic fish: the independence of the dynamics of sub-populations (Kritzer & Sale, 2004); the geographical characteristics of local environment, “*consisting of discrete patches of suitable habitats surrounded by uniformly unsuitable habitat*” (Hanski, 1999); the existence of local and regional scales (Camus & Lima, 2002; Kritzer & Sale, 2004); the existence of behavioural tools allowing the continuity and recolonization of sub-populations, such as homing (Ovaskainen and Hanski, 2004), adaptation, straying and learning (McQuinn, 1997), dispersion of larvae/juveniles (Petitgas et al., 2010); finally the capacity for depletions and recoveries as stated by Petitgas et al. (2010).

This series of conditions give us a framework to define whether the structure of CJM could be considered a metapopulation or not.

4. The CJM population structure

In 2008, a series of six possible scenarios describing the CJM population structure were defined during an international scientific workshop organized in 2008 by the South Pacific Regional Fisheries Management Organization (SPRFMO, 2008b; see www.Sprfmo.int).

From these hypotheses, SPRFMO listed six possible scenarios. Below, for each scenario we first present a definition then describe the role it plays in the daily debate and advisory process.

Scenario 1. Single discrete populations: All CJM in the South Pacific belong to one population that is homogenous in structure throughout the entire distribution area.

Scenario 2. Two discrete populations (off Peru and Chile): CJM in the South Pacific belong to two populations, separated by latitude 20ºS, the southern one extending onto the high seas up to New Zealand and the northern one foremost present in Peruvian and Ecuadorian waters. The populations do not mix during their life.

Scenario 3. Two discrete populations (coastal & high seas): CJM in the South Pacific are assumed to be organized into two populations, one coastal and one in the high seas extending up to New Zealand. The populations do not mix during their life.

Scenario 4. Network of closed populations: Three or more discrete populations, one in Peru, one in and off Chile & one or multiple populations in the high seas. The populations do not mix during their life.

Scenario 5. The superpopulation (= patchy population): CJM are organized in different population “patches” but maintain a high degree of exchanges between the patches resulting in overall correlated population fluctuations.

Scenario 6. The metapopulation: CJM are organized in different autonomous population units that maintain a limited to moderate degree of inter-population exchange.

It was described for CJM by Gerlotto et al (2012). Following Hanski (1999) the authors extended a list of conditions required for a metapopulation to exist and applied it to the case of the CJM. After studying a series of population characteristics, namely spawning areas, growth rates and recruitment for the different exploited populations as defined by SPRFMO (i.e. Centre-South Chile, North Chile, Far North (Peru and Ecuador), offshore (west of 100ºW), the authors conclude that although not all the theoretical conditions are fulfilled, the more likely structure is that of a metapopulation. The central offshore population represents the “source area” from 30ºS to 40ºS and from 80ºW to 98ºW. The other areas (Peruvian area, coastal Centre-South Chile and NE to 30ºN – 98ºW) should be considered as supporting temporal autonomous sub-populations.

Hintzen et al. (2014) established a list of 27 characteristics that condition the population structure. The table 3 shows a summary of the supporting and contradicting pieces of evidence collated in the two former chapters for the six population structure scenarios.

These results indicate that scenarios 1, 2, 3, 4 are not fully compatible with the biological, ecological or habitat observations. The two extreme scenarios, i.e. single and multiple discrete population structures, seem unlikely. Some continuity in the CJM suitable habitat occurs in austral winter, permitting exchanges from the high seas to the Peruvian coast via the Chilean coast. However the connectivity is reduced in austral summer with a threshold at ~19ºS - 22ºS (Bertrand et al., submitted). The degree of separation varies at an inter-annual scale. The lack of exchanges at some periods/season explains why growth patterns (Goicochea et al., 2013) and parasite composition (Oliva et al., 1999) differ between Chile and Peru which present different thermal, trophic and biodiversity conditions. The existence of the threshold between the north and south populations could explain also why "imported" cohorts (Corten, 2014) spawn in a different spawning area than the one where they are born (McQuinn, 1997; Petitgas et al., 2010), which is not the normal behavior: usually homing behavior is strong and makes the fish spawning in their birthplace (Cury, 1994). In the case of CJM, due to the lack of connectivity during the spawning season between north and south, once mature, fish "trapped" in the north cannot go back to the south to spawn, and change their migration route through learning and entrainment (Petitgas et al., 2010). On the contrary, the continuity in the habitat during part of the year explains why inter-habitat movements for juveniles and to a lesser extend for adults may happen (Ashford et al., 2011; Gretchina et al., 2013). The favorable habitat can be highly reduced off Peru during certain years (Gretchina, 2008), and hence, when the suitable habitat shrinks, the main source for CJM may be limited off center-south Chile.

Two main patches of favorable habitat structure the CJM population: one centered in Peruvian waters and the other one in center-south Chile and its extension offshore up to 80ºW (Bertrand et al., submitted). These two areas are favorable to CJM given their temperature and hydrographical conditions. Under normal conditions two separate groups are hypothesized to live in each of these areas, and behave as a metapopulation including individual exchanges during part of their life. Under unfavorable climatic and hydrographic conditions, the suitable habitat may disappear to a large extend, resulting in reduced CJM biomass in the area (Gutierrez et al 2012). In the center-south, climatic and hydrographic conditions are more stable; suitable habitat spans over a wider area and has an opening to the high seas, which allow fish a refuge in case of unfavorable conditions closer to shore. Given these attributes, it is likely that a suitable habitat persists in this area and is therefore host to a resident population unit.

Exchange of individuals from the southern resident population unit to the northern unit have sporadically been observed in the South Pacific, e.g. in 2008 (Corten and Janusz, 2011), as described in chapter 2. This shows that colonization of the northern habitat is possible from the southern population. The inverse is unlikely, as we saw that unfavourable conditions in the south coincide with even worse conditions in the north where suitable habitat may have completely disappeared (ref.).

In conclusion, the new evidence summarized in this study confirms us that, in agreement with Gerlotto et al. (2012), Hintzen et al. (2014) and Bertrand et al. (submitted), the most likely population structure is best described by that of a 'metapopulation'.

5. Toward the definition of a “pelagic fish metapopulation”

We have noted in the introduction the lack of real conclusion in the literature on the compatibility of metapopulations with the biological characteristics of pelagic populations. We will not consider here cases such as eggs or larvae dispersion (e.g. Cowen et al., 2000; Grimm et al., 2002; Camus and Lima, 2002; etc.) based mostly on studies of benthic sedentary species with passive pelagic larvae transport that usually do not fit with pelagic fish biology. The general difficulty to determine whether a pelagic population is a metapopulation or not was probably best evidenced in the HOMSIR project (Abaunza, 2008) on North Atlantic horse mackerel *Trachurus trachurus* which, although most of the conditions for metapopulation for horse mackerel were present, did not want to draw any conclusion (Abaunza et al., 2004); and Secor (2010) on north Atlantic bluefin tuna (*Thunnus thynnus*), who considered that for a series of biological reasons, this fish could not be considered as organized in “*a true metapopulation*”.

We face the same dilemma. Indeed, although the description of the CJM population structure as a metapopulation seems most in line with scientific evidence as synthesized in Table 3, some inconsistencies still exist, relating to the connectivity between the northern and the southern main habitats of CJM (Table 3, item 26 and 27). Here we propose that a number of conditions firstly designed for terrestrial metapopulations may not be applicable to pelagic marine metapopulations. Therefore either “a true metapopulation” does not apply to pelagic fish species or there is need for an *ad-hoc* definition of these population structures.

We must begin with the question: are “pelagic fish metapopulations” (if existing) exactly similar to standard metapopulations? In other words, are there various types of marine metapopulations, one of them being compatible with the pelagic fish specificities? In order to study this point we will follow Gerlotto et al (2012) who explained how the population structures can be seen as a continuum from a single population towards multiple discrete populations through patchy populations and metapopulation structures.

We will consider this continuum using McCall’s basin model (McCall, 1990; Hintzen et al, 2014; Bertrand et al, 2008) as an explanatory tool. With this model we can draw different schemas for the different cases. McCall describes a pit in the basin as a particular habitat, where the conditions for a sub-population to have an autonomous life are fulfilled (figure 6). We categorized four main cases inside the continuum.

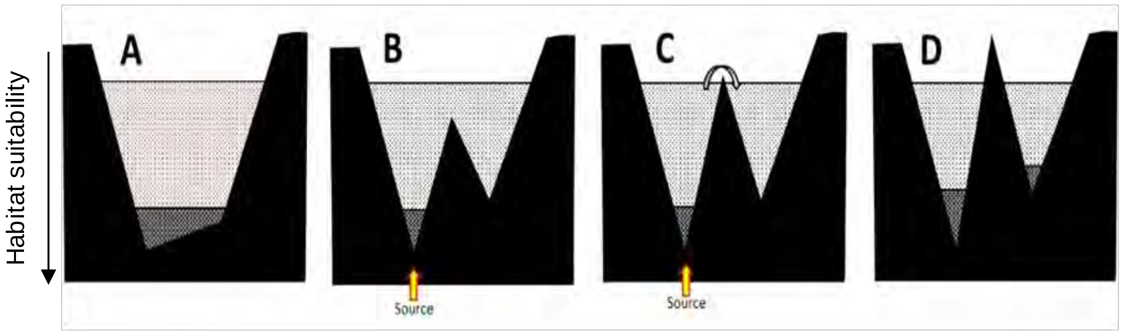

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Figure 6. Description of four cases of population behavior related to environment and habitat adapted from where increases with the depth. Favourable habitat is represented in light grey

while dark grey represents the most suitable habitat. Grey arrow in case C: possibility of transport of individuals from one pit to the other under particular conditions. A to D: see text.

> Case A. Single population. Only one single pit exists. Fish distribution within its potential habitat range habitat occupies the entire basin when environmental conditions are favourable. This case is archetypal of the basin model, where density and area vary with abundance.
>
> Case B. Similar to case A except that one (or more) additional pit exists. Secondary pits have a shallower basin than the “source” pit, which remains the only refuge when conditions are the worst; fish in the other pits can disappear. These secondary pits can be recolonised when conditions become favourable encompassing the entire habitat.
>
> Case C. Similar to case B except that the habitats are not connected anymore, usually due to the existence of territorial borders. Only some individuals or very small groups can move from one habitat to the other when the different habitats present favourable conditions (opening of corridors, passive transports of individuals, etc.). Still, these limited exchanges allow the recovering of lost pits where sub-populations have eventually sunk by the source.
>
> Case D. similar to case C except that there is no exchange at all between the different pits. No source population: if a population collapses, its niche is lost forever. In this case we have two separated population that can diverge.

Within this list of cases, which structures are metapopulations? If we consider the fundamental conditions expressed by Levins (1970), i.e. separate populations acting independently during a long period and some exchanges existing between sub-populations, then only cases B and C can be accepted as metapopulations. The major differences between these two cases deal with the existence or absence of physical or geographical borders that constraint the habitat inside a “territory”, even though the environmental conditions would allow a larger distribution. To go further, we first need to define a number of terms (Fig. 7).

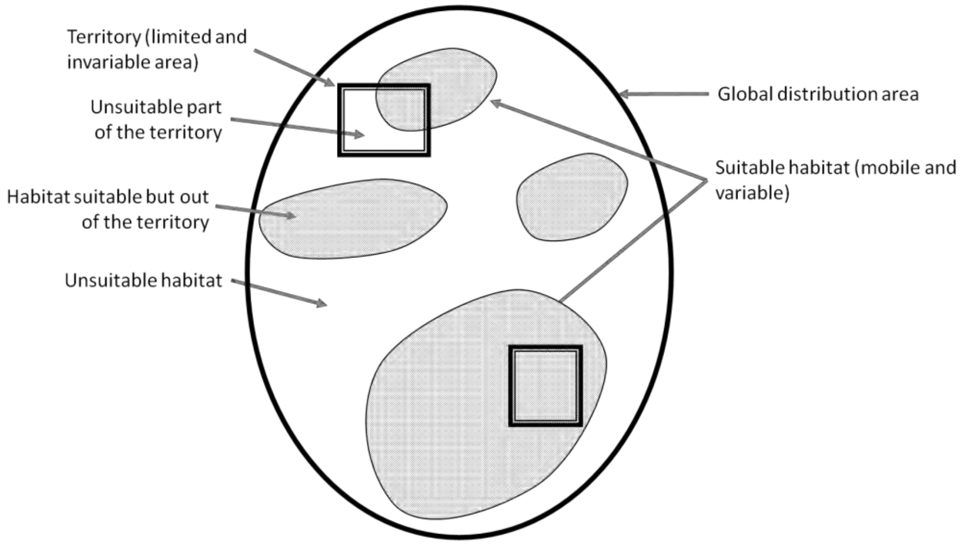

Figure 7. Description of the different spatial characteristics implicated in metapopulation definitions.

- The <u>distribution area</u> corresponds to the zone of possible population distribution defined by overall abiotic conditions.

- Within this distribution area the <u>suitable habitat</u> represents the synthesis of ecological/hydrological conditions that have a positive impact on the life of the species at a given moment. The suitable habitat depends on scale-related oceanographic processes, from large scale patterns (e.g. the subtropical front) to mesoscale or even finer scale features (Bertrand et al. 2008; 2014). Within the distribution area, exchanges between disconnected favourable habitats are achieved through passive or active displacements of the larval/juvenile/adult.

- The territory is a spatially limited geographical area needed by the species to complete its life cycle within the overall distribution area. A territory can be for example a pond for a freshwater fish or a clearly delimited coral reef for marine species (Bay et al. 2008). Its surface is delimited and cannot change even if environmental conditions vary (at the scale of few generations). A territory is surrounded by unfavourable environment preventing the population expansion (Hanski, 1999). Depending on environment variations, habitat suitability may cover part or totality of the whole territory. We extend this territory concept to migratory species. For instance anadromous fish that "obstinately" spawn in a given river (Cury 1994) or herring that need specific physical bottom substrate to spawn (McQuinn 1997). In this case, the territory refers to a specific and transitory, but obligatory phase of the population life cycle.

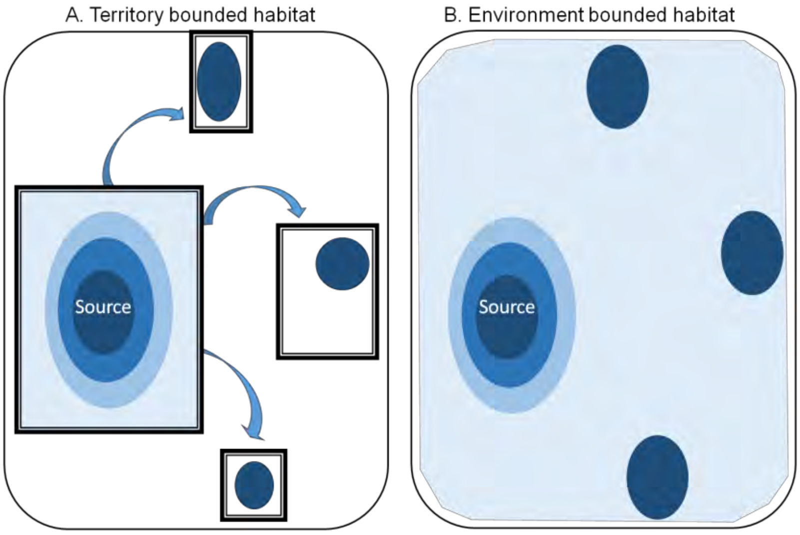

Figure 8. A. Territory-Bounded Habitat (TBH) and B. Environment-Bounded Habitat (EBH) metapopulation conceptual frameworks. The suitable habitat (scale of blue) represents the largest area that can be occupied by a species inside the distribution area (overall rectangles) when environmental conditions are favourable. Territories are represented by rectangles. We schematize four sub-populations, one of which (the source) suffers increasing suit environment conditions: the suitable area surface increases from dark to light blue. In the TBH case the suitable habitat cannot extend farther than the territory borders; only some individuals can migrate (blue arrows). In the EBH, no geographical limit exists and when the suitable habitat

extends it can cover eventually the whole distribution area, letting the source overlapping with the other subpopulations. Based on these definitions, the two metapopulation structures can be described as (Figure 7 and 8):

The "territory-bounded habitat" (TBH) metapopulation, for species linked to a specific territory: environment changes within the territory induce changes on the surface of the suitable habitat up to the territory border. Exchanges between population belonging to different territories occur at the level of individuals by passive transport or active behaviour (e.g. stray in Cury 1994) (case C, figure 6).

The "environment-bounded habitat" (EBH) metapopulation where the only limit of expansion for the habitat is the distribution area: its actual surface is limited by the area where favourable conditions of the local environment are found. Connections between local and global scales are often achieved by large hydrological events, e.g. currents, eddies, etc. For a given sub-population (usually the source), and under favourable environmental conditions, the suitable habitat may expand up to overlapping with the other sub-population habitats. Here the exchanges are at the level scale of cohorts or whole sub-populations (case B, figure 6).

Territory adds additional environmental constraints, shaping the habitat suitability. As each territory is unique, the impact of environmental variability is likely to affect differently each one of them resulting to non-synchronized variations on local biomasses. Asynchrony has been defined as a necessary condition for metapopulation persistence (Hanski, 1999). However pelagic populations, such as the CJM, present from time to time synchronous large scale patterns of abundance with for instance the existence of strong cohorts present in the whole distribution area (Konchina and Pavlov 1999). This is compatible with our definition of EBH, where the effects of large scale climate forcing are not territory-dependent.

TBH is certainly representing the vast majority of metapopulations that have been studied. Not surprisingly, it does not fit with a pelagic population dynamics and life, particularly because of the asynchrony it imposes to the different populations and of the way sub-populations exchange individuals.

Table 4 synthesises the TBH and EBH characteristics that have an impact on the life history of the populations. This explains why any attempt to match pelagic population characteristics to the TBH framework cannot lead to any clear conclusion. On the contrary, it fits with the EBH metapopulation definition and the inconsistencies noted for pelagic fish (e.g. Table 3 for the CJM) disappear.

On this basis we define the “pelagic fish metapopulation” as an EBH-metapopulation, where:

- Three of the four necessary conditions defined by Hanski (1999) for metapopulation existence are fulfilled: (i) discrete-breeding populations; (ii) risk of extinction for all populations; (iii) recolonisation possible. On the contrary asynchrony in local dynamics (4th condition) does not fully apply.

- Other typical characteristics of metapopulations are also present (see Gerlotto et al. 2012): (i) differences in scales between local and regional effects of the environment; (ii) existence of source-sink populations; (iii) autonomy of sub-populations and limited genetic exchanges.

- Exchange or colonisation occur under three situations: (i) conventional exchange of individuals by straying and learning (Cury 1994; McQuinn 1997; Corten 2002) and entrainment (Petitgas et al. 2010); (ii) habitat overlap (Bertrand et al. 2016); (iii) permanent integration of a cohort usually generated by the source (Konchina and Pavlov 1999; Corten 2014) often transported by large hydrological events or when the boundaries between suitable habitats weaken (e.g. Bertrand et al. 2016).

- Substantial changes in population abundance due to synchrony between sub-populations are common.

The definition of these two types of metapopulation (Table 4) is likely to have implication on Darwinian adaptation and speciation mechanisms. Darwinian Theory considers that a large population is usually unable to acquire new important evolving patterns. Inside large populations, *"speciation becomes impossible, at least in the bulk of the species»* (Mayr, 1982). Then speciation –and obviously adaptation- is mostly effective on smaller groups suffering independently particular pressures. Speciation requires populations be temporarily protected from the effect of foreign genes: *"The best way to succeed in this isolation is through extrinsic factors, i.e. (…) geographical barriers»* (Mayr, 1970). Adaptation thus depends on two conditions: (i) an optimal population size, large enough to have a good probability of producing adaptive mutations, and small enough to extend the mutation throughout the genetic patrimony; and (ii) isolated from other sub-population during several generations. In the extreme case of discrete populations, these mechanisms lead to speciation.

TBH metapopulation matches these requisites. In each territory mutations can lead to an adaptation to local conditions. Yet genetic exchanges exist between subpopulations allowing for gene fluxes.

Genuine pelagic populations are often too abundant and too homogeneous (no geographical barriers) to match these requisite. Paradoxically they live in a highly variable environment with no defined territories, which requires fast adaptive capabilities in space and time. Organisation in EBH metapopulation is a way to overcome this paradox. Indeed, one strategy is to present long periods of rather low abundance (population depletions) during which, subpopulation are discrete and adaptive mutation can be selected as in TBH; followed by shorter periods of high abundance where the sub-populations share their mutations that can eventually colonize the whole population.

We suggest the following scheme to illustrate our hypothesis. From time to time, a species increases dramatically its biomass, triggered by linear, non-linear or stochastic climatic or random event (Hsieh et al. 2005) and occupy the whole distribution area. This population expansion can last several generations. It was for instance the case of grey triggerfish *Balistes capriscus* in West Africa, which population increased by several orders of magnitude from 1972 to the early-1980s (Caveriviere et al. 1980). Such coincidence of favourable conditions leading to a demographic explosion is unlikely to be frequent. For instance studies on paleoecology reveal that sardine (*Sardinops sagax*) and CJM populations in Southeast Pacific Ocean do present these short bursts (at scale of years or a few decades) separated by long phases (several decades and up to centuries) of low abundance (Valdés et al. 2008; Gutiérrez et al. 2009; Salvatteci 2013). During episodes of high abundance, when the doors open between bounded sub-populations (fig. 4; see Bertrand et al. 2016), the species can expand in the whole distribution area. It recovers all potential niches lost during the low abundance phase and integrates all the sub-populations (and so the genetic pool) into a single one during a few years/decades. Later, the population comes back to its typical abundance, with autonomous sub-populations, during tens or hundreds of generations. In this case, the successive demographic depletions and explosions could be a way to transmit rapidly to the whole population the favourable mutations selected locally by the species to adapt to highly variable local conditions.

In synthesis, the succession of large and small abundances is (among other possible mechanisms) an evolutionary adaptation to environmental changes within an EBH metapopulation, which allows the species to (i) cope with environmental changes; (ii) recover all the potential niches that could have been lost during the low abundance phases; (iii) optimise its genetic pool.

A drawback of this population strategy is that it makes the species highly sensitive to adaptive predation, especially overfishing, which induces a consistent risk of collapse in exploited populations. As illustrated by CJM, the episode of very high abundance leads to the development of a huge international fishing power. When depletion occurs, this potential fishing effort tends to focus on the remaining parts of the population, inducing a strong overfishing. According to Petitgas et al (2010), a qualitative difference exists between natural depletion and fisheries-induced collapse where recovering "*takes much longer than predicted*". If depletion cannot be considered as "bad news" for the species, collapses linked to overfishing are likely to destroy the structure (as well as the "culture": Corten 2002; Petitgas et al. 2010) of the populations and therefore to introduce risks of permanently very low abundance (or even extinction) for the species.

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Table 1. Growth curve parameters for studies on CJM in Chile and in Peru (from Diaz, 2013)Reference	Location	Method	L_∞ (cm)	K	t_0
Diaz (2013)	Peru	Empirical reading	81.6		
Diaz (2013)	Peru	AFT (ELEFAN I)		0.167	
Goicochea et al. (2013)	Peru	Otholith reading	75.17	0.165	-0.817
Dioses (1995)	Peru	Otholith reading	80.8	0.155	-0.356
Cubillos & Arancibia (1995)	Chile (Centre-South)	AFT (ELEFAN)	78.6*	0.138	
Gili et al. (1995) in Serra & Canales (2007	Chile (centre-south)	Otholith reading	77.8*	0.094	-0.896

(*) The curves are calculated for fork lengths (FL), those calculated with total length (TL) being transformed with the equation TL = 0.514+ 1.091FL (Cubillos and Arancibia, 1995).

Table 2. Limits of tolerance of CJM for a series of hydrological and biological parameters

Parameter	Lower limit	Upper limit	Lower preferendum	Upper preferendum
Oxygen	1 ml/l	n/a	2 ml/l	n/a
Temperature	9º	28º	10º	25º
Salinity	<min. observed	>max. observed	34.9	35.1
Chl-a	0.07mg/m3	26 mg/m3	0.1	?
Oxycline depth	n/A	30 m	?	>40 m
Depth	400 m	0 m	-	-

Table 1. List of the characteristics collected in the literature and their compatibility with the six different structure types (see 3.2.2.). Scenarios are indicated by their number (see text) in columns 3, 4 and 5. From Hintzen et al., 2014

Characteristic (condition) nb	Observation / condition	Supporting	Contradicting	Incompatible with
1	No genetic evidence is found to differentiate fish caught in different regions ranging from Peru to Chile and onto the high seas	1, 5, 6		2, 3, 4
2	No clear segregation in otholith biogeochemistry was found for juveniles to distinguish between fish caught in Peruvian or Chilean waters.	1	2, 4	
3	There is a high degree of similarity in length distribution from Northern Chile and Southern Peru catches	1, 5		
4	Strong cohorts appear all over the Pacific	1, 5		
5	Only a continuous and permanent distribution of adult fish is shown off Chile	1	3	
6	A certain degree of segregation in otholiths biogeochemistry was found for adults to distinguish between fish caught off Peru and Chile	2, 6	1, 5	
7	Differences in growth and estimated growth parameters are observed between fish caught off Peru and Chile	2, 6	5	1
8	A difference in encountered natural mortality between fish off Peru and Chile is observed	2, 4, 6	1, 5	
9	Based on an analyses of the metazoa parasite fauna, a small difference between fish off Peru and the Chilean coast is observed	2, 4, 6	1	
10	A difference in age distribution in the catch taken off Peru and off Chile / high seas is observed	2, 3, 4, 6	1	
11	A difference in estimated recruitment / productivity, obtained from assessment results, is observed between stock assessments separating the Northern and Southern fisheries	2, 6	1	
12	The existence of a ‘few-fish zone’ between ~19-22° South is observed in acoustic and catch geo-referenced data. In addition, the predicted separation in	2, 4, 6	3	1

	coastal habitat during part of the year limits extensive mixing.			
13	A difference in encountered natural mortality between fish off Peru and Chile is observed	2	3	1
14	Spawning is observed in multiple patches / areas throughout the South Pacific and is not limited to one spawning area	2, 3, 4, 6		
15	Analyses show that the 2008 cohort, first captured off Chile, may have migrated under a strong La Nina effect into Peruvian waters in the beginning of 2011	6	3	2, 4
16	Substantial connectivity between fish in Chilean, Coastal and Peruvian areas	1, 5, 6	2, 3, 4	
17	The spatio-temporal SEAPODYM model, parameterized for Jack mackerel, shows that the distribution of adult and juvenile fish is also oriented perpendicular to the coast		3, 4	
18	A recent eastward shift in distribution area of the main catches in the south-central area of the South Pacific has been observed with limited availability of Jack mackerel outside Chilean jurisdictional areas.	1	3, 4	
19	Observations of spawning activity span from the Chilean coast up to 110°W		3, 4	
20	At least two main spawning areas are defined)	4, 6	1, 5	
21	Observations show local spawning activity inside New Zealand waters. Most catches correspond to large and old Jack mackerel	4, 6	1, 5	
22	Analyses of the trend in population units, based on assessment results separating Peruvian and other catches, do not show a close synchrony in development	6	1, 5	
23	No extensive connectivity between fish in Peruvian and Chilean waters or to the high seas except during strong El Niño when there is a flux from offshore to coast and south to north.	6	1, 5	
24	Jack mackerel is considered a highly migratory species with the ability to migrate between potential habitat patches	1, 5, 6		
25	The heterogeneous habitat owing to the Humboldt current system results in	5		

	patchy suitable habitats			
26	No connectivity between coastal Chile and high-seas fish, no connectivity between Peru and high-seas fish	4	1, 6	
27	Habitat is only partly fragmented throughout the year. There is no fragmentation between habitat off Chile and onto the high seas		6	

Table 4. Comparative view of the major characteristics of TBH vs. EBH metapopulation

Main characteristics	**Territory bounded habitat (TBH)**	**Environment bounded habitat (EBH)**
Metapopulation structure	Permanent	Interrupted when sub-population habitats merge
Surface occupied by the sub-populations	Spatially defined by the territory (at least for a critical part of the life cycle)	Spatially variable, limited by the suitable habitats
Biomass of the different sub-populations	Nearly independent (asynchronous), integrating the effects of environment on specific territories	Synchronous when large scale environmental forcing impacts the whole distribution area.
Exchange between sub-populations	Individual passive transport or active behaviour	Transport of larvae or migration of individuals at a scale up to cohorts or sub-populations
Source	The most resilient sub-population; otherwise not functionally different from the others	The most resilient sub-population; the only one susceptible to invade all the other sub-populations
Frequency and intensity of exchanges	Random, sporadic, linked to the locally-controlled rise and fall of the different sub-populations	Massive, episodic, and environmentally controlled, depending of the connectivity between suitable habitats (pits)
Total biomass	The variability is smoothed out by the asynchronous variations of the sub-populations	Extremely variable, each sub-population being submitted to synchronous environmental variations
Speciation/adaptive conditions	Almost permanent	Periodica