Testing the connectivity of *Dissostichus eleginoides* (Patagonian toothfish) between the Pacific coast of southern Chile and the Patagonian Shelf in the southwest Atlantic

Emma Harte

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Abstract

Patagonian toothfish, *Dissostichus eleginoides,* are endemic to the Southern Hemisphere and are commonly associated with sub-Antarctic Islands and seamounts. They are found around the Falkland Islands and an economically valuable long-line fishery, targeting adult toothfish, operates in the Falkland Island Conservation Zones year round. This research explores gaps in the understanding of toothfish early life history by conducting egg buoyancy experiments and particle tracking simulations to resolve important spawning locations, transport pathways and larval retention areas.

Buoyancy of toothfish eggs was estimated up to 21 days post fertilisation. Egg buoyancy followed a similar pattern to other species, where buoyancy initially decreased for several days before returning toward its initial value, although further data is needed to confirm this. Particle tracking simulations were undertaken using the software ICHTHYOP. Particles were released from potential spawning areas around the Burdwood Bank and southern Chile during July 2009 and 2012. These simulations represented spawning corresponding to a good and poor recruitment year respectively.

Results of these particle tracking simulations for 2009 and 2012 suggest that transport from the Burdwood Bank is unlikely to be a major contributor to the recruitment of juveniles around the Falkland Islands or the Patagonian Shelf, with low connectivity (<0.4%) seen across all simulations. In 2009, there was a high level of connectivity between the southern Chilean spawning sites and the Patagonian Shelf (>50%), indicating that larval transport from southern Chile to this area may be important for successful recruitment of juveniles around the Falkland Islands. Connectivity between these areas was weaker in 2012, potentially due to changes in the position and/or density of the boundary current that flows around southern Chile, forced by changes in the phase of the Southern Annular Mode (SAM).

These findings have implications for fisheries management due to the connectivity of early life stages between Chile and the Patagonian Shelf region. Depletion of spawning stock biomass in Chile could impact potential recruitment in the South Atlantic, therefore a co-ordinated management strategy between Chile and the Falkland Islands should be considered.

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Table of Contents

Abstract ii

Acknowledgements iii

1. General Introduction 1

1.1. Regional Southwest Atlantic oceanography 2

1.2. Ecology of the Patagonian Toothfish 6

1.2.1. Distribution *6*

1.2.2. Life history *7*

1.2.3. Population structure *8*

1.3. Fisheries overview 10

1.3.1. Fishery stocks *10*

1.3.2. Patagonian toothfish fishery *11*

1.3.3. Falkland Islands Patagonian Toothfish Fishery *12*

1.4. Study Objectives 15

1.5. Thesis structure 16

2. Buoyancy determination of Patagonian toothfish eggs 17

2.1. Introduction 17

2.2. Methods 20

2.2.1. Fish rearing and condition *20*

2.2.2. Pilot study experimental design *21*

2.2.3. Redesigned study *22*

2.2.4. Data analysis *25*

2.3. Results 26

2.4. Discussion 28

2.5. Chapter conclusions 32

Modelling the distribution of Patagonian toothfish eggs and larvae around the Falkland Islands 34

3.1. Introduction 34

3.2. Overview of models 37

3.2.1. ROMS *37*

3.2.3. ICHTHYOP *38*

3.3. Particle simulations 39

3.3.1. Particle release areas *39*

3.3.2. Particle release characteristics *40*

3.3.3. Particle retention areas *41*

3.3.4. Parameter uncertainties *42*

3.4. Assessment of egg buoyancy within the model 42

3.4.2. Summary of buoyancy assessment *54*

3.4.3. Final model simulations *56*

3.5. Results 57

3.5.1. Connectivity of the Burdwood Bank to the Falkland Islands and the Patagonian shelf *57*

3.5.2. Connectivity of southern Chile to the Falkland Islands and the Patagonian shelf *59*

3.5.3. Retention success from southern Chile to the Falkland Islands and Patagonian Shelf *63*

3.5.4. Oceanographic variability *65*

3.6. Discussion 73

3.7. Chapter conclusions 77

4. General Discussion and Conclusions 79
4.1. Research Objectives 79
4.2. Main research findings 80
  4.2.1. Buoyancy experiments 80
  4.2.2. Particle tracking 81
  4.2.3. Ocean-atmosphere variability 84
4.3. Implications for stock structure and stock assessment 87
4.4. Future research 88
4.5. Conclusions 90

References 94

Appendices 104
Appendix A: Raw density data 104

1. General Introduction

Many fish species have planktonic early life stages (eggs and larvae). During these stages, transport and dispersal are largely via ocean currents. Oceanographic processes can drive patterns of recruitment variability during these stages, and be responsible for persistence in adult populations through modulating environmental conditions encountered (occurrence of unfavorable salinity or temperature conditions) and through connectivity between different spawning grounds and suitable habitat for settlement (Heath & Gallego, 1997; Hinrichsen *et al.,* 2002; Petereit *et al.,* 2014; White et al., 2019). Biophysical interactions also influence dispersal of these early life stages, for example, the density of a fish egg is an important factor in determining the vertical distribution within the water column which in turn influences dispersal patterns and predator-prey interaction affecting survival (Sundby, 1991; Sundby & Kristiansen, 2015).

Dissostichus eleginoides Smitt, 1898 (Patagonian toothfish) have a circum-sub-Antarctic distribution (Collins *et al.,* 2010). Patagonian toothfish fisheries in the Southern Ocean are one of the most profitable and productive fisheries (Canales-Aguirre, 2018; Gordon & Shipley, 2019). In the waters of the Southwest Atlantic surrounding the Falkland Islands the fishery has a large economic value. Despite its economic importance, a complete understanding of the early life history of Patagonian toothfish is still lacking (Collins *et al.,* 2010). This understanding is important for long-term management of fisheries (Chambers & Trippel, 1997). Distribution, spatially and temporally, throughout early life stages is unknown. There is some evidence suggesting egg/larval connectivity from Chilean stocks (Ashford *et al.,* 2012; Randhawa *et al.,* in submission). Links between toothfish recruitment and environmental variability have been made in South Georgia; however links have not been investigated within the Falkland Islands (Belchier & Collins, 2008). This research aims to address these gaps by using modelling to investigate inter-annual variation in retention success and regional oceanography and identify links between Patagonian toothfish stocks.

This chapter provides an overview of the regional Southwestern Atlantic oceanography (Section 1.1), then introduces the Patagonian toothfish and reviews current knowledge relating to their ecology (Section 1.2). Fisheries for Patagonian toothfish in the Southern Ocean and the Falkland Islands will be discussed (Section 1.3) and objectives of the current research will be presented (Section 1.4) together with a thesis outline (Section 1.5).

1.1. Regional Southwest Atlantic oceanography

The Southwest Atlantic region extends from the southeastern tip of Argentina (~55°S) to the coast of Brazil (~5°N) and from the eastern coast of South America to 20°W (FAO, 2001; Combes & Matano, 2014). It encompasses a wide continental shelf, a narrow, steep continental slope and an extensive deep ocean (Fig. 1). The Patagonian Shelf extends from the tip of Tierra del Fuego to the Subtropical Front (38°S - 55°S). It is a relatively shallow submerged continental plateau which extends eastward into the Southwest Atlantic for 400-600 km. Water depths over much of the shelf are less than 200 m with a major surface expression in the form of the Falkland Islands (52°S, 59°W).

The Patagonian Shelf is an obstacle to deep ocean circulation in the Southwest Atlantic. South of the Drake Passage, the Antarctic Circumpolar Current (ACC) is steered northward around the southern and eastern flanks of the shelf, forming the equatorward flow of the relatively fresh and cold Falkland Current in the south (Piola *et al.,* 2013; Combes & Matano, 2014; Strub *et al.,* 2015). This boundary current flows equatorward following the 1000-1500 m isobaths of the continental slope meeting the poleward flowing Brazil Current near 38°S to form the Falkland/Brazil Confluence (Fetter & Matano, 2008; Spadone & Provost, 2009). At 41°S, the mean transport range of the Falkland Current is between 41 and 45 Sv. There are seasonal variations in the Falkland Current transport as well as significant inter-annual variations (Spadone & Provost, 2009; Combes & Matano, 2014).

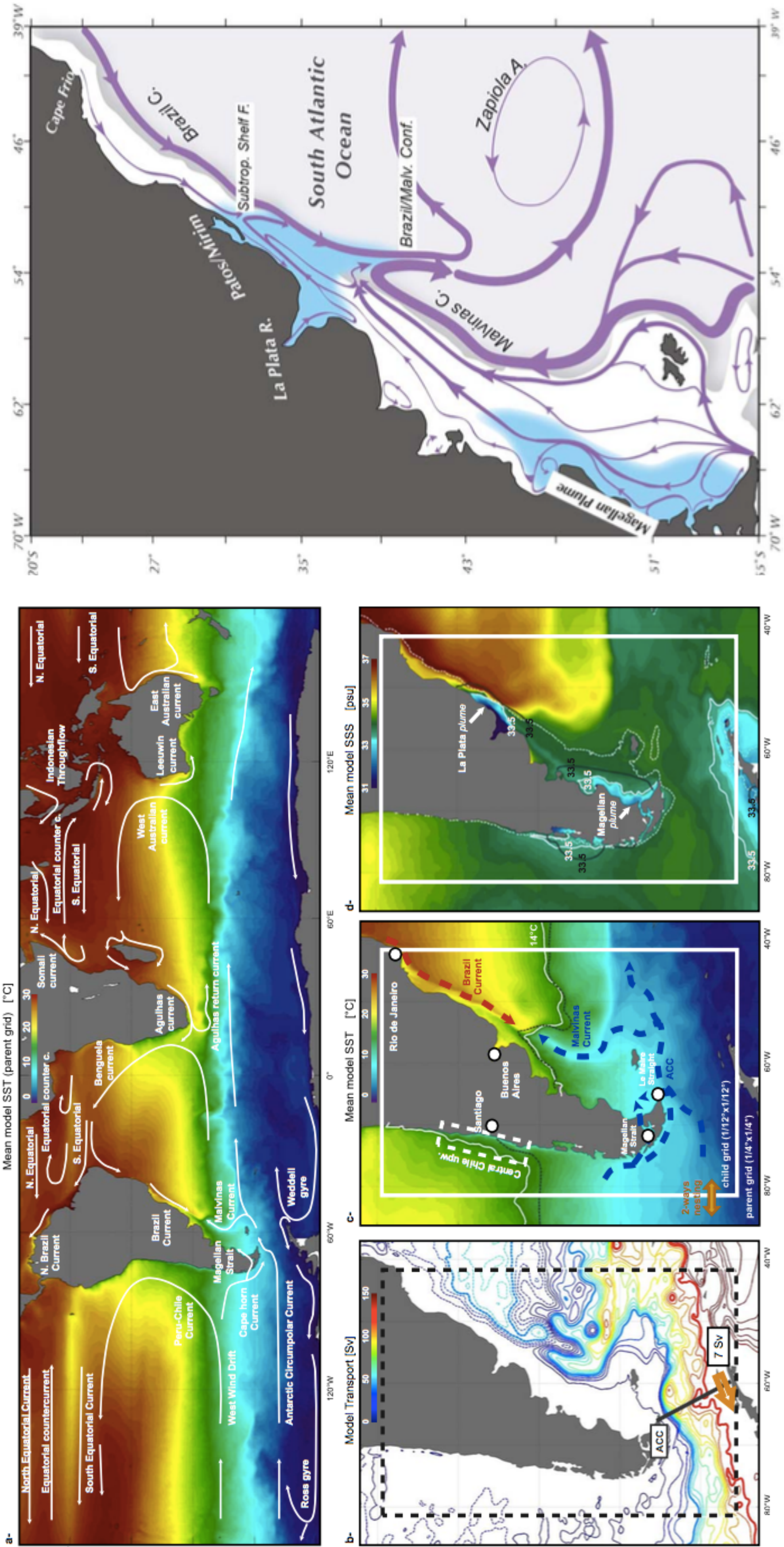


Figure 1. Oceanic circulation of the Southwestern Atlantic and Drake Passage, Adapted from Combes and Matano (2014, pp 732, 738). *Note - Falkland Current is referred to here as the Malvinas Current.*

The Patagonian Shelf is subject to high tidal variability and intense westerly winds (Strub *et al.,* 2015; Combes & Matano, 2018; Piola, *et al.,* 2018). In the southern portion of the Patagonian Shelf, seasonal variation is driven by onshore fluxes from the Drake Passage and recirculation around the Falkland Islands, while inter-annual variability is driven by local wind forcing (Combes & Matano, 2018). In the Southwest Atlantic wind driven circulation, strong tides and the Falkland Current are the dominant flow mechanisms (Glorioso, 2002). These flow mechanisms create high productivity on the south-western Atlantic continental shelf supporting commercially important fisheries around the Falkland Islands and the Patagonian coast (Brown, 2011).

South of the Falkland Islands, the Falkland Current meets the continental slope and splits into two northward flowing streams that wrap around the Falkland Islands comprising, a weaker western branch and a stronger eastern branch (Bianchi *et al.,* 1982). Falkland Current waters have a wide temperature range of 4-15 ^{o}C but a narrow salinity range of 33.7-34.1 psu (Wilson & Rees, 2000). Little data on the seasonal and inter-annual variability of oceanographic parameters are currently available for the shelf waters surrounding the Falkland Islands (Arkhipkin *et al.,* 2004b).

The Burdwood Bank is a submerged continental platform that lies ~200 km south of the Falkland Islands. The Bank rises to depths of 50 - 200 m and is separated from the Patagonian Shelf by a shallow (400 m) channel some 90 km in width (Matano *et al.*, 2019). The bank hosts a rich and highly productive ecosystem and is thought to be the main location for spawning of the Patagonian toothfish on the Patagonian slope (Collins *et al.,* 2010; Brown, 2011; Matano *et al.,* 2019) (Fig. 2).

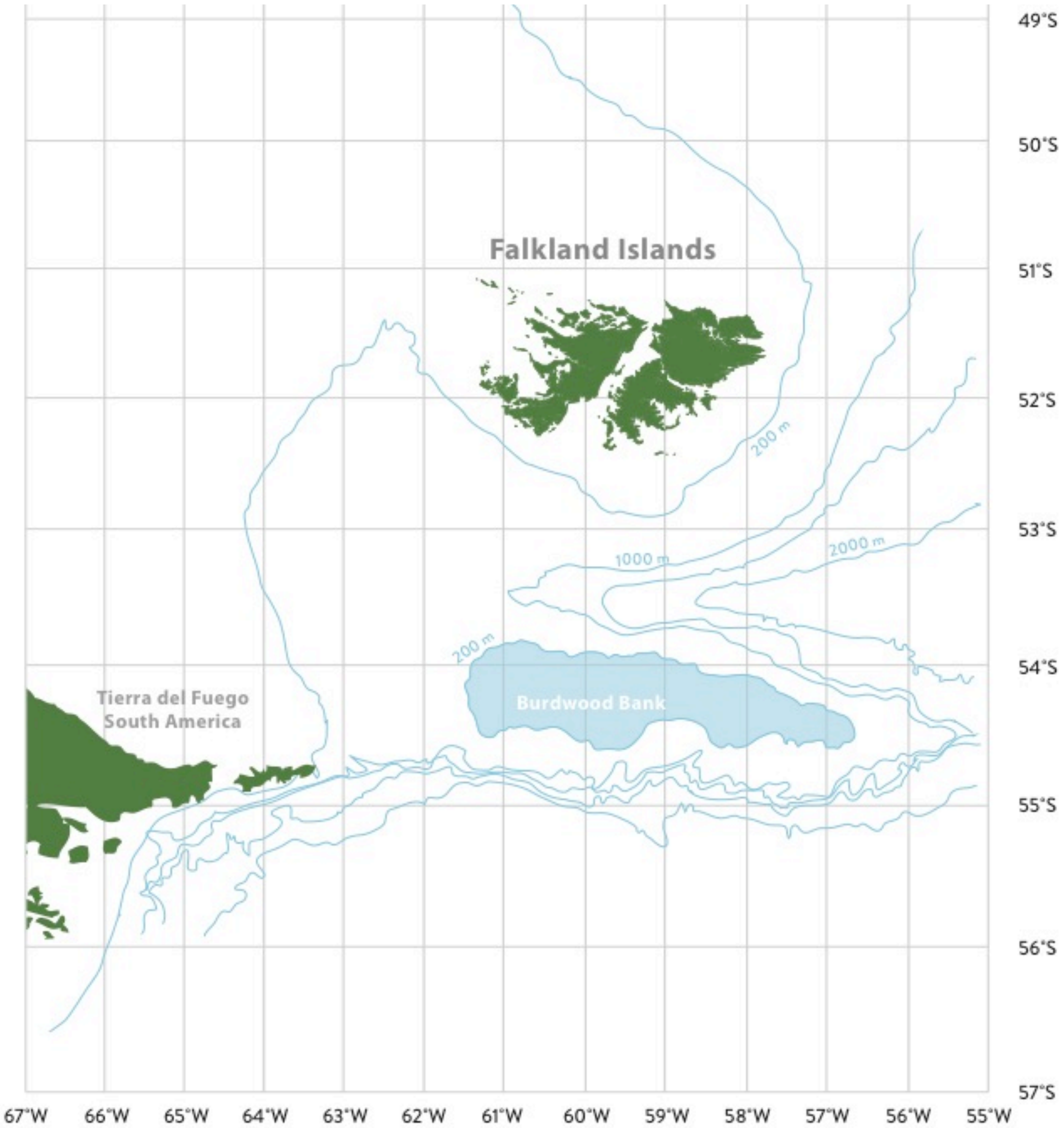


Figure 2. Location of Burdwood Bank in relation to South America and the Falkland Islands. Burdwood Bank is shown as light blue shading.

Numerical simulations identify tides and the ACC as primary divers of circulation over Burdwood Bank (Matano *et al.,* 2019). Model analysis shows a broad anticyclonic current that forms around the Banks rim, with anticyclonic eddies overlying the Bank (Fig. 1). During the summer, tidal mixing creates a strong density gradient between the Bank and the deep ocean, leading to intensified along-isobath flow, which strengthens retention inside the Bank (Matano *et al.,* 2019). During winter, the along-isobath flow in the upper layer is weakened due to the erosion of cross-bank density gradients resulting in reduced residence times over the Bank (Matano *et al.,* 2019). Recent backward particle tracking experiments also point to a potential connection between the Burdwood Bank and marine ecosystems 500-1500 km westward, along the Chilean coast (Matano *et al.,* 2019).

1.2. Ecology of the Patagonian Toothfish

1.2.1. Distribution

Patagonian toothfish are an Antarctic cod of the family Nototheniidae (Canales-Aguirre *et al.,* 2018). Patagonian toothfish are endemic to the Southern Hemisphere and are distributed from the Antarctic Polar Front to 40°S in the Southwest Indian Ocean, 35°S on the Patagonian Shelf and 30°S in the Chilean Pacific (Evseenko *et al.,* 1995; Belchier & Collins, 2008; Arana 2009; Collins *et al.,* 2010). Populations are associated with sub-Antarctic islands and seamounts to the north and south of the Polar Front, with temperature being a likely key factor limiting their distribution (Belchier & Collins, 2008; Collins *et al.,* 2010). Populations north of the Polar Front are found around island groups in the Indian Ocean and in the South Atlantic on the Chilean Shelf, Patagonian Shelf and the Falkland Islands (Belchier & Collins, 2008) (Fig. 3). This research focusses on the connectivity of Patagonian toothfish populations in southern Chile and around the Falkland Islands.

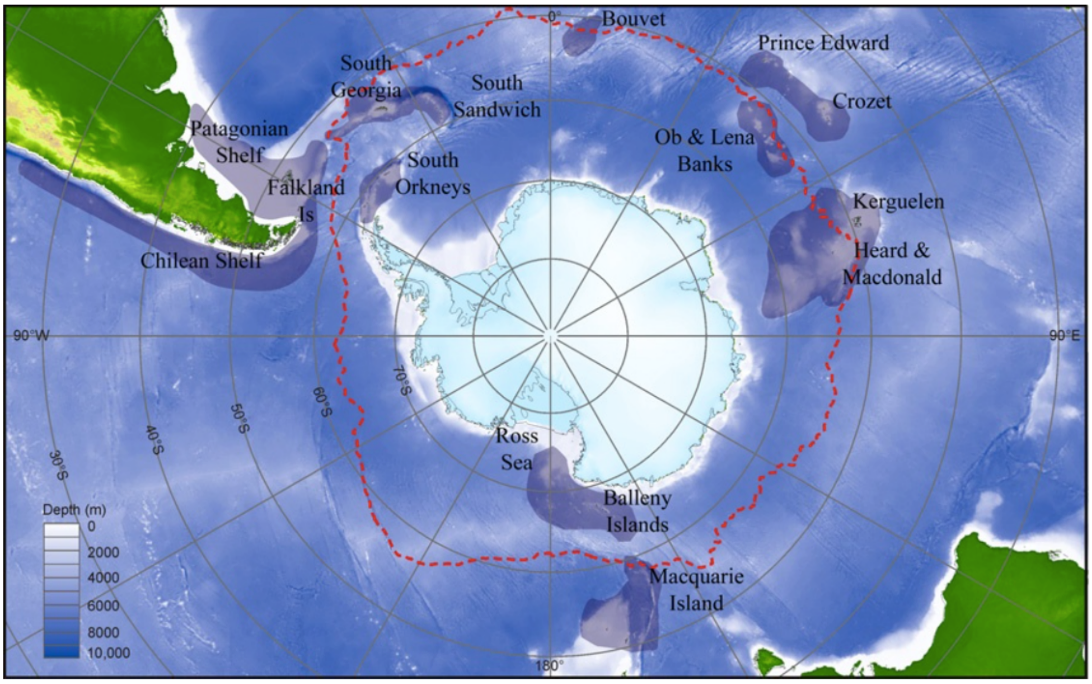


Figure 3. Known distribution of the Patagonian toothfish (*Dissostichus eleginoides*). Toothfish distribution is shown as purple shading and the Polar Front is presented by the red dotted line. [Source: Collins *et al.,* 2010 pg. 234].

1.2.2. Life history

Toothfish are a large, long-lived, demersal species that inhabit a broad bathymetric range over their life cycle (Belchier & Collins, 2008; Arana, 2009; Collins *et al.,* 2010). Adult fish inhabit waters greater than 500 m deep with a maximum depth of around 2500m, although this is likely to vary geographically (Collins *et al.,* 2010). Adult toothfish are generally considered relatively non-migratory and show strong site fidelity (Brown, 2011). Patagonian toothfish can live up to 30 years and reach two meters in length; however, they have low fecundity in relation to their body weight (Young *et al.,* 1995; Laptikhovsky *et al.,* 2006). On the Patagonian Shelf, fecundity (number of eggs produced per individual per annum) of Patagonian toothfish is reported to be between 94,000 and 1,426,000 (Brown, 2011). Sexual maturity in females is reached at a size of 90-100cm total length (9-12 years) and 64-94cm (7-11 years) in males (Zhivov & Krivoruchko, 1990; Yau *et al.,* 2001; Collins *et al.,* 2010).

The spawning grounds of Patagonian toothfish lie in deep waters (approximately 1000 m) over the continental slope with spawning occurring between June and September (Collins *et al.,* 2010). The Burdwood Bank, south of the Falkland Islands, is their only known spawning site on the Patagonian slope and is located towards the northern edge of their distribution range (Collins *et al.,* 2010; Brown, 2011). Reproduction of the Falkland Islands population of Patagonian toothfish is thought to occur on the eastern slope of the Burdwood Bank, with spawning occuring at water depths between 800-1200 m (Laptikhovsky & Brickle, 2005). There is evidence that some individual toothfish at Burdwood Bank do not spawn every year (skip spawning), which may be linked to environmental variability resulting in unfavourable conditions for spawning (Brown, 2011). To the southwest, spawning in Chilean waters does not occur north of 50°S (Arana, 2009). Distribution data for eggs and larvae is scarce and no buoyancy data are available for toothfish eggs; however, observations at South Georgia indicate eggs and larvae are pelagic (Collins *et al,* 2010). Eggs are 4.3-4.7mm in diameter at spawning with development lasting 90 days and hatching thought to occur at around 15mm in October and December (Evseenko *et al.,* 1995; North, 2002; Collins *et al.,* 2010). The larval period is approximately 230 days (Collins *et al.,* 2010).

Most early stage larvae have been captured in the upper 200m of the water column (Canales-Aguirre *et al.,* 2018). Eggs tend to be found further offshore than larger larvae, suggesting oceanographic features are enhancing onshore larval transport and/or larvae are capable of actively swimming inshore to settle (Evseenko et al., 1995; North, 2002; Canales-Aguirre *et al.,* 2018). Due to the extended pelagic duration of eggs and larvae there is the potential for high dispersal and connectivity of toothfish populations through the advection of these stages (Laptikhovsky *et al.,* 2006; Canales-Aguirre *et al.,* 2018).

Juvenile recruitment is associated with settlement of pelagic larvae and shows inter-annual variability (Collins *et al.,* 2010). Around the Falkland Islands strong year classes have been seen every four to five years (Laptikhovsky & Brickle, 2005). The recruitment variability observed at South Georgia Island appears to be linked to environmental variability (Belchier & Collins, 2008). Belchier & Collins (2008) found an inverse correlation between sea surface temperature and recruitment peaks of Patagonian toothfish in South Georgia; the best recruitment resulted from colder water temperatures during the summer six months prior to adult spawning. Links between recruitment and environmental variability have been explored but not fully evaluated in the Falkland Islands (Brown, 2011).

The juvenile phase, lasting 4-5 years, is spent in shallow waters and recruitment may be concentrated to a small area (Collins *et al.,* 2010). Juveniles disperse and gradually migrate down the continental slope into deeper waters at a size of 500-700mm in length. This migration may be associated with both changes in growth rate and diet (Collins *et al.,* 2010). Movement to deeper water is associated with a change to neutral buoyancy that reduces energy needed for movement using currents (Ashford *et al.,* 2012).

1.2.3. Population structure

There is a broad distribution of Patagonian toothfish in the Southern Hemisphere. However, due to the bathymetric range of juvenile and adult toothfish, areas of deep ocean potentially isolate populations (Collins *et al.,* 2010). Understanding movements at different spatial and temporal scales and identifying different populations is important to determine whether commercially valuable fisheries for toothfish should be managed as separate stocks or together as one stock (Collins *et al.,* 2010).

Dispersal of larvae and fish eggs is important in determining recruitment strength, with survival of these stages varying between years and within the spawning season, with recruitment success crucial to fish populations' long-term survival (Chambers & Trippel, 1997; Collins *et al.,* 2010). Spatial and temporal distribution is affected by transport pathways that are dependent on ocean currents at the differing depths and the buoyancy of the eggs and larval stages (Ospina-Alvarez *et al.,* 2012). Neutral buoyancy of pelagic early life stages can affect distribution, dispersal and survival, which can affect population structure (Myksvoll *et al.,* 2013; Petereit *et al,* 2014). Identifying potential transport pathways of eggs and larvae can help in gaining an understanding into the recruitment processes that are occurring around the Falkland Islands and which populations (Falkland Islands or Chilean) contribute to recruitment into the Falkland Islands population of Patagonian toothfish.

Coupled physical and biological models have been used to investigate fish egg and larval transport and subsequently for understanding retention and recruitment (Hinrichsen *et al.,* 2002; Miller *et al.,* 2006; Miller, 2007). Such models have been used to identify the potential transport and dispersion of Patagonian toothfish eggs and larvae in the South Georgia region (Brigden, 2018) and on the Kerguelen Plateau in the Indian sector of the Southern Ocean (Mori *et al.,* 2016). In the Falkland Islands, surface transport pathways were explored alongside otolith chemistry data to understand population dynamics between the Falkland Islands, Burdwood Bank and southern Chile (Ashford *et al.,* 2012; Randhawa *et al.,* in submission). The work showed there are two distinct spawning populations that are contributing to recruitment of Patagonian toothfish around the Falkland Islands, thought to be southern Chile and the Burdwood Bank.

In the Falkland Islands and Patagonian region Patagonian toothfish are genetically distinct from those found at Shag Rocks and South Georgia (Shaw *et al.,* 2004). It is proposed there are unconnected spawning populations along the Patagonian Shelf, to the south of the Falkland Islands at Burdwood Bank and off southern Chile (Laptikhovsky *et al.,* 2006; Arana, 2009; Collins *et al.,* 2010). However, Ashford *et al.* (2012) and Lee *et al.* (2018) have suggested there is some connectivity between southern Chile and the Burdwood Bank spawning sites and the Falkland Islands, identified through particle tracking simulations and otolith shape research. Better understanding of this connectivity is needed to help inform fisheries management [see below]. This study seeks to further explore early life stage connectivity of Patagonian toothfish populations in the region, through the use of particle tracking simulations using the highest resolution model currently available for the Southwest Atlantic region.

1.3. Fisheries overview

1.3.1. Fishery stocks

There are a number of definitions of the stock concept. For management purposes it is based on the homogeneous characteristics of a population unit (Begg *et al.,* 1999a). Ihseen *et al.* (1981) defined a fish stock as "a group of randomly mating, reproductively isolated individuals with temporal and spatial integrity". An essential component of stock assessment for effective fisheries management is stock identification and the connectivity between stocks (Begg *et al.,* 1999a). Overfishing and depletion of stocks can occur if there is a failure to recognise stock structure (Begg *et al.,* 1999a).

Life history parameters are used to identify fish stocks since stocks can exhibit differences in one or more life history parameters within the same species (Begg *et al.,* 1999b). Parameters include distribution, abundance, age-at-maturation, fecundity, survival and growth as well as genetics, parasite analysis and otolith shape and chemistry (Ihssen *et al.,* 1981; Rodhouse *et al.,* 1998). Evidence for the management of stocks as discrete units comes from differences in life history parameters that show fish are reproductively and geographically isolated (Ihssen *et al.,* 1981; Begg *et al.,* 1999b). Understanding the biological and physical structuring mechanisms of fish stocks can help to show factors that affect the stability of an individual stock (Begg *et al.,* 1999b). Genetic discreteness and stock isolation can be maximised by the oceanography of a region that limits mixing of eggs and larvae between neighbouring stocks (Iles & Sinclair, 1982; Palumbi, 1994; Begg *et al.,* 1999b). However, hydrological conditions can also allow mixing of stocks during pelagic egg and larval stages with re-segregation occurring during adulthood (Swain *et al.,* 1980; Begg *et al.,* 1999b). It is important to examine life history parameters over different temporal scales, as life history parameters and spatial boundaries can vary over time (Begg *et al.,* 1999b).

1.3.2. Patagonian toothfish fishery

In the Southern Ocean, the main deep-water demersal fishery is for Patagonian toothfish and is one of the most profitable and productive fisheries (Canales-Aguirre *et al.*, 2018; Gordon & Shipley, 2019). Due to past illegal and unreported catches, historic reported landings for Patagonian toothfish fisheries are likely unreliable (Gordon & Shipley, 2019). Inaccurate reporting of catch has been a problem for management throughout the toothfish fisheries in the Southern Hemisphere (Lack, 2008). Due to their size, delayed onset of maturity and long life span Patagonian toothfish can be vulnerable to overfishing (Bialek, 2003; Canales-Aguirre *et al.*, 2018). Nevertheless well-managed fisheries, including that of the Falkland Islands, have been certified as sustainably managed by the Marine Stewardship Council (Gordon & Shipley, 2019).

During the 1950s, exploratory trawling for Patagonian toothfish, limited to shallow depths, was investigated in Chile (Guerrero & Arana, 2009; Collins *et al,* 2010). In the mid-1980s the development of deep-water capable longline gear which could target adult fish, led to a targeted fishery in Chilean waters and consequently areas in South Georgia, Kerguelen and the Patagonian Shelf. The fishery rapidly expanded in catches due to the high price commanded by toothfish (Collins *et al.,* 2010). Reported legal landings within the CCAMLR area and national territorial waters increased from less than 5000 tonnes to 40,000 tonnes from 1983 to 1992, respectively (Collins *et al.,* 2010).

Demersal longline is the main method of catching adult toothfish. Hooks baited with squid or sardine are deployed at depths up to 2000 m and typically left for 24-48 hours (Collins *et al.,* 2010). There are three types of longlining systems employed in toothfish fisheries, these are: autoline, Spanish (double-line) and the trotline (or umbrella) system (Fig. 4). The success of different longline systems varies considerably with region, likely due to current speeds, bottom topography and potentially toothfish behaviour (Collins *et al.,* 2010).

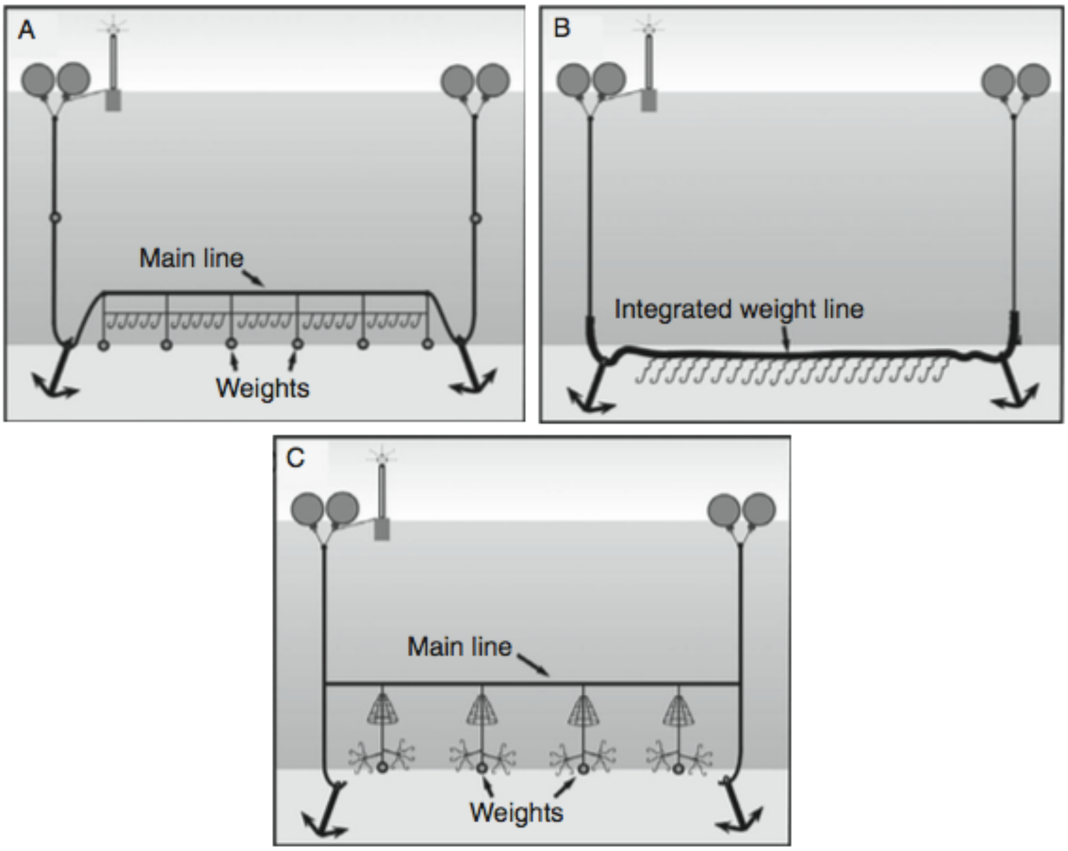


Figure 4. The three-longlinning methods: (A) Spanish double-line system, (B) autoline system and (C) trotline (umbrella) system. [Source: Collins *et al.,* 2010 pg. 277].

Other types of fishing methods include pots, gill nets and bottom trawling. Pots were initially trialled to try and reduce seabird mortality and depredation of catch and are used on the Patagonian Shelf and southern Chile. Potting proved unsuccessful at South Georgia with longlines delivering a higher catch rate (Agnew *et al.,* 2001; Guerrero & Arana, 2009). Gill nets are used by IUU vessels in the Southern Ocean but are banned in CCAMLR waters (Collins *et al.,* 2010) and trawling is used on the shelf-slope at Heard Islands, with toothfish also being caught as by-catch in some trawl fisheries (Collins *et al.,* 2010).

1.3.3. Falkland Islands Patagonian Toothfish Fishery

Since 1987, fisheries have been controlled in Falkland Islands waters (Des Clers *et al.,* 1996). Waters within the Falkland Islands are divided into two zones: Falklands Interim Conservation Zone (FICZ), a 150 nautical mile radius from the centre of the islands declared in 1987 and the Falklands Outer Conservation Zone (FOCZ) which opened to fisheries in 1994 (Fig. 5) (Des Clers *et al.,* 1996).

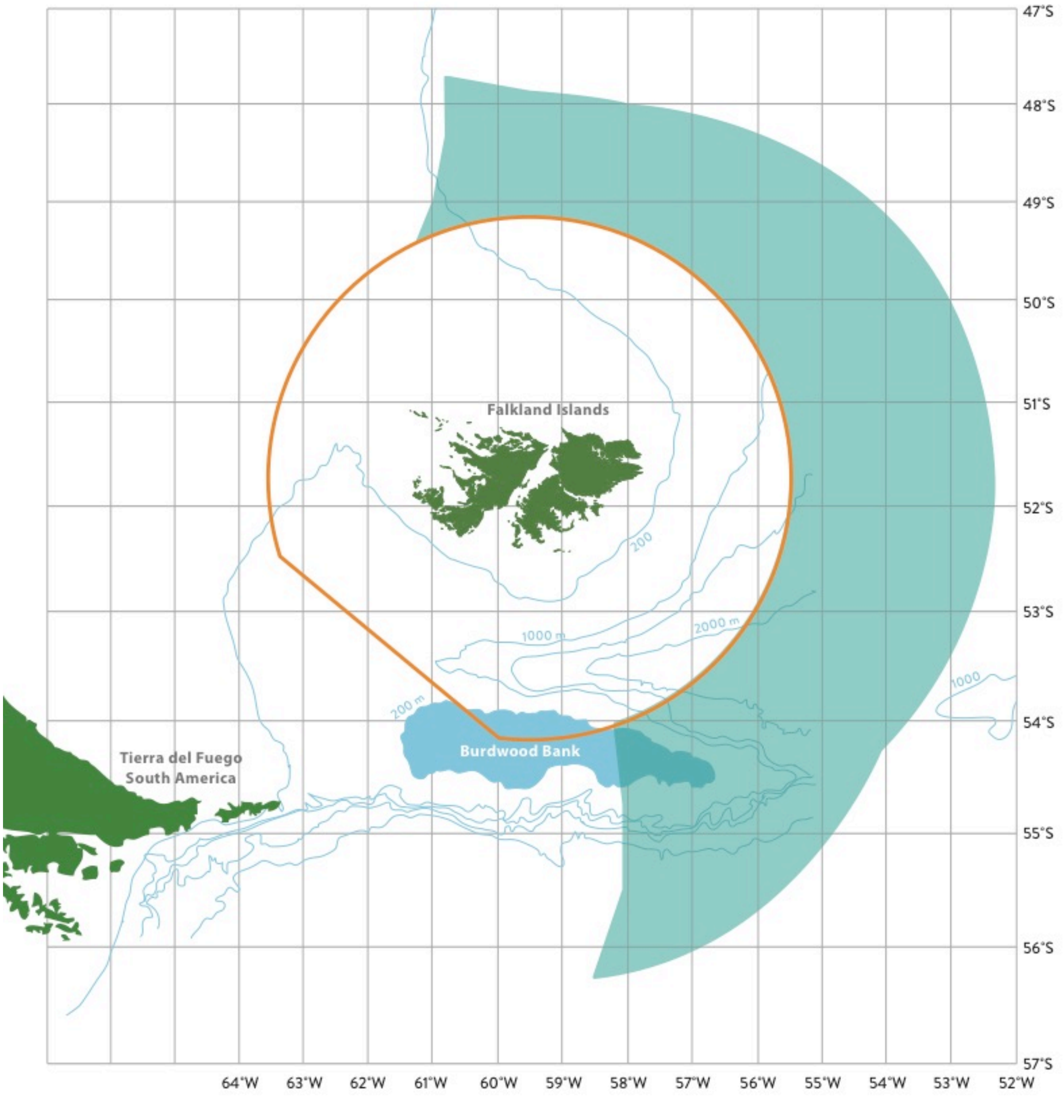


Figure 5. Falkland Island Conservation Zones. Interim Conservation Zone (FICZ) defined by the orange line, Outer Conservation Zone (FOCZ) highlighted in teal.

In 1992, the Falkland Islands Government authorised exploratory fishing of Patagonian toothfish in the FICZ and FOCZ (Andrews *et al.,* 2013) with the establishment of the fishery in 1994 (Des Clers *et al.,* 1996; Laptikhovsky & Brickle, 2005; Collins *et al.,* 2010). Fishing companies responded to the opening of this fishery by creating Consolidated Fisheries Limited (CFL) in which most Falkland Island fishing companies were shareholders.

One vessel, using the longline umbrella gear targets adult toothfish of approximately 60cm in length and which inhabit waters at a depth greater than 600m (Laptikhovsky & Brickle, 2005; Collins *et al.,* 2010; Andrews *et al.,* 2013). Initially the Spanish longline system was used. In 2008, there was a switch to umbrella lines (trotlines). It has been reported that catch per unit effort can be up to ten times higher with umbrella lines than Spanish longlines in the Falkland Island waters (Collins *et al.,* 2010). Quantities of toothfish are also caught in two other Falkland fisheries: 1) finfish trawl, with a commercially viable by-catch and 2) the calamari (*Doryteuthis gahi)* fishery, where toothfish are too small to be commercially valuable (Farrugia & Winter, 2018). Different parts of the toothfish population are accessed by the different fisheries: Calamari trawling occurs on the shelf to the east of the Falkland Islands, finfish trawling occurs on the shelf predominately to the north and west of the islands and longlining on the slope and in deep water (Farrugia & Winter, 2018).

The Falkland Islands stock is managed under the Quota Management System, introduced in 2006, and is treated as a single discrete stock, managed in isolation from the neighbouring Chilean and Argentine stocks, as it is assumed recruitment from these stocks is not significant (Andrews *et al.,* 2013). The maximum sustainable yield for the stock was estimated at 1657 tonnes per annum (t pa) by the CASAL model in 2013, but estimates have ranged from 850 to 1800 t (Andrews *et al.,* 2013). Due to a decreasing trend in Spawning Stock Biomass and an uncertainty in the stock assessment model the total allowable catch (TAC) was set at 1200 t pa in 2008. A further reduction in TAC has been made and is now set at 1040 t pa (Andrews *et al.,* 2013; Falkland Islands Government, 2019). Local fisheries scientists internally review the stock assessment for 2018 this was conducted by Farrugia & Winter, with the most recent external review conducted in 2018 for MSC certification conducted by Andrews *et al.*

The harvest strategy uses a number of measures to reduce uncertainty that includes; precautionary catch limits, overall effort control, data collection and research and a seasonal closure of the main spawning ground. There is a limit of two operating longline vessels under the licensing system, though only one vessel operates in practice, the *FV* CFL Hunter (Andrews *et al.,* 2013).

There is a trigger reference point that is set at 45% of the unexploited spawning stock biomass; at this point an automatic TAC reduction of 20% applies. In 2013 stocks were considered to be in good condition and stable at around 51% of the unexploited stock size, well above the biomass trigger point (Andrews *et al.,* 2013). A limit reference point is also in place: if the current spawning stock biomass to unexploited spawning stock biomass is less than 0.2 the fishery will be closed pending evaluation of conditions required for stock rehabilitation (Farrugia & Winter, 2018). The fishery is well monitored and managed with a long-established observer programme (Andrews *et al.,* 2013). The fishery has been certified by the Marine Stewardship Council as a sustainable fishery and was recertified for the third time in 2018 for five years without conditions (Falkland Islands Government, 2019).

The most recent stock assessment report indicates an estimated toothfish total biomass of 31,891 tonnes and the spawning biomass of 11,293 tonnes in 2017 (Farrugia & Winters, 2018). Maximum sustainable yield was estimated at 1932 t, however, it is the recommendation of the Farrugia &Winters (2018) annual fisheries report to retain a total allowable catch of 1040 t for longline fisheries. This will maintain spawning biomass to unexploited spawning stock biomass ratio at above the trigger reference point while considering possible future decreases in the ratio (Farrugia & Winter, 2018). Toothfish catch was reported in 2017 to be 1520.1 tonnes: 1.9% by weight was caught by calamari trawl, 30.3% by finfish trawl and 67.9% by longline. Over the past five years there has been a general downward trend in longlining catch (Farrugia & Winter, 2018). A shift in fishing behaviour in the southwest of the FICZ in 2016 and 2017 led to an increase in toothfish by-catch exceeding the estimated 330 t taken by trawl fisheries. As a conservation measure, an area in the southwest of the FICZ was closed from early December 2017 to end of January 2018 (Falkland Islands Government, 2019). A toothfish bycatch limit of 1.5% was implemented in 2018 and therefore deeper waters were not exploited by trawl fisheries and the bycatch did not exceed the trawler predictions of 330t (Falkland Islands Government, 2019).

1.4. Study Objectives

In the Falkland Islands there is an active fishery for Patagonian toothfish, which has a large economic value to the islands. There is still not a full understanding of the early life history of the target species, which is important for long-term management of the fisheries. The distribution, spatially and temporally, throughout the early life stages is still uncertain with some evidence suggesting recruitment (egg and larval supply) contribution from the neighbouring Chilean stock.

This research investigates the spatial and temporal distribution of the early life stages of the Patagonian toothfish by completing buoyancy experiments and using particle-tracking simulations. The key objectives of this study are:

1. To empirically estimate toothfish egg buoyancy throughout embryogenesis.
2. Identify potential transport pathways of eggs and larvae from spawning grounds to retention areas and the spawning populations and areas that may contribute to retention and potential recruitment.
3. Compare retention and transport success between years and discuss possible mechanisms leading to variability.

1.5. Thesis structure

The structure of this thesis is as follows:

Chapter two: **Buoyancy determination of Patagonian toothfish eggs**. This chapter experimentally investigates toothfish egg buoyancy and buoyancy changes throughout egg development.

Chapter three: **Modelling the distribution of Patagonian toothfish eggs and larvae around the Falkland Islands**. This chapter describes the modelling approach, model parameterisation, sensitivity analysis and particle tracking simulations that were undertaken. The model outputs are presented and discussed.

Chapter Four: **General discussion and conclusions**. This chapter summarises the main findings of the research and their implications to stock/fisheries management are considered and future research needs are identified.

2. Buoyancy determination of Patagonian toothfish eggs

2.1. Introduction

Marine fish species employ a diverse range of reproductive strategies and tactics to maximise survivorship of their offspring (Murua & Saborido-Rey, 2003). It is thought both tactical variation and strategy are adaptive, where tactical variation is due to environmental fluctuations and strategy is an overall reproductive pattern common to a species (Stearns, 1992; Roff, 1996). Adaptations to specific habitat features that allow for increased chance of survival, feeding and growth are seen in numerous examples of marine fishes (Cowen & Sponaugle, 2009).

The majority of commercially important fish species reproduce through external fertilisation without parental care and spawn more than once in their lifetime (Murua & Saborido-Rey, 2003). Two types of spawning patterns have been described; total spawners and batch spawners (Tyler & Sumpter, 1996). Total spawners release eggs in a short time frame but as a single event or in one unique event, while batch spawners release several batches over a spawning season (Murua & Saborido-Rey, 2003). Many Atlantic cold and temperate water species are batch spawners; Brown (2011) identified toothfish as batch spawners. This strategy of releasing eggs over an extended time frame likely increases the probability of offspring survival (Lambert & Ware, 1984; Murua & Saborido-Rey, 2003).

After spawning, the density of fish eggs and density of the surrounding water determines the vertical distribution of eggs in the water column (Sundby, 1991). Vertical distribution is important for the horizontal dispersal and survival of eggs. The vertical position of eggs in the water column determines predator-prey interactions and dispersal pathways from spawning grounds towards feeding grounds and areas suitable for recruitment (Sundby, 1991; Sundby & Kristiansen, 2015). Buoyancy of an egg can be defined as the difference in specific gravity between the ambient water and the egg. Buoyancy in fish eggs is largely insensitive to variation in temperature and the main determinant of buoyancy is salinity (Sundby & Kristiansen, 2015).

Survival of fish eggs and larvae may be influenced by the environmental conditions that prevail at the time of spawning (Ospina-Alvarez *et al.,* 2012). Key adaptations of adult fish to ensure egg and larval survival, as well as connectivity, appear to be spawning location and timing (Peck *et al.,* 2012). Fish populations may be able to adapt to horizontal transport and dispersal by influencing the vertical position of their eggs and larvae in the water column (Sundby & Kristiansen, 2015). This can be achieved through spawning behaviour; selection of spawning area and depth, and through the production of eggs that have a defined specific gravity that determines their local buoyancy (Sundby & Kristiansen, 2015).

Marine fish eggs are generally either pelagic or mesopelagic and float within precise depth ranges (Coombs, 1981; Kendall, 2001; Sundby & Kristiansen, 2015). Demersal or benthic eggs are mainly found in marine fish spawning in the littoral zone and in freshwater fish (Kunz, 2004). Pelagic eggs are buoyant due to large quantities of dilute aqueous fluid (Craik & Harvey, 1987). Pelagic eggs develop in the upper water layers, are usually small, with most not measuring more than 0.3 mm but can range up to 5.5 mm and are produced in large numbers (Kunz, 2004). All egg types other than pelagic have some type of parental care associated. Pelagic eggs are, on average, smaller than demersal eggs, with external conditions also relating to egg size. Egg size can also vary between populations and stocks (Kunz, 2004). Deep-water marine fish, such as the Patagonian toothfish, tend to produce larger eggs compared to shallow water spawners (Kunz, 2004). It is thought that larger eggs ascend more rapidly in comparison to smaller eggs (Robertson, 1981). Patagonian toothfish are deep-water batch spawners (~1000 m) and produce relatively large eggs (4.3 mm - 4.7 mm) (Evseenko *et al.,* 1995; Collins *et al.,* 2010; Brown, 2011).

Mujica *et al.* (2016) obtained Patagonian toothfish eggs from an experimental farm in southern Chile. They found eggs were 3.1-3.5mm in diameter and hatched between 30 and 33 days post fertilisation. There are no data from the wild available in the Falkland Islands; however there are observations from a hatchery (Falkland Islands Fish Farming Limited) within the Falkland Islands. At the Falklands hatchery, egg size is comparable to Mujica *et al.* (2016) observations and hatching occurs at one month (Love A 2020, pers.comm, 18 February).

Through observations at sea, mainly around South Georgia, Southern Ocean, it is considered that Patagonian toothfish eggs are pelagic and found in the upper 500m of the water column (Evseenko *et al.,* 1995; North, 2002; Collins *et al.,* 2010). The exact values of egg buoyancy are unknown but due to the pelagic early life stages of Patagonian toothfish there is the potential for high dispersal and connectivity of populations (North, 2002; Shaw *et al.,* 2004; Collins *et al.,* 2010; Canales-Aguirre *et al.,* 2018).

Studies have found egg buoyancy in some fish species changes throughout development. Studies on Atlantic cod (*Gadus morhua*) and anchovy (*Engraulis encrasicolus*) found egg buoyancy increases at the beginning of embryonic development and thereafter decreased until hatching (Jung *et al*., 2012; Ospina-Alvarez *et al.,* 2012; Petereit *et al.,* 2014). Buoyancy and changes to buoyancy throughout these early life stages are important to understand, as transport processes between spawning grounds and nursery areas can act as a critical determinant in recruitment success (Shelton & Hutchings, 1982) i.e. Changes in buoyancy will affect position of the egg/larvae in the water which, in turn, will potentially affect dispersal (transport, connectivity) and ultimately recruitment location.

Changes in egg buoyancy should, where possible, be empirically estimated and incorporated into egg dispersal models (Myksvoll *et al.,* 2011; Jung *et al.,* 2012; Ospina-Alvarez *et al.,* 2012; Brigden, 2018). With no empirical data on the buoyancy of Patagonian toothfish eggs, determining initial buoyancy and any buoyancy changes during the early stages of development is a necessary step for biologically relevant modelling. The research in this chapter empirically estimates toothfish egg buoyancy throughout their development that can then be used in particle (egg) tracking simulations (Chapter 3).

There are two methods commonly used to determine specific gravity of fish eggs. Coombs (1981) described a method using a density gradient column; this requires the set-up of a stable column of a continuously graded solution of seawater. Once specimens are introduced they settle at a level of known density where they are neutrally buoyant. The second method is to measure the various basic egg components, lipids, proteins and osmolality of water content, which can be done to a relatively high precision (Sundby & Kristiansen, 2015).

Due to restrictions of available equipment in the Falkland Islands different methods to achieve Coombs' (1981) density gradient column were used to determine egg buoyancy.

2.2. Methods

A pilot study to determine egg buoyancy for Patagonian toothfish was conducted between August 30th and September 14th 2018 in the Falkland Islands. Following on from the knowledge gained in the pilot study, additional buoyancy experiments were conducted in October and November 2019. The experiments were conducted at Falkland Fish Farming Limited (FFFL), in Stanley, Falkland Islands, where wild caught Patagonian toothfish are being reared.

2.2.1. Fish rearing and condition

The toothfish being reared at FFFL were caught off the Burdwood Bank and to the south of Beauchêne Island by the longlining vessel *FV* CFL Gambler and transferred live to the fish farm. The toothfish are approximately 20 years of age and have been sustained at the farm for approximately six years. Toothfish do not have a swim bladder and are more robust, seemingly having less serious decompression injuries when brought from depth to the surface, than species with swim bladders (Agnew *et al.,* 2006). All fish appear to be in good health, with a few minor deformities seen, such as damage to their mouths or eyes likely caused during collection from the Burdwood Bank/Beauchêne Island (Wylie A 2018, pers. comm, 03 September). Although the toothfish are being reared, where conditions differ to the wild, including depth, pressure and diet, it is assumed for this study the eggs being produced are generally representative of those produced in the wild. Ideally we would compare hatchery eggs to wild eggs, but this was not possible for this study.

In previous years eggs and milt were manually removed from the fish, with eggs then being fertilised externally in a beaker. In October 2018 it was observed that there were naturally spawned and fertilised eggs within the adult toothfish tanks, which lead to juveniles being successfully reared. Therefore, in 2019 the fish were left to spawn naturally in their tanks. It is assumed, though not tested, that egg quality is better in naturally spawned eggs (Wylie A 2019, pers. comm. 27 August). Eggs were collected from a collector tank on the side of the main tanks and were placed in batches in incubator tanks.

2.2.2. Pilot study experimental design

Two ten-litre columns, with a closable connection, were used to raise the salinity by 0.1 PSU increments on one side of the column to find neutral egg buoyancy (Fig. 6). A higher salinity stock was added to the left hand column (S_H) and a lower salinity stock to the right hand column (S_L). Salinity stock solutions were made using 10 L of water and Peacock Granular salt that has a sodium chloride content of 99.8%. The connection between columns was closed before removing water. Removing 1000 mL of water from S_L and then opening the connection caused 500 mL of the more saline water to flow into S_L thereby increasing the salinity by 0.1 PSU. The column was then very gently manually mixed to avoid stratification. Temperature (°C) was recorded after every addition of more saline water.

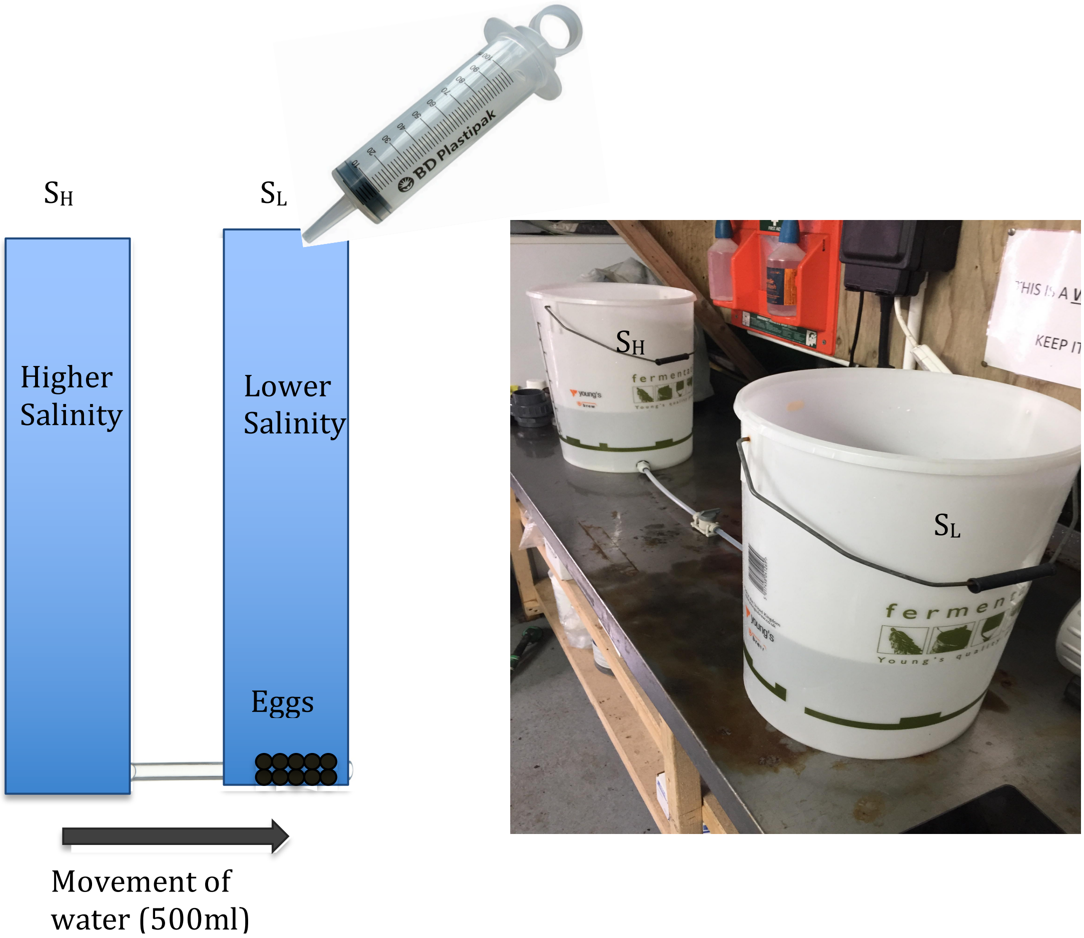


Figure 6. Diagram and photo of the experimental set up for the pilot study conducted in 2018. SH= higher salinity column, SL = lower salinity column.

A random sample of 100 eggs was placed in the lower salinity solution and the number of eggs, positively, neutrally and negatively buoyant, were counted. The salinity was increased as describe above and eggs were again counted. The process was repeated until the lower salinity column had increased by 1 PSU. This was carried out once per day for each batch of eggs (different stages of post fertilisation).

The experimental design for the pilot study had limitations that impacted the accuracy of the data collected. The temperature could not be controlled and therefore on warm days the temperature in the apparatus rose quickly which likely caused temperature shock and egg death within the experiment. The experiment did not have any replication for each day post-fertilisation due to egg death in many experiments. Although the eggs are relatively large, the transparency of the eggs within the experimental set up did not lend itself to easy counting of eggs throughout the water column, which could have led to bias in the data through preferential counting at the surface. The results from the pilot study are therefore excluded from further study.

2.2.3. Redesigned study

Due to the shortcomings of the pilot study in 2018, described above, a different method was utilised to investigate egg buoyancy in the 2019 spawning season. Unlike in the pilot study, whole salinities, i.e. no 0.1 PSU increases only an increase of 1 PSU (from 31 PSU to 42 PSU) were used in this design.

To account for the natural egg density distribution, three 1000 mL glass cylinders were used for each experiment. A different salinity was used in each cylinder, one in which the eggs were positively buoyant, one with a distribution of buoyancies and one negatively buoyant (Fig. 7). Twenty eggs were placed in each salinity and left to settle for 30 minutes. The number of eggs in each salinity that were negatively, neutrally and positively buoyant were counted and recorded. The same salinities were used until the positively buoyant eggs had become negatively buoyant, once this happened the lowest salinity was discarded and a new salinity where the eggs were positively buoyant was used.

Four batches of eggs were used for the experiment. Batch A was naturally fertilised on 28th October 2019, batch B manually fertilised 6th November 2019, batch C manually fertilised 8th November 2019 and batch D manually fertilised on the 9th November 2019.

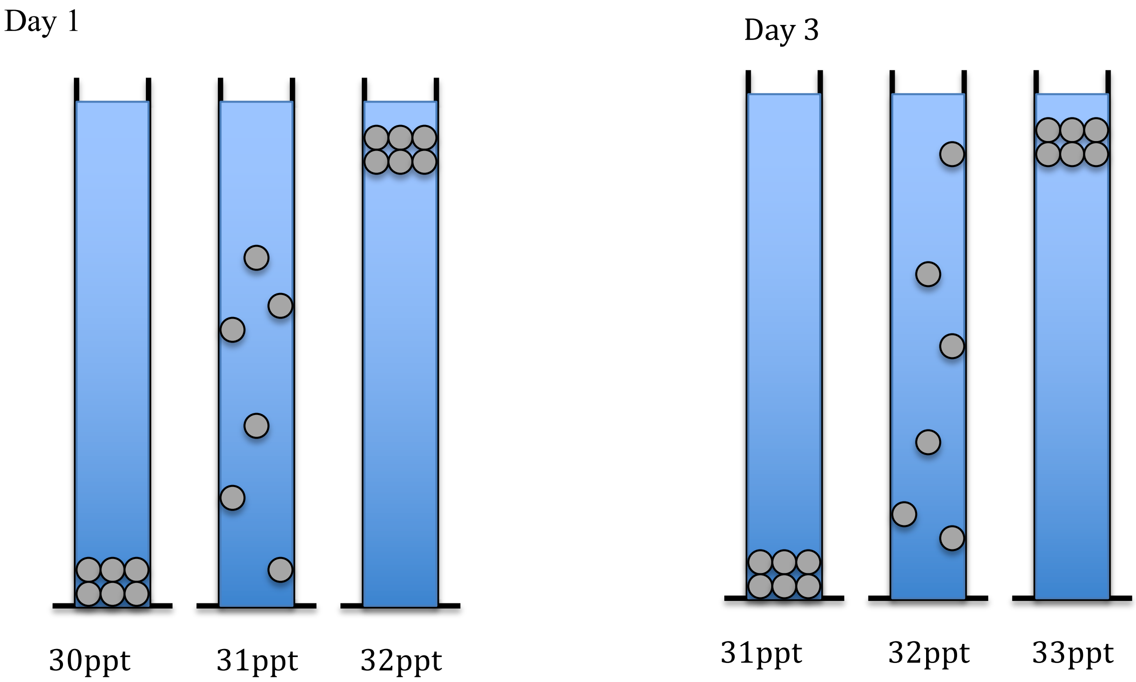


Figure 7. Example of the experimental set up for the redesigned study.

Sundby and Kristiansen (2015) found buoyancy in fish eggs is insensitive to temperature variations, but toothfish egg condition was found to be temperature sensitive in the 2018 pilot study, therefore a constant temperature of 5° C (incubated temperature) was used. To maintain this temperature the cylinders were placed in a fridge. Temperature in each cylinder was measured and recorded at the start and end of each experiment.

There have been observations at the FFFL facility that the eggs are sensitive to light (Wylie A 2019, pers.comm. 28 October). This was overcome by leaving the eggs in a dark fridge whilst waiting for the egg buoyancy to settle. Eggs were not left in the experiment for an extended period of time and a fresh set of eggs from each batch weas used in each experiment. This was due to not having a quick and easy way to distinguish if the eggs had become negatively buoyant or had sunk out because they had become non-viable.

A small sample of 30 eggs was taken at the different stages post-fertilisation and studied under a microscope to ensure fertilisation had occurred and development of the embryo was progressing. Morphology of the embryo was determined and the development of the egg was compared to the known stages shown by Mujica *et al.* (2016) (Fig. 8, 9).

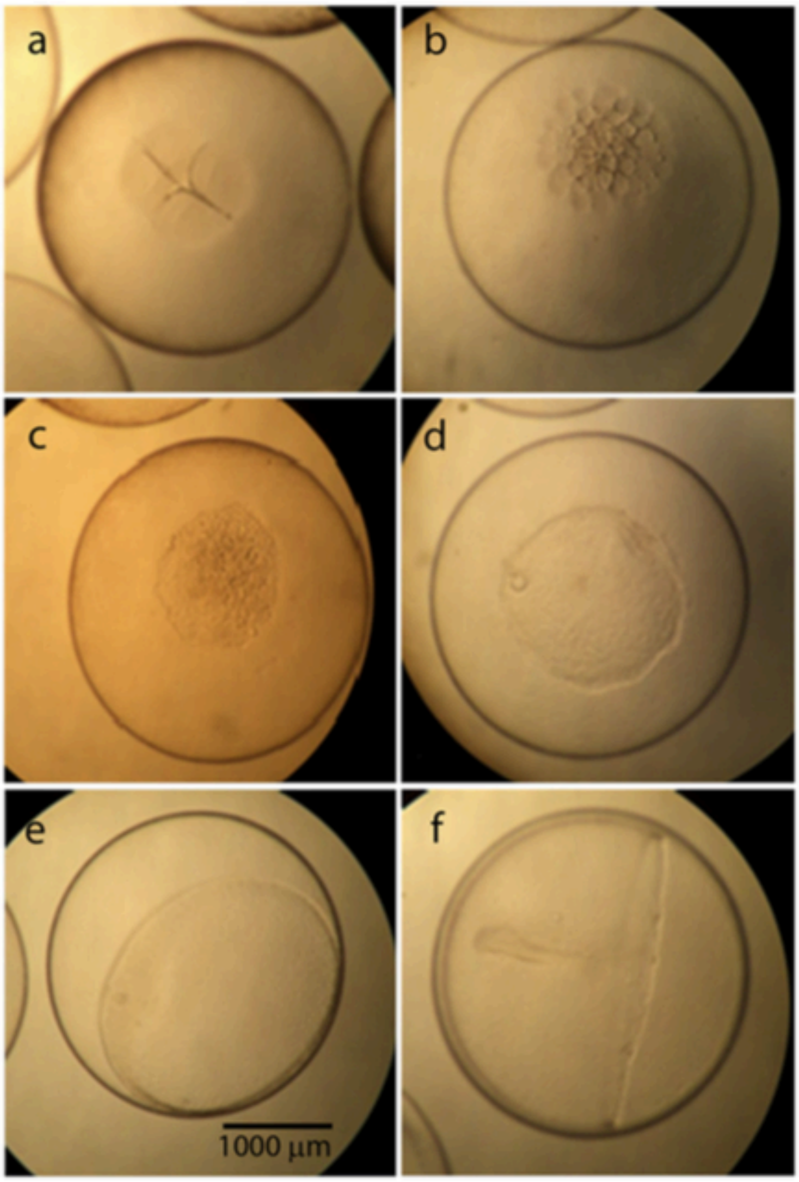


Figure 8. Morphology of *Dissostichus eleginoides* (Patagonian toothfish) embryos: (a) day 0 (fertilisation), (b) day 1, (c) day3, (d) day 4, (e) day 5 and (f) day 6. [Source: Mujica *et al.,* 2016 pg. 676].

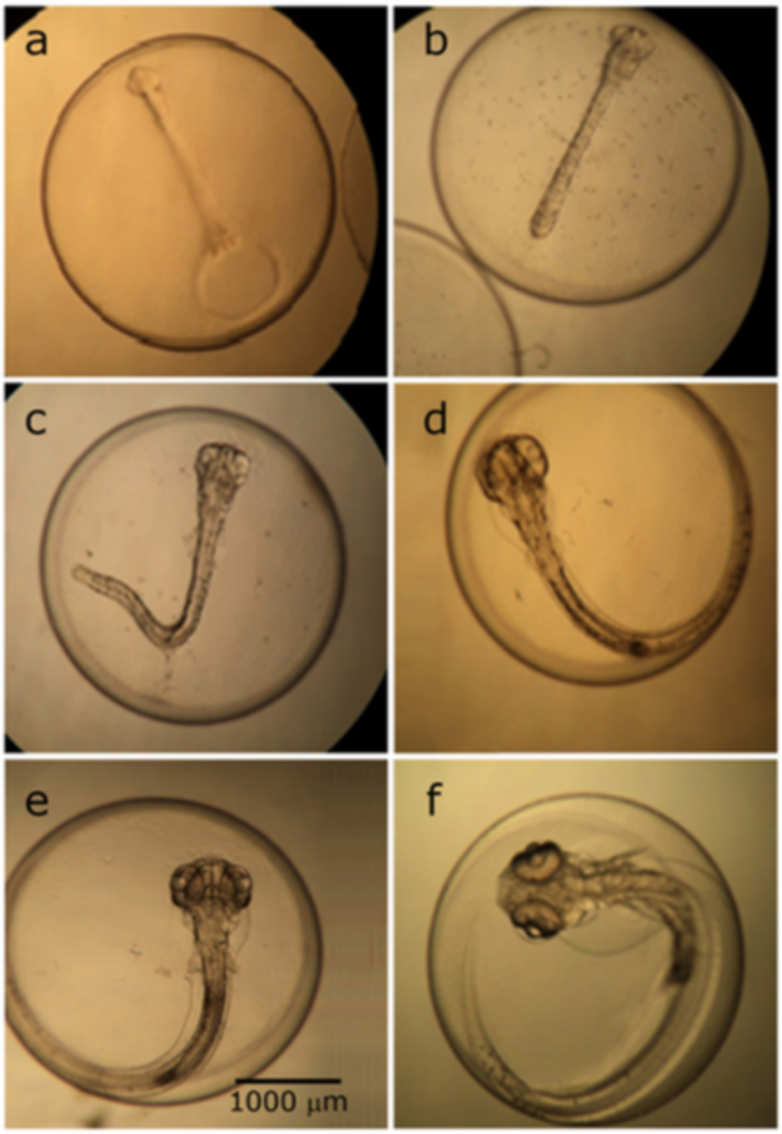


Figure 9. Morphology of *Dissostichus eleginoides* (Patagonian toothfish) embryos: (a) day 7 (b) day 10 (c) day 13 (d) day 17 (e) day 19 and (f) day 24. [Source: Mujica *et al.,* 2016 pg. 677].

2.2.4. Data analysis

Measurements of salinity, temperature and atmospheric pressure were used to calculate the water density in each cylinder for each experiment. From the recorded data the fraction of eggs positively, neutrally or negatively buoyant at each water density, for each day post fertilisation was calculated. Data from each batch were kept separate and not averaged due to high variability between batches, as well as missing replication for some days post fertilisation. There was a two-week period were data were unable to be collected.

Where the data allowed, egg density for each batch and day post fertilisation was assumed using the fraction of eggs positively and negatively buoyant (data found in appendix A). If at one density the majority of eggs were negatively buoyant and at the next density the majority were positively buoyant, neutral buoyancy (therefore egg density) was assumed to be in between the two densities and the middle value was used. When the data did not allow for a middle value to be assumed, less than or greater than was used (Example in Table 1).

Table 1. Example of data that allows for an assumed egg density and where data allowed for a greater than value to be assumed.

2 days post fertilisation				
Density kg/m^3	**Fraction of eggs positive**	**Fraction of eggs Neutral**	**Fraction of eggs Negative**	**Assumed egg density (kg/m^3)**
1026.14	0.1	0	0.9	1026.53
1026.93	0.8	0.2	0	
6 days post fertilisation				
1027.72	0	0	1	
1028.51	0.25	0.05	0.7	>1029.31
1029.31	0	0	1	

2.3. Results

Visual observations of the eggs under a microscope from all four batches showed that fertilisation had been successful and embryo morphology matched the stages shown by Mujica *et al.* (2016).

Results of the egg buoyancy experiments (Fig. 10) show egg buoyancy decreased after fertilisation and then increased again 10-days post fertilisation. Raw data can be found in Appendix A. Batch A's (blue) assumed egg density (calculation described above) increased from 1.026 g/cm^3 at two days post fertilisation to 1.031 g/cm^3 at 10-days post fertilisation. 12-days post fertilisation the assumed egg density began to decrease again to 1.028 g/cm^3 at 15-days post fertilisation.

The assumed density of batch B (red) was lower in comparison to batch A; changes to assumed density in batch B did, however, follow a similar pattern to batch A. Between one- and five-days post fertilisation, assumed density had increased from 1.024 g/cm^3 to 1.030 g/cm^3. At 20 and 21 days post fertilisation, assumed density had decreased from day five but was still greater than density at one-day post fertilisation.

Similar to batch B, batch C (green) estimated density was lower than batch A. The assumed density of batch C at one-day post fertilisation was the same as batch B. At 19-, 20- and 21-days post fertilisation density was greater than in the initial days post fertilisation.

There were three data points collected for batch D (black). At two days post fertilisation batch D had an assumed density value of 1.024 g/cm^3 comparable to the batch B and C at one-day post fertilisation. At 19- and 20-days post fertilisation egg density was greater than at 2-days post. Batch B, C and D all had the same assumed density value at 20-days post fertilisation.

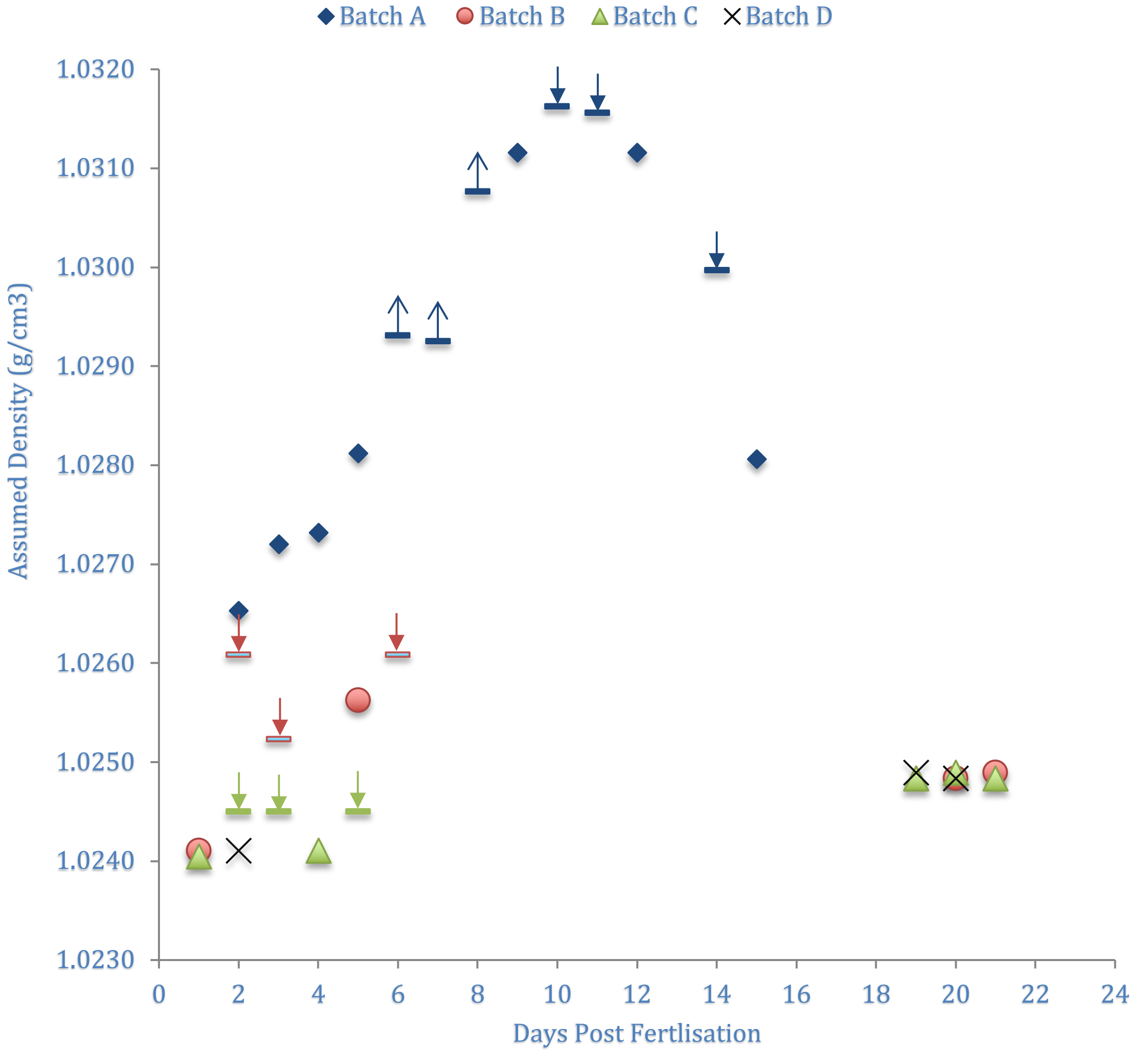


Figure 10. Assumed Patagonian toothfish (*Dissostichus eleginoides)* egg density (g/cm^3) with time post fertilisation, derived from data in Appendix 1. Batch A represented in blue, batch B in red, batch C in green and batch D in black. Arrow direction indicates where assumed density is less than (downward arrow) or greater than (upward arrow) than the value of the bar.

2.4. Discussion

No previous studies have been undertaken on buoyancy of Patagonian toothfish eggs as far as the author is aware. Systematic changes in buoyancy through embryonic development have been seen in a number of studies of different marine fish species (Sundby & Kristiansen, 2015). After fertilisation, the initial stages are characterised by a decrease in buoyancy due to loss of water, with increased salinity in the embryo and yolk, associated with incapability to osmoregulate (Sundby & Kristiansen, 2015). As the embryo develops and osmoregulation capability increases, the egg becomes less dense. Close to hatching, the eggs become heavier with hatched larvae being considerably lighter than the egg (Jung *et al.,* 2012; Sundby & Kristiansen, 2015).

The results from batch A appear to fit with studies from other marine fish species (Jung *et al.,* 2012; Sundby & Kristiansen, 2015); an initial decrease in buoyancy in the first few days post fertilization and then a period of increasing buoyancy. Buoyancy data close to hatching was not collected and therefore it is uncertain if the eggs become heavier again. Batch B showed an initial decrease in buoyancy in the first five days post fertilisation, indicating a similar pattern to batch A in buoyancy changes was being followed; however, data are missing for between five-and twenty-days post fertilisation. The data for batches C and D are limited, therefore buoyancy patterns and changes throughout embryonic development cannot be inferred beyond that the eggs at 19-21 days were slightly denser than at one-day post fertilisation and all three batches had close density values on days were replication was present.

The data show that batch A's density is greater than the other three batches in this study. The eggs started out denser at 1.0265 g/cm^3 compared to 1.024 g/cm^3 in batches B, C and D. This could be due to a number of reasons; once fertilised batch A was exposed to large quantities of light for an extended period of time (Wylie A 2019, pers. comm. 9 November), the quality of the eggs produced was poor, or due to variation in eggs produced by differing females.

Some fish stocks have been found to have eggs with both a pelagic and mesopelagic distribution, where the lightest fraction of eggs are pelagically distributed and the heaviest fraction of the eggs are mesopelagically distributed (Sundby & Kristiansen, 2015). This is the case for anchovy and sardine eggs in the Bay of Biscay, cod eggs in the northern Gulf of St. Lawrence and coastal cod eggs in Norwegian fjords (Boyra *et al.,* 2003; Ouellet *et al.,* 1997; Stenevik *et al.,* 2008). This could explain why batch A had a higher density than batch B, C and D in the initial stages of post fertilisation.

Spawning at the FFFL facility occurred later in the year than in the wild. The first and only batch of naturally spawned eggs were collected on the 28th October 2019. In the wild, fish are thought to spawn during the period of June and September (Collins *et al.,* 2010). The female fish at the farm began releasing eggs into the tanks in July; however the males were not releasing milt or the timing of the milt release was not matched with female egg release. Although for this experiment it has been assumed the eggs produced at the farm are representative of the wild, the late spawning or mistimed spawning of the males could invalidate this assumption. Since natural fertilisation was not occurring, it was decided the female and male fish would be stripped and eggs would be manually fertilised. However, the effect this has on egg quality is unknown.

During the course of the experiment, the egg quality in batch A was questionable. Many of the eggs in the incubator appeared cloudy and non-viable, only viable looking eggs were selected for experimentation. At eleven-days post fertilisation batch A was examined under the microscope, out of 50 arbitrarily selected eggs only one appeared to be viable (did not show a cloudy discolouration, shape deformity and embryo morphology fit with Mujica *et al.,* 2016 observation). It was also observed that the consistencies of the eggs were softer than they should be. Stress, diet, environmental factors and variations between individual age, weight and length of the fish can influence the quality of marine fish eggs (Bogevik *et al.,* 2012; Ochokwu *et al.,* 2015). Due to differing environmental conditions and diet at the FFFL compared to the wild eggs, egg quality at the hatchery may be lower.

There were also complications with batch B during their incubation period. It was noted that there were copepods and protozoans on dead eggs in the incubator, therefore this batch had to go through another disinfection. The disinfection process burns off the chorion of the egg, which may have an effect on the egg's buoyancy. After disinfection a random sample of batch B was analysed under a microscopeand while there were about 20% of deformities it was determined the batch was viable (Love A 2019, pers.comm. 26 November). The batch was used in experiments after re-disinfection and the data is similar to batch C where eggs were not re-disinfected, therefore the results were not discarded.

In 2019, FFFL experienced one of their worst years for obtaining fertilised eggs (Wylie A 2019, pers. comm. 27 November). Because of the low number of fertilised egg batches and late spawning during the timeframe of this experiment, replication was minimal. Due to the absence of sufficient replication, statistical analysis unfortunately could not be carried out. Ideally, the experiment would have been carried out for the entire egg phase, with a large amount of replication to account for natural variability in egg quality and buoyancy. As this was not possible for this research, it would be beneficial for future experiments to be carried out to help validate the findings of this study. If possible Coombs' (1981) density gradient column should be used as this would allow for precise buoyancy values to be found and could be used in future particle tracking simulations, which may increase the accuracy of transport pathways produced by a model.

Limitations of this study include the duration of the buoyancy experiments and minimal replication. Minimal replication leaves uncertainty in true buoyancy values of toothfish eggs. The most complete density profile with the data available from these experiments comes from batch A. Therefore, this profile will be used to inform buoyancy parameterisation in the particle tracking simulations. The short duration of the experiments meant that data could not be collected to hatching, leaving ambiguity about what happens to the buoyancy of batch A post 15-days fertilisation. Based on the literature (Jung *et al.,* 2012; Sundby & Kristiansen, 2015) there are at least two plausible buoyancy scenarios that could occur post 15 days; egg density could remain at the same value as 15-days post fertilisation until hatching (Scenario 1) or alternatively, egg density could decrease from 15-days post to hatching (Scenario 2) (Fig. 11). In Chapter 3, Batch A's density profile and the buoyancy scenarios shown in Figure 11, will be used to test the sensitivity of the results to uncertainty in egg buoyancy post-15 days. The affect of conditions and diet on captive fish which can lead to differing quality (density) of eggs and subsequent larvae is also a limitation to this study.

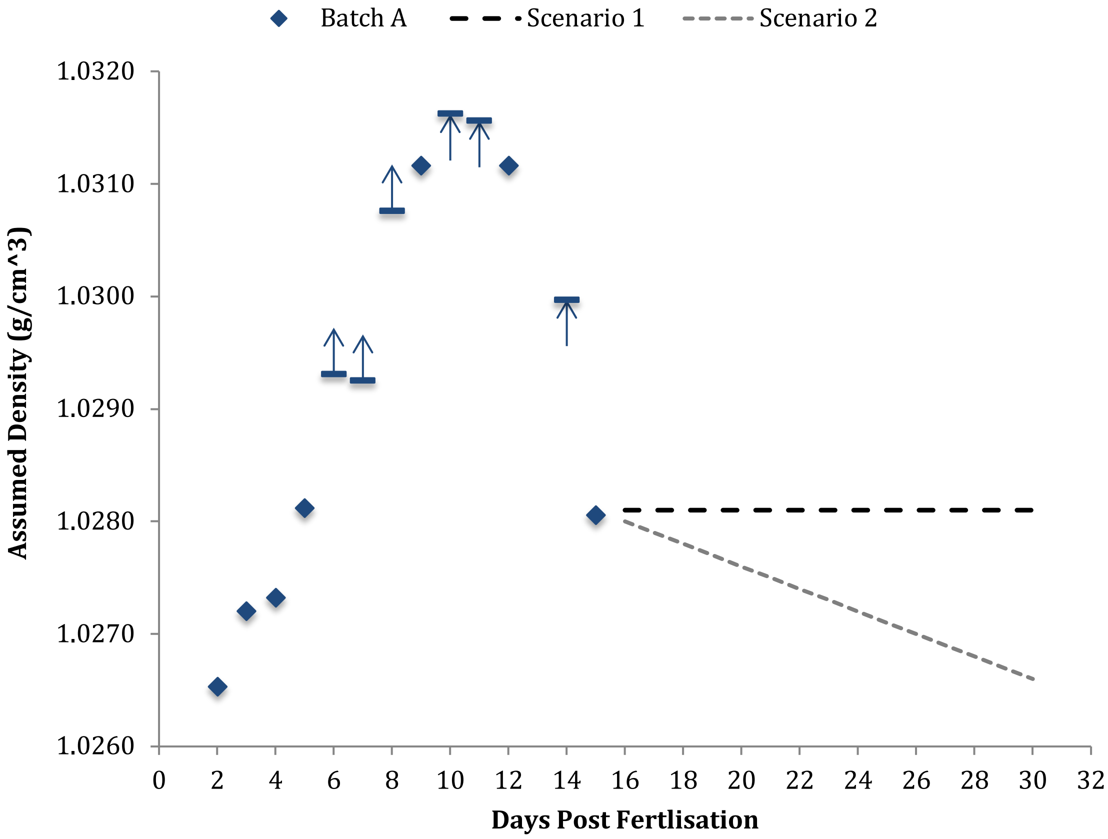


Figure 11. Assumed density profile of batch A with two plausible density scenarios beyond 15 days post fertilisation. Black dotted line - scenario 1 where density stays the same, grey dotted line - scenario 2 where density decreases to hatching.

2.5. Chapter conclusions

This experiment set out to determine the buoyancy of Patagonian toothfish eggs throughout embryonic development to allow for incorporation of buoyancy history into particle tracking simulations of Patagonian toothfish eggs. While the experiment gave an indication of buoyancy history in toothfish eggs during their development, issues arose in the experiment, such as, low replication, late spawning, poor egg quality and an incubator contamination for a batch of eggs being used in the experiment, that introduced uncertainty in the absolute values of buoyancy obtained. The experimental data that were obtained from this study, suggests that Patagonian toothfish eggs change buoyancy throughout embryonic development, following a similar pattern to buoyancy changes observed in several other marine fish species, although further data are needed to confirm this. The buoyancy data gathered from the most complete batch, batch A, will be used to parameterise egg behaviour (density changes through time) within the particle tracking work being completed in Chapter 3. Egg density values obtained from batch A experiments can be used as an informed starting point for the inclusion of egg buoyancy within the model. Uncertainty that remains in the egg buoyancy history (absolute values and density post-15 days) will be addressed in the modelling work by running sensitivity analyses, to cover plausible egg buoyancy scenarios and one scenario where egg buoyancy is not included within the particle tracking simulations.

3. Modelling the distribution of Patagonian toothfish eggs and larvae around the Falkland Islands

3.1. Introduction

Knowledge of life history traits is needed for effective long-term fisheries management, with larval dispersal being an important but poorly understood demographic process (Swearer *et al.,* 2019). Recruitment variability of pelagic eggs and larvae is tied to environmental conditions, which cause differential growth or mortality of individuals, including during the egg and/or larval stages (Hinckley *et al.,* 1996; Chambers & Trippel, 1997; Swearer *et al.,* 2019). Obtaining early life stage dispersal data on fish from direct sampling can be logistically challenging and costly (Cowen & Sponaugle, 2009; Swearer *et al.,* 2019). Fish egg and larval transport has been investigated using coupled biological (individual-based models) and physical ocean models and these models have become a tool for understanding recruitment (Hinrichsen *et al.,* 2002; Miller *et al.,* 2006; Miller, 2007). Biophysical models allow for key abiotic and biotic factors affecting the growth and survival of early life stages of fish to be examined through interacting factors such as temperature, light, turbulence and current transport (Hinrichsen *et al.,* 2011).

Fish species utilise different parts of their environment at different phases of their life cycles, with spatial connections between these locations allowing for completion of their life cycle (Hinrichsen *et al.,* 2011). Connectivity patterns (influenced by atmospheric and hydrographic forcing conditions) across time and space influence recruitment success through changes in dispersion and retention of early life stages from spawning grounds to areas suitable or unsuitable for survival (Heath & Gallego, 1997; Hinrichsen *et al.,* 2002).

Empirical study of larval connectivity is challenging because of the difficulties of conducting studies that quantify dispersal in the ocean. Most dispersal studies are based on predictions from biophysical models with hydrodynamic and particle tracking models dominating the literature (Swearer *et al.,* 2019). Broad scale modelling of velocity fields has been shown to capture long-distance dispersal patterns, particularly among offshore islands where oceanic influences maintain spatial coherence in velocity field (Liggins *et al.,* 2016). Such models have been used adopted to explore oceanic circulation on the Patagonian shelf (Combes & Matano, 2018; Matano *et al*., 2019).

Many marine fish species have pelagic early life stages, with recruitment strength influenced by large scale (>100km) and mesoscale (10-100km) circulation features, particularly in regions with variable and strong currents (Hinckley *et al.,* 1996). The mesoscale frequently describes spawning and nursery grounds of marine fish. Individual-based models (IBMs) are used in conjunction with circulation models to determine pathways of plankton stages of marine organisms (Werner *et al.,* 2007). These models have become key to understanding environmental interactions with marine organisms and factors impacting population connectivity and dispersal. There are several considerations needed in designing a modelling experiment. Spatial scale and model resolution need to be fine enough to capture the underlying physical dynamics in the area of study (Werner *et al.,* 2007). Mesoscale transport processes studied using well-validated models have been deemed essential in modeling early life history (Gallego *et al.,* 2007). Predicted fish egg and larval pathways can be influenced by the horizontal resolution of a model. Therefore horizontal resolution of the model used needs to be fine enough to capture the appropriate horizontal mixing processes prevailing in the study area (Hinrichsen *et al.,* 2002; Gallego *et al.,* 2007; Hinrichsen *et al.,* 2011). This study uses the highest resolution model (see section 3.2.1) presently available for the western South Atlantic region. Along with physical processes, biological processes also need to be considered; spawning time, spawning location, egg buoyancy and larval behaviour should be considered and incorporated where possible (Werner *et al.,* 2007; Ospina-Alvarez *et al.,* 2012).

Numerous studies have used coupled biophysical models to explore transport, retention and connectivity of early life stages of fish populations. For example Lett *et al.,* (2019) modelled the transport of larvae between a main spawning site and two nursery areas of gilthead seabream in the northwestern Mediterranean Sea. Meerhoff *et al.* (2020) assessed larval connectivity in a sandy beach mole crab through a coupled bio-oceanographic model in coastal Uruguay, Santos *et al.* (2018) focused on the European sardine and how spawning patchiness, migration behaviours and egg buoyancy affected the transport and recruitment on the continental shelf in the Western Iberia Upwelling ecosystem. Biophysical models have also been used to study the connectivity and dispersal of Patagonian toothfish, the focus of this study. Mori *et al.* (2016) and Brigden (2018) used coupled models in the Kerguelen Plateau and in South Georgia and Shag Rocks to examine temporal and spatial patterns of dispersal and retention of Patagonian toothfish eggs and larvae. Recent developments in the field call for a greater emphasis and inclusion of larval behaviour in coupled bio-oceanographic models (Leis 2021; *Swearer et al.,* 2019).

Distribution data for early life stages of Patagonian toothfish are scarce. Eggs are known to be pelagic with an extended residence time, which allows for the potential of high dispersal and connectivity of populations through advection (Collins *et al.,* 2010; Laptikhovsky *et al.,* 2006; Canales-Aguirre *et al.,* 2018). Patagonian toothfish eggs have been recorded drifting up to 500km to the North of South Georgia and Shag Rocks from spawning locations (Evseenko *et al.,* 1995; Brown, 2011). No similar data are available for the Falkland Islands, providing motivation for the present study.

To the east of the Falkland Islands topographic features on the shelf slope generate eddies which can cause redistribution of eggs to surface waters (Glorioso *et al.,* 2005; Brown, 2011). The stronger eastern branch of the Falkland Current may transport toothfish eggs to eastern and northern Falkland waters, while to the south and west of the Falkland Islands two quasi-stationary eddies have the potential to cause toothfish eggs and larvae to be retained in these areas (Arkhipkin *et al.,* 2010; Brown, 2011).

Ashford *et al.* (2012) previously used particle tracking simulations and otolith chemistry to test the surface connectivity of Patagonian toothfish early life stages around the Falkland Islands. Velocity fields from the global, primitive equation model OCCAM were used for particle tracking simulations. The model had a horizontal resolution of 1/12° (the highest available at the time) and 66 depth levels. A Lagrangian tracking code was used to simulate trajectory of particles, released in monthly cohorts on day 15 of each month, May to November from 1996 - 2000, from observed spawning locations on the Burdwood Bank, western North Scotia Ridge and the southwestern slope off Chile. Particles were tracked for 320 days post release. The study found otolith and particle trajectory data consistent with spawning areas off southern Chile and the Burdwood Bank supplying retention and recruitment into the Falkland Islands region. For their study, particles were only tracked in the surface layer of the model. However, we know from Evseenko *et al.* (1985) that particles are seen in the upper 700m of the water column, with highest abundances around 200m. From these observations it seems very unlikely that eggs and passive larvae are found directly at the surface (e.g. 0m). To address this limitation, the present study will use simulations with varying egg buoyancy, and therefore egg depth profiles, in an attempt to match previous at sea observations of egg distribution (Evseenko *et al,* 1985). This study will also investigate particle tracks in two different years, 2009 and 2012, to consider inter-annual variability in transport pathways.

To better inform fisheries management of Patagonian toothfish around the Falkland Islands, identification of potential transport pathways, at relevant depths, of early life stages is needed. In particular, a more in-depth understanding of connectivity between spawning areas in Chile and the Burdwood Bank in relation to Falkland juvenile and adult toothfish populations is needed. The aims of the modelling component of this research are: To identify potential pathways of eggs and passive larvae from spawning grounds around the Burdwood Bank and southern Chile and their contribution to areas suitable for retention around the Falkland Islands, as well as to investigate oceanographic mechanisms which may drive recruitment variability between years.

3.2. Overview of models

3.2.1. ROMS

The physical model output used in this study is the AGRIF version of ROMS (Shchepetkin & McWilliams, 2005). The grid extends from 82°W to 46°W and from 60°S to 45.6°S (Fig. 12). The grid has a 1/20° spatial resolution (~3.3km) and 40 vertical levels with higher resolution at the surface. At the surface, the model is forced by monthly climatology heat and freshwater fluxes from the COADS data set (Da Silva *et al.*, 1994) and by daily ASCAT wind stress. The ASCAT wind stress data was obtained from the Centre de Recherche et d'Exploitation Satellitaire (CERSAT), at IFREMER (http://cersat.ifremer.fr/). At the lateral open boundaries, the model is nudged toward the daily averaged temperature, salinity and ocean current from the 1/12° resolution GLORYS12 data-assimilated global ocean model available at http://marine.copernicus.eu (product identifier GLOBAL_REANALYSIS_PHY_001_030). The model forcing also includes the M2 tidal component. The model was run for the period 2008-2017 and the output was averaged every five days. The particle tracking simulations described below were carried out using the five-day averaged velocity fields from the ROMS model runs.

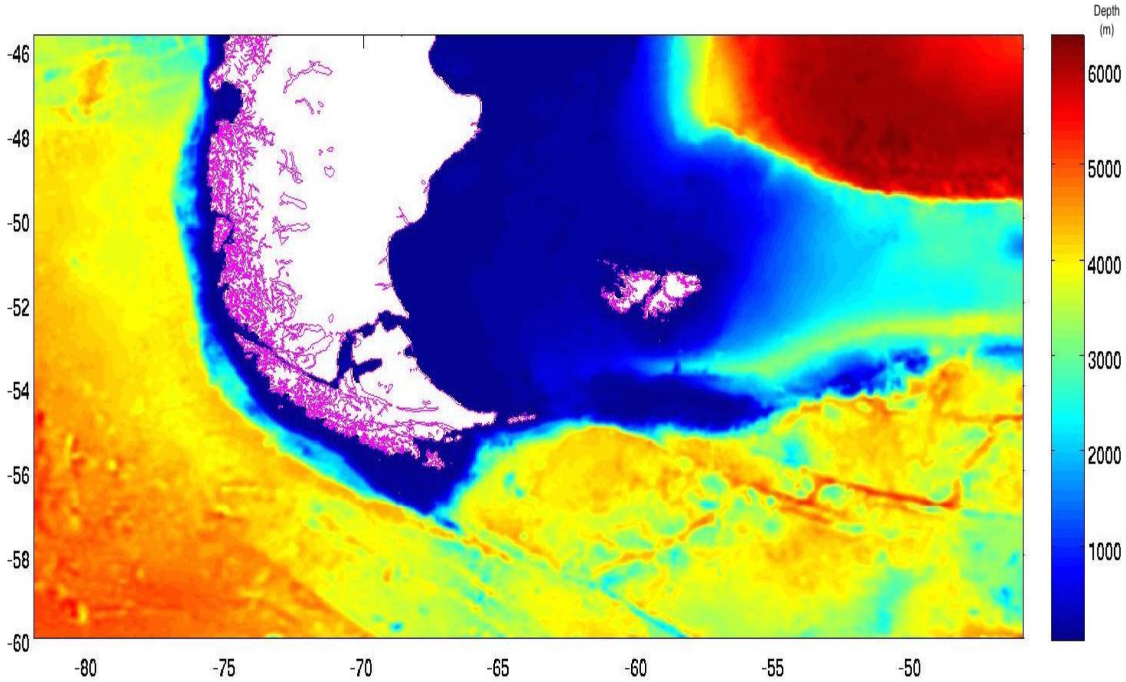


Figure 12. Region covered by the Southwest Atlantic Regional Oceanic Modelling System (ROMS). Shading represents water depth (m). (Source, Combes, V. 2020).

3.2.3. ICHTHYOP

Particle tracking simulations to study the transport of Patagonian toothfish eggs and larvae were carried out using the free Java tool ICHTHYOP/ROMS3D (Version 3_3.3) (http://www.ichthyop.org/). ICHTHYOP was chosen based on the recommendation of Ricardo Matano and Vincent Combes at Oregon State University. Ichthyop is an individual-based Lagrangian particle tracking model, which can be used to study biological and physical factors that may influence fish eggs and larvae (Lett *et al.,* 2008). The tool simulates Lagrangian transport of particles using velocity fields from ocean models such as ROMS. The software uses a standard 4th order Runge-Kutta equation to implement the differentiation of advection/diffusion equations. Ichthyop software has been widely used across a number of studies investigating ichthyoplankton (fish eggs and larvae) dynamics (Ospina-Alvarez *et al.,* 2012; Lett *et al.,* 2019; Deschepper *et al.,* 2020; Martins *et al.,* 2020, McGrath *et al.,* 2020).

3.3. Particle simulations

3.3.1. Particle release areas

Seven particle release areas were chosen around the Burdwood Bank (Fig. 13) and eight in southern Chile (Fig. 14), based on previous reports of female toothfish being found in spawning condition in these areas (Arana, 2009; Brown, 2011) and information provided but FIFD and SAERI. A bathymetric mask of 800-1200m was then used to ensure particles (virtual eggs) were only being released from areas that had appropriate depths for known toothfish spawning (Laptikhovsky *et al.,* 2006; Collins *et al.,* 2010; Brown *et al.,* 2013) (this has resulted in release sites not being of equal size).

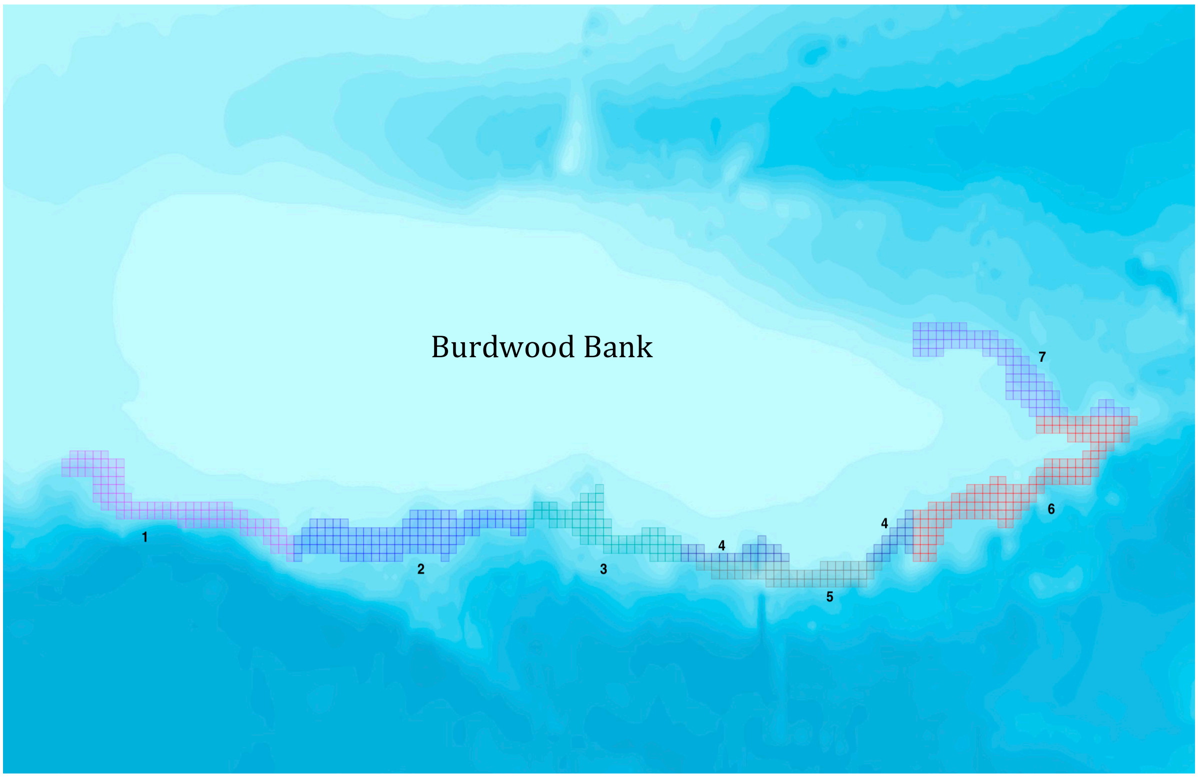


Figure 13. The seven particle release areas from around the Burdwood Bank

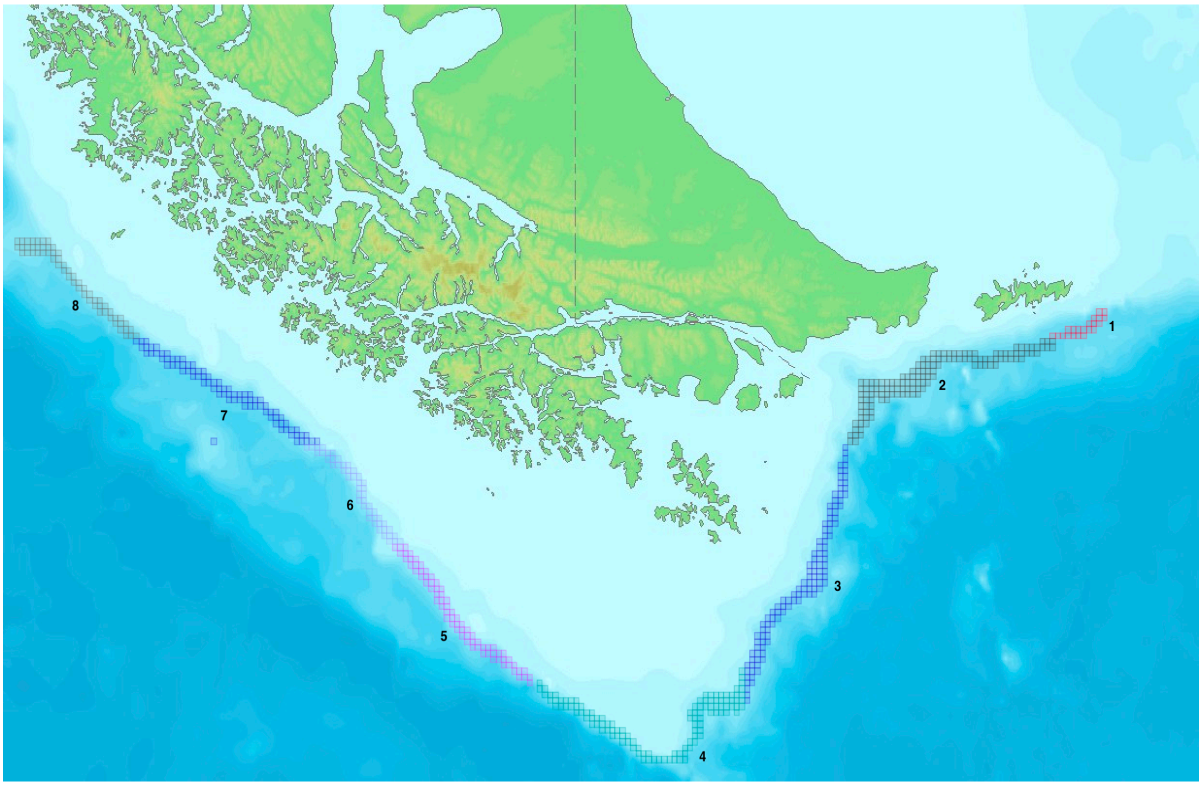


Figure 14. The eight particle release areas from southern Chile.

3.3.2. Particle release characteristics

Particles were released from the above areas on July 31st, the middle of known Patagonian toothfish spawning period (Collins *et al.,* 2010). ROMS ocean model data were available for the years 2008 - 2017. To investigate inter-annual variability in transport pathways, two years out of the ten available were selected. Ideally more years would have been investigated; however, time constraints did not allow for this. Survey data collected by the Falkland Island Government Fisheries Department (FIFD) showed that 2010 was a good year for recruitment whilst 2013 was a poor year for recruitment (T Farrugia 2019, pers.comm. 26 July). Therefore, the years of 2009 and 2012 were chosen as these are the spawning events that would correspond to the years were good/poor recruitment was subsequently seen. For each particle simulation, 10,000 particles were released, with the model distributing the particles evenly across the release areas, relative to area size. The release depth of particles was dependent on whether a particle density profile was included in the simulation: In simulations where density was included, eggs were released from the known toothfish spawning depth of 800-1200m (Collins *et al.,* 2010; Brown, 2011). In simulations where the particle buoyancy profile was neutral, eggs were released between 50 - 200m, as eggs have previously been observed in the upper portion of the water column (Evseenko *et al.,* 1985). Particle simulations were run for 60, 90 and 120 days. Details on these choices are given below (Section 3.3.4).

3.3.3. Particle retention areas

Four retention areas were defined around the Falkland Islands with a maximum depth of 200m. These areas were selected due to recently settled juveniles being previously found in these areas during annual surveys (Arkhipkin *et al.,* 2017) and from input from experts in both FIFD and SAERI, where it is usual to split the waters surrounding the Falklands into 4 zones. A further retention area in waters of less than 200m was also defined to the west of the Falkland Islands on the Patagonian Shelf. This area was selected because it appears sufficiently shallow to provide habitat for larval retention and sufficiently close to allow for subsequent movement of juvenile fish into nearshore habitat around the Falkland Islands (Fig. 15).

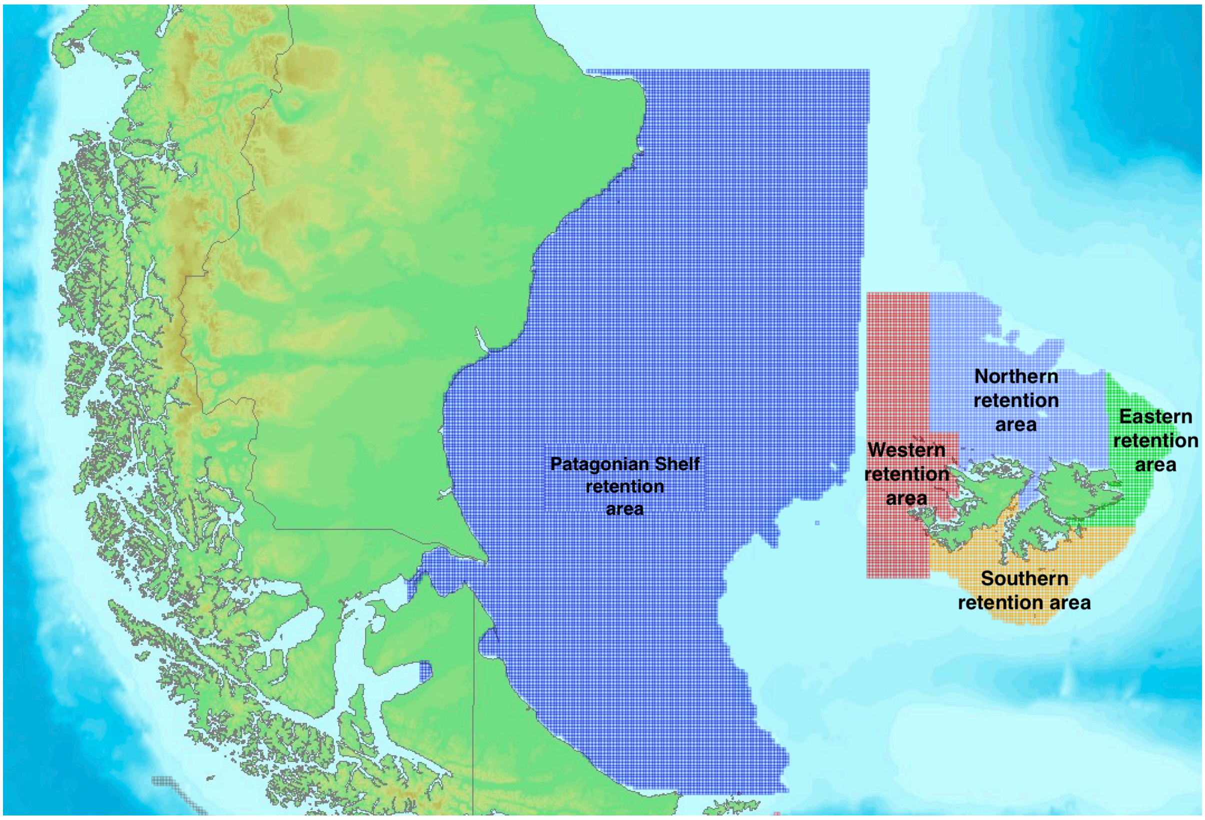


Figure 15. Defined retention areas around the Falkland Islands and on the Patagonian Shelf.

A particle was classified as being successfully retained if that particle was in one of the five retention areas on the last day of the particle simulation. No egg or larval mortality was included in the simulations; therefore potential retention in the model is only based on transport patterns and variability.

3.3.4. Parameter uncertainties

There are uncertainties surrounding Patagonian toothfish egg buoyancy and egg duration in the Southwest Atlantic.

No egg buoyancy data were available in literature for Patagonian toothfish and whilst a partial profile of egg buoyancy was obtained during egg buoyancy experiments at Falklands Fish Farming Limited (FFFL), results were not conclusive (Chapter 2). To account for this uncertainty in egg buoyancy, a series of model simulations with differing buoyancy values were completed and analysed. An appropriate egg buoyancy profile from the simulations was identified from these simulations by comparing egg depth profiles to those reported from previous at sea observations (Evseenko *et al.,* 1985) and egg trajectories leading to areas appropriate for retention and where juveniles have been seen around the Falkland Islands (Arkhipkin *et al.,* 2017). Details of these simulations can be found in Section 3.4.

Egg duration has been described to last 90 days in South Georgia and Shag Rocks (Evseenko *et al.,* 1985). Egg duration at two Patagonian toothfish hatcheries in southern Chile and the Falkland Islands observing egg duration of around 30 days (Mujica *et al.,* 2016; Love A 2020, pers.comm. 18 February). Therefore, particle simulations were completed from both southern Chile and the Burdwood Bank in 2009 and 2012 for 60 days, 90 days and 120 days, comprising of a one-month period where larvae are thought to still be passive particles and an egg duration of 30, 60 and 90 days to account for ambiguity in egg duration. This led to a total of 12 particle simulations being completed and analysed, once a suitable buoyancy profile was determined (Section 3.4).

3.4. Assessment of egg buoyancy within the model

This section examines the depth distribution and trajectory of the particles (virtual eggs) from multiple particle release simulations, in which several realisations of buoyancy profiles were used to ascertain an appropriate buoyancy profile for use in this research. Based on juvenile toothfish surveys conducted by the Falkland Islands Fisheries Department around the Falkland Islands (Arkhipkin *et al.,* 2017) and literature on egg depth distribution, we expect to see eggs (particles) within the upper 200m of the water column (Evseenko *et al.*, 1985) and transported to the retention areas defined in the model, where juveniles are often seen (Arkhipkin *et al.,* 2017) (Fig. 15). Several particle simulations were run using releases from the Chilean spawning areas with a transport duration of 60 days (comprising of a 30-day egg duration seen at FFFL and a one-month larval period), with a release date of 31st July 2009.

First, a simulation was undertaken where particles were released at the known toothfish spawning depth (800-1200m) and forced to the surface quickly where they remained for the entirety of the simulation (Fig. 16a). This simulation was completed to set a base line of where particles would advect if left at the surface. The depth distribution of particles is not consistent with egg distributions reported in the literature (Evseenko *et al.,* 1985). This simulation led to particles being swept east to the Burdwood Bank and into the Falklands Current and generally away from suitable retention areas (>200m) around the Falkland Islands and Patagonian Shelf (Fig. 16b).

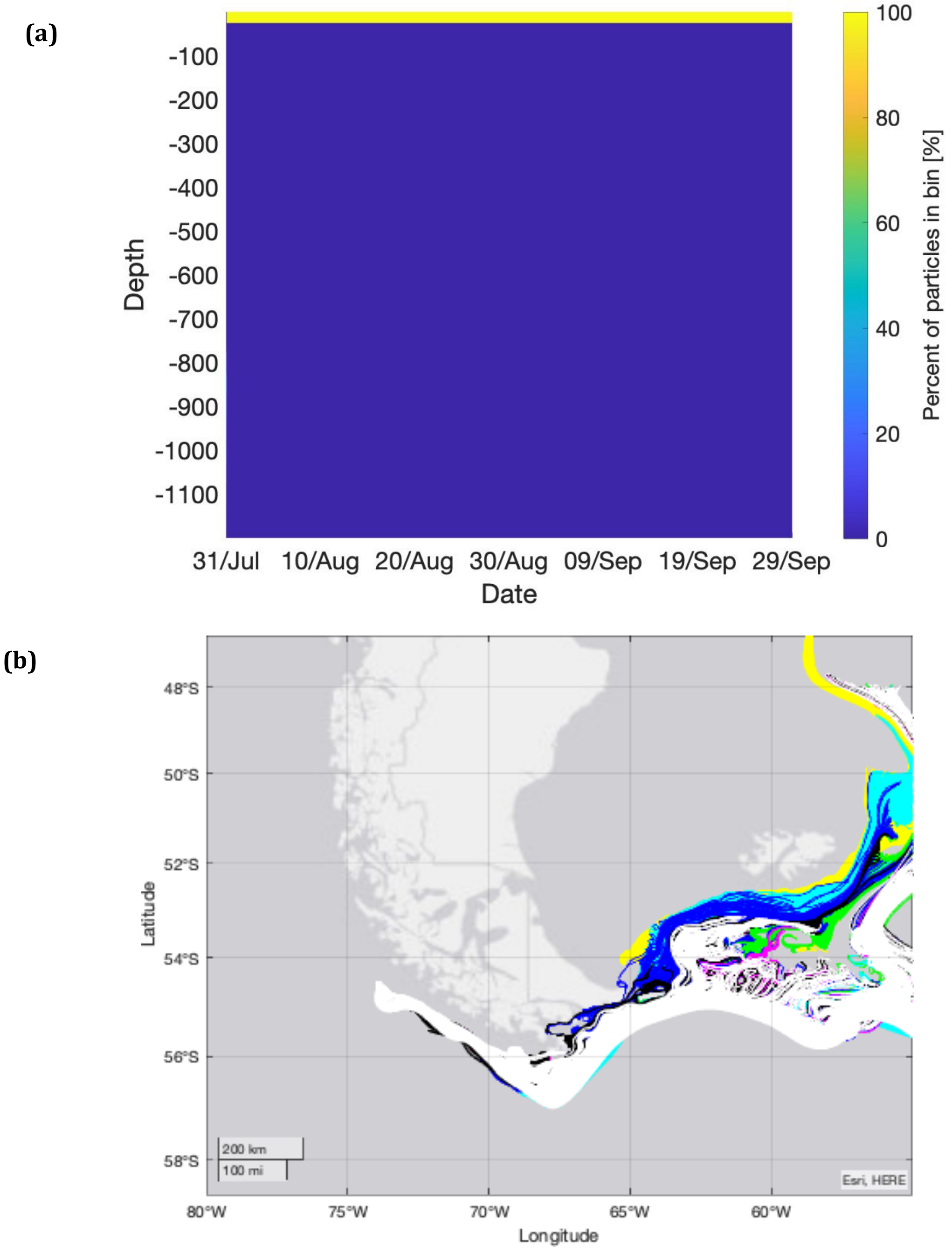


Figure 16. 60-day simulation of particles released from southern Chilean spawning areas on 31st July 2009 where particles are forced to the surface and remain there, a) Depth-time history of particles, b) particle trajectory. Colour represents area from which particles were released (colours do not reference colours in Fig. 14).

The next simulation used a neutral buoyancy profile with particles released at depths between 50-200m. When neutral buoyancy is used within the model simulations, it leads to an egg distribution within the water column consistent with observed egg distributions (Evseenko *et al.,* 1985). Particles are distributed in the upper 200m of the water column, not all particles are found at the surface and few advect at depth greater than 200m (Fig. 17a). Trajectories from this simulation show that particles move up onto the shelf and into areas close to the Falkland Islands (Fig. 17b), which are areas with suitable depth for particles to retain and are areas where juvenile toothfish have previously been identified.

A third simulation utilised the most complete buoyancy profile, batch A, obtained from the experiments conducted at FFFL (Chapter 2, Fig. 10). The depth profile of the particles over the 60-day model simulation time does not seem plausible (Fig. 18a). Particles are advected mainly at depths between 900 – 1500 m, (Fig. 18a), which does not fit with the at sea observations of eggs being found in the upper portion of the water column (Evseenko *et al*., 1985). The particle trajectories result in advection towards the south of the Burdwood Bank and some onwards into the outer portion of the Falklands Current (Fig. 18b). Due to the depth profile of the particles in this simulation not fitting with Evseenko *et al.* (1985) observations, batch A's density profile will not be used in future model simulations.

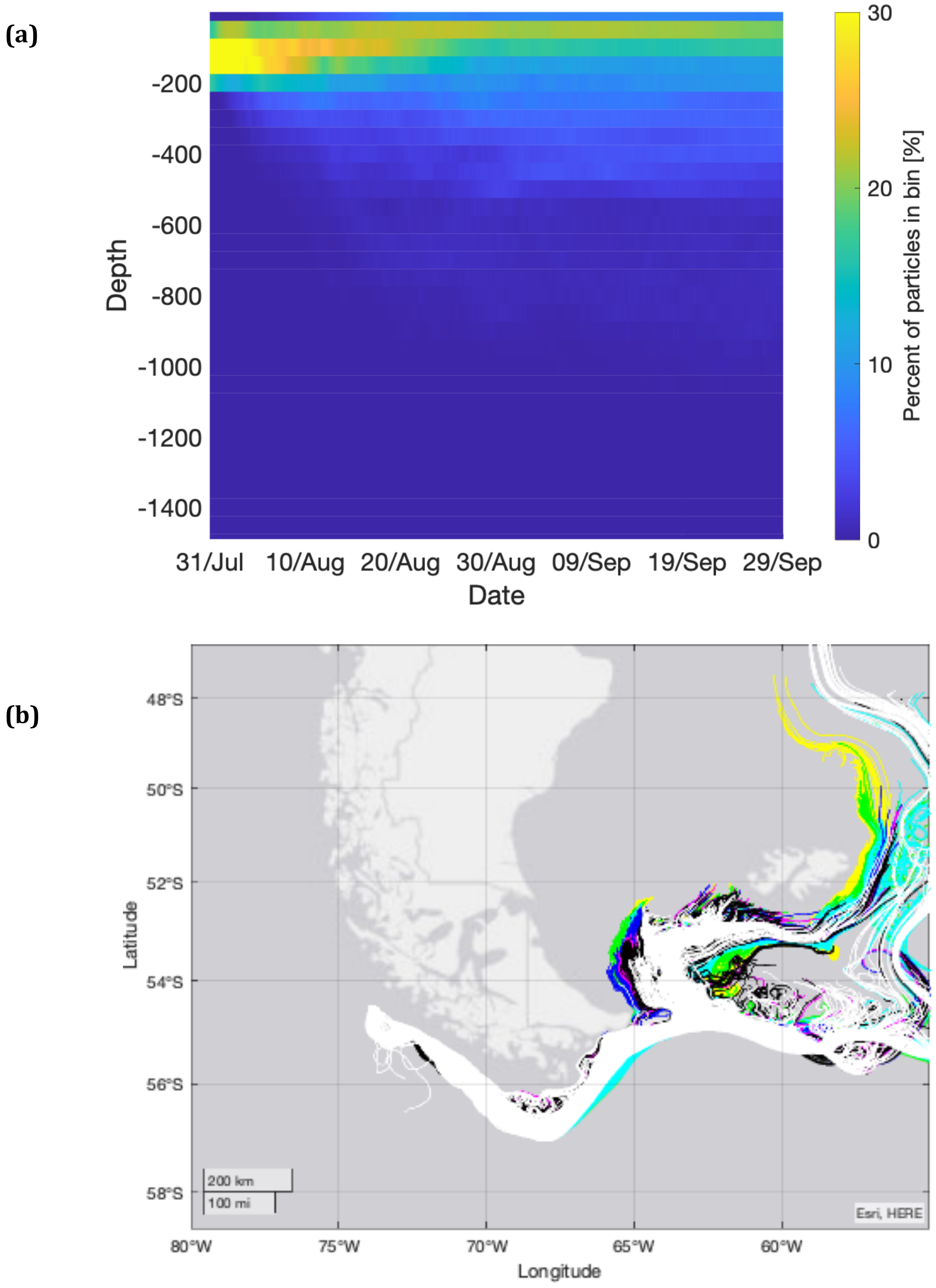


Figure 17. 60-day simulation of particles released from southern Chilean spawning areas on 31st July 2009 with a neutral buoyancy, a) Depth-time history of particles, b) particle trajectory. Colour represents area from which particles were released (colours do not reference colours in Fig. 14).

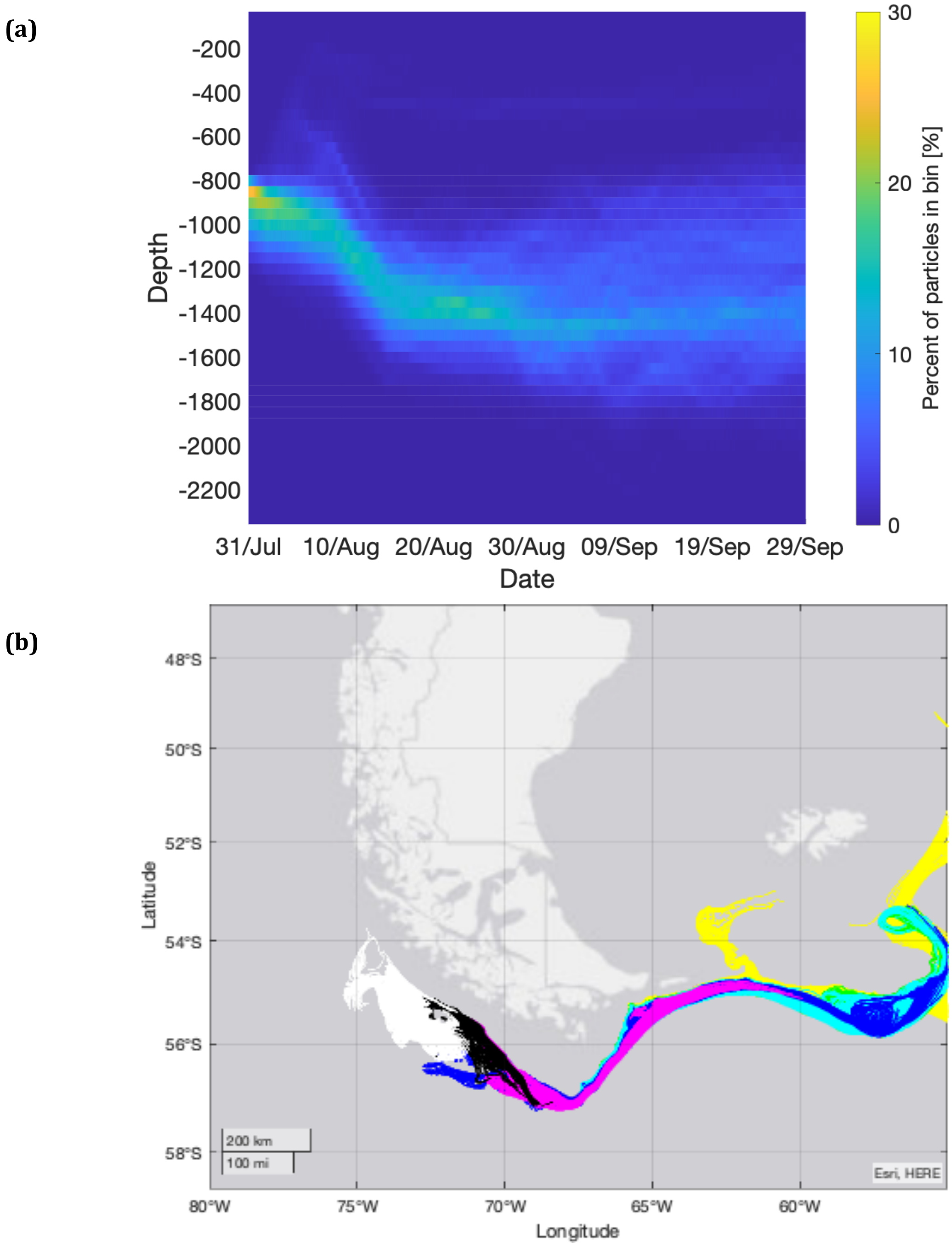


Figure 18. 60-day simulation of particles released from southern Chilean spawning areas on 31st July 2009 using batch A's buoyancy profile, a) a) Depth-time history of particles, b) particle trajectory. Colour represents area from which particles were released (colours do not reference colours in Fig. 14).

The density of batch A eggs appears to be much greater than the other three batches in the experiment. The shape of the buoyancy profile is assumed to be correct as it follows a similar profile to other marine species (Jung *et al.,* 2012; Sundby & Kristiansen, 2015). An inspection of the starting density values for batches B, C and D (1.0241 g/cm^3) suggests there could be a 0.025 g/cm^3 bias in batch A (e.g. the eggs are too dense). A value of 0.025 g/cm^3 was therefore subtracted from batch A's data points, creating a similarly shaped buoyancy profile but at a lower density that agrees with batches B, C and D (Fig. 19).

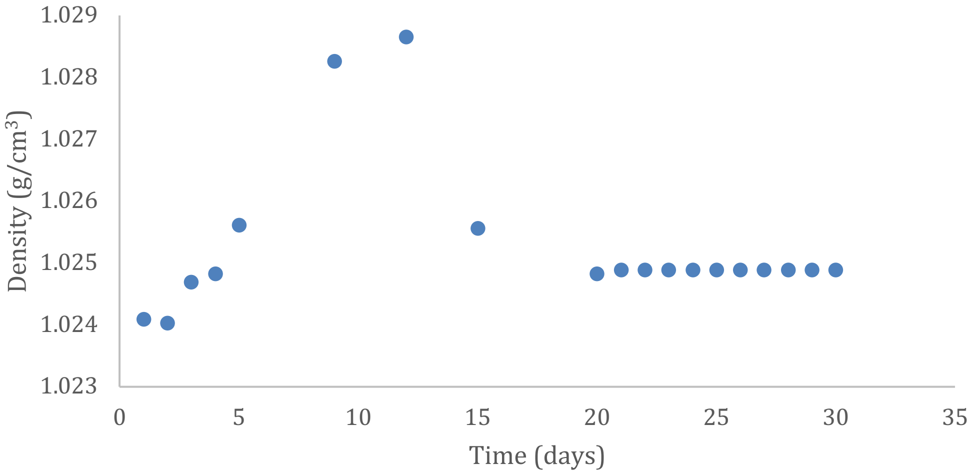


Figure 19. Altered density profile removing a suggested 0.025 g/cm^3 bias from batch A's data points.

This altered profile was then used in further particle simulations (Fig. 20). Only a small percentage of particles was observed in the upper 200m of the water column, between 20- and 30-days post release, with the majority still at depths of between 550 – 800m (Fig. 20a). Around 15% of particles was at the surface around 30 days (time of hatching) and there is only a small percentage of particles distributed between 0 and 200m, with most found below 200m of depth. This depth distribution of particles are inconsistent with previous at-sea observations (Evseenko *et al.,* 1985) (Fig. 20a). Particles are also seen travelling in the Falklands Current and around the Burdwood Bank, but not into areas suitable for retention with water depths of less than 200m (Fig. 20b).

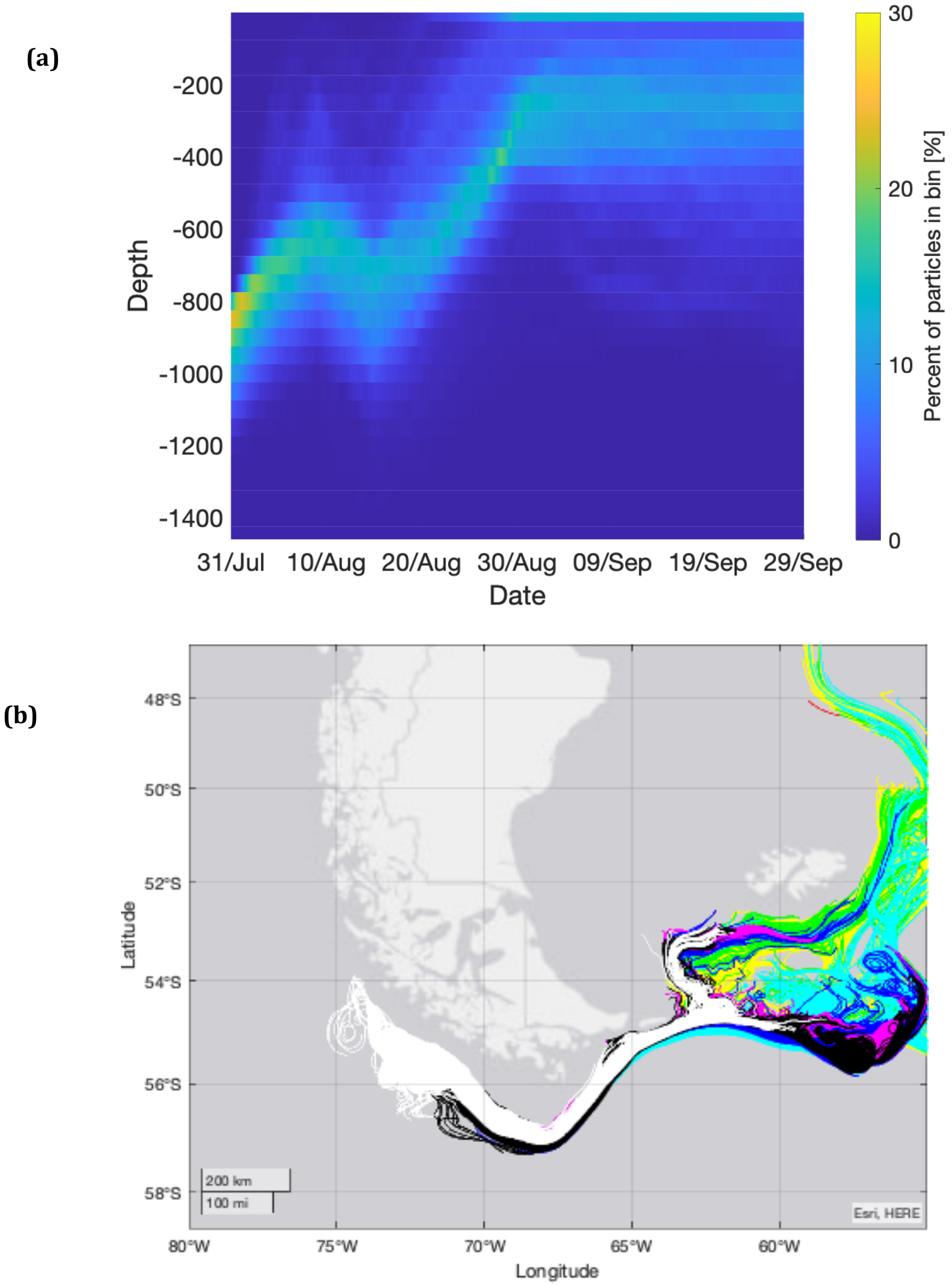


Figure 20. 60-day simulation of particles released from southern Chilean spawning areas on 31st July 2009 with an altered buoyancy profile, a) Depth-time history of particles, b) particle trajectory. Colour represents area from which particles were released (colours do not reference colours in Fig. 14).

To further test the sensitivity of the particle simulations to egg buoyancy, the altered density profile was nudged down three times, each time by 0.001 g/cm^3 (Fig. 21). Further particle simulations using these further altered profiles were then completed (Figs. 22-24).

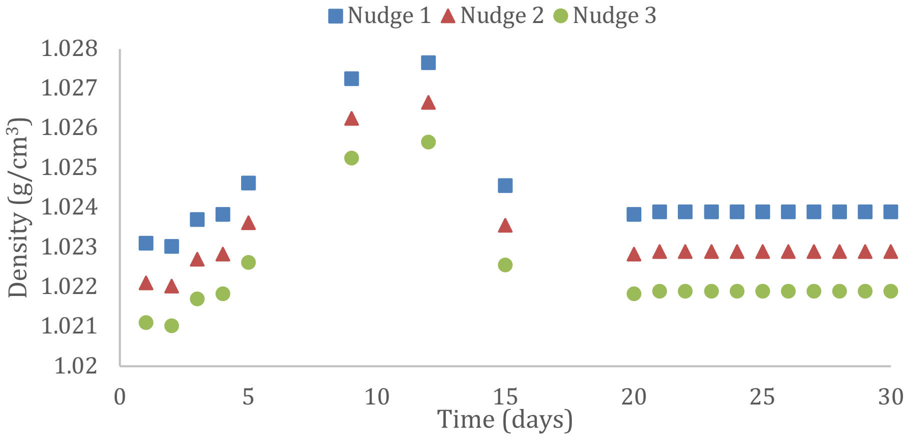


Figure 21. Altered density profile nudged down three times each time by 0.001g/cm^3.

In the particle tracking simulation using the altered buoyancy profile nudged down by 0.01, 60% particles reach the surface (0m) by around 28 days (2 days before hatching is due) (Fig. 22a). Particles are not distributed across the upper 200m of the water column over the 60-day period, as seen with the neutral buoyancy profile (Fig. 17). Particles continue ascending to the upper most layer of the water column. The particles advect towards the Burdwood Bank as well as eastward into the Falklands Current, but again, not onto the shelf into areas with depth suitable for retention (Fig. 22b).

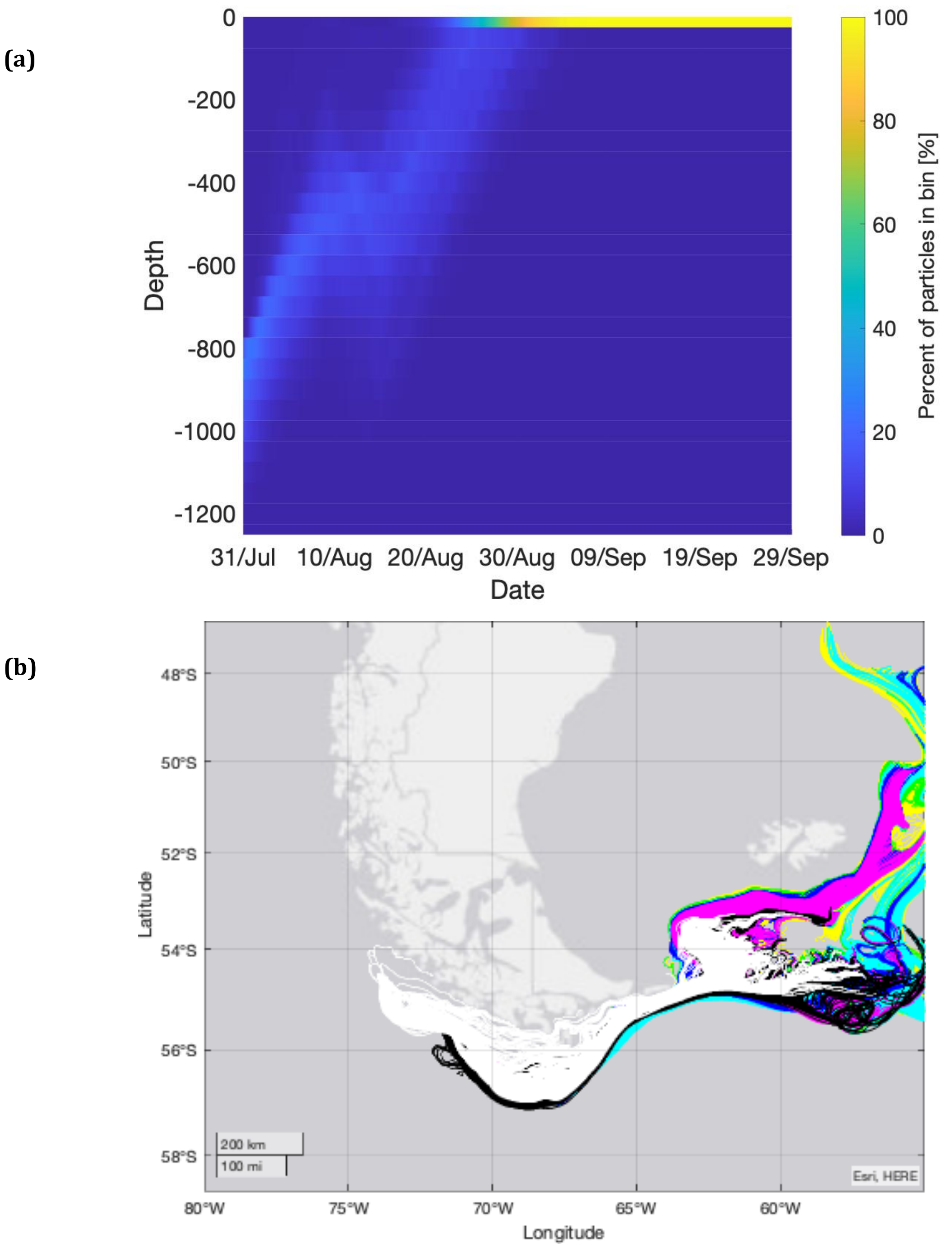


Figure 22. 60 day simulation of particles released from southern Chilean spawning area on 31st July 2009 with the altered buoyancy profile lowered by 0.001g/cm^3**,** a) Depth-time history of particles, b) particle trajectory. Colour represents area from which particles were released (colours do not reference colours in Fig. 14).

In a particle tracking simulation using the altered buoyancy profile nudged down by 0.002g/cm^3, 60% of particles had reached the surface within 20 days, faster than when nudging down by 0.001g/cm^3 (Fig. 23a). Particles follow a similar trajectory to the 0.001g/cm^3 nudge, with particles not moving into areas with depths suitable for retention (Fig. 23b).

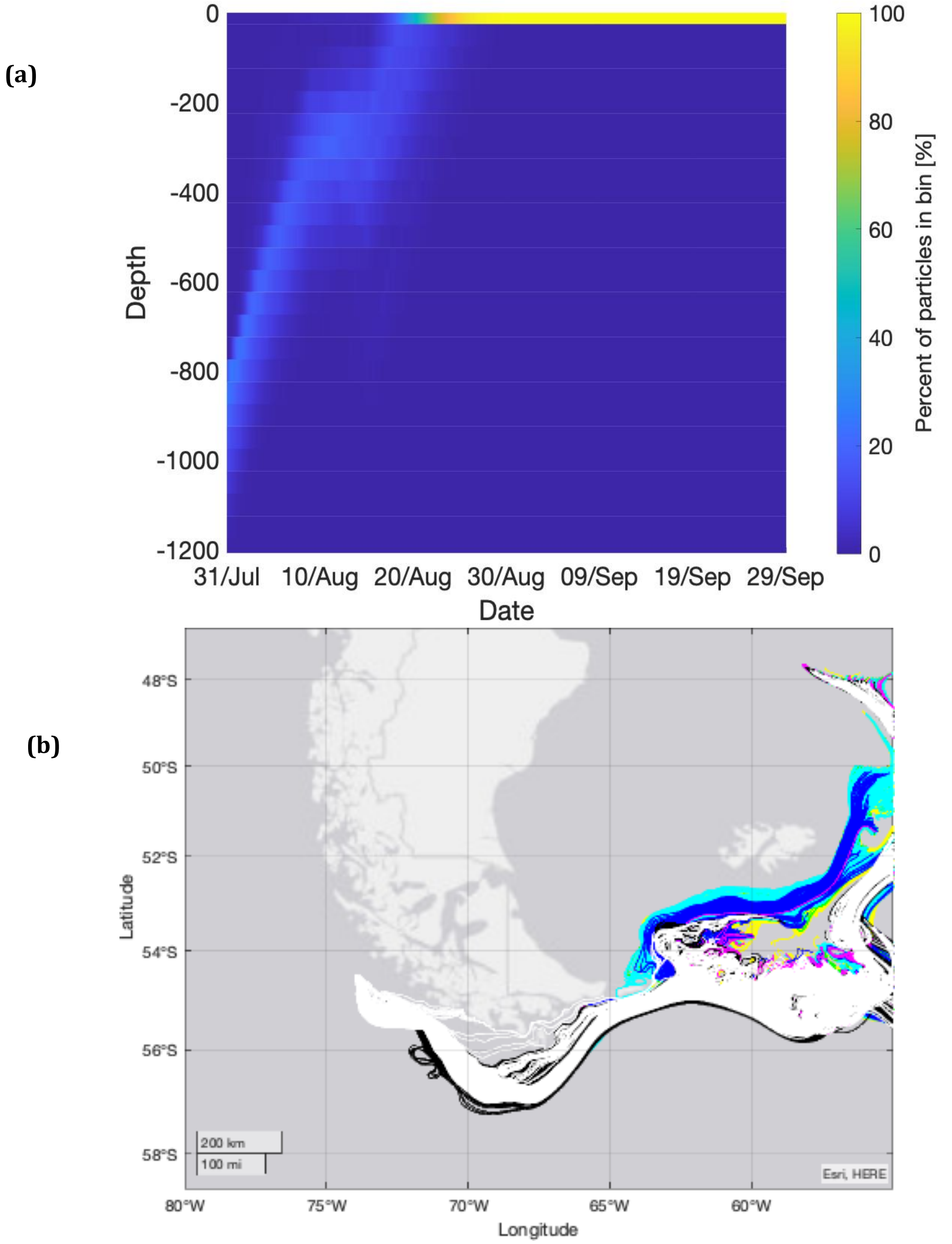
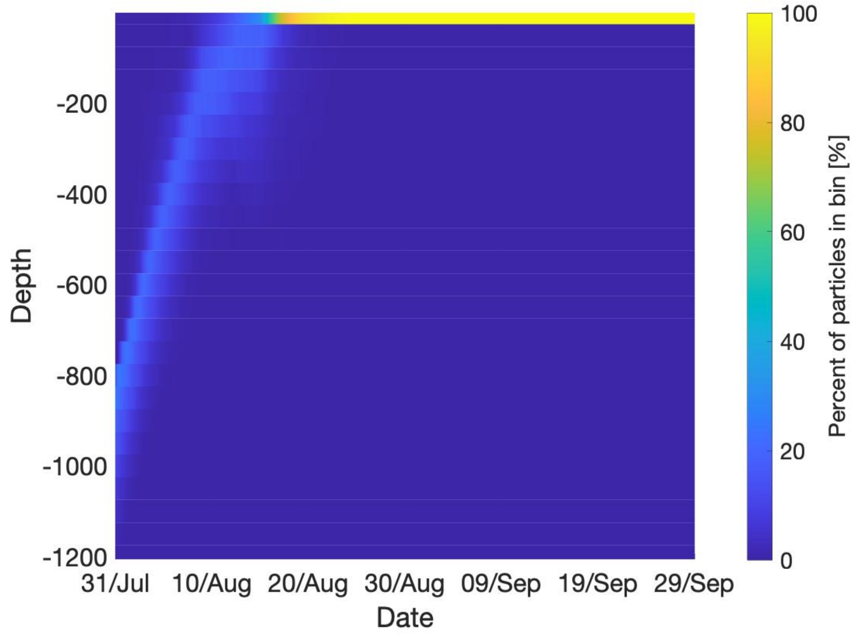


Figure 23. 60 day simulation of particles released from southern Chilean spawning areas on 31st July 2009 with the altered buoyancy profile lowered by 0.02g/cm^3, a) Depth-time history of particles, b) particle trajectory. Colour represents area from which particles were released (colours do not reference colours in Fig. 14).

In a further particle simulation where the altered profile is lowered by 0.003 g/cm^3 particles are reaching the surface the fastest with 60% of particles seen in the upper most layer of the water column by 15 days (Fig. 24a). The depth profile sees the same pattern as the other two nudges with eggs ascending to the surface and remaining there (Fig. 24a). Particle trajectory is also similar to the other two nudges (Fig. 24b).

(a)



(b)

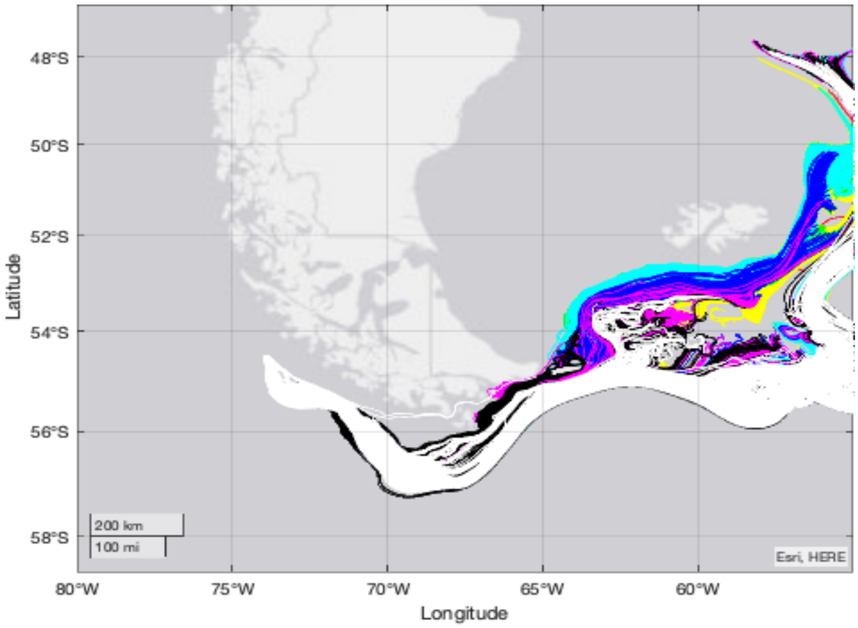


Figure 24. 60 day simulation of particles released from southern Chilean spawning areas on 31st July 2009 with the altered buoyancy profile lowered by 0.03g/cm^3, a) Depth-time history of particles, b) particle trajectory. Colour represents area from which particles were released (colours do not reference colours in Fig. 14).

3.4.2. Summary of buoyancy assessment

A distribution of eggs within the upper 200m of the water column, not just at the surface, seems important in leading to trajectories where particles move up on to the shelf into depths suitable for retention. The simulations using several plausible modifications of the buoyancy profile collected from experiments at FFFL do not produce the distribution of particles within the water column seen when neutral buoyancy is used. From at-sea observations of eggs being mainly found at around 200m (Evseenko *et al.,* 1985), the simulations using egg buoyancy within the model generate depth profiles that are either too dense and do not ascend to areas of the water column where eggs have been observed or particles ascend to the upper most layer of the water column. Trajectories largely do not lead to areas that would be suitable for retention (an area on the shelf less than 200m) or where young juveniles have been found (Arkhipkin *et al.,* 2017) (Table 2).

From the results above, the simulations are likely highly sensitive to particle (egg) density. The depth distribution of particles that fits most closely to observed egg distributions (Evseenko *et al.,* 1985) and which leads to retention into areas where juvenile toothfish have previously been reported (Arkhipkin *et al.,* 2017) is obtained by releasing particles from depths of 50-200m and using a neutral buoyancy within the particle tracking simulations. Therefore, a neutral buoyancy profile will be used for assessing which spawning areas are likely to be important in retention and transport success for Patagonian toothfish and to investigate why some years have good recruitment and others poor recruitment.

Table 2. Summary of simulations completed for the assessment of use of particle buoyancy.

Release Area (See Fig. 14)	Release Date	Particle Buoyancy	Release Depth (m)	Simulation Duration (days)	Does density profile match literature?	Advection of particles to suitable areas?	Figure reference
Southern Chile	31st July 2009	0.09 g/cm^3	800-1200	60	No	No	Fig, 16
Southern Chile	31st July 2009	Neutral	50-200	60	Yes	Yes	Fig. 17
Southern Chile	31st July 2009	Batch A profile (Chapter 2, section 2.3)	800-1200	60	No	No	Fig. 18
Southern Chile	31st July 2009	Altered Profile (Figure 19)	800-1200	60	No	No	Fig. 20
Southern Chile	31st July 2009	Altered profile minus 0.001 g/cm^3	800-1200	60	No	No	Fig. 22
Southern Chile	31st July 2009	Altered profile minus 0.002 g/cm^3	800-1200	60	No	No	Fig. 23
Southern Chile	31st July 2009	Altered profile minus 0.003 g/cm^3	800-1200	60	No	No	Fig. 24

3.4.3. Final model simulations

12 model simulations were conducted releasing particles at depths of 50-200m from areas shown in Figs. 13 and 14 using a neutral buoyancy profile for egg density (Table 3). These simulations were used to analyse connectivity/transport success and retention success around the Falkland Islands and onto the Patagonian Shelf. Here connectivity success is defined as the number of particles retained in each retention area divided by number of particles released from a release area. Similarly, retention success is defined as the number of particles reaching a retention area divided by the total number of particles released (10,000).

Table 3. Summary of the 12 final model simulations conducted.

Release Areas (See Fig. 13, 14)	Release Date	Particle Buoyancy	Release Depth (m)	Simulation Duration (days)	Age at which particles can be considered retained
Southern Chile	31st July 2009	Neutral	50-200	60	59
Southern Chile	31st July 2009	Neutral	50-200	90	89
Southern Chile	31st July 2009	Neutral	50-200	120	119
Burdwood Bank	31st July 2009	Neutral	50-200	60	59
Burdwood Bank	31st July 2009	Neutral	50-200	90	89
Burdwood Bank	31st July 2009	Neutral	50-200	120	119
Southern Chile	31st July 2012	Neutral	50-200	60	59
Southern Chile	31st July 2012	Neutral	50-200	90	89
Southern Chile	31st July 2012	Neutral	50-200	120	119
Burdwood Bank	31st July 2012	Neutral	50-200	60	59
Burdwood Bank	31st July 2012	Neutral	50-200	90	89
Burdwood Bank	31st July 2012	Neutral	50-200	120	119

3.5. Results

3.5.1. Connectivity of the Burdwood Bank to the Falkland Islands and the Patagonian Shelf

In 2009 and 2012, there was no connectivity between particles released from the Burdwood Bank (Fig. 13) and the five retention areas defined around the Falkland Islands and on the Patagonian Shelf (Fig. 15) for either the 60-day simulation or 90-

day simulation and in 2012 there was no connectivity for the 120-day simulation. Particles were swept eastward towards the North Scotia Ridge or were entrained in the Falklands Current (Fig. 25).

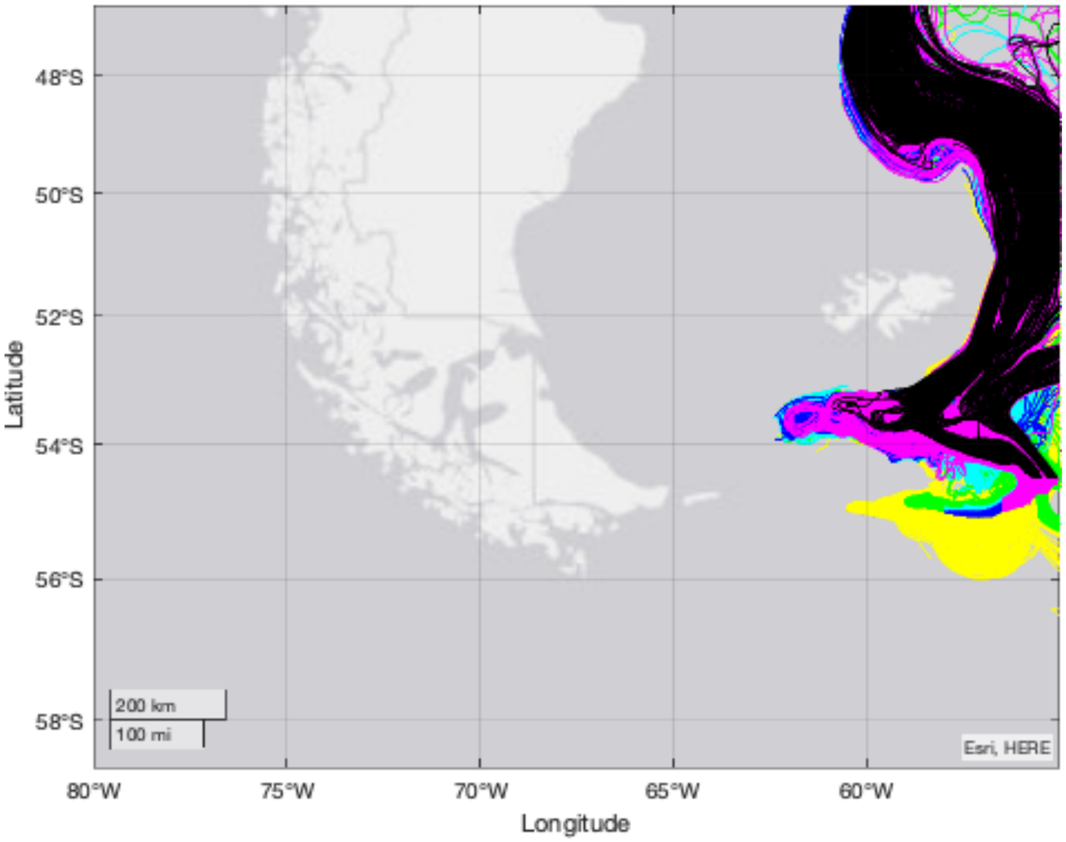


Figure 25. Trajectory of particles released in 2009 from the seven release areas around the Burdwood Bank. The simulation was run for 120 days. Colour represents area from which particles were released (colours do not reference colours in Fig. 14).

The simulation run for 120 days in 2009 led to a very small transport success between Burdwood Bank release site 1 and the northern (0.06%), the eastern (0.37%) and southern (0.12%) retention area. There was no transport success from any of the other six release sites (Fig. 26).

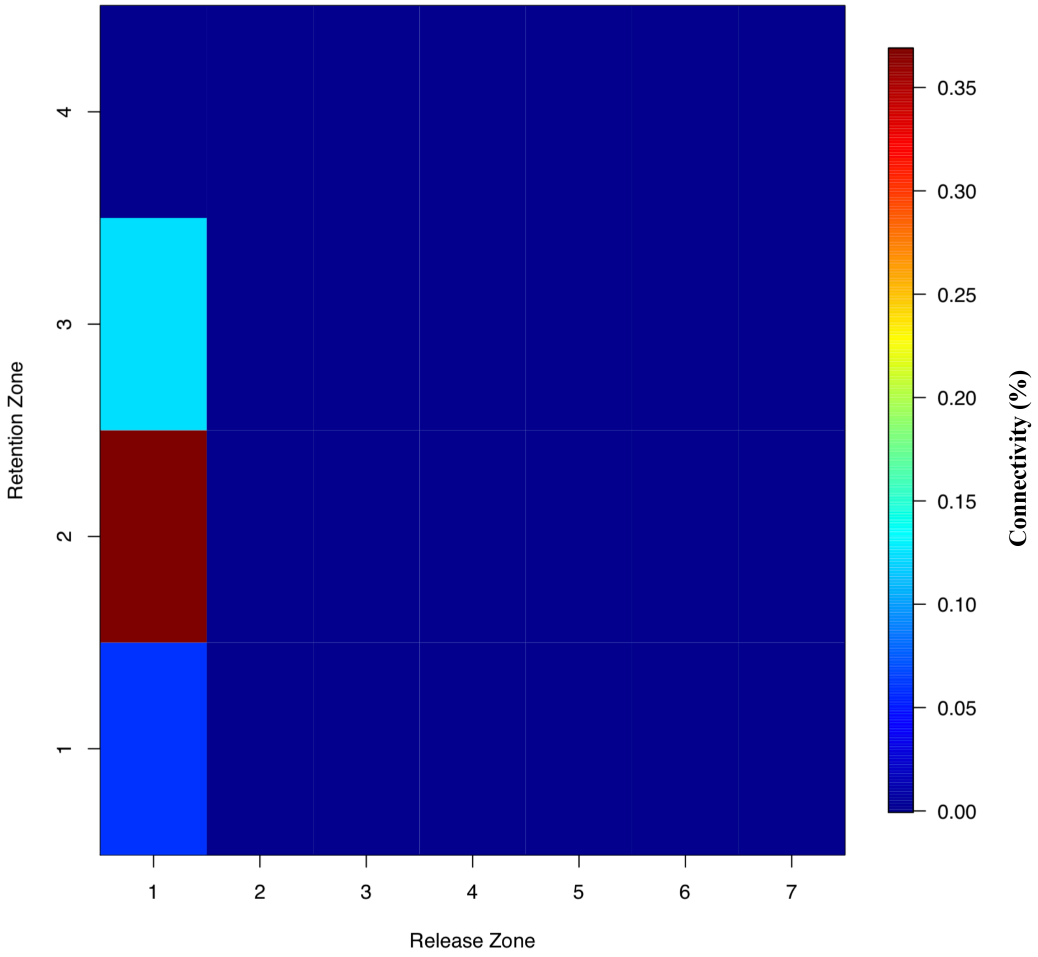


Figure 26. Connectivity matrix between the seven release areas around the Burdwood Bank and the four retention areas around the Falkland Islands (refer to Figure 13 and 15 for geographic locations for release and retention areas respectively).

3.5.2. Connectivity of southern Chile to the Falkland Islands and the Patagonian Shelf

Across all three particle tracking simulation lengths in 2009, the greatest connectivity was found between the southern Chilean release areas of 5, 6, 7 and 8 (Fig.14) and the Patagonian Shelf retention area (Fig.15) with a transport success of greater than 20%. The highest transport success, and therefore connectivity, was seen between release area 5 and the Patagonian Shelf retention area (retention zone 5; >50%). Between the other four release areas and the four retention areas transport success was less than 10% (Fig. 27).

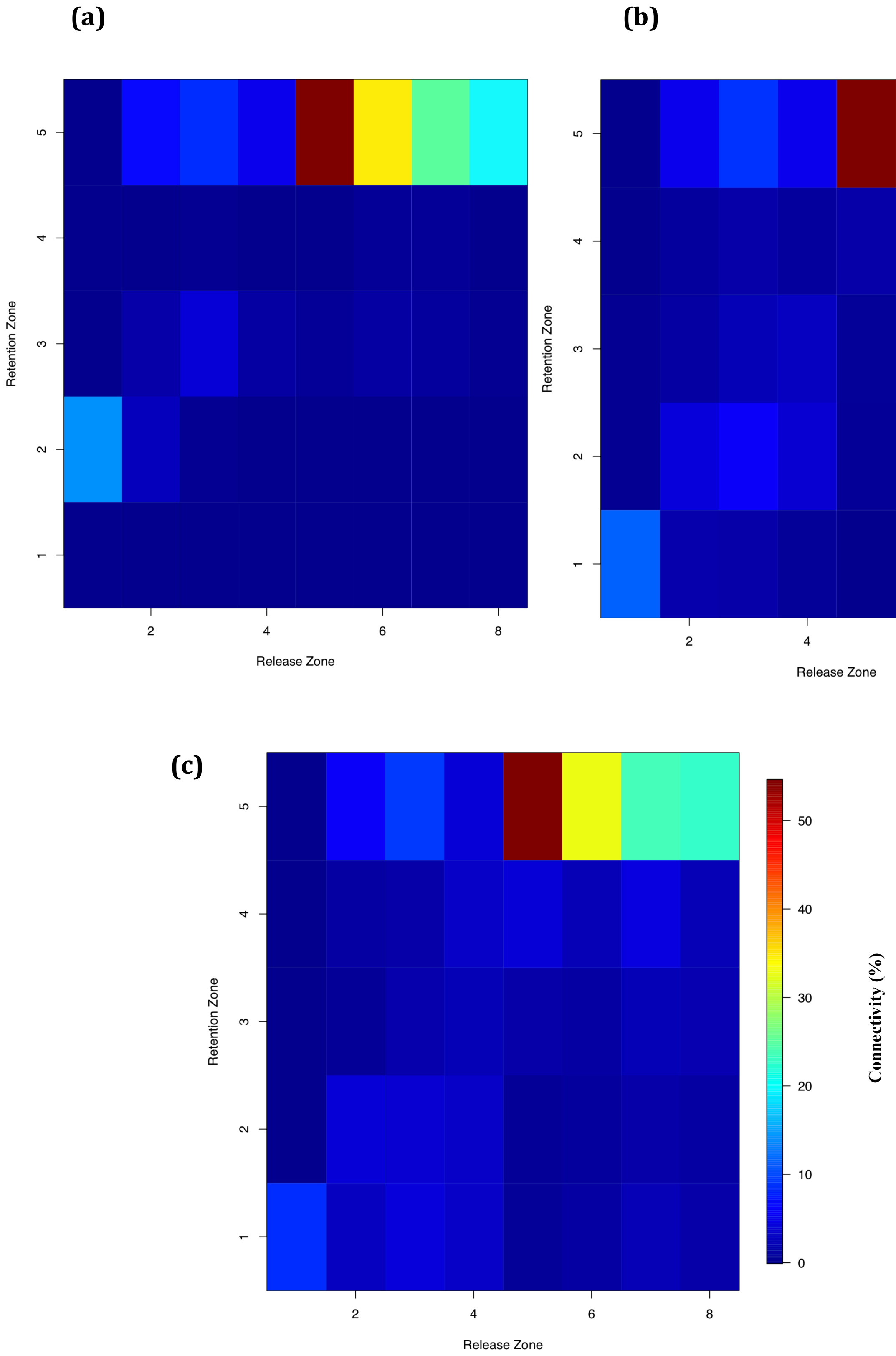


Figure 27. Connectivity matrices for 2009, a) 60 days, b) 90 days, c) 120 days for southern Chilean release areas and the Falkland Islands and Patagonian shelf retention areas (refer to Figure 14 and 15 for geographic locations for release and retention areas respectively).

During 2012, connectivity between release and retention areas varied with the length of the simulation (Fig. 28). In the 60-day simulation, the highest connectivity occurs between release area 7 and the Patagonian Shelf retention area with a 10% transport success between these areas (Fig. 28a). The 90-day simulation shows connectivity is greatest between three sets of release/retention areas: release area 1 and the eastern retention area (7.6% transport success), between release area 3 and the western retention area (7% transport success) and between release area 7 and the Patagonian Shelf retention area (7.4% transport success) (Fig. 28b). Running the simulation for 120 days shows the greatest connectivity is between release area 3 and the western retention area with a transport success of 10.4%. Relatively high connectivity is also found between release area 1 and the northern retention area, which had an 8.5% transport success and 7.6% with the eastern retention area. Release area 2 had an 8.1% transport success to the eastern retention area (Fig. 28c).

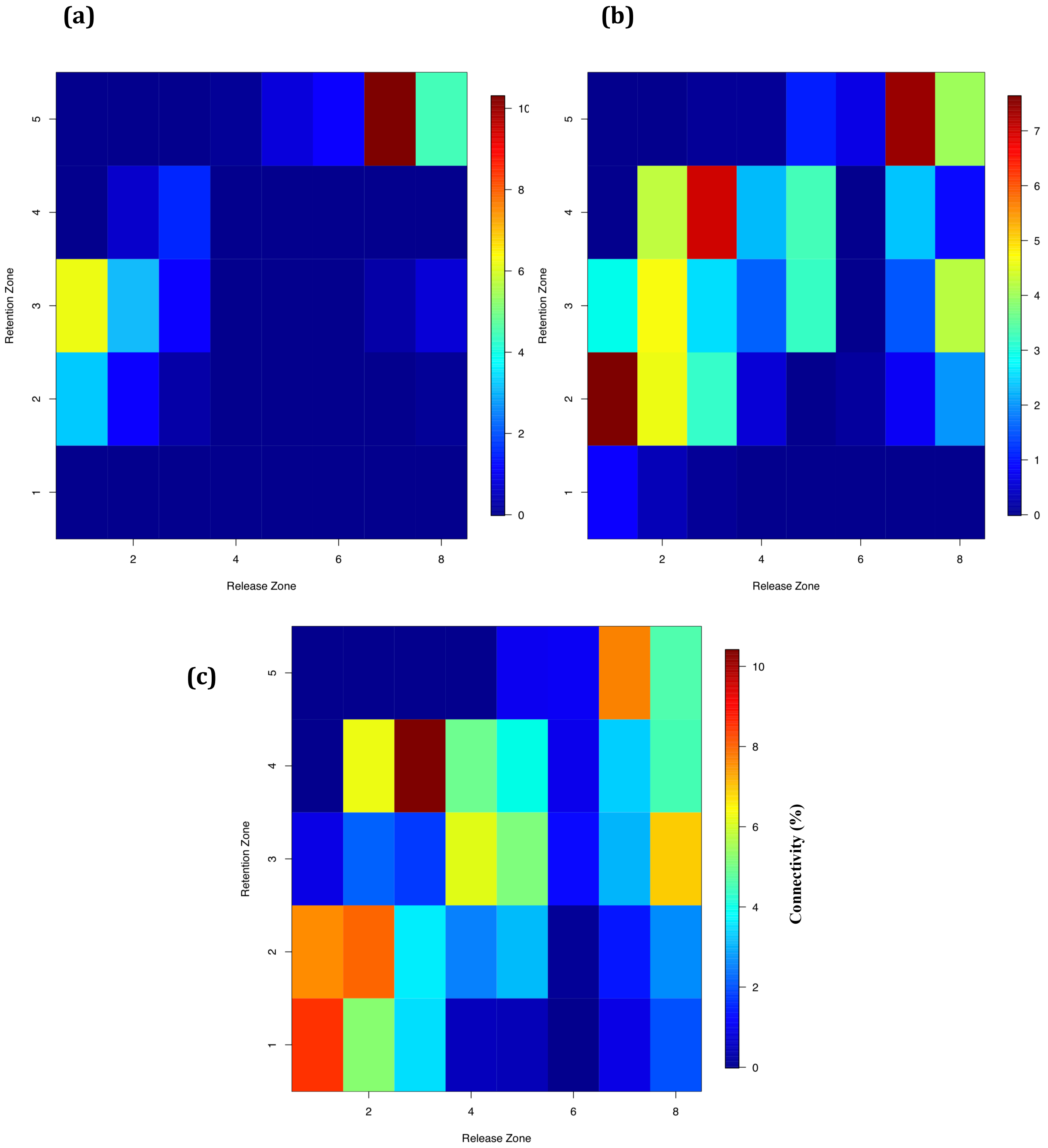


Figure 28. Connectivity matrices 2012, a) 60 days, b) 90 days, c) 120 days for southern Chilean release areas and the Falkland Islands and Patagonian Shelf retention areas refer to Figure 14 and 15 for geographic locations for release and retention areas respectively).

3.5.3. Retention success from southern Chile to the Falkland Islands and Patagonian Shelf

In 2009, the Patagonian Shelf had the most retention success across all retention areas and for all three simulation lengths (17-19%, Fig. 29). All other retention areas had low retention success in comparison. When excluding the Patagonian Shelf, the highest retention (3.17%) is seen in the eastern Falkland Islands area for the 90-day simulation. The 60-day simulation length produced the lowest retention success for all areas except for the Patagonian Shelf. The 60-day simulation resulted in the highest retention success for the Patagonian Shelf and across the different simulation lengths.

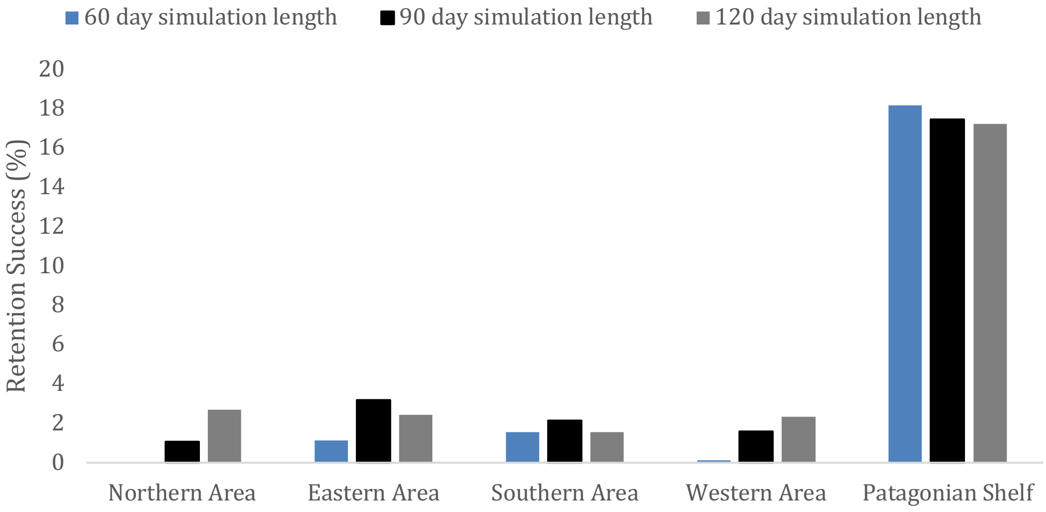


Figure 29. Retention success by retention area for each simulation length in 2009.

In the results from the 2012 particle releases (Fig. 30) a simulation length of 120-days resulted in highest retention for all areas except the Patagonian Shelf, where the 60-day simulation lead to higher retention success of 1.97% compared to 1.54% and 1.64% for this area. The highest retention success of 5.37% was seen in the western retention area for the 120-day simulation (Fig. 30). Retention on the Patagonian Shelf was considerably lower for all three simulation lengths in 2012 when compared to 2009. The 120-day simulation in 2012 lead to higher retention in eastern, southern and western retention areas when compared with the same simulation length in 2009. Retention success in the southern and western retention areas was also greater in 2012 for the 90-day simulation than in 2009.

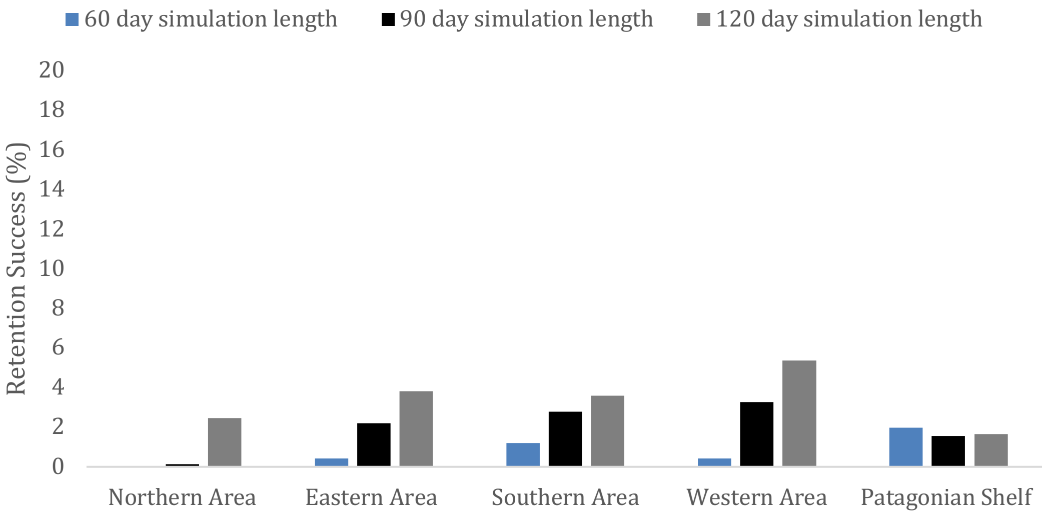


Figure 30. Retention success by retention area for each simulation length in 2012.

Total retention success in 2009 for all five retention areas did not vary greatly with simulation length. Total retention varies between 60 and 90 days by 4.45%, 5.28% between the 60- and 120-day simulation and by 0.83% between the 90- and 120-day simulation (Fig. 31, in black).

In 2012, total retention success for all five retention areas had more variation with simulation length compared to 2009. Variation between 60- and 90-days was 5.9%, there was a difference in retention success of 12.9% between 60 and 120 days and 7% between 90- and 120-day simulation length (Fig. 31, in grey). For all three simulation lengths overall retention success was lower in 2012 compared to 2009.

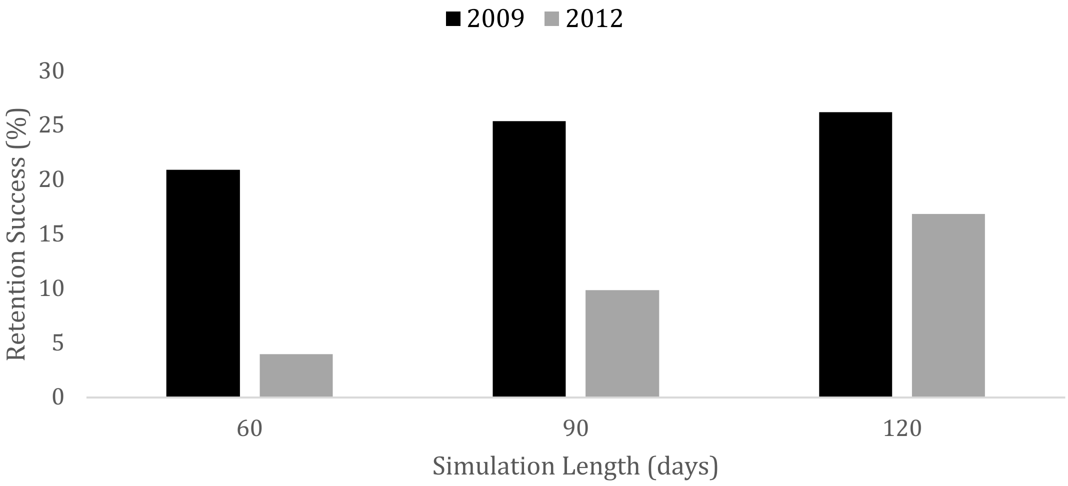


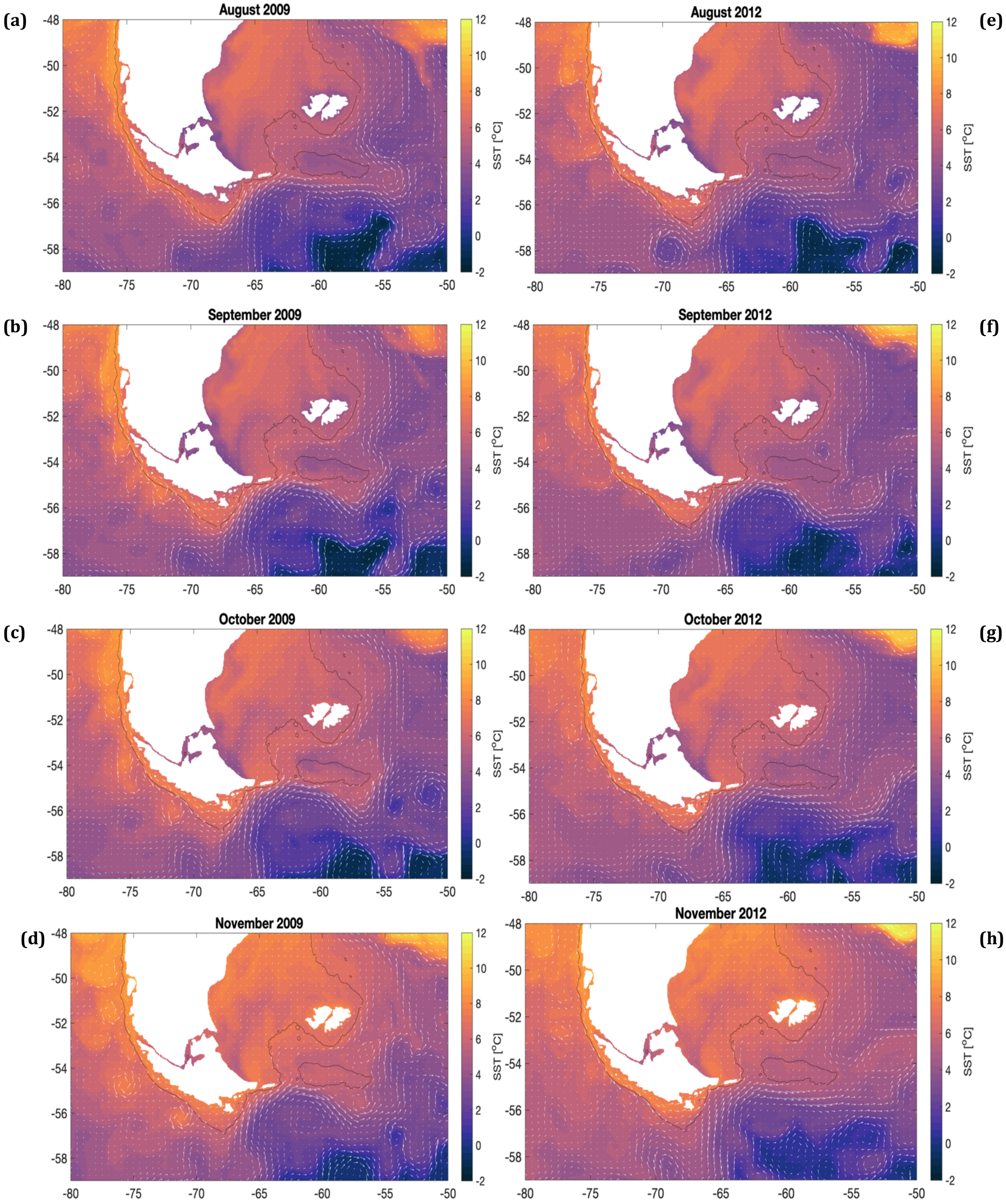
Figure 31. Overall retention success by model simulation length for all five retention areas in 2009 (black) and 2012 (Grey).

3.5.4. Oceanographic variability

Differences in recruitment strength of Patagonian toothfish have been seen in different years in the Falkland Islands region (Laptikhovsky & Brickle, 2005; Collins *et al.,* 2010). Differences are also seen in retention success between the two years studied in the particle tracking simulations. This suggests that changes in the regional circulation, which transport particles, are potentially responsible. Therefore, variability in the regional oceanography between 2009 and 2012 is investigated here. ROMS surface temperatures and upper-ocean current fields are examined to try to understand what aspects of regional oceanography, if any, might be leading to or preventing, transport success between particle release and retention areas (Fig. 13,14).

Surface currents and temperatures around southern Chile show clear differences between 2009 and 2012 (Fig. 32-35). For example, during August 2009 SSTs close to the Chilean coast between 75°W and 65°W were cooler (~1° C) than in August 2012 (Fig. 32a,e & 34a), whereas, further offshore over the southern Chilean particle release areas (Fig. 14) average SSTs in August and September 2009 were warmer (~2° C) than at similar times during 2012 (Fig. 32a-b,e-f & 34a-b). These changes in temperature appear to reflect a shift in the position of the boundary current between 75-65°W that flows around southern Chile (Fig. 1) between 2009 and 2012 (Fig. 33a-d). During 2009, the boundary current hugs the 200-750m isobaths around southern Chile (Fig. 33a-d); however in 2012, the boundary current is displaced further offshore (~100-200 km) and appears to be wider (Fig. 33e-h). Surface velocities inshore of the 200m isobath off southern Chile are also lower (~0.4-0.6 m/s) in 2009 than in 2012 in all months modelled, whereas, velocities offshore of the 200m isobath are generally higher in 2009, particularly east of 70°W and around the southern edge of the Burdwood Bank (Fig. 33, 35).

There appears to be very little difference in the surface circulation in the Falklands Embayment (waters north and west of the Burdwood Bank, south of the Falkland Islands (63°W, 52°S)) between years (Fig. 33, 35). In both years the boundary current splits near 55°S, 64°W, most flow moves east, with some moving through the gap. North of the gap, a jet heads north off the shelf break and turns east to pass south around the Falklands Plateau (Fig. 32-33). Velocities along this pathway are seen to be very similar between 2009 and 2012 for all months (Fig. 35).


August 2009

September 2009

October 2009

November 2009

August 2012

September 2012

October 2012

November 2012

Figure 32. Monthly-mean Sea Surface Temperature (shading) and surface velocity fields (white arrows) for August to November 2009 (a-d) and 2012 (e-h) from SW Atlantic ROMS simulations. Also shown is the position of the 200m isobath (black solid line).

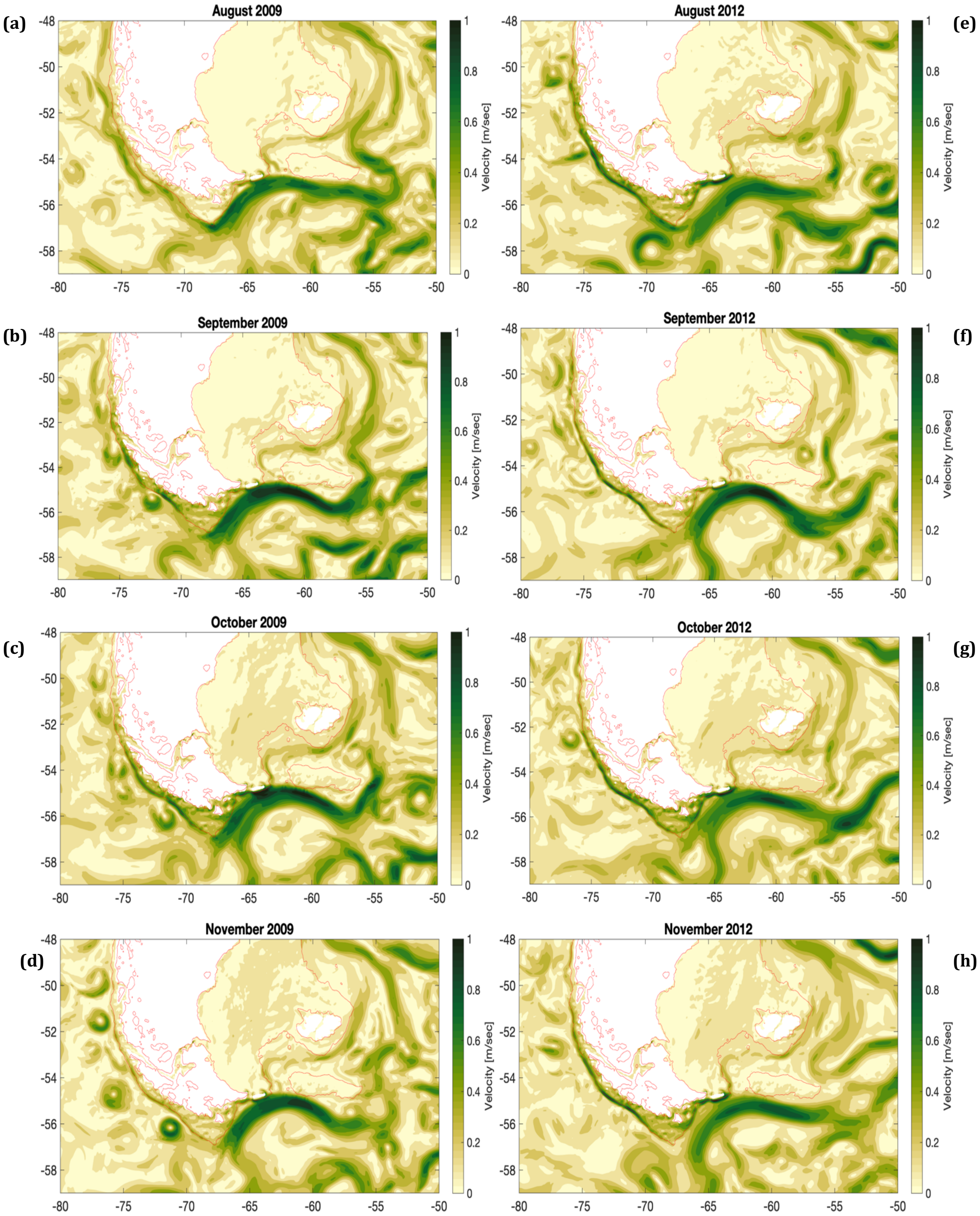


Figure 33. Surface current absolute velocity plots for August to November 2009 (a-d) and 2012 (e-h) from the SW Atlantic ROMS simulation. Also shown is the position of the 200m isobath (red solid line).

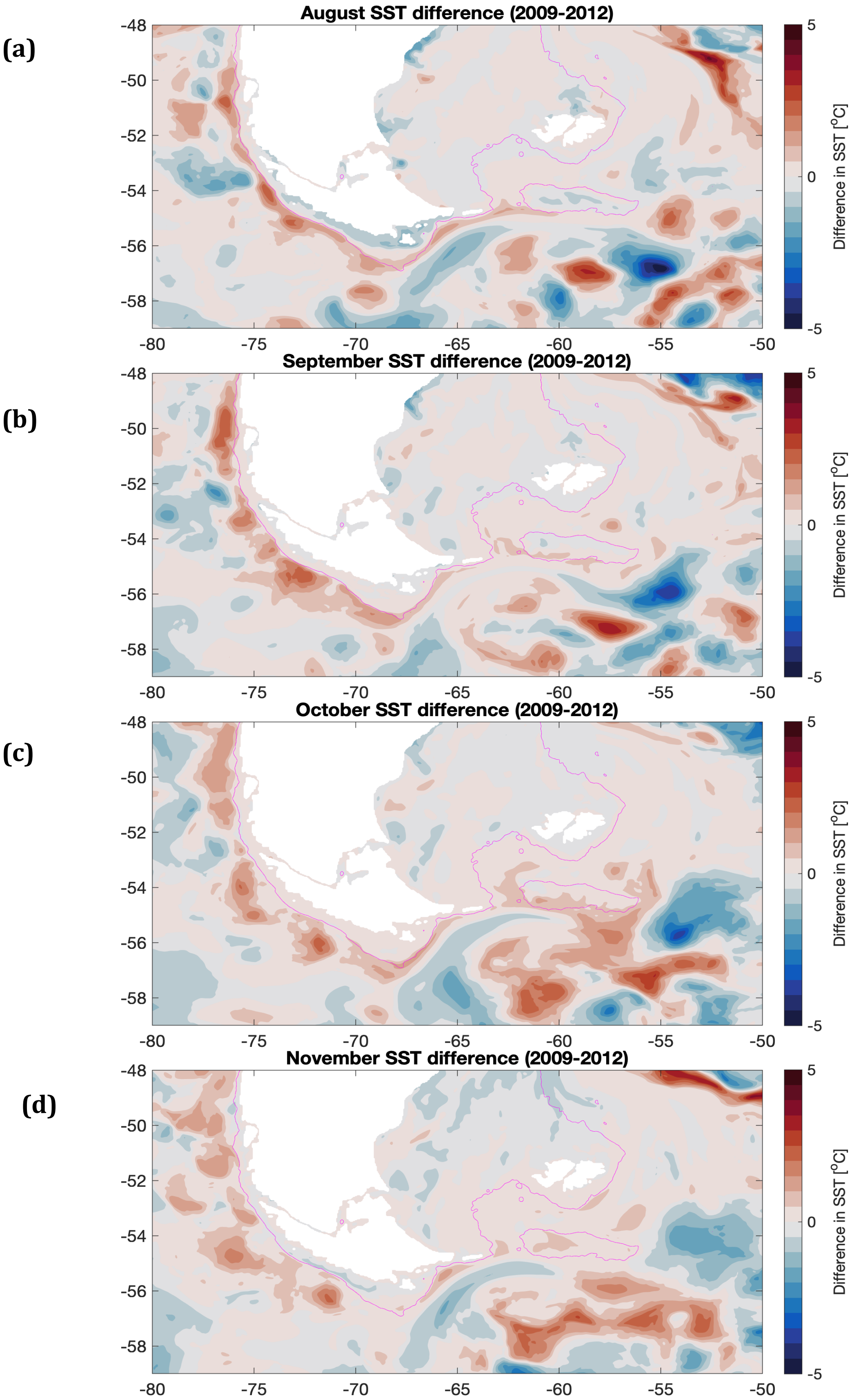


Figure 34. Difference in monthly-averaged sea surface temperature between 2009 and 2012 from ROMS model output for (a) August, (b) September, (c) October and (d) November. Also shown is the position of the 200m isobath (magenta solid line)

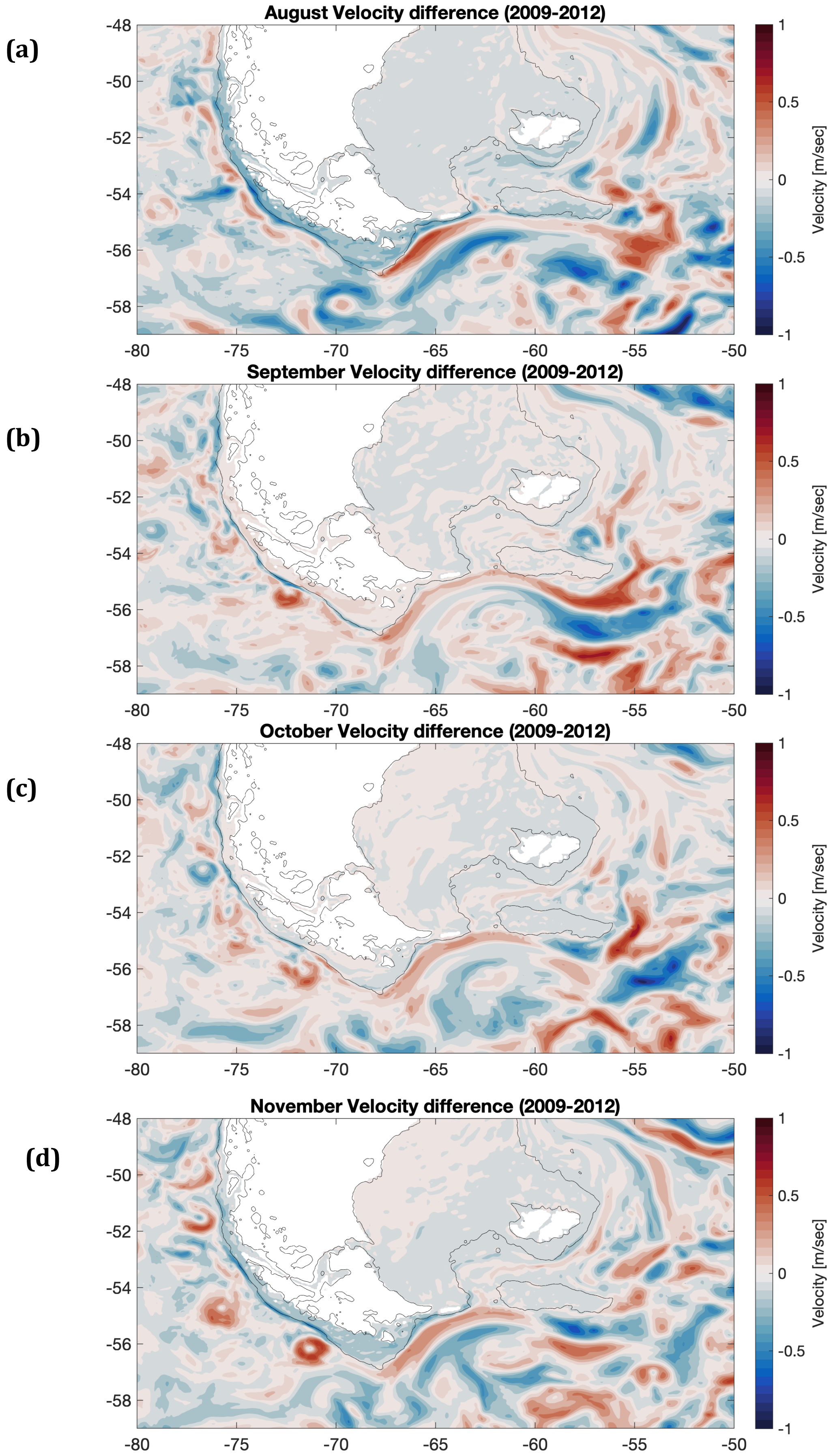


Figure 35. Difference in monthly-averaged absolute sea surface velocities between 2009 and 2012 from ROMS model output for (a) August, (b) September, (c) October and (d) November. Also shown is the position of the 200m isobath (black solid line)

The differences in position and intensity of the boundary current flow around southern Chile between 2009 and 2012 appear to be reflected in the particle trajectories (Fig. 36). In both years particles generally move toward the southeast, down the coast of South America and then either head northward towards the Patagonian Shelf and Falklands Embayment and into the Falkland Current or eastward towards the Burdwood Bank (Fig. 36a-b). However, differences can be seen in particle movement between 2009 and 2012 (Fig. 36c). For example, during 2009 more particles stayed against/on the shelf around southern Chile (Fig. 36 - red shading) whereas in 2012, particles were generally displaced further off the shelf (Fig. 36 - blue shading) reflecting the offshore shift in position in the boundary current (Figs. 33, 35). It is also notable that in 2009, fewer particles moved eastward via the southern edge of the Burdwood Bank and more spread onto the Patagonian Shelf, compared to 2012 (Fig. 36c). Particle trajectories from the southern Chile release areas also appear to be more tightly packed together closer to the shelf edge in 2009 compared to 2012, when particle trajectories span a wider range of latitudes-longitudes between 70-60°W (Fig. 36c).

There was also a notable difference in the depth distribution of particles between 2009 and 2012 (Fig. 37). More particles were seen in the upper 50m of the water column in 2009 compared to 2012 throughout the particle tracking simulation (Fig. 37a-c). During 2009, particles were also on average 25-150m shallower when moving around southern Chile and onto the Patagonian Shelf than in 2012 (Fig. 37d-f).

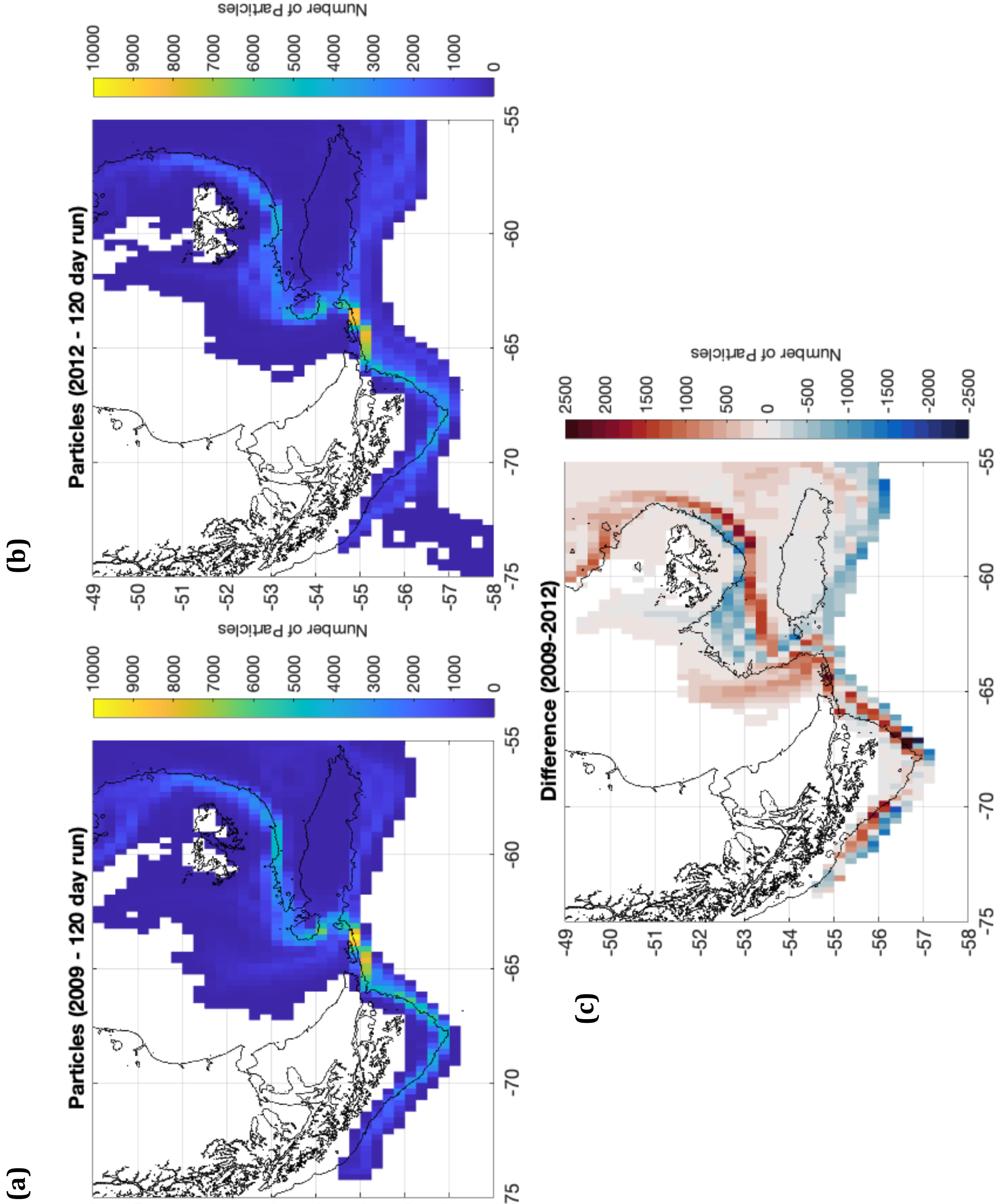


Figure 36. Geographical particle density plots (number particles per 0.25 degree lat-lon bin) for (a) 2009 and (b) 2012 for the 120-day particle tracking simulations and (c) the difference between these (2009 minus 2012). Also shown is the position of the 200m isobath (solid black line).

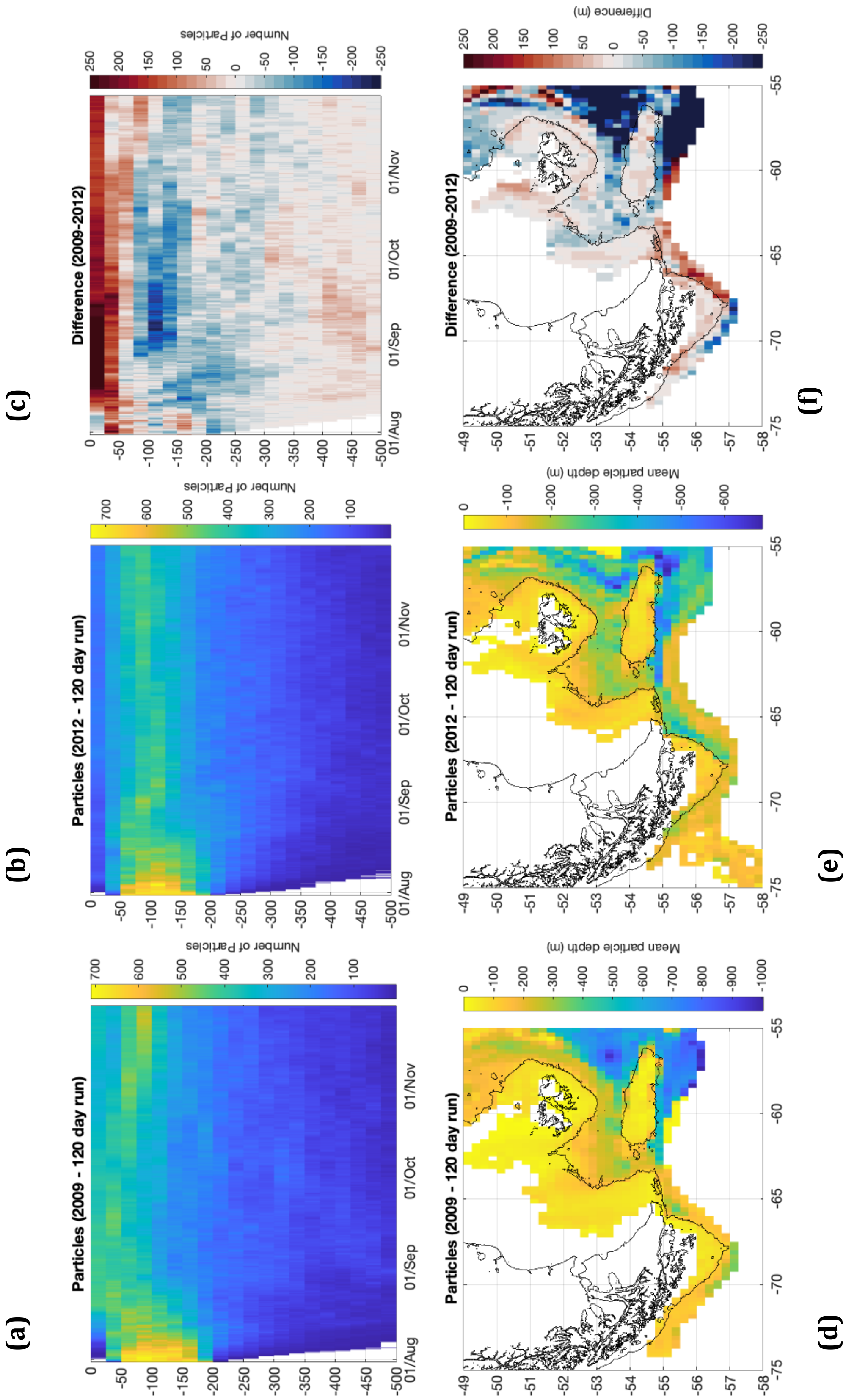


Figure 37. Depth-time distributions of particles from 120-day particle tracking simulations for 2009 (a,d), 2012 (b,e) and the difference between the 2009 and 2012 simulations (c,f). Shown are the number of unique particles per day with 20m depth bins (top panels; a-c) and the mean depths of all particles on 0.25 lat-lon grid (bottom panels; d-f) over the duration of the particle tracking simulations.

3.6. Discussion

It is known that spawning of Patagonian toothfish occurs in southern Chilean waters and in waters belonging to both Argentina and the Falkland Islands around the Burdwood Bank (Arana, 2009; Collins *et al.,* 2010). From satellite tagging of Patagonian toothfish, Brown (2011) identified that spawning behaviour for the Falkland Islands population of Patagonian toothfish occurs at the Burdwood Bank and not in the waters surrounding the Falkland Islands. Brown (2011) therefore suggested that the main spawning area for Patagonian toothfish in the Falkland Islands is the Burdwood Bank. However, studies of otolith chemistry and previous particle tracking simulations suggest that Patagonian toothfish around the Falkland Islands originate from two spatially distinct areas, thought to be southern Chile and the Burdwood Bank (Ashford *et al.,* 2012; Randhawa *et al.,* in submission).

This study has shown that when releasing particles from the Burdwood Bank at the end of July, in five out of the six simulations completed, there was no transport success between release sites around the Burdwood Bank and the Falkland Islands, or the Patagonian Shelf. In the 120-day simulation from 2009, there was limited transport success to three of the retention areas around the Falkland Islands and total transport success was only 0.55%. These results suggest that the Burdwood Bank may not be an important spawning site for the retention of eggs and passive larvae around the Falkland Islands. However, this finding is based on a limited number of particle tracking simulations for 2009 and 2012 and should be investigated further for additional years and additional release schedules.

Connectivity matrices produced for the simulations suggest that the most important spawning site in 2009 was the southern Chile release area 5 with ~50% transport success to the Patagonian Shelf retention area for all three simulation lengths. The release areas located furthest from the retention areas (5, 6, 7, and 8) contributed most to transport success. In contrast, during 2012 the highest transport success was 10.4% between the southern Chilean release area 3 and the western retention area, around the Falkland Islands, suggesting release area 3 was a more important spawning site in this year. Transport success in 2012 was highest from the three closest release areas (1, 2, 3) and for release area 7. Transport success between release areas and retention areas varied between 2009 and 2012, with the biggest variation in transport success to the Patagonian Shelf across the two years. This suggests that transport success may be an important factor driving the variability seen in recruitment success around the Falkland Islands.

When particles were released from Southern Chile, retention in the four areas surrounding the Falkland Islands did not vary greatly between 2009 and 2012. There is however a large difference in retention success between these two years on the Patagonian Shelf for all three of the simulation lengths. In 2009 ~18% of particles released are successfully retained on the Patagonian Shelf compared to ~1.7% in 2012. The difference in retention success on the Patagonian Shelf between 2009 and 2012 provides a possible explanation as to why a good year for recruitment was observed in 2010 around the Falkland Islands in annual juvenile trawl surveys, followed by a poor year in 2013 (T Farrugia 2019, pers. comm. 26 July). Good retention on the Patagonian Shelf could therefore mean good recruitment in the Falkland Islands.

When analysing the data from 2009 and 2012 and excluding the Patagonian Shelf retention area, a greater overall retention success is observed for the four Falkland Islands retention areas overall for the 90 day and 120 day simulations in 2012 compared to 2009 (Fig. 38).

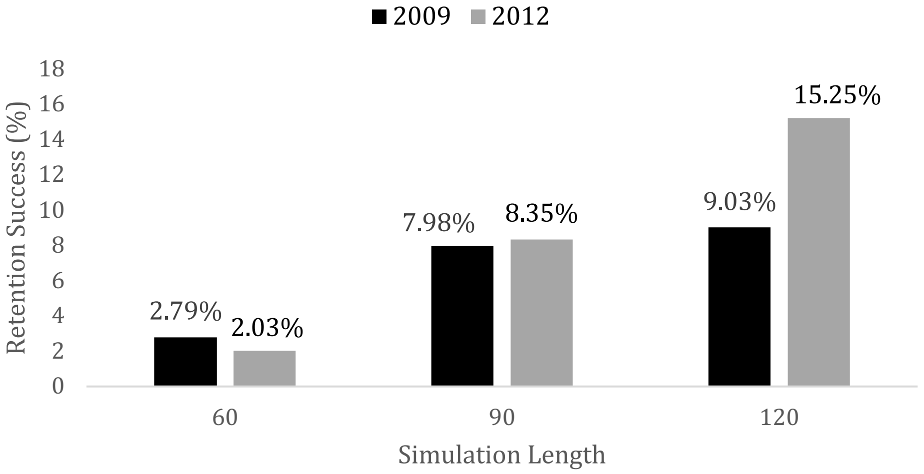


Figure 38. Overall retention success for the four retention areas around the Falkland Islands (this data does not include retention for the Patagonian Shelf) in 2009 (black) and 2012 (Grey).

This pattern, with high retention successes following a spawning event in 2012, is the opposite of what one would expect to see; 2012 was a year that was followed by poor recruitment in 2013 (T Farrugia 2019, pers. comm. 26 July). However, this is only seen when removing the Patagonian Shelf from the data set. Therefore, successful retention onto the Patagonian Shelf could be an important factor for successful recruitment of juveniles into nursery areas around the Falkland Islands. However, this study was limited to examining two years of data and therefore examination and comparison of multiple years where good and poor recruitment has been found is needed to determine whether retention onto the Patagonian Shelf is the key to recruitment differences seen across the years.

Comparing the ROMS surface temperature and upper-ocean current fields between 2009 and 2012 shows possible reasons for seeing more connectivity and retention on the Patagonian Shelf in 2009. Inter-annual differences in the boundary current position, as well as upper-ocean water mass density, may be partitioning the depths and pathways of the particles. In 2009, it appears that the boundary current is trapping particles against the shelf edge leading to fewer particles being exported eastward via flow around the southern edge of the Burdwood Bank (Fig. 36c). Particles that are transported past the western side of the Burdwood Bank are, also on average, shallower in 2009 (Fig. 37c), possibly favouring their subsequent dispersal onto the shallower bathymetry of the Patagonian Shelf. It is also noted that egg buoyancy within the simulations was set to neutral buoyancy, i.e. they have the same density as the parcel of water they were "placed" in and keep that buoyancy throughout the simulations. Warmer SSTs observed in 2009 (Fig. 34) suggest a more buoyant upper-ocean and offer a possible explanation as to why particles in 2009 are, on average, shallower than in 2012. The shallower position of the particles may allow them to move up onto the Patagonian Shelf more easily and/or make them more susceptible to upper ocean events such as wind forcing that likely drive shelf-ocean exchange in this region (Guihou *et al.,* 2020).

Previous particle tracking studies on the Patagonian toothfish in South Georgia and the Antarctic toothfish (*Dissostichus mawsoni)* in the southeast Pacific Basin and Ross Sea have shown that regional and large-scale oceanography can affect dispersal and connectivity of early life stages of these species (Ashford *et al.,* 2012b; Brigden, 2018). In South Georgia, atmospheric forcing including direct wind forcing, local bathymetry and variability in the strength and proximity of the Southern Antarctic Circumpolar Current Front to the South Georgia shelf edge were found to be a significant driver of transport and retention success/loss of toothfish eggs and early larvae (Brigden, 2018). Similarly life history of the Antarctic toothfish in the Ross Sea and the southeast Pacific Basin was found to be structured by the large-scale circulation, such as major gyres and currents, and formation of Antarctic Bottom Water (Ashford *et al.,* 2012b). The present study also suggests that variability of large-scale (>100 km) ocean boundary and upper-ocean temperature are likely important factors in controlling connectivity between toothfish spawning grounds in southern Chile and nursery areas in the Falkland Islands.

The simulations in this study did not include any active larval behaviour nor did they include mortality; thus, retention and connectivity is solely based on transport pathways. Generally, marine organisms are not passive, but are swimming, with vertical migration, and buoyancy changes are all behaviours seen (Fuchs *et al.,* 2007). Therefore, despite a particle being transported to an area that is suitable for retention in these simulations, it does not mean that the particle will be recruited into a population. Population connectivity can be influenced not only by currents/transport pathways but also through larval behaviour, such as horizontal swimming, vertical migration, foraging and predator avoidance (Werner *et al.,* 2007). These behaviours can also reduce dispersal and promote local recruitment (Gerlach *et al.,* 2007). Vertical migration will affect dispersal and connectivity, as larvae located at different depths will be subject to differing currents and therefore their transport trajectories will be altered (Batchelder *et al.,* 2002; Paris & Cowen, 2004). Due to the effect larval behaviour may have on dispersal and connectivity of populations, it is important to identify these behaviours and, where possible, incorporate them into particle tracking simulations (Werner *et al.,* 2007).

Averaged monthly SST along the Chilean coast in 2009 and 2012 has shown there is variation in temperature seen along the coast both between months and between years. These temperature differences could influence adult spawning behaviour and egg development duration along the coast. It is believed that in Chilean, Argentine and Falkland Island waters, Patagonian toothfish are at the edge of their range (Brown, 2011). Spawning areas in Chile and the Falkland Islands are in more confined regions when compared to spawning areas seen around South Georgia. Spawning does not occur north of 50°S in Chilean waters and in the Patagonian region spawning is only seen at the southern side of the Burdwood Bank (Arana, 2009; Brown, 2011). Spawning areas in South Georgia are more widely distributed and are not as restricted (Brigden, 2018). Skip spawning behaviour has been seen in Patagonian toothfish in the southwest Atlantic, with inter-annual variation in the proportion of non-spawning individuals, suggesting fluctuation in suitable environmental conditions, such as temperature, for spawning (Brown, 2011). Unfavourable environmental conditions for spawning and compromise in adult fitness due to a species at the edge of their range may also contribute to the variability seen by Laptikhovsky & Brickle (2005) in recruitment between years as well as variation in transport pathways.

Matano *et al.* (2019) showed a potential connection between the marine ecosystem of the Chilean coast and the Burdwood Bank based on backward particle tracking experiments. The results found in this new study support this finding, with all simulations where particles were released from southern Chile having trajectories where particles reach the Burdwood Bank. Particles released from the Burdwood Bank are swept eastward or follow the anticyclonic current around the Burdwood Bank and then entrain into the Falklands Current and do not connect to any areas in southern Chile. These findings suggest that southern Chile is likely to hold an important source population for Patagonian toothfish located in the Falkland Islands fishery, whilst the Burdwood Bank appears to be a sink population for eggs originating from southern Chile. Analysis of transport and retention success between release sites in southern Chile and the Burdwood Bank as a retention area were not conducted for this research, however further investigation in the future could help in understanding the connectivity between these two populations.

3.7. Chapter conclusions

Based on particle tracking simulations, for the years studied (2009 and 2012), the Burdwood Bank appears to have little to no connectivity with the retention areas around the Falkland Islands or on the Patagonian Shelf and is unlikely to contribute greatly to the supply or retention of Patagonaian toothfish eggs and larvae around the area. Instead, results of the particle tracking simulations for the two years suggest spawning areas in southern Chile are likely the more important source of retention for the Falkland Islands. Overall retention and transport success was found to vary between years, being greatest in 2009 compared to 2012, with the main difference being the number of particles successfully transported onto the Patagonian Shelf. In 2009 (considered to be a spawning year that corresponds to good recruitment around the Falkland Islands), there is high transport success onto the shelf especially from the southern Chilean release area 5. This high transport success on the shelf is not seen in 2012 which is considered to be the spawning event which corresponds to a poor recruitment year. These results suggest that successful transport onto the Patagonian Shelf may be important for recruitment success seen around the Falkland Islands. Analysis of differences in the regional oceanography between 2009 and 2012 also revealed changes in the position and water density of the boundary current around southern Chile, which appear to influence transport and retention success. In 2009, the boundary current was warmer and further inshore, leading to particles being shallower and trapped against the shelf edge, restricting eastward flow towards southern Burdwood Bank and supporting transport and retention success onto the Patagonian Shelf. In contrast, during 2012 the boundary current was further offshore and colder allowing particles to move away from the shelf edge and towards the southern side of Burdwood Bank. These findings highlight aspects of the large-scale regional oceanography that appear to play an important role in regulating the supply of larvae and juveniles into the Falkland Islands fishery.

4. General Discussion and Conclusions

4.1. Research Objectives

This thesis has sought to advance the understanding of transport, dispersal and retention of Patagonian toothfish eggs and larvae around the Falkland Islands to inform understanding of potential recruitment variability. The research attempted to use egg buoyancy data, gathered from empirical buoyancy experiments, in particle tracking simulations to identify likely patterns in the spatial distribution and retention of eggs and larvae. There were three key objectives:

1. To empirically estimate toothfish egg buoyancy throughout embryogenesis.
2. Identify potential transport pathways of eggs and larvae from spawning grounds to retention areas and the spawning populations and areas that may contribute to retention and potential recruitment.
3. Compare retention and transport success between years and discuss possible mechanisms leading to variability.

Previous research suggested the main spawning ground for the Patagonian toothfish in the Falkland Islands fishery is the Burdwood Bank with some recruitment from spawning sites in southern Chile (Collin *et al.,* 2010; Brown, 2011; Ashford *et al.,* 2012). The Falkland Island toothfish stock is managed in isolation from the neighbouring Chilean stock and connectivity of early life stages between these areas is not currently considered in fisheries management (Andrews *et al.,* 2013). Identification of spatial connectivity between locations of spawning and potential retention areas is needed for better informed fisheries management. Recruitment of juvenile toothfish shows inter-annual variability in the Falkland Islands with strong year classes seen every four to five years (Laptikhovsky & Brickle, 2005; Collins *et al.,* 2010); however, the drivers of this variability have been suggested but not evaluated (Brown, 2011).

The findings of this research are summarised below. Knowledge gained from egg buoyancy experiments and particle tracking simulations are discussed and the implications that these results may have for fisheries management are considered. Future research needs are also identified.

4.2. Main research findings

4.2.1. Buoyancy experiments

As far as the author is aware, previous to the current study, no prior experimental buoyancy work appears to have been carried out on Patagonian toothfish eggs. Previous particle simulation work carried out around the Falkland Islands (Ashford *et al.,* 2012) only tracked particles in the upper most layer of the water column. However, observations from around South Georgia Island report that eggs typically occur at around 200m depth (Evseenko *et al.,* 1985). The vertical position, of fish eggs and larvae within the water column determine the extent of their dispersal and transport, with coupled biophysical models being sensitive to initial egg positioning within the water column (Ospina-Alvarez *et al.,* 2012). Therefore, it is important to incorporate knowledge of buoyancy data within any particle tracking simulations. The buoyancy experiments undertaken within the current study using a method adapted from Coombs' (1981) gradient column, resulted in partial buoyancy profiles being obtained. The results demonstrated Patagonian toothfish eggs change buoyancy throughout their embryonic development with a decrease in buoyancy after fertilisation and an increase in buoyancy again 10 days post fertilisation. The experiment allowed for egg density values to be calculated which could then be incorporated into the particle tracking simulations. However, there was variation in density between batches with one batch being much denser than the other three. Several explanations are possible, but of main concern was the quality of eggs being produced by the female toothfish in an aquaculture environment. For this study it was presumed that the eggs being produced are representative of eggs spawned in the wild, however this may not be the case due to egg quality being effected by stress and environmental factors, including light, temperature and pressure and parental diet (Bogevik *et al.,* 2012; Ochokwu *et al.,* 2015).

To address the uncertainty of egg buoyancy, the depth distributions and particle trajectories were analysed from multiple simulations using differing buoyancy profiles. Buoyancy data gathered from FFFL was used in the simulations as well as slightly altered profiles and neutral buoyancy (Chapter 3, Table 2).

4.2.2. Particle tracking

In a modelling study of the surface connectivity of Patagonian toothfish eggs and larvae between spawning grounds and the Falkland Islands, Ashford *et al.* (2012) found two spawning areas are supplying retention and recruitment into the Falkland Islands region. Their study found spawning grounds in southern Chile are likely to be contributing to recruitment in the western and northern areas of the Falkland Islands, whilst the Burdwood Bank supplies recruits to nursery areas to the south and east of the Falkland Islands (Ashford *et al.,* 2012). While Ashford *et al.* (2012) identified connectivity with southern Chile, particles were only tracked at the surface. The current study aimed to use new egg buoyancy data to try to match previous at-sea observations of egg depth distribution (Evseenko *et al.,* 1985).

By analysing transport pathways from simulations using numerous buoyancy profiles of toothfish eggs and larvae (Section 3.4), results show that when particles are forced to remain at the surface or at depths greater than 800m, the resulting trajectories lead to particles not encountering areas around the Falkland Islands or the Patagonian Shelf that have suitable depths for retention. Using a neutral buoyancy profile that keeps particles between depths of 25 and 200m results in a trajectory with particles ending up in areas around the Falkland Islands and on the Patagonian Shelf of less than 200m, which are considered to be suitable for retention. This suggests that eggs and larvae are not being transported solely at the surface nor are they being transported at depth.

Particles were released from seven spawning sites around the Burdwood Bank and eight in southern Chile. Five retention areas were defined around the Falkland Islands and the Patagonian Shelf (Fig. 39).

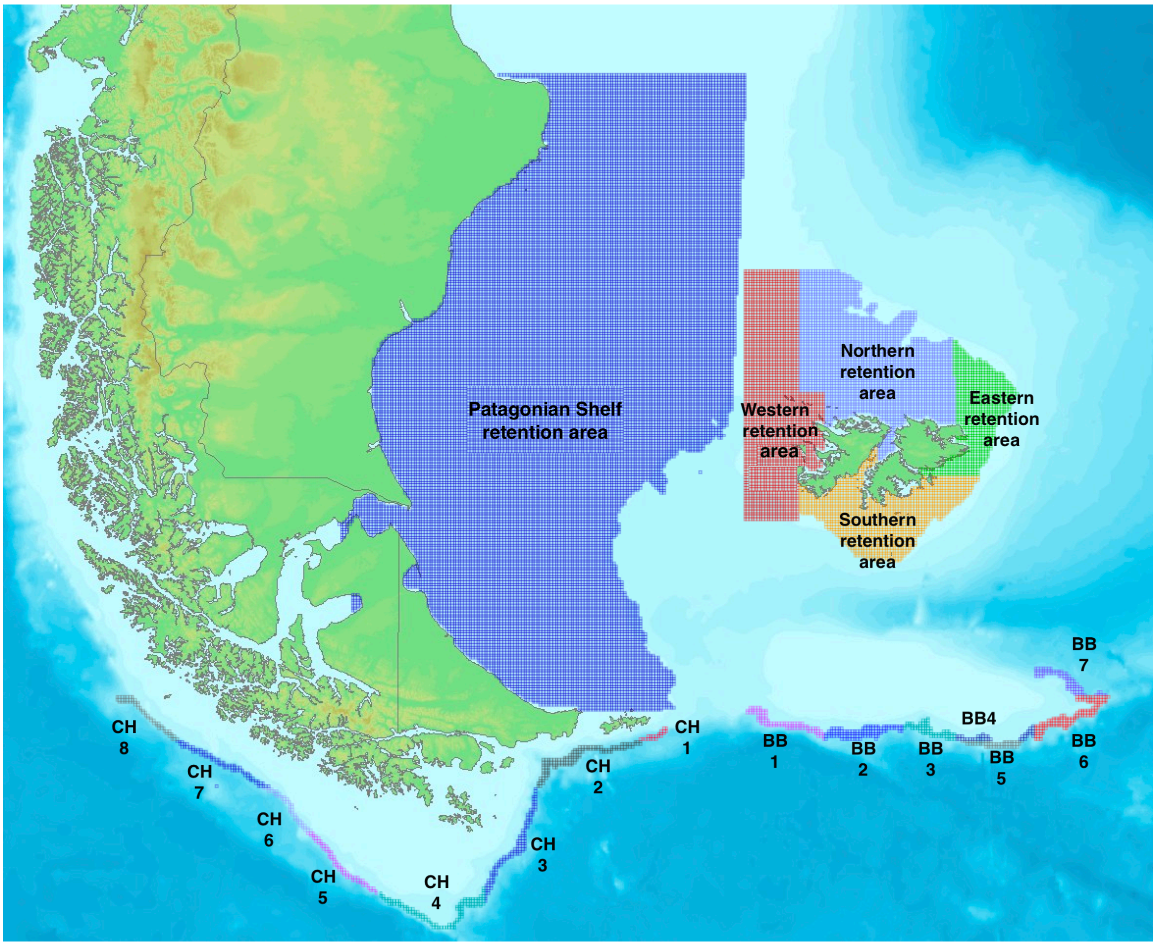


Figure 39. The seven release areas around the Burdwood Bank (BB) and the eight release areas in southern Chile (CH). Retention areas around the Falkland Islands and the Patagonian Shelf are also presented. Areas are shown in different colours to highlight the boundaries of the different release and retention areas.

This study found releasing particles at the end of July in 2009 and 2012, the seven Burdwood Bank spawning sites were not a major contributor to retention areas around the Falkland Islands or on the Patagonian Shelf. This is an important finding as it has been thought that the Burdwood Bank was the main spawning ground supplying recruitment to the Falkland Island toothfish stocks, with only a minimal contribution from southern Chile (Collins *et al.,* 2010; Brown, 2011; Ashford *et al.,* 2012; Andrews *et al.,* 2013). Otolith chemistry data show there are two distinct areas from which toothfish are recruiting, with variable proportions of recruits from each area (assumed to be the Burdwood Bank and southern Chile) in differing years (Ashford *et al.,* 2012; Randhawa *et al.,* in submission). Connectivity analysis between the two years in which simulations were run show in 2009 retention occurred from southern Chilean release areas 5, 6, 7 and 8 whereas in 2012 there is greatest connectivity between areas 1, 2, 3 and 7 (Fig. 39). Instead of the two distinct areas seen in otolith chemistry being the Burdwood Bank and southern Chile, differences in otolith chemistry could possibly be explained by recruitment from two distinct areas from within the southern Chile region, populations further north and from populations closer to the southern tip of Chile. However, further data in additional years is needed to be able to draw firmer conclusions.

Releasing particles from southern Chile, successful retention was seen in all five retention areas in both 2009 and 2012. Strong year classes of recruits have been seen around the Falkland Islands (Laptikhovsky & Brickle, 2005) with the Falkland Island Government Fisheries Department identifying 2010 and 2013 as years where good and poor recruitment were seen, respectively. By running simulations in 2009 and 2012, which are the corresponding spawning events for the good and poor recruitment years, the particle tracking simulations identified that retention onto the Patagonian Shelf from spawning areas in southern Chile may be important for potential recruitment around the Falkland Islands. This result is consistent with a recent particle tracking simulation by Guihou *et al.* (2020) which shows that the main source of water to the Patagonian Shelf is an ocean-shelf exchange across the shelf break (net inflow of 0.65 Sv) that generally occurs south of 52.5°S (e.g., Fig. 2 of Guihou *et al.,* 2020). In turn, Guihou *et al.* (2020) report that the majority of waters flowing on to the shelf originate from the southern Chile and Cape Horn shelves, consistent with the results of the particle tracking simulations reported here. Together, the results of Guihou *et al.* (2020) and the present study highlight the important physical connectivity that exists between southern Chile and Cape Horn shelves and the Patagonian Shelf. This may have important implications for the current fisheries management within Falkland Island waters that currently treat the Falkland Islands stock as a discrete stock from the Chilean stock.

A topic, not focused on in detail in this research, was the connectivity between southern Chile and the Burdwood Bank. The particle tracking simulations showed particles released from southern Chile, though not quantified, are reaching areas of the Burdwood Bank where depth would be suitable for the retention of eggs and larvae to occur. Commercial fisheries for the Patagonian toothfish are active in the Falkland Islands Outer Conservation zone, which encompasses the eastern and southeastern side of the Burdwood Bank (Fig. 5). Matano *et al.* (2019) identified through backward particle tracking simulations from the Burdwood Bank that all trajectories originated from the Pacific Basin and were advected onto the Burdwood Bank by the ACC, with the two northern most jets off the ACC being the main water sources (e.g., Fig. 13, Matano *et al.,* 2019). Their research identifies a potential connection between the ecosystems of Chile and coastal Argentina, with the ecosystem of the Burdwood Bank, a finding similar to this current study. Due to the active fishery around the Burdwood Bank, understanding of the connectivity patterns of populations of Patagonian toothfish at the Burdwood Bank and southern Chile should be a focus of future research.

The particle tracking undertaken in this study has some limitations. Particles were released in one single "spawning" event at the end of July. However, Patagonian toothfish are batch spawners and spawn over a number of months (Collins *et al.,* 2010; Brown, 2011). Ideally, to account for this, multiple release dates would have been used in this study and statistical analysis carried out on transport success between release months. Multiple release dates in one year would likely give a clearer picture into intra-annual variability in both transport and retention success. Inter-annual variability was also an area of interest for this research, with the Falkland Island Government Fisheries department seeing years of good and bad recruitment in their annual juvenile Patagonian toothfish surveys. For this study only two years were chosen, 2009 and 2012, which were the spawning events that would correlate to the years of good and poor recruitment. While comparisons in retention and transport success as well as any differences in regional oceanography were made across these two years, a larger data set, where further good and poor recruitment years are included would allow for more confidence in the results.

4.2.3. Ocean-atmosphere variability

Particle tracking simulations for the two years studied (2009 and 2012) resulted in a difference in retention success between the two years, with the main retention difference being observed on the Patagonian Shelf. Analysis of SSTs and surface current fields of the underlying ROMS model were carried out to begin to understand which aspects of regional oceanography may be leading to the difference in retention and transport success seen between the two years.

Results from particle tracking simulations suggest that important factors leading to retention and transport success between southern Chile and the Patagonian Shelf are the position and water density of the boundary current found around southern Chile. For example, in 2009, when greater transport and retention of particles onto the Patagonian Shelf is observed (Fig. 27, 29), the boundary current is closer inshore and warmer compared to 2012. These conditions appear to retain more particles against the shelf edge and in the upper 0-150 m (Fig. 36, 37), in turn supporting greater transport onto the Patagonian Shelf. The origin of these inter-annual variations in the boundary current, and successful transport between the southern Chilean Shelf and the Patagonian Shelf, are not entirely clear, but are potentially linked to large-scale ocean-atmosphere forcing. A recent study by Guihou et al. (2020) examined the variability and drivers of exchange between the Chilean Shelf and Patagonian Shelf using particle tracking simulations similar to those conducted here. Their results suggest that inter-annual variability of transport onto the Patagonian Shelf, which is primarily sourced from waters around southern Chile (Guihou et al., 2020), can partly be explained by large-scale wind variability, associated with variations in the Southern Annular Mode (SAM) index. A positive (negative) phase of the SAM was found to be associated with decreased (increased) transport onto the Patagonian Shelf (Guihou *et al.,* 2020). Whilst the behaviour of the SAM was not considered in this study, it is interesting to note that during 2009 the SAM was in a neutral phase (0.22), whilst in 2012, it was in a strongly positive phase (2.11) (http://www.nerc-bas.ac.uk/public/icd/gjma/newsam.1957.2007.seas.txt). A positive phase of the SAM during 2012 is anticipated to reduce ocean-shelf transport onto the Patagonian Shelf (Guihou *et al.,* 2020), consistent with the lower connectivity observed between southern Chile and the Patagonian Shelf reported in the present study. Given the potential importance of the SAM, future work could consider examining the influence of the SAM-phase on particle transport success between southern Chile and the Patagonian Shelf. If the SAM has a significant control on transport success between the Chilean and Patagonian Shelf, then observed and forecasted variability in the SAM could be used to help predict recruitment success in a given year and be incorporated into fisheries management.

There are several additional aspects of the regional oceanography, not directly considered in this study, which may have an important control on connectivity and recruitment. In particle tracking simulations, particle trajectories from southern Chile advect towards the Burdwood Bank and the South West Atlantic. To maintain the population of toothfish in southern Chile there must be a mechanism that allows/enhances local retention and subsequent recruitment. For example, eddies can also act as mechanisms for the retention of fish eggs and larvae in local spawning areas (Govoni *et al.,* 2010). In September, October and November 2009, eddies are present of the shelf between 78°W and 70°W that are not seen in 2012. In the particle tracking simulations produced for this study and in Ashford *et al.* (2012) study, particles released from southern Chile were mainly advected away from the region towards the Burdwood Bank, the Falkland Islands and the Patagonian Shelf. Particles released from the Burdwood Bank do not advect towards southern Chile, making southern Chile a source of eggs and larvae and the Burdwood Bank a sink. Eddies seen in the southern Chilean spawning areas in 2009 may act to entrain and retain eggs and larvae in the region and enhance local recruitment for this source population. Understanding the dynamics of the early life history stages in southern Chile is important if the region is supplying recruits to the Falkland Islands as population dynamics here could affect dynamics around the Falkland Islands.

Temperature differences in August and September between the two years modelled along the southern Chilean coast may not be influencing transport pathways in the simulations or the connectivity and retention differences seen in this study. However, temperature may influence adult spawning behaviour as well as egg and larval development rates. Throsen-Rass (as reviewed in Laptikhovsky, 2006) describes egg size in marine fish increases with a decrease in temperature. Smaller eggs would result in higher fecundity and therefore would be expected to be seen in areas of higher water temperatures, such as Chile and the Falkland Islands, where higher fecundity is observed in Patagonian toothfish (Brown, 2011). A disadvantage to a smaller egg size is that development time is generally egg size and temperature specific, whereby warmer temperatures and smaller eggs lead to a reduction in incubation time resulting in early hatching and an increased risk of larval mortality (Duarte & Alcaraz, 1989; Laurel *et al.,* 2008). Fluctuations in temperature also have the potential to directly influence the endogenous reserves, growth and size of larvae, which likely affects survival through predator prey interactions (Laurel *et al.,* 2008). Adult behaviour of skip spawning has been identified in Patagonian toothfish and is possibly linked to unfavourable conditions prevailing before spawning (Brown, 2011). Boucher (2018) found there was a significant difference in the number of spawning females from year to year in the region. This can lead to uncertainties in the estimation of spawning stock biomass and other stock indicators used in stock assessment, as the assumption most individuals are contributing to annual recruitment is nullified (Boucher, 2018). Therefore, along with differences in transport between years, temperature conditions may also be playing a role in the recruitment variability seen around the Falkland Islands and should be investigated further to help with certainty in stock assessments.

4.3. Implications for stock structure and stock assessment

Genetic studies have shown that Patagonian toothfish at South Georgia are genetically distinct from those found around the South American continent and the Falkland Islands (Shaw *et al.,* 2004; Rogers *et al.,* 2006; Canales-Aguirre *et al.,* 2018). Little genetic variation has been found in Patagonian toothfish collected from both the Chilean and Argentinean coasts, providing little evidence of separate stocks (Smith & McVeagh, 2000; Shaw *et al.,* 2004; Canales-Aguirre *et al.,* 2018). While previous tagging, otolith shape and microchemistry and genetic studies have been conducted, there is still uncertainty over the stock structure of Patagonian toothfish around South America and the Falkland Islands.

Findings from this study suggest retention, and therefore likely recruitment, on the Patagonian Shelf and around the Falkland Islands is, in large, originating from southern Chile. Currently the Falkland Island fishery management strategy treats the Falkland stock as a discrete stock and is managed in isolation from the neighbouring Chilean stock (Andrews *et al.,* 2013). If confirmed by subsequent research that the Falkland Islands stock is reliant on recruits from southern Chile then the fisheries management strategy employed in Chilean waters will affect the Falkland Islands stock. Fishery activities occurring on the Patagonian Shelf where egg and larval retention appears to be important for subsequent recruitment of juveniles into the Falkland Islands fishery stock should also be considered. Fisheries data in Argentine waters is limited and due to the current political tensions, data sharing between the Falkland Islands and Argentina seems unlikely; nonetheless fishing on the shelf such as a targeted fishery or fishing that results in the bycatch of young toothfish could affect population dynamics in the Falkland Islands.

In Chile, the Patagonian toothfish fishery is managed by the Subsecretaria de Pesca y Acuicultura with the fishery divided into two categories: industrial in the south and artisanal north of 47°S and since 2005 around 5000 t are caught annually in Chilean waters (Servicio Nacional de Pesca y Acuicultura, 2018). The most recent stock assessment in Chile determined that stock has been reduced below the spawning biomass limit established at 50% B_{MSY}, which qualifies the stock as depleted and overfished (Servicio Nacional de Pesca y Acuicultura, 2018). The Patagonian toothfish management committee is developing a stock recovery management plan; however, this has not yet been implemented into the fishery (Servicio Nacional de Pesca y Acuicultura, 2018b). The status of the Chilean fishery stock is of high concern and should be considered in the Falkland Islands management of their stocks as one or more alternatives in a Management Strategy Evaluation approach to modelling the Falkland Islands stock (Punt *et al.,* 2016). This study's findings and previous genetic studies suggest that a coordinated management strategy between the countries involved in the South American continental shelf fishery for Patagonian toothfish should be considered and stocks should potentially not be managed in isolation.

4.4. Future research

It would be beneficial to carry out further buoyancy experiments under more rigorous conditions. The time frame for the experiment should span the entirety of the egg phase with maximum replication to account for natural variability in egg buoyancy and quality. Greater understanding of buoyancy during the egg phase would allow for more confidence in setting parameters in future modelling work. Issues surrounding egg quality at FFFL arose during this research. Plankton tows in spawning areas during spawning months may allow for the collection of wild Patagonian toothfish eggs. Collection of these eggs would allow for data to be gathered on wild egg buoyancy and could be compared to values found at FFFL. Although not considered for this study due to the restriction of equipment in the Falkland Islands, another way to determine buoyancy of fish eggs to a high degree of accuracy is through the measurement of basic egg components, lipids, proteins and osmolality of water content. The specific gravities of the components can be obtained following methods set out by Jung *et al.* (2014) and Sundby and Kristiansen (2015).

The larval phase is the least understood phase in Patagonian toothfish life cycle. Using the resources of FFFL there may be an opportunity to gain information on larval growth rates and larval behaviour; which can subsequently be incorporated into future modelling work. This research looked at potential retention of eggs and passive larvae and did not include mortality. Larval behaviour is important because if larvae are solely passive then recruitment is impacted by oceanographic factors alone, however, if there is some degree of active behaviour then this may improve the possibility of survival and recruitment through avoidance of predation and movement to areas of more favourable habitat for settlement. As Patagonian toothfish are thought to be at the edge of their range in the Falkland Islands and Chile, environmental fluctuations, which cause unfavourable spawning and recruitment conditions are likely more frequent (Brown, 2011). Understanding the effect temperature has on growth and survival of larvae would be beneficial as survival directly effects recruitment. The software Ichthyop, allows for input of variables including larval behaviour, vertical movement, swimming, lethal temperature and growth rate. Running particle tracking simulations with these parameters would create more certainty in predicted recruitment and transport pathways as well as better identification of connectivity with spawning locations.

Patagonian toothfish are described as batch spawners (Brown, 2011) therefore modelling that includes multiple release dates annually should be carried out. Multiple release dates would allow for the study of intra-annual variation in connectivity and retention. As this study only had one release date, it is unclear that if particles were released earlier or later in the spawning season whether the Burdwood Bank would have higher connectivity to areas of suitable retention and contribute more to retention. This should be explored in greater depth due to the implications that the origin of toothfish recruits has on fisheries management. Understanding where eggs and larvae spawned at the Burdwood Bank recruit to (if not the Falkland Islands) would also be an interesting data gap to address.

While this research began to address potential drivers for recruitment variability between years, only two years were studied. Running the model for additional years would allow for more certainty in the results seen in this research. With the model available in additional years that have been identified as good/poor recruitment years, it would be advantageous to utilise this resource and gain greater understanding of the drivers of recruitment variability. The underlying ROMs model can be used to output averaged SST and surface current field plots for months prior to and during spawning. These plots could be compared over the years, which will give an indication as to whether prevailing boundary current and temperature conditions could be a driving factor behind the recruitment variability seen. Identifying these drivers could improve stock assessment models and allow for the incorporation of environmental oceanographic variables into these models.

This research focused on retention of Patagonian toothfish eggs and larvae on the Patagonian Shelf and around the Falkland Islands, however if further research confirms the majority of recruitment seen in these regions is originating from southern Chile, early life history dynamics in southern Chile become important. From particle tracking simulations (Ashford *et al.,* 2012; Matano *et al.,* 2019; this study) it is becoming clearer that the Burdwood Bank is a sink for Patagonian toothfish from southern Chile whilst southern Chile is a source population for both the Burdwood Bank and the Falkland Islands. Understanding how retention and recruitment function in the region will offer insight into how the population promotes self-recruitment and may inform fisheries management of the region which in turn can affect the Falkland Islands fishery.

4.5. Conclusions

Toothfish are commercially and economically important to the Falkland Islands (Collins *et al.,* 2010). Due to several gaps in knowledge of their early life history, it is unclear whether toothfish are primarily recruiting into the Falkland Islands fishery from spawning occurring on the Burdwood Bank, a submerged continental platform to the south of the Falkland Islands, or from the neighbouring southern Chilean population. A suite of egg buoyancy experiments and numerical particle tracking simulations allows this study to determine the likely spawning locations and transport pathways through which recruitment to the Falkland Islands population could occur and examine how connectivity of populations is influenced by regional oceanography.

A necessary step for biologically relevant modelling is the inclusion of initial buoyancy and any changes throughout the egg development stage (Jung *et al.,* 2012). With no empirical data available on the buoyancy of Patagonian toothfish eggs, experiments were conducted to ascertain buoyancy history of toothfish eggs throughout development to then incorporate the data into particle tracking simulations. The experiments resulted in an indication that the buoyancy history of the eggs followed observed patterns in other marine fish species, an initial decrease in buoyancy before increasing again towards hatching (Jung *et al.,* 2012; Sundby & Kristiansen, 2015) and it seems likely that Patagonian toothfish eggs change density throughout their embryonic development. However variations in buoyancy values between egg batches and lack of sufficient replication lead to an uncertainty in the absolute buoyancy values. Refining these initial estimates of the buoyancy history of toothfish eggs, which is left to future research, could consider measuring the various basic component of lipids, proteins and osmolality of water content within the eggs. These measurements can achieve a relatively high precision for egg density (Sundby & Kristiansen, 2015) and could help further inform knowledge of buoyancy history of toothfish eggs throughout embryonic development.

Due to the uncertainty in egg buoyancy from experiments carried out at FFFL, particle tracking simulations using several possible realisations of egg buoyancy history were carried out. Based on comparisons between these particle tracking simulations, at sea observations of egg distribution at South Georgia (Evseenko *et al.,* 1985) and trawl surveys identifying locations of juvenile nursery areas (Arkhipkin *et al.,* 2017), we conclude that neutral egg buoyancy provides a plausible realisation for egg buoyancy history and was used in the final particle tracking simulations. Distribution of eggs within the upper 200m of the water column, mainly between 50-200m, is needed for particles to advect to areas that have suitable depth for retention. Despite a neutral buoyancy profile providing plausible results, egg buoyancy experiments indicate egg buoyancy history changes throughout development. Identifying these changes and incorporating them into the model may result in more accurate transport pathways being determined. Therefore a case is made that future egg buoyancy experiments may still be beneficial.

Particle tracking experiments were run with 10,000 virtual toothfish eggs released from spawning areas around the Burdwood Bank and southern Chile (Fig. 13, 14), during spawning years, 2009 and 2012, considered to subsequently lead to good recruitment (2010) and poor recruitment (2013) around the Falkland Islands. These experiments have shown that the Burdwood Bank is unlikely to be the primary source for the supply of larvae to the Falkland Islands and the Patagonian Shelf region, as has previously been assumed (Collins *et al.,* 2010; Brown, 2011); rather southern Chile appears more likely to be the primary source of larval supply to the Falkland Islands and Patagonian Shelf and subsequent active movement of larvae to the Falklands region, may be important for the successful recruitment of juveniles to nursery areas around the Falkland Islands. This conclusion is supported by the high (low) level of connectivity observed between southern Chile spawning sites and the Patagonian Shelf during 2009 (2012), which was followed by good (poor) recruitment around the Falkland Islands in 2010 (2013) (T Farrugia 2019, pers.comm. 26 July).

The differences observed in modelled connectivity between southern Chile, the Patagonian Shelf and the Falkland Islands between 2009 and 2012 suggests aspects of the regional oceanography are an important control on larval connectivity. Analysis of numerical model fields identified inter-annual variability in the position and upper-ocean water mass density of the boundary current around southern Chile as playing important roles in successful transport and retention of larvae onto the Patagonian Shelf. A possible origin for this variability in boundary current flow, and successful transport between the southern Chile and Patagonian Shelf, is the phase of the SAM (Guihou *et al.,* 2010); however, further research is needed to support this hypothesis.

The findings of this research could have implications for the fisheries management strategy in place in Falkland Islands waters. The current strategy does not take into account the connectivity of early life stages between southern Chile, the Patagonian Shelf and the Falkland Islands. If southern Chile is contributing to a high level of retention and potential recruits to the Falkland Islands region, through movement onto the Patagonian Shelf and subsequent active larval swimming to the Falkland Island juvenile nursery areas, then the management of the adult spawning population in Chile needs to be taken into account. The status of the Chilean stock as overfished and depleted (Servicio Nacional de Pesca y Acuicultura, 2018) is of high concern if indeed the two populations are connected, as this study suggests. The dynamics of early life stages of Patagonian toothfish in southern Chile are important to understand as if southern Chile is the major contributor to juvenile recruitment around the Falkland Islands; population dynamics in southern Chile will affect the population dynamics around the Falkland Islands. Therefore a coordinated management strategy between Chile and the Falkland Islands should be considered. Fishery activities on the Patagonian Shelf should also be considered in the management of toothfish in Falkland Island waters; however due to heightened political tension between the Falkland Islands and Argentina currently, data sharing and coordination of fisheries is unlikely. Although not studied in detail here, the SAM seems to be an important factor controlling transport success onto the shelf. The SAM phase could therefore potentially be used as a predictor of recruitment success into the Falkland Islands fishery stock and be included in future management strategies.

As with any research, several additional studies could be carried out to further the understanding of the structure of Patagonian toothfish populations in the South Atlantic and southern Chile. Aspects of both the biological and physical drivers behind recruitment variability around the Falkland Islands should be considered. Further studies on biological factors that can affect retention such as egg buoyancy and larval behaviour, as well as possible mortality rates (morality as a result of unsuitable temperatures or depth), should be carried out to allow for better model parameterisation. Incorporating these factors into the particle tracking model utislised here may result in more accurate predicted transport pathways and potential retention and transport success. Analysis of particle tracking simulations in additional years focusing in particular on the influence of the boundary current and/or SAM index on successful transport between southern Chile and the Patagonian Shelf are seen as priorities. Deepening our understanding into factors affecting recruitment, whether biological or physical, will help to inform fishery management strategies in the region, potentially leading to further improvements in an already well managed fishery.

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Appendices

Appendix A: Raw density data

Batch A

Day post fertilisation	**Density (kg/m^3)**	**Fraction Positive**	**Fraction Neutral**	**Fraction Negative**
2	1026.14	0.1	0	0.9
	1026.93	0.8	0.2	0
	1027.72	0.6	0	0.4
3	1026.02	0	0	1
	1026.81	0.35	0.2	0.45
	1027.60	0.8	0.05	0.15
4	1026.14	0	0	1
	1026.93	0	0.05	0.95
	1027.72	0.65	0.05	0.3
5	1027.72	0.15	0	0.85
	1028.51	0.85	0	0.15
	1029.31	0.85	0	0.15
6	1027.72	0	0	1
	1028.51	0.25	0.05	0.7
	1029.31	0	0	1
7	1027.66	0	0	1
	1028.45	0.15	0.05	0.8
	1029.25	0.4	0	0.6
8	1028.39	0	0	1
	1029.18	0	0	1
	1029.97	0	0	1
	1030.76	0.15	0.3	0.55
9	1030.76	0.5	0	0.5
	1031.56	0.6	0	0.4
	1032.35	0.8	0	0.2
	1033.14	0.6	0.05	0.35
10	1031.62	0.65	0	0.35
	1032.42	0.85	0	0.15
	1033.21	0.9	0	0.1
11	1030.76	**0.55**	**0.15**	**0.3**
	1031.56	1	0	0
	1032.35	0.95	0	0.05
	1033.14	1	0	0
12	1029.97	0.3	0	0.7
	1030.76	0.45	0.15	0.4
	1031.56	1	0	0
14	1029.97	0.95	0	0.05
	1030.76	0.7	0	0.3
	1031.56	0.9	0.05	0.05
15	1027.66	0.1	0	0.9
	1028.45	0.75	0.05	0.2
	1029.25	0.35	0	0.65
	1030.04	0.7	0.05	0.25

Batch B

Day post fertilisation	**Density (kg/m^3)**	**Fraction Positive**	**Fraction Neutral**	**Fraction Negative**
1	1023.71	0.3	0.05	0.65
	1024.50	0.95	0	0.05
	1025.29	1	0	0
	1026.08	1	0	0
	1026.87	1	0	0
	1027.66	1	0	0
2	1026.08	1	0	0
	1026.87	1	0	0
	1027.66	1	0	0
3	1025.23	0.75	0	0.25
	1026.02	0.9	0	0.1
	1026.81	0.85	0	0.15
	1027.60	0.95	0	0.05
5	1025.23	0	0	1
	1026.02	0.5	0.2	0.3
	1026.81	1	0	0
	1027.60	1	0	0
6	1026.08	0.8	0.05	0.15
	1026.87	1	0	0
	1027.66	1	0	0
20	1024.44	0.15	0.15	0.7
	1025.23	1	0	0
	1026.02	0.75	0.05	0.2
21	1024.50	0.3	0.15	0.55
	1025.29	0.55	0.1	0.35
	1026.08	0.8	0.05	0.15

Batch C

Day post fertilisation	Density (kg/m^3)	Fraction Positive	Fraction Neutral	Fraction Negative
1	1023.65	0.2	0.1	0.7
	1024.44	1	0	0
	1025.23	1	0	0
	1026.02	1	0	0
	1026.81	1	0	0
	1027.60	1	0	0
2	1024.50	1	0	0
	1025.29	1	0	0
	1026.08	1	0	0
	1026.87	1	0	0
	1027.66	1	0	0
3	1024.50	1	0	0
	1025.29	1	0	0
	1026.08	1	0	0
	1026.87	1	0	0
	1027.66	1	0	0
4	1023.71	0.4	0.2	0.45
	1024.50	0.75	0.1	0.15
	1025.29	1	0	0
	1026.08	1	0	0
	1026.87	1	0	0
	1027.66	1	0	0
5	1024.50	1	0	0
	1025.29	1	0	0
	1026.08	1	0	0
	1026.87	1	0	0
	1027.66	1	0	0
19	1024.44	0.4	0.05	0.55
	1025.23	0.7	0	0.3
	1026.02	0.95	0	0.05
20	1024.50	0.05	0	0.95
	1025.29	0.8	0.1	0.1
	1026.08	0.85	0	0.15
21	1024.44	0.05	0	0.95
	1025.23	0.7	0	0.3
	1026.02	0.75	0.15	0.1

Batch D

Day post fertilisation	**Density (kg/m^3)**	**Fraction Positive**	**Fraction Neutral**	**Fraction Negative**
2	1023.71	0.2	0.05	0.75
	1024.50	0.7	0	0.3
	1025.29	0.95	0	0.05
19	1024.50	0.05	0	0.95
	1025.29	0.9	0	0.1
	1026.08	0.9	0.05	0.05
20	1024.44	0	**0**	1
	1025.23	0.75	0.05	0.2
	1026.02	0.9	0	0.1