


REVIEW

Patagonian toothfish (*Dissostichus eleginoides*) stocks in South American waters and its implications for fishery management

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ABSTRACT. Patagonian toothfish (*Dissostichus eleginoides*) is a highly prized resource in markets due to the quality of its meat. The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) implemented controls and regulations in response to the sharp rise in the illegal fishing of *D. eleginoides* in the 1990s. Today, four fisheries in waters close to the southern tip of South America are managed in accordance with stringent sustainability standards. Even though they are separate management units, both abundance assessments and annual catch allocations are conducted using different criteria regarding stock considerations across the region, leaving one of the fundamental premises of fisheries management unclear. This study examines historical data and recent research to explore the potential differentiation between Patagonian toothfish populations in South American waters, which is crucial for the management of diverse fisheries. Genetic studies, otolith microchemistry, morphometry, parasitic fauna, tagging programs, reproductive characteristics, and the impact of ocean circulation on dispersal and recruitment were analyzed. Tagging studies in the southern hemisphere oceans confirm the species' affinity to specific habitats, suggesting minimal fish exchange between South American fishing grounds. From a fisheries perspective, this review suggests the existence of distinct stocks of the species structured along the shelf and slope of the southern cone of America based on reproduction areas along the continental shelves and slope, the diverse parasitic fauna, the variability in stable isotopes and trace elements of otoliths, and the little significant exchange of fish between current fishing grounds. All of this could lead to considering the *D. eleginoides* fishery as independent exploitation units.

Key words: Stocks, structure, South American fisheries.



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Stocks de merluza negra (*Dissostichus eleginoides*) en aguas sudamericanas y sus implicancias para la gestión pesquera

RESUMEN. La merluza negra (*Dissostichus eleginoides*) es un recurso muy apreciado en los mercados debido a la calidad de su carne. La Comisión para la Conservación de los Recursos Vivos Marinos Antárticos (CCRVMA) implementó controles y regulaciones en respuesta al marcado aumento de la pesca ilegal de *D. eleginoides* en la década de 1990. Hoy, cuatro pesquerías en aguas cercanas al extremo sur de América del Sur se gestionan de acuerdo con estrictos estándares de sostenibilidad. Si bien son unidades de gestión separadas, tanto las evaluaciones de abundancia como las asignaciones anuales de captura se realizan utilizando diferentes criterios en cuanto a consideraciones de *stock* en toda la región, lo que deja sin aclarar una de las premisas fundamentales de la gestión pesquera. Este estudio examina datos históricos e investigaciones recientes para explorar la diferenciación potencial entre las poblaciones de merluza negra en aguas sudamericanas, crucial para el manejo de pesquerías diversas. Se analizaron estudios genéticos, microquímica de otolitos, morfometría, fauna parasitaria, programas de marcaje, características reproductivas e impacto de la circulación oceánica en la

dispersión y reclutamiento. Los estudios de marcaje en los océanos del hemisferio sur confirman la afinidad de la especie con hábitats específicos, lo que sugiere un intercambio mínimo de peces entre las zonas de pesca sudamericanas. Desde una perspectiva pesquera, se sugiere en esta revisión la existencia de *stocks* diferenciados de la especie estructurados a lo largo de la plataforma y el talud del cono sur de América sobre la base de áreas de reproducción a lo largo de las plataformas y el talud continentales, la diversa fauna parasitaria, la variabilidad en los isótopos estables y los elementos traza de los otolitos, y al poco intercambio significativo de peces entre las zonas de pesca actuales. Todo esto podrían llevar a considerar la pesquería de *D. eleginoides* como unidades de explotación independientes.

Palabras clave: *Stocks*, estructura, pesquerías sudamericanas.

INTRODUCTION

Patagonian toothfish (*Dissostichus eleginoides*) is a highly prized resource in markets due to the quality of its meat. From a commercial exploitation perspective, it is the most important fish species in the Southern Ocean (Grilly et al. 2015). Trawl and longline fisheries began in the mid-1980s, with a rapid expansion of illegal fishing in the 1990s (Agnew and Kirkwood 2005), which was drastically reduced by catch and trade controls imposed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) (Agnew 2000). Patagonian toothfish fisheries in the southern hemisphere are highly regulated and are now managed according to strict sustainability criteria. However, this species has low fecundity and high longevity, being able to live up to 50 years (Horn 2002). Length and age at first maturity have been estimated at 80 cm and approximately eight years, respectively (Ruocco et al. 2017). These characteristics make this species highly vulnerable to overfishing (Wöhler and Martínez 2002; Bialek 2003; Canales-Aguirre et al. 2018).

There are currently four fisheries for this species in waters near the southern tip of South America. The first of these occurs around the South Georgia Islands and Aurora Islets (Shag and Black Rocks), and is within the scope of CCAMLR. The other three occur in Argentine and Chilean waters on the South American continental shelf: two are under the management of these countries and the third is under the control of the United Kingdom around

Malvinas Islands. Even though they are separate management units, both abundance assessments and annual catch allocations are conducted using different criteria regarding stock considerations across the region, leaving one of the fundamental premises of fisheries management unclear. While the fishery operating around Malvinas Islands is managed under the assumption of the existence of an individual stock in the area, and having achieved Marine Stewardship Council (MSC) sustainability certification standards in 2014 (Payne et al. 2005; Winter 2017; Farrugia and Winter 2018; Skeljo and Winter 2020), the Argentine-managed fishery considers all fish present on the Patagonian continental shelf in the Atlantic, including those around the Malvinas Islands, as a single unit. As a result, assessments of abundance and catch allocations to the Argentine fleet are based on this assumption and fail to take into account catches in the archipelago, harming stock sustainability (Wöhler et al. 2004; Wöhler and Martínez 2005; Martínez and Wöhler 2006, 2007, 2008, 2010, 2011, 2012, 2013; Martínez et al. 2016; Di Marco et al. 2017, 2018, 2019, 2020). On the other hand, the Chilean fisheries management assumes that there is a single stock distributed on the Argentine shelf (in the operating area of the Argentine fleet) and in the Chilean Pacific, resulting in assessments made under this assumption, but all catches are allocated to the Chilean fleet (Tascheri and Canales 2016; Tascheri 2017, 2018, 2019, 2020). This causes a worrying situation regarding the sustainability of the resource in waters of the continental shelf around South America, which has already been warned on different occasions to both the Argentine

and Chilean fisheries administrations (CM BAC 2019; Martínez et al. 2019).

With the aim of clarifying aspects related to the differentiation of Patagonian toothfish stocks present in the area, this study examined the available scientific evidence regarding the population structure of the species in South American waters, around the South Georgia and South Sandwich Islands (Figure 1). A novel paradigm that incorporates the identification of distinct populations is presented to improve fisheries management within a sustainable framework.

MATERIALS AND METHODS

Articles were identified based on the search of terms through Scopus and Google Scholar databas-

es that provided information and different viewpoints on the Patagonian toothfish population structure in different sectors of its extensive distribution area, with emphasis on those related with the southern cone of the Americas. The combination of keywords *Dissostichus eleginoides*, *D. eleginoides*, Patagonian toothfish, stock, fisheries, South America, southwestern Atlantic Ocean, CCAMLR and fisheries management were used. A total of 171 articles passed the eligibility screening and were considered appropriate for the content analysis. Many of these studies were relatively outdated, while others have recently provided valuable information in this regard. A number of hypotheses were proposed given the comprehensive compilation of information. Based on these hypotheses, specific recommendations were made to enhance fishery management, with a focus on the establishment of separate populations and management units.

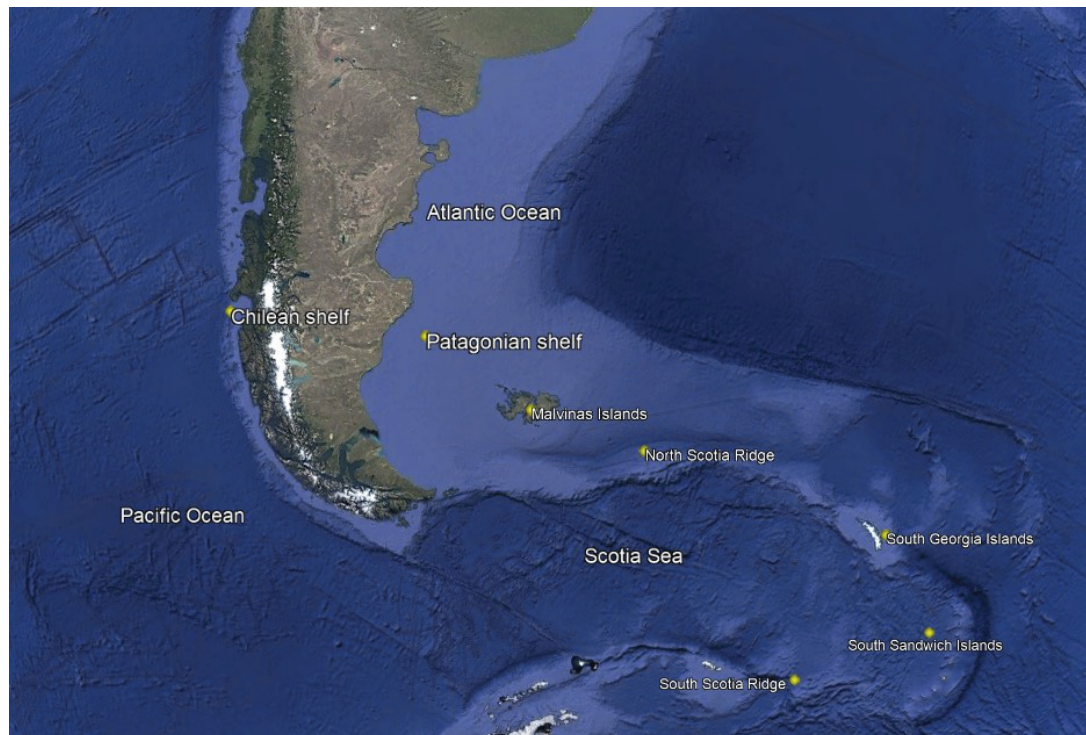


Figure 1. Geographic location of the southern Cone of South America and main geographical features. Source: created by the author based on images available on Google Earth.

RESULTS AND DISCUSSION

Biology and ecology of Patagonian toothfish

The Patagonian toothfish (*Dissostichus eleginoides* Smith 1888) belongs to the Nototheniidae family and is native to Antarctic and subantarctic waters. It is one of two recognized species of the genus *Dissostichus* alongside the Antarctic toothfish (*D. mawsoni*). While *D. mawsoni* inhabits Antarctic waters, *D. eleginoides* prefers lower latitudes. A third species, *D. australis*, has been proposed to exist near South Georgia Islands (Arkhipkin et al. 2022). Unlike *D. mawsoni*, *D. eleginoides* lacks glycoproteins to prevent tissue freezing, restricting its distribution to waters above 1.4 °C (Collins et al. 2010).

Dissostichus eleginoides grows rapidly in its early years, reaching up to 12 cm in the first year, but its growth slows significantly after 4 to 8 years of age (Belchier and Collins 2008; Collins et al. 2010). It can live for over 50 years (Horn 2002; Belchier 2004), grow more than 2 m long and weigh more than 100 kg, reaching sexual maturity between 8 and 12 years of age (Belchier and Collins 2008; Arana 2009; Collins et al. 2010; Ruocco et al. 2019). It mainly inhabits depths of 80 to 2,500 m, with adults found in deeper waters and juveniles in shallower areas.

The Patagonian toothfish is endemic to the southern hemisphere, found in Antarctic and subantarctic waters surrounding the Antarctic continent. It is also present in waters surrounding the southern cone of America, from Ecuador in the Pacific Ocean to Argentina and Uruguay in the Atlantic Ocean, extending at least as far north as 35° S in this area (Cousseau and Perrotta 1998). In the southern regions of the Atlantic, Pacific, and Indian Oceans, it is found in discrete areas including South Georgia Islands, Aurora Islets, South Sandwich Islands, South Orkney Islands, Crozet Islands, Kerguelen Islands, Heard Island, McDonald Island,

Macquarie Island, and Prince Edward Island, as well as seamounts like Banzare, Ob, Lena, and various regions of the Ross Sea (Collins et al. 2010). It is noteworthy that a single specimen of *D. eleginoides* was captured in the northern hemisphere, off the coast of Greenland (Møller et al. 2003), although this is a singular occurrence.

Dissostichus eleginoides has been regarded as a species with limited migratory behavior, displaying strong fidelity to its residence sites (Brown 2011). Although capable of covering extensive distances, this is not a frequent or regular behavior. Rather, it appears to be quite exceptional (Williams et al. 2002; Marlow et al. 2003; Welsford et al. 2011; Martínez et al. 2014; Waessle and Martínez 2018; Burch et al. 2019; Lee et al. 2022; Troccoli et al. 2023), similar to *D. mawsoni* (Grilly et al. 2022). It spawns during the winter in waters near the edge of the shelf and slope (Laptikhovsky et al. 2006; Pájaro et al. 2009; Collins et al. 2010) and has a relatively low fecundity (Young et al. 1995, 1999). First sexual maturity (E50%) occurs when fish are between 8 and 12 years old, although this varies across different sectors of its distribution (Collins et al. 2010). It has been reported that not all adult fish reproduce every year, which is believed to be related to adverse environmental and physiological conditions (Brown 2011; Boucher 2018). Eggs and larvae are pelagic, remaining in the water column for a fairly extended period (Evseenko et al. 1995; North 2002; Collins et al. 2010). Once hatched, the larvae tend to inhabit areas closer to the coasts due to passive or active transport (Evseenko et al. 1995; North 2002; Canales-Aguirre et al. 2018; Harte 2020). Given their extensive pelagic life, it has been suggested that eggs and larvae can be transported long distances from spawning areas by currents (Ashford et al. 2012; Harte 2020; Lee et al. 2021), facilitating the dispersal of individuals and mixing between populations. However, juveniles are primarily found in areas close to the spawning sites, at shallower depths. As they grow, they enter to the adult stock (around 6 to 7 years age), moving to greater depths (Wöhler et al. 2001; Collins et al. 2010).

Lee et al. (2021) indicated that Patagonian toothfish experiences early ontogenetic migrations from spawning areas south of Chile and Burdwood Bank in the continental shelf ecosystem around the Falkland Islands. They observed that migrations after settlement show progressive spatial distribution patterns, with juveniles concentrated in specific areas defined by environmental conditions and the abundant presence of competitors like *Champs-ocephalus esox* and prey like *Patagonotothen ramsayi*. Additionally, ontogenetic changes in the bathymetric distribution of juveniles and adults correspond to variations in the diet. The species is carnivorous and acts as an active predator. Juveniles mainly feed on fish, secondarily on cephalopods (García de la Rosa et al. 1997; Arkhipkin et al. 2003; Barrera Oro et al. 2005; Collins et al. 2007; Méndez Gudiño 2018; Troccoli et al. 2020), and initially on zooplankton (Zhivov and Krivoruchko 1990); while adults are opportunistic predators with a diet centered on fish and to a lesser extent on cephalopods and crustaceans (Collins et al. 2010; Troccoli et al. 2020).

The fisheries of *Dissostichus eleginoides*

The catch of Patagonian toothfish began as bycatch in the early 1980s in trawl fisheries in Argentine and Chilean waters of the Patagonian shelf in the Atlantic and Pacific oceans, around the Kerguelen Island and South Georgia Islands. Subsequently, due to the development of deep-sea longlining aiming primarily on adult fish, the first fisheries targeting the species began in Chilean waters. This quickly expanded in the early 1990s to other fishing grounds, such as the Patagonian shelf in the Argentine Sea and subantarctic islands like South Georgia and Kerguelen (Collins et al. 2010).

Given the high commercial value that its flesh began to acquire, fisheries rapidly expanded across all areas of the species' distribution with significant commercial yields. Thus, the evolution of *D. eleginoides* catches reported by FAO (2023) exhibited a swift increase from the late 1980s, reaching

average values of around 40,000 t between 1992 and 2002, followed by a decrease and stabilization at around 23,000 t from 2005 to the present day (Figure 2). However, it must be noted that the recording of a significant portion of catches, especially during the early and mid-period, was underestimated due to substantial illegal, unreported, and unregulated (IUU) fishing, leading to a significant underestimation of historical total catches of the species (Agnew 2000). Fortunately, these IUU catches have been decreasing since then, owing to various measures implemented by the CCAMLR to counter such activities. These measures include the Catch Documentation Scheme (CDS) and the monitoring and reporting of vessel activities at sea.

In the southern cone of America, three fisheries for Patagonian toothfish are developed in southwestern Atlantic waters (one in South Georgia Islands and two in south Patagonian waters), in addition to a fishery in the Southeastern Pacific, which corresponds to Chile.

The Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) regulates fishing in the South Georgia Islands. The only fishing gear authorized for the directed capture of this species is the bottom longline, equipped with 'umbrella system' designed to mitigate the predation of captured fish by orcas and sperm whales. The fishery is governed through the issuance of annual fishing licenses, treating the stock as an independent unit (GSGSSI 2017), obtaining the sustainability certification from the Marine Stewardship Council (MSC) in 2004 (Andrews and Medley 2018). In 2020, the Total Allowable Catch (TAC) was set at 2,327 t, while the reported catch was 1,884 t (CCAMLR 2021).

The Patagonian toothfish fishery around Malvinas Islands has been operating since 1987 (Des Clers et al. 1996; Laptikhovskiy et al. 2008), and has been managed through the Individual Transferable Quotas (ITQ) system since 2006. The stock assessment considers the existence of a single discrete population, managed independently from neighboring populations on the Patagonian

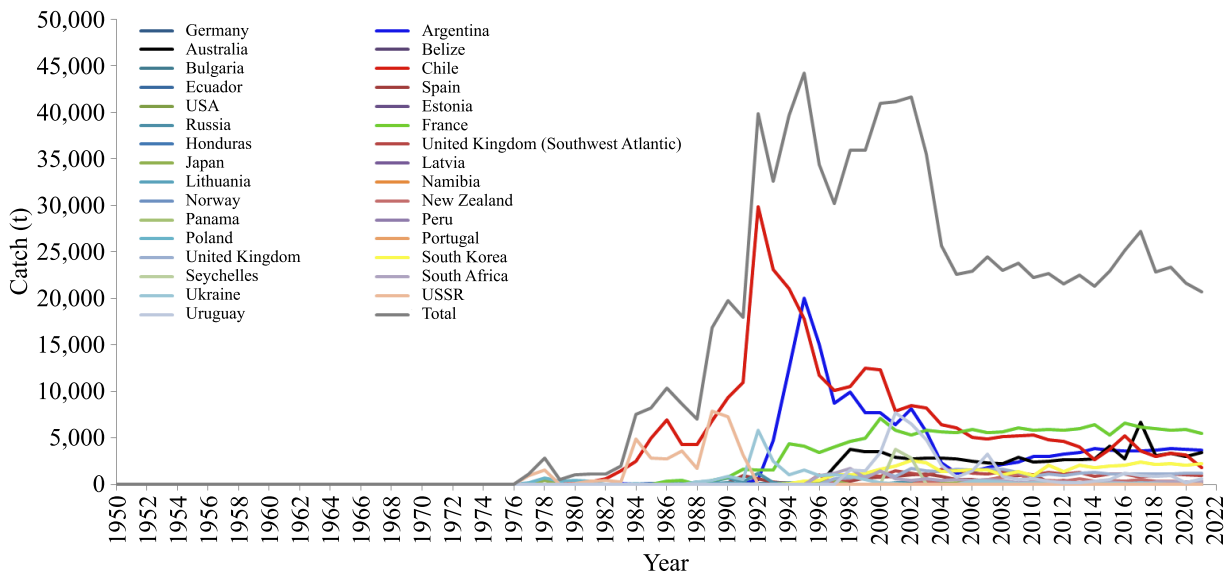


Figure 2. Annual catches of *Dissostichus eleginoides* reported by FAO (2023). Those corresponding to illegal, unreported, and unregulated (IUU) fishing were not included.

shelf and the Chilean Pacific, assuming that the contribution to recruitment of these populations is not significant (Andrews et al. 2013). Targeted fishing is carried out using bottom longlines and has also been certified by the MSC since 2014. For the year 2021, the TAC was set at 1,040 t for the longline fishery (FIFD 2023). The activity takes place year-round, except for a spawning area identified on the eastern and southeastern slope of the Burdwood Bank, which remains closed from June 1st to August 31st as a special conservation measure (FIFD 2018). While this fishery is outside the CCAMLR jurisdiction, compliance with certain established norms within the convention is promoted, such as the Catch Documentation Scheme and vessel monitoring and reporting at sea (Andrews et al. 2018).

In Chile, the Patagonian toothfish fishery is divided into two management areas: one north of 47° S, reserved for artisanal fishermen, where the catch quota is managed globally (Olympic system), and another industrial area south of 47° S, which is managed through Individual Transferable Quotas (ITQ), assigned to the industrial fleet for peri-

ods of 10 years. The industrial fleet consists of 9 vessels, representing 61% of the registered fishing operations (Tascheri 2020). Fishing is conducted using bottom longlines equipped with killer whale guards. In the last three years, catches have exceeded 3,700 t, considering both management units.

On the other hand, the Patagonian toothfish fishery in Argentina was established in the early 2000s (Wöhler et al. 2001). It currently consists of six freezer vessels and uses two types of fishing gear: bottom trawl nets and longlines. In the last five years, the Total Allowable Catch (TAC) has been close to 3,700 t annually, established based on the results of the abundance assessment and the biological potential of the species, conducted by the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP) (Di Marco et al. 2020). This fishery is managed by the Federal Fisheries Council and administered through the Individual Transferable Catch Quota System (ITC), assigned to the legally licensed fleet for periods of 15 years. Although it is not under CCAMLR, it adheres to the Catch Documentation Scheme (CDS) and the monitoring and reporting of fishing activities at sea.

The importance of stock discrimination in fisheries management

Stock identification is a fundamental component for the assessment of fishery resources and effective fisheries management (Begg et al. 1999a). As such, fisheries management needs that stock definitions be evaluated and revised whenever new information or technologies become available (Begg and Waldman 1999). Ignoring the spatial structure of stocks can lead to a misconception of their status and failures in fisheries management. Therefore, the process of stock assessment should include the evaluation of the most appropriate spatial structure (Cadrin 2020).

From a fisheries management perspective, concepts of biological population and stock should be distinguished. A population is a group of fish of the same species that share ecological and genetic characteristics (ICCAT). A stock may correspond to a population, a fraction of it, or several populations (Ricker 1975; Gulland 1983). Stocks for assessment and fisheries management do not always coincide with populations. To identify fish populations and/or stocks, biological or life cycle parameters that may show differences are used (Begg et al. 1999b; Harte 2020). There are different definitions of the concept of fish stock. For Hilborn and Walters (1992), the concept of a stock is essential for fisheries management and refers to relatively large groups of fish that share a common life history and similar biological traits, and are capable of reproducing. A somewhat different definition was given by Ricker (1975), who indicated that a stock can be a portion of a fish population that is considered a unit from the perspective of its utilization, whether current or potential. This last definition aligns with the concept provided by Gulland (1983) who established that the definition of a 'stock unit' for the purposes of fisheries management is an operational matter, meaning that 'a group of organisms can be considered a stock if potential differences within the group and exchanges with other groups can be ignored without invalidating such consideration'.

According to FAO (<http://www.fao.org/glossary/default.asp>), a fish stock can be defined as a group of individuals of a species that occupies a well-defined spatial range, independent of other stocks of the same species. It may be influenced by random dispersal movements and defined migrations due to seasonal or reproductive activity. For the International Commission for the Conservation of Atlantic Tunas (ICCAT), the term stock has different meanings, although in general and in relation to the subject at hand, it constitutes a biological unit of a species that forms a group with similar ecological characteristics and, as a unit, is the subject of assessment and fisheries management. In summary, the term stock is often synonymous with a unit of assessment/management, although there may be migration of a smaller portion of its components to and from adjacent areas. Connectivity between stocks, through the exchange of individuals, affects genetic flow and regulates population size and function, sometimes allowing for the mitigation of anthropogenic disturbances (Hilário et al. 2015). Understanding population connectivity is crucial for spatial management, especially with the intensification of resource exploitation in deep waters (Hilário et al. 2015).

Levins (1969, 1970) introduced the concept of metapopulations in his theory, which has been developed by Hanski (1989, 1994, 1999, 2001), Hanski and Gilpin (1991), Hanski and Simberloff (1997), and Hanski and Gaggiotti (2004), becoming a key component of modern ecological theory. A metapopulation is a set of local populations or subpopulations inhabiting discrete habitat patches, where the dispersal between these patches is sufficient to maintain significant demographic connectivity but not so high as to eliminate independence in local population dynamics (Sale et al. 2006). The metapopulation theory primarily applies to cases where the spatial structure of populations is determined by dispersal barriers within the habitat and requires local populations to be potentially connected through the migration of their components or reproductive products. However, it is dif-

difficult to assume that such a theory could be applied to stocks of Patagonian toothfish located in waters surrounding South America, as their distribution is continuous along the edge of the continental shelf and slope, at least from Ecuador in the Pacific to southern Brasil in the Atlantic.

To manage a fishery after management units were defined, it is helpful and required to determine the exploitation unit, which should generally correspond to the stock unit but not necessarily be restricted to it. According to the FAO (<http://www.fao.org/glossary/default.asp>), a management unit is a fishery unit considered by an authority for management purposes, generally within a jurisdiction and/or with established legal rights. Jurisdiction is interpreted, in this case, as the territorial limits within which some authority can be exercised. According to the terms previously defined, then, a Management Unit can be considered as a fishery, which will have one or more target species and will differ from others occurring in adjacent areas or in the same areas, in this case, if they have different target species.

The evidence for managing stocks as discrete units comes either from the knowledge of clear isolation (insurmountable barriers and/or large distances separating different groups of the same species) or, when that does not occur, from differences in biology or life cycle parameters that demonstrate geographic or reproductive isolation of fish; Begg et al. 1999b). When there is genetic differentiation, a population group can be easily distinguished from another. However, often these differences are not easily detectable, either because some genetic exchange occurs between individuals in different groups, or because isolation may be very recent, so genome differences have not yet manifested. However, if demonstrable reproductive isolation exists, and differentiation in other parameters is verified, the existence of different groups or stocks can be assumed. It has been possible to consider distinct populations in certain locations because different groups of *D. eleginoides* distributed in the southern region of the Atlantic,

Pacific, and Indian Ocean exhibit one or both of these requirements (Smith and McVeagh 2000; Shaw et al. 2004; Rogers et al. 2006; Toomey et al. 2016). However, this aspect has not yet been fully explained in the waters surrounding South America, where the species has substantial fisheries and immediate progress is required in that regard. To manage fisheries efficiently, it is important to identify and define different stocks of the species, in order to assess how fishing effort and fishing mortality are distributed among them, thus managing them separately and optimizing their performance. Effective management of fisheries necessitates the identification and definition of different stocks of the species in order to evaluate the distribution of fishing effort and mortality among them, allowing for the management of each stock separately and the optimization of its performance (Grimes et al. 1987). The alignment of biological and management units requires continuous monitoring through the application of stock identification methods, often requiring responsive management willing to modify fishing management schemes in light of new scientific evidence available (Kerr et al. 2017).

Contributions to the understanding of the population structure of Patagonian toothfish

Numerous studies have been conducted with the aim of examining connectivity and detecting differences among potential populations of Patagonian toothfish in the southernmost region of South America, some of which were compiled by Collins et al. (2010). As indicated by Begg and Waldman (1999), a holistic approach requires the use of various techniques and methodologies to determine the possible existence of different fish stocks or populations. In the case of Patagonian toothfish in the southernmost region of South America, analyses based on reproductive characteristics of the species in the area and aspects of ocean circulation and their potential relationship with the dispersal of reproductive products and recruitment have also been conducted. The following sections will

highlight key aspects of the various themes studied, primarily concerning their contribution to the distinction of stocks or populations in the waters of the southernmost Americas and the sub-Antarctic islands of the Atlantic Ocean.

Genetics studies

Genetic studies have been conducted to distinguish stocks of *D. eleginoides* in the Atlantic, Pacific, and Indian Oceans, and around the southern tip of South America. Smith and McVeagh (2000) found genetic differences in Patagonian toothfish in samples from the southern regions of these oceans compared to those from near the eastern slope of the Burdwood Bank. Additionally, through the analysis of mitochondrial DNA, significant differentiation was observed between the Patagonian shelf and the northern sector of the Scotia Ridge compared to Aurora Islets (Shag and Black Rocks) and South Georgia Islands, while other microsatellite markers were much less successful in showing such differentiation (Shaw et al. 2004). These authors also indicated that fish caught in the northern Scotia Ridge exhibit characteristics of mixing, suggesting that the Polar Front acts as a barrier preventing the dispersal of eggs and larvae, hindering or even preventing exchange between these populations, facilitated by the limited migratory behavior of adult and sub-adult fish.

On the other hand, results from partial sequences of mitochondrial DNA and microsatellites stated that populations of Patagonian toothfish in the South Atlantic (samples originated from the fishery around Malvinas Islands) are distinct from those present in South Georgia (Western Atlantic), Bouvet Island (Eastern Atlantic), and Mount OB (Indian Ocean) (Rogers et al. 2006). This study confirmed genetic differences found by Smith and McVeagh (2000) and Shaw et al. (2004) between populations of South Georgia and Aurora Islets, and the one found on the Patagonian continental shelf around Malvinas Islands. It also coincided in suggesting that the polar front might act as a

barrier to the dispersal of reproductive products, as indicated by Shaw et al. (2004). A recent genetic analysis by Arkhipkin et al. (2022) yielded similar observations.

Using a technique to extract DNA from tissue remnants adhering to otoliths, Toomey et al. (2016) analyzed the genetic structure of specimens from three sectors of the southern ocean region. The sectors studied include Heard and McDonald Islands, Kerguelen and Crozet Islands in the Indian sector, Macquarie Island in the Pacific, and South Georgia and South Sandwich Islands in the Atlantic sector. They found genetic differences in all three sectors using nuclear markers. Such differences among sectors of the three oceans were also attributed to the intervening deep ocean areas, acting as barriers to fish migration, and oceanographic frontal barriers impeding the free dispersal of eggs and larvae. In this context, and within the scope of this study, nuclear markers of *D. eleginoides* from South Georgia and South Sandwich Islands did not differentiate, while differences were evident using mitochondrial markers. Based on a fish tagged in South Sandwich Islands and recaptured near South Georgia, it has been suggested that the northern population of South Sandwich Islands may originate from the South Georgia stock (Collins et al. 2010).

Most genetic studies were conducted to distinguish populations in regions isolated enough that distance or oceanographic conditions prevent fish migration or the dispersal of reproductive products. However, this does not seem to be the case for *D. eleginoides* distributed along the continental shelf or the slope edge in the southernmost South American region, from Ecuador to northern Argentina and Uruguay. The first genetic analysis in this area dates back to Oyarzún et al. (2003a), who did not find significant genetic differences in samples from the central and southern continental shelf of Chile (between 37° S and 43° S). More recently, with the aim of identifying possible differences in Patagonian toothfish from these regions, Canales-Aguirre et al. (2018) used six microsatellites

to test the hypothesis that fish in this region would show very little genetic differentiation due to the presumed habitat continuity or at least the absence of known barriers to gene exchange in that sector. Results from these authors, later confirmed by Arkhipkin et al. (2022), suggest that there is no significant genetic structure distinguishing populations on the South American continental shelf. However, differences were observed with populations from Aurora Islets and South Georgia Islands, which is consistent with findings by Galleguillos et al. (2008). These authors determined that the genetic connectivity between these two groups was 11.3% corresponding to migrants from the Patagonian region to South Georgia, and 0.7% in the opposite direction. They also estimated that the effective population size would be higher on the South American continental shelf compared to the one distributed in South Georgia Islands and Aurora Islets (Shag and Black Rocks). In general, results obtained by Canales-Aguirre et al. (2018) and Arkhipkin et al. (2022) support the hypothesis that the continuity of the deep-water habitat and biological characteristics of the species would influence the lack of differentiation of the Patagonian toothfish on the South American continental shelf. On the contrary, the discontinuity of the seafloor and the presence of the barrier created by the Polar Front and the Antarctic Circumpolar Current would facilitate genetic differentiation of the population of South Georgia.

Otolith microchemistry and morphology

It has been demonstrated that the microchemical composition and morphometry of fish otoliths are useful tools for discriminating stocks (Campana et al. 1994; Campana 1999). Kalish and Timmis (1998) suggested the existence of at least four populations of *D. eleginoides* in the southern regions of the Atlantic, Pacific, and Indian Oceans. These include the South American group, the South Georgia Islands group, the southwestern Pacific group (Macquarie Island), and the southern Indian Ocean

group, represented by fish captured around Prince Edward, Kerguelen, Heard, and McDonald Islands.

Lee et al. (2018) conducted an analysis of otolith morphometric patterns using samples from the southeastern Pacific (Chile), the Atlantic Patagonian continental shelf (north, east, and south of Malvinas Islands, specifically the east of the Burdwood Bank), the area around South Georgia Islands and the Aurora Islets, and South Sandwich Islands. Results of the study showed differences among various catch locations, suggesting three main groupings: one for the southern cone of America, another for South Georgia, and a third for the more southern regions (South Sandwich Islands). Arkhipkin et al. (2022) recently complemented these studies by integrating genetic and morphological analyses of otoliths with meristic and morphometric studies of fish samples from the same regions. These analyses allowed for the differentiation of Patagonian toothfish on either side of the Polar Front, based on differences in the shape of the anterior part of the upper lateral line, the posterior region of the operculum, and the otoliths. A spatial pattern of differentiation was observed between samples from Chile and those from the northern slope of the Argentine Sea. In contrast, samples from the south (Malvinas Islands and Burdwood Bank) exhibited intermediate characteristics, not distinguishable from either of the other two groups, which is consistent with the otolith shape differentiation pattern reported by Lee et al. (2018).

In order to test the information derived from the microchemistry of otoliths from deep sea oceanic fishes, Ashford et al. (2005) analyzed the edges of Patagonian toothfish otoliths to estimate the trace element composition and differentiate them according to catch zones. They found that the microchemical composition allowed for a successful differentiation of some areas, with only 5% of the fish captured on the Patagonian continental shelf of the Atlantic and in the Antarctic sector being misclassified. Furthermore, the composition of otolith edges showed strong differences between catch areas of fish within each region. Thus, fish

captured on both sides of South America were successfully classified, with 79% of them correctly assigned to the Atlantic Patagonian shelf and 84% to the corresponding Pacific shelf. Subsequently, when analyzing the microchemical composition of nucleus of *D. eleginoides* otoliths (formed during the early life stage of fish), a marked difference in four trace elements was found between the north and south of the Polar Front, between the region of South Georgia and the northern Scotia Ridge (Ashford et al. 2006). Samples from South Georgia Islands and Aurora Islets were significantly distinct from the rest of the sampled areas. However, a certain heterogeneity in microchemical composition was highlighted within the samples from the southern Patagonian shelf, which included locations on the northern slope of the Patagonian Atlantic ($43^{\circ} 35' S$), the north, east, and south of the Malvinas Islands, and the eastern and western parts of the northern Scotia Ridge. This suggests that there may be more than one stock in the Atlantic sector, or at the very least, distinct spawning areas for the fish that inhabit these sectors of the Patagonian shelf.

Ashford et al. (2007), working with otolith edge microchemistry (trace and minor elements), demonstrated once again that otolith chemistry reflects hydrography, detecting oceanic gradients along the slopes of continental shelves and between areas separated by strong features such as oceanographic fronts. The trace and minor elements deposited immediately prior to capture along the edges of Patagonian toothfish otoliths clearly allowed for the discrimination of fish originating from frontal zones in the Antarctic Circumpolar Current in the southwestern Atlantic Ocean. Mean values differentiated sampling areas by up to 2.6 standard deviations, suggesting that the Burdwood Bank sector is associated with otolith enrichment with the Mg/Ca ratio; other regions of the Patagonian continental shelf, such as the northern slope and around Malvinas Islands, are associated with an increase in the Mn/Ca ratio; the presence of deep circumpolar water is linked to an elevated Sr/Ca ra-

tio; and there is a noticeable presence of the Ba/Ca ratio showing affinity for the eastern Scotia Ridge, Aurora Islets, and South Georgia Islands. In the Polar Frontal Zone, meanders or eddies may explain certain affinities with neighboring sampling areas, bringing water from the subantarctic and Antarctic Zones to the Northern Scotia Ridge, where there is some mixing between individuals from the south and north of the Polar Front.

The stable isotopes technique using whole otoliths has also proven to be highly useful in identifying the origin of Patagonian toothfish specimens captured on both sides of the Polar Front, between the Atlantic Patagonian shelf and the South Georgia Islands region, and between both regions and Antarctic waters (Ashford and Jones 2007). This analysis allowed for the prediction of the capture area with 100% effectiveness, even surpassing various analyses conducted using otolith microchemistry.

The trace and minor element composition of otolith nucleus from different regions, including the southeastern Pacific (off the coast of Chile) and the Argentine continental shelf near Malvinas Islands, as well as other areas in the southern Atlantic (South Georgia Islands), Indian and Pacific oceans, were once again analyzed by Ashford et al. (2008). As demonstrated in previous analyses (Ashford et al. 2005, 2006, 2007; Ashford and Jones 2007), samples from the southernmost continental shelf of South America were distinct from the rest. They differed in terms of the Mn/Ca, Sr/Ca, and Ba/Ca ratios, as well as Mg/Ca, albeit with intermediate values compared to those obtained in sectors corresponding to the South Georgia Islands, Kerguelen, and Macquarie Island. Subsequently (Ashford et al. 2012), aiming to test the hypothesis that spawning areas in southern Chile contribute to recruitment on the Atlantic South Patagonian shelf (Burdwood Bank and Malvinas shelf), analyzed the otolith microchemistry of fish captured on both sides of the southern cone of South America. Based on the analysis of trace elements deposited in the otolith nucleus during early life stages, they hypothesized that fish distributed both north and south of

Malvinas Islands would receive contributions from reproduction occurring in southern Chile and the Burdwood Bank.

Finally, Farrugia (2018), in his report on the progress of studies related to the stock discrimination included in the action plan for the re-certification of the Patagonian toothfish fishery around Malvinas Islands, mentions ongoing initiatives for otolith analysis (shape, microchemistry, life history) aimed at determining the stock unit being exploited in the fishery. On this way, analyses of trace elements in the otolith cores of juveniles of *D. eleginoides* are being conducted on the shelf surrounding the islands with the aim of identifying potential variations in fish distribution or spatial segregation during early life stages and attempting to establish recruitment patterns associated with different oceanographic conditions. The utility of using otoliths to provide information about the population structure of the species in the area is also being evaluated.

Tagging and recapture

Based on their migratory behavior, species can be classified into two main groups: those that exhibit certain fidelity to residence sites and those characterized by predictable migrations between feeding, breeding, and nursery sites (Quinn and Brodeur 1991). There is a considerable amount of information on tagging and recapture studies of Patagonian toothfish in various sectors of the Atlantic, Pacific and Indian oceans and on the continental shelf and slope around South America. The information derived from these studies has generally been used to determine movements and investigate possible migratory patterns (Williams et al. 2002; Marlow et al. 2003; Brown et al. 2013; Rubilar et al. 2014; Zuleta et al. 2015; Burch et al. 2019; Lee et al. 2022; Troccoli et al. 2023), although it has also been employed to assess the size of stocks subject to exploitation (Tuck et al. 2003; Hillary et al. 2006; Agnew et al. 2006a, 2006b; Roberts and Agnew 2008).

In general, all tagging and recapture studies conducted in all sectors mention above indicate that *D. eleginoides* is a species with strong resident behavior, moving very little from its release location to the recapture site (Collins et al. 2010). However, a small fraction of individuals can cover long distances. Burch et al. (2019), analyzing fish tagged at Heard and McDonald Islands, found that the majority of recaptured fish moved very short distances, up to about 50 km from their release point. However, 2% of recaptured specimens traveled long distances, in some cases exceeding 2,500 km (three fish were recaptured on the Marion and Prince Edward Islands shelf). On the Aurora Islets and South Georgia Islands shelf, Marlow et al. (2003), found that the majority of tagged fish were recaptured at distances very close to the release site, generally less than 25 km. Only two specimens traveled over 100 km, from Aurora Islets (Shag and Black Rocks) towards South Georgia Islands. Meanwhile, on the Macquarie Island shelf, Tuck et al. (2003) reported mainly very short displacements, although a small percentage of individuals can travel greater distances.

Several tagging and recapture experiments were conducted in waters surrounding the southern American cone, yielding significant information regarding movements of the species in the area. Brown et al. (2013), through the use of pop-up satellite tags on specimens near Malvinas Islands, found a high fidelity of the fish to different tagging areas, indicating reduced mobility, generally less than 50 km from the release zone over a six-month period. They described three distinct movement patterns. The first of these is seasonal in nature, involving depth changes during the summer season, while bathymetric movements possibly related to feeding (different prey availability at various depths) and spawning possibly linked to displacements within the water column, characterize the other two. Regarding the latter, authors highlight that during months corresponding to the spawning period, the fish repeatedly moved between waters at depths of 900 to 1,200 m, possibly associated

with spawning. A similar reproductive behavior was previously reported by Laptikovski et al. (2006).

In another tag-recapture program using traditional tags conducted in the area around Malvinas Islands, Farrugia (2018) reported that as in other cases, the vast majority of fish were recaptured within a radius of 30 km from the release site, with times of freedom of up to 232 days. It was also indicated that only one tag from the program carried out on the Patagonian shelf by INIDEP was recovered in the sector of the shelf surrounding Malvinas Islands, about 175 km from its release site, confirming that *D. eleginoides* is a species with a strong fidelity to its residence sites. Subsequently, Lee et al. (2022) conducted a comprehensive analysis of migratory movements of *D. eleginoides* around Malvinas Islands. The majority of individuals (77.6%) exhibited high levels of fidelity to the site of tagging (< 50 km), which, according to these authors, suggests that seasonal spawning migrations are unlikely to occur. However, 9.9% of individuals undertook movements involving greater distances, primarily large fish (> 120 cm) inhabiting deeper areas of the shelf and slope north of 52° S, moving southward toward reproductive areas (North Scotia Ridge, Burdwood Bank and southern Chile).

More recently, Troccoli et al. (2023) have described movements of *D. eleginoides* on the Patagonian shelf of the Atlantic Ocean, both near Burdwood Bank and on the slope north of the Argentine Sea. Based on the recapture of 121 specimens out of the 5,907 tagged during the period 2004-2020, they were able to confirm the same resident behavior in both areas, as previously observed Brown et al. (2013) and Lee et al. (2022). Around 77% of fish in the northern area and 64% in the southern area were recaptured within less than 37 km from the release site, with periods of freedom ranging from 0.5 to 8.6 years. However, about 10% of fish exhibited longer displacements (> 740 km), with one of them covering a distance of 3,540 km, moving from the Atlantic to the Pacific Ocean. Only

two tags from those placed around Malvinas Islands by the Argentine fleet operating in the area were recovered, although the specific release locations of both fish are not known. This pattern of migratory movements also aligns with the findings reported by Marlow et al. (2003) for fish tagged on the slope north of Malvinas Islands (42° S). Out of the total recaptured in that area (14 out of 274 tagged), 12 were obtained within less than 20 km from their release site. Among the remaining fish, one specimen was captured 46 km from the release site after 409 days of freedom, and another was recaptured 322 km southward after 217 days of freedom. Finally, an initiative to study movements of *D. eleginoides* in international waters north and east of Malvinas Islands has been proposed for consideration by CCAMLR by Lam et al. (2019). The study, which plans to use 50 satellite tags, will undoubtedly contribute to understanding the species' migratory movements in the area.

Based on all the available information regarding tagging and recapture experiments, it can be concluded that there is enough evidence to confirm the limited displacements of *D. eleginoides* on the Argentine Patagonian shelf. These displacements are characterized by the absence of regular migrations, which seems to be common to all populations of the species in the southern Atlantic, Pacific and Indian oceans: the majority of fish remain faithful to or near their residence sites, while only a small fraction of them having a tendency to travel long distances (Williams et al. 2002; Marlow et al. 2003; Burch et al. 2019; Lee et al. 2022; Troccoli et al. 2023). However, long-distance migratory movements of fish do not necessarily imply significant genetic contributions to and from other populations or stocks. Even though there are some fish that may exhibit traveler or vagrant behavior, *D. eleginoides* remains considered a fundamentally philopatric species (Kuhn 2007; Welsford et al. 2011). The only exception to this behavior is the result of tagging and recapture studies conducted in the Pacific Ocean off the coast of Chile. Rubilar et al. (2013) reported the tagging of 855 fish be-

tween June 2012 and March 2013 from 47° S to the southernmost Cape Horn (approximately 59° S), of which 11 were recaptured. Surprisingly, despite the low number of recaptures (possibly due to the short time elapsed since release), a noticeable northward displacement was observed from release sites to recapture sites. Meanwhile, Rubilar et al. (2014) mention the capture of 30 fish, confirming the northward migration pattern in Chilean waters. The distance traveled by the fish was significant, exceeding 1,700 km in some cases in less than a year (246 days). In contrast to reports of *D. eleginoides* in other regions of the southern oceans and on the Atlantic Patagonian shelf, only 20% (6/30) moved less than 92.6 km from their release site. There is evidence of only two individuals tagged in Chile that were caught in Argentine waters near the border between the two countries (Troccoli et al. 2023). Zuleta et al. (2015) reported the recapture of a single fish out of the 136 marked during 2014 in the Chilean artisanal fishery (north of 47° S). A fish marked at 43° 26' S was recaptured one degree to the south (42° 34' S), covering a distance of over 120 km in two months after its release, constituting the only available record of a specimen moving southward in Chilean waters.

Spawning characteristics

Patagonian toothfish has a high fecundity compared to other nototheniids. Females can produce between 94,000 and 1,426,000 large-sized eggs (4.3 to 4.7 mm) (Kellermann 1990; Evseenko et al. 1995; Nevinsky and Kozlov 2002; Brown 2011), although in relative terms to their body weight it is much lower than in other teleosts (Young et al. 1995, 1999). Eggs containing 28 oily droplets, like the larvae, are pelagic (Evseenko et al. 1995; North 2002; Mujica et al. 2016). It has been estimated that embryonic development in South Georgia Islands lasts at least about three months before hatching (Evseenko et al. 1995; North 2002).

Larvae hatch with a total length of 14 mm in November on the shelf of South Georgia Islands

(Kock and Kellermann 1991). North (2002), based on larval size and growth rate, predicted that capturing them in that region between November and December would suggest an embryogenesis period of about 3.5 months. On the other hand, it has been reported that in the Kerguelen Islands, larvae can remain in the water for up to 230 days (Krusic-Golub et al. 2005). If this extended duration of the pelagic egg and larval period were confirmed, it would make the species highly susceptible to predation in the early life stages, which, in a way, would not align with the relatively low fecundity of the species.

Small juveniles of Patagonian toothfish exhibit negative buoyancy (Eastman 1993), which facilitates their movement towards the demersal layer near the bottom. These juveniles inhabit shallower waters compared to adults. Thus, recruitment occurs in shallower waters relative to the broad depth range in which the species is distributed. It has been observed that recruitment tends to be variable near Malvinas Islands, with the appearance of a more abundant cohort every 4 to 5 years, approximately (Laptikhovsky and Brickle 2005). However, no reliable relationship between recruitment strength and environmental conditions in that area has been established (Brown 2011; Lee et al. 2021) possibly due to the oceanographic complexity of the region.

Subsequently, as fish grow and become adults, they migrate to deeper waters (Agnew et al. 1999; Wöhler and Martínez 2002), usually close to recruitment sites (Williams et al. 2002). With increased sexual maturation, the neutral buoyancy of adults becomes more pronounced (Eastman 1993). The life cycle of the species is thus marked by significant ontogenetic changes allowing for complex adaptability to achieve connectivity in areas of spawning, breeding, recruitment, and feeding, which may only occasionally involve great distances (Ashford et al. 2012).

Laptikhovsky et al. (2006) described that reproduction of Patagonian toothfish around Malvinas Islands primarily occurs on the eastern slope of

the Burdwood Bank and the westernmost part of the northern Scotia Ridge, where fish from nearby zones would migrate for spawning. They also postulated that after spawning, the fish migrate again from the Burdwood Bank slope to their residence areas, located to the north on the eastern and northern slopes of Malvinas Islands (even up to 40° S), westward in the Chilean Pacific and eastward over the Scotia Ridge. However, Brown et al. (2013), using pop-up tags, found that fish in the eastern and northeastern slope areas of Malvinas Islands do not migrate south during the breeding season. On the contrary, they remain faithful to the tagging sector, with movements involving distances less than 50 km in 79% of cases and not exhibition of repetitive vertical migrations that could be related to reproductive behavior in their residence area.

On the other hand, Martínez et al. (2022) recently demonstrated the existence of reproductive activity along a significant portion of the Argentine Sea slope north of Malvinas Islands, where fish inhabiting that area would reproduce. This finding contradicts the statement by Laptikhovskiy et al. (2006), in the way there would be a minor reproductive peak on the Burdwood Bank during the month of May, although the most significant period for reproduction would occur in July and August. This pattern is similar to the one described for the slope around South Georgia Islands, where a minor reproductive peak occurs in April-May and a major one in July-August (Agnew et al. 1999).

The spawning would occur at an average depth of about 900-1,100 m (Laptikhovskiy and Brickle 2005; Laptikhovskiy et al. 2006; Pájaro et al. 2009; Martínez et al. 2022), although there are records of fish spawning between 700 and 1,900 m deep in the Burdwood Bank slope and slightly to the north. Differential vertical migrations of males and females were reported because of the earlier arrival of males at the spawning areas, where they remain in deep waters awaiting the arrival of females (Laptikhovskiy et al. 2006). Later, during the reproductive peak, both sexes would concentrate between

900 and 1,200 m for spawning (Laptikhovskiy et al. 2006). There is evidence that a certain proportion of adults present in the Burdwood Bank and other regions of the slope of the Patagonian Atlantic shelf do not reproduce every year (Brown 2011; Boucher 2018), which is a characteristic of many teleosts linked to unfavorable environmental conditions or poor physiological conditions of some individuals during the spawning period (Rideout and Tomkiewicz 2011). Arana (2009) observed that individuals undergoing maturation in southern Chile were present in June and July, advanced maturation and spawning occurred in July and August, and post-spawning took place in September and October, while specimens in an advanced state of maturity were detected during the second half of September and early October. Meanwhile, Galleguillos et al. (2008) mentioned that in southern Chile, there would be two spawning peaks: the first and smaller one between April and May and a larger spawning between July and August, coinciding with the report by Laptikhovskiy et al. (2006) for Burdwood Bank.

Pájaro et al. (2005) identified a Patagonian toothfish spawning area in the Argentine Sea along the slope from Cape Horn to the east of Burdwood Bank, based on microscopic analysis of the gonads. Pájaro et al. (2009) confirmed this finding through extensive onboard observer data. These latter authors, analyzing reproduction characteristics of Patagonian toothfish in the Argentine Sea in two distinct sectors (northern slope between 36° S and 48° S and southern slope south of 54° S), found the highest reproductive activity with spawning females and males in the southern sector from Cape Horn to the southern slope of Burdwood Bank and north of the Scotia Ridge between July and August. In contrast, in the sector of the continental shelf edge north of 48° S, no specimens in spawning condition were identified (even with total lengths corresponding to adults), and only a few individuals in maturation and post-spawning stages were captured. This led these authors to postulate that there possibly be very limited reproductive activity

in the northern sector, which would be consistent with the findings of Laptikhovsky et al. (2006) that all fish from the Patagonian Atlantic shelf would reproduce near Burdwood Bank. However recently, information from INIDEP Observer Program for the period 2010-2020 revealed that the slope sector off the Argentine coast north of Malvinas Islands between 37° S and 42° S was home to spawning Patagonian toothfish, indicating reproductive activity (Martínez et al. 2022) (Figure 3). This is a corroboration that with a larger amount of information it was possible to discover new spawning sites for the species, as described by Brigden et al. (2017) for the slope around South Georgia Islands (Figure 4).

Egg and larvae dispersion

Fish, like other living organisms, have evolutionarily developed mechanisms to adapt to the environment in which they inhabit. Among adap-

tations contributing to reproductive success are those linked to the strategy of releasing eggs over a relatively extended period to locate favorable environmental events, in order to increase the probability of survival of early life stages of the life cycle (Murua and Saborido-Rey 2003). To extend spawning periods, individuals often have more than one spawning event during the reproductive season, known as batch spawners, within which the reproductive strategy of Patagonian toothfish would fall (Pájaro et al. 2009; Brown 2011). Following spawning, egg density determines their buoyancy and, consequently, their position in the water column (Sundby 1991). Vertical location in the water column is crucial as it can determine their dispersal or retention, as well as their escape from predators, and thus, their survival. Consequently, fish populations have adapted their breeding areas and times (including spawning depth) to link with oceanic circulation mechanisms that determine their reproductive success.



Figure 3. Spawning areas of *Dissostichus eleginoides* identified in waters of the continental shelf and slope of South America (reproduced from Martínez et al. 2022).

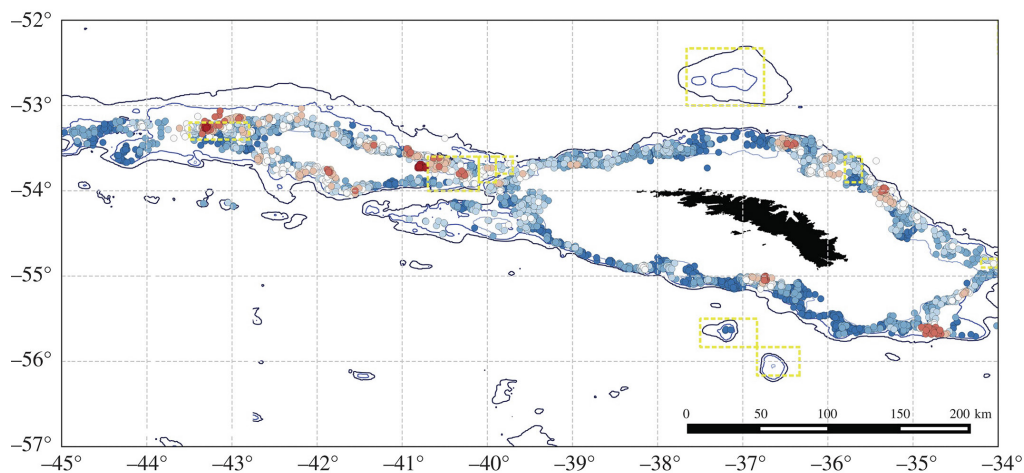


Figure 4. Spawning areas of *Dissostichus eleginoides* near South Georgia Islands and Aurora Islets (Shag and Black Rocks). Reproduced from Brigden et al. (2017).

According to Toomey et al. (2016), the mixing between fish populations can occur through two primary mechanisms: the dispersion of eggs and larvae by currents and the migration of juvenile and adult fish. Such dispersion and migratory movements can occur in the absence of barriers, whether they are generated by topography, such as vast distances of deep ocean or oceanographic fronts that separate waters with different characteristics. Regarding the dispersion of reproductive products in the southernmost American region, where these barriers do not seem to exist, Ashford et al. (2012), Harte (2020), and Lee et al. (2021) analyzed the potential connection between reproductive areas of the Patagonian toothfish located on the continental shelf of southern Chile and the fishing grounds around Malvinas Islands. Through simulations of particle movement in the water column, they established the possibility that spawning areas in the southern Pacific (Chile), driven by the Antarctic Circumpolar Current, contribute to the recruitment occurring in the Atlantic, within the significant southern Patagonian fishing grounds. This is because Patagonian toothfish eggs and larvae are pelagic, meaning they would remain in the neritic region for two to five months (Evseenko et al. 1995; North 2002; Krusic-Golub et al. 2005).

Subsequently, Ashford et al. (2012), aiming to test the hypothesis that spawning areas in southern Chile contribute to recruitment on the Atlantic South Patagonian shelf (Burdwood Bank and Malvinas shelf), analyzed the otolith microchemistry of fish captured on both sides of the southern cone of South America. Based on the analysis of trace elements deposited in the otolith nucleus during early life stages, they hypothesized that fish distributed both north and south of Malvinas Islands would receive contributions from reproduction occurring in southern Chile and the Burdwood Bank. Harte (2020), using experimental density data, suggested that species eggs change buoyancy as embryo development progresses, following a similar pattern of buoyancy change based on developmental stage and egg age as observed in other species of marine fish. This could lead to the assumption that the initial hypothesis of eggs being distributed in the uppermost pelagic layer might not be entirely correct. On the contrary, eggs of *D. eleginoides* could remain in different layers of the mesopelagic with potentially different consequences for their possible dispersion through the Antarctic Circumpolar Current, as proposed by Ashford et al. (2012).

Conducting particle dispersion simulations from the spawning areas in southern Chile and consid-

ering various retention areas on the Patagonian shelf, Harte (2020) surprisingly postulated that Burdwood Bank seems to have little to no connectivity with retention areas around Malvinas Islands or the Patagonian shelf. It is unlikely to contribute significantly to the supply or retention of eggs and larvae of *D. eleginoides* in the region. Instead, results from simulations suggest that spawning areas in southern Chile are likely the most important source of reproductive products for Malvinas Islands fishing grounds. When analyzing the potential processes governing the ontogenetic migration and recruitment strength of *D. eleginoides* in the Patagonian shelf sector around Malvinas Islands, Lee et al. (2021) also proposed that after spawning, eggs and larvae are transported to that area by currents from reproduction areas located south of Chile and Burdwood Bank. The presence of seasonal mesoscale eddies connecting the subantarctic Front with Malvinas Current seems to be of paramount importance for the survival of eggs and larvae of the species. However, Rubilar et al. (2014) found that southern Chile has numerous juvenile rearing and toothfish recruitment areas, suggesting that many of them have not yet been adequately identified and valued. This observation contradicts to some extent the hypothesis that recruitment occurs mainly on the Argentine shelf south and east of Malvinas Islands, indicating that it also takes place in Chilean waters. In this area, juveniles are found in significant numbers, at least from 47° S and up to the border with Argentine waters, implying that the transport of reproductive products, if it occurs, could be a phenomenon of smaller dimensions than assumed by Harte (2020) and Lee et al. (2021).

Length at first sexual maturation

There are different estimations of the length at first sexual maturation of the Patagonian toothfish in the southern region of Atlantic, Pacific and Indian oceans and around the southernmost American region. As a result, this study describes values of length at first maturation ($LT_{50\%}$) estimated by var-

ious authors for different regions where the species is distributed (Table 1).

According to studies conducted by different authors, distinct $LT_{50\%}$ values have been observed among different study areas. However, differences may be attributed to the methods employed in each estimation, especially maturity scales, the technique used for stage assignment (macro or microscopic), and the seasonal coverage of samplings, making comparison challenging. The only thing that seems evident and is repeated in almost all studies is that males mature at smaller body sizes than females. On the other hand, in those estimations corresponding to the southernmost American region, it would appear that values of length at first maturity on the Atlantic continental shelf are quite similar to each other and lower than those corresponding to the Chilean Pacific, with the exception of those reported by Arana (2009). They also seem to be distinguishable from those estimated in the South Georgia Islands area, where differences between males and females are more pronounced. Prenski and Almeida (2000) mentioned that specimens possibly mature at an earlier age in the Patagonian region compared to those from South Georgia Islands due to more precocious development caused by temperature effects. However, later estimates in the Argentine Sea (Pájaro et al. 2009; Ruocco et al. 2017) would indicate that at least males would mature at larger lengths compared to records obtained in the South Georgia Islands.

Parasitic fauna

Parasitic fauna is a useful biological marker and a widely accepted methodology for discriminating fish stocks (MacKenzie 2002; Catalano et al. 2014; Timi and MacKenzie 2015). It has been applied in various fish species from the Southwest Atlantic, and it has been observed that both oceanographic conditions and host characteristics influence parasitic composition and provide insights into stock differentiation (Braicovich and Timi 2008; Timi

Table 1. Length at first sexual maturation (LT_{50%}) of *Dissostichus eleginoides* estimated by various authors in different sectors of the species distribution in the southern region of the Atlantic, Pacific and Indian oceans.

Source	Area	TL _{50%} males (cm)	TL _{50%} females (cm)
CCAMLR (1987)	South Georgia Islands	57.7	110.4
Moreno (1998)	South Georgia Islands	67.0	86.0
Everson y Murray (1999)	South Georgia Islands	78.5	98.2
Agnew et al. (1999)	South Georgia Islands	75.0	101.0
Laptikhovsky y Brickle (2005)	Burdwood Bank and 'East of the Malvinas Islands'	86.0	90.0
Prenski y Almeyda (2000)	Burdwood Bank	76.3	87.1
Pájaro et al. (2009)	Northern slope of the Atlantic Patagonian shelf (39° S-47° S)	84.7	84.7
Pájaro et al. (2009)	Southern slope of Cape Horn-Burdwood Bank (55° S-57° S)	80.7	83.1
Ruocco et al. (2017)	Northern slope (38° S-42° S) and east (54° S-58° S) of the Atlantic Patagonian shelf T	81.1	78.9
Ruocco et al. (2019)	Southern slope (54° S-58° S) of the Atlantic Patagonian shelf T	75.0	76.4
Moreno et al. (1997)	Southern Pacific (Chile)	105.0	117.0
Young et al. (1999)	Southern Pacific (Chile)		128.7
Oyarzún et al. (2003b)	Southern Pacific (Chile)	78.0-94.0	113.0-117.0
Arana (2009)	Southern Pacific (Chile)	81.0	89.0
Duhamel (1991)	Kerguelen Islands	65.0	80.0
Lord et al. (2006)	Kerguelen Islands	63.0	85.0

et al. 2009; Alarcos and Timi 2013; Alarcos et al. 2016; Cantatore et al. 2016).

In the case of *D. eleginoides*, Collins et al. (2010) indicated that 62 different parasite species have been reported. Various studies have demonstrated that the greatest differences in parasitic fauna corresponded to distant localities within its distribution range (Gaevskaia et al. 1990; Rodriguez and George-Nascimento 1996; Brickle et al. 2005, 2006; Brown et al. 2012). When comparing the number of metazoan genera parasitic on *D. eleginoides* from central Chile to those reported by Gayevskaia et al. (1990), Rodriguez and George-Nascimento (1996) found a higher degree

of similarity with those reported for the Malvinas Islands area than with those found in samples from the South Georgia Islands. However, authors indicated that, in geographic terms, the parasite fauna of *D. eleginoides* recorded in South Georgia Islands shows higher taxonomic richness, while fauna recorded in Malvinas Islands exhibited intermediate similarities between Chile and South Georgia Islands. In all studies referring to parasitic fauna in the mentioned ocean sector, differences in parasite species and infestation levels related to ontogenetic development have been reported. Generally, larger fish harbor a greater quantity and variety of parasites, as described by Brickle et al.

(2005, 2006) and Brown et al. (2012). Given that *D. eleginoides* is a major predator of various fish species, its high parasite diversity may be related to its eating habits, albeit it also depends on the existence of possible parasites in the fish's residence area (Gaevsкая et al. 1990).

From the analysis of parasitic fauna of juvenile *D. eleginoides* present on the Patagonian shelf around Malvinas Islands, Brown et al. (2012) identified 15 parasite species in their stomachs with differences in parasitic composition between fish from the northwest and southeast of the islands. These authors proposed that differences in the abundance of one of them (*Elytrophalloides oatesi*) between the shelf around Malvinas Islands and other regions could potentially be used as a biological marker to study migratory movements and the population structure of Patagonian toothfish. The prevalence and abundance of *E. oatesi* in all subantarctic islands were much lower than in the Malvinas region (Brickle et al. 2006; Brown et al. 2012), indicating lower abundance in colder areas. *Elytrophalloides oatesi* shows variable abundance in different regions around the archipelago and is absent in Patagonian toothfish from central-southern Chile (Rodríguez and George-Nascimento 1996; Oliva et al. 2008), which could indicate certain isolation of the fish in both localities.

Alternatives for the management of *Dissostichus eleginoides* fisheries in the southernmost American region based on population structure

Ideally, the scale of assessment models should match the scale of management (Kerr et al. 2017), however this is not always feasible. There are several alternatives available to improve fisheries assessment and management, including changing the scope of stock assessment or incorporating information on stock mixing, modifying the management scale by defining new management unit boundaries, or changing both the assessment and management scales. The scientific evidence reviewed seems clear that the population group of

D. eleginoides located on the island shelf and slope of the Aurora Islets and South Georgia Islands should be managed as a single stock, as is currently practiced. Considering the evidence provided by multidisciplinary studies on various aspects of the biology and population dynamics previously described, three different hypotheses/scenarios were analyzed, each with implications for the fisheries management of Patagonian toothfish in waters surrounding the southernmost American region.

*Maintain the current management scheme of different *D. eleginoides* fisheries in the area*

This scheme involves treating the resource distributed around Malvinas Islands as an individual stock, which is subject to fishing in that area. This contrasts with the consideration of a single stock in the southwestern Atlantic (SWA) under which the Argentine fishery is managed, and the assumption of a common stock composed of Patagonian toothfish distributed in the southern Pacific off the coast of Chile and the Argentine Sea, with the exception of the sector surrounding Malvinas Islands, as assumed in the Chilean fishery management without coordination between the management of different areas (Martínez et al. 2019; Tascheri 2019). In either case, this scenario is not aligned with a sustainable exploitation of the resource and contradicts scientific evidence used to differentiate the stock subjected to exploitation around Malvinas Islands. This differentiation is what allows the ongoing certification of that fishery by the MSC. Furthermore, this scheme also contradicts a potential future certification of fisheries in the operating area of the Argentine and Chilean fleets.

*Progress in the study and potential application of the metapopulation concept, which could characterize the distinct groups of *D. eleginoides* located in the area*

This approach may prove ecologically intriguing, yet it presents certain aspects that may not be easily resolved. On one hand, metapopulation theory necessitates barriers that result in some level

of isolation for subpopulations (Sale et al. 2006), which, in this case, is challenging to assume given the practically continuous distribution of the species from the Pacific to the Atlantic. This would require integrated management or the consideration of managing the various fisheries developed on other subpopulations (including changes in assessment models). Nevertheless, even if practically challenging, this approach could justify more detailed analysis in the future, as it could contribute to characterizing the population structure of *D. eleginoides* in the southernmost region of America.

Accepting the existence of distinct, independently managed, Patagonian toothfish stocks in the seas surrounding the southern region of South America

Considering this approach holds an advantage, stemming from the growing scientific evidence recently provided to suggest the presence of an independent stock around Malvinas Islands. However, while this condition has been assumed and accepted by the MSC for the certification of the fishery conducted there, the search for certainty to firmly establish this circumstance continues. Similarly, while additional research on the extent of exchange between Argentine and Chilean fishing grounds would be beneficial in order to examine the level of isolation that these areas exhibit and consider them as independent stocks, it can initially be deemed that evidence of significant isolation between *D. eleginoides* groups that are exploited by both fisheries may be sufficient to recognize the existence of distinct stocks from a fishing exploitation perspective. If this is the case, different stocks should be defined as independent management units and managed accordingly, as indicated by Martínez et al. (2019) and the CM BAC (2019).

Discussion on the available information for selecting a management alternative

Considering the scientific knowledge about the biology and aspects related to the population structure of *D. eleginoides* summarised in this

analysis, there is some evidence suggesting the presence of distinct Patagonian toothfish stocks located around the southern region of South America and in the Atlantic southwest. Firstly, sufficient scientific evidence has been identified to accept that the Patagonian toothfish distributed over the insular shelf of the Aurora Islets (Shag and Black Rocks) and the South Georgia Islands would constitute a well-differentiated population compared to the fish present on the Patagonian shelf, including genetic aspects and all other types of distinctive characteristics such as those related to reproduction, otolith microchemistry, fish migratory patterns, and egg and larval dispersion, among others, that underpin the existence of a management and exploitation unit around these islands. Literature consensus indicates that this population differentiation has occurred due to isolation generated by the distance from the continental shelf, but primarily by the presence of the Polar Front. Currently, this is the accepted understanding, so both the resource assessment and fishery management are conducted independently for this area, inside the scope of CCAMLR.

Regarding Patagonian toothfish distributed around the southern cone of the Americas, although there are no noticeable barriers to assume complete isolation, we also believe that the available scientific evidence would allow us to consider the existence of differentiated stocks, with a sufficient degree of isolation to establish independent exploitation units. While in this case, scientific works are not entirely consistent regarding the stock unit and the possible interchange and/or contribution that could occur between them, there is a specific precedent for their individual treatment. The majority of studies conducted to define the stock unit of Patagonian toothfish located around the Malvinas Islands concur in demonstrating significant isolation from that found in the rest of the Atlantic Patagonian continental shelf and slope, with a very limited degree of interchange (Marlow et al. 2003; Brown et al. 2013; Lee et al. 2022; Troccoli et al. 2023). This has allowed, in practice, the fishery to

be managed as a single stock and even led to its certification by the MSC under that assumption, albeit with the condition of further advancing the study of the species' population structure in the area. However, as mentioned earlier, some authors have indicated that this stock would receive contributions from the reproductive products (eggs and larvae) of spawning areas located south of Chile and the Burdwood Bank (Ashford et al. 2012; Harte 2020; Lee et al. 2021). In this case, though not explicitly stated, if such contribution were to occur, it would also feed into the main fishing grounds of the Argentine fleet, located immediately west of the Burdwood Bank. This is based on the analysis of the general west-to-east flow of waters governed by the Antarctic Circumpolar Current, with particularly significant velocities in that sector (Matano et al. 2019).

On the other hand, another study conducted to understand the reproductive dynamics of the species in the South Atlantic has posited that all fish distributed in the area would migrate to reproduce on the southern slope of the Burdwood Bank (Laptikhovsky and Brickle 2005). However, it has been subsequently demonstrated that there are other breeding areas in the Argentine Sea, such as the slope west of the Burdwood Bank and extending to Cape Horn (Pájaro et al. 2009). However, the evidence of reproductive activity in the northern slope of the Argentine Sea between 37° S and 42° S (Martínez et al. 2022), along with the behavior of fish that tend to spend a significant portion of their adult lives near these areas (Brown et al. 2013; Lee et al. 2022; Troccoli et al. 2021), does not align with the migratory patterns necessary to support this hypothesis.

Studies by Ashford et al. (2012), Harte (2020), and Lee et al. (2021) proposed that reproductive products of Patagonian toothfish would be carried by currents to the east and then, in the Atlantic, northward. Thus, the spawning occurring in southern Chile and on the Burdwood Bank slope would supply the fishing grounds around the Malvinas Islands. However, to corroborate this scenario, there

would need to be a noticeable migratory movement of adult fish from their residence areas around the Malvinas Islands and the entire northern slope of the Argentine Sea to the more southerly spawning areas upon reaching sexual maturity. Once again, similar to the reproductive dynamics proposed by Laptikhovsky and Brickle (2005), this scheme does not align with the absence of regular migratory patterns of *D. eleginoides* in the area, which instead exhibit strong philopatry. The proposed hypothesis implies that the Chilean stock would be a constant supplier of reproductive products for the Atlantic fishing grounds, leading to a continuous genetic flow between stocks, but in a one-way direction, from west to east. It also doesn't align with the permanent presence of juveniles in all considered areas in the South Pacific. If eggs and larvae are indeed carried by currents at the speeds and distances proposed by Ashford et al. (2012) and Harte (2020), then it's unlikely that juvenile concentrations could remain near the spawning areas, both in the Chilean Pacific (Rubilar et al. 2014) and in the sector near the Burdwood Bank (Wöhler and Martínez 2002). It's also necessary to note that the highest abundance of the species in the area seems to occur near the southern slope of the Burdwood Bank, as inferred from high fishing yields (Martínez and Wöhler 2017). Thus, it's challenging to assume that a subsidiary population would be much smaller but more productive than the main population (Pulliam 1988). Therefore, despite the valuable efforts made to elucidate the recruitment process of *D. eleginoides* in the Atlantic Patagonian sector, we believe that the contribution of different spawning areas to recruitment in distant sectors remains uncertain and further studies are required in this regard.

Perhaps a plausible hypothesis, distinct from what the mentioned authors propose, should be based on the understanding that fish reproduce in different areas all along the continental slope, ranging from the southern Chile (at least 47° S), bordering Cape Horn, to regions of the northern Patagonian slope, and even into the Argentine-Uruguayan Common Fishing Zone (Pájaro et al. 2005, 2009;

Arana 2009; Rubilar et al. 2013, 2014; Martínez et al. 2022). While there are hydrological forcings that suggest that reproductive products could be displaced to areas far from the spawning zones (considering an extended duration of egg and larval stages), it is possible that there are strong and lasting retention mechanisms linked to the spawning areas to prevent these products from moving significantly away from their origin. This is supported by the numerous recruits found in areas close to the reproductive zones along the entire slope. In this context, Ashford et al. (2012), Harte (2020), and Lee et al. (2021) propose dispersion movements that would involve thousands of kilometers within timeframes coinciding with the pelagic stage. As mentioned earlier, the described scheme does not seem to fit the Harden-Jones triangle (1963) since the massive return migration of adult fish to the south and west during the breeding season to their spawning areas is missing. On the contrary, it has been demonstrated through tagging and recapture that this does not occur, as the vast majority of fish remain loyal to their residence area, moving only short distances (generally less than 30-50 km), even over extended periods, as recently demonstrated by Lee et al. (2022) and Troccoli et al. (2023). Therefore, there are likely retention mechanisms for eggs and larvae, both passive and active (in the case of larvae), that mainly allow the reproductive products to remain near the spawning zones and recruit into the adult stock in those areas. Recent studies have highlighted the uniqueness of the Burdwood Bank and its surroundings as a significant site for retaining small organisms with various zooplankton species associations (García Alonso et al. 2019; Spinelli et al. 2020). Both Ashford et al. (2012) and Harte (2020) mention them, although these mechanisms could be much more potent than they have modeled. One of these retention areas is the so-called Malvinas Depression, located northwest and north of the Burdwood Bank but very close to it, where a significant presence of juveniles of Patagonian toothfish were found, including quite young ones (one or two years old),

which has led the Argentine fisheries management to prohibit targeted fishing of the species at depths less than 800 m to prevent their capture (Wöhler et al. 2001; Wöhler and Martínez 2002; Martínez and Wöhler 2017).

Based on the conducted analysis, a possible framework based on available scientific information suggests that the population structure of Patagonian toothfish around South America consists of distinct resident fish stocks that largely remain faithful to their spawning and nursery areas due to the species' evolutionary adaptation to the hydrological and topographical characteristics of the area. This scheme would involve a combination of dispersal and retention mechanisms to ensure that eggs and larvae remain in proximity to the spawning areas, moving only short distances to shallower waters to enhance the survival of young juveniles. As these juveniles grow and approach sexual maturity, they migrate to deeper waters near their nursery areas to join the adult stock. Of course, as is common in fish and other animal populations, there may be a proportion of individuals in both their early life stages (eggs and larvae) and adults that can travel considerable distances and even mix with residents from other areas. These individuals might be responsible for the lack of genetic differentiation across the South American shelf and slope. However, this does not seem to be the rule in the case of *D. eleginoides*; on the contrary, there is sufficient evidence to continue considering the species as philopatric.

The marked affinity for their residency sites, as well as the existence of concrete evidence supporting isolation such as tagging and recapture, stable isotope and trace element variability in otoliths, morphology, the presence of breeding areas along nearly the entire shelf and slope where the species is distributed, the localization of nursery areas associated with each of them, and the differences found in parasitic fauna, allow considering it not unreasonable to suppose the existence of distinct stocks of *D. eleginoides* structured along the shelf and slope around the southern region of South

America. Therefore, and following the conceptual framework of Kerr et al. (2017), it would be highly useful to align the different stocks with different fisheries as exploitation units, sufficiently independent in fishing terms from others existing in the area. As proposed by Begg and Waldman (1999), the concept of a stock really pertains to the interaction between fish assemblages and fishery management, treating it as a homogeneous group for the purpose of fishery management. In this regard, the different stocks of Patagonian toothfish considered in this study fulfill this premise. Initially, and based on the analyzed scientific evidence, there could be assumed to be five differentiated stocks of *D. eleginoides* around the South America and the Atlantic southwest. The first of these corresponds to the Aurora Islets (Shag and Black

Rocks), South Georgia Islands, and could extend to the South Sandwich Islands (Atlantic Subantarctic Islands Stock-ASIS), the second would consist of the fish located near the northern slope of the Argentine Sea, from 39° S to approximately 47° S (North Patagonian Atlantic Stock-NPAS), the third is located around the Malvinas Islands (48° S to 54° S east of the Burdwood Bank-Central Patagonian Atlantic Stock-CPAS), the fourth corresponds to the southern and western sector of the Burdwood Bank (from 54° S west of the Burdwood Bank to 57° S in the Cape Horn region-South Patagonian Atlantic Stock-SPAS), and the fifth is present in the Pacific Ocean sector, mainly along the Chilean coast, although the northernmost extent of its distribution reaches Peruvian and Ecuadorian waters (Pacific Patagonian Stock-PPS) (Figure 5).



Figure 5. Diagram of the geographical distribution of the different proposed stocks/exploitation units of Patagonian toothfish in South America. ASIS: Atlantic Subantarctic Islands Stock; NPAS: North Patagonian Atlantic Stock; CPAS: Central Patagonian Atlantic Stock; SPAS: South Patagonian Atlantic Stock; PPS: Patagonian Pacific Stock.

Notwithstanding, we must remember that the identification of stocks should be recognized as an ongoing process, responsive to changes in fishing arrangements and their assessment, always viewed in the context of a critical examination of all available information and the studies required by the changing condition of the resource, enabling the advancement of new technologies (Brown et al. 1987). Thus, despite all the effort made, and for the purpose of gaining a more precise understanding of the population structure of Patagonian toothfish in waters of South America, multidisciplinary studies may be necessary to complement the current knowledge of various aspects that still remain uncertain. Large-scale analysis of stable isotopes and microchemistry of otolith cores and edges, their morphology, or other methodologies that may emerge in the future, could provide even more evidence about the different stocks proposed and test the formulated hypothesis.

FINAL CONSIDERATIONS

Finally, in light of all the available scientific evidence summarised in this study, and for the purpose of better fisheries management, a series of questions arise and attempt to be addressed. The first of these questions is whether the toothfish present in the waters of the southern cone of South America can be considered a single population. While there are no genetic differences, it is clear that the necessary process of mixing among the individuals that compose it, which must be extensive to characterize a population as a unit, is not fulfilled. This is due to the enormous distribution area that extends from the Pacific, starting in Ecuador and extending into the Atlantic to the south of Brazil, as well as the strong fidelity of the fish to their residence areas, especially in the Atlantic. This fidelity is related to the reproductive and breeding areas that are found throughout the shelf and slope, at least from 47° S in the Chilean Pacific to 39° S off the

Argentine coast, where reproductive activity has also been detected.

On the other hand, the mixing that characterizes populations with a well-defined spawning area where adult fish from the population gather annually to reproduce, facilitating gene exchange, can be discarded based on the scientific evidence collected in this analysis. While some mechanisms that could facilitate certain genetic exchange have been described, such as a few individuals capable of undertaking long migrations or the drift of reproductive products in certain areas (mainly in the southernmost region), it is evident that the vast majority of individuals remain semi-isolated even during the reproductive season. Thus, isolation would not occur due to barriers preventing fish dispersion and mixing, but rather due to their pronounced philopatric behavior. For instance, those fish that reproduce on the slope north of the Argentine Sea, up to 39° S (Martínez et al. 2022), do not mix with those that reproduce during the same period near the Burdwood Bank or in the Chilean Pacific. Therefore, it cannot be asserted that the Patagonian toothfish of the southern cone of South America belongs to a single population in the classical sense of the concept's definition, even though no genetic differences have been detected among different fish groups. The second question, which arises from the first, is whether the existence of more than one population in the southernmost region of South America can be assured. Just as it cannot be asserted that they belong to a single population, we believe that, with the existing knowledge today, it is impossible to ensure the existence of more than one population around the southern cone of America, both in the Pacific and Atlantic. Firstly, genetic studies conducted do not reveal any differentiation, although other tools for population differentiation, such as otolith microchemistry and morphology, parasitology, reproductive dynamics, and tagging-recapture experiences, have shown some differences among fish located in distinct areas. As a result, concrete differences that definitively contribute to possible population differentiation have not been verified

without reasonable doubt. However, we might be witnessing a very early stage in the evolution towards population differentiation, given that all the elements necessary for this process are in place, such as reproductive isolation, distinct feeding and breeding areas, and a very limited gene flow due to the high fidelity to fish residence sites.

One possibility to explain the current pattern of population structure of *D. eleginoides* in the study area is to frame it under the concept of metapopulations. It could be the case of a large metapopulation of the species in the area, ranging from the Ecuadorian shelf and slope in the Pacific to the southernmost tip of Brazil in the Atlantic, consisting of several semi-isolated subpopulations with limited genetic exchange between them due to the reasons mentioned earlier. However, while this framework cannot be ruled out, we believe that there is not yet sufficient evidence to adopt it. Many more studies should be conducted in that direction to test this hypothesis.

The third question that arises is related to the possibility of establishing differentiated management units in different sectors around the southern cone of America. Therefore, is it correct to assume, from a fisheries perspective, the existence of distinct stocks of Patagonian toothfish on the Patagonian shelf, both in the Atlantic and the Pacific? It can be considered that, based on the surveyed scientific studies, and even with the limitations that exist in effectively differentiating potential population groups, it is possible to distinguish different stocks from a fisheries standpoint. A stock is a homogeneous set of fish for the purpose of fisheries management; therefore, the different groups of *D. eleginoides* currently subject to exploitation, both in the southeastern Pacific and on the Patagonian shelf and slope of the Atlantic, possess all the elements to suggest the existence of discrete units from a fisheries perspective (certain reproductive isolation and very limited mixing among them). Thus, it is possible to consider it valid to differentiate the existence of different exploited stocks of Patagonian toothfish around the southern region of South

America, based on updated biological knowledge and their alignment with exploitation units may be the most appropriate and practical approach to improve assessment accuracy and management effectiveness, although the definition of management units may not exactly coincide with the biological boundaries of the stocks.

The fourth question, which is more related to a fisheries management perspective than an ecological concept, is it can be deemed appropriate, for fishing exploitation, to establish distinct independent management (or exploitation) units where different fisheries currently operate. The answer in this case, we believe, should be affirmative. The existence of differentiated management units for different stocks supports proper fisheries management premised on sustainability, adhering to a practical approach of fisheries science. In this way, and given the factual characteristics of current fishing exploitation in the area, at least five independent exploitation units could be established, corresponding to the different stocks proposed in this study. It should be emphasized, in this case, that considering different exploitation units entails a practical and reasonable approach, grounded in scientific studies that provide evidence to support the assumption of stock identification. Thus, the defined exploitation units align with existing fisheries.

Author contributions

Otto C. Wöhler: conceptualization; investigation; supervision; project administration; writing-original draft. Patricia A. Martínez: conceptualization; investigation; writing-review and editing. Gonzalo H. Troccoli: investigation; data curation; visualization; writing-review and editing. Emiliano J. Di marco: investigation; data curation; visualization.

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