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Adapting the Concept of Metapopulations to Large Scale Pelagic Habitats

European Union

Habitat Monitoring Working Group

ADAPTING THE CONCEPT OF METAPOPULATIONS TO LARGE SCALE PELAGIC HABITATS

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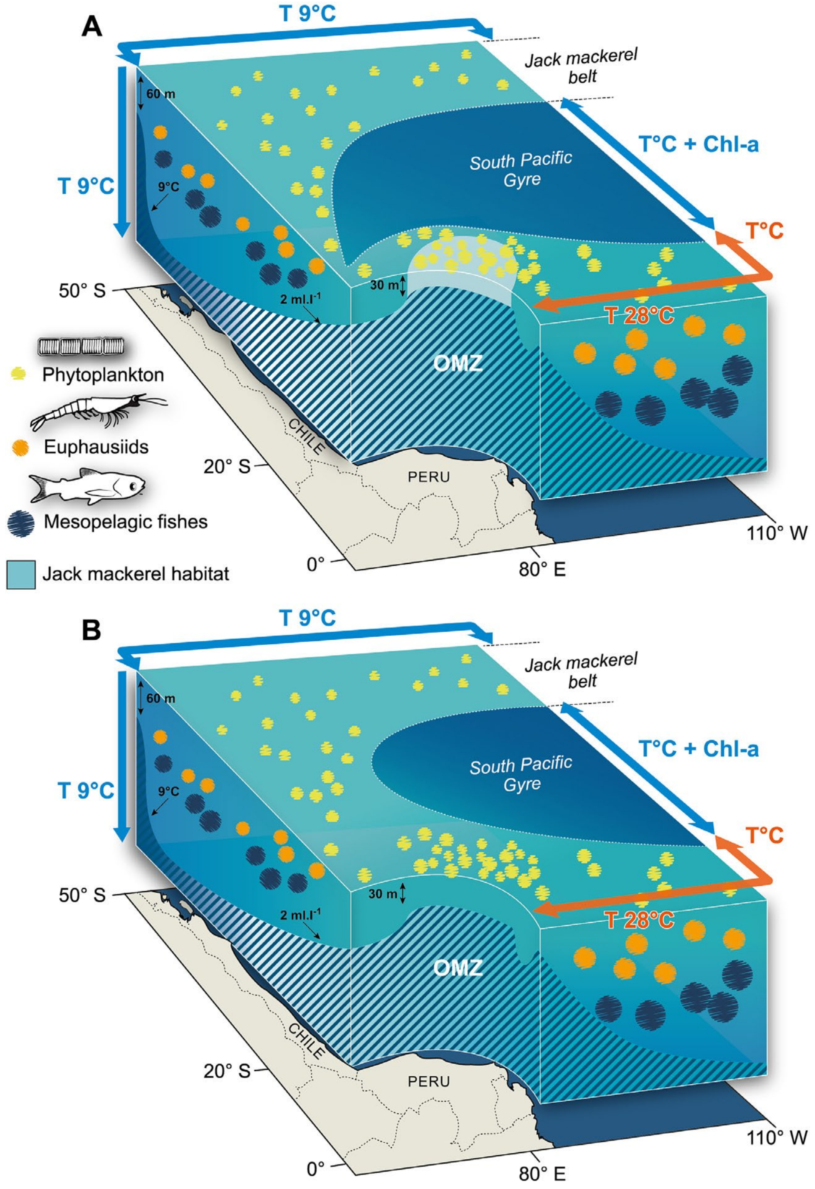

François Gerlotto, Arnaud Bertrand, Niels Hintzen and Mariano Gutiérrez

ADAPTING THE CONCEPT OF METAPOPULATIONS TO LARGE SCALE PELAGIC HABITATS

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ABSTRACT

Metapopulation is an interesting case of population structures allowing a strong resilience to regime shifts. The concept has been studied on various animal species since the first definition by Levin (1969). Results showed that metapopulations are widely observed, and could be the most common type of population. The question of whether large populations of pelagic fish can be organized in metapopulation has been studied since the 1990s, but remains controversial, due to the difficulty to apply to these moving populations the conventional definitions originally fitted to small terrestrial sedentary groups.

Considering the characteristics of pelagic populations that are contradictory with some definitions stated since Levin's, we tried to define a pelagic metapopulation. We observed a continuum in population organization schemes, from one single to several discrete populations, with two metapopulation cases: the "territory-bounded-habitat" (TBH) metapopulation, where each sub-population is confined in a "territory" surrounded by geographical borders that cannot be currently crossed, and the "environment-bounded-habitat" (EBH) metapopulation where the sub-populations lives in moving areas only limited by the favourable conditions of the local environment. We define a pelagic metapopulation as an EBH-metapopulation, where most of the necessary conditions for metapopulation existence are fulfilled.

We analyse EBH metapopulation characteristics on two case studies: a triggerfish and a jack mackerel. We conclude that pelagic metapopulations represent an efficient evolutionary tool that makes local adaptations to changing environmental conditions possible, local adaptations being eventually extended to the whole species during the short episodes of synchronous life when all the sub-populations are connected.

1. INTRODUCTION

Fish populations, and particularly (but not exclusively) pelagic populations, may suffer huge variations of biomass. The literature on this is especially abundant for Clupeids, Engraulids and Carangids, with descriptions of collapses {Dickey-Collas, 2010}, recoveries (Lluch-Belda et al. 1989), expansions (Petitgas et al. 2012) and colonization (Hardie et al. 2006). Until the 1990s, these variations were often attributed to overexploitation by industrial fisheries as stated by Zwolinski and Demer (2012) and many other authors (Pauly et al. 2003; Myers and Worms 2005a; Hilborn et al. 2005; Coll et al. 2008; Hilborn 2011). But it appeared quickly that overfishing could not explain these changes by itself (Cury and Roy 1991) and environmental effects were considered (Zwolinski and Demer 2012; Hutchings and Reynolds 2004; Myers and Worms 2005b; Worms et al. 2009), leading to the introduction of the Environmental approach to fisheries (Garcia 1996).

Already in the late 1970s and early 1980s IMARPE (Peru) was aware that, at least in the case of the Peruvian anchoveta, the 1972-73 collapse was due to the combined effects of overfishing and environmental factors (Csirke 1979, 1980) and biomass as whole, by going through at least two possible "decadal" regimes, with a high abundance one in 1960-1972 and a low abundance one in 1973-1982 (Csirke, 1987), with some other long-term changes in the Peruvian upwelling ecosystem as a whole (Pauly & Tsukayama 1987, *op. cit.*).

A major change towards the international recognition of the significant effects of non-fisheries related factors (*i.e.*, environmental variability) on the inter-annual and decadal changes in the distribution and abundance of some important fish stocks was made in 1983, during the Expert Consultation to examine changes in abundance and species composition of neritic fish resources, organized by FAO in San Jose, Costa Rica, 18-29 April 1983 (Csirke and Sharp 1984, Sharp and Csirke 1983). It was precisely the paper presented by Kawasaki (1983, *op. cit.*) at this meeting the one which contributed to change the paradigm in the analyses of the causes of some major fisheries collapses, first amongst the Costa Rica meeting participants, then in FAO approaches to fish stock assessment and fisheries management, and then worldwide.

Kawasaki's paper brought our attention to the synchronized interdecadal fluctuations in abundance of three far-apart species of Sardinops (off Japan, California and Peru), but it also brought our attention to other cases that were kind of dormant in old data files and past publications. Since, important improvements on the predictive capabilities of the models were obtained using environmental variables input (Cury and Roy 1989; Fréon 1989). Nevertheless the local environment alone could not explain the full story of these dynamics (Gerlotto 2017). During the 1990s and 2000s, changes were often partly attributed to climatic cyclic events (Chavez et al. 2003), although while there were indeed cyclic patterns, these were not always correlated to cycles of the environment (Fréon et al. 2005). In more recent hypotheses population strategy of a species starts to play an important role (Bertrand et al. 2016). Population dynamics clearly show patterns at species level.

One famous example is the r- and K- reproductive strategies (MacArthur and Wilson 1967), or more recently the BOFFFF hypothesis (Hixon et al. 2014). These strategies are related to the population structures. Fisheries scientists had to integrate these and other general theories, and especially the metapopulation theory, elaborated by Levin (1969; 1970).

This concept was applied to diverse cases in terrestrial ecology, from insects to mammals, birds and freshwater fish, and to some particular cases to marine fish (Grimm et al. 2003; see Kritzer & Sale 2004 for a synthesis). One of the great interests of metapopulation theory is that such strategy explains the strong resilience of the populations (Secor 2010): there is no possible genetic drift inside the separated subpopulations, as the low or even null variation of genotypes shows (Poulin et al. 2004; Abaunza 2008) because from time to time, some genetic mixing occur between these sub-populations through exchanges of a few individuals. Such characteristics have been explored by Cury (1994) among others: they explain the high resilience of these populations, even though they may suffer sudden depletions or collapses (McQuinn 1997; Petitgas et al. 2010). It explains also how the species niches lost during a strong depletion can be rather quickly and easily recovered when conditions are favourable.

The typology of population structure in pelagic fish has received little attention since the 1990s (Kritzer & Sale 2004). The question of the existence of metapopulations (among other types) were studied by various authors on a variety of pelagic fish species but providing conclusive arguments were difficult to formulate. McQuinn (1997) was one of the first who presented the hypothesis that north Atlantic herring (*Clupea harengus*) was organized as a metapopulation. His work focussed though on a pelagic species that is known to spawn on gravel habitats in the benthic layer. 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 (*Gadus morhua*) were also a metapopulation. Smedbol and Wroblewski (2002) studied the problems of recovery and interdependency inside the cod metapopulation, and Smedbold et al (2002) concluded: *"under the definition used (…), the northern cod would not be considered a true metapopulation*". Although cod is not a pelagic species, many of its population characteristics are rather comparable with pelagics, especially the fast variation of its biomass related to environmental conditions (Beaugrand et al. 2003), a moderate homing behaviour and pelagic eggs. This species spawns in relatively wide spawning areas susceptible to vary according to climatic conditions, contrary to for instance salmons, or herrings. Smedbol et al. (2002) did not conclude that the cod dynamics could be described as a "true" metapopulation mostly because of the definition used. When the metapopulation theory is applied on genuine pelagic fish, conclusions are even more difficult to draw.

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 assumption for anchovy (*Engraulis encrasicholus*) in the Bay of Biscay, capelin (*Mallotus villosus*) in the Barents Sea, and sardine (*Sardinops sagax*) in California. The HOMSIR project (Abaunza 2008) on North Atlantic horse mackerel *Trachurus trachurus,* did not draw any conclusion although most of the conditions for metapopulation were present (Abaunza et al. 2004).

Fromentin and Powers (2005), then 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. In synthesis, the metapopulation concepts appears to be difficult if not impossible to apply to pelagic populations, as long as the conventional definitions are used.

SPRFMO created in 2018 a scientific working group dedicated to studying habitat (SPRFMO 2018). According to SPRFMO's definition, "***the habitat is the place where a particular population of a species lives. It represents the spatial area that meets the suitable conditions for the species to live and reproduce, perpetuating its presence. Thus, habitat is described by features that define it ecologically, distinguishing it from other habitats in which the same species could not find favorable conditions. A particular case is that of the pelagic habitat that has a fluctuating surface and volume in time and space. This variability has a critical effect on the populations inhabit a geographic area***". The objectives of this new Working Group on "Habitat Monitoring" is to provide environmental indicators associated to the habitat of the main commercial resources fished in the SPRFMO area to complement decision making of fisheries management.

The present work has the ambition to help defining a pelagic habitat and describing the likely population structure of a pelagic species living in such habitat.

The role of habitat seems to be giving low attention in the existing metapopulation theory. Only independent series of environmental characteristics were considered, whereas habitat was never used as a synthetic discriminant pattern. To give an example on a small sample, i.e. the 5 articles published in Fish and Fisheries on fish metapopulations, we found five occurrences of the word "habitat" in McQuinn (1997), 16 in Smedbold et al. (2002), 7 in Kritzer and Sales (2004), 13 in Fromentin and Powerl (2005). Then it appeared 78 times in the paper by Schtickzelle and Quinn (2007), but the authors focused on the description of suitable habitats for salmons and anadromous fish.

One of the major reasons for such a weak application of habitat for defining a population limits is likely that precise three-dimensional and dynamic data were lacking. This has changed recently with the use of other sources of data than fishing and satellite data, and especially acoustic information from the fishing vessels as stated for instance by Melvin et al. (2016). It becomes possible to use habitat characteristics for classifying populations and metapopulations through the definition of their environmental or territorial boundaries (Bertrand et al. 2016) which drive the exchanges between subpopulations in different ways that will be described here. We therefore believe that habitat definitions could be relevant, especially in the case of large and widely distributed marine fish populations: species habitat may well bridge the gap between the field observations and the existing theory. Here we first define what the particular characteristics of marine metapopulations are, then define the different types of marine habitats compatible with metapopulations, and consider different case studies.

2. THE METAPOPULATION

To investigate 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 particular spawning and feeding areas, 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 various authors who defined the metapopulations often presented different although complementary series of conditions for a metapopulation to exist (e.g. Smedbol et al. 2002). 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 and 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 and Lima 2002; Kritzer and 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).

3. THE 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 recently when the concept of "potential habitat" (Zwolinski et al. 2010) was defined.

Defining a "standard" habitat is not easy, as fish is able to live in suboptimal areas, prioritizing one factor (e.g. aggregating in areas with abundant preys although hydrological factors are not favourable). When trying to define what is the ideal habitat of a given species one may need to be looking more closely into the environmental conditions under which the population develops best, grows faster and healthier, and produces more abundant and healthy progenies. It is thus utterly important to look into the "habitat" characteristics (and constrains) where early life history stages (particularly larvae and early juveniles) thrive, allowing them to latter on show up as recruitment to the exploited stock.

Fish species such as herrings, shads, capelins and salmons, need a particular substratum (or habitat), and a fairly narrow favourable environmental window, to spawn and successfully produce new broods or recruits. And their stock units are usually distinguished by their spawning sites and season, even if during their juvenile and maturing stages they may be found sharing the same areas or habitats with fish of the same species that have been spawn in other "tangible habitats". Other pelagic fish species, such as *Sardina pilchardus* and other sardines and small pelagics with pelagic eggs, require, to produce successful recruitments, that their eggs, larvae and early juveniles be placed and/or find themselves also in very particular and favorable environment (or habitat), and usually also depend on a fairly narrow favorable environmental window to spawn successfully, and for the spawning to produce new abundant recruits. And it is highly likely that the "habitats" that characterize these early life history stages will be narrower, and sometimes with different and tighter critical requirements, than that of the later juveniles and adult stages.

Recruitment success is the main factor determining fish stock abundance, and stock abundance variability. But there is a very high natural mortality during the (critical period of) early life history stages and, to a great extent, this high natural mortality during such critical period(s) is determined by the occurrence of a relatively narrow window of ideal environmental conditions (including proper balance of prey items and predators). And in most cases, the failure of a few of these "ideal conditions" may cause a recruitment failure. So, from the biological and population dynamics point of view, looking at the habitat of the early life history stages is probably as important, if not more important, than looking at the habitat of the larger, adult fish that show up in the commercial fishery.

The habitat concept has three major practical applications as far as pelagic populations are concerned:

- It allows independent delimitations 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): this is the potential habitat;

- It is potentially 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 2013, doc SC-01-13);

- 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. 2004a; 2004b; 2016).

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 3-D habitat, from which population structure can be inferred.

When considering habitat of fish populations, the first point to note is that many marine fish, and especially the pelagics, present some characteristics that differ strongly from the usual characteristics of terrestrial habitats, and most of the definitions elaborated for terrestrial organisms fail to describe marine habitats. We face here the difficulty pointed out by Pitcher (2001) and Pitcher et al. (2005) who noted that "*Most marine organisms lack the tangible habitat made of plant architecture that we are familiar with in terrestrial animals. (…) the structural habitat concept itself needs extending only a little to encompass oceanographic structures in ecosystems; for example, the great marine populations of fish are bounded by tangible ocean structures*".

The first point is to define what the different characteristics of habitat inside a continuum of fish distribution types can be in such global environment. We will consider this continuum using McCall's basin model (McCall 1990; Bertrand et al. 2008; Hintzen et al. 2014) as an exploratory and 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: in the deepest pit, most conditions for a sub-population to have an autonomous life are fulfilled (figure 1). We categorized four main cases inside this continuum.

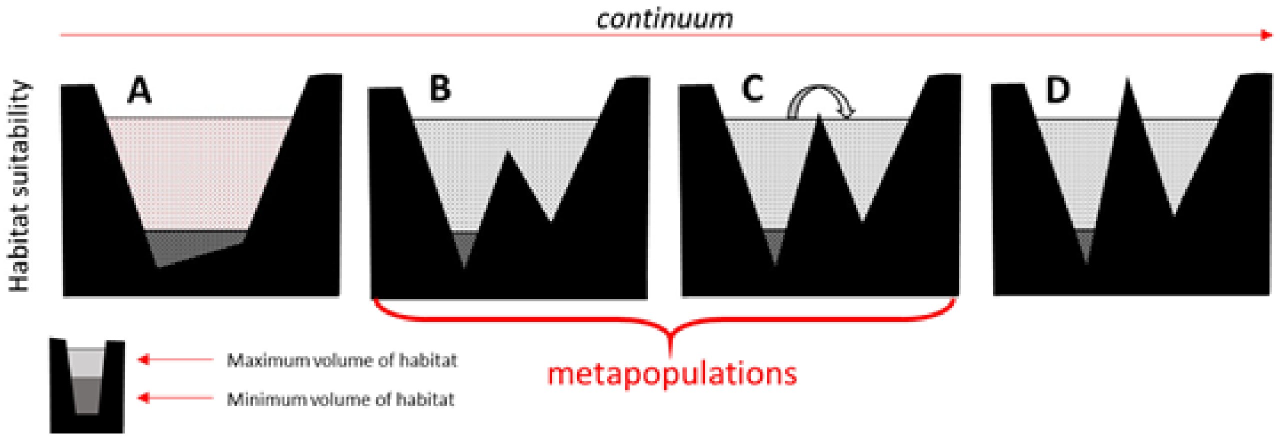

Figure 1. Description of four cases of population behaviour related to environment and habitat adapted from McCall basin model (McCall 1990) where habitat suitability increases with the depth. Favourable habitat is represented in light grey while dark grey represents the most suitable habitat. Grey arrow in case C: possibility of transport of individuals from one pit to the other under particular conditions. A to D: see text in next paragraphs.

Case A. Single population. Only one single pit exists. Fish distribution within its potential 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 pits exist. Secondary pits have a shallower basin than the "source" pit, which remains the only refuge when conditions are worsening; fish in the other pits can disappear. These secondary pits can be recolonized when conditions become favourable encompassing the entire habitat.

Case C. Similar to case B except that the habitats are not connected anymore, e.g. 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 re-colonization from 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 several independent discrete populations that can eventually diverge.

3.1. Two major types of habitat

The fundamental conditions expressed by Levin (1970), i.e. separate populations acting independently during a long period and some exchanges existing between sub-populations, are only compatible with cases B and C which can hence be accepted as metapopulation habitats. 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 wider distribution.

We can further differentiate by applying the definition by Pitcher (2001) between tangible habitats (i.e. geographic) vs. tangible ocean structures (i.e. environmental)

Considering this classification, we can explain the difference between e.g. the herring and the sardine populations: although very close neighbours in terms of taxonomy and evolution, these two species belong to two different groups in population structuring: herring is a species with "tangible habitat" which is limited to bottom areas where benthic eggs can be spawned, while the biology of *Sardina pilchardus* is only depending on environment characteristics (pelagic eggs spawned in favourable environment). Under this criteria, pelagic species such as some Clupeoids (herring, shads, etc.), Salmonids (e.g. Atlantic and Pacific salmons, capelin, etc. (REF)) among others can be separated from other pelagics that are not bounded by a habitat for their spawning.

Therefore, and following Pitcher's discrimination (Pitcher, 2001; Pitcher et al. 2005), the two metapopulation structures applicable to the two different types of habitats can be described as (Figure 2):

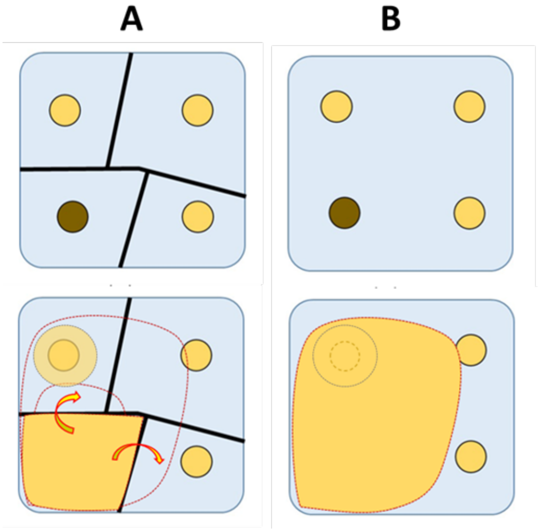

Figure 2. A: Territory-Bounded Habitat (TBH); and B: Environment-Bounded Habitat (EBH) metapopulation conceptual frameworks. The pale blue rectangle represents the largest area that can be occupied by a species

(global distribution area). Territory borders are represented by black lines. We schematize four sub-populations, one of which (the source, below left in each figure) suffers increasing suit environment conditions. Two cases are displayed. Above: the areas (circles) occupied by the four sub populations when suitable environment is the smallest. Below: the largest area occupied by the source sub-population when its suitable environment is expanding (surface surrounded with dotted lines). In the TBH case the suitable habitat cannot extend farther than the territory borders, whatever the surface of the suitable environment; only some individuals can migrate from the source territory to the others (arrows). In the EBH, no geographical limit exists and the suitable habitat extends up to the limits of the suitable environment. It can eventually cover the whole distribution area, letting the source overlapping with the other subpopulations.

3.1.1. 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 1). This category corresponds to Pitcher's "tangible habitat".

3.1.2. The "environment-bounded habitat" (EBH) metapopulation where the only limit of expansion for the habitat is the overall distribution area of the species: its actual surface is limited by the area where favourable conditions of the local environment are found. Connections between local and global scales are achieved by large infrequent 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 scale of cohorts or whole sub-populations (case B, figure 1). This category corresponds to Pitcher's "tangible environment structure".

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 in non-synchronized variations on local biomasses. Asynchrony has been defined as a necessary condition for metapopulation persistence (Hanski 1999). However many pelagic populations, such as Clupeids, Engraulids and Carangids, although usually asynchronous, 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 terrestrial and freshwater 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 1 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 disappear.

4. WHEN DOES A PELAGIC POPULATION BECOME A "PELAGIC METAPOPULATION"?

In the former paragraph we listed the characteristics of a pelagic habitat: variable surface, border limits drawn by environmental factors, no geographical boundaries. We have to go further and define also the pelagic population. Indeed pelagic fish cannot be considered pelagic populations e.g. when their spawning behaviour is driven by an obligatory benthic homing behaviour. For instance, salmons and other anadromous fish which live most of their life in the pelagos but migrate for spawning in precisely delimited territories (Schtickzelle and Quinn 2007) cannot be considered as fully pelagics. A pelagic population may have homing behaviour, but this behaviour should be adaptive: when the usual home is out of reach, fish may spawn in other areas as long as they present favorable environment characteristics: under this definition, herring is not a fully pelagic fish either (McQuinn 1997). Not all the pelagic fish can be considered pelagic populations.

On the basis of this new definitions of pelagic habitats, 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 some or all populations; (iii) recolonization possible. On the contrary asynchrony in local dynamics (4th condition) does not permanently 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 foreign cohort usually generated by the source (Konchina et al. 1996; Corten 2014), transported by large hydrological events or when the boundaries between suitable habitats weaken (e.g. Bertrand et al. 2016; Parada et al., 2017).

- Substantial changes in population abundance due to synchrony between sub-populations are not uncommon, especially during periods of large abundances, but asynchrony is the rule during depleted periods (Gerlotto et al., 2012).

We suggest the following scheme to illustrate our EBH metapopulation hypothesis. Over time, owing to the conjunction of non-linear or stochastic climatic events (Hsieh et al. 2005) and favourable environmental conditions, a species increases substantially its abundance and occupies the majority of the distribution area. This population expansion can last several generations. Such coincidence of particular conditions leading to a demographic explosion is unlikely to be frequent. For instance studies on paleoecology reveal that sardine (*Sardinops sagax*) and South Pacific jack mackerel 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. 2012). During episodes of high abundance, when the environment characteristics make the connections between bounded sub-populations possible (Bertrand et al. 2016) or even allows an overlapping of pelagic habitats, 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 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 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. Usually the episode of very high abundance is followed by an expansion in national or international fishing fleets. When depletion occurs, this potential fishing effort tends to focus on the remaining parts of the population, inducing 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.

4.1. APPLICATION TO TWO CASE STUDIES

Territory-bounded habitats are common in the terrestrial ecosystem, as well as in many aquatic and marine systems (Bay et al. 2008) and is hence already established in the literature.

In the particular case of large marine populations of fish, two cases of what we would describe as TBH metapopulation have been studied in details by McQuinn (1999) on herring, and Schtickzelle and Quinn (2007) on Pacific salmon. Therefore there is no real need to give again another example of TBH metapopulation. On the contrary, the EBH hypothesis has still to be tested on different populations of marine organisms. We selected two cases: one non-exploited semi-sedentary part-time pelagic fish with low abundance, the grey triggerfish (*Balistes capriscus*) in West Africa, and one heavily exploited migratory permanently pelagic fish with high abundance, the South Pacific Jack Mackerel or Chilean Jack Mackerel, CJM (*Trachurus murphyi*). The triggerfish is not fully studied and parts of its biology remain undocumented; but the clear cycle of explosion-deflation and the fact that this species is practically not exploited make it a good example to work on. The CJM is another good example, almost opposite to the triggerfish: its biology is well documented, it is heavily exploited, present in a huge distribution area, it suffered also important phases of explosion-deflation and possibly collapse. Besides, the definition of its population structure is crucial for fisheries management.

4.1.1. The grey triggerfish

Balistes capriscus (Gmelin, 1759) is common all around the intertropical Atlantic Ocean, where it can be observed on both the east and west coasts. This fish is one of the two species of the genus *Balistes* over the West African continental shelf. (Fig. 3), where it reaches a maximal fork length of 45 cm (Caverivière 1991, Gerlotto 2017).

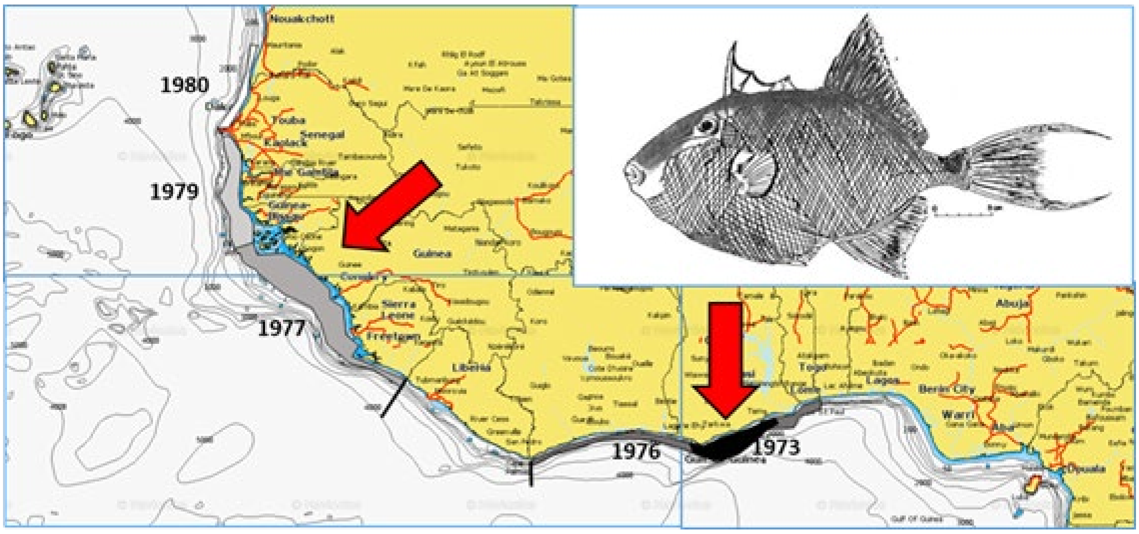

Figure 3. Acoustic surveys displaying the expansion of B. capriscus (above, right: drawing from Opic in Seret, 1981) in West Africa. Surfaces from black (first expansion area) to white (last expansion area): surveys performed in the 1970s by ORSTOM and associated Institutes in West Africa showing the expansion. No survey was performed off Liberia. Red arrows: two abundant sub-populations observed during surveys performed in the 1980s by NORAD (com-plete survey from Mauretania to Nigeria, including Liberia: Strømme et al. 1982).

Biological patterns

A rather complete observation of reproduction cycles and biology was published by Kelly-Stormer et al. (2017) on the grey triggerfish in western Atlantic waters. There was no such study performed in West African waters, but the elements collected in the period of high abundance of this fish in Africa are not contradictory with this work. In synthesis, the grey triggerfish spawns from April to December in West Africa (Caverivière 1982), compared to the period April-September in the Gulf of Mexico (Kelly-Stormer et al. 2017). The female presents a total fecundity of several hundreds of thousands of eggs, emitted by around 10 000 per spawning and a female may spawn up to 10 times during the spawning season (Kelly-Stormer et al. 2017). The overall reproductive patterns are rather similar to most of the tropical fish, with two major differences. (1) If ovaries are not different from the vast majority of ovaries of marine fish, male gonads are quite different: Kelly-Stormer et al. (2017) describes them as “*testes, a spermatic duct, and accessory glands [which] are used to store spermatozoa before spawning*”. Caverivière (1982) noted a similar pattern for the West-African grey triggerfish. (2) Although partly pelagic during the year, the fish displays a territorial behaviour during the reproduction season, when the male builds a nest on the ground to let the female spawning while it expels all the competitors and predators (Garnaud 1960; Simmons and Szedlmayer 2012). Simmons and Szedlmayer (2012) observed that nest substrate is carefully selected, consisting mostly of sand (fine to medium) followed by coarse shell and very fine sand and silt.

Feeding. Usually juvenile may occupy the water column, feeding on planktonic organisms (eggs, passive preys, etc.: Ingram 2001; Wells and Rooker 2004; Casazza and Ross 2008), then become more linked to the benthic domain, (Kelly-Stormer et al. 2017), sedentary, feeding on urchins, molluscs, etc. (Frazer et al. 1991; Vose and Nelson 1994; Blitch 2000).

Population patterns

The grey triggerfish is usually not exploited along the West African coast, except by some artisanal fisheries in Ghana. During the period 1972- 1974, parallel to the collapse of *Sardinella aurita* in Ghana (Ansa-Emmin and Marcille 1976), the populations of grey triggerfish increased substantially, expanding eventually to the whole West African shelf from Nigeria to Senegal and was even observed in Mauretania (Fig. 3).

The highest abundance evaluated during acoustic surveys on the West African shelf reached around one million tonnes, and the Ghanaian fishery (the only one which exploited this biomass) captured up to 18,000 tonnes (fig. 4) (Caverivière et al. 1980; Binet et al. 1991).

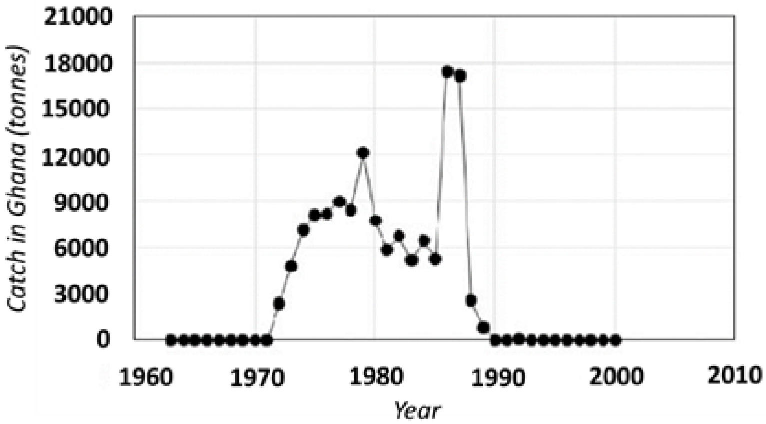

Figure 4. Catch of Balistes capriscus in the Ghanaian fishery, period 1965-2000 (from Gerlotto, 2017)

This expansion, beginning off Ghana, took around 5 to 6 years and involved several generations of fish, as demonstrated by the capture of tons of juvenile *B. capriscus* in Guinea in 1977 (Marchal et al. 1979; 1980), too young to be born elsewhere. Besides, we observed changes in the species behaviour. Contrarily to the standard behaviour detailed above, during the high abundance period, even when becoming adult fish remained pelagic, gregarious, plankton-feeder, living in big dense schools (Robertson 1976). During the 1980s, this high abundance distribution seemed to split into two major sub-populations, as observed during NORAD surveys, one south of Ghana-Ivory coast and one off Guinea (Strømme et al. 1982). As no acoustic survey was performed off Liberia and Sierra Leone before the early 1980s, we cannot know whether the expansion of the Guinean sub-population was triggered by the Ghanaian one or if both were synchronous. Then the stocks dropped off and although not overexploited and even not exploited at all except in Ghana, the triggerfish abundance went back to its original value, i.e. sporadic distribution of a few individuals all along the shelf (fig. 3, 4).

Habitat

B. capriscus tolerates high changes in hydrological characteristics e.g. temperature (from 17°C to more than 28°C) and salinity (from 35%0 to less than 33%0). The species is scattered all over the shelf, from Senegal to Gabon, and exploratory fisheries from the Guinean Trawling Survey during the 1960s (Williams et al. 1968) gave an average density of a few individuals per taw, the maximum measured being slightly below 100 kg in one hour trawling. As noted in the former paragraph, *B. capriscus* depends on the substrate for its reproduction, and requires sandy bottoms. Apart for this period, the fish can be found on other substrates, e.g. muddy or rocky, thanks to its large spectrum of alimentation sources, and even in the pelagos, as happens permanently for other species of the family, e.g. the ocean triggerfish *Canthidermis sufflamen:* Salvetat et al., 2020*)*. Indeed the fish anatomy is principally adapted to feeding on hard passive preys e.g. molluscs and echinoderms; but other aliments have been found in their stomachs, from algae to pelagic preys (mostly passive: eggs, small crustaceans, probably gelatinous organisms) and even Euphausids and Myctophids (Caverivière 1982; 1991; Aggrey-Fynn 2008). In synthesis, the grey triggerfish habitat is versatile, except during the reproduction phase where a particular type of bottom substrate is needed. We have no information on a possible homing related to limited and located bottom spawning areas as in the case of herring, but it seems unlikely that this bottom habitat might produce any strict homing (Thorrold, et al. 2001) considering the large scattered distribution of adults all over the distribution area and the connectivity between favourable spawning areas.

Similar to EBH species e.g. sardine, the spawning is not limited to a given geographical territory, but to a given type of substrate conditions that can be found all along the distribution area. During the period of high abundance, we could see that the fish progressively invaded the totality of the potential distribution area. Then when depleting, it went back to its usually scattered type of distribution. Following these observations, Gerlotto (2017) concluded that triggerfish is organised into an EBH metapopulation. We may submit a hypothesis explaining also why the depletion was as fast as the explosion, despite the lack of fishing pressure and the small number of predators (Marchal et al. 1979; 1980). *B. capriscus* needs to build a nest to spawn in a very well defined type of substrate; this means that the maximum fecundity of this species does not depend only on the number of adults, but also on the area where nests can be built. Besides, such a dramatic change in abundance surely implies that self-organization patterns arise, which change the fish behaviour. This could also answer a question not resolved in the last 1970s by Caverivière et al. (1991) concerning the peculiar reproductive biology of this fish. Indeed, Marchal et al. (1979) found in the samples of the catches in Guinea in 1977 the complete series of maturation stages for females, ending with fully mature ovaries, but very few mature males. We may hypothesize that the complete cycle of spermatozoid maturation is triggered by the behavioural process of building the nest. Then, as long as the fish remains pelagic, such maturation is not possible. This hypothesis would reinforce the idea that the maximum fecundity of the stock is not related to the (variable) number of individuals but to the (unvariable) space available for building nests.

***Balistes capriscus* and metapopulations**

The case of *B. capriscus* is interesting for our study, as it enlightens several points:

- This species is organized into multiple sub-populations all along the Gulf of Guinea presenting non-migrating low abundance stocks.
- The different sub-populations are independent due to the large distances between them and the low migratory behaviour of the species.
- A stochastic non-cyclic event may trigger a huge change in the abundance, which changes the fish biology and behaviour. During this expansion period, all the sub-population gather and follow a synchronous dynamics.
- Such expansion and important biomass is not stable, considering that behavioural changes induces a decrease in the proportion of mature adults.

We face indeed a clear example of EBH metapopulation as it fulfils the specifications for this type of structure: no geographic territory, variability of the distribution area, huge changes in abundance; if the average adult population is demersal and sedentary, the juvenile phase as well as the abundant adult population are pelagic and susceptible to colonize the distribution area. During these high abundance periods all the sub-populations are gathered into a single “superpopulation” (with single genotype) and the whole of the distribution area is occupied, allowing the recovery of lost niches.

4.1.2. The Chilean Jack Mackerel

The Chilean Jack Mackerel (CJM) *Trachurus murphyi* (Nichols, 1920) is one of the 16 species of genus *Trachurus* (www.fishbase.org). It 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. 1993), covering most of the subtropical area of the Southern Pacific from Chilean Patagonia on east (Nakamura et al. 1986), to New Zealand (Nosov and Kalchugin 1990; Paulin et al. 1989) and Australia (OBIS: www.fishbase.org) on west (Figure 5). *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). 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).

The CJM 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 1980s, landings showed a substantial drop since the late 1990s, some western parts of the population being considered as extinct (Gretchina 2008). In the recent years catches remained below 0.5 million tonnes, although indices of recovery have been observed recently (SPRFMO, 2017). Figure 5.

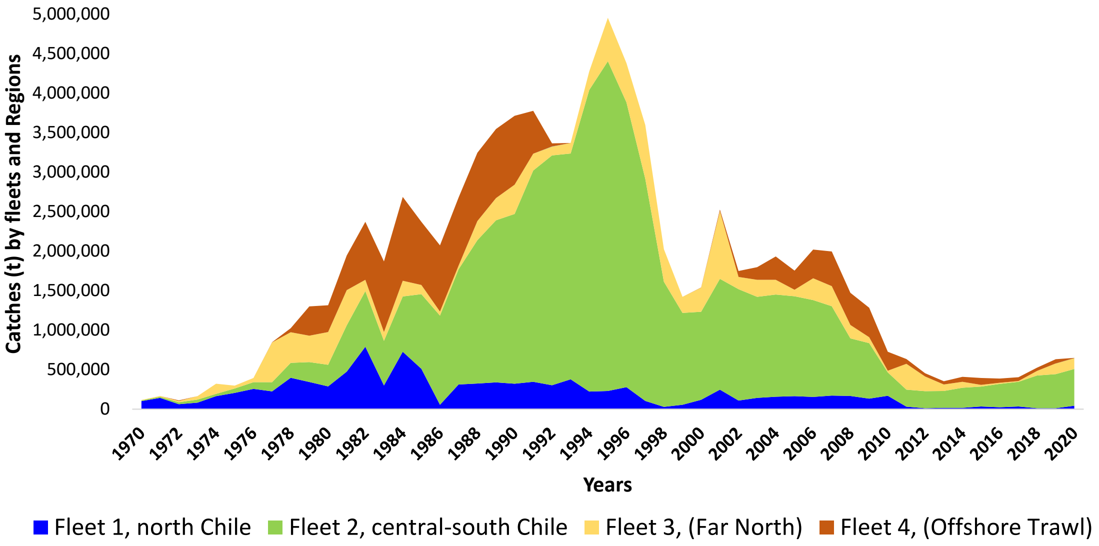

Figure 5. Overall catch data for the Chilean jack mackerel *Trachurus murphyi*, 1970-2020, also dispatched by different fleets, in tonnes. Fishing gear: purse seine in Chile and Peru; pelagic trawl in others cases. Data from www.sprfmo.int

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. 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 6).

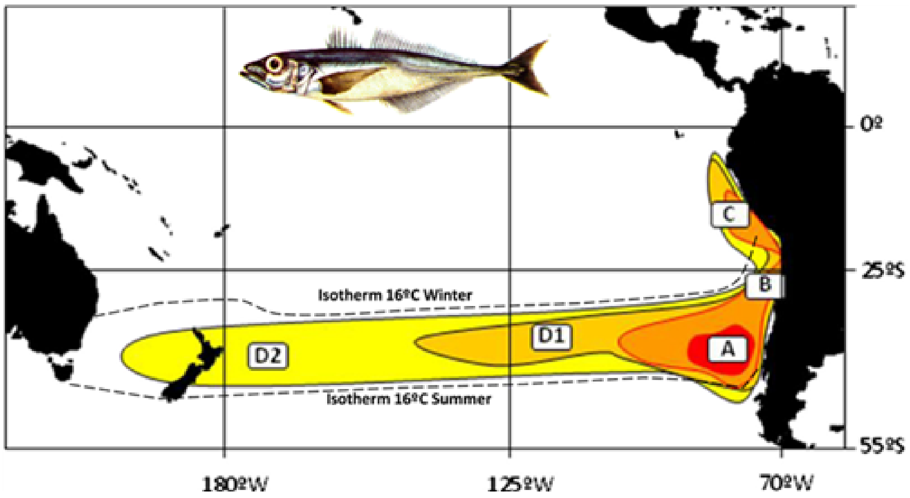

Figure 6. The CJM belt in the South Pacific Ocean, limited by the north (winter) and south (summer) extensions of the 16° isotherm presented in dashed lines. On the same figure are represented the main distribution zone depending of the population abundance, from red (lowest abundance, population limited to the source area off centre-south Chile) to yellow (highest abundance, fish encountered all over the "jack mackerel belt"). The different sub-polulation areas according to SPRFMO are A: centre-south Chile; B: North Chile; C: Peru; D1 : middle Pacific; D2: western Pacific. The largest spawning area is located in region A, followed by C . A temporary spawning area may be found in D2 during periods of high abundance.

Biological patterns

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). Eggs and larvae are pelagic.

There are three major spawning areas: centre-south Chile, Peruvian waters and, less important, the high seas areas (figure 3). 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 2008; 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 off Peru is the coastal sector (outside of the continental shelf) between 14º00'S and 18º30'S (Santander and 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 (Ayón and Correa 2013)

Offshore, Dejnik and Nevinskyi (1994) and Dejnik et al. (1994) studied the ichthyoplankton inside the North and South subdivisions (separated by latitude 15ºS) of the Southern Pacific Ocean. Small concentrations of 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.

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 and Saa 1978; Castillo and Arizaga 1987;

Nosov and Kalguchin 1990; Arcos and Gretchina 1994; Cubillos and Arancibia 1995; Dioses 2013a). Results show a rather wide variety of growth curves attributed mostly to the areas where the studies were performed.

Csirke (2013) notes that in the northern range of its 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. We present in table 1 a synthesis of the results from various authors.

Table 1. Growth curve parameters for studies on CJM in Chile and in Peru (from Diaz, 2013)

Growth curve parameters for studies on CJM in Chile and in Peru	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 and 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 using the equation TL = 0.514+ 1.091FL (Cubillos and Arancibia, 1995)

Population patterns

The bulk of CJM population resides in the Humboldt Current System which is one of the most impacted by climate variability evidenced by the El Niño Southern Oscillations (ENSO) (e.g. Chavez et al. 2008; Ayón et al. 2011; Bertrand et al. 2011). These high variations may induce strong changes in abundance and spatial distribution of fish populations. 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.

Spatial distribution 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).

According to the data of the soviet fishery (1977-1990) and the more recent Russian fishery, during its period of highest abundance the CJM southern extension is limited by the subantarctic cold waters of the Southern Pacific Ocean: depending on the year, the fish can be observed up to south of 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. The author considered that CJM has now completely disappeared from the New Zealand waters.

Although a limited number of studies on migrations using tagging have been published (e.g. Torres 1986), the knowledge on migrations comes from 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.

Besides migrations *sensu stricto*, CJM develops phases of expansion and shrinking depending on the abundance and the hydrology. 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 (Vásquez et al. 2015).

Gretchina et al. (2013) synthesized these observations in their 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 (Dioses 2013b; Gerlotto and Dioses 2013). Bertrand et al. (2016) showed that the 'door' connecting the Chilean and Peruvian favorable areas was likely closed after 2000 when the OMZ became shallower.

Genetic structure of CJM population was studied through four experiments (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 from Chile as well as 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.

From these series of results, plus other studies concerning otholith biogeochemistry (Ashford et al., 2011) , parasites (Avdeyev 1992: MacKenzie. and Longshaw 1995; Brown and Colgan 1986; Cox 1990; Fréon et al. 2005), reproductive distribution, morphological and parasite information (Duran and Oliva 1983; Oliva 1999; Romero and Kuroki 1985; Evseenko 1987a, b; Storozhuk et al. 1987; Kalchugin 1992; Adveyev 1992; George-Nascimento 2000), etc., Glubokov (2008) showed evidence for a population in the central south Pacific Ocean. Ashford et al (2011) found that Chilean jack mackerel caught off Peru may come from a separate self-recruiting population (Serra 1991).

Studies on demographic structures were 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.

i. 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.

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

iii. 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.

iv. 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.

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 that we synthesize below:

(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.

(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. This cohort is the most abundant 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).

(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.

Corten and Janusz (2011), Corten (2014) observed an abundant year class, presumably born in 2008, which appeared in the CSCF 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 they belong 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 event 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.

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. Nevertheless defining a pelagic habitat has always been a challenge, as stated by Smedbol et al. (2002) who stress the difficulty to "to identify suitable habitat for populations occupying demersal and pelagic environments". Recently a series of analyses have been devoted to studying the CJM habitat (Bertrand et al. 2016), and allowed getting a description of its population structure.

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. We may cite particularly two of them which are remarkably strong in the SE Pacific.

- 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). These ENSO affect also the egg and larvae distribution, as stated by Barbieri et al (2004) who showed a strong difference of this index between 1998 (el Niño), the year 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., 2006; 2016) since this fish is unable to live in waters with oxygen concentrations below 1 ml.l, 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} (Bertrand et al., 2006). Besides, the CJM requires a vertical range of oxygenated waters greater than 30 m to live in (Bertrand et al. 2016). As far as salinity is concerned, the range of tolerance of CJM remains much above the maximum variation in the distribution area]33-36[(Bertrand et al. 2004a, 2006).

The environment productivity is another key parameter. *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} (Bertrand et al. 2016).

We present in the table 2 a synthesis of the limits and preferenda of the main hydrological parameters observed and defined for the CJM.

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	-	-

A key publication was produced by Bertrand et al. (2016) who present a model of habitat for the CJM defined by the dynamics of its horizontal and vertical distribution.

- Horizontal distribution. This model is based on interactions between SST and CHL-a for the horizontal distribution (Chaigneau et al. 2013). It 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. 7): 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.

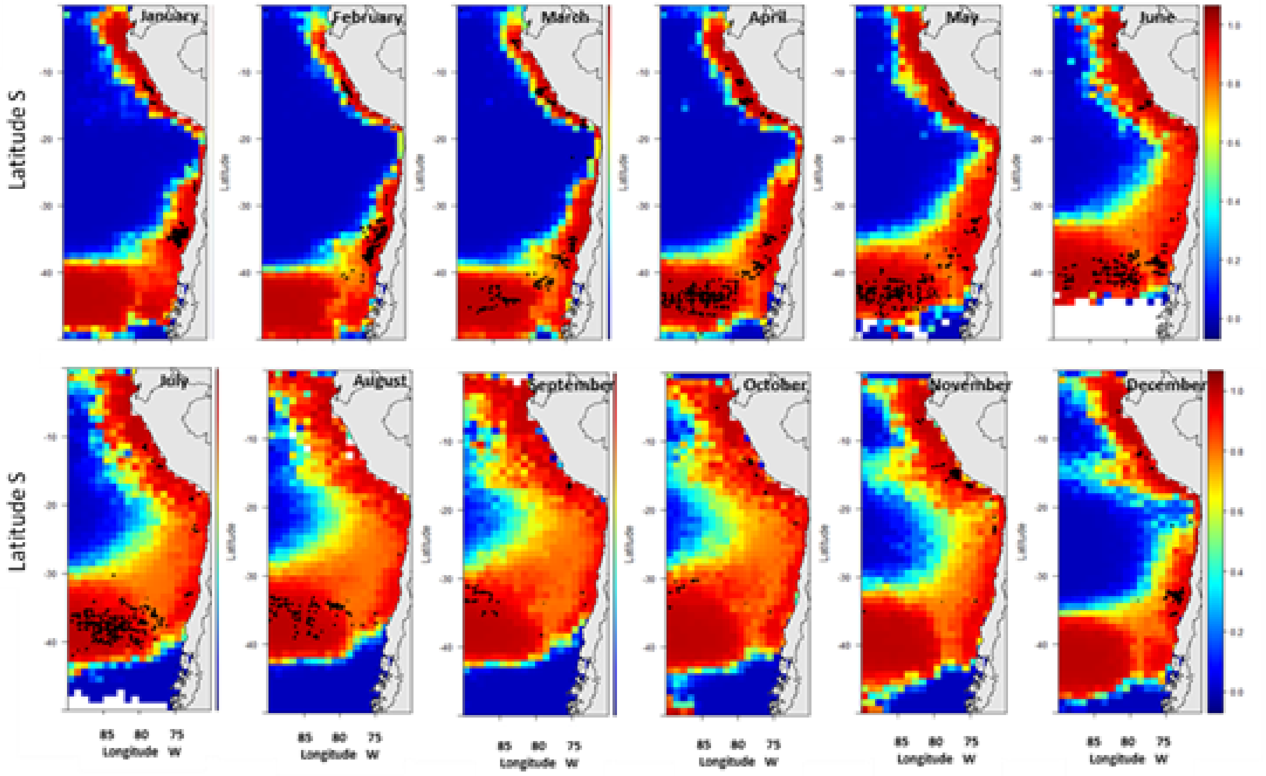

Figure 7. Zoom on the Humboldt Current system of the climatological jack mackerel habitat probability maps from January to December. High probabilities in red; low probabilities in blue. Catch observations are superimposed as black dots (from Bertrand et al. 2016).

– 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; and vertical movements of the water masses (Chaigneau et al.2011).

Using these criteria, the authors built a 3D model of CJM habitat horizontally and vertically limited by temperature, productivity and oxygen (fig. 8). 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. 8), when the oxycline is shallow. This period corresponds to the spawning period for CJM (see above). 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.

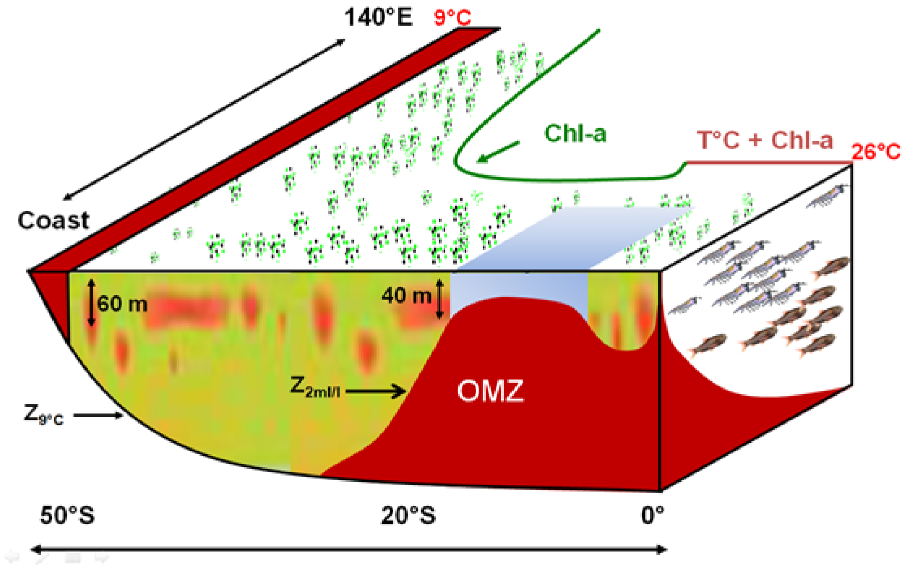

Figure 8. 3D conceptual model of the Jack mackerel habitat in the South Pacific. The habitat is limited by temperature (9ºC), productivity (Chl-a), concentration (2ml/l) and depth (40m) of the dissolved oxygen. Red surfaces correspond to unfavourable habitat delimited in the south by the 9ºC SST isoline 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).

Jack mackerel and metapopulation

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) : single population (scenario 1); two discrete populations off Peru and Chile (scenario 2); two discrete populations, coastal and high sea (scenario 3); network of many discrete populations (scenario 4); one "superpopulation" (= patchy population; scenario 5); one metapopulation (Scenario 6).

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 above for the six population structure scenarios.

Table 3. List of the characteristics collected in the literature and their compatibility with the six different structure types[1]. 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	

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[1] The posible scenarios for CJM are: single population (scenario 1); two discrete populations off Peru and Chile (scenario 2); two discrete populations, coastal and high sea (scenario 3); network of many discrete populations (scenario 4); one "superpopulation" (= patchy population; scenario 5); one metapopulation (Scenario 6).

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 coastal habitat during part of the year limits extensive mixing.	2, 4, 6	3	1
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 patchy suitable habitats	5		
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	

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 population and multiple discrete population structures, seem unlikely since 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. 2016).

Two main patches of favourable habitat structure the CJM population: one centred in Peruvian waters and the other one in centre-south Chile and its extension offshore up to 80ºW (Bertrand et al. 2016). Figure 7. These two areas are favourable 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 unfavourable climatic and hydrographic conditions, the suitable northern habitat may disappear to a large extend, resulting in reduced CJM biomass in the area (Gutierrez et al. 2012). In the centre-south, climatic and hydrographic conditions are more stable; suitable habitat spans over a wider area and has an opening to the high seas, which provides a refuge in case of unfavourable 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 above. 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. The existing threshold between the north and south populations could explain 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 contradictory with the usual homing behaviour (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. Therefore they have to find a new suitable spawning area, which results afterward in changing the migration route of the next cohorts through learning and entrainment (Petitgas et al. 2010).

In conclusion the population characteristics of the CJM are typical to an EBH metapopulation. The CJM overall population follows the same cycle as was observed on the triggerfish: huge distribution area limited by environmental factors exclusively, with independent local dynamics during long periods, synchronous changes in biology during the period of high abundance, existence of separated spawning grounds that show spatial variability related to environment, existence of mechanisms that “close” or “open” connections between the sub-populations, etc. The discrepancies observed by Gerlotto et al (2012), Hintzen et al (2015) and Bertrand et al. (2016) were exclusively due to the inapplicability of conventional metapopulation definition for fish distributed in Environment Bounded Habitats.

5. CONCLUSIONS

These two examples of large pelagic (or semi-pelagic) populations, distributed over wide oceanic areas, demonstrate that the metapopulation concept can be adapted to them. Independently from the case of these two species, we believe that the definition of “Territory-bounded-habitat” and “Environment-bounded-habitat” brings new perspectives in the definition of habitats, which is an important goal for SPRFMO (table 4). This is particularly important for pelagic populations as one major limit when studying moving populations was the lack of definition. When McQuinn (1997) showed that a widely distributed pelagic population like the Atlantic herring, was not entirely comparable to a pelagic population in terms of habitat, as the fish was as linked to its bottom spawning ground as the salmon to its river, he was the first to change dramatically the perspective. Nevertheless this observation was not sufficient, as the difficulties to define the type of population organization of the Chilean Jack mackerel stated clearly. Separating the habitat characteristics into TBH and EBH seems to us a way to resolver to these uncertainties. It answers also (positively) to the question whether the metapopulation concept could apply to pelagic population.

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	Periodic

We have now a framework at our disposal for defining a habitat and the population structure inside this habitat. Applied to the Chilean Jack mackerel, the structuration of this fish into a metapopulation inside an EBH seems quite likely: in this case the global habitat is split into two major “pelagic pits” (and possibly a few minor ones), i.e. centre-south Chile and offshore Peru, separated enough for allowing subpopulation to develop a “Harden-Jones’ migration triangle” where areas for feeding, growing and spawning can be encountered (Harden-Jones, 1968), and being autonomous; but with sporadic exchanges of cohorts thanks to climatic or oceanographic events, as evidenced when observing the CJM cohort migrations.

Separating the habitat characteristics into TBH and EBH seems to us a way to resolve these uncertainties. It answers also (positively) to the question whether the metapopulation concept could apply to pelagic population.

5.1. Summary

Among the different cases of population structures, metapopulation is particularly interesting as it allows adaptation to changing conditions and recovering lost niches, inducing a strong resilience to regime shifts. Researches on various types of animal species, terrestrial as well as aquatic, that have been developed since the first definition of metapopulation by Levin (1969) showed that such organization seems to be widely observed, and could be one of the most common types of population structure (Hanski, 1999). The question of whether the large populations of pelagic fish, such as Clupeidae, Engraulidae, Carangidae, Thunnidae etc., can be organized in metapopulation or not has been studied since the 1990s, but remained unanswered in a large part and is still controversial, due to the difficulty to apply to these large and moving populations the conventional definitions of metapopulation, originally conceived on small terrestrial sedentary groups and mostly focused on wildlife conservation (McCullough 1996).

This question of population organization is not trivial, as these pelagic fish species often represent the biggest catches in the world, FAO evaluating to more than 40 % the contribution of pelagics to the world catch (FAO, 2011). Such importance of pelagic fisheries requires sound stock assessment models be developed for delivering management advices. But models are only efficient if the population structure is well understood.

This opened the more general question of whether a pelagic fish population could be considered as a metapopulation. Considering the different characteristics of pelagic populations that appear contradictory with Levin's definition, we tried to evaluate if the concept of pelagic metapopulation makes sense and how it could be defined. We first observed that there is a continuum in population organization schemes, from one single population to several discrete populations, with two cases which structures were clearly metapopulations: the "territory-bounded-habitat" (TBH) metapopulation, where each sub-population is confined in a "territory" surrounded by geographical borders that cannot be currently crossed, and the "environment-bounded-habitat" (EBH) metapopulation where the sub-populations live in moving –although currently separated- areas where the local environment brings favourable conditions. A few conditions typical to TBH metapopulations cannot be applied on EBH metapopulations, and especially the permanent asynchrony in life histories of the populations. Indeed, from time to time an EBH metapopulation increases dramatically its biomass when the conditions of the global environment make the different local environments evolving synchronously. The history of most of the pelagic populations observed through paleoceanography studies shows that these species suffer successively low (depleted) abundances during long periods (up to centuries) separated by short periods (a few years or decades) of very high abundance. Therefore we define a pelagic metapopulation as an EBH-metapopulation, where most of the necessary conditions for metapopulation existence are fulfilled: discrete-breeding populations; risk of extinction for all populations; recolonization possible; differences in scales between local and regional effects of the environment; existence of source-sink populations; autonomy of sub-populations; and limited genetic exchanges. Only asynchrony in local dynamics does not permanently apply. Nevertheless this episodic phase of synchrony does not forbid the different sub-populations to develop autonomous lives during long periods, allowing them to adapt to changes in the environmental conditions. Exchanges of genetic material is performed conventionally through transport of individuals or exchanges by straying, learning and entrainment; but also through habitat overlap, permanent integration of a cohort transported by large hydrological events or when the environmental boundaries between suitable habitats weaken.

Some effects of this EBH metapopulation characteristics on evolution and on fisheries management are presented. We conclude that pelagic metapopulations do exist and represent an efficient evolutionary tool that makes local adaptations to changing environmental conditions possible, adaptations that are eventually shared by the whole species during the short episodes of synchronous life when all the sub-populations are connected.

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