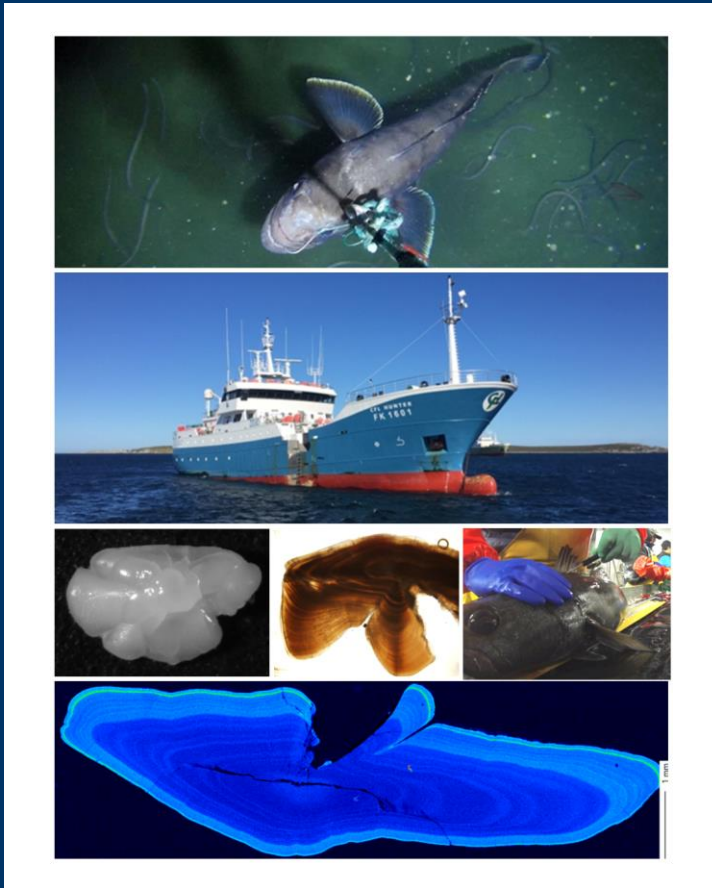


# Stock identification of Patagonian toothfish: an interdisciplinary approach



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# **Stock identification of Patagonian toothfish *Dissostichus eleginoides* in the southwest Atlantic: an interdisciplinary approach**

## **Executive Summary**

The stock structure of Patagonian toothfish in the southwest Atlantic is still poorly understood. On a larger spatial scale, there is well-documented genetic differentiation between toothfish found on the Patagonian Shelf and around South Georgia and South Sandwich Islands. However, toothfish population structure across the Patagonian Shelf is less certain in the context of where it fits into a possible stock structure continuum, extending across possible sympatric discrete, spatially complex (e.g. metapopulation or source-sink) and panmictic population structures.

Separate spawning populations south of Diego Ramirez Islands in Chilean waters and the eastern Burdwood Banks in Falkland Islands waters have been identified; with otolith microchemistry analysis suggesting that larvae settling on the Falkland Shelf originate from a combination of these two spatially distinct areas. Annual spawning migrations have been inferred for Patagonian toothfish from foraging areas on the Patagonian shelf and slope located in the north and east of the Falkland Islands to spawning areas on the Burdwood Bank. However, early satellite-tagging work undertaken in Falkland Islands waters showed high site fidelity and limited movement of adult toothfish, leading to the conclusion that the part of the stock targeted by the longline fishery (primarily older, adult individuals) is most likely confined to Falkland Islands waters.

The aim of this research programme was to provide an improved understanding of the complex stock structure dynamics for Patagonian toothfish in the southwest Atlantic, specifically in relation to the shelf, slope, and deep-sea plains around the Falkland Islands. To achieve this, an integrated approach was used whereby a range of complementary methods were incorporated to improve our understanding of life-history stages identified as potential pathways of population connectivity.

Otolith shape analyses revealed high site fidelity across their distribution, and possible stock separation among early adult fish within localised areas on the Patagonian Shelf. Based on these results limited mixing appeared to occur between southern Chile and Burdwood Bank spawning areas; and feeding grounds off the continental slope and deep-sea plains to the north-east of the Falkland Islands.

Analyses of abundance distributions were undertaken to assess the spatial-temporal persistence (stability) of toothfish nursery area hotspots around the Falkland Islands and to describe their subsequent ontogenetic migration pathways into their adult deep-water habitats. Results indicate spatially discrete hotspots exhibiting high temporal variability. This variability is defined through oceanographic influence that drives larval dispersal and survival on the Shelf. Juvenile toothfish appear to follow persistent ontogenetic migrations, linking distinct recruitment areas with their respective component of the adult population on the Patagonian slope. Evidence of mixing among cohort groups during their ontogenetic migration into deep-sea adult habitats was limited, reflecting a mixed population based on oceanographically defined egg and larval dispersal.

A large-scale tag-recapture programme using conventional and satellite tags was established in June 2016 to improve understanding of the movement patterns of toothfish within the region; and to quantify the exchange between adults on the northern and eastern slope, and the spawning grounds on the Burdwood Bank (and possibly southern Chile). Analyses based on

results over the first 6 years of data were used to elucidate the movement patterns as well as the extent that these are driving connectivity during the adult life-history stages of Patagonian toothfish in the region. Tagging and recapture results indicated that the majority of individuals (78%) displayed high site fidelity (<50 km). However, 10% of individuals undertook large-distance movements across oceanographic and physical boundaries. These were characterised by large (>120 cm) fish inhabiting the slope and deep-sea plains (north of 52°S) undertaking southward (direction = 150 - 240°) home-range relocations to spawning areas on the Burdwood Bank, North Scotia Ridge and southern Chile.

Otolith microstructure and trace element analysis were applied to infer time-resolved elemental profiles that reflect the early ontogeny of juvenile Patagonian toothfish from key nursery areas on the Patagonian Shelf. Results revealed significant ontogenetic shifts in elemental profiles across the early life-history of Patagonian toothfish. From these, key biological benchmarks were identified, including (i) the hatch date distribution (mid-September to late October; mean = 3 October); (ii) the dispersal period of pelagic larvae until their entry onto the Patagonian shelf (0 to 50 days post-hatch); (iii) the entry phase from the shelf extent to inshore waters (<100 m depth; 50 to 100 days post-hatch); (iv) settlement into a demersal habitat (109 days post-hatch); and (v) subsequent migration into juvenile nursery areas (<150 m depth; 120 days post-hatch).

Results from a recent genetic study suggests two independent evolutionary lineages within the '*D. eleginoides*' complex and their differentiation into two distinct taxonomic entities as separate species based on genomic and morphometric data. Results also implied a complex level of restricted connectivity between local populations of Patagonian toothfish, specifically between fish captured from (1) southern Chile and the Falkland Islands; and (2) Falkland Islands and the high seas (North of Falkland Islands), illustrating the Falkland Islands as an intermediate zone of mixing.

This long-term research programme investigating the stock structure of Patagonian toothfish on the Patagonian Shelf revealed complex patterns. Research results indicate high levels of uncertainty in terms of understanding the extent of connectivity during the early life-history phases of egg and larval dispersal. Further, evidence of connectivity across the region through the active migration of adults appears to occur on a relatively small scale. Current results demonstrate that the stock structure arising from the retention of mixed contingents across the Falklands Shelf remains discrete (within the Falkland Islands Conservation Zone) until adult life-history stages. Based on these findings a range of management measures were provided:

1. The maintenance of current management measures concerning (1) the prohibition of trawling, and (2) restrictions on longline-based commercial fisheries during spawning from June to August on the Burdwood Bank.
2. Revise the 'move-on' rule to ensure the protection of shelf-based newly recruited toothfish on a proactive basis.
3. Based on remaining uncertainty, a 'status quo' management approach should be following with the assumption that there is one discrete toothfish stock present in Falkland Islands waters.
4. Continue to build on data sharing and research collaborations with regional partners, specifically Chile, Argentina and the high seas fishing fleet (South Korea).
5. The continued investment in stock structure research to ensure a sustainably managed Patagonian toothfish fishery.

6. Maintain and build fisheries-independent research surveys for (1) the monitoring of nursery areas, (2) the monitoring of deep-sea ontogenetic migratory transition zones (3) their expansion to encompass a seasonal component and (4) increase alignment among the two survey data collection protocols.
7. The incorporation of routinely collected environmental data (CTD) into open access global satellite monitoring programmes (e.g. EU Copernicus Environmental Monitoring Service).
8. Maintaining the tag-recapture programme objectives, specifically for the continued tagging of ~1000 toothfish per year within the Falkland Islands Conservation Zones for meeting stock assessment and stock structure research objectives.

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## 1. Introduction

### 1.1. The importance of understanding stock structure

The 'stock' concept as a population unit in fisheries science forms the basis of assessment and management (Baranov 1918, Russell 1931). The 'unit stock' of a fish population refers to a reproductively isolated group of organisms whose demographic and genetic trajectory is largely independent from other such groups of the same species (Waples 1998). An independent genetic trajectory implies that young fish in the population are entirely spawned from adults in the same population. This isolation is expected to be reflected in demographic independence of stock, recruitment, mortality, and age composition, reflecting the population parameters that are estimated by stock assessment models (Cadrin 2020).

A thorough understanding of population structure is therefore crucial when delineating stock boundaries for assessing stock status, informing the development and implementation of relevant management measures. Almost all fish populations have some spatial structure and mixing patterns, falling along a continuum across broadly defined (1) sympatric discrete (2) spatially complex and (3) panmictic population categories (Cope & Punt 2011, Ciannelli et al. 2013, Brophy et al. 2016, Kerr et al. 2020). A sympatric discrete population refers to reproductively and genetically isolated populations, which may occupy overlapping habitats, at least during one phase of their life cycle. On the opposite end of the scale, a panmictic population refers to interbreeding individuals that are heterogeneously distributed over space. A spatially complex population consists of contingents (sub-populations) that exhibit a degree of independence in local population dynamics containing variable connectivity among them (Hawkins et al. 2016, Cadrin et al. 2020). Such a structure includes both (classical) metapopulations, and source-sink populations (Sinclair & Iles 1989). In the case of a classical metapopulation, these consist of similar, discrete locally breeding subpopulations or contingents which are genetically connected via relatively rare dispersal events (Fronhofer et al. 2012, Hawkins et al. 2016). A source-sink population structure is characterised by 'donor' groups contributing to 'receptor' components that, while able to survive and grow successfully, become non-breeding vagrants with limited ability to reconnect with the source (Fronhofer et al. 2012, Hawkins et al. 2016). Receptor groups in a source-sink metapopulation structure commonly stem from poor habitat quality (Hawkins et al. 2016), driven by spatial (e.g. dispersal beyond the distributional areas of the population) and energetic (e.g. predation, disease, and starvation) processes (Sinclair & Iles 1989).

Stock boundaries are, however, often an oversimplification of complex populations and do not always accurately represent biological population structure (Zemeckis et al. 2014, Kerr et al. 2017, Berger et al. 2021). Complexities in stock structure that are not accounted for may have important implications for stock assessments and fisheries management arrangements (Cope & Punt 2011, Zemeckis et al. 2014, Kerr et al. 2020, Moore et al. 2020). For example, what is assumed as a single closed stock within a defined management area may reflect multiple individual stocks (Smedbol & Stephenson 2001, Clausen et al. 2007). This is of particular importance when different contingents, fished as a single stock, possess varying levels of productivity (Dickey-Collas et al. 2010, Ying et al. 2011). The implementation of conservative population parameters can then lead to the under-fishing of contingents with high productivity, or over-fishing of less productive contingents should less conservative population parameters be assumed (Tuck & Possingham 1994, Begg et al. 1999, Kerr et al. 2017). Political boundaries cut across the distributions of many species, creating shared stocks between nations (Abrantes et al. 2020), and management units containing only a portion of a larger stock can also produce misleading results for stock assessments (Begg et al. 1999, Gullestad & Sundby 2020). For example, climate-driven changes in species distributions can result in changes in the proportion of a catch in an area, leading to incorrect estimations of abundance

(Hutchings 1996). Further, in the situation where stocks are undergoing rebuilding from past over-harvesting, differential restoration between unidentified stock components can lead to an inability to anticipate future recruitment to these stocks (Begg et al. 1999, Dickey-Collas et al. 2010). Inappropriate assumptions of stock structure may also have implications for resilience and model-based investigations of the effects of climate change on their distribution and abundance (Ciannelli et al. 2013). The maintenance of diversity within a structured population provides an important stabilising (portfolio) effect, conferring resilience and maintaining productivity, not just on the species alone, but across associated ecosystems (Hilborn et al. 2003, Schindler et al. 2010).

The inclusion of spatial structure in stock assessment models themselves is extremely data intensive (Cope & Punt 2011, Mormede et al. 2020). Stock identification methods are therefore frequently used to assist in identifying self-sustaining components within natural populations (Cadrin 2020), prior to conducting stock assessments, with a concomitant resolve to increase data provisions at the scale of management needs (Cope & Punt 2011, Janßen et al. 2018). Stock identification methods are therefore considered as essential partners to stock assessment (Zemeckis et al. 2014). However, the most practiced implementation of stock identification results are through alternate management measures (Kerr et al. 2017).

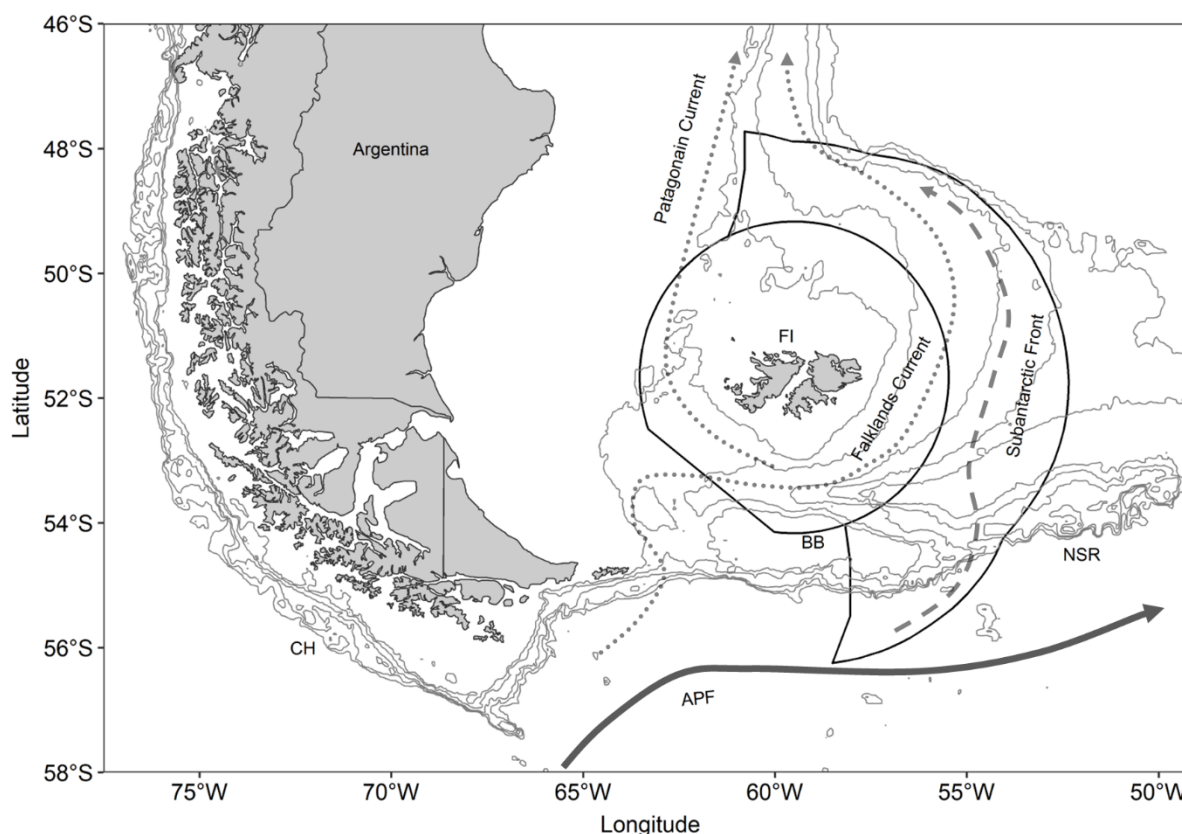
## **1.2. Study area: The Patagonian Shelf**

This research programme was implemented across the Patagonian Shelf, with a specific focus on the shelf, slope and deep-sea plains around the Falkland Islands in the southwest Atlantic (Figure 1). In the southwest Atlantic, the Patagonian Shelf (0 to 200 m) extends along the southern portion of the continental shelf of eastern South America, from the tip of Tierra del Fuego (~55°S), northwards around the Falkland Islands. To the south of the Falkland Islands lies the Burdwood Bank (Matano et al. 2019), a shallow (50 to 200 m) underwater plateau that is separated from the Patagonian Shelf by a narrow (80 km, 400 m deep) channel to the west, extending through a deep trough (>2500 m) to the east where it aligns with the North Scotia Ridge.

The main oceanographic feature of the Patagonian Shelf is the Falkland Current, a north-flowing branch of the Antarctic Polar Front (APF), following the continental shelf-break to the west of the Burdwood Bank and along the southern and east extent of the Falkland Islands (Croxall & Wood 2002, Arkhipkin et al. 2013). South of the Falkland Islands, the weaker Patagonian Current diverges to the west, extending northward (Ulibarrena & Conzonno 2015). A second north-flowing extension of the APF, the Subantarctic Front (SAF) wraps around the eastern extent of the Burdwood Bank, flowing northward where it eventually converges with the Falkland Current and Patagonian Current at 50°S (Ashford et al. 2012, Matano et al. 2019). Oceanographic data indicate that this current is dynamic and shifting with irregular mesoscale eddies occasionally observed breaking through the main current stream along the northern edge of the Burdwood Bank, and linking up with the Falklands Current to the south of the Falkland Islands around Beauchene Island (Song et al. 2016, Fraser et al. 2017).

The Patagonian Shelf and Slope are among the most productive areas in the southwest Atlantic. High densities of macroplanktonic euphausiid and hyperiid amphipods occur in frontal zones around the Falkland Islands, attracting and sustaining important fish and squid resources (Agnew 2002, Arkhipkin et al. 2013), taken by multinational fishing fleets operating in the region.





**Figure 1: Map of the study area identifying the main oceanographic and physical features: APF: Antarctic Polar Front, BB: Burdwood Bank, NSR: North Scotia Ridge, FI: Falkland Islands, CH: southern Chile.**

### 1.3. Study species: Patagonian toothfish

The Patagonian toothfish *Dissostichus eleginoides* Smitt 1898 (family Nototheniidae) is a large (>200 cm TL, >150 kg weight), benthopelagic predatory fish. They have a wide geographic distribution in the Southern Ocean, occurring across the continental shelf, slope, and deep-sea plains of southern Patagonia and Chile; on plateaus surrounding subantarctic islands (e.g. South Georgia, Kerguelen, Heard and McDonald Islands), banks and seamounts (Eastman 1993, Collins et al. 2010). On the Patagonian Shelf, they are broadly distributed in the eastern Pacific as far north as Ecuador, off the narrow Chilean Shelf extending southwards, around Cape Horn, and over the Argentinean and Falklands Shelf in the southwest Atlantic northwards to 30°S. South of the Falkland Islands, they occur over the Burdwood Bank and across the North Scotia Ridge.

### 1.4. Management approach

On the Patagonian Shelf, outside of CCAMLR waters, the species is managed independently by nations according to international boundaries. The species is also targeted by international fleets on the high seas, outside of national jurisdictions. For example, Korean vessels fishing to the north and northeast of the Falkland Islands, and over the North Scotia Ridge have captured a total of nearly 12,000 tonnes between 2013 and 2019 (Park et al. 2021). Catches over the Patagonian Shelf have followed the global pattern, peaking at over 40 000 tonnes in 1995, prior to the implementation of stringent management measures since 2004. Management advice for Patagonian toothfish in the Argentinean, Chilean and Falkland Islands fisheries are based on statistical catch-at-age models which are used to estimate relative biomass (Henriquez et al. 2016, Skeljo et al. 2022). The Chilean Patagonian toothfish stock is

targeted both by industrial and artisanal longline fisheries (Moreno et al. 2006). The stocks are categorised as overfished, with overfishing occurring (Henriquez et al. 2016). Off Argentina, Patagonian toothfish are predominantly (98%) targeted by a deep-sea trawl fishery. The spawning stock biomass is currently estimated to be at 30.3% of the unfished state, corresponding to their defined precautionary biological reference point. Based on this, the Argentine management authority has maintained a 3700 tonnes TAC, with the stock considered to be in a rebuilding state (Godelman et al. 2021). In the Falkland Islands, both the targeted longline fishery as well as the bycatch components arising through the shelf-based inshore trawl fisheries are accounted for in the modelling framework (Skeljo et al. 2022). A total allowable catch (TAC) is then decided in accordance to a set of harvest control rules. The TAC has been set at 1040 tonnes since 2015, with a spawning stock biomass maintained at between 40 to 45% of the unfished state. The stock stands at an acceptable level of abundance, and is projected to increase under the current fishing pressure (Skeljo et al. 2022). To date, models have assumed that single self-replenishing stocks of Patagonian toothfish occur within political boundaries.

## **1.5. Basis of current management units**

### **1.5.1. The Antarctic Polar Front as a population boundary**

Strong genetic heterogeneity has been shown across the APF using both microsatellite and mitochondrial DNA analyses (Shaw et al. 2004, Rogers et al. 2006, Canales-Aguirre et al. 2018). These results have suggested the APF as a major barrier to larval dispersal with deep-water troughs and distance inhibiting movements of adults. Trace element analysis undertaken from the edge and nucleus of Patagonian toothfish otoliths have indicated a sharp population boundary in the vicinity of the APF, with large-scale variation in trace element concentrations from Patagonian populations in relation to subantarctic Islands to the south (Ashford et al. 2005, 2006). This prior evidence of population isolation across the APF has also been corroborated through heterogeneity in whole otolith  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  isotopes (Ashford & Jones 2007). Further, there is no reported evidence of tagged fish being recaptured after movements across the APF (Williams et al. 2002, Marlow et al. 2003, Agnew et al. 2006, Brown et al. 2013a). Medium-scale movements undertaken by tag-recaptured fish have, however, been reported between the South Sandwich Islands to South Georgia (>740 km; Roberts and Agnew, 2008); and from Heard Island to Kerguelen (>210 km) and Crozet (>1025 km; Williams *et al.*, 2002). This reflects that adult Patagonian toothfish are capable of large-scale movements, although these appear to be infrequent. Juvenile Patagonian toothfish are negatively buoyant, however, adults are inferred to become neutrally buoyant at maturity, therefore reducing the energy needed for large-scale movement (Eastman 1993).

### **1.5.2. The South American Continental Shelf**

Microsatellite evidence indicates no significant genetic structuring among populations of the South American continental shelf (Canales-Aguirre et al. 2018). However, genetic markers vary greatly in their ability to resolve the extent to which the population consists of a single or multiple phenotypic or contingent stocks (Beebee & Rowe 2008). Population connectivity may be driven through aspects of their biology including (1) the continuity of the deep-sea habitat in the region enabling the active migration or movement in adults and, (2) dispersal during a protracted egg and larval period (Canales-Aguirre et al. 2018).

Spawning of Patagonian toothfish occurs in discrete areas off southern Chile (Arana 2009), the Burdwood Bank (Laptikhovskiy et al. 2006, Boucher 2018), and the western edge of the North Scotia Ridge (Laptikhovskiy et al. 2006). Around the Falkland Islands, a self-sustaining population was thought to be maintained through annual spawning migrations from foraging areas on the slope and shelf to the north and east of the Falkland Islands with the spawning

areas on the Burdwood Bank (Laptikhovsky et al. 2006). Connectivity may also occur on a slower scale, driven through their ontogenetic migrations from nursery areas to their deep-sea habitats, onwards to their southern spawning areas. On the Patagonian Shelf and slope, these downslope migrations are thought to occur over a more protracted period compared to other areas of their range that contain narrow shelves (Laptikhovsky et al. 2006). However, more recent research results show that annual spawning migrations are unlikely. Large adults that were monitored over a nine month period using archival satellite pop-up tags showed high site fidelity and limited connectivity (Brown et al. 2013a). Further, otolith microchemistry reflects distinct nucleus and edge signatures among areas sampled around the Falkland Islands and Chilean Shelf, suggesting restricted connectivity and the possibility of more than one South American population (Ashford et al. 2005, 2006). Further, the parasite fauna of juvenile Patagonian toothfish indicated spatial separation between individuals inhabiting areas to the northwest and southeast of the Falklands Shelf (Brown et al. 2013b).

Particle simulations in a wind-driven oceanographic model identified wide dispersal of Patagonian toothfish eggs and larvae, from spawning areas on southern Chile and the Burdwood Bank across the Patagonian Shelf (Ashford et al. 2012). In combination with otolith trace element analyses, models predicted recruitment of juveniles from southern Chile to the northern Patagonian Shelf, and region of mixed recruitment from southern Chile and the Burdwood Bank to the south of the Falkland Islands (Ashford et al. 2012). These results are therefore suggestive of large-scale connectivity driven through early life-history dispersal. The absence of spawning in the northern extent of their range, combined with the prospect of high site fidelity (in the absence of annual spawning migrations) identifies important questions in terms of connectivity and the closure of the adult – spawning - recruitment life cycle. There is growing evidence that the spatial structure and population dynamics of Patagonian toothfish may be more complex than currently assumed.

## 1.6. Aims and objectives

The aim of this research programme was to provide an improved understanding of the complex stock structure dynamics for Patagonian toothfish in the southwest Atlantic, specifically in relation to the shelf, slope, and deep-sea plains around the Falkland Islands. To achieve this, an integrated approach was used (Izzo et al. 2017, Kerr et al. 2017) whereby a range of complementary methods were incorporated to improve our understanding of life-history stages identified as potential pathways of population connectivity (Figure 2). In particular, we focused on five research approaches.

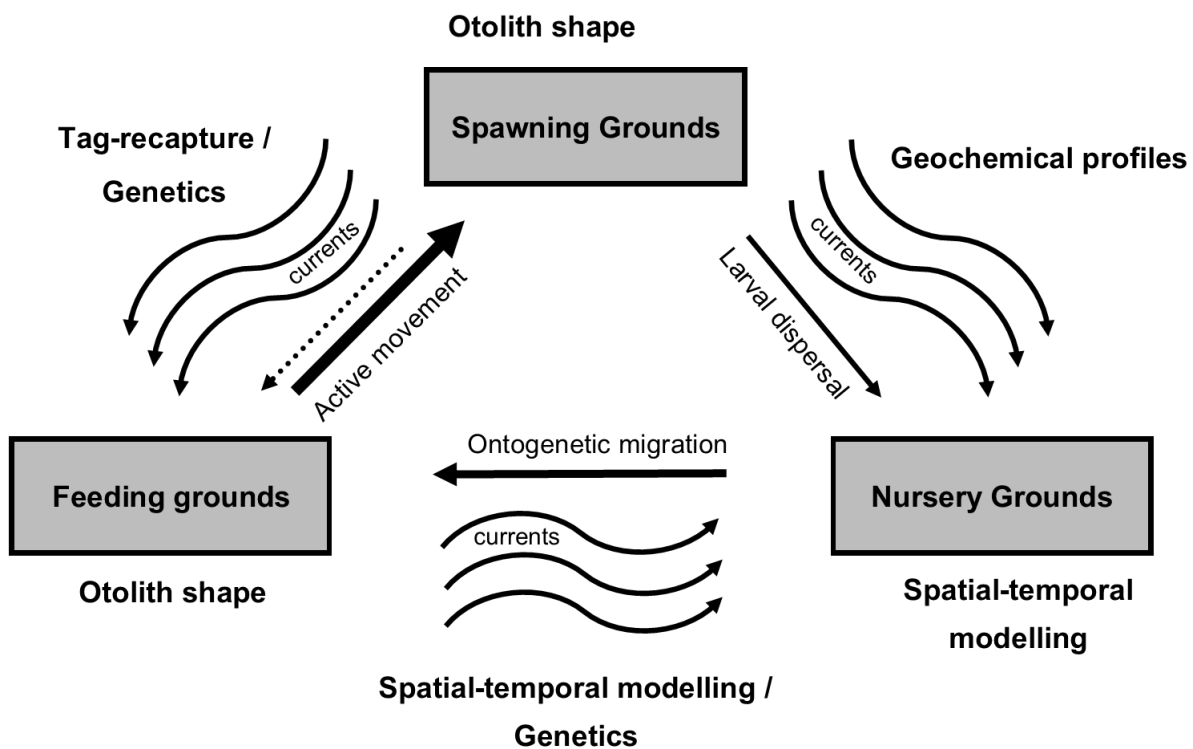
Approach 1 – Morphometric outlines (Lee et al. 2018): Otolith shapes of Patagonian toothfish (*Dissostichus eleginoides*) and Antarctic toothfish (*D. mawsoni*) were investigated for geographic variability within seven regions across the Patagonian Shelf, and South Georgia and the South Sandwich Islands (SGSSI). The approach was applied to assess connectivity across localised spawning and adult foraging habitats, to provide insights into the stock structure of Patagonian toothfish on the Patagonian Shelf.

Approach 2 – Spatial-temporal patterns of early life-history stages (Lee et al. 2021): Ontogenetic migrations were identified as a life-history stage that could lead to increased connectivity between nursery areas and sub-adult habitats. A series of spatial-temporal models were developed to define the spatial units within which early life-history stages occur in shelf waters around the Falkland Islands. The temporal dynamics of these units in the presence of variable interacting environmental (e.g. temperature, currents), chemical (e.g. salinity, oxygen), physical (e.g. depth), and ecological (e.g. inter- and intra-specific competition) drivers were investigated to improve our understanding of (1) recruitment, (2) nursery areas habitats, and (3) ontogenetic migratory pathways.

Approach 3 – Tag-recapture programme (Lee et al. 2022): Deep-sea movement patterns during the adult life-history stages were explored using a medium to long-term tag-recapture programme. We aimed to elucidate the movement patterns as well as the extent that these are driving connectivity during the adult life-history stages of Patagonian toothfish in the region. These were investigated specifically in terms of closing the life cycle and providing a linkage between the adult (non-spawning) component on the northern extent of their range with southern spawning areas.

Approach 4 – The early life-history patterns prior to the settlement of juveniles into a demersal habitat remain elusive and largely unexplored. We applied a complementary approach using otolith microstructure and trace element analysis (by LA-ICM-PS) to infer time-resolved elemental profiles that reflect the early ontogeny of juvenile toothfish from key nursery areas on the Patagonian Shelf.

Approach 5 - Genomics (Arkhipkin et al. 2022): Genetic (mtDNA sequences and genome wide nuclear single nucleotide polymorphisms) and morphological data were used to critically evaluate the taxonomic status of toothfish north (Chile and Patagonian shelf) and south (South Georgia and South Sandwich Islands) of the APF. The stock structure of toothfish within the regions was also investigated.



**Figure 2: Model depicting key life-history stages (boxes), and the approaches undertaken in the current research to investigate potential connectivity pathways (arrows) of Patagonian toothfish on the Patagonian Shelf.**

The current research report aims to incorporate the results into the context of other contemporary findings to describe a tentative life cycle for Patagonian toothfish on the Patagonian Shelf. The primary focus of this approach is to identify the nature and extent of resource sharing on a spatial and temporal basis, and evaluate the biological appropriateness of the current stock boundaries. Using this information, a selection of viable management approaches is reviewed that can be considered for sustainable fisheries management. Finally, a range of research, monitoring and management recommendations are provided to inform the continued movement towards an ecosystem-based approach to fisheries management.

## 2. Research programme findings

Analyses of otolith shape from an extensive component of their distribution highlighted distinct separation along the APF (Approach 1 - Lee et al. 2018). Otolith shape analyses revealed high site fidelity across their distribution, and possible stock separation among early adult fish within localised areas on the Patagonian Shelf. Based on these results limited mixing appeared to occur between southern Chile and Burdwood Bank spawning areas; and feeding grounds off the continental slope and deep-sea plains to the north-east of the Falkland Islands.

Analyses of abundance distributions were undertaken to assess the spatial-temporal persistence (stability) of toothfish nursery area hotspots around the Falkland Islands and to describe their subsequent ontogenetic migration pathways into their adult deep-water habitats (Approach 2 - Lee et al. 2021). Results indicate spatially discrete hotspots exhibiting high temporal variability. This variability is defined through oceanographic influence that drives larval dispersal and survival on the Shelf. Juvenile toothfish appear to follow persistent ontogenetic migrations, linking distinct recruitment areas with their respective component of the adult population on the Patagonian slope. Evidence of mixing among cohort groups during their ontogenetic migration into deep-sea adult habitats was limited, reflecting a mixed population based on oceanographically defined egg and larval dispersal.

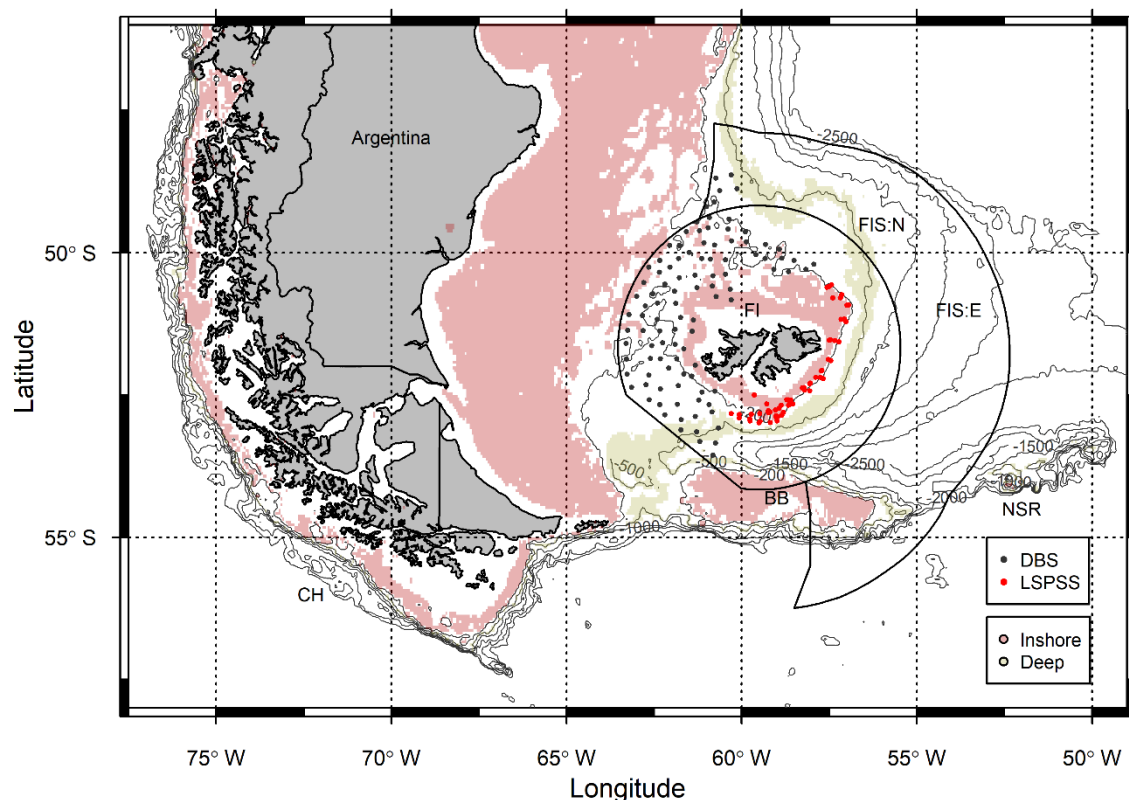
Analyses based on data collected from a large-scale tag-recapture programme were used to elucidate the movement patterns as well as the extent that these are driving connectivity during the adult life-history stages of Patagonian toothfish in the region (Approach 3 - Lee et al. 2022). Tagging and recapture results indicated that the majority of individuals (78%) displayed high site fidelity (<50 km). However, 10% of individuals undertook large-distance movements across oceanographic and physical boundaries. These were characterised by large (>120 cm) fish inhabiting the slope and deep-sea plains (north of 52°S) undertaking southward (direction = 150 - 240°) home-range relocations to spawning areas on the Burdwood Bank, North Scotia Ridge and southern Chile.

Otolith microstructure and trace element analysis were applied to infer time-resolved elemental profiles that reflect the early ontogeny of juvenile Patagonian toothfish from key nursery areas on the Patagonian Shelf (Approach 4 - Lee et al. 2023). Results revealed significant ontogenetic shifts in elemental profiles across the early life-history of Patagonian toothfish. From these, key biological benchmarks were identified, including (i) the hatch date distribution (mid-September to late October; mean = 3 October); (ii) the dispersal period of pelagic larvae until their entry onto the Patagonian shelf (0 to 50 days post-hatch); (iii) the entry phase from the shelf extent to inshore waters (<100 m depth; 50 to 100 days post-hatch); (iv) settlement into a demersal habitat (109 days post-hatch); and (v) subsequent migration into juvenile nursery areas (<150 m depth; 120 days post-hatch).

Results from a genetic study suggests two independent evolutionary lineages within the '*D. eleginoides*' complex and their differentiation into two distinct taxonomic entities as separate species based on genomic and morphometric data (Approach 5 - Arkhipkin et al. 2022). Results also implied a complex level of restricted connectivity between local populations of Patagonian toothfish, specifically between fish captured from (1) southern Chile and the Falkland Islands; and (2) Falkland Islands and the high seas (North of Falkland Islands), illustrating the Falkland Islands as an intermediate zone of mixing.

Based on the findings of this research, in combination with material from prior studies of its biology, it is possible to start piecing together a tentative life cycle for Patagonian toothfish on the Patagonian Shelf (Figure 3). This can also identify further gaps in our knowledge that can be used to define future research priorities for improved management. Throughout the discussion below, the terminology defined by Cadrin (2020), Hawkins *et al.* (2016) and

Ciannelli *et al.* (2013) were used, whereby a population refers to a group of interbreeding individuals that exist together in time and space. We therefore refer to the Patagonian toothfish population as that encompassing the full Patagonian range. The Patagonian toothfish population across the Patagonian Shelf is discussed in the context of a possible stock structure continuum, extending across possible sympatric discrete, spatially complex and panmictic population structures (see a further description of the stock structure continuum in Section 1.1).



**Figure 3: Map depicting the full Patagonian range occupied by Patagonian toothfish across the study area. Solid lines reflect the conservation zones of the Falkland Islands, including juvenile inshore (50 to 150 m) and sub-adult deep-sea areas (401 to 600 m) for which monitoring data are limited. Black points reflect stations from the demersal biomass trawl survey including deep-sea stations used in 2018 (DBS), and red points indicate Loliginid squid pre-season trawl survey stations.**

## 2.1. Connectivity of Patagonian toothfish across their life-history

### 2.1.1. Genetic units

Previous genetic evidence using microsatellites, mitochondrial and nuclear DNA, suggests a single population across the Patagonian region, independent of those to the south of the APF (Smith & McVeagh 2000, Shaw *et al.* 2004, Rogers *et al.* 2006, Canales-Aguirre *et al.* 2018). This clear differentiation in self-sustaining units on either side of the APF was validated through the use of otolith shape analyses (Approach 1 - Lee *et al.*, 2018). Further, genomic data are indicative of two independent evolutionary lineages within the '*D. eleginoides*' complex and their differentiation into two distinct taxonomic entities as separate species (Approach 5 - Arkhipkin *et al.* 2022). A complex level of restricted connectivity was also identified between local populations of Patagonian toothfish, specifically between fish captured from (1) southern Chile and the Falkland Island; and (2) Falkland Islands and the high seas (North of Falkland Islands), illustrating the Falkland Islands as an intermediate zone

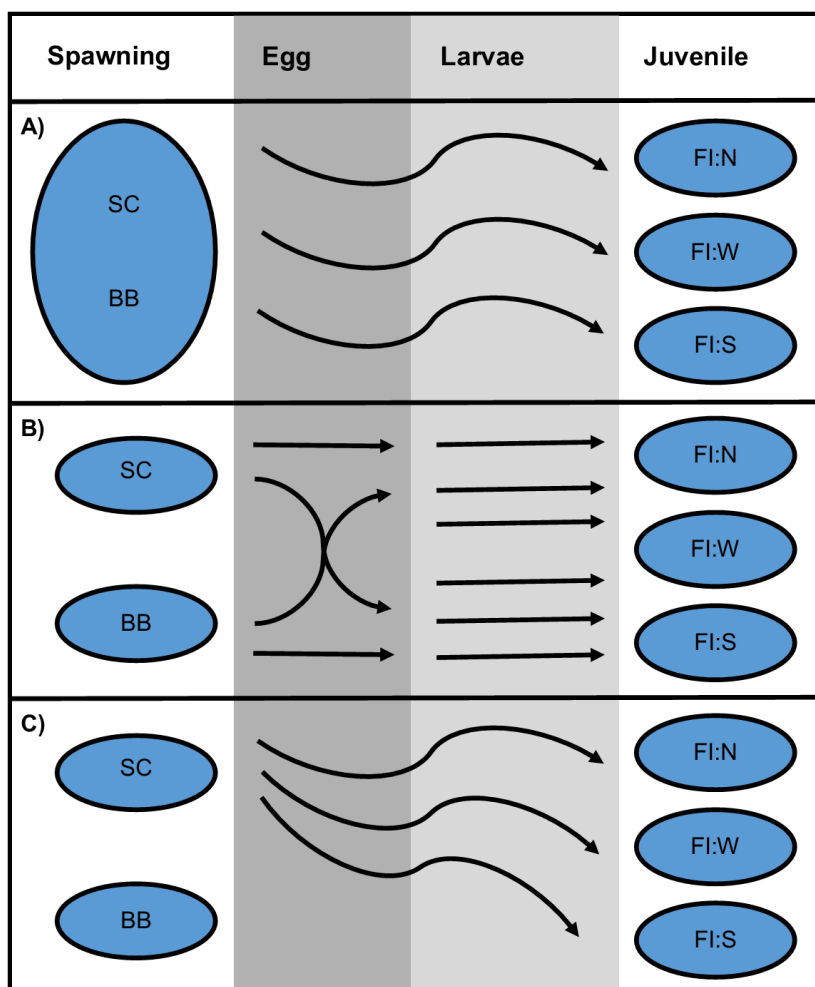
of mixing (Approach 5 - Arkhipkin et al. 2022). These findings were supported on the basis of variability (and similarities) in otolith shape among localised regions representing stock contingents on the Patagonian Shelf between Chile, the Burdwood Bank and a Falkland Islands North - High Seas intermediate zone (Approach 1 - Lee *et al.*, 2018).

### 2.1.2. Spawning

Evidence from previous research identified two discrete spawning localities off southern Chile, and the Burdwood Bank (Laptikhovskiy et al. 2006, Arana 2009). The North Scotia Ridge has also been suggested as a probable spawning area in the region (Laptikhovskiy et al. 2006). No spawning has been observed on the shelf, slope and deep-sea plateau in waters north of the Falklands Trough (*ca.* 53.5°S) despite extensive monitoring by FIFD fisheries observers since 1994 (Laptikhovskiy et al. 2006). Spawning has been recorded over May (minor peak) on the Burdwood Bank, and from July to August across both areas (Laptikhovskiy et al. 2006, Arana 2009). On the Burdwood Bank, spawning is thought to take place at depths of 900 to 1200 m, during which distinct vertical movements of 150 to 580 m take place (Laptikhovskiy et al. 2006, Brown et al. 2013a).

It remains unclear to what extent the spawning areas are indeed discrete units, or instead comprise a continuum extending from southern Chile, across the entire extent of the Burdwood Bank onto the North Scotia Ridge. Results from otolith shape analyses clearly reflect these as discrete population units, although samples from waters intermediate to these areas were not included in the study (Approach 1 - Lee *et al.*, 2018). Results from otolith chemical analyses were inconclusive, with high variability in core signatures either being indicative of (1) a continuous spawning area, (2) the mixing of eggs from discrete areas prior to hatching, or (3) the retention of juveniles around the Falkland Islands from only a single discrete area (Figure 4). Finally, this result may also indicate that inter-individual variability is simply greater than the extent of environmental variability across the region, although, given the results obtained from other studies on otolith chemistry (Ashford et al. 2005, 2012) and shape analyses (Approach 1 - Lee et al. 2018) for Patagonian toothfish in the region, this consideration is unlikely.

A clear delineation of the reproductive potential of fish across the range was not investigated in the current research programme. An understanding of the role of the spawning life-history phase in population connectivity has evolved as an emergent theme requiring research attention (see 3.2.4.2).



**Figure 4: Hypothetical depiction of possible scenarios explaining high variability in microchemistry signatures and what this implies in terms of the retention of juveniles from discrete or continuous spawning areas. A.) Continuous spawning area with eggs and larvae spread evenly across the Falklands Shelf. B.) Discrete spawning areas with mixing taking place during the egg phase, or (C.) retention of early juveniles from a single discrete spawning area. BB - Burdwood Bank; SC - Southern Chile; FI:N – Falkland Islands northern shelf; FI:W – Falkland Islands western shelf; FI:S – Falkland Islands southern shelf.**

### 2.1.3. Egg and larval dispersal and retention

The early life-history of Patagonian toothfish prior to settlement on the shelf is elusive. Indeed, during two research surveys, undertaken by the FIFD during November 2015 (Pompert et al. 2015) and December 2018 (Lee *et al.*, 2019), no Patagonian toothfish eggs or larvae were found, despite the occurrence of 100s of larvae from other species in the region (e.g. *Patagonotothen* spp., *myctophid* spp., *Macrourus* spp., *Sprattus fuegensis*). Until now, the information gathered has largely been based on tank-rearing experiments in Chile (Mujica et al. 2016) or from sparsely sampled specimens (n = 43) obtained over extensive time periods (1978 to 2001) predominantly from south of the APF (Evseenko *et al.*, 1995; North, 2002). Specimens sampled during these surveys included three larvae collected from the upper 3 m layer in waters over the northeastern edge of the Burdwood Bank (200 m depth) in December 1997. Based on evidence from the literature, these samples represent the only reliable record of larval Patagonian toothfish attained for the Patagonian population. From the combined sample collected in this study (i.e. across genetically discrete units), the egg and larval period have been described as pelagic, occurring in the upper 250 m of the water column. Further,



these results provide an egg phase duration ranging between 30 and 105 days. The timing, depth and dispersal characteristics that occur during the egg phase for the Patagonian population, have therefore remained uncertain.

Through the computation of particle trajectories in an oceanographic simulation model, Ashford *et al.* (2012b) predicted potential dispersal pathways, and retention possibilities for juvenile Patagonian toothfish on the shelf around the Falkland Islands (Table 1). However, due to knowledge gaps, results were wide ranging (0 to 28.5%), depending on the month of release, dispersal period, and retention area. Through results achieved from otolith microstructure and chemical analyses, we were able to identify the timing of key early life-history events including (1) the hatch date distribution (mid-September to late October; mean = 3 October ± 8.47 days); (2) a period of natal dispersal (0 to 50 days post-hatch, dph; mean = 22 November); and (3) entry of pelagic larvae onto the Patagonian shelf (50 to 100 dph; 1 January); (4) settlement into a demersal habitat (100 to 120 dph; 31 January); and (5) the start of a downslope ontogenetic migration into juvenile nursery areas (>120 dph; Approach 4 - Lee *et al.* 2023). Results from the current research programme indicated a mid-July to late-August release date and a 60 - 140-day period of egg and larval dispersal from spawning areas to the shelf-edge (Approach 4 - Lee *et al.* 2023). These refinements seem to provide positive validation for the retention of dispersed eggs and larvae from both spawning areas with a dominance of input from southern Chile to the western shelf, and mixed retention in the south and northeast. Model predictions indicate that all egg and larval dispersal arising from the North Scotia Ridge would be retained in the High Seas to the north of the Falkland Islands (Ashford *et al.* 2012).

**Table 1: Mean percentage (range) of simulated particles (representing egg and larval dispersal) released between May and July 1996–2000 from (a) Burdwood Bank and (b) southern Chile, present in the northern and southern FICZ at 50–300 days (table taken from Ashford *et al.*, 2012b). Refined scenarios based on recent results have been highlighted in grey.**

a)						
Month	Destination	Mean % in FICZ at day				
		50	100	200	250	300
May	North	2.6 (0–5)	3 (0–8)	0	0	0
	South	17(0–38.5)	11 (0–26)	1.5 (0–5)	1.5 (0–5)	1.5 (0–5)
June	North	1(0–2.6)	1 (0–5)	1 (0–5)	0	0
	South	16 (5–26)	7 (0–23)	0.5 (0–2.5)	1 (0–5)	1.5 (0–8)
July	North	3.6 (0–13)	0.5 (0–2.6)	0	0	0
	South	15(5–20.5)	11 (5–15)	3 (0–10)	1.5 (0–8)	2 (0–10)
b)						
May	North	1.8 (0–4)	7.5 (3–11)	13 (6–22)	3(1.5–6)	1.5 (0–3)
	South	17(4.5–31)	27 (16–44)	5 (0–10)	2 (0–3)	2.3 (0–6)
June	North	0.8 (0–4)	10(1.5–25)	10 (6–17)	2 (0–6)	1.8 (0–4)
	South	14.5 (3–26)	22.5 (10–40)	3 (0–4)	3 (0–10)	2 (0–4)
July	North	2.4 (0–4)	12 (3–24)	9 (4–19)	3.5 (1.5–9)	10
	South	11 (3–25)	28.5 (15–46)	3.3 (1.5–10)	3.5(1.5–12)	3.5(1.5–10)

Further support for spatial-temporal variability of a mixed stock origin was provided through species distribution models of age-structured cohorts (Approach 2 - Lee *et al.* 2021). Retention hotspots that serve as nursery areas for juvenile Patagonian toothfish showed strong spatial-temporal variation, specifically to the northeast, west and south of the Falkland Islands

(Approach 2 - Lee et al. 2021). The retention of early juveniles in these areas as discrete units is strongly suggestive of recruitment from separate spawning areas, or spawning periods (Hare & Richardson 2014). A discrete hatch date distribution, however, precludes separate spawning periods (Approach 4 - Lee et al. 2023). The spatial-temporal abundance patterns of juvenile Patagonian toothfish in nursery areas were largely driven by mesoscale oceanographic features, specifically eddies forming off the northeast of the Burdwood Bank (Approach 2 - Lee et al. 2021). The increased presence of these oceanographic features provides an important link between the Subantarctic Front (and Burdwood Bank spawning area) with the Falklands Shelf leading to higher levels of larval retention and recruitment; specifically, to the southern (2015 and 2017) and northeastern (2015) nursery areas. Results obtained from spatial-temporal patterns in subsequent year classes indicate that in the absence of retention hotspots, low levels of stable recruitment continue to occur to the northwest of the Falkland Islands, thought to originate from southern Chile (Ashford et al. 2012). The greater oceanic influence through these eddies was identified in otolith chemical profiles of fish retained in the southern and northeastern areas during these years of high recruitment (Approach 4 - Lee et al. 2023). Heterogeneity in otolith core chemistry for Patagonian toothfish sampled from the northern and southern Falklands Shelf has been linked to a southern Chile or Burdwood Bank natal origin (Ashford et al. 2012). Variability in otolith shape of fish from the northern foraging grounds only indicated minor association with the Burdwood Bank and complete isolation with southern Chile (Approach 1 - Lee et al., 2018). However, otolith samples used in the study were from adult individuals, and environmental stability through high site fidelity may have masked any association with original spawning areas.

The balance of results therefore favours a mixed stock origin with a self-sustaining population dominated by input during high recruitment cohorts from the Burdwood Bank spawning population to the southern and northeastern shelf. Finally, results obtained from Approach 2 (Lee et al. 2021) and Approach 4 (Lee et al. 2023) provide the distinct potential for further refining of model predictions through the provision of known retention areas (i.e. nursery hotspots) and dispersal periods in a given year, and the inclusion of these in predictions inferred through particle simulation oceanographic models (see 3.2.4.3).

#### **2.1.4. Demersal juveniles and sub-adults**

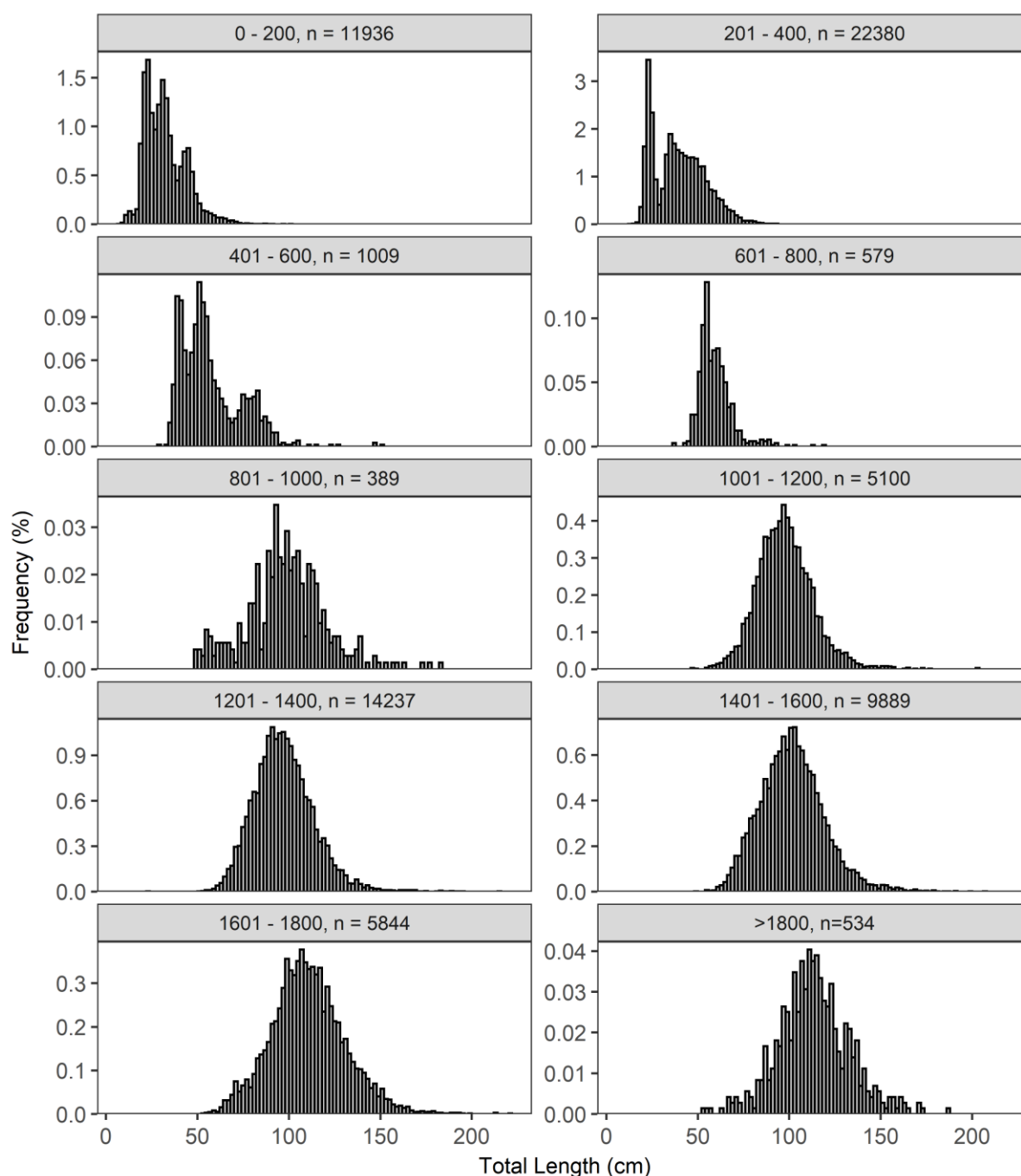
Benthic juveniles appear on the shelf for the first time at length of 5 to 15 cm during late January to early February (Arkhipkin & Laptikhovskiy 2010). In Approach 4 (Lee et al. 2023), settlement into a demersal habitat was identified at 110 days post-hatch, with a mean date of settlement on 10 January (in the peak of the austral summer). In Approach 2 (Lee et al. 2021), persistent (stable) nursery area hotspots were identified to the northwest, along with opportunistic (spatially and temporally variable) areas to the south and northeast of the Falkland Islands (see discussion above). Nursery areas were characterised by the presence of quasi-stationary upwelling regions where cold, productive subantarctic waters were pushed up onto the Falklands Shelf.

The recruitment of juveniles into discrete nursery areas proves vital in defining their abundance and ontogenetic migratory pathways over the next three to five years. During their juvenile life-history stages (ages 0+ to 3+), it was shown how a spatially progressive (related to previous age) down-slope ontogenetic migration occurred into deeper waters (Approach 2 - Lee et al. 2021; Approach 4 - Lee et al. 2023). Predictable pathways were identified adjacent to the areas of initial recruitment. As such, juvenile Patagonian toothfish that were retained in the southern nursery area migrated southwards; those within the northeast nursery area migrated towards the northern and eastern slope; and those to the west migrated southwest towards the western extent of the Falklands Trough, thus linking up with the southern ontogenetic migratory corridor. By age 4 (50 to 60 cm TL) the majority of juvenile toothfish (>97% by number) had migrated past the shelf edge into waters >400 m. This is indicative that

the stock structure, as defined by recruitment patterns, is largely retained throughout the juvenile to sub-adult life-history stages, with no evidence of large-scale mixing taking place on the shelf up to the point of their entrance into deeper waters of the slope.

Difference in the otolith shape of Patagonian toothfish sampled from adult fish (TL > length-at-50% maturity) on the Burdwood Bank and the northern Slope provides retrospective validation of isolation over the course of their life-history from their recruitment into nursery areas, and through their spatially discrete ontogenetic migrations (Approach 1 - Lee *et al.*, 2018). A second consideration is that these results indicate that abundance on the eastern slope is largely driven by the northeast nursery area; while the southward direction of the ontogenetic migrations of fish from the southern and western nursery area appear to feed into the southern slope, the Falklands Trough, the Burdwood Bank and possibly even as far as the southern Chilean adult components of the population.

The term sub-adult is defined as juvenile fish that use adult habitats rather than spatially discrete juvenile nursery and ontogenetic pathway habitats (Hare & Richardson 2014). Information on the sub-adult component of the population that occurs between 400 m and 800 m is scarce, mainly due to it forming a gap between the maximum depths targeted by commercial trawlers (400 m) and longline operations (generally >900 m). However, length-frequency data (n = 1588; 2015 to 2021) indicates that this region largely comprised fish with lengths between 35 and 75 cm, reflecting fish between 3 and 5 years old (Approach 2 - Lee *et al.*, 2021; Figure 5). These sub-adult cohorts can be followed with increasing depths, although a clear convergence with older adult life-history stages occurs at depths between 600 and 1000 m. The sub-adult to adult components of the population are therefore thought to be more or less separated along this depth range (Laptikhovskiy *et al.* 2006, Arkhipkin & Laptikhovskiy 2010). These results indicate that the final stages of the sub-adult ontogenetic migration take place across the same down-slope spatially discrete patterns, as defined in Approach 2 (Lee *et al.* 2021) until convergence with the adult component of the population.



**Figure 5: Length frequency distribution at different depths for Patagonian toothfish sampled on the Patagonian Shelf and Slope between 2015 and 2021 (n = 71897).**

**2.1.5. Adults**

The length at which 50% of the population reaches maturity for both the Falkland Islands and southern Chile is reported as 81 to 86 cm (male) and 89 to 90 cm (female), respectively (Laptikhovsky et al. 2006, Arana 2009). Histological evidence suggests that maturity may be reached at smaller sizes (Falkland Islands; females = 79.1 cm), although the majority of individuals (55.8 to 85.6%) are not active participants in spawning on an annual basis (Boucher 2018, Yates et al. 2018). On the Kerguelen Plateau, the ontogenetic migration of Patagonian toothfish is thought to stop between 600 and 1200 m where they settle at their preferred depth to feed and grow as they approach maturity (Péron et al. 2016). Length-frequency distributions around the Falkland Islands reflect similar patterns (Figure 5). Fish

occupying these depths reflect a consolidation of sub-adult cohorts entering the deep-sea adult population (Arkhipkin & Laptikhovsky 2010).

Results of Approach 1 (Lee *et al.*, 2018), provide little evidence of movement in sub-adult and early adult fish (70 to 120 cm). These indications were further validated by results from tag-recapture data showing high levels of site fidelity across their Falklands distribution (Approach 3 - Lee *et al.*, 2022). However, despite high site fidelity, small-scale (44.40% of recaptured fish moved between 11 and 50 km) to medium-scale (12.50% of recaptured fish undertook movements of 51 to 200 km) movement, defined as foraging activity does seem to occur (Approach 3 - Lee *et al.*, 2022; Brown *et al.*, 2013a). At this stage in the life-history, the stock structure therefore remains defined according to the dispersal and subsequent retention of larvae within nursery areas, and the associated ontogenetic migratory pathways into adjacent deeper waters. Upon reaching maturity, fish that were retained as larvae on the Burdwood Bank continue their ontogenetic migration into deeper waters for spawning. The extent of their spawning on an annual basis remains uncertain and requires further research (Boucher 2018, Yates *et al.* 2018). Fish that were previously retained as larvae on the west, northeast and southern areas of the Falklands Shelf, consisting of southern Chile and Burdwood Bank contingents, utilise these adult areas on the southern, northern and eastern slope exclusively as feeding zones to grow and increase body condition for migrations to spawning grounds.

Two sets of movement behaviours appear to be initiated when fish reach spawning condition. Fish begin what appears to be (1) a range relocation towards spawning grounds; in combination with (2) a continuation of their ontogenetic migration into deeper waters (Approach 3 - Lee *et al.*, 2022). Due to the absence of northern spawning grounds, this would suggest a continued southward dispersal and replacement pattern undertaken by larger fish that were retained as larvae on the Falklands Shelf and High Seas. Many fish, however, do not appear to be undertaking this home-range relocation. Either they are unable to reach suitable condition to undertake a migration, or this is attained relatively late in their life-history. While return feeding migrations have been proposed, results from Approach 1 (Lee *et al.* 2018) indicating clear differences in the otolith shape among local regions, and Approach 3 (Lee *et al.*, 2022) showing an absence of southward migrations, suggest that this is not a common occurrence. Further, results suggest that natal homing may be apparent in their southward home-range relocations, although this requires further investigation (see Section 6.4.3. Data Collection and Monitoring: Tag-recapture Programme). Given their long life-history, a tag-recapture programme of six years is relatively short, and further patterns may become evident over time.

## **2.2. Stock structure: Spatially complex population**

Large-scale uncertainty remains in our understanding of the stock structure for Patagonian toothfish in the region. The absence of clear genetic heterogeneity across the region suggests that sympatric discrete populations are unlikely (Arkhipkin *et al.* 2022). Similarly, evidence of genetic structuring and high site fidelity as described through results from otolith shape (Lee *et al.* 2018) and tag-recapture analyses (Lee *et al.*, 2022) indicate a definitive panmictic population structure is also not reflective of the Patagonian toothfish population in the region. Results across studies are suggestive of a spatially complex population, i.e. a metapopulation type structure (Smedbol & Stephenson 2001, Ciannelli *et al.* 2013). Life-cycle connectivity from juvenile retention areas around the Falkland Islands, through progressive life-history stages to southern spawning locations, suggests deviation from a distinct source-sink model (Approach 2 - Lee *et al.* 2021; Approach 3 - Lee *et al.* 2022). Nonetheless, characteristics of this structure do appear to exist as reflected in high site fidelity outside of the spawning areas (Approach 3 - Lee *et al.* 2022), possibly indicative of vagrants (Sinclair & Iles 1989).

The key question of where along the continuum Patagonian toothfish in the region lie, in terms of a classical metapopulation vs panmictic type stock structure, relates to the extent of

connectivity among discrete or continuous spawning areas; specifically, to the extent that spawning areas are indeed structured as discrete units as opposed to a continuous zone extending across the southern range. Evidence, however, suggests discrete spawning areas occurring across their southern range are likely. A second interacting factor relates to the extent that return home-range relocations of reproductively capable adults (Approach 3 - Lee *et al.* 2022) are a reflection of natal homing to discrete spawning areas, or simply a movement to the area most suitable for spawning. The occurrence of natal-homing would suggest a classical metapopulation type structure, even despite the indication of large-scale mixing of contingents during the process of egg and larval dispersal.

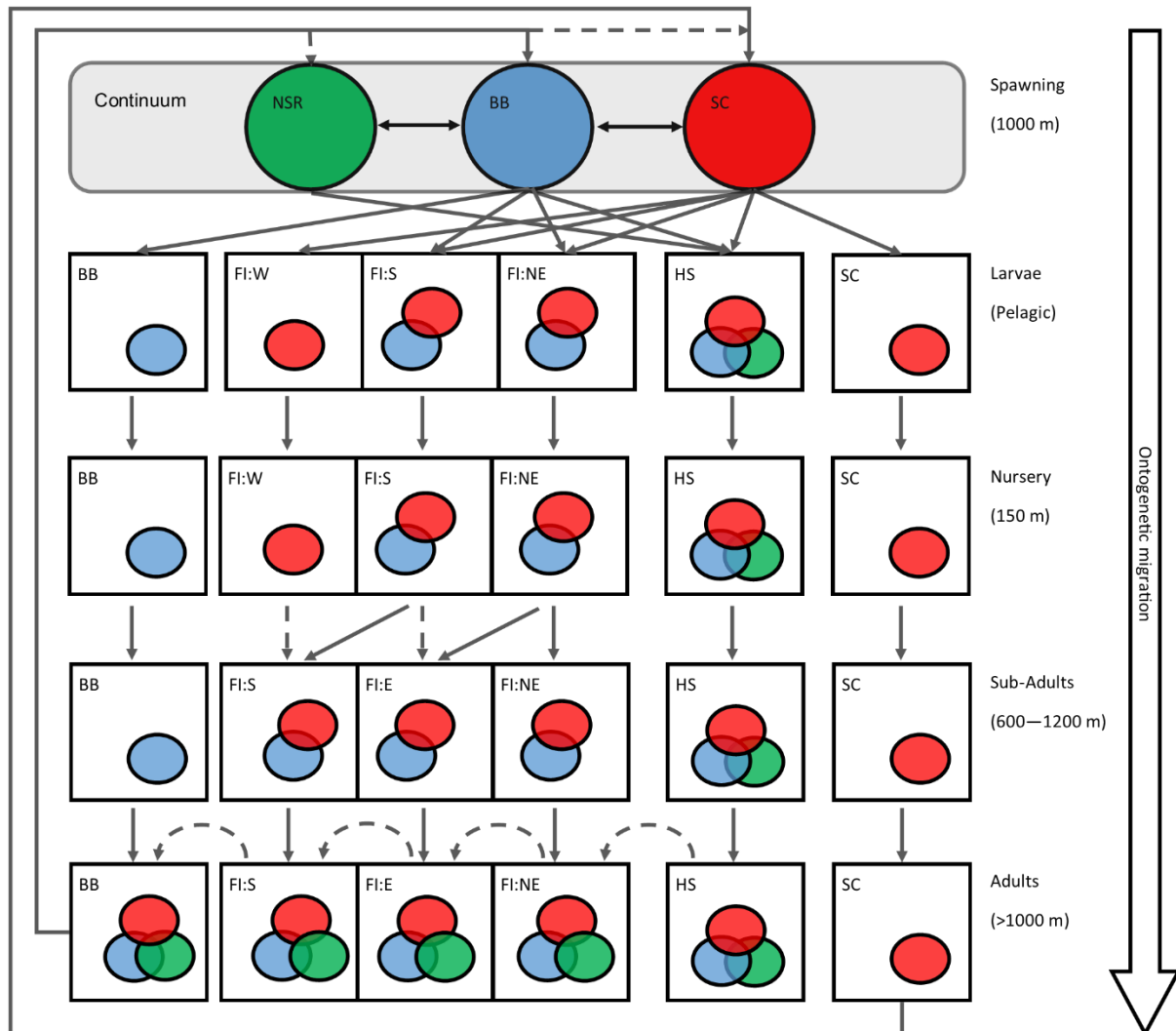
The stock structure for Patagonian toothfish on the Patagonian Shelf and deep-sea plateau may be a reflection of a spatially complex classical metapopulation type structure with aspects of source-sink dynamics according to the 'member-vagrant hypothesis'. The population structure is comprised of at least three contingents, arising from southern Chile (SC), Burdwood Bank (BB) and North Scotia Ridge (NSR) spawning stocks (Figure 6). Spawning occurs between May and August across the population. A component of the southern Chile contingent is retained within Chilean waters across all life-history stages (Arana 2009; Approach 1 - Lee *et al.* 2018), also reflecting a distinct member group according to the 'Member-Vagrant Hypothesis' (Sinclair & Iles 1989). Similarly, a component of the Burdwood Bank contingent is retained within this area from larval, through to the spawning life-history stages (Ashford *et al.* 2012b; Approach 1 - Lee *et al.* 2018). Egg and larval dispersal from the North Scotia Ridge spawning stock are all retained on the High Seas to the north of the Falkland Islands (Ashford *et al.* 2012). Early juveniles that are retained on the shelf around the Falkland Islands arise from both the southern Chile and Burdwood Bank spawning areas. The compositions of individuals from each contingent are not known, but high levels of mixing are hypothesised.

Early juveniles from the Burdwood Bank spawning area are retained across the southern (Ashford *et al.* 2012) and northeastern extent (Approach 4 - Lee *et al.* 2023) of the Shelf, with years of high recruitment driven by oceanographic processes (Approach 2 - Lee *et al.*, 2021). Early juveniles that are retained from the southern Chile spawning therefore appear to be less vulnerable to oceanographic variability and are distributed more consistently across the shelf regions around the Falkland Islands, in particular to the western shelf (Ashford *et al.*, 2012b; Approach 2 - Lee *et al.*, 2021). The stock structure is largely retained throughout the subsequent nursery and ontogenetic migratory life-history phases until maturity is reached. However, there is some evidence of mixing of contingents on the Falklands Shelf through (1) the merging of the western and southern ontogenetic migratory pathways into a single southern channel; (2) the eastward ontogenetic migration of juveniles from the southern and northeast nursery areas.

Upon reaching maturity, a considerable proportion of the population (9 to 25% covering all contingents) initiate large-scale southern dispersal movements defined as home-range relocations towards what may be their original spawning contingent (natal homing). Many individuals that were dispersed as eggs and larvae to these northern areas, however, do not appear to undertake a home-range relocation, remaining as non-spawning (but spawning capable) inhabitants (i.e. vagrants displaying source-sink characteristics). This means that the stock structure across the adult deep-sea habitats consists of (1) non-spawning (but spawning capable) vagrants retained as larvae from the three spawning contingents; potential migrants (2) passing through or (3) yet to undertake their home-range relocations to their respective spawning grounds; or (4) individuals that have undertaken a return migration, although there is currently only limited evidence available to support this hypothesis (i.e. a return feeding migration as hypothesised by Laptikhovskiy *et al.* (2006a) and Boucher (2018)).

The adult life-history stages occurring on the Burdwood Bank spawning grounds therefore consist of (1) locally retained fish; (2) returnees of Burdwood Bank contingents that were

dispersed as eggs and larvae to the High Seas and Falklands Shelf; and (3) North Scotia Ridge and Southern Chile contingents passing through as they undertake home-range relocations towards their respective spawning grounds. This reinforces the importance of the Burdwood Bank population, not only as an important spawning stock contingent driving recruitment across the Patagonian Shelf and slope, but also as a major connectivity hotspot for Southern Chile and North Scotia Ridge contingents as they pass through to their respective spawning grounds.



**Figure 6: Hypothetical life-cycle for Patagonian toothfish depicting the stock structure based on findings of this thesis. The three spawning stock contingents (NSR = North Scotia Ridge, BB = Burdwood Bank, SC = Southern Chile) that make up the metapopulation are depicted passing through areas of interest across key life-history stages. Regions of interest: BB = Burdwood Bank, FI:W = Falkland Islands west, FI:E = Falkland Islands East, FI:S = Falkland Islands South, FI:NE = Falkland Islands North East, HS = High Seas, SC = Southern Chile. Dashed lines indicate movement across areas.**

### **3. Application of findings**

#### **3.1. Management approaches**

Understanding where the Patagonian toothfish population structure lies in terms of a discrete sympatric – spatially complex – panmixia continuum provides a framework in which to define suitable management units (Hawkins et al. 2016). For a population displaying sympatric or distinct source-sink characteristics, the emphasis is on management of the source population (i.e. southern Chile, Burdwood Bank and North Scotia Shelf). At the other end of the extreme, a classical metapopulation approaching panmixia requires consideration as an integrated single unit.

While a broad spectrum of potential techniques is available, Kerr *et al.* (2017) described five core approaches that have been applied to integrate new information on complex population structure and mixing of marine fish into assessment and management. These will be discussed below in relation to the findings of the current research and their potential application in the development of improved assessment and management measures for Patagonian toothfish around the Falkland Islands. It is important to note that these management approaches are not mutually exclusive. In the current context, multiple approaches have been incorporated over time, and are noted in the discussion below.

##### **3.1.1. Status quo management**

The status quo management approach reflects the situation wherein there is insufficient information to change current management practices, providing a default position. The basis for following this approach involves the situations wherein (1) levels of uncertainty or the reliability of current data is inadequate to provide credible or robust advice for management, (2) the presence of stock units that span international boundaries characterised by complex politics, or (3) a combination of the above. These factors are largely applicable in the current context wherein each geographical area is managed independently according to political boundaries, with the assumption of no mixing of contingents. The degree of stock mixing across these political boundaries is therefore an important source of uncertainty in the assessment of Patagonian toothfish.

Through improved collaborations (see 3.2.3), the achievement of strategic research objectives (see 3.2.4), and enhanced monitoring (see 3.2.5), changes in the relative abundance of unique populations can be tracked. Further, sufficient scientific consensus is available, both in terms of stock structure and life-history dynamics, for the incorporation and implementation of additional approaches for meeting management objectives. These will be further developed in the sections below.

##### **3.1.2. ‘Weakest link’ management**

The weakest link management approach reflects the situation wherein there is some knowledge of spatial structure, but insufficient information exists to explicitly manage all spawning components. Therefore, the assumed weakest spawning component is protected through management measures. Although not necessarily the ‘weakest link’, based on management objectives, this would involve the introduction of measures to protect the Burdwood Bank contingent of the stock. The justification for the selection of the Burdwood Bank as the ‘weakest link’ is based on it being the spawning area that can be comprehensively controlled by the Falkland Islands Government.

The relative contribution of the Burdwood Bank contingent to the abundance of Patagonian toothfish across life-history stages and areas (see 3.2.4.1) is not known. Further, how this



contribution varies on a spatial-temporal scale according to oceanographic processes (see section 3.2.4.3) is yet to be identified. However, the occurrence of this contingent in spatial units across the spawning area itself (Burdwood Bank), nursery areas (Burdwood Bank, northeastern and southern shelf), and the ontogenetic pathways that link these (southern and southeast pathway) have been identified. Options for the implementation of management measures to protect the Burdwood Bank contingent can therefore be pursued using this approach.

At present, management measures have already been implemented for the protection of the Burdwood Bank spawning area. For example, no trawling is permitted on the Burdwood Bank, and longline based commercial fisheries are prohibited from fishing in the area during spawning from June to August (see 3.1.3). In addition, management measures have been initiated with the objective of reducing bycatch of juvenile Patagonian toothfish on the Shelf. These entail a 'move-on rule' in which vessels are required to exit the spatial unit (pre-defined 0.5°W x 0.25°S grid-squares) wherein they are fishing for 10 days, after triggering an action (defined as Patagonian toothfish catch >1.5% of daily aggregated trawl catch calculated for each respective vessel).

The implementation of a weakest link management approach can be considered as an extreme version of precautionary principles, in the presence of uncertainty. The greatest drawback of this is that it can also lead to an under-utilization of the population, and therefore not be effective in optimizing long-term yield (Punt & Donovan 2007). In contrast, the weakest link management approach can also result in a displacement of effort to contingents that are not being protected, leading to an overall loss of biomass and decrease in yield (Crowder et al. 2000, Abbott & Haynie 2012).

### **3.1.3. Spatial and temporal closures**

Spatial and temporal closures can be implemented in situations where there is knowledge of spatial structure, but insufficient information exists to alter the scale of assessment. Spatial and temporal closures are usually used to protect vulnerable life-history stages, sometimes at specific times of the year (e.g. spawning populations).

A year-round closure has been implemented on the Burdwood Bank to trawl-activity, as well as to commercial longline operation during the Patagonian toothfish spawning season. However, nursery and juvenile life-history stages remain susceptible to fishing pressure. Based on data from long-term monitoring programmes (biomass surveys, pre-season surveys), spatially and temporally variable nursery area hotspots can be reliably predicted. Further, the increasing persistence with age in the abundance of shelf-based juveniles and sub-adults across ontogenetic pathways, reflect stable spatial zones as a focus point for the implementation of management measures (Approach 2 - Lee *et al.*, 2021). Due to the low abundance of Patagonian toothfish in their nursery areas relative to species targeted by commercial fisheries (*Merluccius hubbsi*, *D. gahi*), along with their small size (6 to 15 cm, 4 to 10 g), newly recruited juveniles are unlikely to be protected by the move-on rule described above. Further, closed areas are likely to create problems due to overlap with other important commercial fisheries across the region. Additional spatial and temporal closures need to be investigated in relation to gear-restrictions (mesh size restriction), and implemented on a proactive basis according to thresholds and triggers, defined according to a robust monitoring framework (see 3.2.5.1).

### **3.1.4. Integration of stock composition into management**

The incorporation of stock composition into management decisions can be applied in situations where there is knowledge of stock mixing, but insufficient information exists to

explicitly model connectivity within a stock assessment. An understanding of the stock composition for Patagonian toothfish around the Falkland Islands is not currently known, although there is a clear potential for this to be achieved (see 3.2.4.1). Understanding stock composition in a given year, may provide higher levels of resolution for the implementation of weakest link management (see 3.1.2) or spatial and temporal closures (see 3.1.3), protecting stock components of importance (based on management objectives), without adversely affecting overall yield. Further, the development of time series of composition data across life-history stages, can subsequently be used to identify oceanographic, anthropogenic or environmental drivers of these changes. Relevant management measures can then be incorporated to mitigate these changes.

### **3.1.5. Alteration of stock boundaries**

The alteration of stock boundaries is a management approach wherein sufficient information is available on population structure, which allows updating and redrawing stock boundaries to improve the alignment of biological populations and management units. In the current context, high levels of uncertainty still characterise our understanding of the stock structure within the region. What is evident is that some levels of connectivity among the three spawning stock contingents are likely. Increased collaborative efforts with Chile and Argentina would be beneficial in terms of developing a unified framework for assessments. From this broad perspective of unified management, and based on assessments derived from the overall population, improved management objectives can be identified that are based on the incorporation of the approaches described above.

## **3.2. Management recommendations**

The results of this work have filled important gaps and together with prior research, has provided important baseline information in terms of understanding the stock structure for Patagonian toothfish in the region. However, fundamental information is still required to build up a complete picture. These themes described below are based on information requirements pertaining to two key life-history periods that appear to be the driving force in terms of stock structure within the region: the dispersal of eggs and larvae through oceanographic processes and home-range relocations undertaken by spawning capable adults.

### **3.2.1. Maintain and revise current management measures**

Management measures that have already been implemented for the protection of the spawning stock and juvenile components of the population should be maintained and further developed in terms of future research. Specifically, restrictions of trawling on the Burdwood Bank should be maintained. Similarly, the prohibition of longline fishing on the Burdwood Bank during spawning from June to August should be maintained.

The 'move-on rule' requires further revisions to ensure the protection of shelf-based newly recruited toothfish on a proactive basis (see 3.1.3). This aspect has been further refined in a recent report undertaken by FIFD providing a range of data management, monitoring and fisheries management recommendations in this regard (Skeljo 2023). In particular, potential candidates for a new threshold could be either in absolute (100 - 200 kg of toothfish bycatch per vessel-day) or relative terms (0.5 - 1.0% of toothfish bycatch per vessel-day).

### **3.2.2. Stock assessment**

Current results demonstrate that the stock structure arising from the retention of mixed contingents across the Falklands Shelf remains discrete (within the Falkland Islands Conservation Zone) until adult life-history stages. Considering the currently available

information, for the purpose of stock assessment it is recommended to assume that there is one discrete toothfish stock present in Falkland Islands waters.

### 3.2.3. Collaborations

A key theme that has arisen across this research reflects the shared Patagonian toothfish population across political boundaries. It is therefore important for increased collaborative research, monitoring and communications to take place between the scientific departments of Chile, Argentina, and the Falkland Islands. This is already starting to occur between Chile and the Falkland Islands, with the development of new research projects in this regard that may provide further clarity in terms of understanding the stock composition in areas south of the spawning grounds (see 3.2.4.1). Further, future findings may push for further collaborative efforts in terms of assessments for the Patagonian toothfish population as a combined stock, or the inclusion of data from specified contingents that straddle international boundaries.

### 3.2.4. Research priorities

#### 3.2.4.1. *Research priority 1: The identification of mixed stock origin on the Patagonian Shelf*

The aim of this study would be the identification of markers that can be used to develop a time-series, describing the proportions of each contingent across the population. While otolith shape was shown to be effective in discriminating fish captured across areas, it is unclear to what extent this is a reflection of (1) the stock contingent from which they arise, or the area within which they have spent their lives up to the point of capture (i.e. a reflection of high site fidelity adjacent to the area of larval retention; Approach 1 - Lee *et al.*, 2018). Otolith microchemistry analysis may provide the key missing component for identifying the stock composition of Patagonian toothfish across the region. The specific objectives for such a study would be to identify elemental signatures in the core region of otoliths from the three spawning contingents (Chile, Burdwood Bank and North Scotia Ridge), and compare these with signatures from fish dispersed across the Patagonian Shelf. Such a collaborative project has already been initiated between the Falkland Islands and Chile through the sharing of otolith samples.

#### 3.2.4.2. *Research priority 2: Identification of stock reproductive potential*

Key questions pertaining to the reproductive biology for Patagonian toothfish were identified in the current study, with a key focus on the extent of potential skipped spawning in their adult, deep-sea, northern habitats. Further research is required to characterise the active spawning depth, seasons, and maturity schedule in Patagonian toothfish across contingents. In addition, it is essential to estimate the proportion of each spawning stock contingent that fails to undertake home-range relocations, or actively participate in spawning (i.e. skipped spawners as discussed in Approach 3 - Lee *et al.*, 2022). Related to this, further research should be undertaken to evaluate the extent of spawning periodicity that takes place in Patagonian toothfish among contingents across the Patagonian Shelf.

#### 3.2.4.3. *Research priority 3: Early life-history transport on the Patagonian Shelf*

Improving our understanding of oceanic transport and their role in population connectivity during egg and larval dispersal has emerged as a key driver of stock structure dynamics for Patagonian toothfish. Such approaches have already been investigated through the important works undertaken by Ashford *et al.* (2012b) as well as by Mori *et al.* (2016) on the Kerguelen Plateau. The predictive abilities of these works can be enhanced through the incorporation and validation provided by recent research findings, such as the (1) incorporation of known

larval retention areas based on spatial-temporal distribution models (Approach 2 - Lee *et al.*, 2021), (2) improved understanding of spawning behaviour (see 3.2.4.2); and updated estimates of the larval period prior to settlement (Approach 4 - Lee *et al.* 2023).

### **3.2.5. Data collection and monitoring**

#### *3.2.5.1. Fisheries-independent surveys*

Demersal biomass surveys represent the most important high-resolution data source supporting the evaluation of demersal resources based on fishery-independent data around the Falkland Islands. Together with the Patagonian longfin squid pre-season surveys, annual data have been collected from across the Patagonian Shelf around the Falkland Islands since 2015. There are four aspects that can be considered for these data to be used for monitoring Patagonian toothfish stocks for the implementation of effective management measures. These are specifically related to the monitoring of (1) nursery areas, (2) deep-sea ontogenetic migratory transition zones (3) expansion to encompass a seasonal component and (4) increased alignment among the two survey data collection protocols.

Shallow coastal waters are essential recruitment and nursery grounds for Patagonian toothfish (Approach 2 - Lee *et al.*, 2021). It is necessary to develop fishery-independent survey protocols to collect reliable information from areas for monitoring recruitment patterns into identified nursery areas. The inclusion of extensive, high intensity bottom trawl stations may have negative effects on habitats in these sensitive ecosystems (Pitcher *et al.* 2017). Careful control of sampling efforts and monitoring of benthic community changes in these areas should therefore be considered. Considerations should also be given for the development and inclusion of zooplankton survey programmes for monitoring potential egg and larval retention in nursery areas and species interactions that occur at this life-history stage.

In addition, it is important for the inclusion of deep-sea stations between 400 and 600 m for which data is extremely limited (see Figure 3). The acquisition of data from these depths is critical for understanding the linkages between the juvenile and sub-adult population on the shelf, with the adult population in deeper waters. Such an extension has indeed been undertaken (for example in 2018; Gras *et al.* 2018), and subsequent surveys can easily be extended to incorporate these stations.

Finally, the inclusion of a winter demersal biomass survey component is essential for obtaining (1) seasonal spatial-temporal patterns in abundance, as well as (2) the provision of reliable data and validation on recruitment strength. These data would significantly reduce uncertainty and provide increased resolution for use in predictive modelling of recruitment, timing, strength, and spatial usage for the implementation of proactive management measures (see 3.1.2 and 3.1.3). Such a survey has already been undertaken during 2017 and 2022, with a further one proposed for 2023.

Each of these aspects mentioned in the paragraphs above can equally be argued along the basis of their importance to many other commercially important fish species, and the species complex surrounding their interactions (Approach 2 - Lee *et al.*, 2021). For example, results of Approach 2 - Lee *et al.* (2021) identified inter-specific interactions among juvenile Patagonian toothfish with icefish (competition) and rock cod (predator-prey relationship) across their nursery and shelf-based life-history stages. In the deep-sea environment, very little is known in terms of the population dynamics and life-history for the ridge-scaled grenadier, a species showing strong vulnerabilities to overexploitation, and a key prey source for sub-adult Patagonian toothfish (Arkhipkin *et al.* 2003, Lee *et al.* 2019a). Monitoring changes in a multi-species assemblage in a dynamic environment therefore provides further context into how the effective management of fisheries needs to be considered within an ecosystem-based framework (Link 2010, Campana *et al.* 2020, Franco *et al.* 2020).

There is an increasing need for the alignment of protocols across the two fisheries independent surveys undertaken by the Falkland Islands Government. Patagonian longfin squid pre-season surveys utilise full commercial fishing gear, longer (two hour) stations with fewer participating staff (see Approach 2 - Lee *et al.*, 2021). The resolution of data collected from demersal biomass surveys is therefore far greater, given the staff capacity involved, and the effort applied for stations. Given the multi-faceted approach and multiple objectives applied to both these surveys, greater alignment can only reduce uncertainty and provide an improved ability to monitor Patagonian toothfish spatial and temporal patterns across the region. While this outcome is desirable, the increased alignment of protocols is restricted by the budget and personnel constraints at FIFD. The current status is therefore to maximize the opportunities provided by the surveys in their current form.

#### 3.2.5.2. *Environmental monitoring*

Oceanographic factors have been shown to be key drivers of larval dispersal across the region (Approach 2 - Lee *et al.*, 2021). There is an urgent need for routine analysis of long-term trends of environmental change, and the identification of what this means for Patagonian toothfish recruitment to the Falklands Shelf (see 3.2.4.3). These data can be used as contextual information for the implementation of direct and indirect management measures:

- Direct: the protection of juvenile cohorts as they undertake their migration across the shelf through the implementation of an appropriate spatial management approach.
- Indirect: Reduce the impact of fishing on age truncation through appropriate sustainability measures. Long-lived spawners (such as occurs in toothfish) provides a storage effect whereby a stock will persist as long as enough adults outlive periods unfavourable to successful spawning and recruitment.

Further, the distributional response of Patagonian toothfish and the species and habitats upon which they rely to environmental change is not known. Environmental change is likely to modify spatial and temporal patterns through range expansions and contractions (Campana *et al.* 2020), particularly for species at the extent of their range, like Patagonian toothfish.

Environmental (CTD) data are already collected by FIFD on a routine basis. The incorporation of these data into satellite monitoring programmes will reduce uncertainty in these products, providing benefits in its extraction and use as environmental drivers for future research objectives.

#### 3.2.5.3. *Tag-recapture programme*

The guidelines and protocols that were established for the tagging programme have been demonstrated as effective, providing a high-quality data set. Recapture rates have remained high during the course of the programme and consistent patterns are emerging from the data, providing valuable insights into the stock structure and movement patterns of Patagonian toothfish within the Falkland Islands Conservation Zones; and indeed, across the wider southwest Atlantic. From 2023, tag-recapture data has been included within the stock assessment. These factors re-assert the importance for maintaining the tag-recapture programme objectives, specifically for the continued tagging of ~1000 toothfish per year within the Falkland Islands Conservation Zones. The best approach for achieving this should be determined through further discussion in collaboration with industry, and the FIFD Patagonian toothfish scientific team.

According to the current approach, an annual target of 400 toothfish (40%) should be tagged by FIFD observers per year. As stated in the FIFD observer manual for longliners, the specific objective for scientific fisheries observers at sea is to tag an average of 25 fish per week / 4

fish per biological sampling day at sea. This objective should be undertaken according to the following approach:

- Observers should tag the first 4 suitable fish from lines targeted for tagging. It is recommended to conduct the tagging at the beginning of the haul as it is more likely the fish will be in better condition for tagging.
- There should be flexibility regarding the time period to conduct tagging across multiple lines per day so that the objective can be achieved. This is specifically in cases when a particular targeted line may have yielded fewer than 4 toothfish suitable for tagging within an initial 15-minute time period.

During the first 6 years of the tag-recapture programme this target has not been achieved, and the numbers of fish tagged by FIFD observers has been substantially lower compared to tagging surveys (83.75% for surveys vs 16.25% for FIFD Observers).

It is recommended that a pulsed tagging protocol (see Approach 3 - Lee *et al.*, 2022) should be included as an objective on further research surveys undertaken on the CFL Hunter. These surveys have been the driver of tagging effort during the first 6-years of the tag-recapture programme. Such surveys can be incorporated into an annual programme as follows:

- Pulsed-tagging as a primary objective: In the absence of increased FIFD observer tagging effort, a single two-week pulsed tagging survey will be required on an annual basis. The intention of such a trip would be to tag up to 1000 fish covering the full spatial extent of the toothfish distribution in the FCZ.
- Tagging as a secondary objective: Should tagging rates be improved by FIFD observers, tagging can be included in future surveys as a secondary objective. Such objectives would be related to covering shortfalls in the number of tags deployed, and the deployment of tags in areas with low sampling effort.

Discussions should further build towards collaborations in this venture with the intention to (1) extend the spatial scale of the study and (2) quantify and improve the reporting of recaptures in areas outside of the Falkland Islands (see 3.2.3).

### **3.3. Conclusion**

This research programme applied an integrated approach to define aspects of the stock structure of Patagonian toothfish on the Patagonian Shelf to reveal complex patterns. Connectivity is largely driven during the early life-history phases of egg and larval dispersal, although high levels of uncertainty remain. Further, evidence of connectivity across the region through the active migration of adults appears to occur on a relatively small scale. Current results demonstrate that the stock structure arising from the retention of mixed contingents across the Falklands Shelf remains discrete (within the Falkland Islands Conservation Zone) until adult life-history stages. The movement patterns described for the adult component of the stock are providing important contributions to our understanding of the linkages between these mixed contingents and the southern spawning areas. Considering the currently available information, for the purpose of stock assessment we assume that there is one discrete toothfish stock present in Falkland Islands waters.

Data programmes initiated and used in the current studies are all relatively short (2015 to 2021), for the acquisition of data and identification of patterns for a long-lived species with well over a 30-year history of exploitation. Nonetheless, the results of this research contribute meaningfully to management through improved confidence in and transparency of the advice. Further, this research provided an important platform for the enhancement and extension of current monitoring programmes through key collaborations, and the development of future research priorities to inform management objectives.

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