ORIGINAL RESEARCH

# Migratory patterns of Patagonian toothfish (*Dissostichus eleginoides*) in the southwestern Atlantic Ocean

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**ABSTRACT.** The Patagonian toothfish (*Dissostichus eleginoides*) is a commercially valuable demersal fish present in the southern hemisphere. Therefore, understanding movements of the species across time and spatial scales would enhance our understanding of its behavior within the Argentine and Chilean Patagonian platform. The Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP, Argentina) initiated a tag-recapture program for *D. eleginoides* in 2004. A total of 5,907 specimens, mostly juveniles (< 82 cm total length), have been tagged and released in waters off the edge of the Argentine shelf and slope between 37° S and 47° S (northern Sector of the Argentine fishing ground), and east of De los Estados Island and south of Tierra del Fuego (54° S-57° S –southern Sector of the Argentine fishing ground). A total of 121 specimens were recaptured: 25 (20.7%) were recovered in the northern Sector, 84 (69.4%) in the southern Sector and 12 (9.9%) in waters of the Pacific Ocean in Chile. A total of 67.5% were recaptured within 20 nm (37 km) of the release site and 15% traveled distances of less than 120 nm. A smaller fraction (5%) traveled distances between 120 and 400 nm and only 12.5% were recaptured at more than 400 nm. Using a Generalized Additive Model, it was determined that variables Days at liberty, Sector and Time of tagging were influential in the distance traveled by specimens. From the present work, it seems evident that this species possesses high site fidelity and lacks cyclic migratory movements involving a substantial component of the stock in the American southern cone.

**Key words:** Tagging, recapture, fishing ground, stock.

**Patrones migratorios de la merluza negra (*Dissostichus eleginoides*) en el Océano Atlántico Sudoccidental**

**RESUMEN.** La merluza negra (*Dissostichus eleginoides*) es un pez demersal presente en el hemisferio sur, muy valioso comercialmente. Por ello, comprender los movimientos en diferentes escalas temporales y espaciales contribuiría a conocer más acerca del comportamiento que presenta la especie en la plataforma patagónica argentina y chilena. Desde 2004, el Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP, Argentina), inició un programa de marcado y recaptura de *D. eleginoides*. Un total de 5.907 ejemplares, en su mayoría juveniles (< 82 cm de largo total), fueron marcados y liberados en sectores ubicados en aguas del borde de la plataforma y talud de la Argentina entre 37° S y 47° S (Sector norte del caladero argentino), y al este de la Isla de los Estados y sur de Tierra del Fuego (54° S-57° S –Sector sur del caladero argentino). Actualmente, fueron recapturados 121 ejemplares, 25 (20,7%) se recuperaron en el Sector norte, 84 (69,4%) en el Sector sur y 12 (9,9%) en aguas del Océano Pacífico en Chile. El 67,5% fue recapturado a menos de 20 mn (37 km) del lugar de liberación y 15% recorrió distancias inferiores a las 120 mn. Una fracción menor (5%) recorrió distancias entre 120 y 400 mn y solo 12,5% se recapturó a más de 400 mn. Mediante un Modelo Aditivo Generalizado se determinó que las variables Días en libertad, Sector y Época de marcado influyeron en la distancia recorrida de los ejemplares. A partir del

OPEN ACCESS

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Received: 21 December 2022
Accepted: 2 June 2023

ISSN 2683-7595 (print)
ISSN 2683-7951 (online)

https://ojs.inidep.edu.ar

Journal of the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP)

presente trabajo, parece evidente que la especie en el cono sur americano carece de desplazamientos migratorios regulares que involucren a una parte significativa del *stock*.

**Palabras clave:** Marcado, recaptura, caladero, *stock*.

## INTRODUCTION

The Genus *Dissostichus* comprises two important commercial species: *D. mawsoni* and *D. eleginoides* (Collins et al. 2010). The first one is distributed in Antarctic waters, while the second reaches lower latitudes (Gon and Heemstra 1990). Patagonian toothfish (*D. eleginoides*) has a wide distribution in the southern hemisphere (Collins et al. 2010; Nelson 2016), with its populations often separated by vast expanses of deep ocean (Shaw et al. 2004; Ashford et al. 2006; Rogers et al. 2006; Ashford and Jones 2007). Patagonian toothfish is a demersal species inhabiting shelves and slopes of subantarctic islands of the Southern Ocean (South Georgia Islands, South Sandwich Islands, South Orkneys, Crozet, Kerguelen, Heard, McDonald, Macquarie and Prince Edward, banks such as Banzare, Ob and Lena, and regions of the Ross Sea) and waters surrounding the southern American cone, from Peru and Chile in the Pacific Ocean to Argentina and Uruguay in the Atlantic (Cousseau and Perrota 2004). The species inhabits mainly the deep shelf, continental slope and submarine canyons from 80 to 2,500 m depth (Prenski and Almeyda 2000; Arkhipkin and Laptikhovsky 2010; Lee et al. 2021). Its ontogenetic cycle is characterized by a pelagic behavior during early development stages (eggs and larvae) (Evseenko et al. 1995; North 2002) and a demersal behavior from juvenile to adult. Several studies in the South Atlantic (Agnew et al. 1999; Arkhipkin et al. 2003; Arkhipkin and Laptikhovsky 2010; Collins et al. 2010; Péron et al. 2016; Lee et al. 2021) and Indian Ocean (Duhamel 1981; Duhamel and Pletikosic 1983; López Abellán 2005; Welsford et al. 2011) have indicated a correlation between larger fish and their distribution at greater depths. This ontogenetic shift in habitat is common in deep-sea fish (Agnew et al. 1999). However, spatial segregation between individuals may also be related to biological factors, such as trophic (Troccoli et al. 2020) or reproductive behavior (Brown et al. 2013a; Boucher 2018) and environmental variables, such as currents and their physical variables (Lee et al. 2021).

In the process of managing a fishing resource, it is essential to be aware of the existence of unitary stocks in order to determine whether a fishery can be managed independently or integratedly with other jurisdictions (Ying et al. 2011; Hawkins et al. 2016; Kerr et al. 2017; Cadrin 2020). There are many factors contributing knowledge about differentiation of stocks, such as the understanding of fish movements in different temporal and spatial scales (Brown et al. 2013a; Lee et al. 2022). The abundance of certain populations may be subject to change in response to any variation of relevant factors (Cianelli et al. 2013). The identity of the southwest Atlantic toothfish stock (SA) has been the subject of various studies. There is a well-documented genetic differentiation between individuals from Patagonian shelf and those from South Georgia and South Sandwich Islands (Shaw et al. 2004; Rogers et al. 2006; Canales-Aguirre et al. 2018). However, detailed population structure of the species on the Argentine and Chilean Patagonian shelf is still unknown. So far, genetic studies in the area have not demonstrated any differentiation justifying the presence of more than one population in the Chilean Pacific and Argentine Atlantic (Shaw et al. 2004; Rogers et al. 2006; Canales-Aguirre et al. 2018; Arkhipkin et al. 2022). Notwithstanding, other complementary approaches, such as tag-recapture (Brown et al.

2013a; Lee et al. 2022), otolith microchemistry (Ashford et al. 2006, 2007; Ashford and Jones 2007), parasitology (Brickle et al. 2006; Brown et al. 2013b), otolith shape (Lee et al. 2018), reproductive characteristics (Laptikhovsky et al. 2006; Pájaro et al. 2009; Boucher 2018) and oceanographic modelling of dispersal patterns (Ashford et al. 2012), indicate some heterogeneity along the slope of the southern American cone, suggesting the existence of different stocks in the area (Wöhler et al. in press).

Tag-recapture programs established in different fisheries around the world (Williams and Lamb 2002; Williams et al. 2002; Marlow et al. 2003; Tuck et al. 2003; Agnew et al. 2006b; Dunn et al. 2007; Roberts and Agnew 2008; Brown et al. 2013a; Rubilar et al. 2013; Lee et al. 2022) have been a very useful tool to understand the geographic and bathymetric movements of fish, contributing to understand fish growth, behavior and population structure (Collins et al. 2010). The so-called ‘conventional tags’ enable the determination of the distance traveled from the release point to the recapture point, which can be correlated with a specific timeframe. Specimens of the Genus *Dissostichus* are suitable for tagging and recovery studies as they are relatively robust and, given the lack of a swim bladder, do not sustain serious decompression injuries when captured and brought to the surface from the depths in which they inhabit (Agnew et al. 2006a). As a result, numerous studies have investigated their movement patterns through this approach (Williams et al. 2002; Marlow et al. 2003; Tuck et al. 2003; Agnew et al. 2006b; Roberts and Agnew 2008; Petrov and Tatarnikov 2010; Stacy et al. 2021; Lee et al. 2022; Grilly et al. 2022).

The Patagonian toothfish tag and recapture program has been in place in Argentine waters since 2004 to learn more about possible migratory movements of the species in the southwestern Atlantic. This article analyzed results derived from the aforementioned program as a contribution to our understanding of migratory movements of the juvenile toothfish fraction and the population structure present in the Argentine Patagonian shelf.

## MATERIALS AND METHODS

In 2004, researchers from the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP) launched the Tag and Recapture Program based on an experience conducted onboard of a commercial longliner. Individuals were tagged with an Australian-made standard anchor T-bar tag (Hallprint, Adelaide), similar to the ones used in various toothfish tagging programs at the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). The Program became a mandatory activity for fishing vessels with an individual transferable quota fishing for the species at the beginning of 2007. The program focuses on specimens that have been tagged in two sectors of the fishing ground of the Argentine commercial fleet: one corresponding to the northern Sector (NS), bordering the slope between 37° S and 47° S, where the longline fleet operates; and the other to the southern Sector (SS), located to the east of De los Estados Island (54° 30′ S-55° 00′ S and 64° 00′ W-58° 00′ W) and south of Tierra del Fuego (55° 00′ S-57° 30′ S and 67° 00′ W-64° 00′ W), which is visited by both longliner and trawler fleets.

With the progressive withdrawal of longliners as from 2017, specimens were only tagged in research surveys conducted onboard of short-set trawlers at shallower depths, contemplating a conditioning time for the tagged fish in water tanks before discarding those that did not recover properly and therefore increase the survival rate of those released. Fish were selected, prioritizing those with the best general condition, measured (cm) and weighed (g). Tags were inserted with a gun on the left side of the dorsal part of the fish, in the area of muscle between the second and third spine of the first dorsal fin (Figure 1). Data on geographical position (longitude and latitude), date and depth of the capture and subsequently release sites were recorded. The release position remained the same or very close to the one from which the capture was obtained.

All tagged specimens were recaptured by commercial fleets. When a tagged toothfish was caught, observers onboard recorded its tag number, size, weight, and sex. Vessel operators recorded data if no observer was present. Recaptures in Chilean waters were recorded by both freezer and artisanal fleets. Observer records included tag number, size, weight, sex, date, time, depth, latitude, and longitude. In some cases, tags were recovered after processing, leaving only the date and position of recapture available.

Estimated traveled distances by specimens and potential trajectories were visualized from tag and recapture position data by using Google Earth v. 7.3.3 Pro. They were divided into four categories: Short Distances (< 20 nm), Short Intermediate Distances (20-120 nm), Long Intermediate Distances (120-400 nm) and Long Distances (> 400 nm). Considering that toothfish is a deep-sea species, a trajectory on the edge of the slope between the release position and the recapture position was assumed, and the minimum distances that the fish would have traveled in nautical miles (1 nm = 1,852 km) were measured. Subsequently, displacement of specimens was analyzed with a Generalized Additive Model (GAM), using the 'mgcv' package of the R program version 4.3.0. These models are an extension of general linear models replacing the linear predictors with additive predictors through a smoothing function or spline (Hastie and Tibshirani 1986; Wood 2006). Four different transformations were tested on the response variable (log, square root, cube root and box cox) to reduce the spread of data. The log transformation provided the best-validated model fit. Continuous explanatory variables considered influential in the traveled distance were the length of tagged specimens (TL), the period of time between the release and the capture (Days at liberty –DL), and the tagging Depth (D). Factors considered were the sector in which specimens were tagged (northern and southern) and the season (spring, summer, autumn and winter). The general model was the following:

Figure 1. Position of the body where the T-bar style tag was implanted. In some specimens two tags were implanted.

$$\text{Log(Distance)} = \mu + s(TL) + s(DL) + s(D) + \text{Sector} + \text{Season} + \text{Error}$$

Family = Gaussian, Link = 'Identity'

where $\varepsilon \sim N(0, \sigma^2_\varepsilon)$. First, the existence of collinearity between variables was verified to eliminate any variable correlated with another (Zuur et al. 2009). Once definitive variables were obtained, the best model was chosen based on the stepwise selection process according to the Akaike Information Criteria and Generalized Cross Validation (Akaike 1973; Burnham and Anderson 2004; Wood 2012). In both cases, the lower the value the better the model obtained will be. In addition, the adjusted multiple determination coefficient was calculated for each model, and the explanatory capacity of the model built through the explained deviance was calculated. Subsequently, influential points were eliminated, obtaining the final model. Finally, its graphic validation was carried out using the gam.chek function ('mgcv') and those variables significant to the final model were plotted (Fernández Casal et al. 2022).

## RESULTS

A total of 5,907 toothfish have been tagged in the northern Sector (NS) and southern Sector (SS) since the beginning of the Program in 2004. A total of 5,528 specimens were tagged onboard the longline fleet and 379 on the trawler, from which, 26.04% were tagged in the NS, while the remaining 73.96% were tagged in the SS (Figure 2; Table 1). To date, a total of 121 specimens have been recaptured, of which 25 (20.7%) were recaptured in the NS, 84 (69.4%) in the SS, and 12 (9.9%) in Pacific waters off the Chilean coast (Table 1; Figure 3). At the same time, 3 specimens from Chilean waters and 2 tagged in the

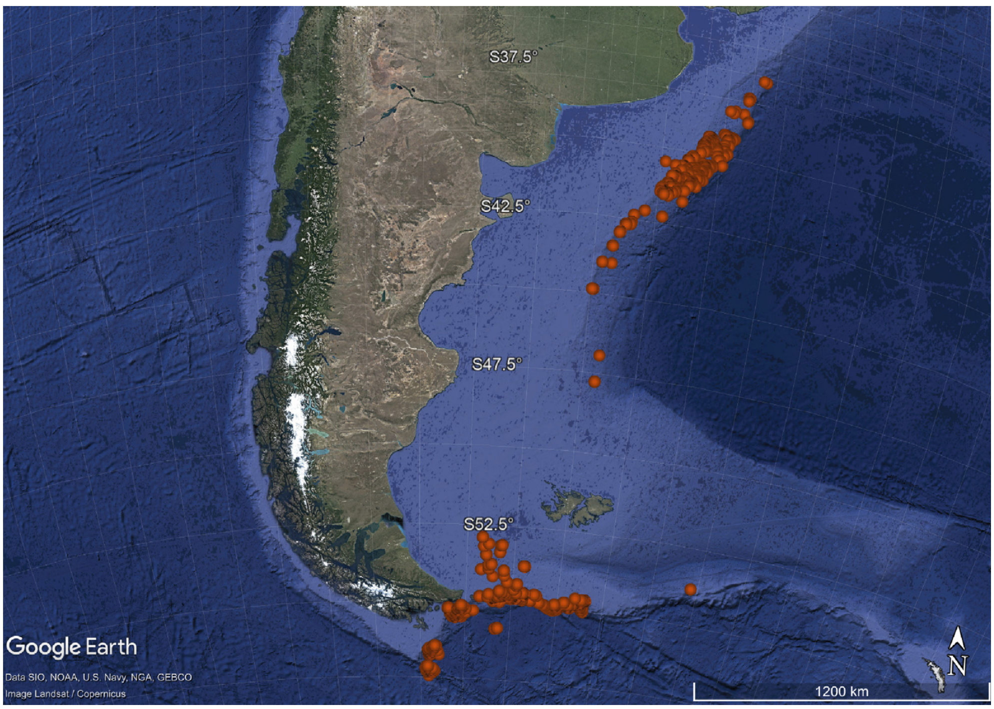


Figure 2. Release position of tagged toothfish specimens in the Argentine Exclusive Economic Zone (EEZ).

Table 1. Number and percentage of toothfish specimens tagged and recaptured in the northern, southern, and Pacific Ocean sectors, indicating recapture rate per year (%).

| | Tagged | | Recaptured | | | |
|---|---|---|---|---|---|---|
| Year | Northern | Southern | Northern | Northern | Pacific | Percentage |
| 2004 | 247 | 247 | 0 | 0 | 0 | 0.00 |
| 2005 | 0 | 0 | 0 | 0 | 1 | 0.00 |
| 2006 | 0 | 0 | 0 | 0 | 0 | 0.00 |
| 2007 | 14 | 763 | 0 | 0 | 0 | 0.00 |
| 2008 | 300 | 755 | 4 | 3 | 0 | 0.66 |
| 2009 | 368 | 685 | 4 | 5 | 0 | 0.85 |
| 2010 | 223 | 705 | 2 | 23 | 2 | 2.91 |
| 2011 | 37 | 465 | 1 | 23 | 1 | 4.98 |
| 2012 | 99 | 154 | 9 | 13 | 1 | 9.09 |
| 2013 | 92 | 244 | 1 | 4 | 4 | 2.68 |
| 2014 | 0 | 0 | 0 | 2 | 0 | 0.00 |
| 2015 | 0 | 0 | 2 | 2 | 0 | 0.00 |
| 2016 | 0 | 0 | 2 | 2 | 0 | 0.00 |
| 2017 | 28 | 32 | 0 | 1 | 2 | 5.00 |
| 2018 | 130 | 223 | 0 | 3 | 0 | 0.85 |
| 2019 | 0 | 40 | 0 | 2 | 1 | 7.50 |
| 2020 | 0 | 56 | 0 | 1 | 0 | 1.79 |
| Total | 1,538 | 4,369 | 25 | 84 | 12 | 2.05 |
| Percentage | 26.04 | 73.96 | 20.66 | 69.42 | 9.92 | |

area corresponding to the Argentine Patagonian shelf, around Malvinas Islands, were also recaptured in the SS. The majority of tagged specimens in each year were juveniles in size (Figure 4). Juvenile fish consisted of 75.18% of fish tagged across the sample period, ranging from 53.75% (2012) to 100% (2019).

From their release site, 67.5% were recaptured at a distance of less than 20 nm, while 15% traveled short intermediate distances less than 120 nm. The smaller fraction (5%) covered distances between 120 and 400 nm (longer intermediate distances) and 12.5% were recaptured at greater distances (more than 400 nm) from their tagging locations. Only 9.9% of the fish left the Argentine fishing ground. Most of specimens (87.5%) covered distances of under 400 nm, remaining inside the same sector, whose length was estimated to be around 370 nm for both sectors. In the NS, 83% (25) of tagged specimens moved within 400 nm. Seventy-seven percent of them (23) were even recaptured at less than 20 nm. Only 17% (5) of the total was recaptured at distances greater than 400 nm, exceeding the limits of that sector of the Argentine fishing ground. In the SS, 89% (81) of the fish moved less than 400 nm from their release site, and 64% of the total (58) moved less than 20 nm. The remaining

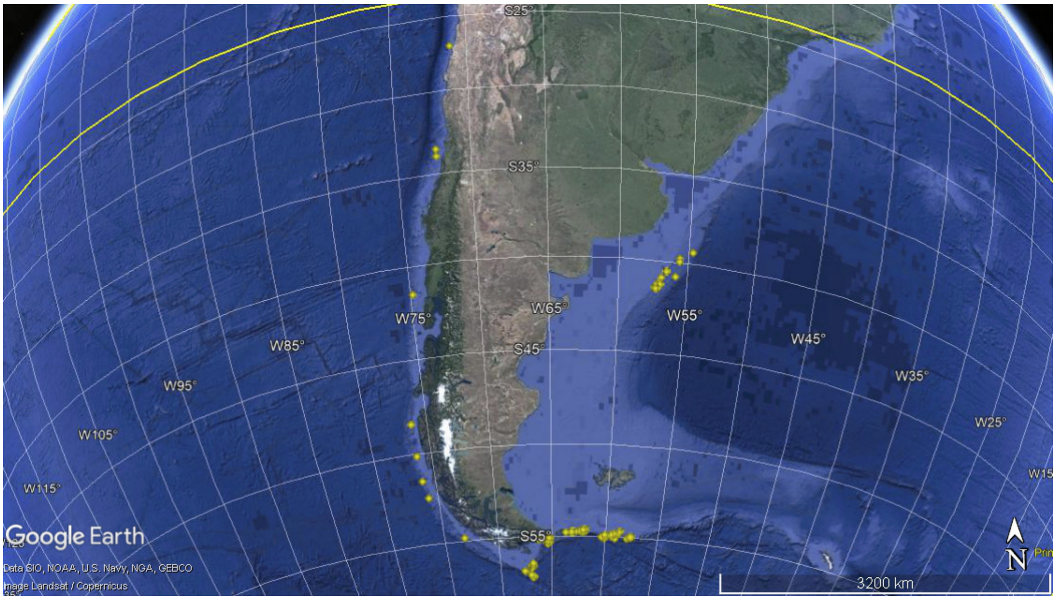


Figure 3. Reported recapture positions of tagged toothfish specimens in the Argentine Exclusive Economic Zone (EEZ).

11% (10 fish) were recaptured at a distance greater than 400 nm from the release site (Figure 5). The predominance of short distances traveled after being tagged and released demonstrates the affinity of the species for its residence sites in the NS and SS of the Argentine fishing ground.

There was no clearly defined direction pattern observed in the fish tagged in the NS (Figure 6). Most of the specimens exhibited a distinct pattern of movement towards the southeast and east. However, one specimen that traveled a moderate distance went in the opposite direction towards the northeast. Furthermore, the specimens that traveled the greatest distances all moved towards the south. Only five of the recaptured fish crossed the NS of the Argentine fishing ground, migrating over long distances (up to approximately 1,500 nm), three of which were recaptured near the Namuncurá/Burdwood Bank, and the rest in southern Chile (Figure 7). A unified directional movement was also not observed for fish tagged and recaptured in the SS of the Argentine fishing ground (Figure 8). Both westward and eastward directions were observed for fish undertaking movements less than 100 nm. Those that moved greater distances did essentially to the west-northwest (Figure 9). Regarding specimens tagged in the SS, 11 of them exceeded the limits of the Argentine fishing ground, eight of which traveled distances in the direction of central-north Chile, between 477 nm (885 km) and 2,100 nm (3,889 km). The vast majority of the tagged fish (64%) remained close to their release sites. A single specimen was reported to the east, tagged at 54° 53′ S-59° 08′ W and caught at 55° 00′ S-57° 37′ W by the longliner ‘CFL Hunter’ in waters near the Malvinas Islands (Martínez, unpublished data).

The variables Days at liberty, Sector, and Season of tagging influenced on the traveled distance in GAM results (Table 2). The final model was defined by these three variables, which explained 34.4% of the variability of the model. The length of fish at the time of tagging and the depth of release were not significant in the movements of toothfish. This hypothesis and the homogeneity of variances seems to be adequate from validation graphs for normality (Figure 10).

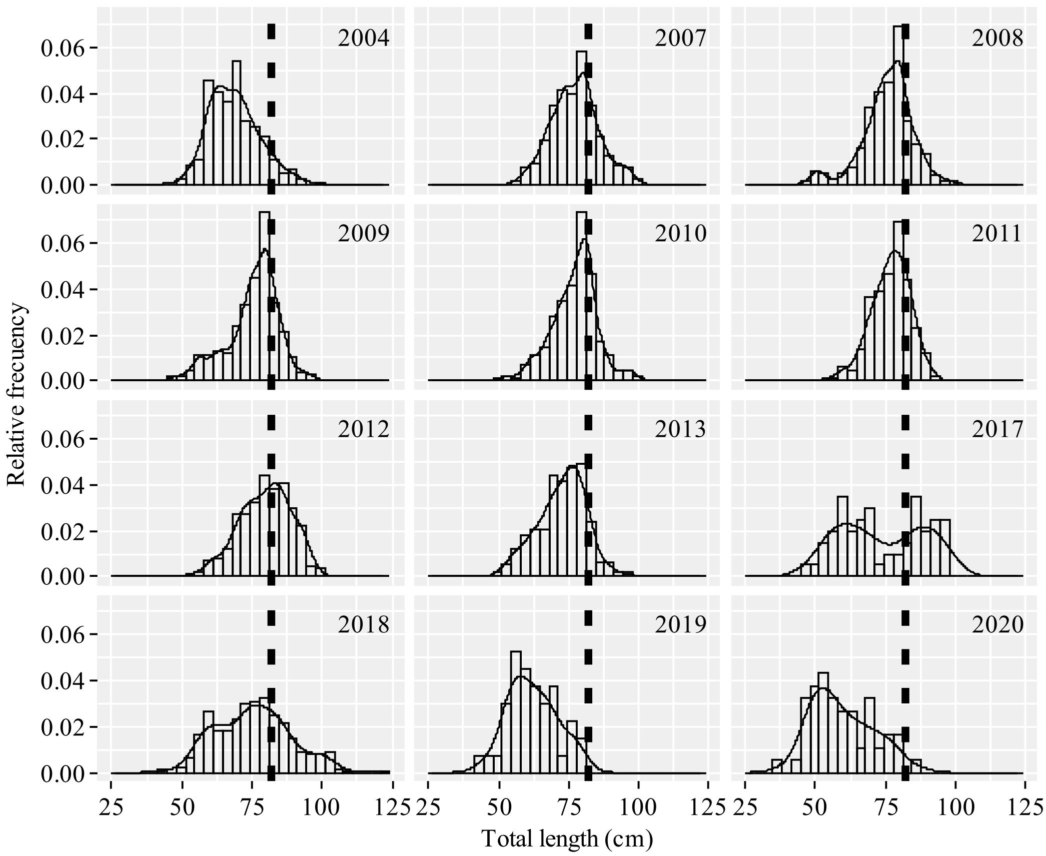


Figure 4. Distribution of relative frequencies of grouped lengths of tagged toothfish specimens per year. The black dotted line represents the length of first maturity estimated at 82 cm (Pájaro et al. 2009).

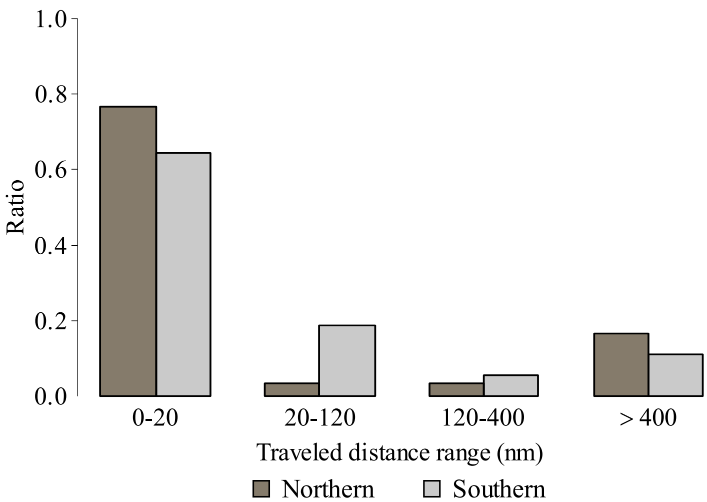


Figure 5. Ratio of recaptured toothfish specimens based on the range of distance traveled in the northern and southern Sector.

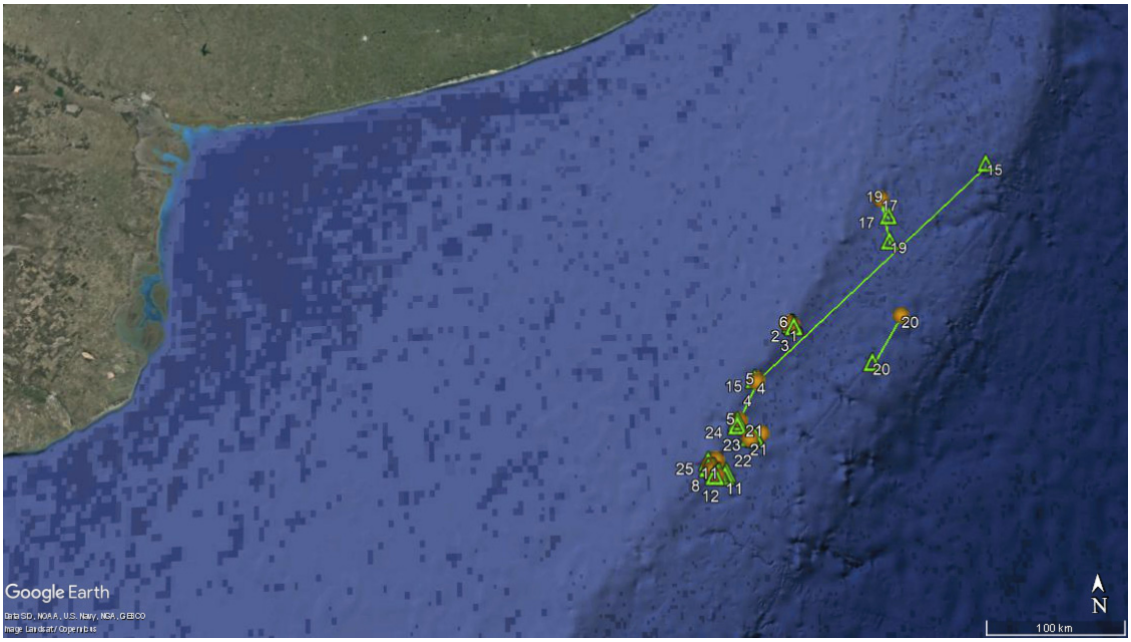


Figure 6. Migratory movements corresponding to distances of less than 400 nm in the northern Sector of the Argentine fishing ground.


Figure 7. Possible migratory route of specimens tagged in the northern Sector of the Argentine fishing ground and recaptured more than 400 nm away from it. Orange circles indicate the tagging position and yellow ones the recapture position. The five specimens that traveled long distances did so in a southerly direction.

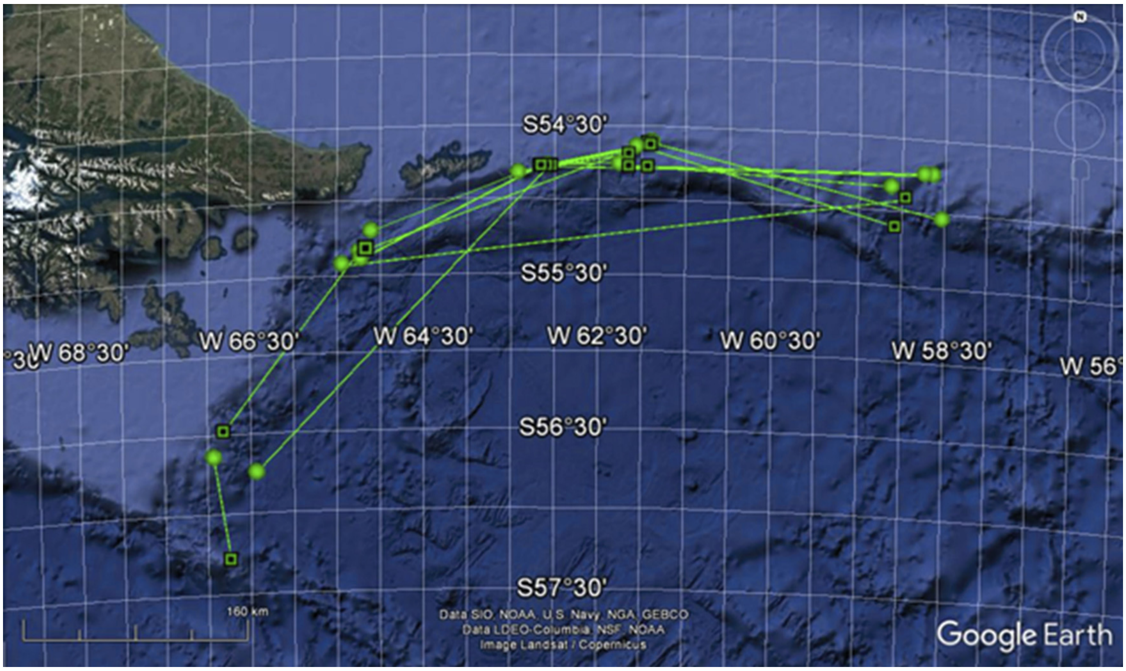


Figure 8. Possible migratory route of specimens tagged in the southern Sector of the Argentine fishing ground with intermediate movements. Circles indicate the position of tagging and squares point out the position of recapture.

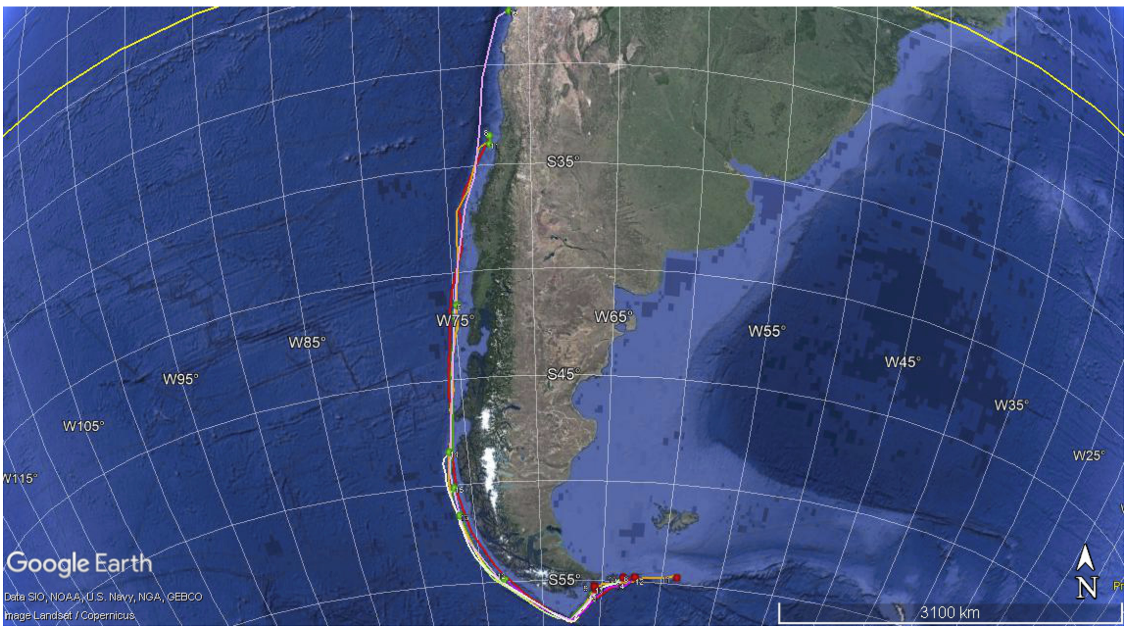


Figure 9. Possible migratory route of specimens tagged in the southern Sector of the Argentine fishing ground that presented greatest displacements. Red circles indicate the tagging position and green circles the recapture position.

Table 2. Model selection table to determine which variables influence the distance traveled by toothfish. For each case, the explained deviance (%), degrees of freedom (EDF), Akaike values (AIC), Generalized Cross Validation (GCV), R2 and p-value are indicated.

| Variable | Explained deviance | Accumulated deviance | EDF | AIC | GCV | R2 | p-value |
|---|---|---|---|---|---|---|---|
| Null | 0 | 0 | 2.00 | 523.74 | 4.53 | 0 | 0 |
| TL | 2.95 | 2.95 | 3.00 | 522.15 | 4.47 | 0.02 | 0.06 |
| + Days at liberty | 16.85 | 19.8 | 7.94 | 509.18 | 4.02 | 0.16 | < 0.01 |
| + Sector | 5.6 | 25.4 | 9.01 | 506.20 | 3.83 | 0.18 | < 0.01 |
| + Depth | 0 | 25.4 | 10.15 | 504.88 | 3.89 | 0.19 | 0.79 |
| + Season of tagging | 8.6 | 34 | 13.28 | 496.37 | 3.64 | 0.27 | < 0.01 |

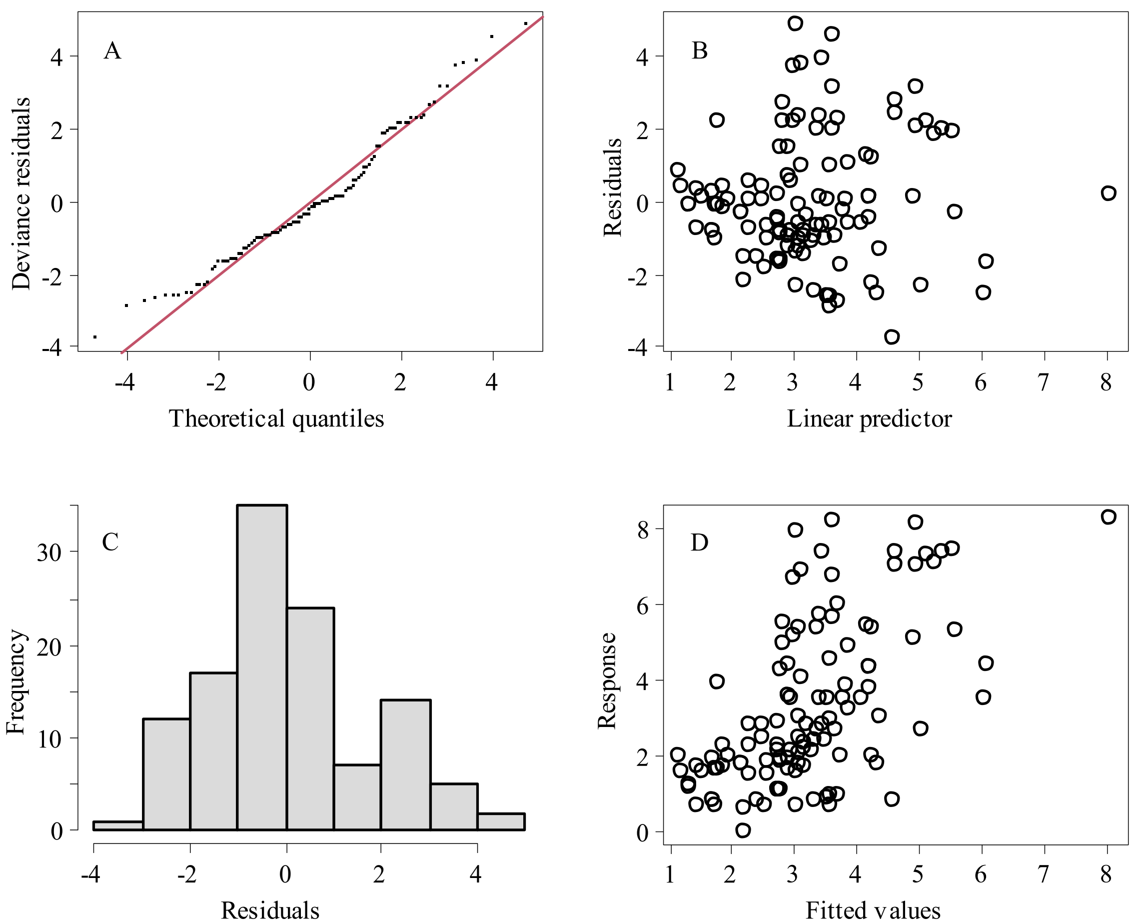


Figure 10. Diagnosis of the final GAM model indicating the quantile-quantile graph (qqplot) (A), residuals versus adjusted (B), histogram of residuals (C), and observed versus adjusted values (D).

Although model's influential variables showed an increase in the distance covered as a function of the number of days at liberty, this trend significantly decreases in specimens with longer periods at liberty (Figure 11 A). However, it should be noted that the decrease in this trend with longer periods at liberty was based on small sample sizes. There were specimens with liberty periods ranging from a minimum of 3 days to a maximum of 3,176 days (8 years and 8 months). The specimen that traveled the longest distance (2,099 nm), did so in a period of 2,261 days (6 years and 3 months) and the one that followed it (1,769 nm) required 2,651 days. However, other fish were recaptured within 20 miles (37 km) of their release sites, even after longer periods at liberty. One extreme case was a fish recaptured just 18 nm from where it had been tagged, 7 years and 8 months after its release (2,762 days) (Figure 11). The specimen that remained at liberty the longest (8 years and 8 months), was recaptured at a distance of 1 nm from where it has been released, being a record of resident behavior.

Specimens tagged in the southern fishing ground of the distribution area showed a trend of greater displacement (Figure 11 B) and an increase in the distances traveled by specimens during winter months (Figure 11 C).

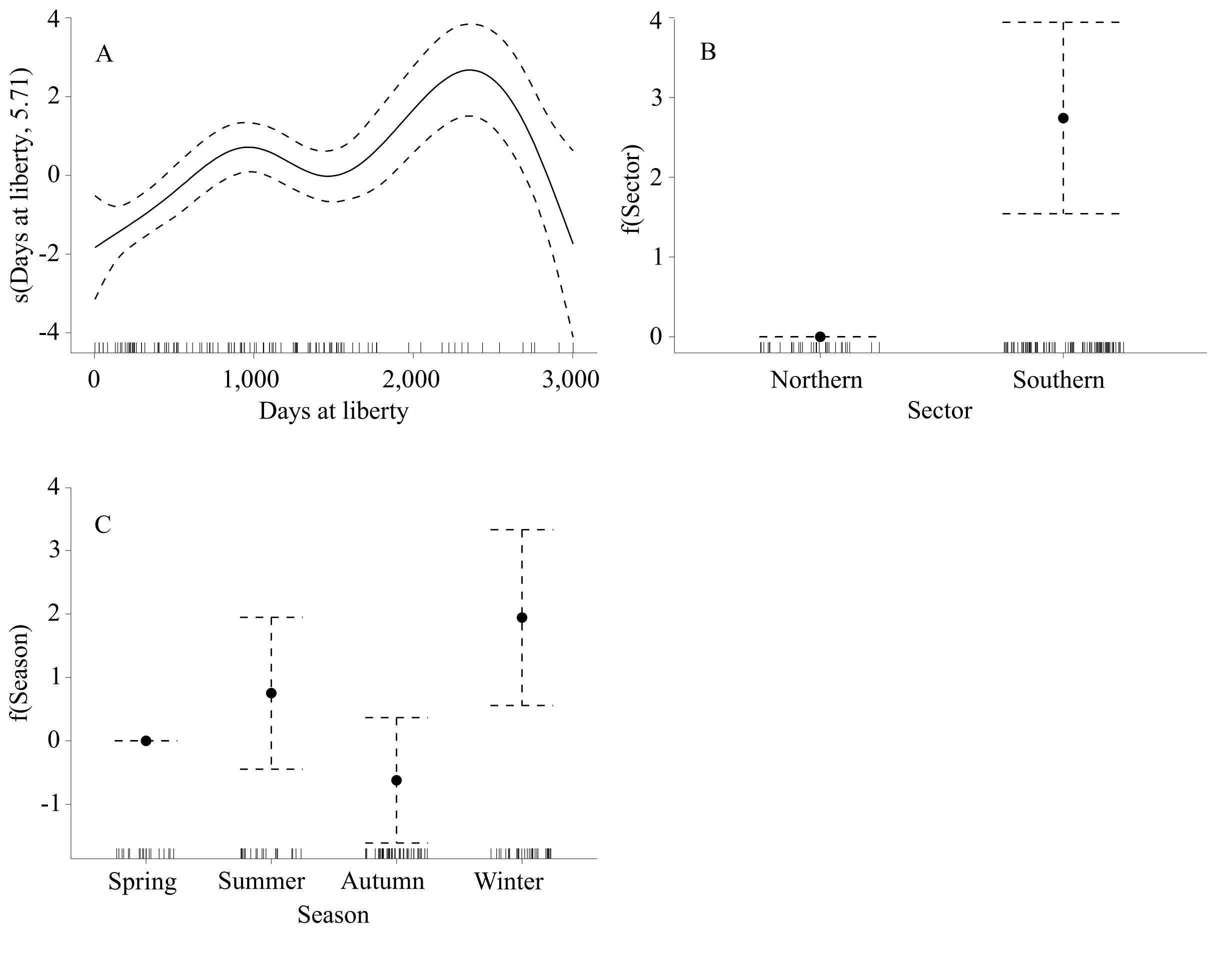


Figure 11. Smoothing terms corresponding to the explanatory variables of the final GAM model used. A) Days at liberty. B) Sector. C) Season.

## DISCUSSION

This study provides the first description of the movement patterns of Patagonian toothfish in Argentine shelf/edge waters between 37° S and 47° S east of De los Estados Island (54° 30′ S-55° 00′ S and 64° 00′ W-58° 00′ W) and south of Tierra del Fuego (55° 00′ S-57° 30′ S and 67° 00′ W-64° 00′ W). The tag and recapture program for toothfish on the Argentine Patagonian shelf provided the first direct observation of movement patterns of the juvenile fraction from shelf areas to deeper areas in the slope and Chilean Pacific. Our results show different levels of individual movement variation. From a fishing perspective, the lack of a significant exchange of fish between current fishing areas allows to consider the existence of different stock units of the species.

**Tagging program**

Results regarding the migratory behavior of the species are quite consistent with those obtained in other toothfish-tagging programs established in different parts of the world (Williams and Lamb 2002; Williams et al. 2002; Marlow et al. 2003; Tuck et al. 2003; Agnew et al. 2006b; Dunn et al. 2007; Roberts and Agnew 2008; Brown et al. 2013a; Rubilar et al. 2013, Grilly et al. 2022; Lee et al. 2022). The tagging program established in the Argentine toothfish fishery covered the extremes of the distribution of the species on the Patagonian shelf, both in northern and southern fishing grounds. The recapture rate until 2020 was estimated at 2.05% (Table 1). This is a higher rate than those estimated from tag-recapture programs at both Chilean waters (1.29%) (Rubilar et al. 2013) and South Georgia Islands (1.3 and 1.7%) (Marlow et al. 2003). However, other tagging programs had substantially higher recapture rates, such as 5.25% in Malvinas Islands (Lee et al. 2022), 11.9% in Shag and Black Rocks (Marlow et al. 2003) and 17.7% in Heard Island and McDonald Islands from 1998 to 2014 (Welsford et al. 2014).

Tagged specimens were recovered in NS and SS zones, including some that migrated to waters outside the Argentine Exclusive Economic Zone (EEZ). In those cases, recaptured specimens were reported by foreign fishing vessels. The number of recaptures, number of days at liberty and the good general condition of recaptured specimens indicated that fish successfully survived the tagging process, similar to observations reported by Williams et al. (2002) and Agnew et al. (2006a). The gradual withdrawal of longline vessels from the fishery since 2013 (Troccoli et al. 2022) may have had an impact on the Patagonian toothfish recapture rate in the Argentine EEZ. Currently, the trawler fleet only operates in the sector between De los Estados Island and Namuncurá-Burdwood Bank. The absence of fishing operations in the NS of the Argentine fishing ground and to the south of Namuncurá-Burdwood Bank may have resulted in an interruption of recaptures in these areas.

Another possible cause of the low recapture rate may be given by the component of the population selected to be tagged in this Program, which predominantly comprised fish < 82 cm TL. Strong management regulations govern the Argentine toothfish fishery, including restrictions on minimum fishing depths, percentage of juveniles in the catch, hook size, and other measures to prevent excessive capture of juveniles of the species (Martínez and Wöhler 2016). This situation has been observed in other toothfish tagging programs, such as in the CCAMLR working group report from 2009, where the Scientific Committee agreed that one of the main reasons behind the low number of recaptures in Subareas 48.6 and 58.4 was likely the small size of fish tagged in comparison to the overall size distribution of fish caught. On the other hand, the possibility that the low recapture rate was associated with a limited fishing effort in relation to the size of the stock in the Argentine fishing ground should not be ruled out.

## Migratory movements

A key aspect in studying movement patterns of species involves understanding the magnitude and frequency of proposed migrations (Allen et al. 2018). That is why it is important to define movement patterns in relation to a defined spatial area. Examples of such patterns include migrations (moving to and from specific locations), homing (returning to a location), home ranges (repeated movement within an area), habitat usage (movement to use resources within a set area), or nomadism (no boundaries) (Gruss et al. 2011).

Other toothfish tagging programs (Williams and Lamb 2002; Williams et al. 2002; Marlow et al. 2003; Collins et al. 2010; Brown et al. 2013a; Lee et al. 2021) have reported the same movement patterns observed at the NS and SS in this study. Even after spending more than eight years at liberty, most of the recaptured specimens (67.5%) maintained a distance of less than 20 nm (37 km) from where they have been released. In addition, the fact that the majority of the fish (87.5%) moved a distance < 400 nm, which is an approximate measurement for both the NS and the SS where vessels fish for Patagonian toothfish in the Argentine EEZ, would indicate that almost all the fish would not move beyond the habitual residence area within each sector of the fishing ground. On the contrary, only very few specimens (12.5%) traveled great distances, with some cases reportedly traveling up to 2,099 nm (3,887 km) to the waters of central Chile. Since the transition to adulthood is primarily characterized by migration to greater depths, Brown et al. (2013a) hypothesized that long-distance migrations may take place during the juvenile stage. Dunn and Hanchet (2006) and Dunn et al. (2007) found that the greatest distances traveled by *D. mawsoni* in Antarctic waters were undertaken by juvenile and sub-adult fish (< 100 cm TL). Rogers et al. (2006) also indicated that possibly the juvenile fraction of the population is the one with the greatest capacity for migration. On the other hand, Marlow et al. (2003) and Burch et al. (2019) have indicated that some adult fish can cross oceanographic fronts and migrate great distances. Recent findings from a Malvinas Islands-based tag and recapture program (Lee et al. 2022) are in line with these results and with reports of other authors that have observed these movements in different regions of the world (Williams et al. 2002; Marlow et al. 2003; Tuck et al. 2003; Brown et al. 2013a). Only a very small percentage of recaptured specimens (10%) traveled significant distances, while the majority (78%) remained less than 27 nm from their release point. Similar results were reported for Antarctic toothfish in the southern ocean (Grilly et al. 2022) where only 7% of the specimens moved great distances, while the rest demonstrated a sedentary behavior. Results of this work do not clearly show any differential migratory pattern related to the size of tagged specimens. While some juvenile individuals tagged in the Argentine EEZ traveled great distances, a similar proportion of the few adult individuals released after tagging also did so. Thus, the percentage of 'great travelers' was relatively similar in both cases.

The analysis carried out in order to establish a possible relationship between the distance traveled by the fish and the time elapsed in freedom after being tagged, did not yield evidence to demonstrate that the fish that remained in freedom for the longest were those that moved the most. However, the trend drops drastically for the oldest records. Considering this, two of the fish that remained the longest in the wild (> 7 and 8 years) were recaptured a short distance from their tagging site. These results are in line with those of Welsford et al. (2011) in the Kerguelen plateau around Heard and McDonald Islands, who did not find a clear relationship between the distance traveled and the time since the fish was released.

The majority of specimens were caught less than 100 km from the tagging site within 1,000 days of being released, while others traveled at least 2,000 km during the same period. In accordance with the findings presented here, Marlow et al. (2003) also found no clear relationship between days at liberty and the distance covered by specimens of *D. eleginoides* in South Georgia Islands. However, Dunn y Hanchet (2006) suggested that *D. mawsoni* appear to have a positive trend between greater fish displacement and longer time at liberty. In contrast to the above, Grilly et al. (2022) found no relationship between time at liberty and long-distance movements for the same species.

Specimens from the southern fishing ground traveled the most distance. In the northern fishing grounds, displacements involved shorter distances and were oriented towards deeper southeast areas of the edge of the continental shelf. Similar results were also found by Grilly et al. (2022) for *D. mawsoni.* Patagonian toothfish are believed to move primarily from shallower waters to greater depths, corresponding to the ontogenetic migration of the species throughout its range (Williams 2002; Arkhipkin and Laptikhovsky 2010; Péron et al. 2016; Lee et al. 2021), so juvenile fish are recruited to the adult stock as they grow.

On the contrary, the nearby displacements in the SS did not present a pattern of preferential direction in their migrations. Between the Namuncurá/Burdwoord Bank and Diego Ramírez Islands (Chile), intermediate displacements were oriented to the east and west, possibly following the edge of the crescent-shaped slope. Movements directed towards the bank can be attributed to both reproductive and feeding functions (Pájaro et al. 2009; Boucher 2018). Seabeds with similar characteristics to the aforementioned landform have unusually high biomass of benthic organisms that form refuge habitats for smaller fish, which may provide attractive feeding opportunities for larger predators (Welsford et al. 2014; Schejter et al. 2016; Matano et al. 2019; Riccialdelli et al. 2020).

Regarding few specimens that moved long distances, all reported recaptures indicate a movement towards Chilean shelf and slope waters. Records coincide with those observed by Rubilar et al. (2013) in the Chilean toothfish tagging program, whose preliminary results show a net movement of fish from the south to the north of Chile. This fact is particularly surprising, considering that no migrations have been described that could indicate a return of the fish to the southernmost areas. The exception could be addressed by three individuals tagged in southern Chile and recaptured in nearby areas of southern Argentina, indicating in this case a moderate movement in a southeasterly direction. These results demonstrate some exchange between the fish that inhabit Chilean and Argentine jurisdiction, although of small magnitude given the total number of fish tagged and recovered.

Laptikhovsky et al. (2006) speculated that Patagonian toothfish in Malvinas Islands migrate in one of two ways: an ontogenetic migration from shelf waters to bathyal waters where adults live, and a seasonal migration of adults that spans more than 1,000 km around the islands between feeding and reproduction grounds. Brown et al. (2013) using satellite tags in the same region stated that toothfish would not regularly make large-scale migrations between feeding areas to the north and east of Malvinas Islands and the spawning grounds at Namuncurá/Burdwoord Bank. This apparent absence of regular migrations of individuals was related to the fact that toothfish is a long-lived animal and would not need to spawn every year (Laptikhovsky and Brickle 2005; Boucher 2018). An absence of annual migratory behaviour and high site fidelity was also inferred on the basis of significant difference in otolith shape among localised regions on the Patagonian shelf between southern Chile, the Burdwood Bank and a Malvinas north-high seas intermediate zone (Lee et al. 2018). In the present work, an increase in distances traveled by specimens tagged in winter, whose months coincide with those of the reproductive period, was observed. However, considering that the majority of specimens tagged here were juveniles, an ontogenetic or feeding movement rather than a reproductive migration is more likely. On the other hand, reproductive activity of Patagonian toothfish in the northern slope of the Argentine EEZ (between 37° S and 43° S) has recently been observed, which support the hypothesis that the fish in this region would reproduce directly there and would not require a migration to higher latitudes for this purpose (Martínez et al. 2022).

## CONCLUSIONS

From the present work, it seems evident that Patagonian toothfish in the Argentine EEZ possess characteristic high site fidelity and lacks regular migratory movements involving a substantial component of the stock or population. This behavior supports the hypothesis of isolation between different fishing grounds of the species that is subject to exploitation around the American southern cone. Rather than being caused by physical or oceanographic barriers, this isolation is supposed to be related to the very philopatric behavior of the species. If the fish remain faithful to their residence areas and these are associated with nearby breeding areas, then this behavior would facilitate isolation. Results of the current study confirm the importance of research investigating the population structure of toothfish across the region. The current findings allow us to assume the possible existence of different groups of fish or stocks, characterized by a certain isolation, which could, from a fishing perspective, be considered individually, since there is a significant shortage of fish migration between current fishing locations. However, much more research is required to confirm this hypothesis.

## ACKNOWLEDGEMENTS

The authors express their gratitude to fishing companies that collaborated by providing instruments and supplies, and made their vessels available to carry out the tag and recapture of Patagonian toothfish program. They also extend their gratitude to the crews who collaborated with the tasks onboard. INIDEP contribution no. 2302.

**Author contributions**

Gonzalo H. Troccoli: conceptualization, methodology, software, validation, formal analysis, investigation, resources, writing-review and editing, visualization. Patricia A. Martínez: conceptualization, investigation, writing-review and editing, supervision, project administration, funding acquisition. Emiliano J. Di Marco: methodology, software, validation, formal analysis. Juan A. Waessle: software, resources. Otto C. Wöhler: conceptualization, investigation, resources, writing-review and editing, supervision, project administration, funding acquisition.

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