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Critical appraisal of research approaches to inform evidence of connectivity of *Trachurus murphyi* – a systematic review of 11 topics

Connectivity Task Team

Report to the 12th South Pacific Regional Fisheries Management Organisation Scientific Committee meeting by the Chilean jack mackerel Connectivity Task Group

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Executive summary

A systematic review on 11 key topics was undertaken to critically appraise sources of information that may be useful in evidencing population structure and connectivity of jack mackerel. Each topic was reviewed in a standardized approach and provided the background and rationale for the use of the approaches / field of study; a description and critical appraisal of methods described in the international literature; explored whether identified methods have previously been applied to jack mackerel or other small pelagic (and their effectiveness); and discussed the feasibility / limitations of these methods within the context of the High Seas of the South Pacific.

A workshop was held in Lima, Peru, on 26 – 27th September 2024, attended by more than 35 delegates from 5 SPRFMO member delegations. The workshop provided an opportunity to review the results of the systematic review and undertake a prioritization exercise to identify those topics which, based on strength of evidence and logistical considerations, would be the most relevant topics for evidencing connectivity of jack mackerel.

Overlaps in approaches and techniques for data collection to inform the topics were identified, highlighting opportunities for optimizing sampling efforts and data collection. Participants of the workshop agreed that all 11 topics that were systematically reviewed would be relevant for evidencing connectivity of jack mackerel in the South Pacific, however, prioritization of topics based on strength of evidence and logistical considerations, identified 4 topics as priority areas to focus immediate future efforts. Specifically: Genetics, Tagging methods, Early stages & Reproduction.

Should funding become available, the JM connectivity TG proposes that a sampling and research programme, aiming to collect the data required to inform the 4 high priority topics be developed. Recommendations and considerations for these next steps are provided.

1 Introduction

The complexity of the Chilean jack mackerel (*Trachurus murphyi* - hereafter referred to as jack mackerel), population structure and connectivity, leads to a source of uncertainty for its fisheries assessment and management, e.g., where several hypotheses have been proposed in the past (SPRFMO 2008). In order to further explore different stock structure hypotheses, the Jack Mackerel Connectivity Task Group (JM Connectivity TG - composed of delegates from Chile, Peru and the EU) has carried out a systematic review on several key topics in order to compile an overview of existing knowledge to identify the sources of information that may be useful in evidencing population structure and connectivity of jack mackerel. Specifically, 13 topics of relevance were identified by the JM Connectivity TG for inclusion in the systematic review (SC11-JM02). These topics were then systematically reviewed, and a concise summary provided, covering: the background and rationale for the use of the approaches / field of study; a description and critical appraisal of methods described in the international literature; whether these methods have previously been applied to jack mackerel or other small pelagic (and their effectiveness); and the feasibility / limitations of these methods within the proposed multidisciplinary study. The results of these systematic reviews are presented in section 4, noting that two topics were merged based on high overlap in subject areas (resource condition was merged with habitat and reproduction) (Table 1). In addition, the topic 'accompanying fauna' was not reviewed because following discussion by the JM connectivity TG, it was only considered a marginally informative topic for evidencing connectivity of jack mackerel in the context of SPRFMO.

The aim of critically appraising these different topics was to identify and prioritize those approaches which may be most effective for evidencing jack mackerel connectivity. Subsequently, the identified approaches could be integrated into a sampling program should funding become available.

Table 1. Identified topics of relevance for inclusion in the desk study (from SC11-JM02).

Topics	Main goals
Age and growth	Determination of age and growth in juveniles and adults
Early stages	Age and growth evaluation of larval stages and/or early juveniles
Fisheries dynamics	Historical trends in spatio-temporal fishing indicators (e.g. catch, yield, size/age structure)
Genetics	Determination of the structure and the spatial and temporal population genetic variability
Geometric morphometry	Characterization and comparison of the morphometry of jack mackerel individuals and otoliths from different areas
Habitat	Habitat characterization at different stages (in conjunction with data from early-stage zones, and associated with oceanographic characteristics, e.g., Species Distribution Modelling of JM in collaboration with the Habitat Monitoring WG).
Microchemistry	Trace elements incorporated into otolith growth may inform migration patterns
Parasitology	Comparative evaluation of the parasitic fauna between areas and/or population units
Reproduction	Evaluation of reproductive aspects and the spatio-temporal variation.
Tagging methods	Review and evaluation of tagging methods (e.g., spaghetti tags, pop-up tags) to provide additional information on fish movements and migration.
Trophic ecology	Evaluation of the spatio-temporal variability of diets

2 Approach

Key topics were identified through several JM Connectivity TG meetings and were presented in SPRFMO document SC11-JM02. The SPRFMO Scientific Committee agreed on the appropriateness of these topics for exploring jack mackerel connectivity at SC11.

Subsequently, an online workshop (workshop 1) was organized 18th July 2024 attended by 41 SPRFMO SC delegates from a range of delegations (Chile, Peru, Korea, EU, United States, Ecuador, Panama, and observers) where the approach for the systematic review was agreed upon, and delegates volunteered to contribute to writing the systematic review for each of the topics. Peruvian and Chilean delegates provided the majority contribution and both delegations contributed to all topics.

Each topic was systematically reviewed in a standardized approach which was discussed and agreed upon at workshop 1. Briefly this consisted in a standardized and replicable approach to searching the literature where:

- Google Scholar was used to search (noting down search words used) international literature, government and non-governmental reports relevant to the topic. The review had a primary focus on peer-reviewed literature but could be supplemented by grey literature.
- Each relevant paper that was cited in the review was saved in a google drive that was available to all JM Connectivity TG members.
- Metadata for references were compiled in a shared spreadsheet (e.g., author names, article title, year, DOI, etc.).

Assigned members (see authors and affiliations in Sections 4.1 - 4.11) from all delegations worked collaboratively in each topic section to develop a review which covered sections describing:

- The background and rationale for the use of the approaches / field of study
- A description and critical appraisal of methods described in the national and international literature
- Whether these methods have previously been applied to jack mackerel or other small pelagic (and their effectiveness)
- The feasibility / limitations of these methods within the SPRFMO context.

Where there were diverging views between authors, each point of view / statement of fact, was backed by references (compiled in shared document & folder) and further discussed in a subsequent workshop (Pre-SC workshop on JM Connectivity).

The pre-SC workshop on JM Connectivity was held in Lima, Peru, on 26 – 27th September 2024, with the majority of participants in person and a few joining online via Zoom. The first day of this workshop was an opportunity for authors of each topic to present key findings from their systematic reviews, identify gaps in knowledge and for questions and discussion on each topic. The second day was an opportunity to further explore gaps and discuss approaches followed by a prioritization exercise to identify those topics which, based on strength of evidence and logistical considerations, would be the most relevant topics for evidencing connectivity of jack mackerel in the South Pacific and which could be applied within a JM connectivity sampling and research program should funding become available.

3 Outcomes and next steps

Overlap in approaches

Overlaps in approaches and techniques for data collection to inform the topics were identified highlighting opportunities for optimizing sampling efforts and data collection (see Section 4.1 - 4.8 for further details). Among them, otolith collection was relevant to several topics, including Age and growth, Morphological geometry, and Otolith microchemistry. In addition, it was identified that sampling of larvae, juveniles and adults would be required for several topics, for example Fisheries dynamics and Habitat (use). Genetics was considered to provide one of the highest weights of evidence and was also identified as useful for Geometric morphometry, Trophic ecology, Age and growth, Otolith microchemistry, Parasitology, Reproduction, and Early stages.

Synergies and overlaps in approaches between topics can be useful to consider when planning subsequent sampling and research programmes. Noting that a sampling programme aiming to cover all 11 topics would likely be logistically unfeasible. Therefore, a prioritization approach was undertaken to identify those topics most relevant to undertake as part of a research programme in the first instance.

Prioritization of topics

The pre-SC12 workshop on jack mackerel connectivity concluded that all 11 topics systematically reviewed would be relevant for evidencing connectivity of jack mackerel in the South Pacific. However, a prioritization exercise was undertaken to help identify those topics that could be most informative in providing evidence of jack mackerel connectivity in addition to considering their logistical feasibility. This was undertaken in a three-step process:

1. Following a summary of the systematic reviews of each topic, and subsequent discussions, on the first day of the pre-SC12 workshop on jack mackerel connectivity, workshop participants voted on whether they considered the topic could provide higher, moderate, or lower strength of evidence of jack mackerel connectivity. This semi-quantitative approach did not consider interactions or comparisons with other topics and was simply used as an initial starting point for further discussion.
2. The number of votes for each topic from step 1 was used to provide a relative ranking of strength of evidence of each topic for informing jack mackerel connectivity. The relative ranking of each topic to others was discussed by participants as part of an interactive workshopping process. Following discussions, it was felt that topics fit into 3 broad categories: topics which provide lower, moderate and higher strength of evidence for informing jack mackerel connectivity (x - axis of Figure 1)

3. Finally, logistical considerations for each topic were discussed. Based on common criteria and information presented across topics in the sections ‘Applicability to jack mackerel or other small pelagic’ and ‘Feasibility and/or limitations of the approach’ of the systematic review, several criteria were identified which were used to broadly assess logistical feasibility. Experts participating in the workshop were asked to discuss in small groups whether, each topic could evidence jack mackerel connectivity considering whether:

    a. Fisheries dependent data (cheaper) vs fisheries independent data (more expensive) was required?

    b. Historical data only could be used? Yes (cheaper) vs No (more expensive)

    c. Samples could be obtained on a vessel (quick / cheap) vs samples that required removing / transporting (slower / more expensive)

    d. Required a high number of samples (e.g., thousands) vs low number of samples (e.g., tens – hundreds)?

    e. The cost of processing each sample was considered low (cheaper) vs high (more expensive)?

    Scoring of logistical ease was undertaken for each topic, where a score of 1 was allocated to answers indicating cheaper / quicker options and 0 for more expensive / time consuming answers. Where there was no clear-cut answer to the questions a score of 0.5 was allocated; for example, a topic that requires both fisheries dependent and fisheries independent data in order to evidence connectivity of jack mackerel. Participants of the pre-SC12 workshop agreed that the scoring, although somewhat subjective, provided an approximation and comparative view of the logistical ease of each topic (Figure 1).

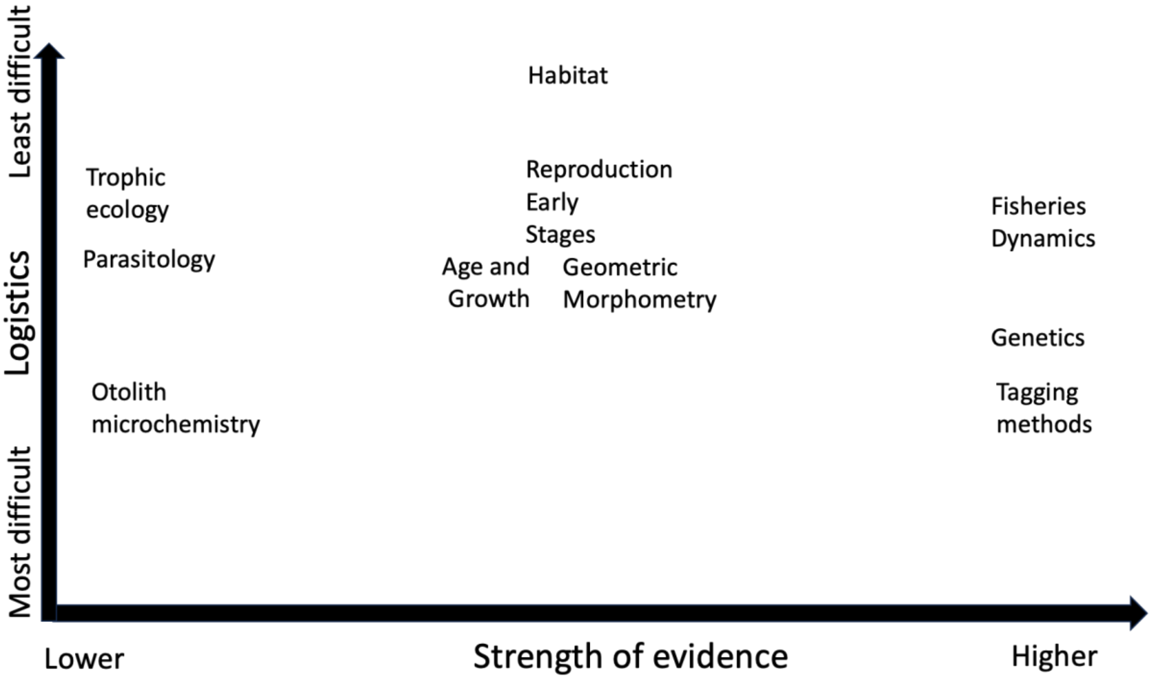

Figure 1. Final prioritization of the topics based on perceived strength of evidence of each topic for informing jack mackerel connectivity and logistical feasibility. Scales for axes are qualitative and range from lower to higher. Following discussions, topics could only be broadly aggregated into 3 categories of strength of evidence: topics which provide lower, moderate and higher strength of evidence for informing jack mackerel connectivity.

Three broad priority groups were identified (Figure 1):

- Topics providing **higher strength of evidence** consisted of Fisheries dynamics, Genetics and Tagging methods
- Topics providing **moderate strength of evidence** consisted of Habitat, Reproduction, Early stages, Geometric morphometry and Age and growth,
- and topics providing **lower strength of evidence** consisted of Trophic ecology, Parasitology and Otolith microchemistry.

Topics providing higher strength of evidence spanned a range of logistical ease, with Tagging methods considered the most logistically challenging across topics (on par with Otolith microchemistry), followed closely by Genetics, whereas Fisheries dynamics was considered to have similar logistical feasibility to topics in the moderate strength of evidence group (e.g. Trophic ecology, Early stages and Reproduction). Habitat, which was classified as a moderate strength of evidence group, had the highest feasibility.

Noting that all of the 11 topics systematically reviewed were considered relevant for evidencing connectivity of jack mackerel in the South Pacific by workshop participants, the final selection of high priority topics considered in balancing strength of evidence and logistics. This was done as part of an interactive process during day 2 of the pre-SC12 workshop.

- It was decided that for the purposes of the prioritization, those topics providing lower strength of evidence would not be considered as high priority to include in a sampling programme in the first instance.
- Topics providing higher strength of evidence were initially all considered as a high priority to include in the sampling programme, but it was deemed financially unfeasible to undertake all three as part of the sampling and research programme. However, much of the sampling undertaken for the topic of Fisheries dynamics was / is being collected in on-going work of the JM working group and can be progressed with in-kind contribution. Workshop participants strongly recommended that JM connectivity TG actively collaborate with the JM Working Group on the topic of fisheries dynamics to further support evidence of jack mackerel connectivity in the South Pacific.
- The three most logistically feasible topics identified as providing moderate strength of evidence were considered for inclusion as high priority topics (Habitat, Early Stages and Reproduction). However, it was agreed that a sampling programme would be more achievable with fewer topics. The types of approaches identified as useful within the topic of Habitat (e.g, species distribution modeling) was identified as on-going work in the Habitat Monitoring working group. Similarly to the topic of Fisheries dynamics, workshop participants strongly recommended that JM connectivity TG actively collaborate with the Habitat Monitoring working group to co-develop distribution models of jack mackerel to identify key areas for any sampling and differences in distribution of different life stages and possible movement based on habitat suitability to further support evidence of jack mackerel connectivity in the South Pacific.

Based on the considerations discussed above, it was agreed by consensus that the topics Genetics, Tagging methods, Early stages and Reproduction were the highest priority areas which should be proposed as part of any future sampling and research programme aiming to evidence connectivity of jack mackerel in the South Pacific.

Genetic connectivity is inferred through the analysis of population genetic structure (Hellberg et al., 2002; Hohenlohe et al., 2021). This approach assesses the geographic and temporal distribution of genetic variability within a species using different molecular markers. Genetic differentiation between populations has been studied with traditional genetic tools (See Section 4.4 for further details). Genetic studies have been applied to pelagic fish, where their apparent lack of geographical barriers, migratory behavior, large population sizes, and long life cycles seem to promote low levels of genetic differentiation undetectable by traditional methods (Cowen et al., 2007). Nowadays, high-throughput sequencing techniques, mainly WGS, are widely applied in studies of population structure, genetic connectivity and metapopulation, successfully applied for pelagic fishes. The genetic variability, plus the disponibility of both markers related to neutral and adaptive responses provide evidence of fluctuation in population genetic variability and connectivity (Nesbø et al., 2000, Bourret et al. 2023, Da Fonseca et al., 2024).

Tagging methods, consists in tracking and studying individual fish by attaching a physical tag to their bodies (see Section 4.10). Tags can be external (visible on the surface) or internal (implanted within the fish) and are used to gather data on movement patterns, population dynamics, growth rates, and behavior (Jacobsen & Hansen, 2004). The topic of tagging methods is considered to have a higher strength of evidence for studying functional connectivity in jack mackerel across its distribution range, as it provides evidence of actual fish movement and has been tested to determine stock boundaries and population structure in species such as western mackerel (Bakken & Westgård, 1986), Atlantic bluefin tuna (Block et al., 2005), Pacific herring (Hay et al., 2001), Northeast Atlantic mackerel (Iversen et al., 2002), and North East Atlantic mackerel (Uriarte et al., 2001), among others. However, their implementation requires significant logistical considerations.

Early stages refer to the distribution and abundance of eggs and larvae throughout their range (see Section 4.2). This topic was classified as having a moderate strength of evidence regarding jack mackerel connectivity. It provides insights into reproductive mixing, spawning distribution, and functional connectivity through the use of biophysical models to assess larval dispersal, as demonstrated for species such as mackerel, horse mackerel, and sardine (Álvarez & Chifflet, 2012), the Mediterranean anchovy (Ospina-Álvarez et al., 2012), and the Japanese jack mackerel (Sassa et al., 2014), among others. In synergy with the Habitat topic, it also provides information on the potential occurrence of spawning grounds through the implementation of stage-specific species distribution models. The logistical requirements for this approach were assessed as moderate.

The topic of Reproduction (see section 4.9), when considered for understanding connectivity patterns, focuses on understanding the reproductive cycle and its comparison throughout the distribution of the target fish species. This approach is considered fundamental to understanding the mechanisms that regulate reproductive processes, identification of reproductive cycles and strategies in the face of changes in the environment. It is important to highlight that each species presents particularities in its type of reproduction, making it unique for each stock, adapting to the conditions of life in the ocean (Xin Jun et al., 2022). Knowledge of reproductive strategies and spawning patterns are essential to understand the population dynamics of any fish species (Hilborn and Waters,1992) with fecundity being one of the reproductive parameters that should be analyzed (Murua et al., 2003).

Next steps

Should funding become available for subsequent work, the JM connectivity TG proposes to develop a research and sampling programme aiming to collect the data required to inform the 4 high priority topics identified. Specifically the JM connectivity TG recommends:

1. Developing spatial distribution estimates of jack mackerel, in collaboration with the Habitat Monitoring Working Group, to identify important environmental drivers of distribution and inform key areas for sampling, across different life stages.
2. Organize workshops (workshop 1) for preliminary discussion on individual priority topics to identify key practical requirements and considerations for sampling, e.g., the minimum number of samples, spatial distribution and temporal coverage.
3. Organize a workshop (workshop 2) to explore and discuss how the findings from the sampling and research programme would be considered and integrated across multiple lines of evidence, including when findings are not aligned. For example, if one approach suggests connectivity where another does not. In order to facilitate discussions on research findings, it is recommended consensus be achieved prior to finalizing a sampling and research programme that, using the systematic review as a starting point:
    - 3.1. Identifies key hypotheses on connectivity and a description of how these hypotheses could be tested using the priority topics.
    - 3.2. Weight of evidence to support different hypotheses are agreed a priori (i.e., whether some approaches provide stronger evidence than others)
    - 3.3. Description of hypotheses and weight of evidence given to these should be agreed by consensus and clearly recorded, for example as a decision tree.
4. Organize a multi-day workshop (workshop 3) to design a sampling and research programme that provides a clear plan for collecting data across the 4 combined identified high priority topics Genetics, Tagging methods and Reproduction / Early Stages to evidence jack mackerel connectivity.
    - 4.1. It is recommended that external subject matter experts attend the workshops and provide independent advice on the proposed sampling approaches.
5. Co-develop sampling protocols to ensure data equivalence across all SPRFMO members involved in the sampling programme.
6. SPRFMO members collaborate with national, international and industry partners to undertake the identified sampling.
7. Results of the sampling and research programme are summarized, communicated and used to support a sustainable ecosystem-based approach to fisheries management. Noting that data and results from a sampling and research programme would have application for informing fisheries management beyond an increased understanding of connectivity of JM.

Given the large spatial and temporal scale required to evidence connectivity of jack mackerel across its range in the South Pacific, the JM connectivity TG suggests that a large sampling and research programme be developed. It is anticipated that this connectivity work programme would require initial funding to support tasks 1-3 in the order of $40,000 with delivery of outputs for SC14. Subsequently, funding in the order of $75,000 (NZD) per year for 6 years would be required to complete a sampling and research programme. It is anticipated that funding would be supplemented by in-kind contributions from participating delegations to the equivalent value (SC11-JM02) with additional funding sought from industry partners who have expressed interest in these projects, including for application of the data to fisheries management beyond an understanding of connectivity of JM.

Recommendations

It is recommended that the Scientific Committee:

Notes

- The collaborative approach, strengthened working relationships, hard work and consensus achieved by members when engaging in the systematic review and the workshops.

Agrees

- That the approach (systematic review and workshop) is appropriate for identifying priority topics of research towards evidencing connectivity of jack mackerel in the South Pacific.
- That all of the 11 topics systematically reviewed are considered relevant for evidencing connectivity of jack mackerel in the South Pacific, however, prioritization of topics based on strength of evidence and logistical considerations, identified 4 topics as priority areas to focus future efforts. Specifically: Genetics, Tagging methods, Early stages & Reproduction.

Recommends

- That funding be provided for the sampling design and implementation of the 4 identified priority topics of research for evidencing JM connectivity (Genetics, Tagging methods, Early stages & Reproduction).
- That the JM connectivity TG actively collaborate with the Habitat Monitoring Working Group and the JM Working Group to co-develop habitat modelling and understanding in fisheries dynamics to further support evidencing connectivity of jack mackerel in the South Pacific.

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4 Systematic reviews of identified topics

4.1 Age and growth

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KEY SEARCH WORDS USED: “Jack Mackerel” +” Age” + ”Growth” + ”Otoliths” + ”Microstructures” + “Age Validation”.

4.1.1 Background and rationale

Determining the age of jack mackerel is relatively challenging (Goicochea et al., 2016; Cerna et al., 2016; Horn & Maolagáin, 2020). So far, most methods have relied on readings of whole otoliths, but the estimated parameters and interpretation of the methods are not entirely conclusive. So, uncertainty remains under discussion (SPRFMO, 2022b).

The origins of studies on the age and growth of *T. murphyi* in the South Pacific, date back to the 1970s with Kaiser (1973) and Carrera et al. (1978) on otolith readings as complete structures in samples off the coast of Chile. Later, other structures such as scales were employed for studies (Nekrasov, 1982, 1987; Nosov, 1989). However, the estimates varied between the methods and techniques used up to that point, and it was in the 1990s, greater efforts were made to reduce the uncertainty of these estimates. During this time, Kochkin (1994) studied the internal structure, estimating a maximum age of 10 years. Babayan and Bulgakova (1994), and Cubillos and Grechina (1998) focused their studies on catch size structures using the length frequency analysis (LFA) method. Alegría et al. (1995) examined whole and sectioned otoliths, observed daily growth zones and estimated ages up to a maximum of 14 years. Based on the analysis of the classification of the otolith edge and daily zones, they estimated that opaque zones formed annually in the otoliths. After more than a decade, concerns arose regarding the existing estimates in response to critical declines in biomass. Within the framework of SPRFMO, an integrated approach to estimating growth parameters was recommended to address the uncertainty in the age determination of jack mackerel.

The growth parameters estimated by Dioses (2013) and Goicochea et al. (2013) from annual ring readings were similar in growth rate to those estimated by Díaz (2013) through LFA, although with a variable asymptotic length. In the Western Pacific, Horn (1993) examined *T. murphyi* otoliths in New Zealand waters using cross-sections, broken, and burned methods, but found difficulties in identifying rings with the latter techniques. In 2020, Horn and Maolagáin estimated a high growth rate and a low asymptotic length through cross-sectional analysis. They argue that there are

differences in age across the jack mackerel's distribution, with younger fish found off the South American coast and older fish in New Zealand waters. Horn and Maolagáin (2020) hypothesized that the population in the Southeast Pacific areas would have smaller sizes corresponding to younger groups. This approach could be related to the proposal by Gerlotto et al. (2012), suggesting two main spawning areas: one off the southern coast of Peru and northern Chile with concentrations of juveniles, and another in central-southern Chile with concentrations of adults. Meanwhile, Arcos et al. (2001) suggest that the population is distributed across three habitats: a nursery area north of 30°S, a feeding area in the coastal zone of central-southern Chile, and a spawning area in the oceanic region off central Chile.

4.1.2 Critical appraisal of methods

Based on micro increments, Goicochea et al. (2013) determined that the first fully formed ring reaches an average size of 19.5 cm total length (TL). In 2016, Goicochea et al. adapted two criteria for interpreting daily increments based on the work of Cermeño et al. (2008): individual mark readings (IMR) and group band readings (GBR). According to the first criterion, jack mackerel reach sizes between 19.5 to 20.8 cm TL at one year of age, while with the second criterion, they reach 28.4 cm TL. Additionally, two types of ring formation patterns were identified: rings with narrow radii or tight formation sequences (Type I) and rings with wide radii or well-separated formations (Type II). They also suggest quarterly formation of each ring with the first criterion and biannual formation with the second. On the other hand, Cerna et al. (2016) used microstructure analysis to determine that the size at one year of age is 22 cm Fork Length (FL). They identified the formation of secondary growth zones starting from day 23 post-hatching and observed a high initial growth rate followed by a growth cessation of growth between days 50 and 80, after which growth gradually declined. This study emphasizes that the first macro-ring, assigned as one year according to annual readings, does not correspond to the annulus, as the number of primary microincrements formed was fewer than 200. They suggest that the first macro-ring of annual periodicity corresponds to the second macro-ring estimated from conventional whole otolith readings. Araya et al. (2019) conducted direct validation of daily growth in jack mackerel in captivity by marking individuals with alizarin red solution. Their results for fish between 18 and 23 cm TL identified three microstructural zones: the first zone, associated with the larval stage, extended from the first to the third week; the second zone, characterized by increased otolith growth with the appearance of secondary growth centers, lasted until the fourth month of life; and the third zone, marked by a significant reduction in otolith growth rate. Arancibia et al. (2021) estimated the growth using daily increments. Finally, Cerna et al. (2022) employed three methods to validate the age of jack mackerel: 1) daily readings of microincrements in sagittal otoliths of age-0 fish to validate the first ring; 2) modal progression of strong annual classes to validate the first, second, and third rings; and 3) radiocarbon analysis of otoliths to validate absolute age in fish over 38 cm FL. The Laird-Gompertz model adjustment estimated an average size of 22 cm FL at the end of the first year of

life. Cerna et al. (2016) and Araya et al. (2019) provide descriptions of microstructures and the interpretation of hyaline rings at a macroscopic level. Both studies describe three growth zones alternating between larval stage growth, a period of rapid growth, and a zone of reduced otolith growth rate. These growth patterns may have impacted the interpretation of hyaline ring formation macroscopically, leading to confusion in determining the first annulus.

These results highlight differences in the interpretation of hyaline marks in the early years of the jack mackerel, *T. murphyi*. In the Peruvian region, the formation of the first annulus has been estimated to occur between 19.5 and 20.8 cm TL, whereas estimates from the Chilean side exceed 23 cm TL. Generally, if these estimates are accurate, they would suggest a difference in growth rates between populations, which is currently under discussion in the SPRFMO SC. In this regard, it is important to analyze the size structure of the population. The stock off the Southeast Pacific has been represented by sizes smaller than 45 cm TL (Gerlotto and Dioses, 2013), while in the western waters, the size structure is larger, above 50 cm TL, and this has been increasing in recent years in landings on the coasts of New Zealand (Horn et al., 2019).

To this date, otolith microstructure (OM) analysis has been applied only to validate the first annulus in this species. Nonetheless, OM is particularly useful to reveal patterns related to ontogenic or environmental changes experienced by fish (Panfili et al. 2009). Growth in early stages is mainly controlled by water temperature and food availability, influencing microincrement width (Camapana and Thorrold 2001). Differences in these environmental parameters between spawning areas should be reflected in the OM. This approach has been used to successfully identify population units of small pelagic fish such as *Clupea harengus* (Brophy et al. 2006) and *Engraulis ringens* (Niklitschek et al. 2018).

4.1.3 Applicability to jack mackerel or other small pelagic

Effective management of fish populations requires knowledge of their growth rates, which involves determining the age of the fish to establish a relationship between size and age. Studies on the age and growth of fish are essential for obtaining information on recruitment, longevity, mortality, and fishing fluctuations due to various annual cohorts. This contributes to the planning of a rational exploitation of these populations. Such studies allow for the description of the current status, past history, and future prospects of a fishery (Khan & Khan, 2014).

In general, despite numerous efforts aging**,** the jack mackerel *T. murphyi* within the genus *Trachurus* is one of the species for which age determination is particularly challenging, especially in the early years of life. This is due to the observation of diffuse annual zones, clusters, or numerous discontinuous marks (Horn & Maolagáin, 2020). These characteristics may reflect endogenous processes and environmental effects in a process where they reach maturity at one year of age (Leal et al., 2013). Such difficulties have been noted by ICES for several species within the genus

Trachurus (ICES, 2020) and for *T. murphyi* in the Southeast Pacific (Dioses, 2013; Goicochea et al., 2013, 2016; Cerna et al., 2016; Araya et al., 2019; Cisterna & Arancibia, 2017; Arancibia et al., 2021; Cerna et al., 2022). In this regard, despite the results of published studies, questions remain due to the lack of validation of the periodicity of microstructures between larval and pre-recruit stages

(Araya et al., 2019), the need to corroborate the radiocarbon validation method (Cerna et al., 2022), the necessity for a deep understanding of the processes of daily, seasonal, and annual microstructure formation (Goicochea et al., 2016),incomplete coverage of the population structure within the species' distribution range (Horn & Maolagáin, 2020), or the potential impact of sample size on estimates (SPRFMO, 2022a).

Based on these studies, the availability of the population structure of jack mackerel may respond to the dynamics of the resource itself, with seasonal migrations related to feeding and spawning processes (Serra, 1991; Cubillos et al., 2008; Bertrand et al., 2016). This migratory dynamic might explain the colonization of larger individuals (Gerlotto et al., 2012; Serra et al., 2014) reported in New Zealand (Penney & Taylor, 2008; Horn & Maolagáin, 2020). Meanwhile, otoliths store information about both the life history of the fish and the environment, making them valuable tools for understanding life cycle events, migration patterns, and population structure (Campana, 2005).

4.1.4 The feasibility and/or limitations of the approach

Several factors may be affecting the estimates of growth parameters and the determination of the age of the jack mackerel, from validation processes to the techniques used in aging. To begin with, many of the methods and their estimates shown in Table 1 have not been validated. Growth parameter estimates are often influenced by sampling biases and imperfect data (SPRFMO, 2022a), and procedures must be well-defined, considering aspects such as the selection of representative samples to be used as preliminary reference in the interpretation by readers (Horn & Maolagáin, 2020).

The current state of aging for *T. murphyi* reveals that it is one of the most complex species to age among marine pelagic organisms. Despite numerous studies, a conclusive determination of the age of this species has not been achieved, as it does not adhere to the typical daily and annual pattern formation principles observed in otoliths of other species. This situation presents short- and medium-term challenges for improving the understanding of size structure variations across its distribution, maturity processes, and a robust interpretation of growth marks at the microstructure level during validation processes. This includes incorporating environmental effects on otolith deposition processes and effective sample size, as well as appropriate size structure, with joint collaboration from the member countries of the SPRFMO SC.

In particular, we observed that growth is a fundamental aspect in the life history of fish (Khan & Khan, 2014). Although there are few studies that support or allow differentiating between different population stocks from the growth perspective, the limitations mentioned above could be complemented with other approaches, such as capture, mark and recapture studies (Panfili et al., 2002), as well as otolith morphometric analysis, otolith microchemistry and otolith microstructure analysis.

Table 2. Parameters of the von Bertalanfy equation of the Jack Mackerel *T. murphyi* of the relationship LH fork length and age in years, estimated with various methods and by different authors, updated from Dioses et al. (2013) and Cerna et al. (2016).

N°	Authors	Structure	Method	Loo	k	to	Area
1	Kaiser (1973)	Otolith	Annual ring	70.1	0.184	-0.341	Northern - Central Chile
2	Carrera et al. (1978)	Otolith	Annual ring	108.3	0.109	-0.877	Central Chile
3	Abramov & Kotlyar (1980)	Otolith	Annual ring	72.5	0.093	-2.233	Peru
4	Aguayo & Ojeda (1981)	Otolith	Annual ring	45.9	0.167	-0.882	Northern Chile
5	Nekrasov (1982)	Scale	Annual mark	74.3	0.086	-2.676	Peru
6	Shevchuk (1982)	Otolith	Annual ring	90.4	0.115	-1.429	Peru - Chile
7	Castillo & Arrizaga (1987)	Otolith	Annual ring	65.2	0.074	-2.410	Southern Chile
8	Nekrasov (1987)	Scale	Annual mark	96.0	0.060	-2.617	Peru
9	Nosov (1989)	Scale	Annual mark	77.8	0.077	-1.613	Peru
10	Kochkin (1994)	Otolith	Annual ring	74.2	0.111	-0.811	Peru
11	Shcherbitch (1991)	Otolith	Annual ring	91.2	0.091	-1.583	--
12	Babayan & Bulgakova (1994)	Length	LFA	94.5	0.099	--	South Pacific
13	Alegría et al. (1995)	Otolith	Daily ring	78.5	0.154	-0.098	Northern Chile
14	Alegría et al. (1995)	Otolith	Annual ring	53.5	0.111	-1.797	Northern Chile
15	Alegría et al. (1995)	Otolith	Annual ring*	48.4	0.184	-0.945	Northern Chile
16	Arcos & Arancibia (1995)	Otolith	Annual ring	79.9	0.068	-2.369	Central - Southern Chile
17	Arcos & Arancibia (1995)	Otolith	Annual ring*	70.7	0.088	-2.107	Central - Southern Chile
18	Cubillos & Grechina (1998)	Length	LFA	78.6	0.144	--	Chile
19	Li et al. (2011)	Otolith	Annual ring	73.8	0.107	-1.080	Central - Southern Chile
20	Dioses (2013)	Otolith	Annual ring	80.8	0.155	-0.356	Peru
21	Díaz (2013)	Length	LFA	81.6	0.167	--	Peru
22	Goicochea et al. (2013)	Otolith	Annual ring	75.2	0.165	-0.817	Peru
23	Cisterna & Arancibia (2017)	Otolith	Daily ring	75.0	0.160	-0.130	Central Chile
24	Horn & Maolagáin (2020)	Otolith	Annual ring*	51.9	0.223	-0.500	New Zealand
25	Arancibia et al. (2021)	Otolith	Daily ring	75.0	0.160	-0.190	Peru - Chile
26	Arancibia et al. (2021)	Otolith	Annual ring	74.7	0.100	-0.500	Peru - Chile
27	Arancibia et al. (2021)	Otolith	Otolith weight	75.0	0.150	-0.480	Peru - Chile
28	Cerna et al. (2023)	Otolith	Annual ring	64.9	0.130	-2.630	Chile
29	Cerna et al. (2023)	Otolith	Annual ring*	56.9	0.170	-2.330	Chile

* Transverse sections

4.1.5 References

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4.2 Early Life-stages

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KEY SEARCH WORDS USED: "early life stages", "*Trachurus murphyi*", "Jack mackerel", "connectivity"

4.2.1 Background and rationale

Three interacting aspects of population structure are evaluated in interdisciplinary stock identification: distribution, dispersal, and geographic variation - but no single source of information can support inferences of all three. Information on geographic distribution (e.g., fishery monitoring, fishery-independent surveys) can define a species range, spatial continuity, areas of high abundance, spawning areas, nursery areas, and fishing grounds for each fleet (Cadrin et al., 2023). Functional connectivity is evaluated from information on dispersal of early life history stages (e.g., plankton surveys, bio-physical models) and movement of juveniles and adults from conventional tags, electronic telemetry or 'natural tags' (e.g., parasites, otolith chemistry). The geographic structure of spawning aggregations, coupled with the reproductive behaviour of adult fish (e.g., natal homing, spawning site fidelity, straying, entrainment, resident or migratory life history strategies), and an understanding of the required environmental conditions, can inform patterns of population heterogeneity, mixing, or reproductive isolation (Kerr et al., 2017).

Cowen et al. (2000) investigate marine larval population connectivity, focusing on whether populations are "open" or "closed." An "open" population is one significantly influenced by larval immigration from other populations, while a "closed" population relies mainly on local larval production. The study combines field observations, larval dispersion models, and ocean current analyses to assess connectivity between different marine populations. By using biophysical models that integrate data on larval behavior and ocean currents, the authors simulate larval dispersion under various scenarios. The findings indicate that marine population connectivity is more complex than previously thought. Rather than being fully open or closed, populations exhibit a spectrum of connectivity influenced by oceanographic and biological conditions.

Blaxter (1982) and Bakun (1996) examine key factors related to connectivity and larval stages in engraulids fish, particularly focusing on how large-scale oceanographic patterns shape marine population dynamics, including the dispersion and survival of larvae. These patterns play a critical role in linking different populations and habitats, which is essential for preserving genetic diversity and ensuring population sustainability. Additionally, Allain et al. (2003) emphasize the importance of mesoscale ocean processes in influencing the dispersion and connectivity of anchovy larvae in the Bay of Biscay.

The occurrence of JM eggs in the southeastern Pacific has been summarized by Gerlotto et al. (2012), revealing an extensive region with positive records bounded by the subtropical front (Evseenko 1987). This region extends from the oceanic zone off central Chile and narrows towards the coastal transition zone of the southeastern Pacific along northern Chile and Peru. The spatial structure of the JM spawning area off central-southern Chile has been described by Núñez et al. (2008) and Cubillos et al. (2008) and later by Vásquez et al. (2015), indicating a persistent spring spawning area with interannual variability in mean egg and larval densities. The presence of JM eggs within the Exclusive Economic Zone of northern Chile has been documented by Braun & Valenzuela (2008), revealing year-round occurrences of eggs and larvae. While JM eggs off Peru are less documented, the recurrent presence of JM larvae has been reported by Ayon et al. (2013) in long-term monitoring, showing interannual variability in mean densities and suggesting decadal shifts in geographic centroids of distribution.

Alvarez and Chifflet (2012) analyzed the spatial distribution of eggs and larvae of three pelagic species (mackerel, horse mackerel, and sardine) in the Bay of Biscay during the years 1998, 2001, and 2004. It was found that the prevailing currents affect mackerel and horse mackerel larvae more, as their spawning areas are far from the continental shelf, where the currents are stronger. Studies by Parada et al. (2010) within the southeastern Pacific highlight the critical importance of larval dispersal for connectivity in the Chilean jack mackerel (JM) population. Parada et al. (2012) emphasize the role of ocean currents in shaping larval dispersion and retention. Meanwhile, Vásquez et al. (2013) revealed that oceanographic features such as fronts and eddies significantly influence the dispersion and connectivity of JM larvae, underscoring the need to account for these factors in understanding JM population structure. These findings are further supported by Vásquez et al. (2015), whose larval dispersion models show how ocean currents and other environmental variables affect larval dispersion and connectivity. This kind of research is crucial for understanding recruitment patterns in JM population and supporting sustainable fisheries management in the region.

4.2.2 Critical appraisal of methods

Studies on larval connectivity use the following methods:

Direct Observation: Field observations are conducted to record the presence and distribution of jack mackerel larvae in different areas and time periods.

Modeling: Coupled biophysical models and numerical ocean circulation models are used to simulate larval dispersal by integrating ocean currents and other environmental factors.

Genetic Markers: These are used to identify genetic patterns that help infer connectivity in JM population based on the analysis of larval and adult population samples.

Empirical Methods (Tagging and Recapture): JM larvae are tagged, and data from their subsequent recapture are recorded to infer dispersal and connectivity patterns.

Otolith Microchemistry: The otoliths (calcareous structures in the inner ear) of the larvae are analyzed to identify chemical signatures that reveal the mobility and location history of the larvae in the marine environment.

Acoustic Tracking: Acoustic techniques are used to track the movement of tagged larvae in the ocean, providing data on dispersal patterns and behaviour of jack mackerel larvae.

In the works of Sassa et al. (2014) and Vásquez (2013), sampling of JM larvae and data collection on oceanographic conditions such as temperature, salinity, and currents were conducted to analyze how these factors influence the distribution and growth of the larvae. Similarly, Barbieri et al. (2004) sampled JM eggs and larvae in different areas off central-southern Chile to investigate their spawning strategy in relation to environmental conditions, as well as the acoustic tracking of this species. These approaches reflect the principles discussed in foundational studies such as Cowen & Sponaugle (2009), which examine the importance of larval dispersal in population structure, and Levin (2006), which explores how oceanographic conditions affect connectivity.

The studies by Fink-Jensen and Avigliano in 2021 highlight the use of otolith microchemistry to track movements and analyze fish connectivity. The former investigates the stock structure and migrations of capelin (a pelagic fish) in Greenland, while the latter reviews works for the application

of this technique in Latin American fish. Both studies demonstrate the effectiveness of otolith microchemistry in providing data on mobility patterns and connectivity between different habitats.
Genetic techniques are effective tools for assessing genetic and population diversity. In the works of Steinke et al. (2016) and Planes et al. (2009), genetic analyses were used to investigate population structure and connectivity between different life stages or populations during dispersal and connectivity. Bode et al. (2019) validated larval dispersal models using genetic kinship data, as did Gary et al. (2020), who included DNA analysis in fish larvae and genotyping to identify parental relationships and dispersal.

These combined methods allow for a more comprehensive view of JM larval connectivity and are crucial for the effective management and conservation of this species in marine ecosystems.

4.2.3 Applicability to jack mackerel or other small pelagic

Studies of the early life stages of jack mackerel in the Peruvian sea (Santander & Flores, 1983; Dioses et al., 1989) have shown their constant presence in this ecosystem. Despite not having a specific sampling design, valuable inferences have been made based on the information collected, identifying significant patterns related to larval dispersal and some ecological aspects. Although the current design is not optimal, it has allowed for the detection of signals of change and variability in these stages. However, implementing a specific sampling design could significantly improve the quality of information and its interpretation, especially in the analysis of larval dispersal and connectivity. The sampling platforms, equipment, and expertise available at IMARPE could be redirected to this line of research, although additional ship time would be necessary to obtain optimal results. This need for improvement is emphasized in the context of the study by Ayón & Correa (2013), who analyzed the spatial and temporal variability of JM in Peru from 1966 to 2010. Their research, based on historical and contemporary data, revealed significant variations in the distribution and density of larvae related to environmental variability. Studies conducted in the oceanic zone off central-southern Chile, through systematic surveys covering an area of over 1 million km² between 1999 and 2020, have revealed the recurrent occurrence of JM eggs and larvae at the highest recorded densities throughout its range (Lang et al., 2021). Although these research surveys are no longer being conducted, the collected data provide crucial input for an integrated study of the spatial structure of JM spawning in the southeastern Pacific. The extensive coverage of this spawning area was made possible by using industrial fishing vessels as scientific research platforms in a public-private collaboration, a practice that could be reactivated within the framework of an integrated SPRFMO project. In northern Chile, seasonal planktonic surveys were carried out from 1981 to 2007 under IFOP projects, revealing the recurrent presence of early JM stages in a region extending up to 80 nautical miles offshore. As in Peru, sampling platforms and equipment could be directed towards studying JM spawning in this region.

These studies highlight the importance of continuous monitoring for effective fisheries management and marine resource protection, especially in species with a large potential spawning area with high larval dispersal activity. Implementing studies with techniques such as modeling (circulation) and genetic markers, in addition to direct observations, is recommended. Furthermore, integrating historical information on the distribution and abundance of JM eggs and larvae can support the development of stage-specific species distribution models, aiding in understanding the extent and variability of potential spawning habitats for this species.

4.2.4 The feasibility and/or limitations of the approach

In this sense, the possibility of conducting studies using some of the methods employed to study connectivity within the SPRFMO framework is quite promising, such as direct observation. While there is capacity to obtain samples of early stages, certain limitations may arise. These could be linked to the wide potential spawning area of JM (Gerlotto et al., 2012) and to oceanographic conditions at the time of sampling that may not favour the presence of spawning adult schools in certain regions of the evaluated area (e.g. during El Niño events). Therefore, it is necessary to ensure that sampling is systematic, covering a broader area and conducted during the key spawning period, particularly during spring (October to December) when the main spawning season take place (Gretchina et al., 1998, Oyarzún et al., 1998, Perea et al., 2013). This would depend heavily on field expeditions occurring within that timeframe and in regions where early life stages of JM have been recorded. These samples are crucial for applying some of the proposed methods, such as the studying otolith microchemistry and conducting molecular tagging studies, which can offer valuable insights into connectivity and population structure.

Regarding modeling approaches, there is the feasibility of evaluating larval connectivity through biophysical modeling, building on previous studies conducted on this species (e.g., Parada et al., 2010; Vásquez et al., 2015; Parada et al., 2017). The availability of high-resolution ocean circulation models for the study region, along with key biological information, provides essential inputs for these modeling efforts, enabling a more accurate assessment of larval dispersal and connectivity in JM population. On the other hand, creating joint historical databases of the distribution and abundance of JM eggs and larvae, combined with environmental information from remote sensing and field data, presents promising opportunities for implementing stage-specific distribution models. These models could help study potential environmental constraints on larval connectivity in JM. However, a potential limitation of these methods is the limited information available on the distribution of young-of-the-year fish, which is necessary to validate the dispersal patterns simulated by biophysical modeling.

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4.3 Fisheries dynamics

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KEY SEARCH WORDS USED: “fisheries”+ “fisheries dynamics” +”Jack mackerel”+ “small pelagics”

4.3.1 Background and rationale

The Chilean jack mackerel, a medium-sized pelagic fish, plays a crucial role in commercial fishing worldwide (see https://www.sprfmo.int/). Its extensive migration and wide distribution across the eastern South Pacific Ocean present a challenge in identifying distinct stock units (Gerlotto et al., 2012; Gerlotto et al., 2021). In this sense, the understanding of the complex population dynamics and structure of Jack mackerel is essential for effective and sustainable resource management. Moreover, the sensitivity of this species to environmental changes (Arcos et al., 2001) further underscores the importance of accurately identifying stock units (Hintzen et al., 2014). With the study of fishery dynamics, we can gain insights into the spatio-temporal trends and enhance our comprehension of the intricate population structure of Jack mackerel.

4.3.2 Critical appraisal of methods

The study of fishing dynamics involves analyzing indicators such as landings, catches, fleet characteristics, fishing effort, among other factors (Ñiquen et al., 2013, Vásquez et al 2020). These fishery indicators are closely linked to environmental variables, highlighting the environment as a key factor that influences fluctuations in fish and their fisheries (Espino 2013). In this sense, fishery dynamics allows us to analyze the impact of drivers, such as climate and fishing, on a species under study. An example of this is the work made by Zwolinski et al. (2012), focused on the sardine of the California Current system. This work not only provided some insight into the population structure of this species but also analyzed the combined effect of fishing effort and climate variability to explain the collapse of the sardine. Understanding fishery dynamics also helps to assess the availability of the resource, its distribution, and aggregation (Bertrand et al., 2006). This information is used to develop population dynamics models for the resource as well as statistical species distribution models (e.g. ENM or SDM), intermediate complexity models, or even ecosystem models, which will be described below. Additionally, the combined impact of fishing and environmental factors is examined as a regulatory mechanism for fish species, including adults and specific age groups such as juveniles and larvae (Ayon & Correa, 2013). Fishery dynamics could also include the analysis of fishing gears, locations, market demand, and the economic aspects related to a fishery. Although fisheries dynamics is a broad field of study, in the following section, we illustrate some guidelines that address different problems related to this topic in Jack mackerel.

4.3.3 Applicability to jack mackerel or other small pelagic

In terms of exploitation, records show that Jack mackerel has been part of a fishery since the 1960s, and in some countries, such as Peru, there is evidence that ancient settlements fished for this species (Lavallée et al. 2011; Csirke 2013). During the 1980s and 1990s, this resource became one of the most exploited in the world, with landings arriving close to 5 million tons according to FAO world records (FAO 2024). However, fluctuations in landings, linked to changes in availability in the stock due to environmental changes, have created high levels of uncertainty about the overall state of the stock, as well as its population structure throughout the South Pacific. In this context, fishery dynamics have been contributing to the development of the following topics:

Shedding light on understanding stock structure

The population dynamics of Jack mackerel and its fishery have been studied using the SEAPODYM model (Dragon et al., 2017). This study aimed to understand how environmental and fishery factors influence the population dynamics of Jack mackerel and to identify the core habitat of the species. It also used acoustic and fishery information from various sources to estimate the spatio-temporal population dynamics across the South Pacific Ocean. Another study (Parada et al., 2017) developed a conceptual framework for the spatial population structure of Jack mackerel and the species' life cycle. However, this study did not provide information on the total distribution of the resource, which is essential for a comprehensive understanding of the species' life history and population structure.

Combination of drivers: fishery and environment

Fishery dynamics allows us to analyze the impact of drivers, such as climate and fishing, on a species under study. In this sense, the study by Lima et al. (2020) explored the combined effect of stock dynamics, fishing (using fishing efforts), and climate (using sea surface temperatures, SST), to explain the sharp decline in Jack mackerel catches in the Humboldt Current ecosystem. According to this study, using a fishery dynamics model, based on the relationship between the abundance of fish stocks, the effort exerted by the fishing fleet, and ENSO (i.e. El Niño Southern Oscillation) variability, the population trends of Jack mackerel could be explained by changes in fishing effort, which appear to be driven by economic forces and El Niño variability. The study of the ENSO variability impact on the spatial distribution of Jack mackerel has also been explored by Yañez et al. (1996) and Naranjo et al. (2015). Their main conclusion is that El Niño seems to have a strong impact over the distribution of this species, and that this could also affect the catchability of its fishery. The impact of El Niño on the Jack mackerel fishery in south-central Chile (Arcos et al., 2001) through an analysis of the catch-at-size relationship with SST in El Niño 1+2 and El Niño 3.4 zones

allowed a first approximation of the conceptual model for Jack mackerel in Chile. This study characterizes three zones (an early-stage nursery zone, a spawning zone, and a feeding zone), which could be fundamental for identifying a stock structure. Additionally, they find that latitudinal differences in size structure of this species could be explained by changes in oceanographic conditions. Sustaining efforts to develop further studies to include the entire distribution of Jack mackerel, would be important. Another study (Zhang et al., 2015) highlights the importance of studying decadal spatio-temporal changes in the location of the fishery, based on the analysis of fishing effort and catch per unit effort (CPUE). This would be fundamental for fishing efficiency and management.

Development of simulation tools:

Indicators generated through the study of fishery dynamics serve as inputs for fostering the development of tools such as stock assessment models (SAM). In the management of Jack mackerel within the framework of the SPRFMO, several SAMs have been developed (SPRFMO 2010: SWG-09-JM-01), which ultimately led to the creation of the Joint Jack Mackerel (JJM) model, which is currently used to assess the population status of Jack mackerel in the South Pacific Ocean (SPRFMO 2023: SC11-Report-Annex 7). This tool allows for ongoing monitoring of the resource and its fishery throughout its range of spatial distribution, which is essential for achieving sustainable development of this species (Sexton et al., 2017). Additionally, simulation tools such as species distribution models (SDM) or ecological niche models (ENM), have been developed to understand the influence of the environment on the spatial distribution of species (see Melo-Merino et al., 2020). These tools, which can use variables such as catches, landings, or geo-referenced biomasses (Alglave et al., 2022), address scientific questions aimed at understanding diverse research questions also including insights into the population structure. Integrated studies, such as that of Bertrand et al. (2017), using acoustic data and Jack mackerel catches in the South Pacific Ocean, have attempted to explain the habitat of this species in three dimensions. This study is a valuable contribution that seeks to reduce the uncertainty of the Jack mackerel population based on the study of their habitat. Finally, more complex models, such as the end-to-end models, have been developed to explore the effect of fishing in an ecosystem context. The study by Oliveros-Ramos (2014) makes use of the OSMOSE simulation platform in the northern Humboldt Current system, while Fulton et al. (2013) makes use of two ecosystem modelling platforms (ATLANTIS and EwE) to model the Southeastern waters of Australia, both containing a mackerel species as a modelled group, and explore the plausibility of a range of alternative spawning biomass estimates for different stock hypothesis.

4.3.4 The feasibility and/or limitations of the approach

The study of fishery dynamics can help provide evidence of the connectivity of the Jack mackerel population, and inform the stock management of the fishery. In particular, this line of research can complement the analysis of other critical stock connectivity tools, such as otolith growth analysis,

capture-mark-recapture studies as well as genetic analysis (Kerr et al. 2017). While the use of models is proving an interesting alternative to understanding connectivity and migration of fish populations (Dragon et al. 2017), its application to the Jack mackerel population has shown limitations in terms of data inputs and assumptions and should require further study. Additional challenges remain, in relation to the relationship between environmental changes and Jack mackerel population migration and movement, in particular, in respect to ENSO and decadal climatic patterns. In this sense, simulation tools could prove to be a useful contribution to connectivity studies in Jack mackerel.

The development of this line of research is feasible and extremely important, especially given the efforts to constantly monitor this species. In order to fill gaps in this discipline and contribute to the identification of stocks based on fisheries dynamics, its critical to promote the development of protocols and methodologies to collect information on fishing indicators in a systematic manner throughout the area of distribution of the species. In addition, it is important to address research questions beyond the local scale, and promote the development of comparative studies throughout the species' distribution.

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4.4 Genetics

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KEY SEARCH WORDS USED: “genetic variability” + “population structure” + “NGS” + “Jack Mackerel”

4.4.1 Background and rationale

Genetic connectivity is inferred through the analysis of population genetic structure (Hellberg et al., 2002; Hohenlohe et al., 2021). This approach assesses the geographic and temporal distribution of genetic variability within a species using different molecular markers. Genetic differentiation between populations has been studied with traditional genetic tools such as RFLP-PCR, mitochondrial DNA (mtDNA) and microsatellites; however, these methods may be limited by an insufficient number of loci in highly vagile and large marine fish populations, which are expected to exhibit subtle genetic structures (Hauser & Ward, 1998; Zarraonaindia et al., 2012; Cunha et al., 2024; Weist et al., 2024). Currently, genomic techniques provide accuracy and improve the statistical power in estimating population parameters (Walters & Schwartz, 2020). By generating hundreds to thousands of genomic markers like single nucleotide polymorphisms (SNPs), the understanding of marine populations has greatly enhanced, integrating insights from a molecular to an ecological level (Oleksiak & Rajora, 2019). In recent decades, the decreasing costs of Next Generation Sequencing (NGS) (Wetterstrand, 2024), has strengthened the population genomics studies, allowing the simultaneous analysis of many loci (regions of the genome) (Luikart et al., 2003). These modern approaches make it possible to find molecular markers regardless of the absence of prior genomic information (Bernatchez et al., 2017; Oleksiak & Rajora, 2019).

At present, population genomics plays an important role in resolving discrepancies in the delimitation of biological stocks and fishing units to prevent the loss of genetic diversity, overexploitation of stocks (Benestan, 2019), and therefore, the collapse of important fisheries (Cadrin, 2020). Genetic studies have been applied to pelagic fish, where their apparent lack of geographical barriers, migratory behaviour, large population sizes, and long-life cycles seem to promote low levels of genetic differentiation (Cowen et al., 2007), undetectable by traditional methods. Among the main groups of small pelagic fish of fishing importance are the mackerels (Manuzzi et al., 2024; Fuentes-Pardo et al., 2023; Bourret et al., 2023; Rodríguez-Ezpeleta et al., 2016), anchovies (Engraulidae) (Zhang et al., 2020), sardines (Clupeidae) (Da Fonseca et al., 2024), and herrings (Kongsstovu et al., 2022; Reid et al., 2018; Lamichhaney et al., 2012). An interesting example is the Atlantic horse mackerel Scomber scombrus, with two contingents or spawning components (north and south) in the northwest Atlantic. Under this complex structures the meristic markers (MacKay & Garside, 1969), otolithic forms (Castonguay et al., 1991), and low-resolution genetic markers such as mtDNA (Lambrey de Souza et al., 2006) or microsatellites (Gíslason et al., 2020), were unsuccessful in distinguishing contingents. However, a small but significant genetic differentiation was observed using genome-wide markers like SNPs (Bourret et al., 2023).

4.4.2 Critical appraisal of methods

Advances in technologies have made various molecular markers available for accessing genetic variability of living organisms (Schlötterer, 2004; Holliday et al., 2018), as well as a better understanding of the underlying factors shaping such variability (Bernatchez, 2016). Over the past decades, mtDNA markers have been widely used, even despite their maternal inheritance (Ladoukakis & Zouros, 2017). In certain cases, evolutionary forces may leave different signals in genetic variation, potentially leading to incorrect interpretations if a single method is used (Karl et al., 2012; Grant, 2016; Marchi et al., 2021). Furthermore, in highly mobile marine species, such as pelagic fishes, where extensive gene flow is expected, mtDNA has shown limited power to detect subtle signals of genetic differentiation compared to more polymorphic genetic markers (Healey et al., 2020; Andersson et al., 2024). On the other hand, microsatellites are DNA markers along the genome (Tautz & Renz, 1984; Bennett, 2000; Chambers, 2000; Liu, 2007) with biparental inheritance. These are more abundant in non-coding regions (Metzgar et al., 2000; Ellegren, 2004), making them less susceptible to natural selection and thus useful for reflecting neutral variation (Ellegren, 2004). Even though these markers have great potential in detecting genetic differentiation between populations (Chambers, 2000), it requires the analysis of a high number of loci, which could be a practical disadvantage compared to other methods.

Nowadays, high-throughput sequencing techniques are the most widely applied in genetic connectivity studies, as they allow the exploration of population variations across the genome. Techniques based on genomic complexity reduction (e.g., GBS and ddRAD-seq, which use restriction enzymes) and whole-genome sequencing (WGS, e.g., pool-seq, lcWGS, and WGS) are the frequent ones used for non-model and model species, respectively. GBS and ddRAD-seq have been widely used in economically important pelagic fish species, such as S. scombrus (Bourret et al., 2023), Engraulis japonicus (Zhang et al., 2020), Seriola rivoliana (Mendoza-Portillo et al., 2020), and Sardina pilchardus (Antoniou et al., 2023), demonstrating their effectiveness in finding structuring signals that could not be previously identified with traditional genetic methods. On the other hand, the WGS method has identified differentiations not detectable by RAD-seq techniques, suggesting that more regions need to be covered, both neutral and adaptive loci (Clucas et al., 2019a,b; Szarmach et al., 2021). Although achieving sufficient coverage to genotype individuals at a population scale can be very costly, an effective alternative is to sequence groups or pools of individuals (pool-seq; Schlötterer et al., 2014). With the help of a high-quality genome, the pool-seq method successfully detected genetic structuring in Trachurus trachurus (Fuentes-Pardo et al., 2023). Recently, low-coverage WGS (lcWGS) has emerged as a solution that sacrifices the depth of coverage while resolving population structure with larger sample sizes (Lou et al., 2021). This method has been applied in pelagic fish such as Clupea harengus (Kongsstovu et al., 2022) and S. pilchardus (Da Fonseca et al., 2024), where SNPs were able to confirm and correct stocks previously considered for sustainable fisheries management.

SNPs variants under selection or locally adapted loci have become a key point of discussion due to their high resolving power compared with neutral loci. Local adaptation refers to the idea that members of local populations often exhibit a greater mean fitness in their natural habitat than in others (Benestan, 2019). This process involves the spread of advantageous phenotypic traits-associated genetic variants due to directional selection driven by local environmental conditions (Vatsiou et al., 2015). Simulation-based modelling has demonstrated that inferences about local adaptation based only on neutral genetic markers run the risk of misidentifying the underlying mechanisms driving population structure (Landguth & Balkenhol 2012). This is particularly evident in marine species, where large effective population size and high gene flow reduce the neutral population divergence but contribute to adaptive divergence through selection. For example, in Atlantic herring, nearly 170,000 neutral SNPs could not discriminate between two main populations, while 10 SNPs under selection in genomic regions related to the timing of reproduction, differentiated them (Han et al., 2020).

4.4.3 Applicability to jack mackerel or other small pelagic

Jack and horse mackerels of the Trachurus genus are medium-sized pelagic fishes belonging to the family Carangidae. Due to their high mobility in the pelagic zone, some species are economically important transboundary resources for regional fisheries. Their economic relevance has prompted considerable research on certain taxa, including studies on population genetic variability, but for most members of the genus, such information remains limited or absent. Research on genetic structure and connectivity patterns has primarily focused on the East Atlantic and Mediterranean Sea, with T. trachurus being the species with the most available genetic data.

For Trachurus murphyi, reports done by Chile indicate no genetic differentiation (Galleguillos & Torres 1988; Arancibia et al., 1996; Sepúlveda et al., 1996; Cárdenas et al., 2009; Serra et al., 2010; Canales-Aguirre et al., 2010; Galleguillos et al., 2012; Serra et al., 2014; Ferrada-Fuentes et al., 2023). However, the lack of significant differentiation could be due to either extensive gene flow among sampled localities, large population sizes, or insufficient resolution power of the genetic methods used. Cárdenas et al., (2009) studied adult fish from 3 sites of Chile, New Zealand, and one oceanic site off the Chilean coast, using four heterologous microsatellite markers and the mtDNA control region. They reported no significant differences, except for a comparison between San

Antonio and the oceanic sample in the control region, contradictory with their microsatellite analysis. Serra et al., (2010), Canales-Aguirre et al. (2010) and Ferrada-Fuentes et al., (2023) used different microsatellite loci across Chile, Peru, and New Zealand, found no genetic differences among localities

Even the increase of the sample size and the geographic coverage, conclusions were limited by the use of the number of heterologous microsatellites and the lack of a temporal sampling design. Later, one small sample site from Peru (Lobos de Afuera island) and two from Chile (Talcahuano and Chiloé) were analysed using only eight species-specific microsatellite loci, reporting non-significant differentiation (Galleguillos et al., 2012). Even though this result was consistent with previous studies, they cautioned against the small sample size (15 specimens per location). It is important to highlight that the reduced number of molecular markers and of sampling size do not allow conclusions to be made about the population structure. Serra et al. (2014) and Ferrada-Fuentes et al., (2023) also analyzed microsatellite loci in localities across the South Pacific Ocean (Peru, Chile, and New Zealand), compared samples from spring and summer (reanalyzed in Canales-Aguirre et al., 2024),. Although there was an improvement in the sampling size, the small number of molecular markers used limited the resolution of the genetic analysis. However, the availability of genetic markers for this species remained limited to less than ten microsatellite loci. Recently, Ferrada-Fuentes et al., (2023) reported SNPs to identify 11,588 neutral and 484 adaptive loci in 332 individuals from 16 locations across Chile, Peru, and New Zealand (samples collected between 2007-2022), reporting low differentiation in oceanic Chilean locations with neutral loci, and strong differentiation between New Zealand and all locations in the South Pacific Ocean (Chile and Peru) with adaptive loci. Regarding this study, concerns about the sampling design and the interpretation of the statistical analysis were expressed (SPRFMO, 2023). Some have suggested that the highly migratory behaviour of adult fish and the potentially wide dispersion of eggs and larvae could explain the lack of genetic differentiation in pelagic marine species (Graves, 1998; Hauser & Ward, 1998), including some Trachurus species (Karaiskou et al., 2003, 2004; Kasapidis & Magoulas, 2008). Later, this generalisation was revisited with the availability of more sensitive genetic methods, which in some cases, revealed subtle genetic structure when thousands of neutral SNPs are analysed, as well as putative local adaptation based on non-neutral loci (Hauser & Carvalho, 2008; Fuentes-Pardo et al., 2023).

In the Eastern Atlantic and Mediterranean Sea, early studies on the genetic structure of T. trachurus showed no genetic differentiation when analysing mtDNA sequences (Karaiskou et al., 2003; 2004). These studies covered a large part of the species' range, from the Aegean Sea to the Balearic Sea in the Mediterranean, and from the coasts of Portugal to the North Sea. Subsequently, other genetic and non-genetic studies for stock identification of T. trachurus were conducted in ICES fishery areas and the Mediterranean Sea (Abaunza et al., 2008). Analyses using three mitochondrial markers (Comesaña et al., 2008), and four microsatellite loci (Kasapidis & Magoulas, 2008) found no evidence of genetic structure. The consensus explanation for the lack of genetic structuring was that the species' dispersal ability appears to counteract the factors that could promote isolation

between geographically distant individuals or those coming from different spawning aggregations (Comesaña et al., 2008; Kasapidis & Magoulas, 2008). Contrary to previous reports, Sala-Bozano et al., (2015) found genetic differentiation between individuals of T. trachurus from the coasts of Norway and Ireland, showing temporal variations over three years. This suggests the presence of different populations that inhabit or visit the North Sea at different times. Recently, the first largest and most comprehensive genomic study of the Atlantic horse mackerel was conducted by Fuentes-Pardo et al. (2023). They applied the pool-seq approach on 11 pools of individuals from most of the geographical range in the northeast Atlantic and western part of the Mediterranean Sea, based on spatial and temporal data. While low genome-wide differences were found among locations with neutral markers, potentially adaptive loci and a putative chromosomal inversion explained high differentiation. The population structure analyses identified five genetic groups, consistent with the stock delimitation proposed by Abaunza et al. (2008).

In the Western Pacific, early genetic studies in greenback horse mackerel (Trachurus declivis) have been reported using traditional markers. Smolenski et al., (1994) reported a lack of differentiation between Southeastern Australia and Tasmania using RFLPs of mtDNA. However, differentiation between temporary samples within Tasmania suggests the possibility of genetically distinct schools. For T. picturatus, a species whose geographic range partially overlaps with T. trachurus, genetic differences were initially detected between the southern Aegean Sea (Mediterranean) and Portugal (Northeast Atlantic) using mtDNA (Karaiskou et al., 2003). However, a subsequent evaluation with PCR-RFLP analysis of the mtDNA control region did not support these results (Karaiskou et al., 2004). Later, Moreira et al., (2019) obtained similar results using mtDNA markers. Moreira et al., (2020) suggested a metapopulation model with significant seasonal gene flow. However, for other Trachurus species distributed in the Eastern Atlantic and Mediterranean (Trachurus trecae, T. mediterraneus), genetic studies have reported contrasting results. Existing data are limited, often relying on a small number of loci or a single type of molecular marker and lacking temporal replicates to assess the stability of the observed signal (Sardinha & Naevdal, 2002; Karaiskou et al., 2003, 2004).

Among small pelagic fish, a long-distance migratory species is the Atlantic mackerel Scomber scombrus, with genetically differentiated populations in the Northeast and Northwest Atlantic (Nesbø et al., 2000). Recently, Bourret et al. (2023) studied populations using ddRAD-seq, finding significant genetic separation between the northern and southern contingents and achieved a genetic assignment accuracy of over 85% for the two contingents. For the European sardine S. pilchardus, five microsatellite loci resolved some but limited population structure (Kasapidis et al., 2011). In contrast, a subsequent study using SNPs obtained from WGS of 108 individuals, from the Eastern Mediterranean to the archipelago of the Azores, identified two possible barriers to gene flow and at least three genetic clusters (Da Fonseca et al., 2024). For C. harengus, SNP-based genomic analysis revealed significant adaptation of populations to different environmental

conditions and spawning behaviours, suggesting that population structure is more complex than usually typically considered in stock management (Kongsstovu et al., 2022; Andersson et al., 2024).

4.4.4 The feasibility and/or limitations of the approach

Genetics is one of the main approaches for evaluating the connectivity of marine populations due to its cost-efficient methods and significant contribution to the understanding of population structure.

Genetic information serves as a natural label that avoids the difficulties associated with the capture and release of wild organisms, which are necessary in other approaches.

Connectivity studies using GBS and RAD-seq are very common at a wide variety of species, mainly due to their efficiency, low cost, and versatility; however, they have some limitations. For example, uncontrolled genomic fragmentation often results in many markers from intergenic regions, making it difficult to answer questions about selection processes (Holliday et al., 2018). Additionally, high levels of missing data can occur due to insufficient sequencing depth or polymorphic restriction sites (Holliday et al., 2018). Alternatively, the WGS and lcWGS are promising options that have been recently applied, though they require a good-quality reference genome for the SNP calling and a large number of individuals per population (Lou et al., 2021; Fuentes-Pardo & Ruzzante, 2017). Fortunately, two Trachurus genomes have already been, T. trachurus (Genner & Collin, 2022) and T. murphyi (genome not published, Ferrada-Fuentes et al., 2024), which will provide important information for future WGS studies. The analysis of neutral and adaptive loci should also be considered to understand fluctuation in population genetic variability and connectivity. For instance, when interbreeding between two or more groups is interrupted or reduced, these groups will eventually develop distinct genetic pools, indicating restricted connectivity or local adaptation under high gene flow. Likewise, markers under selection, in addition to neutral markers, reflect environmental influence and offer insights beyond other approaches where differences may arise from phenotypic plasticity rather than reflecting restricted gene flow and the presence of distinct populations.

As was previously highlighted, different aspects such as sample size, temporal replicability, coverage of different habitat types (spawning, nursery and feeding sites), and key life history stages (early life stages and reproductive period) of pelagic fish species, deserve careful attention during the sampling design. Therefore, population structure analysis with a spatial and temporal criterion, and an holistic approach, should be prioritised for jack mackerel, due to its possible low levels of genetic differentiation, and population expansions and contractions influenced by environmental drivers in a shorter term (EL Niño and La Niña events), medium-term (PDOs), and longer-term climate change. In this sense, a well stratified sampling design should be proposed, in order to properly capture the dynamics of this species throughout its distribution range, taking into account the different hypothesis to be evaluated (SPRFMO, 2021).

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4.5 Habitat

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KEY SEARCH WORDS USED: “habitat”+”Jack mackerel”+ “small pelagics” “habitat + jack mackerel + connectivity + small pelagic”

4.5.1 Background and rationale

Connectivity, defined as the exchange of larvae, juveniles, or adults across a species' range (Palumbi, 2003), is a vital component of population and fishery ecology, influencing fundamental processes such as population dynamics, evolution, and community responses to climate variability (Kool et al., 2013). Habitat connectivity plays a crucial role in shaping the population structure of marine species (O’Donnell et al., 2022). Identifying connectivity between essential habitats throughout a species' lifespan is key to understand the ecology of the species and is useful for fishery management, as it determines the appropriate spatial scale for fishery assessment and management efforts (Begg & Waldman, 1999). In this sense, abundance and distribution of fish are subject to the extension or shrinking of their habitat (Bertrand et al. 2010). Moreover, different pelagic species utilize multiple habitats during different life stages, so connectivity between these habitats is crucial to allow for ontogenetic migrations and access to resources (Perry et al., 2018). In addition, as human activities continue to eliminate or fragment habitats, an understanding in connectivity becomes increasingly important. However, determine connectivity is extremely challenging, as it requires understanding the demographic consequences of fish movement across potentially large spatial scales in complex climate variability.

These factors constitute a significant challenge, especially for highly migratory species with wide distribution ranges like the Chilean jack mackerel (Trachurus murphyi, hereafter referred to as JM). The species' ability to undertake long-distance migrations that often cross international jurisdictions or ocean boundaries (Rooker et al., 2014) and the often poorly understood migratory behaviors make this work even more challenging. This is further complicated by the fact that most biological information about JM in the South Pacific is focused on national Exclusive Economic Zones (EEZs).

Although some multidisciplinary research has been conducted in the past to study the population structure of the jack mackerel (e.g. Serra et al., 2010, 2014) and their relationships with the climate variability (Bertrand et al., 2016; Grados et al., 2021), the need for a comprehensive and integrated research plan to better understand the origin and admixture of populations or subpopulations of JM in the southern Pacific has been highlighted (SC9-JM08, SPRFMO-SC9-Final-Report). To address this, the Task Group on Connectivity of JM was established. Its terms of reference include conducting a desktop analysis to compile all existing knowledge and data on the species and issues related to stock identity, as well as hierarchically analyzing the evidence to identify sources of information related to population connectivity (SPRFMO-S10-Final-Report). This document reviews the implications of habitat connectivity in studying the population structure of pelagic organisms, with a focus on the JM.

4.5.2 Critical appraisal of methods

Connectivity is likely to depend not only on the distance between the essential habitats during the lifespan of species, but also on the presence of movement among them. Especially in species with separated larval, juvenile and adult habitats, this connectivity can have important contributions to the population structure and the sustainability of the species.

Connectivity between spawning and juvenile habitats

Most marine species have life histories that include at least one potentially widely dispersive stage. For several species, this dispersive stage is typically the pelagic larval stage, where the larvae may be transported by ocean currents. The extent of successful dispersal is a major determinant of population dynamics, alongside overall birth and death rates (Pineda et al., 2007). When dispersal is combined with factors that influence the survival of dispersed organisms, the concept of population connectivity becomes relevant. Understanding the drivers of larval dispersal is an inherently biophysical problem: biological in the sense of processes that influence offspring production, growth, development, and survival; physical in the sense of advection and diffusion properties of water circulation; and biophysical in the sense of interactions between certain larval traits (e.g., vertical swimming behavior) and physical properties of the environment that operate at various scales. Information on the true scale of larval dispersal is often limited because dispersal distances are notoriously difficult to measure directly. Several means of determining dispersal distances exist, ranging from studies of single spawning events and subsequent dispersal of the young to more synthetic estimations over multiple generations.

Both direct and indirect methods using geochemical and genetic markers, as well as sophisticated coupled biophysical models are available (see Cowen & Sponaugle, 2009 for a review). Given the extensive effort required to track a single reproductive event from a single source location, alternative methods must be sought to identify realistic dispersal kernels. One alternative approach to estimating dispersal distances, with the potential to calculate dispersal kernels, is the use of high-resolution biophysical models. Although considerable caution is warranted in the use of models, one clear advantage over the aforementioned indirect and direct methods is that models allow for multiple releases of virtual larvae. While each individual model run is equivalent to an isolated measurement of a dispersal event, the modeling approach enables repeated measures across time and space, thereby capturing expected environmental variability and allowing for the construction of a connectivity matrix. Models are also powerful tools when combined with field and empirical methods. In addition to their utility in resolving spatial scaling patterns, models are critically important for understanding the processes contributing to these patterns.

Connectivity between juvenile and adult habitats

Gillanders et al (2003) review a total of 110 studies in which most of them (~98%) showed movement from juvenile to adult habitats in fish. This horizontal transfer of organisms between juvenile to adult habitats can result in substantial movement of biomass in which nursery habitats can be define. Nursery habitats are a subset of juvenile habitats. Generally, a habitat is considered as a nursery if juvenile fish occur at higher densities with lower rates of predation or have higher rates of growth compare to other habitats. However, this consideration does not address if these juvenile habitats successfully transfer the higher juvenile biomass to the adult populations (Beck et al. 2001). In this sense, it is critical to measure movement of individuals from juvenile to adult habitats.

Different methods have been used to determine movement from juvenile to adult habitats (Table 2 in Gillanders et al. 2003). These methods generally involve identifying changes in size or age structure of organisms in different habitats or sites, over time either as individuals or as a group. Though direct measurements are preferred, much of the information on movement of juveniles comes from indirect sources, like differences in distribution, abundance and size structure, and differences in physical stages of maturity.

Connectivity across adult habitat

Fish connect habitats through the exchange of biomass and energy via ontogenetic migrations, larval dispersal, and daily movement. Given that mobile species, such as the JM, utilize multiple oceanic habitats, understanding patterns and processes at a seascape level is crucial (Perry et al., 2017). As environmental variability, climate change, and human activity can modify and fragment the habitats of marine species, affecting connectivity patterns, it becomes imperative to define environmental thresholds and critical climate processes. For mobile species, it is expected that their spatial structure and migratory patterns will adapt to significant habitat changes or fragmentation, with medium-term consequences being less severe compared to stationary species (Caldwell and Gergel, 2013). Marine connectivity encompasses a range of interlinked forms, including genetic, functional and structural. **Functional connectivity** relates to the movement of organisms through the ocean as a result of their ecological characteristics, such as habitat preference and dispersal ability (Olds et al. 2016). In contrast, **structural connectivity** relates to the physical characteristics of the ocean that allow for movement, for instance, oceanographic features such as eddies, currents and fronts, or benthic (seafloor) structure (Wells et al. 2008).

4.5.3 Applicability to jack mackerel or other small pelagic

Others studies focused in the study of spatial and temporal connections of small pelagic cohorts (Silva et al., 2019), the study showed low movements between different regions in the sardine of Europe.

In general, we can observe, for the case of small pelagic fish, they can exhibit complex population structures, with a varying degrees of connectivity driven by a combination of larval dispersal, adult migration and recruitment dynamics. Accounting for these spatial and temporal patterns is crucial to understand the habitat connectivity of marine species.

Evaluating functional connectivity in the marine ecosystem is particularly challenging, especially for species with wide distributions that form large schools with heterogeneous age structures. Among the tools available for studying functional connectivity, mark-recapture investigations are especially powerful, particularly when tags are applied at young-age specimens (Neilson et al., 2006). For the JM, there have been no successful large-scale mark-recapture studies across its distribution range. The understanding of its functional connectivity primarily comes from observations and direct tracking of certain cohorts through commercial fisheries, which have demonstrated long-distance migrations across the South Pacific (i.e. Corten, 2014). Although the feasibility of a tagging system for JM will be evaluated in a specific chapter of this desk study, it is worth noting that the current configuration of the JM fishing industry, where the majority of the catch is destined for human consumption, enhances the applicability of developing a regional tag-recapture program to study functional connectivity. Understanding larval dispersal is crucial for assessing functional connectivity, especially in species with a long pelagic larval duration, such as JM. However, estimating and predicting larval dispersal poses a challenge for species with a wide spawning range and a multiple-spawning reproductive strategy. Larval transport can be inferred from the spatial distribution of spawning and larvae of different ages, as previously suggested for JM (Vásquez et al., 2013). While individual larvae have been tracked (i.e. Almany et al., 2007), the majority of dispersal estimates are derived from biophysical simulations and population genetic approaches. Genetic evidence suggests mean dispersal distances of marine fish species are in the order of ten to thousands of kilometers (Cowen et al. 2007). This approach has been widely used in small pelagic species (e.g., Ospina-Álvarez et al., 2015) to assess functional connectivity between spawning and nursery grounds. Given the availability of high-resolution circulation models for the southeastern Pacific and previous experiences with JM (Vásquez et al., 2015), the application of biophysical modeling schemes can be a highly effective tool in a multidisciplinary population connectivity project.

Habitat suitability models are valuable tools for assessing seascape structural connectivity, which represents ecological linkages and flows across heterogeneous environments. These flows typically involve the movement of organisms, energy, nutrients, or genetic material. The magnitude and location of these exchanges are shaped by patterns of intra- and inter-habitat connectivity, with the latter being especially crucial for species whose movements span multiple habitat types (Stuart et al., 2021). Habitat suitability models for JM have already been developed (e.g. Li et al., 2016; Bertrand et al., 2016), revealing that horizontal patterns of productivity and temperature and vertical patterns of dissolved oxygen can play a determining role in the structural connectivity of the habitat at different temporal scales. The applicability of this methodology within an integrated regional approach, utilizing a more extensive database of JM records across its distribution area, could enhance our understanding of the structural connectivity patterns throughout the South Pacific. This is particularly important in relation to ENSO dynamics, the primary modulator of interannual habitat changes in the southeastern Pacific (Arcos et al., 2001; Ñiquen & Bouchon, 2004).

4.5.4 The feasibility and/or limitations of the approach

It is critical to measure movement of individuals if we want to understand which juvenile habitats contribute more per unit area to the production of individuals that recruit to adult populations. In the case JM this becomes increasingly important due to the gap in knowledge about this specie population structure and the extensive fishery that each habitat can be subject. In this sense, is necessary to collect data in all the distribution of JM (juvenile and adult habitats) that will allow management and conservation efforts to focus on those habitats that make the greatest contributions to adult populations.

For the data collection, based on the methods explain above, there is a clear need to obtain information on abundance and size distribution of organisms from a range of juvenile and adult habitats, and to sample at multiple locations within each type of habitat.

The feasibility of a mark-recapture program to assess functional connectivity will be evaluated in a specific chapter of this desk study. However, it is worth noting that the current configuration of the JM fishing industry, where the majority of the catch is destined for human consumption, enhances its applicability. Some limitations may arise in tagging juvenile individuals due to the size of the tags.

There is potential to improve JM occurrence databases through the SPRFMO Secretariat to support habitat suitability modeling approaches at various spatio-temporal scales. High-resolution 3D circulation models and surface satellite data are available for environmental variables describing the habitat. However, one limitation is the vertical extent of observations, despite the availability of validated 3D hydrodynamic models. Another limitation is the low observation coverage of JM spawning across its distribution area, which is crucial for modeling connectivity between spawning and nursery grounds.

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4.6 Otolith Microchemistry

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KEY SEARCH WORDS USED: “Jack Mackerel” + ”Microchemistry” +”Otoliths” + ”Trace elements” + ”Stable isotopes”.

4.6.1 Background and rationale

Otoliths are polycrystalline structures that increase in size through the periodic deposition of materials throughout the fish life (Morales-Nin, 1984). They are metabolically inert, so it is unlikely that the deposited material will be reabsorbed or altered (Campana & Neilson, 1985). They are composed by an organic protein matrix (1-3%), calcium carbonate in its crystalline polymorph aragonite (95-98%) and trace elements (<1%). Some elements reflect the chemical composition of the water in which the fish inhabits (Campana, 1999). Since water bodies often differ in trace element concentrations, populations can often be distinguished by the chemical signature retained in the otoliths (Begg and Waldman, 1999; Sturrock et al., 2012). However, the elemental composition of otoliths is influenced by various extrinsic factors (e.g., temperature, salinity, pH) and intrinsic factors (e.g., diet, ontogeny, genetics), so the relationship between the chemical concentration in the otolith and the environment is not completely understood (Reis-Santos et al., 2008; Izzo et al., 2016).

Otolith chemistry has increasingly gained attention as a tool for analyzing various aspects of fish biology, such as population dynamics, migration patterns, exposure to hypoxia and pollution, and habitat connectivity (Hüssy et al., 2020). The chemical analysis of different areas in the otolith can answer different questions about the life history of the fish. For example, otolith core chemical analysis is often used to identify spawning and nursery areas (Brown, 2006; Rooker & Secor, 2004), while analysis of transects from the core to the edge of the otolith allows the evaluation of environmental variability and migration patterns (Elsdon and Gillanders, 2003; Volpedo & Vaz-dos-Santos, 2015). These characteristics suggest that otoliths chemical print is a good natural marker for fish populations and can be used to discriminate between population units or stocks (Panfili et al., 2002).

Regarding the jack mackerel Trachurus murphyi, only two studies have been carried out based on microchemistry. Markwitz et al. (2000) performed micro-measurements of stable Sr content in otoliths using micro-PIXE, relating them to macro measurements from 2D maps to determine the pattern of strontium deposition; despite not being a stock determination study, it proposes Sr as an element that can evidence environmental changes. On the other hand, Ashford et al. (2011) used LA-ICP-MS methodology to detect Sr:Ca, Ba:Ca, and Mg:Ca ratios in the core and rim of otoliths.

They observed spatial heterogeneity between the putative boundaries of the South-Western and South-Eastern Pacific Ocean, and between Peru and Chile in edge analysis. However, they did not find clear differences indicating defined population boundaries between Chile, Peru, and New Zealand in the core analysis, with the exception of a small, highly distinct group in northern Peru. These results suggest a complex spatial structure defined by survival and connectivity driven by the oceanographic conditions of the Subtropical Front.

4.6.2 Critical appraisal of methods

Undoubtedly, the characteristics of teleost fish otoliths allow the application of microchemistry analysis to elucidate connectivity and life history of different hydrobiological resources. Currently, there are two methods widely used for microchemistry analysis, and ideally are performed simultaneously: Trace elements analysis and Stable isotopes analysis.

Trace element analysis is usually performed through Inductively Coupled Plasma Mass Spectrometry (ICP-MS) to measures element:Ca ratios in the otolith. ICP-MS samples can be extracted from the otolith through solution-based (SB-ICP-MS) extraction or laser ablation (LA-ICP-MS) (Campana, 1999). The more common elements analyzed for stock discrimination and connectivity studies are Sr, Ba and Mg. Strontium is highly correlated to salinity and often used to detect changes between fresh and estuarine waters from sea water, Ba also is sensitive to changes in salinity and otoliths from fishes with higher growth rates have higher Ba:Ca ratios, and Mg is highly physiologically regulated, where higher Mg:Ca ratios indicate a higher metabolism (Hüssy et al. 2020). Nonetheless, other element:Ca ratios can be used depending on their concentrations and spatial variability (Niklitschek et al. 2018).

The second method is Stable Isotopes analysis through Isotope-Ratio Mass Spectrometry (IRMS) to measure stable isotopes proportions (e.g. 18O:16O, noted δ18O). The most commonly used are 18O and 13C, but other stable isotopes can be used if required. Oxygen 18 has the characteristic of being completely regulated by the environment, mostly by salinity, and by temperature to a lesser extent. In salinity homogeneous environments as the Southern Pacific Ocean, it can be used to analyze changes in temperature (Campana, 1999). On the other hand, 13C is directly correlated to the dissolved inorganic carbon (DIC) concentration of the environment, but between 10-30% of the 13C concentration in the otoliths comes from the fish’s diet (Campana, 1999).

However, the process of dissolved ion transport across several membranes prior to accumulation in the otoliths is not yet clear; this indicates that otoliths are subject to the understanding of how certain processes such as feeding habits and diet, ontogenetics , genetics , temporal variability of chemical signatures in sea water, lack of chemical heterogeneity in the environment, among others, affect the chemical composition of the otolith as well as the need to sample all sources contributing to the evaluated population (Tanner et al., 2016).

4.6.3 Applicability to jack mackerel or other small pelagic

In 2018 Moreira et al. evaluated the existence of different population units of the Blue Jack Mackerel, Trachurus picturatus, in the North-Eastern Atlantic Ocean based on the analysis of elemental and isotopic signatures using solution-based inductively coupled plasma mass spectrometry (SB-ICP-MS) and Isotope-Ratio Mass Spectrometry (IRMS) for detecting Sr:Ca, Ba:Ca, Mg:Ca, Pb:Ca, Li:Ca, Fe:Ca, and Mn:Ca ratios, as well as δ18O and δ13C isotopes. They found variability in chemical composition among the sampled areas; however, they could not determine the existence of distinct populations since it was not possible to precisely identify if any areas had shared the same habitat. They suggested including complementary techniques for a better understanding of the connectivity and population structure of this species. Subsequently, Moreira et al. (2022) conducted another study on the same species to infer its scale of geographic variation between fishing areas and years. They analyzed Li:Ca, Mg:Ca, Sr:Ca, and Ba:Ca ratios using LA-ICP-MS. Their results suggest some degree of self-recruitment in the fishing areas and that the four sampled subpopulations in the North-East Atlantic are primarily connected through larval and juvenile dispersal. They concluded that T. picturatus populations in this area should be considered and managed as distinct population units.

The determination of stock structure in Mediterranean horse mackerel T. mediterraneus was also addressed with this approach. Turan (2006) used morphometry and chemical composition of otoliths to discriminate populations. He analyzed trace elements Ba, Ca, K, Mg, Mn, and Na using ICP-OES from otoliths of samples from four Mediterranean seas. However, the results showed no clear geographic pattern, and he suggested incorporating molecular genetic techniques to aid in population differentiation.

In other pelagics such as Engraulis encrasicolus, microchemistry of otolith cores from fish of different ages was evaluated to assess differences in spawning areas, but no results were observed in spawning patterns (Guidetti et al., 2013). Cuevas et al. (2019) used LA-ICP-MS to measure trace elements in Engraulis ringens cores and edges, and compared their ratios between central Chile and northern Patagonia, finding highly significant differences in the core's chemical print, suggesting two different spawning zones. However, the low significant differences in edge analysis suggest that mixing between populations occurs during the year or that they represent pocket units from a larger population unit. Similarly, microchemical analysis of Rastrelliger brachysoma otoliths identified four mackerel populations; however, they recommended confirming the study with mitochondrial DNA analysis, life history studies, and population dynamics of the four populations individually (Koolkalya et al., 2020). On the other hand, Fink-Jensen (2021) used microchemical analysis from core to edge of otoliths in Mallotus villosus, successfully tracking the fish's residency throughout its life and linking otolith chemical signature patterns to sea physicochemical changes.

4.6.4 The feasibility and/or limitations of the approach

The delineation of population units of the genus Trachurus based on otolith microchemistry constitutes a promissory study (Fujinami et al, 2024; Ashford et al. 2011). There is only one study in that line in Trachurus murphyi¸ which concluded that there is high heterogeneity in the chemical composition of otoliths across the Southern Pacific Ocean based in otolith edge analysis, but did not find differences in chemical composition of the otolith cores, suggesting a common spawning zone for T. murphyi in the oceanic waters of the Southern Pacific Ocean (with the exception of a tiny group in northern Peru) and concluding that the connectivity in this species is driven by oceanographic conditions related to the Subtropical Front (Ashford et al. 2011). Nevertheless, this study did not account for the effect of ontogeny in the chemical composition of otoliths, and other studies have reported that the otolith chemical print may vary interannually (Campana & Thorrold, 2001; Hamer et al. 2003; Swearer et al. 2003), which could have influenced the heterogeny found in the analysis of the otolith edge. To reduce the ontogenic effect, individuals of the same age class should be analyzed, and sampling should consider the year of capture and seasonality in order to reduce the effect of interannual and seasonal variations in the otolith chemistry that could mislead researchers' interpretations (Campana, 1999; Gillanders, 2002; Tanner et al. 2016).

The scarce research on T. murphyi's otolith chemical print lays the necessity to carry out new research, improving the methodology by assessing and reducing the effects of extrinsic factors that may affect the otolith chemistry and incorporate stable isotopes analysis beside trace elements (Rooker & Secor, 2004) with a holistic approach, using complementary techniques as molecular genetics, otolith morphometrics (Tanner et al. 2016), and comprising a wider spatio-temporal range (Nazir & Khan, 2021) to reach a more complete understanding of the population structure and the stock identification, collaborating among the SPRFMO member countries.

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4.7 Geometric morphometry

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KEY SEARCH WORDS USED: "otolith shape"+ "body shape" + "stock discrimination"+"Jack Mackerel"

4.7.1 The background and rationale

Oceanographic features such as currents, fronts, and upwelling cells have been recognized as possible factors driving population differentiation within species. The shape of otoliths is species-specific and often varies geographically within species in relation to environmental factors (e.g., temperature, salinity) and other environment-associated attributes (e.g., diet composition) (Cardinale et al., 2004; Vignon and Morat, 2010; Mille et al., 2016).

Body morphometric analysis is one of the widely used methods for differentiating fish stock units (e.g., Taylor and McPhail, 1985; Melvin et al., 1992; Hurlbut and Clay, 1998; Turan, 2004). The study of morphometric characters, in addition to being one of the first techniques to be used for this purpose, has been subject to numerous improvements in recent years, due to the development of new methods and tools to record, describe and analyze shapes in fish (Rohlf and Bookstein, 1990; Marcus et al., 1996; Cadrin and Friedland, 1999; Moreira et al. 2020).

The body shape of a fish is defined from the interaction between environmental and genetic factors, especially those that occur linked to early stages of development. Therefore, body shape represents a phenotypic expression but influenced by environmental variations. Morphometric variations with growth can change between different locations, and these can be used for the discrimination of stock units (Cadrin and Friedland, 1999).

In fact, for this purpose, phenotypic traits may be a usable complement to genetics. This is because low or weak gene flow can interfere with the detection of significant genetic differences. Although morphometric differences between localities may indicate a source of population separation, or the existence of different stock units, these differences may also be caused by the influence of the environment and if there is a high mixture of individuals from different localities, the differences would then be undetectable (Murta et al., 2008).

Otolith shape should vary among stocks as long as they remain at least partially segregated. Consequently, otolith shape analysis is used independently or in combination with other disciplines to identify (phenotypic) fish stocks (Campana and Casselman, 1993; Cadrin et al., 2014; Volpedo and Vaz-dos-Santos, 2015).

Body shape analysis implies: (1) capturing with a standardized photography the outline of the body, (2) establish a network of landmarks and/or fitting a geometrical model based on predefined techniques, considering the effect of fish size, and (3) based on multivariate analysis discriminate and classify groups of individuals.

Otolith shape analysis implies: (1) capturing the outline of the otolith, (2) fitting a geometric model to concisely describe the outline, and (3) using multivariate analysis of model parameter estimates to detect patterns of variance, discriminate groups, and classify individuals to groups.

The use of otolith shape analysis to identify stocks is increasing due to the development of quantitative methods for describing otolith shape, the availability of open-source software to carry out the process, and access to digital collections of otolith images (Cadrin et al., 2014).

The preference for otoliths over bodies, scales, and bones for shape analysis relies on the fact that otoliths are metabolically inert. This means that once deposited, otolith material is unlikely to be resorbed or altered, remaining unaffected by short-term changes in fish condition (e.g., starvation). Additionally, since otoliths are composed of calcium carbonate, their shape remains unaffected by the mode of fish preservation (excluding acidic preservatives, which promote dissolution).

The method for body shape analysis considers:
1) Photographs are taken with a digital camera (without using digital or optical zoom) of each complete specimen.
o Each individual is previously mounted on a white PE surface, which has an undercut where it is guaranteed that the specimen is properly arranged. As a standard method, the left side of each individual should be photographed, orienting their head to the left.
o Because the fins are retracted and it is of interest to be able to identify the exact location of the fin insertions, as part of the landmarks, colored head pins are provided to properly demarcate the insertions prior to photography.
o Before each photograph, a meter scale (in mm) must be placed as a reference ruler to calibrate the photograph and for subsequent measurements in it.

o It must be ensured that the photograph obtained is as sharp as possible and that the camera is always located in a vertical plane towards the object, therefore, photographs on inclined or blurred planes must be avoided or discarded.

2) To obtain morphometric variables, the methodology proposed by Winans (1987) is followed, which uses a network of measurements between landmarks.

o Because not all measurements are significantly related to the morphometry of jack mackerel, it is proposed to reduce the possible combinations of measurements to those chosen by Arancibia et al. (1996) and Hernández et al. (1998), based on the work of George-Nascimento and Arancibia, (1992).

o These measurements correspond to the straight lines between the points: (1-2), (1-3), (1-4), (2-3), (2-4), (3-4), (3-6), (4-5), (5-6), (5-8), (6-7), (7-8), (7-10), (8-9), which will be measured with a sensitivity of 1 mm.

o The combinations of measurements between numbers 1 to 5 will allow a characterization of the jack mackerel's head area while the rest of measurements are associated to the body shape.

3) Processing and Analysis

o Each photograph will have the information of the sample number and the existence of a reference of the measurement scale, which is with the purposes to calibrate the measurements to be made with an accuracy of less than 1 mm.

o The use of opensource software, for example Image Tool for Windows version 3.00, developed by the University of Texas Health Center at San Antonio has been utilized in previous studies of JM.

o Each JPEG image is calibrated by measuring or establishing a reference line of 10 scale meter units, which will be equivalent to 10 mm in length. Then, the measurements will be carried out, according to the plan for linking morphometric landmarks in the sequence formulated in the previous section.

o In this software, the measurements are automatically transferred to a spreadsheet, with which the measurements are stored in a digital file.

o The measurements thus obtained correspond to the Cartesian coordinates (x, y) and in pixels of the afore mentioned points and then are converted to distances (in mm).

o The method based on digital photographs reduces preparation and processing time of samples in the laboratory, reduces sources of measurement error and offers greater sensitivity in measurements.

4) Effect of fish size

o In order to obtain morphometric expressions independent of the size of the individual and to make the variance of the data constant, a function must be used that transforms the original information, which is possible through simple transformations in proportion of height (George-

Nascimento & Arancibia, 1992; Arancibia et al., 1996), through logarithmic transformations (Schaefer, 1991) or multivariate transformations (Winans, 1984).

o It is recommended, after testing which of these transformations manages to effectively remove the effect of size on the shape of the individual, through the use of Principal Component Analysis (PCA) for the total measurements made in each described function and an Analysis of Covariance (ANACOVAS) for the first three main components resulting from each PCA, the transformation initially applied by Schaefer (1991)

o In order to obtain components free of the effect of size on the shape of fish, it is proposed to use the function of Schaefer, (1991). In a similar way this correction has been use by Murta et al. (2008) in Atlantic horse mackerel, Trachurus trachurus, and for other species (Ihssen et al., 1981b; Hurlbut and Clay, 1998).

o A source of "noise" or element that can interfere in the analysis process is based on the simultaneous collection of samples, the sexual maturity of individuals, in such a way that they ideally represent groups of aggregations in similar reproductive conditions.

5) Statistical analysis

To identify the morphometric characters that explain greater differences between localities, an exploratory Multiple Discriminant Analysis (MDA) is applied using locality as a source of variation, on a covariance matrix (Winans, 1987).

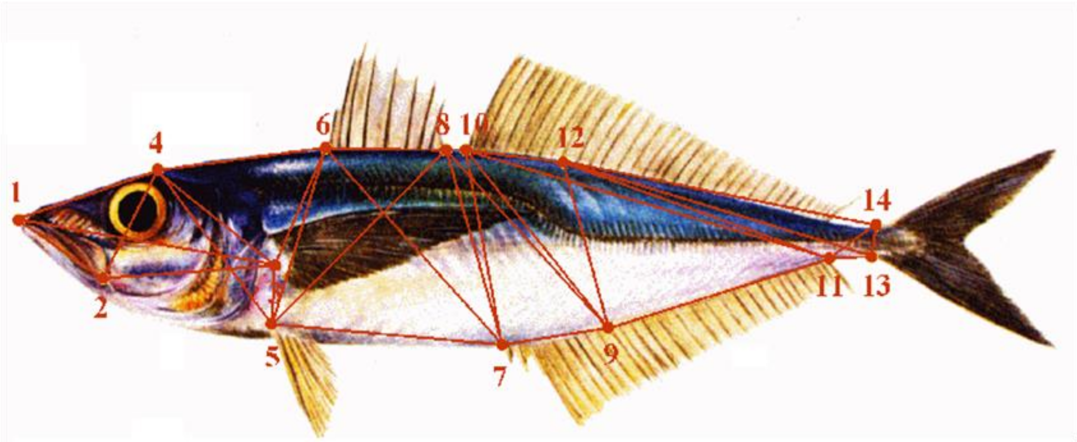

Figure 2. Example of landmarks consider in *Trachurus murphyi* and image prepared for analysis

The method for otolith shape analysis is well summarized by Stransky (2014) as follows:

1) Capturing the outline of the otolith.
    - Images of otoliths are usually recorded with digital cameras that are mounted on microscopes.
    - Image processing tools are used to enhance contrast of the image, transforming color or grayscale images to black-and-white silhouettes of the structure.
    - Image analysis software includes search algorithms to trace the outline.
2) Fitting a geometric model to concisely describe the outline.
    - The goal of mathematically modeling an outline is to describe the form accurately (i.e., achieve a good statistical fit) with the fewest number of model parameters.
    - Most outline models require the outline to be transformed into a series of radial distances from a central point to locations on its perimeter. Each radius of the series is spaced by an equal step angle of rotation from the previous radius. The unrolled series of radii is then treated as a truncated time series to be fit by the statistical model of choice. The shape can also be expressed as tangent angle functions rather than radius functions.
    - Commonly used methods for fitting outlines are Elliptic Fourier analysis and Discrete Wavelet analysis. While Elliptic Fourier analysis focuses on the overall otolith shape differences, Discrete Wavelet analysis is sensible to local differences along the otolith contour (Neves et al., 2022).
3) Using multivariate analysis of model parameter estimates to detect patterns of variance, discriminate groups, and classify individuals to groups.

- A rich selection of variables is produced from the outline shapes and then suited to parametric methods such as discriminant analysis, as well as nonparametric classification techniques such as decision trees.
- As with all multivariate analyses, standard statistical diagnostics should be explored to test assumptions and detect outliers.
- It is possible to derive a large number of shape parameters, so cross-validation of classifications from discriminant analysis (i.e., classification of extrinsic specimens with known group membership) is essential for evaluating model performance (Campana and Casselman, 1993).

The following table recap the image process software and multivariate test used to analyze otolith shapes and discriminate stocks:

Author	Specie	Image analysis software / package	Multivariate analysis
Bacha et al. (2014)	European anchovy Engraulis encrasicolus	TNPC 5.0 (NOESIS)	- Non-metric multidimensional scaling (nMDS) - Cluster analysis - Cross-validation - PERMANOVA
Cerna et al. (2019)	Peruvian anchovy Engraulis ringens	Image-Pro Plus software (Media Cybernetics, Bethesda, MD, USA)	- Generalized additive model (GAM) - Canonical discriminant analysis (CDA)
IFOP (2014)	Jack mackerel Trachurus murphyi	Image-Pro Plus (Media Cybernetics, Bethesda, MD, USA) R	- Principal component analysis (PCA) - MANOVA
Jemaa et al. (2015)	European sardine Sardina pilchardus	TNPC 5.0 (NOESIS)	- Principal component analysis (PCA) - Linear discriminant analysis (LDA) - Jackknife cross-validation - PERMANOVA
Khemiri et al. (2018)	European anchovy Engraulis encrasicolus	Shape 1.3 (Iwata & Ukai, 2002)	- Canonical discriminant analysis (CDA)

			- MANOVA - Cross-validation
Machuca et al. (2019)	Peruvian anchovy Engraulis ringens	Image-Pro Plus 5.1 (Media Cybernetics, Bethesda, MD, USA) SHAPE versión 1.3 (Iwata & Ukai 2002)	- MANOVA - Tukey multiple comparison analyses - Canonical discriminant analysis
Moreira et al. (2019)	Blue jack mackerel Trachurus picturatus	ImageJ v. 1.50i (Rasband, 2009) SHAPE, vers. 1.3 (Iwata and Ukai, 2002)	- Linear discriminant function analysis (LDFA) - Jackknifed (leave-one-out) cross-validation - PERMANOVA - Canonical analysis of principal coordinates (CAP)
Muniz et al. (2020)	Atlantic chub mackerel Scomber colias	Paintnet ImageJ Shape ver. 1.3 (Iwata and Ukai 2002)	- PERMANOVA - Linear discriminant function analysis (LDFA) - Canonical analysis of principal coordinates (CAP)
Neves et al. (2023)	European sardine Sardina pilchardus	R package “ShapeR” (Libungan & Pálsson, 2015)	- Linear discriminant analysis (LDA) - Jackknife cross-validation analysis - Hierarchical cluster analysis - PERMANOVA
Tuset et al. (2019)	Blue jack mackerel Trachurus picturatus	ImageJ 1.50i (Rasband, 2009) Age and Shape (version 1.0; Infaimon SL©, Barcelona, Spain)	- Principal component analysis (PCA) - PERMANOVA - Clustering
Turan (2006)	Mediterranean horse mackerel Trachurus mediterraneus	MorFISH v. 1.0 (Turan & Oral, 2005)	- One-way ANOVA - Discriminant function analysis (DFA) with jackknifed classification

			- Hierarchical cluster analysis - Mantel’s (1967) test
Vasconcelos et al. (2018)	Blue jack mackerel Trachurus picturatus	SHAPE, vers. 1.3 (Iwata and Ukai, 2002)	- MANOVA - Canonical discriminant analysis - Jackknife cross-validation
Zhang et al. (2013)	Japanese Spanish mackerel Scomberomorus niphonius	Image-Pro Plus version 6.0 (Media Cybernetics, Bethesda, MD, USA)	- Stepwise canonical discriminants (CDAs)

4.7.2 Applicability to jack mackerel or other small pelagic

There are several examples of using otolith shape analysis to discriminate small pelagic stocks at both global and regional scales. These examples include different species of genus Trachurus.

Regarding small pelagic fish:

- Bacha et al., (2014) investigated the population structure of the European anchovy Engraulis encrasicolus in the southwestern Mediterranean and the Atlantic Ocean through an analysis of otolith shape indices and elliptical Fourier descriptors and using multivariate statistical procedures. Their results identified three distinct anchovy populations: the Alghero-Provençal basin, the southern Alboran Sea and the Atlantic Ocean (Morocco and Gulf of Cadiz).
- Khemiri et al., (2018) investigated the stock structure of European anchovy Engraulis encrasicolus caught in the open sea and in the coastal area of the Gulf of Tunis, Bizerte lagoon and Ichkeul lake using otolith shape (Fourier) analysis and comparing them with a canonical discriminant analysis, suggesting a clear differentiation between open sea and inland groups.
- Jemaa et al. (2015) analyzed European sardine Sardina pilchardus at 15 localities in the northeast Atlantic and Mediterranean using otolith shape ratings and elliptical Fourier descriptors. They identified three distinct groups: Group A corresponding to the northern Mediterranean Sea and Gulf of Gabès; group B to Atlantic Morocco-south Alboran-Algerian-Provençal coasts; and group C to the European Atlantic coast. The results underline the importance of considering phenotypic stock identification for sustainable fisheries and effective conservation.
- Neves et al. (2023) performed a comparative analysis using the Elliptical Fourier descriptor (EFd) and the Discrete Wavelet descriptor (DWd) to reconstruct the population structure and connectivity patterns of the European sardine (Sardina pilchardus). Both descriptors

supported the division of Mediterranean populations into three main groups and suggested migration between adjacent areas, including localities in the north Atlantic, the eastern Mediterranean and across the Strait of Gibraltar, connecting the Atlantic and the western Mediterranean.

- Machuca et al. (2019) analyzed the peruvian anchovy Engraulis ringens in three zones off the coast of Chile: 1) Arica-Iquique, 2) Coquimbo, and 3) Talcahuano-Valdivia, and performed a morphometric analysis that included basic measurements, shape indices, and contour analysis (elliptical Fourier analysis). They found significant differences between zone 3 and zones 1 and 2, concluding that otolith shape analysis could be used to discriminate between population units, with better results achieved using elliptical Fourier coefficients compared to shape indices alone.
- Cerna et al. (2019) analyzed the phenotypical variability in otolith shape of the Peruvian anchovy Engraulis ringens across three zones (I, II, and III) from north to south along the Chilean coast, using juvenile and adult fish. They utilized shape indices and elliptical Fourier harmonics in their analysis. The results support the hypothesis that juveniles and adults of anchoveta have remained segregated throughout their entire, or at least a fraction of, their life cycle, mainly between the extreme northern and southern zones.

Regarding Jack mackerel:

- Vasconcelos et al. (2018), analyzed the population structure of blue jack mackerel (Trachurus picturatus) in the northeast Atlantic. For this purpose, they applied analyses of geometric morphometry and otolith shape in three areas: Madeira, Peniche and the Canary Islands. The results showed significant differences between areas, indicating the existence of at least three distinct populations of this species in the northeast Atlantic.

- Moreira et al. (2019) evaluated the efficiency of otolith shape to infer the population structure of blue jack mackerel (Trachurus picturatus) in the northeast Atlantic, through otolith shape indices and elliptical Fourier descriptors by uni- and multivariate statistical analyses, identifying three distinct spatial groups: group 1 with samples from the Azores; group 2 with samples from the Canary Islands; and group 3 with samples from Madeira and mainland Portugal.
- Tuset et al. (2019), quantified the phenotypic variability of otolith outline of blue jack mackerel (Trachurus picturatus) in the Canary Islands using wavelets, revealing three phenotypes (M1, M2 and M3) in similar proportions. These phenotypes showed temporal variations related to spawning, recruitment and feeding, but not to sex, age or size. The results support a model of local migratory triangles and contingent theory.
- Turan (2006) evaluated the shape and otolith chemistry of Mediterranean horse mackerel (Trachurus mediterraneus) to assess the feasibility of using these natural marks to

discriminate populations from the Black, Marmara, Aegean and eastern Mediterranean Seas and showed differentiation between samples from the middle Black Sea (Sinop) and Aegean Sea (Izmir) for both otolith shape and chemistry.

- Zhang et al. (2013) investigated the geographic variability of the sagittal shape of otoliths of Japanese Spanish mackerel (Scomberomorus niphonius) in three spawning grounds: Qingdao in the middle Yellow Sea, Lvsi in the southern Yellow Sea, and Huanghua in the Bohai Sea. Using discriminant function analysis with standardized otolith shape indices and Fourier harmonics, they identified a clear separation between the Bohai Sea and Yellow Sea groups, suggesting that the two schools should be managed as separate units.
- Muniz et al (2020), used two-year-old Atlantic chub mackerel (Scomber colias) individuals collected between January and April 2018 from six sampling sites (45 fish per site) in the northeast Atlantic (Azores, Madeira, Canary Islands and mainland Portugal - Matosinhos, Sesimbra and Portimão) to perform analyses of body morphometry and otolith shape using univariate and multivariate statistics. This research showed the existence of three main groups: Canary Islands, Azores-Madeira and mainland Portugal.
- IFOP (2014) conducted a multidisciplinary study to identify the population structure of Jack mackerel Trachurus murphyi in the South Pacific Ocean, which included the analysis of otolith shape indices and elliptical Fourier descriptors. They found that differences in the otolith contour analyses were explained by fish sizes and sampling locations. However, determining which of these categories has greater discriminative or classificatory power is challenging due to a significant level of correlation between both categorical variables.

4.7.3 The feasibility and/or limitations of the approach

Its feasibility depends on the creation of a standardized procedure for capturing and analyzing images of fish (for body shape analysis) and otoliths across different locations (e. g., Peru, Chile, EU, etc.) to ensure consistency. This procedure should include the following aspects:

1. Criteria for sampling selection: sex, size

2. Criteria for capturing the image: camera, lighting, background, image resolution, distance between the camera, the individuals and the and the otolith, orientation, and alignment

3. Software for image processing: preferably open-source

4. Approach/algorithm for mathematically modeling the outlines

5. Multivariate test

Difficulties in obtaining samples simultaneously at all the specified sample points

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4.8 Parasitology

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KEY SEARCH WORDS USED: Biomarkers; parasites; biological tags, parasites assemblages.

4.8.1 Background and rationale

Fish population research is essential for managing fisheries, promoting conservation, and comprehending the dynamics of ecosystems. Moreover, comprehension of fish population dynamics is essential for conservation and sustainable fisheries management (Mackenzie & Abauza, 1998). As indicators of fish populations, parasites have a distinctive viewpoint, even though more conventional techniques such as genetic analysis and population surveys yield useful data, mostly because it is feasible to differentiate between various fishing stocks by considering ecological and geographic elements that affect their prevalence and distribution (Mosquera et al., 2003).

The association of the parasite and the host involves two types of parasites: the host-specific ones that represent an evolutionary system and the general parasites, closely associated with an ecological process. To determine if a parasite is valid to be used as a biological marker, it must meet the following conditions i) existence of different levels of infection in each characterized area; ii) that they are not very or short-lived parasites; iii) that the infection has a certain regularity over time; iv) that the parasites are easily detectable and identifiable; and, v) that its pathogenicity is preferably low. The use of parasites that have simple life cycles, such as ectoparasites, monogeneans, many protozoa and/or crustaceans, is the easiest to use as biomarkers (MacKenzie and Abaunza, 1998).
MacKenzie & Abaunza (2005) developed two approaches for using parasites as biomarkers or biological labels. While one approach involves the selection of a small number of parasite species based on specific criteria known as “biological tags” or biomarkers (Williams, MacKenzie, & McCarthy, 1992), the other approach involves complete parasite assemblages (community and infracommunity of parasites) in addition to the use of more sophisticated statistical techniques (Brickle & MacKenzie, 2007).

Parasite communities within fish populations exhibit distinct species compositions that can vary geographically. Different fishing stocks often have unique parasite profiles due to differences in habitat, water quality, and host availability. Determining the prevalence and intensity of different groups of parasites can be decisive in understanding fish populations. Parasites have been used for the discovery of multiple species in supposedly single-species fisheries (George-Nascimento, 1996; Braicovich & Timi, 2008; Henríquez et al., 2011) and to recognize individual populations in large group of fish (Moser & Hsieh, 1992).

Baldwin et al. (2011) conducted a completed review that examined the effectiveness of various methods, including fish morphometrics, artificial tags, fish genetics, parasite genetics, and parasites as biological tags, in identifying marine fish subpopulations. The study focused on the Pacific sardine (Sardinops sagax) on the west coast of North America. The authors concluded that combining fish and parasite-based techniques can be a useful alternative for fish stock studies, especially for pelagic fish species whose stock structure can be difficult to determine. Increasing the number of spatial and temporal scales that are simultaneously studied through methodology integration may help clarify fish stock structure over limited geographic areas and provide strategies for the effective management of marine fish species.

There are several examples worldwide of the use of parasites as biological tags for determination of fish stocks. For instance, a study on Atlantic cod (Gadus morhua) in the North Sea found that parasite species composition differed between fish populations from different regions, reflecting local environmental conditions (Skovgaard et al., 2009). Other example was showed by Cavaleiro et al. (2018) in the Mediterranean Sea, using parasites to differentiate between populations of commercially important species such as european sea bass (Dicentrarchus labrax) and gilthead sea bream (Sparus aurata). These studies have revealed significant variations in parasite communities among different populations, influenced by factors such as water temperature, salinity gradients, and the availability of intermediate hosts.

In Chile, George-Nascimento et al. (2013) confirmed the existence of two anchovy Engraulis ringens stocks in 3 fishing areas (Caldera, Talcahuano, and Valdivia) using parasites communities as biological tags of fish populations. It is important to highlight that there are only 1000 km between these three sampling sites, and it was possible to determine these stocks using this methodology.

The same principles apply in freshwater fish. Carraro et al. (2017) reported that have utilized parasites to assess population structure and connectivity among fish populations inhabiting different river systems. Brown trout (Salmo trutta) in European rivers have demonstrated distinct parasite profiles between populations, indicating localized transmission patterns associated with specific river habitats and environmental conditions.

4.8.2 Critical appraisal of methods

The most commonly used methodologies in these cases generally propose two approaches for the use of parasites as biomarkers. One of them consists of selecting a small number of parasite species according to the selection criteria described in the literature. Many hosts will then be screened specifically for these parasites. The most appropriate criteria for selecting parasites as parasite biomarkers can be summarized as follows:

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• Significantly different levels of infection in the target host in different parts of the study area.
• Parasites with single-host life cycles, such as monogenetic trematodes and most parasitic crustaceans, are the easiest to use. However, if the life cycles and ecology of parasites are well

known, especially those whose life cycles involve stages of development in different hosts, they can also be used.

• Persistence time of the parasite in the final host. It must be more than a year.

• Parasites must be easily identified, so that dissection in the host is minimal, otherwise time would be a limitation.

• Avoid highly pathogenic parasites.

In the second approach, entire parasite assemblages are analyzed using multivariate statistical techniques such as discriminant analysis or multivariate logistic regression. This approach is most appropriate for large, valuable host species with rich and varied parasitic faunas (George-Nascimento, 2000).

Parasites typically have complex life cycles involving specific hosts, including intermediate hosts such as invertebrates or other fish species. The presence of certain parasite species or life stages can indicate specific migration patterns or feeding behaviors of fish populations. This can help trace the origins and movements of fish populations, providing insights into their stock structure. For instance, research on salmonids has shown that differences in parasite infection patterns correlate with distinct migratory routes and spawning grounds among different populations (Egidius et al., 2020).

4.8.3 Applicability to jack mackerel or other small pelagic

Utilizing parasites as indicators to distinguish between fishing stocks has practical implications for fisheries management. By analyzing parasite data alongside traditional methods, managers can gain a more comprehensive understanding of stock boundaries, migration patterns, and population health. This knowledge informs sustainable fishing practices and conservation efforts, helping to prevent overexploitation and preserve genetic diversity within fish populations (Thieltges et al., 2021). Fisheries regulations and management plans can be tailored based on insights gained from parasite-based stock differentiation, promoting long-term sustainability (Baldwin et al., 2012). There are some examples of studies in which parasites have been used to analyze the population structure of the jack mackerel stock in the South Pacific:

Reference	Period of time	Geographic coverage	Parasitic analysis	samples	Number of species
George Nascimento and Arancibia, 1992	between March and April 1990	-Chile (Iquique (Sector costero), Constitución (Sector oceánico), Talcahuano (Sector costero))	-Collection of endo- and ectoparasites with stereoscopic microscopy. -Univariate and multivariate statistical analysis of infracommunities and communities of component parasites. -Descriptors: prevalence, abundance, and parasite composition.	1.383	14

Aldana et al., 1995	between January and October 1990	-Chile (Iquique, caldera, Coquimbo, Talcahuano).	-Reproductive and morphometric aspects of the parasite species	1.189	1
Arancibia et al., 1996 (FIPA 1994-19)	between June 1995 and March 1996 (quarterly samples)	-Chile (Iquique, Coquimbo, San Antonio, Talcahuano and Valdivia).	-Parasite collection with stereoscopic microscopy under complete necropsy of each individual. -Univariate and multivariate exploratory statistical analysis. -Descriptors: prevalence, and parasitic composition	1.137 3.444	12
Oliva, 1999	between November 1993 and August 1994	-Perú (Paita, Callao), Chile (Arica, Iquique, Antofagasta, Coquimbo, Talcahuano).	-Parasitological analysis included a complete necropsy of each host fish. Collection of endo- and ectoparasites with stereoscopic microscopy. -Univariate and multivariate statistical analysis (reanalysis of historical data). Descriptors: prevalence, intensity, composition and parasite richness.	3.034	21
George Nascimento, 2000	1990 a 1996	-Chile norte (Iquique, caldera, Coquimbo) -Chile centro-sur (San Antonio, Talcahuano Valdivia).	-Collection of endo- and ectoparasites with stereoscopic microscopy. -The analysis criteria considered ordering those taxa that appeared more than 20 times (11 taxa), considering a host range between 32 and 37 cm. -A non-parametric discriminant analysis was performed to determine if the parasite composition could identify the geographic origin of the fish. -Univariate and multivariate statistical analysis on infracommunities and communities of component parasites. Descriptors: Prevalence, abundance and parasite composition.	3.946	15
Serra et al., 2010 (FIPA 2007-27)	between January and March 2008	-Perú (Isla Lobos de Afuera (norte) , Parácas (centro sur); Chile (Iquique, Caldera, Coquimbo, Talcahuano, (centro sur), Puerto Montt (sur) Chiloé (sur oceánica), Nueva Zelandia.	- Exploratory univariate and multivariate statistical analysis. - Alcohol fixation of parasite samples. - Descriptors: Average infection intensity, prevalence, abundance.	809	18
Serra et al., 2014	between March	-Perú (Pimentel (norte), Cañete, Olleros		1.733	18

(FIPA 2010-18)	and August 2011	y Tambo de Mora (centro); Ancón y Chimbote (sur); Chile (Iquique and Mejillones (norte), Couimbo, Talcahuano costa (centro) Chiloé costa and oceánico (sur); Nueva Zelandia.	- Exploratory univariate and multivariate statistical analysis. - Alcohol fixation of parasite samples. - Descriptors: Average infection intensity, prevalence, abundance		
George Nascimento y Oliva, 2014	1990 to 2007	-Perú (Paita, Callao), Chile (Arica, Iquique, Antofagasta Caldera, Coquimbo, Talcahuano.	-Review of the studies on parasites in jack mackerel from 1992 to 2000. -Univariate and multivariate statistical analyses of infracommunities and communities of parasites		

THE FEASIBILITY AND/OR LIMITATIONS OF THE APPROACH

Continued research is essential to refine our understanding of parasite-host interactions and their utility in fisheries management. Challenges include the need for standardized sampling protocols, integrating parasite data with other ecological parameters, and adapting to changing environmental conditions. Advances in molecular techniques and data analysis will enhance the precision and reliability of parasite-based assessments in identifying and distinguishing between fishing stocks.
Parasites represent valuable indicators of fish populations, offering insights into stock structure, migration patterns, and environmental conditions. Their ability to distinguish between fishing stocks based on species composition and ecological interactions enhances our ability to manage fisheries sustainably. By integrating parasite analysis into broader ecosystem studies, we can improve the understanding of fish populations

Finally, the study of parasites provides a better understanding of fish populations that complements traditional fisheries management approaches. Leveraging their role as indicators enhances our capacity to protect and sustainably manage fish stocks, supporting both ecological health and socio-economic benefits derived from fisheries. It is important to note that a consensual sampling protocol is necessary to improve the accuracy of the results.

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4.9 Reproduction

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KEY SEARCH WORDS USED: “reproduction” + “small pelagics” + “populations” “ connectivity” + “Trachurus”.

4.9.1 Background and rationale

Connectivity is defined as the movement of individuals or subpopulations, provided that the level of exchange is sufficient to impact the demographic rates of local populations.To study and determine the life cycle of marine species is a complex dutty, specially the reproductive part due to the external fertilization and the production of a huge amount of very small propagules with high dispersive capability that its nature presents (Cowen & Sponaugle, 2009). Even though it is harder to analyze marine populations than terrestrial populations, the concept of connectivity is critical to understand the functioning of stocks and communities (Sheaves, 2009). The scales and patterns of

connectivity of marine populations are helpful to determine the management strategies to be implemented in order to conserve marine resources and biodiversity (Calo et al. 2013).

The termed connectivity is applied for marine ecosystems like the extent to which discrete populations are linked by dispersal (either larvae, juveniles or adults) (Palumbi, 2003). Connectivity can be explained with different terms depending on the scale considered and how it is measured (Saenz-Agudelo, et al. 2011). The demographic connectivity is known to be used as a parameter for understanding the dynamics of populations and how they respond to natural and/or human disturbances (Schiegg et al. 2006; With, 1997). In marine organisms, most of the populations function as metapopulations where sub-populations are connected by larval dispersal (Figueira & Crowder, 2006; Sale et al. 2005).

The identification of a stock has been considered essential to provide an appropriate management of the species (Vaz-dos-Santos, 2009), because an error in this can lead to the overexploitation of a resource (BEGG et al., 1999). For this reason, and in response to the great interest in obtaining better sustainability, fecundity studies have taken on great relevance in total population assessments, productivity and population dynamics studies, as well as in determining the characteristics of a population, subpopulation and stocks (De Martini and Sikkel, 2006).

Studies on reproduction are fundamental to understanding the mechanisms that regulate reproductive processes, which allow the identification of reproductive cycles and strategies in the face of changes in the environment. It is important to highlight that each species presents particularities in its type of reproduction, making it unique for each stock, adapting to the conditions of life in the ocean (Xin Jun et al., 2022). An example of biological response to environmental variables is the gonadal maturation process, which has a wide range of variation within the same population (Xin Jun et al., 2022). Therefore, studying the maturation and spawning process of fish is important to estimate changes in populations and to ensure the adequate utilization of fishery resources in order to ensure the sustainability of populations.

Information on reproductive parameters such as size at maturity, spawning season, sex ratio and fecundity are fundamental elements required for the proper advice and management of fish stocks (Vasconcelos, 2017). Knowledge of reproductive strategies and spawning patterns are essential to understand the population dynamics of any fish species (Hilborn and Waters,1992) with fecundity being one of the reproductive parameters that should be analyzed (Murua et al., 2003). In addition, knowledge about fecundities and types of fecundities are of great importance in fisheries because it determines the most appropriate method to use to estimate egg production, a tool used to calculate the biomass of a species, in order to provide better management (Jennings et al., 2001; Ganias, 2013).

4.9.2 Critical appraisal of methods

In small pelagic species of cosmopolitan nature, such as chub mackerel (Scomber japonicus), which is a widely distributed species that inhabits warm waters of the Atlantic, Indian and Pacific oceans, numerous studies of reproductive aspects have been carried out with the intention of knowing more about its biological aspects such as growth and reproduction, as a consequence of its wide distribution and high level of commercialization, the biological information of its reproductive cycle is indispensable for stock management purposes (Cikes Kec and Zorica, 2012). The estimation of fecundity varies depending on the strategy that each species presents, in the case of species that are partial spawners, the number of reproductive periods of the species is evaluated, the number of spawning periods per reproductive period and the number of eggs per spawning period and the number of eggs per spawning period (Hunter and Goldberg, 1980). Another way to compare fecundities among different species is the relative fecundity, which is calculated as the fecundity per reproductive period divided by the body weight of the specimen. Another species that has a wide geographic distribution is the jack mackerel (Trachurus Trachurus), so in order to develop an adequate management, its distribution area is usually divided into populations or stocks that are relatively independent from others (Abaunza, 2004).

In Jack mackerel, there are standardized and worldwide known methodologies with respect to biological sampling, gonad collection, the use of gonadal maturity scales and histological processing of gonads. However, it is in the estimation of reproductive parameters where there is a point of divergence between different authors investigating Jack mackerel reproduction in different latitudes.

4.9.3 Applicability to jack mackerel or other small pelagic

Different authors have described the considerations to be taken to carry out fecundity studies, taking as a reference that for studies of this type, samples should be collected during spawning periods or seasons (Brown - Peterson et al. 2011), collecting only females in hydrated condition. Vasconcelos et al. (2017) describe in their work on "Strategy for regulating the fecundity of blue jack mackerel off Madeira Island" that they performed histological cuts of sections between (3-5 µm), subsequently stained with toluidine blue and digitized using a visual image analysis system (Leica DFC 290). The methodology applied in this study consisted of taking three sub-samples between 0.02 - 0.05 g and applying the gravimetric method, which consists of shaking each sub-sample to facilitate the separation of the smaller oocytes and sieving them in order to eliminate the smaller oocytes. The remaining oocytes were then placed in a Petri dish to record the number and size of advanced stage oocytes.

Buitron and Perea (1998) describe that fertility calculations should be made by collecting only hydrated ovaries, which are subjected to histological discarding by means of the freezing method

described in order to discard females with the presence of FPO. Oocyte counting is performed by gravimetric method, following the methodology described by Hunter and Goldberg (1980). Cengiz (2020) mentions that for the estimation of fecundity in mackerel, the gravimetric method was used; however, they add Gilson's fluid and shake the sample to ensure the separation of tissue and oocytes, preventing this from influencing the count. The different methods used to estimate fecundity involve measurements of gonad volume, weight and area. Similarly, a number of sub-sampled 100 to 150 mg of the central part of the gonad, then subjected it to Gilson's fluid (Agger et al., 1974) ensuring the dissolution of the membrane covering the oocytes.

On the other hand, Cassia and Ciechomski (1980) mentioned that it is preferable to count mature oocytes in the migratory nucleus phase instead of hydrated oocytes, arguing that this is not only because it is difficult to find hydrated ovaries, but also because it avoids counting hydrated oocytes that could become atretic.

Like most marine species, environmental factors are predominant for the development of biological aspects. In this case, one of the most important factors that constantly regulate the variations or reproductive response of fish is temperature (IMARPE Internal Report, 2019) specially the small pelagic species which are sensitive to climate change (Checkley et al. 2009). Sexton et al. (2017) mentions that the influence of the warm tropical water southwards along the coast of Tasmania is involved in the variations of the spawning periods of Trachurus declivis. This has been reinforced by Neira (2011) who suggested that sea surface temperature (SST) influenced significantly the spawning selection concluding that Jack mackerel spawns in waters with SSTs between 17.2 and 20.1°C. The sensitivity to environmental conditions is important in regions where stock sizes of small pelagic fisheries fluctuate substantially, such as the California Current ecosystem (Rodríguez-Sánchez et al., 2002).

The development of maturity scales arose as a necessity in the face of the problem of cataloging the stages of maturity with empirically elaborated scales. According to the literature, the calculation of spawning times is calculated by taking the IGS data, considering the values more as spawning peaks or important reproductive times.

4.9.4 The feasibility and/or limitations of the approach

In most of the research conducted, the analysis of reproductive aspects is highly linked to multidisciplinary studies for a better characterization of the population structure and connectivity between populations. In addition, compared to other methods, the calculation of fecundity and reproductive indicators is more economical, widely known and accessible because of the biological information of the resources.

In order to carry out research based on reproductive aspects of Jack mackerel, it is necessary to analyze only the adult population (above 26 cm LT) which present an evident oocyte development during a period of at least one year, since this would allow to analyze the complete reproductive cycle of the species. Methodologies applied for the development of thesis and research work usually takes even two additional months, so the sampling time should consider a total of fourteen months to analyze the changes that may occur within a year. As for the sampling area to be considered in the sampling, it is important that it covers the entire area in which the resource is found, in this case, from the north of Peru to the south of Chile.

Most of the methodologies are applicable in the studies of the reproductive aspects of Jack mackerel, with the exception of histochemical studies, which are difficult to perform, since they have not been applied before and the necessary equipment and reagents are not available. On the other hand, statistical software is available to estimate sex ratio and gonadal maturity size. A possible limitation is the obtaining of samples, due to the presence or absence of the resource, due to environmental variations, which often means that these are not available for purchase in the markets, generating information gaps.

Gray et al. (2012) described that latitudinal and longitudinal variations in the duration and timing of peak reproductive activity are common in species of fish that are widely distributed. This information is according to what we found in the reproductive periods of jack mackerel in Peru and Chile.
This work is feasible to carry out in Peru since it is part of the activities that are carried out as part of the monitoring of the fishery.

4.9.5 References

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4.10Tagging methods

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KEY SEARCH WORDS USED: “tagging”+“stock discrimination”+“Jack Mackerel”

4.10.1Background and rationale

Jack Mackerel (Trachurus murphyi) is a pelagic fish species distributed in the South Pacific Ocean, which plays an important role in the marine ecosystem and the fisheries economy. As a straddling species, it has a wide distribution and extensive migrations, which has made it difficult to establish distinguishable stock units (Serra, 1991; Arcos and Grechina, 1994). Identifying stock units for appropriate management and understanding spatial patterns are essential to achieving fisheries management objectives. In this context, tagging methods could provide insights regarding stock identification, population structure, migration patterns, distribution, and habitat. So, tagging can provide:

- Data on the movement patterns and distribution, population structure, and help to identify stocks and their boundaries (e.g. Hamre, 1970; Begg et al., 1997; Block et al., 2005).

- Information about -seasonal- migration routes, and habitat use/preference aids in predicting population responses to environmental changes (e.g. Sarno et al. 1994, Martinez et al., 1998).
- Information for spawning and nursery grounds identification (e.g. Cote et al., 1998, Eiler & Bishop, 2016).
- Data to contribute to more precise estimates of stock size, recruitment, and mortality rates (e.g. Everson et al., 2012).

4.10.2 Critical appraisal of methods

Tagging methods could be classified as conventional and electronic.
Conventional tags have often been used for stock identification, sometimes as the main objective or as a complement to other tagging study objectives (Jacobsen & Hansen, 2004). Also, it has proven to be effective in the study of migration patterns, habitat use, and stock structure in various pelagic species (Dragesund et al., 1980; Hamre, 1970; Schweigert et al., 2001; Uriarte et al., 2001; Iversen, 2002).

The ***conventional tags*** may include (i) external tags such as ribbons, threads, wires, plates, disks, dangling tags, and straps (McFarlane et. al., 1990); (ii) external marks, defined as a mark visible on the outside of the fish and employed to identify individual fish or groups of fish, but without any information regarding reporting format. Examples of external marks are visible modifications of the fish body (or fins), pigments, stains, brands, and meristic or morphometric characteristics (Coombs et al., 1990); (iii) internal tags which are inserted or injected into the fish (body cavity, muscle or cartilage) and carried internally such as plastic or glass tubes, metal plates, small pieces of magnetized metal, or semi-electronic tags transmitting information (by radio waves) when an electrical current is induced ; (iv) internal marks such as marks in the bone structure, produced chemically (alizarin or oxytetracycline) or leaving distinctive "marks" on the bone structures. As mentioned above, although this type of tagging has been used successfully, the disadvantage is that they usually provide only snapshot information, and less accurate information on the continuous long-term.

On the other hand, ***electronic tags***, also known as telemetry and bio-logging, are widely used to study animal behavior (e.g., horizontal and vertical movements), ecology, survival, and environmental responses (Jepsen et al., 2015, Sippel et al., 2015). These devices include the transponder tags to detect the position of a fish to be accurately determined relative to a research vessel when they receive a pulse from sonar (Mitson & Storeton-West, 1971; Greer Walker et al., 1978); archival tags for recording depth or temperature to provide position and physiological indicators of the fish at regular time intervals; and continuous radio (inland environments) or acoustic (coastal and oceanic environments) transmission tags, which do not depend on recovery but do depend on transmitter size, power source, range and signal rate (Cote et al., 1998; Niezgoda et al., 1998). Regarding pelagic species, electronic tagging studies have been used mainly in tunas, sharks, and batids (e.g., Sibert et al., 2003, Block et al., 2005, Sibert et al., 2006, Wearmouth & Sims, 2009, Eveson et al. 2012), nevertheless, as tags become smaller and more varied, the possibility of tagging small pelagic species increases. Table 3 shows the advantages and disadvantages of the different tagging methods

Table 3. Tag methods classification showing their advantages and disadvantages focus on pelagic species

Tag method	Tag type	Advantages	Disadvantages
Conventional	External tags	Low cost and easy to apply. Suitable for wide ranges of sizes. Broad geographic coverage.	Impact on biological processes. High loss rate. Possible obstruction/entanglement.
Conventional	External marks	Low cost and easy to apply. Minimal impact on the individual	A limited number of codes. Marks may deteriorate/disappear.
Conventional	Internal tags	Little or no impact on biological processes. Suitable for a wide range of sizes and species. High recovery rate compared to external tags.	Need for expensive equipment. Laborious recovery.
Conventional	Internal marks	Simple, fast, and economical (chemical marking). Natural marks without additional manipulation.	Complicated application in natural populations
Electronic	Passive integrate transponding (PIT)	Precise individual identification. Long-lasting durability and lifespan. Non-invasive once implanted. Accurate and reliable data. Resistant to adverse conditions	Require specialized equipment for reading (Stationary or handheld readers). Limited detection range. It can be expensive.
Electronic	Transponding	Precise determination of the position concerning a sonar. Detailed data on behavior. Does not require physical recovery for reading.	Require specialized equipment for reading. It can be expensive. Limited to short-term studies. Limited range depending on the transmitter.

Electronic	Archival tags or data storage (DSTs)	Record detailed data such as depth, temperature, and geographical position. Provide information over long periods.	Expensive and requires specialized equipment. Data recovery and analysis can be laborious. Battery life may be a limitation.
Electronic	Continuous transmission tags (Acoustic)	Provide real-time data on the movement of the fish. Not dependent on the physical recovery of the device.	Require expensive receiving equipment. Range and effectiveness depend on transmitter size and power source. They can be expensive and complicated to implement.

4.10.3 Applicability to jack mackerel or other small pelagic

There are many studies focused on tagging, and most of them mentioned that the success of tagging experiments depends on several factors such as handling and tagging mortality of the marked individuals, loss of tags, and the success in detecting or reporting tagged fish during the recovery process (Jacobsen & Hansen, 2004). While there is no perfect tagging method as all carry some degree of negative impact (although these effects may be minimal or undetectable in some cases), method selection should be based on a careful evaluation of the advantages and disadvantages, considering the species, size, life stage, habitat, study duration, and specific objectives (Jepsen *et al*. 2015). Furthermore, it is recommended that controlled pilot studies be conducted, whenever possible, to quantify the potential impacts of tagging before undertaking large-scale studies (Bridger & Booth, 2003; Jepsen et al., 2005) which would be the case of jack mackerel. Table 4 recaps some studies focused on tagging methods in small pelagics.

Table 4. Some studies of tagging in small pelagics and *Trachurus* genus in different regions

Author(s)	Species	Region	Tagging method	Goals
IMARPE (1967)	Anchoveta (*Engraulis ringens*)	Peru	Conventional tag: External tag	Migration
Hamre (1970)	Mackerel (*Scomber scombrus*)	The Skagerrak and the North Sea	Conventional tag: Internal tag	Stock structure
Ichihara *et al.* (1972)	Yellowtail (*Seriola quinqueradiata*)	Goto Islands of western Japan	Electronic tag: transmission tags	Movement (migration)

Carlson & Reintjes (1972)	Atlantic menhaden *(Brevoortia tyrannus)*	Beaufort, North Carolina	Conventional tag: Internal tags & marks	Migration and stock structure
Pristas & Willis (1973)	Menhaden *(Brevoortia tyrannus)* *(Brevoortia patronus)*	Beaufort, North Carolina	Conventional tag: Internal tag	Movement (migration) and stock structure
Tasto (1973)	Jack mackerel (*Trachurus symetricus*)	Southern California and Baja California, Mexico	Conventional tag	Movement (migration) and stock structure
Dragesund *et al*. (1980); Hamre (1989)	Atlantic herring (*Clupea harengus*)	North-East Atlantic	Conventional tag	Stock identification.
Bakken & Westgard (1986)	Mackerel (*Scomber scombrus*)	North Sea and Southwest of Ireland	Conventional tag	Migration patterns and identify stocks.
Sarno *et al.* (1994)	Saithe *(Pollachius virens)* Pollack *(Pollachius pollachius)*	Loch Ewe, Scotland	Electronic tag: transponder tag	Movement (migration)
Begg et al. (1997)	School Mackerel (*Scomberomorus queenslandicus*) spotted mackerel (*S. munroi*)	Australian east-coast waters	Conventional tag	Movement and stock structure
Martinez *et al*. (1998)	Anchovy (*Engraulis ringens*)	North of Chile	Conventional tag	Migration
Hay *et al*. (2001)	Pacific herring (*Clupea pallasi*)	British Columbia	Conventional tag: External & Internal tag	Migration and stock Identification
Schweigert et al. (2001)	Pacific herring (*Clupea pallasi*)	British Columbia	Conventional tag: microtags	Stock structure and migration

Uriarte & Lucio (2001)	Caballa (*Scomber scombrus*)	Northwest Atlantic	Conventional tag	Stock identification and migration
Uriarte et al. (2001)	Caballa (*Scomber scombrus*)	Northwest Atlantic	Conventional tags: Steel internal tag	Stock identification, migration, and recruitment process
Iversen (2002)	Chub mackerel (*Scomber scombrus*)	North-East Atlantic	Conventional tag	Stock identification and migration
Serra *et al.* (2010)	Jurel (*Trachurus murphyi*)	South of Chile	Conventional tags with external pit tags Electronic tag: External & Internal tag	Feasibility study on the use of different tags in Jack mackerel
Eiler & Bishop (2016)	Arenque Pacífico (*Clupea pallasi*)	Prince William Sound	Electronic tag: Acoustic transmission	Stock structure and migration
Wiff *et al.* (2023)	Reineta (*Brama australis*)	South of Chile	Conventional tag: External tag	Migration

Although there are few studies on stock identification, structure, and migration of jack mackerel (*Trachurus murphyi*) using tagging methods, it is crucial to elucidate these aspects for effective management. So, we think that, at least, the following topics should be considered:

- Tagging experiments on captive jack mackerel and study of the impacts of tagging (behavior and mortality) and tag retention.
- A study of the recovery rate, for conventional tags or data storage tags (DST), is essential to evaluate the project´s feasibility on a larger scale.
- Fieldwork (planning and marking system) must be conducted according to a structured plan, with international cooperation (SPFRMO members, NGOs, etc.) to ensure comprehensive coverage and collection of representative data.

4.10.4 The feasibility and/or limitations of the approach

Its feasibility depends on:

- ***Spatial coverage***: Tagging jack mackerel in the context of the SPRFMO requires effective international cooperation, as jack mackerel are widely distributed in the South Pacific. Many members must show and make an effective commitment to carry out this hard task which includes deciding and studying what type of tags to use (e.g., conventional, electronic), the possibility of conducting controlled pilot studies, how many, and how the data will be recovered and analyzed.
- ***Funding and Resources***: Successful implementation of tagging programs depends on adequate funding and available resources for catching, tagging, and monitoring fish.

Limitations include

- ***Recovery rates***: Low tag recovery rates can be a significant challenge, especially for conventional tags.
- ***Costs***: For example, if the decision is made to use electronic tags, high costs will be associated which may limit their use, especially in large-scale studies as is the case of jack mackerel.
- ***Impact of tagging***: Tagging devices can alter fish behavior and survival, which could bias study results. Minimizing these impacts is essential to obtaining representative data.

In summary, implementing a jack mackerel tagging program is a feasible approach that can provide valuable insights into the stock structure and dynamics of this species in the South Pacific. To achieve these goals of this program, it is essential to plan meetings and workshops that facilitate the exchange of knowledge and coordination between members. Furthermore, international collaboration is crucial to ensure adequate spatial coverage and accurate and representative data collection.

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4.11Trophic ecology

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KEY SEARCH WORDS USED: “trophic”+“Jack Mackerel”

4.11.1Background and rationale

The jack mackerel (*Trachurus murphyi*) It is distributed from Ecuador (1°30'S) to the Strait of Magellan (55°S), while in the Southwest Pacific Ocean it is distributed to New Zealand and Tasmania, being found mainly between 30° and 50°S, constituting what is known as the “jack mackerel belt” (Arcos et al. 2001; Medina & Arancibia 2002; Cisterna & Arancibia 2017). The northern Humboldt Current system (NHCS) is considered a facultative predator, i.e., it is able to move between different habitats to feed and thus access different sources of energy (Konchina, 1981). This resource exhibits a strong seasonal migration pattern (Jones 1990, Serra 1991, Arcos et al., 2001), aggregating in large schools in the coastal zone for feeding purposes in highly productive sub-Antarctic waters, especially in the fall and winter (Serra 1991, Cornejo 1991, Gretchina 1998, Miranda et al., 1998), to later migrate to oceanic waters for spawning purposes in subtropical waters (Serra, 1983, Evseenko, 1987). Indeed, there is evidence of its ability to feed on neritic and oceanic prey in the epipelagic zone off Peru and

Chile (Alegre et al., 2015; Medina and Arancibia, 2002). Indeed, the jack mackerel feeds mainly on euphausiids, copepods, crustacean larvae, being able to include mesopelagic fish when it is in the oceanic zone, and anchoveta and some coastal fish when it is located in the neritic zone (Alegre et al., 2015; Alegre et al 2013., Medina and Arancibia 1998; Medina and Arancibia, 2002).

In the case of euphausiids, it has been shown that production is higher than commonly estimated (Ballon et a., 2011). In this regard, it has been established that the higher zooplankton production at northern Humboldt Current system (NHCS) could be related to a more efficient use of primary production by zooplankton and/or a strong connection between the coastal and the offshore pelagic ecosystems. This last argument may particularly apply to the euphausiids, which were the main source of dietary trophic carbon for anchovy and which inhabit both near- and offshore ecosystems (Espinoza and Bertrand, 2008), as well as for jack mackerel and chub mackerel (Alegre et al., 2015).

On the other hand, the jack mackerel population follows the distribution pattern of its prey both after the shelf break (euphausiids) and offshore (mesopelagic fishes) that could be directly affected by oxygen whereas jack mackerel are not. This hypothesis can be rejected since Bertrand et al. (2006) showed that mesopelagic fishes, as observed by acoustic, can take refuge within the OMZ while jack mackerel are restricted to the oxygenated surface layer. Similarly, in the HCS, more than of 75% of macrozooplankton biomass (in particular euphausiids, a main jack mackerel prey, Alegre et al., 2015), migrate within the OMZ during the day (Escribano et al., 2009, Ballón et al., 2011). We can thus deduce that jack mackerel is directly affected by oxygen whereas euphausiids and mesopelagic fishes are not. In addition to productivity, oxygen seems therefore a fundamental factor controlling jack mackerel distribution and exchanges from southern areas into Peruvian waters.

These patterns observed for jack mackerel are similar to the case of sardine but opposite to the case of anchovy (Bertrand et al., 2011). Anchovy, sardine and jack mackerel are gregarious fish and obligate ram ventilators. (Bertrand et al., 2010, Bertrand et al., 2011) showed that anchovy does not seem affected by a very shallow oxycline (<10m) while sardine and jack mackerel avoid such areas. It is natural to assume that large fish and dense aggregations of larger actively swimming fish such as jack mackerel require more oxygenated waters and more vertical habitat (deeper oxycline).

Therefore, it is important to know the connectivity of these environments in terms of their trophic ecology as it plays an important role in shaping the population structure of marine species (O'Donnell et al., 2022). In addition, different fish species often migrate and use during different life stages these environments, so connectivity in terms of their feeding is crucial to enable ontogenetic migrations and access to prey (Perry et al., 2018)

4.11.2 Critical appraisal of methods

It is recognized that trophic interactions can reveal connections between ecosystems, and that predator-prey relationships depend on the spatial and temporal scale of observation (Bertrand et al 2004). A common method for studying trophic relationships is based on analyses of stomach contents (Caddy & Sharp 1988, Hyslop 1980). It has been widely used as an indicator of the diet of marine organisms and is useful for describing prey-predator interactions. Through this method, useful information can be obtained to quantify the energy flow in the marine food web, identifying the most relevant species in this structure, either as predators or prey (Rodhouse and Nigmatullin 1996; Cortes 1997; Santos et al. 2001). This methodology is limited by the degree of digestion of prey in the stomach contents, being necessary to analyze a high number of stomachs to improve the accuracy of the dietary estimate (Keller et al. 2016). However, complementary analyses such as stable isotopes have been successfully used to obtain more information and precision in the results (Connan et al. 2005; Schmidt et al. 2006; Drazen et al. 2008; Leclerc et al. 2012; Junqueira et al. 2020; Choy et al., 2015; Selleslagh et al., 2015).

Indeed, stable isotope ratios of carbon (^{13}C) have been used in some studies to trace the flow of sources of organic matter from inshore to offshore, or from surface to bottom (Barros et al. 2010; Choy et al., 2015). It reflects the primary source of carbon in the foraging habitat.

Stable isotope ratios of nitrogen (^{15}N) have been used to know the source of nitrogen and the trophic level of the prey (Rossman et al., 2016). This increases by ~3.4‰ from one step to the next in the food chain (Stephens et al., 2023) and is very useful for estimating the trophic position of the consumer.

Stable isotope ratio analysis has notable limitations (Riekenberg et al. 2021), such as:

- It is often not accurate in representing the host-parasite relationship and leads to an incomplete understanding of the food web. In addition, it has low prey taxonomic resolution and high cost (Post 2002; Bearhop et al. 2004; Hussey et al. 2010; Layman et al. 2012; Hussey et al. 2014).
- Trophic position estimates use averages, which obscure specific individual variations affecting the understanding of trophic interactions

4.11.3 Applicability to jack mackerel or other small pelagic

Species are linked through trophic relationships which denote transfers of energy and nutrients which commonly are called trophic structure, and is referred to the way in which organisms use food resources (Shackell et al., 2010). In this way, a healthy marine ecosystem has a food web with highly interconnected linkages, which can denote the complexity of the ecosystem (Menge, 1995). Thus, a strong connection between the coastal and the offshore pelagic ecosystems is likely one of the reasons for the high fish productivity of the NHCS, because it allows to jack mackerel and small pelagic fish to gain access to feed on the euphausiids (Espinoza and Bertrand, 2008). Euphausiids are a rich source of energy and nutrients, and are the food base of migratory predators (e.g.,

mysticete whales). Energy load is a key factor in the physiological dynamics of individuals (Ney, 1993) and, basically, feeding strategies dictate the level of predation of the predator on the prey. So, this component could be an attribute of euphausiids for their predators to make use of this prey, which is abundant and relatively easy to capture (Garvey & Whiles, 2016).

This means, connectivity, which is seen as the exchange of individuals of a species between spatial units (Polis et al., 1997). allows the continuity of these energy flows in the trophic webs. This leads to the fact that these individuals may have differences in habitat use, as well as changes in migration patterns (McCarthy and Waldron, 2000). According to Moreira et al. (2020), it is necessary to know the connectivity patterns within metapopulations as well as spatio-temporal amplitude to implement the sustainable management of fisheries

4.11.4 The feasibility and/or limitations of the approach

Therefore, taking into account the above mentioned, it is proposed to examine the connectivity of Jack mackerel using stable isotope ratios. One of the main advantages is that, depending on the tissue, analyses can identify what the fish predated weeks and even months and years ago. The isotopic stability technique is one of the most robust techniques for trophic ecology studies. To achieve this, it is necessary to demonstrate whether there are differences in the isotopic signatures of individuals in various habitats, and must be established and shown to be reasonably consistent within the time frame and spatial scale of the study (Herzka et al., 2001).

Nowadays, the quantitative assessment of the trophic relationships among connected habitats by using stable isotopes is crucial (Claudino et al., 2015; Conway-Cranos et al. 2015; Selleslagh et al. 2015). Using stable isotope analysis has been achieved a simplified food web model in the Northern Humboldt Current System (NHCS), characterized by increase of 13C and 15N from copepods to marine mammals, and decreasing trend of 13C values from inshore to offshore (Espinoza and Bertrand, 2017), which is similar to other upwelling ecosystems (Sydeman et al. 1997; Miller et al.,2008).

The ability of jack mackerel to move into different habitats makes it a good candidate to study trophic connectivity. Thus, 13C and 15N values can be used to quantify the isotopic niche of this species in different habitats (Jackson et al. 2011). The overlap between isotopic niche inshore and offshore may be used as evidence of connectivity (Newsome et al., 2007).

4.11.5 References

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